TREATISE ON
INVERTEBRATE PALEONTOLOGY

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VOLUME 1 (OF 3)
MOLLUSCA 6
BIVALVIA

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EDITORIAL PREFACE

The aim of the *Treatise on Invertebrate Paleontology,* as originally conceived and consistently pursued, is to present the most comprehensive and authoritative, yet compact statement of knowledge concerning invertebrate fossil groups that can be formulated by collaboration of competent specialists in seeking to organize what has been learned of this subject up to the mid-point of the present century. Such work has value in providing a most useful summary of the collective results of multitudinous investigations and thus should constitute an indispensable text and reference book for all persons who wish to know about remains of invertebrate organisms preserved in rocks of the earth's crust. This applies to neozoologists as well as paleozoologists and to beginners in study of fossils as well as to thoroughly trained, long-experienced professional workers, including teachers, stratigraphical geologists, and individuals engaged in research on fossil invertebrates. The making of a reasonably complete inventory of present knowledge of invertebrate paleontology may be expected to yield needed foundation for future research and it is hoped that the *Treatise* will serve this end.

The *Treatise* is divided into parts which bear index letters, each except the initial and concluding ones being defined to include designated groups of invertebrates. The chief purpose of this arrangement is to provide for independence of the several parts as regards date of publication, because it is judged desirable to print and distribute each segment as soon as possible after it is ready for press. Pages in each part bear the assigned index letter joined with numbers beginning with 1 and running consecutively to the end of the part.

The outline of subjects to be treated in connection with each large group of invertebrates includes (1) description of morphological features, with special reference to hard parts, (2) ontogeny, (3) classification, (4) geological distribution, (5) evolutionary trends and phylogeny, and (6) systematic description of genera, subgenera, and higher taxonomic units. In general, paleoecological aspects of study are omitted or little emphasized because comprehensive treatment of this subject is given in the *Treatise on Marine Ecology and Paleoecology* (H. S. LADD, Editor, Geological Society of America, Memoir 67, 1957), prepared under auspices of a committee of the United States National Research Council. A selected list of references is furnished in each part of the *Treatise.*

Features of style in the taxonomic portions of this work have been fixed by the Editor with aid furnished by advice from representatives of the societies which have undertaken to sponsor the *Treatise.* It is the Editor's responsibility to consult with authors and co-ordinate their work, seeing that manuscript properly incorporates features of adopted style. Especially he has been called on to formulate policies in respect to many questions of nomenclature and procedure. The subject of family and subfamily names is reviewed briefly in a following section of this preface, and features of *Treatise* style in generic descriptions are explained.

A generous grant of $35,000 has been made by the Geological Society of America for the purpose of preparing *Treatise* illustrations. Administration of expenditures has been in charge of the Editor and most of the work by photographers and artists has been done under his direction at the University of Kansas, but sizable parts of this program have also been carried forward in Washington and London.

In December, 1959, the National Science Foundation of the United States, through its Division of Biological and Medical Sciences and the Program Director for Systematic Biology, made a grant in the amount of $210,000 for the purpose of aiding the completion of yet-unpublished volumes of the *Treatise.* Payment of this sum was provided to be made in installments distributed over a five-year period, with administration of disbursements handled by the University of Kansas. An additional grant (No. GB 4544) of $102,800 was made by the National Science Foundation in January, 1966, for the two-year period 1966-67, and this was extended for the calendar year 1968 by payment of $25,700 in October, 1967. Expenditures planned are primarily for needed assistance to authors and may be arranged through approved institutions located anywhere. Important help for the Director-Editor of the *Treatise* has been made available from the grant. Grateful acknowledgment to the Foundation is expressed on behalf of the societies sponsoring the *Treatise,* the University of Kansas, and innumerable individuals benefited by the *Treatise* project.

ZOOLOGICAL NAMES

Many questions arise in connection with zoological names, especially including those that relate to their acceptability and to alterations of some which may be allowed or demanded. Procedure in obtaining answers to these questions is guided and to a large extent governed by regulations published (1961) in the *International Code of Zoological Nomenclature* (hereinafter cited simply as the *Code*). The prime object of the *Code* is to promote stability and universality in the scientific names of animals, ensuring also that each name is distinct and unique while avoiding restrictions on freedom of taxonomic thought or action. Priority is a basic principle, but under specified conditions its application can be modified. This is all well and good, yet nomenclatural tasks confronting the zoological taxonomist are formidable. They warrant the complaint of some that zoology, including paleozoology, is the study of animals rather than of names applied to them.

Several ensuing pages are devoted to aspects of zoological nomenclature that are judged to have chief importance in relation to procedures adopted in the *Treatise*. Terminology is explained, and examples of style employed in the nomenclatural parts of systematic descriptions are given.

TAXA GROUPS

Each taxonomic unit (taxon, pl., taxa) of the animal and protistan kingdoms belongs to some one or another rank in the adopted hierarchy of classificatory divisions. In part, this hierarchy is defined by the *Code* to include a species-group of taxa, a genus-group, and a family-group. Units of lower rank than subspecies are excluded from zoological nomenclature and those higher than superfamily of the family-group are not regulated by the *Code*. It is natural and convenient to discuss nomenclatural matters in general terms first and then to consider each of the taxa groups separately. Especially important is provision that within each taxa group classificatory units are coordinate (equal in rank), whereas units of different taxa groups are not coordinate.

FORMS OF NAMES

All zoological names are divisible into groups based on their form (spelling). The first-published form (or forms) of a name is defined as original spelling (*Code*, Art. 32) and any later-published form (or forms) of the same name is designated as subsequent spelling (Art. 33). Obviously, original and subsequent spellings of a given name may or may not be identical and this affects consideration of their correctness. Further, examination of original spellings of names shows that by no means all can be distinguished as correct. Some are incorrect, and the same is true of subsequent spellings.

Original Spellings

If the first-published form of a name is consistent and unambiguous, being identical wherever it appears, the original spelling is defined as correct unless it contravenes some stipulation of the *Code* (Arts. 26-31), unless the original publication contains clear evidence of an inadvertent error, in the sense of the *Code*, or among names belonging to the family-group, unless correction of the termination or the stem of the type-genus is required. An unambiguous original spelling that fails to meet these requirements is defined as incorrect.

If a name is spelled in more than one way in the original publication, the form adopted by the first reviser is accepted as the correct original spelling, provided that it complies with mandatory stipulations of the *Code* (Arts. 26-31), including its provision for automatic emendations of minor sort.

Incorrect original spellings are any that fail to satisfy requirements of the *Code*, or that represent an inadvertent error, or that are one of multiple original spellings not adopted by a first reviser. These have no separate status in zoological nomenclature and therefore cannot enter into homonymy or be used as replacement names. They call for correction wherever found. For example, a name originally published with a diacritic mark, apostrophe, diaeresis, or hyphen requires correction by deleting such features and uniting parts of the name originally separated by them, except that deletion of an umlaut from a vowel is accompanied by inserting "e" after the vowel.

Subsequent Spellings

If a name classed as a subsequent spelling is identical with an original spelling, it is distinguishable as correct or incorrect on the same criteria that apply to the original spelling. This means that a subsequent spelling identical with a correct original spelling is also correct, and one identical with an incorrect original spelling is also incorrect. In the latter case, both original and subsequent spellings require correction wherever found (authorship and date of the original incorrect spelling being retained).

If a subsequent spelling differs from an original spelling in any way, even by the omission, addition, or alteration of a single letter, the subsequent spelling must be defined as a different name (except that such changes as altered terminations of adjectival specific names to obtain agreement in gender with associated generic names, of family-group names to denote assigned taxonomic rank, and corrections for originally used diacritic marks, hyphens, and the like are excluded from spelling changes conceived to produce a different name).

Altered subsequent spellings other than the exceptions noted may be either intentional or unintentional. If demonstrably intentional, the change is designated as an emendation. Emendations are divisible into those classed as justifiable and those comprising all others classed as unjustifiable. Justifiable emendations are corrections of incorrect original spellings, and these take the authorship and date of the original spellings. Unjustifiable emendations are names having their own status in nomenclature, with author and date of their publication; they are junior objective synonyms of the name in its original form.

Subsequent spellings that differ in any way from original spellings, other than previously noted exceptions, and that are not classifiable as emendations are defined as incorrect subsequent spellings. They have no status in nomenclature, do not enter into homonymy, and cannot be used as replacement names.

AVAILABLE AND UNAVAILABLE NAMES

Available Names

An available zoological name is any that conforms to all mandatory provisions of the *Code*. Such names are classifiable in groups which are usefully recognized in the *Treatise,* though not explicitly differentiated in the *Code*. They are as follows:

1) So-called *"inviolate names"* include all available names that are not subject to any sort of alteration from their originally published form. They comprise correct original spellings and commonly include correct subsequent spellings, but include no names classed as emendations. Here belong most genus-group names (including those for collective groups), some of which differ in spelling from others by only a single letter.

2) Names may be termed *"perfect names"* if, as originally published (with or without duplication by subsequent authors), they meet all mandatory requirements, needing no correction of any kind, but nevertheless are legally alterable in such ways as changing the termination (e.g., many species-group names, family-group names, suprafamilial names). This group does not include emended incorrect original spellings (e.g., *Oepikina,* replacement of *Öpikina*).

3) *"Imperfect names"* are available names that as originally published (with or without duplication by subsequent authors) contain mandatorily emendable defects. Incorrect original spellings are imperfect names. Examples of emended imperfect names are: among species-group names, *guerini* (not *Guérini*), *obrienae* (not *O'Brienae*), *terranovae* (not *terra-novae*), *nunezi* (not *Nuñezi*), *Spironema rectum* (not *Spironema recta,* because generic name is neuter, not feminine); among genus-group names, *Broeggeria* (not *Bröggeria*), *Obrienia* (not *O'Brienia*), *Maccookites* (not *McCookites*; among family-group names, Oepikidae (not Öpikidae), Spironematidae (not Spironemidae, incorrect stem), Athyrididae (not Athyridae, incorrect stem). The use of "variety" for named divisions of fossil species, according to common practice of some paleontologists, gives rise to imperfect names, which generally are emendable (*Code,* Art. 45e) by omitting this term so as to indicate the status of this taxon as a subspecies.

4) *"Vain names"* are available names consisting of unjustified intentional emendations of previously published names. The emendations are unjustified because they are not demonstrable as corrections of incorrect original spellings as defined by the *Code* (Art. 32,c). Vain names have status in nomenclature under their own authorship and date. They constitute junior objective synonyms of names in their original form. Examples are: among species-group names, *geneae* (published as replacement of original unexplained masculine, *geni,* which now is not alterable), *ohioae* (invalid change from original *ohioensis*); among genus-group names, *Graphiodactylus* (invalid change from original *Graphiadactyllis*); among family-group names, Graphiodactylidae (based on junior objective synonym having invalid vain name).

5) An important group of available zoological names can be distinguished as *"transferred names."* These comprise au-

thorized sorts of altered names in which the change depends on transfer from one taxonomic rank to another, or possibly on transfers in taxonomic assignment of subgenera, species, or subspecies. Most commonly the transfer calls for a change in termination of the name so as to comply with stipulations of the *Code* on endings of family-group taxa and agreement in gender of specific names with associated generic names. Transferred names may be derived from any of the preceding groups except the first. Examples are: among species-group names, *Spirifer ambiguus* (masc.) to *Composita ambigua* (fem.), *Neochonetes transversalis* to *N. granulifer transversalis* or vice versa; among genus-group names, *Schizoculina* to *Oculina (Schizoculina)* or vice versa; among family-group names, Orthidae to Orthinae or vice versa, or superfamily Orthacea derived from Orthidae or Orthinae; among suprafamilial taxa (not governed by the *Code*), order Orthida to suborder Orthina or vice versa. The authorship and date of transferred names are not affected by the transfers, but the author responsible for the transfer and the date of his action may appropriately be recorded in such works as the *Treatise*.

6) Improved or *"corrected names"* include both mandatory and allowable emendations of imperfect names and of suprafamilial names, which are not subject to regulation as to name form. Examples of corrected imperfect names are given with the discussion of group 3. Change from the originally published ordinal name Endoceroidea (TEICHERT, 1933) to the presently recognized Endocerida illustrates a "corrected" suprafamilial name. Group 6 names differ from those in group 5 in not being dependent on transfers in taxonomic rank or assignment, but some names are classifiable in both groups.

7) *"Substitute names"* are available names expressly proposed as replacements for invalid zoological names, such as junior homonyms. These may be classifiable also as belonging in groups 1, 2, or 3. The glossary appended to the *Code* refers to these as "new names" *(nomina nova)* but they are better designated as substitute names, since their newness is temporary and relative. The first-published substitute name that complies with the definition here given takes precedence over any other. An example is *Marieita* LOEBLICH & TAPPAN, 1964, as substitute for *Reichelina* MARIE, 1955 (*non* ERK, 1942).

8) *"Conserved names"* include a relatively small number of species-group, genus-group, and family-group names which have come to be classed as available and valid by action of the International Commission on Zoological Nomenclature exercising its plenary powers to this end or ruling to conserve a junior synonym in place of a rejected "forgotten" name *(nomen oblitum)* (Art. 23,b). Currently, such names are entered on appropriate "Official Lists," which are published from time to time.

It is useful for convenience and brevity of distinction in recording these groups of available zoological names to employ Latin designations in the pattern of *nomen nudum* (abbr., *nom. nud.*) and others. Thus we may recognize the preceding numbered groups as follows: 1)*nomina inviolata* (sing., *nomen inviolatum,* abbr., *nom. inviol.*), 2) *nomina perfecta (nomen perfectum, nom. perf.),* 3) *nomina imperfecta (nomen imperfectum, nom. imperf.),* 4) *nomina vana (nomen vanum, nom. van.),* 5) *nomina translata (nomen translatum, nom. transl.),* 6) *nomina correcta (nomen correctum, nom. correct.),* 7) *nomina substituta (nomen substitutum, nom. subst.),* 8) *nomina conservata (nomen conservatum, nom. conserv.).*

Additional to the groups differentiated above, the *Code* (Art. 17) specifies that a zoological name is not prevented from availability a) by becoming a junior synonym, for under various conditions this may be re-employed, b) for a species-group name by finding that original description of the taxon relates to more than a single taxonomic entity or to parts of animals belonging to two or more such entities, c) for species-group names by determining that it first was combined with an invalid or unavailable genus-group name, d) by being based only on part of an animal, sex of a species, ontogenetic stage, or one form of a polymorphic species, e) by being originally proposed for an organism not considered to be an animal but now so regarded, f) by incorrect original spelling which is correctable under the *Code*, g) by anonymous publication before 1951, h) by conditional proposal before 1961, i) by designation as a variety or form before 1961, j) by concluding that a name is inappropriate (Art. 18), or k) for a specific name by observing that it is tautonymous (Art. 18).

It is worthy of mention that names published for collective groups (see later discussion under "Genus-Group Names") are authorized by the *Code* (Art. 42c) for use in zoological nomenclature and therefore may be construed to be available names which are treated for convenience exactly as if they were generic names.

Unavailable Names

All zoological names which fail to comply with mandatory provisions of the *Code* are unavailable names and have no status in zoological nomenclature. None can be used under authorship and date of their original publication as a replacement name *(nom. subst.)* and none preoccupies for purposes of the Law of Homonymy. Names identical in spelling with some, but not all, unavailable names can be classed as available if and when they are published in conformance to stipulations of the *Code* and they are then assigned authorship and take date of the accepted publication. Different groups of unavailable names can be discriminated, as follows.

9) *"Naked names"* include all those that fail to satisfy provisions stipulated in Article 11 of the *Code,* which states general requirements of availability, and in addition, if published before 1931, that were unaccompanied by a description, definition, or indication (Arts. 12, 16), and if published after 1930, that lacked accompanying statement of characters purporting to serve for differentiation of the taxon, or definite bibliographic reference to such a statement, or that were not proposed expressly as replacement *(nom. subst.)* of a pre-existing available name (Art. 13,a). Examples of "naked names" are: among species-group taxa, *Valvulina mixta* PARKER & JONES, 1865 (=*Cribrobulimina mixta* CUSHMAN, 1927, available and valid); among genus-group taxa, *Orbitolinopsis* SILVESTRI, 1932 (=*Orbitolinopsis* HENSON, 1948, available but classed as invalid junior synonym of *Orbitolina* D'ORBIGNY, 1850); among family-group taxa, Aequilateralidae D'ORBIGNY, 1846 (lacking type-genus), Hélicostègues D'ORBIGNY, 1826 (vernacular not latinized by later authors, Art. 11,e,iii), Poteriocrinidae AUSTIN & AUSTIN, 1843 (=fam. Poteriocrinoidea AUSTIN & AUSTIN, 1842) (neither 1843 or 1842 names complying with Art. 11,e, which states that "a family-group name must, when first published, be based on the name then valid for a contained genus," such valid name in the case of this family being *Poteriocrinites* MILLER, 1821).

10) *"Denied names"* include all those that are defined by the *Code* (Art. 32,c) as incorrect original spellings. Examples are: Specific names, *nova-zelandica, mülleri, 10-brachiatus;* generic names, *M'Coyia, Størmerella, Römerina, Westgårdia;* family name, Růžičkinidae. Uncorrected "imperfect names" are "denied names" and unavailable, whereas corrected "imperfect names" are available.

11) *"Impermissible names"* include all those employed for alleged genus-group taxa other than genus and subgenus (Art. 42,a) (e.g., supraspecific divisions of subgenera), and all those published after 1930 that are unaccompanied by definite fixation of a type species (Art. 13,b). Examples of impermissible names are: *Martellispirifer* GATINAUD, 1949, and *Mirtellispirifer* GATINAUD, 1949, indicated respectively as a section and subsection of the subgenus *Cyrtospirifer; Fusarchaias* REICHEL, 1949, without definitely fixed type species (=*Fusarchaias* REICHEL, 1952, with *F. bermudezi* designated as type species).

12) *"Null names"* include all those that are defined by the *Code* (Art. 33,b) as incorrect subsequent spellings, which are any changes of original spelling not demonstrably intentional. Such names are found in all ranks of taxa.

13) *"Forgotten names"* are defined (Art. 23,b) as senior synonyms that have remained unused in primary zoological literature for more than 50 years. Such names are not to be used unless so directed by ICZN.

Latin designations for the discussed groups of unavailable zoological names are as follows: 9) *nomina nuda* (sing., *nomen nudum,* abbr., *nom. nud.*), 10) *nomina negata (nomen negatum, nom. neg.),* 11) *nomina vetita (nomen vetitum, nom. vet.),* 12) *nomina nulla (nomen nullum, nom.*

null.), 13) *nomina oblita* (*nomen oblitum, nom. oblit.*).

VALID AND INVALID NAMES

Important distinctions relate to valid and available names, on one hand, and to invalid and unavailable names, on the other. Whereas determination of availability is based entirely on objective considerations guided by Articles of the *Code,* conclusions as to validity of zoological names partly may be subjective. A valid name is the correct one for a given taxon, which may have two or more available names but only a single correct name, generally the oldest. Obviously, no valid name can also be an unavailable name, but invalid names may include both available and unavailable names. Any name for a given taxon other than the valid name is an invalid name.

A sort of nomenclatorial no-man's-land is encountered in considering the status of some zoological names, such as *"doubtful names," "names under inquiry,"* and *"forgotten names."* Latin designations of these are *nomina dubia, nomina inquirenda,* and *nomina oblita,* respectively. Each of these groups may include both available and unavailable names, but the latter can well be ignored. Names considered to possess availability conduce to uncertainty and instability, which ordinarily can be removed only by appealed action of ICZN. Because few zoologists care to bother in seeking such remedy, the "wastebasket" names persist.

SUMMARY OF NAME GROUPS

Partly because only in such publications as the *Treatise* is special attention to groups of zoological names called for and partly because new designations are now introduced as means of recording distinctions explicitly as well as compactly, a summary may be useful. In the following tabulation valid groups of names are indicated in boldface type, whereas invalid ones are printed in italics.

DEFINITIONS OF NAME GROUPS

nomen conservatum (nom. conserv.). Name unacceptable under regulations of the *Code* which is made valid, either with original or altered spelling, through procedures specified by the *Code* or by action of ICZN exercising its plenary powers.

nomen correctum (nom. correct.). Name with intentionally altered spelling of sort required or allowable by the *Code* but not dependent on transfer from one taxonomic rank to another ("improved name"). (*See Code,* Arts. 26-b, 27, 29, 30-a-3, 31, 32-c-i, 33-a; in addition change of endings for suprafamilial taxa not regulated by the *Code.*)

nomen imperfectum (nom. imperf.). Name that as originally published (with or without subsequent identical spelling) meets all mandatory requirements of the *Code* but contains defect needing correction ("imperfect name"). (*See Code,* Arts. 26-b, 27, 29, 32-c, 33-a.)

nomen inviolatum (nom. inviol.). Name that as originally published meets all mandatory requirements of the *Code* and also is not correctable or alterable in any way ("inviolate name").

nomen negatum (nom. neg.). Name that as originally published (with or without subsequent identical spelling) constitutes invalid original spelling, and although possibly meeting all other mandatory requirements of the *Code,* cannot be used and has no separate status in nomenclature ("denied name"). It is to be corrected wherever found.

nomen nudum (nom. nud.). Name that as originally published (with or without subsequent identical spelling) fails to meet mandatory requirements of the *Code* and having no status in nomenclature, is not correctable to establish original authorship and date ("naked name").

nomen nullum (nom. null.). Name consisting of an unintentional alteration in form (spelling) of a previously published name (either available name, as *nom. inviol., nom. perf., nom imperf., nom. transl.*; or unavailable name, as *nom. neg., nom. nud., nom. van.,* or another *nom. null.*) ("null name").

nomen oblitum (nom. oblit.). Name of senior synonym unused in primary zoological literature in more than 50 years, not to be used unless so directed by ICZN ("forgotten name").

nomen perfectum (nom. perf.). Name that as originally published meets all mandatory requirements of the *Code* and needs no correction of any kind but which nevertheless is validly alterable by change of ending ("perfect name").

nomen substitutum (nom. subst.). Replacement name published as substitute for an invalid name, such as a junior homonym (equivalent to "new name").

nomen translatum (nom. transl.). Name that is derived by valid emendation of a previously published name as result of transfer from one taxonomic rank to another within the group to which it belongs ("transferred name").

nomen vanum (nom. van.). Name consisting of an invalid intentional change in form (spelling) from a previously published name, such invalid emendation having status in nomenclature as a junior objective synonym ("vain name").

nomen vetitum (nom. vet.). Name of genus-group taxon not authorized by the *Code* or, if first published after 1930, without definitely fixed type species ("impermissible name").

Except as specified otherwise, zoological names accepted in the *Treatise* may be understood to be classifiable either as *nom-*

ina inviolata or *nomina perfecta* (omitting from notice *nomina correcta* among specific names) and these are not discriminated. Names which are not accepted for one reason or another include junior homonyms, senior synonyms classifiable as *nomina negata* or *nomina nuda,* and numerous junior synonyms which include both objective *(nomina vana)* and subjective types; rejected names are classified as completely as possible.

NAME CHANGES IN RELATION TO TAXA GROUPS

SPECIES-GROUP NAMES

Detailed consideration of valid emendation of specific and subspecific names is unnecessary here because it is well understood and relatively inconsequential. When the form of adjectival specific names is changed to obtain agreement with the gender of a generic name in transferring a species from one genus to another, it is never needful to label the changed name as a *nom. transl.* Likewise, transliteration of a letter accompanied by a diacritical mark in manner now called for by the *Code* (as in changing originally published *bröggeri* to *broeggeri*) or elimination of a hyphen (as in changing originally published *cornu-oryx* to *cornuoryx*) does not require *"nom. correct."* with it.

GENUS-GROUP NAMES

So rare are conditions warranting change of the originally published valid form of generic and subgeneric names that lengthy discussion may be omitted. Only elimination of diacritical marks of some names in this category seems to furnish basis for valid emendation. It is true that many changes of generic and subgeneric names have been published, but virtually all of these are either *nomina vana* or *nomina nulla.* Various names which formerly were classed as homonyms are not now, for two names that differ only by a single letter (or in original publication by presence or absence of a diacritical mark) are construed to be entirely distinct.

A category of genus-group taxa and names for them calls for special notice. This comprises assemblages of identifiable species which cannot with any certainty be placed in a known genus. Such assemblages are recognized by the *Code* as valid zoological entities called **collective groups,** with names for them "treated as generic names in the meaning of the *Code*" (Art. 42c). They differ from genera in that collective groups require no type species. Particularly for dealing with fossil assemblages of dissociated skeletal remains of echinoderms (chiefly crinoids) procedures based on definition of collective groups must find place in the *Treatise.* Names for these will uniformly be labeled as applied to collective groups with accompanying abbreviation *"coll. coll."* (for Latin *collectio collectiva,* collective group or assemblage), thus distinguishing them from names for genera. An example is *Pentagonopentagonalis* YELTYSHEVA, 1955 *(coll. coll.),* no type species. The species *P. bilobatus* YELTYSHEVA, 1960, is available as the type species of *Obuticrinus* YELTYSHEVA in YELTYSHEVA & STUKALINA, 1963, in accordance with its original designation as such by these authors.

Examples in use of classificatory designations for genus-group names as previously given are the following, which also illustrate designation of type species as explained later.

Kurnatiophyllum THOMPSON, 1875 [**K. concentricum;* SD GREGORY, 1917] [=*Kumatiophyllum* THOMPSON, 1876 *(nom. null.); Cymatophyllum* THOMPSON, 1901 *(nom. van.); Cymatiophyllum* LANG, SMITH & THOMAS, 1940 *(nom. van.)*].

Stichophyma POMEL, 1872 [**Manon turbinatum* RÖMER, 1841; SD RAUFF, 1893] [=*Stychophyma* VOSMAER, 1885 *(nom. null.); Sticophyma* MORET, 1924 *(nom. null.)*].

Stratophyllum SMYTH, 1933 [**S. tenue*] [=*Ethmoplax* SMYTH, 1939 *(nom. van. pro Stratophyllum); Stratiphyllum* LANG, SMITH & THOMAS, 1940 (*nom. van. pro Stratophyllum* SMYTH) (non *Stratiphyllum* SCHEFFEN, 1933)].

Placotelia OPPLIGER, 1907 [**Porostoma marconi* FROMENTEL, 1859; SD DELAUBENFELS, herein] [=*Plakotelia* OPPLIGER, 1907 *(nom. neg.)*].

Walcottella DELAUBENFELS, 1955 [*nom. subst., pro Rhopalicus* SCHRAMM, 1936 (*non* FÖRSTER, 1856)].

Cyrtograptus CARRUTHERS, 1867 [*nom. correct.* LAPWORTH, 1873 (*pro Cyrtograpsus* CARRUTHERS, (1867), *nom. conserv.* proposed BULMAN, 1955 (ICZN 1963, p. 105, Opinion 650)].

Pentagonopentagonalis YELTYSHEVA, 1955 *(coll. coll.),* for species based on crinoid-stem parts [no type species] (ICZN pend.).

FAMILY-GROUP NAMES; USE OF *"NOM. TRANSL."*

The *Code* specifies the endings only for subfamily (-inae) and family (-idae) but all family-group taxa are defined as coordinate, signifying that for purposes of priority a name published for a taxon in any category and based on a particular type genus shall date from its original publication for a taxon in any category, retaining this priority (and authorship) when the taxon is treated as belonging to a lower or higher category. By exclusion of -inae and -idae, respectively reserved for subfamily and family, the endings of names used for tribes and superfamilies must be unspecified different letter combinations. These, if introduced subsequent to designation of a subfamily or family based on the same nominate genus, are *nomina translata,* as is also a subfamily that is elevated to family rank or a family reduced to subfamily rank. In the *Treatise* it is desirable to distinguish the valid alteration comprised in the changed ending of each transferred family-group name by the abbreviation *"nom. transl."* and record of the author and date belonging to this alteration. This is particularly important in the case of superfamilies, for it is the author who introduced this taxon that one wishes to know about rather than the author of the superfamily as defined by the *Code,* for the latter is merely the individual who first defined some lower-rank family-group taxon that contains the nominate genus of the superfamily. The publication of the author containing introduction of the superfamily *nomen translatum* is likely to furnish the information on taxonomic considerations that support definition of the unit.

Examples of the use of *"nom. transl."* are the following.

Subfamily STYLININAE d'Orbigny, 1851
[*nom. transl.* Edwards & Haime, 1857 (*ex* Stylinidae d'Orbigny, 1851)]

Superfamily ARCHAEOCTONOIDEA Petrunkevitch, 1949
[*nom. transl.* Petrunkevitch, 1955 (*ex* Archaeoctonidae Petrunkevitch, 1949)]

Superfamily CRIOCERATITACEAE Hyatt, 1900
[*nom. transl.* Wright, 1952 (*ex* Crioceratitidae Hyatt, 1900)]

FAMILY-GROUP NAMES; USE OF *"NOM. CORRECT."*

Valid name changes classed as *nomina correcta* do not depend on transfer from one category of family-group units to another but most commonly involve correction of the stem of the nominate genus; in addition, they include somewhat arbitrarily chosen modification of ending for names of tribe or superfamily. Examples of the use of *"nom. correct."* are the following.

Family STREPTELASMATIDAE Nicholson, 1889
[*nom. correct.* Wedekind, 1927 (*pro* Streptelasmidae Nicholson, 1889, *nom. imperf.*)]

Family PALAEOSCORPIIDAE Lehmann, 1944
[*nom. correct.* Petrunkevitch, 1955 (*pro* Palaeoscorpionidae Lehmann, 1944, *nom. imperf.*)]

Family AGLASPIDIDAE Miller, 1877
[*nom. correct.* Størmer, 1959 (*pro* Aglaspidae Miller, 1877, *nom. imperf.*)]

Superfamily AGARICIICAE Gray, 1847
[*nom. correct.* Wells, 1956 (*pro* Agaricioidae Vaughan & Wells, 1943, *nom. transl. ex* Agariciidae Gray, 1847)]

FAMILY-GROUP NAMES; USE OF *"NOM. CONSERV."*

It may happen that long-used family-group names are invalid under strict application of the *Code.* In order to retain the otherwise invalid name, appeal to ICZN is needful. Examples of use of *nom. conserv.* in this connection, as cited in the *Treatise,* are the following.

Family ARIETITIDAE Hyatt, 1874
[*nom. correct.* Haug, 1885 (*pro* Arietidae Hyatt, 1875) *nom. conserv.* proposed Arkell, 1955 (ICZN pend.)]

Family STEPHANOCERATIDAE Neumayr, 1875
[*nom. correct.* Fischer, 1882 (*pro* Stephanoceratinen Neumayr, 1875, invalid vernacular name), *nom. conserv.* proposed Arkell, 1955 (ICZN pend.)]

FAMILY-GROUP NAMES; REPLACEMENTS

Family-group names are formed by adding letter combinations (prescribed for family and subfamily but not now for others) to the stem of the name belonging to genus (nominate genus) first chosen as type of the assemblage. The type genus need not be the oldest in terms of receiving its name and definition, but it must be the first-published as name-giver to a family-group taxon among all those included. Once fixed, the family-group name remains tied to the nominate genus even if its name is changed by reason of status as a junior homonym or junior synonym, either objective or subjective. Seemingly, the *Code* (Art. 39) requires replacement of a family-group name only in the event that the nominate genus is found to be a junior homonym, and then a substitute family-group name is accepted if it is formed from the oldest available substitute name for the nominate genus. Authorship and date attributed to the replacement family-group name are determined by first publication of the changed family group-name, but for purposes of the Law of Priority, they take the date of the replaced name. Numerous long-used family-group names are incorrect in being *nomina nuda,* since they fail to satisfy criteria of availability (Art. 11,e). These also demand replacement by valid names.

The aim of family-group nomenclature is greatest possible stability and uniformity, just as in case of other zoological names. Experience indicates the wisdom of sustaining family-group names based on junior subjective synonyms if they have priority of publication, for opinions of different workers as to the synonymy of generic names founded on different type species may not agree and opinions of the same worker may alter from time to time. The retention similarly of first-published family-group names which are found to be based on junior objective synonyms is less clearly desirable, especially if a replacement name derived from the senior objective synonym has been recognized very long and widely. To displace a much-used family-group name based on the senior objective synonym by disinterring a forgotten and virtually unused family-group name based on a junior objective synonym because the latter happens to have priority of publication is unsettling.

Replacement of a family-group name may be needed if the former nominate genus is transferred to another family-group. Then the first-published name-giver of a family-group assemblage in the remnant taxon is to be recognized in forming a replacement name.

FAMILY-GROUP NAMES; AUTHORSHIP AND DATE

All family-group taxa having names based on the same type genus are attributed to the author who first published the name for any of these assemblages, whether tribe, subfamily, or family (superfamily being almost inevitably a later-conceived taxon). Accordingly, if a family is divided into subfamilies or a subfamily into tribes, the name of no such subfamily or tribe can antedate the family name. Also, every family containing differentiated subfamilies must have a nominate *(sensu stricto)* subfamily, which is based on the same type genus as that for the family, and the author and date set down for the nominate subfamily invariably are identical with those of the family, without reference to whether the author of the family or some subsequent author introduced subdivisions.

Changes in the form of family-group names of the sort constituting *nomina correcta,* as previously discussed, do not affect authorship and date of the taxon concerned, but in publications such as the *Treatise* it is desirable to record the authorship and date of the correction.

SUPRAFAMILIAL TAXA

International rules of zoological nomenclature as given in the *Code* (1961) are limited to stipulations affecting lower-rank categories (infrasubspecies to superfamily). Suprafamilial categories (suborder to phylum) are either unmentioned or explicitly placed outside of the application of zoological rules. The *Copenhagen Decisions on Zoological Nomenclature* (1953, Arts. 59-69) proposed to adopt rules for naming suborders and higher taxonomic divisions up to and including phylum, with provision for designating a type genus for each, hopefully in such manner as not to interfere with the taxonomic freedom of workers. Procedures for applying the Law of Priority and Law of Homonymy to suprafamilial taxa were outlined and for dealing with the names for such units and their authorship, with assigned dates, when they should be transferred on taxonomic grounds from one rank to another. The adoption of terminations of names, different for each category but uniform within each, was recommended.

The Colloquium on zoological nomenclature which met in London during the week just before the XVth International Congress of Zoology convened in 1958 thoroughly discussed the proposals for regulating suprafamilial nomenclature, as well as many others advocated for inclusion in the new *Code* or recommended for exclusion from it. A decision which was supported by a wide majority of the participants in the Colloquium was against the establishment of rules for naming taxa above family-group rank, mainly because it was judged that such regulation would unwisely tie the hands of taxonomists. For example, if a class or order was defined by some author at a given date, using chosen morphologic characters (e.g., gills of pelecypods), this should not be allowed to freeze nomenclature, taking precedence over another later-proposed class or order distinguished by different characters (e.g., hinge-teeth of pelecypods). Even the fixing of type genera for suprafamilial taxa might have small value, if any, hindering taxonomic work rather than aiding it. At all events, no legal basis for establishing such types and for naming these taxa has yet been provided.

The considerations just stated do not prevent the Editor of the *Treatise* from making "rules" for dealing with suprafamilial groups of animals described and illustrated in this publication. At least a degree of uniform policy is thought to be needed, especially for the guidance of *Treatise*-contributing authors. This policy should accord with recognized general practice among zoologists, but where general practice is indeterminate or nonexistent our own procedure in suprafamilial nomenclature needs to be specified as clearly as possible. This pertains especially to decisions about names themselves, about citation of authors and dates, and about treatment of suprafamilial taxa which on taxonomic grounds are changed from their originally assigned rank. Accordingly, a few "rules" expressing *Treatise* policy are given here, some with examples of their application.

1) The name of any suprafamilial taxon must be a Latin or latinized uninominal noun of plural form, or treated as such, a) with a capital initial letter, b) without diacritical mark, apostrophe, diaeresis, or hyphen, and c) if component consisting of a numeral, numerical adjective, or adverb is used, this must be written in full (e.g., Stethostomata, Trionychi, Septemchitonina, Scorpiones, Subselliflorae). No uniformity in choice of ending for taxa of a given rank is demanded (e.g., orders named Gorgon*acea,* Millepor*ina,* Rugos*a,* Scleractin*ia,* Stromatopor*oidea,* Phalang*ida*).

2) Names of suprafamilial taxa may be constructed in almost any way, a) intended to indicate morphological attributes (e.g., Lamellibranchiata, Cyclostomata, Toxoglossa), b) based on the stem of an included genus (e.g., Bellerophontina, Nautilida, Fungiina), or c) arbitrary combinations of letters, (e.g., Yuania), but none of these can be allowed to end in -idae or -inae, reserved for family-group taxa. A class or subclass (e.g., Nautiloidea), order (e.g., Nautilida), or suborder (e.g., Nautilina) named from the stem of an included genus may be presumed to have that genus (e.g., *Nautilus*) as its objective type. No suprafamilial name identical in form to that of a genus or to another published suprafamilial name should be employed (e.g., order Decapoda Latreille, 1803, crustaceans, and order Decapoda Leach, 1818, cephalopods; suborder Chonetoidea Muir-Wood, 1955, and genus *Chonetoidea* Jones, 1928). Worthy of notice is the classificatory and nomenclatural distinction between suprafamilial and family-group taxa which respectively are named from the same type genus, since one is not considered to be transferable to the other (e.g., suborder Bellerophontina Ulrich & Scofield, 1897; superfamily Bellerophontacea M'Coy, 1851; family Bellerophontidae M'Coy, 1851). Family-group names and suprafamilial names are not coordinate.

3) The Laws of Priority and Homonymy lack any force of international agreement as applied to suprafamilial names, yet in the interest of nomenclatural stability and the avoidance of confusion these laws are widely accepted by zoologists above the family-group level wherever they do not infringe on taxonomic freedom and long-established usage.

4) Authors who accept priority as a determinant in nomenclature of a suprafamilial taxon may change its assigned rank at will, with or without modifying the terminal letters of the name, but such change(s) cannot rationally be judged to alter the authorship and date of the taxon as published originally. a) A name revised from its previously published rank is a "transferred name" *(nom. transl.),* as illustrated in the following.

Order CORYNEXOCHIDA Kobayashi, 1935

[*nom. transl.* MOORE, 1955 (*ex* suborder Corynexochida KOBAYASHI, 1935)]

b) A name revised from its previously published form merely by adoption of a different termination, without changing taxonomic rank, is an "altered name" *(nom. correct.)*. Examples follow.

Order DISPARIDA Moore & Laudon, 1943

[*nom. correct.* MOORE, 1952 (*pro* order Disparata MOORE & LAUDON, 1943)]

Suborder AGNOSTINA Salter, 1864

[*nom. correct.* HARRINGTON & LEANZA, 1957 (*pro* suborder Agnostini SALTER, 1864)]

c) A suprafamilial name revised from its previously published rank with accompanying change of termination (which may or may not be intended to signalize the change of rank) is construed to be primarily a *nom. transl.* (compare change of ending for family-group taxa -idae to -inae, or vice versa, and to superfamily) but if desired it could be recorded as *nom. transl. et correct.*

Order ORTHIDA Schuchert & Cooper, 1931

[*nom. transl.* MOORE, 1952 (*ex* suborder Orthoidea SCHUCHERT & COOPER, 1931)]

5) The authorship and date of nominate subordinate and superordinate taxa among suprafamilial taxa are considered in the *Treatise* to be identical since each actually or potentially has the same type. Examples are given below.

Subclass ENDOCERATOIDEA Teichert, 1933

[*nom. transl.* TEICHERT, 1964 (*ex* superorder Endoceratoidea SHIMANSKIY & ZHURAVLEVA, 1961, *nom. transl. ex* order Endoceroidea TEICHERT, 1933)]

Order ENDOCERIDA Teichert, 1933

[*nom. correct.* TEICHERT, 1964 (*pro* order Endoceroidea TEICHERT, 1933)]

Suborder ENDOCERINA Teichert, 1933

[*nom. correct.* TEICHERT, 1964 (*pro* suborder Endoceracea SCHINDEWOLF, 1935, *nom. transl. ex* order Endoceroidea TEICHERT, 1933)]

6) A suprafamilial taxon may or may not contain a family-group taxon or taxa having the same type genus, and if it does, the respective suprafamilial and family-group taxa may or may not be nominate (having names with the same stem). The zoological *Code* (Art. 61) affirms that "each taxon [of any rank] has, actually or potentially, its type." Taxa above the family-group level which may be designated as having the same type genus (such designations not being stipulated or recognized by any articles of the zoological *Code*) are considered to have identical authorship and date if the stem of names employed is the same (illustrated in preceding paragraph), but otherwise their authorship and date are accepted as various. Examples showing both suprafamilial and familial taxa in a group of spiders follow.

Class ARACHNIDA Lamarck, 1801

[*nom. correct.* NEWPORT, 1830 (*pro* class—not family—Arachnidae LAMARCK, 1801) (type, *Araneus* CLERCK, 1757, validated ICZN, 1948)]

Subclass CAULOGASTRA Pocock, 1893

[type, *Araneus* CLERCK, 1757]

Superorder LABELLATA Petrunkevitch, 1949

[type, *Araneus* CLERCK, 1757]

Order ARANEIDA Clerck, 1757

[*nom. correct.* DALLAS, 1864 (*pro* Araneidea BLACKWALL, 1861, *pro* Araneides LATREILLE, 1801, *pro* Aranei CLERCK, 1757, validated ICZN, 1948) (type, *Araneus* CLERCK, 1757)]

Suborder DIPNEUMONINA Latreille, 1817

[*nom. correct.* PETRUNKEVITCH, 1955 (*pro* Dipneumones LATREILLE, 1817) (type, *Araneus* CLERCK, 1757)]

Division TRIONYCHI Petrunkevitch, 1933

[type, *Araneus* CLERCK, 1757]

Superfamily ARANEOIDEA Leach, 1815

[*nom. transl.* PETRUNKEVITCH, 1955 (*ex* Araneides LEACH, 1815) (type, *Araneus* CLERCK, 1757)]

Family ARANEIDAE Leach, 1815

[*nom. correct.* PETRUNKEVITCH, 1955 (*pro* Araneadae LEACH, 1819, *pro* Araneides LEACH, 1815) (type, *Araneus* CLERCK, 1757)]

Subfamily ARANEINAE Leach, 1815

[*nom. transl.* SIMON, 1892 (*ex* Araneidae LEACH, 1815) (type, *Araneus* CLERCK, 1757)]

TAXONOMIC EMENDATION

Emendation has two measurably distinct aspects as regards zoological nomenclature. These embrace 1) alteration of a name itself in various ways for various reasons, as has been reviewed, and 2) alteration or taxonomic scope or concept in application of a given zoological name, whatever its hierarchical rank. The latter type of emendation primarily concerns classification and inherently is not associated with change of name, whereas the other type introduces change of name without necessary expansion, restriction, or other modification in applying the name. Little attention generally has been paid to this distinction in spite of its significance.

Most zoologists, including paleozoologists, who have signified emendation of zoological names refer to what they consider a material change in application of the name such as may be expressed by an importantly altered diagnosis of the assemblage covered by the name. The abbreviation *"emend."* then may accompany the name, with statement of the author and date of the emendation. On the other hand, a multitude of workers concerned with systematic zoology think that publication of *"emend."* with a zoological name is valueless, because more or less alteration of taxonomic sort is introduced whenever a subspecies, species, genus, or other assemblage of animals is incorporated under or removed from the coverage of a given zoological name. Inevitably associated with such classificatory expansions and restrictions is some degree of emendation affecting diagnosis. Granting this, still it is true that now and then somewhat radical revisions are put forward, generally with published statement of reasons for changing the application of a name. To erect a signpost at such points of most significant change is worthwhile, both as aid to subsequent workers in taking account of the altered nomenclatural usage and as indication that not to-be-overlooked discussion may be found at a particular place in the literature. Authors of contributions to the *Treatise* are encouraged to include records of all specially noteworthy emendations of this nature, using the abbreviation *"emend."* with the name to which it refers and citing the author and date of the emendation.

In Part G (Bryozoa) and Part D (Protista 3) of the *Treatise,* the abbreviation *"emend."* is employed to record various sorts of name emendations, thus conflicting with usage of *"emend."* for change in taxonomic application of a name without alteration of the name itself. This is objectionable. In Part E (Archaeocyatha, Porifera) and later-issued divisions of the *Treatise,* use of *"emend."* is restricted to its customary sense, that is, significant alteration in taxonomic scope of a name such as calls for noteworthy modifications of a diagnosis. Other means of designating emendations that relate to form of a name are introduced.

STYLE IN GENERIC DESCRIPTIONS

CITATION OF TYPE SPECIES

The name of the type species of each genus and subgenus is given next following the generic name with its accompanying author and date, or after entries needed for definition of the name if it is involved in homonymy. The originally published combination of generic and trivial names for this species is cited, accompanied by an asterisk (*), with notation of the author and date of original publication. An exception in this procedure is made, however, if the species was first published in the same paper and by the same author as that containing definition of the genus which it serves as type; in such case, the initial letter of the generic name followed by the trivial name is given without repeating the name of the author and date, for this saves needed space. Examples of these two sorts of citations are as follows:

Diplotrypa NICHOLSON, 1879 [**Favosites petropolitanus* PANDER, 1830].

Chainodictyon FOERSTE, 1887 [**C. laxum*].

If the cited type species is a junior synonym of some other species, the name of this latter also is given, as follows:

Acervularia SCHWEIGGER, 1819 [**A. baltica* (=**Madrepora ananas* LINNÉ, 1758)].

It is judged desirable to record the manner of establishing the type species, whether by original designation or by subsequent designation.

Fixation of type species originally. The type species of a genus or subgenus, according to provisions of the *Code,* may be fixed in various ways originally (that is, in the publication containing first proposal of the generic name) or it may be fixed in specified ways subsequent to the original publication. Fixation of the type species of a genus or subgenus in an original publication is stipulated by the *Code* (Art. 68) in order of precedence as 1) *original designation* (in the *Treatise* indicated as OD) when the type species is explicitly stated or (before 1931) indicated by "n. gen., n. sp." (or its equivalent) applied to a single species included in a new genus, 2) defined by use of *typus* or *typicus* for one of the species included in a new genus (adequately indicated in the *Treatise* by the specific name), 3) established by *monotypy* if a new genus or subgenus includes only one originally included species which is neither OD nor TYP (in the *Treatise* indicated as M), and 4) fixed by *tautonymy* if the genus-group name is identical to an included species name not indicated as type belonging to one of the three preceding categories (indicated in the *Treatise* as T).

Fixation of type species subsequently. The type species of many genera are not determinable from the publication in which the generic name was introduced and therefore such genera can acquire a type species only by some manner of subsequent designation. Most commonly this is established by publishing a statement naming as type species one of the species originally included in the genus, and in the *Treatise* fixation of the type species in this manner is indicated by the letters "SD" accompanied by the name of the subsequent author (who may be the same person as the original author) and the date of publishing the subsequent designation. Some genera, as first described and named, included no mentioned species and these necessarily lack a type species until a date subsequent to that of the original publication when one or more species are assigned to such a genus. If only a single species is thus assigned, it automatically becomes the type species and in the *Treatise* this subsequent monotypy is indicated by the letters "SM." Of course, the first publication containing assignment of species to the genus which originally lacked any included species is the one concerned in fixation of the type species, and if this named two or more species as belonging to the genus but did not designate a type species, then a later "SD" designation is necessary. Examples of the use of "SD" and "SM" as employed in the *Treatise* follow.

Hexagonaria Gürich, 1896 [**Cyathophyllum hexagonum* Goldfuss, 1826; SD Lang, Smith & Thomas, 1940].

Muriceides Studer, 1887 [**M. fragilis* Wright & Studer, 1889; SM Wright & Studer, 1889].

Another mode of fixing the type species of a genus that may be construed as a special sort of subsequent designation is action of the International Commission on Zoological Nomenclature using its plenary powers. Definition in this way may set aside application of the *Code* so as to arrive at a decision considered to be in the best interest of continuity and stability of zoological nomenclature. When made, it is binding and commonly is cited in the *Treatise* by the letters "ICZN," accompanied by the date of announced decision and (generally) reference to the appropriate numbered Opinion.

Worthy of repetition is the lack of requirement of a type species for definition of collective groups *(coll. coll.)*, but when differentiated and named these are treated for convenience as genera in the meaning of the *Code* (Art. 42c).

HOMONYMS

Most generic names are distinct from all others and are indicated without ambiguity by citing their originally published spelling accompanied by name of the author and date of first publication. If the same generic name has been applied to 2 or more distinct taxonomic units, however, it is necessary to differentiate such homonyms, and this calls for distinction between junior homonyms and senior homonyms. Because a junior homonym is invalid, it must be replaced by some other name. For example, *Callopora* Hall, 1851, introduced for Paleozoic trepostome bryozoans, is invalid because Gray in 1848 published the same name for Cretaceous-to-Recent cheilostome bryozoans, and Bassler in 1911 introduced the new name *Hallopora* to replace Hall's homonym. The *Treatise* style of entry is:

Hallopora Bassler, 1911, *nom. subst.* [*pro Callopora* Hall, 1851 (*non* Gray, 1848)].

In like manner, a needed replacement generic name may be introduced in the *Treatise* (even though first publication of generic names otherwise in this work is avoided). The requirement that an exact bibliographic reference must be given for the replaced name commonly can be met in the *Treatise* by citing a publication recorded in the list of references, using its assigned index number, as shown in the following example.

Mysterium de Laubenfels, *nom. subst.* [*pro Mystrium* Schrammen, 1936 (ref. 40, p. 60) (*non* Roger, 1862)] [**Mystrium porosum* Schrammen, 1936].

For some replaced homonyms, a footnote reference to the literature is necessary. A senior homonym is valid, and in so far as the *Treatise* is concerned, such names are handled according to whether the junior homonym belongs to the same major taxonomic division (class or phylum) as the senior homonym or to some other; in the former instance, the author and date of the junior homonym are cited as:

Diplophyllum Hall, 1851 [*non* Soshkina, 1939] [**D. caespitosum*].

Otherwise, no mention of the existence of a junior homonym generally is made.

Synonymic homonyms. An author sometimes publishes a generic name in two or more papers of different date, each of which indicates that the name is new. This is a bothersome source of errors for later workers who are unaware that a supposed first publication which they have in hand is not actually the original one. Although the names were separately published, they are identical and therefore definable as homonyms; at the same time they are absolute synonyms. For the guidance of all concerned, it seems desirable to record such names as synonymic homonyms and in the *Treatise* the junior one of these is indicated by the abbreviation "jr. syn. hom."

Identical family-group names not infrequently are published as new names by different authors, the author of the later-introduced name being ignorant of previous publication(s) by one or more other workers. In spite of differences in taxonomic concepts as indicated by diagnoses and grouping of genera and possibly in assigned rank, these family-group taxa are nomenclatural homonyms, based on the same type genus, and they are also synonyms. Wherever encountered, such synonymic homonyms are distinguished in the *Treatise* as in dealing with generic names.

SYNONYMS

Citation of synonyms is given next following record of the type species and if two or more synonyms of differing date are recognized, these are arranged in chronological order. Objective synonyms are indicated by accompanying designation "(obj.)," others being understood to constitute subjective synonyms. Examples showing *Treatise* style in listing synonyms follow.

Calapoecia Billings, 1865 [**C. anticostiensis;* SD Lindström, 1883] [=*Columnopora* Nicholson, 1874; *Houghtonia* Rominger, 1876].

Staurocyclia Haeckel, 1882 [**S. cruciata* Haeckel, 1887] [=*Coccostaurus* Haeckel, 1882 (obj.); *Phacostaurus* Haeckel, 1887 (obj.)].

A synonym which also constitutes a homonym is recorded as follows:

Lyopora Nicholson & Etheridge, 1878 [**Palaeopora? favosa* M'Coy, 1850] [=*Liopora* Lang, Smith & Thomas, 1940 (*non* Girty, 1915)].

Some junior synonyms of either objective or subjective sort may take precedence desirably over senior synonyms wherever uniformity and continuity of nomenclature are served by retaining a widely used but technically rejectable name for a generic assemblage. This requires action of ICZN using its plenary powers to set aside the unwanted name and validate the wanted one, with placement of the concerned names on appropriate official lists. In the *Treatise* citation of such a conserved generic name is given in the manner shown by the following example.

Tetragraptus Salter, 1863 [*nom. correct.* Hall, 1865 (*pro Tetragrapsus* Salter, 1863), *nom. conserv.* proposed Bulman, 1955, ICZN pend.] [**Fucoides serra* Brongniart, 1828 (=*Graptolithus bryonoides* Hall, 1858)].

ABBREVIATIONS

Abbreviations used in this division of the *Treatise* are explained in the following alphabetically arranged list.

Abbreviations

Aalen., Aalenian
Aarsber., *Aarsberetning*
Abhandl., *Abhandlung(en)*
Abstr., Abstract
Abt., *Abteilung*
aff., *affinis* (related to)
afhandl., *afhandling*
Afr., Africa, -an
Ala., Alabama
Alb., Albian
Alg., Algeria
Am., America, -n
Amman., Ammanian
Anis., Anisian
Ann., *Anñaes, Année, Annalen, Annales,* Annual, *Annuaire*
ant., anterior
append., appendix
approx., approximately
Apsheron., Apsheronian
Apt., Aptian
Aquitan., Aquitanian
Arbeit., *Arbeiten*
Arch., Archipelago, Archives, *Archivos*
Arg., Argentina
Argov., Argovian
Ariz., Arizona
art., article
Artinsk., Artinskian
Astart., Astartian
Atl., Atlantic
auctt., *auctorum* (of authors)
Aus., Austria
Auvers., Auversian
AV, attached valve
Avd., *Avdelingen*

Bajoc., Bajocian
Barrem., Barremian
Barton., Bartonian
Bathon., Bathonian

B.C., British Columbia
Bd., *Band*
Beil., *Beilage*
Belg., *Belgique,* Belgium
Blackriv., Blackriveran
B.M. (N.H.), British Museum (Natural History)
Boh., Bohemia
Bol., *Boletim, Boletín*
Boll., *Bolletino*
Br.I., British Isles
Brit., Britain, British
Bulg., Bulgaria
Bull., Bulletin
Byull., *Byulletin*
Burdigal., Burdigalian

C., Centigrade, Central
ca., *circa*
Calabr., Calabrian
Caledon., Caledonia
Calif., California
Callov., Callovian
Cam., Cambrian
Campan., Campanian
Can., Canada
Caradoc., Caradocian
Carb., Carboniferous
Carib., Caribbean
Carn., Carnian
Cat., *Catalogue(s)*
Cauc., Caucasus
Cenoman., Cenomanian
cf., *confer* (compare)
Charmouth., Charmouthian
Chatt., Chattian
Chazy., Chazyan
Chemung., Chemungian
cht., chart
Cincinnati., Cincinnatian
circ., circular
cm., centimeter
Co., Company, County
Coblenz., Coblenzian
col., color
Coll., Collection(s)
coll. coll., *collectio collectiva* (collective group)
Colom., Colombia
Comm., Commission
commun., communication
Comun., *Comunicaciones*
Congr., Congress
Coniac., Coniacian
cont'd., continued
Contrib., Contribution(s)
Corall., Corallian
cosmop., cosmopolitan
Cr., Creek
Cret., Cretaceous
Cuis., Cuisian
Cumberland., Cumberlandian
Czech., Czechoslovakia

Dalmat., Dalmatia
Dan., Danian
D.C., District of Columbia
Desmoines., Desmoinesian
Denkschr., *Denkschrift(en)*
Denm., Denmark
Dept., Department
Dev., Devonian
diagram., diagrammatic
Dinant., Dinantian
Distr., District
Dol., Dolomite
Domer., Domerian
Domin., Dominican
Dorset., Dorsetshire
Downton., Downtonian

E., East
ed., edited, editor
edit., edition
e.g., *exempli gratia* (for example)
emend., *emendatus(-a)*
Eng., England
enl., enlarged
Eoc., Eocene
err., *errore* (by error)
espec., especially
est., estimated
Est., Estonia
et al., *et alii* (and others, persons)
Eu., Europe
Exped., Expedition
ext., exterior
Extr., Extract, *Extrait*

F., Formation
fam., family
fasc., fascicle, *fascicule*
fig., figure(s)
Fla., Florida
Fören., *Förening*
Förhandl., *Förhandlingar*
Forhandl., *Forhandlinger*
Fr., *Français(e),* France, French
FV, free valve

G.Brit., Great Britain
gen., genus
Geol., Geological, *Geologische,* Geology
Ger., German, Germany
Gloucs., Gloucestershire
Gotl., Gotland
Gr., Great., Group
Greenl., Greenland
Guadalup., Guadalupian
Hamilton., Hamiltonian
Handl., *Handlingar*
Hauteriv., Hauterivian
Helvet., Helvetian
Hemis., Hemisphere
Hettang., Hettangian
Hist., History
holo., holotype
hom., homonym
Hung., *Hungarica,* Hungary

I., Isle(s)
ICZN, International Commission on Zoological Nomenclature
i.e., *id est* (that is)
Ill., Illinois
illus., illustrated, -ions
Inc., Incorporated
incl., inclined, including
Ind., Indiana
Ind.O., Indian Ocean
Indon., Indonesia
Inf., Inferior
int., interior
Internatl., International
Inv., Investigation(s), -al
Ire., Ireland
Is., Island(s)

Jahrb., *Jahrbuch*
Jahrg., *Jahrgang*
Jan., January
Jour., Journal
jr., junior
Jur., Jurassic

Kans., Kansas
Kimmer., Kimmeriyskian (Cimmerian)
Kimmeridg., Kimmeridgian
Kinderhook., Kinderhookian
Kuialnik, Kuialnikian
Ky., Kentucky

L., **Low.**, Lower
La., Louisiana
Ladin., Ladinian
lat., lateral
Leonard., Leonardian
Lias., Liassic
Lief., *Lieferung*
litt., letters
Llandeil., Llandeilian
Llandov., Llandoverian
loc., locality
Lond., London
long., longitudinal
Ls., Limestone
Ltd., Limited
Ludlov., Ludlovian
Lusitan., Lusitanian

Lutet., Lutetian
LV, left valve

m., meter
M., Middle
M, monotypy
Maastricht., Maastrichtian
Madag., Madagascar
Maeot., Maeotian
mag., magnification
Mag., *Magazin*
Malac., Malacological
Man., Manitoba
Mass., Massachusetts
Mbr., Member
Md., Maryland
Me., Maine
Meded., *Mededeelingen*
Medin., Medinan
Medit., Mediterranean
Mem., Memoir(s), *Memoria, Memorie*
Mém., Mémoire(s)
Mesoz., Mesozoic
Mex., Mexico
Mich., Michigan
Mio., Miocene
Min., Minutes
Minn., Minnesota
Misc., Miscellaneous
Miss., Mississippi, Mississippian
Missouri., Missourian
missp., misspelling
Mitteil., *Mitteilungen*
mm., millimeter(s)
Mo., Missouri
mod., modified
Mon., Monograph, *Monographia, Monographie*
Monatsber., *Monatsberichte*
Monatsh., *Monatshefte*
Mongol., Mongolia
Mont., Montana
Morg., Morganian
Mt., Mount, Mountain
Mtg., Meeting
Mts., **Mtns.**, Mountains
Mus., Museum

n., **n**, new
N., North
Nach., *Nachrichtsblatt*
N.Am., North America(n)
Namur., Namurian
Nat., Natural
Natl., National
N.Car., North Carolina
N.Dak., North Dakota
NE., Northeast
Neb., Nebraska
Neocom., Neocomian
Neog., Neogene
Neth., Netherlands
Nev., Nevada
Newf., Newfoundland
Niag., Niagaran
N.J., New Jersey
no., number
nom. conserv., *nomen conservatum* (conserved name)
nom. correct., *nomen correctum* (corrected or intentionally altered name)
nom. dub., *nomen dubium* (doubtful name)
nom. imperf., *nomen imperfectum* (imperfect name)
nom. neg., *nomen negatum* (denied name)
nom. nov., *nomen novum* (new name)
nom. nud., *nomen nudum* (naked name)
nom. null., *nomen nullum* (null, void name)
nom. oblit., *nomen oblitum* (forgotten name)
nom. subst., *nomen substitutum* (substitute name)
nom. transl., *nomen translatum* (transferred name)
nom. van., *nomen vanum* (vain, void name)
nom. vet., *nomen vetitum* (impermissible name)
Nomencl., Nomenclature
Nor., Norian, Norway
Notizbl., *Notizblatt*
Nouv., *Nouvelle(s)*
N.S., Nova Scotia
NW., Northwest
N.Y., New York
N.Z., New Zealand

O., Ocean
obj., objective
Oblast., *Oblastnoi*
Occas., Occasional
OD, original designation
Okla., Oklahoma
Oligo., Oligocene
Onondag., Onondagan
Ont., Ontario
Op., Opinion
Ord., Ordovician
Ore., Oregon
orig., original
Otapir., Otapirian
Oxford., Oxfordian

p., page(s)
Pa., Pennsylvania
Pac., Pacific
Pak., Pakistan
Paläont., Paläontologie
Palaeont., Palaeontological
Paleoc., Paleocene
Paleog., Paleogene
Paleont., Paleontological
Panaman., Panamanian
pantrop., pantropic
Patag., Patagonia
pend., pending
Penn., Pennsylvanian
Perm., Permian
pers., personal
Philip., Philippines
Philos., Philosophical
Piacenz., Piacenzian
pl., plate(s), plural
Pleist., Pleistocene
Pliensbach., Pliensbachian
Plio., Pliocene
Pol., Poland
Pont., Pontian
Port., Portugal
Portland., Portlandian
post., posterior
Pref., Prefecture
Prelim., Preliminary
Proc., Proceedings
Prof., Professional
prov., province(s)
pt., part(s)
pubbl., *pubblicato*
publ., publication(s), published
Purbeck., Purbeckian

Quart., Quarterly
Quat., Quaternary
Que., Quebec
Queensl., Queensland

R., River
Raurac., Rauracian
Rec., Recent, Record(s)
Rech., *Recherches*
reconstr., reconstructed, -ion
Rept., Report(s)
Repub., Republic
rev., revised
Rev., Review, *Revista, Revue*
Rhaet., Rhaetian
Rhinel., Rhineland
Richmond., Richmondian
Roy., Royal
RV, right valve
Ryaz., Ryazian

S., Sea, South
S.Am., South America
Santon., Santonian

Sarmat., Sarmatian
Sci., Science, Scientific, *Scientifique*
Scot., Scotland
Scyth., Scythian
SD, subsequent designation
SE., Southeast
sec., section(s)
Senon., Senonian
Sequan., Sequanian
ser., serial, series, *seriia*
sér., *séries*
Sess., Session
Sh., Shale
Sib., Siberia
Sil., Silurian
Sinemur., Sinemurian
sing., singular
Sitzungsber., *Sitzungsberichte*
Skrift., *Skrift(er)*
s.l., *sensu lato* (in the wide sense, broadly defined)
SM, subsequent monotypy
Soc., *Société*, Society
Somalil., Somaliland
Sonderabdr., *Sonderabdruck*
sp., species (**spp.**, plural)
Spitz., Spitzbergen
sr., senior
s.s., *sensu stricto* (in the strict sense, narrowly defined)
Ss., Sandstone
Staffords., Staffordshire
Stephan., Stephanian
Str., Strait(s)
Subantarct., Subantarctic
subfam., subfamily
subj., subjective
subtrop., subtropical
summ., summary
superfam., superfamily
suppl., supplement(s)
SW., Southwest
Swed., Sweden
Switz., Switzerland
syn., synonym

t., *tome*
T, tautonymy
tab., table(s)
temp., temperate
Tenn., Tennessee
Terr., Territory, -ies
Tert., Tertiary
Tex., Texas
Tithon., Tithonian
Toarc., Toarcian
Tongr., Tongrian
Tournais., Tournaisian
Trans., Transactions
transl., translated, -ion
transv., transverse
Tremadoc., Tremadocian
Trenton., Trentonian
Trias., Triassic
trop., tropical
Turon., Turonian

U., **Up.**, Upper
Univ., *Universidad, Università, Universität, Université, Universitets,* University
Ural., Uralian
Urug., Uruguay
U.S., United States
USA, United States of America
USSR, Union of Soviet Socialist Republics

v., **vol.**, volume(s)
Va., Virginia
Valang., Valanginian
var., variety
Venez., Venezuela
Verhandel., *Verhandelingen*
Verhandl., *Verhandlung(en)*
Virgil., Virgilian
Vise., Visean
Volg., Volgian

W., West
Wandrawan., Wandrawanian
Wash., Washington
Waverly., Waverlyan
Weald., Wealdian
Werfen., Werfenian
Westphal., Westphalian
Wis., Wisconsin
Wolfcamp., Wolfcampian
Wyo., Wyoming

Ypres., Ypresian
Yugo., Yugoslavia

Z., Zone
Zeitschr., *Zeitschrift*
Zool., Zoological, *Zoologie, Zoologisch,* Zoology

REFERENCES TO LITERATURE

Each part of the *Treatise* is accompanied by a selected list of references to paleontological literature consisting primarily of recent and comprehensive monographs available but also including some older works recognized as outstanding in importance. The purpose of giving these references is to aid users of the *Treatise* in finding detailed descriptions and illustrations of morphological features of fossil groups, discussions of classifications and distribution, and especially citations of more or less voluminous literature. Generally speaking, publications listed in the *Treatise* are not original sources of information concerning taxonomic units of various rank but they tell the student where he may find them; otherwise it is necessary to turn to such aids as the *Zoological Record* or NEAVE's *Nomenclator Zoologicus.* References given in the *Treatise* are arranged alphabetically by authors and accompanied by index numbers which serve the purpose of permitting citation most concisely in various parts of the text; these citations of listed papers are enclosed invariably in parentheses and, except in Parts C and N, are distinguishable from dates because the index numbers comprise no more than 3 digits. The systematic descriptions given in part C are accompanied by a reference list containing more than 2,000 entries with the index numbers marked by an asterisk, and in Part N (containing over 1,000 entries), they are italicized.

The following is a statement of the full names of serial publications which are cited in abbreviated form in the *Treatise* lists of references. The information thus provided should be useful in library research work. The list is alphabetized according to the serial titles which were employed at the time of original publication. Those following it in brackets are those under which the publication may be found currently in the *Union List of Serials,* the United States Library of Congress listing, and most library card catalogues. The names of serials published in Cyrillic are transliterated; in the reference lists these titles, which may be abbreviated, are accompanied by transliterated authors' names and titles, with English translation of the title. The place of publication is added (if not included in the serial title).

The method of transliterating Cyrillic letters that is adopted as "official" in the *Treatise* is the so-called Anglo-American method given by the Geographical Society of London. It follows that names of some Russian authors in transliterated form derived in this way differ from other forms, possibly including one used by the author himself. In *Treatise* reference lists the alternative (unaccepted) form is given enclosed by square brackets (e.g., Chernyshev [Tschernyschew], T.N.).

List of Serial Publications

Académie Impériale des Sciences, St. Pétersbourg, Mémoires (Akademiya Nauk SSSR Leningrad).
Académie Royale des Sciences, Arts et Belles-Lettres de Dijon, Mémoires.
Académie Royale des Sciences, des Lettres et des Beaux-Arts de Belgique, Bulletin. Bruxelles.
Académie des Sciences de l'Institut de France, Mémoires. Paris.
Académie des Sciences Mathematiques et Naturelles, Bulletin. Belgrade.
Académie des Sciences de Paris, Comptes Rendus, Mémoires.
Académie des Sciences de Roumanie, Comptes Rendus. Bucharest.
Académie des Sciences de l'URSS, Comptes Rendus; Institut Paléontologique, Travaux; Institut Paléozoologique, Travaux [Akademiya Nauk SSSR, Doklady]. Leningrad.
Académie Tchèque des Sciences, Bulletin International, Classe des Sciences Mathématiques, Naturelles et de la Médecine.
Academy of Natural Sciences of Philadelphia, Journals; Proceedings.
Academy of Science of St. Louis, Bulletins; Memoirs; Transactions.
Accademia Gioenia dell Scienze Naturali di Catania, Atti; Bollettino.
Accademia dei Lincei, Classe di Scienze Fisiche, Matematiche e Naturali, Atti; Memorie; Rendiconti. Roma.
[R.] Accademia delle Scienze, Atti; Memorie. Torino.
[R.] Accademia delle Scienze dell 'Istituto di Bologna, Memorie.
Accademia di Scienze, Lettere ed Arti, Atti. Palermo.
Acta Musei Nationalis Pragae (see Národního Musea v. Praze, Sborník).
Acta Palaeontologia Sinica. Peking.
Akademie der Wissenschaften und der Literature zu Mainz, mathematisch - naturwissenschaftlichen Klasse, Abhandlungen. Wiesbaden.
[K.] Akademie der Wissenschaften zu Wien, mathematische-naturwissenschaftliche Klasse, Denkschriften; Sitzungsberichte.
Akademija Znanosti Umietnosti. Ljubljana.
Akademiya Nauk SSSR, Geologicheskii Muzei A. P. Karpinskii. Moskva, Leningrad.
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Akademiya Nauk SSSR Leningrad, Doklady; Trudy, Izvestiya. Moskva, Leningrad.
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Allan Hancock Pacific Expedition, Reports. Los Angeles.
American Association for the Advancement of Science, Proceedings; Publications. Washington, D.C.
American Association of Petroleum Geologists, Bulletins. Tulsa, Okla.
American Journal of Conchology. Philadelphia, Pa.
American Journal of Science. New Haven, Conn.
American Malacological Union, Pacific Division, Reports. Buffalo.
American Midland Naturalist. Notre Dame, Ind.
American Museum of Natural History, Bulletins; Novitates; Memoirs. New York.
American Naturalist. Lancaster, Pa.
Anales del Instituto de Biología Universidad de Mexico. Mexico City.
Anatomical Record. Philadelphia, Pa.
Annales Générales des Sciences Physiques. Bruxelles.
Annales Hébert et Haug. Paris.
Annales de Paléontologie. Paris.
Annales des Sciences Naturelles, Zoologie. Paris.
Annals and Magazine of Natural History. London.

Annuario Museo Zoologico Università Napoli (Italia).
Archiv für Biontologie (Gesellschaft Naturforschender Freunde). Berlin.
Archiv für Molluskenkunde. Frankfurt.
Archiv für Naturgeschichte. Berlin, Leipzig.
Archives de Biologie. Paris.
Archives Néerlandaises de Zoologie. Leiden.
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Arkticheskii i Antarkticheskii Nauchno-issledovatel'skii Institut, Trudy. Leningrad.
Arquivos do Instituto Biológico (de defesa agricola e animal). São Paulo.
Australia Bureau of Mineral Resources, Geology and Geophysics, Bulletins; Explanatory Notes; Reports. Canberra.
Australia, Geological Society of, Journals. Adelaide.
Australian Journal of Marine and Freshwater Research. Melbourne.
Australian Museum, Memoirs; Records. Sydney.
Australian Zoologist. Sydney.
[K.] Bayerische Akademie der Wissenschaften, mathematisch-physikalische Klasse, Abhandlungen; Sitzungsberichte. München.
Bergens Museums Aarbog, Afhandling og Aarsberetning. Bergen.
Biologia Centrali-Americana, Zoology. London.
Biological Bulletin. Woods Hole, Mass.
Biological Reviews (*see* Cambridge Philosophical Society). Cambridge, Eng.
Biological Society of Washington, Proceedings.
Bolitim Instituto Oceanográfico Universidade São Paulo. São Paulo.
Bombay Natural History Society, Journals.
Boston Society of Natural History, Memoirs; Occasional Papers; Proceedings.
Bristol Naturalists' Society, Proceedings.
British Association for the Advancement of Science, Reports. London.
British Museum (Natural History), Bulletins; Scientific Reports. London.
Bulletin of American Paleontology. Ithaca, N.Y.
Bulletin Biologique de la France et de la Belgique. Paris.
Bulletin Scientifique de la France et de la Belgique. London, Paris, Berlin.
Bulletin of Zoological Nomenclature. London.
The Cabinet Cyclopedia, Natural History. London.
Cahiers Géologiques de Seyssel (Ain).
Cahiers Géologiques de Thoiry.
California Academy of Sciences, Occasional Papers; Proceedings. San Francisco.
California Fish and Game, Bulletins. San Francisco, Sacramento.
California, Geological Survey of, Palaeontology. San Francisco.
California, University of, Geological Sciences, Bulletins; Publications. Berkeley and Los Angeles.
California, University of, Publications in Zoology. Berkeley.
Cambridge Philosophical Society, Biological Reviews and Biological Proceedings. Cambridge, Eng.
Canada, Geological Survey of, Department of Mines and Resources, Mines and Geology Branch, Annual Reports; Bulletins; Memoirs; Museum Bulletins; Victoria Memorial Museum Bulletins. Ottawa.
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Canadian Naturalist and Geologist. Montreal.
Carnegie Institution of Washington, Papers; Publications; Department Marine Biology. Washington, D.C.
Carnegie Museum, Annals; Memoirs. Pittsburgh, Pa.
Centennial and Bicentennial Congress of Biology, Proceedings. Singapore.
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Chemical Society of Japan, Bulletins; Journals. Tokyo.
Chicago Academy of Sciences, Bulletins; Transactions.
China, Geological Survey of, Palaeontologia Sinica, Memoirs. Peking.
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Cincinnati Society of Natural History, Journals.
Commission Géologique du Portugal, Communications, Travaux. Lisbon.
Conchological Club of Southern California, Minutes. Los Angeles.
Conchologists' Exchange (*see* Nautilus). Philadelphia, Boston.
Connecticut Academy of Arts and Sciences, Memoirs; Transactions. New Haven, Conn.
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Evolution. Lancaster, Pa.

Fauna und Flora des Golfes von Neapel (*see* Stazione Zoologica di Napoli). Berlin.

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Geologica Hungarica; Series Geologica; Series Palaeontologica. Budapest.

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Geological Society of Australia, Journals. Adelaide.

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[K.K.] Geologische Bundesanstalt Wien, Abhandlungen; Jahrbuch; Verhandlungen.

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[K.K.] Geologische Reichsanstalt Wien (*see* Geologische Bundesanstalt Wien).

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SOURCES OF ILLUSTRATIONS

At the end of figure captions an index number is given to supply record of the author of illustrations used in the *Treatise,* reference being made either (1) to publications cited in reference lists or (2) to the names of authors with or without indication of individual publications concerned. Previously unpublished illustrations are marked by the letter "n" (signifying "new") with the name of the author.

STRATIGRAPHIC DIVISIONS

Classification of rocks forming the geologic column as commonly cited in the *Treatise* in terms of units defined by concepts of time is reasonably uniform and firm throughout most of the world as regards major divisions (e.g., series, systems, and rocks representing eras) but it is variable and unfirm as regards smaller divisions (e.g., substages, stages, and subseries), which are provincial in application. Users of the *Treatise* have suggested the desirability of publishing reference lists showing the stratigraphic arrangement of at least the most commonly cited divisions. Accordingly, a tabulation of European and North American units, which broadly is applicable also to other continents, is given here.

Generally Recognized Divisions of Geologic Column

EUROPE	NORTH AMERICA
ROCKS OF CENOZOIC ERA	**ROCKS OF CENOZOIC ERA**
NEOGENE SYSTEM[1]	**NEOGENE SYSTEM**[1]
Pleistocene Series (including Recent)	Pleistocene Series (including Recent)
Pliocene Series	Pliocene Series
Miocene Series	Miocene Series
PALEOGENE SYSTEM	**PALEOGENE SYSTEM**
Oligocene Series	Oligocene Series
Eocene Series	Eocene Series
Paleocene Series	Paleocene Series
ROCKS OF MESOZOIC ERA	**ROCKS OF MESOZOIC ERA**
CRETACEOUS SYSTEM	**CRETACEOUS SYSTEM**
Upper Cretaceous Series	**Gulfian Series (Upper Cretaceous)**
Maastrichtian Stage[2]	Navarroan Stage
Campanian Stage[2]	Tayloran Stage
Santonian Stage[2]	Austinian Stage
Coniacian Stage[2]	
Turonian Stage	Woodbinian (Tuscaloosan) Stage
Cenomanian Stage	**Comanchean Series (Lower Cretaceous)**
	Washitan Stage
Lower Cretaceous Series	
Albian Stage	Fredericksburgian Stage
Aptian Stage	Trinitian Stage
	Coahuilan Series (Lower Cretaceous)
Barremian Stage[3]	Nuevoleonian Stage
Hauterivian Stage[3]	
Valanginian Stage[3]	Durangoan Stage
Berriasian Stage[3]	
JURASSIC SYSTEM	**JURASSIC SYSTEM**
Upper Jurassic Series	**Upper Jurassic Series**
Portlandian Stage[4]	Portlandian Stage
Kimmeridgian Stage	Kimmeridgian Stage
Oxfordian Stage	Oxfordian Stage
Middle Jurassic Series	**Middle Jurassic Series**
Callovian Stage (or Upper Jurassic)	Callovian Stage (or Upper Jurassic)
Bathonian Stage	Bathonian Stage
Bajocian Stage	Bajocian Stage
Lower Jurassic Series (Liassic)	**Lower Jurassic Series (Liassic)**
Toarcian Stage	Toarcian Stage

Pliensbachian Stage	Pliensbachian Stage
Sinemurian Stage	Sinemurian Stage
Hettangian Stage	Hettangian Stage
TRIASSIC SYSTEM	TRIASSIC SYSTEM
Upper Triassic Series	**Upper Triassic Series**
Rhaetian Stage[5]	(Not recognized)
Norian Stage	Norian Stage
Carnian Stage	Carnian Stage
Middle Triassic Series	**Middle Triassic Series**
Ladinian Stage	Ladinian Stage
Anisian Stage (Virglorian)	Anisian Stage
Lower Triassic Series	**Lower Triassic Series**
Scythian Stage (Werfenian)	Scythian Stage
ROCKS OF PALEOZOIC ERA	ROCKS OF PALEOZOIC ERA
PERMIAN SYSTEM	PERMIAN SYSTEM
Upper Permian Series	**Upper Permian Series**
Tartarian Stage[6]	Ochoan Stage
Kazanian Stage [7]	Guadalupian Stage
Kungurian Stage	
Lower Permian Series	**Lower Permian Series**
Artinskian Stage[8]	Leonardian Stage
Sakmarian Stage	Wolfcampian Stage
Asselian Stage	
	PENNSYLVANIAN SYSTEM
CARBONIFEROUS SYSTEM	**Kawvian Series (Upper Pennsylvanian)**
Upper Carboniferous Series	
Stephanian Stage	Virgilian Stage
	Missourian Stage
	Oklan Series (Middle Pennsylvanian)
	Desmoinesian Stage
Westphalian Stage	Bendian Stage
	Ardian Series (Lower Pennsylvanian)
	Morrowan Stage
	MISSISSIPPIAN SYSTEM
	Tennesseean Series (Upper Mississippian)
Namurian Stage	Chesteran Stage
Lower Carboniferous Series	Meramecian Stage
Visean Stage	**Waverlyan Series (Lower Mississippian)**
	Osagian Stage
Tournaisian Stage	Kinderhookian Stage
Strunian Stage	
DEVONIAN SYSTEM	DEVONIAN SYSTEM
Upper Devonian Series	**Chautauquan Series (Upper Devonian)**
Famennian Stage	Conewangoan Stage
	Cassadagan Stage
Frasnian Stage	**Senecan Series (Upper Devonian)**
	Chemungian Stage
	Fingerlakesian Stage

Middle Devonian Series	**Erian Series (Middle Devonian)**
Givetian Stage	Taghanican Stage Tioughniogan Stage
Couvinian Stage	Cazenovian Stage
Lower Devonian Series	**Ulsterian Series (Lower Devonian)**
Emsian Stage	Onesquethawan Stage
Siegenian Stage	Deerparkian Stage
Gedinnian Stage	Helderbergian Stage
SILURIAN SYSTEM	**SILURIAN SYSTEM**
Ludlow Stage	**Cayugan Series** Includes age equivalents of middle and upper Ludlow (in New York)
Wenlock Stage	**Niagaran Series** Includes age equivalents of upper Llandovery, Wenlock, and lower Ludlow (in New York)
Landovery Stage	**Medinan Series** Includes age equivalents of lower and middle Llandovery (in New York)
ORDOVICIAN SYSTEM	**ORDOVICIAN SYSTEM**
	Cincinnatian Series (Upper Ordovician)
Ashgill Stage	Richmondian Stage Maysvillian Stage Edenian Stage
Caradoc Stage	**Champlainian Series (Middle Ordovician)** Mohawkian Stage Trentonian Substage Blackriveran Substage
Llandeilo Stage	Chazyan Stage
Llanvirn Stage	
Arenig Stage **Tremadoc Stage**[9]	**Canadian Series (Lower Ordovician)**
CAMBRIAN SYSTEM	**CAMBRIAN SYSTEM**
Upper Cambrian Series	**Croixian Series (Upper Cambrian)** Trempealeauan Stage Franconian Stage Dresbachian Stage
Middle Cambrian Series	**Albertan Series (Middle Cambrian)**
Lower Cambrian Series	**Waucoban Series (Lower Cambrian)**
EOCAMBRIAN SYSTEM	**EOCAMBRIAN SYSTEM**
ROCKS OF PRECAMBRIAN AGE	**ROCKS OF PRECAMBRIAN AGE**

RAYMOND C. MOORE

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[1] Considered by some to exclude post-Pliocene deposits.

[2] Classed as division of Senonian Subseries.

[3] Classed as division of Neocomian Subseries.

[4] Includes Purbeckian deposits.

[5] Interpreted as lowermost Jurassic in some areas.

[6] Includes some Lower Triassic and equivalent to upper Thuringian (Zechstein) deposits.

[7] Equivalent to lower Thuringian (Zechstein) deposits.

[8] Equivalent to upper Autunian and part of Rotliegend deposits.

[9] Classed as uppermost Cambrian by some geologists.

PART N

MOLLUSCA 6

BIVALVIA

By †L. R. Cox, N. D. Newell, D. W. Boyd, C. C. Branson, Raymond Casey, André Chavan, A. H. Coogan, Colette Dechaseaux, C. A. Fleming, Fritz Haas, L. G. Hertlein, E. G. Kauffman, A. Myra Keen, Aurèle LaRocque, A. L. McAlester, R. C. Moore, C. P. Nuttall, B. F. Perkins, H. S. Puri, L. A. Smith, T. Soot-Ryen, H. B. Stenzel, E. R. Trueman, Ruth D. Turner, and John Weir

VOLUME 1

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[Volume 1, p. i-xxxviii, *N*1-*N*489; Volume 2, p. *N*491-*N*952; Volume 3 (to follow)]

DEDICATION

By Raymond C. Moore and Norman D. Newell

Part N of the *Treatise on Invertebrate Paleontology,* devoted to the great group of mollusks named Bivalvia, here is dedicated to the memory of Leslie Reginald Cox, one of the chief contributing authors both to this and other *Treatise* volumes concerned with the Mollusca. He died quite unexpectedly on August 5, 1965, at the age of 67 just after completion of a typescript draft of his chapter on General Characters of Bivalvia, which follows, but before illustrations planned by him had been organized. He had already finished work on many bivalve families, including preparation of figures for genera included in them. The magnitude of loss to paleontology and especially to the *Treatise* caused by his death goes without saying. Whereas no previously published unit of this series has been designated to honor an individual paleontologist, it seems highly appropriate that Part N on Bivalvia should be dedicated to Dr. Cox.

Except to record that Dr. Cox's scientific career is almost entirely linked with the British Museum (Natural History), where in later years he was Deputy Keeper of the Palaeontology Department, and that his research activities broadly and mainly embraced groups of post-Paleozoic Mollusca represented by fossils from all parts of the world, the scope and importance of his very numerous published contributions are not pertinent for review by us here. Rather, it is desirable to stress the extraordinary degree of Dr. Cox's dedication to objectives of the *Treatise,* for without any financial remuneration to him or even financial assistance from *Treatise* sources, he not only labored indefatigably to achieve utmost quality of his own chapters in this collaborative project but unstintingly furnished aid to other *Treatise* workers. The wisdom of his counsel and generosity in drawing on his time and accumulated knowledge for the benefit of others, including both of us in disposing of editorial and organizational problems, are irreplaceable assets. In short, without trace of provincial outlook, scientifically or politically, LESLIE R. COX epitomizes the able, energetic, best possible *Treatise* collaborator, who is indispensable for achieving the high aims of leadership in authoritative, comprehensive presentation of present-day knowledge of invertebrate fossils, both for understanding of them as remains of once-living animals and for practical use of them in solving geologic problems.

Acknowledgment of work done by Mr. C. P. NUTTALL, British Museum (Natural History), in revising parts of the text, in completing illustrations, and in adding to literature references, deserves record. This help has been extremely valuable, and because of his substituting as far as possible for Dr. Cox, special appreciation is expressed to Mr. NUTTALL.

GENERAL FEATURES OF BIVALVIA

By †L. R. COX (with additions by C. P. NUTTALL and E. R. TRUEMAN)
[British Museum (Natural History), London]

CONTENTS

NAME AND CHARACTERS OF CLASS

NAME BIVALVIA

Probably more disagreement on the name to be applied to this class has arisen than in the case of any other major taxon. Of some 13 names for the bivalve mollusks which have been introduced in the literature, those of Pelecypoda GOLDFUSS and Lamellibranchia (or Lamellibranchiata) DE BLAINVILLE were preferred (to an almost equal extent) by malacologists for many years. Until fairly recently, in fact, it is only in occasional works that we find the Linnean name Bivalvia, and in still fewer do other names appear, such as Conchifera LAMARCK and Acephala CUVIER. The designation Bivalvia, however, has now been revived in several major works of reference, notably F. HAAS's monumental contribution to the revised edition of BRONN's *Klassen und Ordnungen des Tierreichs* (1929-56), J. THIELE's *Handbuch der systematischen Weichtierkunde* (1934-35) and the Russian *Osnovy Paleontologii* (1960). It has thus become increasingly familiar to the present generation of workers, and has been accepted for use in the present *Treatise*

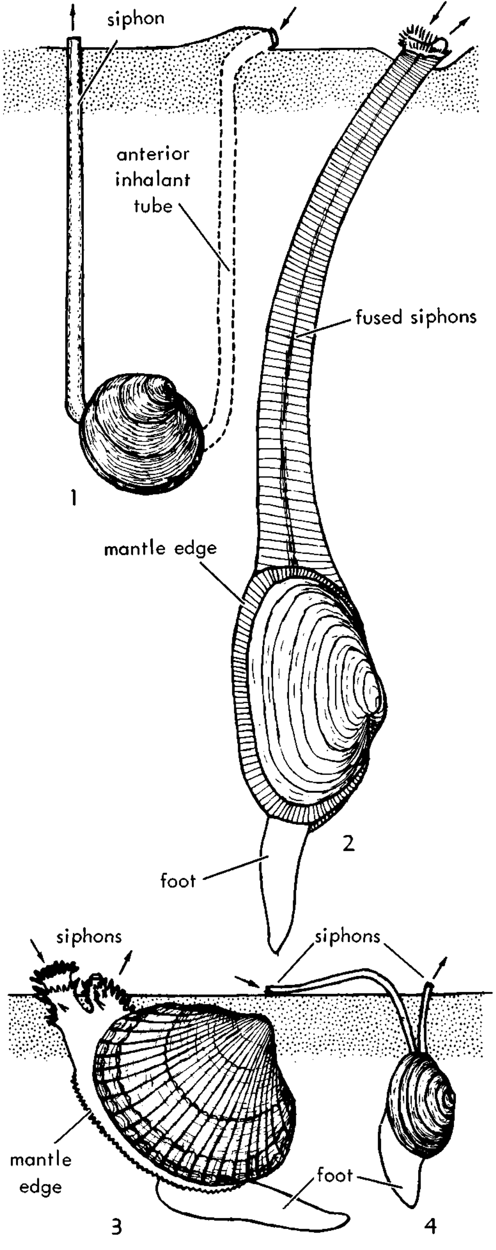

Fig. 1. Habitat of bivalves—burrowing types (Cox, n).——*1. Loripes lucinalis* (Lamarck), suspension-feeder with anterior inhalant tube punched through sediment by foot, ×1.——*2. Mya arenaria* Linné, deep-burrowing suspension-feeder with fused siphons, ×0.4.——*3. Cardium edule* Linné, shallow-burrowing suspension-feeder with short siphons, ×0.7.——*4. Tellina tenuis* da Costa, shallow-burrowing deposit-feeder with long unconnected siphons, ×0.6.

in the hope that this course will promote stability and uniformity in nomenclature.

Used by various early workers from the time of Buonanni (1681) onward, the name Bivalvia was adopted by Linné in 1758 in the 10th edition of the *Systema Naturae* (p. 645) for a subdivision of the group Testacea of the class Vermes; no diagnosis was given, the subdivision being defined by listing the genera included in it. In fact, these consisted of all the Linnean genera of the class as still understood, with the exception of *Teredo,* which was included in the group Intestina. Among the Linnean species of *Anomia* were certain forms now classified as Brachiopoda, but otherwise the Bivalvia included no non-molluscan elements. If objections to the name are raised on the ground that there are other groups of invertebrates protected by tests with two valves (e.g., Brachiopoda, some Crustacea, and even certain Mollusca recently recognized to be Gastropoda), it may be answered that a name is merely a name, and neither a key to recognition nor a definition. This consideration apart, it can at least be said that all Bivalvia have tests with two valves, whereas not all have an axelike foot[1] or platelike gills.[2]

MAIN CHARACTERS OF BIVALVIA

The Bivalvia are aquatic mollusks which fundamentally are bilaterally symmetrical and laterally compressed, and very commonly are elongated in an anteroposterior direction. They invariably are provided with a shell consisting of two wholly or partly calcified valves lying on left and right sides of the body. The shell is external except in a few forms. Typically, the two valves are of equal convexity; but in some forms bilateral symmetry has been lost, usually as the result of cementation of one valve to the substrate, and the valves differ in size to a varying extent. The valves (except in some aberrant genera) are connected dorsally by an only partially calcified, elastic structure (**ligament**), and open and close by hinging along an axis

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[1] The name Pelecypoda was derived from the Greek words πέλεκυς, axe, and πούς, ποδός, foot.

[2] The name Lamellibranchia was derived from the Latin words *lamella,* thin plate, and *branchiae,* gills.

which passes through or close to this. Typically, the hinge axis has an approximately anteroposterior direction. The two valves thus open along their anterior, posterior, and ventral margins, most widely along the last. The valves are closed by the action of muscles **(adductor muscles)**, two or one in number, attached to the inner face of each; these muscles, by drawing the valves together, oppose the action of the ligament, which acts as a spring tending to open them.

The mantle consists of two lobes, one lining each valve. These lobes are joined dorsally, but elsewhere their edges are either completely free or joined only along part of their length. The body of the mollusk normally occupies a dorsal position within the shell and mantle, to the latter of which it is fused. Ventrally, the mantle encloses a relatively large space (**mantle cavity**).

The animal lacks a head, radula, and jaws. Cephalic sensory organs (eyes, tentacles, etc.) found in other mollusks are thus absent, but in many Bivalvia they are replaced by organs with similar functions located mainly along the periphery of the mantle. The **mouth** and **anus** are usually at opposite ends of the body and the intestine is convoluted to a varying extent. The mouth lies between two pairs of ciliated, flaplike structures known as **labial palps**, which assist in conducting food to it. The stomach contains a peculiar structure, the crystalline style (present also in certain gastropods), which aids the digestion of carbohydrates.

A **foot** present in most Bivalvia is an extensile structure which most commonly serves mainly for burrowing. Most forms have a pair of **gills** or ctenidia which are suspended within the mantle cavity from the body and are arranged symmetrically with regard to the median plane of the mollusk. Their detailed structure varies considerably. The nervous system includes visceral and pedal ganglia, together with cerebral and pleural ganglia which are fused in most forms but separate in some. A pedovisceral commissure is lacking. Reproduction is without copulation. Most marine Bivalvia pass through a pelagic larval stage.

BIOLOGY OF BIVALVIA

HABITATS AND FOOD

The Bivalvia are essentially aquatic animals. No members of the class can respire, feed, or remain active except in an aqueous medium. The period for which any species can survive, inactive, when removed from such an environment depends largely on its capacity to close its two valves hermetically so that loss of moisture is reduced to a minimum. Of marine forms, those accustomed to life attached to rocks and other objects in the intertidal zone, where they may be exposed for several hours daily, are most tenacious of life. Specimens of the oyster *Crassostrea virginica* (GMELIN) are said to have revived after being kept for as long as ten weeks out of water and specimens of *Mytilus* can survive for a month or more under such conditions. Most marine forms, however, remain alive only for a few days out of water. Some fresh-water bivalves that live in pools which dry up periodically, particularly in hot climates, are the most retentive of life of all bivalves. Usually for aestivation they burrow more deeply into the muddy bottom before it becomes dry, but at times they merely lie loose on the floor of the former pool. Some Unionidae and Sphaeriidae are known to be dormant for as much as six months in every year, and are probably capable of survival for even longer periods. A case is on record of an Australian unionid, probably *Velesunio ambiguus* (PHILIPPI), which made a full recovery on reimmersion after being kept out of water (for much of the period in a dry drawer) for as long as 498 days.

The laterally compressed form characteristic of the great majority of bivalves renders them well adapted for burrowing in sandy or muddy substrates, a process accomplished with the aid of their extensile foot. Many burrowers ascend toward the

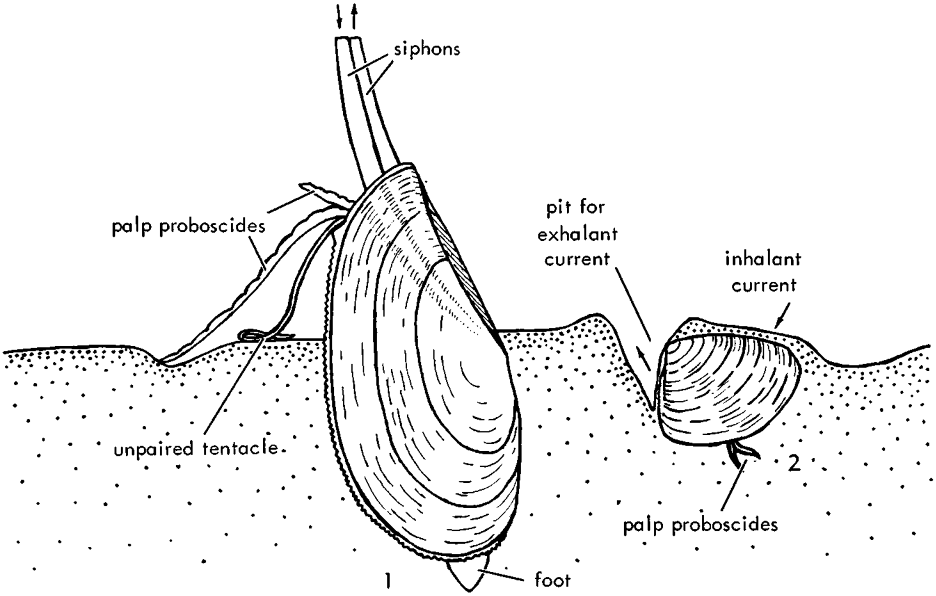

FIG. 2. Habitat of bivalves—nuculacean shallow-burrowing deposit-feeder groping for food by means of palp proboscides *(43)*.——*1. Yoldia limatula* (SAY), form with posterior siphons, ×2.5.——*2. Nucula nucleus* (LINNÉ), showing posterior pitlike opening forced through sediment for exhalant stream, inhalant stream being drawn in anteriorly between shallowly buried shell margins, ×1 *(189)*.

sea floor in order to feed, withdrawing to a greater depth when this activity ceases, as when the bottom is uncovered between tides. Some can burrow rapidly when attacked by an enemy (Fig. 1). Many shallow burrowers, such as *Cardium,* emerge to the surface of the sea floor from time to time and can migrate laterally, again with aid of their foot. The movement of such forms is not, however, a gentle creeping. *Cardium,* for example, moves by a series of jerks or even leaps resulting from the sudden straightening of its bent foot.

Some of the deeper burrowers lead a more or less sedentary life. Usually it is necessary for some communication to be established, either continuously or at frequent intervals, with the relatively clear bottom water. Most bivalves accomplish this with the aid of their two siphons, inhalant and exhalant, and as these structures constitute posterior extensions of the mantle, the usual position occupied by the deeper burrowers is with the anteroposterior axis of the mollusk almost vertical, the anterior end of the shell facing downward and the siphons extending upward from the other end. The deepest burrowers are thus those with the longest siphons, and some species of such genera as *Mya* and *Lutraria* live permanently buried to a depth of as much as 30 cm. in the bottom sediment. It is not, however, to be assumed that the normal position of life of all burrowers is with the plane of the valve margins vertical or almost so; evidence has been found recently that some Tellinidae lie below the surface with the commissure horizontal and right valve uppermost. The Lucinidae have no inhalant siphon, but draw in a current through an inhalant tube which is driven through the sediment by an up-and-down motion of the end of an extensile vermiform foot, and is lined with hardened mucus. This tube projects from the shell at its anterior end, which points obliquely upward, buried perhaps to a depth of 6 to 8 cm.

In *Nucula,* which is without siphons, the shell is buried so shallowly that it is possible for the inhalant current to be drawn in between its anterior margins; at the same time, a passage is maintained for the exhalant current, which passes between the more deeply buried posterior margins, by repeated extrusions of water expelled from the mantle cavity by sudden contractions of the adductor muscles (Fig. 2). *Solemya* is thought to be able to exist for considerable periods buried in soft sediment without any communication with the clear water above, but is exceptional if not unique in this respect.

While great numbers of Bivalvia are thus burrowers in unconsolidated sediment, others have become borers in solid rock (Fig. 3). *Hiatella* is able to bore into relatively soft rock by the mechanical action of the two valves of the shell, which are forced apart repeatedly by sudden pressure of water expelled from the siphons after their partial withdrawal into the borehole (Fig. 3,*2*). In this case, however, individuals unable to find a suitable spot for penetration can exist just as well without boring.

The genus *Pholas* can penetrate harder types of rock. Its shell, the surface of which bears rows of toothlike protrusions, rasps its way forward by a rocking motion of its valves produced by the two adductor muscles acting alternately. The foot forms a sucker which grips the end of the burrow, changing position frequently, with the result that a hole circular in cross section is bored (Fig. 3,*5*).

Lithophaga bores into calcareous formations, including coral rock, with the aid of an acid secretion from which its own shell is protected by a thick periostracum. The mollusk is held in position by byssal threads attached to the side of the burrow (Fig. 3,*1*). In all these cases the cavity widens inward, the shell growing as it bores; the mollusk, therefore, can never emerge from the cavity. The siphons, however, must always be capable of becoming extended as far as the opening, and the depth of penetration is limited by this factor. Some of the smaller species of *Tridacna* can bore mechanically obliquely downward

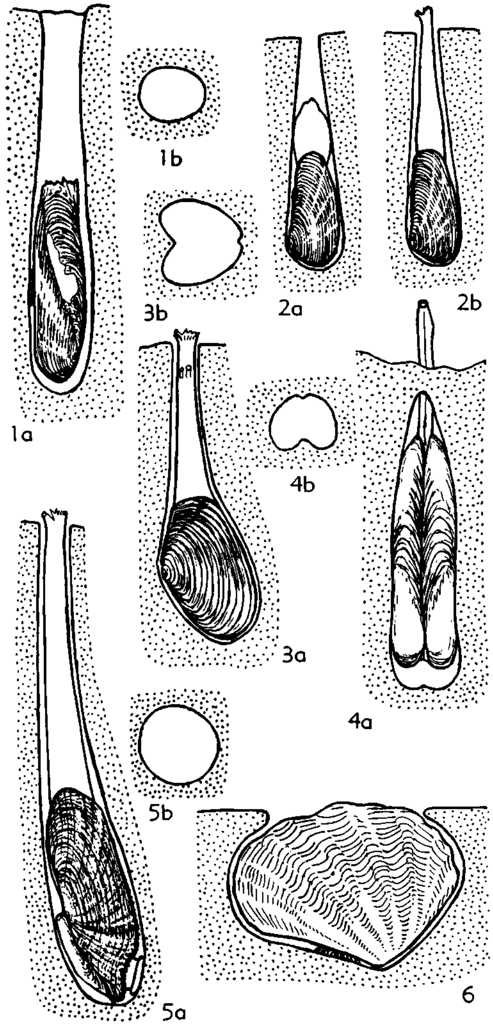

FIG. 3. Habitat of bivalves—rock-borers (surface of rock directed upward) showing relations to their crypts (Cox, n).——*1. Lithophaga cumingiana* (REEVE); *1a,* longitudinal section of crypt with animal attached to its wall by byssus threads; *1b,* transverse section of crypt showing oval shape; both ×0.4.——*2. Hiatella gallicana* (LAMARCK), longitudinal sections of crypt with animal in place; *2a,* siphons withdrawn, gripping walls of crypt; *2b,* siphons extended; both ×0.3.——*3. Platyodon cancellatus* (CONRAD); *3a,* longitudinal section of mechanically bored crypt without rotation of animal; *3b,* cross section of crypt with shape like that of shell; both ×0.2.——*4. Adula californiensis* (PHILIPPI); *4a,* longitudinal section of crypt enclosing animal with extruded siphons seen from dorsal side, umbones of shell abraded by mechanical action in boring; *4b,* transverse section of crypt; both ×0.7.——*5. Pholas dactylus* LINNÉ; *5a,* longitudinal section of crypt with side view of animal attached by sucker-like foot while boring; *6b,* cross section of crypt; both ×0.3.——*6. Tridacna crocea* LAMARCK, side view of animal in cavity bored obliquely downward in coral rock, at first held in place by byssus thread, ×0.3.

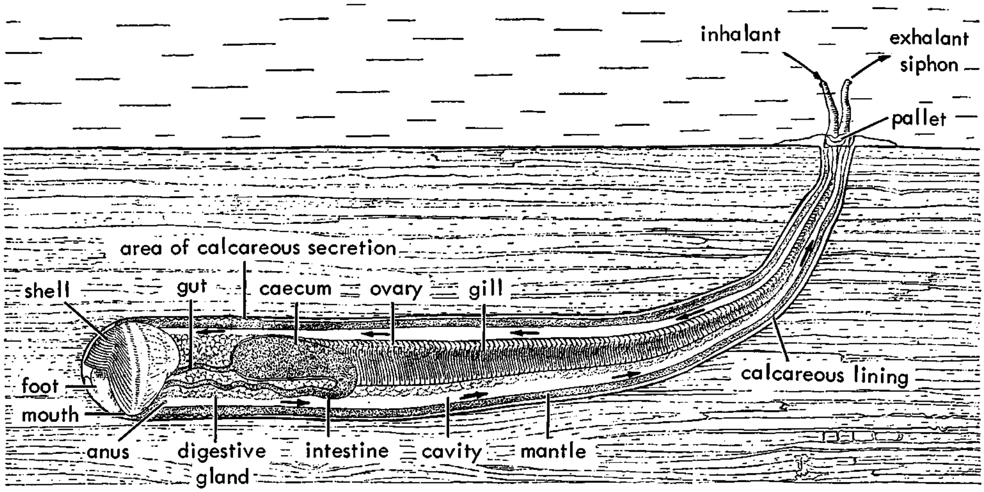

Fig. 4. Habitat of bivalves—wood-borer *Teredo,* side view of animal with posterior extremity permanently fixed to burrow entrance, boring effected by rasplike bivalve shell with wood particles broken down by enzyme in capacious caecum and waste thrown off through anus and carried away by exhalant-siphon stream, ×1 (Lane, 1961).

into coral rock. During the process the mollusk is oriented with its hinge margins facing downward. The byssus, which in this peculiar genus projects through a gap between these margins, pulls the shell against the rock and facilitates its penetration. The process stops when the opposite margins of the valves, which must remain capable of opening, are almost flush with the surface of the rock (Fig. 3,6).

The wood-boring Teredinidae ("shipworms") are the most highly specialized boring bivalves (Fig. 4). As in the case of *Pholas,* the anterior end of the valves of the shell has a rasplike surface and penetration is mechanical. The wood particles are, however, ingested by the animal, which is not, therefore, completely dependent on the outside water for food. The valves are much reduced in size and cover only a small part of the animal, which is wormlike and extends along the whole length of the boring. The latter, which is lined with calcium carbonate, and therefore the mollusk itself, may be of very considerable length (up to 1.2 m. in some species of the genus *Bankia*). Its opening can be closed by two calcareous paddle-shaped structures known as **pallets,** so that (unlike the rock-borers) the animal can seal itself off from the exterior.

Bivalves form an important element of the benthonic epifauna. Some rely on the weight or shape of their shell to maintain their position on the sea floor. Others, which live on rocky or coarse bottoms, attach themselves to stationary objects by one of two methods. The first is by means of their **byssus,** and the second is by **cementation** of one of the valves of the shell. The byssus, well developed, for example, in *Mytilus, Arca,* and *Pinctada* (pearl oyster), is typically a bunch of threads, secreted by glands at the posterior end of the foot and projecting through a gap between the valve margins (Fig. 5). In *Anomia,* however, it consists of a rigid calcareous plug which passes through a foramen in one of the valves. The Ostreidae, Spondylidae, and Chamidae are examples of living families in which attachment of one valve to some solid object is effected by a calcareous cement secreted by the equivalent of the byssal glands. The rudists of the Cretaceous Period are the most notable example of this mode of life provided by the fossil record.

The genus *Pinna* combines byssal attachment with a burrowing mode of life. The shell is conical or fan-shaped and lives half or more buried in the muddy sea floor with its pointed (anterior) end lowermost and its broader end projecting into the relatively clear water above. The byssus, by which *Pinna* is attached to buried stones or other objects, emerges from between the valve margins close to the anterior end of the shell (Fig. 6). Some species of the Limidae and of the genus *Musculus* (family Mytilidae) construct quite elaborate nests from byssus threads. When the mollusk has surrounded itself by one of these structures, which usually occupy holes in rocks or similar positions, its vulnerable trailing tentacles are protected from predators.

The most active living Bivalvia belong to the family Pectinidae. Many species of this group can swim near the sea bottom, propelled by sudden expulsions of water from the mantle cavity, produced by clapping their valves together. When not active in this manner the mollusk rests on one valve on the sea floor (Fig. 7). Some Limidae can also swim in a similar manner. In this family the valve margins remain more or less vertical during the process, whereas their position remains nearly horizontal in the Pectinidae.

No living Bivalvia are pelagic except in the larval state. It has, however, been suggested that *Bositra,* a Jurassic genus which until recently was not considered distinct from *Posidonia* of the Carboniferous, led a pelagic existence. The evidence for this conclusion has been summarized by JEFFERIES & MINTON *(78),* who postulate that the means of propulsion was similar to that employed in the Pectinidae.

Bivalves are most abundant in the sublittoral zone, but some forms have been dredged from very deep sea floors. The deepest record for a member of the class is of an unnamed species of *Axinulus* (family Thyasiridae) from 10,415-10,687 m. in the Tonga Trench *(185).* CLARKE *(22,23)* has listed three species as occurring off Bermuda at a depth of 5,199 m. (2,843 fathoms) and six species as having been found in the South Atlantic at depths exceeding 4,572 m. (2,500 fathoms). The Nuculacea are well represented in the abyssal bivalve fauna, and other forms include certain thin-shelled Pectinacea (e.g., *Pseudamussium, Propeamussium*) and the septibranch genera *Poromya* and *Cuspidaria.*

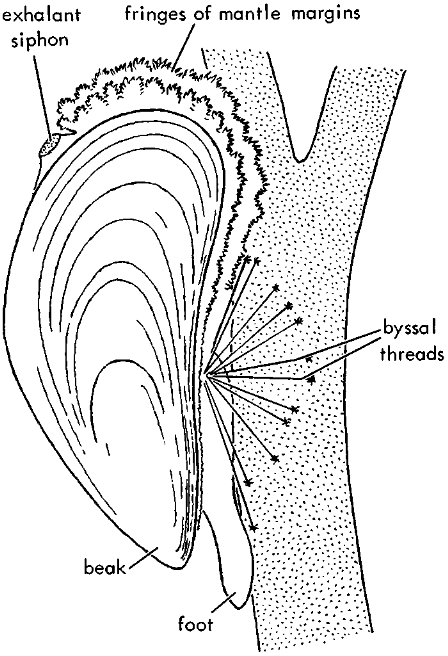

FIG. 5. Habitat of bivalves—*Mytilus edulis* LINNÉ, Rec., cosmop, side view of animal with extruded foot attached by byssus threads to branching object, fringes of mantle and exhalant siphon seen at posterior extremity, ×1 (Cox, n).

From a purely marine environment, bivalves pass into less saline waters of landlocked seas such as the Baltic, parts of the Caspian, and into estuaries. Some marine forms (e.g., *Mytilus, Cardium, Macoma*) are notably tolerant of brackish-water conditions, and other genera exist only in such environments. Bivalves confined to fresh water include the Unionacea and the family Etheriidae, in which one valve of the oyster-like shell is cemented to stones. The genus *Dreissena,* while probably unrelated to the marine mussel *Mytilus,* resembles it both in shape and in its byssal attachment.

The great majority of Bivalvia have been divided, according to their feeding habits, into suspension-feeders and deposit-feeders. Those of the first group feed on phytoplankton, relying for their supply on the inhalant current in which large numbers of microscopic protists (chiefly diatoms and dinoflag-

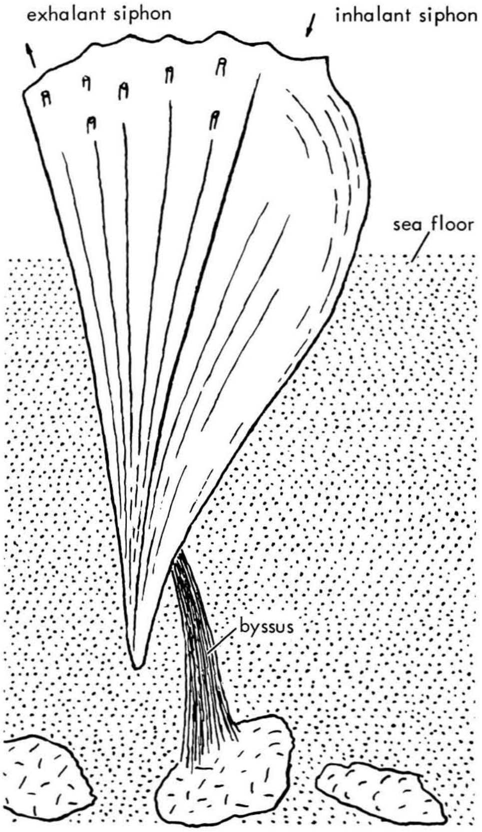

FIG. 6. Habitat of bivalves—*Pinna* sp. in living position partly buried in sea bottom with pointed anterior end lowermost, attached by byssus to stones or other objects in sediment, ×0.5 (Cox, n).

ellates) are suspended. These are strained off by the ctenidia of the mollusk and conveyed to the mouth by a process to be described in a later section (p. *N*16). Deposit-feeders live on organic debris and bottom-living diatoms contained in the mud or sand of the sea floor into which they burrow. The organ used to collect the food is usually the inhalant siphon. In most such forms this is long and slender and not attached to the exhalant siphon, and its tip ranges over the surface of the sediment in search of food. In the Nuculacea, however, the collection of food-bearing sediment is the function of the two palp proboscides, appendages of the labial palps. Only one small group of Bivalvia, the septibranchs (Poromyacea), has acquired a carnivorous habit. The branchial apparatus is here converted into a mechanism for trapping small

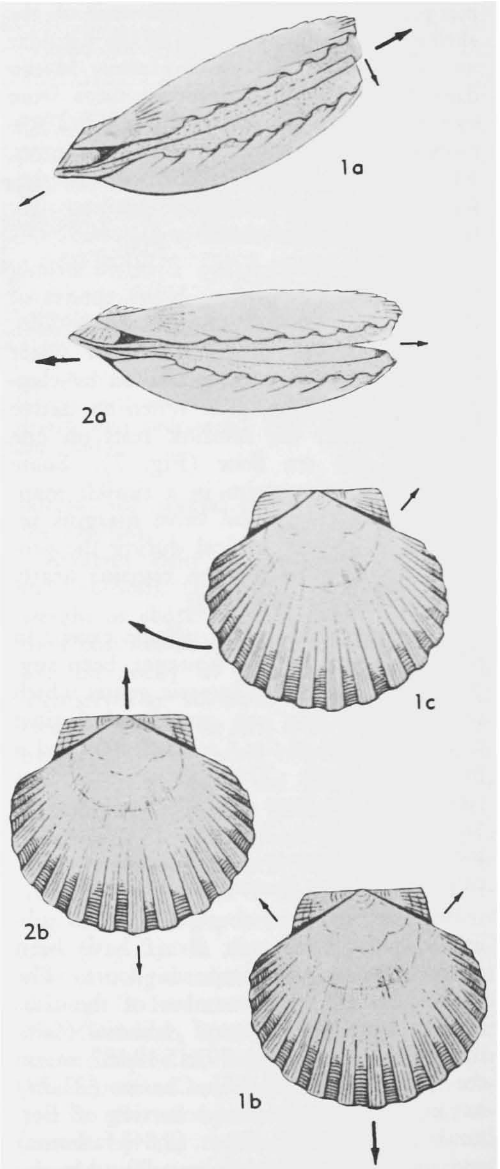

FIG. 7. Habitat of bivalves—free-swimming scallop *Pecten* sp., edge and lateral views showing *(1a-c)* forward swimming and *(2a,b)* "escape" movement, direction of movement indicated by larger arrows and that of propelling water jets by smaller arrows, ×0.25 *(142)*.

worms and crustaceans drawn into the mantle cavity.

Reference has already been made to the ingestion of wood particles by the shipworms (Teredinidae). Some small bivalves of the superfamilies Cyamiacea and Erycinacea are commensal with echinoderms, crustaceans, and other invertebrates, while *Entovalva* is parasitic in the esophagus of holothuroids. *Vulsella* lives commensally in sponges.

DURATION OF LIFE

Direct observations on the duration of life in Bivalvia in their natural habitats obviously present considerable difficulty, and much of the available information on longevity in this group, summarized by COMFORT (1957), is based on the counting of growth rings or rugae and the assumption that these are annual. As might be expected, some of the smaller bivalves are the shortest-lived. A life span of less than one year is reported for one species of *Sphaerium* and of less than two years for a second species of this genus. The duration of life of marine bivalves varies greatly. A few examples are as follows: *Tellina tenuis* DA COSTA, 5 years; *Mya arenaria* LINNÉ, <8 years; *Mytilus edulis* LINNÉ, 8 to 10 years; *Ostrea edulis* LINNÉ, >12 years; *Cardium (Cerastoderma) edule* LINNÉ, 14 years; *Pecten maximus* (LINNÉ), 22 years; *Mercenaria mercenaria* (LINNÉ), 25 to 40 years.

No reliable observations seem to have been made on the life span of the largest living bivalve, the "giant clam" *Tridacna gigas* (LINNÉ), statements that this species can live to an age of 100, 200, or even 300 years being based on conjecture. There is good evidence, however, that some of the larger fresh-water mussels live to a considerable age. Specimens of *Margaritifera margaritifera* (LINNÉ) 100 years and 70 to 80 years in age have been mentioned in the literature.

MORPHOLOGY OF BIVALVIA SOFT PARTS

MANTLE AND SIPHONS

The **mantle** is the name given to the integument which surrounds the vital organs of the mollusk and which secretes and then forms the lining of the shell. It consists of two **lobes**, one corresponding to each valve, which are joined along their mid-dorsal margin. Dorsally the mantle lobes enclose the **body** or **visceral mass**, to which they are fused, but ventrally they surround a relatively large space, the **mantle cavity**. This plays a fundamental part in the life of the mollusk. Not only does it form a respiratory chamber and an enclosure through which all foods must pass to reach the mouth, but it is also the receptacle into which excreta and genital products are discharged before being expelled into the surrounding medium. Interchange of water between the mantle cavity and the exterior is maintained by two currents, an **inhalant current**, oxygenated and food-bearing, and the other an **exhalant current,** which removes the deoxygenated water and with it the waste products of metabolism and, usually, the genital products. The exhalant current invariably leaves the mantle cavity at its posterior end; the inhalant current enters posteriorly in the great majority of bivalves, but anteriorly and to some extent ventrally in some forms (Fig. 8). An extensile muscular organ, the **foot**, projects from the body of the mollusk into the mantle cavity along the median plane in an anteroventral direction, and can be protruded beyond the margins of the shell. This structure is discussed later (p. *N*14).

The margins of the mantle have three folds (Fig. 9), each with a definite function. The outer fold secretes the **outer calcareous layer** of the shell and the **periostracum.** The middle fold usually bears tentacles or other sensory organs. The inner fold contains radial muscles (**pallial muscles**) which are attached to the interior of the shell along a well-defined line **(pallial line)**, more or less parallel to the margin. They control the flow of water into and out of the mantle cavity.

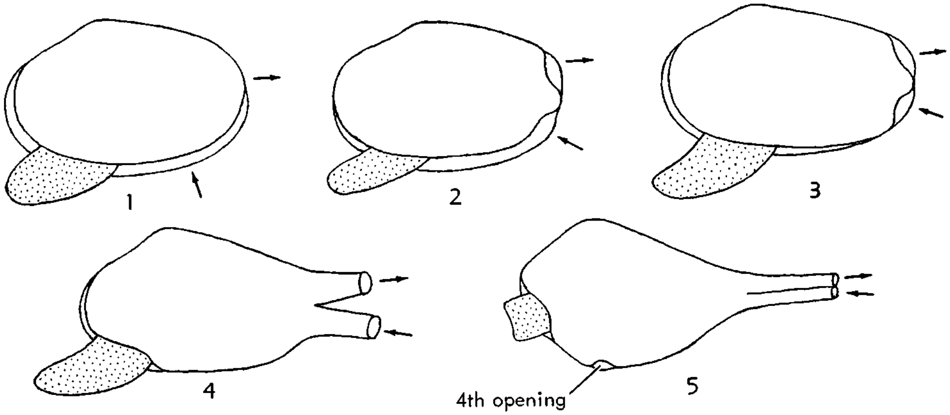

FIG. 8. Bivalve mantle and siphons—diagrams showing degrees of closure of mantle margins, foot (stippled) protruding anteroventrally and shell supposedly removed with mantle margins represented as confluent where fused together (arrows indicate direction of inhalant and exhalant currents) (Cox from Hescheler).——*1*. Margins completely open, unfused.——*2*. Margins fused only at single posterior place between exhalant and main openings.——*3*. Margins fused only at two posterior points so as to define exhalant and inhalant openings and separate these from main opening.——*4*. Margins fused except at openings for siphons and at anterior pedal opening.——*5*. Margins fused all around except for openings indicated in *4* and an additional opening of uncertain function.

In some bivalves the mantle cavity is completely open along its anterior, ventral, and posterior margins, although the inhalant and exhalant streams are localized. Such forms include the Nuculidae, Glycymerididae, Anomiidae, Arcidae, Trigoniidae, Pectinidae, Spondylidae, Plicatulidae, Limidae and Dimyidae, together with certain species of *Crassatella*. The Pteriidae and related families, together with the Pinnidae and the Ostreidae, may be considered to belong to the same group, as there is no direct fusion of the mantle margins, although in each lobe the margin is joined to the adjacent gill demibranch.

In most members of the Bivalvia the mantle-lobe margins are fused along some part or parts of their length, in varying degrees of intimacy *(195)*. Fusion may affect the inner of the three folds only, both inner and middle folds, or all three folds, and in the case of the middle and outer folds the inner surface only, or both surfaces, may be involved. In each case, moreover, attachment may be by ciliary junctions only, by adherence between the cuticular boundaries of epithelial cells, or by actual union of the tissues. Without entering into details regarding the intimacy of fusion, we may review the remaining bivalves according to the positions where fusion occurs.

In some forms the lobe margins are fused at a single place at the posterior end of the mantle cavity, a relatively small opening, through which the exhalant current passes, being thus separated from the main opening, through parts of which the foot can be extruded and the inhalant current can pass. Bivalves in which this condition exists include Mytilidae, Carditidae, Astartidae, most Lucinidae, and Crassatellidae, some Unionidae, and the genus *Pisidium*. In *Solemya* a more extended line of fusion separates the two openings, reaching halfway along the ventral margin. In some species with a single place of fusion the part of the mantle ending in the exhalant opening can be extended beyond the margin of the shell to form a tubelike projection (**siphon**), although a relatively short one. The entry of the inhalant current tends to be localized close to the point of fusion, indicating an approach to the condition found in the next group.

In another group of Bivalvia the mantle margins are fused in two places, leaving two more or less contiguous posterior openings, the upper (more dorsal) one for the exhalant current, and the lower for the inhalant current, together with a third opening for the foot. The marginal region of the mantle is usually extensible at the two posterior openings to form siphons of varying length. The pedal opening occupies the whole length of the ventral and anterior margins in most bivalves belonging to this group (e.g., *Malletia, Yoldia,* most *Nuculana,* many Lucinidae, most Corbiculidae, Mutelidae, Donacidae, Psammobiidae, Tellinidae, Scrobiculariidae, Veneridae, Cardiidae, Mactridae, Mesodesmatidae, Poromyidae, Cuspidariidae, and some other forms). It is somewhat reduced, by further fusion of the ventral margins in the Chamidae and Tridacnidae and becomes a small anterior orifice in *Modiolarca, Dreissena,* the Pholadidae, Teredinidae, Verticordiidae, Lyonsiidae, and a few other forms.

Finally, in a few bivalves there are three places of fusion of the lobe margins, leaving four openings. The fourth opening lies between the pedal and inhalant ones and is usually small. Its function is uncertain. Forms with four mantle openings include the Pholadomyidae and Clavagellidae, *Solen, Lutraria, Panopea, Thracia, Myochama,* and *Chamostrea.*

The siphons, which are contractile, can be withdrawn partly or wholly between the two valves of the shell by means of **siphonal retractor muscles,** which are local modifications of the pallial muscles. To provide space for the withdrawal of the siphons the line of insertion of these muscles recedes inward in many forms to give rise to an embayment in the pallial line, known as the **pallial sinus** (Fig. 10). The length of the siphons varies considerably, being greatest in the more deeply burrowing forms. They are separated along their whole length in the Donacidae, Psammobiidae, Tellinidae, Scrobiculariidae, Mesodesmatidae, and some other forms, all of which are deposit-feeders. In other groups (e.g., Mactridae, Pholadidae, Clavagellidae, many Laternulidae, *Solen, Lutraria,* and some Veneracea) they are fused along their entire length, forming a single tubelike projection from the shell. In a few forms, including *Petricola* and *Teredo,* they are united at their base but free and divergent distally. When united and not completely retractable into the shell the siphons may be protected by a special coating of epidermis. The degree of intimacy of fusion of the margins of the mantle lobes where these are extended to form the siphons varies in the same way as elsewhere, as described above. Details have been given by YONGE *(195).*

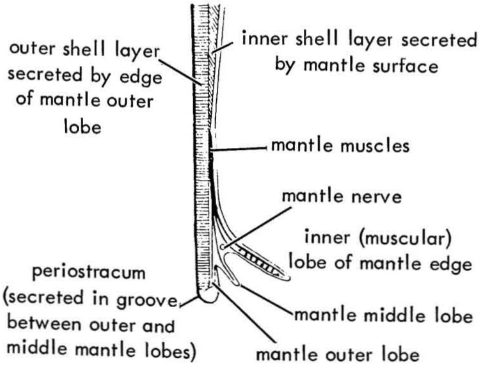

FIG. 9. Bivalve mantle and siphons—section of mantle edge and associated shell and periostracal layers (Yonge, 1953).

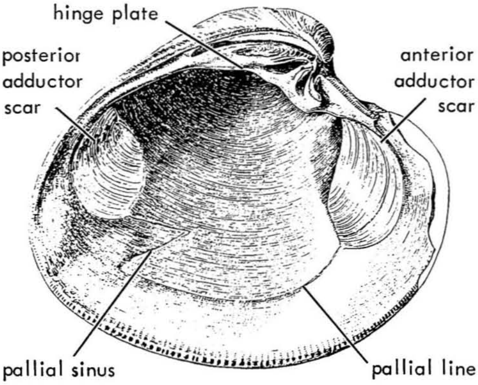

FIG. 10. Bivalve mantle and siphons—interior of shell of *Venus campichiensis mortoni* (CONRAD) from Miocene of Maryland showing attachment impression of mantle (pallial line and sinus), ×1 (Dall, 1904).

The foregoing account applies to the great majority of siphonate bivalves, in which two siphons occur, both posterior in position. In a few genera (e.g., *Kellia* and *Lasaea,* both belonging to the Erycinidae), however, the inhalant siphon is anterior and the exhalant one posterior; and in some

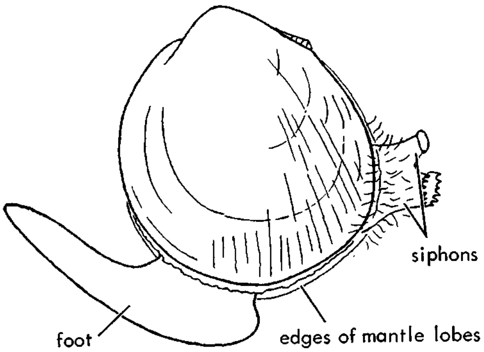

FIG. 11. Bivalve foot and siphons—*Cardium (Laevicardium) crassum* GMELIN, Recent, British Isles, with foot and siphons protruded, ×0.7 (Cox, mod. from Forbes & Hanley).

(e.g., Lucinidae) only one siphon, a posterior exhalant one, is present. In the Lucinidae this siphon is unique in that it is reversible, contracting into the mantle cavity by turning itself inside out.

When the mollusk is respiring and feeding, the valves of the shell are opened slightly and the mantle edge with its tentacles is protruded slightly beyond the margins. In a number of genera belonging to the superfamily Leptonacea, in all of which the shell is quite small, the mantle is reflected to a varying extent over its exterior, until in such forms as *Chlamydoconcha, Entovalva, Ephippodonta,* and *Scioberetia* the shell is completely internal.

Dorsally, the two mantle lobes are united along a line of primary continuity, the **mantle isthmus**, and from either end of this their margins may be joined for some distance by secondary fusion in one of the ways already described. Thin projections of the mantle extend between the hinge teeth of the two valves, which thus do not fit together so very closely, as is commonly supposed.

FOOT AND BYSSUS

The **foot**, which in the typical bivalve is an anteroventrally directed extensile muscular process projecting from the body of the mollusk into the mantle cavity, is primarily an organ for burrowing and locomotion, although it may have secondary uses (Fig. 11). It can be extruded beyond the valve margins when the animal is active and is of various shapes, depending to some extent

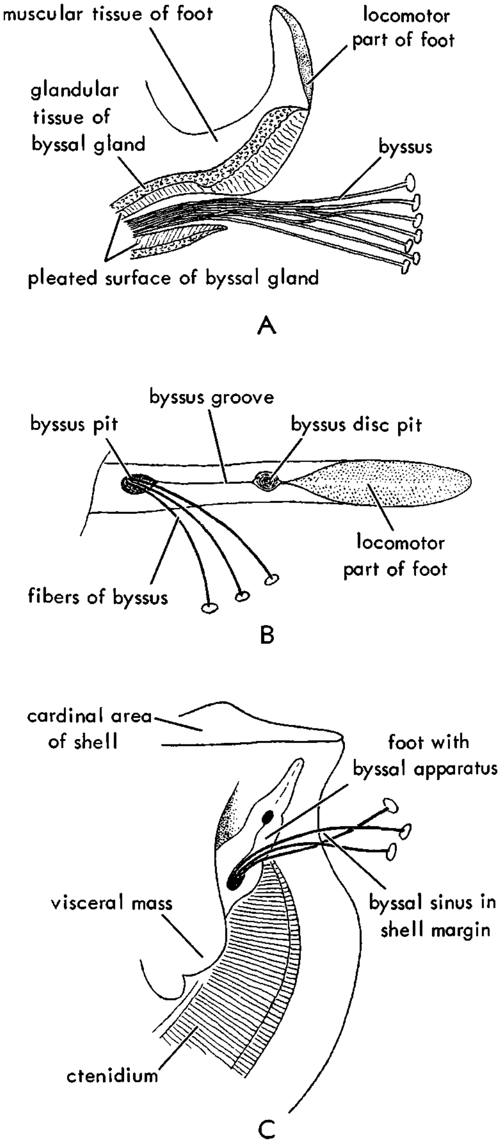

FIG. 12. Foot and byssus of Ceylon pearl oyster *Pinctada vulgaris* (SCHUMACHER), Recent, south Asia, enl. (Cox from Herdman, 1904).——*A*. Sagittal section.——*B*. Ventral surface of foot attached by three byssal fibers, foot elongated for making fourth byssal fiber.——*C*. Anterior part of animal, foot resting in mantle cavity and three byssal fibers projecting through byssal sinus of shell margins.

on the mode of life of the bivalve. The **byssus**, an important structure associated with the foot and secreted by the byssal gland or glands, is typically a bundle of hairlike threads by means of which the mollusk can attach itself to other objects, such as rocks and seaweed (Fig. 12). Attachment may be throughout life (as in genera such as *Mytilus* and *Pteria*), or only during a particular phase in the animal's existence. In many bivalves the byssus is absent or merely vestigial in the adult stage, but is present (if only as a single thread) in the early postlarval ontogeny of a great many forms and has a definite function. In *Mya,* for example, it enables the young animal to anchor itself temporarily to sand grains and other objects, pending the development of structures essential to its adult burrowing mode of life (Fig. 13). YONGE *(196),* therefore, has suggested that the byssus is essentially an early postlarval structure retained, by neoteny, in those adult bivalves in which it is present. Most byssiferous species can cast off the byssal threads and replace them by new ones, and some, including *Mytilus,* can move over a vertical surface by planting a succession of such threads and hauling themselves along, leaving a trail of disused threads attached to the surface over which they are moving. Among bivalves in which the adult has a well-developed byssus the foot has usually lost its function as an organ of locomotion, although there are exceptions. Such forms belong largely to the Pteriomorphia, but also include representatives of other groups widely scattered taxonomically. Their foot is commonly a slender, finger-like or tonguelike structure, possibly with a ventral keel.

The structures associated with formation of the byssus consist (where fully developed) of the **byssal pit**, a cavity at the posterior end of the foot; the **byssal gland** or **glands**, situated around the byssal pit and along the foot; and the **byssal groove**, which starts from the byssal pit, runs along the underside of the foot, and ends in a small depression (byssus disc-pit) forming a sucker. The byssal glands secrete a sticky fluid which accumulates in the byssal pit and along the byssal groove, and solidifies immediately on contact with water to form each byssal thread. The end of the foot plants the distal end of the thread on the object of attachment, while the proximal end remains attached within the byssal pit. Chemically, the material of the typical byssus consists of a protein of the albuminoid group, and its composition is similar to that of the organic material present in the molluscan shell.

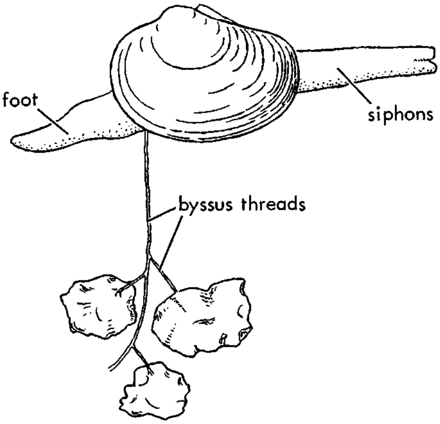

FIG. 13. Bivalve foot and byssus—*Mya arenaria* LINNÉ, Recent, juvenile specimen (length, 2.3 mm.) showing byssus attached to sand grains prior to adoption of burrowing existence (Cox, mod. from Yonge).

Byssally attached Pteriomorphia include most Mytilacea, Pteriacea, Anomiacea, the Pinnacea, and many Pectinacea and Limacea. In the Anomiacea the byssus, where present, is a rigid calcified structure, projecting through a foramen in the lower (right) valve, but in the Eocene genus *Carolia* it became obsolete during growth and the foramen gradually sealed up; in *Placuna* (Upper Tertiary-Recent) the calcified byssus is present only in very early stages of ontogeny. The Pinnacea differ from most byssiferous forms in their burrowing mode of life. The animal lives almost completely buried in the muddy substrate, with the pointed anterior end of the shell directed downward; the well-developed byssus, consisting of numerous silklike strands, emerges from the ventral margin close to this end and is attached to buried stones. As already mentioned, the genus *Musculus* [Mytilidae] and some Limidae construct protective nests from strands of the byssus. In the Ostreacea and in Pectinacea having one valve cemented to the substrate, cementation is effected by the foot, the cementing calcium carbonate originating in the byssal gland. In the Ostreidae the foot then atrophies; it becomes merely vestigial in the Plicatulidae and Dimyidae, but remains better developed, although reduced, in adult *Spondylus* and in *Hinnites*. A byssus is absent in highly mobile members of the Pectinidae.

In the Nuculacea, the superfamily commonly thought to retain the greatest number of primitive features, the foot is a relatively large but not greatly elongated organ broadening distally (when expanded) to a flat, disclike "sole" with marginal crenulations. It has been variously regarded as a primitive structure retaining a creeping sole comparable to that of many gastropods, or as a highly specialized structure adapted for rapid burrowing in soft substrates. The former interpretation seems to be refuted by our knowledge that members of this group do not creep about on a hard sea bottom but are shallow burrowers. A small byssal gland has been observed in a number of species of the superfamily, but it is functionless in the adult stage. A massive byssus is present in those Arcacea (e.g., *Arca* itself, typified by *A. noae* LINNÉ) which grow attached to rock surfaces, but it is absent in burrowing members of the family.

In more advanced bivalve groups also retention of the byssal gland in the adult mollusk depends largely upon the mode of life. The gland is absent in adult Unionacea, Arcticacea, Lucinacea, Mactracea, Tellinacea, Solenacea, Pholadacea, Clavagellacea, and Poromyacea, all of which are burrowing or boring forms. A byssus is also absent in the Chamacea, a group in which one valve of the shell is cemented to the substrate. On the other hand, it is well developed in the mussel-like Dreissenacea, in the Tridacnacea, and in some Lyonsiidae. A small byssal gland is found in adult Trigoniacea, Crassatellacea, Corbiculacea, and Cyamiacea, and in some Carditacea, Glossacea, Leptonacea, Carditacea, Veneracea, and Myacea. Many Leptonacea show a marked tendency to attach themselves by means of a few byssal threads. Some live commensally in the burrows of other invertebrates, attaching themselves to the walls.

The foot itself is of various shapes in the groups just mentioned, hatchet-like, tongue-like or even wormlike. In some forms, such as the Cardiidae and Arcidae, it has a pronounced knee-shaped bend. A broad sole, used for burrowing and not for creeping, is developed in a number of genera, particularly in the families Veneridae and Tellinidae. In a few small forms belonging to the Leptonacea, on the other hand, a broad, flat-soled foot is actually used for creeping over solid surfaces.

CTENIDIA AND LABIAL PALPS

The conversion of the well-developed gills or **ctenidia** from organs of respiration into an apparatus concerned largely with the collection of food in most forms is among the most characteristic features of the Bivalvia. The extension of the mantle cavity in an anteroposterior direction along the whole length of the shell has provided space for enlargement of the two ctenidia. Attached by membranes to the body of the mollusk, these lie on each side of the cavity, with their front end to the left and right of the foot, if they are not completely posterior or dorsal to the latter. They converge in a posterior direction and in many forms are connected together at their posterior end. Each ctenidium consists of a hollow, longitudinally directed **axis** and of a series of thin leaflike or lathlike hollow structures (**filaments**) attached to it, usually on both sides. The structures on each side of the axis constitute a **demibranch**, and in many bivalves the two demibranchs are more or less symmetrical with regard to the axis. The demibranchs may be described as **inner** and **outer** according to their position, closer to the sagittal plane of the mollusk or to the mantle. The outer demibranch is absent in the Lucinidae (see Fig. 20,*J*). In most bivalves both demibranchs extend in a ventral direction from the axis, but in some forms the outer demibranch

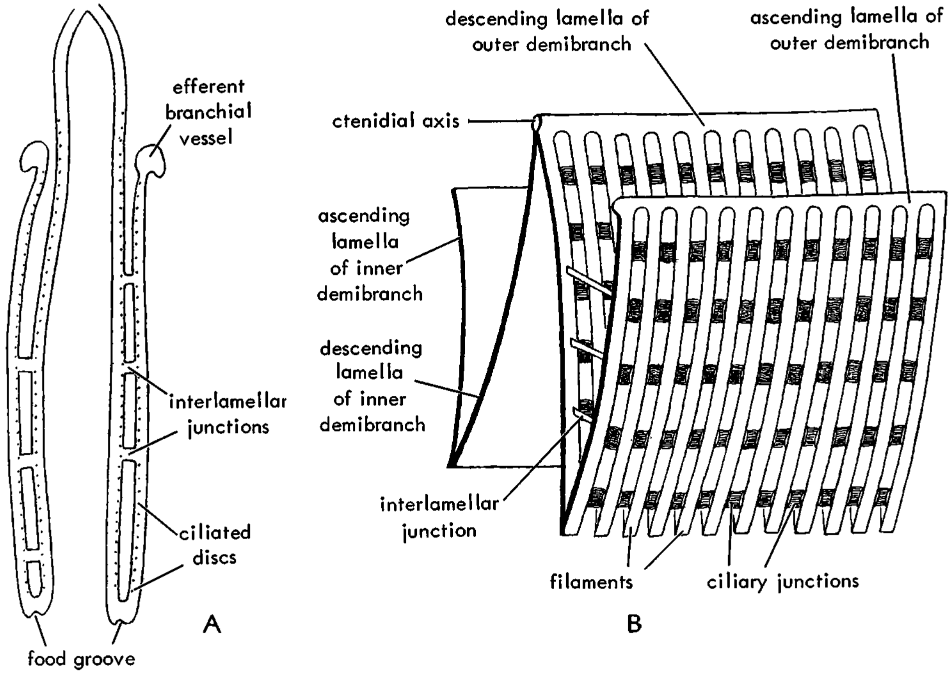

FIG. 14. Filibranch ctenidium of *Mytilus edulis* LINNÉ (Cox, n).——*A*. Side view of corresponding filaments of two demibranchs showing interlamellar junctions and positions of ciliated discs, ×40.——*B*. Part of ctenidium viewed obliquely, nearer demibranch with 12 filaments joined by ciliary junctions (not to scale and thickness of filaments not indicated, ciliary junctions far fewer than in nature).

extends either wholly or partly in a dorsal direction (Fig. 14,*A*). The structure of the ctenidia varies considerably in complexity and has served as the basis of a system of classification of the Bivalvia, associated with the name of PELSENEER, which has been widely used by students of living Mollusca.

The simplest and presumably most primitive type of ctenidium found in the Bivalvia is comparable to the bipectinate ctenidium of the Archaeogastropoda, the demibranchs being symmetrical or slightly asymmetrical and formed of simple, broad, leaflike filaments. Adjacent filaments are unconnected or have at the most only loose and sparse ciliary attachments. Bivalves with this type of ctenidium, consisting of the superfamilies Nuculacea and Solemyacea among Recent forms, have been grouped together under the name Protobranchia.

In most other bivalves the filaments constituting the demibranchs are narrow, elongated, lathlike structures, and, except in a few forms (Fig. 14,*B*), each is bent back upon itself so as to have a reflected (usually ascending) limb, as well as the proximal (usually descending) limb which is attached to the axis. Each series of filament limbs forms a sheet or **lamella,** so that a typical ctenidium consists of four lamellae, a descending and ascending one in each demibranch. The lamellae are flat in some forms and thrown into folds or **plicae** in others. Adjacent filaments in a lamella may be attached in two ways. Each filament may bear on its sides small brushlike patches of cilia (**ciliated discs**) which merely interlock with those of the next filament and can be separated from them without much difficulty; or else adjacent filaments may be connected at regular intervals by strands of cellular organic tissue, so that they cannot be separated. The two lamellae of a demibranch may be joined at intervals back to back in a similar manner. In many forms such junctions are so exten-

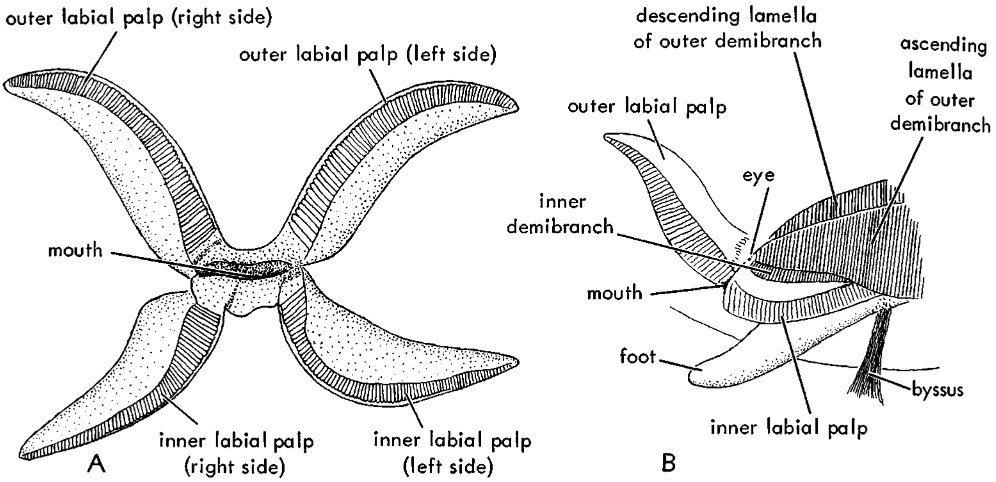

Fig. 15. Labial palps of *Mytilus edulis* Linné, enl. (Cox, n).——*A*. Anterior view of mouth and lips showing their relation to palps, outer ones (normally contiguous to lower) reflected upward and all four palps turned into transverse plane.——*B*. Left-side view of palps, outer one (cut at base and turned away) normally contiguous to inner palp with anterior end of ctenidium between them.

sive that the faces of the demibranchs are interrupted only by series of transversely aligned pores (**water pores** or **ostia**), while the space between the two lamellae of the same demibranch is reduced to a series of transverse tubular cavities.

Bivalves with ciliary interfilamental junctions constitute the group Filibranchia of Pelseneer, and form the superfamilies Arcacea, Trigoniacea, Anomiacea, Mytilacea, Pteriacea, and Pectinacea. Interlamellar junctions are absent in the first three of these groups but present in the last three. Bivalves with interfilamental and interlamellar junctions formed of organic tissue constitute the Eulamellibranchia of the same author, and comprise all other living superfamilies except those already mentioned as forming the Protobranchia, and the Poromyacea, referred to below. It is to be noted that in this classification the Ostreacea, Limacea, and Pinnacea are included in the Eulamellibranchia and thus separated taxonomically from superfamilies of the Filibranchia, to which all other evidence suggests they are most closely related.

Ctenidia are absent in one superfamily, the Poromyacea, which constitute the Septibranchia of Pelseneer's classification. They are replaced by a horizonal longitudinal muscular septum dividing the mantle cavity into dorsal and ventral chambers, which communiciate only by narrow slits in the septum. This is the superfamily already mentioned as consisting of carnivorous feeders.

The **labial palps** are structures in the mantle cavity which belong to the same physiological system as the ctenidia (Fig. 15). They consist of two pairs (right and left) of usually acutely triangular, leaflike, contiguous flaps or **lamellae** forming prolongations of the upper and lower lips of the mouth but extending posteriorly. When they occupy their normal positions the lamellae belonging to the upper lip fold down so that their joined proximal ends are in front of the mouth, and in each pair (right or left) the one belonging to the upper lip lies on the outer side of the one belonging to the lower lip; for this reason they are termed **outer** and **inner lamellae,** respectively.

The labial palps of the Nuculacea are remarkable both for their large size and for the presence of **palp proboscides**, extensile tentacle-like processes attached to the posterodorsal corner of the outer of each pair of lamellae. When the animal is feeding, the proboscides are extruded between the

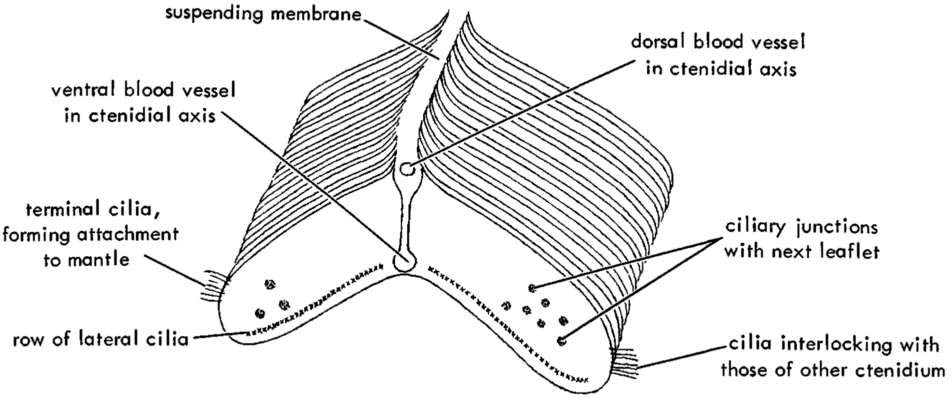

FIG. 16. Protobranchiate ctenidium of *Nucula* sp., diagrammatic oblique view of region from just in front of posterior adductor muscle to well behind foot, showing ten pairs of leaflets or filaments with cilia indicated only on nearest ones (Cox, n).

opened valve margins of the shell just behind the foot and function as food collectors in much the same manner as the inhalant siphon of other deposit-feeders. The material collected is conveyed along a ciliated groove to the **palp pouch**, at the proximal end of the pair of palp lamellae; the latter then proceed to sort it by a complicated process, with the ultimate result that the part finally accepted reaches the animal's mouth.

It is only in the Nuculacea that the ctenidia function mainly as respiratory organs. Their role in suspension-feeders may now be briefly described. The surfaces of the gill lamellae bear innumerable minute cilia, the beating of which creates a complicated series of currents within the mantle cavity, details of which vary in different genera (Fig. 16). Water from the surrounding medium, oxygenated and bearing food and other particles in suspension, is drawn in through the inhalant opening or siphon. When the inhalant current has entered the mantle cavity its velocity is at first checked, with the result that heavier particles, inorganic or otherwise, sink to the ventral edge of the mantle; together with later rejected material, these are carried by movements of cilia on the mantle, to be discharged (as the result of sudden contractions of the adductor muscles) as **pseudofeces**. They are most commonly ejected

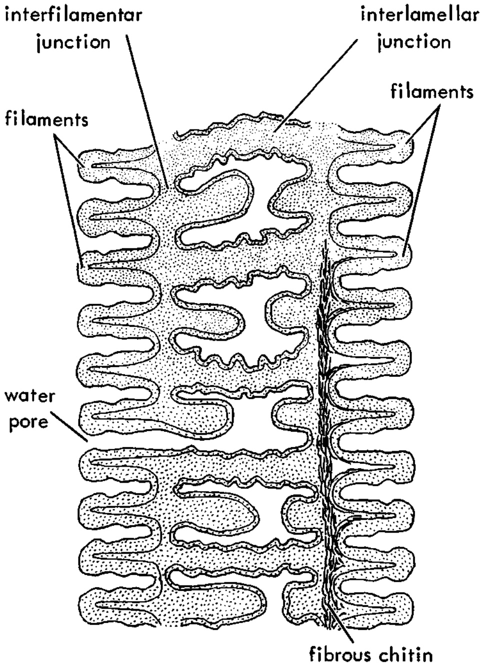

FIG. 17. "Eulamellibranch" type of gill structure in *Tellina nitida* PERRY indicated by horizontal section through outer demibranch passing through ten filaments of each lamella with illustration of interlamellar and interfilamentar junctions of organic tissue, much enl. (Cox, n, after *143*).

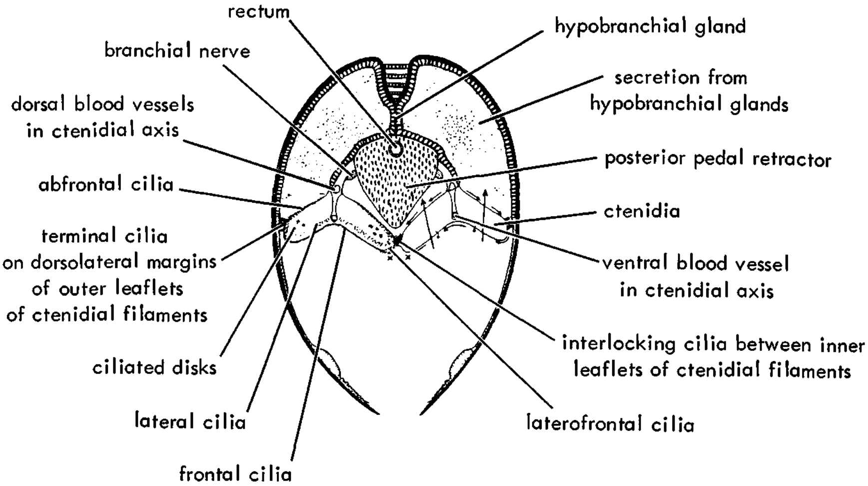

Fig. 18. Semidiagrammatic transverse section of *Nucula turgida* Leckenby & Marshall, Recent, northern Europe, showing relations of organs in region immediately in front of posterior adductor muscle, arrows on ctenidial filaments indicating direction of beat of abfrontal lateral, laterofrontal, and frontal cilia, ×20 *(189).*

through the pedal and inhalant openings. The inhalant current then impinges on one of the ctenidia, where the remaining suspended particles or organisms are strained off, entangled in mucus, and carried by ciliary movements along the ventral parts of the ctenidium to the corresponding labial palp, between the lamellae of which the anterior end of the inner demibranch of the ctenidium commonly terminates (Fig. 17). Further sorting and partial rejection takes place between the palp lamellae, the opposed inner surfaces of which bear ciliated ridges and grooves. The accepted lighter material passes along the **food groove**, at the angular junction of the two lamellae (Fig. 18), eventually reaching the animal's mouth.

In most bivalves the inner demibranchs of the two ctenidia are joined to the foot where this lies between them and to one another posterior to it (Fig. 18-20). At the same time the outer demibranchs are joined to the mantle. In the protobranchs and many filibranchs the junctions, if present, are by interlocking cilia, but in other forms they are by vascular tissue. As a result, a space (**epibranchial chamber**) dorsal to the ctenidia is partitioned off from the re-

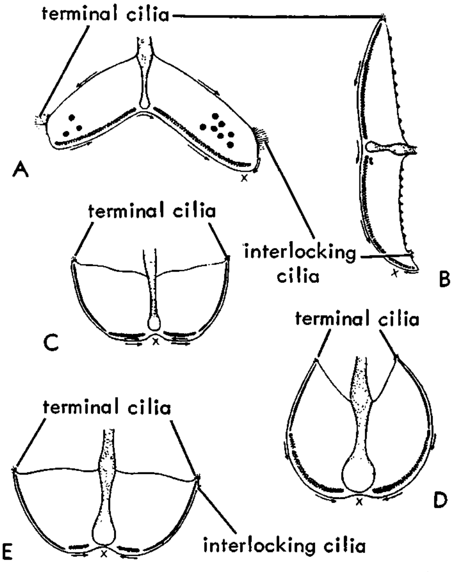

Fig. 19. Ctenidial filaments (semidiagrammatic) of protobranch bivalves, ciliary junctions between adjacent filaments of same ctenidium in black and extent of chitinous support rods (and so of lateral cilia) shown by cross hatching; arrows indicate beat of frontal cilia (and abfrontals in *Nucula*) and crosses show position of anteriorly directed ciliary currents *(189).*——*A. Nucula.*——*B. Solenomya.*——*C. Lembulus.*——*D. Yoldia.*——*E. Malletia.*

mainder of the mantle cavity. This space is continuous with the exhalant opening or siphon at the posterior end of the cavity. The water from which suspended particles have been strained off by the ctenidia passes through the ostia, or spaces between the filaments, and then is directed dorsally into the epibranchial chamber, along which it passes posteriorly to form the exhalant current.

It would hardly be expected that traces of such soft organs as ctenidia would be preserved in fossils. There is, however, an interesting record of the discovery of specimens of *Laevitrigonia* in the Portland Beds (Upper Jurassic) of Wiltshire, England, in which the ctenidia and some other organs were thought to be preserved in a silicified state. The discovery was mentioned and the identity of the preserved structures accepted by so competent a malacologist as S. P. Woodward, as well as by some of his contemporaries; a plate illustrating the remains was, moreover, prepared for a London journal which, unfortunately, ceased publication before the plate could appear. The present writer (who possesses a copy of the plate) has made unsuccessful attempts to trace the specimens, which originally belonged to the amateur geologist Etheldreda Benett and were apparently taken to Philadelphia by Thomas Wilson, who acquired her collection. Judging by the illustrations, the identification as filibranch ctenidia of the preserved structures seems plausible.

DIGESTIVE SYSTEM

A bivalve has no head and its **mouth** (Fig. 21,*2,3*) is a small orifice situated in a median position at the anterior end of the body, above the front of the foot. In dimyarian forms it lies just behind the anterior adductor muscle. The mouth is continued on each side by a groove (**oral groove**) along which food passes to it from the corresponding labial palp and ctenidium. Above and below the mouth and the adjacent part of each oral groove are the two **lips**, which are usually merely raised folds of the epithelium covering the body. As already seen, the labial palps are expanded continuations of these lips.

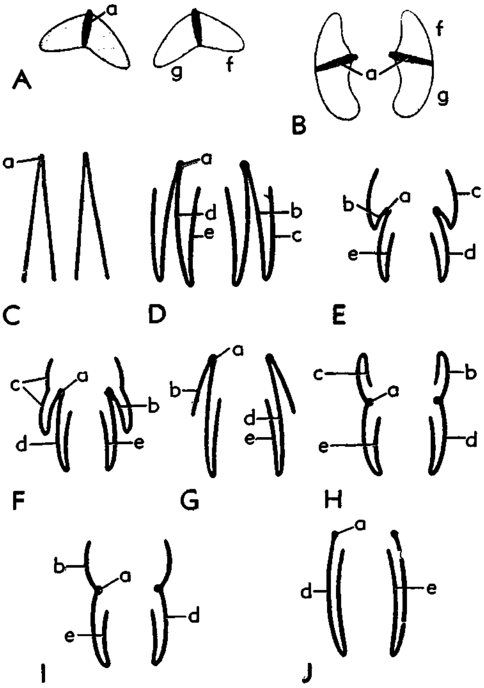

Fig. 20. Diagrammatic transverse sections of bivalve gills *(143)*.——*A. Nucula*.——*B. Solenomya*.——*C. Dimya, Anomia aculeata*.——*D*. Most Bivalvia.——*E. Donax faba*.——*F. Donax variabilis, Corbicula, Tapes, Venus, Isocardia*.——*G. Lasaea*.——*H. Tellina* (posterior part of gills).——*I. Lyonsia, Pandora, Scrobicularia*.——*J. Lucina, Montacuta*. [Explanation: *a*, axis; *b*, direct (usually descending) lamella of outer demibranch; *c*, reflected (usually ascending) lamella of outer demibranch; *d*, direct or descending lamella of inner demibranch; *e*, reflected or ascending lamella of inner demibranch; *f*, leaflets of outer demibranch; *g*, leaflets of inner demibranch.]

Jaws and a radula are absent, and a short **esophagus** leads from the mouth to the stomach, into which ducts open from the surrounding **digestive gland** or **liver**. The function of the **stomach** is to sort out and to pass on to the intestine such indigestible matter as has not already been rejected by the ctenidia and labial palps and discharged from the mantle cavity, and to carry out preliminary digestion of nutritive matter. In the latter process an important part is played by the **crystalline style**, a rodlike structure of hyaline mucroprotein which is secreted in the **style sac**, a posterior diverticu-

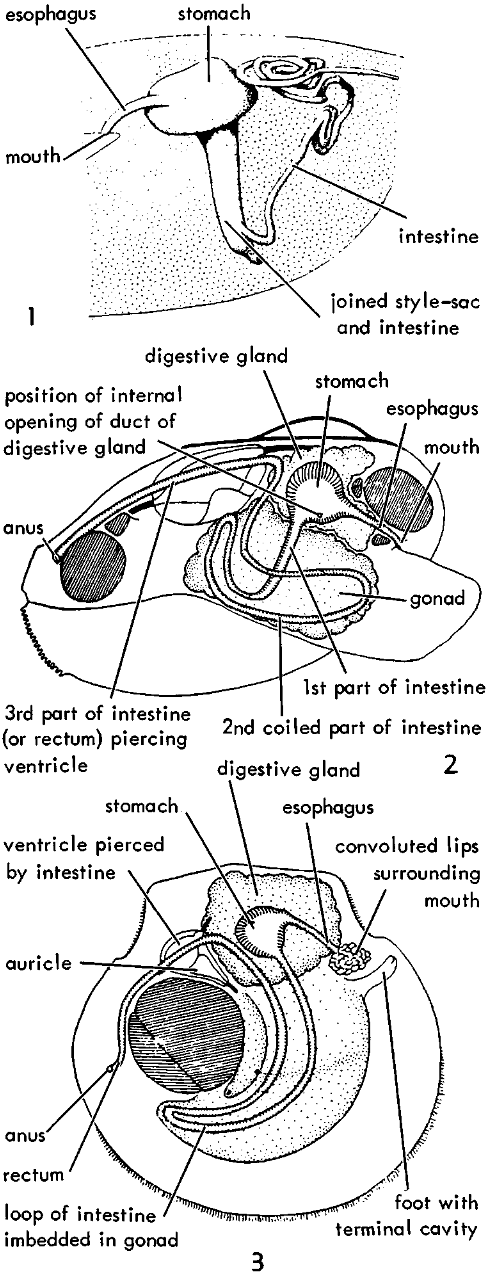

FIG. 21. Digestive systems of bivalves.——*1. Macoma balthica* (LINNÉ), ×4 *(55)*.——*2. Anodonta, ca.* ×1 (Bullough, 1958).——*3. Pecten, ca.* ×1 (Bullough, 1958).

lum of the stomach (Fig. 21,*1*). The style rotates continuously as the result of ciliary action, with its distal end projecting into the stomach and its head bearing against a hardened patch of the stomach wall (**gastric shield**). Its head is thus gradually worn away and the enzyme which it contains is stirred up with the contents of the stomach, acting as a ferment for the digestion of carbohydrates. The partially digested food then passes into the digestive gland, in the diverticula of which intracellular digestion and absorption occur. In the protobranchs, however, the crystalline style is absent, its place being taken by a rotating rod of fecal matter, the **protostyle;** the soluble products of digestion are absorbed in the stomach and intestine, and there is no intracellular absorption in the digestive gland. The style is much reduced in the septibranchs, a carnivorous group.

From the stomach the fecal matter passes posteriorly into the **intestine**, which either emerges from the style sac or forms a separate tube close to it. The intestine first takes a ventral course and then forms from one to several coils which invade the upper part of the foot; it next ascends dorsally and turns in a posterior direction, to form the **rectum,** which passes over the posterior adductor and ends on the posterodorsal side of the latter, in the **anus**. This lies near the exhalant opening or the proximal end of the exhalant siphon, and the exhalant current carries the feces away.

Before reaching the posterior adductor, the rectum passes through the **pericardial cavity** (space surrounding the heart), within which is the ventricle which in most forms is wrapped round and appears to be pierced by it. The fecal matter carried by the intestine forms a string of mucus-bound material, which is naturally more compact in deposit-feeders than in suspension-feeders. This is discharged at the anus as a series of **fecal pellets**, which may be oval, rodlike, or ribbon-like and commonly have a series of longitudinal grooves corresponding to ridges (**typhlosoles**) on the interior of the intestine. In *Nucula* the pellets are rodlike, with a varying number of grooves. In the Pectinidae they are usually rodlike and tri-

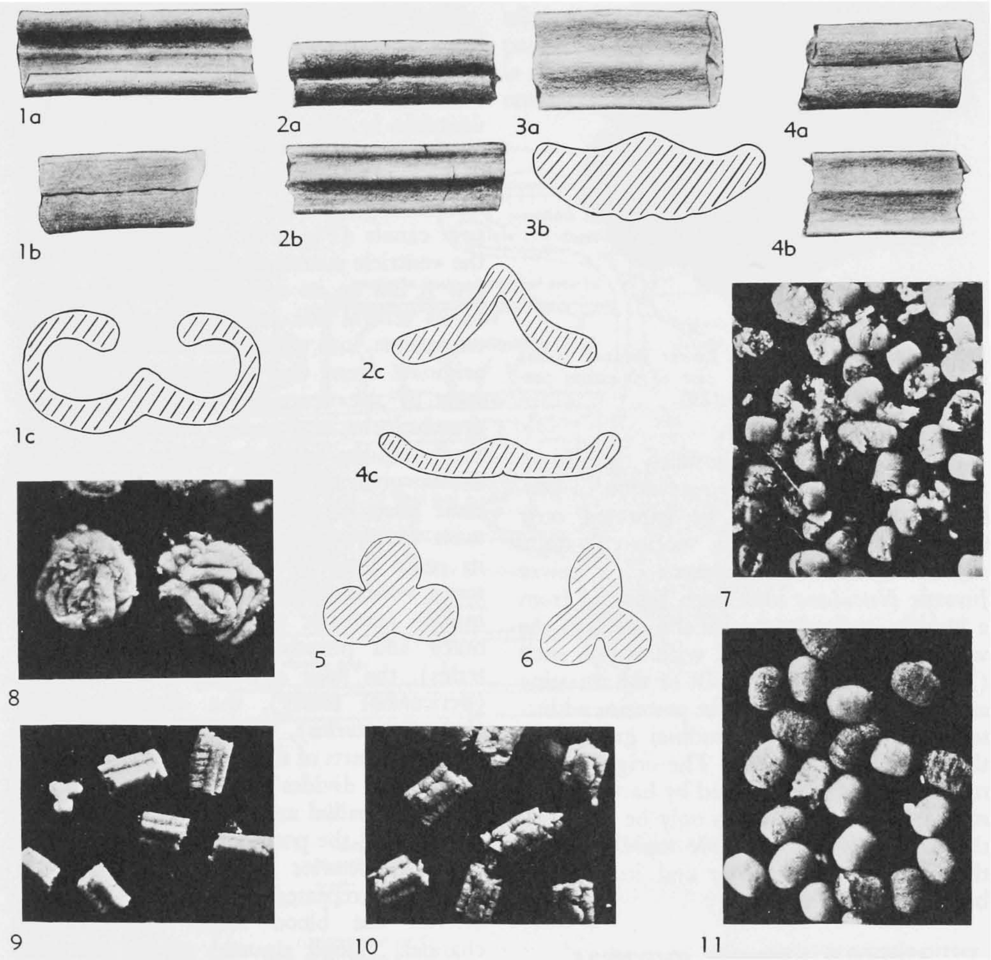

Fig. 22. Bivalve fecal pellets (various magnifications, not to scale) *(106)*.——*1. Mytilus edulis* Linné; *1a,b,* side views; *1c,* cross section.——*2. Modiolus modiolus* Linné; *2a,b,* side views; *2c,* cross section.——*3. Musculus marmoratus* (Forbes); *3a,* side view; *3b,* cross section.——*4. Modiolus phaseolinus* (Philippi); *4a,b,* side views; *4c,* cross section.——*5. Chlamys varia* (Linné), cross section.——*6. Chlamys opercularis* (Linné), cross section.—— *7. Moerella donacina* (Linné).——*8. Pecten maximus* (Linné).——*9. Chlamys tigerina*(Müller).——*10. Chlamys varia* (Linné).——*11. Arcopagia crassa* (Pennant).

angular or trefoil-shaped in cross section, although in *Pecten maximus* (Linné) the rod becomes wound into a mucus-bound ball (Fig. 22,*7-11*). In the Mytilidae they are ribbon-like and fragile, with cross sections of various shapes (Fig. 22,*1-6*). In the Tellinidae they are ovate-cylindrical and smooth. The pellets from a specimen of *Mytilus edulis* Linné about 8 cm. long are about 1.5 mm. wide and may be up to 5 cm. long, although usually they are broken up into shorter lengths. From a specimen of *Moerella donacina* (Linné) 1.5 cm. long the pellets average 0.36 mm. in diameter and nearly four-thirds of that amount in length. The diameter of the pellets from a specimen of *Nucula* 1 cm. long is about 1.5 mm. and their length is up to about 1 mm. Each species in any community has its characteristic pellets.

FIG. 23. *Nuculana* sp., from Lower Jurassic (Lias) of England, specimen with cast of intestine preserved, ×6 *(28)*.

Fecal pellets disintegrate fairly quickly on the sea floor, and their preservation in geological deposits would be expected only when consolidation has occurred quite rapidly. Interesting specimens of a Lower Jurassic *Nuculana* have been reported from a locality in England with the mold of the whole intestine preserved within each shell (Fig. 23). The several coils of the intestine and its termination near the posterior adductor, as well as the longitudinal grooves on the molds, are well seen. The original fecal matter has become replaced by hard ferruginous material, and it can only be supposed that this change took place rapidly, before the intestine could decay and its contents become dispersed.

CIRCULATORY SYSTEM

The blood of the Bivalvia is a clear, transparent fluid in which are suspended colorless amoebocytes which can pervade all tissues of the mollusk, assisting in the transport and assimilation of food, in excretion, and in conveyance of calcium carbonate for shell formation. In most forms it contains no special oxygen-carrier like the haemocyanin of gastropods and cephalopods, but merely bears oxygen in solution; hemoglobin, however, is present in some species. Circulation is maintained by regular pulsations of the heart, and during its circuit the blood at first becomes deoxygenated and contaminated with waste products of metabolism, and is then reoxygenated and purified.

The heart, which lies within the fluid-filled **pericardial cavity** situated in the mid-dorsal region of the body, consists of the **ventricle** and of two **auricles** or **atria.** The ventricle is elliptical in form and extends along the whole length of the cavity, and the auricles are large sacs which lie on its left and right sides and open into it by narrow canals (Fig. 24,*2*). In most bivalves the ventricle surrounds the rectum, but in a few it lies on its dorsal side and in others on its ventral side. In the majority of forms two aortae, into which the blood is pumped, originate from the anterior and posterior ends of the ventricle respectively; in the protobranchs and many filibranchs, however, only the anterior aorta is present, but it soon gives off an artery which serves the same parts of the animal as the posterior aorta when present. The anterior aorta (or its main branch) divides into various arteries, which supply the anterior part of the mantle (**anterior pallial arteries**), the stomach and intestines (**gastro-intestinal arteries**), the floor of the pericardial cavity (**pericardial artery**), the digestive gland (**hepatic arteries**), the foot (**pedal artery**), and other parts of the animal. The posterior aorta soon divides into two large arteries (**posterior pallial arteries**) which supply the two sides of the posterior part of the mantle and the posterior adductor muscle. After traversing repeated subdivisions of these arteries the blood seeps into irregular channels (**blood sinuses**) which permeate the connective tissue of the animal. It is within these sinuses, in the epithelium of the mantle and body of the mollusk, that reoxygenation of the blood from water drawn into the mantle cavity largely takes place, although, as seen below, some part of the blood undergoes this process on its passage through the ctenidia.

The **venous system**, consisting of various veins and sinuses, collects the blood thus distributed by the arterial system, and conveys it back to the heart. Most of the blood from the stomach, digestive gland, and intestines is conveyed, by the visceral veins, to the **kidneys** (or **nephridia**), a pair of organs situated one on each side of the body. Each kidney has more or less the form of a U-shaped tube, the lower limb of the U being oriented longitudinally. This lower limb, traversed by a **longitudinal vein,** has glandular walls penetrated by narrow diverticula, and in it the waste products of metabolism are removed from the blood during its passage along the vein. The upper limb is a thin-walled **bladder** from which the excretory products are discharged into the

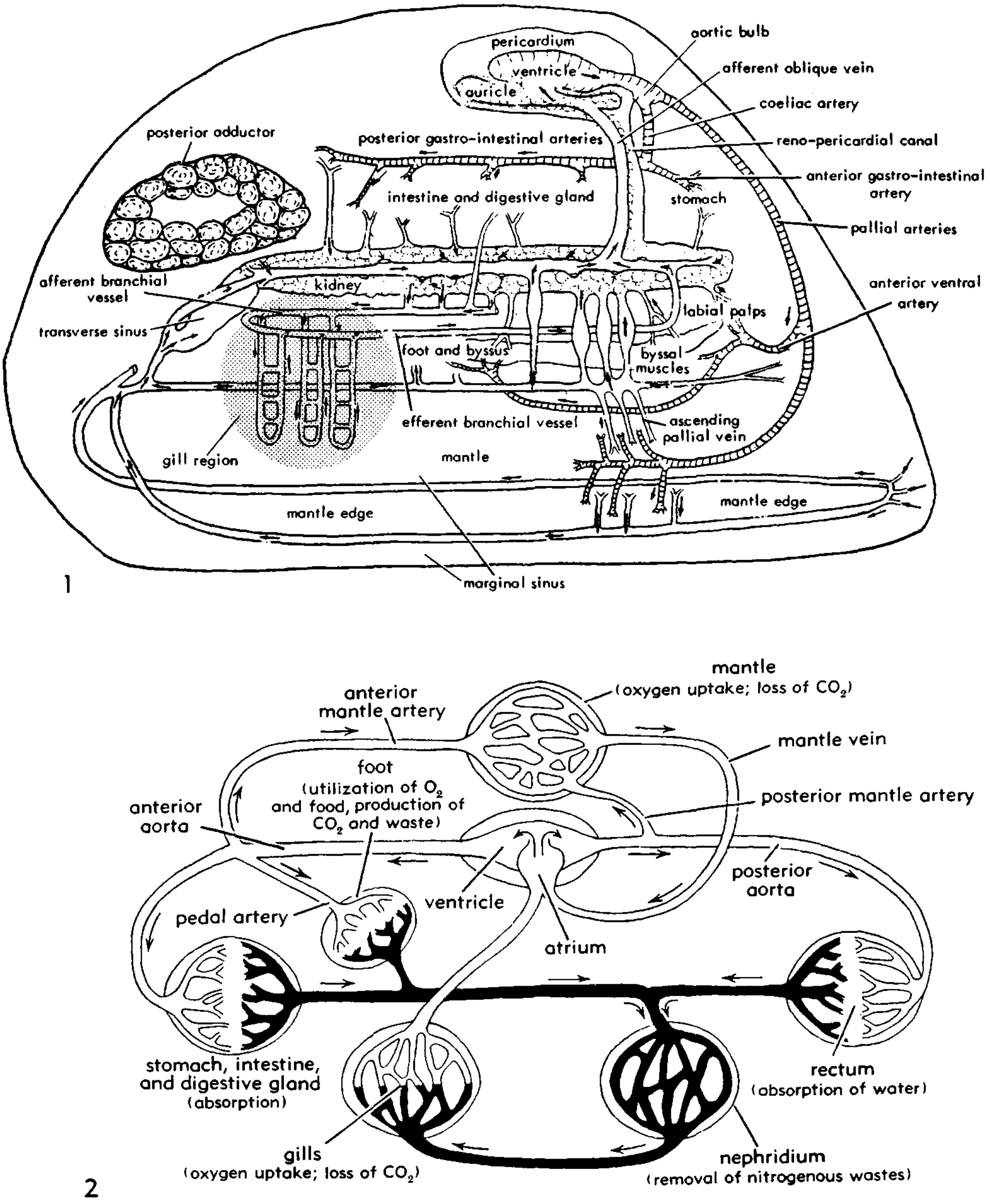

FIG. 24. Circulatory systems of bivalves shown diagrammatically.——*1. Mytilus edulis* LINNÉ, enl. arterial system hatched, venous system clear *(181)*.——*2.* Generalized bivalve, oxygenated blood clear, deoxygenated blood black *(62)*.

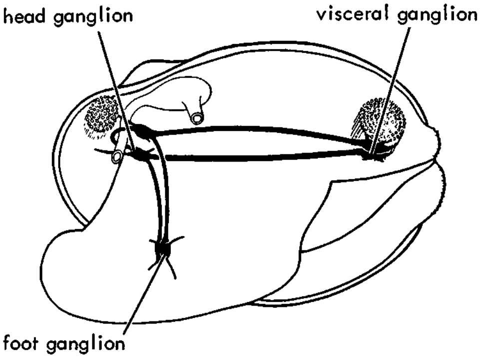

Fig. 25. Nervous system of bivalve, diagrammatic *(18)*.

mantle cavity at a point near the genital opening.

In some bivalves the venous blood from the mantle is conveyed direct to the auricles, bypassing the kidneys. In some forms, including *Mytilus,* it passes to the kidneys through ribbon-like passages known as **plicate canals,** in which further oxygenation occurs (Fig. 24,*1*). A varying proportion of the blood stream is conveyed by a vein direct from each kidney to the corresponding auricle. Part, however, completes its return journey to the heart by a longer course, as it circulates first through one of the ctenidia, passing thence to the auricle either by a direct vein or (as in *Mytilus*) via the anterior end of the kidney.

Special devices are incorporated in the circulatory system of many bivalves to allow the foot or siphons to be extended by flooding with blood.

NERVOUS SYSTEM AND SENSE ORGANS

The nervous system in most Bivalvia consists of three pairs of **ganglia,** symmetrically arranged except in inequivalve forms (Fig. 25). The ganglia on each side (left and right) are generally widely separated and joined by long connectives. The **cerebropleural ganglia** lie in an anterior position not far behind the anterior adductor (when this is present) and close to the esophagus, above which the commissure joining them passes. They innervate the labial palps, the anterior adductor, and the anterior part of the mantle. The **pedal ganglia** lie close together in the foot and are joined by connectives to the ganglia already mentioned. The **visceral ganglia** lie below the rectum, behind the foot and close to the posterior adductor, and are also joined by connectives to the cerebropleural ganglia. They innervate the ctenidia, heart, pericardium, posterior part of the mantle, siphons, and posterior adductor. A nerve (**pallial nerve**)

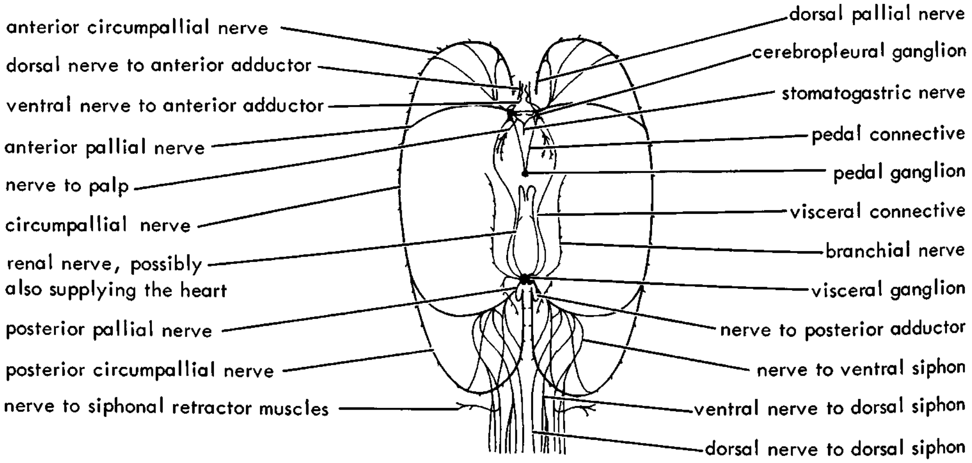

Fig. 26. Nervous system of *Psammocola (Psammobella) tellinella* (Lamarck), Recent, northern Europe *(55)*.

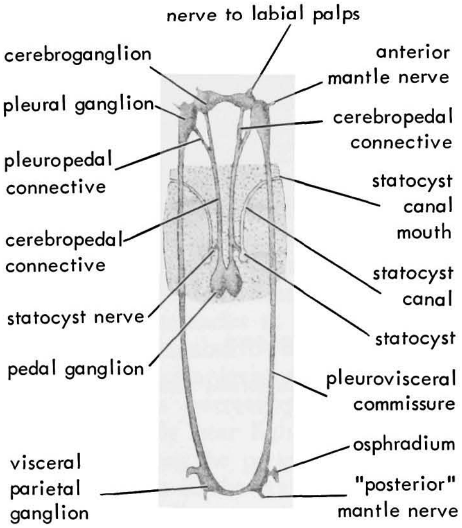

FIG. 27. Nervous system of *Nucula (69).*

runs close to and more or less parallel to the mantle margin on each side, and is connected anteriorly with the cerebropleural ganglion and posteriorly with the visceral ganglion (Fig. 26).

Only in certain protobranchs (e.g., *Nucula*) are there distinct cerebral and pleural ganglia, the latter lying behind the former at the beginning of the visceral connectives. Other protobranchs show successive stages in the fusion of these two ganglia, and in *Yoldia* they are completely united. In the Ostreidae, in consequence of the disappearance of the foot, the pedal ganglia are absent or almost so (Fig. 27).

As there is no head, anteriorly situated sense organs have virtually disappeared in the Bivalvia, although two vestigial eyes are found in the Mytilidae and Pteriidae. In the former family these are small dark spots at the proximal end of the most anterior filament of each inner demibranch. Many bivalves possess a pair of **otocysts** in the foot, above the pedal ganglia. They are minute hollow, oval bodies which lie just below the epithelium and open into the mantle cavity by a small canal. They are thought to be organs of orientation. Two **osphradia**, pigmented sensory patches of the epithelium, are present on the wall of the mantle cavity close to the attachment of the gills. They are probably chemoreceptors, their function being to test the quality of the incurrent water.

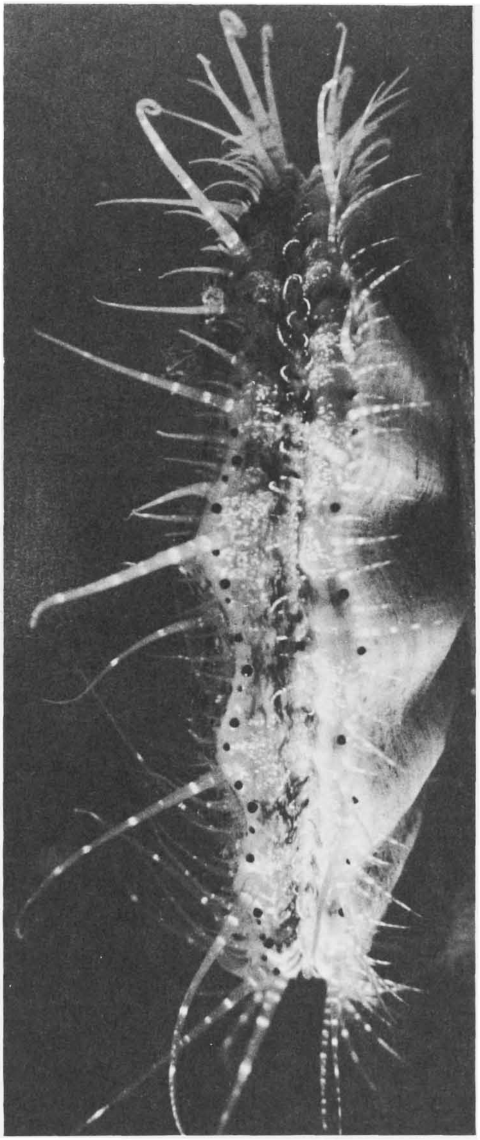

FIG. 28. Sense organs of *Chlamys (Pseudamussium) septemradiatus* (MÜLLER), Recent, northern Europe; anterior view showing tentacles and eye spots along mantle margin, ×3 (photo by W. J. Rees, published by permission).

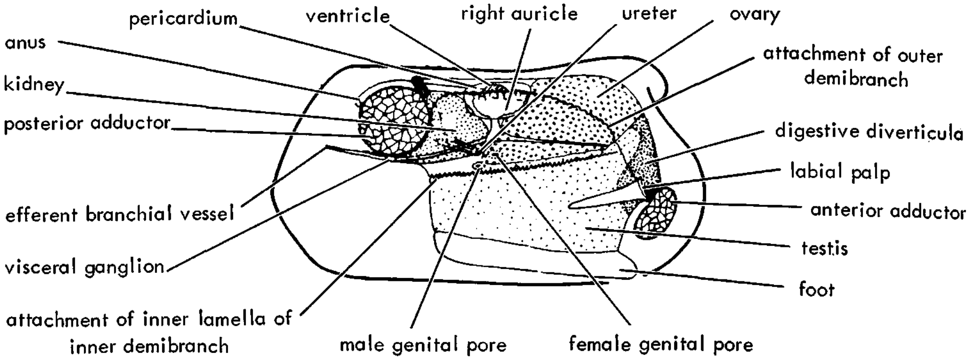

FIG. 29. Reproductive system of *Entodesma saxicola* (BAIRD), Recent, California; visceral mass viewed from right side after removal of right ctenidium, ×2 *(191)*.

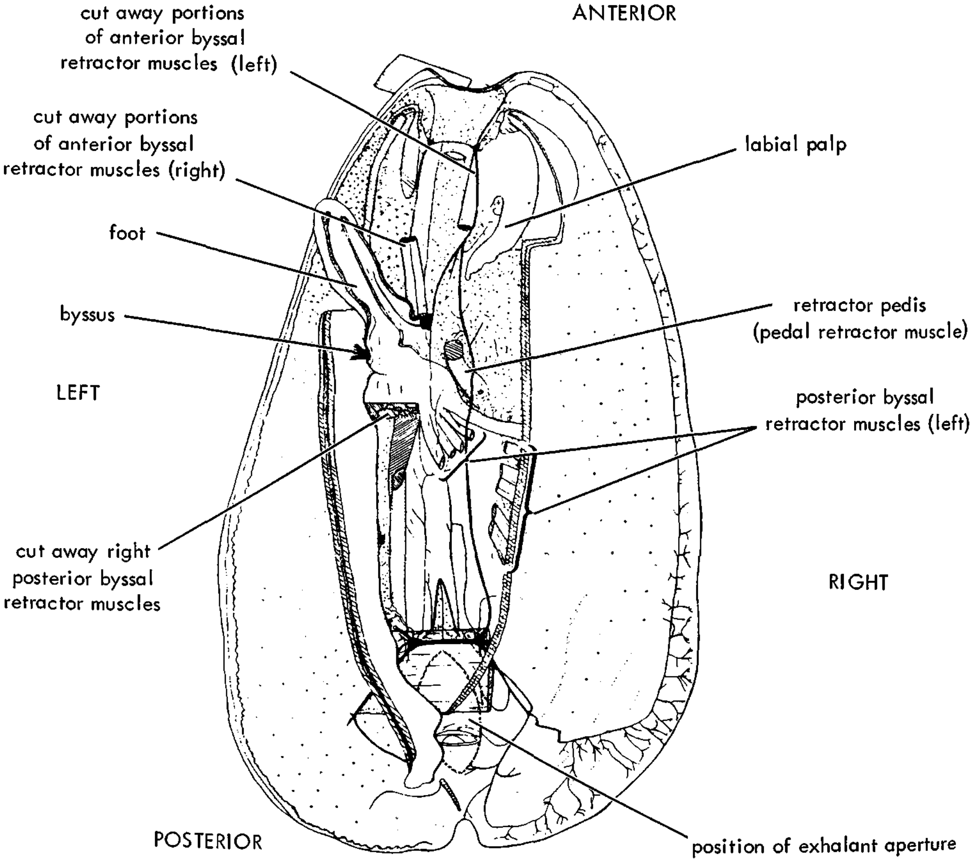

FIG. 30. Dissection showing soft parts of *Mytilus edulis* LINNÉ, ×1.3 *(181)*.

The unfused parts of the mantle edges and the extremities of the siphons are the regions where sensory organs have mainly developed. **Sensory tentacles** occur along the mantle edge in many bivalves and are highly developed in the Limidae and the swimming Pectinidae. In some genera (e.g., *Pecten, Spondylus*) the mantle edge between these tentacles bears small but quite elaborate, irregularly distributed **eyes** (Fig. 28), while in *Cardium* fairly complex eyes are carried by tentacles at the ends of the siphons. Many nonburrowing bivalves have eyes of varying complexity along the mantle edges, while in burrowing forms the siphons commonly bear light-sensitive spots. Sensory cells may be present singly or as scattered groups in the wall of the mantle cavity. In *Mytilus* a pair of abdominal sense organs lie on the ventral side of the posterior adductor muscle and may serve to detect vibrations of the sea water.

REPRODUCTIVE ORGANS AND SEXUALITY

Reproductive organs in the Bivalvia are relatively simple. They consist of a pair of **gonads** which are usually placed symmetrically on the two sides of the visceral mass, each forming a branching system of follicles surrounding the intestine (Fig. 29). In *Mytilus* the gonads extend into the mantle cavity of both valves and in *Anomia* into the mantle cavity on the right side of the body only. According to Coe *(24)*, 96 percent of species in which sexual conditions have been investigated are unisexual (or dioecious), the remainder exhibiting various grades of ambisexuality. In some the ovary and testis are distinct glands, discharging their products through separate ducts, but in others different parts of the same gonad, or even the same parts, may function as ovary and testis, and then there is only one duct. In some of the more primitive genera the ducts open into the kidneys and the genital products reach the mantle cavity through the same outlet (**renogenital pore**) as the renal excreta. In other forms the efferent ducts lead direct to the mantle cavity, ending on the same papillae as the renal openings, or else discharging through distinct pores. The genital ducts are short and devoid of glands. Their outlets lie along the dorsal gill passage, so that the genital products are usually caught up by the exhalant stream.

In many species fertilization takes place in the surrounding water, between ova and spermatozoa which have been discharged from the mantle cavities of the parent animals. In others fertilization takes place in the mantle cavity. In many such cases one of the gametes (usually the spermatozoan) is drawn in with the inhalant current, but self-fertilization is known to occur in hermaphrodite species. The larvae are usually soon expelled from the mantle cavity, but some species incubate their young in a **brood chamber**, usually between the lamellae of the gill demibranchs.

Of the approximately 10,000 described species of living Bivalvia, about 400 are known to be ambisexual—that is, their individuals do not function solely as males or as females during their lifetime. Coe has distinguished four grades of ambisexuality, the differences between which, however, are not altogether clear-cut. They are as follows:

1) *Functional hermaphroditism.* Both ova and spermatozoa are produced simultaneously for a period by the same individual, although there may be a brief initial period of unisexuality, usually male (**protandrous hermaphroditism**).

2) *Consecutive sexuality.* In this type there is a single reversal of sex during the lifetime of the mollusk, usually from male to female.

3) *Rhythmic consecutive sexuality.* A series of alternating male and female phases occurs during life. A well-known example is that of *Ostrea edulis* Linné, in which each adult oyster passes through one male and one female phase each year. In any interbreeding population roughly one-half of the individuals start as males each season and change to females while the other half undergoes the reverse change, so that both sexual types are always present.

4) *Alternative sexuality.* In every season the sex of each adult remains unchanged, but in successive seasons changes of sex, affecting part of the population only, occur.

This type of sexuality has been observed mainly in certain oysters, among them *Ostrea virginica* Gmelin.

MUSCULATURE

Many of the muscles in the Bivalvia are attached to the interior of the shell and leave on it a series of scars, some well impressed, others superficial and seen only in very well-preserved fossils (Fig. 30). A description of the arrangement of the shell-attached muscles will, therefore, appropriately form a link between the foregoing account of the soft parts and a

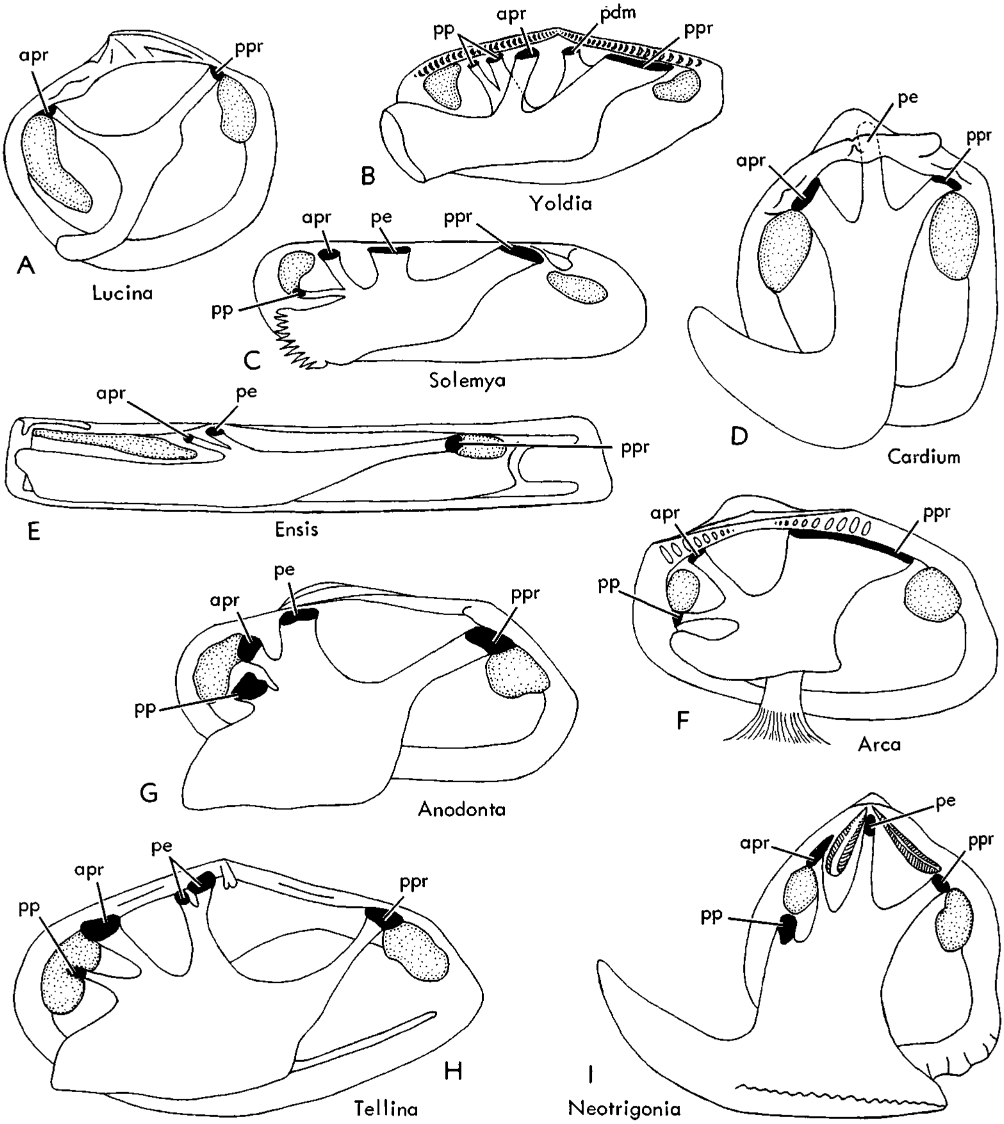

Fig. 31. Diagrams showing pedal musculature in dimyarian bivalves, illustrated by right valves viewed from inside (adductor scars stippled, pedal scars black, except in pedal elevator of *Cardium* which is attached in umbonal cavity under hinge plate), not to scale (all modified from Pelseneer, 1911, except *B, C, E, G,* and *I.*——*A. Lucina.*——*B. Yoldia (66).*——*C. Solemya* (Pelseneer, 1891).——*D. Cardium.*——*E. Ensis (126).*——*F. Arca.*——*G. Anodonta* (Brück, 1914).——*H. Tellina.*——*I. Neotrigonia* (Pelseneer, 1891). [Explanation: *apr,* anterior pedal retractor; *pdm,* dorsomedian pedal muscles; *pe,* pedal elevator; *pp,* pedal protractor; *ppr,* posterior pedal retractor].

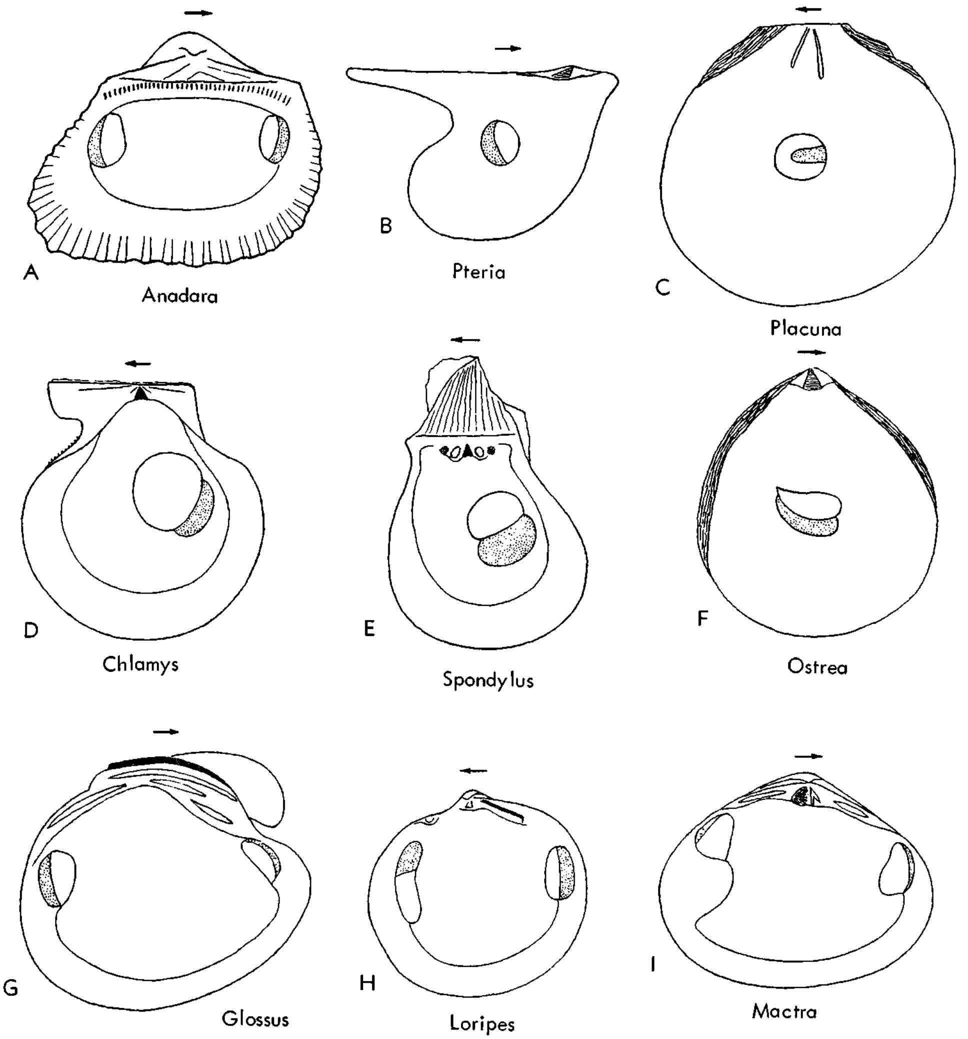

FIG. 32. Adductor-muscle scars in selected bivalve genera, not to scale (arrows directed anteriorly), showing attachment areas of striated or "quick" muscle (unshaded) and smooth or "catch" muscle (stippled) (Cox, n).

discussion of the general features of the shell. For treatment here they may be classified as the adductor muscles, the pallial muscles, the muscles of attachment of the foot and byssus, and a miscellaneous group. No account will be given of muscles which lie entirely within the soft parts of the mollusk, such as the intrinsic muscles of the foot, ctenidial muscles, and muscles of the auricles and ventricle (cardiac muscles).

ADDUCTOR MUSCLES

The **adductors**, the largest and strongest muscles found in the Bivalvia, extend between the two valves and serve to draw them together, opposing the tendency of the ligament (p. *N*58) to open them. Fundamentally they are two in number and are designated, according to their positions, as the **anterior** and **posterior adductors.** Their

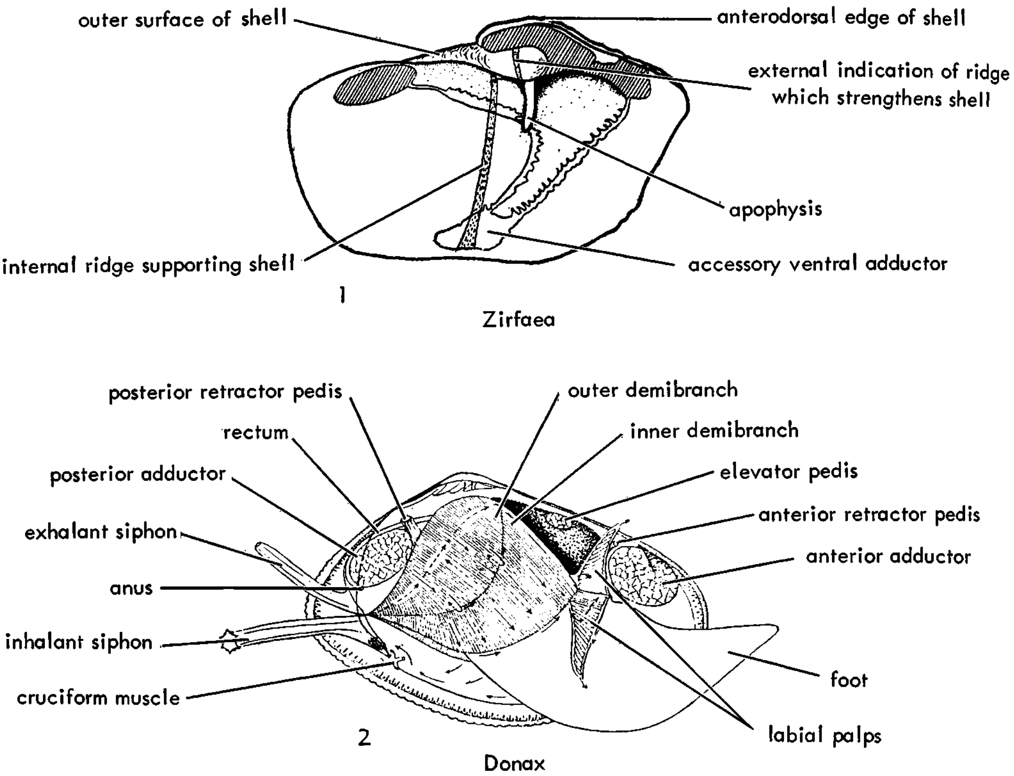

FIG. 33. Bivalve musculature.——*1. Zirfaea crispata* (LINNÉ) showing attachments of anterior adductor and accessory muscles, ×1.5 (Purchon, 1955).——*2. Donax vittatus* (DA COSTA) showing cruciform and other muscles in relation to various anatomical features, ×2 *(190)*.

scars of attachment are usually circular or oval in shape and in many forms do not differ greatly in size. Bivalvia in which two adductor muscles are present are described as **dimyarian** (Fig. 31), and dimyarian forms in which the two muscles do not differ greatly in size are called **isomyarian** or **homomyarian.** Use of these last two terms is usually extended to apply to such genera as *Lucina,* in which the anterior adductor is larger than the posterior one and dorsoventrally elongated, and *Ensis* and *Pharus,* in which the anterior adductor, like the shell itself, is greatly elongated in an anteroposterior direction.

The scars of the two adductors usually lie within the dorsal half of the shell, but well below the axis about which the two valves hinge (Fig. 32). In the genus *Cucullaea* one scar is located on a raised platform on the interior of the shell; in the mussel-like genera *Septifer* and *Dreissena* the anterior scar occupies a septum in the umbonal angle. In some genera of the rudists the scars are borne by processes protruding prominently into the cavity of the shell. Such muscle-bearing structures are known as **myophores.** In the great majority of forms, however, the adductor scars are flush with or form shallow depressions of the general inner surface of the shell. In the Pholadacea (Fig. 33) the anterodorsal part of the shell is broadened and reflected dorsally over the umbo and the anterior adductor is attached to the reflected part, thus lying on the dorsal side of the hinge axis. Usually the two adductors contract or relax in union, but in a few genera (e.g., *Solecurtus, Hiatella,* and members of the Pholadidae) they are capable of contracting alternately, so that the valves can rock about a transverse axis.

Among numerous representatives of the Bivalvia, however, we find all stages in the progressive diminution of the anterior adductor, and in many genera this muscle is absent, at least in the adult stage. Forms in which it is small or absent are termed **ani-**

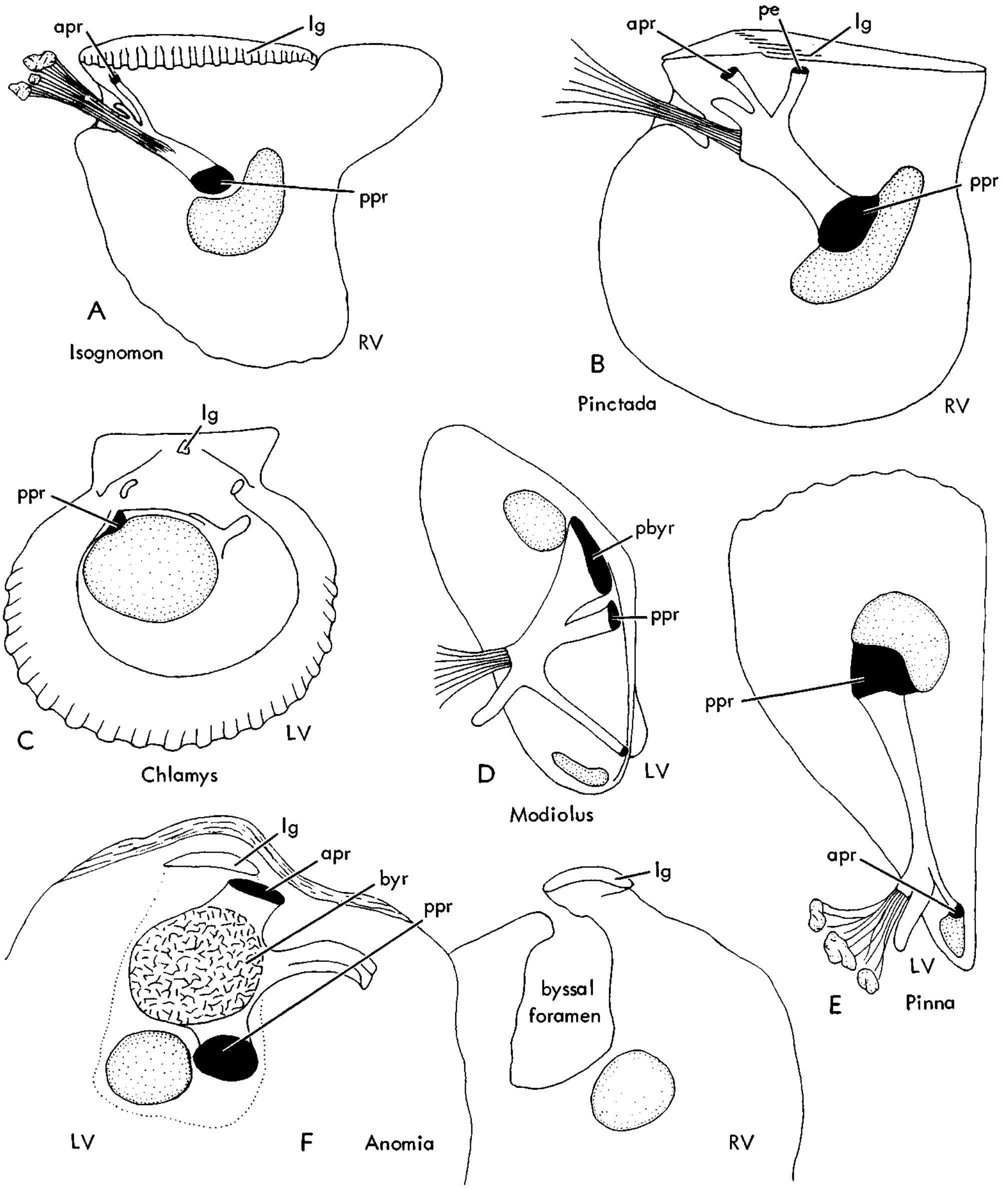

FIG. 34. Diagrams showing pedal musculature in heteromyarian and monomyarian bivalves, illustrated by valves viewed from inside (adductor scars stippled, pedal scars black), not to scale (all modified from *132*, except *B* and *E*).——*A. Isognomon.*——*B. Pinctada (113).*——*C. Chlamys.*——*D. Modiolus.*——*E. Pinna* (Rosewater, 1961).——*F. Anomia.* [Explanation: abbreviates as for Fig. 31 and, in addition, *byr,* byssal retractor; *lg,* ligament; *LV,* left valve; *pbyr,* posterior byssal retractor; *RV,* right valve.] [Note that pedal and byssal muscles are attached only to left valves in *Chlamys* and *Anomia.*]

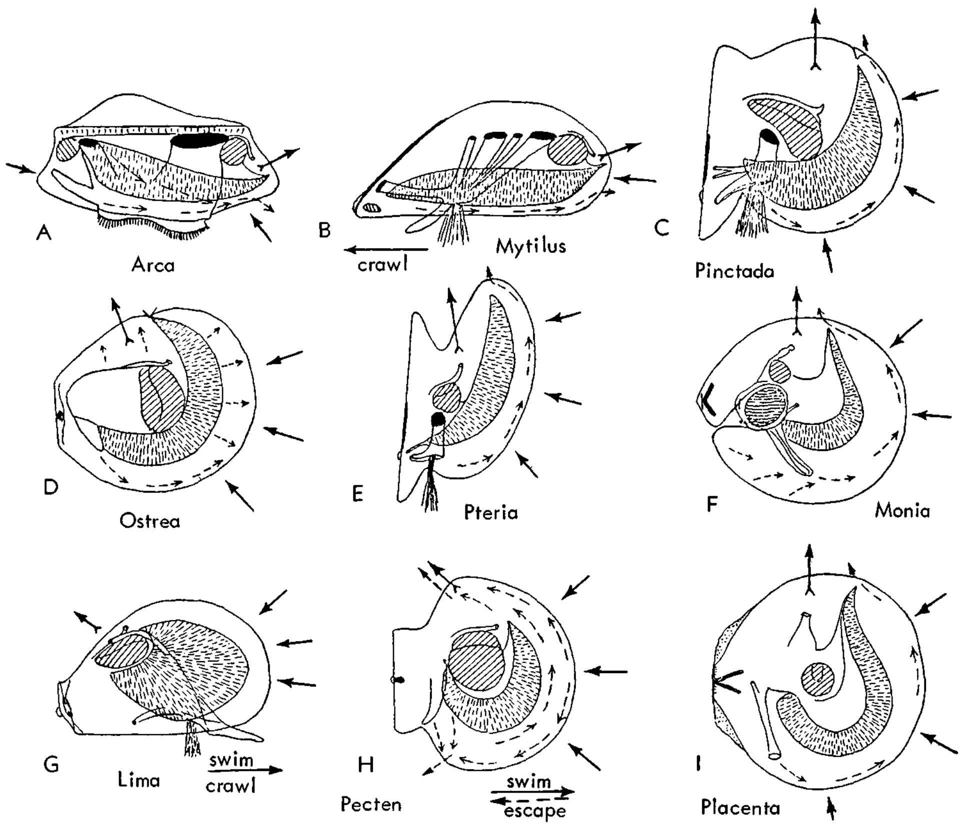

FIG. 35. Bivalve musculature in dimyarian *(A)*, heteromyarian *(B)* and monomyarian *(C-I)* genera (with left valve and mantle removed) showing adductors (oblique ruled), pedal muscles (left-valve attachments in black) in relation to ctenidia (broken-line pattern), plain arrows indicating inhalant currents, feathered arrows exhalant currents, and broken arrows cleansing currents in mantle cavity (diagrammatic, not to scale) (*193*, from various sources). [*A, B, G*, viewed from left side; *C-F, H*, viewed from above; *I*, viewed from underside (animal lies on concave right valve in life).]

somyarian,[1] and among them we may distinguish those that are **heteromyarian** (anterior adductor much reduced) and those that are **monomyarian** (only posterior adductor present) (Fig. 34, 35). Under certain earlier taxonomic schemes such names as Anisomyaria and Dimyaria were considered to designate major taxa of the Bivalvia, but it is now realized that the degree of reduction of the anterior adductor is not a satisfactory criterion in classification. Thus *Tridacna,* although now thought to be fairly closely related to the Cardiidae, a typical homomyarian family, possesses only one adductor, while on the other hand *Dimya,* considered to be close to the monomyarian family Plicatulidae, has two well-defined although small adductors. Stages in the disappearance of the anterior adductor are well shown in the Mytilidae. In some species of *Botula* the two muscles differ very little in size; in *Modiolus* the anterior adductor, although still well developed, is considerably the smaller of the two; in *Mytilus* it is very small, and in *Choromytilus* it is absent. In many of the earlier Pteriacea a small anterior adductor is present, whereas in modern forms this muscle is absent in the adult stage. When the anterior ad-

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[1] Some authors use "anisomyarian" as a synonym of "heteromyarian."

ductor is absent or much diminished in size there is a general tendency for the posterior adductor to assume a more central position, as it is then best able to perform its function of drawing the valves together when so located.

In most bivalves the adductors are formed of two distinct bundles of muscle fibers, each attached to its own part of the complete adductor scar. These two types of muscle have been termed "nacreous" and "vitreous"; the fibers of the former type are smooth and those of the latter type striated, either transversely or obliquely. The "vitreous" or striated muscle (termed "quick" muscle by some workers) is believed to function during the rapid closing of the two valves, whereas the "nacreous" muscle (also termed "catch" muscle) acts more slowly and serves to hold the two valves of the shell closed for considerable periods. In dimyarian forms the "nacreous" muscle generally occupies the more peripheral part of the scar (anterior or posterior as the case may be) and the "vitreous" muscle the part closer to the middle of the shell, but in the anterior adductor of the Lucinidae the former type occupies the dorsal half of the muscle. The distinctions between the types are particularly well defined, and the two parts of the adductor scar are commonly distinguishable in monomyarian families (e.g., Pectinidae, Spondylidae, Plicatulidae, Ostreidae). In the Pectinidae (in swimming representatives of which the striated muscle functions during the rapid opening and closing of the valve) the attachment area of this part of the muscle forms the anterior three-quarters of the scar, whereas in *Plicatula* it forms only its anterior quarter. In the Ostreidae there is less difference in the size of the two areas, that belonging to the striated muscle occupying the dorsal half of the whole scar.

PALLIAL MUSCLES

The muscles of the mantle are known collectively as **pallial muscles**. Radially directed muscle fibers are present within the entire mantle, but are strongest near its periphery and attached to the interior of the shell along a line or narrow band (**pallial line**) which for all or part of its length is parallel and fairly close to the margin (Fig. 36). The function of these marginal radial muscles is to withdraw the mantle edge well within the valves of the shell before they are closed. Concentrically directed muscles also extend round the margin of the mantle close to its free edge. The pallial line is distinctly impressed on the interior of the shell in most homomyarian and some heteromyarian forms, running from the lower margin of one adductor scar to that of the other.

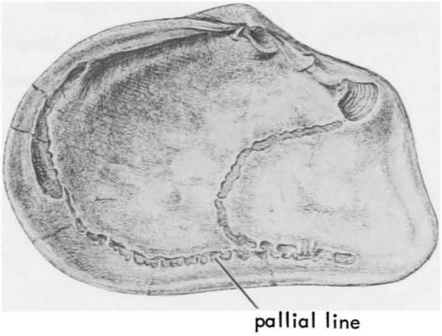

FIG. 36. *Mya truncata* LINNÉ, interior of right valve showing muscle attachments of mantle along pallial line, ×0.7. Pallial sinus at right (Wood, 1857).

In most forms in which the anterior adductor has been completely lost, a line of mantle attachment representing the original pallial line stretches from the posterior adductor towards the hinge line, following a direction more or less parallel to the anterior margin of the shell, but it is shorter than in most dimyarian forms owing to displacement of the remaining adductor towards the center of the shell. In the Pteriidae a continuous pallial line is replaced by a series of irregularly spaced pits, each marking the insertion of fanlike muscles for the retraction of the mantle margin. In the Pinnacea, a heteromyarian group, primary mantle attachment exists only along the two adductor muscle insertions and there is no pallial line like that present in the Mytilidae, another heteromyarian group. In the Pteriacea and Anomiacea the considerable area of the mantle posterior to the single adductor is unattached to the shell near its margin, and the unattached area is even more extensive in

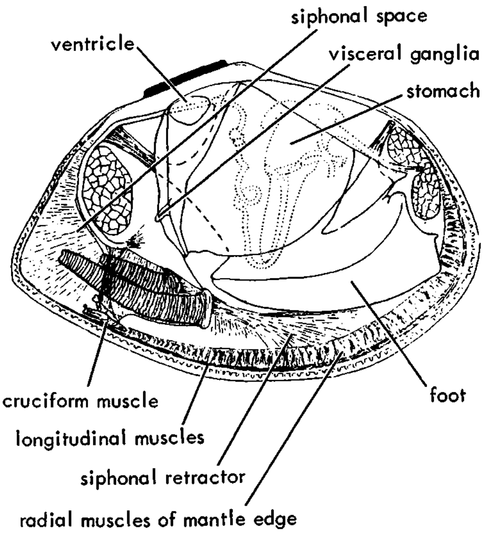

FIG. 37. *Tellina tenuis* DA COSTA showing mantle muscles, cruciform and siphonal retractor muscles, ×3 *(190)*.

the Pinnacea, for the reason just stated. Special **pallial retractor muscles** (posterior only in the first two superfamilies, posterior and anterior in the third) exist, however, in these groups, and serve to withdraw these parts of the mantle far within the shell when stimulated. In the Pectinacea, Limacea, and Ostreacea a secondary line of posterior pallial attachment has become developed, passing around the adductor scar on its posterior side and upward towards the hinge line. Except in the Limidae this line of secondary pallial attachment is less distinct than the true pallial line, and in the Ostreidae even the latter cannot be clearly seen in many species.

In the dimyarian family Solenidae, in which the shell is much elongated in an anteroposterior direction, a line of pallial attachment runs along the dorsal margin from the posterior adductor (Fig. 36).

JAWORSKI *(77)* has interpreted the fine radial ridges seen on the interior of the shells of some members of the Ostreidae and Chamidae, particularly near the margin, as reflecting the radial musculature of the mantle, suggesting that where there has been particular pressure on the mantle the musculature has affected the secretion of shelly matter. He has thus dismissed the theory of some other workers that these ridges, seen also on the lip of the lower valve of many hippurites, are impressions of the cirri (tentacles) of the mantle edge. In some species, particularly of the family Lucinidae, the musculature of the general surface of the mantle leaves numerous small attachment scars, in the form of pits or furrows, on the interior of the shell.

In siphonate forms, with the exception of the Lucinidae (in which the single siphon, the exhalant one, is invaginable), **siphonal retractor muscles** are present as modifications of the radial muscles of the mantle margin, and serve to withdraw the siphons partly or wholly within the shell (Fig. 37). Except when the siphons are short, these muscles are attached to the interior of the shell along an embayment of the pallial line known as the **pallial** sinus, the space within the embayment accommodating the retracted siphons. Bivalves with a simple pallial line are described as **integripalliate** and those with an embayed pallial line as **sinupalliate**, but the distinction between these two types is not of fundamental significance. In forms with a deep pallial sinus (e.g., Tellinidae) the lower border of the sinus may coincide with the marginal part of the pallial line for a considerable distance, and in the Solenidae, in which the pallial line bends back close to the dorsal margin before joining the dorsally and relatively anteriorly placed posterior adductor scar, the upper border of the sinus may also coincide with part of it (Fig. 36).

The Pholadidae are remarkable for the development of an **accessory ventral adductor**, the insertion of which in each of the two valves forms an irregularly shaped area at the posterior angle of the pallial line, where it bends back to form the sinus. This muscle must be interpreted as having arisen from pallial muscles at this point by the fusion of those on the two sides across the shell. The **cruciform muscle** found in the Tellinacea and some Solenidae occupies a very similar position. Located just below the base of the siphons, it consists of two bundles of muscle fibers running transversely from one valve to the other and intersecting at an acute angle, so as to form a cross

(Fig. 33,37). In many Recent specimens their small circular scars of attachment are just visible near the posterior angle of the pallial line. YONGE has suggested that their function is to take the strains that occur during the extrusion and retraction of the siphons (Fig. 38).

ATTACHMENT MUSCLES OF FOOT AND BYSSUS

The number and positions of attachment of the various pedal muscles vary in different genera. Such muscles have almost completely disappeared in the Plicatulidae, Chamidae, and Laternulidae, and are absent in the Spondylidae and Ostreidae, in the last of which families the foot itself has atrophied. In equivalve genera the pedal muscle scars are equal in number and similarly arranged in the two valves, but this may not be the case in inequivalve forms.

The **anterior pedal retractor** is usually attached on the posterodorsal or posterior side of the anterior adductor scar. In some forms (e.g., *Ensis*) the muscle divides into two bundles, each with its area of attachment. In others there is a tendency for the attachment of this muscle to migrate ventrally along the posterior margin of the adductor scar. The anterior retractor is absent in most monomyarian forms, such as the Pectinidae, and small dorsally placed muscles formerly identified as such in *Pteria* and some species of *Lima* are now regarded as elevator muscles. The anterior retractor is present in the heteromyarian families Pinnidae and Mytilidae. In *Mytilus* this muscle arises from the base of the byssus and is attached to the shell very close to the umbo, but in the related genus *Choromytilus* it is attached in a much more posterior position. In the Pholadidae the anterior pedal retractor is attached to a process or **apophysis**, usually narrow and spoonlike, which projects into the interior of the shell from under the beak.

The attachment of the **posterior pedal retractor** is usually on the dorsal side of the posterior adductor scar, but in some forms it has migrated to the ventral side of this muscle and when present in the Limidae it is on its posteroventral side. In byssiferous forms the posterior retractor is joined to the byssus and forms its retractor as well as that of the foot. In the Mytilidae and Arcidae this muscle tends to become extended in a direction parallel to the dorsal margin. Actually, in *Mytilus edulis* LINNÉ it is split up into three to six bundles, the most anterior of which arises from the base of the foot itself and constitutes the pedal retractor, while the others form byssal retractors. On the shell, however, the scars of the individual bundles are merged together. In *Anomia* the posterior retractor is modified to form the byssal muscle or muscles, developed on the left side only, its commonly duplicated scars occupying a position which is anterior and slightly dorsal to median, facing the foramen in the right valve through which the calcified byssus passes. In the Pectinidae also the posterior retractor (if developed at all) is present only on the left side, its scar being situated along the dorsal margin of the adductor scar. In the Pteriidae a posterior retractor is present on both left and right sides, its scar in each valve lying on the antero-

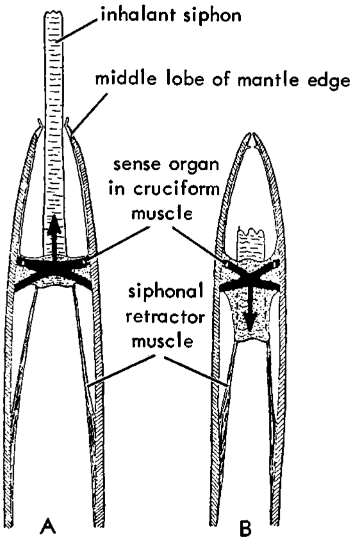

FIG. 38. Bivalve musculature—semidiagrammatic ventral views of inhalant siphon attachments in Tellinidae and Semelidae showing how cruciform muscle acts as tie taking backward strain when siphon is extruded *(A)* and forward strain when it is withdrawn *(B)* *(190)*.

dorsal side of the adductor scar. In both cases the line of junction of the scars is indistinct. In *Isognomon,* on the other hand, the adductor scar is crescentic, with its hollow side facing dorsalward, and the pedal retractor lies within the concavity, well separated from the adductor. In nonbyssiferous members of the Pectinidae and Limidae and in the Vulsellidae the posterior retractor, like the anterior one, has disappeared, although a small foot is present.

A **pedal protractor muscle**, serving to extend the foot, is fairly widespread in the Bivalvia, although it has not been observed in some families. In some genera (e.g., *Pleiodon*) its place of insertion in the shell is on the posterior side of that of the anterior retractor, or it may migrate anteriorly so as to encroach on the anterior adductor scar, in some (e.g., *Tellina, Donax, Montacuta*) almost dividing it in two; or it may lie on the ventral side of that adductor (e.g., *Glycymeris, Limopsis, Arca, Trigonia, Cardium,* and other forms). In some Nuculacea there are two **anterior protractors**, inserted close to the dorsal margin just posterior to the top of the anterior adductor scar, and in front of the anterior retractor scar.

A **pedal elevator muscle**, best developed in the Cardiidae, Tellinidae, Psammobiidae, and Unionidae, among living families, is a thin bundle of muscle fibers attached to the shell very commonly in the umbonal cavity, in which case its scar is represented by an umbonal protuberance in fossil specimens which are internal molds. Small paired or single pedal elevator muscles are present near the hinge margin in *Pinctada, Pteria, Isognomon, Malleus,* and some species of *Lima.*

MISCELLANEOUS SHELL-ATTACHED MUSCLES

The visceral mass is secured in place by muscles which leave attachment scars on the interior of the shell in some species. Thus in some Unionacea (e.g., *Spatha*) visceral attachment muscles leave two impressions, a rather large, crescentic one behind the anterior adductor and a smaller, more elongated one in a mediodorsal position. In the Pholadidae an **anterior retractor muscle of the visceral mass** is inserted in each valve a little behind the anterior adductor scar, while the **posterior retractor of the visceral mass** is inserted within or close to the posterior adductor, first dividing into two bundles in some species. In *Solemya* a narrow band on the interior of the shell ascends obliquely from the posteroventral corner of the anterior adductor scar towards the dorsal margin, where it broadens out to merge with the pedal retractor scars. It marks the attachment of muscles of the integument of the visceral mass.

A small **gill retractor** muscle exists in *Anomia,* some Ostreidae, Pectinidae and Solenidae, and probably in other forms. In *Hemipecten* its attachment is just in front of the middle of the valve. NEWELL *(113)* has recorded that areas of attachment of two gill muscles can be detected on the interior of the right valve of *Chlamys islandica* (MÜLLER), a large crescentic one below the adductor scar and a small one above it.

Not all the scars visible on the interior of bivalve shells are definitely assignable to muscles of known function, and some have been alluded to merely as "accessory muscle scars." Several such scars are well seen in some modern species of the Nuculacea, particularly on the dorsal part of the surface. SCHENCK *(146)* has applied such noncommittal terms as "median muscle scar" and "punctiform scars" to them, while HEATH *(66)* has termed two of them the "dorsomedian" and "ventromedian" scars. Such scars are numerous and conspicuous on some of the Paleozoic nuculaceans. The Ordovician *Babinka* has radially directed pyriform scars between its adductor scars, with smaller and less conspicuous scars below them. STENZEL *(154)* has called attention to a small scar, which he terms that of "Quenstedt muscle," a short distance below the center of the ligamental area in all species of Ostreidae. As no foot is present in this family, the muscle in question cannot function as a pedal muscle, although it may have arisen as a modification of one.

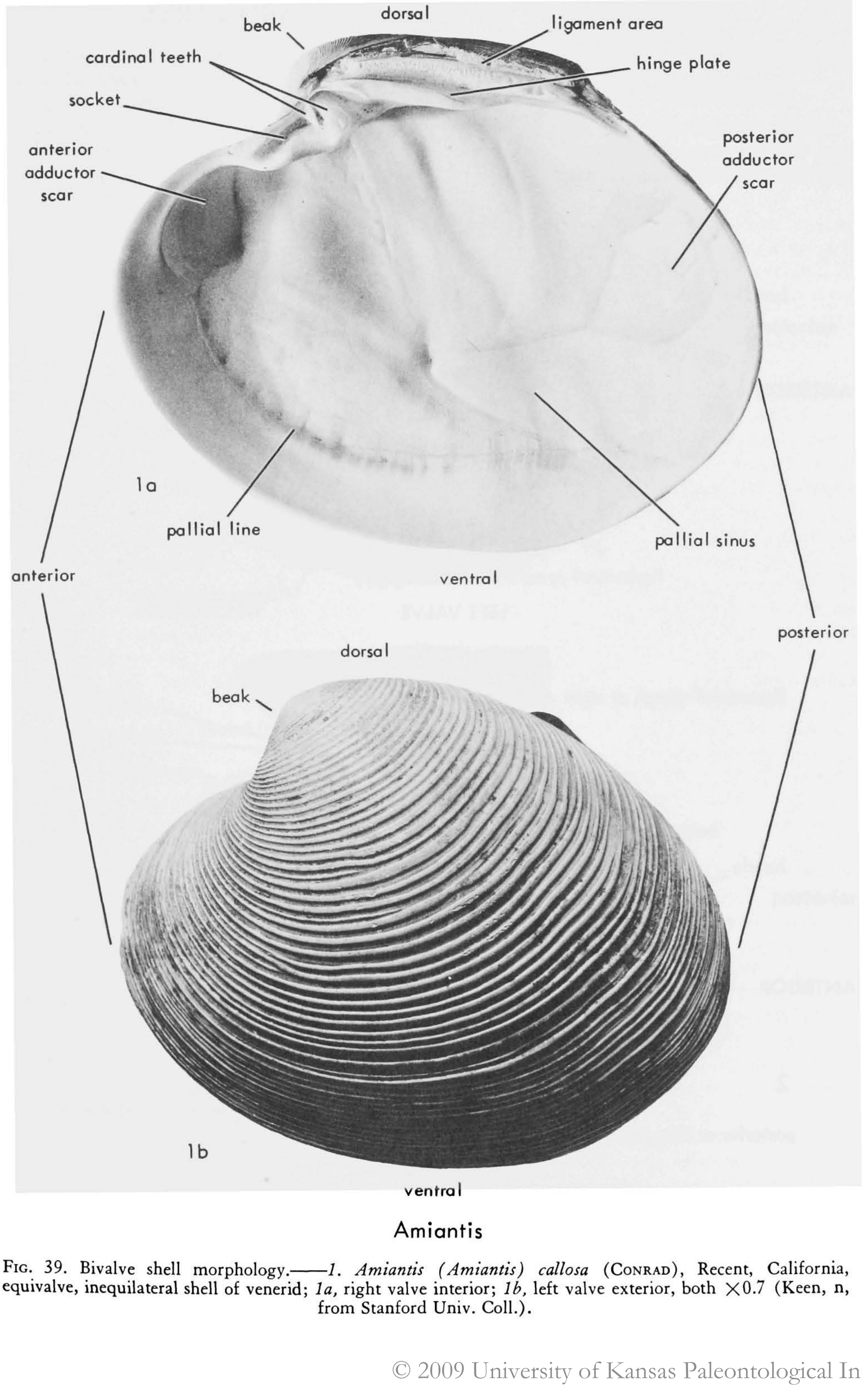

Fig. 39. Bivalve shell morphology.——*1. Amiantis (Amiantis) callosa* (Conrad), Recent, California, equivalve, inequilateral shell of venerid; *1a,* right valve interior; *1b,* left valve exterior, both ×0.7 (Keen, n, from Stanford Univ. Coll.).

MORPHOLOGY OF BIVALVIA HARD PARTS

GENERAL EXTERNAL FEATURES OF SHELL

In the class Bivalvia the shell consists of two usually convex, calcareous structures (**valves**) of various shapes which open and close by hinging along an imaginary straight line (**hinge axis** or **cardinal axis**) that coincides with or is close to one margin (**hinge margin**) (Fig. 39-42). The structures belonging to this part of the shell (ligament, hinge teeth, hinge plate, etc.,

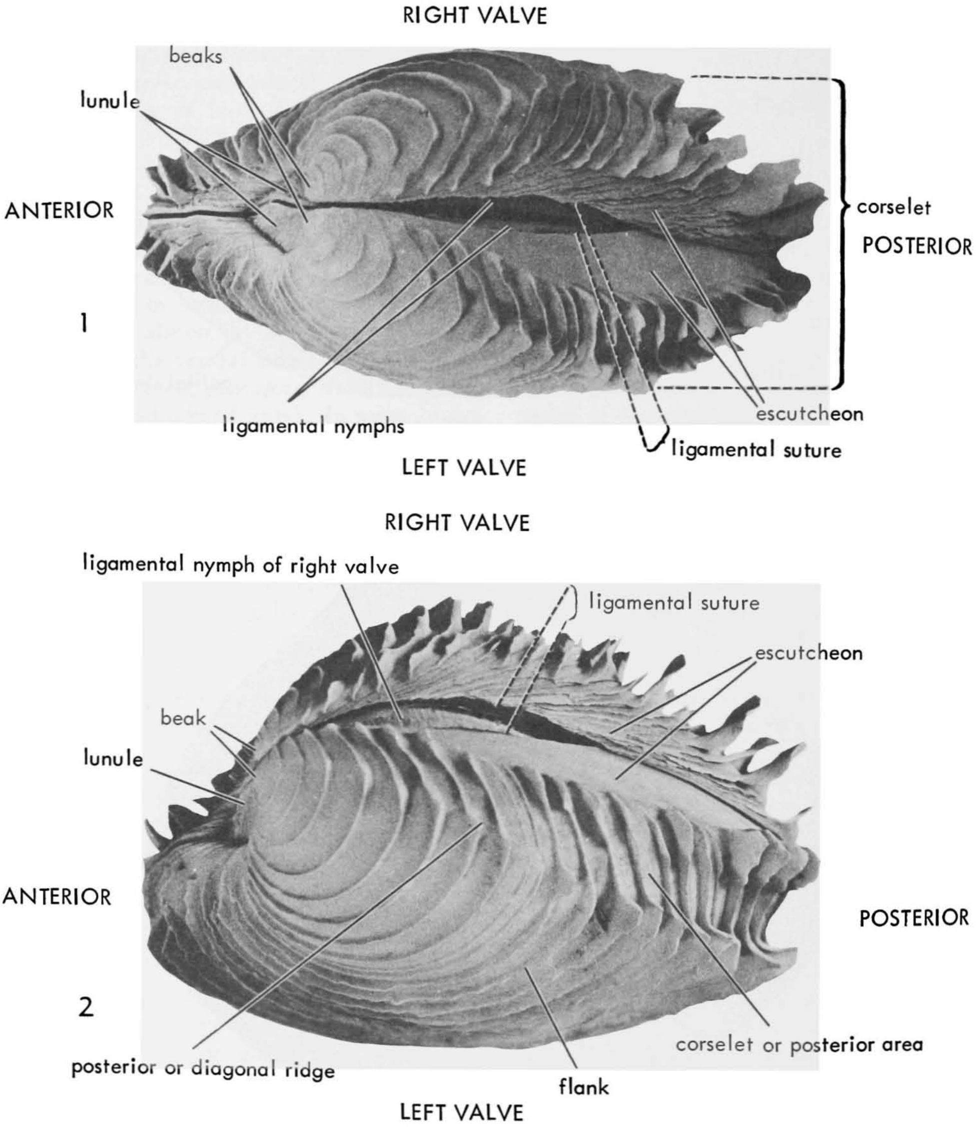

FIG. 40. General external features of shell—*Circomphalus foliaceolamellosa* (DILLWYN), Neog., Medit., Rec., W.Afr.——*1.* Dorsal view.——*2.* Specimen viewed obliquely from above left. Note slight size difference between LV and RV lunules and escutcheons, ×1.4 (Nuttall, n).

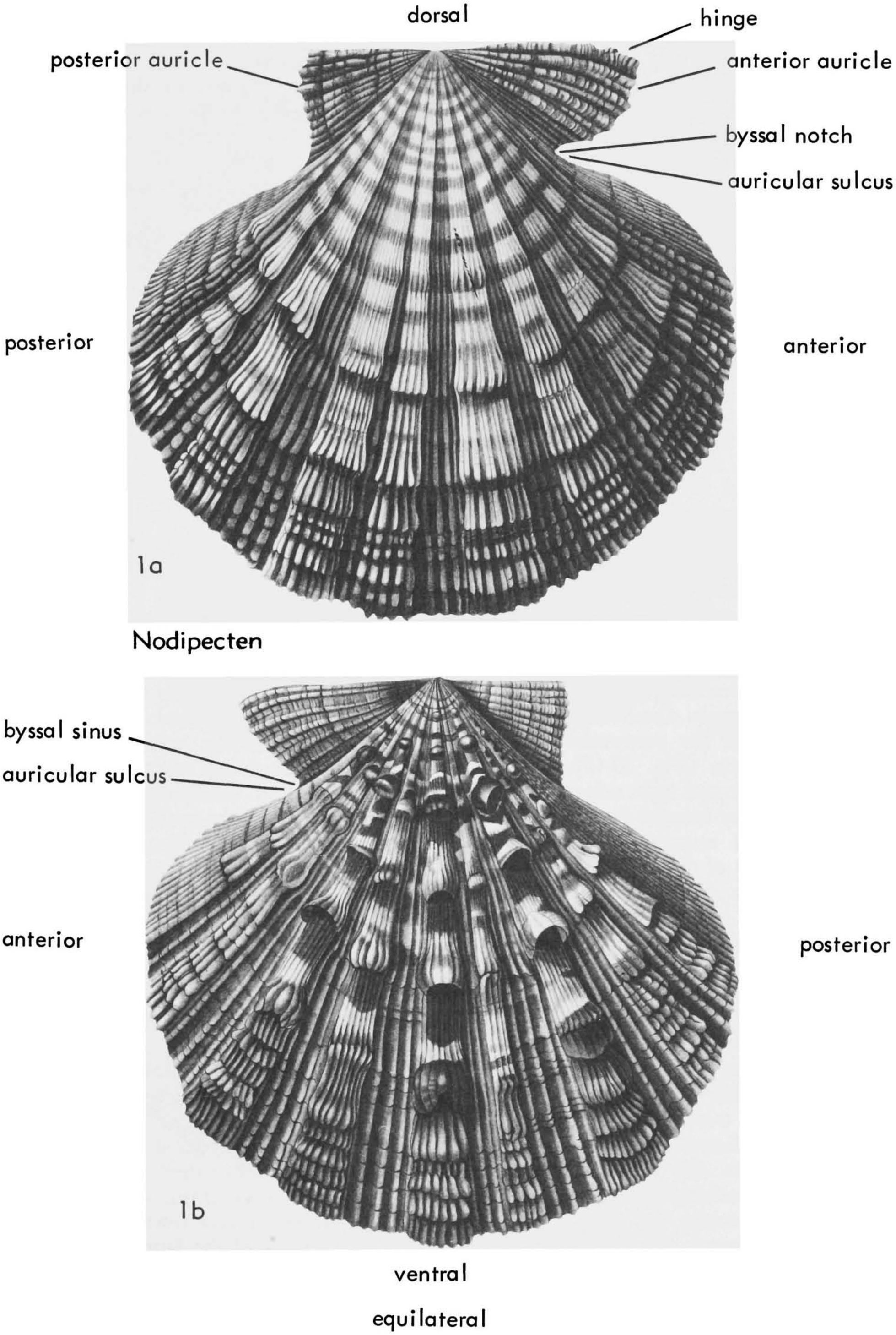

FIG. 41. Bivalve shell morphology.——*1. Chlamys (Nodipecten) nodosa* (LINNÉ), Recent, off Florida, equivalve, equilateral pectinid; *1a,b,* right and left valve exteriors, ×0.5 (Chenu, 1844).

described later) which function during opening and closing of the valves are collectively known as the **hinge**. In typical homomyarian bivalves the hinge occupies a strictly **dorsal** position in relation to the soft parts; on the opposite margin (along which the valves open most widely), is **ventral;** one end of the shell is **anterior,** as it lies relatively close to the mouth of the animal, and the other end is **posterior**, as it lies relatively close to the anus (Fig. 39). In heteromyarian bivalves the corresponding parts of the shell do not occupy similar positions in relation to the soft parts.

The point is discussed later (p. *N*78) and the conclusion is reached that, for lack of any alternative directional terminology, it is desirable to regard the hinge in all Bivalvia as dorsal and to designate the other three "points of the compass" as ventral, anterior, and posterior, although the oro-anal axis may, in fact, diverge widely from the antero-posterior direction taken as parallel to the cardinal axis. The various parts of the margin of the shell may thus be termed the **dorsal, anterior, ventral,** and **posterior margins**, the dorsal margin in many forms consisting of two parts, the **anterodorsal margin** anterior to the beaks (see below) and the **posterodorsal margin** posterior to them (Fig. 39-42). The two valves lie on left and right sides of the body and are therefore termed the **left valve** and the **right valve** respectively. In most bivalves these are of equal size, and in some although not in all respects mirror images of one another; but in some forms they are unequal. Usually the line of junction of the two valves (**commissure**) lies within a single plane, and in equivalve forms this coincides with the **sagittal plane** of the animal (Fig. 42).

The measurement of length and height in bivalve shells poses certain problems. Some workers would wish to define the **length** as the distance between two planes perpendicular to the cardinal and hinge axes and just touching both the anterior and posterior extremities of the shell. The **height** is measured perpendicular to the length.

Most experienced workers achieve a certain consistency in deciding on the cardinal axes of bivalves and one particularly useful aid is that this axis normally lies parallel to a line through the adductor scars of many dimyarian shells. In some forms, including many species of *Donax* and *Macoma,* the ligament is set at a noticeable angle to this imaginary axis and acts as a hinge about which the valves turn when opening and closing.

It must therefore be stressed that the axes can only be determined with certainty in genera with cardinal areas (e.g., *Arca, Gervillia, Malleus, Pinctada, Pteria, Lima, Pecten*). In dealing with other genera it is often safer, especially when measurements are made for statistical purposes, to take the maximum shell length and then the maximum height perpendicular to it. The **inflation** of bivalve shells may be defined as the distance between two planes parallel to the plane of the commissure which touch the outermost parts of the two valves. [The term thickness is not recommended for use in this connection, as it is also commonly applied to the calcareous wall of the shell.]

When describing the outline of a bivalve (i.e., as seen in lateral view), recourse is usually made to such terms as suboval, subtrigonal, suborbicular, and the like (Fig. 43). It is preferable wherever possible, however, to use terms such as mytiliform, pectiniform, and ensiform, which evoke the shapes of well-known genera. In the same way, species of *Pinna* are best described as either being wedge-shaped or ham-shaped, rather than trigonal. The geometrical terms mentioned above are mostly very imprecise and their main usefulness lies in comparisons; for instance, the statement that one species of *Dosinia* is more quadrate in outline than another is informative.

Starting with the larval shell or **prodissoconch** (p. *N*94), growth of a bivalve shell proceeds by successive increments along the margins of the two valves. The increments are broadest in a direction determined by the shape of the adult shell and are narrow close to the dorsal margin, where they converge from either end toward the prodissoconch. A valve of the latter is commonly preserved on each valve of the adult shell, forming a small, noselike angle termed the **beak** (Fig. 39), which adjoins the dorsal

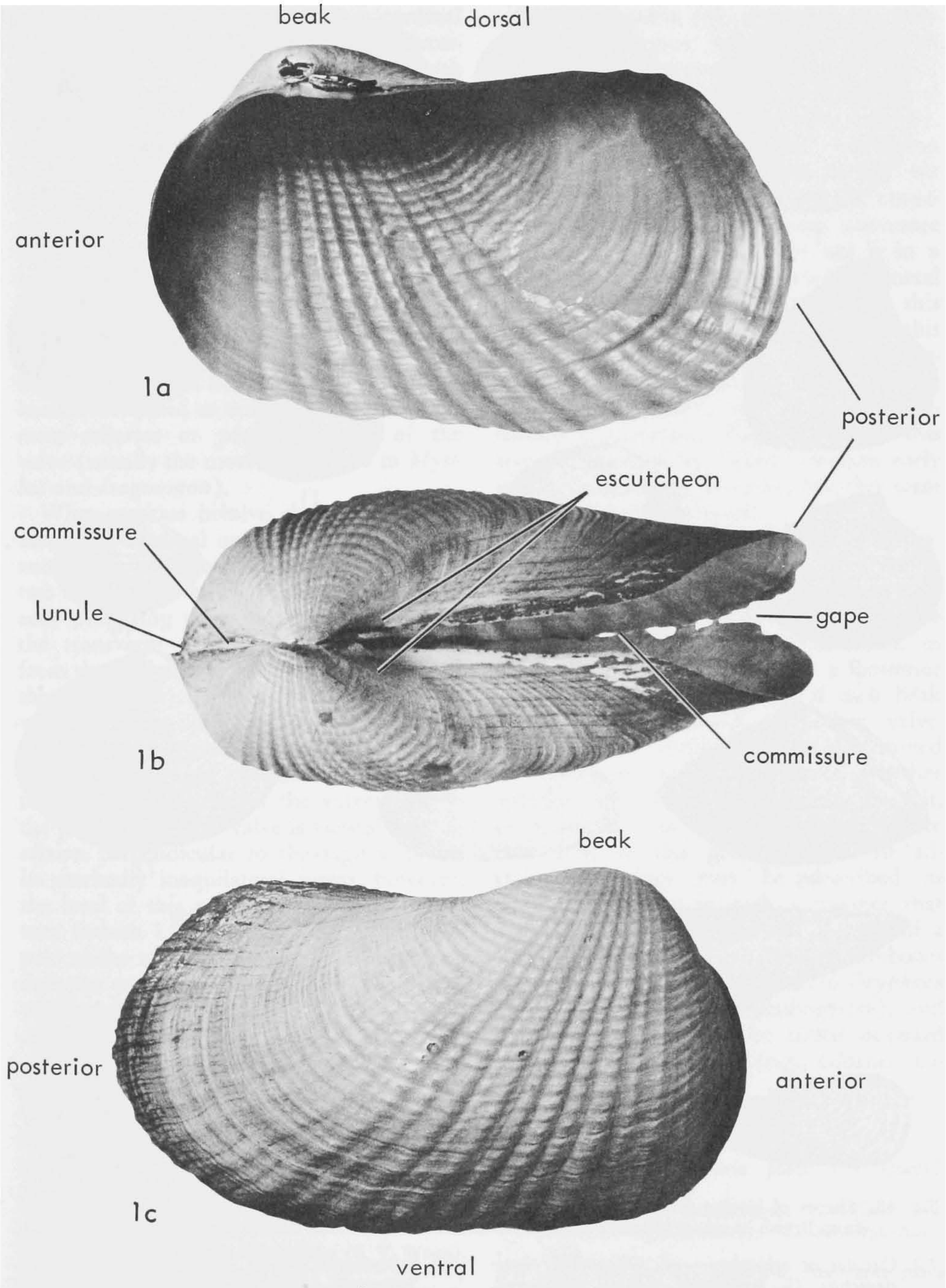

FIG. 42. Bivalve shell morphology.——*1. Pholadomya (Pholadomya) candida* G. B. SOWERBY, Recent, Caribbean, equivalve, inequilateral pholadomyid; *1a,b,* right valve interior and dorsal views of both valves; *1c,* right valve exterior; all ×0.7 (Cox, n).

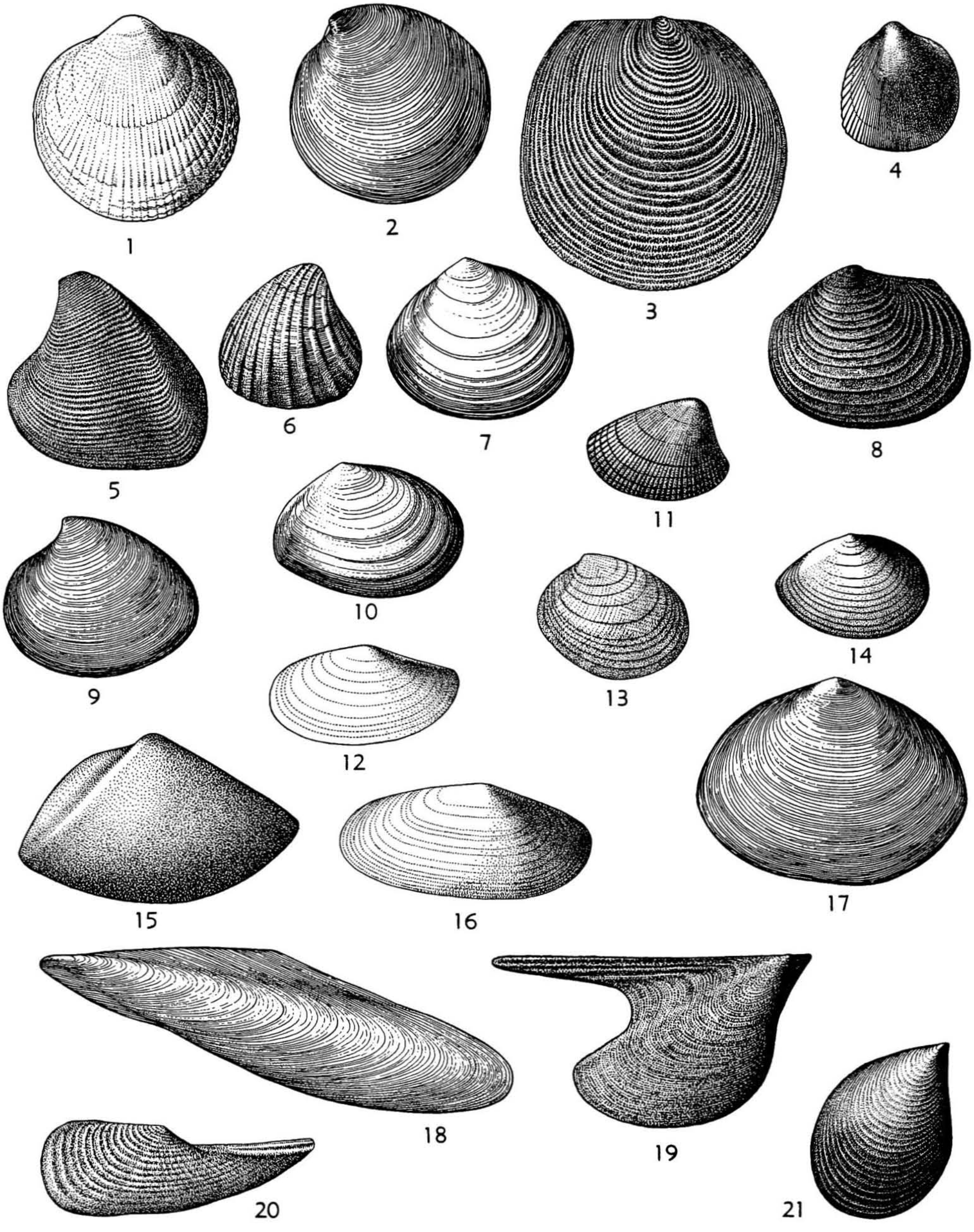

Fig. 43. Shapes of bivalve shells, illustrating terms commonly used to describe them, all ×1 except *14* (from British Museum (Natural History), *British Mesozoic Fossils, British Caenozoic Fossils*).

1,2. Circular or orbicular.——*1. Glycymeris plumstediensis* (J. Sowerby), L.Eoc., Eng.——*2. Dosinia exoleta* (Linné), Pleist.-Rec., N.Eu.

3,7. Subcircular or suborbicular.——*3. Steinmannia bronni* (Zieten), L.Jur.(U.Lias., Toarc.), N. Eu.——*7. Macoma obliqua* (J. Sowerby), Plio.-Pleist., Eng.

4,8. Subquadrate.——*4. Nemocardium nitens* (J. Sowerby), L.Eoc., Eng.——*8. Lucina concinna* (Damon), U.Jur.(Kimmeridg.), Eng.

5,6. Trigonal.——*5. Opis trigonalis* (J. de C. Sowerby), Jur.(U.Lias.-Bajoc.), Eng.——*6. Cardita deltoidea* (J. Sowerby), L.Oligo., Eng.

9. Trigonally suboval. *Astarte semisulcata* (Leach), Pleist., Eng., Rec., Arctic.

margin in most forms lacking a cardinal area (p. *N*103). Indications of the successive increments are preserved as growth lines on the surface of the shell. If, in the adult shell, the beak occupies a position close to the middle of the length, the shell is described as **equilateral** (Fig. 41), but if the beak lies closer to one end or the other the shell is described as **inequilateral** (Fig. 42). In the great majority of bivalves the beak lies anterior to mid-length, but in some genera the reverse is true. Its position is best described by citing the ratio between its distance from the anterior end of the shell and the total length of the latter. The beak is described as **terminal** if it forms the most anterior or posterior point of the valve (usually the most anterior, as in *Mytilus* and *Isognomon*).

When various bivalve shells are viewed along the cardinal axis from beyond their anterior or posterior end, it is seen that the two beaks only rarely form the most dorsally projecting parts of the shell. Usually the transverse profile of each valve rises from them to a point termed the **summit** of the valve before curving round towards the ventral margin. In more or less equilateral forms the summit usually coincides with the point of maximum curvature of the longitudinal dorsal profile of the valve; that is, the profile when the valve is viewed in a direction perpendicular to the sagittal plane. In markedly inequilateral forms, however, the level of this point of maximum curvature (which I propose to call the **umbonal pole** of the valve) lies nearer the beak than does the summit and occupies a less dorsal position than the latter.[1]

The term **umbo** (pl., **umbones**) has been used by different workers in different senses. As understood by MURRAY (1771) in his explanation of the terminology of LINNÉ, it is the point of the valve most distant from the sagittal plane. For many authors it is synonymous with "beak," for others with "summit" or else with the abovementioned point of maximum curvature (umbonal pole), while others use it in a rather indefinite sense to denote the general region of the valve which surrounds this point and extends to the beak. It is in this last sense that I recommend its employment, although in parts of the present *Treatise* it is probably used with a more restricted connotation. The umbones in this sense were called the *"nates"* by some early workers, including MURRAY, but this term has now been abandoned.

The **umbonal cavity** is the part of the interior of the valve that lies within the umbo. The umbones are described as **prosogyrate** if they curve in such a manner that the beaks point in an anterior direction, as **opisthogyrate** if they point in a posterior direction, and as **orthogyrate** if each beak points directly toward the other valve. Usually these conditions are determined by the position of the beaks, whether anterior to mid-length, posterior to it, or more or less median, but there are exceptions to this generalization. In addition, umbones may be described as **coiled** if incurved in such a manner that their transverse outline forms a spiral of a complete whorl or more. Coiled umbones are commonly prosogyrate (but in *Gryphaea* and *Exogyra* they are opisthogyrate), and in addition, they may be coiled outward from the sagittal plane (e.g., *Glossus, Di-*

FIG. 43. *(Continued from facing page).*

10. Suboval. *Macoma calcarea* (GMELIN), Pleist., Eng., Rec., Arctic.

11. Subtrigonal. *Nucula pectinata* J. SOWERBY, L.Cret.(Alb.), Eng.

12. Subelliptical. *Yoldia oblongoides* (S. V. WOOD), Pleist., Eng.

13,14. Oval.——*13. Acila cobboldiae* (J. SOWERBY), Pleist., Eng.——*14. Abra splendens* (J. DE C. SOWERBY), L.Eoc., Eng., ×3.

15. Donaciform or rhomboidal. *Tancredia donaciformis* LYCETT, Jur.(Toarc.-Bajoc.), Eng.

16. Elongate elliptical. *Gari edwardsi* (MORRIS), L.Eoc., Eng.

17. Elliptical. *Scrobicularia plana* (DA COSTA), Pleist.-Rec., N.Eu.

18. Lanceolate or modioliform. *Gervillella sublanceolata* (D'ORBIGNY), L.Cret.(Apt.-Alb.), N.Eu.

19. Alate (bialate) or pteriiform. *Pteroperna plana* MORRIS & LYCETT, M.Jur.(Bajoc.), Eng.

20. Rostrate or nuculaniform. *Cercomya undulata* (J. DE C. SOWERBY), Jur.(Bajoc.-Oxford.), Eng.

21. Mytiliform. *Inoceramus (Pseudomytiloides) dubius* J. DE C. SOWERBY, Jur.(U.Lias., Toarc.), Eng. (Nuttall, n).

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[1] In *Glossus* it actually faces ventralward.

ceras), in which case the term **spirogyrate** has been applied to them.

In many shells one or more ridges or carinae originate at the beaks. Most commonly such a ridge passes over the umbo on the posterior side of the umbonal pole and runs diagonally across the surface of the valve to (or toward) an angle in the outline of the latter which may be considered to separate the ventral from the posterior margin. This ridge is usually termed the **posterior ridge** or **diagonal ridge** (Fig. 40), but within the Trigoniacea, in many genera of which it is very pronounced, it has been designated as the **marginal carina.** This sector of the surface of a valve, running posteroventrally from the umbo, is commonly termed the **posterior slope**, irrespective of the presence or absence of a ridge. The diagonal ridge separates two parts of the surface of the valve which in some genera (most Trigoniacea, *Protocardia,* etc.) have a different type of ornamentation. The part posterior to the ridge is known as the **corselet** (or merely as the **area** in the Trigoniacea), while the median part, extending anteriorly from the ridge to an undefined limit, is known as the **flank** (Fig. 40,*2*). A broad radial depression (or **sulcus**) of the flank may lie on the anterior side of the diagonal ridge (e.g., some Trigoniacea, *Crassatella*). In some genera one or more radial sulci are present even when no diagonal ridge is developed.

In many bivalves, notably Veneridae and Lucinidae, a heart-shaped morphologically differentiated area occurs anterior to the umbones. This is termed the *lunule*[1] (Fig. 40, 42). The lunule corresponds to the track (on the outside of the shell) of growing anterodorsal hinge structures. An analogous structurally differentiated area behind the umbones is termed the **escutcheon** (Fig. 40, 42). The escutcheon sometimes is itself bounded by a ridge known as the **escutcheon ridge.** It may also fall within the further differentiated posterior area termed the corselet. The corselet may be bordered by the posterior ridge (or carina) or alternatively be circumscribed by a groove as in the Lucinidae. Both the lunule and the escutcheon are composed of the same shell layer as the dentition.

The ligament, the elastic structure by which the two valves are joined dorsally, is described in later sections of this introduction, but allusion may here be made to external features of the calcareous part of certain shells which are associated with it. The **nymphae** or **nymphs** are narrow lunate platforms (one in each valve) which in many bivalves extend from the beaks along part of the posterodorsal margin, lying at the bottom of the escutcheon when one is present (Fig. 40,*1*). Each has a more or less flattened side facing toward the opposite valve and a deep groove separating it from the posterodorsal margin. They serve for the attachment of the ligament, and when this has been removed they are just visible in dorsal view of the shell. The elongate space, with the nymphs inside, left on removal of the ligament is termed the **ligament suture.** In many Pteriomorphia the dorsal margin in both valves, or only in one, forms the base of a flat or slightly concave, commonly triangular area (**cardinal area**) which makes a well-marked angle with the plane of the commissure (Fig. 44). As the result of the presence of this area the two beaks are well separated. It may bear a single triangular transverse depression, a series of transverse depressions, chevron-like grooves, or longitudinal grooves, the relations of which to the ligament are explained later (p. *N*60-*N*62).

The Pectinacea, Pteriacea and, to a less marked extent, the Limacea, comprise shells in which part of the straight hinge margin lying on either side of the beak forms the margin of a triangular, relatively compressed part of the valve known as an **auricle** or **wing** according to its length (Fig. 41). The auricles and wings may be clearly delimited from the remainder of the valve (termed **body** of valve, or, in the Pectinidae, **disc**), or their lower border may be less distinct. In most Pteriacea the beaks lie close to the anterior end of the hinge margin so that the anterior auricle is small or even obsolete; the posterior wing is elongate and acutely pointed at its tip in some species.

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[1] H. Dodge (1950, *Jour. Paleontology,* v. 24, p. 500) has called attention to the inappropriateness of the terms "escutcheon" and "lunule" and has suggested their replacement by "vallis" and "sigilla," respectively, but they are now very firmly entrenched in the literature.

When the two valves are drawn together by the adductor muscles, many bivalve shells are completely closed along all margins. In some, however, these still remain open **(gape)** in one or more places (Fig. 42). Most commonly the gape affects the posterior margins. This condition is obviously essential in species with long siphons that cannot be completely retracted, but it also exists in some forms with relatively short siphons. A gape for the extrusion of the foot **(pedal gape)** may affect the anterior or anteroventral margins, and an opening for the passage of the byssus is found in all species firmly attached by this structure. In *Arca* the **byssal gape** is commonly broad and may give rise to much irregularity of the ventral margin, while in *Mytilus* it is a narrow cleft. In the Pectinacea, Limacea, and Pteriacea the byssal opening, when present, is close to the anterior auricle. In *Chlamys* and some other Pectinacea it is present in the right valve only and lies at the base of a deep notch **(byssal notch)** below the anterior auricle (Fig. 41). In *Tridacna* a broad, almost cordate byssal gape affects the hinge margin immediately in front of the beaks. In *Anomia* a deep embayment of the margin of the right valve or even an enclosed foramen connected to the margin only by a groove serves as the byssal opening.

INTERNAL CALCAREOUS STRUCTURES OF HINGE

The hinge teeth, hinge plate, and structures serving for ligamental attachment will be discussed together, leaving the ligament to be dealt with by Dr. E. R. Trueman in an ensuing part of this introduction. The ligament, composed of elastic horny material, connects the two valves dorsally, at the same time acting as a spring tending to open them. The function of the **hinge teeth,** which lie below the actual axis (usually passing through the ligament) about which the two valves hinge, is to guide them into the exact position in which they will fit tightly together when they are closed by the adductor muscles, and to interlock so that any rotational or shearing movements

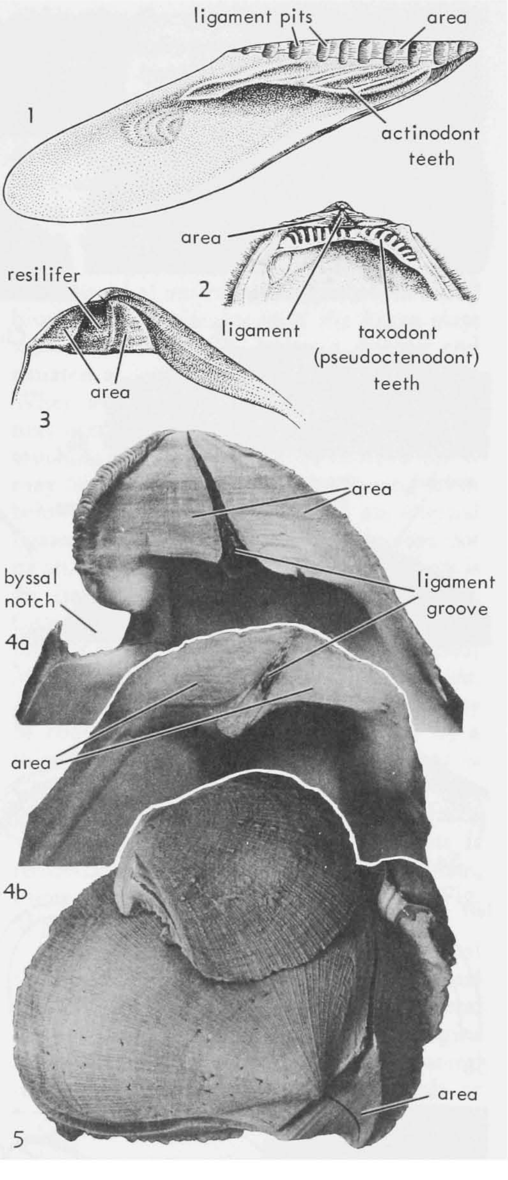

Fig. 44. General features of shells, with cardinal areas (Nuttall, n, except as stated otherwise).——*1. Gervillella sublanceolata* (d'Orbigny), L.Cret. (Apt.-Alb.), Eng., LV, ×0.3.——*2. Limopsis aurita* (Brocchi), Mio.-Rec., Eu., Medit., RV, ×2.6 (from *157a*).——*3. Plagiostoma gigantea* J. Sowerby, L. Lias., Eng., RV, ×0.5.——*4. Pedum spondyloideum* (Gmelin), Pleist.-Rec., Red Sea; *4a,* RV; *4b,* LV, ×1.3.——*5. Spondylus pacificus* Reeve, Rec., Pac., colony showing deep area on attached RV, much reduced in LV, ×1.

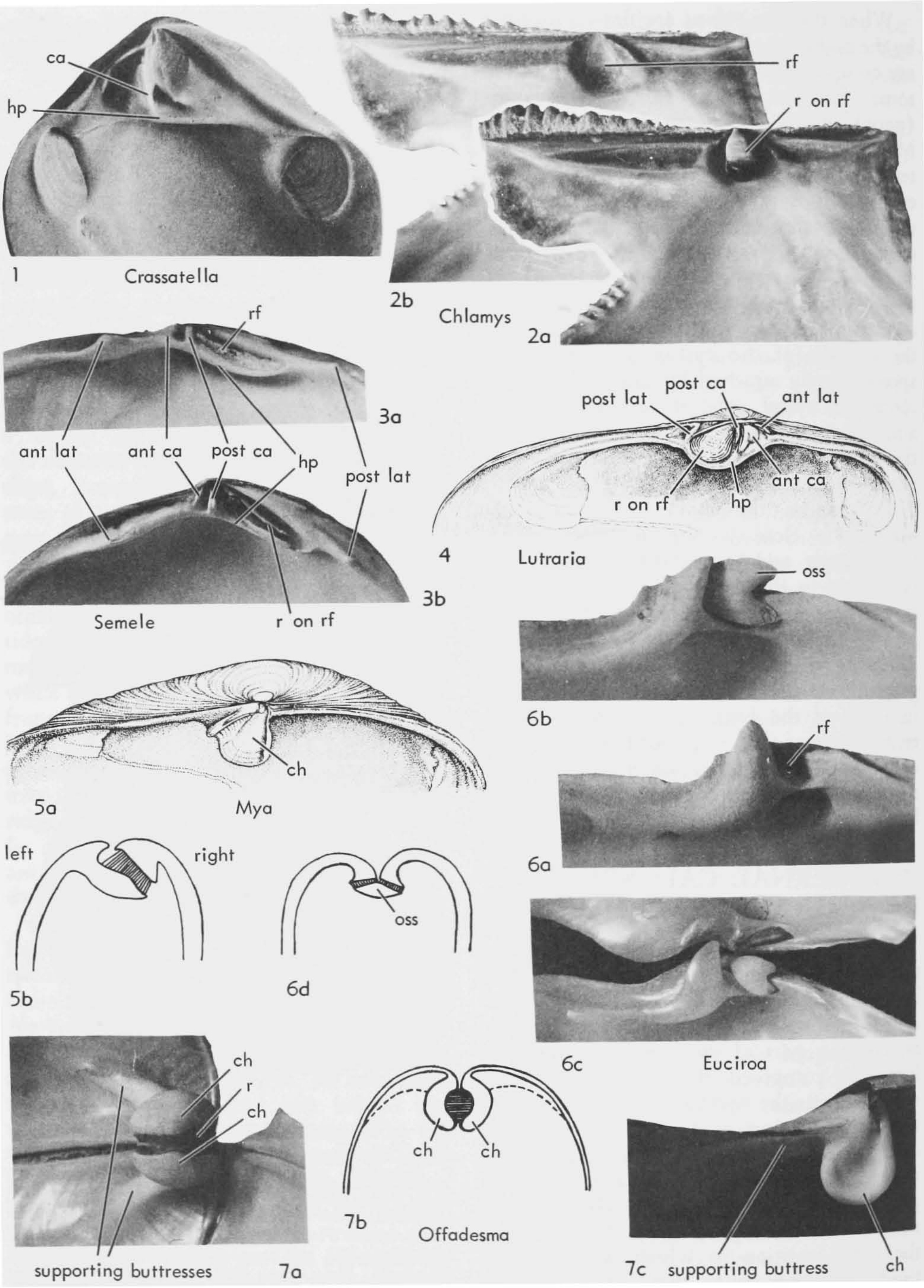

FIG. 45. Internal calcareous structures of the hinge (Nuttall, n, except as otherwise stated). Ligamental attachments.——*1*. RV of *Crassatella tumida* LAMARCK, Eoc.(Lutet.), France; resilium touching beak, ×1. ——*2*. *Chlamys* sp., Rec.; *2a*, RV showing partly calcified resilium; *2b*, after removal of resilium, ×2.——

of the valves are prevented (Fig. 45). It is clear that those bivalves, such as deep burrowers or rock-borers, that lead a relatively sheltered existence are less in need of a hinge apparatus that is thoroughly effective in performing these functions than those liable to be exposed to disturbed conditions. In *Spondylus,* which lives under such conditions, it is often impossible to separate the two valves of the shell without breaking the teeth. In most bivalves the two valves can be separated once the ligament is ruptured, some much more readily than others. It is evident from the way in which the teeth interlock that there will usually be a socket along the hinge of one valve for the reception of each tooth of the other valve, except perhaps for weak teeth which are merely projections of the dorsal margins. Thus, although a thin film of the mantle separates structures belonging to one valve from those of the other, an artificial mold of the dentition of one will reproduce the features of that of the other, apart from small details.

In the Bivalvia as a whole a great variety in the basic pattern of the structure of the hinge is observed, but in most forms striking homologies exist in arrangement of the teeth throughout any one major taxon. In addition, many show progressive changes in the dentition which can be shown to have occurred during the course of geological time. Thus the dentition constitutes the most satisfactory and practicable basis of classification within the class, while it is also an invaluable aid in evolutionary studies. Hinge teeth are found in the earliest known Bivalvia, and it seems scarcely necessary to indulge in speculations as to their origin. The suggestion that they arose from ribbing on the exterior of the shell has no supporting evidence.

In many forms some or all teeth in each valve are borne by a **hinge plate** (cardinal platform of some authors), an undercut shelly plate situated below the beak and the proximal parts of the dorsal margins and lying approximately in the plane of the valve margins (Fig. 45). The **nymph,** already mentioned (p. *N*46) as serving for attachment of an external ligament in many bivalves, is continuous with the hinge plate when this is present. It has a sloping end situated at some distance behind the beaks. When an internal ligament is present, this may occupy a depression in the hinge plate, touching the beak, as in *Crassatella,* or it may be borne by a process projecting from below the beak. DALL termed an internal ligament a **resilium** and any structure for its attachment a **resiliifer.**[1] **Chondrophore** is an alternative term for a projecting resiliifer. Commonly a spoonlike structure, this is present only in the left valve in the genus *Mya,* but in many genera (e.g., *Laternula, Periploma*) it occurs in both valves. It may be connected to the wall of the valve by a thin supporting buttress (or clavicle), as in *Laternula* and *Periploma.* In some genera, particularly in the superfamilies Pandoracea and Poromyacea, the internal ligament is reinforced by an accessory calcareous plate, known as the **lithodesma** or **ossiculum** (Fig. 45).

In many groups of the Bivalvia it is usual to refer to two categories of teeth, **cardinal teeth** lying just below the beaks and **lateral teeth** situated close to the dorsal margins at some distance from the beaks. Lateral teeth are described as **anterior laterals** or

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[1] Also known as *resilifer.*

FIG. 45. *(Continued from facing page).*

3. Semele elliptica (G. B. SOWERBY), Rec., Columbia; *3a,* RV hinge line viewed obliquely; *3b,* normal view, both showing weak external ligament and strong resilium in elongate sunken groove on hinge plate, ×1.——*4. Lutraria angustior* PHILIPPI, Rec., E.Atl. and Medit.; LV with resiliifer on prominent hinge plate, ×0.7 (from *157a*).——*5. Mya arenaria* LINNÉ, Pleist. and Rec., Arctic; N.Atl., N.Pac.; *5a,* oblique view of strong chondrophore of LV, ×0.5; *5b,* same, transverse section (from *157a*).——*6, Euciroa eburnea* (WOOD-MASON & ALCOCK), Rec., Ind.O.; *6a,b,* RVs, lithodesma or ossiculum missing and present, ×3.3; *6c,* both valves in juxtaposition, ×2.7; *6d,* transverse section.——*7. Offadesma angasi-* (CROSSE & FISCHER), Rec., N.Z., with spoon-shaped chondrophore mounted on strong posterior supporting buttress or clavicle; *7a,* both valves of broken specimen, ×2.3; *7b,* section; *7c,* LV, ×3. [Explanation: *ant,* anterior; *ca,* cardinal tooth; *ch,* chondrophore; *hp,* hinge plate; *lat,* lateral tooth; *oss,* ossiculum or lithodesma; *post,* posterior; *r,* resilium; *rf,* resiliifer.]

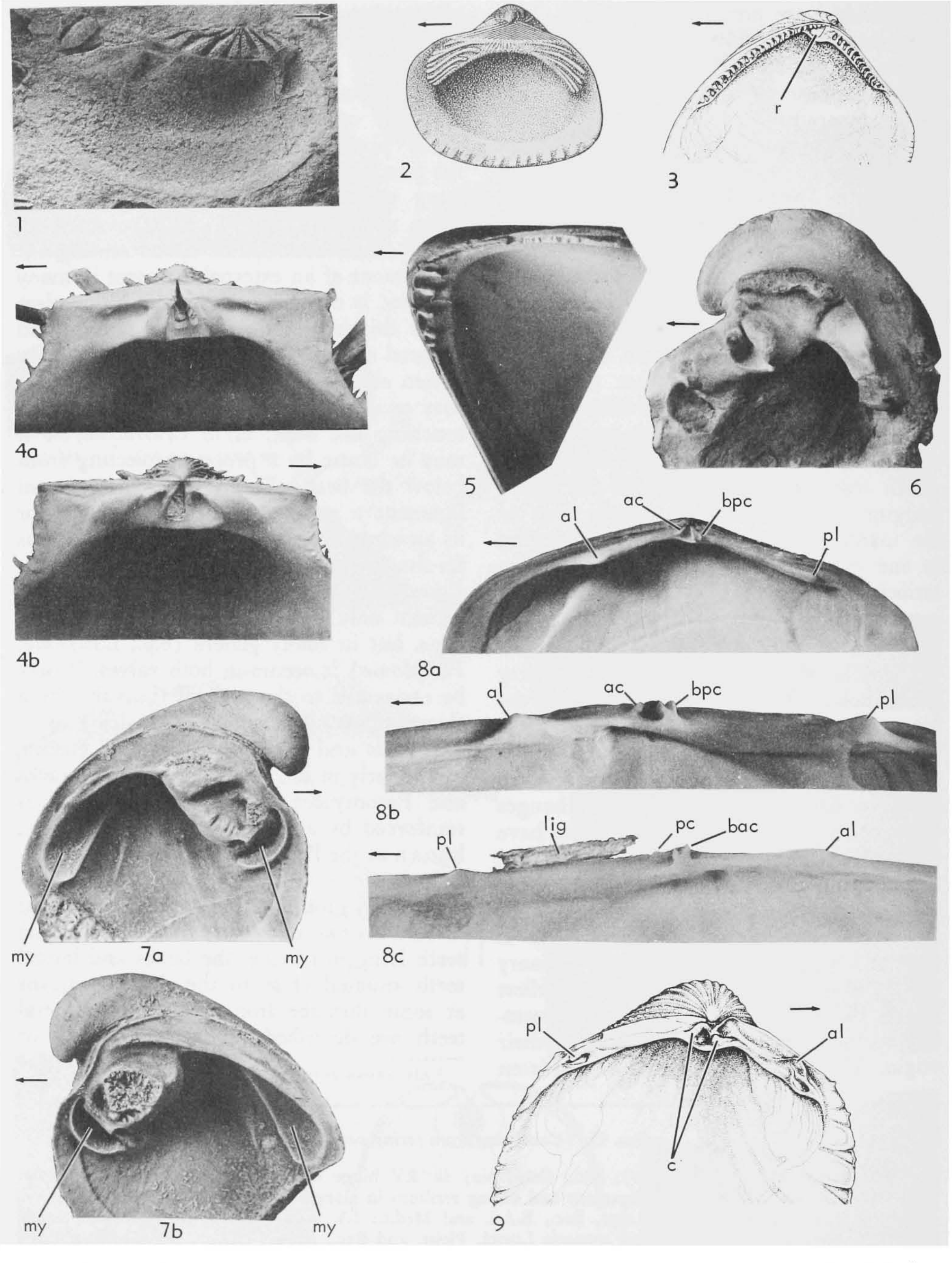

Fig. 46. Internal calcareous structures of the hinge—types of dentition (Nuttall, n, except *3* and *9,* from *157a*).——*1.* Actinodont, *Lyrodesma caelata* Salter, Ord.(Llandeil.), Eng., ×2.——*2.* Taxodont, *Cucullaea donningtonensis* (Keeping), Cret.(Neocom.-Apt.), Eng., ×0.5.——*3.* Taxodont, *Nucula turgida* Leckenby & Marshall, Rec., E.Atl.-Medit., ×3.——*4.* Isodont, *Spondylus imperialis* Chenu, Rec., China Sea; *4a,b,* ×1.——*5.* Dysodont, *Mytilus edulis* Linné, Rec., Eu.-E.N.Am.-W.N.Am.-Japan, ×3.——*6.* Pachyodont, *Pachyrisma grande* (Morris & Lycett), Jur.(Bathon.), Eng., ×0.4.——*7.* Pachyodont, *Mega-*

posterior laterals according to the end of the shell to which they are the more closely situated (Fig. 45). Cardinal teeth tend to radiate from the beaks, whereas lateral teeth commonly have a longitudinal orientation, parallel to the adjacent margin of the valve. There is some disagreement as to whether the term "lateral" should be restricted to teeth of which even the proximal end is well separated from the beaks, or if it should also refer to elongate longitudinal teeth (found, for example, in many Unionidae), although their proximal end is close to the beak. The term **pseudolateral** teeth has been applied to this latter category. Many authorities on the Unionidae apply the term **pseudocardinal** to teeth agreeing with the above definition of cardinals but differing from the cardinal teeth of other groups in their very irregular form. Cardinal teeth may be described as **prosocline or opisthocline** according to whether they slope (from their lower end) toward the anterior end of the shell or away from it, and as **orthocline** if they are almost perpendicular to the hinge axis. In view of the function of hinge teeth it is natural that their shape and development should depend to some extent on the shape of the shell within any major taxon. Thus in *Glossus,* a genus in which the umbones are placed very far forward and are strongly prosogyrous, anterior lateral teeth are absent and the much elongated cardinals are almost parallel to the dorsal margin instead of diverging radially, as in less inequilateral forms. Many such instances could be cited.

Hinge teeth are absent in some bivalves, including members of a number of families found in Paleozoic rocks; among these are the Solemyidae, which have survived to the present day. Such edentulous forms have been described as cryptodont (from the Greek κρυπτός, hidden, ὀδοντόω, to furnish with teeth). There are also edentulous (or anodont) genera belonging to families in which hinge teeth are usually well developed Examples are *Anodontia,* of the Lucinidae, and *Anodonta,* of the Unionidae. Several other terms including the letters "-odont" have been introduced in connection with hinge dentition, and it is important to distinguish their use as descriptive adjectives from those for names of taxonomic categories, in some cases with definitions extended beyond their literal meaning. In this section they are used in an adjectival sense; a number of "-odonta" names that have been proposed for major taxa are included in the list on p. *N*118.

One of the more simple types of dentition, described as **taxodont** (Greek τάξις, a single rank or line) consists of a series of short, straight or chevron-shaped teeth occupying the entire length of the dorsal margins (Fig. 44,*2;* 46,*2,3*), except that in some forms they are interrupted just below the beaks by a small triangular recess (resiliifer). Most commonly the teeth are not quite perpendicular to the hinge margin but slightly oblique, those on one side of the beak sloping inward so as to converge toward the series on the other side in a ventral direction. The taxodont type of hinge is met with very early in the geological history of the Bivalvia in representatives of the superfamily Nuculacea, but it has also arisen as a secondary development in the Arcacea. For this reason primary taxodont dentition has been described as **ctenodont** (Greek κτενίον, small comb) and the secondary type as **pseudoctenodont** (Fig. 44,*2*). An uneven series of small transverse teeth simulating taxodont teeth occurs in the nonmarine genera *Palaeomutela* of the Permian and *Pleiodon* of the present-day fauna. Such teeth have been termed **pseudotaxodont.**

Actinodont (Greek ἀκτίς, ray) dentition is another type that appeared very early in the history of the Bivalvia (Fig. 44,*1;* 46,*1*). The teeth radiate from the beak and the outer ones are more or less elongate, usually

Fig. 46. *(Continued from facing page).*

lodon cucculatus J. de C. Sowerby, Dev., Ger.; *7a,b,* ×1.3.——*8.* Heterodont, *Tellinella interrupta* (Wood), Rec., Carib.; *8a-c,* ×1.——*9.* Heterodont, *Acanthocardia echinata* (Linné), Rec., NE.Atl.-Medit., ×1. [Explanation: *ac,* anterior cardinal; *al,* anterior lateral; *bac,* bifid anterior cardinal; *bpc,* bifid posterior cardinal; *c,* cardinal teeth; *lig,* ligament; *my,* myophore; *pc,* posterior cardinal; *pl,* posterior lateral; *r,* resiliifer. Arrows indicate anterior of shell.]

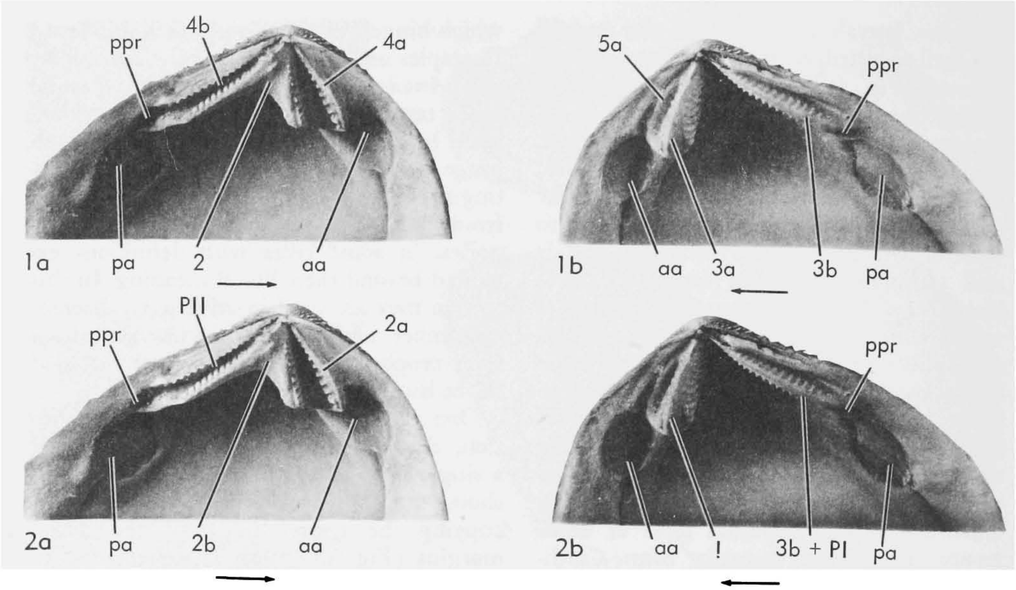

FIG. 47. *Neotrigonia margaritacea* (LAMARCK), Rec., Tasmania, ×1.3, showing notation for trigoniid dentition: *(1a,b)*, usual interpretation, and *(2c,d)* ODHNER's interpretation (mod. from Cox, 1952). [Explanation: *aa*, anterior adductor; *pa*, posterior adductor; ppr, posterior pedal retractor.]

diverging only slightly from the dorsal margin to which they are adjacent. In the lower Middle Cambrian genus *Lamellodonta* VOGEL the dentition approaches this pattern, but short subumbonal teeth are lacking, and the lamelliform teeth that are anterior and posterior to the beaks number only one or two on each side.

The term **schizodont** (Greek σχιζω, to split) has little value. It was originally applied primarily to the type of dentition found in the family Trigoniidae, in which the median tooth of the left valve, one of a small number radiating from the beaks, is broad and bifid (Fig. 47). This feature has no particular significance, as bifid teeth are found in other groups, including many heterodonts, discussed below. Forms belonging to the fresh-water superfamily Unionacea have been described as schizodont, as their dentition shows some similarity to that of the Trigoniacea, although not in this particular respect. The types of hinge found in these two superfamilies probably arose independently from the actinodont type. As already mentioned, there is no clear differentiation of the teeth into cardinals and laterals.

The **heterodont** (Greek ἕτερος, different) type of dentition was so termed because of the presence of distinctly differentiated cardinal and lateral teeth (Fig. 46,*8,9*). This condition is not, however, obvious in all bivalves to which the term is applied; in other words, use of the adjective is influenced to some extent by taxonomic considerations. The lateral teeth are obscure in many representatives of some heterodont families (e.g., Veneridae), and they are absent in other families (e.g., Thyasiridae, Psammobiidae, Solenidae, Hiatellidae). When laterals are present, they may belong to both anterior and posterior categories or only to one. Posterior laterals, when present in heterodont forms, lie entirely posterior to the ligament.

Pachyodont dentition (Greek παχυς, thick, stout) consists of heavy, blunt, amorphous teeth (Fig. 46,*6,7*). These mostly correspond to the definition of cardinals, but certain lamellar teeth present in some Megalodontidae (oldest family in which this type of dentition appears) could be termed laterals. In later groups (Diceratidae and rudists) there are two teeth in one valve and one tooth in the other. Some of these form elongate, projecting structures in many rudists, particularly the Hippuritidae and Radiolitidae, and are commonly associated with other heavy processes (**myophores**) for attachment of the "adductor" muscles (Fig. 46,7).

The typical **isodont** dentition (Greek ἴσος, equal) is that of the genera *Spondylus* and *Plicatula,* in which there are two equal teeth in each valve, placed symmetrically on either side of a triangular or rounded resilium pit and received in corresponding sockets in the other valve (Fig. 46,*4*). In the Pectinidae the hinge teeth are also symmetrically arranged with regard to the resiliifer but differ from those of the two genera just mentioned. Narrow, lamelliform teeth, one to three in number on each side and termed **cardinal crura** (sing., **crus**), radiate from the apex of the resiliifer, remaining close to the dorsal margin of each auricle. In some species of the family blunt ridges, each swelling out distally into a low tubercle, mark the lower boundary of the interior of the auricles; these ridges are termed **auricular crura.** The apparently feeble and relatively ineffective dentition found in some mytiliform shells, and consisting of small denticles situated close to the beak, is termed **dysodont** (Greek prefix δύσ, badly, ineffectively) (Fig. 46,5).

For recording the hinge structure of any species there is no satisfactory substitute for clear illustrations. Formulae which have been devised to represent hinge dentition are unsatisfactory alone, as they do not indicate the shapes and relative sizes of the various teeth, their exact positions, or the angle that each forms with the adjacent dorsal margin. It is, however, an advantage to be able to letter the teeth in an illustration according to some standard notation. The earliest attempt to represent hinge teeth by a formula was that of STEINMANN, who designated each tooth by the numeral 1 and each socket by a cipher (0). Beginning at the anterior end of the hinge it was thus possible to represent the dentition of one valve by some such formula as 101010 and that of the opposite valve by reversing the 1's and the 0's. This crude method did not enable lateral teeth to be distinguished from cardinals, nor did it take into account teeth developed merely in a rudimentary form. DALL attempted to remedy such defects by introducing separate symbols for lateral teeth, by recording rudimentary teeth (by symbols placed in parentheses), and by adding a symbol for the resiliifer, but his system was rather confusing and was never widely adopted.

A system of hinge-tooth notation devised by BERNARD and MUNIER-CHALMAS has been much more widely accepted. It was based on ontogenetic studies carried out on heterodont bivalves and enables homologies between teeth of different genera to be indicated. To explain this system it is necessary to anticipate part of the section of this introduction dealing with ontogeny. The actual larval shell has small transverse crenulations rather like taxodont teeth along its hinge line. In the immediately ensuing postlarval stages of heterodonts these primitive crenulations are replaced by lamellae parallel to the dorsal margins (Fig. 48). There are usually two of these lamellae along the anterior part of the hinge in the right valve, one belonging to the left valve fitting between them; in addition, a further lamella may be developed as a projection of the hinge margin of the left valve. Similar lamellae may or may not be developed along the posterior part of the hinge. At this early stage the ligament is internal, separating the posterior lamellae from the anterior ones; in many genera it subsequently assumes an external position, but the effects of this original separation of the dental elements remain. The posterior lamellae give rise only to posterior lateral teeth, when these are present in the adult shell, but otherwise they disappear. The anterior lamellae, however, give rise to all the cardinal teeth, as well as to the anterior laterals, when present. The lamellae are assigned roman numerals, of which *I* and *III* (also, in some forms, *V*) represent those of the right valve, while *II* and *IV* (also, in some forms, *VI*) represent those of the left valve. The numbering is from the lowest (most ventral) tooth upward.

Cardinal teeth arise by the swelling out and detachment of the proximal ends of the

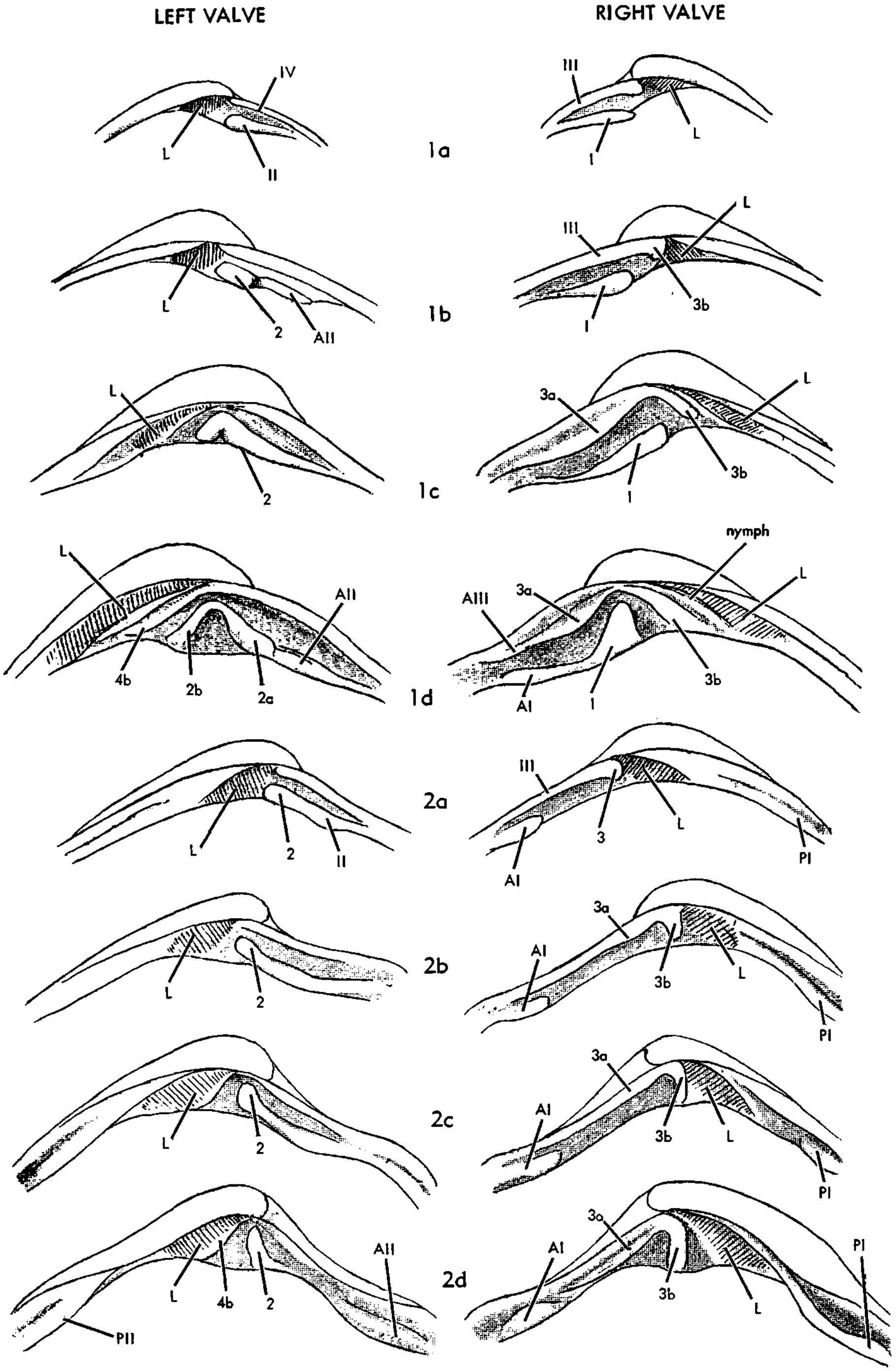

Fig. 48. Internal calcareous structures of hinge. Ontogenetic development of two species from lower Miocene of Bordeaux region, France (mod. from Bernard, 1895-97).——*1*. Corbiculoid (*ex* cyrenoid) type illustrated by *Gouldia deshayesiana* (Basterot); *1a*, at 0.4 mm.; *1b*, 0.64 mm.; *1c*, 0.96 mm.; *1d*, 1.2 mm. ——*2*. Lucinoid type illustrated by *Loripes neglecta* (Defrance); *2a*, at 0.32 mm.; *2b*, 0.48 mm.; *2c*, 0.64 mm.; *2d*, 0.96 mm. [Explanation: *L*, ligament.]

lamellae, and are designated by arabic numerals corresponding to the roman numerals of the lamellae from which they are formed. The lamella *I* is not known to give rise to more than one cardinal, which receives the number *1,* and when its distal end persists as an anterior lateral tooth, this lamella is designated as *AI*[1] (Fig. 48, 49). The remaining lamellae have the potentiality for giving rise to two cardinals each. Thus, lamella *II* in some forms bends up to the beak as the juvenile shell grows and then bends down again, producing two cardinal teeth, to the posterior (downbent) one of which Bernard assigned the number *2b* and to the anterior (upbent) one the number *2a;* but in some forms it merely bends up and gives rise to a single tooth which was designated as *2a* by Bernard, merely as *2* by many authors, and as *2b* by Douvillé.[2] The proximal end of lamella *III* bends down to give rise to one cardinal tooth, designated as *3b,* while the same end of its unbent part swells out to form a cardinal designated as *3a;* both of these teeth are usually distinguishable. The proximal end of lamella *IV* may advance beyond the beak and above tooth *2,* to bend down next to the ligament to form a posterior cardinal tooth to which the number *4b* is assigned; more rarely, the same end of its unbent part may swell out to form a marginal cardinal tooth just in front of the beak, which is given the number *4a.* Usually only *4b* is present, but according to Bernard, both *4a* and *4b* can be recognized in some species of *Corbula.* A tooth identified as *5b* is distinguishable in some species of *Astarte.* In all cases, when the primitive lamellae or their distal ends remain as lateral teeth, these receive the symbols, *AI, AII,* etc., and *PI, PII,* etc., *"A"* standing for anterior and *"P"* for posterior. The socket which receives any particular tooth is conveniently designated by the symbol for the tooth, to which is added an accent (for example, *AI'* is the socket that receives *AI*).

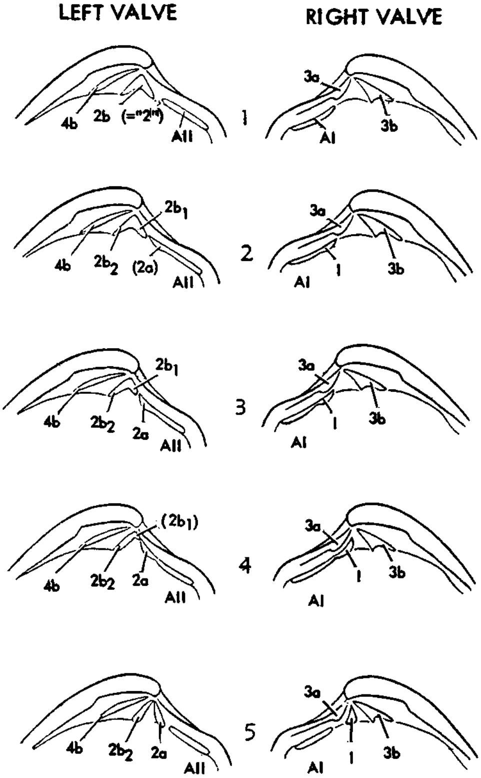

Fig. 49. Internal calcareous structures of the hinge. Generalized evolutionary changes between the Lower Jurassic and Lower Cretaceous (Lias to Neocomian) in members of the families Arcticidae and Veneridae. This shows (in LV) gradual production of *2a* as a swelling which eventually becomes separated at the rear of *AII;* simultaneously the anterior half of bifid *2b* atrophies. In RV, the median cardinal *1* can be seen separating from *AI* (Casey, 1952, fig. 1, p. 125).——*1.* Lucinoid type.——*2.* Arcticoid (*ex* cyprinoid) type.——*3.* Advanced arcticoid type.——*4.* Early corbiculoid (*ex* cyrenoid) type.——*5.* Corbiculoid type.

It follows from the above account that with the Bernard notation all teeth in a right valve have odd numbers and all teeth in a left valve even numbers; also that, in a closed heterodont shell with every theoretically possible cardinal tooth developed, a series of pairs of teeth, diverging chevron-like and numbered upward, would be

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[1] Bernard designated the lateral teeth as *LA I, LP I,* etc., but inclusion of the *"L"* makes hinge formulae unnecessarily long and might even cause confusion, as the same letter has also stood for "ligament" and for "left."

[2] This tooth commonly is bifid, however, its anterior and posterior branches being assigned the symbols $2b_1$ and $2b_2$ by Casey, who has studied evolutionary changes in hinges of Mesozoic Arcticidae and Veneridae (see Fig. 49). Casey, like Douvillé, has based his conclusions on historical rather than ontogenetic studies (such as employed by Bernard). We must note yet again that the Theory of Recapitulation cannot fully explain their different observations.

stacked upon tooth *1,* the tooth designated by the letter *a* being the anterior one of each pair and that lettered *b* the posterior one. In almost every known hinge, however, one pair or another is incomplete.

In the construction of hinge formulae it is usual to follow STEINMANN's method of arranging the symbols for the teeth of each valve in alignment, starting with the anterior end of the hinge, but the symbols are separated by spaces instead of by ciphers. The whole hinge is usually represented by placing the formulae for the two valves one above the other, separated by a line (as numerator and denominator of a fraction). The symbol for each cardinal tooth is placed above or below the space representing its socket in the other valve. If a tooth is developed only in a rudimentary form its symbol is usually placed in parentheses.

BERNARD distinguished between two main types of heterodont dentition. In the first type, which he termed the **lucinoid type** (Fig. 48,*2;* 49,*1*), usually only two cardinal teeth occur in each valve, *3a* and *3b* in the right, and *"2"* (see above) and *4b* in the left, *"2"* occupying the so-called pivotal position immediately below the beaks. The chief families with dentition of this type are the Lucinidae, Cardiidae, Carditidae, Astartidae, and Crassatellidae, and the first four of these are among the earliest heterodont families to appear in the geological record. The hinge formula for bivalves with lucinoid dentition (omitting teeth *5b* and *6b,* recognizable in a few Astartidae) is as follows:

$$\begin{array}{ccccccccccc} AI & & AIII & 3a & & 3b & & PI & & PIII & \\ \hline & AII & & & 2 & & 4b & & PII & & (PIV) \end{array}$$

(in single line this is given as *AI, AIII, 3a, 3b, PI, PIII / AII, 2, 4b, PII, (PIV).*

In the second type, which BERNARD termed the **cyrenoid type** (a name which must now presumably be emended to **corbiculoid** (Fig. 48,*1;* 49,*4,5*), there are usually three cardinal teeth in each valve, *3a, 1,* and *3b* in the right, and *2a, 2b,* and *4b* in the left, tooth *1* occupying the pivotal position below the beaks. The chief families in which this dental pattern is developed most typically are the Corbiculidae and Veneridae, and the hinge-formula reads as follows:

$$\begin{array}{ccccccccccccc} AI & & AIII & 3a & & 1 & & 3b & & PI & & PIII & \\ \hline & AII & & & 2a & & 2b & & 4b & & PII & & (PIV) \end{array}$$

or *AI, AIII, 3a, 1, 3b, PI, PIII/AII, 2a, 2b, 4b, PII (PIV).*

The **arcticoid** ("cyprinoid") (Fig. 49,*2,3*) type of dentition, introduced by CASEY, is more or less intermediate between the two just described. Tooth *1* is present at the posterior end of the anterior lateral *AI* and has not advanced to a pivotal position below the beak; *3b* is conspicuously bifid. Tooth *2b* is bifid in some but not in all forms, while *2a,* if distinguishable at all, is present only as a tubercle at the proximal end of *AII.* The hinge formula of a representative of the Arcticidae would thus read:

$$\begin{array}{cccccccccccccc} AI & & AIII & 3a & & (1) & & 3b & & (5b) & PI & & (PIII) & \\ \hline & AII & & & (2a) & & 2b & & 4b & & & PII & & (PIV) \end{array}$$

or *AI, AIII, 3a, (1), 3b, (5b), PI, (PIII) / AII, (2a), 2b, 4b, PII, (PIV).*

Attempts have been made by DOUVILLÉ and others to apply the BERNARD notation to several nonheterodont groups, in none of which has the early ontogeny of the shell been investigated adequately. It would certainly be useful to have an acceptable symbol for each hinge tooth in genera belonging to these groups, but not if this implies homologies which have not been proved to exist. Thus, four entirely different Bernardian hinge formulae have been suggested for the Trigoniacea (two shown in Fig. 47), three assuming that homologues of lateral teeth are present, the fourth that there are only cardinal teeth. DOUVILLÉ also considered that the two teeth in the rudist left valve were homologues of the laterals *AII* and *PII* (later reidentified as *AII* and *PIV*), whereas the single tooth in the right valve should be designated as *3b* (later *3*). The present *Treatise* designated the three teeth in question merely as *1, 3* and *2* respectively. DOUVILLÉ's application of cardinal hinge teeth notation to the Unionidae, (e.g., *5a, 3a, 3b/4a, 2a, 2b, 4b,* has not met with general acceptance. [See Addendum (p. *N*908) for more on bivalve dental notation.]

TRANSPOSED HINGES

There are many recorded cases where certain hinge teeth of the two valves are transposed, those present in one valve corresponding in number and positions to those usually found in the other (Fig. 50). Such occurrences resemble sinistrality in gastropods in that they may constitute individual abnormalities in particular species, while in certain cases they have been considered to have greater taxonomic significance. There appears to be a particular tendency for abnormal transposition to occur in certain families, notably the Astartidae, Crassatellidae, and Unionidae. An investigation carried out by POPENOE & FINDLAY (1933) showed that in *Astarte* one specimen in 130 exhibited this phenomenon and in *Cardita* one specimen in 180, and these authors quote a statement by DALL that in one lot of *Goodallia* examined nearly one-third had the hinge reversed. They also found that transposition did not affect the complete hinge (that is, posterior laterals, cardinals, and anterior laterals) in any of the species studied. In some specimens the cardinals and anterior laterals were transposed while the posterior laterals were developed normally in the respective valves; in other specimens it was only the posterior laterals that were transposed. On the other hand, EGGLETON & DAVIS have recorded that in a living population of the freshwater genus *Sphaerium* there was a transposition rate of 12.1 percent, and of the transposed specimens 40.5 percent had the posterior laterals only reversed, 41.0 percent the anterior laterals and cardinals, and the remainder (18.5 percent) all the teeth. NEWELL found that all the teeth were transposed in a Permian specimen of *Permophorus albequus* (BEEDE), probably the geologically oldest shell in which the phenomenon has been observed.

The case of the Chamidae, a family in which one valve is cemented to the substrate, has attracted considerable attention because transposition of the hinge teeth goes hand-in-hand with reversal of the valve of fixation. The fixed valve invariably has two teeth and the free valve one tooth. The so-called "normal" condition is when fixation is by the left valve and the "inverse" condition when it is by the right valve; the two valves can be distinguished readily because the umbones are strongly prosogyrous in all specimens. ODHNER considered that "normal" and "inverse" specimens should be referred to different genera, *Chama* and *Pseudochama,* but not all authorities are in agreement with this conclusion, some believing that both types of shell could even belong to a single species.

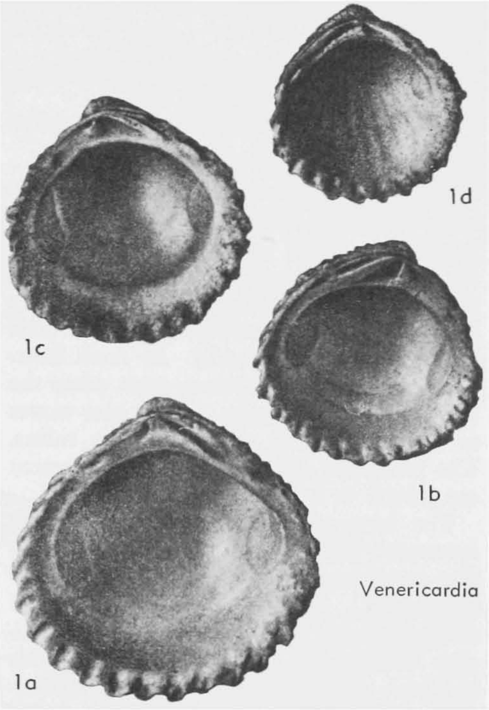

FIG. 50. Bivalve shells with transposed hinges.——*1. Venericardia parva* LEA, Eocene (Claiborne), Alabama; *1a,b,* normal right and left valves, ×14; *1c,d,* right and left valves having transposed cardinal and anterior lateral teeth, ×15 *(136).*

Some discussion has arisen as to how BERNARD's notation should be applied to specimens with transposed hinge teeth. While some authors have advocated interchanging the symbols between the two valves, others have maintained that the apparent transposition could have resulted from the suppression or accentuation of tooth elements belonging properly to the valves in which they are found so that symbols appropriate to that valve should be used. It seems advisable to refrain from applying any notation to transposed hinges, particularly as no observations have been made on the ontogeny of shells in which they occur.

LIGAMENT

By E. R. Trueman

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The shell in the Bivalvia consists characteristically of two lateral calcified valves joined by a horny ligament; being parts of the same structure, these are all formed in the same manner. The term **ligament** may be used to describe all parts of the shell joining the valves dorsally. Its main function is to cause the valves to open when the adductor muscles relax, and it also serves to unite the dorsal margins of the valves. The form and composition of the ligament are related to both of these functions.

The form of the ligament, which with reasonable probability represents the primitive condition, is termed the **primary ligament** *(127)*. Such a ligament consists of the superficial periostracum and the lamellar and fibrous layers (Fig. 51,*A*). This ligament somewhat resembles that of *Limopsis*. It is secreted respectively by the inner surface of the outer mantle fold (formerly termed the periostracal groove), the outer surface of the same fold, and a specialized region of the general outer surface of the mantle, the mantle isthmus. The primary ligament represents the basis of the ligament throughout the Bivalvia except where it is largely or completely lost, as in the Pholadacea.

Previous authors *(34, 76, 127)* have used different nomenclature in describing the principal layers of the ligament. For instance, the lamellar layer corresponds to the outer layer or to what Dall considered the ligament proper, while the fibrous layer has been variously referred to as the inner layer, cartilage, or resilium. But the terms **lamellar** and **fibrous layers**, first used by Newell *(113)*, are probably those most generally acceptable. The terms outer and inner layer are certainly confusing when used in combination with the terms internal or external to describe the location of the ligament on the valves. In the ligament of *Ostrea*, for example, both layers are situated internally, whereas in the Semelidae *(167)* the ligament is in two parts, along the valve margins and between the valves, and both parts contain lamellar and fibrous layers. The structure of these layers is generally quite distinct. The lamellar layer consists of nearly parallel lamellae of protein which lie parallel to the growth surface of the layer when they are being secreted but subsequently may lie obliquely (Fig. 51,*B*,*C*). This layer is characteristically dark brown in color and has undergone hardening by aromatic tanning. The fibrous layer shows growth lines, which may correspond to the laminations of the lamellar layer, so that both structures may be considered to represent phases of secretory activity of the mantle epithelium. The fibrous layer also shows a fibrous structure in which the long axis of each fiber is normal to the growth surface at the point of its secretion (Fig. 51). The horny organic material of the ligament, termed **conchiolin**, largely consists of protein material. In the periostracum and outer layers the conchiolin is hardened by quinone tanning and is not calcified, whereas the inner layer is calcified, though to a less extent than the inner layer of the valves (a notable exception to this being observed in the Pectinidae, where the main part of the inner layer is not calcified but is extensively tanned *(166)*.

The primary ligament appears to persist unmodified in some genera (e.g., *Monia*, Anomiidae; *Lima, 195,* Fig. 51,*A*), but usually some degree of secondary extension is provided at either end of the ligament or at both ends. The secondary ligament may consist of either periostracum (e.g., *Entodesma, Mytilimeria, 191,* and *Mytilus, 195,* Fig. 51,*B*), or of a fourth layer of the ligament, the **fusion layer** (e.g., in *Pinna, 192; Glossus (Isocardia), 123,* and *Tellina, 164,* Fig. 51,*C*). The fusion layer is secreted by the outer surface of the outer folds of the mantle edge after they have become fused in early postlarval life, and its appearance is somewhat intermediate between the periostracum and the lamellar layer. It generally plays only a minor role in the mechanical operation of the ligament, functioning simply as a union or cover between the dorsal margins of the valves as in *Pinna (192)*. In *Tellina (164)* this layer forms a

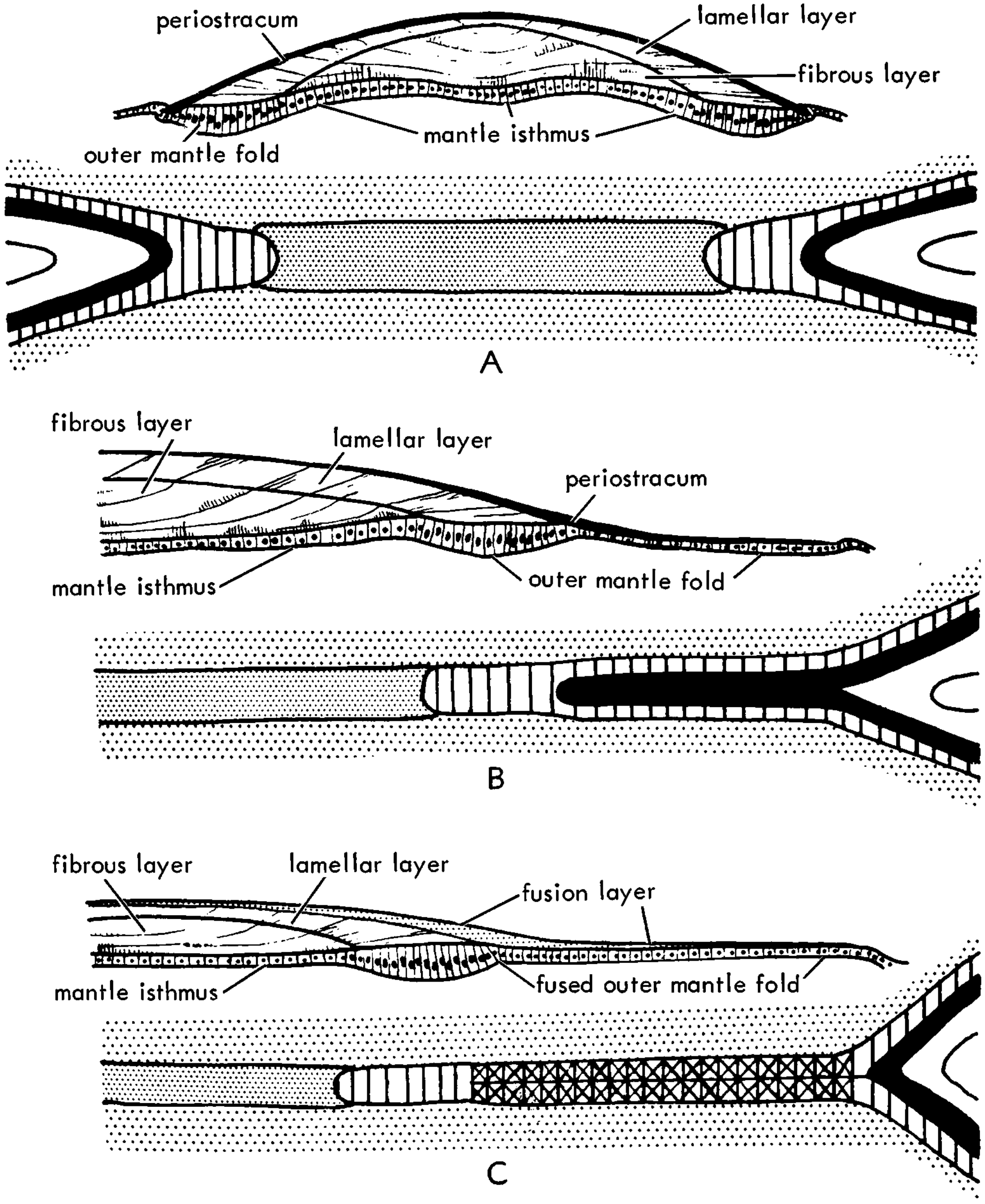

FIG. 51. Bivalve ligaments (diagrammatic) (Trueman, n).——*A*. Primary ligament.——*B*. Primary ligament with periostracal secondary extension (e.g., *Mytilus*).——*C*. Primary ligament with secondary extension produced by fusion layer (e.g., *Tellina*). [Explanation: Upper diagram of each pair represents median longitudinal section of ligament and lower diagram shows dorsal aspect of mantle tissues involved in its secretion. *Coarse stipple*, general outer surface of mantle secreting fibrous layer of valves; *fine stipple*, mantle isthmus secreting fibrous layer of ligament; *vertical rules*, outer surface of outer mantle fold secreting outer calcareous layer of valve and lamellar layer of ligament; *black*, inner surface of outer mantle fold secreting periostracum; *cross hatching*, fused outer mantle folds secreting fusion layer.]

relatively long posterior extension of the primary ligament and has been described as the posterior cover. The anterior cover appears to be formed by the anterior lamellar layer in this genus, but in the Solenidae the fusion layer extends both in front of and behind the primary ligament *(125)*. Discrimination between periostracum and the fusion layer depends on the degree of fusion of the mantle folds and the extent of the pallial muscles has been used to distingush between them *(124)*. Where the outer surfaces of the outer folds of the mantle are fused, leading to secretion of the fusion layer, pallial attachment is lost. Pallial muscle attachment is retained where the valves are joined by periostracum.

The ligament is formed in a characteristic manner in each group of bivalves, being situated either between the cardinal areas of the valves, as in *Ostrea* and *Mya,* or conspicuously along the valve margins, as in *Tellina* and *Cardium*. The ligament may be either elongated or condensed, with primary and secondary constituents variously developed. No general description will cover all cases but the terms **amphidetic** and **opisthodetic** *(112)* may be usefully employed to express the relation of the mantle isthmus to the umbones. Thus a symmetrical condition of the mantle isthmus between the umbones gives an amphidetic ligament, as in *Glycymeris* and *Pecten*. In an opisthodetic ligament, the mantle isthmus is mainly posterior to the umbones, as in *Mytilus* and *Tellina*. The terms **alivincular** and **parivincular** are used to describe the form of the ligament *(34),* an alivincular ligament being a flattened structure situated between the cardinal areas of the valves with the lamellar layer both anterior and posterior to the fibrous layer, as in *Ostrea (165)* (Fig. 52,*A*). The parivincular ligament is usually conspicuous along the posterior margins of the valves and is cylindrical in shape, as in *Tellina (164)* (Fig. 52,*D*). It has probably evolved from an opisthodetic ligament situated between the valve margins, as in *Mytilus* or *Pinna* (52,*C*).

During growth of the bivalve shell the ligament elongates, and it is functionally essential that a straight longitudinal hinge axis be maintained. To lengthen a straight line on the border of a rounded body, either the axis of the ligament must descend or the outline of the body must be elongated. The method of growth of the postlarval ligament of most bivalves falls into these two broad categories. In some the hinge axis elongates largely by ventral growth of the ligament, as in *Ostrea (165)*. The early (and dorsal) part of these ligaments commonly becomes worn away and the inner layer exposed, replacement taking place by addition to the ventral surface, as most markedly occurs in *Hinnites*. This appears to be a modification associated with attachment by cementation, as has also been described for *Etheria (196)*. Indeed, alivincular ligaments of the general form of that of *Ostrea* commonly occur in cemented genera such as *Spondylus*. The ratio between anterior-posterior length and the dorsoventral thickness is usually of the order of not more than 3 or 4 : 1. Other bivalves, as in *Mytilus,* show extension of the dorsal valve margin, and the axis of the ligament exhibits little ventral migration but considerable posterior extension to form an opisthodetic ligament. For opisthodetic ligaments the length to thickness ratio is rarely less than 10 : 1.

The alivincular ligament may be oriented more or less symmetrically about the umbones (amphidetic), as in *Ostrea, Spondylus,* and *Limopsis* (Fig. 52,*A*), but in some genera, for example *Pteria* (Fig. 52,*B*), it is inclined from the umbones into a condition which appears to be somewhat intermediate between amphidetic and opisthodetic ligaments (Table 1). During growth an alivincular ligament becomes fractured dorsally, being replaced by ventral secretion *(165),* while the cardinal area of an opisthodetic ligament is similarly changed because of the tangential growth of the valves. In the latter, replacement takes place by posterior growth of the anterior lamellar layer (Fig. 52,*D*), which occurs very markedly in *Glossus (123)*.

The principal exceptions to the above classification of the ligament are the **multivincular** and **duplivincular** ligaments. The multivincular ligament found in *Isognomon (76, 113, 114, 169),* for example, develops from an alivincular ligament by the addition posteriorly of successive areas of fibrous layers **(resilia)**, which are completely isolated from each other by the lamellar layers (Fig. 52,*F*). The ligament of young *Isognomon* resembles that of *Pteria* (Fig. 52,*B*) *(76)*. The production of these successive resilia can only take place by the development of successive areas of

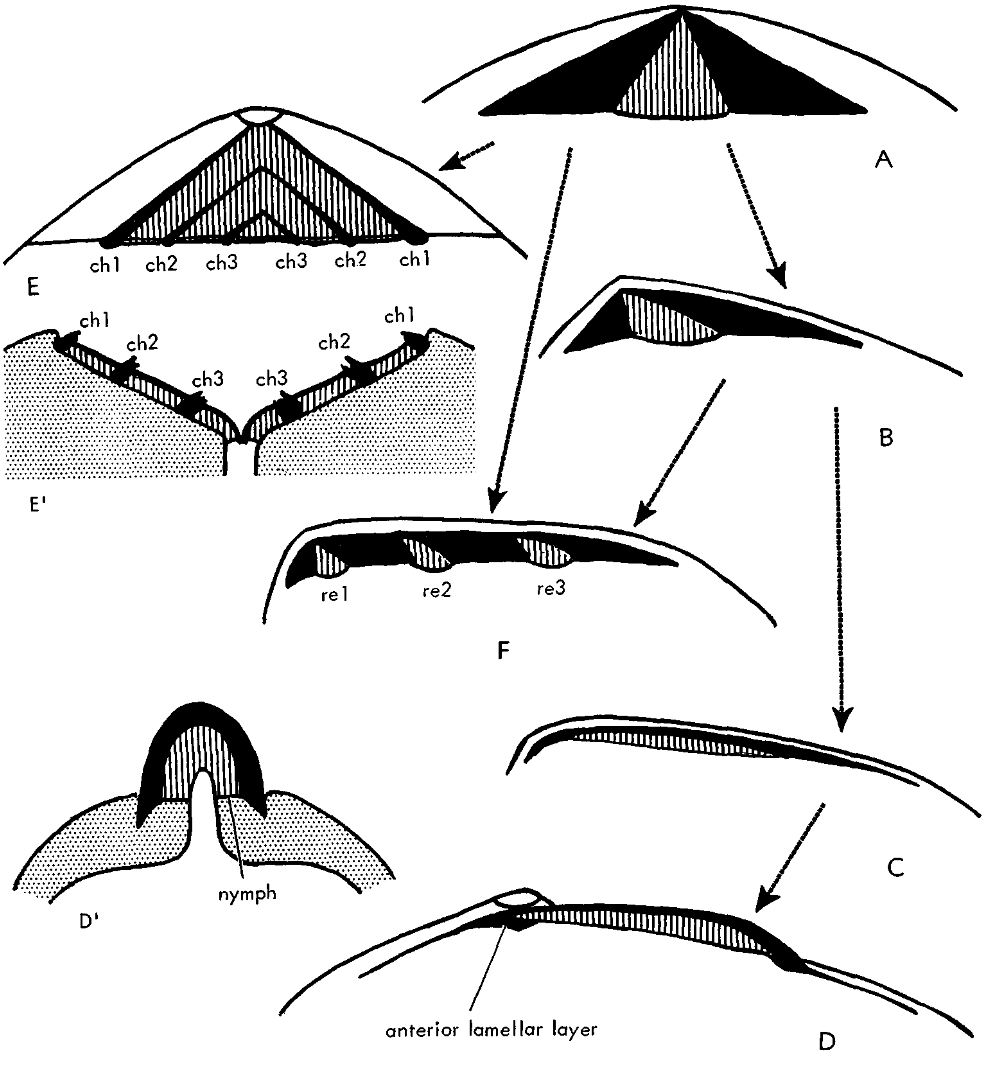

FIG. 52. Bivalve ligaments, diagrammatic sections showing location of ligament in relation to right valve (Trueman, n).——*A*. Alivincular amphidetic ligament comparable to primary ligament (e.g., *Limopsis*).——*B*. Alivincular ligament intermediate in form between amphidetic and opisthodetic.——*C*. Opisthodetic ligament placed directly between valve margins (e.g., *Mytilus*) (=*tr.*, Table I).——*D*. Opisthodetic parivincular ligament (e.g., *Cardium*) showing anterior lamellar layer with posterior growth below ligament in cardinal area, accompanying transverse section *(D')* showing C-spring shape of ligament and nymph.——*E*. Duplivincular ligament (e.g., *Arca*) with true lamellar layer *(ch1)* comparable to that of primary ligament and similar successive chevrons *(ch2, ch3)* shown in longitudinal *(E)* and transverse *(E')* sections.——*F*. Multivincular ligament (e.g., *Isognomon*) showing first-formed fibrous layer *(re1)* and successive resilia *(re2, re3)*. [Explanation: *Black*, lamellar and fusion layers of ligament; *vertical rules*, fibrous layer of ligament; *stippled pattern*, calcareous shell of valves in section. Arrows indicate inferred possible evolutionary relationships between different ligament types.]

secondary mantle isthmus epithelium *(169)*. The duplivincular ligament *(114)*, found, for example, in *Arca,* has bands of lamellar layer on the cardinal area of the valves, giving the appearance of a series of chevrons (Fig. 52,*E*). The ligament is amphidetic and new chevrons usually occur centrally and grow centrifugally. The fibrous layer runs continuously from end to end of the ligament, but it is usually partially (as in *Glycymeris*) or completely (as in *Arca noae*) divided into two lateral halves. It has been suggested *(126)* that the mantle in many of the Arcoida has divided, during ontogeny, into two lobes in the region of the mantle isthmus. Considerable interumbonal growth of the valves takes place in the cardinal area, and, as the umbones move apart in ontogeny, so, also, does the earliest formed ligament, producing a chevron effect. In its earliest ontogenetic stages this ligament is not unlike the primary ligament and, indeed, in the Limopsidae this condition persists.

The insertion of the ligament into the valves generally exhibits an arrangement characteristic of the form of the ligament, and it is often possible to infer the nature of the ligament from the valves even in Paleozoic shells. Many of these have ligament areas similar to those of modern shells *(76)*.

Table 1 shows the structure of the ligament in representative genera and indicates the form of attachment of the ligament, particularly the fibrous layer, to the valves. Distinction usually can be made between the chevron pattern of the duplivincular ligament and the insertion of the fibrous layer in a resiliifer or along the thickened margins of the valve (nymphs).

It is difficult to utilize the ligament as a factor of importance in classification of the Bivalvia because of its adaptive characters. It is notable that the form of the larval ligament shows little variation throughout the group and resembles the primary ligament. Differentiation takes place immediately following settlement, being closely related to the change in habitat and the increase in shape and size of the valves. The development of diverse forms of adult ligaments from a fundamentally similar larval ligament is largely dependent on the growth pattern of the mantle and shell complex, and the effect on this of selective processes.

However, Table 1 does show something of the phylogenetic distribution of the ligament. In the Palaeoheterodonta and Heterodonta opisthodetic and parivincular ligaments with a well-developed fusion layer commonly occur. The most obvious exceptions to this are clearly adaptive modifications, such as in *Mya* or *Lutraria* to deep burrowing *(171)*, the Pholadidae to rock-boring, and *Etheria* to cemented attachment *(196)*. The parivincular ligament, in the form of a C spring, reaches its maximum development in genera such as *Arctica, Cardium,* and *Tellina,* but, even so, in the Semelidae and Scrobiculariidae, closely related to the last genus, there is also an internal or cardinal ligament which functions as the only part of the ligament under compression when the valves are closed *(167)*. The parivincular ligament has probably evolved to its present form by the upward growth of a ligament situated transversely between the dorsal margin of the valves, somewhat resembling that of *Mytilus* (Fig. 52,*C*). An opisthodetic parivincular ligament also occurs in *Malletia,* but this cannot be taken as indicating close affinity between the Palaeotaxodonta and Heterodonta.

The Palaeotaxodonta and Cryptodonta have ligaments which are essentially the same as those of other bivalves. They are groups which have undergone a considerable degree of adaptive radiation, as is indicated by the diversity of their ligament form (Table 1). Quite distinct from the previous groups, the ligament in the Arcacea and Limopsacea is generally characterized by interumbonal growth and duplivincular structure, the major exception to this being *Limopsis* where the ligament resembles the primary ligament. The juvenile stage of the duplivincular ligament before the development of chevrons, represented in Figure 52,*E* by the ligament nearest the umbo, is comparable to the primary ligament. Bivalves with duplivincular ligaments could give rise to forms with alivincular ligaments by a neotenous retention of the primary ligament perhaps consequent on relatively less interumbonal growth of the valves.

TABLE 1. *Some Characteristics of Ligaments in Representative Genera of Bivalves.*

[Explanation: ab, absent; al, alivincular; am, amphidetic; ca, cardinal area (or subcardinal area); ch, chevron pattern; co, calcareous ossicle; du, duplivincular; mu, multivincular; ny, nymph; op, opisthodetic; pa, parivincular; pr, present; re, resilia (placed between resilifers); tr, transverse between dorsal valve margins; *Etheria ligament much modified subsequent on attachment by cementation.]

	Placement	Type	Fusion layer	Lamellar layer	Fibrous layer	References
PALAEOTAXODONTA						
Nuculacea--Nucula	am	al	ab	tr	re	TR
Nuculanacea--Nuculana	am	al	ab	tr	re	127
Malletia	op	pa	?		ny	TR
CRYPTODONTA						
Solemyacea--Solemya	op	tr	ab	tr	re	127
PTERIOMORPHIA						
Arcacea--Arca	am	du	ab	ch	ch	127
Limopsacea --Limopsis	am	al	ab		re	113
Glycymeris	am	du	ab	ch	ch	TR
Mytilacea--Mytilus	op	tr	ab	tr	ny	TR
Pinnacea--Pinna	op	tr	pr	tr	ny	192
Ambonychiacea--Myalina	op	du	?	ch	ch	115
Pteriacea--Pteria	am/op	al	?		re	TR
Isognomon	op	mu	ab	tr	re	169
Pectinacea--Pecten	am	al	?	tr	re	166
Pterinopecten	am	du	?			113
Spondylus	am	al	?		re	TR
Ostreacea--Ostrea	am	al	ab		re	165
PALAEOHETERODONTA						
Anthracosiacea--Anthracosia	op	pa	?		ny	TR
Unionacea--						
Anodonta	op	pa	pr		ny	TR
PALAEOHETERODONTA (continued)						
Unionacea--Etheria	op	al*	ab			196
Trigoniacea--Trigonia	op	pa	pr		ny	TR
HETERODONTA						
Lucinacea--Diplodonta	op	pa	pr		ny	2
Crassatellacea--Astarte	op	pa	pr		ny	TR
Cardiacea--Cardium	op	pa	pr		ny	TR
Mactracea--Lutraria	op	ca	ab	ca	re	171
Solenacea--Ensis	op	pa	pr		ny	126
Tellinacea--Tellina	op	pa	pr		ny	164
Donax	op	pa	pr		ny	TR
Abra		(pa+ca)	pr		(re+ny)	167
Dreissenacea--Dreissena	op	tr	ab		ny	TR
Glossacea--Glossus	op	pa	pr		ny	124
Veneracea--Venus	op	pa	pr		ny	126
Petricola	op	pa	pr		ny	126
Glauconome	op	pa	pr		ny	126
Myacea--Mya	op	ca	ab	ca	re	170
Pholadacea--Zirfaea	ab					TR
ANOMALODESMATA						
Pandoracea--Cochlodesma	op	ca	pr		re	3
Lyonsia	op	ca	?		re,co	191

Index numbers for references correspond to those in list at end of chapter; TR denotes observations by Trueman.

Although the duplivincular ligament has been shown to occur in the ancestry of pteriaceans, scallops, and marine mussels, in all but the Arcoida it was replaced before the Jurassic, the two former groups having followed similar evolutionary trends *(115)*. Attainment of the monomyarian condition may be followed by secondary symmetry of the valves and ligament as has occurred in the evolution of *Pecten (193)*. But in the Dysodonta, as in all other bivalves, the ligament shows adaptive radiation in forms as diverse as *Pecten, Pinna,* and *Isognomon,* so that while the structure of the ligament may provide additional clues to phylogeny this evidence should not be used independently.

In all Bivalvia closure of the valves causes a condition of stress in the ligament, the lamellar and fusion layers being stretched and the fibrous layer compressed. In the ligament of *Mytilus* (Fig. 53), which may be taken as a fairly generalized example, the neutral axis of the structure lies approximately between the fibrous and lamellar layers. The orientation of the molecules of the lamellar layer is such that the tensile stress is imposed along their principal axis, while the structure of the fibrous layer is more suited to compression. When the fibrous layer is subjected to tension it readily fractures, as in an alivincular ligament such as that of *Ostrea,* where during growth it comes to lie above the axis. Some measure of the efficiency of operation of the ligament has been obtained by a study of the mechanical properties of the intact and isolated ligament. The ligament of the Pectinidae, in which the main part of the inner layer is not calcified, has been

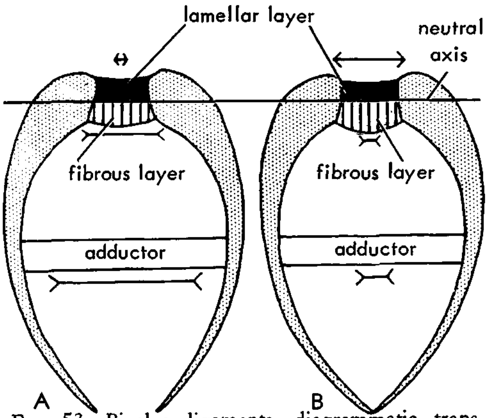

FIG. 53. Bivalve ligaments—diagrammatic transverse sections of *Mytilus* with valves gaping *(A)* and closed *(B)*, relative length of arrows adjacent to ligament layers and adductor muscle indicating change in their dimensions on closure of shell *(171)*. [Explanation: *Stippled pattern,* calcareous shell of valves in section; *black,* lamellar layer of ligament; *vertical rules,* fibrous layer of ligament; *horizontal line intersecting ligament,* approximate neutral axis of ligament.]

shown to be the most efficient mechanically *(168)*. It is notable that this family includes most of the few free-swimming bivalves. In few burrowing forms is the ligament strong enough to open the valves against resistance of the substratum, and it is usually supplemented either by the foot, as in *Tellina* and *Anodonta,* or by hydrostatic pressure of the water contained within the mantle cavity, as in *Mya (170)*.

The main ligament types may be briefly surveyed with regard to their design and to their mechanical efficiency of operation. The duplivincular ligament is a relatively ineffective structure. It provides a flexible attachment between the valves, acting more as a hinge than an opening mechanism, and the foot is probably used to push the valves open. The alivincular ligament, although it may be fractured dorsally, maintains an opening moment throughout the life of an individual bivalve. In certain genera, such as *Ostrea* and *Pecten,* where the foot is reduced or absent, it is the sole means of opening the valves and must maintain a sufficient opening moment. A somewhat similar condition must occur in *Mytilus,* where the long opisthodetic ligament is among the most powerful. The parivincular form probably represents the most highly evolved ligament mechanism and its mode of growth by posterior extension and replacement of the fractured umbonal region is both simple and efficient, more so than the repetition of duplivincular or ventral migration of the alivincular ligaments. It may be considered that an elongated opisthodetic ligament represents the most effective way that the bivalves have evolved of overcoming the allied problems of growth of an exoskeletal structure and its continued function, both as a means of uniting the valves dorsally and of causing the shell to gape ventrally. Perhaps this is the reason for the dominance of the opisthodetic ligament in the Heterodonta.

[*End of section by E. R. Trueman.*]

SUPPLEMENTARY CALCAREOUS STRUCTURES

PLATES ACCESSORY TO SHELL VALVES

In the Pholadidae the two valves of the shell are supplemented by plates located along the dorsal margin and, in some genera, along the ventral margin. These plates are of various shapes, and some are likely to be mistaken for gastropod shells of a simple type, such as *Scutum.* At the anterior end of the dorsal margin is the **protoplax,** an almost flat, longitudinally elongated, spearhead-like plate which is either in one piece or divided longitudinally into two; it may be chitinous or calcareous. Behind it is the **mesoplax,** a transversely elongated plate, commonly with infolded margins, which lies athwart the umbonal region of the shell and protects the posterior part of the anterior adductor muscle; this is always calcareous and may also consist either of one piece or of two. The **metaplax** is a long, narrow, usually calcareous plate which extends dorsally behind the umbones, covering the gap between the shell margins (Fig. 54). The **hypoplax,** also usually calcareous, is an elongate plate extending along the posterior end of the ven-

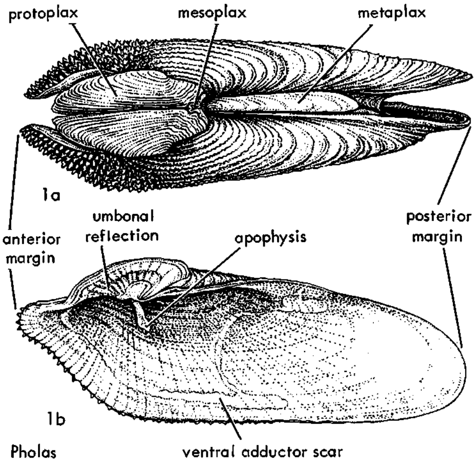

FIG. 54. Bivalve supplementary calcareous structures —*Pholas dactylus* LINNÉ, Recent, Europe, showing dorsal *(1a)* and interior lateral *(1b)* views, ×0.8 *(157a)*.

tral margin, covering the gape of the two valves. The complete series of plates is not developed in any known species, the number present ranging from one to three (or four when one is divided). The mesoplax occurs most commonly; it is, however, absent in the genus *Barnea*.

Comparable to these structures is a small triangular plate present in the genus *Caestocorbula* (Corbulidae), occurring on the left side along the posterodorsal margin.

PALLETS OF TEREDINIDAE

Pallets, which are peculiar to the Teredinidae, are small, paired calcareous structures that serve to close the end of borings when the siphons are retracted (Fig. 55). Each consists of a rodlike proximal part (**stalk**) and a broader distal part which may be bladelike or cuplike, or may consist of a series of funnel-shaped structures, each emerging from the one below it. The maximum length of the pallets of the shipworm *Teredo navalis* LINNÉ is about 5 mm., while that of a typical *Bankia capensis* (CALMAN) is about 30 mm. The stalk of the pallet fits into a groove between the siphons and the end of a duplication of the mantle (**collar**) that covers their proximal end. Fossil teredinid pallets are known from the Paleocene onward.

SECONDARY ADDITIONS TO SHELL

In some Pholadidae an anterior (pedal) gape of the margins becomes closed after a certain stage of growth by an evenly rounded extension of the shell proper, known as the **callum.** In many of the Martesiinae this extends around the anterodorsal part of the shell and between the beaks, covering the anterior portion of the anterior adductors. In *Jouannetia* the presence of the callum gives the shell an almost spherical shape, the left valve partly covering the right valve; at the same time a tonguelike posterior secondary extension of the shell is present in the right valve only. In some Pholadidae a tubular secondary structure (**siphonoplax**) forms a continuation to the posterior end of the shell, protecting the proximal end of the siphons.

TUBULAR PROTECTIVE STRUCTURES

Under this heading may be included the tubular structures built by certain bivalves

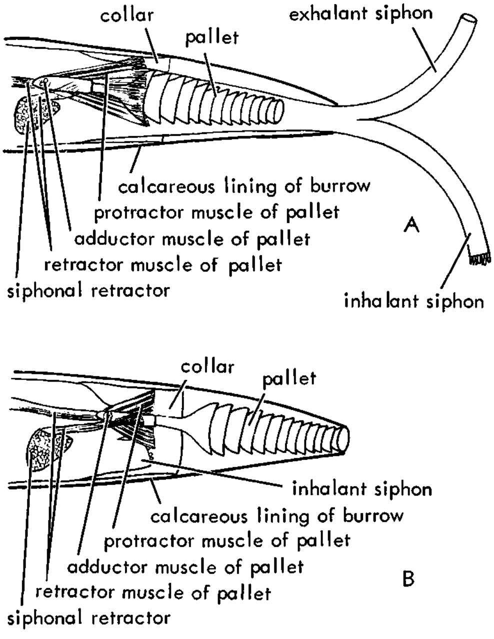

FIG. 55. Bivalve supplementary calcareous structures —*Xylotrea gouldi* JEFFREYS, Recent, Europe, posterior part of adult showing left side with siphons extended and pallets retracted *(A)* and with siphons contracted and pallets protracted *(B)* *(149)*.

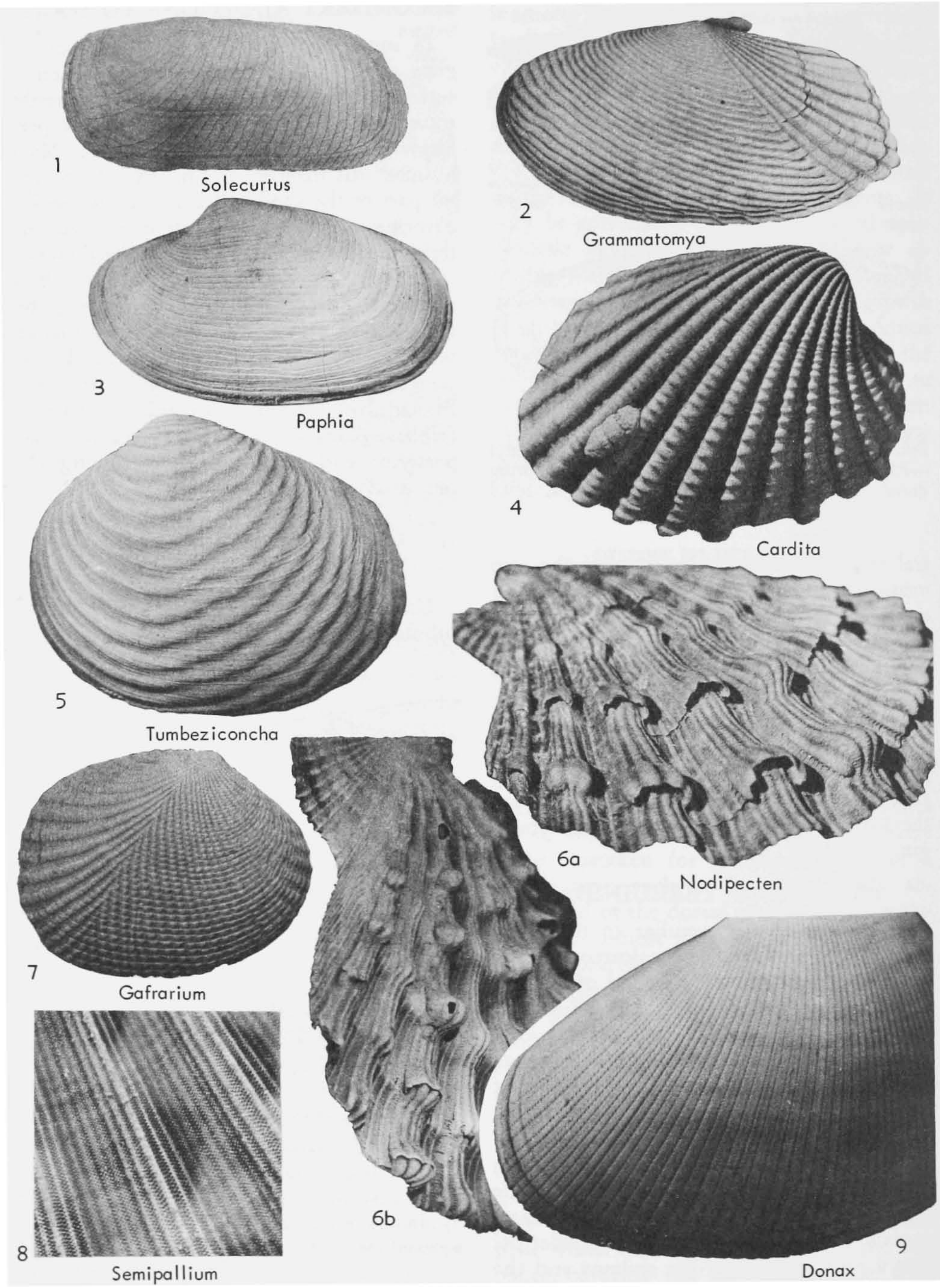

FIG. 56. Bivalve shell sculpture (Nuttall, n).——*1. Solecurtus philippinarum* (DUNKER), Recent, East Indies, imbricate surface, the unevenly grooved appearance given by overlapping lamellae with externally flush edges, ×1.——*2. Grammatomya pulcherrima* (DESHAYES), Recent, Indian Ocean, anterior part of shell with diagonal ribs and posterior part with radial ribs, ×1.7.——*3.Paphia neglecta* (MARTIN), Mio.-Plio., E.Indies, surface with basically concentric or commarginal grooves which are slightly undulating

for their encasement, usually when the two valves are so reduced as to form an inadequate protection for the soft parts. *Teredo,* the shipworm, secretes a constantly thickened calcareous lining to its borings into wood. The borings may twist about irregularly owing to the necessity of avoiding one another during penetration, and when further progress is impossible the animal secretes a calcareous wall at the innermost end of its tube and then ceases to grow. In places where the wood decays away the tube is left as the sole protection of the animal, and the thickness of its wall, usually not more than 0.5 mm., may be increased to as much as 2 mm. One teredinid, *Kuphus,* does not bore into wood, but burrows vertically into mud on the sea floor, lining its burrow with a calcareous tube with irregular growth rings; this tube may be a meter or more in length, up to 60 mm. in diameter, and 5 mm. or more thick. At its lower end the tube is sealed by one or more arched laminae, and at its upper end are two relatively small openings for the siphons, separated by a partition. Similar tubes are known as fossils from the Eocene onward and are particularly abundant in the lower Miocene in the Indian Ocean and Antillean regions, and elsewhere.

Gastrochaena may bore deeply enough into rock or other shells to render further protection unnecessary, but if penetration is only partial an "adventive" protective structure may be built over its shell. This commonly takes the form of a claviform tube or of an elongated botryoidal structure. *Fistulana,* which belongs to the same family, always secretes a rather fragile, straight, elongate, club-shaped tube, which is sealed at its anterior end and open at the other. In the position of life the tube is oriented vertically in sandy sediment; a partition divides it into two chambers, in the lower of which the animal lives, the upper serving to protect its siphons.

An elongate calcareous tube, smooth or with transverse fringes, is also secreted in the Clavagellidae. The much-reduced shell lies at its broader, anterior end, with the left valve merged in the wall of the tube in *Clavagella* and both valves in *Penicillus.* At the anterior end there is communication between the interior and exterior of the tube through a series of tubules, long and spinelike in some species, short in others. In *Penicillus* a convex, perforated disc recalling the rose of a watering can forms the anterior end of the tube, and above it is a tubule-bearing collar. Some Clavagellidae live in cavities in hard rock, but many live in a silty substrate with the tube vertical and its anterior end lowermost. It has been suggested that the mollusk can bury itself more deeply in the substrate by drawing silty water into the tube through the anterior perforations.

SHELL SCULPTURE

Most bivalve shells retain on their surface, as irregularly spaced lines and coarser markings, a record of interruptions in secretion of the shell at its margins during growth or of changes in the rate of secretion (Fig. 56, 57). These markings, termed **growth lines** and **growth rugae**, form a series of conformable curves the course of which is commonly described as "concentric" by conchologists, although commarginal would be a more appropriate term.[1]

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[1] Compare *"collabral,"* introduced by the writer with a similar connotation in gastropod terminology.

FIG. 56. *(Continued from facing page).*

and irregular, ×2.——*4. Cardita ovalis* (REEVE), Plio.-Rec., E.Indies, surface with strong radial rounded ribs and furrows, ribs bearing beadlike prominences in umbonal region and transverse bars toward shell margins, ×2.——*5. Mactra (Tumbeziconcha) thracioides* (ADAMS & REEVE), Rec., Peru, surface with excentric undulations, ×1.3.——*6. Chlamys (Nodipecten) nodosus* (LINNÉ), Rec., trop. W.Atl., oblique views *(6a,b)* showing strong radial ribs which bear secondary riblets and are crossed by concentric or commarginal growth rugae, tubercles hollow and not all of them entire, ×1.3.——*7. Gafrarium* sp., Pleist., E.Indies, surface with divaricate ribs interrupted by concentric or commarginal grooves, ×2.——*8. Semipallium tigris* (LAMARCK), Rec., E.Indies, with reticulate honeycombed surface on which main sculpture consists of radial ribs bearing secondary riblets, ×4.——*9. Donax punctatostriatus* HANLEY, Rec., trop.W.Am., showing pitted (punctate) radial grooves, ×2.

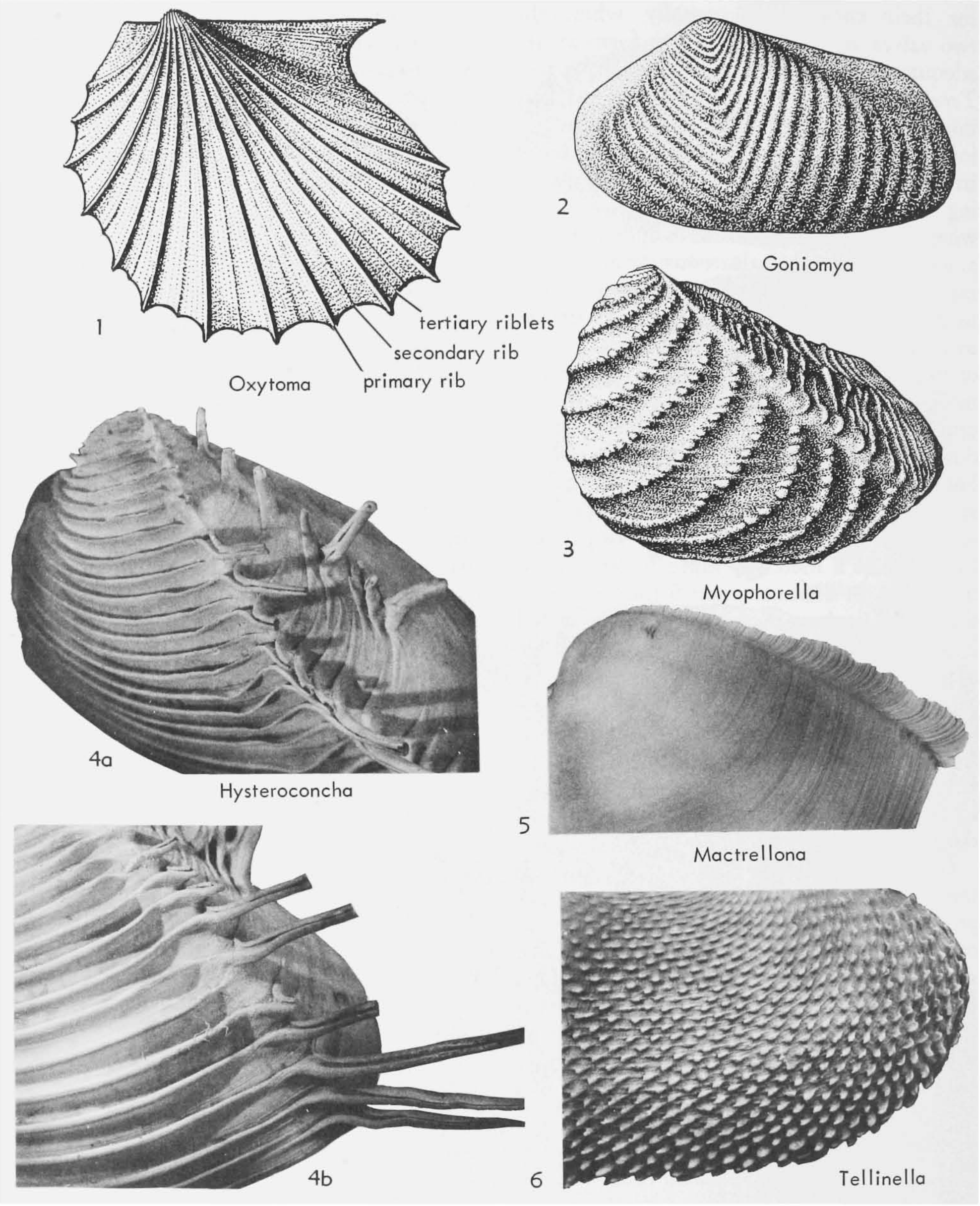

FIG. 57. Bivalve shell sculpture (Nuttall, n).——*1. Oxytoma inaequivalvis* (J. SOWERBY), L.Jur.(Lias.), Eng., surface with radial ribs of three size orders, ×1.3.——*2. Goniomya literata* (J. SOWERBY), M.Jur. (Bajoc.), Eng., with divaricate surface sculpture, ×1.——*3. Myophorella hudlestoni* (LYCETT), U.Jur. (Oxford.), Eng., surface with diagonally arranged pustules or nodes on anterior part of shell and irregular concentric lamellae on posterior slope, ×0.7.——*4. Pitar (Hysteroconcha) lupinaria multispinosa* (G. B. SOWERBY), Rec., Peru, with rows of spines on posterior slope, oppositely disposed to those of muricid gastropods, and remainder of shell surface marked by strong concentric lamellae (*4a,b,* different views of shell), ×2.——*5. Mactrellona alata* (SPENGLER), Rec., off S.Am.W.coast, surface marked by carina on posterior slope (at margin of corselet), ×1.——*6. Tellinella asperrima* (HANLEY), Rec., E.Indies, with hooked spines disposed concentrically or commarginally but also making diagonal patterns (divaricate), ×2.7.

Many bivalves have shells which are otherwise smooth, but a great number have a relief pattern, known as **sculpture** or **surface ornament**, which is of a more or less regular nature and (except for minor variations) is similar in all representatives of a species. The sculpture consists most commonly of one of two components or of a combination of these two. The first component is a **concentric** one and attributable to rhythmic changes in the rate of secretion of shelly matter along the mantle margins. The second component is a **radial** one and consists of elements diverging from the direction of the beak and crossing the concentric elements, although not at right angles except on one sector of the surface. Radial sculpture must result from the continuous enhanced secretion of shelly matter by particular groups of cells along the mantle margins during growth of the valve.

This analysis is oversimplified, however, as in many shells there are elements of sculpture crossing the directions just described obliquely at various angles. Thus in *Goniomya* there are steep, ventrally converging ribs which meet to form a series of downward pointing V's. In *Divaricella* and *Acila,* on the other hand, two series of parallel, oblique riblets meet in an obtuse angle to form chevrons pointing toward the summit of the shell. In the Trigoniidae oblique ribbing ranges from almost concentric to almost radial. Obliqueness of ornament is at the most a generic character found in families widely scattered taxonomically, and in some genera (e.g., *Ceratomya*) it is merely a specific character. Its existence shows that in some bivalves a condition associated with enhanced secretion of shelly matter shifts progressively along cells of the mantle margin during growth.

The various elements of ornament have been loosely classified into those projecting above the general level of the surface of the valve and those that are engraved into the surface, although, as protruding and engraved elements are obviously complementary, this distinction is not fundamental. According to their relative width and prominence, the projecting elements are termed **folds, undulations, costae** (or **ribs**), **costellae** (or **riblets**), **threads, lines,** etc., and the incised elements **grooves, striae,** etc. The terms **interval** and **interspace** are applied to the grooves separating two costae. Costae may be rounded or flat-topped and prominent or relatively depressed. When both radial and concentric components are present, one type may be confined to the intervals between the elements of the other, or the two may be superposed where they cross. Concentric threads may override radial costae, or, when both components are strong, **pustules, beads, tubercules,** transverse **bars** (as on the ribs of certain Arcidae), etc., may arise at the points of intersection. In some bivalves layers of growth project at intervals, forming lamellae, which extend in the direction of growth (**imbricate**) in many forms but are **erect** in others. Where they cross the ribs the imbricating lamellae may protrude prominently to form **scales,** as in *Tridacna* and many Pectinidae, or even sharp **spines.** In many Limidae concentric elements in the intervals between the ribs are small pinprick-like depressions or **puncta.** It is virtually impossible in a brief review to describe at all adequately the various ornamental patterns found on bivalve shells or to mention all the descriptive terms that have been employed in describing them.

In the majority of radially ornamented shells the radial elements remain constant in number after their first appearance, but in some they increase during growth, by bifurcation or by the intercalation of new elements in the intervals between the earlier formed ones. Some Pectinacea (e.g., *Oxytoma*) have a pattern of regularly arranged riblets of two or more orders of strength; the strongest **(primary)** ones are the first to appear. In some species the surface ornament of the two valves differs to a varying extent, not only when the valves are pronouncedly unequal (as in *Pecten s.str.*) but also (although more rarely) when they are of much the same size. The latter observation applies to some species of *Chlamys,* to representatives of the genera *Cucullaea* and *Indogrammatodon,* and to species of a number of other groups.

Mention must also be made of changes in sculptural pattern that take place during growth in some bivalves. Many Unionidae

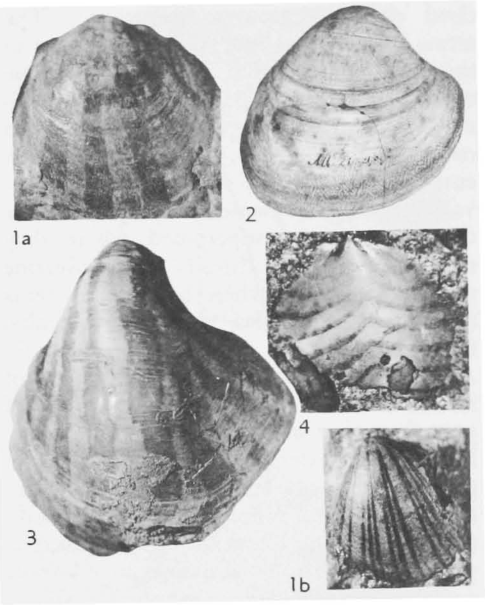

FIG. 58. Preservation of color patterns in fossils (Nuttall, n).——*1. ?Streblopteria sublobata* (PHILLIPS), L.Carb., Eng.; *1a,b,* ×2.5.——*2. Venilicardia lineolata* (J. SOWERBY), a silicified specimen from the Blackdown Greensand, Cret.(Alb.), Eng., ×1. ——*3. Exogyra columba* (LAMARCK), Cret. (Cenoman.), France, ×2.——*4. Pernopecten sowerbyi* (McCOY), L.Carb., Ire., ×2. [Photographs by N. Tanti, B. M. (N. H.).]

are remarkable for the radial, wavy, or zigzag ribs which are present on their earlier-formed growth stages only. In some Trigoniidae the pattern of the ribbing in the neighborhood of the umbones is quite different from that on the later-formed part of the shell. In the Pteriidae, the left valve of *Pteroperna costatula* (EUDES-DESLONGCHAMPS), from the Bathonian, has radial ribs in the young state but is later devoid of ribbing. A great number of similar cases could be cited.

In strongly costate shells, such as *Tridacna, Lopha,* and many species of *Plicatula,* undulations of the whole ventral margin correspond to the external ribbing. In other bivalves with external costae the marginal region is **scalloped** internally; that is, it bears a series of regular flutings (each corresponding to an external costa), separated by flat or concave intervals with well-marked edges converging toward the actual shell margin. This type of internal marginal ornament is found, for example, in many Pectinidae, Cardiidae, Carditidae, and Arcidae. When the internal marginal ornament is still finer, it consists of what are usually called **denticles** or **denticulations.** Most commonly these also correspond to external radial ornament, but in some Nuculidae, Astartidae, and Crassatellidae they are present in shells which are apparently smooth externally. In such cases they correspond to radial structural elements belonging to an inner layer of the shell.

COLORATION

[Revised by C. P. NUTTALL, British Museum (Natural History)]

Coloration can be correlated to a certain extent with the taxonomic arrangement of Bivalvia. In the first place, chemically dissimilar groups of pigments are found in different major taxa. In addition, certain types of color patterns, or even the absence of coloration, can be characteristic of particular families and genera. Coloration naturally was given considerable prominence in older conchological monographs; although it may be extremely constant within a species, a very large proportion of exceptions is found and unfortunately these lead to the creation of many synonyms.

While some bivalve shells are devoid of coloration, we find among the majority every gradation of color ornament from a slight uniform or irregular tinting to dense coloration, localized or otherwise, and to patterns of considerable complexity. When a definite pattern distinct from irregular mottling is present this may consist of radiating sectors or rays of various widths, of concentric bands, of series of spots or blotches, of chevrons or zigzagging lines and bands, or (as in certain Veneridae) of complicated mosaics composed of geometrical (commonly triangular) figures of various sizes. When zigzagging ornament is present, corresponding angles of successive zigzags tend to have a radial alignment *(188a).*

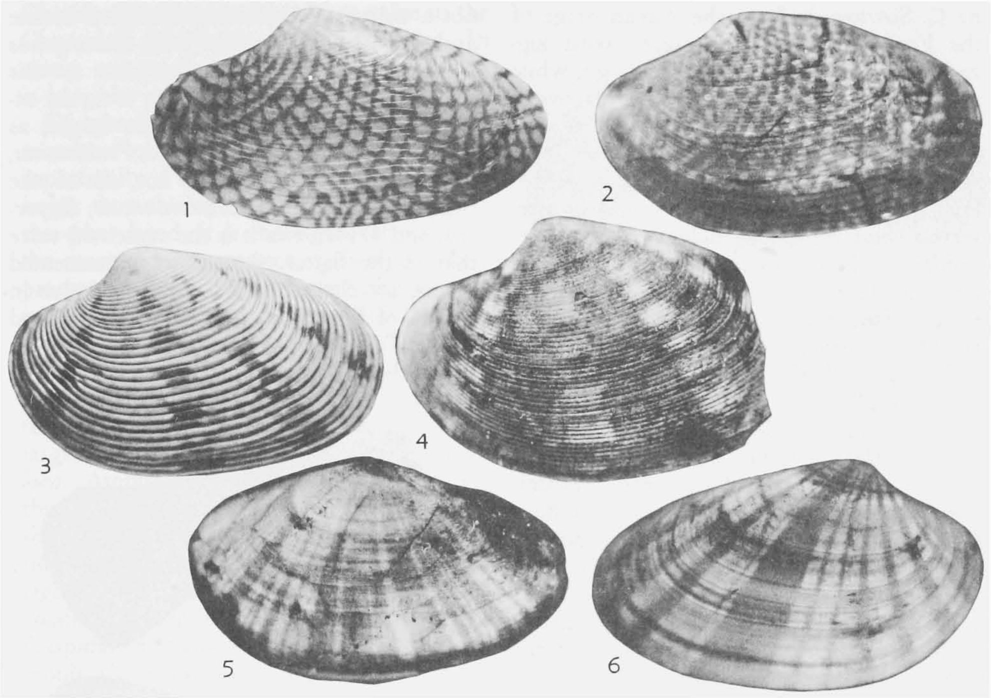

Fig. 59. Photography under ultraviolet light revealing negative or reversed color patterns. None of the fossils (except *Macrocallista,* fig. 6) showed any trace of color patterns when viewed in normal light, but fluoresced strongly under ultraviolet light. Under normal light *Macrocallista* shows concentric banding (Nuttall, n).——*1. Paphia undulata* (Born), IndoPac., Rec., ×2.——*2.* The closely related *Paphia neglecta* (Martin), Neog., Borneo, ×2.3 (see Fig. 56 for normal photo of same species).——*3. Paphia lirata* (Philippi), China Sea, Rec., ×1.2.——*4.* A similar pattern shown by *Paphia* sp., Neog., Borneo, ×2.3.——*5. Tellinella* sp., Neog., Borneo, ×2, showing patterns typical of the genus.——*6. Macrocallista laevigata* (Lamarck) from the Calcaire Grossière of Damery (Eoc., Lutet., France), ×2. [Photographs by N. Tanti, B. M. (N.H.).]

The coloration is not purely superficial, but may penetrate well into the calcareous test. The pigments are thought to be waste products of metabolism, derived from the diet or other sources, and secreted in the shell as a means of disposal *(24b)*. As in the gastropods, it is improbable that the color ornament can have any protective function in the great majority of bivalves which live buried in sediment. Some bottom-living forms, notably the pectinids, appear remarkably well camouflaged. In some evolutionally less advanced genera (e.g., *Pteria, Pinctada, Malleus, Pinna*), the pigments, notably porphyrins, are soluble in acid. In other forms the pigment is intimately associated with the conchiolin that forms the organic matrix of the shell and cannot be separated from it.

Traces of color ornament have been observed in fossil bivalves of various ages, although their preservation is less common than in gastropods (Fig. 58). Possibly the oldest of such bivalves on record is a specimen of *Leiopteria pseudolaevis* (Oehlert) from the Devonian of France, described by the author of the species as bearing dark, radially arranged specks. Both Newton and Brill have described a number of Carboniferous Pectinacea of various genera bearing colored spots, rays, concentric bands, or chevrons. Triassic species, specimens of which are recorded to have color ornament preserved, include the pectinacean *Pleuronectites laevigatus* (von Schlotheim), while Jurassic forms include representatives of *Entolium, Plagiostoma,* and *Plicatula.* A silicified specimen of *Venilicardia lineolata* (J.

de C. Sowerby), from the Albian Stage of the English Cretaceous, covered with zigzagging markings, has been described, while specimens of the Upper Cretaceous oyster *Exogyra columba* (Lamarck) from various European localities not uncommonly bear wavy radial lines. Other Upper Cretaceous bivalves recorded as having traces of preserved color ornament include various Pectinidae and a specimen of *Inoceramus*. Among Tertiary bivalves the nonmarine genus *Congeria* seems to be particularly retentive of such ornament.

Comfort (1950) has mentioned that certain mollusks containing porphyrin pigments fluoresce under ultraviolet light; but it is not clear whether this phenomenon is confined only to dyes of this type. Preliminary experiments with fossil bivalves have shown that fluorescence is widespread but of rather sporadic occurrence (Fig. 59). Good preservation seems essential and the shell must be cleaned, because the matrix itself usually fluoresces, thus obscuring the pattern. This phenomenon should prove a useful tool for paleontologists, particularly those working on Tertiary material, and has obvious applications as an aid in making identifications and in assessing the probable relationship of various species. It has also been found that the inside of a shell often will fluoresce, showing in strong relief the pallial line and muscle scars which are formed of prismatic aragonite.

[*End of section revised by C. P. Nuttall.*]

INEQUIVALVE BIVALVES

The two valves of a bivalve shell may differ in convexity, shape, and ornament (Fig. 60,*1*). Such differences are pronounced in many forms in which one valve is cemented to the substrate, and they also exist in many species of certain byssally attached groups, such as the Pteriacea and Pectinacea. In addition, slightly to moderately strongly inequivalve forms are found in other groups well dispersed taxonomically. Whether it is the left or the right valve that is the more strongly convex is usually a generic or specific character and not a matter of individual variation in one and the same species. The fresh-water genus *Etheria*, however, is an exception to this statement. In cemented forms it is the attached valve that is usually the larger, as in most Ostreidae, Spondylidae, *Prohinnites*, Chamidae, and most but not all of the rudists, although in *Pseudomonotis, Eopecten*, and *Myochama* it is the cemented valve that is the flatter. Among these cemented forms, attachment is by the right valve in genera of Pectinacea in which it exists, and in the Terquemiidae and Myochamidae. It is by the left valve in the Ostreidae and

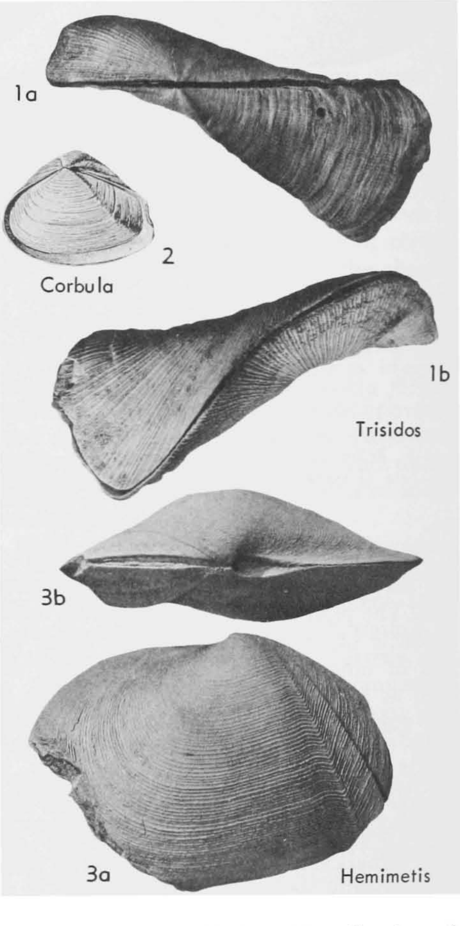

Fig. 60. Inequivalve bivalves (Nuttall, n).——*1. Trisidos tortuosa* Linné, Rec., IndoPac., both strongly inequivalve and inequilateral; *1a,b*, ×0.5 (Nuttall, n).——*2. Corbula caloosae* Dall, Pleist. (Caloosahatchie), Florida (Dall).——*3. Hemimetis* sp. aff. *H. plicata* (Valenciennes), Neog., E.Indies; *3a,b*, ×1.

Chondrodontidae, and by either valve in the Chamidae, Diceratidae, and Etheriidae. In many cemented forms the attached valve is irregular and variable in shape.

Of byssally attached bivalves, inequivalve members of the large and long-ranging superfamily Pteriacea have the left valve larger than the right. In the Pectinidae, on the other hand, it is the right valve that is the more strongly convex if there is a very pronounced difference between the two, as in *Weyla* of the Lias, *Neithea* of the Cretaceous, and *Pecten s.str.* of the Tertiary. When, however, the difference is only slight, either valve may be the larger. In the superfamily Arcacea the left valve is larger than the right in the genus *Cucullaea*. Among burrowing bivalves in which the two valves are pronouncedly dissimilar, the Corbulidae and Thraciidae may be mentioned; in both of these families it is the right valve that is the larger. The same condition exists in some Myidae, but in the Cuspidariidae it is the left valve that is commonly the more convex. In the Tellinidae the two valves are dissimilar because their margins are sinuous, and the posterior end of the shell is commonly bent toward the right (Fig. 60,*3*). Slight differences between the two valves exist in certain species of other families, even the Veneridae.

Dissimilarity between the two valves is frequently accompanied by discordance of their margins. In *Oxytoma* the ventral margin of the left valve overlaps that of the right valve considerably, while in *Cucullaea* a similar but less pronounced overlap exists. In *Corbula,* on the other hand, the ventral margin of the right valve overlaps that of the left (Fig. 60,*2*).

SEXUAL DIMORPHISM

In the Bivalvia sexual dimorphism is most evident in the Unionidae. In many species of this family the shell of the female tends to be shorter than that of the male but more gibbose posteriorly, where the gills are modified to form a brood chamber. The differences in shape of the shell are in some cases so marked that males and females have been described as different species. Sexual dimorphism is scarcely apparent in most marine species. Work on the pearl oysters *(Pinctada)* has now led to the conclusion that differences in shape formerly thought to be sexual have no such significance. A conjecture that in the species *Astarte sulcata* (DA COSTA) specimens with internal marginal crenulations are females and those devoid of them males has proved to be false, as crenulations are present in the majority of specimens of both sexes.

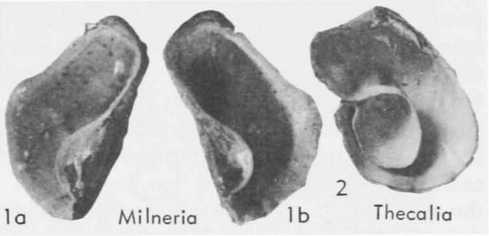

FIG. 61. Sexual dimorphism of bivalves (Cox, n). ——*1. Milneria minima* DALL, Rec., Calif.; *1a,b,* valves with brood pouches, ×6.7.——*2. Thecalia concamerata* (BRUGUIÈRE), Rec., S.Afr.(Capetown), right valve, ×2.

The only known cases in which the shell is very noticeably modified in the female are those of the genera *Thecalia* and *Milneria,* both of which belong to the family Carditidae. In *Thecalia* the ventral margins are infolded to form a shelly pocket serving as a brood chamber within the main shell (Fig. 61,*2*). In *Milneria* the corresponding margins are impressed to form a hemispherical indentation which serves the same purpose and can be covered by an extension of the mantle (Fig. 61,*1*). The males in both genera have only a narrow byssal gape of the corresponding part of the margins.

STRUCTURE OF SHELL WALL

The wall of the shell consists, when complete, of a thin coat of dark flexible horny material (**periostracum**), secreted by the inner face of the outermost of the three lobes of the mantle edge, and of the main calcareous portion, of which the outermost layer is secreted by the outer face of the same lobe, and the inner part, which does not extend peripherally beyond the pallial line, by the general surface of the mantle (*see Treatise,* p. *I*22, Fig. 14). The outer layer thickens from the beak radially, as the shell was smaller when the part nearest the beak was secreted, whereas the inner part thickens in the reverse direction as it is secreted continually during growth. The calcareous part of the test has been called the **ostracum,** but as this term, as originally defined, was restricted to the outermost layer, secreted by the mantle edge, its use is best avoided.

Unlike the calcareous part of the shell, the periostracum is not interrupted along the dorsal margins, but shares with the ligament the role of connecting the two valves. It is particularly thick in many of the larger fresh-water mussels, serving to protect the calcareous part of the shell from acid corrosion. In many marine bivalves it is thin, and it has commonly been removed by erosion by the time the shell is full-grown. It is particularly well developed in *Solemya,* in which it is the only part of the shell present in later growth stages, forming a wide border (usually radially cracked in museum specimens) to the calcareous portion. The substance of which the periostracum consists long ago received the name **conchiolin.** It is now known to be a quinone-tanned protein (a scleroprotein) composed of a number of amino acids.

The more solid part of the shell consists mainly of aragonite, of calcite, or of both of these forms of calcium carbonate, but it may also contain very small quantities of other minerals. It is permeated by an extremely fine mesh of conchiolin very similar in composition to the material of which the periostracum is composed. The exact composition of this organic component has been found to differ in different species and also in calcitic and aragonitic layers when both are present in the same shell. It contains at least 11 amino acids, present in varying proportions.

Each distinguishable layer of the calcareous wall of the shell is composed of one of the two forms of calcium carbonate mentioned, but the structure varies and several types (some grading into others) can be recognized. These have been described by Bøggild *(13).* **Nacreous structure,** confined to aragonite and never forming the outermost layer, consists of thin leaves of the mineral of the order of thickness of 1 micron, which are orientated almost parallel to the inner surface of the shell and are separated by very thin films of conchiolin, with the result that they tend to flake away. This structure, with its characteristic luster, is well displayed by mother-of-pearl, which forms the inner layer of the shell of *Pinctada,* the pearl oyster. The nacreous layers of some shells, such as *Mytilus,* are more compact and less lustrous.

Prismatic structure may occur both in calcitic and in aragonitic layers of the shell wall, but it is only when composed of calcite that the prisms may be aggregated together so regularly that the part of the test composed of them resembles inorganic mineral structures. The prisms may be single or branched, and their size differs considerably in different species. They are very commonly but not invariably oriented perpendicularly to the surface of the shell, so that sections of the prismatic layer parallel to the surface of the shell show a network of polygons. The prisms may be oblique to the surface, however, and their long axes may be radially or otherwise arranged. Their optic axes may be regularly or quite irregularly oriented. Most frequently each prism is a crystallographic entity, extinguishing as a whole under crossed nicols. In some cases, however, the mode of extinction shows that each is an aggregate of small, irregularly arranged crystals (*complex prismatic structure*). In other cases each large prism consists of numerous fine ones with a feather-like arrangement *(composite prismatic structure).*

Other types of structure give rise to the appearance of the shell commonly termed *porcelaneous.* **Crossed-lamellar structure** (confined to aragonite except in a few genera) is widespread in the Bivalvia (Fig. 62). It clearly gives much more strength to the shell than a nacreous or prismatic structure. The shell layer concerned consists of a series of more or less parallel rectangular lamellae which on the whole are perpendicular to its surface but tend to bend around close to the latter in some species until almost

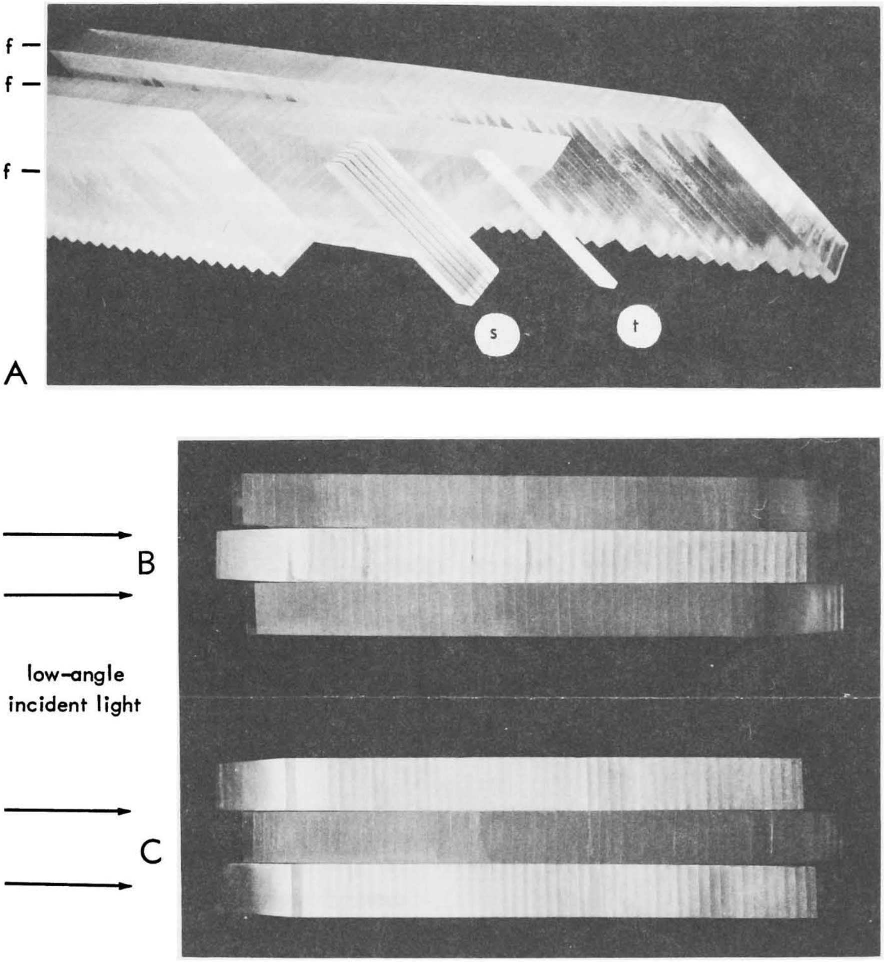

FIG. 62. Crossed-lamellar structure: parts of three first-order lamellae *(f)* each of which is about 15μ wide.——*A*. Model showing the cross relationship of second-order lamellae within three adjacent first-order lamellae. Upper surfaces of first-order lamellae are parallel to growth surfaces within shell. Isolated second-order lamella *(s)* is shown to be composed of six third-order lamellae *(t)*. In each second-order lamella the "unit crystals" (third-order lamellae) are relatively much smaller and more numerous than shown in model.——*B*. Three first-order lamellae in plane of light source.——*C*. Same, rotated 180°. Alternation of light-dark pattern on adjacent first-order lamellae is a useful criterion for recognition of crossed-lamellar structure in shells partially recrystallized *in situ*. In the model used here, low-angle incident light on three adjacent first-order lamellae, viewed normal to growth surfaces, is reflected *up* by second-order lamellae dipping toward light, and *down* by second-order lamellae dipping away from light. Air spaces between second-order lamellae of model allow light to be reflected. (Model and photos by Copeland MacClintock, Yale University, n.)

tangential to it. The longer sides of the lamellae are parallel to the surface, and their direction is usually parallel to the growth lines, rather than radial. These primary lamellae, which mostly extend across the whole thickness of the shell layer, are about 0.02-0.04 mm. thick and up to several mm. in length, although in some forms they are short and branched. They thin out as a wedge between other lamellae at each end. They are themselves built up of transverse secondary lamellae less than 1 micron thick. These are inclined so as to form an angle of 41 degrees with the longer sides of the primary lamellae, adjacent series sloping in opposite directions. Notwithstanding its complex structure, each primary lamella extinguishes under crossed nicols as if it were a single crystal.

The **foliated structure** found in the calcite of some bivalve shells is similar to the aragonitic nacreous structure in that it consists of more or less parallel leaves of the mineral, but it is coarser, less regular, and without luster. The leaves may be parallel to the surface of the shell, oblique, or perpendicular to it. Two other types of structure found in bivalve shells have been described by BØGGILD. The first is the **complex structure,** confined to aragonite, and resembling crossed-lamellar structure except that it is more intricate. The second is the **homogeneous structure**, too fine for its details to be observable under the microscope, extinguishing in one direction over large parts of the shell under crossed nicols.

Apart from trace elements and organic constituents, the composition of bivalve shells ranges from entirely aragonitic to entirely calcitic, the latter being the rarer condition. Among Recent forms, those belonging to the Ostreidae and Anomiidae are almost wholly calcitic. Of extinct families, the Buchiidae and Oxytomidae are thought to have had entirely calcitic shells. Some calcite is present in almost all the Mytiloida and Pterioida, which together constitute the Anisomyaria of some older classifications, but only in a few other groups, which include the rudists. In the great majority of bivalve shells at least two calcareous layers are distinguishable and the number is greater in many species. Of the part of the shell not secreted by the mantle edge, particular reference must be made to that formed where the adductor muscle or muscles are attached. This commonly differs in structure from the surrounding material secreted by the general surface of the mantle and becomes buried under this material as the muscles migrate ventralward and the shell is thickened during growth. It has been called the hypostracum, but as this term was originally introduced with another meaning it seems preferable to adopt OBERLING's name **myostracum** for it. When there are more than two calcareous layers besides the myostracum, a transverse section must be cut through the shell if it is wished to determine which were secreted by the edge of the mantle and which by its general surface.

A nacreous layer is present in the Nuculacea, Mytilacea, Pteriacea, Pinnacea, Unionacea, Trigoniacea, Clavagellacea, and some Pholadomyidae, among Recent shells. Its presence is usually regarded as a primitive feature and it was probably more widespread in Paleozoic bivalves, in most of which, however, it has become transformed into calcite in the course of fossilization. It was present in Paleozoic Pectinacea, although it is wanting in later representatives of this superfamily.

Prismatic calcite forms the outer layer of the shell in the Pteriidae, Isognomonidae, Inoceramidae, Malleidae, Pinnidae, and Oxytomidae (right valves only). In *Trichites* (Pinnidae) and in many species of *Inoceramus* this layer is particularly thick. In *Hippurites* the thick outer layer of the shell is composed of compact prismatic calcite. Prismatic aragonite forms the outer layer of the shell in the Unionacea, Trigoniacea, Lucinidae, Donacidae, and in some Nuculidae, Veneridae, and Pholadomyidae. It forms the inner layer in the Limidae, Spondylidae, Astartidae, and Laternulidae, and in some Mactridae and Hiatellidae. Crossed lamellar calcite is rare, but forms the outer layer of the shell in the Buchiidae and at least some Oxytomidae, as well as in some Jurassic species of *Gryphaea*. Crossed lamellar aragonite is widespread, particularly in heterodont bivalves, in which it commonly forms the outer layer and less commonly a middle layer. Irregularly foliated calcite is characteristic of many Ostreidae and of the Anomiidae, forming almost the whole test. It also forms the outer layer of the shell in the Spondylidae and many Pectinidae. The "complex" and "homogeneous" types of aragonitic structure most commonly form the innermost layer of the shell, particularly in a number of heterodont genera, but both types form the outer layers in some species. Details and illustrations of the structure of the shell wall of many species have been published, notably in BØGGILD's monograph.

Investigations have been carried out by LOWENSTAM *(93, 94, 95)*, DODD *(40)*, and others with the object of determining what factors govern the relative proportions of calcite and aragonite secreted in shells (such as some species of *Mytilus*) in which both minerals are present as interdigitating inner layers. The results have indicated that secretion of aragonite is favored by higher temperature of the sea water. Seasonal fluctuations in percentage of aragonite in the shell also have been observed. That changes in shell mineralogy can occur during ontogeny has been demonstrated by STENZEL *(155)*, who has found that the prodissoconch of the oyster *Crassostrea virginica* (GMELIN) is aragonitic, whereas the adult shell is mainly calcitic.

Molluscan shells contain, in addition to calcium carbonate and an organic constituent, minute quantities of trace elements, particularly magnesium, strontium and barium, the proportions of which can be determined by spectrographic techniques. According to TUREKIAN & ARMSTRONG *(172)*, the amounts, expressed in parts per million, present in various bivalve genera investigated are as follows:

Trace Elements in Bivalve Shells
(in parts per million)

Element	Mg	Sr	Ba
Arca	69-140	1200-2500	6-41
Glycymeris	140-220	1600-1900	6-29
Pecten	440-4700	660-1200	6-12
Lucina	53-89	1000-1500	6-7
Macoma	125-320	1400-1800	7-33
Tellina	59-180	1600-5000	6-17
Cardium	88-190	1200-1800	7-12
Chione	65-98	1100-1600	8-18
Average[1]	354	1570	12

[1] For all Bivalvia examined.

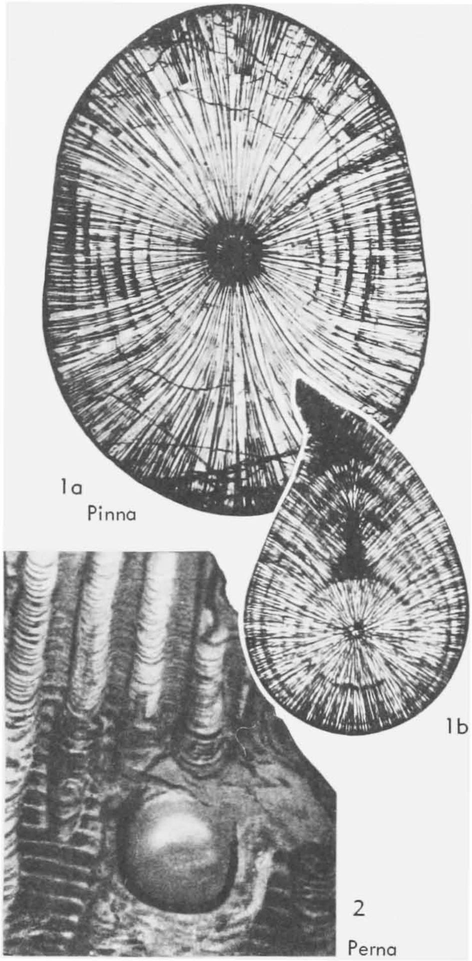

FIG. 63. Pearls in bivalves.——*1. Pinna nobilis* LINNÉ, Rec., E.Atl.O.; *1a,b,* transverse sections through pearls composed of prismatic calcite, ×8 *(147)*.——*2. Perna oblonga* RÖMER-BÜCHNER, U. Mio., Ger.(Mainz basin), attached "half pearl," ×3.5 (Zilch, 1936).

The results obtained by the authors cited and by other workers show that the trace element composition of the shell depends on a number of factors. Although the composition is related to that of the water in which the mollusk lives, there are noticeable discriminations against magnesium and strontium, less marked in the former than the latter, and a slight enrichment in barium. The concentrations of the trace elements also depend on the salinity and temperature of the water, on the ratio of calcite to aragonite in the shell, and on the species under consideration. Bivalvia are on the whole richer in strontium and barium than gastropods, while some analyses suggest that they are poorer in magnesium.

In some bivalves the wall of the shell is traversed by minute tubules, present only in its innermost layer, in its innermost and middle layers, or throughout its whole thickness. It is otherwise compact in most genera. Some of the rudists are a notable exception. In the Radiolitidae the wall of the shell is cellular, and in the Caprinidae it is traversed by longitudinal canals. In some species of the Ostreidae parts of the shell are cellular or cavernous.

PEARLS

Pearls are calcareous growths formed within sacs in the tissues of the mantle of the mollusk or as blister-like excrescences (blister pearls) on the interior of the shell. Pearls of the first type may, however, become expelled from the soft tissues and cemented to the interior of the shell. The ultimate cause of the formation of pearls is irritation of the outer epithelium of the mantle arising from the presence of the larva of a parasite or of small extraneous objects such as sand grains, or from unknown causes. The formation of a pearl sac, lined with elongate epithelial cells, results from a series of changes set in motion when the outer epithelium is damaged by the intruding object or organism; this then usually acts as a nucleus around which the pearl is secreted. If, however, the extraneous object becomes lodged between the wall of the shell and the mantle epithelium without damaging the latter, a blister pearl may be the result.

The mineral constitution and structure of a pearl depend on the mineral-secreting tendency of the part of the mantle where it is formed. When this part of the mantle secretes nacreous aragonite, as in the pearl oyster *Pinctada* and the fresh-water clam *Margaritifera,* lustrous aragonitic pearls are formed. Such pearls are built up of concentric layers, consisting mainly of aragonite with a fibrous radial structure, separated by thin films of conchiolin; in some pearls a certain amount of calcite enters into their composition. In *Pinna* the inner nacreous layer of the shell is restricted to a relatively small part of the interior, the greater part of the test consisting of prismatic calcite (Fig. 63,*1*). Many *Pinna* pearls in consequence consist of radiating prisms of calcite. Pearls formed by *Ostrea* are also calcitic but have a less distinctly crystalline structure.

The geologically oldest reported traces of fossil pearls consist of rounded depressions on the surface of an internal mold of *Megalodon* from the Upper Triassic of Hungary. Pits on a number of similarly preserved specimens of *Inoceramus* from the Cretaceous also have been regarded as molds of pearls, although this interpretation has been queried. Pearls in the solid, attached to oyster shells, are known from the Jurassic. Isolated pearls of Cretaceous age have been found in several areas. Specimens from the Chico Formation of California are believed to have been formed by the species *Inoceramus subundatus* MEEK; they now consist of concentric lamellae of calcite, but it is uncertain if they were originally aragonitic and have undergone subsequent change. Isolated small, lustrous, aragonitic pearls found in the London Clay (Lower Eocene) of southern England are believed to have been formed by a species of *Pinna.* Other pearls, some of them lustrous, have been found attached to specimens of *Isognomon* from Tertiary deposits at a number of European localities. Records of fossil pearls are, in fact, now fairly numerous (Fig. 63,*2*).

ORIENTATION AND AXES

RELATION TO BIOLOGIC FEATURES

A directional terminology is essential for morphological descriptive work in biology, and use of the six basic terms anterior, posterior, dorsal, ventral, left, and right was long ago extended from the vertebrate animals, to which they essentially refer, to invertebrates, with exception of the more primitive groups. In this process criteria other than the simple ones of the usual direction of the animal's movements and of the position of the various parts of its body in relation to gravity or to the supporting surface had to be considered and in certain cases (as in the application of "dorsal" and "ventral" to the Brachiopoda) somewhat arbitrary decisions made. The Bivalvia present no perplexing directional problems, although they are specialized for a sedentary or at least a relatively inactive life and have no head. When typical homomyarian forms move by ploughing their way through sediment with the aid of their foot their movement is usually more or less in the direction toward which one end of the shell points, and this is the end of the shell nearest the mouth. Added to these facts are their clear analogies with other and more active classes of the Mollusca, such as the Gastropoda and Polyplacophora, in which the application of the standard directional terms is obvious. If most importance should be attached to one particular feature in determining the basic directions it is here suggested that this feature should be the mantle isthmus, in all cases to be regarded as dorsal and extending anteroposteriorly. This would conform with the theory that the Bivalvia arose from a cap-shaped or low-conical, bilaterally symmetrical univalve mollusk by the shell bending and two embayments forming along a median line, giving rise to two valves hinging along the isthmus between the embayments (this *Treatise,* page *I*22). On the side of the body opposite the unmistakably dorsal shell was the broad foot by means of which this ancestral form crept over the substratum.

The basic directions, as so determined, agree with those as generally accepted for homomyarian bivalves, less attention being paid to the foot, which, no longer used for creeping, is to be accepted as commonly extending anteroventrally instead of indicating the exact ventral direction. Difficulties arise, however, when anisomyarian and monomyarian bivalves are considered. In these groups the anterior adductor tends to move to a position close to the anterior end of the hinge line before it disappears completely and the posterior adductor tends to assume a median position. The organs of the body are displaced accordingly; the mouth, followed by the adjacent end of each ctenidium, moves close to the dorsal margin, and is in turn followed by the much reduced foot. In consequence, if emphasis is placed on the positions of these organs, the conclusion is likely to be reached that the mantle isthmus, that is, the hinge, does not occupy a strictly dorsal position and may even be almost anterior.

YONGE has approached the subject by suggesting that the "mantle-and-shell" and the body may be considered as separate although interacting entities, each with certain definable axes, the mutual relationships of which afford a basis for comparison of the various bivalve groups. The cardinal axis or hinge axis, determined solely by the mantle-and-shell, is the only one which we have so far discussed. The term **anteroposterior axis** begs the question as to how exactly these basic directions are to be decided upon. FISCHER *(48)* defined the anteroposterior direction as that of a straight line touching the lower margins of the two adductors. This definition, of course, ignores monomyarian forms, and is, incidentally, based on structures belonging to the mantle-and-shell rather than to the body of the mollusk. JACKSON *(76)* considered the anteroposterior axis to be a straight line "passing through the mouth and middle of the posterior adductor muscle and nearly or quite coinciding with the termination of the intestine." This definition could be made to relate solely to the body by shortening it to "passing through the mouth and anus," and this axis whose direction will in some cases be rather different from JACKSON's "anteroposterior axis" would preferably be termed the "oro-anal axis."

The group of figures previously given (Fig. 35) compares the position of the cardinal or hinge axis with the oro-anal axis in several bivalves. It can be seen that it is dangerous to conclude too much from the fact that these axes tend to diverge as the monomyarian condition is reached. There are some homomyarian forms in which the oro-anal axis is by no means parallel to the cardinal axis (Fig. 64). The following figures were obtained: *Paphia,* 15°; *Lucina,* 0° to 15°; *Arca,* 25°; *Limopsis,* 35°. Moreover, variations of between 10° and 35° were found in diffierent species of *Modiolus.* In *Tridacna* the reorientation of the soft parts within the shell that has accompanied the loss of the anterior adductor is even more

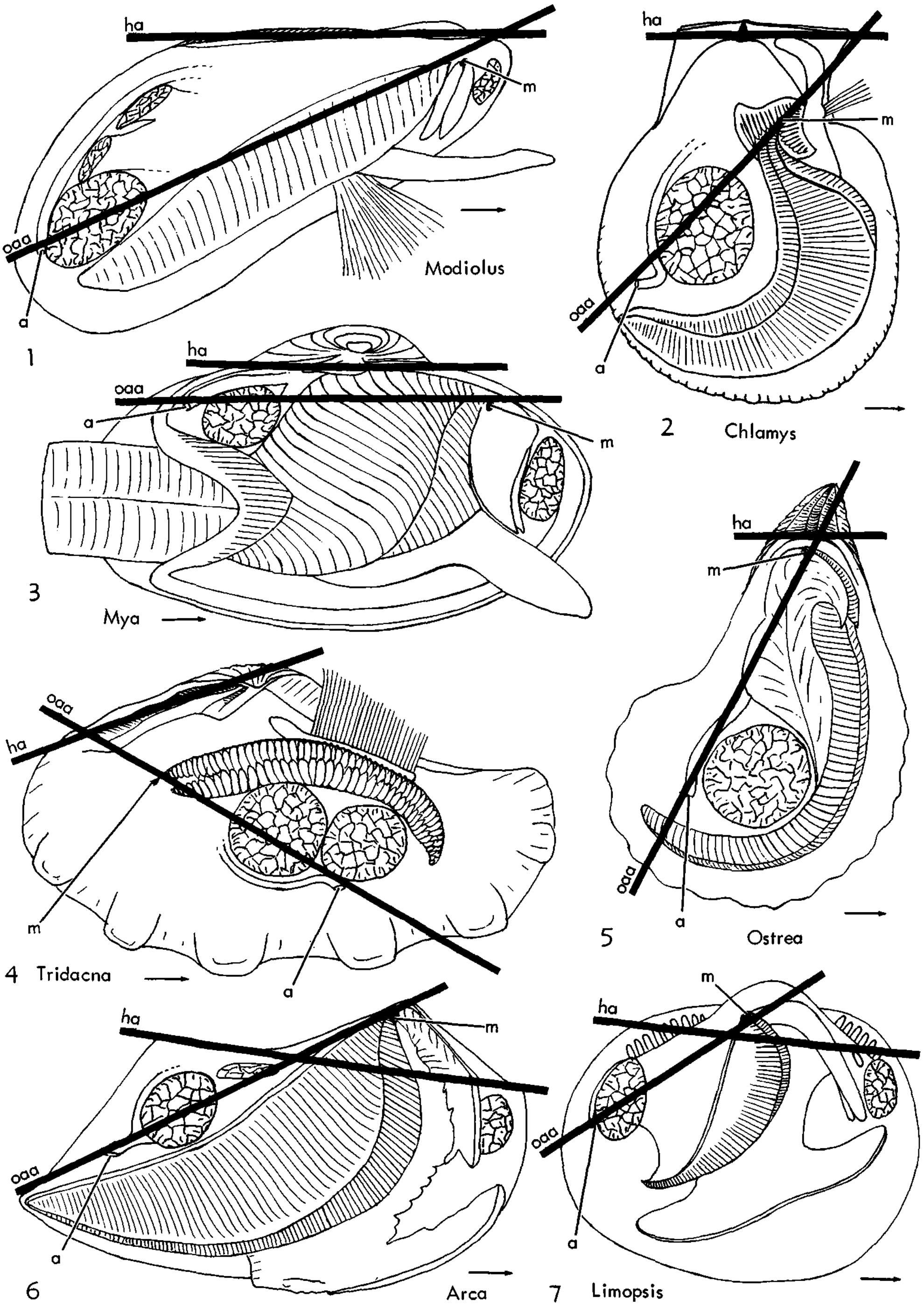

FIG. 64. Orientation and axes of bivalves showing relationship of oro-anal and hinge axes (*1, 3, 5,* after *76; 2, 4, 6,* after *150; 7* after *132*). [Explanation: *a,* anus; *ha,* hinge axis; *m,* mouth; *oaa,* oro-anal axis.]

remarkable (Fig. 64,*4*). The mouth lies close to the hinge line and on the same side of the beak as the ligament, and the byssus protrudes through a broad gape of the margins on the other side of the beak. The remaining adductor has moved to the opposite side of the shell to that in which it normally lies, with the anus just below and behind it. Thus the oro-anal axis forms an angle of about 120° with the cardinal axis. If use of the usual directional terms is to be based on a convention that the anteroposterior direction must be indicated by the oro-anal axis, it is clear that the paleontologist, dealing with many extinct genera in which the exact arrangement of the soft part is unknown, will find the terminology impracticable, and that even the student of Recent bivalves will find it most inconvenient. The only practicable course, apart from introducing a new series of directional terms, is to regard the cardinal axis as the criterion for determining the anteroposterior direction, and this, indeed, has long been the practice with the majority of workers. It has determined the traditional way of orienting bivalve shells with the cardinal axis horizontal for purposes of illustrating their side view.

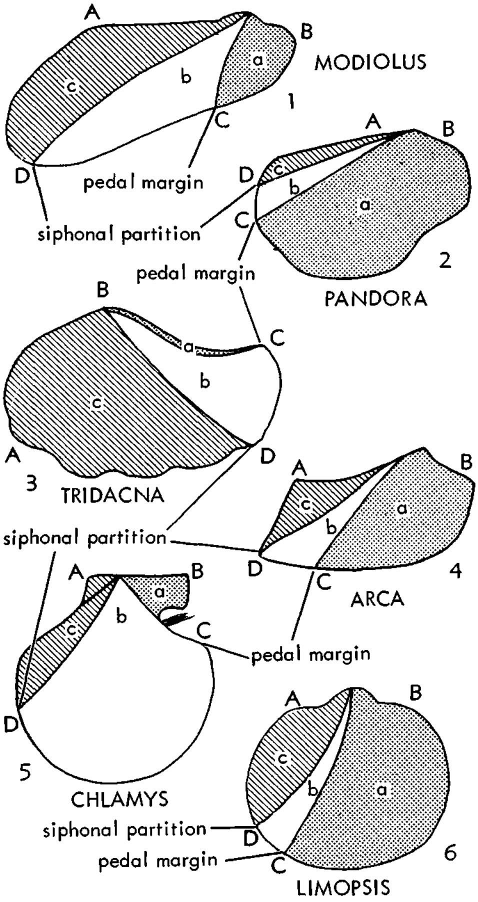

FIG. 65. Zonation of bivalve shell surfaces by interconnection of successive peripheral positions of pedal margin and siphonal partitions defining areas (a) with free borders at all growth stages adjacent to pedal margins, (b) with free borders adjacent to inhalant aperture, (c) with free borders next to exhalant region (*150*, mod.). [Explanation: A, B, upper limits of suprabranchial and infrabranchial chambers; D, C, outer limit of siphonal partition between these chambers; C, outer limit of inhalant region.]

While the direction of the cardinal axis is more easily ascertained in practice than that of any axis defined by reference to soft parts or even muscle scars, it must be admitted that it cannot always be determined with mathematical precision. When there is a long, straight hinge margin, as in the Arcacea, Pteriacea, and Pectinacea, the axis obviously almost coincides with this margin. When there is a ligamental nymph, its upper surface will usually indicate the direction of the axis. In many genera, however, it is necessary to determine this by trial with actual shells in which the valves open and close. Added to this is the fact that, as ANTHONY *(4)* showed by observation on living specimens, there is a slight vacillation of the hinge axis when the valves open and close in individual specimens of some species, particularly burrowing ones with a relatively simple hinge apparatus. Much statistical work has been based on measurements of the length and height of shells made in directions intended to be parallel and perpendicular to the hinge axis or "anteroposterior" axis. As these directions are usually determined by rapid inspection, it is to be suspected that the subjective element in posing each specimen for measurement may be so great as largely to vitiate the results. Measurements for statistical purposes should be of quantities ascertainable quite objectively, such as the maximum distance between the anterior and posterior margins irrespective of the exact direction of the measurement.

The paleontologist will naturally ask to what extent the external features of the shell, apart from gapes of the margins already mentioned, indicate the positions of various soft organs. STASEK *(151)* recognized four particularly significant points on the margin (Fig. 65). Two *(A,B)* situated more or less dorsally, one posterior and the other anterior to the beak, represent respectively the upper limits of the suprabranchial and infrabranchial chambers. Of the other two, *D,* situated along or close to the posterior margin, represents the siphonal partition between these chambers, and *C,* the position of which varies greatly, represents the other limit of the inhalant aperture or region. Thus the pedal or byssal opening lies between *B* and *C.* Radial lines joining the points *C* and *D* to the beak separate three sectors of the surface of a valve which, although varying greatly in relative size in different genera, appear to correspond to functionally equivalent regions of the soft parts. It is usually difficult to distinguish these sectors using the shell alone except when, for instance, a pallial sinus enables us to position *D,* and the posterior end of the pedal gape reveals the approximate position of *C.* Nevertheless

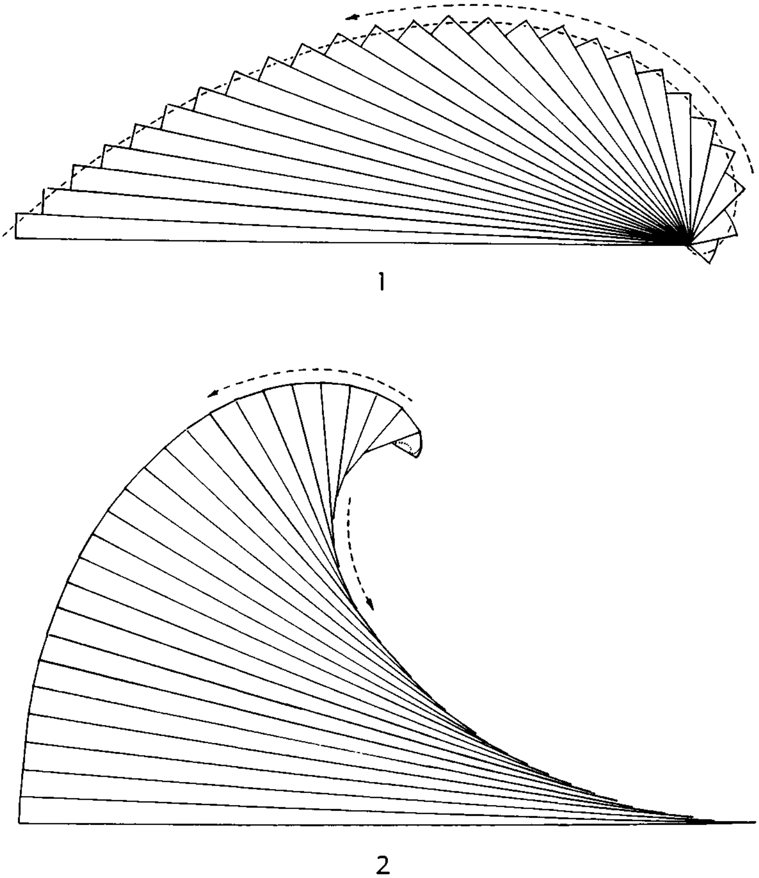

FIG. 66. Bivalve shell geometry—two constructions showing different methods of adding equal-arc increments resulting in gnomonic growth. In these examples secretion is shown decreasing uniformly from a maximum (lower left) to zero (lower right) *(92)*.——*1.* Valve lacking cardinal area.——*2.* Cornucopia-like shell.

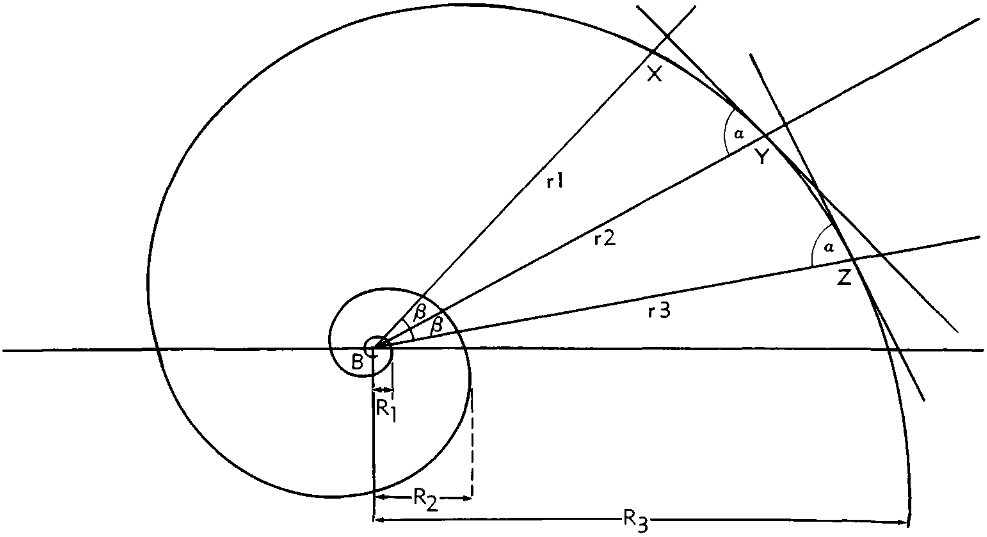

Fig. 67. Bivalve shell geometry—properties of the logarithmic or equiangular spiral. Triangles *BXY* and *BYZ*, in which the angle at *B* (β) is the same, are always similar. Angle (α) formed between tangent and radii *r1, r2, r3*, is always constant (Cox, n).

Stasek's approach should prove well worth pursuing by paleontologists.

In many shells there is a posterior area with ornament quite different from that on the flank of the valve; two parts of the valve are commonly separated by a carina. *Protocardia* and many Trigoniidae are well-known examples. Many authors, following Hyatt *(73)*, term this area the **siphonal area**, on the assumption that it is secreted by the part of the mantle edge that forms the exhalant and inhalant openings, protruded in many species to form siphons. Further observations, however, appear to be necessary before any generalizations can be made regarding the position of the boundary between the two types of ornament or of the diagonal carina in relation to these openings. From our knowledge of living representatives of the family, it appears that in the Trigoniidae, in which a posterior area is commonly particularly well differentiated, the mantle margins are completely open.

It will be seen that the review above does not give the paleontologist an easy answer to the problem of reconstructing the arrangement of soft parts in extinct genera. One constant connection between the body and the "mantle-shell" is that the rectum seems invariably to curl over the dorsal side of the posterior adductor. Other useful guides are given by general shell features such as gapes, and pedal and adductor scars, discussed in previous sections.

RELATION TO SHELL CHARACTERS

With shells belonging to extinct families there may not be an infallible means of distinguishing between the left and right valves or (as amounts to the same thing) of deciding which are the anterior and posterior ends. The following general guidance may, however, be given.

1) When ligamental nymphs are present, these are invariably on the posterior side of the beaks.

2) If a pallial sinus is seen on the interior of the shell, this is invariably near the posterior end.

3) If only one adductor muscle scar is present, this lies posterior to the middle of the shell, although in some cases only slightly so; if one adductor scar is very much larger than the other, it is the posterior one.

4) If the beaks lie near one end of the

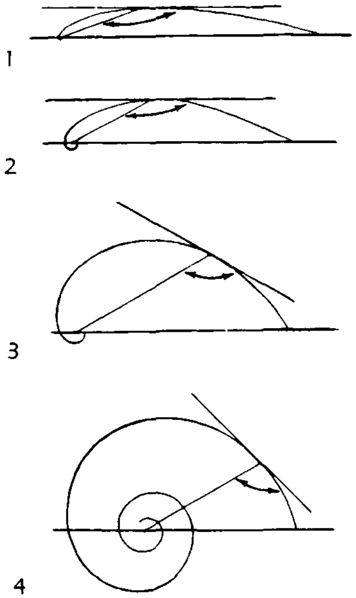

Fig. 68. Bivalve shell geometry.——*1-4*. Sections through beak and front edge of shell showing correlation between decrease in angle of equiangular spiral and increase of shell convexity *(92)*.

shell, the shorter end is very commonly the anterior end. It is always anterior in alate shells of the Pteriacea and in mytiliform shells, but there are some genera in which the beaks are posterior to mid-length, including *Nucula,* and various members of the Erycinacea, Mactracea, and Tellinacea.

5) If one end of the shell tapers to a narrow rostrum, this is usually the posterior end.

6) If there is a single diagonal umbonal ridge, this usually crosses the posterior part of the valve.

7) In the Nuculacea a careful study of the arrangement of the pedal retractor and protractor scars can indicate at which end of the shell the foot protruded; this end must have been anterior (Driscoll, *44*).

GEOMETRY OF SHELL

By †L. R. Cox and C. P. Nuttall

[British Museum (Natural History)]

With many exceptions, which obviously include all cases of irregular growth arising from fixation to the substrate or other factors, bivalve shells may be regarded as geometrical structures which grow in accordance with definite laws. The fundamental observation that gives the clue to these laws is that from an early postlarval stage when the shell acquires definitive form its shape (in all three dimension) remains virtually unchanged as it continues to grow. Accordingly, fairly young shells can usually be identified specifically without great difficulty by comparing them with adult ones. Any addition to the shell during a period of growth thus forms what is termed a **gnomon** to the existing shell (Fig. 66); it increases its volume and surface area without changing its shape. The geometrical constructions explaining shell coiling in general have been based since the first part of the nineteenth century on the logarithmic or equiangular spiral, main properties of which are shown in the explanation of Figures 67 and 68. Our knowledge of bivalve shell geometry in particular is largely due to the work of Thompson (1942), Lison (1949), Owen (1953), Stasek (1963), Raup (1966), and Carter (1967).

In the simplest case, the commissure may be considered to lie in a plane passing through the cardinal axis and to constitute the generating curve of the valve. During growth this plane may be imagined to rotate about an axis passing through the umbonal region, while the generating curve, without changing its shape, increases continuously from a negligibly small size to dimensions of the full-grown valve. The fact that growth of the generating curve is itself gnomonic means that, whatever its shape, every point along its margin (in other words, each shell-secreting cell or group of cells) is displaced outward continuously within its plane along a straight line radiating from the beak. However, on the three-dimensional surface traced out by the revolving, expanding generating curve, all such points will follow divergent spiral curves.

Lison *(92)* has explored the subject not only theoretically but also practically by observations on bivalves with radial ornament. He has shown that, if many radially ribbed valves are carefully examined, there is one rib, and one only, that lies entirely within a single plane, so that every part of it appears straight when viewed longitudinally. This rib is termed by him the **directive rib**, and the plane in which it lies the **directive plane** (Fig. 69). He also defines the angle between the directive plane and the plane of the commissure as the **angle of incidence** (Fig. 70). The course of this rib over the directive plane may be studied, either by cutting a transverse section through the valve along the rib or by turning the valve so that its transverse profile coincides with the whole length of the rib.

By making actual measurements on a number of different bivalves LISON was able to verify the conclusion that the directive rib forms a **logarithmic spiral**. He also

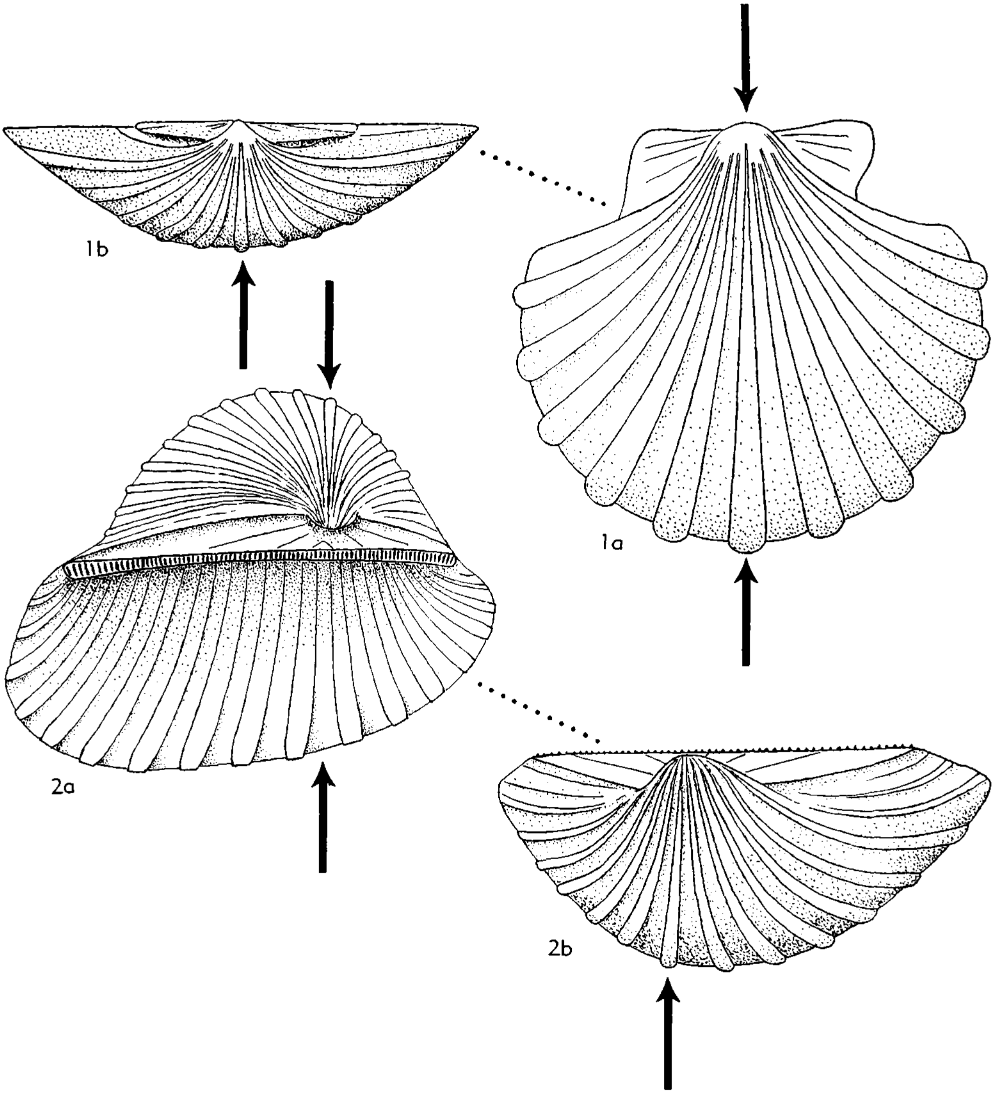

FIG. 69. Bivalve shell geometry—drawings of shells showing directive rib (Cox, n).——*1. Pecten; 1a,b,* views normal to plane of right valve and to beak.——*2. Anadara; 2a,b,* views oblique and normal to beak of left valve.

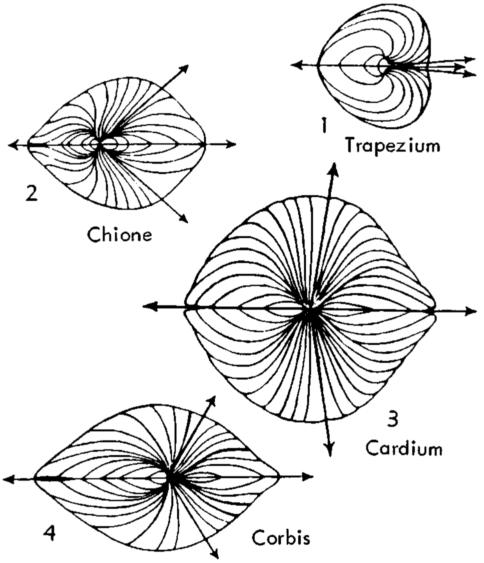

FIG. 70. Bivalve shell geometry—views of shells showing change in appearance with differing angles of incidence between directive plane and plane of commissure (arrows indicate position of these planes) *(92)*.——*1. Trapezium oblongum* (LINNÉ), Rec., E.Atl.——*2. Chione reticulata* (LINNÉ), Rec., E. Atl.——*3. Cardium orbita* G. B. SOWERBY, Rec., E. Atl.——*4. Corbis fimbriata* (LINNÉ), Rec., E.Atl.

showed, both theoretically and by measurement, that the other radial elements of the shell form three-dimensional (i.e., turbinate or gauche) logarithmic spirals (**helicospirals**), since their projections on the directive plane are logarithmic spirals (actually all with the same constant angle as the directive spiral), and the deviation of any point on them from the directive plane is proportional to its distance from the pole (i.e., beak of the valve) (Fig. 66,*1*). LISON also pointed out that in shells with a cardinal area, the area itself might form a spiral surface to which similar laws are applicable, both surfaces having the same directive plane. The hypothetical construction shown in Figure 66,*2* may well be applied to patelliform and bellerophontid gastropods and some spiriferid brachiopods with a high area may approach it. Bivalves such as *Arca* and *Spondylus* seem to represent a balance between Figure 66,*1* and *2* (i.e., secretion at lower right is more than zero).

In shells with almost orthogyrate umbones (e.g., *Pecten, Glycymeris*) the directive plane is nearly perpendicular to the plane of the generating curve (valve margins) and more or less bisects the valve, but in shells which have prosogyrate or opisthogyrate umbones and are commonly more or less inequilateral the angle of incidence may be much smaller (Fig. 67). For example, both in prosogyrate *Codakia* and opisthogyrate *Tellina* the angle of incidence is about 10°; but in the former the directive plane lies close to the commissure behind the umbo, and in the latter case the reverse is true.

LISON stated that the calculation of such quantities as the surface area or volume of a shell from a series of simple measurements presents mathematical problems of considerably complexity, but he showed that the form of a bivalve shell in which the valve

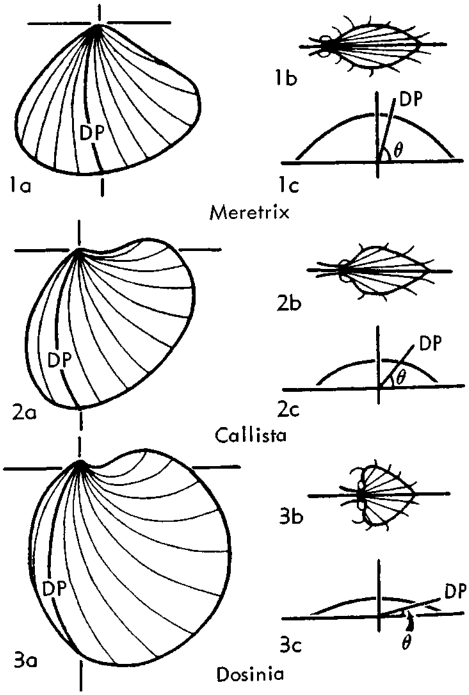

FIG. 71. Bivalve shell geometry—side and edge views of shells with sections showing relationship between directive plane *(DP)* and shape of lunule in some venerids with varying angle of incidence *(θ)* (Carter, 1967, *20a*).——*1. Meretrix,* with angle of incidence approximately 80°.——*2. Callista,* with angle of incidence approximately 50°.——*3. Dosinia,* with angle of incidence approximately 20°.

margins are plane can be fully defined mathematically, for purposes of comparison with other shells, in terms of the angle of the directive spiral, the angle of incidence of the directive plane, and three functions, obtained by a graphical method, expressing the shape of the generating curve.

This approach to the subject cannot, of course, be demonstrated easily by visual inspection if the shell lacks radial ribbing, except in rare specimens with an umbonal ridge that proves to lie within the directive plane. The angle of incidence is clearly interdependent with several features of the shell, particularly convexity of the valve, position of the umbo, the extent to which it is prosogyrate or opisthogyrate, and relative development of the lunule and escutcheon (Fig. 71).

A rather different way of interpreting shell geometry in terms of three growth components has been developed by OWEN *(121, 122, 124)* and YONGE (*194a* and this *Treatise,* p. *I*26), who attached more importance to a line which was originally termed the normal axis (and now designated as demarcation line) than to the directive rib (Fig. 72). It originates at the beak and crosses the growth lines where they are most distant from the plane of the commissure. In radially ornamented shells it coincides with a rib or other element of sculpture, and it forms part of a logarithmic spiral of one of the types (planispiral, helicospiral) already discussed. It is identical with the directive spiral in equilateral shells like *Pecten* and *Glycymeris* (in which it coincides with the median rib or interspace).

In such shells the direction of displacement in three-dimensional space of any point on the secreting edge of the mantle at any particular moment is considered to be the resultant of two components, a radial one (directed outward from the beak in the plane of the generating curve) and a transverse component (directed perpendicularly to this plane, to the rotation of which it is due). The normal axis or **demarcation line** therefore may be defined alternatively as the locus of points on the surface of the valve where the transverse component has its maximum effect.

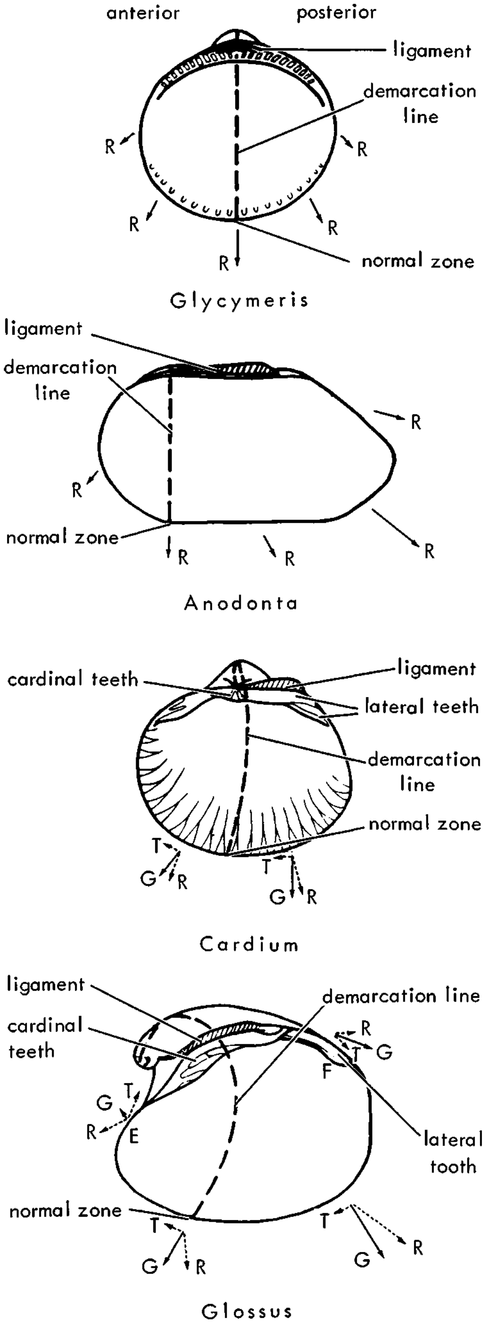

FIG. 72. Bivalve shell geometry—diagrams showing growth components of valves radially *(R)* and tangentially *(T)* with resultant growth direction *(G) (122).*

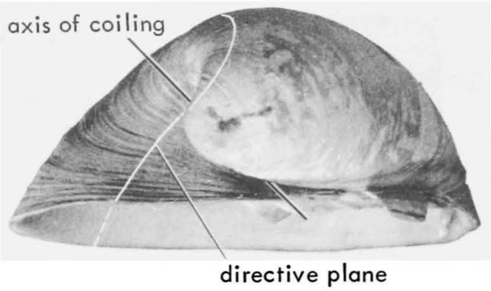

FIG. 73. *Glossus humanus* (LINNÉ), Neog.-Rec., Eu., slightly oblique view showing approximate position of axis of coiling and directive plane, ×0.78 (Nuttall, n).

In inequilateral forms the demarcation line diverges from the directive rib. Both OWEN and YONGE hold the view that in many bivalve shells a gradual twisting around of the generating curve occurs within its own plane, which is due to a third component, tangential to its margin. The effect of the tangential component would be, as it were, to "bow" all elements of radial ornament in the direction in which it acts. Thus, if this direction is toward the posterior end of the shell, the median rib, planar and "directive" in the absence of the tangential component, becomes bowed at right angles to its length so as to present a posteriorly facing convexity. If taken to a logical conclusion, it will be seen that some rib posterior to it, which would have had a posteriorly facing concavity in the absence of the tangential component, now becomes flattened out by virtue of the latter, becoming, in fact, the "directive" rib of LISON.

No mathematical calculations of the type made by LISON have been attempted to test the true relationship of the demarcation line in relation to the generating curve.

In addition, STASEK *(151)* has shown from careful measurements of certain inequilateral forms that considerable scope for disagreement in positioning of the demarcation line exists. For all these reasons, we agree with him that this term is too imprecise. STASEK also pointed out that confusion seems to have arisen from considering the three components of growth as forces acting to effect shell shape by a sort of vector addition. He rightly stressed that they simply describe the directions in which growth has occurred.

OWEN's rejection of the usefulness of LISON's concept of the directive plane cannot be accepted. He based his argument mainly on examples such as *Chama* and *Glossus* in which this plane apparently does not exist. In fact, it would seem that, apart from irregular forms such as oysters, all bivalves do possess a directive plane which is normal to the axis of coiling of the valve. Confusion may have arisen because in many cases it is impossible to find a straight or directive rib. In most species of *Chama,* all the ribs appear as turbinate spirals, because the directive plane is parallel, or almost so, to the valve surface. In the case of *Glossus* (Fig. 73) each valve grows in the same way as a virtually planispiral gastropod. To explain the form of *Glossus,* with its unusually coiled umbones, it is not necessary to postulate a gradual twisting round of the generating curve (and of the coiling axis) as growth proceeds. In multispiral genera such as *Diceras* the helicoid spiral stage, exhibited by most gastropods, is reached; the coiling axis passes through the nucleus and down through the "columella." In such cases no rib could be straight or "directive" and the directive plane (by definition perpendicular to the coiling axis) would merely touch the earliest part of the shell.

More recently RAUP (1966) has produced computer-constructed theoretical shell forms applicable to all of the important molluscan classes and to brachiopods. These are based on four parameters: 1) shape of the generating curve *(S)* which corresponds to the commissure in bivalves and brachiopods, and the aperture of ammonoids and gastropods; 2) rate at which the whorl expands *(W)*; 3) distance of the generating curve from the axis of coiling *(D)*; and 4) rate of whorl translation *(T)* (i.e., the rate at which the generating curve moves down the y-axis), to produce asymmetrical forms such as spired gastropods and inequilateral bivalves (Fig. 74,*1*). These parameters other than the shape of the generating curve (which is normally unrelated to any geometrically correct figure) may be altered to produce different shell forms (Fig. 74,*2*). These findings appear to be an amplification of Lison's work, and it seems likely that some mathematical relationship exists between angle of incidence and ratio of increase along the x-axis (*W* and *D*) compared with increase along the y-axis *(T)*.

So far, the exceptions to equiangular spiral growth and the problems associated with bivalvedness have been largely ignored. We may see that when the generating curve has turned through an angle greater than 180° from the definite beginning of the spiral course, the earlier part of the spiral (that is, part of the umbo of the valve) begins to project beyond the plane of the commissure (i.e., the generating curve at this later growth stage).

Both Stasek *(151)* and Raup *(140b)* have explored some of the methods by which mutual interference of the umbones of the

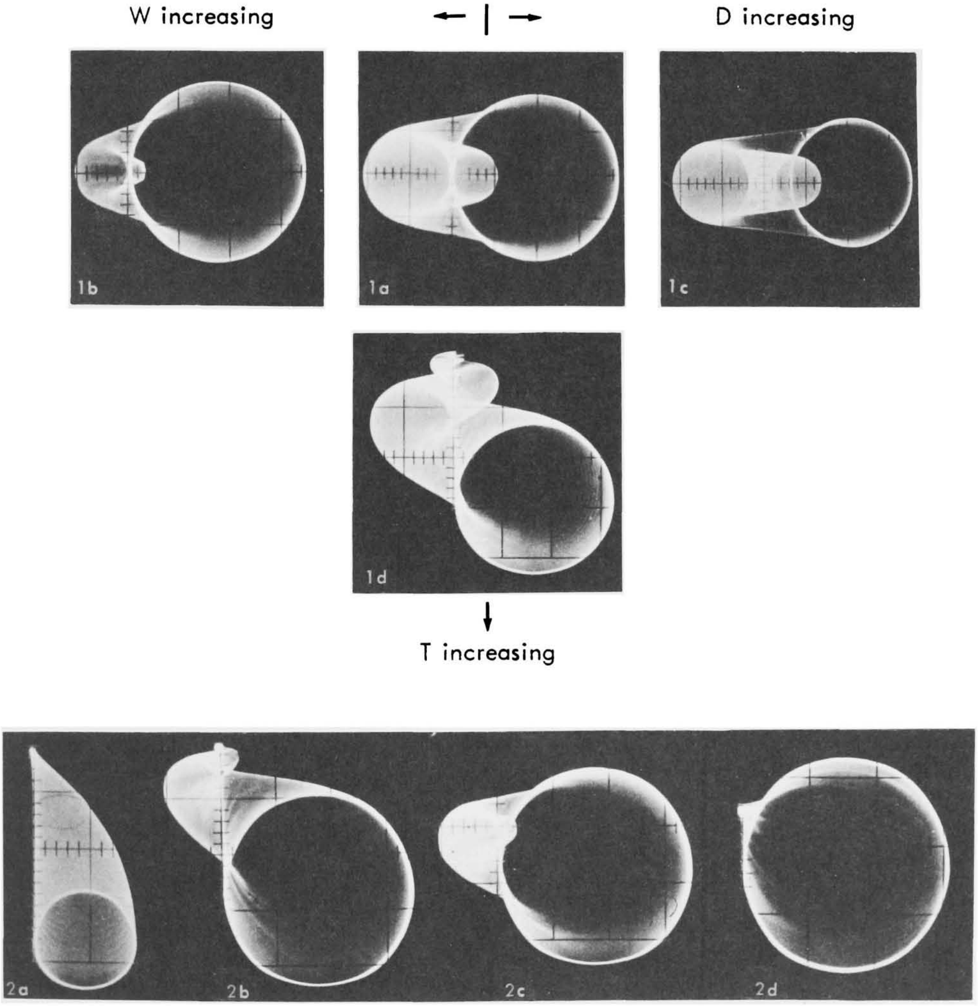

Fig. 74. Bivalve shell geometry—parameters and models of shell forms in mollusks *(140)*.——*1*. Explanation of parameters used in construction of theoretical shell forms (generating curve in all cases circular); *1a*, typical planispiral gastropod; *1b*, bellerophontid gastropod; *1c*, evolute ammonoid; *1d*, spired gastropod.——*2*. Models of shell forms found in Bivalvia; *2a*, typical rudist with high *W* and high *T*; *2b*, *Diceras*, with relatively low *W* and intermediate *T;* *2c*, *Gryphaea*, with relatively low *W* and low *T;* *2d*, slightly inequilateral shell of typical form with high *W* and low *T* (see p. *N*88).

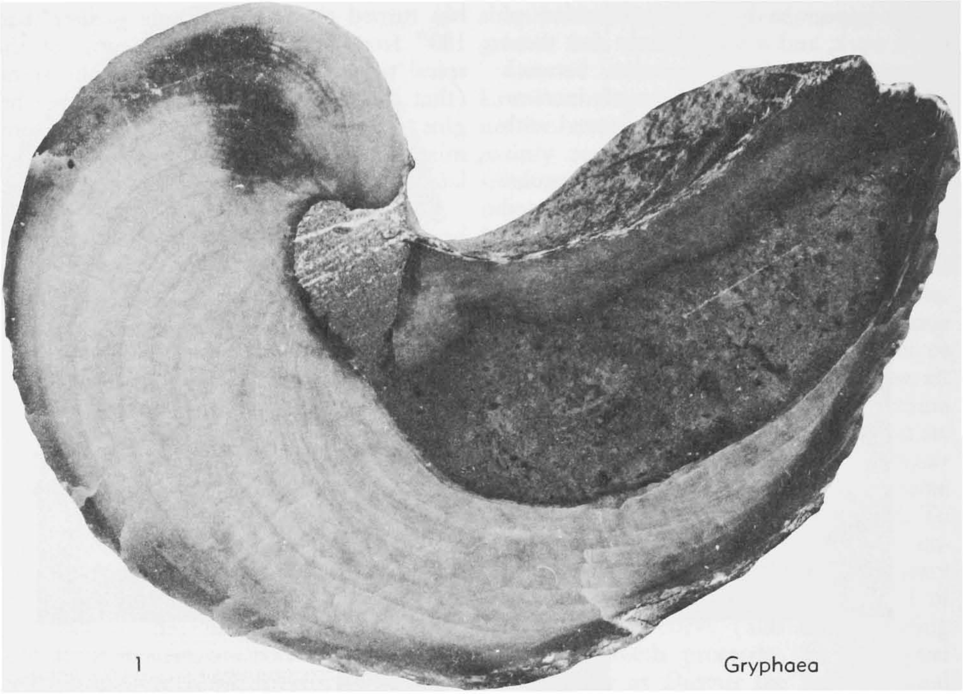

FIG. 75. Bivalve shell geometry—longitudinal section through *Gryphaea arcuata* LAMARCK, L.Jur.(Lias.), Eng., showing how mutual interference of umbones in growth of valves is avoided even when plane of generating curve is coiled through more than 180°, ×2 (Nuttall, n).

two valves is avoided. In the first place, the rate of whorl expansion is usually very high and the umbo does not project, because adult size is reached before the spiral has moved through half a whorl. Another important property of this rapidly expanding type of spiral shell is that it provides plenty of space for the attachment of adductor muscles in a mechanically advantageous position. Their strength will be in proportion to their cross-sectional area and in order for them to be effective this must be as large as possible in relation to the mass and volume of the shell. This problem is avoided by the possession of raised platforms or myophores, found in forms such as rudists which do not exhibit rapid whorl expansion.

In genera such as *Arca,* the umbones are separated by a broad cardinal area. In some shells (e.g., *Pecten, s.str.*) one valve is slightly concave and lies entirely below the projecting umbo of the convex valve. In *Gryphaea* the umbo and much of the earlier part of the left valve becomes infilled with callus which would serve to keep the shell balanced on the substrate (Fig. 75). As in many other oyster-like genera, the right valve is built up by the internal addition of successively larger lamellae. As interlocking teeth are absent, the valves are held together by the single adductor muscle and the ligament, the attachment of which must change position throughout growth. In this way the right valve is free to move away from the left umbo.

A high translation rate in genera such as *Diceras* and *Glossus* causes the umbones not only to be prosogyrate but also to coil outward from one another. In some shells (e.g., *Ceratomya, Corculum*) one umbo either lies slightly in front of the other or alternatively the valves rotate about slightly different axes, so that when the valves open the umbones pass sideways on to each other rather like the blades of a pair of scissors.

In a few shells (e.g., *Ensis ensis, Tellina (Peronaea) planata*) one umbo is known to penetrate the other. In any case, it is probable that in most bivalves, even when a cardinal area is absent, a certain amount of growth occurs along all parts of the dorsal margin of the two valves, as a result of which the umbones remain just sufficiently separated to allow the two valves to hinge freely along this margin.

It must be emphasized that the basis of the foregoing discussion, namely, that bivalve shells retain the same shape throughout growth, is only an approximation to the truth. The periodicity of elements of concentric ornament, in addition to irregularities resulting from pauses and accidents during growth, obviously must mean that every addition to the shell is not exactly gnomonic, and in many shells study of the growth lines will indicate a slight progressive change in shape as the valves grow. Nevertheless, the approach to study of the geometry of bivalve shells outlined above throws much light on its characteristics and provides a basis, not yet fully explored, for the comparison of shells of different species.

[*End of section by L. R. Cox and C. P. Nuttall.*]

ONTOGENY

EMBRYONIC AND LARVAL DEVELOPMENT IN MARINE BIVALVES

Three types of early development have been distinguished in marine Bivalvia. In the commonest (**planktotrophic**) mode of development the mollusk emerges from the egg early in ontogeny and passes through the full succession of swimming larval stages, leading a pelagic life and feeding on phytoplankton for a relatively long period before sinking to the bottom and undergoing metamorphosis (Fig. 76). A second type (**direct development**) involves the omission of any pelagic larval stage, the young bivalve hatching out only when sufficiently advanced for bottom life. The third type (**lecithotrophic larval development**) is more or less intermediate between the other two; the developing animal, when an embryo within the egg, derives sufficient nutrient matter from the relatively large yolk mass to sustain it during a definite but rather short ensuing larval life. It has no need to feed on phytoplankton before settling and undergoing metamorphosis. In such species as *Pandora inequivalvis* Linné the animal passes through the entire series of free-swimming larval stages, but very quickly. In other cases (*Ostrea chilensis* Philippi) the animal does not hatch out until it is a fairly advanced veliger (Fig. 77). **Brood protection,** by which the ova are retained and fertilized and the embryo undergoes a varying degree of development in a brood pouch, usually within the gills of the parent animal, may be associated with all three types of development, although it is most common in the second and third types. Even direct development, however, may occur in species that discharge their ova for external fertilization.

The embryology and larval history have been investigated under laboratory conditions in a number of species which undergo development of the first type. The quantity of eggs shed into the surrounding water by each spawning individual is enormous (5 to 12 million in the case of *Mytilus edulis* Linné), while spermatozoa are discharged in still greater and quite incalculable numbers. The diameter of the yolk-mass of ripe eggs is between 40 and 85μ, the size (70 μ in *M. edulis* and 50μ in *Cardium edule* Linné) being fairly constant in any one species. In *M. edulis* the spermatozoa have a head 5μ long and a tail 35μ long. The ova are at first enclosed in a thin gelatinous membrane.

After fertilization, cleavage proceeds rapidly and the invagination process of gastrulation is complete within about 12 hours in a number of species in which it has been investigated. A circle of relatively large cilia forms at the front end of the larva, anterior to the mouth, and, in a period varying from 12 to 24 hours after fertilization, the young animal enters upon the **trochophore** stage of its existence. Beating of the cilia causes it to rotate, and as the result of this movement the enclosing membrane ruptures and the larva commences a swimming existence (Fig. 78). With rapid development of the

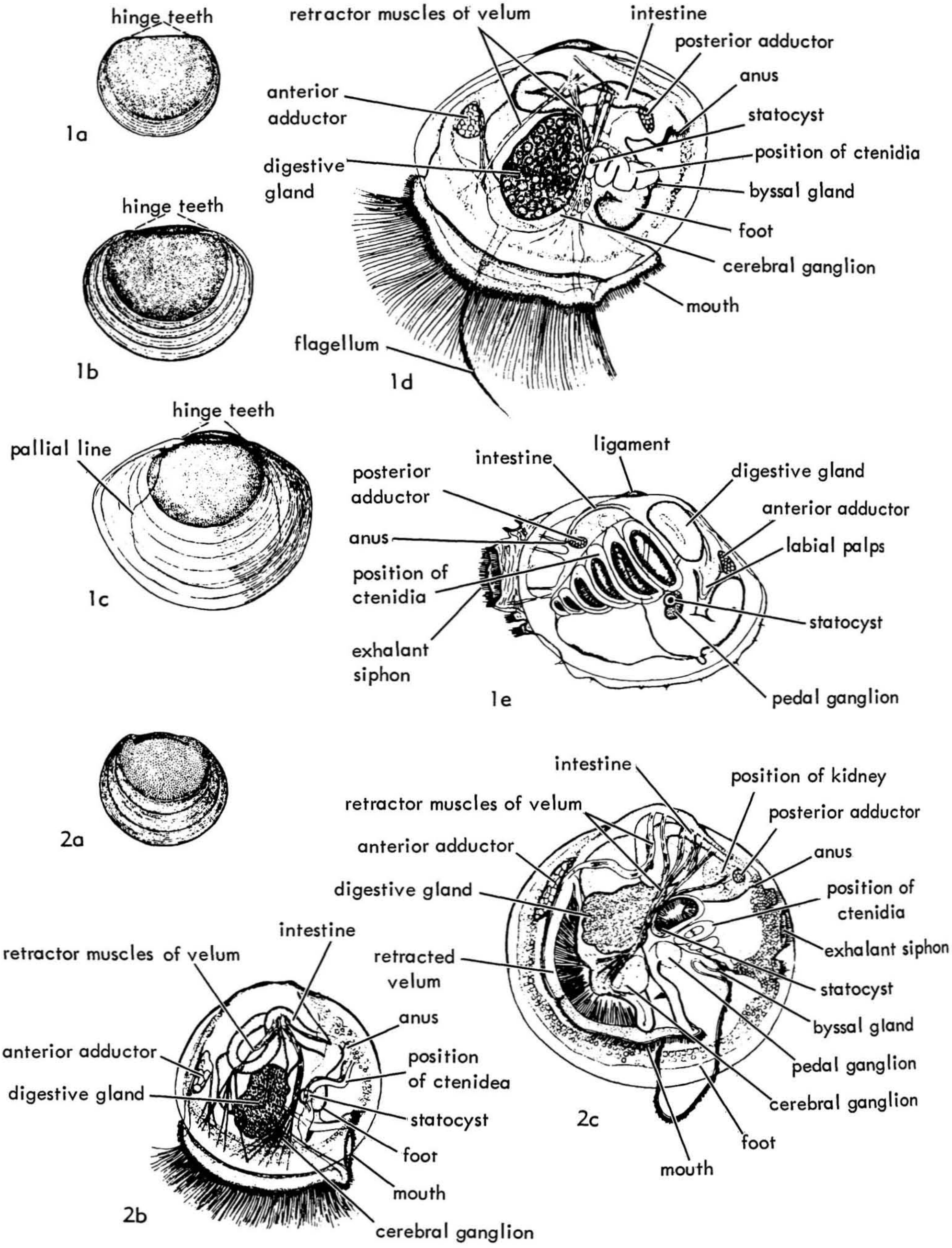

FIG. 76. Bivalve ontogeny—shells and anatomical features of larvae, all much enl. *(180)*.——*1. Cultellus pellucidus* (PENNANT), Rec., E.Atl.; *1a,* prodissoconch I (=veliconch); *1b,c,* later larval growth stages of shell; *1d,e,* anatomy of larva and animal at early postlarval growth stage.——*2. Zirfaea crispata* LINNÉ, Rec., E.Atl.; *2a,* prodissoconch and early subsequently formed shell; *2b,c,* anatomy at young and late larval stages.

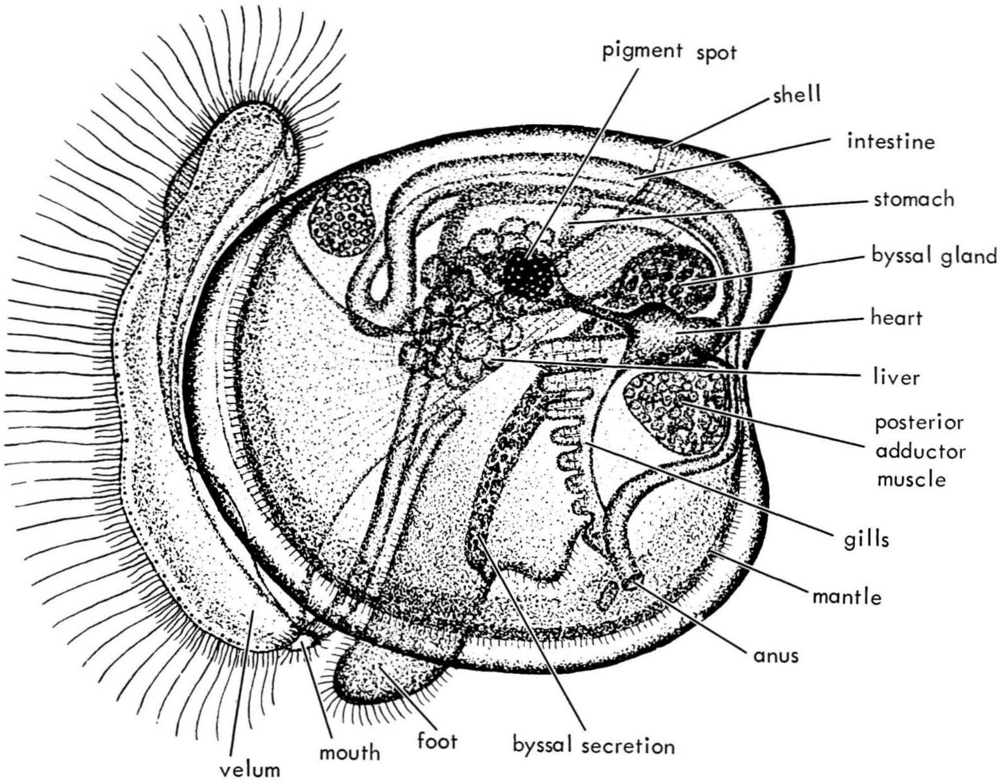

FIG. 77. Bivalve ontogeny—anatomy of veliger larva of *Ostrea virginica* GMELIN, Rec., W.Atl., much enl. (Prytherch, 1934).

velum (an anterior crownlike structure with long cilia) from the ciliated region already mentioned, the larva passes (17 to 48 hours after fertilization) into the **veliger** stage. Whereas trochophore larvae do not ascend into the plankton, velum-bearing larvae constitute one of its most important elements, and as such have been intensively studied in recent years.

The earliest-formed shell is secreted by the shell gland, which begins to appear on the posterodorsal part of the larva as soon as invagination has occurred. It is at first a patch of relatively large cells which form a thickened part of the ectoderm and begin to secrete a thin cuticle. The patch soon becomes divided into left and right halves along a median line (the future hinge line). In each half the cells become flattened and start secreting a calcareous shell valve. The two valves grow rapidly until, about three days after fertilization, they are large enough to cover the soft parts. At the same time larval retractor muscles, which serve to contract the whole body of the larva so that it can be withdrawn between the valves, have developed; in *Cardium edule* there are three pairs of these. Rudiments of the mantle have also arisen from the line of junction of shell gland tissue and ordinary epithelial cells, forming lateral folds that have begun to grow downward as left and right mantle lobes.

Whereas the term **veliger** was originally and is still commonly applied to the velum-bearing larva up to the time of metamorphosis, some authors, following WERNER (1937), now consider the veliger stage proper to end when secretion of the valves of the shell is taken over from the shell gland by the mantle. At this stage a primitive digestive system (esophagus, stomach,

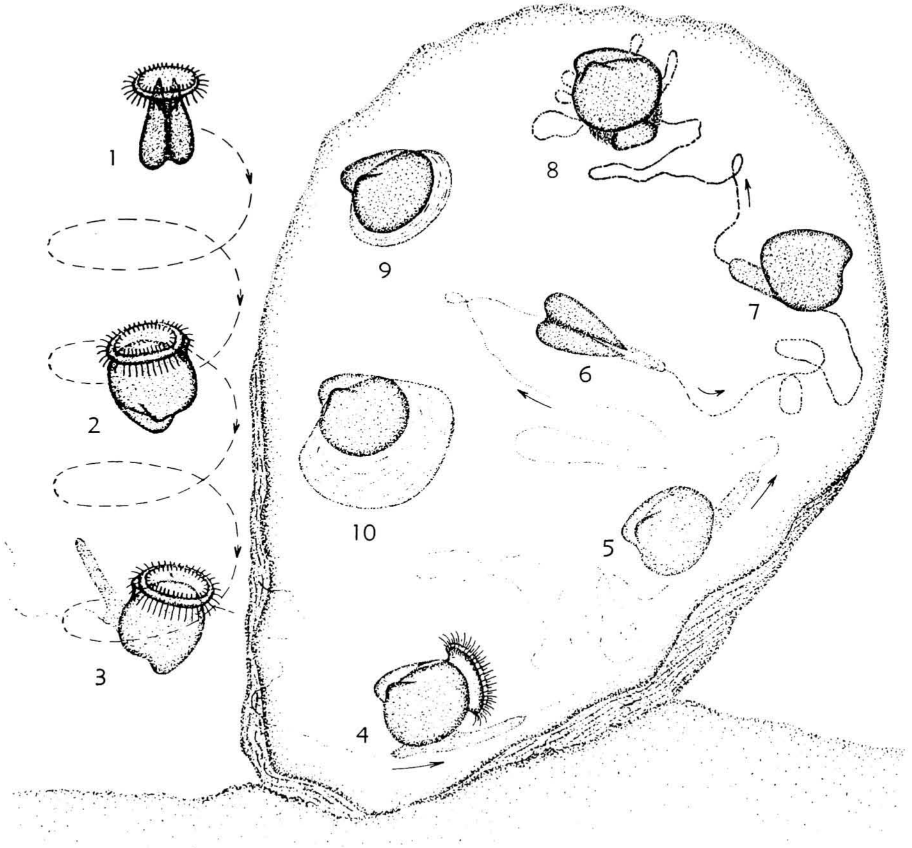

FIG. 78. Bivalve ontogeny—diagram of "settling" steps in development of *Ostrea virginica* GMELIN, Rec., W.Atl., much enl., with earlier stages proportionally most enl. (Prytherch, 1934).——*1,2*. Side and end views of swimming larvae.——*3,4*. Searching phase of larval growth.——*5-7*. Crawling phase of larval growth.——*8*. Fixation of larva to substrate.——*9,10*. One and two-day old spats.

intestine, and rectum) has appeared, together with a rudimentary anterior adductor in addition to the retractor muscles just mentioned. The two valves are D-shaped, hinging along a straight, toothless margin where they are joined by their outer cuticle, and are thin, translucent, and devoid of growth lines. The term prodissoconch having been originally applied to the complete larval shell, this earlier stage has been termed by WERNER (followed by other authors) the **prodissoconch I**, commonly abbreviated to "prod. I." It is virtually the same as the **protostracum** of BERNARD. The size of the prodissoconch I ranges from about 70 to 150 microns and is, again, fairly constant in any one species.

Secretion of the two valves is taken over by the mantle in an average period of about 10 days after fertilization, the total time elapsing before metamorphosis varying according to the species and temperature, and ranging perhaps from 2 to 6 weeks. The shell borne by the larva during the last and longest period of its existence is termed by WERNER the **veliconch.**[1] The veliconch consists of the prodissoconch I and of a newly added zone of mantle-secreted shelly matter, the **prodissoconch II**, on which distinct growth lines are visible. It slowly loses the D-like form of prodissoconch I and at the same time its convexity usually increases,

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[1] Originally, *veliconcha*, but better abbreviated to *veliconch* for uniformity with prodissoconch, etc.

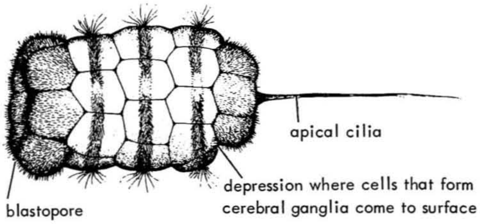


FIG. 79. Bivalve ontogeny—embryo of *Yoldia limatula* SAY, Rec., Atl., 45 hours old, much enl. *(43)*

distinct umbones commonly appear, and it acquires a variety of shapes—oval, trapeziform, or subtrigonal, according to the genus to which it belongs. A ligament and primitive hinge teeth, described more fully below, appear. The size of the velum increases and the digestive system becomes more elaborated, while further permanent soft organs (cerebral ganglia, gills, foot and byssal gland, siphons, posterior adductor) gradually become differentiated. The term **pediveliger stage** has been applied to a late larval stage marked by the coexistence of a velum and of a foot that has undergone rapid growth in preparation for a creeping existence. The length of prodissoconch II at metamorphosis ranges from about 0.2-0.6 mm. and may vary considerably in a single species.

Among bivalves that combine lecithotrophic development with a short free-swimming larval stage, the Nuculacea (several species of which have so far been investigated) are of particular interest. Instead of having a velum of the usual type, these forms develop a barrel-shaped structure, consisting of about five rows of large polygonal cells, which encases the growing larva and its shell (Fig. 79). About three of these rows bear cilia, the beating of which causes the larva to rotate and swim. The whole structure breaks up and is discarded at metamorphosis.

Prodissoconch II is ill-defined or absent in larval shells that have undergone lecithotrophic development, but stages I and II are both distinguishable on the prodissoconch of forms in which development to the bottom stage has been direct. They differ, however, in appearance from the corresponding stages of planktotrophic larval shells and can be distinguished by an experienced worker. It is believed that examination of the prodissoconchs of fossil bivalves, when well enough preserved, will throw light upon the mode of early development.

EMBRYONIC AND LARVAL DEVELOPMENT IN FRESH-WATER BIVALVES

Fresh-water bivalves belonging to the family Dreissenidae have a free-swimming

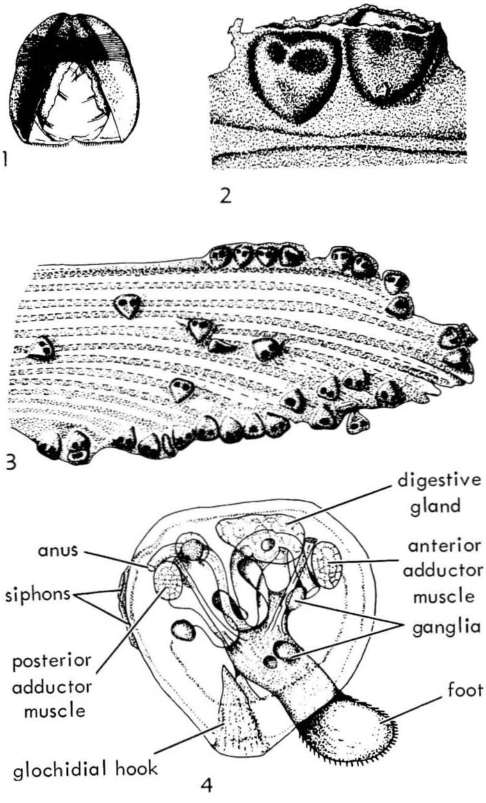


FIG. 80. Bivalve ontogeny—early growth stages of fresh-water mussels, much enl. (Guthrie & Anderson, from Lefevre & Curtis 1910 [1912]).——*1*. Hooked glochidium of *Symphynota* before attachment to fish.——*2*. Young glochidia of *Anodonta* 24 hours after attachment to fin of carp.——*3*. Same, 36 hours after attachment, glochidia well embedded in tissue of fin.——*4*. Juvenile *Symphynota* after end of parasitic phase, adult structures developed in association with persistent glochidial hook.

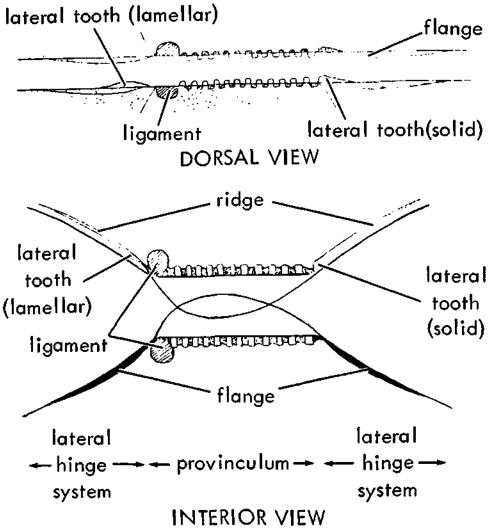


FIG. 81. Bivalve ontogeny—components of larval hinge showing terminology *(141)*.

larval life and pass through trochophore and veliger stages like most marine forms. The early development of *Dreissena* has been more thoroughly investigated in the laboratory than that of any other bivalve. Members of the families Corbiculidae and Pisidiidae undergo direct development in brood pouches within the mantle cavity of the mother, usually between the gill lamellae.

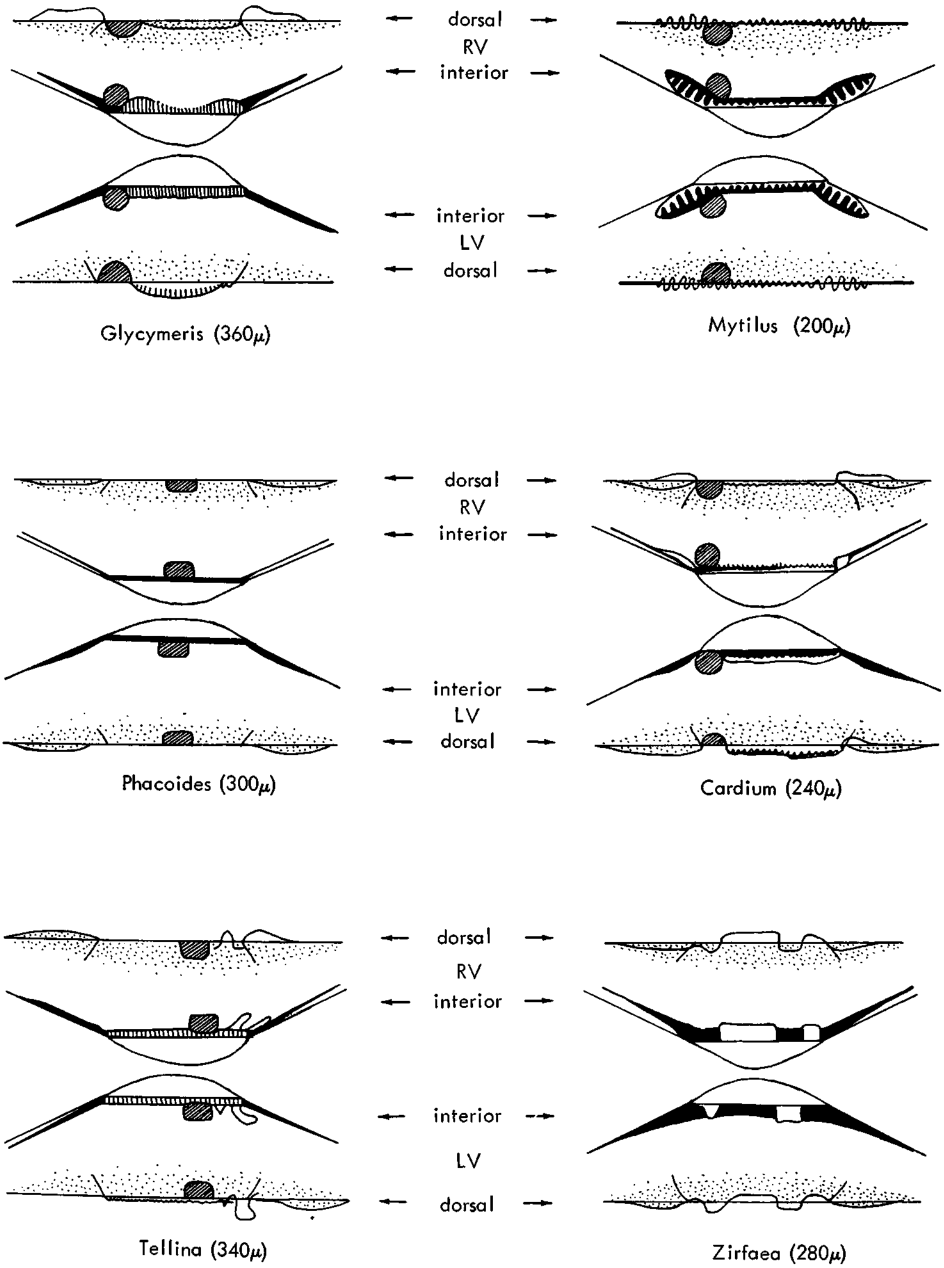
Many of the Unionacea are of particular interest in passing through a stage in which the larva is parasitic on fishes. In *Anodonta* and *Unio,* for example, the eggs are fertilized in the suprabranchial chamber of the parent mollusk and then pass to the interlamellar spaces of the gills, where development proceeds to a certain stage, when some stimulus (such as the movement of a passing fish) results in the expulsion of the larva into the surrounding water. This larva, termed the **glochidium**, already has a shell of two valves joined by a strong larval adductor muscle. There is no mouth or anus, a larval mantle serving as an organ of nutrition. A rudimentary foot is present, bearing a long filament. In the glochidium of *Anodonta* the margin of each valve opposite the hinge bears a barbed, hooklike projection; this is absent in that of *Unio,* but the corresponding part of the margin is extremely sharp. If the glochidium is successful in reaching a fish it attaches itself to a fin or gill by grasping it by means of the two valves of its shell, drawn together by the adductor (Fig. 80,*1-3*). A cyst soon forms in the tissues of the fish, and within this the larva completes its development, emerging when it is ready for bottom life (Fig. 80,*4*). The duration of the parasitic period depends to some extent on the temperature; for *Unio* it is usually 14 to 20 days but may be as long as 36 days; for *Anodonta* it is said to range from 12 to 80 days. The shell of the glochidium may remain as a prodissoconch at the umbo of the adult unionid, but it is usually removed by erosion.

The larval history of an African freshwater bivalve, *Mutela bourguignati* (ANCEY), includes a parasitic stage which is quite unlike that of glochidium-producing unionids. The eggs first develop in the inner demibranchs of the gills into spherical larvae covered dorsally and laterally by a thin pellicle; anteriorly each larva bears a tentacle about 70 times its length. When about 0.2 mm. in diameter the larvae are discharged into the surrounding water and proceed to become parasitic on fish. Each one (termed the *haustorial larva* at this stage) develops into a bud which remains clear of the host and a stalk which penetrates into the latter and through which nourishment is conveyed from it. The two shell valves, enclosing the developing vital organs of the mollusk, originate within the bud. Eventually, when about 1 mm. long, the young bivalve is released to assume its bottom life, soon casting off the long stalk which it bears. Many South American unionids produce yet another type of larva, known as the *lasidium larva,* but their developmental history has yet to be worked out in detail.

A question which paleontologists still have to investigate is when the Unionacea first acquired a parasitic larval habit during their long geological history.

HINGE STRUCTURES OF PRODISSOCONCH

No differentiated hinge structures are seen in the straight-hinged or D-shaped stage of the larval shell (prodissoconch I), but after the transition to the mantle-secreted prodissoconch II a larval ligament and a series of larval teeth appear (Fig. 81). Rees *(141)*, after studying 77 types of bivalve pelagic larvae from the North Sea, was able to distinguish 18 basic types of larval hinge in this particular material. He



Glycymeris (360μ)

Mytilus (200μ)

Phacoides (300μ)

Cardium (240μ)

Tellina (340μ)

Zirfaea (280μ)

Fig. 82. Bivalve ontogeny—dentition of prodissoconch hinges in six North Sea genera, Rec. (diameter of larval shells in microns indicated) (Cox, from *141*).

found that these were characteristic of definite superfamilies, except that one type was common to the Pectinacea and Anomiacea, and another to the Ostreacea and Pteriacea. The straight median part of the hinge margin, termed the **provinculum**, bears the most obvious teeth, and REES recognized four main types of such dentition. In the first type each valve bears several or numerous small rectangular teeth or crenulations (recalling the taxodont teeth of the Nuculacea and Arcidae) arranged along a relatively thick provinculum; in the second type there are only one to three strong rectangular teeth along a relatively thick provinculum; in the third type the teeth form one or more elongated projections on a thin provinculum; and in the fourth type the right valve has a thin strip of small spiky provincular teeth. Teeth are entirely lacking on the provinculum in the Lucinacea and the Erycinacea.

Further structures, constituting the **lateral hinge system**, may be present along the valve margins anterior and posterior to the provinculum (Fig. 81, 82). In the left valve these parts of the margins have a projecting flange which is received in the right valve between the thin edge of the dorsal margin and an internal ridge. The proximal end of this ridge may bear a toothlike projection consisting either of a lamina underlying the marginal flange of the other valve or of a more solid tooth that comes into contact with the outer edge of the provinculum of the other valve when the shell is closed. Special teeth, variously shaped and commonly larger than those already mentioned, are also present in some species, usually at one end of the provinculum. The short transverse larval ligament is external in the Solenacea but internal in the other groups studied. When internal it occupies a recess interrupting the denticles of the provinculum, and its position is posterior except in the Lucinacea (in which it is median), in the Erycinacea and Tellinacea (in which it is anterior to mid-length), and in many Ostreidae.

RANSON'S (1948) work on the prodissoconch in the Ostreidae is of interest as showing that its hinge structure may vary to some extent in the same family. He found that three different types of hinge are present and used them as a basis for generic classification. The types are *(a)* provinculum with five teeth, ligament just beyond anterior end of provinculum, further series of crenulations along anterodorsal margin; *(b)* provinculum with two teeth at each end and gap in middle, ligament well beyond anterior end of provinculum; *(c)* teeth as in *(b)* but ligament below provinculum, between its center and anterior end. The very anterior position of the ligament in the larva of many species of Ostreidae is an unusual feature, and was long ago commented upon by BERNARD.

CHANGES DURING AND AFTER METAMORPHOSIS

When the larva assumes a bottom life (the episode of "spatfall" in the case of oysters) significant changes take place in its organization, the most important being the degeneration of the velum, which is no longer required as an organ for swimming and food collecting, and the loss of the larval retractor muscles. The byssus gland begins to function, for, as already seen, the byssus may play an important part in adaptation of the young mollusk to its new mode of life. At this stage the foot begins to grow rapidly when it is to function as an organ of locomotion and burrowing in the adult mollusk. In the Ostreidae, on the other hand, this organ performs its last function by holding the left valve in position while the fluid that cements it to the substrate is poured out by the byssal gland; this task accomplished, it quickly atrophies. In probably all bivalves the later larval stages have two equal adductor muscles, but in forms in which the adult is monomyarian the anterior of these dwindles away very rapidly after settlement. The loss is almost complete in about 90 hours in the case of *Ostrea edulis* LINNÉ, by which time the length of the shell has increased from 0.3 mm. at the time of spatfall to 0.6 mm. Loss of the anterior adductor is accompanied by migration of the posterior adductor and by changes in the positions of the internal organs, resulting in wide divergence between directions of the oro-anal and cardinal axes.

These changes are also almost completed within a few days after settlement. The gills continue to grow by increase in the number of filaments, and other soft organs which are to be retained in the adult mollusk continue to develop. Whereas the prodissoconch is devoid of ornament, the ribbing and other sculptural features characteristic of the adult shell commonly appear even on the earliest growth stages of the **dissoconch** (postlarval shell), which, except in attached forms, rapidly assumes the shape of the full-grown shell.

We are indebted to BERNARD and others for our knowledge of the earlier stages in the development of the hinge structures of the dissoconch. BERNARD made large collections of prodissoconchs and young dissoconchs, mainly from Recent shell sands and from various fossiliferous formations of Tertiary age, and was able to construct series showing successive ontogenetic stages in a number of species, in many cases confirming his identifications by examining prodissoconchs still preserved on the beaks of adult shells. His most important observations relate to the heterodonts and have been summarized when explaining the system of hinge notation which he devised in collaboration with MUNIER-CHALMAS. Similar work on some other important groups still living, such as the Unionacea and Trigoniacea, and on many extinct groups (if only the necessary material is obtainable) has yet to be accomplished, and should throw light on the relations of these groups to the heterodonts. His work on various Palaeotaxodonta and Pteriomorphia may be reviewed briefly.

In all the bivalves investigated the denticulations or crenulations of the provinculum persist in the earlier dissoconch stages and at first even increase in number and size, although they ultimately disappear. A hinge plate (if present in the adult shell) gradually becomes defined on the ventral side of the provinculum and extends beyond this anteriorly and posteriorly. The dissoconch teeth then appear on it in succession and the ligament undergoes a series of changes.

In Arcoida investigated by BERNARD the first two teeth (i.e., one in each valve) arise simultaneously on the posterior side of the beak below the provincular crenulations, to be followed very soon after by the first anterior pair. These earliest teeth (like the first few that succeed them) have a longitudinal orientation, and those in the right valve are dorsal to those in the left. Except for two small pairs that appear next in some species on the dorsal side of the earliest ones, the next few (but not necessarily all) subsequent teeth arise in order at the two extremities of the series, and not by intercalation between previously formed teeth at the middle of the hinge or elsewhere. (Investigations by subsequent workers suggest that this does not apply to all Arcoida.) In *Glycymeris obovata* (LAMARCK) the first two pairs of definitive teeth are present when the shell is 0.4 mm. long, and there are five pairs when the length is about 0.7 mm. The later-formed teeth have from the first the orientation (whether dorsoventral or longitudinal) they possess in the adult shell, and during growth the inner end of each of the earlier-formed, longitudinal teeth, occupying the middle of the hinge line, usually bends ventralward; the whole tooth eventually assumes a dorsoventral orientation. In *Nucula* and *Nuculana,* the development of the hinge teeth follows much the same course as in the Arcoida, but all teeth except the very first pair are chevron-shaped from the beginning, the downbending of the inner end of each being regarded by BERNARD as an "exaggeration and acceleration" of the process observed in the Arcoida. In *Malletia,* on the other hand, several of the earliest-formed teeth are at first straight and longitudinal. In *Nucula* and *Malletia* there is evidence of the obliteration by the ligament of some of the earlier-formed teeth, lying at the middle of the hinge, during growth of the shell.

In *Mytilus* a few small, almost longitudinal teeth develop along the posterodorsal margin some distance beyond the row of crenulations persisting from the prodissoconch, but are obliterated as the ligament extends posteriorly. Similar teeth appear along the margin anterior to the beak, also beyond the row of crenulations, and some of these persist to form the dysodont teeth of

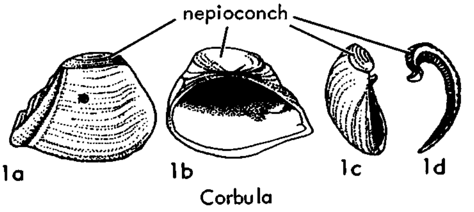


FIG. 83. Bivalve ontogeny—*Corbula costata* J. DE C. SOWERBY, U.Eoc.(Barton), Eng., showing change in valve shape from early form (nepioconch) as growth proceeds *(188)*.

the adult mussel. In a species of *Pteria* it was found that definitive teeth do not make their appearance until a later stage in ontogeny than in the forms just mentioned. From the first these belong to two distinct series; the posterior teeth are elongate lamellae almost parallel to the hinge margin, the more ventral ones appearing first; the anterior teeth are short, and tuberculate or lunate in shape.

It is to be assumed that, as soon as secretion of the shell and ligament are taken over by the mantle with the resulting appearance of prodissoconch II, the ligament becomes differentiated into its fibrous, calcareous and its lamellar, noncalcareous parts. It would also be expected that the ligament of the adult shell would be derived from that of prodissoconch II. In the Nuculidae BERNARD observed that this early ligament expands in a ventral and anterior direction as the hinge plate develops and gives rise to the definitive ligament, which remains internal. In *Mytilus edulis,* on the other hand, he found that, at an early stage in the development of the dissoconch (length 0.6 mm.), a second ligamental depression appears a short distance posterior to the original depression. It is from this second center that the definitive ligament develops rapidly, until ultimately it extends along a considerable part of the posterodorsal margin; the original ligament apparently atrophies. The exact process involved in the lateral separation of the two constituents of the ligament in forms in which there is a cardinal area has yet to be observed. In the early ontogeny of members of the Arcoida it can be seen how the ligamental depression, at first internal, becomes marginal and then mainly external. Actual secretion of new ligament cannot, however, take place externally to the margin, since the mantle does not extend beyond the latter. In forms in which the lamellar ligament is inserted in grooves on the cardinal area, diverging to form the arms of chevrons, it is clear that the original center of secretion of lamellar ligament at the margin must divide into two, which draw apart and trace out divergent courses on the cardinal area as this increases in width and the hinge line in length. Further paired centers of secretion must then arise in turn at the middle of the hinge and separate in a similar manner. In the Noetiidae, however, there are no such paired centers of secretion, the ligamental grooves on the cardinal area being perpendicular to the hinge margin.

ABRUPT POSTNEANIC CHANGES IN SHELL CHARACTERS

In addition to the changes in features of the shell corresponding to the transition from prodissoconch I to prodissoconch II and from the latter to the early dissoconch (the neanic shell of HYATT's terminology), a study of the ontogeny in some species shows that rather abrupt changes in shape and ornament may occur at later periods. In some instances the mollusk is apparently free-living for some time after metamorphosis and then becomes cemented; in other cases it is not at present possible to correlate the change in shell characters with a known episode in life history.

WRIGLEY *(188)* has called attention to several such cases of discontinuity. In some species of *Corbula* there is a distinct apical shell (much larger than the protoconch) which appears perched on top of the complete shell, from which it can be detached. In the Eocene species *Corbula costata* J. DE C. SOWERBY (Fig. 83) this apical shell, termed by WRIGLEY the nepioconch, is about 10 mm. long, ornamented with fine, regular concentric threads, and devoid of a carina, whereas immediately following the discontinuity in growth the ornament changes to irregular concentric rugae and a posterior carina appears. Two such abrupt changes are observable in the Eocene species *Callocardia nitidula* (LAMARCK) and *Plicatula filamentosa* CONRAD, the first marking the transition from the nepioconch to the mesoconch (in WRIGLEY's terminology), and the second the change from the mesoconch to the part of the shell bearing the adult ornamental pattern. In *Plicatula* (Fig. 84,*1*) the nepioconch is smooth, the mesoconch is ornamented with fine radial threads, while the last-formed part of the shell bears broad radial ribs.

In the Chamidae the adult shell is inequivalve and rather irregular in form as the result of attachment by one valve, while the umbones are strongly prosogyrate and the hinge teeth (2 in the attached and 1 in the free valve) are thick, amorphous, and longitudinally elongate, as the result of the coiling of the valves that has taken place during growth. The early dissoconch, about 2.5 mm. in length, preserved at the umbo in some specimens, is, however, equivalve and very different from the adult shell in shape and appearance; it was obviously unattached. In the genus *Echinochama,* in which the change is strongly marked, this neanic shell is rectangular in outline, with anterior beaks and ornament of a few regularly spaced, thin concentric lamellae (Fig. 84,*2*). The dentition, consisting of two cardinal teeth and one elongate anterior lateral in each valve, is quite unlike that of the adult shell. It is difficult not to believe that this early, heterodont-like shell throws considerable light on the origin and affinities of the Chamidae. It may also be significant that no such neanic shell has ever been found in any of the Mesozoic rudists, some so similar to *Chama* in adult form and dentition.

In the family Pectinidae, those species which have been included in the genus *Hinnites* DEFRANCE resemble a typical *Chlamys* in shape and ornament until they become attached by the growing part of the

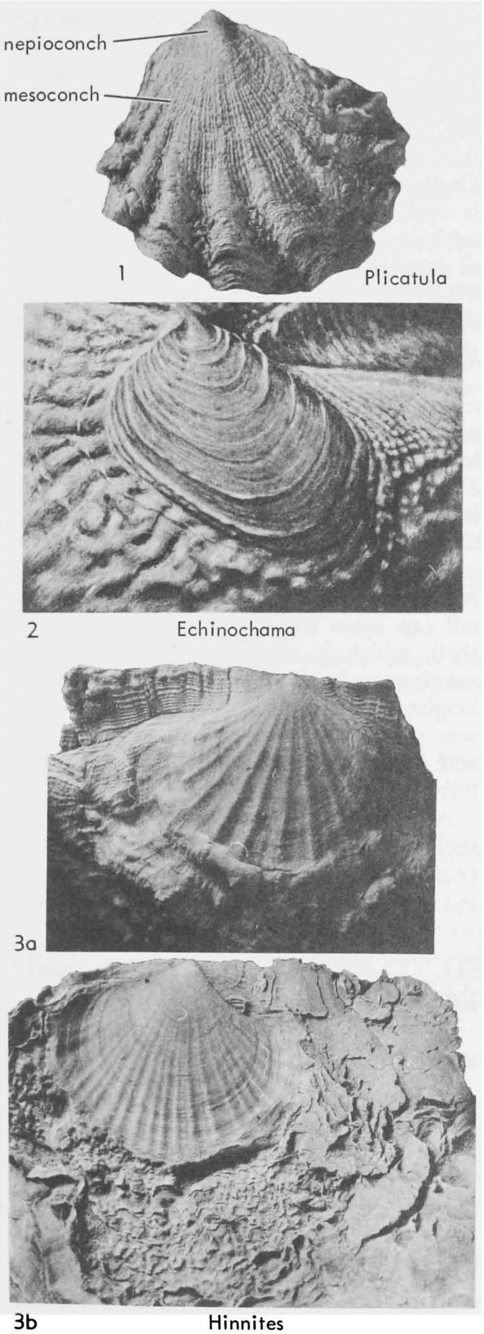


FIG. 84. Bivalve ontogeny—changes in shell characters during and after metamorphosis (Nuttall, n).——*1. Plicatula filamentosa* CONRAD, Eoc.(Claiborn.), Ala., showing early (nepioconch) and intermediate (mesoconch) growth forms, ×2.——*2. Echinochama arcinella* (LINNÉ), Rec., E.Atl., umbo of left valve with preserved nepionic shell, ×17 (from Odhner, 1919).——*3. Hinnites crispus* (BROCCHI), Plio., Italy; *3a,b,* changes from early pectiniform to later oyster-like shape, ×1.

FIG. 85. Bivalve ontogeny—*Penicillus (Penicillus) pulcher fossile* (SIEVERTS), Mio., E.Indies(Brunei), showing changes in form subsequent to nepionic shell, ×4 (Sieverts, 1934).

surface of the right valve and develop an irregular form. The early shell is commonly preserved at the summit of both valves and its right valve has a well-defined anterior auricle and a byssal notch (Fig. 84,*3*). In the European Neogene species *Hinnites crispus* (BROCCHI) attachment may not occur until the shell is more than 20 mm. high. In *Prohinnites,* of the Lower Cretaceous, a juvenile shell, regular in form, is commonly preserved in the right valve, with its margin surrounded by the surface of attachment, but it lacks a byssal notch. This fact seems to afford evidence that *Prohinnites* and *Hinnites* arose by convergence from different stocks.

Among more ancient bivalves, a very remarkable instance of change in form and ornament at a moderately advanced stage in ontogeny is that observable in the genus *Slava* BARRANDE, from the Silurian of Bohemia. The earlier-formed shell, which is about 15 to 35 mm. in height, is elevated and subtrigonal in shape, with prominent but prosogyrous umbones, and sits like a tall cap upon the later-formed part of the shell, which is almost circular in outline, ranging up to about 55 mm. in length and height, and bears fine radial riblets. *Slava* was not attached at any stage in growth and reasons for the sudden change in the form of its shell are unknown.

A number of other striking changes in shell form during ontogeny could be cited (e.g., *Penicillus,* Fig. 85).

MORPHOLOGICAL TERMS APPLIED TO BIVALVIA SHELLS AND SOFT PARTS AFFECTING SHELL

Terms considered most important are given in boldface type (as **accessory muscle**); use is not recommended of those printed in italics (as *epidermis*).

accessory muscle. Any muscle other than adductor and pallial muscles, with scar of attachment to shell (convenient noncommital term when referring to scars of muscles of uncertain function).

acline. Perpendicular to hinge axis or almost so (applied to hinge teeth or, in some genera, to direction of elongation of body of shell). Same as orthocline.

actinodont. With teeth radiating from beak, outer ones more or less elongate (applied to certain bivalves of early origin).

adductor muscle. Muscle, commonly one of 2, connecting 2 valves of shell, tending to draw them together.

adductor scar. Impression on interior of shell where adductor muscle was attached.

alate. With wings or auricles.

alivincular. Type of ligament not elongated in longitudinal direction nor necessarily situated entirely posterior to beaks, but located between cardinal areas (where present) of respective valves, with lamellar layer both anterior and posterior to fibrous layer; example, *Ostrea.*

allomorphism. See xenomorphism.

amphidetic. Extending on both anterior and posterior sides of beaks (applied to ligament or ligamental area); example, *Arca.*

anachomata. *See* chomata.

anisomyarian. With one adductor muscle (anterior) much reduced or absent.

anodont. Lacking hinge teeth. Same as edentulous.

anterior. Direction parallel to cardinal axis more nearly approximating to that in which mouth of animal faces.

anterior lateral tooth. Lateral tooth situated in front of beaks.

anterodorsal margin. Margin of dorsal part of shell in front of beaks.

apophysis. Projecting structure, such as that serving for attachment of pedal muscle in Pholadidae or adductor muscle in some rudists.

arcticoid type. Type of heterodont dentition intermediate between lucinoid and corbiculoid types; formerly termed cyprinoid type.

auricle. Earlike extension of dorsal region of shell, commonly separated from body of shell by notch or sinus.

auricular crura (sing., **crus**). Blunt internal ridges, swelling out distally as low tubercles, marking lower border of auricles in some Pectinidae.

auricular sulcus. External furrow at junction of auricle with body of shell.

auriculate. With auricles.

basal margin. Edge of shell opposite hinge, i.e., ventral margin according to terminology here adopted.

bead. Small rounded protuberance on rib.

beak. Noselike angle, located along or above hinge margin, marking point where growth of shell started.

bialate. With 2 wings or auricles.

body of shell. In alate or auriculate shells, entire shell with exception of wings or auricles.

bourrelet. Either of two portions of bivalve ligamental area flanking resilifer on its anterior and posterior sides; each comprises growth track and seat of the lamellar ligament. [The posterior bourrelet is flattish in all oysters except the Exogyrinae, in which it is a narrow sharp-crested spiral ridge on the LV and a corresponding groove on the RV.]

branchitellum (pl., **branchitella**). Point on posteroventral shell margin of oysters nearest to palliobranchial fusion, commonly forming conspicuously projected posteroventral tip on LV, especially in sickle-shaped oysters; aboral end of gills points toward it.

buttress. Internal projection from wall of shell supporting hinge plate or chondrophore.

byssal foramen. Opening in right valve in Anomiidae for passage of calcified byssus.

byssal gape. Opening between margins of shell for passage of byssus.

byssal notch. Indentation below anterior auricle of right valve in many Pectinacea for passage of byssus or protrusion of foot.

byssal sinus. Embayment of margin below anterior auricle of left valve in many Pectinacea, corresponding to byssal notch of right valve but usually shallower.

byssiferous. Possessing a byssus.

byssus. Bundle of hairlike strands by which temporary attachment of bivalve can be made to extraneous objects.

callum. Secondary calcareous structure present in some Pholadidae, forming anterior extension of shell proper and closing pedal gape in adult.

cancellate. Consisting of intersecting radial and commarginal threads.

cardinal area. Flat or slightly concave, commonly triangular surface extending between beak and hinge margin in many bivalves, and partly or wholly occupied by ligament.

cardinal axis. Imaginary straight line along which 2 valves of shell are hinged.

cardinal costa. Ridge or rib demarcating cardinal area from outer surface of shell.

cardinal crura (sing., **crus**). Narrow lamelliform teeth radiating from apex of ligament pit in Pectinacea.

cardinal platform. Shelly internal plate bearing hinge teeth, situated below beak and adjacent parts of dorsal margins and lying in plane parallel to that of commissure. Same as hinge plate.

cardinal tooth. Hinge tooth situated close to beak.

carina. Prominent keel-like ridge.

carinate. With carina or sharp angulation.

cartilage. Old term for internal ligament.

catachomata. *See* chomata.

caudate. With narrow, tail-like extremity.

chevron groove. V-shaped furrow on cardinal area in some Arcacea and early Pectinacea for insertion of ligament.

chomata (sing., **choma**). Collective term for anachomata, which are small tubercles or ridgelets on periphery of inner surface of RV, and catachomata, which are pits in LV for reception of anachomata; both generally restricted to vicinity of hinge, but may encircle whole valve.

chondrophore. Process with hollowed-out surface for attachment of internal ligament.

cicatrix. Scar (of muscle attachment).

clavicle. Shelly buttress supporting chondrophore in some genera.

closed. Not gaping anywhere along margins (applied to shell valves).

commarginal. With direction on part of surface of shell under consideration determined by former position of shell margin. (New term suggested for direction usually described as concentric.)

commissure. Line of junction of 2 valves.

compressed. Relatively flattened.

concentric. With direction coinciding with that of growth lines. (By no means concentric in literal and geometrical sense of term; *see* commarginal.)

conchiolin. Material (protein) of which periostracum and organic matrix of calcareous parts of shell are composed.

convexity. Degree of inflation.

corbiculoid type. Heterodont dentition with 3 cardinal teeth in each valve, middle one of RV occupying median position below beaks. Formerly termed cyrenoid type.

corselet. Differentiated posterior area.

cordate. Heart-shaped.

costa. Moderately broad and prominent elevation of surface of shell, directed radially or otherwise.

costella. Rather narrow linear elevation of surface of shell.

costule. Same as costella.

crenate. With notches along edge or crest (as of ribs).

crossed-lamellar. Type of shell structure composed of primary and secondary lamellae, latter inclined in alternate directions in successive primary lamellae.

cruciform muscles. Two bundles of muscle fibers present in Tellinacea and some Solenidae, joining valves posteroventrally and intersecting to form cross.

cryptodont. Lacking hinge teeth (applied to certain groups of early origin only).

ctenodont. With numerous short hinge teeth transverse to margin (applied to certain groups of early origin only).

ctenolium. Comblike row of small teeth on lower side of byssal notch in some Pectinacea.

cuneiform. Wedge-shaped.

cyclodont. With arched hinge teeth curving out from below hinge margin, hinge plate being small or absent.

cyrenoid type. See corbiculoid type.

demarcation line. Imaginary line on surface of valve originating at beak and marking locus of points on successive positions of margin where transverse growth component has had maximum effect. Forms dorsoventral profile when valve is viewed from one end.

denticle. Small rounded toothlike protuberance.

denticulation. Same as denticle.

dentition. Hinge teeth and sockets, considered collectively.

diagenodont. With differentiated cardinal and lateral teeth located on hinge plate, laterals not exceeding 2 or cardinals 3 in either valve; example, *Astarte.*

diagonal ridge. Ridge running diagonally from umbo toward posteroventral part of valve.

dimyarian. With 2 adductor muscles.

directive rib. Rib, forming part of surface ornament of shell, that lies entirely within single plane.

directive spiral. Spiral curve formed by directive rib within its own plane.

disc. In Pectinacea, whole of valve except auricles.

discordant margins. Margins of closed valves not in exact juxtaposition, but one overlapping other.

dissoconch. Postlarval shell.

divaricate. Type of ornament composed of pairs of rather widely divergent costules or other elements.

dorsal. Pertaining to region of shell where mantle isthmus was situated and valves are connected by ligament (i.e., to region of hinge).

duplivincular. Type of ligament with lamellar component repeated as series of bands, each with its 2 edges inserted in narrow grooves in cardinal areas of respective valves; example, *Arca.*

dysodont. With small weak teeth close to beaks (as in some Mytilacea).

ear. Small extension of dorsal region of shell, commonly separated from body by notch or sinus. Same as auricle.

edentulous. Lacking hinge teeth.

emarginate. With margin interrupted by notch or sinus.

ensiform. Shaped like genus *Ensis,* with outline resembling curved sword.

entire. Lacking sinus (applied to pallial line).

epidermis. Term used by some authors for periostracum.

equilateral. With parts of shell anterior and posterior to beaks equal in length or almost so.

equivalve. With 2 valves of same shape and size.

escutcheon. Typically lozenge-shaped dorsal differentiated area extending posteriorly from beaks and sometimes bordered by ridge in each valve.

escutcheon ridge. Ridge extending posteriorly from beak in each valve and forming border of escutcheon.

excurrent. Forming passage for current of water expelled from mantle cavity (applied to mantle opening or siphon).

exhalant. Same as excurrent.

exogyrate. Shaped like shell of *Exogyra,* that is, with left valve strongly convex and its dorsal part coiled in posterior direction, with right valve flat and spirally coiled.

falciform. Sickle-shaped.

fascicle. Small bunch (of ribs).

fasciculated. Arranged in small bunches.

fibrous ligament. Part of ligament characterized by fibrous structure and in which conchiolin is commonly impregnated with calcium carbonate; secreted by epithelium of mantle isthmus and elastic chiefly to compressional stresses.

flabelliform. Fan-shaped.

flank. Median part of surface of valve, limited posteriorly by posterior ridge where present.

fluted. With series of narrow parallel rounded excavations (like flutings of architectural column).

fold. Rather broad undulation of surface of shell, directed either radially or commarginally.

foot. Protrusible muscular structure extending from mid-line of body, anteroventrally in more typical bivalves, and used for burrowing or locomotion.

foramen. Opening, hole.

fossette (or fosset). Socket, as for cardinal tooth.

fulcrum. Old term for chondrophore.

funnel plates. Transverse laminae in wall of radiolitid lower valve, inclined downward funnel-wise toward axis and combining with radial laminae to produce cellular structure.

fusion layer. Part of ligament secreted where mantle edges are united dorsally by secondary fusion (i.e., anteriorly and posteriorly to mantle isthmus).

gape. Localized opening remaining between margins of shell when valves are drawn together by adductor muscles.

gill retractor muscle. Muscle present in a few Bivalvia attaching one of gills to shell.

globose. Tending toward spherical shape.

growth line. Line on surface of shell, one of usually irregularly arranged series, marking position of margin at some stage of growth.

growth ruga. Irregular wrinkle on surface of shell of similar origin to growth line but corresponding to more pronounced hiatus in growth.

growth thread. Threadlike elevation of surface of similar origin to growth line.

gryphaeate. Shaped like shell of *Gryphaea,* that is, with left valve strongly convex and its dorsal part incurved and with right valve flat.

height. Distance between 2 planes parallel to cardinal axis and perpendicular to plane of commissure, which just touch most dorsal and ventral parts of shell.

heterodont. With distinctly differentiated cardinal and lateral teeth.

heteromyarian. With one adductor muscle (anterior) much reduced.

hinge. Collective term for structures of dorsal region which function during opening and closing of valves.

hinge axis. Imaginary straight line about which 2 valves of shell are hinged.

hinge line. Term applied loosely by many authors to part of shell bordering dorsal margins and occupied by or close to hinge teeth and ligament; used by some in same sense as hinge axis.

hinge margin. Edge of shell that approximates most closely to hinge axis.

hinge plate. Shelly internal platform bearing hinge teeth, situated below beak and adjacent parts of dorsal margins, and lying in plane parallel to that of commissure.

hinge tooth. Shelly structure (usually one of a series) adjacent to dorsal margin and received in socket in opposite valve; hinge teeth serve to hold valves in position when closed.

homomyarian. With 2 adductor muscles equal in size or almost so.

hyote spines. Hollow, tubular and cylindrical shell outgrowths open distally at their tips as well as on their distal flanks, arising periodically from thin edges of shell margin of oysters. [The tip ends are rounded, ear-shaped openings, typically developed on *Hyotissa hyotis* (LINNÉ, 1758).]

hypoplax. Elongate accessory plate extending along posterior end of ventral margin in some Pholadidae.

hypostracum. Term used in 2 different senses: 1) inner layer of shell wall, secreted by entire epithelium of mantle (original sense); 2) part of shell wall secreted at attachments of adductor muscles (later sense: *see* myostracum).

imbricate. Overlapping like tiles or shingles on a roof.

incremental line. Same as growth line.

incurrent. Forming passage for current of water drawn into mantle cavity from medium (applied to mantle opening or siphon).

inequilateral. With parts of shell anterior and posterior to beaks differing appreciably in length.

inequivalve. With one valve larger than other.

inflated. Strongly convex.

inflation. Distance between 2 planes parallel to plane of commissure and touching outermost parts of 2 valves.

inhalant. Same as incurrent.

inner [layer of] **ligament.** Same as fibrous ligament.

integripalliate. With pallial line devoid of sinus.

interband. Longitudinal band on surface of lower valve of radiolitid rudist, separating 2 bands designated as siphonal bands.

interdentum. Shelly plate present in some Unionidae bridging space between pseudocardinal and lateral teeth.

interspace. Depression between adjacent costae or other linear surface elevations.

interval. Same as interspace when applied to surface ornament.

inverse. Term formerly applied to chamid in which attachment is by LV or rudist in which attachment is by RV.

isodont. With small number of symmetrically arranged hinge teeth; examples, *Spondylus, Plicatula.*

isomyarian. With 2 adductor muscles equal in size or almost so; same as homomyarian.

keel. Projecting ridge; same as carina.

lamella. Thin plate.

lamellar ligament. Part of ligament characterized by lamellar structure and containing no calcium carbonate; secreted at mantle edge and elastic to both compressional and tensional stresses.

lamelliform. Like thin elongate plate.

lamina. Thin plate.

lanceolate. Lance-shaped, i.e., tapering to point at one end, rounded at other.

lateral hinge system. Hinge structures present in some prodissoconchs anterior and posterior to provinculum.

lateral tooth. Hinge tooth partly or wholly located some distance from beaks.

left valve. Valve lying on left-hand side when shell is placed with anterior end pointing away from observer and commissure vertical, the hinge being uppermost.

length. Distance between 2 planes perpendicular to cardinal axis and just touching anterior and posterior extremities of shell.

lenticular. Shaped like biconvex lens.

ligament. Horny elastic structure or structures joining 2 valves of shell dorsally and acting as spring causing them to open when adductor muscles relax.

ligament fulcrum. Narrow lunate platform extending posteriorly from beak along dorsal margin and serving for attachment of ligament; same as nymph.

ligament groove. Narrow depression in cardinal area for attachment of fibers of ligament.

ligament pit. Relatively broad depression in cardinal area for attachment of ligament.

ligament ridge. Narrow ridge or lamina formed by projection of outer layer of shell wall into body cavity of many rudists (particularly hippuritids and radiolitids), thought to have served for attachment of ligament.

ligament suture. Elongated space behind umbones apparent after erosion of ligament.

lithodesma. Small calcareous plate reinforcing internal ligament in some genera; same as ossiculum.

longitudinal. Direction parallel to that of cardinal axis.

lucinoid type. Type of heterodont dentition with 2 cardinal teeth in each valve, anterior one in LV occupying median position below beaks.

lunule. Depression, commonly cordate in shape, present anterior to beaks in many bivalves.

mantle. Integument that surrounds vital organs of mollusk and secretes shell.

marginal carina. Ridge in Trigoniacea that runs from umbo to posteroventral angle of shell and delimits posterior area.

mesoconch. Part of dissoconch formed at an intermediate stage of growth and separated from earlier and later formed parts by pronounced discontinuities.

mesoplax. Transversely elongated accessory plate lying athwart umbonal region in some Pholadidae.

metaplax. Long narrow accessory plate covering gap between posterodorsal margins in some Pholadidae.

modioliform. Shaped like shell of *Modiolus;* differing from mytiliform in that beaks are not quite terminal and anteroventral region forms slight bulge.

moniliform. Composed of row of beads like a necklace.

monomyarian. With only 1 adductor muscle (posterior).

multivincular. Type of ligament consisting of serially repeated elements of alivincular type; example, *Isognomon.*

muscle scar. Impression on interior of shell marking former place of attachment of a muscle.

myophore. Process for attachment of muscle (usually adductor).

myostracum. Part of shell wall secreted at attachments of adductor muscles.

mytiliform. Shaped like shell of *Mytilus.*

nacreous. Type of shell structure consisting of thin leaves of aragonite parallel to inner surface of shell and exhibiting characteristic luster.

nates. Old name for umbones, as here defined.

nepioconch. Earliest formed part of dissoconch, when separated from later part by pronounced discontinuity.

nepionic. Earliest postlarval stage.

nodose. Bearing tubercles or knobs.

normal. Term formerly applied to chamid in which attachment is by RV or to rudist in which it is by LV.

nymph. Narrow lunate platform extending posteriorly from beak along dorsal margin and serving for attachment of ligament.

oblique. Most extended in direction neither parallel nor perpendicular to cardinal axis, but intermediate between these.

obliquity. Angle between straight dorsal margin and line bisecting umbonal angle (in terminology of some authors); or between dorsal margin and most distant point of ventral margin (in terminology of others).

opisthocline. Sloping (from lower end) in posterior direction (term applied to hinge teeth and, in some genera, to body of shell).

opisthodetic. Located wholly posterior to beaks (term applied to ligament).

opisthogyrate. Curved so that beaks point in posterior direction (term applied to umbones).

orbicular. Circular.

orthocline. Perpendicular to hinge axis or almost so (term applied to hinge teeth and, in some genera, to body of shell).

orthodont. Type of hinge in which direction of teeth is parallel to cardinal margin or almost so.

orthogyrate. Curved so that each beak points neither anteriorly nor posteriorly, but directly towards other valve (term applied to umbones).

oscule. Orifice in upper valve in some rudists, usually near margin.

ossiculum. Small calcareous plate reinforcing internal ligament in some genera; same as lithodesma.

ostracum. Term used in 2 senses: 1) outer part of calcareous wall of shell, secreted at mantle edge (original usage); 2) entire calcareous wall of shell (usage of some later authors).

outer [layer of] **ligament.** Same as lamellar ligament.

ovate. Shaped like longitudinal section of egg.

override. To pass over without interruption (commarginal over radial elements of ornament).

pachyodont. With heavy, blunt, amorphous teeth.

pallet. Small calcareous structure present in Teredinidae, one of pair closing end of boring when siphons are retracted.

pallial. Pertaining to the mantle.

pallial line. Line or narrow band on interior of valve close to margin, marking line of attachment of marginal muscles of mantle.

pallial region. Marginal region of shell interior adjacent to pallial line.

pallial retractor muscles. Muscles withdrawing marginal parts of mantle within shell where there is no distinct line of muscle attachment.

pallial sinus. Embayment of pallial line forming line of attachment of siphonal retractor muscles.

parivincular. Longitudinally elongated type of ligament, located posterior to beaks and comparable to cylinder split on one side with severed edges attached respectively along dorsal margin of 2 valves.

pedal elevator muscle. Thin bundle of muscle fibers attached to shell in umbonal cavity and serving to raise foot.

pedal gape. Opening between margins of shell for protrusion of foot.

pedal levator muscle. Same as pedal retractor muscle.

pedal protractor muscle. Muscle present in some genera, attached to shell interior and serving to extend foot.

pedal retractor muscle. Muscle attached to shell interior serving to retract foot.

periostracum. Thin coat of horny material covering calcareous part of shell.

pillar. Inward projection of outer shell layer extending longitudinally up lower valve in hippuritids.

plica. Fold or costa involving entire thickness of wall of shell.

porcelaneous. With translucent, porcelain-like appearance.

posterior. Direction parallel to cardinal axis more nearly approximating to that in which anus faces and exhalant current is discharged.

posterior area. Part of surface of valve posterior to posterior ridge.

posterior lateral tooth. Lateral tooth situated posteriorly to beaks and (in heterodonts) posteriorly to ligament.

posterior ridge. Ridge passing over or originating near umbo and running diagonally towards posteroventral part of valve.

posterior slope. Sector of surface of valve running posteroventrally from umbo.

posterodorsal margin. Margin of dorsal part of shell posterior to beaks.

primary ligament. Part of ligament representing original condition of structure, consisting of periostracum and lamellar and fibrous layers, but excluding secondary additions, notably fusion layer.

primary riblet. On shell with riblets of different orders of strength, riblet that appears early in ontogeny and remains stronger than those appearing later.

prionodont. Type of hinge in which teeth are developed in direction transverse to cardinal margin; virtually same as taxodont.

prismatic. Type of shell structure consisting of prisms of calcite or of aragonite.

prodissoconch. Shell secreted by the larva or embryo and preserved at beak of some adult shells.

prodissoconch I. Earlier-formed part of prodissoconch, secreted by shell gland of larva.

prodissoconch II. Later-formed part of prodissoconch, secreted by mantle edge.

prosocline. Sloping (from lower end) in anterior direction (term applied to hinge teeth and, in some genera, to body of shell).

prosocoelous. Same as prosogyrate.

prosodetic. Located anterior to beaks.

prosogyrate. Curved so that beaks point in anterior direction (term applied to umbones).

prosopon. Term recently proposed as suggested improvement on "surface ornament" or "sculpture."

protoplax. Flat, spearhead-like accessory plate, in 1 piece or divided longitudinally into 2, situated at anterior end of dorsal margin in some Pholadidae.

protostracum. Same as prodissoconch I.

provinculum. Median part of hinge margin of prodissoconch, usually bearing small teeth or crenulations.

pseudocardinal. Tooth irregular in form situated close to beak (as in some Unionacea).

pseudoctenodont. With numerous short teeth transverse to hinge margin, but descended from forms in which some teeth were longitudinally directed and more or less elongate.

pseudolateral. Lateral tooth (as here defined), proximal end of which is close to beak.

pseudopillar. Low, broad inward projection of shell wall present in some radiolitids.

pseudotaxodont. With numerous irregular short hinge teeth transverse to hinge margin and known to be unrelated to ctenodont and pseudoctenodont forms.

punctate. With pinprick-like depressions.

punctum (pl., **puncta,** never punctae). Pinprick-like depression of surface.

quadrate. Square, or almost so.

Quenstedt muscle. Small muscle of unknown function represented by scar below ligament area in Ostreidae.

radial. Direction of growth outward from beak at any point on surface of shell, commonly indicated by direction of costa or other element of ornament.

resiliifer (or **resilifer**). Recess or process for attachment of internal ligament.

resilium. Internal ligament, irrespective of composition.

reticulate. With network of oblique intersecting threads or other elements of ornament.

rhomboidal. Shaped like rhomb, figure with 4 equal sides and no right-angled corners.

rib. Moderately broad and prominent elevation of surface of shell, directed radially or otherwise; same as costa.

riblet. Rather narrow linear elevation of surface of shell; same as costella.

right valve. Valve lying on right-hand side when shell is placed with anterior end pointing away from observer and commissure vertical, the hinge being uppermost.

rostrate. With pointed, beaklike end.

sagittal plane. Anteroposteriorly directed plane of symmetry of shell and soft parts.

scale. Localized projection of outer layer of shell, commonly situated on a costa.

scalloped. With series of regular internal flutings corresponding to ends of external costae; term applied to shell margin.

schizodont. With 1 tooth (median of LV) broad and bifid.

sculpture. Regular relief pattern present on surface of many shells.

secondary riblet. On shell with riblets of different orders of strength, riblet that appears somewhat later in ontogeny than primary ones and remains weaker than these.

sinupalliate. Possessing pallial line with posterior embayment (or pallial sinus).

sinus. Indentation, embayment.

siphon. Tubelike extension of mantle for passage of inhalant or exhalant current.

siphonal area. Posterior sector of surface of shell, commonly demarcated anteriorly by umbonal ridge; secreted where mantle edge has openings or is produced to form siphons for passage of respiratory currents.

siphonal band. Longitudinal band (one of 2) on surface of some rudists (mainly radiolitids) differing in ornament from rest of surface and thought by some to have been secreted at part of mantle edge where respiratory current entered or left shell.

siphonal retractor muscles. Muscles serving to withdraw siphons partly or wholly within shell.

siphonoplax. Tubular secondary calcareous structure forming posterior extension of shell in some Pholadidae and protecting proximal end of siphons.

socket. Recess for reception of hinge tooth of opposite valve.

spine. Thornlike protuberance of surface of shell.

spirogyrate. Coiled outward from sagittal plane; term applied to umbones.

squamose. Bearing scales.

stria. Narrow linear furrow or raised line on surface of shell.

submargin. One of dorsal edges of disc or body of shell in Pectinacea, adjoining lower border of auricle.

sulcus. Radial depression of surface of shell.

summit. Most dorsal point of profile of valve when latter is viewed along cardinal axis or from side with cardinal axis horizontal.

surface ornament. Regular relief pattern present on surface of many shells.

taxodont. With numerous short hinge teeth, some or all transverse to hinge margin.

teleodont. With differentiated cardinal and lateral teeth, as in diagenodont forms, but with additional elements giving rise to more complicated hinge; example, *Venus*.

terminal. Forming most anterior or posterior point of valve; term applied to beak.

thickness. Used by some authors to denote the shell measurement here termed inflation, but also commonly applied to the distance between the inner and outer surfaces of wall of shell.

thread. Narrow elevation of surface of shell.

transposed hinge. Condition in which certain hinge teeth present in one valve occupy positions of teeth usually found in other.

transverse. Direction perpendicular to that of cardinal axis in plane of valve margins.

trapeziform. With 4 straight sides, only 2 of which are parallel.

trapezoidal. With 4 straight sides, no 2 of which are parallel.

trigonal. Three-cornered.

truncate. With curvature of outline interrupted by straight cut.

tumid. Strongly inflated.

umbo. Region of valve surrounding point of maximum curvature of longitudinal dorsal profile and extending to beak when not coinciding with it. (Many authors treat beak and umbo as synonymous, but with most shells two distinct terms are needed.)

umbonal angle. In pectinoid shells, angle of divergence of umbonal folds. In other shells, approximate angle of divergence of posterodorsal and anterodorsal parts of longitudinal profile.

umbonal cavity. Part of interior of valve that lies within umbo and under hinge plate (where present).

umbonal depression. Small depression at tip of umbo in some Arcacea.

umbonal fold. In pectinoid shell, ridge originating at umbo and setting off body of shell from auricle.

umbonal pole. Point of maximum curvature of longitudinal dorsal profile of valve.

valve. One of the calcareous structures (2 in most bivalves) of which shell consists.

veliconch. Shell borne by veliger larva; identical with prodissoconch when larva is pelagic.

ventral. Pertaining to or located relatively near to region of shell opposite hinge, where valves open most widely.

ventricose. Strongly inflated.

vinculum. Secondary shelly matter associated with basic dental structures; commonly takes form of bridge between two adjacent teeth, thus causing dentition to appear simpler than it is.

wing. More or less elongate, triangular, distally acute or obtuse, terminal part of dorsal region of shell in Pteriacea, Pectinacea, etc.

xenomorphic (adj.). Pertaining to xenomorphism.

xenomorphism. Special sculpture at the umbonal region of the unattached valve resembling the configuration of the substratum onto which the attached valve is or was originally fixed. Known in the Anomiidae, Gryphaeidae, Ostreidae and other pleurothetic and cemented families. It is on the right valves in oysters and on the left valves in *Anomia* (see STENZEL, KRAUSE & TWINING, 1957, p. 98-99). Erroneously called allomorphism by some authors.

EVOLUTIONARY HISTORY OF BIVALVIA

The hypothesis that the Bivalvia were derived from a primitive univalve mollusk with a depressed uncoiled shell, perhaps numerous pedal muscles, and a line of pallial muscles close to the margin, has been expounded in Part I of this *Treatise* (p. *I*21-*I*22). Several authors have pointed out that the Monoplacophora, in which a whole series of shell-attached muscles is present, correspond better to the theoretical concept of the ancestral form than any other molluscan group at present known. Attention has, moreover, been called to the fact that the early Bivalvia include the genera *Babinka* and *Myoplusia,* both of which were characterized by multiple accessory muscles which may represent the retention of a primitive condition. The possibility of the derivation of a two-valved form from a group of univalve mollusks has, moreover, recently received unexpected confirmation by the discovery of two-valved opisthobranch gastropods and by observations on their ontogeny, although in this case the actual process of valve division is not in the manner postulated in the hypothesis mentioned.

Other interesting problems are connected with the origin of the class. Did the Bivalvia arise from a more primitive molluscan group as an adaptation to a particular environment and mode of life? Or, approaching the matter from a slightly different theoretical aspect, if they originated as chance mutations, were they successful in establishing themselves because they proved to be well suited to a particular environment and mode of life? Were the earliest bivalves epifaunal like the presumed ancestral form, or infaunal, adopting immediately a burrowing existence in the sea-floor sediment? Is there any evidence that the class arose polyphyletically? It is not proposed here to adopt any particular standpoint on these theoretical matters, but merely to record what is at present known of the earliest appearances of the various groups of Bivalvia in the fossil record.

Unfortunately difficulties arise at the outset owing to uncertainty as to whether some of the earlier forms with two-valved tests were Mollusca or Crustacea. The very earliest fossils which have been regarded by some workers as Bivalvia are two small species from the Lower Cambrian of New York State described by BARRANDE as *Fordilla troyensis* and by WALCOTT as *Modioloides* [originally *Modiolopsis*] *prisca,* both types of their respective genera. *F. troyensis* is about 4.5 mm. long, *M. prisca* only 2 mm. Both came from sequences of slates and shales with interbedded limestones and little at present can be said about their paleoecology. ULRICH & BASSLER, who have redescribed and refigured these remains, are of the opinion that both were Crustacea and not Bivalvia. Neither possessed features definitely identifiable as hinge teeth or as adductor muscle scars and, according to the authors cited, *Fordilla* had a test with a "calcareo-phosphatic structure."

Of equally doubtful affinities are some rather small internal molds, up to about 8 mm. in length, from the Lower Cambrian of eastern Portugal, first described by DELGADO. He considered these to represent nine species of Bivalvia, distributed among six previously known genera, including *Ctenodonta,* and details were given of the exact number of taxodont teeth seen in the specimen supposed to belong to this genus. In a revision of this assemblage by TEIXEIRA five of the species were considered identical and were referred to *Modiolopsis* (although on no certain evidence), while no conclusion was reached as to whether the remainder were Bivalvia or Crustacea. The supposed *Ctenodonta* has been refigured by VOGEL, who has recorded that its "taxodont teeth" were a product of the imagination. It does not, in fact, seem possible to say definitely if these Portuguese specimens are Bivalvia or Crustacea. The formation yielding them was a bluish-grey fine-textured shale containing siliceous concretions.

The problematic Ribeirioida [Tecnophoridae & Ribeiriidae], in which the two halves of the test are joined along the dorsal margin and hinge teeth are absent, first appeared in the late Lower Cambrian. Many authorities have referred this group to the Arthropoda, although not on altogether convincing grounds. Whether or not these forms are correctly placed here, they are morphologically intermediate between the Monoplacophora and undoubted Bivalvia.

The oldest species so far discovered that can be referred with confidence to the Bivalvia is *Lamellodonta simplex* VOGEL, described in 1962 from beds in the Zaragoza province of Spain dated by trilobites and brachiopods as lower Middle Cambrian. It is an oval, equilateral shell up to 18 mm. in height and 14 mm. in length, with well-developed hinge teeth, consisting of lamellae parallel to the adjacent dorsal margin and symmetrically arranged on the two sides of the beak, from below which corresponding pairs diverge at a very obtuse angle; two lamellae with an intervening socket are present on each side of the beak in some specimens, one lamella in others. Neither adductor scars nor the position of the ligament have been observed, but the ligament is thought to have been external. The matrix of the specimens is a very fine-grained quartzite. VOGEL concludes from the equilateral form of the shell that the mollusk crept about on the sea floor or possibly lived on seaweed. As, however, an equilateral shell is not a criterion of a nonburrowing mode of life, it is equally possible that *Lamellodonta* burrowed at least intermittently into the fine sandy substrate. While it would be rash to acclaim this form as the ancestor of all the Bivalvia (for earlier members of the class may yet be found), VOGEL's diagram (Fig. 86) suggesting its its relationship to main groups of the class found in later rocks deserves consideration. The discovery of this genus is of great interest, particularly as it does not support the theory, once widely accepted in consequence of R. T. JACKSON's demonstration of the presence of taxodont-like teeth on most prodissoconchs, that the most primitive bivalve was a form with taxodont dentition belonging to the Nuculacea.

Records of unmistakable Bivalvia from the later stages of the Cambrian (apart from the Tremadocian, included in the system by British but not by other authors) seem nonexistent. We find evidence in two widely separated areas, however, that diversification of the Bivalvia already had begun to take place in the Tremadocian, although (apart from the doubtful forms already mentioned) members of the class do not appear until a later stage of the Ordovician in most regions. Thus THORAL has reported the occurrence of the genus *Babinka,* as well as of a nuculacean bivalve in the Tremadocian of the Montagne Noire area of France. This discovery of *Babinka* is of interest, as in Bohemia, the part of Europe from which it was originally described, it does not appear until the Llanvirnian Stage. In both areas the genus occurs in siliceous nodules. Reference has already been made to the suggestion, based on the multiple muscle scars of this genus, of its possible derivation from the Monoplacophora. It has small but distinct cardinal hinge teeth, and a study of these and of its elongated anterior adductor scar has led McAlester to the conclusion that it was the ancestor of the heterodont superfamily Lucinacea. This author therefore considers that, like *Lucina* at the present day, it burrowed shallowly into sandy sediment, using a slender, wormlike foot to punch a tubular hole upward through this deposit for the passage of the inhalant current. From the Tremadocian of Argentina Harrington has described representatives of the three genera *Ctenodonta, Palaeoneilo,* and *Cosmogoniophorina.* The record of the first two, which belong to the Nuculacea, combined with Thoral's identification of a representative of this superfamily in French beds of the same stage, at least confirms the general view that the group is a very primitive one. On the other hand, an assumption that the Nuculacea arose more or less directly from *Lamellodonta* is not very plausible in view of the considerable modifications in the dentition and form of the shell that would have taken place in such a process. Still less acceptable would be a theory that *Babinka* arose from *Lamellodonta.* The problem of the original diversification of the Bivalvia is thus still unsolved.

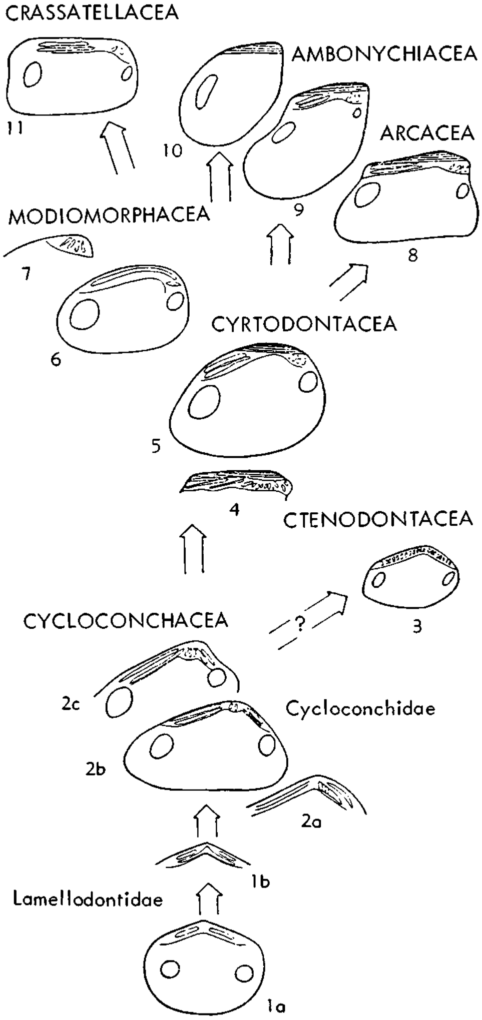


Fig. 86. Reconstruction of the phylogeny of early Paleozoic bivalves suggesting relationship of *Lamellodonta* to main groups (after Vogel, *176*).——*1. Lamellodonta simplex* Vogel.——*2. Actinodonta* Phillips (*2a, A.* sp.; *2b, A. acuta* Douvillé; *2c, A. cuneata* Phillips).——*3. Ctenodonta planodorsata* Ulrich.——*4. Cyrtodonta gibbosa* Hind.——*5. Cyrtodonta grandis* Ulrich.——*6. Redonia* Rouault.——*7. Modiolodon* Ulrich.——*8. Parallelodon* Meek & Worthen.——*9. Gosseletia* Barrois.——*10. Myalina* de Koninck.——*11. Cypricardinia* Hall.

Cosmogoniophorina, originally described from the Ordovician of Sweden, belongs to an important Paleozoic family, Modiomorphidae, the affinities of which have given rise to some disagreement. The shell in this group is rectangular or oval in shape, elongate, and strongly inequilateral, with the beaks near the anterior end. Hinge teeth are lacking in this particular subgenus, but in other members of the family they are of the actinodont type, consisting of lamellae radiating from the beak, the posterior ones commonly elongated and parallel to the adjacent margin. It is easier to conceive that the Modiomorphidae could have evolved from *Lamellodonta* than the other forms just mentioned, the symmetrically arranged hinge teeth of that genus giving rise to asymmetrical, actinodont dentition as the part of the shell anterior to the beaks became reduced in length; to attempt a functional interpretation of this change in shape would, however, be pure guess-work.

Unlike the later Mytilacea, which some of them resembled in shape, the Modiomorphidae do not appear to have been byssally attached.

It is in the succeeding Arenigian stage of the Ordovician that the Bivalvia, now still further diversified, can be said to have become successfully established. Even now, however, their distribution appears to have been restricted, and it seems that sandy sediments were their most favored environment. The Armorican Sandstone of northern France has yielded the most varied fauna of this stage, while a few further forms have been found in the Montagne Noire area, in southern France. In Wales the Abercastle and Porth Gain beds of St. Davids have yielded a small assemblage described in 1873 by HICKS, who dated the beds erroneously as Tremadocian, while in the USA the St. Peter Sandstone of Minnesota has yielded a few species described by SARDESON. Among these Arenigian bivalves the Nuculoida are represented by *Ctenodonta* and *Nuculites,* the Modiomorphidae by *Modiolopsis* and *Redonia,* and a further actinodont family, Cycloconchidae, by *Actinodonta.* The genus *Lyrodesma,* type of the family Lyrodesmatidae, which made its first appearance in the Armorican Sandstone, seems also to have been related to the actinodonts, although the posterior teeth of its radiating series are not greatly elongated. The Cyrtodontidae, represented in each of the areas mentioned by one or other of the genera *Cyrtodonta, Cypricardites,* and *Vanuxemia,* is of interest as being the earliest known group in which the ligament was placed on a distinct cardinal area. The hinge teeth in the Cyrtodontidae are arranged very similarly to those of the actinodonts, and derivation of the family from that group is a reasonable assumption. Although it is doubtful, in the absence of a distinct byssal gape, if the Cyrtodontidae were byssally attached, epifaunal mollusks, a very plausible tree of descent indicates that they could well have been the ancestors of the predominantly epifaunal bivalves here grouped in a subclass Pteriomorphia. A striking species from the Armorican Sandstone was classified by BARROIS as a *Parallelodon,* a genus of Arcoida otherwise not known until later in the geological record. It certainly has the shape and dentition of a *Parallelodon,* but it is not clear if it has a distinct cardinal area. Unfortunately, the specimen cannot be traced. The Montagne Noire has yielded a winged shell apparently belonging to the Pteriacea, referred by its describer, THORAL, to the genus *Pterinea* with a query.

Among the remaining Arenigian bivalves we may also note *Davidia* and *Sluzka.* These are two of several edentulous Paleozoic bivalves which, for lack of evidence as to their relationship to one another and (except for the long-ranging genus *Solemya,* mentioned again later) to post-Paleozoic taxa, are here grouped together as a subclass Cryptodonta (Palaeoconcha of an alternative nomenclature). Finally, *Coxiconcha* [*Sanguinolites*] *pellicoi* (DE VERNEUIL & BARRANDE) is an elongate form with cardinal teeth and a gaping posterior extremity, interpreted by DOUVILLÉ as an early permanent burrower, a forerunner of such families as the Pholadomyidae and Pleuromyidae, included in this *Treatise* in a subclass to which DALL's name Anomalodesmata is applied. This form does not, however, appear to have been sinupalliate, so that the depth to which it could burrow was probably restricted.

Passing, now, to the Llanvirnian and Llandeilian stages of the European Ordovician succession and their equivalent, the Chazyan stage of the USA, we find the Nuculacea, Modiomorphidae, and Cyrtodontidae still well represented. *Babinka* reappears in the Llanvirnian Stage of Bohemia, its type area, and is not met again. The cryptodont genera *Edmondia* and *Cardiomorpha* make their appearance in these stages, together with representatives of the mytiliform, byssiferous family Ambonychiidae (with little doubt an offshoot from the Cyrtodontidae), and a further early representative of the Pteriacea, described under the genus *Leptodesma.* The earliest known species of *Conocardium,* a very distinctive genus possibly related to the Ribeirioida, occur in Llandeilian beds in southern Scotland and in the Chazyan of the USA. Finally, beds of the same stage and area have yielded a form described as a *Cypricardinia;* if the generic reference is correct, this is the earliest known heterodont, unless *Babinka* is so regarded. *Lyrodesma,* of the Lyrodesmatidae is recorded also from the Lower Ordovician Armorican Sandstone of northern France.

Succeeding stages of the Ordovician, equivalents of the Caradocian and Ashgillian of the British succession, have yielded extensive bivalve faunas in a number of areas, particularly Sweden (*Leptaena* Limestone), Norway, France (Grès de May), southern Scotland, Bohemia, Kazakhstan, the USA (Minnesota, New York, Maryland, Ohio), and Canada. These faunas consist largely of groups encountered in earlier beds (Nuculacea, Cyrtodontidae, Ambonychiidae, Lyrodesmatidae, actinodonts [Modiomorphidae, with Allodesmatidae now added], *Conocardium* and various cryptodonts). Alone among these groups, the Nuculacea have persisted with only relatively slight changes to the present day, and further reference will not be made to them. The Pterineidae now begin to assume importance. Possible Myalinidae make their appearance. The earliest appearance of the Lucinacea (if we except the problematic *Babinka*) is marked by the presence of the genus *Paracyclas* in the Upper Ordovician of Scotland. Among the cryptodonts are some genera *(Rhytimya, Cuneamya, Sphenolium)* that give every appearance of having been permanent (although perhaps not very deep) burrowers and have been thought by some authorities to have been, like *Coxiconcha pellicoi* already mentioned, among ancestors of the Anomalodesmata. Upper Ordovician rocks have yielded the earliest Bivalvia which are thought to have bored into hard coral limestone. The genera in question are *Corallidomus* WHITFIELD and *Semicorallidomus* ISBERG, from Ohio and Sweden respectively, and both have been referred to the Modiomorphidae [Modiolopsidae].

In most areas the Silurian bivalve fauna differs very little in generic composition from that of the Ordovician, but the appearance of *Palaeopecten* WILLIAMS, found both in North America and in Wales, is to be noted. *Protopecten* HIND, from Scotland, also seems to have belonged to the Pectinacea. These forms, the earliest known representatives of this superfamily, differ from the Pteriacea from which they were presumably derived in their almost equilateral outline. *Palaeopecten,* like all Aviculopectinidae, had a distinct cardinal area with grooves corresponding to a duplivincular ligament. Bohemia is remarkable for its varied Silurian bivalve fauna described in a monumental monograph by BARRANDE. This fauna is particularly rich in members of the Cryptodonta, some *(Praecardium, Paracardium, Panenka)* with strong radial costation and much external resemblance to many Cardiidae found in much later formations. It is, however, highly improbable that these forms were ancestral to the Cardiidae, or that *Praelucina,* another cryptodont found with them, had any affinity with the Lucinidae. On the other hand, *Prolucina,* represented by large internal molds from the Silurian of Gotland, Sweden, clearly showing the impression of the characteristic elongated lucinoid anterior adductor scar, must undoubtedly belong to the Lucinacea. *Megalomoidea,* found in the Silurian (Guelph) of North America, marked (if the views here adopted are correct) the initiation of an important line of descent, the pachyodonts, that was to lead eventually to the remarkable sedentary bivalves, the rudists, of the Cretaceous.

During the Devonian Period the Bivalvia became very abundant and diversified. Faunas of this age, including numerous representatives of the class, have been described from every continent, particularly important monographs dealing with material from the USA, Germany, and Belgium. Some groups encountered in earlier rocks (including the Praecardiidae, Edmondiidae, Ambonychiidae, Modiomorphidae, and Conocardiidae) persist. Pectinacea and Myalinidae assume importance for the first time, the first group being represented by such genera as *Aviculopecten, Lyriopecten, Pterinopecten,* and *Posidonia.* The Pteriacea, with *Pterinea, Limoptera, Lepto-*

desma, and other genera, are abundant in some formations. *Parallelodon,* a possible member of which appeared, as already seen, in the Ordovician Armorican Sandstone, is represented by a number of typical species in the Devonian. *Carydium,* a new type of actinodont, also occurs. The earliest representatives of the Solemyidae, not separable more than subgenerically from the living genus *Solemya,* make their appearance. Although mytiliform shells referred by early authors to *Mytilus* or *"Modiola"* occur in earlier rocks, it is probable that these belonged to the Modiomorphidae and perhaps in some cases to the Myalinidae. True Mytilidae, belonging to the genus *Modiolus,* are, however, encountered in the Devonian. The Trigoniacea, very doubtful members of which have been reported from the Upper Ordovician and Silurian, are represented in the Devonian by several genera of Myophoriidae. The pachyodonts are represented by *Megalodon, Eomegalodon,* and *Prosocoelus.* Finally, certain genera which, like *Cypricardinia* and the lucinoids *(Paracyclas, Prolucina)* already mentioned as appearing in earlier rocks, and accepted as early heterodonts, are found in the marine Devonian; these are *Montanaria, Crassatellopsis, Cypricardella, Mecynodon,* and possibly others. The Devonian is the oldest fossiliferous system in which nonmarine formations are extensively developed, and it is interesting to note that fresh-water bivalves very similar in external appearance to some modern Unionidae are found in such rocks, both in Great Britain and in North America. They are referred to a genus *Archanodon.*

The marine faunas of the Carboniferous were marked by the dominance of most of the same groups as during the Devonian. New families to appear were the Pinnidae (including forms not separable generically from the modern *Pinna*) and the Limidae (*Palaeolima*). Among the Carboniferous Pectinacea were forms in which the ligament had advanced beyond the duplivincular stage of the Aviculopectinidae to the type found in modern members of the superfamily. These forms are referable to the genus *Pernopecten* (from which *Entolium* of the Mesozoic may not be separable). Among the Pectinacea there also arise what was probably the earliest bivalve genus to be cemented to the substratum, an oyster-like form described by DE KONINCK as *Pachypteria,* a genus united in the present *Treatise* with *Pseudomonotis,* based on a Permian species. This genus, in which fixation was usually by the right but occasionally by the left valve, has been regarded as a possible ancestor of the oysters. Among the Mytilidae we may note the appearance of elongate, cylindrical forms which have hitherto been included in the genus *Lithophaga,* although it has not been established that they bored into limestone, like modern representatives of this genus. The Carboniferous heterodonts include *Astartella,* in which the hinge teeth are very similar to those of modern members of the Astartidae. Finally, Carboniferous cryptodonts with the shell form of permanent burrowers, such as *Chaenomya, Solenomorpha, Wilkingia,* and *Sanguinolites,* approach some of the later Anomalodesmata very closely. *Wilkingia* and *Chaenomya* seem to be the earliest bivalves known to have been sinupalliate.

The Carboniferous system is particularly notable for the nonmarine bivalves which are locally abundant in the strata associated with coal seams and have been intensively studied in recent years because of their use in correlation. Among these forms, the genus *Naiadites* has close affinities with the marine *Myalina.* The origin of such genera as *Carbonicola, Anthracosia,* and *Anthraconaia* is puzzling, as it is doubtful if these relatively small bivalves were descendants of the large *Archanodon* of the Devonian.

In most areas the marine bivalve faunas of the Permian do not differ greatly in generic composition from those of the Carboniferous. New families to appear, however, were the Bakevelliidae (Pteriacea with a multivincular ligament) and the heterodont groups Myoconchidae, Permophoridae, and Crassatellidae. The Permian genera *Undulomya, Palaeocosmomya,* and *Praeundulomya* are here accepted as members of the Pholadomyidae, although it is not known if they were sinupalliate. The Australian Permian is noteworthy for the occurrence of *Megadesmus, Cleobis, Myonia,* and other genera united in the family Megadesmatidae. Many specimens attain a considerable size. These forms have been regarded as burrowers and early members of the Myacea, but they lack a posterior gape and pallial sinus and their systematic position may need reconsideration. Restricted to the Permian is the very characteristic genus *Eurydesma,* first described from Australia and since recorded from Pakistan, Kashmir, South Africa, and South America. Notwithstanding its globose shape, the general features of the shell indicate that this genus should be referred to the order Pterioida, but the relationship of the Eurydesmatidae, of which it is the type genus, to other families of this order has still to be established. The *Inoceramus*-like genus *Atomodesma,* found in the Permian of Timor and Pakistan, seems referable to the same family.

The successors of the small fresh-water bivalves of the Carboniferous, included with them in the family Anthracosiidae, are found in Permian nonmarine deposits in Russia, Africa, and elsewhere. Commonly occurring genera are *Palaeanodonta* and *Palaeomutela,* the latter characterized by its pseudotaxodont dentition. Reference must also be made to the very peculiar endemic fauna of the (probably) Permian Corumbatai Formation of Brazil and Uruguay, which includes such genera as *Plesiocyprinella, Terraia, Ferrazia, Pinzonella,* and *Cowperesia,* none obviously related to forms found in other areas. This assemblage is neither a typical fresh-water nor a marine one, but was possibly derived from a marine fauna which had become isolated in a large land-locked basin.

A few groups that had formed important constituents of the upper Paleozoic bivalve faunas lingered on and became extinct during the Triassic Period, but some had already died out. Of the cryptodonts, *Edmondia* and *Sanguinolites* are unrepresented in the Triassic; only one species of *Wilkingia* [*Allorisma*] has been described, and merely two or three of *Cardiomorpha.* The last known *Conocardium,* the only Triassic species of the genus recorded, occurs in the Rhaetic of Burma. *Myalina,* so common in the Carboniferous and Permian, is represented in the Triassic by only a few species. The Aviculopectinidae continued into and died out during this period, but, apart from *Aviculopecten* itself, the upper Paleozoic genera were replaced by others, such as *Eumorphotis, Claraia,* and *Leptochondria.* Certain pectinacean groups attained great importance, forming a very characteristic element of some of the bivalve faunas of the period. These were the Monotidae and the Halobiidae, the latter represented mainly by the genera *Halobia* and *Daonella.* Their thin, flattened, radially ribbed shells occur in enormous numbers in some deposits. Costate Pectinidae (*Chlamys* and other genera), the presence of which in earlier rocks is doubtful, became well established during the Triassic. Of the Pteriacea, the peculiar family Cassianellidae is virtually confined to this system. The genus *Bakevellia* persisted and was joined by other genera of the Bakevelliidae *(Hoernesia, Gervillia, Gervillella),* while the earliest representatives of the derivative family Isognomonidae (including *Isognomon* itself) appeared. The Triassic was also marked by the appearance of the families Plicatulidae and Ostreidae. Among the earliest representatives of the latter are small, smooth, gryphaeate forms found in the Upper Triassic of Sicily and the Bear Islands, while the plicated genus *Lopha* includes the species *L. montiscaprilis* (KLIPSTEIN), of the Carnian of the Alps. The relationship of these early Ostreidae to the plicated Triassic oyster-like forms included in the genus *Enantiostreon,* which were attached by the right valve and are here referred to the family Terquemiidae, has yet to be determined. Of the Limidae, *Mysidioptera,* in which anterior auricles are virtually lacking, was the most characteristic Triassic genus.

During the Triassic the Myophoriidae reached the acme of their development. In the preceding periods this family had been represented mainly by smooth-shelled genera such as *Schizodus,* but now many of its numerous representatives were quite elaborately ornamented. The first Trigoniidae, descendants of the Myophoriidae, are found in the Upper Triassic. This period was also marked by the reappearance of pachyodonts. *Megalodon,* which presumably had retreated during the Carboniferous and Permian to some region not yet located, flourished greatly in the calcareous sediments laid down towards the close of the Triassic and, like the related genus *Conchodus,* occurs in great number in the Rhaetic limestones of the Alps. Heterodonts were not very much in evidence during this period, but the appearance of the Carditidae (genus *Palaeocardita*) is to be particularly noted as it is not until the Cretaceous that comparable ribbed members of the family are to be found again. The genera *Protocardia* and *Eotrapezium,* the oldest known genera of the Cardiidae and Arcticidae respectively, appear at the very top of the Triassic, and *Corbula* a little lower. The Triassic Period also saw the incoming of some common Mesozoic genera of the Pholadomyidae (*Homomya, Pachymya (Arcomya),* and, more rarely, *Pholadomya*), and also of *Pleuromya.* Finally, fresh-water deposits of the period have yielded true Unionidae, very similar in appearance to modern representatives of the family.

The marine bivalve faunas of the Jurassic have quite a different aspect from those of the Triassic, owing largely to the abundance of Trigoniidae, Ostreidae, Limidae, and Pholadomyidae. Among the Arcoida the genus *Parallelodon* persists from the Paleozoic, and *Cucullaea* and *Grammatodon* from the Triassic. *Indogrammatodon,* a well-characterized subgenus of *Grammatodon,* is abundant in the Middle and Upper Jurassic in the area surrounding the Indian Ocean. *Eonavicula,* the obvious ancestor of the modern *Arca,* and *Barbatia* make their appearance. Mytilidae are usually abundant, and include radially ribbed forms *(Arcomytilus, Musculus),* although *Modiolus* is the commonest representative of the family. *Gervillella* assumes importance among the Bakevelliidae and *Isognomon* becomes more abundant. Among the Pectinacea, *Oxytoma,* which had appeared near the top of the Triassic, occurs commonly, especially in the Lias, while *Meleagrinella* is frequent at some horizons. The genus *Buchia,* particularly characteristic of boreal regions, makes its appearance in the Upper Jurassic. The Pectinacea include many species of modern aspect, some inseparable from the genus *Chlamys,* but a group of highly inequivalve forms, *Weyla,* occurs in the Lias of South America, North and East Africa, and elsewhere. The peculiar genus *Eopecten,* cemented to the substratum by the tip of its flat right valve, is reminiscent of the upper Paleozoic *Pseudomonotis* but has the hinge characters of a true pectinid. Most of the Jurassic Limidae differ very little from modern representatives of the family, but the genus *Ctenostreon,* with its thick shell and broad spinose ribs, was evidently adapted for life recumbent on the sea floor. Among the oysters, gryphaeate forms are abundant at many horizons of the Jurassic and their relationship to the flatter smooth oysters *(Liostrea)* has given rise to much speculation. Rather less frequent and virtually confined to post-Liassic beds are representatives of *Exogyra.* Ribbed oysters *(Lopha)* are common in the Middle and Upper Jurassic. The genus *Eligmus,* a ribbed, oyster-like form that was the earliest representative of the Malleidae, characterizes the Bathonian and Callovian of some areas.

Hippopodium, possibly the last survivor of the Modiomorphacea, is remarkable, not only for its thick, heavy shell, but also for its discontinuous range and localized distribution. Found in the Hettangian to Pliensbachian stages of the Lias in northwestern Europe, it is known otherwise only from the uppermost Jurassic of East Africa. *Megalodon* of the Trias was succeeded in the Jurassic by other pachyodont genera of the same family, notably *Pachyrisma* and *Pterocardia.* In the Oxfordian the genus *Diceras,* which is thought to have been derived from the Megalodontidae, acquired the habit of fixation by the tip of one valve and initiated lines of descent that led to the various rudistid groups of the Cretaceous. Throughout the Jurassic the commonest heterodont family was the Astartidae, represented by *Astarte* and other genera, among which *Opis* was remarkable for its strongly prosogyrate umbones. Of the Cardiniidae, a family that had appeared during the Triassic, the genus *Cardinia* was very abundant throughout the Lias and then died out. The Arcticidae increased greatly in importance during the Jurassic, newly appearing genera including *Isocyprina, Anisocardia, Pronoella,* and *Pseudotrapezium.* The Lucinidae, Cardiidae, and Corbulidae maintained their positions and the Fimbriidae made their appearance. Sinupalliate, presumably relatively deep-burrowing forms included *Pholadomya, Homomya, Goniomya, Pleuromya, Thracia,* and *Gresslya.* In addition to various Unionidae, Jurassic fresh-water deposits have yielded representatives of the heterodont genus *Neomiodon.* Those of central Asia contain a variety of rather small forms which have been referred to two families Ferganoconchidae and Pseudocardiniidae.

Many genera pass up from the Jurassic into the Cretaceous. The range of *Buchia* terminated in the Lower Cretaceous, while genera that did not continue into the Tertiary included *Oxytoma, Gervillia,* and *Opis.* The family Inoceramidae, which had existed but remained relatively unimportant during the Jurassic, burst forth into a great variety of species during the Cretaceous, some remarkable for their very large size and thick shells. Among the Pectinidae the genus *Neithea,* with one valve flat or concave and the other strongly convex, and with ornament of radial ribs usually of different orders of prominence, was particularly characteristic of the Cretaceous. Ostreidae occur in profusion and include many exogyrate as well as gryphaeate forms. The Trigoniidae are locally abundant and include a number of genera, such as *Pterotrigonia,* which are virtually although not in all cases strictly confined to the system. Among the heterodonts, the Arcticidae were still abundant and many attained a greater size than those of the Jurassic. The Veneridae gained steadily in importance. Radially ribbed genera of Carditidae, missing during the Jurassic, reappeared. Among the burrowers *Panopea* replaced the usually smaller *Pleuromya.*

The most notable of all Cretaceous bivalves were the rudists, particularly abundant in the Tethyan province although a few found their way to more northerly latitudes. The majority were cemented to the substratum and many lived gregariously, the lower valve acquiring a conical shape like some corals. Some rudists attained a very large size although in many cases they were not proportionately heavy owing to the cellular structure of their shells. None of the rudists survived beyond the Maastrichtian Stage. The Chamidae, the earliest members of which appeared in the Upper Cretaceous, resembled the rudists in their attachment by the tip of one valve and in the number of hinge teeth in the adult shell. It is, however, probable that they were of quite independent origin and derived from a heterodont family.

With the incoming of the Cenozoic Era bivalve faunas assumed a modern aspect, and many included a great number of species of all sizes. As Tertiary time advanced, marine geographical provinces become more strongly differentiated than during any other period. It is possible here to call attention to only a few points of particular interest relating to Cenozoic bivalves. During the Eocene a group of gryphaeate and exogyrate oysters, quite similar to those of the Cretaceous, made their appearance. Their geographical distribution, however, was very restricted, being virtually confined to central Asia and northern Africa. Pectinidae are abundant in many Tertiary formations and some genera, for example *Amussiopecten* of the Miocene, are of value as stratigraphical indices. The modern groups of highly inequivalve Pectinidae (genus *Pecten*) first appeared in the Oligocene, flourished in the Miocene, and still survives. During the Tertiary the once so abundant family Trigoniidae became restricted to Australasian seas and at the present day only one genus, living off eastern Australia, exists. The Cardiacea showed extraordinary potentialities for evolutionary diversification under the fresh-water and brackish conditions that prevailed during late Miocene and Pliocene times in southeastern Europe and adjacent parts of Asia. The great number of cardiid genera that existed in the area at that time constitute the family Lymnocardiidae. *Congeria,* a characteristic genus found in many of the same deposits, is referred to the family Dreissenidae, typified by the genus *Dreissena,* which, although so much like the marine *Mytilus* in external appearance, is believed to have been derived from some heterodont group. The marine genus *Tridacna,* commonly associated with coral formations, is notable, not only because it includes the largest bivalves still living, but also because of the extraordinary rotation that the soft parts have undergone in relation to the shell. It is thought to have been derived in Tertiary times from some genus of Cardiidae. Modern representatives of the freshwater superfamily Unionacea include, in Africa, India, and South America, genera of the remarkable family Etheriidae, in which one valve becomes cemented to other objects and the shell acquires an irregular, oyster-like appearance.

SELECTION OF NAMES APPLIED TO HIGHER TAXONOMIC CATEGORIES OF BIVALVIA

[Names are listed in latinized form although some (as indicated) were originally introduced in vernacular; authors whose names are not included are Gray *(56, 57),* Latreille *(88, 89),* de Blainville *(12),* Menke *(104),* M'Coy *(148),* Bronn *(17),* Fischer *(48),* Hertwig *(68),* von Vest *(175),* and Lameere *(87).* Most names based on those of genera are omitted.]

Actinodonta Douvillé, 1913 (*42,* p. 438, as "actinodontidés"). Introduced for group of lower Paleozoic bivalves of undefined taxonomic rank characterized by more or less longitundinally extended, divergent teeth on both sides of beaks. Accepted as suborder of order Taxodonta and scope extended by Dechaseaux (*38,* p. 266).

Adapedonta Cossmann & Peyrot, 1909 (*27,* p. 92). Proposed for 1 of 7 suborders of order Eulamellibranchia. Contents, Gastrochaenidae, Myacea, "Panopaeacea," Solenacea.

Ambonodonta Grobben, 1892 (*60,* p. 42). Proposed for 1 of 3 subclasses into which bivalves are divided. Contains (as orders) Eutaxodonta (=Arcidae), Heterodonta, Schizodonta, Anisomyaria.

Ameodontida Stenzel, Krause & Twining, 1957 (*156,* p. 43). Proposed for 1 of 8 orders into which bivalves are divided. Contents, Nuculacea, Nuculanacea.

Anisomyaria Neumayr, 1883 (*111,* p. 393, 412, as Anisomyarier). Proposed for 1 of 5 orders into which bivalves are divided; unites Monomyaria and Heteromyaria. Latinized by Steinmann (1888).

Anomalodesmacea Dall, 1889 (*32,* p. 452, 460). Proposed for 1 of 3 orders into which bivalves are divided, in which "archaic anodontism still persists as the characteristic of chief importance." Original contents, Solemyacea, "Anatinacea," Myacea, Clavagellacea, Pholadacea. Name changed to "Anomalodesmata" by some authors.

Asiphonida Fleming, 1828 (*50,* p. 381). One of 2 major subdivisions of the bivalves, characterized by complete openness of mantle margins.

Astartedonta Korobkov, 1954 (*85,* p. 56, 134). Proposed as 1 of 3 suborders of order Heterodonta. Contents, Astartacea, Crassatellacea.

Asthenodonta Dall, 1895 (*34,* p. 557). Proposed for a group of order Teleodesmacea with hinge "usually degenerate or obsolete, owing to modifications due to the burrowing habit." Contents, Myacea, Adesmacea [=Pholadacea].

Autolamellibranchiata Grobben, 1894 (*61,* p. 73). Proposed for 1 of 2 orders into which bivalves are divided and consisting of all members of class except Protobranchia.

Colloconchida Cox, 1960 (*29,* p. 85). Proposed for 1 of 5 orders of subclass Pteriomorphia and consisting only of the Ostreacea.

Cryptodonta Neumayr, 1883 (*111,* p. 393, as "Cryptodonten"). Order of thin-shelled, toothless Paleozoic bivalves, many of which had been described by Barrande from Bohemia. Name latinized by Fischer (1886). Same as "Palaeoconchae."

Ctenodonta Dechaseaux, 1952 (*38,* p. 262); attributed by this author to Douvillé (1912), who, however, had merely cited the generic name *Ctenodonta* Salter. Adopted for suborder of order Taxodonta to include Nuculacea and the cryptodonts.

Cyclodonta Dall, 1895 (*33,* p. 548). Proposed for group with "teeth arched, springing from below hinge margin, with hinge plate obscure or absent." Contents, Cardiacea, Tridacnacea, Isocardiacea.

Cyrenina Stenzel, Krause & Twining, 1957 (*156,* p. 133). Proposed for 1 of 2 suborders of order Heterodontida. Equivalent to "cyrenoid type" of Bernard.

Cyrenodonta Korobkov, 1954 (*85,* p. 56, 141). Proposed for 1 of 3 suborders of order Heterodonta. Equivalent to "cyrenoid type" of Bernard.

Desmodonta NEUMAYR, 1883 (*111,* p. 388, 411, as "Desmodonten"). Proposed for order in which 2 equal muscle scars and pallial sinus are present and in which hinge teeth are lacking or irregular and intimately connected with chondrophore. Contents, Pholadomyidae, Corbulidae, "Anatinidae," Mactridae, "Paphidae" [Mesodesmatidae], "Glycimeridae," ?Solenidae. Name latinized by FISCHER (1886).

Dimyaria LAMARCK, 1812 (*86,* p. 105, as "acéphalés dimyaires"). Proposed for 1 of 2 major taxa of bivalves; characterized by 2 adductor muscles. Name latinized by HERRMANNSEN (1846).

Diogenodonta DALL, 1895 (*34,* p. 538). Proposed for group of order Teleodesmacea defined as "laterals usually 1 or 2, and cardinals 3 or less." Contents, Cypricardiacea, Astartacea, Cyrenacea, Carditacea, Chamacea, Rudistae, Lucinacea, Leptonacea.

Dysodonta NEUMAYR, 1883 (*111,* p. 393, 412, as "Dysodonten"). Proposed for order of bivalves in which hinge teeth are wanting or irregular and 1 adductor only or 2 very unequal adductors are present; as originally proposed, identical with "Anisomyaria" of same author. Name latinized by FISCHER (1886).

Eleutherorhabda RIDEWOOD, 1903 (*143,* p. 185). Proposed for 1 of 3 orders of Bivalvia; characterized by ciliated discs forming only means of adherence of adjacent gill filaments. Contents, Dimyidae, Anomiidae, Arcidae, Trigoniidae, Mytilidae, "Melinidae," Spondylidae, Pectinidae, "Aviculidae."

Eudesmodontida COX, 1960 (29, p. 85). Proposed for 1 of 8 orders of subclass Heteroconchia. Contents, Allorismacea, Laternulacea, Clavagellacea, Pholadacea.

Eulamellibranchia PELSENEER, 1889 (*129,* p. 52, as "eulamellibranchiés"). Proposed for 1 of 5 subclasses of bivalves distinguished on basis of gill characters; in this group branchial lamellae are intimately connected by organic tissue. Contents, "Submytilacea," "Conchacea," Myacea, Pholadacea, "Anatinacea." Name latinized by COOKE (1895).

Eutaxodonta GROBBEN, 1892 (*60,* p. 42). Proposed for 1 of 4 orders of subclass Ambonodonta; hinge taxodont. Contents, Arcidae.

Filibranchia PELSENEER, 1889 (*129,* p. 52, as "filibranchiés"). Proposed for 1 of 5 subclasses of bivalves distinguished on basis of gill characters; in this group the 2 branches of same filament have no cross connections. Contents, Arcidae, Trigoniidae. Name latinized by COOKE (1895).

Foliobranchia MENEGAUX, 1889 (*103,* p. 142, as "foliobranches"). Proposed for 1 of 4 major taxa into which bivalves are divided on basis of gill characters; in this group (same as "protobranchiés" of PELSENEER) each demibranch consists of row of simple flattened leaflets. Contents, Nuculacea, Solemyacea. Name latinized by PERRIER (1897).

Gastrodeuteia PURCHON, 1959 (*138,* p. 225). One of 5 stomach types in Bivalvia; equated with Septibranchia, 1 of 3 orders into which class is divided.

Gastropempta PURCHON, 1959 (*138,* p. 228). One of 5 stomach types in Bivalvia, regarded as 1 of 3 suborders of 3rd order into which class is divided. Consists of many Eulamellibranchia.

Gastroproteia PURCHON, 1959 (*138,* p. 225). One of 5 stomach types in Bivalvia; equated with Protobranchia, 1 of 3 orders into which class is divided.

Gastrotetartika PURCHON, 1959 (*138,* p. 226). One of 5 stomach types in Bivalvia, regarded as 1 of 3 suborders of 3rd order into which class is divided. Consists of some Filibranchia and many Eulamellibranchia.

Gastrotriteia PURCHON, 1959 (*138,* p. 226). One of 5 stomach types in Bivalvia, regarded as 1 of 3 suborders of 3rd order into which class is divided. Consists of most of Filibranchia.

Hemibranchia PERRIER, 1897 (*133,* p. 2121). Proposed for 1 of 6 orders of bivalves. Contents, Septibranchia, Anatinacea, Tellinacea.

Hemidapedonta COSSMANN & PEYROT, 1909 (*27,* p. 92). Proposed for 1 of 7 suborders of order Eulamellibranchia. Contents, Tellinacea, Psammobiidae, Donacidae.

Heterodonta NEUMAYR, 1883 (*111,* p. 388, 412, as "Heterodonten"). Proposed for order of bivalves in which hinge teeth are clearly differentiated into cardinals and laterals. Name latinized by FISCHER (1886).

Heteromyaria PHILIPPI, 1853 (*134,* p. 361). One of 3 orders into which bivalves are divided, characterized by 2 very unequal adductor muscles.

Homomyaria ZITTEL, 1881 (*197,* p. 17). One of 3 subdivisions of order Asiphonida; hence definable as siphonless bivalves with 2 equal adductor muscles.

Integripalliata D'ORBIGNY, 1843 (*120,* p. 14, as "intégropaléales"). One of 2 suborders into which order "orthoconques" is divided. Name latinized as "Integropallialia" by WOODWARD (1854) and as "Integripalliata" by ZITTEL (1881).

Isodonta DALL, 1895 (*34,* p. 524). Proposed for group in order Prionodesmacea to include Pectinacea and Anomiacea. Name based on adjective "isodonte" introduced by FISCHER (1886, p. 936).

Isofilibranchia IREDALE, 1939 (*74,* p. 230, 409). One of 7 orders into which subclass Prionodesmacea is divided. Contents, Mytilidae.

Lipodonta IREDALE, 1939 (74, p. 229). One of 7 orders into which subclass Prionodesmacea is divided (given as alternative name for Palaeobranchia). Contents, Solemyidae.

Lucinina STENZEL, KRAUSE & TWINING, 1957 (*156,* p. 101). Proposed for 1 of 2 suborders of order Heterodontida. Equivalent to "lucinoid type" of BERNARD.

Lucinodonta KOROBKOV, 1954 (*85,* p. 56, 81). Proposed for 1 of 3 suborders of order Heterodonta. This and the Astartedonta correspond to the "lucinoid type" of BERNARD.

Macrociliobranchia ATKINS, 1938 (*5,* p. 425). One of 2 major groups into which bivalves are divided on basis of cilia of laterofrontal tracts of gill filaments. Contents, Protobranchia, Filibranchia (emend.), Eulamellibranchia, Septibranchia.

Microciliobranchia ATKINS, 1938 (*5,* p. 426). One of 2 major groups into which bivalves are divided on basis of cilia of laterofrontal tracts of gill filaments. Consists of Pseudolamellibranchia as emended to include certain groups formerly classified as Filibranchia.

Monomyaria LAMARCK, 1812 (*86,* p. 104, as "acéphalés monomyaires"). Proposed for 1 of 2 major taxa of bivalves, characterized by single adductor muscle. Name latinized by HERRMANNSEN (1847).

Naiadacea WHITE, 1942 (*182,* p. 59). Cited as suborder, consisting of Unionacea. The earliest work traced in which this very old name is applied to a taxon ranking higher than those of family group.

Neotaxodonta KOROBKOV, 1954 (*85,* p. 56, 170). Proposed as 1 of 6 orders into which Bivalvia are divided. Contents, Arcacea.

Oligodonta MARCH, 1912 (*101,* p. 113). Proposed for 1 of 2 divisions of order Heterodonta and consisting of forms with BERNARD's "lucinoid type" of dentition.

Orthoconchae D'ORBIGNY, 1843 (*120,* p. 14, as "orthoconques"). Proposed for 1 of 2 orders into which bivalves are divided, characterized by symmetry of shell and soft parts and by vertical position of plane of valve margins during life. Name latinized by GEINITZ (1845).

Pachyodonta STEINMANN, 1903 (*152,* p. 242). Proposed for a division of the Heterodonta consisting of *Megalodon, Diceras,* and the rudists.

Palaeobranchia IREDALE, 1939 (*74,* p. 232). One of 7 orders into which subclass Prionodesmacea is divided and consisting of Solemyidae. *See* also Lipodonta.

Palaeoconchae NEUMAYR, 1883 (*111,* p. 392). Proposed for order of thin-shelled, toothless bivalves, many of which had been described by BARRANDE from the Paleozoic of Bohemia. *See* also Cryptodonta.

Palaeoheterodonta NEWELL, 1965 (*116,* p. 16). Proposed for 1 of 6 subclasses into which Bivalvia are divided. Contents, Modiomorphacea, Unionacea, Trigoniacea.

Palaeolamellibranchia IREDALE, 1939 (*74,* p. 229, 305). Proposed for 1 of 7 orders into which subclass Prionodesmacea is divided and consisting of Trigoniidae. Identical with Schizodonta.

Palaeotaxodonta KOROBKOV, 1954 (*85,* p. 55, 72). Proposed for 1 of 6 orders of Bivalvia. Contents, Nuculidae, Nuculanidae, Malletiidae.

Pantodonta DALL, 1895 (*34,* p. 537). Proposed for a group belonging to order Teleodesmacea defined as "laterals exceeding 2 in any one group." Contents, Allodesmatidae.

Parafilibranchia IREDALE, 1939 (*74,* p. 230, 403). Proposed for 1 of 7 orders into which subclass Prionodesmacea is divided. Contents, Anomiidae, Placunidae.

Pleuroconchae D'ORBIGNY, 1843 (*120,* p. 15, as "pleuroconches"). Proposed for 1 of 2 orders of bivalves, characterized by asymmetry of shell and soft parts; normal position resting on one valve with plane of valve margins horizontal. Latinized by GEINITZ (1846).

Pleurodonta MARCH, 1912 (*101,* p. 112). Proposed for 1 of 2 orders of bivalves; main characteristic stated to be presence of embryonic teeth as crenulations on prodissoconch. Unites Dysodonta and Taxodonta as suborders.

Pliodonta MARCH, 1912 (*101,* p. 113). Proposed for 1 of 2 divisions of order Heterodonta and consisting of forms with BERNARD's "cyrenoid type" of dentition.

Praeheterodonta DOUVILLÉ, 1912 (*41,* p. 1680, as "préhéterodontes"). Proposed for a group of undefined taxonomic status, consisting of myophoriids, trigoniids and "préastartidés" (*Prosocoelus, Desertella, Megalodon, Palaeocardita,* etc.). Accepted as order and name latinized by DAVIES (1935).

Prionodesmacea DALL, 1889 (*32,* p. 453, 460). Proposed for 1 of 3 orders of bivalves; chief characteristic stated to be "transverse plication of hinge." Contents, Nuculacea, Arcacea, Naiadacea, Trigoniacea, Mytilacea, Pectinacea, Anomiacea, Ostreacea.

Prionodonta MACNEIL, 1937 (*98,* p. 457). Proposed as suborder of order Filibranchia, to include Cyrtodontacea, Parallelodontacea, Glycymeracea, and Arcacea. DALL (*32, 34*) had introduced term "prionodont" in same sense as "taxodont" but had not given it Latin form or systematic status.

Protobranchia PELSENEER, 1889 (*129,* p. 52, as "protobranchiés"). Proposed for 1 of 5 subclasses into which bivalves are divided, to include forms with primitive gills. Name latinized by GROBBEN (1892).

Pseudoctenodonta DECHASEAUX, 1952 (*38,* p. 267). Proposed for 1 of 3 suborders of order Taxodonta. Contents, Arcidae, Parallelodontidae.

Pseudolamellibranchia PELSENEER, 1889 (*129,* p. 52, as "pseudolamellibranchiés"). Proposed for 1 of 5 subclasses into which bivalves are divided, to include forms with filamentous gills in which connections exist between adjacent filaments and two branches of same filament. Name latinized by COOKE (1895).

Pteriomorphia BEURLEN, 1944 (*10,* p. 144). Proposed for an order of bivalves to include the Pteriacea, Pectinacea, Ostreacea, Anomiacea, Mytilacea, and Arcacea.

Pteroconchida Cox, 1960 (29, p. 853). Proposed for 1 of 5 orders of subclass Pteriomorphia. Contents, Pteriacea, Pinnacea, Pectinacea, Limacea, Anomiacea.

Rostroconchida Cox, 1960 (*29,* p. 85). Proposed for 1 of 5 orders of subclass Pteriomorpha. Contents, Conocardiacea.

Rudista de Blainville, 1825 (*12,* p. 516). Proposed as 1 of 4 orders of class Acephalophora. (Lamarck had previously treated "les rudistes" as a family.)

Schizodonta Steinmann, 1888 (*153,* p. 238, 250). Proposed as 1 of 6 orders of bivalves, to include only the Trigoniidae.

Septibranchia Pelseneer, 1888 (*128,* p. 1031). Proposed for a "sub-group" of bivalves in which gills are transformed into muscular partition dividing pallial cavity into 2 chambers.

Sinupalliata d'Orbigny, 1843 (*120,* p. 14, as "sinupaléales"). Proposed for 1 of 2 suborders of order "orthoconques." Name latinized as "Sinupallialia" by Woodward (1854) and as "Sinupalliata" by Zittel (1881).

Siphonida Fleming, 1828 (*50,* p. 408). One of 2 major subdivisions of the bivalves, characterized by fusion of mantle margins in 1 or more places.

Subfilibranchiata Cossmann & Peyrot, 1909 (*27,* p. 92). Proposed for suborder of order Anisomyaria. Contents, Mytilacea, Anomiacea.

Synaptorhabda Ridewood, 1903 (*143,* p. 186). Proposed for 1 of 3 orders into which bivalves are divided; characterized by cellular tissue forming junctions between gill lamellae and between gill filaments.

Taxodonta Neumayr, 1883 (*111,* p. 388, 412, as "Taxodonten"). Proposed for 1 of 5 orders into which bivalves are divided; characterized by presence of numerous hinge teeth, undifferentiated into cardinals and laterals, arranged in row. Name latinized by Fischer (1886).

Teleodesmacea Dall, 1889 (*32,* p. 453, 460). Proposed for 1 of 3 orders into which bivalves are divided; in this group the "various types of hinge have been harmoniously combined." Contents, Tellinacea, Solenacea, Mactracea, Carditacea, Cardiacea, Chamacea, Tridacnacea, Leptonacea?, Lucinacea, Isocardiacea?, Veneracea, Rudista?.

Teleodonta Dall, 1895 (*34,* p. 551). Proposed for group belonging to order Teleodesmacea characterized by "most perfected type of modern teeth." Contents, Veneracea, Tellinacea, Solenacea, Mactracea.

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FORM, FUNCTION, AND EVOLUTION

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CONTENTS

INTRODUCTION

A most challenging aspect of biology is the interpretation of raw data into a meaningful picture of interrelationships between component parts of individuals, various elements of the biota, and the environment that contains them—the field of interpretive biology. The challenge is greatly magnified in paleontologic interpretation, where soft parts, natural biotic assemblages, and total representation of environments are rarely encountered, and the dimensions of time and evolution must be considered. Yet it is in the imaginative interpretation of fossils, and its application to a variety of scientific and philosophical problems, that the great potential of paleontology lies. Interpretive paleontology has gained considerable impetus from the "new systematics" with its emphasis on fossils as biological entities having a given set of soft parts, definite population characteristics, environmentally adaptive morphology, and distinct ecologic relationships. The study of adaptive functional morphology, defining relationships between the animal, its skeletal components, the environment, and the path of evolution, is basic to all paleontologic interpretation.

The Mollusca, and in particular the Bivalvia, are among the best suited of invertebrates for interpretive studies and have been the subject of many pioneer works by neontologists and paleontologists. The following factors contribute to their utility:

1) The molluscan animal shows a wide range of variation in morphology and anatomy, reflecting its successful adaptation to a great variety of habitats. The soft parts of many living mollusks, and in particular Bivalvia and Cephalopoda, are well studied.

2) The soft parts of the Bivalvia are reflected to varying degrees in the morphology of the shell, the two having evolved as an integral unit rather than separate entities. It is thus possible to reconstruct many aspects of the soft body contained within fossil shells, providing additional information for the interpretation of functional morphology, ecology, and evolutionary trends in ancient forms.

3) The shell of the Bivalvia commonly reflects, in its varying shapes and structures, the preferred habitat and mode of life of the animal (Fig. 87). Once defined for living Bivalvia, the shell-habitat relationships may be used extensively in the interpretation of evolutionary trends as a response to changing environment or habitat or both.

4) The ecology of living Mollusca has been better documented than for most phyla of invertebrates, and this information is directly applicable to the interpretation of paleoecology, environmental selectivity in evolution, and adaptive value of morphological and anatomical features. The Bivalvia are probably better known than other classes of mollusks, but in total, the ecologic information for many taxa is still insufficient for detailed interpretive studies.

5) The Mollusca have had a long and successful evolutionary history. They are among the principal invertebrates in many Paleozoic rocks, and dominate most Mesozoic and Cenozoic deposits. The Bivalvia follow this trend, having undergone several successful periods of adaptive radiation, and are now at a peak in their evolutionary history. Many lineages can be traced well back into the Cenozoic, and many modern families had their roots in Mesozoic or older rocks. Numerous genera extend back at least to the Cretaceous. It is therefore possible in many Bivalvia to make direct comparisons between Recent and fossil anatomy and morphology—the ideal situation in interpretive studies.

6) A great deal of adaptive homeomorphy has taken place in the evolutionary history of the Bivalvia, so that even in distantly related bivalves, similar (convergent) shell structures or forms are produced in response to the same environmental controls. It is thus possible to interpret the functional morphology of many extinct groups in light of its adaptive value in living homeomorphic counterparts. This is a much neglected aspect of interpretive paleontology that can greatly enhance intensive study of Paleozoic bivalves.

7) Bivalves are common and normally well-preserved fossils, especially those with calcite shell layers, and it is possible to collect populations of species showing the es-

sential morphologic features for interpretive studies in beds of all ages.

8) The majority of living Bivalvia are, wholly or in part, marine shelf dwellers, and easily available for *in situ* study. Many can be raised and observed under laboratory conditions, providing an easy method of obtaining data on the functional aspects of morphology which can be related to fossils.

CONCEPTS AND METHODOLOGY

A clear set of procedures for collecting and analyzing data in multifaceted interpretation has not yet been devised owing to its youthful stage of development in invertebrate paleontology. The current methodology, the problems set out for study, and the pitfalls encountered are all basic, and pertinent to whatever sophistication the future brings to this phase of the science. It is obvious that interpretive study of fossil Bivalvia, and particularly extinct groups, is a far more complicated process than similar analysis of the living fauna, where one can be certain at the outset of anatomical and environmental characteristics and their relationship to the shell.

DATA COLLECTING

The ability of paleontologists to interpret fossils beyond basic systematics has been hindered by a lack of basic data necessary for complete analysis, or even for the primary job of relating form, function, and habitat. Applicable field data extend far beyond a large collection of well-preserved fossils from rocks of a certain formation and age—the normal information found in collections throughout the world. Three aspects of data collecting deserve special consideration.

The first deals with the fossils themselves. The best base unit for interpretive study of a species is the population, a statistically valid sampling of the gene pool as it is reflected in the preserved fossils. The adaptive value of any structure cannot be fully evaluated for any taxon until its normal range of variation is known, or until it can be determined whether the form of the structure is predominantly a product of genetic or environmental control. It would be meaningless to analyze the functional significance of a flaring auricle on specimens of *Crassostrea* when it could be demonstrated through population analysis in a single oyster bed that this structure was only a variation of the normal shell form produced by crowding; the structure would not be functionally equivalent to the auricles of pectinoids or pterioids. An integral part of defining population characteristics is the study of the animal throughout its range in space and time.

Adaptive features of bivalves related to temperature, salinity, turbulence, or other regionally variable factors of the environment can be detected in fossils only through the study of numerous populations along time planes, throughout the geographic range of the species.

Ontogeny plays an important roll in the study of form, function and environmental relationships. Collections representing the stages of growth are as necessary as those depicting normal adult variations in a species. Changes in growth form, relative development of morphological and anatomical features, and living habit are well known in the life histories of various Bivalvia. For example, numerous Pectinidae are byssally attached during juvenile development, but become free-living forms as adults. These commonly have more inequilateral juvenile shells, with relatively enlarged auricles and a deeper byssal notch than found in the adult stage. Thus the functional significance of form and structure changes markedly with growth, necessitating study of all ontogenetic stages.

If development of a morphologic or anatomical feature can be intimately related to change in life habit during ontogeny, the adaptive value of that developing structure can be interpreted more meaningfully as structural and environmental changes are studied concurrently. Such analysis may provide a key to the functional adaptations of extinct bivalves whose characters are reflected in the ontogeny of living species.

Much is to be gained in interpretive paleontology by recording the overall com-

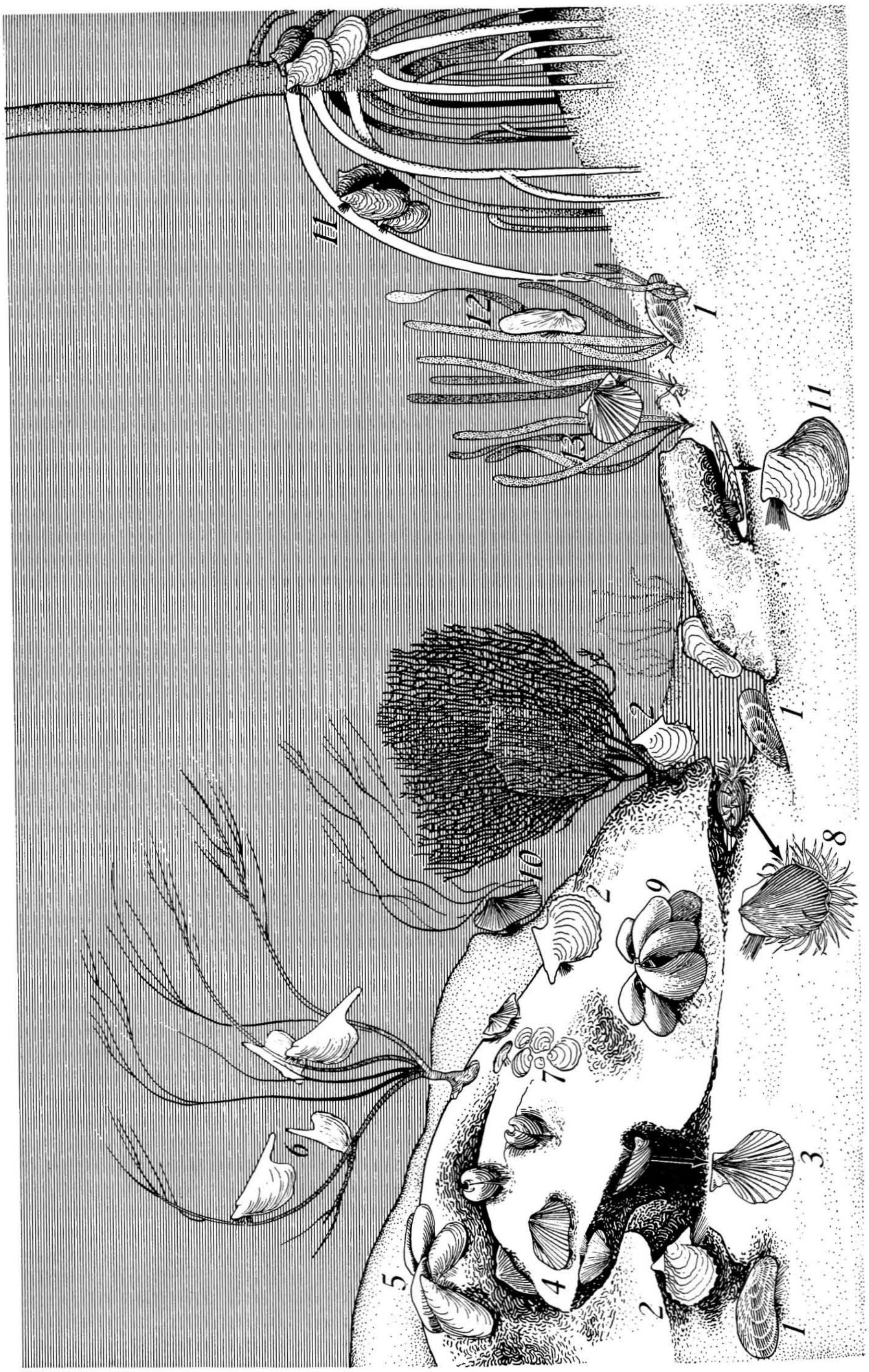

FIG. 87. Habitat and orientation of byssate epifaunal Bivalvia (Kauffman, n).

position and relative abundance of the biota associated with taxa whose functional morphology is under study. This serves two basic purposes. First, it may reflect environmental control on occurrence of particular taxa, since the entire biota better depicts the physical and chemical aspects of the depositional environment than does a single taxon or a few. Thorough knowledge of environmental influence on a taxon is critical to the functional interpretation of its morphology. Secondly, analysis of associated fossils and their relative state of preservation is useful in determining whether or not the taxa under study are natural associates of the bulk of the biota and of the sedimentary environment with which they occur, or whether they represent introduced, thanatocoenosic elements. The critical implications of this to the interpretation of form and function in fossil Bivalvia, relative to ancient environments, are obvious. Too often this factor has been ignored, and functional interpretation of fossils related to paleoenvironmental situation *not* affecting the animal in life.

The second aspect of collecting data for interpretive studies is the relationship of the fossil to the rock. This again is a frequently neglected observation.

Meaningful study of functional morphology depends upon knowledge of substrate-animal relationships during life. For extant genera and species also occurring in the fossil record this can be accomplished by direct observation of living counterparts, but for more archaic groups of bivalves the paleontologist must rely equally on broadly applicable neontologic data and evidence from fossil-rock relationships to define normal life habit, and subsequently to interpret the functional significance of morphologic features. Conjoined valves of fossil Bivalvia are commonly found preserved in or near living position, but this information is too often lost in collecting procedures. If pertinent observations on the orientation of coattached Paleozoic Bivalvia relative to bedding had been made more frequently in the past, then the argument might be resolved as to whether forms like *Cyrtodonta* (veneriform), *Cycloconcha* (telliniform), and *Cymatonota* (soleniform) were relatively immobile, semi-infaunal, shallow infaunal, or deep infaunal elements, or vagrant forms. These genera possess many shell features characteristic of living moderate-depth to deep-infaunal bivalves which move infrequently through the sediment, but those whose interior morphology is known have an entire pallial line, probably indicating lack of siphons or short siphons not adapted to deep burrowing. Their living infaunal counterparts all possess siphons at least half as long as the shell.

Observations on the degree of fragmentation, spatial distribution, secondary orientation, and size distribution of various elements in a fossil-bearing deposit yield much data applicable to interpretation of the depositional environment, degree of faunal mixing, and ecologic relationships affecting any taxon. These data are useful in determining the probability of whether or not a particular fossil-sediment association reflects the normal habitat of the animal, and thus the environment to which its anatomy and morphology are adaptive. A highly fragmented deposit indicates considerable transport and reworking, and co-occurrence of fragmented and unfragmented species of the same general resistivity is characteristic

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FIG. 87. *(Continued from facing page).*

[EXPLANATION: Shells somewhat enlarged relative to substrate, not necessarily to scale; water depth less than 50 feet, direction of current movement from left to right (modeled mainly from author's observations in nearshore waters east of Florida keys).]

1. Semi-infaunal forms. *Arcuatula* (ribbed modiolid); also *Pinna* and *Atrina* (not shown).

1-2,5,7,9,12. Closely attached forms.——*1. Arcuatula,* also smooth-shelled *Modiolus s.s.* (on rock).——*2.* Some *Pinctada.*——*5. Mytilus.*——*7. Anomia.*——*9. Brachidontes.*——*12. Amygdalum.*

2-4,8,10-11. Fissure-dwellers.——*2.* Some *Pinctada.*——*3.* Some *Chlamys.*——*4.* Some *Barbatia,* usually not nestling.——*8. Lima.*——*10.* Some *Arca,* rare and usually not nestling.——*11. Isognomon* (e.g., *I. radiatus*).

2,6,11,13. Free-swinging forms.——*2.* Some *Pinctada.*——*6. Pteria.*——*11. Isognomon alatus* GMELIN.——*13. Leptopecten.*

4,10. Nestlers.——*4. Barbatia.*——*10. Arca.*

of mixed assemblages. Secondary reworking of shells, in many cases into an unnatural environment for the transported species, is commonly indicated by strong linear orientation of shells not in living position, by deposits packed with shells of species not normally crowded or gregarious in their habitat, or by deposits yielding shells of a very narrow size range.

The physical characteristics of fossil-bearing rocks provide a considerable quantity of environmental information necessary to the study of adaptive morphology; this constitutes a third type of basic field data required for interpretive paleontology. Bedding commonly reflects rate, continuity, and energy gradients of deposition. Sedimentary structures such as cross laminations, flow casts, ripple marks, and mud cracks are primary indicators of energy conditions, amount and direction of current and wave action, and water depth. Particle size and mineralogy give important clues to depth, distance from strand, circulation, and energy conditions. Sediment and skeletal chemistry reflect water chemistry and paleotemperature.

Many additional relationships are known; it should suffice to declare that sediment study provides the greatest amount of information concerning environments in which fossil organisms lived. Inasmuch as precise definition of environment is necessary to understand the adaptive value of organic structures, it follows that interpretive paleontology demands equally close field examination of the physical and biotic characteristics of rocks.

COMPARATIVE ANATOMY AND MORPHOLOGY

These are the primary tools of interpretive paleontology, and the degree to which they can be applied to the study of fossil Bivalvia is directly correlative with: 1) the amount of data available on the antomy, morphology, physiology, geographic and ecologic variation, and life habit of living counterparts; 2) the degree to which soft parts, physiologic processes, and environmental preferences are reflected in the morphology of the shell (the common fossil), and how well these relationships are understood; 3) the level of phylogenetic relationship between fossil bivalves and their living counterparts; and 4) the precision with which the paleoenvironment can be defined and compared with that supporting modern counterparts.

At present, the basic anatomy, soft-part and shell morphology, and geographic ranges of the common shelf-dwelling marine, brackish-, and fresh-water Bivalvia are reasonably well documented and these data are directly applicable to interpretive molluscan paleontology. It may be assumed that structures found in common between Recent and fossil Bivalvia probably had similar function(s), especially in phylogenetically related or homeomorphic forms. In general the soft parts and the shell of bivalves have been studied as separate entities by biologists (in particular Yonge, 1952, 1953, *47,* 1958, 1962) and paleontologists. Yet interpretive biology is based on their interrelationship, and conceives the body and mantle-shell as evolving in unity.

Little is known about the physiology, and ecologic or geographic variation of modern bivalves—a considerable gap in the Recent data required for the study of adaptive structures in fossils. Physiological adaptation may be the primary impetus for evolutionary modification to cope better with a given set of environmental conditions. Many questions concerning bivalve adaptation can be answered once molluscan physiology is better studied, such as the relationship of shell structure, mineralogy, and isotope chemistry to the containing environment. The works of Epstein & Lowenstam (1961), Lowenstam (1954, 1960, 1961, 1963), Urey, *et al.* (1951), and others have just touched on this interpretive potential.

Ecologic data of a generalized nature is scattered through the Recent bivalve literature, but is detailed for few species and generally inadequate for comparative studies. Many paleontologists find it necessary to make their own observations of living bivalves *in situ* (Fig. 87). The most neglected aspects of Recent bivalve ecology are: 1) the lack of data concerning behavior; 2) the paucity of community studies and ecologic interrelationships within communities; 3) general lack of knowledge concerning ecological control on morphologic variation; and 4) almost total absence of data on how living communities of animals are reflected in shell accumulations of the substrate (the potential fossil deposits) with which they are associated. The basic premises of paleoecology and environmental interpretation using fossils depend upon clearly establishing these relationships and testing criteria for the recognition of biocoenotic as opposed to thanatocoenotic accumulations, or for dividing mixed assemblages. Establishing natural associations of fossils and environments, picking the "in place" assemblage from the total assemblage of shells in an ancient sediment, is critical to interpreting the adaptive value of structures in fossils and matching the adaptation to the proper paleoenvironment. My own investigations along the Atlantic shelf and in the Caribbean suggest that the majority of sublittoral sediments contain shells representing a mixture of molluscan species naturally associated with the deposit, and forms introduced from other environments; the latter commonly dominate inshore (depths of 50 feet or less), the former dominate offshore.

The soft parts of most living Bivalvia are reflected to a high degree, relative to other shelled invertebrates, in the morphology of the valves: shell form and inflation, muscle insertion areas, characteristics of the pallial line, marginal gapes, dentition, ligamenture, and a variety of interior structures such as platforms, internal ribs, and shallow furrows. Exceptions are forms like *Tridacna* and *Pecten* in which torsion of the animal in evolution has taken place somewhat independent of the shell and these gross anatomical modifications are not well reflected on the valve interiors. This close relationship between soft parts and mantle-shell implies not only that the Bivalvia are well suited for studies of functional morphology, but also that the general characteristics of soft parts in fossils can be accurately deciphered and integrated with shell morphology to allow interpretation of adaptive trends in the entire animal. The intricate relationship between the body of the animal and the mantle-shell in most bivalves suggests that they constitute a single study unit in interpretive paleontology, and have evolved as an integrated whole.

It is strange therefore that the mantle-shell and the soft parts of Bivalvia commonly have been treated as separate but interacting evolutionary phenomena, independently adapting to the same set of environmental conditions (YONGE, 1953, 1958). STASEK (1953) termed this the theory of independent entities and he reviewed its prevalence in molluscan literature. The philosophy of independent entities is expressed in many ways. At least a partial split of malacologists consists of those interested in soft-part morphology, anatomy, and physiology, and those primarily concerned with shell characteristics. Further, single studies of adaptive trends in molluscan evolution commonly deal with the evolution and adaptive morphology of the mantle-shell and the soft body as distinct, unrelated entities (YONGE, 1953). STASEK demonstrated convincingly that the inability of many workers to relate evolutionary trends in the mantle-shell with those of the soft body partially reflects their failure to orient consistently the mantle-shell *relative to* the body and thus develop a uniform system of orientational terms. He described the theory of transformation, and the use of transformation diagrams as a means of relating the body and mantle-shell of Bivalvia. This theory is based on the concept that "comparable regions of the body are always adjacent to comparable regions of the mantle shell, the differences between distantly related bivalves being the result of variation in the relative proportions of body and mantle-shell as a unity" (STASEK, 1963, p. 213). I concur with this philosophy and have utilized the concept of evolutionary unity between body and mantle-shell in a recent interpretive study of Cretaceous *Thyasira* (KAUFFMAN, 1967,*11*).

FUNCTIONAL MORPHOLOGY

Relating soft parts to features of the shell is probably the most critical and basic step in interpreting functional morphology and adaptive evolution in the Bivalvia. It allows partial reconstruction of soft parts and subsequently life habit in fossil forms, and in bivalves of all ages provides a far greater spectrum of data needed for evaluation of evolutionary change. Development of a functional adaptive trait rarely involves only a single structure but rather encompasses a suite of functionally integrated features. It follows that functional interpretation of structures as separate entities is not as meaningful as interpretation based on whole systems of interrelated features—anatomical and morphological. Thus, development of a plicate commissure in evolution of various ostreids does not simply reflect an adaptation to strengthen the shell against current action and predation, but involves interrelated phenomena such as an increase in mantle area and absorption potential, increase in area devoted to sensory perception along the mantle, decrease in gape necessary for feeding without decrease in water intake area (thus providing protection against fouling by large particles), and provides better stability for the shell on its substrate in the face of high-energy environments. Interpretive paleontology must deal with the bivalve—shell and body—as a whole unit to obtain a biologically complete and objective analysis of form and function.

RUDWICK (1961, 1964) added considerable impetus to detailed studies of functional morphology with his works on brachiopods and oysters and proposed an orderly process of functional analysis, the paradigmatic method. The four basic steps of this approach have been simply stated by CARTER (1967) as follows:

1) *Perception:* detailed examination and comparison of a structure or set of interrelated structures with related living and fossil parallels. From this one or more plausible functions are suggested for the structure.

2) *Specification:* testing suggested functions against idealized structural specifications relevant to each, taking into account the limitations of properties for materials involved. A paradigm, the structure capable of fulfilling the postulated function with maximum efficiency attainable under limitations imposed by the materials, is conceptualized for each postulated function.

3) *Evaluation:* comparison of the observed structure with the paradigm for each postulated function, providing an evaluation of the degree of efficiency with which the structure could have fulfilled each function. This is a measure of the degree of possible functional efficiency.

4) *Interpretation:* choosing the most applicable paradigmatic analysis, that which most closely approaches the structure being analyzed.

This organized and logical approach to the study of form and function in any element of the biota has considerable merit. Its demonstrated success in treating brachiopods and bivalves is strong recommendation for its use in interpretive paleontology generally.

HOMEOMORPHY AND TAXONOMIC LEVELS OF COMPARISON

Critical comparison of structures, or structure complexes, between living and fossil bivalves furnishes the bulk of evidence used in the study of functional anatomy and morphology. The majority of works dealing with form and function in fossil bivalves utilize this principle of direct comparison, but in some cases place more emphasis on phylogenetic than on morphologic ties in interpretation. The degree of attempted interpretation in many cases seems more nearly correlative with close phylogenetic relationship, normally at the generic or genus-group level, than it does with structural similarity. LADD (1957, p. 32) generally stated this widespread philosophy as follows: "The shape of a fossil shell may be a clue to its environment or mode of life if the shell closely resembles a living species or genus that is restricted to a certain environment. If there is no close living relative, interpretations should be made with caution." Although there is merit to this concept, it partially places emphasis on the wrong criteria as a basis for attempting interpretation, and decreases the potential scope and age span of detailed study in adaptation and functional morphology. Structural similarity, even between unrelated forms, should have priority in interpretation, whether similar whole shells are being compared, or like structures on otherwise dissimilar shells. Only through such a philosophy can the functional significance of spines on productid brachiopods be interpreted from living *Spondylus,* or the protective calcareous cup of various reef-builders—archeocyathids, solitary anthozoan corals, richthofeniid brachiopods, and rudist bivalves—be critically compared.

Comparative anatomy and morphology between closely related living and fossil bivalves can be applied widely as an interpretive concept back to the Cretaceous, and in many taxa to the Jurassic. A few Triassic and late Paleozoic comparisons are possible. Most interpretive studies accordingly deal with Jurassic or younger organisms. Paleozoic and Triassic bivalves are sorely in need of interpretive work, especially basic studies of form and function, and this can be accomplished only by following the leads of NEWELL (1937, 1942) and RUDWICK (1964) in emphasizing morphologic homology over close phylogenetic relationship. In comparative studies treating older fossil bivalves it seems necessary to utilize two working concepts: 1) high-level taxonomic comparison, in particular within the family and superfamily, and 2) recognition and use of homeomorphy in interpretation.

In adaptive radiation, principal anatomical and morphological features, and the fundamental functions they perform, become well defined early in the evolutionary history of a main phylogenetic branch (order, superfamily, or family level), and later diversification of the lineage is concerned with secondary modification of these basic structures and functions to meet small-scale environmental demands of various niches. At higher taxonomic levels, in fact, a close similarity of basic form and function exists among nearly all members of a phylogenetic branch, making it possible to compare with confidence like structures and their functional significance in only distantly related genera of the same family or superfamily. If the family or superfamily conceptually replaces the genus as the main phylogenetic level of comparison in interpretive paleontology, many extinct Paleozoic and archaic Mesozoic bivalve genera can be subjected to critical studies in form and function, adaptive value of evolutionary trends, and paleoecology. *Parallelodon* can thus be interpreted, in detail, in light of the anatomy, morphology, and function in *Arca; Pterinea* can be compared with *Pteria,* and *Aviculopecten* with living pectinoids. In such comparisons, where a considerable amount of geologic time and evolution are involved, some major morphologic differences are expected, and in fact occur, between comparable taxa. However, if functional morphology is studied not as a series of individual interpretations of isolated characters, but rather as interpretation of functionally integrated suites of characters, then a few structural differences between otherwise similar forms do not seriously detract from the sum of applicable data gained by comparative analysis of their entire shells. Determining the functional significance of independent characters is an initial step leading up to determination of interacting character suites, but is not itself a means to an end.

This concept can be expanded to allow comparison between similarly adapted forms belonging to distinct families of bivalves by changing emphasis from broad phylogenetic to homeomorphic relationships. Thus the living habit and functional morphology of Ordovician *Cymatonota* (family Modiomorphidae) can probably be interpreted from living *Solen* (family Solenidae). Although *Cymatonota* probably lacked elongate siphons characteristic of modern "jackknife clams," the sum total of its shell characters, including anterior and posterior gapes, closely resemble those of the elongate, deep infaunal *Solen.* This infers that shells of both genera were similarly adapted to rapid burrowing and an infaunal habitat with the long axis of the shell approximately perpendicular to the substrate, but that *Cymatonota* probably lived with the posterior tip of the shell exposed at the sediment-water interface. CARTER (1967,*4*) has made similar functional comparisons of the spines and concentric lamellae in *Hysteroconcha* (Veneridae) and *Hecuba* (Donacidae), remarkably convergent, unrelated bivalves from opposite sides of the Northern Hemisphere.

These examples demonstrate the broad homology of structures and functions that is common in bivalve evolution. The bivalve shell is a simple and efficient solution to the problem of protecting the soft parts that was derived early in the evolution of the class and has limited diversification potential, compared with something like an arthropod carapace. The basic adaptive radiation of the shell took place early in the Paleozoic, when most of the available marine habitats were explored and partially or wholly occupied. A variety of basic attached epifaunal groups were established in the Ordovician, as were infaunal protobranchs, ancestral lucinoids, and other ecologic groups which, except for an apparent lack of elongated siphons in most genera, had shell characteristics of various living sessile infaunal bivalves (e.g., *Cyrtodonta, Cycloconcha, Cymatonota*) and may have lived mostly buried in the substrate with the feeding margins exposed. Since the early and middle Paleozoic, no great change in these basic, adaptive shell forms has occurred, although some additional types have been added by further radiation (for example, cemented epifaunal elements—ostreids, spondylids, rudists, etc., niches of which during the Paleozoic were largely occupied by brachiopods). Instead, both related and unrelated groups of bivalves have repeatedly developed modified versions of these basic shell forms during radiation into the principal infaunal and epifaunal niches.

The second working concept in comparing the functional anatomy and morphology of fossil and Recent bivalves therefore stresses the study of structures divorced from phylogenetic relationships, within the framework of a classification based on adaptations and ecology. Such an approach takes advantage of widespread homeomorphy of shell features and its interpretive significance in bivalves of all ages. Thus the possible "rudder" function of the subtriangular posterior auricle and extended posterior shell flank in orienting free-swinging, byssally attached, epifaunal bivalves so that the inhalant margins face into the current and exhalant apertures away from it (Fig. 88) can be evaluated on a wide variety of morphologically similar but distantly related fossil and Recent genera. Among these are various Pteriacea (living *Pinctada,* Mesozoic-Cenozoic *Pteria,* Silurian-Mississippian *Leiopteria,* Devonian *Cornellites, Limoptera,* Ordovician-Pennsylvanian *Pterinea*), Mesozoic-Cenozoic Isognomonidae, Cretaceous Inoceramidae, the Pectinidae (living *Leptopecten*) and many others. The zigzag commissure occurs in an equally broad spectrum of taxa, and uniformly seems to be an adaptation to: 1) strengthening the shell during growth; 2) increasing the marginal mantle area, and number of associated sensory perceptors; 3) decreasing the minimum gape necessary for feeding and respiration, thus decreasing the size range of harmful particles able to filter between the valves and enter the mantle cavity, and other functions. Structural homeomorphy provides a successful means of comparing and interpreting form and function on a variety of bivalves without regard to age or phylogenetic relationships. It is one of the most valuable tools of interpretive paleontology, and is particularly applicable to the study of Paleozoic and early Mesozoic bivalves.

CONCEPTS OF ADAPTATION

Prior to documenting relationships between anatomy, morphology, adaptive function, and evolutionary trends in the Bivalvia, the concept of adaptation used here merits brief discussion. The whole problem of adaptation is adequately discussed elsewhere (for example, Pittendrigh, 1958).

Carter (1967) has recently reintroduced and discussed the question of whether or not all structures of an animal and its shell are, by definition, adaptive and functional. This is pertinent to the study of form and function in fossils because there is no way to observe the animal in life other than through its modern counterpart. If, in fact, features of the shell can be demonstrated as being nonadaptive or nonfunctional in living bivalves, these must be defined and avoided in the more subjective paleontologic interpretations.

Carter (1967) and before him others have pointed out that selectively neutral characters are very rare in living animals, and modern evolutionary theory incorporates this observation. Two types of nonfunctional characters are defined however, pleiotropic genetic effects and vestigial effects. Pleiotropic structures are basically formed when one gene locus gives rise to manifold morphologic consequences. Accessory structures formed during evolutionary development of a primary adaptive structure would be considered pleiotropic if they did not have a function or were not beneficial in any way to the animal. Normally, such accessory structures are not detrimental to the animal either, i.e., they are neutral, but it is conceivable that if the adaptive significance of the primary, genetically linked structure was far greater than detrimental effects of secondary structures, these features would not immediately be selected against. Conceivably a single structure will have both advantageous (adaptive) and detrimental effects, but will be retained if the former significantly outweighs the latter.

A second type of nonfunctional character is the vestigial structure, initially developed as an adaptive feature, and later in evolution losing its function due to changes in the demands of the environment or further modification of the animal so that its function is bypassed or replaced. Elongate spines on a hypothetical bivalve, adapted initially for protection against a certain predator who constantly attacked one area of the shell, would become vestigial if that predator became extinct and was not replaced in the area occupied by the bivalve, and if these spines had no other beneficial function. If they were otherwise detrimental they would probably be quickly eliminated from the lineage by natural selection or the stock would become extinct. A variation on the vestigial structure, but having an ontogenetic rather than a phylogenetic connotation, would be a spine formed at the commissure of the bivalve during growth as a support for an outgrowth of the mantle edge acting as a sensory receptor, but with continued growth deserted by the mantle sensor for a newly forming spine at the growing edge. This spine, now a permanent and unused part of the shell, might well be considered ontogenetically "vestigial" if it performed no secondary function. "Organizer" structures, necessary in early ontogeny as a base for the development of adult features, may similarly become ontogenetically vestigial.

The conclusion of most workers has been that nonfunctional structures are too rare and too hard to define, especially on fossils, to give them much consideration in interpretive biology. In fossil bivalves it is probably best to consider all structures functional, and adaptive, unless it can be demonstrated through careful evolutionary study that they are phylogenetically vestigial and on the wane. Few studies to date allow such observations. The lack of an obvious function for a bivalve structure probably reflects our lack of basic data concerning form, function, behavior, and habitat in living forms more than it suggests nonfunctionality.

Although it is conceivable that a bivalve structure may be adapted to a single function, and that this may be unrelated to other functional aspects of the individual, most commonly a structure has more than one known function and closely interacts with other structures, in various combinations (character suites) in performing these operations. It is further valid to define primary and secondary adaptation of structures whose function(s) changes with growth. In the broad sense, all structures of the bivalve shell, no matter what primary function they were selected for, are secondarily functional in providing a protective cover for the soft parts of the animal. Because functional character suites commonly include interacting parts of the shell, mantle, and soft body, total definition of these interacting characters and the intricate relationships they have to the function(s) performed, is commonly not possible in fossils. We are obligated however to utilize fully what characters are preserved for paleontologic interpretation; by critical comparison with the whole living counterpart, and imaginative thinking, reconstruction of complex form and function relationships is often possible in fossil bivalves.

In succeeding chapters dealing with specific structures and their probable function in bivalves, adaptations are listed as primary and secondary. This is basically an ontogenetic classification. Primary structural adaptations are considered as those which develop with growth to adapt the animals better at the time of their formation, to cope with the environment. Secondary adaptations are functions undertaken after the formation of a primary structure that are not necessarily related to the moment of growth but better adapt the entire animal, throughout its existence, to the immediate environment in a way distinct from that of the primary adaptation. Thus, in plicate ostreids and brachiopods, RUDWICK (1964) suggested that development of a zigzag commissure has a *primary* function of producing increased sensory perception along the mantle margin, as well as decreasing the gape of the shell, and correspondingly the size range and amount of sediment that can potentially slip between the valves during periods of sensory "scanning," feeding, and respiration, while not decreasing water-intake area. Plicae produced by the continued growth of the zigzag margin are *secondarily* adaptive in strengthening the entire shell, giving it greater stability on the substrate, and possibly preventing encrustation by certain kinds of epibionts. The primary function of a structure produced at the growing edge of the shell may continue throughout life even as the growing edge proceeds beyond it. The shell itself is such a structure, providing needed protective cover at the time of formation and throughout life. Spines or shell flutes adapted to support the animal on the substrate and keep the feeding margin off the bottom are produced at the mantle edge and continue to act in this capacity throughout life of the bivalve. In many cases, primary and secondary adaptations are difficult to define; their definition depends mainly on the detail with which the ontogeny and ecology of the living bivalve is known, and the degree of similarity between fossil and living forms. It may be easier to define the secondary adaptation of a structure whose function at the growing edge of the shell is poorly known.

Primary and secondary adaptation, as used here, does not imply a ranking of the importance of a structure to the survival of the animal, nor does it necessarily suggest which of its functions was the main factor in its natural selection during evolution of the lineage. These are harder and more subjective things to define in Bivalvia than are form and function. Some workers disagree with this, stating that adaptations affecting the animal during growth are the main factors in natural selection. Conceivably however, the plicae produced by the zigzag commissure in certain bivalves (or brachiopods) could have a far greater survival value in certain environments than the mantle folding that produced them, and be the main factor favoring the selection for the crenulated mantle edge and zigzag commissure—the so-called primary adaptations.

This paper is not designed as a complete compendium of functional interpretations given to various bivalve structures. Much of this information lies hidden in otherwise wholly taxonomic studies, or in obscure articles; the job of assembling it has just begun. The man purposes of the paper are: 1) to present a fair representation of current thinking in the field of interpretive paleontology as it applies to bivalves, both in regard to concepts and absolute interpretation; 2) to discuss the principal inferences that have been made concerning the form and function of common structures, both singularly and in adaptive suites in the Bivalvia; and 3) to demonstrate through a select study the potential interpretive value of this discipline in paleontology.

FUNCTIONAL MORPHOLOGY OF BIVALVE SHELL

In paleontology, functional morphology basically involves detailed study of the shell and its component parts, soft parts insofar as they are reflected in the shell, interpretation of probable function(s) for shell structures and soft parts, and reconstruction of the environment—the selective force on morphologic adaptation. These data are then applicable to interpretation of paleoecology, evolutionary trends, sedimentary environment, biogeography, and a variety of other disciplines.

Although RUDWICK's (1961) paradigmatic method of analysis suggests a procedure for analyzing the function of single structures in fossils, a broader pattern of analysis has not been defined. To discuss the total aspect of functional interpretation in Bivalvia there must be some ordering of data, a classification of topics and animals. The disadvantages of relating form and function to a system of phylogenetic relationships have been discussed and rejected as too confining on interpretative potential. Form (morphology), habitat (environment), and mode of life (ecology)—the specific adaptation, and the selective factors controlling its existence or nonexistence, are deemed the most important elements in the study of functional morphology, regardless of age and phylogeny. The following discussion is organized within this framework and oriented toward interpretation using the shell, the potential fossil. Form is classified as a series of morphologic features or suites of structures found in major areas of the shell (interior, exterior, commissure, etc.). Environments are classified in terms of their principal components: substrate, energy conditions, salinity, turbidity, etc. Bivalve living habit is divided into broad categories, each containing adaptive groups with certain unique morphologic features. In general, these categories are as follow:

1) Epifaunal Bivalvia (Fig. 87)
    a) Byssate free-swinging forms *(Pteria)*
    b) Byssate, closely attached, exposed forms; solitary *(Modiolus)* and gregarious *(Mytilus)*
    c) Byssate nestlers *(Arca, Barbatia)*
    d) Byssate fissure dwellers (some *Chlamys, Lima)*
    e) Cemented forms *(Ostrea, Chama)*
    f) Free living epifauna; swimmers *(Pecten)* and nonswimmers *(Glycymeris,* in part)
2) Semi-infaunal Bivalvia (Fig. 87)
    a) Sessile *(Pinna, Arcuatula)*
3) Infaunal Bivalvia
    a) Mobile detritus feeders *(Solemya)*
    b) Sessile detritus feeders *(Tellina, Nucula)*
    c) Filter feeders (Veneridae)
    d) Borers *(Lithophaga)*

In many of these categories, the major adaptive features of the soft parts and shell displayed by component taxa are strikingly similar, suggesting that study of the broader aspects of adaptation and functional morphology is a necessary and rewarding prerequisite for detailed studies of form and function. Some of these more generalized features will be treated first.

SHELL AS PROTECTIVE COVER

Because of their relative immobility and general lack of complex sensory receptors compared to the other main classes of Mollusca, the Bivalvia are potentially more subject to harmful influences of the environment, in particular predation, than their relatives. The swimming pectinids and limids are principal exceptions, and both have highly developed sensory areas (tentacles, eye spots) at the mantle edge. NEWELL (1965, p. 1) attributed this condition to secondary evolutionary degeneration from the condition of the hypothetical ancestral mollusk through loss of the head and its complex sensory structures, and general adoption of a passive mode of life in which feeding is accomplished either by filtering of water or sifting of sediment for particulate organic matter. This has limited the evolutionary potential of the group. In shell and body the Bivalvia have evolved along relatively simple themes, and have repeatedly, in unrelated groups, solved the problem of coping with the environment in much the same way.

With simple sensory perception, the bivalve animal probably reacts less efficiently and responds less quickly in advance of impending harm than does a gastropod or cephalopod. Further, it is generally not able to defend itself beyond closing the valve and few forms have escape mechanisms such as swimming or "jumping." Perhaps the study of bivalve physiology and biochemistry will reveal more complex sensitivity and protective chemical response than we are now aware of, but even so, the bivalve occupies one of the most precarious ecologic positions among the Mollusca. Survival of the Bivalvia as an evolutionary experiment, particularly in association with more complex and partially predatory groups of arthropods, cephalopods, and early fishes during the early and middle Paleozoic depended upon a high degree of external protection for the soft body of the animal. This was achieved prior to (in the protomollusk) or early in bivalve development by evolution or modification of the external shell and by adaptation to protective habitats, or both, in particular partial or total burial in the substrate. Most early and middle Paleozoic groups apparently lacked strong siphons but many otherwise show infaunal adaptations and were probably buried up to the feeding margin or had short siphons and were completely infaunal. The earliest known Bivalvia had two-valved, hinged, protective shells, many of them quite strong, and there is no evidence to imply that they did not completely enclose the soft parts. If the earliest history of bivalve evolution were known, we would expect to find grades between a naked or partially shelled protomollusk and completely shelled Bivalvia with soft parts totally contained between the valves, developing nearly parallel in time to the rise of potential predators.

It is obvious that the primary adaptive function of the shell in Bivalvia is protection and that any accessory structure of the containing valves, no matter how complex or for what environmental stimulus it was selected, shares in this protective function as well. Shell spines, possibly adapted primarily for supporting sensory receptors or for support on the substrate, also strengthen the shell and make it more difficult for a predator to get to the soft parts. Plicae produced by growth of zigzag mantle folds at the commissure, possibly adapted primarily for increasing the sensory area of the mantle edge, or as an aid in sediment screening, act secondarily to strengthen the shell and provide additional protection to the soft parts.

All Bivalvia during their ontogeny have a protective shell of two valves which in some groups subsequently becomes greatly modified and reduced so as not completely to enclose the mantle or body or both. In most cases these appear to be secondary modifications of the Bivalvia developed relatively late in evolution. Most forms in which the shell does not completely enclose the soft parts have compensated for this loss of protection by adapting the living habit to deep burial (*Mya:* see Cox, 1968, fig. 1, no. 2) or burial in hard substrate (*Zirfaea: ibid.,* fig. 3), by secreting secondary protective tubes around burrows (*Teredo: ibid.,* fig. 4), by inhabiting deep substrate declivities or building nests *(Lima),* or through other structural and ecologic modifications of the normal bivalve features and living habits.

FORM AND ORNAMENT OF SHELL EXTERIOR

Great diversification in form (shape and convexity), structures, and surface ornamentation of the bivalve shell is apparent from the living and fossil record. This reflects adaptive radiation of the shell and soft parts, in unity, into a considerable variety of aquatic niches. Shell form and exterior morphology are highly reflective of environmental demands and strikingly similar in even distantly related bivalves occupying the same niche. This suggests a closer correlation of form with habitat than with phylogenetic derivation and explains the great morphologic diversity among such highly adaptive groups as the Pectinidae, Ostreidae, and Mesozoic Inoceramidae. Pectinoids range from equilateral, subequally inflated swimmers *(Amusium)* and inequivalve swimmers *(Aequipecten)* and semiburrowers to prosocline, strongly auriculate byssally-attached forms *(Chlamys, Leptopecten),* to irregular oyster-like, cemented shells *(Hinnites).* The Cretaceous Inoceramidae show equivalent variety, ranging from thin nearly equal valves *(Mytiloides),* to highly inequivalve rudist-like shells *(Volviceramus)* and include byssate and nonbyssate lineages. Other families are much more conservative but are found in fewer major habitats. The degree of phylogenetic consistency in morphologic features of the shell, therefore, generally reflects the relative radiation into available aquatic niches; the greatest variety in morphology is directly correlative with the number of distinct habitats occupied. In general, epifaunal groups are more variable than those of the infauna; they are also subject to a greater variety of environmental pressures and available habitats.

Within any given ecologic niche, however, the bivalve shell form is relatively consistent among related and unrelated groups. The outstanding exceptions (e.g., *Tridacna*) do not detract from the general pattern and its application to interpretive paleontology. One and rarely two or three basic designs dominate; each is an efficient solution to a particular set of environmental demands. This tends to support NEWELL's contention that the evolutionary potential of bivalves is restricted (1965, p. 1). The bivalve shell is a simple cover with limited possibilities as to shape and convexity. One or a few basic shell forms were apparently developed early in the evolutionary history of the Bivalvia for each major habitat occupied, and subsequent evolution has only repeated and elaborated on these basic patterns. Relatively few new major specializations such as shell cementation, accessory plates, and severe modification of the shell in certain boring bivalves (e.g., *Martesia, Teredo, Bankia*) or to the bizarre Cretaceous rudists, have developed since early Paleozoic radiation. Thus the adaptive significance and function of thin, streamlined, strongly auriculate, slightly biconvex shells byssally attached to raised surfaces and swinging free to varying degrees in the current (Fig. 87), can be compared critically in such diverse groups as the living Pteriidae *(Pteria, Pinctada)*, Pectinidae *(Leptopecten)*, Isognomonidae *(Isognomon)*, Cretaceous Inoceramidae (some *Mytiloides, "Inoceramus" fibrosus* lineage), and possibly Paleozoic Pterinopectinidae *(Pterinopectinella)*, Aviculopectinidae *(Aviculopecten, Girtypecten)*, and Myalinidae *(Myalina)*.

Many schemes for the description of shell form in the Bivalvia have been presented. That of SHROCK & TWENHOFEL (1953) and NEWELL (1942), based on a series of linear dimensions and angles measured relative to a base horizontal, the hinge axis, has been widely utilized and supplemented by various additional axes, angles, and dimensions (for example, see YONGE, 1955; median axis, anteroposterior axis, demarcation line, etc.). However, attempts to integrate closely shell structures, based on this system of orientation, with features of the soft body have been largely unsuccessful.

STASEK (1963) has shown clearly that soft-part orientation varies independently of valve orientation in the standard system; the maximum length axis of the shell does not necessarily reflect the maximum length axis of the contained body. Thus, statements such as that by PELSENEER (1906) that development of the monomyarian condition in bivalves was accompanied by shortening of the anteroposterior axis and proportional increase in the dorsoventral (height) axis of the body are not necessarily meaningful in that they attempt to relate changes in one system (soft parts) relative to a system of orientation applied to the shell (STASEK, 1963, p. 199). The difficulty encountered in successfully relating evolutionary changes in the distribution of soft parts to modification of the shell described within the standard orientation system has led authors such as YONGE (1953, *47*, 1958, 1962) to envision the Bivalvia as consisting of two separate but interacting entities, the body and the mantle-shell (STASEK, 1963, p. 195). Such reasoning inevitably leads to the study of bivalve evolution from two, unrelated points of view. This view does not suit the concepts of interpretive paleontology, and in particular does not lend itself to the study of form and function, where the soft parts and the shell continually interact (in character suites) in adapting to and functioning in the immediate environment.

STASEK's (1963) contention that the body and mantle-shell evolve and interact in unity is well taken, and his proposed system of consistently relating evolution in shell form and structure to changes in the body—his theory of transformation—is dealt with in the preceding section (COX, 1968) and is worthy of careful consideration by students of interpretive molluscan biology and paleontology. In this system, main anatomical areas of the body can be delineated within sections of the shell by tracing consistently recognizable points of juncture between soft parts through ontogeny and evolution as marked on the shell by changes in sculpture or structure. This allows the paleontologist to reconstruct broadly the distribution of soft parts in fossil shells and to interpret more completely the function of shell structures and the evolutionary significance of their change through time. Recognition of an intricate evolutionary relationship between shell and soft parts defines a second primary function for the whole bivalve shell—a support for the enclosed soft parts. STASEK encouraged use of both the standard orientation system and transformation diagrams in studying bivalves, the latter being most useful in studies of form and function. The morphology of the Bivalvia has been thoroughly treated in the preceding section *(6)*, and the reader is referred to the detailed glossary, discussion, and extensive diagrams presented there for explanation of terms used in succeeding pages.

The observation that shell form and exterior morphology are strikingly similar among phylogenetically distantly related bivalves occupying similar niches strongly suggests that gross features of the shell are of major adaptive significance. This broad aspect of form and function has not been treated as much as many of the finer structures of the shell distinguished in published works, and so discussion here is given within the framework of the habitat groups previously described.

BYSSATE FREE-SWINGING BIVALVES

Bivalves of this type are characterized by having hydrodynamically streamlined shells (Fig. 88). They are moderately to strongly prosocline, attached anterodorsally, with a rounded anterior margin and commonly a projecting posteroventral flank. Beaks are reduced and auricles strongly developed, especially the posterior one. Prominent marginal reentrants commonly occur beneath the auricles and are generally coincident anteriorly with the byssal gape and posteriorly with the exhalant aperture or region. Shells are equivalve to moderately inequivalve and only slightly inflated, with maximum convexity umbonal or dorsocentral. Most have thin, smooth shells, although many fossil representatives are costate. Living *Pteria*, some *Pinctada* (Pteriidae), certain Isognomonidae (e.g., *Isognomon alatus* GMELIN), some Pectinidae *(Leptopecten)*, and probably extinct fossil forms such as Cretaceous Inoceramidae of the *"Inoceramus" fibrosus* or *tegulatus* lineage and *Oxytoma* (Pseudomonotidae?), Jurassic *Gervillia* (Isognomonidae), certain Triassic monotids, possibly late Paleozoic Aviculopectinidae *(Pseudaviculopecten, Aviculopecten)*, Silurian-Mississippian *Leiopteria* (Pterineidae) and Devonian *Pterinea* and *Cornellites* (Pterineidae) belong to this form group.

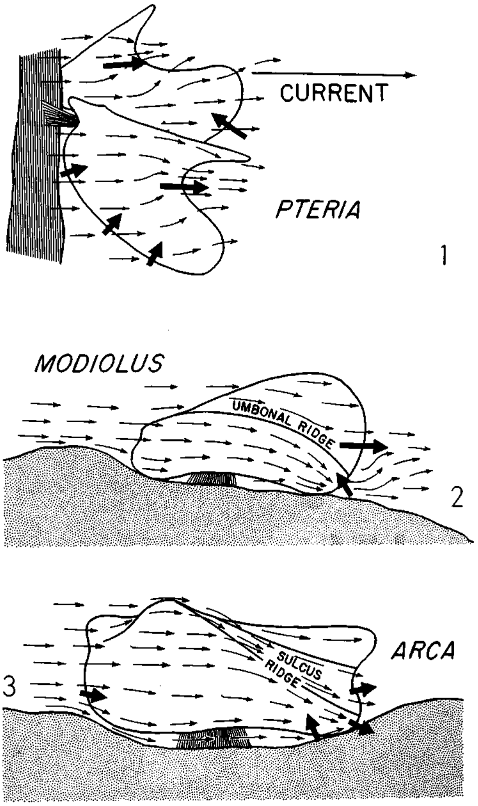


FIG. 88. Relation of inferred water-flow patterns (small arrows) to shell morphology and preferred orientation of selected byssate bivalves and to location of their inhalant and exhalant regions (heavy arrows). Shape of shell surface influences channeling of water first over incurrent areas and then over waste-bearing excurrent areas. *Pteria (1)* shown as attached to upright straight stalk (compare Fig. 87,6); *Modiolus (2)* and *Arca (3)* shown as attached to hard substrates typical of sublittoral areas (compare Fig. 87, *1,10*) (Kauffman, n).

In general the byssate, free-swinging Bivalvia are inhabitants of shallow inner sublittoral environments and all appear to be almost totally restricted to the continental shelves. Living forms are attached by a set of relatively long byssal threads to raised, firm substrates such as sea whips, algae,

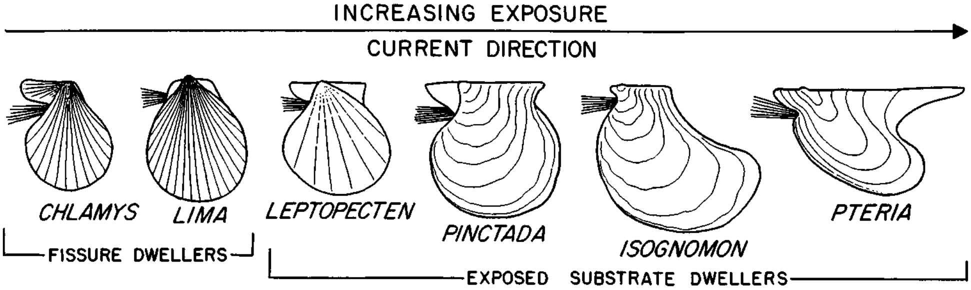


FIG. 89. Shell form of loosely attached byssate bivalves in relation to their exposure to currents (Kauffman, n).

grasses, projecting coral branches, wrecks, logs, and the like. In the shallow water preferred by most species they are subject to at least periodically strong currents and wave action; some are continually buffeted. *Pteria,* some *Pinctada,* and *Isognomon alatus* I have observed alive in the southern Atlantic and Caribbean areas, swing on the fully extended byssus to varying degrees during periods of normal feeding so that the plane of the commissure approaches or parallels the direction of the prevalent current. They are capable of retracting the byssus, thus pulling the shell up tight against the substrate when alarmed. Preferred orientation is with the plane of the commissure near vertical and the hinge axis slightly inclined to the horizontal in *Pteria* and *Isognomon alatus;* this is often modified by the nature of the available substrate and growing space. *Pinctada* is more variably oriented, with the commissure plane vertical to flat-lying. In nearly all cases these are solitary animals; *Isognomon* also grows in clusters.

The general shell form is well adapted to exposure on elevated surfaces in a set of relatively high-energy environmental conditions. In its preferred orientation, the subequivalve to moderately inequivalve, slightly inflated shell offers little resistance to currents, and with maximum convexity situated toward the leading edge of the shell, acts as a crude airfoil. The narrow shell is further adaptive in clustering *Isognomon* to more efficient packing of upright individuals into a tight aggregation. Studies on a limited number of living specimens in this morphogroup showed preferred attachment on the lee side of elevated objects, making the streamlining of the shell an even more effective adaptation for minimizing the chance of damage in severe current or wave action (Fig. 87). The enlarged posterior auricle and extended posteroventral margin of many forms functions as an effective rudder, insuring the most advantageous orientation of the shell in the face of currents (as long as the byssus is extended so as to allow a degree of play). There is a suggestion in limited studies of living free-swinging byssate forms that the highest degree of streamlining—the least convexity and greatest inclination—as well as the most pronounced posterior "rudders" (auricle and extended posteroventral margin) are found on forms occupying the most elevated and exposed habitats (Fig. 89).

The absence of projecting beaks and their strong prosogyrous inclination on many byssate bivalves is further adaptive to streamlining the shell, as may be the lack of coarse surface ornament on many members of this group. The adaptive role of surface sculpture in free-swinging byssate forms deserves considerable study and is not fully understood. Costation has been cited frequently as functioning to strengthen the shell against various energy factors and predation, providing a series of radially arranged structural ribs. This is especially critical at or near the thin shell margin. Costae and plicae would also serve to break up currents flowing over the shell surface, producing a layer of turbulent rather than lamellar flow, reducing hydraulic friction at the shell-water interface, and improving the ability of the shell to withstand currents or wave action. Yet most living members of this group are relatively thin-shelled and have smooth to finely lamellate outer shell surfaces. *Leptopecten,* a living exception, is strongly costate, with partially plicate marginal areas and commissure adapted primarily for increasing the area covered by complex mantle sensors, or acting as a sediment screen in turbulent water, as in other pectinids, or both. It thus represents a unique case. Several fossil representatives of the byssate, free-swinging epifaunal group are also costate, especially the Paleozoic pteriiform bivalves, and it would seem that general loss of radiating surface ornamentation was an evolutionary trend among inhabitants of the niche. A possible advantage of smooth shells over costate ones would be to increase the friction of water flow over the surface, and thus provide a stronger orienting force on the rudder-like shell, insuring its optimum positioning relative to current direction.

The functional significance of reentrants in marginal outline beneath the auricles has been little studied but in this group is probably of great importance. The byssal notch is primarily a product of retarded lateral shell growth around the byssal gape, keeping the gape open for extrusion of the foot and implantation of byssal threads, and for movement of the shell up and down the byssal axis. Also, depth of the byssal notch probably is related to strength of the byssal anchorage and amount of shell rotation on the byssus in the plane of the commissure. Further correlation is seen between the axis bisecting the byssal gape and the byssal axis (i.e., the line joining the center of the byssal notch and byssus with its point of origin on the foot). Thus the mean direction in which the byssus extends out from the byssal notch and implants on the substrate can be determined relative to the height-length coordinates of the shell, and a preferred angle of byssal attachment defined between shell and substrate. For an exposed byssate organism like *Pteria,* adapted in form to maintain a preferred orientation, keeping the angle of byssal attachment constant is critical not only to current orientation but also to proper feeding and waste removal, as subsequently discussed. The deep byssal notch, and small but prominent anterior auricle above it in many members of this group limit rotation of the shell on the byssus within the plane of the commissure, and thus help to maintain a consistent shell orientation. The deeper and narrower the notch and more parallel its sides, the tighter the restriction on movement.

Cox (Fig. 35) has indicated for *Pteria* and *Pinctada* that inward directed currents used in feeding and respiration enter the mantle cavity through the anteroventral and ventral portions of the shell and that outward directed currents leave the shell, bearing wastes, in the mid-posterior region, in the position of the posterior marginal reentrant below the main auricle. On a piece of coral or vegetation growing approximately vertical from the substrate, a typical *Pteria, Pinctada,* or *Isognomon* generally attaches to the lee side of the structure in a near-vertical position (*Pinctada* variable and typically more inclined, ranging to horizontal), but owing to the projecting anterior auricle, with the hinge axis inclined downward or upward (if attached in a fork) posteriorly (Fig. 87-88). In this orientation the incurrent areas face directly or diagonally into the prevailing water currents, and the excurrent area directly away from these currents so that exhaled waste material is removed quickly. For this system to act efficiently a consistent orientation must be maintained and is partially insured by restricted rotation on the byssus, as previously discussed. The posterior reentrant of the shell, at the excurrent aperture, is further functional in this system by creating a depressed posterior area on the shell into which currents are channeled as they pass over the valves (Fig. 88). Increased current flow brought about by this channeling at the position of the exhalant aperture would further insure rapid removal of waste and prevent deleterious concentration of these products in the water surrounding the shell. Current flow studies, such as those carried out by RUDWICK on brachiopods (1961), will be necessary to substantiate this function.

BYSSATE CLOSELY ATTACHED BIVALVES IN EXPOSED HABITATS

This group includes both solitary and gregarious forms which are variously adapted for relatively immobile attachment by short byssal threads close to the exposed surface of hard substrates (Fig. 87). The Bivalvia have adapted to this habitat in two principal ways, characterized by equivalve to subequivalve *Modiolus s.s.* or *Mytilus,* normally attached with the plane of the commissure nearly perpendicular to the substrate, and inequivalve forms like *Anomia,* in which the plane of the commissure parallels the substrate. *Pinctada,* partially a free-swinging byssate genus, also has representatives which approach *Anomia* in habitat and attach loosely to the substrate with the flat valve down and the plane of the commissure parallel or moderately inclined to the surface. It occupies a habitat intermediate between those of *Anomia* and *Pteria* or *Isognomon.* Both principal types of closely attached bivalves have solitary and gregarious representatives; gregarious mytiloids seem to have greater mobility in orientation (i.e., looser byssal attachment) than solitary forms like *Modiolus s.s.,* or flat-lying forms like *Anomia.* Both adaptive types solve the problems of their environment well; both are also known to a lesser extent as inhabitants of depressions and fissures on hard substrates, as is *Pinctada,* especially in intertidal or very shallow-water situations where this habitat affords extra protection.

The groups of byssate, closely attached bivalves, with few exceptions, are inhabitants of shelf environments and are concentrated in, and especially adapted to, high-energy shallow-water conditions of the littoral and shallow sublittoral benthic zones. The greatest diversity of forms is normally found in less than 50 feet of water. Strong wave and current action, periodic exposure and high turbidity, agitated well-lighted waters, and episodes of rapid scour and sedimentation are characteristic of their preferred environment. Unlike the free-swinging byssate forms (e.g., *Pteria*) which may survive intense current and wave action by moving with the flow of the current, Bivalvia of this group adapt to these conditions in having hydrodynamically streamlined shells which are normally tightly affixed to the substrate by means of a short byssus. The gregarious habit affords further protection to contained animals in that it essentially creates the effect of an individual protective depression for all but the outside members of the cluster.

The dominant bivalves in this group are solitary (many *Modiolus s.s.*) or gregarious forms (e.g., *Mytilus, Brachidontes*) oriented with the plane of the commissure approximately perpendicular to the substrate (Fig. 87,*3*). The predominantly thin shells are elongated along the anterior-posterior axis, equivalve to subequivalve, and moderately to highly inflated (except some mytiloids secondarily adapted in their low convexity to more efficient packing in gregarious clusters, as in *Isognomon*). Beaks are anterior, strongly prosogyrous and normally incurved, not projecting much above the hinge line. Maximum inflation is along the normally well-defined umbonal ridge extending from the beak area to the posteroventral margin. Auricles, if developed, are poorly defined and posterior, usually consisting of a flattened, projecting posterodorsal flank. A small anterior lobe anterior or ventral to the beaks is a common feature. Shells are characteristically subtriangular with the narrowest angle anterior. A single, shallow, concave reentrant in marginal outline is found anteroventrally to mid-ventrally in most forms and marks the site of a narrow, elongate byssal slit. Most shells are smooth, but fine to moderately strong costae occur on some genera *(Brachidontes).* Included in this ecologic group are fossil and Recent Mytilidae (e.g., *Mytilus, Brachidontes, Septifer, Modiolus s.s.*) in fresh to marine waters, Dreissenidae *(Dreissena)* from fresh (Recent) to marine (Cretaceous) environments and probably extinct forms like the early Paleozoic Ambonychiidae *(Ambonychia), Mytilarca* and probably various Mesozoic Inoceramidae *(Mytiloides),* to name a few.

The form of the shell is hydrodynamically streamlined for current flow passing from anterior to posterior and it is assumed that this is the preferred orientation during attachment to the substrate; this has not been substantiated by direct observation. Certainly clustering not only reduces the need for hydrodynamic streamlining and selective orientation to maintain stable attachment in strong currents, but also imposes a stronger orienting force on the animal—the availability of living space. Clustered individuals are therefore less likely to be oriented relative to current direction. It is postulated that in the evolution of mytiloid bivalves the primary adaptive value of the characteristic shell form was hydrodynamic streamlining. Development of the clustering habit was probably secondary and was accompanied by subsequent modifications of the basic form such as greater attenuation of the beak-umbo area and lateral flattening of the valves to allow greater efficiency in packing of shells within the cluster.

Only a posterior auricle is developed on the majority of mytiloid bivalves and this is poorly defined at best, being a flattened triangular extension of the posterodorsal flank not commonly separated from the main body of the shell by a definitive sulcus (more so in Paleozoic forms, e.g., Ambonychiidae), and angulate to broadly rounded at its extremity. This structure is the most exposed part of the shell when it is normally oriented with the recessed margin (site of byssal slit) nearly parallel to the surface of the substrate. As such it probably functions as a stabilizing rudder, helping the shell maintain a relatively constant position in the face of currents within the limited scope of free play allowed the shell by the short byssus. The limited mobility of the shell around the byssal axis in most mytiloids negates the need for a deep byssal notch and its stabilizing function. No function has been postulated for the anterior lobe in forms like *Modiolus* other than that it spatially accommodates the anterior adductor muscle internally, keeping it distant from the main area of the mantle cavity and its contained viscera (Fig. 34,*D*).

The umbonal ridge (posterior ridge, diagonal ridge of Cox, 1968) probably performs an important function in feeding and excretion within mytiliform groups. It obviously provides internally, by its inflation, needed space in the mantle cavity for proper distribution of the soft parts. If the preferred orientation of mytiliform groups is with the anterior end of the shell approximately facing into the current and closely attached to the substrate by a short byssus, with the plane of the commissure approximately perpendicular to the surface, then currents passing over the attachment surface would be partially channeled beneath the projecting umbonal ridges, especially in forms like *Modiolus s.s.* and *Dreissena* (Fig. 88), between the ridges and the attachment surface. A series of eddies would probably result. These currents, bringing in fresh food and oxygen would first pass over the inhalant aperture, lying just ventral to the termination of the umbonal ridge (Fig. 35), and in leaving the area of channeling posteriorly, secondly pass over the exhalant aperture, above or at the tip of the ridge, carrying away waste products. This remains to be tested.

A wide range of surface sculpture characterizes closely attached byssate forms, from very smooth shells *(Modiolus s.s.,* many *Mytilus),* to coarsely lamellate and costate groups *(Brachidontes,* many Ambonychiidae). Although shells lacking radiating elements dominate, there appears to be no consistent pattern of ecologic occurrence for costate as opposed to noncostate forms. Adaptive value can be attributed to both types of surfaces. The smooth-shelled forms can be packed more closely in clustered species than those with raised surface ornament. Costate shells are stronger than shells of equivalent thickness lacking costation, an important consideration in high-energy situations, and in addition are harder to extract from close quarters, in a rocky depression or in a cluster. The costae provide additional surface area and therefore increase friction against the walls of the depression or adjacent shells, as do coarse concentric lamellae.

The second adaptive morphotype included within the group of byssate, closely attached Bivalvia is less common but equally well suited for life in exposed, high-energy, shallow shelf environments, their preferred habitat. The Jurassic to Recent Anomiidae *(Anomia, Paranomia, Pododesmus)* dominate this group. Some *Pinctada* approximate the same living habit. Most living representatives of the Anomiidae cling tightly to exposed, firm substrates by means of a short, broad byssus extending from the point of origin on the foot, through a hole or notch in the dorsocentral part of the lower (right valve) to the substrate (Fig. 34,*F*). Some are depression- or fissure-dwellers, especially in shallow water. The byssus is calcified to varying degrees, and relatively inflexible. The shells are moderately to highly inequivalve, with the right (lower) valve flat, perforated for the byssus, and smaller in diameter than the inflated, irregular left (upper) valve. Valves are moderately thin, rugose to concentrically wrinkled, rarely with radiating costae, and round to ovate in outline. The lower valve commonly conforms closely to the shape of the attachment surface. Populations are highly variable. Most forms live as solitary individuals or loosely clustered, though shells may be crowded on a surface. The calcified byssus and close fit between the lower valve and substrate prevent significant movement of the shell around the byssal axis, especially when it is drawn down tightly against the substrate.

In most respects shells of this type are adaptive to the rigors of the environment in the same way as cemented bivalves, limpets, and cranioid brachiopods. Their flat lower valve and convex upper valve differentiate them from typical cemented forms and identify them with byssate bivalves, however. The large byssal notch or perforation in the lower valve functions uniquely in allowing firm attachment by a short, calcified, ventrally directed byssus. This insures that the shell will not be buffeted against the substrate or easily torn loose in strong currents. A relatively much longer and more flexible byssus results from extrusion through a byssal gape between the valves, and other means of stabilizing the shell in heavy currents must be developed, as in *Pteria*. The form of the upper valve in Anomiidae, though irregular, is most commonly round, with maximum convexity dorsocentral, the flanks being flattened and the surface irregularly wrinkled. As such, it is crudely streamlined in the face of currents and allows easy water passage over it, restricting the possibility of uprooting the shell by strong currents. No studies have demonstrated whether Anomiidae show preferred orientation in currents. If hydrodynamic stability were important, it would be expected that the dorsal margin of the valves would face approximately into the flow. The rough, irregular surface of many Anomiidae may further function to cut down the effects of strong currents on the shell by creating a layer of turbulent flow, with its relatively low hydraulic friction, close to the valve surface. Costae may serve the same function, as well as providing additional strength to the commonly thin shells.

Pinctada seems to occupy a position intermediate between free-swinging and closely attached byssate epifaunal bivalves, and incorporates characters of both morphologic groups. In shell outline it has many of the characteristics of free-swinging byssate forms, being prosocline, strongly auriculate, with relatively low convexity, and a prominent byssal notch (Fig. 89). It differs from typical free-swinging forms like *Pteria* in being more quadrate and less prosocline in outline and in being markedly inequivalve (right valve flat to slightly convex, left valve moderately convex). The byssus is directed more laterally out of a prominent notch in the right valve. Yonge (1953) considered *Pinctada* to represent an important evolutionary step between byssate and cemented Bivalvia and cited the normal living habit as being closely attached to the substrate, right valve down and the plane of the commissure parallel or at a slight angle to the surface. In this orientation it approaches the anomioid habit. My *in situ* observations of *Pinctada radiata* Leach in the inner sublittoral zone of Florida and the Caribbean Islands contradict this to some extent. In shallowest waters (10 feet or less) continually buffeted by waves and in areas where no vertical substrate is present (e.g., sea fans, sea whips, branching coral), as on a denuded reef, *Pinctada radiata* grows as Yonge described, although as many are attached with the plane of the commissure inclined at a moderate to high angle to the substrate as are found lying flat on the surface. These are still relatively mobile on the byssus and dominantly face dorsally or anteriorly into the current. The preferred habitat in these areas, however, seems to be attachment to the lee sides or in branch junctions of sea whips and fans, predominantly the former, in much the same manner as *Pteria*. The dorsal margin is moderately to steeply inclined upward and the flat valve lies against the upright surface. This seems to be the habitat for which its streamlined shell is best adapted.

It is significant that *Pinctada* combines the shell characteristics of two distinct morphogroups, free-swinging and closely attached byssate epifaunal bivalves, and occupies both niches equally well. Contrary to YONGE's (1953) opinion, *Pinctada* seems to be among the more generalized and adaptive of the byssate epifaunal bivalves, and its form might be expected to be ancestral to more specialized groups of both niches. The predominance of this shell form in certain early Paleozoic byssate bivalves like *Pterinea* supports this.

BYSSATE EPIFAUNAL NESTLERS

Bivalves of this group are typified by many fossil and Recent Arcidae (Fig. 31,*F*, 35,*A*). Shells are subrectangular to subovate, elongated anteroposteriorly, moderately to highly inflated, prosocline, and normally have prominent, inflated moderately projecting incurved beaks and umbones, characteristically prosogyrate but ranging to opisthogyrate and situated mid-anteriorly. The hinge line is elongate, straight, and commonly projects onto small triangular auricles anteriorly and posteriorly. A shallow mid-ventral concave reentrant in the marginal outline marks the large byssal gape. Costate, thick to moderately thick shells dominate. Typical examples are living and fossil *Arca, Barbatia,* Mesozoic *Nemodon,* and Paleozoic *Parallelodon.* Not all Arcacea are included, since many of the more ovate genera are unattached, partially or wholly infaunal elements (e.g., *Noetia,* some *Anadara*).

The byssate epifaunal nestlers inhabit nearshore, shallow-water environments, predominantly at depths less than 100 feet, and prefer depressions in firm substrate for attachment to exposed surfaces. On reefs they are often found in crevices between coral heads, or within coral branches (Fig. 87). They are common in wave-cut depressions in limestone benches, on the roots of marine plants, attached to the protected sides of vegetation and hard reef blocks, and many species occupy the protected photonegative undersurfaces of rocks and growing reefs, where their range overlaps that of the byssate fissure-dwellers like *Lima* and certain *Chlamys* (Fig. 87). Inasmuch as the typical shell of the byssate nestler seems highly adapted to habitation of exposed surficial depressions in hard substrata, the habitation of the even more protected undersides of rock surfaces probably represents secondary adaptation to a new niche for additional protection.

The subrectangular arcoid shell form is structurally well adapted for nestling in crevices, and in this habitat is firmly anchored against uprooting by strong current and wave action or predator attack. The large, partially reinforced byssus extends mid-ventrally through a large gape into the base of the depression occupied and the shell is raised and lowered vertically on this structure by a powerful set of pedal-byssal muscles capable of rapid contraction (Fig. 31,*F*). In normal orientation the long axis of the shell approximately parallels the long axis of the depression, which the living forms are able to enlarge or modify in shape by rotational manipulation of the shell on the byssal axis, grinding both shell and substrate until a snug fit is insured upon contraction. When withdrawn into the depression, the shell, tapered ventrally and elongated parallel to the depression, acts like a broad wedge in a crack and cannot be moved easily either sideways or back and forth. Lamellate costae, by providing additional surface friction, aid in preventing its easy removal, wedging into smaller side depressions and strengthening the shell. The shell will break before the force of the byssus is overcome by simple prying from below. Thus, in form and direction of byssal extension, the shell functions as a virtually immovable protective shield for the soft parts in its preferred habitat. The auricles may function in this group as supporting shell structures for enlargement of the taxodont hinge and ligament area; increase in the area covered by ligamental material and in the number of interlocking teeth further strengthens the enclosing valves by prohibiting their easy disarticulation or rotation in the plane of the commissure by predators and strong wave or current action.

When feeding the shell is raised on the byssus and the valves gape ventrally near the bottom of the depression occupied. Two external features of the shell apparently have an important function in the feeding process. As in mytiliform bivalves, many arcoids possess a strong umbonal ridge and have maximum convexity located dorsocentrally. Similarly, water flowing over the attachment surface is initially channeled between the umbonal ridge or axis of maximum inflation and the base of the depression, along the inhalant areas of the mantle edge (anterior, ventral) and passes out of the trough thus created into open water as it flows past the posterior exhalant aperture (Fig. 88), continually providing clean water for feeding and respiration and flushing out waste products. Flanges or frills of periostracum around the anterior, ventral, and posterior edges of the shell and along the umbonal ridge function in many species of *Barbatia* and some *Arca* as a sediment screen over the feeding edges and in some cases may nearly seal off a narrow depression from possible infiltration of harmful material into the mantle cavity. They further enclose the main water channel. This is important in turbid, high-energy environments preferred by many arcoids.

Large triangular interareas between the hinge line and beaks of typical arcoids support the primitive ligament composed of numerous thin sheets. The broad attachment area is necessary to accommodate enough ligamental material, arranged in this inefficient manner, to open the valves. In the Bivalvia possessing more advanced, compact types of ligaments, this area is greatly reduced.

BYSSATE FISSURE-DWELLERS

Byssus-attached inhabitants of fissures mainly include partially or wholly photonegative species of bivalves belonging to two morphologic groups, one or both of which may have become adapted to the habitat secondarily during its evolution without additional significant modification in form. The primary habitats are the underside of rocks, deep, relatively dark declivities and fissures, reef tunnels, spaces inside root bundles of aquatic plants, and similar niches with good water circulation, weak light, and good protection from strong wave or current action. Some of the included species sparsely occupy other, more exposed surfaces if their preferred habitat is not available. In addition to the principal inhabitants (e.g., pectinoids, Limidae, certain Pteriidae, *Isognomon* such as *I. radiatus*), various arcoids primarily adapted for exposed depression-dwelling secondarily occupy this niche in abundance, especially in very shallow waters, thus gaining added protection from currents, waves, and exposure. Energy conditions being rarely severe in these habitats, and the number of predators being somewhat limited, arcoids occupying them are less dependent on individual depressions for firm anchorage and exist in great numbers, tightly fastened to relatively flat surfaces where depressions are not available. It appears that few arcoids bother to excavate or modify their own depressions, as they do on exposed surfaces. The same habits are shown by deep-water arcoids for many of the same reasons.

Similarly, because of the strong adaptive value of their shell morphology for habitation of exposed shallow-water depressions on hard substrates, fissure-dwelling arcoids are considered to be secondary occupants of this niche which have not developed distinct shell characters that may be considered specifically adapted to it. Oysters, mytiloids, anomioids, and a few other groups are occasional inhabitants of fissures and the undersides of rocks, especially at their edges, and in very shallow-water or littoral habitats. None are considered primarily adapted to this habitat, but they gain added protection from it under severe conditions.

The principal bivalves inhabiting these niches (besides arcoids) are byssate species of *Lima* (Limidae), *Chlamys* (Pectinidae), the more rounded or quadrate forms of Isognomonidae (e.g., *Isognomon radiatus* ANTON), and related forms. Certain of the more rounded to quadrate Pteriidae are also known from it (e.g., some *Pinctada*). Though distantly related, these bivalves share many things in common. They are all byssate and attached loosely by relatively long flexible threads protruding anterodorsally from a prominent byssal gape between the valves; the shells are capable of considerable movement about the byssus. The valves are not streamlined for ready orientation in the face of currents, however, as is *Pteria,* but are predominantly round to ovate, slightly inequilateral (prosocline except for *Lima*: opisthocline), with the height axis longest. Posterior auricles are relatively small, and posteroventral projection of the valves absent or small-scale (Fig. 87,*2-3, 8, 11*); the shells would not act as an effective rudder for orientation in currents, as does the posteriorly extended *Pteria.* Convexity ranges from low to moderate; small anterior auricles and a shallow byssal notch occur in *Isognomon* and *Lima;* a pronounced auricle and notch characterize *Pinctada, Chlamys,* and related genera.

These forms are thus not well adapted for free-swinging byssal attachment on surfaces exposed to intense current or wave action, and would be hydrodynamically unstable, easily twisted and torn loose in such a habitat. Two of the primary inhabitants, typified by *Lima* and *Chlamys,* have highly developed sensory tentacles or projected sensory regions (eye spots) at the mantle edge; in *Lima* the tentacles cannot be fully withdrawn into the shell and are easy prey for predators, especially fishes, when the shell lies exposed. Most forms are costate or coarsely lamellate, with moderately thick shells.

Shells having the form of *Lima, Chlamys,* and more ovate *Isognomon* and *Pinctada* might therefore appear to be adaptive to crevice, fissure, cave, and rock undersurface habitats primarily in a negative way—a simple round to ovate disc lacking special adaptive form or structure to deal with high-energy environments, or (in *Chlamys* and *Lima*) lacking the shell symmetry ideal for swimming, seeking protection and survival in this habitat where such modifications are unnecessary. This is not compatible with the evolutionary record of byssate bivalves, which shows these relatively equilateral forms as modifications of the more streamlined early and middle Paleozoic shells obviously belonging to exposed, byssate, epifaunal organisms or potentially free-swimming groups.

Few thoughts have been published on the adaptive advantage of rounded to ovate, nearly equilateral shell forms in epifaunal bivalves other than "freedom of organization" of the soft parts internally (YONGE, 1953), and its obvious value in the swimming habit. In swimming, the rounded shell provides a broad nearly equidimensional disc which maintains a stable horizontal attitude in the water and offers sufficient resistance to allow "gliding," once the thrust phase of the process has been completed by water currents expelled from between the valves, or by rapid clapping together of the valves. Notably, both *Chlamys* and *Lima* include swimming species, and specifically the fissure-dwelling limids are reported to be among the best swimmers in the genus group. Not only is the secretive habitat and swimming ability of forms like *Lima scabra* BORN functional in protecting the nonretractile tentacles from predators or current-wave damage, but this and other species gain additional protection from their ability to build "nests" of byssal threads around the shell and tentacles, within the protected fissure habitat.

If the primary function of round shells in epifaunal organisms is, at least in Limidae and Pectinidae, the swimming habit, then the occurrence of predominantly rounded to ovate shells on byssate fissure-dwellers of these groups has little significance and suggests secondary adaptation of the animal to the habitat to seek further protection, without shell modification other than slight loss of symmetry. This is an unsatisfactory explanation for the occurrence of the more rounded to ovate *Isognomon* and *Pinctada* in the same habitat, belonging to groups which never developed the swimming habit, and may represent only part of the answer.

It is possible that round or ovate shell form has definite adaptive value because it allows optimum free spatial distribution of soft parts within it. Other shell-morphologic aspects of survival being minimized as they would be in a protected fissure habitat, the round shell form could have been selected for genetic conjunction with a decentralization of soft parts. Yonge (1953) has partially dealt with this problem.

A final possible function of rounded shell form in attached epifaunal Bivalvia is that it provides relatively greater areal distribution of sensory receptors at the mantle margin. The high degree of sensor development in Limidae and Pectinidae, among the most disclike epifaunal bivalves, suggests that this is feasible. In the design of a simple disc cut on one side by a hinge line, the percentage of marginal valve area potentially supporting mantle sensors is directly proportional to the relative length of the hinge line and the arc of the commissure it subtends. The development of auricles, depth of subauricular notches, amount of plication, size of inhalant and exhalant apertures, and relative distribution of sensors are additional individual variables. In design, an optimum coverage is attained in pectiniform shells having the hinge line, except for the part extending onto the auricles, relatively short and the commissure area potentially supporting sensory receptors (eye spots) forming an arc approximately 330° to 350°, nearly a full sensory spectrum. Of course, variations are seen in the distribution of sensors around the margins of pectinids, none or few being present dorsolaterally just beneath the auricles, but this lack of sensory coverage is compensated for by auricular sensors (Waller, 1967). The sensory tentacles of limids cover a slightly smaller arc on the commissure, but are long and thus able to compensate for this, giving equivalent sensory coverage. The mantle edges of *Pinctada* and *Isognomon* also perform a sensory function, but are much more finely tentaculate and lack highly specialized cells or structures.

The contention may be made, therefore, that the more rounded to ovate shell form in epifaunal Bivalvia, where it is permitted to exist by the environment or specialized structures and behavior of the animal (e.g., swimming), or both, is highly adaptive and selected for in evolution, functioning to increase the area of sensory reception around the commissure and thus the ability of the animal to be forewarned of impending danger. A high degree of sensory reception may be more important in photonegative habitats, where light intensity is low, than in more exposed, well-lighted areas. I have observed frequently that many epifaunal Bivalvia, even those without specialized light-sensitive areas, as in Pectinidae, are highly sensitive to abrupt changes in light intensity and will close the valves and contract on the byssus if, for example, a diver or large fish passes between them and the light source, even at a considerable distance. The ability to detect such a change is minimized in a diffused light situation, as in fissures, caves, or rock undersides. It is possible that this is compensated for in the more rounded shell form and more highly developed sensory receptors at the mantle margin. Considerable work needs to be done to substantiate this hypothesis, and to investigate further the possibility that increased sensory perception is necessary for effective feeding in these photonegative environments. Only in these ways can the predominantly round to ovate shell form in fissure-dwelling epifaunal Bivalvia be considered a functional adaptation specifically for this habitat.

Coarse concentric lamellae (e.g., *Isognomon, Pinctada*) and strong, commonly fluted or lamellate costae (e.g., *Chlamys, Lima,* some *Pinctada*) not only strengthen the shell of byssate fissure-dwelling bivalves but also make it harder to extract from narrow crevices. In this habitat, the shell is normally attached with the ventral margin facing outward. Flutes and raised lamellar plates on costae and coarse concentric lamellae also face outward in this orientation angled like barbs against the fissure walls. They function to hold the shell in place, reinforcing the byssus, when its extraction is attempted by predators.

CEMENTED EPIFAUNAL-BIVALVES

This group includes a variety of forms and unrelated taxa which have in common cementation of the shell, normally by calcareous deposits, to hard substrate during part or all of their life cycle. The primary function of this habit is obvious; it provides continued, stable orientation of the bivalve and protects against destruction by dislodgement in the preferred habitat, commonly one of high-energy wave and current conditions. Although some cemented Bivalvia have been reported from considerable depth, the great majority are shelf-dwellers and are concentrated in the inner sublittoral benthic zone, the maximum known diversity being in marine water less than 100 feet deep. Most commonly, cemented Bivalvia prefer exposed or semiexposed substrate surfaces subject to periodically intense wave and current action, good lighting and agitation, periods of turbidity, and an abundant food supply. Representatives of this habitat group are primarily the living and fossil Ostreidae (*Ostrea, Crassostrea, Pycnodonte, Exogyra, Gryphaea, Arctostrea,* etc.), Spondylidae *(Spondylus)*, Pectinidae *(Hinnites)*, Plicatulidae *(Plicatula)*, Chamidae *(Chama, Echinochama)*, the highly diverse Mesozoic rudists, and the late Paleozoic-early Mesozoic pseudomonotids. Many parallels may be found among late Paleozoic Brachiopoda. The general evolutionary history of the Bivalvia suggests that cementation was a secondary adaptation in some cases of mobile or partially byssate epifaunal bivalves to a completely sessile habitat (e.g., Monotidae, Pectinidae) (YONGE, 1953). The origin of ostreids (NEWELL, 1960), chamids, and rudists (YONGE, 1967) has been investigated but is still not clear.

Cemented epifaunal Bivalvia include both solitary (e.g., *Spondylus*) and gregarious groups (e.g., many Ostreidae). Shell form within populations is highly variable owing to the "molding" effect of the substrate. Gregarious crowding in beds (as in *Crassostrea*) introduces a second source of variability in form, structure, and ornament, with lateral shell growth commonly impeded, auricles eliminated, and sculpture patterns disrupted. Not only is the gross character of the substrate reflected in the general form of the valves, especially the attached valve, but in some Ostreidae the fine detail of the surface is preserved on the outer surface of both valves, being imprinted on their thin growing edges in the area of attachment as they lay in conjunction against the substrate surface. STENZEL, KRAUSE & TWINING (1967) have termed this phenomenon xenomorphic growth. Many authors have also reported a great plasticity of shell form and ornament in attached bivalves in response to environment. For example, elongate *Crassostrea virginica* (GMELIN) grows in areas of strong current and more rounded forms of the same species are found in quiet-water situations.

It seems that with such variability imposed on cemented Bivalvia by environmental factors, little can be said about the adaptive value of form or specific structures beyond the stabilizing function of the cementing habit itself. Some broad patterns are worthy of comment, however. Three principal morphotypes characterize cemented bivalves: 1) uncoiled groups such as *Spondylus, Pseudomonotis, Crassostrea, Ostrea* (many Ostreidae which have slightly coiled early stages but basically are elongated to rounded, with uncoiled valves as adults); 2) bivalves with strongly coiled shells either approximating the plane of valve symmetry *(Gryphaea)* or coiled out of the plane of symmetry (*Exogyra,* some rudists like *Toucasia,* many Chamidae); and 3) cuplike bivalves with an enlarged, subconical attached valve and a caplike upper valve (many rudists, such as *Durania* and various radiolitids). Each type has specific adaptive value within the preferred nearshore habitat, but they are not clearly separated as distinct groups and intergrade with some cemented forms transitional between morphologic types.

These groups have two things in common besides cementation. They are predominantly thick-shelled and inequivalve, many grossly so (e.g., rudists), with the attached valve most inflated in the great majority. The adaptive significance of thick shells is obvious in shallow-water environments where periodically intense wave and current action, as well as potential abrasion by saltating sediment particles can be expected; the shell is considerably strengthened against the rigors of such an environment, and the animal is better protected from both high-energy conditions and predators. In fossil oysters, thick-shelled species are rarely found bored by predatory gastropods as compared to the amount of gastropod-inflicted mortality in thin-shelled bivalve species.

The prevalence of the inflated lower valve (left or right depending on the group) in cemented Bivalvia suggests that this characteristic is also highly adaptive to the shallow-shelf environment. Many authors have cited the functional significance of a deep bowl-shaped lower valve in littoral ostreids as being its ability to retain a considerable amount of water, practically enveloping the soft parts, during times of intertidal exposure. It has been cited but not clearly demonstrated that species of *Crassostrea* develop deeper lower valves in intertidal situations than in subtidial habitats. However, since most cemented forms are not intertidal at present, and apparently were not in the past, this function cannot be considered the primary factor in natural selection. The possible advantageous effects of a deep lower valve acting as a more efficient means of supporting the soft parts in bivalves oriented with the plane of the commissure approximately parallel to the substrate, as opposed to equivalve forms or those with more inflated upper valves, has not been fully investigated. It seems logical, however, to conclude that this would be a better system of support (and thus have adaptive value) than having the viscera and mantle largely supported by the upper valve (as in *Anomia*), hanging pendent from a necessarily strong set of mantle and body muscles in the mantle cavity, even though their buoyancy in water would partially offset the strain imposed on the musculature.

The inequivalve nature of most cemented bivalve shells have two additional functional aspects. First, cemented bivalves are largely exposed and wholly sessile, and thus at the mercy of the environment. Among other things, their survival depends upon keeping the feeding margin elevated above the surrounding substrate to prevent clogging and suffocation. In reef areas of sediment bypass, this is not so much a problem, but for most cemented forms attached to hard substrate in areas of active sedimentation it becomes critical. The formation of an inflated lower valve by predominantly upward growth of the valve margins from the site of cementation insures adequate elevation of the feeding margin and survival as long as the rate of marginal growth exceeds the rate of sedimentation. The tall conical Cretaceous rudists represent maximum development of this adaptation in the Bivalvia. My own observations in Chesapeake Bay and Florida support the existence of a direct relationship between the depth of lower valves, original orientation of the attached shell, and rate of sedimentation in living species of oysters at all growth stages. The upward direction of marginal growth during ontogeny is considered a primary adaptation to survival, and the resultant bowl-shaped lower valve a secondary product of this which continues to function in the adult stage for the same purpose. That this is not wholly an environmentally controlled phenomenon, but rather a genetic character selected for its adaptive value, is evidenced by the fact that cemented bivalves now almost totally restricted to areas of sediment bypass (reef-dwelling spondylids and chamids, for example) still retain the relatively more inflated character of the attached valve. A variety of "sculptural" elements also function to keep the feeding margin elevated, among them costal spines *(Spondylus)*, coarse raised lamellae *(Chama)*, and coarse costae or plicae *(Lopha)*.

Secondly, the stresses placed on the ligament or resilium in opening the shells of cemented bivalves are entirely distinct from those encountered by byssate forms like *Mytilus* or *Pteria*. The attached valve is immovable, so that the gape necessary for feeding and respiration must be created completely by raising the upper valve against the force of gravity. This feat demands overcoming the entire weight of the upper valve and a considerably greater amount of force than necessary to move the same sized valve on a pterioid sideways half the distance. Unequal stresses are placed on the ligamental material, in most cases a resilium. It is thus advantageous to the proper functioning of the ligament to have the upper valve of the cemented shell as small, flat, and thin as possible, without deleting its protective value. Reduction in convexity and thickness characterize the upper valves of many cemented taxa; in most the thickness remains sufficient for protection against predators and high-energy water movement. The most efficient system in cemented Bivalvia would be a lower valve which was deep enough to contain all soft parts except the upper mantle flap, and an upper valve acting as a light, flat cap fitting just inside the lower valve. Such a form was developed by some cemented bivalves, in particular Cretaceous rudists. The coarsely perforate nature of some rudist upper valves suggests that they acted as a permanent screen or filter analogous to that of richthofeniid brachiopods (Rudwick, 1961) and may rarely have been raised. The shape and convexity of the upper valve must be considered in this hypothesis. Whereas a thin flat cap might be the most efficient geometric form relative to functioning of the ligament or resilium, it is advantageous only in areas of slow deposition or sediment bypass. In areas of more rapid and constant sedimentation, such a valve form (or one that was externally concave) fitted just inside the periphery of the lower valve and oriented horizontally, would act as a sediment trap, increasing the danger of deleterious sediment infiltration around the mantle edge into the mantle cavity or mantle-shell interspaces. Consequently, the upper valves of most cemented bivalves are slightly convex (outward) and are functional in that they shed material falling onto them. Flat to concave upper valves seem to predominate in groups which were either reef-dwellers (rudists) or else oriented on the substrate so that upper valves tilt toward the substrate and easily shed sediment (e.g., *Exogyra*).

The preceding remarks apply generally to adaptive form in all cemented epifaunal bivalves and specifically cover most of the points that have been made about the group of basically uncoiled forms (e.g., *Crassostrea, Ostrea, Hinnites, Spondylus*). Variation in other features of this particular group have functional significance. The size of the attachment area is highly variable among uncoiled forms and typically occupies one-third to two-thirds of the lower valve. Its size is commonly dependent on and reflective of the energy conditions of the surrounding environment, inasmuch as its primary function is anchorage. As such it has potential as a paleoecologic tool. Kauffman (1965,*8*) has noted the possibility that average and maximum attainable size of the attachment surface may be in part genetically controlled in that it is related to growth form of the shell. In this study an evolutionary trend is defined in time-successive species and subspecies of *Lopha* toward relatively much larger attachment areas as the lineage adapted to shallowing of the Cretaceous seas and increased wave and current action. Some groups of extinct oysters (e.g., certain species of *Gryphaea, Exogyra*) rarely developed large attachment areas, even in high-energy environments, but apparently became detached early in adult life and lay free on the substrate, developing other stabilizing features such as broad auricles, folds, and sulci. This would tend to substantiate possible broad genetic control on size of the area.

Variously developed auricles, folds and sulci, especially posteriorly, are found on cemented, uncoiled bivalves. In many cases these serve no obvious function unless they increase the sensory mantle area, as in pectinids. In cemented forms with small attachment areas, however, and especially in those that become detached in later life, these are functionally important as supports for the shell on the substrate, providing essentially a three-point stability with the inflated valve down. They are most highly adapted to resting on soft surfaces. In the evolution of certain Cretaceous *Lopha* (Kauffman, 1965, *8*), species adapted to relatively deep, quiet-water, shelf habitats and soft substrates had minute attachment areas, became detached as adults, and developed at that time prominent posterior auricles for support on the substrate. Auricles disappeared and the shell became more symmetrical as the lineage adapted to shallow water, high-energy conditions; the attachment area increased markedly in relative size, and the shell became cemented throughout life. Flattening and lateral spreading of the flanks of oyster shells in quiet water habitats with soft substrate represents a similar adaptation.

Sculpture in uncoiled cemented bivalves is highly variable, from nearly smooth surfaces to coarsely plicate or spinose shells having fine to coarse concentric lamellae. Plicae, costae, spines, flutes, and coarse lamellae function primarily to strengthen the shell, provide additional support by increasing surface area in contact with the substrate, keep the feeding margin elevated above the bottom, and possibly discourage predation (particularly by gastropods) and certain types of epibionts from encrusting the shell. In addition to these functions, the spines of *Spondylus* support sensory extensions of the mantle margin at the time of formation, elevating them well above the shell surface, and providing an effective "early warning" system.

Coiling of the lower valves in cemented epifaunal bivalves is well defined in wholly attached taxa like *Chama* and forms in which the adult probably became detached and lay free on the substrate (some *Gryphaea* and *Exogyra*). The direction and trace of coiling is relatively constant in most forms. It is thus not an environmentally produced variation possibly reflecting change in original shell orientation relative to the substrate due to increase in sedimentation rate or reorientation of the substrate itself. This is a common cause of coiled variants in normally uncoiled ostreids *(Crassostrea)*. Although obviously controlled genetically in wholly cemented forms like *Chama,* the adaptive significance of coiling has yet to be clearly defined and it may be a vestigial character. The functional value of a coiled shell in free-living adults of this group is more obvious. In such bivalves, it is critical that after detachment the lower valve should remain anchored in a ventral position and that growth at its margins should proceed upward to offset the effects of sedimentation and keep the feeding margin above the sediment-water interface. The angle of marginal growth in coiled shells like *Gryphaea* accomplishes this efficiently, and in addition produces a deep, bowl-shaped, relatively heavy lower valve capable of being buried by rapid sedimentation, or sinking into soft substrate for a considerable distance before exposing the feeding margin of the valve to clogging or smothering through sediment burial. Because of the relatively tight coiling angle which approximates the plane of valve symmetry in many *Gryphaea* (e.g., *G. mucronata* GABB and *G. newberryi* MEEK & HAYDEN, in the American Mesozoic), the shell, if it had remained in a single orientation relative to the substrate surface (either attached or unattached), eventually would have coiled over so that the feeding margin would be buried in the sediment and the lower (attached) valve would become partially dorsal in position. A series of shell reorientations during the life of the animal would have been necessary, therefore. The first was probably at the time of detachment, and subsequent changes in position were probably produced by periodic tilting of the shell in or on the substrate toward the "ventral" margins. The impetus for this tilting was continued upward growth of the "ventral" shell margin (in terms of conventional orientation), shifting the center of gravity of the shell in a "ventral" direction, and creating a weight imbalance which could be compensated for only by tilting, perhaps triggered by rocking of the shell during times of exceptional bottom currents.

This theory applies mainly to gryphaeoid forms with coiling in or near the plane of valve symmetry. Forms with beaks coiled laterally, approaching the exogyroid condition, normally developed auricles, folds, and sulci posteriorly to help support the shell on the substrate after detachment and were reoriented less frequently. The type of coiling in *Exogyra,* helical and posteriorly out of the plane of symmetry, was adapted to keeping the feeding margin above the substrate without continual reorientation of the shell. Once attached, the shell grew in a low helical spiral upward and outward, with the plane of the commissure slanted at an angle, allowing the flat to concave upper valve to shed sediment. The heavy adult shell eventually titlted backward, coming to rest on the posterior auricle or flared posterior margin produced in many species, as an additional supporting surface on the substrate. A similar case probably can be made for many coiled rudists and rudist-like bivalves during the Mesozoic. Costae and strong lamellae strengthen the already thick resistant shell and provide improved anchorage in the substrate.

The tall, conical to barrel-shaped lower valve of Cretaceous rudists like *Durania* and *Barrettia* functioned both as a very thick protective cover for the soft parts and for keeping the feeding margin well elevated above the substrate when oriented vertically. These were the predominant reef-forming types of rudists during the Cretaceous. By direct observation of Caribbean rudist reefs and analogy to living and fossil corals, these forms lived predominantly upright in clusters on the reef structure, their lower parts embedded in biogenic debris, their upper parts exposed or cemented togther by mutually secreted calcareous deposits, algae, coral, and other reef-dwellers. In this environment, the rounded cross section and conical to cylindrical form of many genera may be considered adapted to tight packing of individuals on the reef, providing mutual support against vigorous wave and current action. Longitudinal costae and ridges on many forms (e.g., *Biradiolites*) potentially could interlock to furnish additional support in clustered rudists. Many of the tall cylindrical to conical forms had small attachment bases and would have been easily toppled as adults, were it not for support in the upright position furnished by these various structures, partial burial, and the clustering habit. Recumbent examples of normally upright rudists have been noted for many taxa; these individuals are characterized by abnormal flattening on one side of the lower valve and enlargement of the attachment area, providing a flat stable surface at the shell-substrate interface.

Rudists with more irregular cross-sections and regular to irregular, gentle or moderate coiling of the valves (for example, some *Caprinuloidea, Titanosarcolites*) were not well adapted for an upright posture and close packing, and lay recumbent on the substrate as adults, their flattest flanks or outside of the coil ventral in position, or both, and the feeding margin elevated above the substrate by upward curvature of the lower valve or both valves where equidimensional (e.g., *Titanosarcolites*). This living habit was effective for highly inequivalve rudists with a small cap valve (e.g., some caprinids) in areas of active sedimentation, despite the recumbent posture. The degree of spiral coiling and curvature of the coils were directly proportional to the possible elevation of the feeding margin above the substrate. In peculiar forms like *Titanosarcolites,* however, in which the valves are subequal, long, narrow, slightly coiled, slightly spiral structures, the feeding margin was not greatly elevated above the substrate as the shell lay recumbent on the surface. These could only have existed in areas of minimal sedimentation rate or bypass conditions. Most recumbent rudists not only have the flattest side in contact with the substrate, but also the most coarsely ornamented flank, costae and ridges functioning to stabilize the shell on the sediment surface and prevent skidding in the face of currents. The attachment area of many recumbent rudists is enlarged to provide firmer anchorage.

The rudists are complex, bizarre bivalves and have many unique structures which cannot be listed or interpreted in detail here. The interesting papers of ZAPFE (1937), YONGE (1967) and CHUBB (1956) interpreting rudist morphology are recommended to the reader. Two additional exterior features of the rudist shell deserve mention.

Many rudists, in particular forms like *Biradiolites,* have a basically long conical shell with subcircular cross section but are slightly flattened on one side. The site of flattening is marked by two shallow depressions separated by a low ridge and extending the length of the shell. These have been called "siphonal areas," and are variously interpreted as being supporting troughs for extruded incurrent and excurrent siphons, or merely depressions for channeling incoming and outgoing currents. Conclusive arguments have not been presented for either interpretation, or even for the existence of siphons in rudists.

The apertures of the lower valves in forms like *Durania* are surrounded by flattened, grooved to fluted areas on top of the shell wall not covered by the upper valve when in normal apposition. Similar smooth, grooved, downfolded flanges of shell material are found around the edges of the lower valve, outside of the commissure in *Thyrastylon* and related forms. The exposed surfaces of both structures are smooth and appear to have functioned as supports for lobes of fleshy material, probably extensions of the mantle, during life. Quite possibly these mantle flaps were continually exposed and could not be withdrawn into the body chamber of the lower valve. As such, they would provide an effective sensory device. Like modern Bivalvia, the sensory cells of the animal were probably concentrated at the mantle edge. It has also been suggested that the exposed mantle contained symbiotic zooxanthellae, as do living *Tridacna* in the same environment, on the exposed edges of the mantle lobes.

FREE-LIVING EPIFAUNAL BIVALVES

This group includes forms that normally lie exposed on the substrate surface without attachment by shell cementation or byssal threads (except possibly during early ontogeny). Two basic assemblages dominate this habitat among living and fossil bivalves whose ecology is well known; the contention has been made that many early Paleozoic Bivalvia occupied this habitat, but this has not been substantiated. The Pectinidae and possibly some Limidae represent the main group; the other is composed of scattered representatives of families otherwise dominated by shallow infaunal elements. Certain *Glycymeris,* Cardiidae and Veneridae (e.g., *Gemma*) have been observed living free on the substrate with the plane of the commissure horizontal, with or without a thin veneer of sediment on the upper valve.

The two main groups of free-living epifaunal bivalves are distinctly adapted to their different modes of life, but have in common a generally rounded, nearly equilateral, orthocline to slightly prosocline or opisthocline shell, a relatively short hinge line, and a dominance of strong, moderately heavy to thick valves with small auricles, or lacking auricles. The rounded shell form with a short hinge line is adaptive in that it provides a high degree of sensory perception, particularly in the pectinoids with their highly developed, light-sensitive mantle "eye spots." In shells of this design, the mantle margin containing sensory receptors of various types (light, vibration, chemical, etc.) achieves its maximum peripheral coverage (percent of total shell periphery covered) and most even distribution among the Bivalvia, with effective reception around an arc approaching 340°. Many of the Pectinidae also have sensory mantle areas around the auricles, projecting through the auricular gapes to compensate in coverage for loss of receptors in areas directly ventral of the auricles. Although mantle sensory areas are not as highly developed in forms like *Glycymeris* or *Gemma,* effective coverage is still achieved by the rounded shell design. Fully exposed, unattached bivalves are especially susceptible to predation because they may be moved, manipulated, or attacked from any side, and a high degree of sensory reception is critical to their existence.

Exposed populations of *Glycymeris* and *Gemma* which have been observed adapt similarly to the shallow-water environment they prefer. The shells are rounded in outline and moderately to highly biconvex. The valves are basically equal, thick and strong, being reinforced in *Glycymeris* by broad, heavy costae, and they can withstand considerable rolling and saltation in the face of currents or wave action. Both genera are capable of shallow burrowing (most species are dominantly infaunal), but observed free-living surface forms make little effort to do so in normal energy conditions and will gape and feed during times of relative immobility, oriented wtih the plane of the commissure parallel to the substrate. The inflated, rounded shell form permits considerable rolling of the valves across the substrate but this can be considered beneficial only in the sense that it guarantees a continually fresh food supply. Otherwise it is detrimental and restricts the periods spent in feeding to times of relative stability. In total, the adaptive morphology of these bivalves does not seem best suited for exposed surface habitats but rather for shallow infaunal living, where most Veneridae, Glycymerididae, and Cardiidae are found. They are apparently able to adapt marginally to more exposed environments, occur locally in great numbers on substrate surfaces, and grow to adult proportions in this environment. The shallow infaunal living habit, with the shell erect or lying flat on one or the other valve in *Glycymeris* (Atkins, 1936, p. 217; Yonge, 1955) and *Gemma* (personal observation), makes them subject to frequent exposure by wave and current scour in the high-energy environments they prefer. Their ability to feed and respire on the substrate surface is adaptive to their survival.

In contrast, the Pectinidae are highly adapted to this habitat. Although some are capable of weak byssal attachment as adults, it is not commonly employed by most species lying exposed on the substrate surface; it is frequently a juvenile mode of life. Exposed, free-living pectinoids inhabit a variety of environments, ranging from shallow-water and even intertidal situations subject to strong water movement, to abyssal depths and quiet-water conditions. Most prefer relatively firm substrates of varying grain size over hard or soft sediment. They live independently, though commonly are crowded on a surface, and are typically oriented with the right valve down and the plane of the commissure nearly horizontal.

Two features of the pectinoids are considered primary adaptations to this mode of life (see Waller, 1967). The shell form is rounded and nearly equilateral, being erect, with small unequal auricles, or slightly prosocline. Various forms are subequivalve, left convex, or right convex, and in part this is correlative with habitat and swimming ability. The left valve of some species is slightly concave. The beak projects only slightly above the hinge line, which extends laterally onto the small triangular to subquadrate auricles dorsolaterally. A byssal notch is developed beneath the anterior auricle at some time during ontogeny. Surface sculpture ranges from very fine concentric growth lines *(Amusium)* to coarse costae and partially developed plicae.

The adaptive advantage of a disc-shaped shell in sensory perception has been discussed. The pectinoid shell form is the best adapted among the Bivalvia for this purpose, allowing evenly distributed, nearly complete sensory coverage, except just below the auricles, around a peripheral arc of the shell approximating 340°. Coverage is less in forms with a long hinge line and large auricles, even though these too bear mantle sensors; it is maximum in forms like *Amusium, Placopecten,* and *Propeamusium* where the auricles are small, subequal, and slanted laterally toward the beak area. The development of "eyes" around the mantle margin of Pectinidae represents one of the most sensitive photic receptor systems among the Bivalvia. This, in conjunction with the broad sensory coverage provided by the shell form, and their swimming habit, greatly increases the ability of pectinoids to react quickly to impending danger and thus to survive in an exposed habitat. These factors offset the greater susceptibility to predation of relatively thin-shelled scallops resting loose on the substrate.

The disc-shaped shell is also well adapted to swimming in pectinoids (and some Limidae). Swimming is effected by rapid clapping of the valves (especially when alarmed) and by forceful ejection of water from within the valve out through dorsolateral shell gapes below the auricles (Fig. 35,*H*). Periods of "gliding" occur between swimming pulses. The plane of the commissure lies horizontal or gently inclined to the bottom during the main phases of swimming. To maintain an approximately horizontal position in the water, and to allow gliding of the shell between periods of propulsion, equilaterality of the valves is important, and adaptive to the swimming habit. Strongly inequilateral shells would be unbalanced and would tilt laterally during swimming and gliding. Although some of the inequilateral pectinoids like *Chlamys,* with its greatly enlarged anterior auricle, are good swimmers, the most equilateral forms, having subequal auricles *(Placopecten, Amusium,* etc.) are reported to be the best swimmers, suggesting a relationship between form and swimming ability. Shell weight, proportional to thickness and size of accessory structures (auricles) or sculpture, also affects swimming ability. The most lightweight pectinids *(Amusium, Propeamussium, Chlamys radiata)* are better adapted for swimming than thick-shelled forms. For this reason, young specimens of various genera are reported to be more active swimmers than adults. The lightweight shell and active swimming of *C. radiata* is further adaptive to the preferred soft-mud habitat of this species, preventing it from sinking into the substrate.

Relative valve convexity is an important consideration in the various habitats occupied by pectinoids. Subequal valves of low convexity characterize the best swimmers, like *Amusium,* and closely approximate good hydrodynamic streamlining necessary during swimming and gliding. But many inequivalve forms are also classified as good swimmers (e.g., *Pecten, Aequipecten*); most of these are left-convex. Apparently the left-convex shell offers less resistance than right-convex forms to being lifted off of the substrate by the initial spurts of swimming. Once water-borne, it is less liable to sink rapidly between swimming spurts than right-convex shells, the flat right valve offering greater resistance per unit area to sinking than an inflated valve of comparable size. The flatter right valve in these shells is also better adapted to resting on the substrate in a stable position. It has yet to be determined whether a correlation exists between the degree of convexity in the left valve and swimming ability, although it seems reasonable to think that such a relationship exists.

Few good swimmers are found among strongly right-convex pectinids, but shells of this form appear to be well adapted for a more sessile existence on the substrate. They are commonly found partially buried in the sediment, with the convex right valve situated in a depression up to a point just below the commissure. In some forms the upper valve is relatively flat to concave and covered with a thin veneer of sediment, which effectively conceals the bivalve from predators. The sediment depression is formed, once the shell has settled after a swimming episode, by rapid ejection of water from the right side of the disc, directed at the substrate. The scallop then lifts itself off the bottom by means of another water jet and settles into the depression thus created. Sediment stirred by this action settles as a thin film on the upper valve. This would be detrimental to cemented forms like oysters and cause fouling when the valves were gaping, but this is not a problem in scallops, which can quickly remove the veneer by rapid clapping of the valves. The deep lower valve is adaptive in that it allows firm implantation of the shell into the substrate while still keeping the commissure elevated above the bottom, retaining sufficient water to keep the animal alive in intertidal situations.

The auricles of pectinids function to extend the hinge line and ligamental area beyond the narrow beak region, providing a stronger articulation and decreasing ability of the valves to be rotated in the plane of the commissure. They also support additional mantle sensors. Reentrants beneath the auricles occur anteriorly at the site of the byssal gape and below it at the anterior water-expulsion gape. A shallower reentrant lies below the posterior auricle at the dorsal edge of the water-expulsion gape on some taxa. A relationship between the shape and depth of these notches and rate or force of water expulsion may exist but it is not presently known. The byssal notch ranges from deep *(Chlamys)* to shallow or absent *(Amusium)* and its depth is directly related to the strength and frequency of byssal attachment. The notch itself allows the byssal gape to be kept open and helps to stabilize the valve on the byssus, restricting movement in the plane of the commissure. In the ontogeny of certain pectinoids, the juvenile shell is strongly attached by the byssus, and the byssal notch is deep, whereas the adult rarely or never attaches and the byssal notch becomes weak or disappears. The gape becomes correspondingly more restricted in these adults and may actually be subsequently closed off. These trends may be traced in the ontogeny of auricular growth lines.

Finally, surface sculpture of the pectinoid bivalves shows interesting adaptive trends. Plicae and, to a lesser extent, costae strengthen the shell at its growing margin, and overall. They are functional in this respect and much needed in areas of high predation rates, strong current, and wave action. Plicae also reflect development of a crenulate commissure which is functionally important in feeding and sensory perception (see subsequent discussion). A general relationship, with many exceptions, can be seen between development of radiating ornamentation and swimming ability and between radiating sculpture and energy conditions of the habitat. Typical pectinoids of deep quiet-water habitats of the outer shelf (*Amusium, Propeamussium, Placopecten,* etc.) are predominantly smooth-shelled forms or finely costate. These are among the best swimmers, and are characterized by nearly symmetrical, subequal valves, and reduced auricles of similar size. In general, free-living epifaunal pectinoids in shallow-water, high-energy habitats have coarsely costate to plicate valves, comparably stronger and better able to cope with an active environment than shells of the deep-water groups. These aid also in anchoring the shell on the substrate surface. Many are good swimmers, others poor, but none attain the ability of *Amusium* insofar as their swimming is known. In shallow-water habitats, no work to date has demonstrated a correlation between strength of radial sculpture and swimming ability. Certain plicate forms seem to equal costate pectinoids in this respect.

If it can be demonstrated that smooth-shelled pectinids and limids are consistently better swimmers than costate or plicate forms, it would be worth investigating the possibility that greater friction created between water and shell by partial or total lamellar flow over smooth surfaces gives greater lift and gliding ability to forms like *Amusium* than the layer of turbulent water flow that would be created over the costate or plicate surface of typical *Chlamys, Aequipecten,* or *Pecten.*

The Limidae contain many excellent swimmers which are adapted in much the same way to this form of mobility as the Pectinidae. Most limids are fissure-dwellers which remain byssally attached for considerable lengths of time, however, including some of the most able swimmers. When exposed on the substrate and actively swimming, the subrounded to ovate, subequivalve, slightly biconvex shell functions as well as many pectinoids, even though it is generally more inequilateral than scallop shells. Swimming may be jerky, with short gliding periods between thrusts created by rapid clapping of the valves, or languid, with slower rhythmic clapping. Water jets are apparently emitted from only one side of the shell during swimming, and the plane of the commissure tends to be inclined to the substrate surface. The trailing tentacles of the Limidae aid in swimming and probably help to offset the posteromedian center of gravity caused by the more opisthocline shell form and the unequal thrust of the single water jet.

SEMI-INFAUNAL BIVALVES

Bivalves in this group are sessile to slightly mobile organisms with the shell normally buried one-half or more of its length in the substrate, but with the posterior portion of the shell, containing the main inhalant and exhalant apertures, permanently exposed; these do not have elongate siphons.

The principal semi-infaunal bivalves belong to the Pinnidae, long, slender, subtriangular, thin fragile shells with slight to moderate convexity (Fig. 6). Maximum inflation occurs along an angulated mid-line. Sculpture ranges from concentric growth lines and coarse lamellae or undulations without radial elements, to variously costate and weakly plicate forms. In *Atrina* the radial elements are fluted or bear spines. Pinnidae predominate in inner shelf environments, including shallow-water areas of high current and wave activity. The shells are embedded in soft sandy, silty, or clayey substrates with the narrow umbonal tip of the shell downward and the mid-shell axis vertical. Some are attached by byssal threads to particles beneath the substrate surface. The broad "posterior" margin of the shell extends above the surface of the substrate one-third to one-half the length of the shell. The animal is capable of vertical burrowing but lateral movement is restricted. The exposed shell is almost totally composed of the prismatic layer and is very fragile. Commonly, it is heavily encrusted by epibionts. Yonge (1953) and Rosewater (1961) have discussed the adaptive morphology and anatomy of the Pinnidae in detail.

The shell form of the Pinnidae, elongate subtriangular with low convexity and a diamond-shaped to lenticular cross section, is highly adapted to vertical penetration of the substrate. It is easily retracted into the sediment, when oriented with the narrow tip down, offering minimum frictional resistance. No projecting surfaces, other than surface sculpture, retards its downward movement. Vertical orientation and semi-burial function to anchor it against currents and predators, and greater stability can be achieved by additional downward burrowing. If the plane of the commissure is aligned into the current, the exposed shell has a streamlined profile (cross section) and does not offer much resistance to current or wave action; no studies have conclusively demonstrated that this is the preferred orientation, however. The burrowing habit may also be an adaptation for protection of the animal, which lies primarily within the buried portion of the valves. The thin shells of the Pinnidae are easily crushed or broken. If fully exposed, as rarely in reef fissures, they afford only minimal protective cover to the soft parts. Mantle receptors called "eyes" but apparently not light sensitive, are situated on the mantle edge around the exposed portion of the valve; thus necessary sensory perception is attained over nearly the entire shell margin subject to predation or damage in the semi-infaunal Pinnidae.

Radiating surface sculpture serves two obvious functions. It strengthens the shell, especially where needed at the growing edge (the main site of predator attack). Secondly, it gives increased anchorage to the shell when buried and in contact with the substrate. Spines and flutes in *Atrina* are especially effective in this respect, being inclined upward toward the sediment-water interface and concave on the upper surfaces. Once buried, they act as barbs, preventing vertical withdrawal of the shell from the substrate. In addition, they may function when first formed as supports for sensory tentacles or narrow extensions of the mantle margin, although the position of the concave troughs on their upper surfaces appears to be wrong for this function; they should face ventrally. Spines and flutes may also serve to discourage epibiont encrustation on the exposed valve surface, at least particular types.

In addition to Pinnidae, certain modioliform Mytilidae (i.e., *Arcuatula*) occupy the semi-infaunal habitat, especially in littoral or very shallow-water niches. *A. demissa* is the best known form, commonly occurring singly or in gregarious masses one-third to one-half buried, oriented nearly vertically, among root masses of vegetation or in grass mats and mud. The posterior feeding margin remains exposed. Like the Pinnidae they are byssally attached and apparently capable of downward movement by uprooting the byssus and reimplanting it at a lower level among the roots. Unlike the Pinnidae, semi-infaunal mytilids are not specifically adapted for this niche in form, being similar to closely attached exposed forms such as *Modiolus s.s.,* commonly found isolated on hard substrates and nestled into crannies or depressions near the sediment-water interface (i.e., bases of sponges, sea fans, or patch-reef coral masses). The shell of *Arcuatula,* slightly more elongate than that of normal *Modiolus,* is probably adaptive in allowing occupation of narrow spaces between roots and easier penetration of root masses. Costae, generally limited to semi-infaunal modiolids, may further aid in wedging the shell into its "burrow" by increasing surface friction. Otherwise, the semi-infaunal modiolids should probably be considered secondarily adapted to this habitat, seeking it after development of the normal exposed epifaunal habit for additional protection as the stocks radiated into shallow-water and littoral niches. The fact that *Modiolus s.s.* tends to take on a similar habitat in the shallow end of its range, even though it is primarily exposed epifaunal in habit, supports such a contention.

Individual species of characteristically infaunal groups sometimes take on the semi-infaunal habitat with the posterior edge of the shell exposed during active feeding (e.g., many protobranchs, like *Yoldia,* burrowing arcids, and venerids), or when partially exhumed by scour. This is especially true in probing detritus-feeders. These forms are basically infaunal elements; many are strongly siphonate, and do not occupy the semi-exposed niche continually. They are treated with the infaunal Bivalvia.

INFAUNAL BIVALVES

Included in this group are sessile and mobile bivalves which spend part or all of their life buried beneath the substrate. Most forms draw fresh water and food into this protected habitat through open sediment

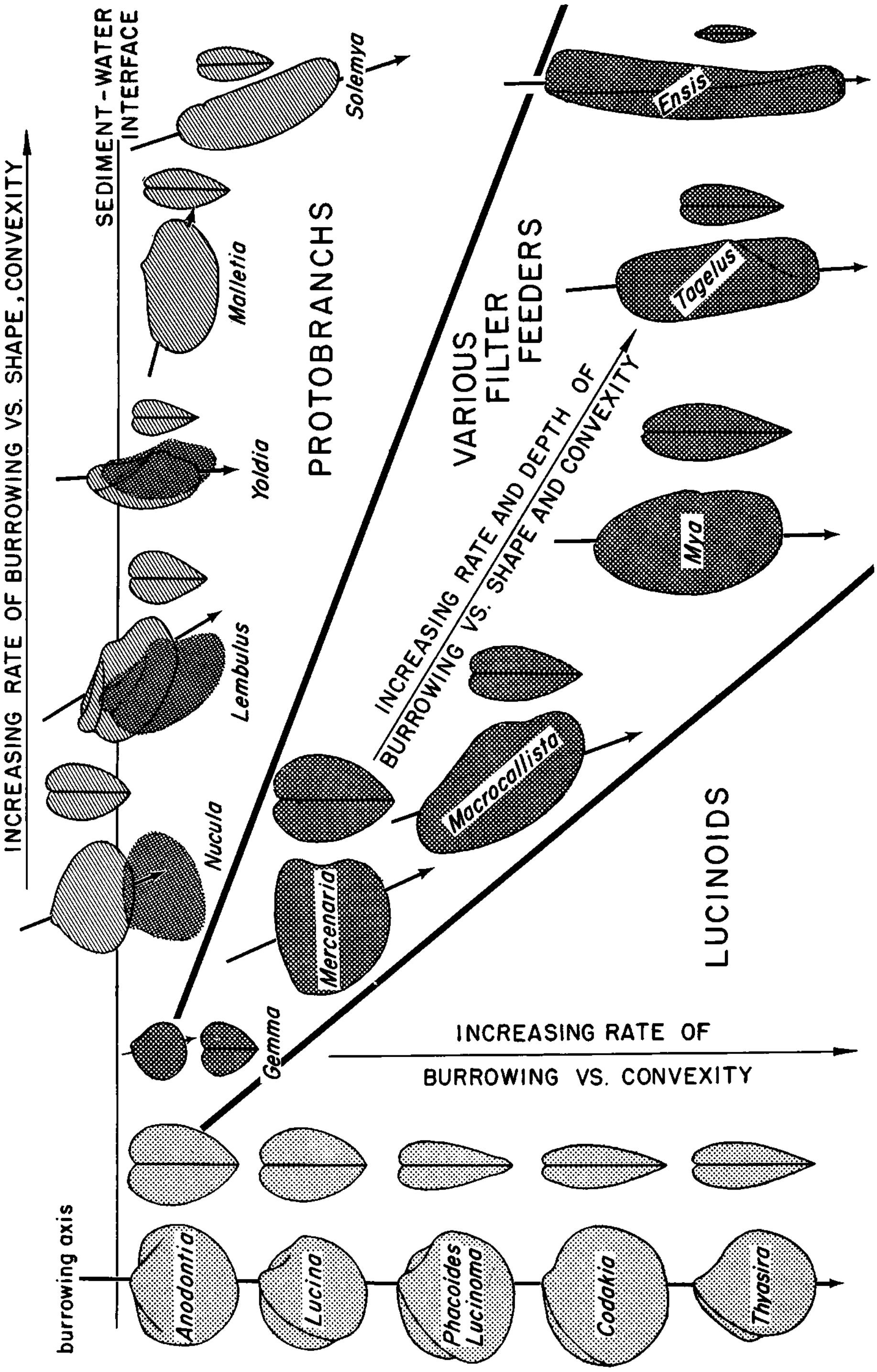


Fig. 90. General relationships in Recent Bivalvia of shell outline and convexity to depth and rate of burrowing (Kauffman, n).

tubes or fleshy siphons, or both. Many feed on organic debris within the sediment. A great variety of taxa have adapted to the infaunal habitat, which affords natural protection from many but not all molluscan predators, and from most rigorous environmental conditions. Although most infaunal elements occupy relatively soft, unconsolidated substrates and thus are still subject to scouring by waves or currents, some (e.g., *Teredo, Lithophaga,* various Pholadidae) have developed the ability to bore into partially or wholly lithified material or wood, attaining the ultimate protection afforded by the infaunal habit, a semipermanent burrow, relatively indestructible, enclosing the animal throughout life. Evolutionary simplification of the ancestral Bivalvia producing loss or retarded development of complex cephalic structures, including highly developed sensors (eyes, long tentacles, proboscis) probably left the early radiating bivalve stocks more vulnerable to elements of the environment than other main molluscan classes. Although development of an enclosing bipartite calcareous shell was the primary adaptation to protection and survival, development of the infaunal habit and structures to cope with it was an equally significant evolutionary event. Inasmuch as this would have been the most natural and available protective habitat to early Bivalvia, and would have afforded them relatively greater protective value than most others, it was one of the first invaded during early Paleozoic radiation. Invasion of the infaunal niche by several groups had occurred by Early Ordovician time, and Ordovician form equivalents to the solenoid jackknife clam *(Cymatonota),* tellinids *(Cycloconcha),* nuculids *(Ctenodonta)* and other living infaunal elements are well known. The lack of a pallial sinus in many of these groups probably indicates that they lacked siphons, or had short ones, and that most early infaunal elements were therefore buried only up to the inhalant and exhalant apertures, or completely buried just below the sediment-water interface. At least one Late Ordovician genus, *Lyrodesma,* contains species with a shallow pallial sinus [e.g., *L. poststriatum* (EMMONS)] and probably had at least short siphons (JOHN POJETA, personal communication, July, 1967).

Compared to the variety of available habitats and energy conditions encountered by epifaunal Bivalvia, the infaunal environment is relatively more uniform. This has had a profound effect on the variety of shell forms developed by infaunal bivalves. Although infaunal taxa are varied, and function in many different manners within the substrate (mobile to sessile, detritus- and filter-feeding, etc.) they are remarkably uniform in the gross adaptive characteristics of the shell (Fig. 90). Thus a similar set of environmental controls act on mobile protobranchs moving horizontally through the sediment in search of organic detritus, and on vertically boring, sessile, siphonate filter-feeders. The main factors controlling external shell form appear to be rate of movement through the substrate and depth of burial, including the anatomical modifications these demand. Maintaining stability and a preferred orientation in the substrate imposes further control on the shell form of infaunal bivalves.

Therefore, although a number of ecologic divisions may be made among the infaunal Bivalvia, as previously listed, the adaptive value and function of shell form, various structures, and ornamentation can be concurrently discussed for all of them. Thus, the adaptive streamlining of the shell for rapid movement through the substrate is

FIG. 90. *(Continued from facing page).*

[Dark arrows indicate approximate axis of burrowing. All shells shown in normal living position, but not necessarily at uniform scale.]

For lucinoids, a consistent depth zonation is not implied; although some studies accord with depth relationships here depicted, others indicate a different ordering.

For various filter-feeders, the general depth zonation discernible in the diagram agrees with field observations, but spacing of the drawings does not indicate absolute depth differences.

For protobranchs, indicated depth distribution is approximately to scale. The dual images of *Nucula, Lembulus,* and *Yoldia* represent ultimate depth and position attained by burrowing (dark background) and progress toward these (light background) in the time it would take *Malletia* and *Solemya* to attain their normal burrowing depth, as shown.

nearly identical in the vertical burrowing, sessile filter-feeders *Solen* and *Ensis,* as it is in the horizontal burrowing, vagrant deposit-feeder *Solemya* (Fig. 90). Even more significantly, both *Solemya* and *Ensis* are capable of limited swimming when exposed on the surface, because of similar shell design and distribution of soft parts, although they are unrelated bivalves with distinct habitats.

The shape and relative convexity of infaunal bivalve shells are closely correlative with the depth and rate of burrowing, and energy expended in burrowing for all ecologic groups except the very specialized rock- and wood-borers. The following generalized observations apply to an amazingly high percentage of infaunal elements.

Obese bivalves with a rounded to broadly ovate outline are dominantly very shallow infaunal elements which burrow slowly, utilizing large quantities of energy, and once buried remain relatively stationary. Various Cardiidae (e.g., *Dinocardium, Laevicardium*) and Veneridae *(Gemma)* characterize this group. *Nucula* is the most similar detrital-feeding protobranch. Deeper-burrowing bivalves are generally less convex and more elongated, with the axis of elongation approximately coinciding with the direction of burrowing (Fig. 90). Their shells are thus more streamlined and better adapted to easy penetration of the sediment when pulled down on the implanted foot. *Mya* and *Ensis* are typical examples of deep infaunal bivalves (Fig. 90). Depth in each case is measured by the depth of burial relative to the length of the shell, not by the absolute distance below the sediment-water interface. Thus for bivalves that burrow straight down or at a moderate to high angle to the interface, low convexity and elongation of the shell along the burrowing axis are adaptive in that they decrease resistance of the shell to movement through the substrate and require less energy in burrowing. TRUEMAN, BRAND, & DAVIS (1966) have demonstrated this experimentally on four infaunal bivalves of varying shape: round, obese *Cardium;* wedge-shaped, moderately convex *Donax;* ovate moderately convex *Macoma;* and elliptical, very slightly inflated *Tellina.* Mechanical penetration tests on the shells indicated that the ease of burrowing decreased in the following order: *Tellina, Donax, Macoma,* and *Cardium,* in order of increasing shell convexity and decreasing elongation.

All other factors being equal, this information suggests that in the order given these shells would be buried with *Tellina* deepest and *Cardium* shallowest in the substrate. If convexity and elongation were the principal factors controlling depth of burrowing in infaunal bivalves, living species should be depth-zoned on the basis of their shape and this zonation would be directly applicable to the interpretation of infaunal habitat in fossils. It would be expected that forms like *Cardium* and *Gemma* would constitute the shallowest zone, followed in order by geometric forms represented by: 1) *Mercenaria,* 2) *Astarte* or *Crassatella,* 3) elongate *Macrocallista,* 4) *Mya* or *Panope,* 5) *Tagelus,* and 6) *Ensis* (Fig. 90). Observation on living species indicates that this zonation is only partially realized, and that other factors besides shell form also determine depth of burial. Among these, TRUEMAN, BRAND, & DAVIS (1966) listed: 1) ability to rock the shell during burrowing, which aids in speed of penetration; 2) size and nature of the foot, and its ability to probe and anchor in the substrate; 3) presence or absence of external ornamentation, which retards burrowing rate; 4) gape of the shell during burrowing, gaping hindering penetration; 5) ability to produce powerful water jets to clean out sediment ahead of the burrowing animal; 6) size of shell, larger ones being harder to pull into the sediment than smaller ones with the same shape; and 7) available energy used in burrowing, especially once the shell has penetrated below the substrate and burrowing becomes more difficult owing to greater drag imparted to the shell. In their test case, TRUEMAN, BRAND, & DAVIS *(41)* found that *Cardium, Macoma,* and *Tellina* burrowed to the depth of the shell in similar times (*Cardium* slightly slower), *Tellina* being aided by its streamlined shape, *Cardium* and *Macoma* by their rocking motion during burrowing. *Donax,* streamlined and with a very powerful foot, burrowed faster.

Thus streamlined shell shape, with slight convexity and elongation approximately along the burrowing axis, is primarily adapted to a rapid rate of burrowing, although even here it is not the only controlling factor. It is a useful interpretive tool in paleontology in this respect. In certain groups it also reflects depth of burial, as in the venerids, but in most cases it is related to burial depth only insofar as this depends upon rate and it is not possible to set up a reliable depth zonation of infaunal forms purely on these characters for use in interpretive paleontology. This is driven home in the protobranchiate Bivalvia *(45)*, all of which are relatively shallow burrowing detritus-feeders. Three basic geometric forms dominate this group (Fig. 90): the inflated ovate to subtriangular *Nucula;* elongate, posteriorly attenuated, moderately convex shells like *Yoldia, Nuculana,* and *Lembulus;* and very thin, slightly convex, anteroposteriorly elongated shells like *Malletia* and *Solemya.* At approximately the same burial depth *Nucula* burrows very slowly and remains relatively sessile, once buried. *Nuculana, Lembulus* and *Yoldia* are moderately fast burrowers, vertically or at an inclined angle, but remain stationary, once in place with the attenuated posterior end commonly above the substrate. *Solemya* burrows rapidly, orients horizontally in the substrate, and is sessile to moderately mobile. *Malletia* burrows very rapidly and is a vagrant detritus-feeder, moving just below the substrate surface. None are deep burrowers, even though the form of *Solemya* and *Malletia* closely approximates that of certain deep infaunal bivalves.

It is interesting to note that in bivalves which may be depth zoned on their form (Fig. 90), the angle of burrowing and eventual living position change from orientation with hinge axis approximately horizontal to one with the hinge axis nearly vertical, as in *Ensis.* Development of an elongate shell is correlative with elongation of the foot and migration of the point of pedal extrusion from the ventral to the anterior margin, causing a compensatory change in shell orientation during burrowing so that the long axis lines up with the foot and the shell offers least possible resistance to burrowing. Thus, elongation of an infaunal bivalve shell in the evolution of a lineage normally takes place along the burrowing axis and reflects not only adaptation to deeper or more more rapid burrowing, or both, but also may indicate a change in living orientation.

Not all depth zonation or differences in burrowing rate are reflected in varying outline of infaunal bivalves. Decrease in shell convexity alone is adaptive to deeper and faster burrowing (Fig. 90, left). Inflation of the valves appears to be the main factor determining resistance of the shell to penetration of the substrate; decrease in inflation in an evolving lineage commonly permits more efficient burrowing and gives rise to depth zonation among related forms of different convexity but similar outline. Thus the rounded, obese venerid *Gemma* occupies a much shallower habitat and burrows more slowly than the thin platter-like *Dosinia.* In the Lucinacea, rate of burrowing among basically round to ovate shells seems to be primarily a function of inflation and a graded series is inferred from the modern literature and *in situ* observations with tumid forms like *Anodontia,* the slowest burrowing lucinoids, followed in order of increasing rate by inflated *Lucina, Lucinoma, Codakia,* and *Thyasira* (Fig. 90). The latter is also more elongated along the burrowing axis (dorsoventral in the Lucinacea). My own observations suggest a similar depth zonation for all but *Anodontia,* a relatively deep but slow-burrowing form. STANLEY (personal communication, 1967), however, has documented different depth ordering.

Sulci and folds on infaunal Bivalvia normally reflect internal partition of the soft parts and development of interior supports for attachment of muscles, gills, or other organs. They may function externally to strengthen the shell, and in some forms deep sulci terminate near the exhalant aperture and may function secondarily to channel currents passing over the shell into the exhalant area, insuring dispersal of wastes. They aid in anchoring the shell in the substrate, but are a hindrance to burrowing, destroying the streamlining of the shell as it passes through the substrate. For this reason they are rarely present anteriorly, or along the leading edge of the shell in burrowing position. The nature of this leading edge, anterior in many infaunal filter-feeders such as the Veneridae, ventral in the Lucinacea, is closely related to the rate of burrowing, inasmuch as it is the first part of the shell to penetrate the substrate and the ability of the bivalve animal to pull the shell into the sediment depends partially upon the ease of penetration. Gently tapered, relatively flat flanks terminating in a narrowly rounded leading edge represents the most successful burrowing design, as characterized by the wedge-shaped *Donax,* deep-burrowing bivalves like *Tagelus* and *Solen,* and rapidly burrowing forms like the protobranchs *Malletia* and *Solemya.* Increase in convexity and curvature of the flanks, or decrease in curvature of the leading edge, lessen the ability to burrow rapidly.

A well-defined lunule is present in many infaunal bivalves (e.g., *Mercenaria*) and in its position anterior to the beaks, this depressed area would seem to hinder burrowing in the same way as an anterior sulcus—by increasing resistance to movement through the sediment. Notably, the lunule is best defined in shallow or slow burrowers, poorly developed or absent in deep or rapidly burrowing Bivalvia, or both. The function of the lunule has not been adequately interpreted. CARTER (1967,*3*) noted that it has been postulated to be functional in burrowing by acting as a pressure plate preventing the animal from moving upward as the foot is extended downward. These two structures are not always significantly opposed, however. He further suggested that it may function as an area of compensatory growth, maintaining the valve margins in the plane of junction (commissure plane) during rotation of the growth direction. No function has been proposed for the escutcheon, also common in infaunal bivalves.

Most infaunal Bivalvia are smooth or have fine concentric ornamentation, and this condition is adaptive to more rapid burrowing by decreasing friction between the shell surface and the sediment that is inherent in more ornate forms. Coarse lamellae (*Lucina,* some venerids), concentric ribs *(Callista, Antigona),* costae and plicae (Cardiidae) cancellations *(Chione)* and spines or raised flutes on ridges *(Pitar, Hysteroconcha, Hecuba)* occur on many infaunal bivalves. As in other Bivalvia, coarse surface ornamentation is functional in strengthening the valves, and anchoring or stabilizing the shell in the substrate. Raised areas, such as lamellae, flutes, and spines, would seem to be exceptionally useful in anchorage, as well as discouraging predation or encrustation. That these ornamental characters are functional in these respects is strongly suggested by the dominance of coarse surface sculpture in the groups of shallow-burrowing bivalves, and their general absence in deep-burrowing forms. Shallow infaunal elements are frequently subject to scouring or exposure from currents and waves and to higher predation rates, especially from gastropods. In CARTER's study of *Hysteroconcha* and *Hecuba (4)* he concluded that spines along the umbonal ridge were of minimal importance to stabilizing the animal in the substrate, inasmuch as they were not properly oriented for this function and the animal was not totally buried while feeding. He further rejected the possibility that they were supports for mantle sensors, like those of *Spondylus,* or form an effective sediment screen used in feeding (they are too far apart). He concluded that they most likely function as defensive structures against predation, inasmuch as they are long and sharp, but relatively strong, guard the most vulnerable part of the shell (being situated at the siphonal junction), and are oriented to face the direction of normal predatory approach of starfishes and gastropods.

BORING BIVALVES

Bivalves which have developed the ability to excavate permanent burrows into hard substrates are specialized, secondarily derived lineages, many of which arose relatively late in the evolution of the class. The oldest genera which possibly occupied this niche are Ordovician *Corallidomus, Endodesma,* and *Conocardium* (POJETA, personal communication, 1967). Boring bivalves are common, but like the rudists, their highly specialized nature does not warrant detailed discussion here, and only a few general aspects of form and function are dealt with.

The primary habitats are rock, wood, coral, or other calcareous shelly material, and tightly compacted mud, each providing a very high degree of protection to the contained animal. Secondary calcareous tubes are sometimes secreted within the burrows for additional protection *(Teredo)*. This permanent, built-in protective cover, and the necessity of developing boring shell structures for hard substrate, produced far greater experimentation in shell form than is found in most habitats where the shell is primarily designed for protection.

The shell form is basically similar in most boring bivalves, being elongated along the boring axis, except where secondarily reduced, as in *Teredo* (Fig. 4), in which case the animal remains elongate and the shell becomes restricted to the anterior (boring) end. In cross-section most boring bivalve shells are round to subround. This basic form, essentially a narrow cylinder, is highly adapted to the boring habitat in that it is the most efficient possible shape with respect to energy required for the penetration of hard substrates because it greatly restricts the diameter of the burrow necessary to contain the animal. Only *Tridacna,* which bores as a juvenile shell up to approximately 6 inches in length, and *Platyodon,* a *Mya*-like shell with ovate cross-section, have basically different form among the common borers. The functional morphology of *Tridacna,* among the most highly specialized bivalves, is treated by YONGE (1936, 1951) and ROSEWATER *(29),* and is excluded from the following discussion.

Boring is accomplished by chemical solution (e.g., *Lithophaga*) and mechanical grinding (e.g., *Botula, Pholas*) anteriorly (except *Tridacna*), aided by highly specialized structures and glands on the foot such as the sucker disc of *Pholas* and *Teredo* which grips the substrate during grinding, or the specialized siphons used to grip the walls of the excavation during boring in *Hiatella.* As expected, the grinding anterior end of the shell is highly modified in various borers. The anterior margin is usually moderately and evenly rounded, thickened in some forms, and equipped in a few with accessory toothlike projections *(Pholas)* or a bevelled cutting edge to aid in grinding. The anterior end of the shell is most commonly the widest part, and the boring diameter created by it thus is wide enough to accommodate the rest of the valves and animal. The posterior end of the shell is commonly attenuated and modified to various extents as a sheath protecting the base of the long siphons (e.g., Pholadidae). In some forms the siphons cannot be totally withdrawn into the shell, and thus a permanent posterior gape is developed. The need for withdrawal of the siphons is greatly lessened in this habitat by added protection afforded by the bore hole and, in certain forms *(Teredo)* a secondary calcareous tube secreted wtihin the boring by the animal. The shipworms (e.g., *Teredo*) represent the maximum known modification of the shell to its boring habitat. Here the valves are reduced to a series of small anterior grinding plates, leaving the soft parts mostly naked within the protective burrow and its inner calcareous tube (Fig. 4). *Teredo* and *Pholas,* among others, have a modified sucker disc on the foot that anchors the shell against the bottom of the hole during grinding, and helps the valves by changing positions of attachment. A large anterior shell gape allows this sucker disc permanent access to the substrate. All borers have greatly reduced beaks and umbones, adaptive to streamlining of the shell to fit the bore hole created at the anterior margin. A byssal gape occurs mid-ventrally in forms like *Botula;* this allows the large byssus to provide firm reinforcement of the shell in the bore hole during periods of mechanical abrasion anteriorly at the base of the excavation. In chemical borers like *Lithophaga,* which secretes an acid-bearing mucus anteriorly dissolving the carbonate rock at the base of the boring, a thick layer of periostracum functions to protect the calcareous shell of the animal from the acid.

Various types of surface sculpture aid boring bivalves in stabilizing the shell against the walls of the bore hole while downward pressure is being exerted to deepen it by mechanical erosion, i.e., grinding of the shell edge against the substrate. Costae and lamellae are the principal types of sculpture; spinose to fluted plicae occur in *Pholas* and related genera. In some forms (e.g., *Hiatella*), internal water pressure within the mantle cavity, forces the valves outward against walls of the bore hole to anchor the shell in the hole during grinding, or as means of grinding itself. The ornamentation of the shells in forms like *Teredo* is zoned into distinct regions. The anteriormost zones are characterized by short hard spines used in boring as the shells are rotated in the hole.

Accessory shell plates called pallets are developed in the Teredinidae at the ends of the siphons and act as opercula, effectively closing off the tube when the siphons are retracted.

COMMISSURE

The commissure is defined as the line of junction between valves exclusive of the hinge line—that part of the dorsal margin between the most lateral extent of the hinge teeth. In most equivalve and subequivalve taxa the commissure lies at the outer edge of both valves, but in inequivalve forms (e.g., *Corbula*) it may lie within the outer edge of the larger valve. A number of functionally important structures are associated with the commissure, among them various valve gapes, marginal crenulations, denticles, folds (plicae edges), and raised structures like spines or marginal flutings.

VALVE GAPES

In various Bivalvia the valve margins are not totally in contact around the commissural line but rather gape locally when the valves are tightly closed. In epifaunal Bivalvia, all byssate forms, and many free-living (Pectinidae) and cemented forms (e.g., *Hinnites*) have a byssal gape during their ontogeny which ranges in position from mid-ventral *(Modiolus)* to anterodorsal *(Chlamys),* and from broadly lanceolate *(Lima)* to slitlike *(Brachidontes)* in shape. The gape functions for passage of the reduced foot out of the shell to implant byssal threads on the substrate, and upon contraction of the foot, for byssal threads to pass into the shell to the byssal gland of the foot. The shape of the gape reflects the distribution of threads on the substrate, and thus the degree of anchorage and amount of expected movement about the byssal axis. It is critical in strongly byssate forms that the gape be kept open so that: 1) the byssus may be repaired by the foot if threads are broken; 2) a new byssus may be formed in taxa capable of shedding or uprooting the byssus and moving to a new location when necessary *(Lima);* 3) orientation of the shell on the byssus may be controlled; and 4) the shell may be moved along the byssal axis by pedalbyssal retractor muscles; this is protective, and allows normally free-swinging forms to draw up tight to the substrate when subjected to dangerous ecological situations. Retarded lateral shell growth around the byssal gape keeps it open as long as the byssus is functional, producing a reentrant in the shell margin—the byssal notch or sinus. The gape closes or becomes restricted if byssal attachment is lost in ontogeny, as in many Pectinidae.

In various Pectinidae and *Spondylus,* gapes occur at the lateral ends of the auricles. Waller *(43)* noted that these function as openings for sensory eye spots on the mantle margin in pectinids and in their positioning compensate for the loss of sensory coverage in water expulsion areas just below the auricles. In swimming, the Pectinidae propel the shell through the water not only by clapping of the valves, but by forceful expulsion of water jets through lenticular dorsolateral gapes just below the auricles with abrupt closing of the valves. The narrow shape of the gapes, which remain open after the shell is closed tightly, restricts the water forced through them, producing a high-velocity jet.

Various bivalves have elongate shell gapes in the area of foot and siphonal extrusion. In deep-burrowing Bivalvia *(Ensis, Mya, Panope)* these become greatly enlarged and may actually be large enough for extrusion of the foot and siphons during burrowing without broad opening of the valves. This is adaptive to rapid burrowing, since the gaping shell in most infaunal bivalves hinders the burrowing process by destroying shell streamlining. In forms with siphonal gapes, these obviously allow active feeding and respiration, and possibly full extension of the siphons, when the valve is otherwise closed. In the extreme case of certain *Mya,* the gape is necessary to accommodate the extruded siphon, which is too large to retract into the shell when it is fully closed. In addition to the above-named gapes, many bivalves have been noted to have minute openings between the valves when fully closed, extending over a considerable area of the commissure. These are probably sensory in function, allowing direct communication between sensors at the mantle edge and the outside environment.

CRENULATIONS AND DENTICLES

Crenulations refer to regularly scalloped areas, or alternating evenly developed, raised and recessed sections of the commissural margin which interlock when the valves are closed and are expressed primarily on the valve interior. They normally occur around the ventral and ventrolateral margins of the shell (e.g., *Mercenaria, Nucula*). Denticles are small, raised, irregularly developed, circular to elongate nodes normally found just within the dorsolateral margins of forms like *Lopha, Ostrea,* and around the byssal gape of various pectinoids. Some have sockets to receive them on the opposite valve, others do not. Both structures strengthen to some extent the valve margin by providing supporting ribs or blocks to the thinnest area of the shell subject to the most frequent attacks by predators. Where they interlock or are received by sockets, both structures further function to prevent rotation of the valves in the plane of the commissure, giving additional protection from predators. Some have very specialized functions. A series of elongate denticles grouped around the byssal gape in pectinoids has been termed the ctenolium, which functions to separate and support the byssal threads at the point where they leave the shell so that they will not twist in the current. This insures a relatively constant orientation of the shell on the byssus, important in feeding and withstanding currents for some species. The presence or absence of denticles is a generic character in Ostreidae but their function other than additional support is not yet known. Denticles and crenulations may serve to anchor the free edge of the mantle in some forms; this would be especially important in females of dimorphic species which use the gills or mantle flaps as areas of egg storage and incubation before eggs are let loose into the water, or for larval implantation (Unionidae). It has been postulated that the individuals of *Astarte* and *Crassatella* with marginal crenulations within a population are females, and those without crenulations are males. Possibly the crenulations function in reproduction in these forms.

MARGINAL FOLDS

Most Bivalvia have a relatively flat commissure, but in many plicate forms the commissure margin is folded in varying degrees. The folds range from very coarse, producing a zigzag pattern at the commissure *(Arctostrea,* some *Lopha),* to broadly sinuous *(Lopha),* to small and angular or blocky (Pectinidae). Secondarily they produce strengthening plicae on the shell, which in turn perform a number of functions in various bivalves. Their primary functions, when formed at the valve margin, are far more significant. Four principal functions have been postulated for mantle folds and the folded shell margins they produce. These have been discussed by RUDWICK (1964).

Folding of the mantle and the shell around it greatly increases the area along the mantle edge relative to a given amount of distance along the marginal outline of the valve, i.e., a given arc. This functions not only for increased feeding and respiration capabilities, to the degree that the mantle margin is involved in creating currents and sorting particles, but also greatly increases the potential number of sensory receptors distributed around the mantle margin. These are primarily situated in the outer edge of the mantle lobes. Such an increase affords greater protection to exposed epifaunal bivalves.

The folded shell margin produced by the mantle also functions to reinforce the relatively thin shell material characteristic of the peripheral border. The folds provide a series of vertical to inclined lightweight struts directed against the outer shell surface. Less weight is required in reinforcing the shell in this manner than by thickening it an equivalent amount. The interlocking marginal folds further serve to prevent rotation of the valves in the plane of the commissure. Reinforcement is especially necessary in exposed epifaunal Bivalvia so commonly attacked in the region of the commissure by predators.

Schmidt (1937) and later Rudwick (1964) have discussed the possible role of the folded commissure in sediment screening on brachiopods and oysters. In bivalves with flat commissures a considerable gape is required for effective feeding and respiration; in larger forms this gape is greater than the width of most particles in the associated sediment so that during turbidity, a great number and size range of particles can potentially wash into and clog the mantle cavity if the valves are open. Folding of the mantle and shell margin greatly increases the absolute linear dimension of the commissure and the area of the mantle edge contained within it. This means that the gape between the valves can be decreased in bivalves with a folded margin without decreasing the water intake area along the commissure. Narrowing the gape not only prevents large particles from washing in but diminishes the amount of possible sediment infiltration. It further makes mantle tentacles, normally very short, more functional in sediment-screening since they are brought closer together in the process. As shown by Rudwick, the amount of protection from sediment infiltration afforded by a folded mantle depends upon the strength, relative amplitude, and angularity of the crests, as well as on how uniform the reduced slit is over the entire commissure. A completely uniform-sized gape is the ideal situation, but rarely developed. In angular folds, the maximum opening along the slit is at the crest of each fold; the opening is most restricted on zigzag commissures with angular crests on the fold. Small, triangular, secondary calcareous deposits inside the crests of the folds are formed by some species to help partially seal off the more open crestal areas.

Rudwick *(31)* has suggested that although the restricted uniform gape, made possible by angular folding of the mantle and commissure, may function in all of the preceding ways, the primary function of this arrangement is sensory. He proposed that slight, even gaping of the shell is only the first step in opening the valves more fully for feeding, and that this initial gape is basically an early warning system exposing the sensory mantle edge completely to the surrounding environment without much danger of fouling. If the water were found free of harmful elements (predators, turbidity), the valves would then gape even further for feeding, possibly to a point where marginal folds were no longer functional as sediment screens.

DENTITION AND ASSOCIATED STRUCTURES

The dentition of the Bivalvia has received a considerable amount of study and has an important role in classification at all taxonomic levels. Its evolution in the class has been speculated on many times. It is unusual that so few authors have attempted to interpret in detail the function of the dental apparatus, especially in view of its considerable diversity. The bivalve dentition is composed of interlocking teeth and sockets which in many groups are differentiated into cardinal and lateral structures, of different size, or have become greatly modified, or even lost. Structures associated with the dentition are various pits and plates for muscle attachment or ligamental material.

The teeth and sockets of the Bivalvia perform three obvious functions. They provide a means of partially or wholly locking the valves together so that they cannot be easily separated by predators (e.g., starfishes, echinoids, gastropods), high-energy water movement, buffeting, or transportation. They secondly prohibit to varying degrees independent rotation of the valves in the plane of the commissure. Again this constitutes a basic form of protection against predators and physical environmental factors. Starfishes, or large gastropods like *Busycon* with a broad muscular foot capable of independent pressure in various regions, certainly are able to put torquelike stresses on the valves when they envelop their prey. Thirdly, the teeth and sockets provide an interlocking joint mechanism partially involved in the rotation of the valves (gaping) along the hinge axis. NEWELL *(18)* has correctly pointed out that in many bivalves the ligament and not the teeth constitute the fulcrum around which the valves gape. No additional major functions have been proposed, to my knowledge, for dentition in the majority of bivalves. A few, such as the boring Teredinidae and *Pholas,* have specialized hinge structures which do not function as normal teeth but rather create a ball joint around which the valves are independently rotated by muscles, functioning as individual cutting tools at the base of the bore hole.

For each of the three main functions of the dentition, general adaptive trends can be cited in the Bivalvia. A detailed functional analysis of dentition cannot be attempted until careful interpetive studies define the precise function of individual dental units, to date much neglected. As a locking device, the taxodont, schizodont, cyclodont, heterodont, heavy isodont (e.g., *Spondylus*), and diagenodont dentition patterns provide strong juncture between the valves and in addition effectively oppose rotation in the plane of the commissure. The great majority of bivalves characterized by these dental types are shallow infaunal or epifaunal elements exposed to rigorous environmental conditions and frequent predation where strong hingement is necessary. The Arcidae, Veneridae, Trigoniidae, Astartidae, Nuculidae, Nuculanidae, Crassatellidae, and Spondylidae are among these. Weaker hingement is found in reduced isodont (Pectinidae), dysodont, asthenodont, anomalodont and edentulous hinge areas, but the relationship to habitat is not as clearly defined. Many of these are deep-burrowing and deep-boring bivalves such as *Mya, Pholas,* and *Ensis* (Fig. 90), which are protected from severe wave and current action, and have a lower predation rate; a strong hingement is not selected for by the environment. Others, however, have preferred habitats directly affected by the conditions selecting for strong hingement, including the shallow infaunal *Anodonta* (fresh water), the various Mytilidae (byssate epifaunal), various Ostreidae (attached epifaunal), and the Pectinidae (free-living epifaunal). Many of these outstanding exceptions can be accounted for because other adaptations to the environment counteract the need for strong hingement—swimming habit in *Pecten,* strong byssal attachment and long efficient ligament in mytilids, cementation in ostreids, etc. However, this does not detract from the caution with which nature of the hinge must be used as a key to habitat in living and fossil bivalves.

The distribution of teeth on the hinge line appears to be directly related to the symmetry of many bivalve shells. Teeth and sockets are subequally distributed around the beak of symmetrical shells, and stretched out on the hinge line in the direction of symmetry imbalance. Thus, long posterior lateral teeth and short anterior laterals would be expected on shells which are truncated anteriorly and projected posteriorly, as in *Crassatella.* This correlation between skewness of the hinge structures and asymmetry of the shell is an adaptation which distributes, as evenly as possible, the protective locking mechanism and the stresses imposed on the hinge area by opening and closing of inequilateral valves.

The length of the hinge line relative to the circumference of the shell margins is correlative to the degree of valve rotation permitted in the plane of the commissure. Elongate hinge lines, like those of the Arcidae or various heterodonts (e.g., *Crassatella*) are better adapted to prevent individual rotation of the valves than short hinge lines (with exception of those with deeply interlocking teeth, as in *Spondylus*) found in various dysodont mytilids, all other factors being equal. In both hingement and protection against rotation, the ligamental structures give added support to the dentition. The efficiency of the dentition in permitting free lateral movement of the valves (gaping) around the ligamental fulcrum, while still maintaining juncture, seems to be correlative with the size of the teeth, their orientation, their penetration, their anchorage in the sockets, and their curvature.

Various structures associated with the hinge complex do not function in the above manner but have specialized roles. Broad spoon-shaped depressions (chondrophores) between cardinal teeth in forms such as *Mya* and triangular pits (resilifers) in the center of the hinge of *Pecten* and various Ostreidae contain a pad of fibrous, calcified ligamental material (the resilium) which is compressed when the valves are closed and expands upon relaxation of the adductor muscles to open the valves.

In Ostreidae, which have no teeth and sockets in the strict sense, the entire hinge plate, consisting of a central resilifer and lateral cardinal plates, is covered with ligamental material which not only functions to open the valves but also to hold them together. Marginal denticles may have a minor role in articulation. Hingement is aided in many Ostreidae (e.g., *Crassostrea*) by the concave nature of the resilifer on one valve and the convex nature of its counterpart on the other, so that they form a crude locking apparatus when in apposition. In *Isognomon* and related genera, several resilifer pits are spread across the hinge line, separated by flat plates. These are opposed and do not function as crude teeth and sockets, as in *Crassostrea.* The locking effect of a number of fibrous ligament pads filling these pits along the hinge line, however, is essentially that of true dentition, though not as stable by far.

A hinge plate usually supports some or all of the dentition but on some forms is extended centrally as a shelf, beyond the dentition and over the umbonal cavity, forming a platform for muscle attachment. In *Septifer* this receives the short anterior adductor, keeping it out of the way of the main byssal muscles which pass through a notch in the platform and attach in the umbonal cavity. Highly specialized muscle attachment surfaces, analogous to the cardinal process on brachiopods, are developed on some bivalves, such as the coral-boring *Diplothyra* and wood-boring Teredinidae. These are recessed plates or surfaces situated on various-length shafts originating on the hinge plate, and are termed apophyses. They appear to be a special and bizarre adaptation placing an attachment platform in the mantle cavity, adjacent to the viscera, for the implantation of muscles with a specialized function.

LIGAMENTURE

Ligamental material is variously distributed internally and externally on the bivalve shell and functions primarily to open the valves upon relaxation of the adductor muscles, either by expansion of a compressed internal band or pad of fibrous, calcified conchiolin (resilifer) or by contraction of stretched external sheets (lamellar and fusion layers of the ligament). Only duplivincular ligamenture constitutes an exception; it has little role in opening the valves and merely acts as a flexible attachment. As previously mentioned, the ligament secondarily, and in some bivalves primarily (e.g., *Anodonta, Ostrea*) functions to articulate the valves and prevent their individual rotation in the plane of the commissure, especially when dentition is weak or absent. The structure of the ligament in Bivalvia and its function have been fully described by NEWELL (1937, 1938), COX (1968) and OWEN (1958) and particularly in the experimental work of TRUEMAN (1949, 1950, 1951). As COX pointed out, the ligament is a highly variable and adaptive structure in the Bivalvia, showing considerable diversification even within single lines of evolution. The type of ligament (duplivincular, alivincular, parivincular, etc.), because of its characteristic trace where implanted on the shell, or the specialized structures adapted to receive it (e.g., resilium), can be reconstructed in most fossil Bivalvia, as can the placement of different layers. Fibrous ligament lies below the hinge axis, usually in a resilifer or chondrophore; lamellar and fusion layers lie externally. The distribution of various layers is to some extent also reflected in the trace of the pallial line (OWEN, 1958, and others). The gap between the ends of the pallial line and the ends of the primary ligament (reflected in fossils by the structures that contain it) is the area of anterior and posterior extension of the fusion layer.

The positioning of the ligament on the dorsal margin of the valves, like the dentition, is correlative in many bivalves with the symmetry of the shell so that stresses placed on the ligamental material in opening the valves will be as equally distributed as possible. Posterior elongation of the ligament in Mytilidae (alivincular) and Veneridae (parivincular) and addition of multivincular resilia behind the anterior beaks of *Isognomon* as the shell elongates posteriorly is a reflection of this relationship. The distribution of different types of ligamental material (e.g., fibrous, lamellar, or fusion layers; ligament sheets or pads; duplivincular, alivincular, or parivincular), and their density or reinforcement due to calcification is similarly adaptive. It is postulated but not conclusively demonstrated that the depth and size of ligament insertion areas on the valves (grooves, resilifers, nymphae) and the amount of ligament that is "internal" (concealed beneath the dorsal valve margins), is correlative with the ability or force of the ligament to open the valves, though not to the same extent as the nature of the ligament itself.

Cox *(6)* has pointed out the relative mechanical efficiency of various ligament types which, in order of increasing effectiveness are: duplivincular, alivincular, and parivincular (multivincular is still differentiated by some workers and probably fits between the last two types). It seems that a correlation exists between ligament type, its strength and efficiency, and the habitat of the bivalve, although no thorough study has been done to verify this. Many infaunal bivalves must not only overcome the weight of the valves in gaping but also partially or wholly the containing force of the sediment. Correspondingly, parivincular ligaments are common among the infaunal bivalves. Byssate epifaunal bivalves attached to exposed surfaces, where they are extremely vulnerable to harmful effects of the environment, and lacking strong dentition depend on the ligament for valve attachment as well as gaping. Most of these have strong, efficient multivincular *(Isognomon)*, parivincular, or advanced alivincular ligaments *(Mytilus)*. Some *(Pteria)* have weaker alivincular types. Many strongly cemented bivalves (e.g., *Ostrea*), fissure-dwellers *(Chlamys, Lima)*, and swimming forms *(Pecten, Lima)* are probably less dependent on strong ligamenture because of their unusual living habits, and have weaker alivincular ligamenture. There are many exceptions to this generalized pattern; nevertheless, such an approach may be a useful interpretive tool in evaluating evolution of the bivalve ligament. Thus, the apparent development of a mytilid-like advanced alivincular or parivincular ligament from an isognomonid multivincular type in the evolution of Cretaceous Inoceramidae (KAUFFMAN, 1965,9) can be interpreted as development of a more efficient and powerful ligamenture adaptive to a change of ecology from a prone, weakly byssate (or unattached) living habit on the substrate to strongly byssate, erect, free-swinging attachment to elevated objects. NEWELL *(18, 19)* has shown similar evolutionary trends in Late Paleozoic pectinids and mytilids. It is apparent that the functional significance of various types and arrangements of ligamenture deserves considerable study so that it is more applicable to the interpretation of similar, well-documented evolutionary changes.

INTERIOR SHELL STRUCTURES AND SOFT-PART MORPHOLOGY

The interior morphology of the bivalve shell is as complex, if not more so, than that of the exterior and in many cases closely reflects the soft-part morphology of the animal. The relationship between the two has not been adequately studied by either neontologists or paleontologists, possibly reflecting the common practice of zoologists to treat the mantle-shell and animal as distinct evolving entities (YONGE, 1953), and of the paleontologists to rely heavily on external features and dentition in systematics. Study of the probable nature and distribution of soft parts in fossils, a highly rewarding aspect of interpretive paleontology, is a much neglected field, although it has a long history. It demands a thorough understanding of the relationships between shell and soft parts so that one may be constructed from the other. The adductor-muscle scars and pallial line are commonly documented interior features on fossil bivalve shells. Other internal structures, however, equally reflective of the soft parts, have largely been ignored. These include smaller muscle attachment areas, interior buttresses, and muscle platforms, blood-vessel impressions, mantle-fluid channels, and other features. Thorough study of these, and an understanding of their function, allows relatively detailed reconstruction of the soft parts in ancient bivalves.

Stasek (1963) has pointed out additional difficulties in relating shell morphology with soft parts—the employment of two different systems of orientation and a lack of understanding of how one varies relative to another. His stated theory of transformations for relating both soft parts and shell in distinct taxa is based on the concept that comparable regions of the body are always adjacent to comparable regions of the mantle-shell, allowing a series of basic points to be identified on the shell of the bivalve which mark the position of various organs or regions of soft-part morphology. If these points are reflected by structures on the inner or outer shell surface that can be traced through ontogeny, they can be connected (Fig. 65), dividing the shell into distinct zones reflecting major anatomical areas or the position of particular structures, or both. Their history of development can thus be studied within a taxon, or they can be compared between diverse bivalves, indicating adaptive differences and evolutionary change in both soft and hard parts, in unity, and providing additional data for the interpretation of functional morphology in fossils. For more detailed comparison between taxa, a basic grid can be constructed on these points (Stasek, 1963, fig. 6). No matter what variation in form is developed on even distantly related Bivalvia, many of these points are identifiable through ontogeny or on the adult shell on the great majority of bivalves, or both. Thus, in comparing two distinct bivalves, if a basic grid is constructed on one and the critical points noted within it, a deformed grid using the same points can be constructed on the second (Stasek, 1963, fig. 7), allowing identification of comparable soft part areas and structures, and demonstrating evolutionary differentiation between them.

This is a potent paleontologic tool which has two primary applications to the study of form and function. First, in defining points of reference where shell and soft parts can be related, it makes possible a system of orientation common to both, and introduces a reliable means of identifying, from shell morphology alone, the probable distribution and development of soft-part morphology in considerable detail. Structures of the shell are brought to light as markers for some internal structure which rarely have been noted and interpreted by paleontologists. The work to date only introduces the possibilities; it is primarily up to the paleontologist to seek additional reflections of soft parts in the shell morphology.

Secondly, the transformation diagram is a major tool of comparative morphology in which most extinct bivalves, of all ages, may be critically compared with a living counterpart, either related to the fossil, or homeomorphic and similarly adapted to the environment. Such an approach would be a considerable boon to the study of Paleozoic Bivalvia, in particular for the interpretation of their evolution and degree of morphologic sophistication. Eventually we may be able to reconstruct soft-part morphology in such detail through this method that it will be possible to discuss the functional advantage of an enlarged foot, gill reorientation, an expanded mantle cavity, or ventrally migrating palps in the evolution of Paleozoic bivalve lineages with no related living counterparts. Features of the shell interior discussed below are all natural reference points for the construction of transformation grids because they reflect direct contact between the shell and particular structure(s) of the soft-part morphology.

MUSCULATURE AND PALLIAL LINE

The study of musculature in Bivalvia is one of the most successful means of delineating the general aspects of soft-part morphology and is a primary tool in the study of form and function. The musculature of the principal groups of living bivalves is well documented except for relationship of minor muscles of the gills and visceral mass to the shell, where they utilize it for insertion. At least the principal areas of muscle insertion, the adductors, pedal and byssal retractors, and the main pallial muscles are commonly preserved on fossil bivalves of all ages. Although these were generally ignored in earlier paleontologic works or described only in a cursory manner, a great deal of attention has been focused on musculature in recent years, and it has an important role in systematics and evolutionary studies. Their study is especially critical in Paleozoic forms. The most important aspect of musculature still to be investigated in paleontology is the spatial interrelationship between all muscle-insertion areas on the shell and other features of the animal morphology, so that the evolutionary significance and functional meaning of changes in muscle systems can be interpreted in detail, and the fossil soft-part morphology more completely reconstructed. Transformation diagrams and multivariate analyses will probably be the primary tools of such an undertaking.

Adductor muscles.—The principal muscle-insertion areas recognizable on fossil and Recent Bivalvia are those of the adductor muscles. These were defined early in the history of bivalve research and have been significant bases for classification. The terms dimyarian (equal or subequal adductors), anisomyarian or heteromyarian (unequal adductors, anterior one smallest), and monomyarian (single posterior adductor) are familiar to all students of paleontology. The adductors function primarily to close the valves, and through prolonged contraction to keep them closed against the tensional and compressive forces of the ligament. YONGE (1953, *47*) and OWEN (1958) pointed out that the adductors probably originated as hypertrophied pallial muscles at the ends of the mantle embayments on the hypothetical ancestral bivalve. They are well developed on all fossils definitely identified as Bivalvia where the musculature can be distinguished in well-preserved material. Although primitive adductor muscles may have been dominantly of a single type of tissue, the muscles of most living bivalves are divided into two parts, in some cases *(Pecten, Ostrea)* strikingly so. These are termed the catch and quick portions and are composed of nonstriated and striated muscle components, respectively. The quick portion is adapted for rapid contraction and closing of the valves and is especially functional as a defense mechanism, for cleaning the mantle cavity and valve surface, and in swimming (Pectinidae, Limidae). The catch portion is designed to keep the valves closed against the force of the ligament and is capable of sustained contraction. A comparative study of the size and distribution of these parts relative to the overall morphology and habit of various bivalves would be a rewarding and much needed endeavor.

YONGE *(47)* has discussed in considerable detail the basic differences between dimyarian, anisomyarian, and monomyarian musculature, their origin and evolution, and generally their functional significance relative to bivalve morphology and the mantle-shell of various kinds of bivalves. Many important details concerning the effects of anterior-adductor-muscle reduction and loss on the distribution and operation of associated soft parts are contained in this work and applicable to the study of form and function. The functional advantages of the anisomyarian and monomyarian conditions are treated only generally, probably because YONGE envisions these conditions as being secondarily produced by evolution in the following sequence of events, and therefore not in themselves a selected primary adaptation: 1) development of byssal attachment in dimyarian bivalves, producing a permanent fixed point for the foot and therefore restricting its ability to reorient, relative to other animal morphology, during evolutionary change in the form of the animal and its shell; 2) progressive reduction of the anterior one-half of the body without compensating shift of the foot and byssus, so that they become relatively more anterior in position and disproportional to other morphologic features; 3) secondary adaptation of the mantle-shell to the trend in 2), and reduction of the anterior adductor, as part of the mantle-shell complex.

Yonge envisioned the equilateral dimyarian byssate shell as being less adaptive to the epifaunal environment than one which is posteriorly elongated. Reduction of the anterior portion of the shell allows clustering of individuals while still keeping the inhalant and exhalant apertures, posterior in position and projecting above the substrate, free from restriction of circulation. Given the alternative of reducing either the anterior or posterior end of the animal following byssal attachment, posterior restriction would have been detrimental in that it would have restricted the ability of the inhalant and especially exhalant apertures to function properly, assuming they could not compensate in their placement relative to other soft parts.

The monomyarian condition arose by eventual loss of the anterior adductor and was accompanied by a trend toward horizontal orientation of the shell and eventual attachment (Yonge, 1953, *47*). Many monomyarians, however, retained an erect living posture (some *Pinctada,* Ambonychiidae). The tendency toward horizontal orientation, as in the pectinoids, created selective pressures for a more rounded, inequivalve shell, reflecting reorientation of the soft-part morphology, and creating the most stable geometric form for this living orientation. Centralization of the posterior adductor was a secondary result of this trend. Yonge *(47)* discussed this in detail and considered the adaptive significance of this change to be primarily increased freedom of internal orientation of animal morphology, the soft parts being distributed around the centralized posterior adductor. Development of the rounded, horizontally oriented shell and body morphology is envisioned as a return to the basic shell form—the fundamental symmetry of bivalve shell growth—by Yonge. It is made possible in development of the monomyarian condition by destruction of the influence of the anteroposterior axis of the body on the symmetry of the mantle-shell. This basic molluscan symmetry is already greatly affected in Bivalvia by evolutionary simplification of the head region so dominant in cephalopods and gastropods.

The placement of the adductor muscles on the bivalve shell is critical in that they function most efficiently when situated so as directly to oppose forces placed on the shell by the ligamental material. Dimyarian muscles shift laterally, becoming more distant from the beak, as the shell lengthens in an evolving lineage. Anisomyarian musculature reflects uneven pressures exerted on the anterior and posterior adductors in closing the valves and keeping them closed, by marked reduction of the anterior half of the shell and soft parts. In monomyarians the relationship between shell symmetry and placement of the ligament and adductor muscle is best expressed, and centralization of the muscle in an evolving lineage can be correlated with increasing valve symmetry and centralization of the ligament (Pectinidae). The size of the adductor muscles, and the relative distribution of striate and nonstriate tissue, are general indications of their strength and can be interpreted to varying degrees from the nature of the muscle insertion area. In general (many exceptions exist), the depth of the insertion area, the roughness of its surface, and the presence or absence of buttresses are thought to correlate with the strength of the muscle or the amount of pressure exerted on it when contracted, or both.

The shape of the adductors may also be diagnostic of function, but this is not fully understood. For example, what is the functional significance of a subcentrally situated ovate adductor impression on *Pycnodonte* as opposed to a comma-shaped impression on *Lopha* in the same position? In some cases these merely reflect the morphologic structures adjacent to them as they pass through the visceral mass and mantle cavity (Lucinacea); but also the detail of their shape may reflect not only the distribution of stresses on the muscle but the various types of muscle tissue. In some bivalves the catch and quick portions of the adductor are clearly marked by different surface features of the muscle impression, by a distinct line separating them, or by marked constrictions in the outline of the attachment surface. A considerable amount of functional interpretation can result from definition of the relative size of adductor muscle components. For example, the large striated muscle portion of the adductor in ostreids reflects the ability of the animal to clean the mantle cavity and shells of sediment by rapid and forceful closure of the valves.

The unusual irregular, dorsoventrally elongate shape of the lucinoid anterior adductor impression is an excellent example of how impression form may be interrelated with other aspects of the morphology and therefore have considerable interpretive potential. Lateral constriction of the muscle provides anteriorly space for the upward passage of the vermiform foot between the adductor and mantle attachment area to form and occupy the anterior sediment tube used in feeding and respiration (Fig. 91). Posteriorly compression of this muscle provides additional space in the mantle cavity necessary for the retraction and coiling of the enlarged foot. A constriction in the center of the scar denotes the contact between catch and quick muscle portions. Finally, the vertical elongation of the scar reflects its ability to satisfy the preceding spatial requirements and still maintain a size necessary to perform its main function of closing the valves. Vertical elongation also brings the ventral tip of the muscle, with its ciliated surface used in sorting, in contact with the main currents flowing into the mantle cavity for feeding and respiration.

Pallial line.—The pallial line is a band or series of pits made by the insertion of muscles attaching the mantle to the shell. Peripheral to this the mantle hangs free. The line extends subperipherally between the adductors of dimyarian bivalves, and between the posterior adductor and the hinge area of monomyarians. In some dimyarians the line extends subperipherally beyond the adductors along the dorsal and dorsolateral margins. Here it essentially acts as a secondary dorsal adductor in addition to its role of mantle attachment. The extent to which the pallial line continues dorsally is controlled by the extent of fusion of the outer layers on the outer mantle lobe adjacent to the mantle isthmus, and associated extension of the ligamental fusion layer laterally beyond the region of the primary ligament (Owen, 1958). The pallial line dorsally connects the point where the fusion layer terminates, with the adductor muscle. The dorsal extent of the pallial line may therefore be used to determine the layers involved in mantle fusion adjacent to the isthmus and the extent of the ligamental fusion layer in fossil bivalves. That fusion of the inner two mantle layers, and the inner surface of the outer layer do not produce loss of dorsal pallial attachment, whereas outer mantle fusion and development of a fusion layer does restrict it, suggests strongly a functional replacement of one for the other in evolution. The distance between the ends of the primary ligament and the inner edges of the adductor muscles in dimyarians has been thought by Owen (1958) to correspond to compensatory lateral shift of the adductors, with elongation of the animal and shell through evolution, to the position on the shell where they are most efficiently placed to perform their function of closing the valves.

The pallial line reflects the insertion of more than one band of pallial muscles, usually distinct bands of radially arranged longitudinal muscle strands. These may be differentiated in some fossils by slight differences in the texture of the insertion areas. The degree of manipulation of the free mantle flap made possible by these muscles may be reflected in the strength of their insertion and the distinctness of separate bands. Two basic types of pallial muscle attachment are developed in the Bivalvia, and most forms have one or the other: 1) continuous pallial muscle insertion along a track (e.g., *Mercenaria*), the pallial line as strictly defined, and 2) discontinuous insertion reflected in a linear series of discrete pits along the line of pallial attachment (e.g., *Isognomon*) or by local clusters of muscles (e.g., *Pinna*). In many cases the second type of pallial line is much farther within the shell than the first. Although the functional advantages of one over the other system have not been well defined, it is postulated that continuous pallial attachment provides greater control in manipulation of the free mantle edge, but that discontinuous attachment, which involves bundles of longer fibers than developed in continuous musculature, is better adapted to rapid contraction of the mantle over longer distances. The pitted system occurs in many

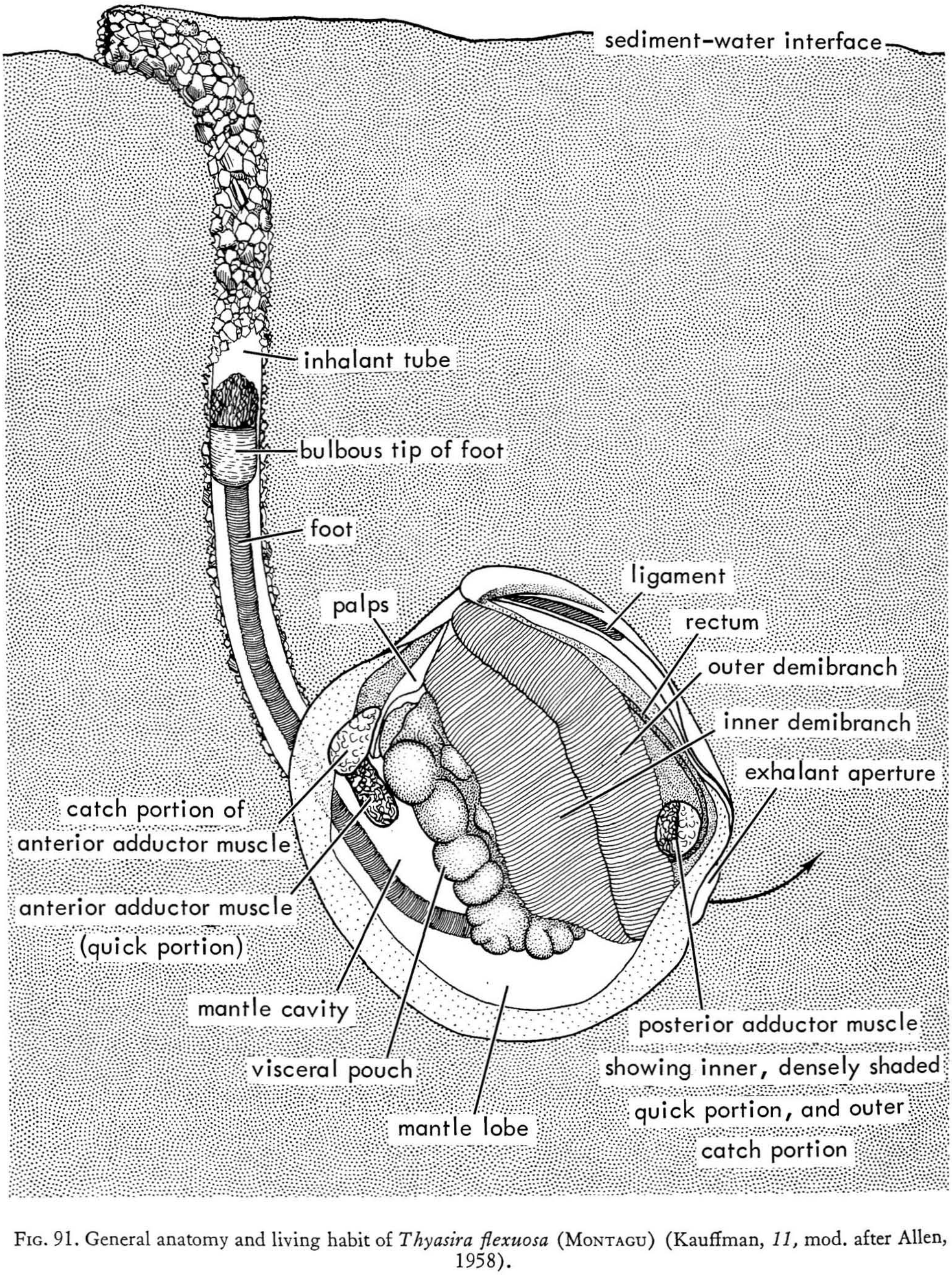


FIG. 91. General anatomy and living habit of *Thyasira flexuosa* (MONTAGU) (Kauffman, *11,* mod. after Allen, 1958).

Animal shown in living position at shallower depth than normal, anterior inhalant tube broken away in center to show elongate vermiform foot with bulbous tip. Sediment grains encasing tube enlarged to accentuate structure, no sediment-size selection being implied. Backward-directed arrow (lower right) indicates direction of current flow from exhalant nonsiphonate aperture, here somewhat extruded to show its position.

epifaunal bivalves which have a large expanse of thin delicate shell beyond the line of pallial attachment composed mainly of prismatic calcite (or other outer ostracum) and periostracum. The shell is easily broken by predators and in high-energy current situations, and it is highly advantageous for the animal in this situation to have the ability to withdraw the free edge of the mantle rapidly far into the shell when threatened. The more central position of the pitted pallial line would therefore be as adaptive as the bundled musculature itself. Such flexibility of free mantle extension and contraction may also be adaptive to rapid repair of the shell over a larger area once broken.

An obvious feature of the pallial line in infaunal Bivalvia is a distinct reentrant posteroventrally, the pallial sinus. This marks the position of the siphons where developed (although very short siphons do not necessarily produce a sinus) and embayment of the mantle attachment to allow them free movement. The bifurcating axis of the sinus generally reflects the direction of siphon extrusion. The size of the sinus is only grossly related to the size of the siphons, and more closely reflects their degree of fusion, strength, and degree of extrusibility. In Lucinacea, a reentrant of the inner shell layers, contained within the pallial line, between the pallial line and the anteroventral edge of the anterior adductor muscle insertion area delineates the position of an incurrent channel between the anterior sediment tube (Fig. 91), and the mantle cavity. This channel allows extension of the foot out through the tube and entrance of inflowing currents used in feeding and respiration.

Pedal and pedal-byssal musculature.—The foot is one of the most complex and adaptive structures of the bivalve, and it would be expected to have a complex system of operational musculature. This is certainly the case. YONGE *(47)* has reviewed the development of the principal pedal and pedal-byssal musculature on a variety of bivalves and the subject has been treated in detail and illustrated in this volume by Cox *(6)*. Some general adaptive trends are evident from these data. The primitive pedal musculature is envisioned by many authors as consisting of numerous subequal dorsocentrally inserting muscles between the anterior and posterior adductors (McALESTER, 1964) for the operation of a ventrally extending foot. Decentralization and functional differentiation in the muscle system, inequality of musculature, and general decrease in numbers of muscles in younger forms reflect evolutionary trends producing a great diversification in the types and functions of the foot, and in living habits among the Bivalvia. Numerical decrease in numbers of pedal muscles to perform a particular function is considered an evolutionary advance producing greater efficiency of operation and simplifying the musculature transgressing the mantle cavity. This trend does not apply to all bivalves, however. For example, Ordovician nuculoids do not have multiple pedal scars, whereas younger ones do (J. POJETA, personal communication, 1967). Reference to the pedal musculature developed on many different groups of Bivalvia (Fig. 31, 34) obviates functional relationships between size and distribution of muscles and the size and function of the foot. Strong musculature necessary to operate the digging foot of *Mercenaria, Anodonta, Cardium,* and *Yoldia* is reflected by large or numerous pedal muscle scars (developed as solutions to the same problem) or both; loss or degeneration of the foot accompanying byssal attachment and cementation produces a marked decrease in the development of pedal muscles.

The rate of burrowing and relative energy required in penetrating the substrate are strongly reflected in the pedal musculature of infaunal bivalves. For example, rapid burrowing requires forceful penetration of the substrate by the foot so as to obtain a deep anchorage. In some rapid burrowers (e.g., *Tellina*) a large pedal protractor is placed in near opposition to the retracted foot for this purpose. Infaunal bivalves not well adapted in form for rapid burrowing and which require a considerable amount of energy in the process (e.g., the moderately inflated *Anodonta*) have proportionately larger protractor muscles, or more of them *(Yoldia)*. Manipulation of the foot in the burrowing process requires additional strong muscle control, reflected by the great development of pedal elevators and retractors on most actively burrowing infaunal bivalves. The complicated relationships between the direction a foot extends from the shell and operates, its necessary force and scope of activity, and the placement of pedal retractors, elevators, and protractors on various Bivalvia would be an excellent line of investigation and would be wholly applicable to the interpretation of form and function. It is obvious from known examples that the placement of muscles relative to the direction of extension of the foot is critical and that a delicate balance must be maintained between the vector forces of protractors, elevators (where developed), and retractors. Shift in one during evolution might be expected to bring about compensatory shift in the others or else be accompanied by significant alteration of shell form, or soft-part morphology, or all three. For example, if *Cardium* is taken as a model of a simple ventral to ventroanterior projecting foot system in a rounded shell (Fig. 31), the equal placement of the pedal elevator, anterior retractor, and posterior retractor, and subequal development of the latter two might be expected as the most efficient and balanced system of operation, the foot being drawn straight up by equal force from the three muscles. Posterior elongation of the shell and a shift from mid-ventral to anteroventral projection of the foot during evolution, as in a form like *Anodonta* (Fig. 31) drastically imbalances this system. The pedal elevator remains below the umbo but due to anterior placement of the beak on such a form comes to lie close to the anterior retractor, adjacent to the adductor muscle. To compensate for this, the posterior retractor enlarges and shifts backward with the posterior adductor, coming into apposition with the projection of the foot and taking over as the principal retractor force. When such interrelationships are fully understood it should be possible to reconstruct relative vector forces from the muscle-insertion areas of fossils and interpret the size, projection, and operation of the foot.

The foot is reduced or lost in many attached Bivalvia and the pedal musculature greatly simplified (Fig. 34) to a dominant pedal or pedal-byssal retractor with or without small accessory protractor and anterior retractor muscles. This reflects the dominant motion in byssate bivalves of extension or contraction of the shell on the byssus, with rapid contraction especially adapted to survival by pulling the shell tight against the substrate or byssal attachment area. Correspondingly, the pedal-byssal retractor normally lies directly opposed to the direction of byssal extension, the optimum position for efficient operation. Once the position of the pedal-byssal insertion area and the byssal gape are known on fossil shells, the direction of extension of the byssus can be determined and the position of the shell relative to the attachment surface reconstructed. This in turn allows numerous functional interpretations based on other aspects of the shell morphology. Thus in *Modiolus, s.s.* (Fig. 34,*D*) the large pedal-byssal retractor and main (posterior) pedal retractor are side by side in the posterodorsal corner of the shell and projection of the byssus is anteroventral. In *Isognomon* (Fig. 34,*A*) projection of the byssus is dorsoanterior and the main retractor muscle is centrally situated, directly opposed to the byssus in a posteroventral direction.

Other muscles.—Numerous small muscles attached to the shell within the pallial line serve the mantle and other soft parts and are sometimes preserved in fossil shells. Besides the pallial line the mantle is attached by numerous small radial pallial muscles scattered over the surface. These produce small pits on the shell in some cases and function also to retract the mantle when agitated. In taxa where the mantle is not attached over a large area posteriorly *(Pteria)* special bundles of mantle retractor muscles attach centrally in the shell. Clusters of muscles around the pallial sinus in siphonate bivalves serve to withdraw the siphons by contraction; in some cases these are easily distinguished on fossils and usually larger than the mantle muscles. Gill-muscle scars have been pointed out in the Early Ordovician prelucinoid *Babinka* (McAlester, 1964) but are not commonly visible on the interior surface of bivalve shells. Newell (1937, 1938, 1942) has tentatively identified them on a variety of taxa. They form an arc which probably defines the orientation of the gills, its long axis parallel to a line connecting the ends of the arc. This could be a useful tool for determining the position and orientation of gills in other fossils if the insertion areas are preserved. Cox *(6)* has reviewed minor musculature in detail.

Muscle platforms and buttresses.—Raised areas around and below muscle insertion surfaces reinforce the adductor muscle attachment and buttress it against the predominant direction of force during operation. *Glycymeris* and various Arcidae, and especially forms like *Cucullaea* display these well. Internal ribs accomplish the same function. These may be the result of flexure of the entire shell, as posteroventral sulci (externally) or internal supporting folds (e.g., many Ostreidae), or solid internal ribs *(Leptosolen)*, or hollow internal ribs (Cretaceous *Endocostea*). In the Lucinacea and possibly other bivalves the internal fold formed by the primary exterior sulcus marks the line of gill attachment and may be a platform for the gill muscles, or a buttress for gill support as well as attachment of the posterior adductor muscle.

Other features.—Various grooves and lines have been documented on the interior of bivalve shells and related in various ways to soft-part morphology. Fine, radiating sinuous grooves and raised lines have been interpreted as traces of radiating mantle attachment muscles (retractors), as impressions of mantle tentacles, and as traces of pallial fluid canals or blood vessels within the mantle. The arcuate track of one major blood vessel has been identified by its imprint on the central part of the shell in various Lucinaea and Ostreidae.

Space.—In the study of functional morphology of bivalves it has often been overlooked that the size of the mantle cavity and the distribution of soft-part morphology within it represent spatial relationships critical to the survival and efficient operation of the animal, and can be defined in fossils. Utilizing inflation of the valves internally, the trace of the pallial line, and various lines of evidence such as musculature which reflect the size and distribution of soft parts, the size and available space in the mantle cavity can be generally reconstructed. In forms like the Lucinacea, where the vermiform foot must be totally withdrawn and coiled in the mantle cavity to allow currents to enter anteriorly, or the Unionidae which retain the larval young on the gills of the female, an enlarged mantle cavity is necessary and is variously reflected in the shell morphology. In unionids this is shown by the greater inflation of the female shell, especially along the umbonal ridge. In lucinaceans it may be represented by lateral compression and submarginal position of the anterior adductor muscle, and posterior repositioning and size reduction of the gills.

EVOLUTION AND INTERPRETATION

The documentation of form and function is a necessary first step of interpretive paleontology and considerably broadens the scope with which paleontology can be applied to the solution of geologic and biologic problems. For the sake of simplicity, functions have been defined for major features of the bivalve shell, the potential fossil, and for interacting structures of the shell and its contained soft parts, as discrete entities. This step must precede integrated analysis and does not deny the existence of complex functionally interacting systems or suites of soft-part and shell morphology. These are too variable and complex to attempt description here for all Bivalvia; their characteristics depend largely on the lineage in question.

Therefore, in order to document the concept of functionally integrated character suites, the ability to define them in paleontology, and the application of this and associated paleontologic, biologic, and geologic data to broad problems of science, a selected example is presented. Although this does not incorporate all possible lines of interpretive research, it serves to point out its potential. The interpretation of evolutionary trends is basic to nearly all ventures into this field.

CRETACEOUS THYASIRA OF NORTH AMERICAN INTERIOR

The unique lucinacean *Thyasira* Leach has worldwide distribution in cold to warm temperate, Recent marine waters, and the anatomy, morphology and living habit of modern representatives have been thoroughly studied (Allen, 1958). Structurally, the animal is unusually adapted to life in restricted cool water, infaunal habitats, including oxygen-poor, hydrogen sulfide-rich environments with a limited food supply, supporting an otherwise impoverished molluscan assemblage. Soft-part morphology is well defined in features of the containing shell. The earliest known fossil representatives occur in Cretaceous rocks of North America. Kauffman *(11)* recently described those of the Western Interior for the first time, defining two main evolving species complexes containing five definable lineages, with seven species and ten subspecies distributed through 11 Campanian ammonite zones (see Fig. 97). Populations and ontogenetic series of well-preserved specimens showing interior shell morphology were available for study from 20 stratigraphic levels spanning about 4.75 million years. Radiometric dating indicates individual subspecies have an average time range of 0.86 million years; the more restricted subspecies range through 0.63 million years of time. This is slightly longer than comparable ammonite zones in the same rock sequence. Evolution within Cretaceous lineages was relatively conservative, and has been since the Cretaceous, the fossil forms being closely comparable in shell morphology, and soft parts indicated by it, to living species of the Atlantic Realm. These factors made the study of Cretaceous *Thyasira* an ideal test case for multifaceted inter-

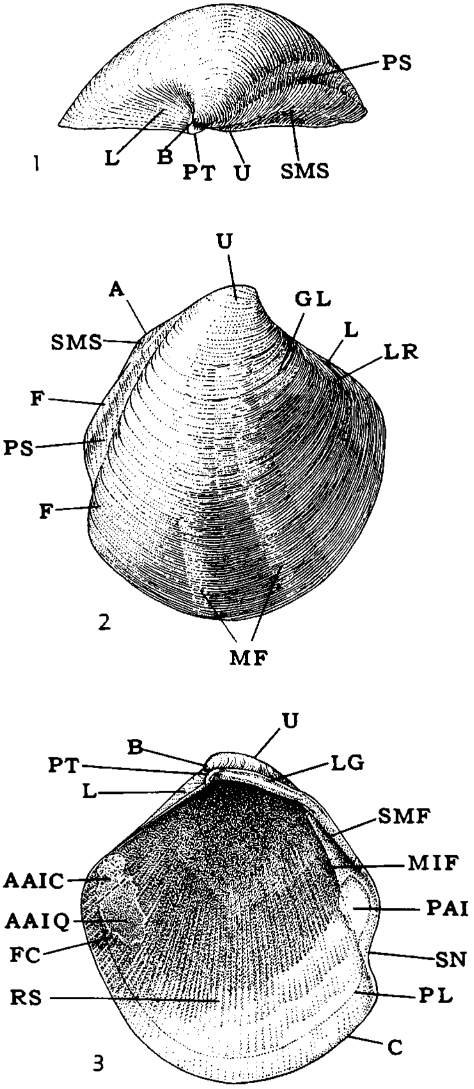


Fig. 92. Morphology of *Thyasira flexuosa* (Montagu) right valve, *(1)* dorsal, *(2)* exterior, and *(3)* interior views (Kauffman, *11*). [Explanation: *A,* posterior auricle; *AAIC,* anterior adductor insertion area for catch portion of muscle; *AAIQ,* anterior adductor insertion area for quick portion of muscle; *B,* beak; *C,* commissure; *F,* fold on valve exterior; *FC,* foot canal or incurrent channel, reentrant between antero-ventral edge of adductor muscle scar and inner edge of pallial line, marking position of channel or opening in mantle margin leading from proximal end of anterior inhalant tube to mantle cavity (foot projects outward and feeding currents flow inward through this channel); *GL,* growth line; *L,* lunule; *LG,* ligament groove; *LR,* marginal ridge of lunule; *MF,* medial flattened areas on shell exterior; *MIF,* main or primary interior fold; *PAI,* posterior adductor muscle insertion area; *PL,* pallial line; *PS,* primary sulcus of valve exterior; *PT,* pseudocardinal tooth; *RS,* radiating interior striae; *SMF,* submarginal fold of valve interior; *SMS,* submarginal sulcus of valve exterior; *SN,* notch in marginal outline formed by its intersection with primary sulcus; *U,* umbo.]

pretive analysis utilizing comparative morphology and ecology between closely related fossil and living taxa.

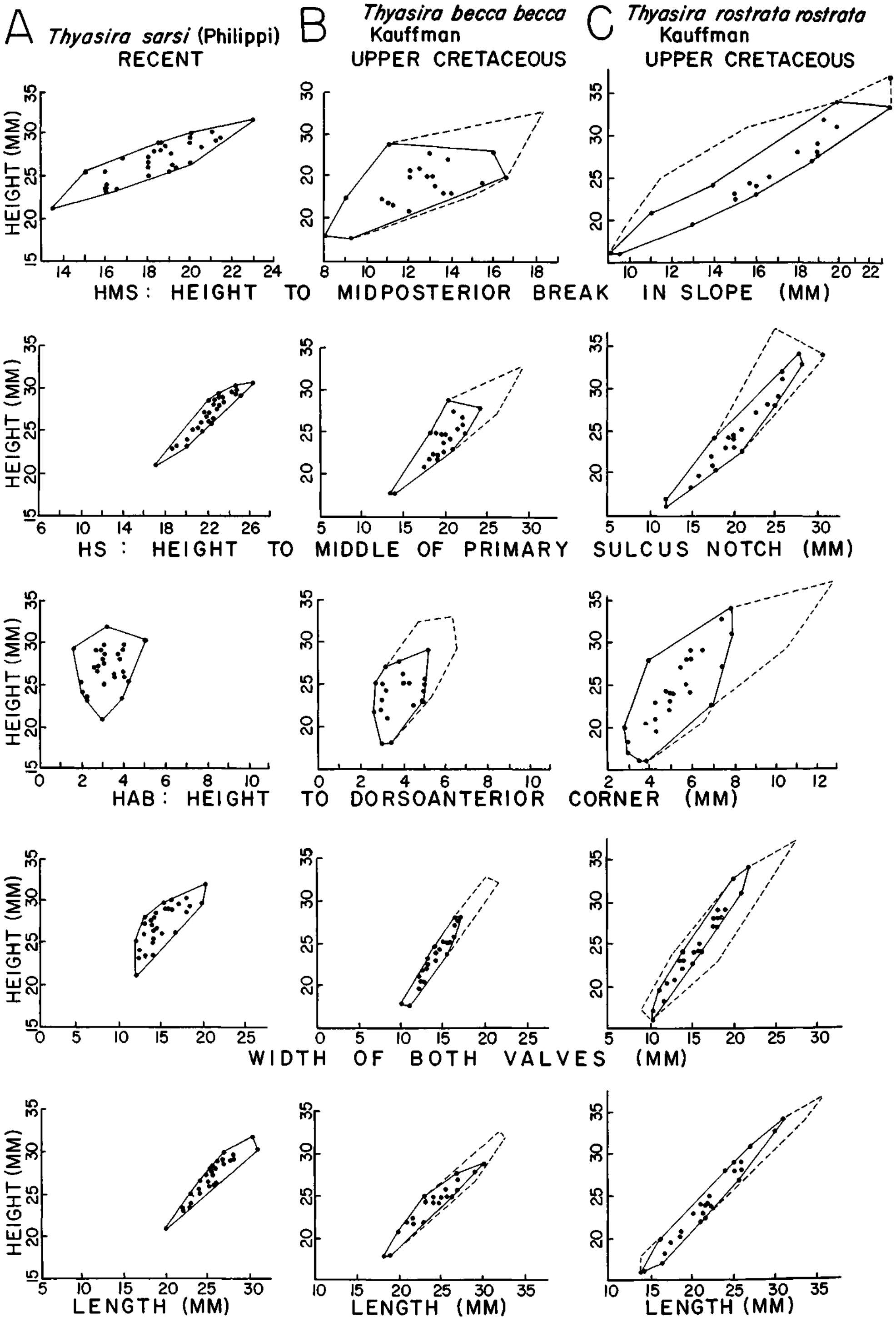
Shell.—Comparative studies demonstrated that the interior and exterior shell morphology of Cretaceous and Recent *Thyasira* were similar in all aspects but size and shell thickness. Cretaceous species are consistently larger and have thicker shells than most Recent Atlantic species to which they are related, with the exception of forms like *Thyasira sarsi* (Philippi). Fossil and Recent shells are equivalve, moderately biconvex, slightly to moderately prosocline and round, subround or subtriangular in outline. They are characterized externally by prosogyrous beaks, a shallow lunule, narrow escutcheon, fine concentric ornamentation, and a prominent posteroventrally directed sulcus, posterior to which is a strong asymmetrical fold and a smaller submarginal sulcus below the dorsoposterior border. Internally the hinge is edentulous or pseudodentate, very slightly thickened, and the posterior ligamental groove long and narrow. The external sulci are expressed internally as folds. A round posterior adductor insertion area of moderate size is located astride the main fold; the anterior adductor is irregular, elongate in a dorsoanterior-ventroposterior direction, well implanted, separated ventrally from the entire pallial line, and constricted centrally. Radial grooves and low ridges cover the shell interior. Figure 92 shows additional detail.

Biometric analysis of shell characters on Cretaceous populations compared to similar variation plots in the closely allied living species *Thyasira sarsi* provided a means of depicting expected limits of population variation in fossil species and thus a basis for separating phenotypic variation from evolutionary change in time successive Cretaceous populations of each lineage. It further demonstrated the conservative nature of Cretaceous to Recent evolution in *Thyasira* and confirmed the close comparability of fossil and Recent forms. The same variable and conservative characters are found on both (Fig. 93 is a sample of this analysis) and the degree of variation shown by any character or character-pair is closely comparable on living and fossil species of the same evolving complex. Equally as significant is the close similarity in character plots of the entire sample—all collections of the species from all geographic areas and throughout its time span (Fig. 93). This marks the degree of phenotypic conservatism within the species, and further aids in separating taxa in an evolving lineage.

Functional morphology of the shell.—*Thyasira* lives erect, deeply burrowed in the substrate (Fig. 91). The shell is similarly oriented during burrowing once erected on top of the substrate; the foot extends midventrally, penetrating deep into the sediment and anchoring by expansion of the bulbous tip. The shell is then pulled straight down, ventral edge leading, by contraction of pedal muscles aided by a rocking motion of the shell. Most *Thyasira* have an externally simple shell which is well adapted for burrowing and this mode of life.

Low to moderate shell convexity, the nearly smooth outer surface, and the gradually tapering ventral and ventrolateral flanks are features streamlining the shell for vertical burrowing, creating a tapered smooth wedge adapted for easy penetration of the substrate. Elongation of the shell along the height axis occurs in many species (Fig. 92) and further streamlines the shell by reducing the length dimension relative to height, and diminishing the size of the penetration track and the frictional drag imparted to the shell by the substrate during penetration. The smoothly rounded to ovate marginal outline, lacking projecting auricles, is similarly adaptive.

Both the lunule and escutcheon face away from the burrowing direction and could act as buttresses against the overlying sediment to counteract the force of the foot against the substrate when extended ventrally. Folds and sulci are considered disadvantageous to rapid burrowing in bivalves, creating an irregular surface to be pulled through the sediment, and probably increasing the amount of frictional drag to be overcome as well as the necessary energy output. These lie dorsal to the main incising part of the shell in *Thyasira,* which


A *Thyasira sarsi* (Philippi)
RECENT
B *Thyasira becca becca* Kauffman
UPPER CRETACEOUS
C *Thyasira rostrata rostrata* Kauffman
UPPER CRETACEOUS
HEIGHT (MM)
HMS: HEIGHT TO MIDPOSTERIOR BREAK IN SLOPE (MM)
HS: HEIGHT TO MIDDLE OF PRIMARY SULCUS NOTCH (MM)
HAB: HEIGHT TO DORSOANTERIOR CORNER (MM)
WIDTH OF BOTH VALVES (MM)
LENGTH (MM)
15
20
25
30
35

minimizes their effect on burrowing, and the functional significance of their internal counterparts, the primary and submarginal folds in *Thyasira,* far surpasses any deleterious effect they may have on burrowing. The primary sulcus internally provides a strong buttress for the attachment of the gills and posterior adductor muscle, and the submarginal sulcus becomes the lower edge of the ligamental groove. Median flattened areas along the burrowing axis of many species (Fig. 92) may be advantageous in that they slightly diminish the outside convexity of the shell and further cut down on its resistance to burrowing.

In living species there seems to be a general but poorly documented correlation between convexity, outline of the valves, burrowing speed, and burrowing depth. The broadest, roundest shells belong to shallower infaunal species with a slower rate of burrowing than the less convex shells elongated along the height (burrowing) axis (e.g., *Thyasira flexuosa,* Fig. 92). A similar interpretation is applied to the variable Cretaceous *Thyasira* (see Fig. 95).

Soft-part morphology.—ALLEN (1958) studied in detail the anatomy and morphology of living *Thyasira,* characterized in Figure 91 by the common Atlantic species *T. flexuosa* (MONTAGU), shown here in living position. Like other Lucinacea, the internal morphology of *Thyasira* deviates strikingly from the usual infaunal plan and mode of adaptation to habitat, typified by the Veneridae. These deviations are primarily concerned with the foot, mantle cavity, gills, inhalant and exhalant apertures, mantle fusion, and sorting and feeding mechanisms. These are reflected in the internal morphology of the shell on both fossil and living species. The animal is adapted to a deep infaunal existence in fine substrate, oriented vertically (Fig. 91), in areas of poor productivity and potential oxygen deficiency or high hydrogen-sulphide content, or both.

The foot is highly modified, long and slender with a bulbous, expandable tip bearing mucous-secreting glands. It reaches ten times the length of the shell in some Lucinacea and when retracted lies coiled in the mantle cavity, considerably enlarged to receive it. The foot has three functions, burrowing, locomotion (not common), and formation of an anterior agglutinated sediment tube leading from the water-substrate interface to the anterior margin of the shell and carrying the principal inhalant currents used in feeding and respiration. It may also have a role in detritus-feeding but this has not been documented. It is well adapted for both burrowing and tube formation. In burrowing its form and length allows deep penetration and firm anchorage in the substrate with each thrust, and thus rapid penetration. The tube is formed by the joining of successive agglutinated sediment collars formed around the mucous-secreting tip of the foot. Periodically the foot is extruded through the tube to clean or repair it, and possibly also for feeding, creating in-

FIG. 93. (Facing page) Comparative population variations in Recent and Cretaceous species and subspecies of *Thyasira* (Kauffman, *11*).

[EXPLANATION: Graphs show close similarity in range of variation of each character pair for single populations of living and Cretaceous species, providing comparative basis for species and subspecies concepts. Slightly greater variation shown by fossil species in some character-pairs is attributed to preservation factors. Range of variation for all specimens of fossil subspecies, regardless of locality and relative position within their known stratigraphic range, is closely comparable to that of single populations with exception of size range.]

A. Thyasira sarsi (PHILIPPI), Rec., from Grand Banks, north Atlantic, at depth of 130 fathoms. Population of 30 valves (USNM 52733, Division of Mollusks).

B. Thyasira becca becca KAUFFMAN, U.Cret., from single layer of concretions in middle part of *Baculites scotti* Zone of Pierre Shale, Fall River County, South Dakota. Solid line and plotted points represent population of 23 specimens, broken line showing boundary of scattergram based on measurements of all known specimens of subspecies from all different localities.

C. Thyasira rostrata rostrata KAUFFMAN, U.Cret., from zone of limestone concretions (zone of *Baculites* sp. with weak flank ribs) in Steele Shale, Lost Soldier-Ferris district, Wyoming. Solid line and plotted points represent population of 26 specimens, broken line showing boundary of scattergram for measurements of all known specimens from all known localities.

ward directed currents, or as a plug during times of turbidity.

Expansion of the mantle cavity to accommodate the foot when retracted and coiled is produced by: 1) reduction of the size of the gills and their reorientation (compared to simple dorsal pendants) dorsoposteriorly, buttressed against the main interior fold and facing anteroventrally; 2) development of lateral body pouches on either side of the mantle cavity, possibly reflected in some species by the point of maximum valve convexity; and 3) lateral compression of the anterior adductor muscle.

The anterior adductor muscle and its insertion area are larger than the posterior adductor, elongate dorsoventrally or along a dorsoanterior-ventroposterior axis, irregular and generally constricted centrally at the junction between the striate and nonstriate part of the muscle (Fig. 91). The lower half of the insertion area is separated anteriorly from the pallial line. This separation, the incurrent channel, allows free passage of the foot in front of the muscle and out the mid-anterior portion of the commissure to form the sediment tube used in feeding and respiration. Incoming currents pass between the tube and the mantle cavity through this channel. Thus, lateral compression of the muscle is functional both anteriorly and posteriorly.

The apertures of *Thyasira* are highly modified as a result of the anterior inhalant tube. Unlike other Lucinacea with a long posterior exhalant siphon, *Thyasira* is nonsiphonate and no sinus is developed in the pallial line, even though many species prefer a deep infaunal habitat. The posterior inhalant aperture is poorly defined and formed only by partial cuticular fusion of the inner mantle lobe. It no longer functions in feeding and respiration; currents entering through it are weak and function to create vortices in the main rejection track current for the sorting and cementing of pseudofeces. The posterior exhalant aperture is well developed and retains an excretory function.

The formation of a long inhalant tube in *Thyasira* permits individuals to burrow deeply into soft sediment, some of which is chemically deleterious to many other infaunal elements, while still drawing adequate food and oxygen from waters above the interface. Many environments inhabited by Thyasiridae are characterized by a limited food supply. To adapt to these conditions the sorting mechanisms are greatly reduced, concentrated anteriorly and the food-selectivity of the animal considerably diminished compared to more normal infaunal groups like the venerids. The gills are reduced in size and lose their particle-sorting structures. Palps are similarly restricted in size, and all ciliary sorting surfaces except those of the anterior adductor muscle and anterior mantle lobes are lost or greatly reduced. These modifications make possible acceptance of a wide range of particulate organic matter, decidedly adaptive in a food-poor habitat. Further modifications of the mantle are treated in ALLEN (1958) and KAUFFMAN (1967, *11*).

In the initial evolution of the Lucinacea, including the poorly known pre-Cretaceous history of *Thyasira,* and subsequently in the development of Cretaceous to Recent lineages of Thyasiridae, evolutionary changes in shell and animal morphology had to be integrated with normal feeding and respiration. Critical to the feeding-oxygenation process are the spatial relationships of the soft parts and fluid flow within the mantle cavity. The three basic spatial relationships that had to be maintained during evolution, and therefore integrated as a selective force in the evolutionary process, were as follows: 1) Efficient operation of gills in feeding and respiration depends upon even bathing by most incurrent waters. Thus, to allow initial sorting of material by cilia at the mouth of the anterior channel, and elimination of harmful or unusable particles by countercurrents before the incoming water is distributed across the gills, the gills themselves must maintain a critical distance from the point at which incurrent waters enter the mantle cavity. 2) The most even bathing of the gills would be expected if: a) this distance was sufficient to allow the water to spread out within the cavity, and b) the gills faced perpendicular to the incoming currents. 3) The mantle cavity must be large enough to accommodate the coiled vermiform foot when completely withdrawn from the sediment tube, and still allow normal respiration and filter feeding to take place within it. Retention of these critical spatial relationships plays an important role in the evolution of Cretaceous *Thyasira.*

REFLECTION OF SOFT-PART MORPHOLOGY ON SHELL: FORM AND FUNCTION

Much of the unique soft-part morphology of *Thyasira* is reflected in detail on the shell interior, providing a firm basis for reconstruction of the basic soft parts in fossils, and considerably broadening the scope of possible interpretation of form, function, ecology, and evolution in Cretaceous species closely resembling living forms. The size of the mantle cavity is defined by the pallial line, inner edge of the adductor muscle insertion areas, and the interior inflation of the shell; the presence or absence of lateral mantle pouches is not documented in shell morphology, except possibly the point of maximum shell inflation dorsocentrally. The function of an enlarged mantle cavity has been discussed.

The adductor and pallial musculature is well defined by moderately impressed insertion areas on the shell interior. These are more coarsely striated than the surrounding shell at the adductor insertions. Their shape accurately records the shape of the muscle at insertion. The elongated shape of the anteroir-adductor-insertion area reflects lateral compression of this muscle to provide additional space medially in the mantle cavity for the coiled foot, and ventroanteriorly for the incurrent channel between the mantle cavity and sediment tube. The ventroanterior separation of the anterior adductor insertion from the pallial line marks the position of the incurrent channel and defines, by the angle of this narrow reentrant, the steep angle at which the foot projected outward in tube formation, the probable inclination of the sediment tube extending from the shell to the surface, and the point and direction at which incoming currents entered the mantle cavity. A prominent medial constriction in the anterior adductor insertion area on some species defines the juncture of the ventral striated and dorsal nonstriated muscle fibers (Fig. 91). The relatively large area of striated muscle, and the coarsely ornate surfaces of the adductors indicating firm muscle implantation, probably reflect the ability of the animal to close the valves forcefully and quickly. This creates a powerful downward jet of water which clears sediment along the ventral margin of the shell during burrowing. The large size of the anterior adductor is partly due to its lateral compression and compensating ventral elongation in order to maintain an area of musculature anteriorly adequate in size for closing the valves. Ventral elongation is also probably related to food sorting, extending one of the main ciliated areas of the mantle cavity (the ventral part of the muscle) to a position adjacent to the anterior inhalant channel. This further increases the area of ciliated surface available to create inhalant currents and sort particles at the mouth of the incurrent channel. The smaller, more rounded posterior adductor muscle is defined by an insertion area midposteriorly astride the main interior fold, which functions as a buttress for the implantation and bracing of the muscle.

Both posterior sulci on the shell exterior produce interior folds. The small submarginal fold forms the base of the ligamental groove. In addition to muscle support, the main posteroventrally directed fold internally marks the line of gill attachment in *Thyasira,* functions as a supporting buttress for the gills, and may actually represent the surface on which the gill muscles insert, although no trace of these has been found. The orientation of the gills in the mantle cavity can be determined from this structure and their approximate size reconstructed using modern representatives. From such data the critical spatial relationships between the gills and incurrent channel, and their orientation relative to the point and direction of current entry into the mantle cavity can be defined on fossils. Similarly, the distribution of the visceral pouch, foot, and other structures generally can be reconstructed in Cretaceous *Thyasira.*

The entire pallial line is well defined and marks the point of insertion of a continuous arc of mantle muscles used in retracting and manipulating the free mantle edge.

Radial grooves and ridges within the pallial line are probably the tracks of these and additional, functionally similar mantle muscles scattered over the valve interior. The lack of siphons in *Thyasira* is reflected in the lack of a pallial sinus.

It is apparent from the preceding discussion that the soft-part morphology can be reconstructed in considerable detail on fossil *Thyasira* by direct comparison with similar living species. The interpretation of form and function is coincidently greatly enlarged in scope, and the interrelationship of characters, that is the recognition of functional character suites, is made possible. Thus, the compression of the anterior adductor muscle is related to formation of an incurrent channel anteriorly and enlargement of the mantle cavity centrally, and therefore to the nature of the foot, the anterior sediment tube, the position of the incurrent channel on the commissure and the orientation of the gills to face it. It further reflects distribution and nature of ciliary sorting mechanisms, and its size, bipartite nature, and implantation are related to the force with which the valves can be closed in burrowing and cleaning of the mantle cavity. Obviously, many aspects of the soft-part morphology and many different inter-related functions can be depicted by thorough examination of a single structure.

Conversely, many structures may be modified by evolution and interact to perform a single function, and this too is better defined on fossils when the details of the soft parts are known through comparative morphology. For example, the creation of a functional inhalant current anteriorly in *Thyasira* is dependent on and evidenced by 1) the vermiform foot and the inhalant sediment tube it creates; 2) the ability of the mantle cavity to receive the large foot; 3) the alteration of the anterior adductor muscle insertion area so that an incurrent channel is formed between the pallial line and the muscle; 4) the ventral elongation and expansion of the muscle and its contained cilia to help create currents down the tube and act as a principal particle sorting mechanism; 5) the ability of the gills to be oriented through evolution so that they face the incoming current at this point; and 6) the degeneration and secondary development of the posterior inhalant aperture with its reduced role in taking small quantities of water into the mantle cavity to aid in particle sorting.

Having defined these basic form and function relationships, the next obvious step in an interpretive study would be to document their adaptive value in the behavior and preferred habitat of the animal—their ecologic inferences—and how closely this might be defined in the fossil. The close morphologic comparison between living and fossil *Thyasira* alone would imply but not demonstrate that their habitats and ecologic implications were very similar.

COMPARATIVE ECOLOGY

The ecology of living *Thyasira* is as unique as its morphology, which is specifically adapted to an infaunal habitat excluding many other burrowing mollusks. The similarity of shell and inferred soft parts of fossil *Thyasira* to living forms suggests a similar ecology. This can be demonstrated by analysis of the physical aspects of the rock, geographic distribution, shell orientation, and faunal associates of Cretaceous *Thyasira* from the Western Interior of North America. Temperature, depth, substrate type, sediment and water chemistry, the amount of available food, and competitor mollusks are the principal environmental controls on the distribution of living forms.

HABITAT OF LIVING THYASIRA

The living posture of *Thyasira* is shown in Figure 91; the animal is capable of burial up to 10 times the length of its shell, although normally it is found shallower. Upon reaching the preferred depth of burrowing the foot projects upward from the mid-anterior margin, forming the agglutinated inhalant tube by cementing together collars of mucous-cemented sediment formed around the tip of the foot. The top of the tube is bent over and probably faces into the current, providing additional force to drive inhalant waters down the tube. The reclining top of the tube further protects against quantities of sediment washing into the aperture.

Living *Thyasira* demonstrate a strong preference for dark clay mud substrates, with or without silt- to cobble-size detritus. They prefer substrates without associated coarse clastic debris (Fig. 94). Some species live in fine- to medium-grained sand; none have been reported from coarser clastics except when mixed with mud or fine sand. Soft clay mud is preferred to compact material. Many living species have the ability to inhabit, and actually prefer, oxygen-poor or hydrogen sulphide-rich substrate in areas of low productivity which ecologically exclude many other infaunal bivalves or both. *Thyasira* flourishes best in areas of low competition and is frequently abundant only with a restricted assemblage of associated mollusks. The greatest diversity of living species of *Thyasira,* in both hemispheres and all major ocean basins, is in the mid-temperate latitudes, between 30° and 55° north or south latitude. Though distributed throughout the world, *Thyasira* is rare in Arctic, Antarctic, and Tropical seas (Fig. 95). Many species, or species groups have their maximum abundance in progressively deeper, cooler waters going from north to south in their geographic range (Fig. 96). Temperature and not depth is therefore the main controlling factor in distribution. The greatest diversity and abundance of living *Thyasira* is in the outer part of the inner sublittoral zone and the outer sublittoral zone of continental shelves (200 to 600 feet), but they are known from shallow waters of the inner shelf out to 7,500 feet or more in depth.

Living *Thyasira* are well adapted to their preferred environment. The foot and streamlined shell insure rapid deep burrowing in the substrate, as previously described. Formation of the anterior inhalant tube is a striking adaptation, permitting *Thyasira* to be a deep-burrower without development of massive siphons. The tube

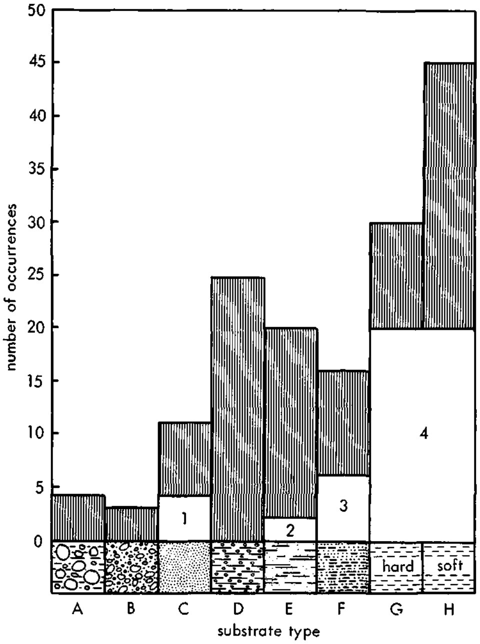


FIG. 94. Distribution of living and Cretaceous species of *Thyasira* (fossil forms from Western Interior only) relative to substrate type (Kauffman, *11*).

The diagram demonstrates a primary preference of *Thyasira* for clayey substrates without associated coarser sediment (especially where soft) and a strong secondary selection of clay containing sand, silt, or pebbles. The genus is poorly represented on substrates consisting of coarse clastics. Agreement between distribution of Cretaceous (white areas numbered 1 to 4) and Recent (vertically ruled areas) *Thyasira* with respect to substrate types is noteworthy, attention being called to the fact that plotted occurrence of Cretaceous forms is superposed on the plot for Recent and the latter not stacked on the former.

A. Coarse cobbles in a pebble-clay-sand matrix.
B. Pebbly sand.
C. Coarse to fine sand, silty sand, and sandy silt.
D. Pebbly clay.
E. Sandy clay.
F. Silty clay.
G. Firm clay, usually dark, without associated coarser clastic material.
H. Soft clay without coarser clastic material.
1. Sandstone, usually with calcareous cement and little admixed clay.
2. Sandy shale, usually cemented secondarily into concretionary masses by calcium carbonate.
3. Silty shale, usually cemented secondarily into concretionary masses by calcium carbonate.
4. Clay shale cemented secondarily into concretionary masses by calcium carbonate.

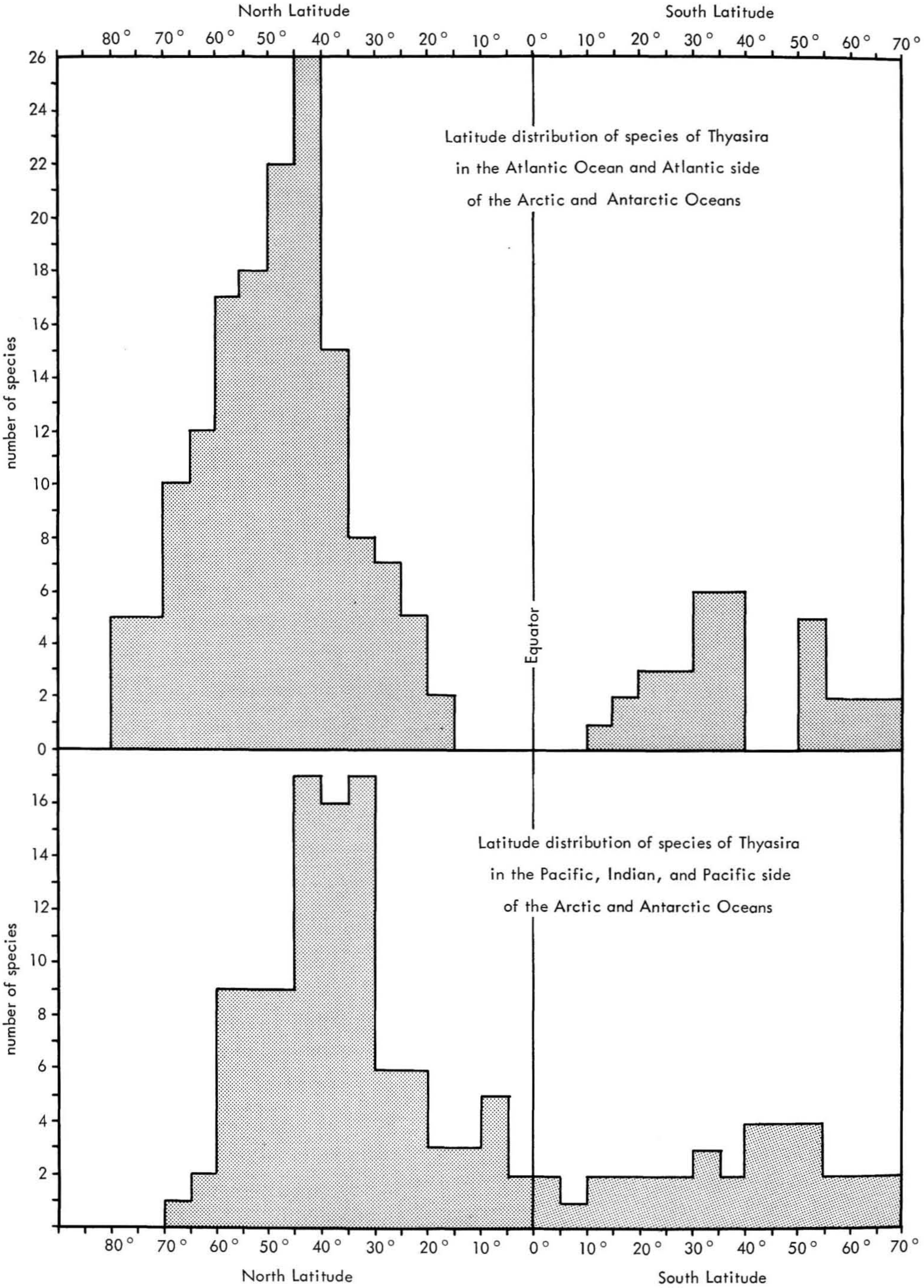


FIG. 95. Species diversity of living *Thyasira* relative to degrees of latitude, generally reflecting water temperatures (Kauffman, *11*).

is a relatively stable, lasting, incurrent structure which does not require continual energy output by the animal to operate, and is easily repaired by the foot. It provides a closed incurrent system between surface waters and the mantle cavity. This isolation of soft parts within the mantle cavity and tube, as well as an apparently broad tolerance of deleterious sediment chemistry, allows the animal to flourish in chemically unfavorable substrates which exclude many infaunal bivalves with exposed soft parts (siphons, foot, etc.). The reduction of palps and sorting mechanisms, and the ability to accept a broad size range of particulate food, adapts *Thyasira* to life in waters of low productivity where it can outcompete other infaunal mollusks.

HABITAT OF CRETACEOUS THYASIRA

Many lines of evidence support the assumption that Cretaceous *Thyasira* had the same habitat requirements, and adaptations to them, as living forms. Being a deep-burrower, the shells remain in close apposition after death as long as they are not exhumed and worked by currents. They gape and separate easily once exposed, being edentulous and having a small thin ligament incapable of keeping them together in the face of currents. It would be assumed that bivalved fossil shells which are not gaping might be contained in living posture. Ninety-five percent of the Cretaceous *Thyasira* studied from the Western Interior are bivalved specimens with valves in normal apposition. When bedding can be defined in rock containing them, the shells are invariably oriented nearly perpendicular to the laminae with the beak dorsal. Single valves, on the other hand, lie in the plane of the bedding, predominantly convex upward. The orientation of fossil bivalve shells parallels the living position of Recent species (Fig. 91). It can be concluded from this that they lived similarly in the substrate. The trace of a sediment tube found with one fossil specimen confirmed this as the living orientation.

An analysis of the rock associated with Cretaceous *Thyasira* from the North American Interior showed a strong dominance of dark clay shale, silty in some cases but without coarse clastics, and a secondary association with fine- to medium-grained sandstone (Fig. 94). Fossils occur mainly in concretions associated with the shales. These are secondary structures formed during early diagenesis and do not represent the original sediment type. Comparison of these data with the substrate distribution of living species (Fig. 94) shows a close correlation. Pyrite scattered through the shale and concretions containing *Thyasira* may reflect reducing conditions in Cretaceous sediments similar to those associated with some living species. The evidence conclusively points to highly similar substrate preferences for fossil and living species.

The geographic distribution and diversity gradients of Cretaceous *Thyasira* from the North American Western Interior, exclusive of two localities in Alberta and one questionable Cretaceous specimen from Greenland, are shown in Figure 97, superimposed on a lithology distribution map of the interior basin during the time span of known Cretaceous species (Campanian). This clearly demonstrates a geographic range in the northern hemisphere during the Cretaceous compatible with living distribution (Fig. 95). More significantly, species and subspecies diversity gradients increase south-

FIG. 95. *(Continued from facing page).*

Maximum diversity of forms is observed between latitudes of 30° and 55° in both hemispheres and both major ocean basins, especially between latitudes 30° and 45°. The smaller numbers of species in southern latitudes than in northern probably reflects difference in collecting and research in the two areas, rather than environmental differences. A southern shift of maximum diversity in the Indo-Pacific area as compared to the Atlantic may be due to the influence of cold marginal currents and upwellings along the steep eastern Pacific margin with very narrow shelf, the broad and shallow Atlantic shelf being affected by the warm Gulf Stream. [Comparison of this diagram with Figure 97 indicates close correlation of species-diversity gradients for Recent and Cretaceous species of *Thyasira* in relation to latitudes.]

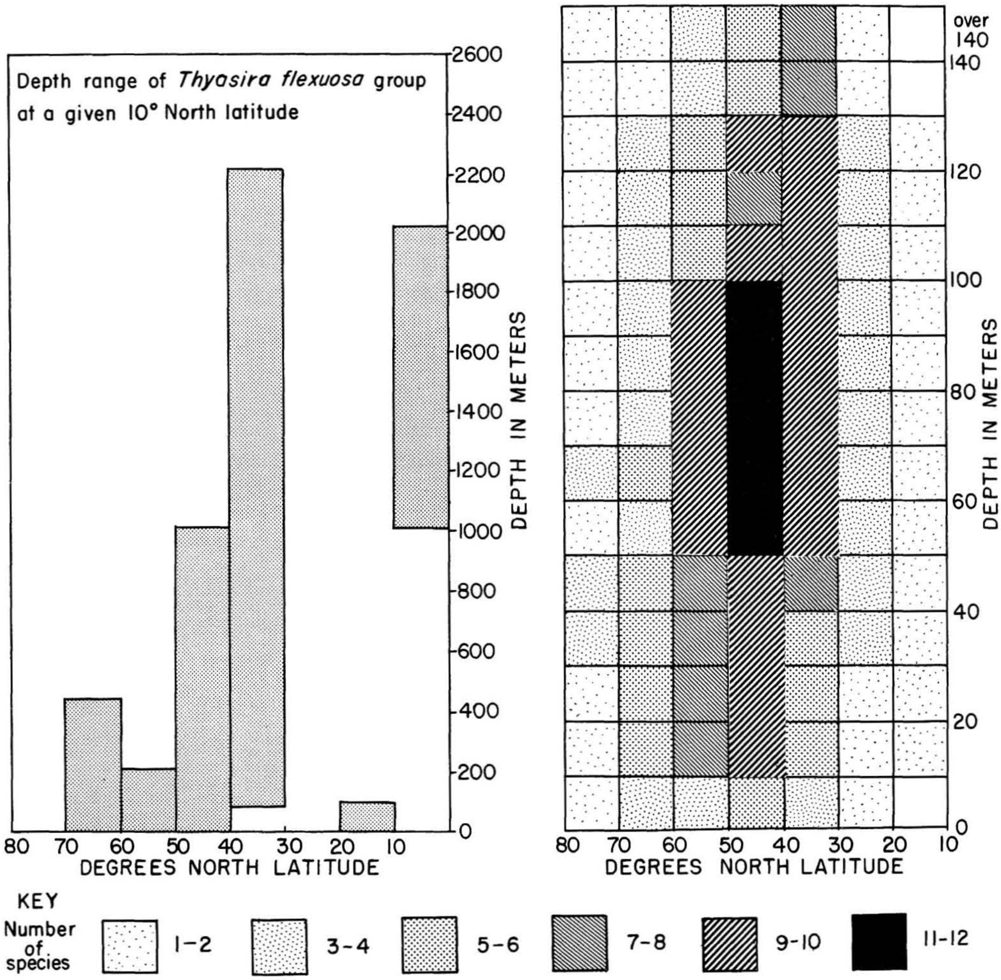


Fig. 96. Depth distribution of living *Thyasira* species in northern latitudes (Kauffman, *11*).

A general shift of bathymetric range from shallow water in most northerly latitudes to progressively deeper waters toward the south indicates temperature control of species distribution. The graph on the left is based entirely on forms belonging to the *Thyasira flexuosa* complex, for which data are sparse and ranges not significant between latitudes 10° and 30°. The graph on the right represents all species for which records of depth distribution are available, pattern density indicating number of species in 10° latitude bands. Although the total bathymetric range of the genus is nearly equivalent in all areas between 10°N and 80°N, maximum diversity in any 10° band shifts toward deeper and cooler waters in the south. Overall maximum species diversity occurs between 40°N and 50°N at depths of 50 to 100 m., defining optimum environmental conditions for *Thyasira*.

ward, reaching a maximum in Wyoming and Colorado during various parts of the Campanian, between 38° and 44° North Latitude. Although this may be in part a product of more concentrated work in these areas, it is not wholly subject to sampling error; scattered large Campanian collections from Canada and Greenland have not yielded abundant *Thyasira* in equivalent facies. The data strongly suggest that similar geographic distributions were shown by Cretaceous and Recent species and that environmental gradients affecting diversity, mainly temperature, were likewise similar during the Campanian in the Western Interior.

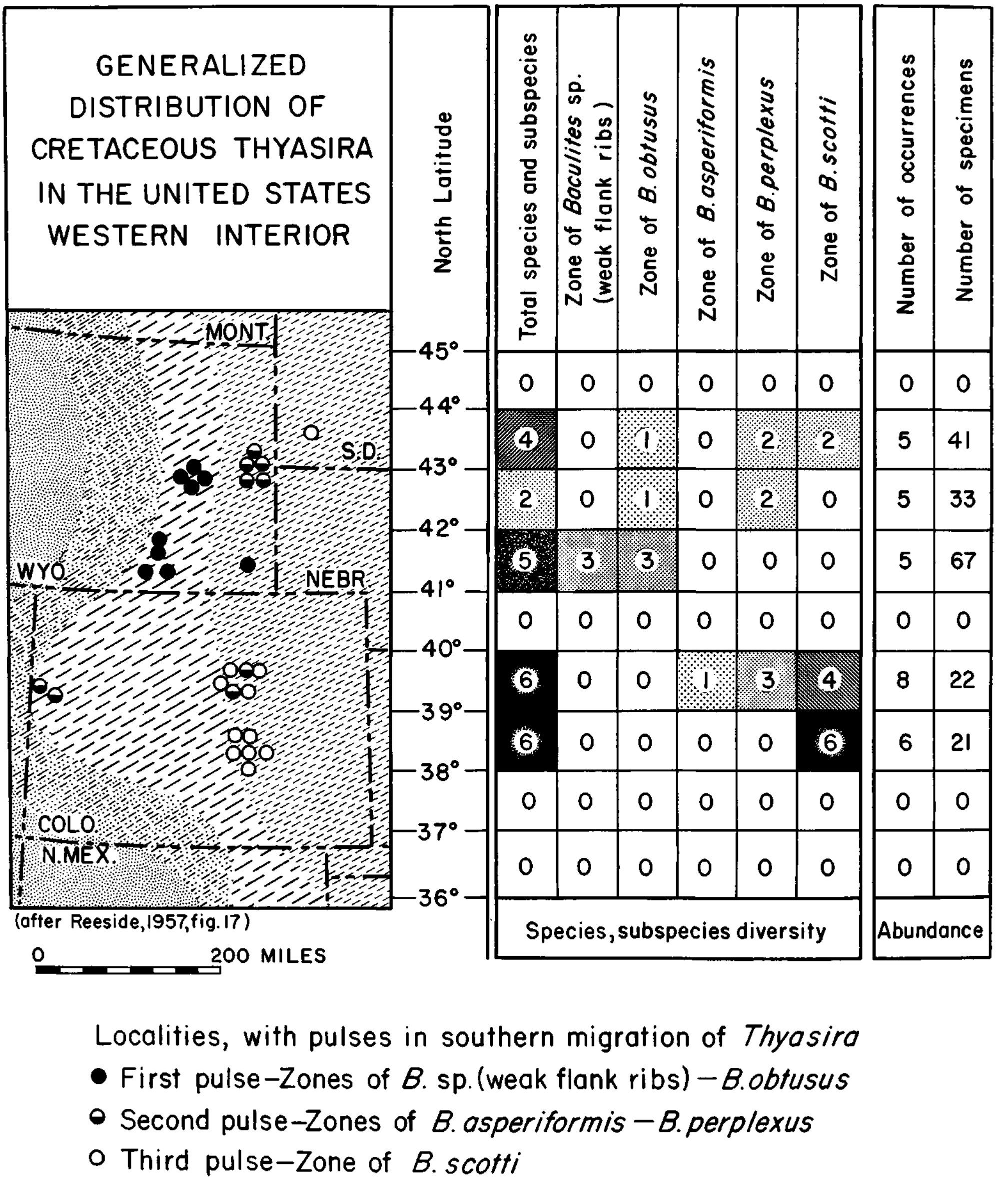
TABLE 1.—*Communities, Biotic Association of Mollusks, and Environmental Characteristics Summarized for Living Thyasira. Families Arranged in Order of Number of Recorded Molluscan Associations.*

ASSEMBLAGE		Arctic Macoma community (Ockelmann, 1958)	Amphiura filiformis community (Petersen, 1913, 1916)	Amphiura chiaji community (Petersen, 1913, 1916)	North Atlantic-Mediterranean assemblages (Allen, 1958)	North Atlantic-Mediterranean assemblages (Allen, 1958)	Astarte crenata community (Ockelmann, 1958)	Arca glacialis-Astarte crenata community (Sparck, 1933)	Boreal Foraminifera community (Thorson, 1957)	Maldane sarsi-Ophiura sarsi community (Thorson, 1957)	Foraminifera community (Ockelmann, 1958)	Amphilepas norvegica-Pecten vitreus community (Petersen, 1913, 1916)	Total for genus	Total for family
		SHALLOWER										DEEPER		
DEPTH RANGE (METERS)		4-50	15-100	15-100	11-140	11-140	25-550	30-550	100+	200-600	200-780	300+		
SUBSTRATE		clay, sandy clay	soft mud	soft clay, silty clay	soft mud	soft mud	soft clay	soft mud	soft mud	soft mud	soft clay	soft mud		
TEMPERATURE		cold	cool	cool	cool	cool	cold	steady negative	cold	cold	cold	cold		
PRODUCTIVITY		low	low-mod.	low	?low	?low	?low	low	low	?low	?low	low		
COMMONLY ASSOCIATED MOLLUSCAN GENERA		11	7	4	3	4	9	4	1	6	5	2	56	
BIVALVIA - TOTAL		11	5	4	3	3	9	4	1	4	5	2	51	
Thyasiridae	Thyasira	X	X	X	X	X	X	X	X	X	X	X	11	12
	Axinopsida	X	--	--	--	--	--	--	--	--	--	--	1	
Nuculidae	Nucula	X	X	X	X	--	X	--	--	X	--	--	6	6
Semelidae	Syndosmya	--	X	X	X	--	--	--	--	X	--	--	4	5
	Theora	--	--	--	--	--	--	--	--	X	--	--	1	
Nuculanidae	Nuculana	X	--	X	--	--	--	--	--	--	--	--	2	4
	Portlandia	--	--	--	--	--	X	--	--	--	X	--	2	
Astartidae	Astarte	X	--	--	--	--	X	X	--	--	X	--	4	4
Pectinidae	Pecten	--	--	--	--	--	--	X	--	--	--	X	2	4
	Propeamussium	X	--	--	--	--	X	--	--	--	--	--	2	
Arcidae	Arca	--	--	--	--	--	X	X	--	--	X	--	3	3
Lucinidae	Lucina	--	--	--	--	X	--	--	--	--	--	--	1	2
	Myrtea	--	--	--	--	X	--	--	--	--	--	--	1	
Cuspidariidae	Cuspidaria	X	--	--	--	--	X	--	--	--	--	--	2	2
Hiatellidae	Hiatella	X	--	--	--	--	X	--	--	--	--	--	2	2
Tellinidae	Macoma	X	--	--	--	--	--	--	--	--	--	--	1	1
Arcticidae	Arctica	--	X	--	--	--	--	--	--	--	--	--	1	1
Cardiidae	Cardium	X	--	--	--	--	--	--	--	--	--	--	1	1
Corbulidae	Corbula	--	X	--	--	--	--	--	--	--	--	--	1	1
Myidae	Mya	X	--	--	--	--	--	--	--	--	--	--	1	1
Limidae	Lima	--	--	--	--	--	--	--	--	--	X	--	1	1
Mytilidae	Dacrydium	--	--	--	--	--	X	--	--	--	--	--	1	1
GASTROPODA - TOTAL		0	2	0	0	0	0	0	0	2	0	0	4	
Turritellidae	Turritella	-	X	--	--	--	--	--	--	--	--	--	1	1
Aporrhaidae	Aporrhais	--	X	--	--	--	--	--	--	--	--	--	1	1
Philinidae	Philine	--	--	--	--	--	--	--	--	X	--	--	1	1
Acteocinidae	Cylichna	--	--	--	--	--	--	--	--	X	--	--	1	1
SCAPHOPODA - TOTAL		0	0	0	0	1	0	0	0	0	0	0	1	
Dentaliidae	Dentalium	--	--	--	--	X	--	--	--	--	--	--	1	1

BIOGEOGRAPHY

Having established a general geographic and environmental correlation in the distribution of Cretaceous and living *Thyasira* (Fig. 95-97), this analysis may be carried one step further with the fossil material. Unlike the living species, the distribution of Cretaceous forms can be analyzed separately in a series of distinct time periods (ammonite zones) and then compared to give a progressive paleogeographic interpretation (Fig. 97).

Thyasira appeared abruptly in the Western Interior Cretaceous and disappeared similarly at the point of its maximum southern migration (Fig. 97). It is limited in the entire Interior Cretaceous to a relatively short sequence of Campanian rocks. Considering the generally widespread warm maritime climate that characterized much of the Cretaceous, and the cool-water temperatures preferred by living *Thyasira*, the most logical interpretation of its brief invasion is that it accompanied a short-term



North Latitude	Species, subspecies diversity						Abundance	
	Total species and subspecies	Zone of *Baculites* sp. (weak flank ribs)	Zone of *B. obtusus*	Zone of *B. asperiformis*	Zone of *B. perplexus*	Zone of *B. scotti*	Number of occurrences	Number of specimens
45°–44°	0	0	0	0	0	0	0	0
44°–43°	4	0	1	0	2	2	5	41
43°–42°	2	0	1	0	2	0	5	33
42°–41°	5	3	3	0	0	0	5	67
41°–40°	0	0	0	0	0	0	0	0
40°–39°	6	0	0	1	3	4	8	22
39°–38°	6	0	0	0	0	6	6	21
38°–37°	0	0	0	0	0	0	0	0
37°–36°	0	0	0	0	0	0	0	0

FIG. 97. Distribution, diversity, and abundance of Western Interior species of *Thyasira* in relation to Late Cretaceous migration pulses and sediment distribution (Kauffman, *11*).

The map (based on REESIDE, 1957, fig. 17) indicates in highly generalized manner the lithologic nature of substrates in early Campanian to initial middle Campanian time (Zone of *Baculites scotti*), patterns representing (in west-to-east sequence) sand, sandy mud, fine gray mud, and fine black mud. A strong preference of Cretaceous *Thyasira* for fine muds without associated coarser clastics is noteworthy, just as in living species (Fig. 94).

The chart shows a shift in southernmost occurrences of *Thyasira* in progressively younger Campanian ammonite-based zones, implying migratory pulses which are keyed to localities marked on the map. Maximum species diversity is found at the southern end of the genus range during each pulse. Close correlation exists between overall latitude distribution and maximum diversity gradients in Cretaceous and Recent species of *Thyasira* (Fig. 95). Constriction of the seaway indicated near the

TABLE 2.—*Abundance of Thyasira and Faunal Associates, Structure of Molluscan Assemblages, and Dominant Lithology at Localities Yielding Thyasira from Upper Cretaceous of Western Interior United States.*

USGS LOCALITIES	D5	D65	D255	D709	D714	D1012	D1215	D1216	D1410	D1564	D1864	D1865	D1866	D2909	D2910	D3256	D3260	D3332	D3933	D3945	D4162	D4747	3763	3779	10459	10666	22838	22840
LITHOLOGY	sh tb	sh sc	sh ic	sh lc	sh lc	sh tb	sh tb	sh ic	sh lc	sh tb	sh ic	sh ic	sh ic	sh ic	sh tb	sh lc	sh ic	sh lc	sh tb	sh lc	sh ic	sh sc	ss	ss s	sh lc	sh sc	sh lc	sh ic
ASSEMBLAGE	H	H	H	D	D	D	D?	D	D	?	H	H	H	?	?	?	?	?	?	D	?	?	?	?	?	?	D	D?
BIVALVIA	1	3	6	2	3	3	4	4	4	3	2	1	1	2	2	3	1	1	4	2	2	3	1	1	2	2	5	4
Thyasira	R	R	C	C	R	R	R	R	C	R	R	C	C	R	R	C	R	R	R	R	C	R	R	C	C	R	R	R
*Inoceramus	-	R	C	-	R	-	R	C	C	-	R	-	-	R	R	R	-	-	C	-	-	R	-	-	-	C	R	R
Lucina	-	-	R	R	R	C	C	C	C	R	-	-	-	-	-	C	-	-	C	R	C	-	-	-	-	-	R	C
*Cymbophora	-	-	R	-	-	R	-	-	R	-	-	-	-	-	-	-	-	-	-	-	-	R	-	-	-	-	R	-
Pteria	-	-	R	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	R	-	-	-	-	-	R	-	-	R
"Ostrea"	-	-	R	-	-	-	R	R	-	R	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Nucula	-	R	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	R	-
GASTROPODA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0
Aporrhais?	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	R	-	-	-
Lunatia?	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	R	-	-	-
CEPHALOPODA	2	2	3	3	3	4	3	2	5	1	2	2	2	1	1	1	1	1	1	2	1	1	1	1	2	1	3	2
*Baculites	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	R	C	C	R	C	C	C	C	C
*Hoploscaphites	R	R	R	-	-	-	-	-	-	-	R	R	R	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
*Didymoceras	-	-	-	C	C	C	-	C	C	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	R	-
*Oxybeloceras	-	-	-	R	R	C	-	-	R	-	-	-	-	-	-	-	-	-	-	R	-	-	-	-	-	-	R	-
*Anapachydiscus	-	-	-	-	-	R	C	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	R
*Placenticeras	-	-	R	-	-	-	-	-	R	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
*Menuites	-	-	-	-	-	-	R	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
*Scaphites	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	R	-	-	-
*Eutrephoceras	-	-	-	-	-	-	-	-	R	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
SCAPHOPODA	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Dentalium	-	-	R	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	R	-	-	-	-	-	-
MOLLUSKS - TOTAL	3	5	10	5	6	7	7	6	9	4	4	3	3	3	3	4	2	2	5	4	3	5	2	2	6	3	8	6

*Extinct genus

[EXPLANATION. *Lithology: ic,* ironstone concretions (siderite-limonite); *lc,* limestone concretions, usually argillaceous; *s,* shaly; *sc,* siderite concretions; *sh,* shale, usually dark, noncalcareous, thin-bedded; *ss,* sandstone, usually fine- to medium-grained, argillaceous; *T,* Tepee Butte limestone masses, irregular light-colored argillaceous limestone bodies.

Fossil assemblages: H, Hoploscaphites assemblage; *D, Didymoceras-Oxybeloceras* assemblage; *?* indicates not enough data available to define principal assemblages.

Abundance: R, rare, five or fewer specimens; *C,* common, more than five specimens per collection.

flooding of cool Arctic waters into the central interior or the basin deepened abnormally due to tectonic phenomena for a short period of time so that bottom temperatures came within the range supporting abundant *Thyasira* today, or both influences operated.

As shown in Figure 97, Cretaceous *Thyasira* show three migratory pulses during the Cretaceous. The initial pulse carried them to southern Wyoming, a younger one to central Colorado, and a terminal one to south-central Colorado. In each case they were primarily distributed in clay-mud facies (Fig. 97), and maximum diversity was at the southern end of their range. These pulses are thought to represent steps in the flooding of the interior seaway by Arctic waters; a rate of flooding and faunal migration can thus be calculated since the

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FIG. 97. *(Continued from facing page).*

southern margin of the map may account for elimination of the southern tail of the distribution curve in fossil species that normally occurs in Recent species distribution (Fig. 95).

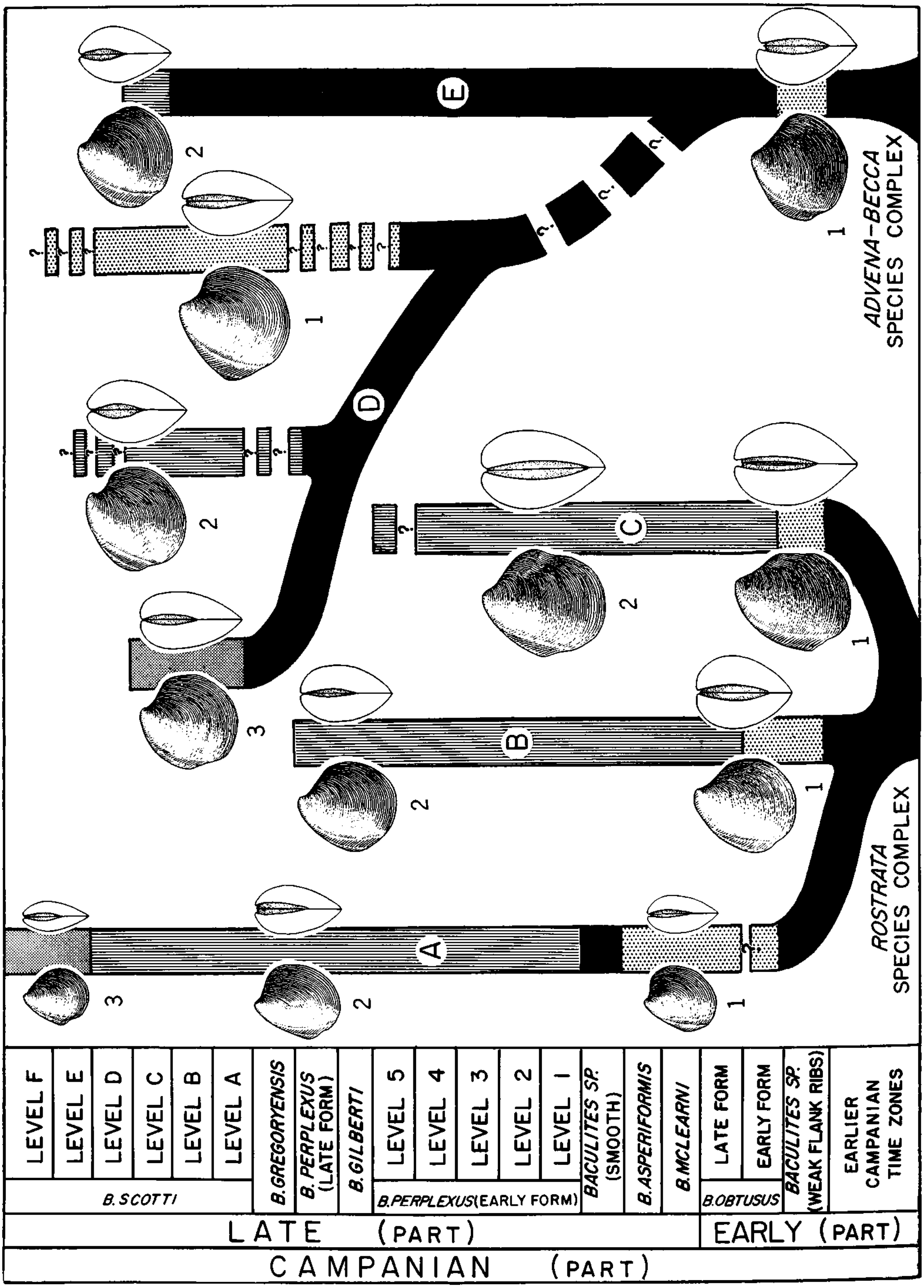

Fig. 98. Phylogeny and evolution of Cretaceous *Thyasira* in Western Interior of North America (Kauffman, *11*).

duration of *Thyasira* in the Western Interior is known. The strange diversity gradient, strongly skewed with the southern tail of the distribution missing, was probably produced by a relatively abrupt transition zone between Arctic and warm southern waters, or by a marked constriction and shoaling of the seaway in southern Colorado, or both. Both factors would have limited southern extension of Thyasiridae because they did not produce environmental situations preferred by *Thyasira* then and now.

COMMUNITY RELATIONSHIPS

Extensive survey of the Recent molluscan literature reveals that living *Thyasira* are abundant only in association with restricted molluscan assemblages of relatively uniform composition. Table I presents a summary of association data for published communities of marine animals containing abundant *Thyasira*. The most diverse associated molluscan assemblage contains 10 genera and 14 species, including *Thyasira* and excluding rare taxa (Arctic *Macoma* community). On the average, only four to five molluscan genera are associated. In the boreal foraminiferal community of OCKELMANN (1958) *Thyasira* is the only abundant mollusk (Table 1). The restricted nature of the assemblages reflects the cool-water environment, low productivity, and chemically unsuitable substrate to which *Thyasira* is so well adapted. Infaunal bivalves strongly dominate the assemblages; gastropods and epifaunal organisms are rare. The most consistent associates of *Thyasira* are other Lucinacea (*Axinopsida, Lucina, Myrtea*—all similarly adapted, like *Thyasira*, to the environment), Nuculanidae (*Nuculana, Portlandia*), Nuculidae (*Nucula*), Semelidae (*Abra* or *Syndosmya, Theora*), Astartidae (*Astarte*), and Pectinidae (*Pecten, Amusium*, or *Propeamussium*). Except for the free-living, swimming pectinids, these are all infaunal filter- and detritus-feeders which show a strong preference for fine-grained substrate. This basic assemblage is not uncommonly supplemented by *Cuspidaria* and *Arca*. *Turritella* and *Aporrhais* are the most abundant associated gastropods, but still comparatively rare.

Comparison of molluscan assemblages associated with Cretaceous *Thyasira* to those characterizing Recent occurrences reveals an interesting correlation, although it is complicated by the abundance of extinct taxa in the Cretaceous which have no living counterparts (e.g., ammonites, Inoceramidae). Cretaceous molluscan associates are listed in Table 2. Eighteen genera of Cretaceous mollusks, ten of them extinct, occur with *Thyasira* in deposits of the Western Interior. A maximum of ten genera and a minimum of two were found in any

FIG. 98. *(Continued from facing page).*

[Heavy black lines show hypothetical phylogenetic relationships (doubtful where broken, indicating lack of specimens representing lineage in some time intervals). Coarse dotted pattern marks range of oldest subspecies in each lineage. Vertical ruling designates youngest subspecies in each lineage. Fine dotted pattern represents distinct species phylogenetically arranged within lineages from which they were derived. Interrupted and queried portions of ranges denote possible extension of established ranges based on vague stratigraphic data.]

A. *Thyasira quadrula* lineage, characterized by reduction of the anterodorsal flank, increased inclination of the anterodorsal slope, decrease in convexity and span of apical angle, posterior migration and straightening of primary sulcus, and dorsal migration of primary sulcus notch. [*1, T. quadrula quadrula; 2, T. quadrula arrecta; 3, T. triangulata.*]

B. *Thyasira rostrata* lineage, characterized by decrease in convexity and in relative size of escutcheon, decrease in relative height and projection of beaks, increase in apical angle with expansion of anterodorsal flank and decrease of anterodorsal slope. [*1, T. rostrata rostrata; 2, T. rostrata cracens.*]

C. *Thyasira beauchampi* lineage, characterized by decrease in convexity, expansion of anterodorsal auricle and anterior sulcus, decrease in curvature and prominence of beak and umbo, and straightening of primary sulcus with dorsal migration of notch. [*1, T. beauchampi beauchampi; 2, T. beauchampi rex.*]

D. *Thyasira becca* lineage, characterized by decrease in relative height followed by increase, increase and subsequent decrease in projection of anterodorsal flank, convexity, and beak inclination, posterior migration of primary sulcus, and decrease in projection and angularity of mid-posterior marginal beak in slope. [*1, T. becca becca; 2, T. becca cobbapi; 3, T. cantha.*]

E. *Thyasira advena* lineage, characterized by decrease in convexity, slight increase in height relative to length, posterior migration of primary sulcus, decrease in inclination of beaks, increase in relative projection of beaks and depth of concave notch anterior to them. [*1, T. advena advena; 2, T. advena browni.*]

single occurrence (including *Thyasira*), yielding an average of 4.6 genera (and species) per occurrence. This is comparable with the rstricted nature of modern *Thyasira*-rich assemblages. The diversity is even less if the extinct ammonites, the ubiquitous Mesozoic epifaunal *Inoceramus,* and the mactroid *Cymbophora* (Cretaceous only) are omitted, because they have not been replaced in their niches by living counterparts. Although infaunal bivalves also dominate Cretaceous assemblages with *Thyasira,* epifaunal organisms are more abundant owing to the special adaptations of *Inoceramus* to living on soft mud bottoms, and the surface area for attachment of other epifaunal bivalves *(Pteria, Ostrea)* provided by the large upper valves of flat-lying inoceramids.

Exclusive of extinct mollusks, Cretaceous forms associated with abundant *Thyasira* are taxonomic parallels of living associates. Lucinidae *(Lucina), Nucula, Aporrhais,* and *Dentalium* are among these. The data suggest similar community relationships and environmental control on molluscan diversity and taxonomic representation in *Thyasira*-rich assemblages of the Cretaceous and Recent. This is further evidence for parallel habitat preference and ecologic adaptation in fossil and Recent *Thyasira.* The data further suggest the presence of two basic communities containing *Thyasira* during the Cretaceous, represented by distinct assemblages of mollusks, in particular ammonites. Contrary to popular opinion, the ammonites were probably strongly affected by bottom environments in their distribution; many may have been basically vagrant benthonic organisms. It is considered necessary to include them in the definition of bottom communities.

The first assemblage is characterized by *Hoploscaphites* and *Baculites* without additional ammonites. *Inoceramus* and *Thyasira* are the only commonly associated bivalves. *Lucina* is rare. *Pteria,* scaphopods, and gastropods are known sparingly but exclusively in this assemblage. The second assemblage is characterized by a diversity of ammonites and identified by *Didymoceras* and *Oxybeloceras* without *Hoploscaphites,* gastropods, scaphopods, or *Pteria. Inoceramus, Lucina,* and *Thyasira* are abundant and locally the other associated mollusks are diverse, including *Ostrea, Nucula, Cymbophora,* and *?Lunatia.* Due to the greater diversity and numbers of specimens, as well as the occurrence of *Ostrea* and the mactrid *Cymbophora* in the second grouping, the assemblages are thought to reflect depth zones with the *Didymoceras-Oxybeloceras* assemblage the shallowest. Both are thought to be middle shelf assemblages indicating 200 to 400 feet in depth, using the criteria of KAUFFMAN (1967,*10*).

PHYLOGENY, EVOLUTION, AND INTERPRETATION

The described Cretaceous *Thyasira* from the Western Interior fall into five distinct lineages, each with two or more subspecies and species in evolutionary succession. These can be grouped into two phylogenetic complexes on the basis of gross morphology (Fig. 98). The *Thyasira rostrata* complex includes erect shells elongated along the burrowing axis (height axis); the *T. advena-T. becca* complex includes rounded obese *Thyasira.* Each complex undergoes a principal Campanian radiation (Fig. 98); the *rostrata* complex in the early Campanian, and the *advena-becca* complex in the late Campanian. The pattern of radiation is dissimilar between them in that the late Campanian phase was more abrupt; it was also correlated with the extinction of two major lineages belonging to the *rostrata* complex (Fig. 98), suggesting competition and replacement of the *rostrata* complex by the *advena-becca* complex in the same habitat (as evidenced by similar lithologies containing them).

The members of each lineage are characterized by particular morphologic features, some of which begin to merge toward the point in time of initial radiation of the complex. These characters are shown in Figure 98. The *T. quadrula* species group has reduced beaks and a straight posterior margin (Fig. 98, column A); the *T. rostrata* lineage has inflated shells, dorsally projecting beaks, and rounded posterior margins

(Fig. 98, column B). The *T. beauchampi* lineage includes very large forms with an anterior sulcus (Fig. 98, column C); the *T. becca* lineage has rounded, inflated shells with strongly prosogyrous beaks and an angulate, projecting anterior margin (Fig. 98, column D); and the *T. advena* lineage has inflated rounded shells with a sloping anterior margin and reduced suberect beaks (Fig. 98, column E).

Species co-occurrence is not uncommon among Cretaceous *Thyasira.* In most cases the associated species belong to quite dissimilar lineages; a member of the *rostrata* species complex is found with a member of the *advena-becca* complex in the same concretion, both bivalved and in living position. This situation suggests that the co-occurring species occupied distinct microniches within the primary dark mud habitat. Shell morphology strongly suggests that they were depth zoned. By analogy to living thyasirids and other infaunal Bivalvia, the rounded, inflated shells of the *advena-becca* complex probably belonged to slower and shallower burrowers than the narrower ovate shells of the *rostrata* complex, elongated along the burrowing axis. Where closely related species occur together in the same sediment, one is always very rare and obviously not competing well with its similarly adapted relative in the same niche.

Evolutionary trends in Cretaceous *Thyasira* from the Western Interior are similar in four of the five lineages; the lineage of *T. beauchampi* shows opposite trends toward widening of the valves and shallow burrowing adaptations. In the lineages of *T. quadrula, T. rostrata,* and less strikingly *T. advena* and *T. becca* (Fig. 98), the principal evolutionary changes through the Campanian are: 1) vertical elongation of the shell along the burrowing axis and consequent reduction of length; 2) decrease in convexity of the valves; 3) decrease on some species of the projection of anterior and posterior flanks and reduction of auricles, where present; 4) ventral and slightly inward shift of the anterior adductor insertion area correlative with reduction of the projecting anterior flank; this brings about ventral shift in the incurrent channel, the point of current entry into the mantle cavity, and the point at which the inhalant tube meets the shell (Fig. 99); and 5) posterior shift and straightening of the primary sulcus with reduction in size of the posterior fold

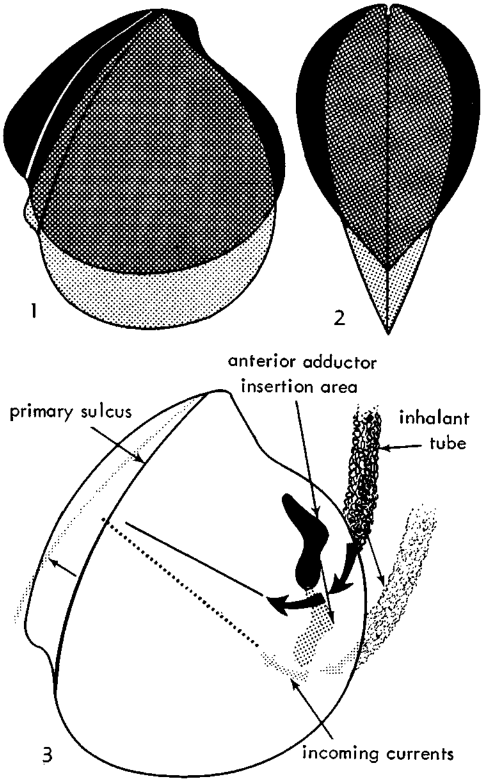

Fig. 99. Main evolutionary trends in Cretaceous *Thyasira* (Kauffman, n).

1. Diagrammatic right lateral view of shell showing decrease in length and flank projection, accompanied by increase in height (burrowing axis) during evolution of older species (black) to younger ones (dotted pattern).
2. Diagrammatic anterior view of shell indicating decrease in convexity during evolution of older species (black) to younger ones (dotted pattern).
3. Diagrammatic view of left valve interior demonstrating ventral migration of anterior adductor insertion area, incurrent channel, connection of inhalant tube, and direction at which incoming currents enter mantle cavity, as well as posterior migration and straightening of primary sulcus and internal fold formed by it. [Solid line connecting incurrent channel with sulcus trace marks approximate direction of water approach to front of gills in early forms. Dotted line indicates same in more advanced forms. Dark areas represent original position and light areas advanced position of features indicated (anterior adductor insertion area, inhalant tube, primary sulcus).]

and flank. These are particularly well shown in the *Thyasira quadrula* lineage (Fig. 98, column A).

The interpretation of these trends—the reason for selection of the traits during evolution of the lineages—is perhaps the primary contribution of multifaceted interpretive study as it utilizes all other data. Study of the comparative ecology between living and fossil Thyasiridae, and the nature of the sediment containing Cretaceous species strongly suggests that all lineages were basically adapted for the same habitat and that all members of each lineage occupied this preferred habitat during the Campanian. The evolutionary trends cannot be interpreted in terms of a changing environment, therefore, but rather must be attributed to improved adaptation within the same general habitat. This interpretation is limited only by the gross environmental data available from the study of the containing rock. Based on general analysis of form and function in other Lucinacea (Fig. 90), and in unrelated homeomorphic infaunal bivalves, the evolutionary trends of Cretaceous *Thyasira* can be interpreted as follows:

Vertical elongation along the burrowing axis and complimentary reduction in shell length, projection of auricles or lateral flanks, and shell convexity better adapt the shell to rapid and deep burrowing by streamlining its shape, reducing frictional drag, and increasing its penetration potential when pulled down on the anchored foot. This obviously has high survival value as the thin, weakly hinged shell is highly susceptible to predation or current damage when exposed on the water-substrate interface. This change in shell form brings about the observed downward and inward shift of the anterior adductor insertion area, and the incurrent channel beneath it, because of shortening and rounding of the anterior margin in more advanced species. It also shifts the direction in which incurrent waters enter the mantle cavity from mid-anterior to ventroanterior.

Recalling the critical spatial relationships which must be maintained in the thyasirid shell, 1) the enlarged mantle cavity to receive the coiled foot, 2) the distance between the incurrent waters as they enter the mantle cavity and the gills, and 3) the orientation of the gills relative to the direction in which incurrent waters flood the mantle cavity, it is apparent that all of these would be upset by the change in shell form and shift of the anterior adductor muscle, anterior incurrent channel, and direction of incurrent flow were there not a compensating shift in the soft parts affected.

Posterior migration of the primary sulcus, which internally marks the attachment base of the gills, reflects a posterior shift of the gills internally. This partially or wholly compensates for the loss of space in the mantle cavity produced by lateral compression of the shell and inward shift of the anterior margin and adductor insertion area. Sufficient room for the coiled foot is thus retained. Straightening of the primary sulcus with its posterior migration decreases its slope relative to the horizontal hinge axis. The gills, which buttress against this structure, are thus reoriented with their leading edge facing ventroanteriorly rather than mid-anteriorly. This brings them into proper orientation perpendicular to the new direction of incurrent flow in the younger, more streamlined species. Posterior shift of the gills accompanies inward shift of the anterior incurrent channel through reduction of shell length and anterior flank projection, insuring that the critical spacing between gills and incurrent channel is maintained (Fig. 99).

In summary, adaptation of the shell for more rapid burrowing in *Thyasira* created a spatial imbalance of the feeding and respiration systems internally, in turn creating strong selection pressures for compensatory migration and realignment of the gills. It is postulated that these changes were effected in unison, not singly in any particular order, as a series of interacting selective pressures. The complex structural changes brought about by better adaptation of the shell for burrowing points out that form and function is not a simple study of isolated structures and their operation, but must be considered in terms of interacting morphologic suites performing numerous interrelated functions.

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CLASSIFICATION OF BIVALVIA

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CONTENTS

INTRODUCTION

The Bivalvia are wholly aquatic benthos which have undergone secondary degeneration from the condition of the ancestral mollusk, possibly, but not certainly, a monoplacophoran-like animal (Yonge, 1953, 1960; Vokes, 1954; Horný, 1960; McAlester, 1966; and others). The changes have involved loss of the head and adoption of

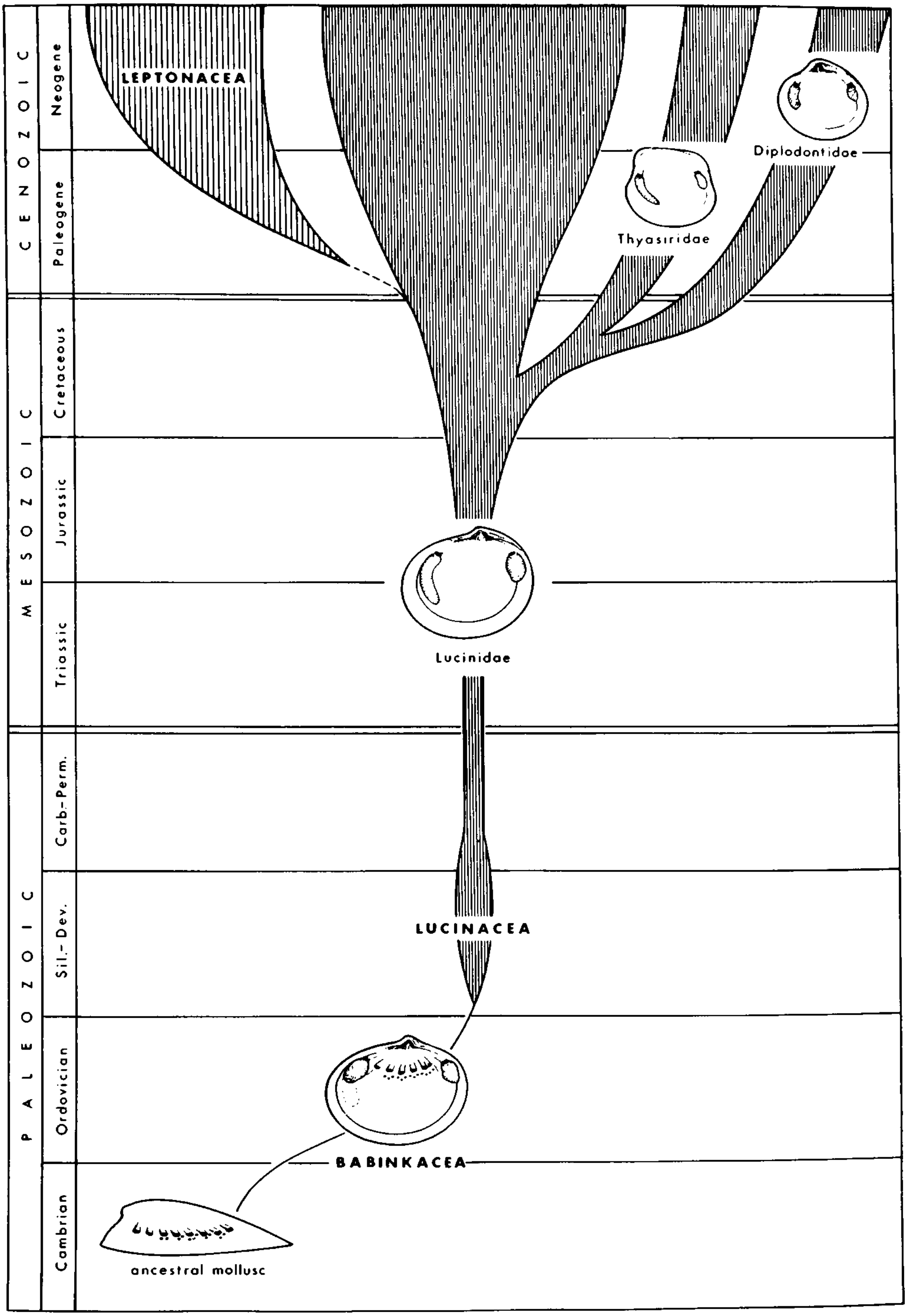

FIG. 100. Hypothetical derivation of certain Bivalvia from monoplacophoran-like ancestor (McAlester, 1966).

a passive mode of life in which feeding is accomplished by filtering of water or sifting of sediment for particulate organic matter (Fig. 100). These adaptations have limited the evolutionary potential severely, and most structural changes have followed variations of rather simple themes. The most evident adaptations have affected articulation of the valves, modes of defense, anchorage, and burrowing, and efficiency in feeding. Habitat preferences are correlated with the availability of food and with chemistry, temperature, agitation and depth of water, and with firmness of the bottom on or within which they live. The morphological clues to genetic affinity are few. Consequently, parallel trends are rife, and it is difficult to arrange the class taxonomically in a consistent and logical way that takes known history into account.

The problem of classifying the bivalves is further complicated by the fact that critical characters sought in fossil representatives commonly are concealed by rock matrix or are obliterated by the crystallization or dissolution of the unstable skeletal aragonite. The problem of studying morphological details is especially difficult among the older fossils which should provide evidence of the relative times of phyletic divergence. Among these, morphological details generally are inadequately known, partly owing to limitations of the materials but even more as the result of insufficient work on the group and lack of application of adequate skills and preparation techniques. In all of the history of work on older bivalves, very few examples of outstanding morphological work on these fossils can be cited. Sound morphological studies, although minimized today, are more than ever needed for understanding ecology of the group and for development of trustworthy classification and phylogenetic interpretation of the bivalves.

The present outline of classification undertakes to synthesize and integrate best features of the most widely used systems. It is neither basically new nor based on adequate morphologic and phylogenetic information. Its superiority over other systems may be claimed on the grounds of simplicity of the adopted nomenclature and the weighing of both anatomical and paleontological data.

It must be stressed that the result is a compromise. No classification of Bivalvia in the present state of knowledge will be wholly acceptable to all students of the group. It is hoped, however, that the arrangement will better serve needs of both neontologists and paleontologists than others that have been suggested.

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DEVELOPMENT OF CLASSIFICATION

FAMILY-GROUP CATEGORIES

Many of the major fossil and living groups of bivalves, now generally regarded as superfamilies, are highly distinctive and accordingly they had been discriminated by the middle of the nineteenth century. Several were known even by vernacular names long before the time of Linné. It is evident that many of the family-group taxa have been astonishingly conservative, with long and continuous records that extend far back into the Paleozoic where well-preserved specimens may be relatively scarce and origins of higher categories are generally conjectural. Where the fossil record is good, abundant evidence shows that general shell characters in many groups have been quite stable through hundreds of millions of years. This fact is contrary to a view sometimes voiced that the soft anatomy is somehow more revealing of affinities than shell morphology and that shell characters alone are inadequate and unreliable as indicators of phylogeny. This view reflects lack of understanding of geologic time and the richness of the fossil record.

SUPRAFAMILIAL CATEGORIES

The building blocks of bivalve taxonomy have been the family groups many of which have not been very controversial. Real difficulties arise, however, when attempts are made to group well-defined superfamilies into orders and subclasses. Excellent reviews of the history of efforts to devise a stable system of bivalve higher categories have been published by HAAS (1929-56), IREDALE (1939), PURCHON (1958), COX (1960), and MORTON (1963), and are not taken up in detail here. It is sufficient to say that, lacking graded morphological series of living or fossil forms suitable for joining many of the family-group taxa, systematists have sought more or less arbitrarily to base ordinal groupings on single-organ systems. But most such traits are now known to be individually plastic and are demonstrably variable within families or even within genera. The experience of more than two centuries of work on the subject encourages the view that a simple keylike classification of the bivalves cannot adequately reflect their relationships at the level of orders and subclasses. Consequently, many of the diagnoses given in this volume are ambiguous and even repetitive.

EARLY SEARCH FOR TAXOBASES

The degree of fusion of the mantle margins, together with the character and number of the resulting apertures or siphons, was regarded by LINNÉ (1758) as a primary basis for the discrimination of orders. In this belief, he was followed for a time by many students: for example, CUVIER (1797, 1800), LAMARCK (1801), DUMÉRIL (1806), FLEMING (1822-28), LATREILLE (1825), D'ORBIGNY (1843-47), WOODWARD (1851-56), ADAMS & ADAMS (1854-58), and ZITTEL (1881-85).

In addition to the presence or absence of well-developed siphons, LAMARCK (1812) stressed the progressive reduction and loss of the anterior adductor muscle in some groups as important and useful, as did PHILIPPI (1853) and ZITTEL (1881-85). GRAY (1821) and LANKESTER (1883) thought that the form and function of the foot furnished a reliable basis for recognition of suprafamilial groups. LINNÉ (1758) and D'ORBIGNY (1843-47) also used the equality or inequality of the valves as a convenient taxonomic criterion. All of these views have influenced the classification herein adopted.

The objective of efforts to classify the Bivalvia was utilitarian, of course, with little thought of phyletic history of the assemblage. The characters enumerated still figure prominently in all classifications but are now generally regarded as supplementary features that may appear independently in unrelated groups. Loss of the anterior muscle (e.g., in Pectinidae and Tridacnidae), or cementation by one valve and acquisition of an oyster-like growth form (e.g., *Ostrea, Hinnites, Mulleria*), are illustrations of parallel adaptations in groups that are otherwise unlike.

CONTRIBUTIONS FROM PALEONTOLOGISTS

STOLICZKA (1870-71), a paleontologist who was impressed by the general stability and homogeneity of form and structure of family groupings of bivalves throughout their history, proposed to base higher categories on overall resemblance to chosen type genus, and on this basis he established nine orders, the names of which were based on the stems of generic names. This taxonomic device had already been experimented with by RAFINESQUE (1815), FÉRUSSAC (1822), and ADAMS & ADAMS (1854-58). Experience showed that it had a sound basis, and the orders of STOLICZKA, with modifications and additions, have become the superfamilies of later workers.

Over the years, the list of generally recognized major groups has grown from the nine orders in STOLICZKA's classification to the 47 superfamilies in the present treatment, with others sure to follow as the study of Paleozoic bivalves progresses. Throughout the nineteenth century the unwieldy number of family-group taxa prompted many efforts to regroup the class into a few convenient morphological divisions.

The paleontologists NEUMAYR (1884, 1891), STEINMANN (1888), DALL (1889, 1895, 1896-1900, 1913), and DOUVILLÉ (1896, 1907, 1912, 1913) introduced the historical-phylogenetic point of view into efforts to classify the bivalves. They demonstrated that general shell form and details of the articulating apparatus, that is, the hinge teeth plus the ligament, were commonly quite stable through time, but they also pointed out many exceptions, as for example, the highly variable hinges of the dysodonts and fresh-water mussels (Unionacea). The French paleontologist BERNARD (1895, 1896,*4*, 1896,*5*, 1897, 1898) shared these views and made elaborate studies of ontogenies of the hinge in several living bivalves in which he undertook to trace dental homologies among separate major groups. Unfortunately, his work was not well documented and was halted by his early death. This promising field of investigation has been almost totally neglected subsequently, save for a few outstanding exceptions (e.g., DAVIES, 1935, CASEY, 1952) and uncertainties exist about the applicability of some of BERNARD's conclusions.

DALL and DOUVILLÉ both advocated that close attention should be paid to the entire organism, and they believed that observations on the comparative anatomy of living species could be harmonized with paleontological evidence based on geological chronology and shell characters. To them it was obvious that special consideration must be given to characters that are preserved in the fossil record if the historical facts of bivalve evolution are to be given due recognition in classification.

These authors also made some limited use of the poorly understood differences in shell fabric, or microstructure, later summarized by BØGGILD (1930) and OBERLING (1955, 1964). Much work remains to be done in this field to sort out the relative influences of phylogeny and ecology in determining the shell microstructure of each group. It seems clear that shell fabric yields important contributory evidence (*e.g.*, unionaceans have prismatonacreous shells; oysters possess prismatofoliaceous calcite shells), but the full phylogenetic implications have yet to be worked out. Unfortunately, original shell microstructures are rarely preserved in bivalves older than Pennsylvanian, and commonly they are destroyed even in geologically quite young fossils. Furthermore, it is now well established that in some groups environmental modifications of shell microstructure have been introduced, whereas in others this microstructure apparently is quite stable. Most of the outlines are yet to be determined.

DOUVILLÉ's great contribution was his emphasis on broad adaptive levels in reaching phylogenetic conclusions about the bivalves and he tried to utilize dental homologies indicated by BERNARD. In this DOUVILLÉ recognized the hazard of confusing examples of similar adaptation with close genetic affinity, and he undertook to make use of all lines of evidence. He did not complete a formal taxonomic arrangement of the bivalves, but his work was incorporated in a classification of Tertiary bivalves by DAVIES (1935) that stands as a monument to DOUVILLÉ. Unfortunately, DAVIES' work did not incorporate many pre-Tertiary forms, nor will his classification accommodate them.

DOUVILLÉ distributed all bivalves among three branches according to three main modes of life. These were 1) "normal" or vagrant epifaunal bivalves, 2) fixed or "sedentary' epifaunal forms, either suspended by a byssus or cemented by one valve for part of the life span, and 3) burrowing, or boring, infaunal bivalves (desmodonts of NEUMAYR). It was recognized by DOUVILLÉ that many members of these branches had undergone secondary radiation leading to structural similarities among unrelated stocks, the details of which he tried to understand by combining studies of comparative anatomy and paleontology (DAVIES, 1933). Paleontologic and morphologic evidence supports the probable unity of most of his "sedentary" branch, but his "normal" and "burrowing" branches are not very homogeneous either historically or anatomically (Fig. 100). Little is known about the adaptive significance of particular structural types of ornamentation, dentition, ligament, and shell microstructure. And many challenging fundamental prob-

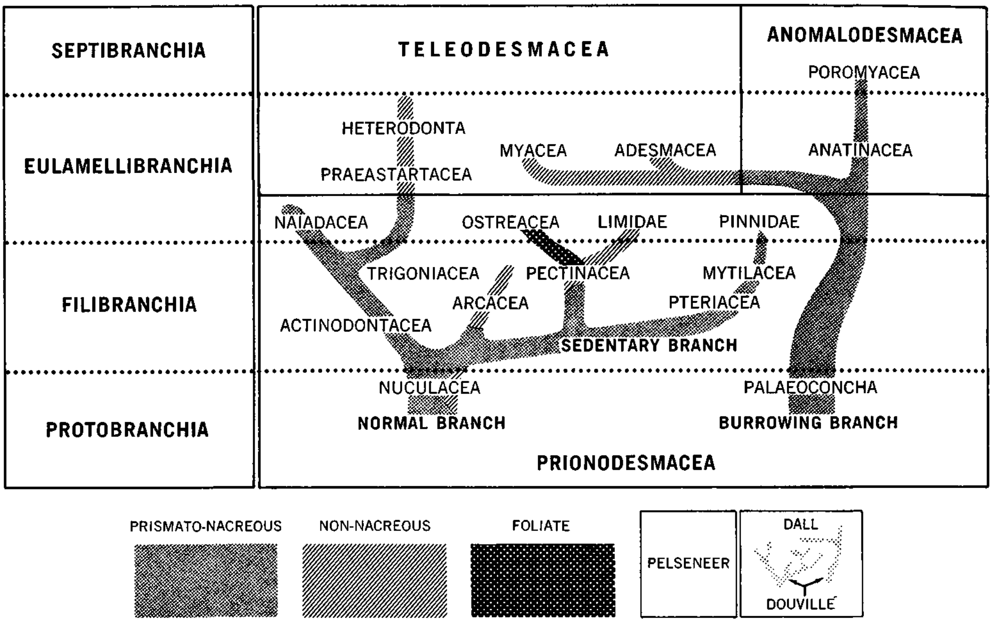

Fig. 101. Schematic comparison of classification of Dall and Douvillé (based in part on geologic history), with the "horizontal" classification of Pelseneer based mainly on ctenidial grade (Newell, n).

lems of the bivalves are not better understood than they were in the nineteenth century.

PELSENEER SCHOOL

In spite of the considerable amount of paleontologic evidence that was early available and general agreement that a phylogenetic approach to classification must take into account all lines of evidence, there developed a school of anatomists that ignored the fossil evidence and the integrity of superfamilies as defined by aggregate characters and turned to comparative studies of the bivalve ctenidia (Fig. 101) as a primary basis for higher classification (Fischer, 1880-87; Pelseneer, 1889, 1891, 1906, 1911; Ridewood, 1903).

More recently, Adkins (1936-38) has classified the bivalves according to whether they possess one or another of two types of laterofrontal cilia on ctenidial filaments. Purchon (1958) has based a system on stomach type in which he recognized five grades. Stasek (1963) has experimented, as a primary taxobasis, with the degree of association of ctenidia and labial palps (Table 1). The philosophical objection to this approach is that it cannot take into account the total organism, and provides no grounds for recognizing parallel evolution. The practical objection is that reliance on a single anatomical feature generally is not applicable to fossils, and makes no provision for evaluation of paleontologic evidence, the court of final appeal with respect to phylogeny in groups that have a good fossil record.

Studies of comparative anatomy of living species are of biologic interest and of course are essential for phylogenetic conclusions. They are only supplementary, however, and cannot provide needed evidence of the historical course of evolution. Ridewood (1903) showed that a sequence of stages can be recognized in the union of adjacent gill filaments and that identical grades of gill structure have been acquired in bivalves that otherwise are unlike. Furthermore, other bivalves closely similar in many characters may have different grades of ctenidia. For example, the Ostreacea, Pinnacea, and Limacea have gills of eulamellibranch grade, although they have much in common with

TABLE 1. SOME CHARACTERISTICS OF EXTANT BIVALVE SUPERFAMILIES

Subclasses and Superfamilies	Gill Grade				Gill Cilia		Stomach Type					Labial Palps			Shell Microstructure			
	Protobranch	Filibranch	Eulamellibranch	Septibranch	Atkins, Type 1	Atkins, Type 2	Purchon, Type 1	Purchon, Type 2	Purchon, Type 3	Purchon, Type 4	Purchon, Type 5	Stasek, Type 1	Stasek, Type 2	Stasek, Type 3	Nacreous	Cross Lamellar	Foliate	Homogeneous
PALAEOTAXODONTA																		
Nuculacea	x	--	--	--	x	--	x	--	--	--	--	x	--	--	x	x	--	--
Nuculanacea	x	--	--	--	--	--	x	--	--	--	--	--	--	--	--	--	--	x
CRYPTODONTA																		
Solemyacea	x	--	--	--	--	--	?	--	--	--	--	--	--	--	--	--	--	x
PTERIOMORPHIA																		
Arcacea	--	x	--	--	--	x	--	--	x	--	--	--	--	x	--	x	--	--
Limopsacea	--	x	--	--	--	x	--	--	x	--	--	--	--	--	--	x	--	--
Mytilacea	--	x	--	--	x	--	--	--	x	--	--	x	--	--	x	--	--	--
Pinnacea	--	--	x	--	--	x	--	--	x	--	--	--	--	--	x	--	--	--
Pteriacea	--	x	--	--	--	x	--	--	x	--	--	--	--	x	x	x	--	--
Pectinacea	--	x	--	--	--	x	--	--	--	x	--	--	--	x	x	x	x	--
Anomiacea	--	x	--	--	--	x	--	--	--	x	--	--	--	x	--	--	x	--
Limacea	--	--	x	--	--	x	--	--	--	x	--	--	--	--	--	x	--	--
Ostreacea	--	--	x	--	--	x	--	--	x	--	--	--	--	x	--	--	x	--
PALAEOHETERODONTA																		
Unionacea	--	--	x	--	--	--	--	--	--	x	--	x	--	--	x	--	--	--
Trigoniacea	--	x	--	--	x	--	--	--	--	x	--	x	--	--	x	--	--	--
HETERODONTA																		
Lucinacea	--	--	x	--	x	--	--	--	--	x	--	--	--	x	--	x	--	--
Chamacea	--	--	x	--	x	--	--	--	--	x	--	--	x	--	--	x	--	--
Leptonacea	--	--	x	--	x	--	--	--	--	--	--	--	--	x	--	x	--	--
Chlamydoconchacea	--	--	x	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Cyamiacea	--	--	x	--	x	--	--	--	--	x	--	--	--	x	--	x	--	--
Carditacea	--	--	x	--	x	--	--	--	--	x	--	--	x	--	--	x	--	--
Crassatellacea	--	--	x	--	x	--	--	--	--	x	--	x	--	x	--	x	--	--
Cardiacea	--	--	x	--	x	--	--	--	--	--	x	--	x	--	--	x	--	--
Tridacnacea	--	--	x	--	x	--	--	--	--	--	x	--	--	--	--	x	--	--
Mactracea	--	--	x	--	x	--	--	--	--	--	x	--	--	x	--	x	--	--
Solenacea	--	--	x	--	x	--	--	--	--	--	x	--	--	x	--	x	--	--
Tellinacea	--	--	x	--	x	--	--	--	--	--	x	--	--	x	--	x	--	--
Dreissenacea	--	--	x	--	x	--	--	--	--	--	--	--	--	--	--	x	--	--
Gaimardiacea	--	--	x	--	--	--	--	--	--	--	--	--	--	--	--	x	--	--
Arcticacea	--	--	x	--	x	--	--	--	--	--	--	--	--	--	--	x	--	--
Glossacea	--	--	x	--	x	--	--	--	--	--	x	--	x	--	--	x	--	--
Corbiculacea	--	--	x	--	x	--	--	--	--	--	x	--	--	--	--	x	--	--
Veneracea	--	--	x	--	x	--	--	--	--	--	x	--	x	x	--	x	--	--
Myacea	--	--	x	--	x	--	--	--	--	--	x	--	--	x	--	x	--	--
Gastrochaenacea	--	--	x	--	--	--	--	--	--	--	--	--	--	--	--	x	--	--
Hiatellacea	--	--	x	--	--	--	--	--	--	--	--	--	--	--	--	x	--	--
Pholadacea	--	--	x	--	x	--	--	--	--	--	x	--	--	x	--	x	--	--
ANOMALODESMATA																		
Pholadomyacea	--	--	x	--	x	--	--	--	--	--	--	--	--	--	x	--	--	--
Pandoracea	--	--	x	--	x	--	--	--	--	x	--	--	--	x	x	--	--	--
Poromyacea	--	--	--	x	--	--	--	x	--	--	--	--	--	x	x	--	--	--
Clavagellacea	--	--	x	--	x	--	--	--	--	x	--	--	--	x	x	--	--	--

Superfamilies not represented by extant bivalves include the following:

Superfamily	Soft Parts and Shell Microstructure
Ambonychiacea	No information
Archanodontacea	No information
Babinkacea	No information
Conocardiacea	Shell microstructure complex
Ctenodontacea	No information
Cycloconchacea	No information
Cyrtodontacea	No information
Edmondiacea	No information
Hippuritacea	Shell microstructure complex, varying with families
Megalodontacea	No information
Modiomorphacea	No information
Praecardiacea	No information

the Pectinacea, Mytilacea, and Anomiacea, which have filibranch gills. In four families —Arcidae, Anomiidae, Pteriidae (Aviculidae), and Spondylidae—RIDEWOOD found that one or two species had advanced a step beyond the rest of the family. The family-group taxa, based on multiple character complexes, are thereby fragmented.

These facts are adequate evidence of parallel evolution through a series of functional grades and are not indicative of relationship. PELSENEER (1906), in his taxonomic treatment, divided the anisomyarians (considered together with the Arcoida by many paleontologists as a phylogenetic unit) according to grades of gill structure into the Filibranchia and Eulamellibranchia. Later (PELSENEER, 1911), recognizing the incongruity of the resulting associations, he redistributed some of the families in an intermediate group, the Pseudolamellibranchia, which was heterogeneous as regards grade of gill structure, combining families with eulamellibranchiate gills (Ostreidae, Limidae, Pinnidae) and others possessing filibranch gills (Vulsellidae, Pectinidae). Thus, he abandoned gill structure as the primary anatomical basis in favor of overall resemblance. A comparison of PELSENEER's scheme with the classifications of DALL and DOUVILLÉ is shown in Figure 101.

A modified version of PELSENEER's 1906 treatment of the bivalves is followed in a leading zoological treatise (FRANC, 1960), in which the Filibranchia still contain some forms with eulamellibranch gills (Pinnidae, Limidae, Ostreidae) and the Eulamellibranchia include others with filibranch gills (Trigoniidae). These groups simply illustrate mosaic evolution in which gill characters have evolved at differing rates in different lines. The original purpose of PELSENEER, to provide a simple method of keying the various bivalves according to grade of gill structure, is thus defeated, and there is no semblance of consistency in his search for a natural classification.

HORIZONTAL VERSUS VERTICAL SYSTEMS

In spite of general doubts about the validity of PELSENEER's orders of Bivalvia, YONGE (1959), COX (1959), OWEN (1959), and PURCHON (1959), in a symposium on primitive bivalves, recently marshalled evidence of the homogeneity of the bivalves with primitive comblike gills, the Protobranchia, which they proposed to elevate from ordinal status to a subclass of the Bivalvia. All other bivalves they would segregate in one or more additional subclasses. This conclusion, retrograde, I believe, has been adopted by MORTON & YONGE (1964). The Protobranchia are based on ctenidial characters shared by the family Solemyidae, and the nuculoids. Otherwise dissimilar, the two groups are characterized by simple gills, which, structurally, are reminiscent of the gills of certain gastropods.

Both *Solemya* and the nuculoids are detritus-feeders, unlike the majority of bivalves which strain suspended material from water. Thus, the protobranchs share in common the quality of primitiveness of the ctenidia. Here similarity ends, however. The nuculoids, clearly a homogeneous group, differ in almost every other feature from *Solemya*. Both groups are extremely ancient, having been separate for at least a half a billion years, and no paleontologic evidence indicates that either was derived from the other. Were they closely related, the fossil record should show some evidence of parallel trends, but the shells have always been quite unlike and remarkably stable.

The Solemyidae and nuculoids apparently have shared the same habitat and apparently have occupied similar niches throughout their known history without any tendency to develop similar shell characters. Since they are unlike morphologically, are not connected by intermediate forms, and have reacted differently within the same habitat, one might infer that in fact they are only distantly related to each other. Classifying these two groups together simply because of similarities in one organ (gill structure) is no more defensible than placing all nacreous shells or all monomyarian shells together. Modern work on the genus *Solemya* tends to emphasize innumerable points of difference from nuculoids. Horizontal classification based on a single-organ system has an element of utility, of course, but it does not reflect the intricacies of phylogeny.

In the light of existing knowledge about the bivalves, an overall phylogenetic classification has not been devised, and experience shows that a simple classification free from innumerable inherent inconsistencies cannot be achieved as yet. Ultimately, the older fossils will provide the needed evidence for grouping morphologically dissimilar superfamilies on the basis of common origin. This may be accomplished only by working upward through genus, family, superfamily, order, and subclass, with a critical eye to the fossil evidence. Phylogenetic relationships are best deduced from the geologic history of the class, and this is poorly known. A wholly satisfactory classification cannot be obtained by arbitrarily forcing family group taxa into ready-made higher categories.

Neumayr's and Douvillé's influence is evident in the great French *Traité de paléontologie* (Dechaseaux, 1952) and the Russian *Osnovy paleontologii* (Ebersin, 1960). However, both display extensive modifications necessitated by progress and differing emphases on the subject. Dall's superior knowledge of the bivalves is reflected in his last major revision (1913), and no subsequent student of the group has been able to combine such encyclopedic knowledge and scholarship.

With some noteworthy modifications, the groupings adopted herein are similar to those recognized by L. R. Cox (1960), many of which we had discussed together, but the nomenclature is not the same.

CLASS—SUBCLASSES—ORDERS

NAME OF CLASS

Even the name applied to the bivalve mollusks has been a source of widespread disagreement. The malacologists of the world in recent years have been about evenly divided in preferences between the two terms Pelecypoda Goldfuss, 1820, and Lamellibranchiata (or Lamellibranchia) de Blainville, 1824 (Lamellibranches, 1814), and no possibility of winning universal adoption of either of these two names seems to exist. Following the examples of Haas (1929-56) and Thiele (1934-35), however, a strong swing now is seen toward compromise on the term Bivalvia Linné, 1758 (Yonge, 1959; Purchon, 1959; Franc, 1960; Ebersin, 1960; Cox, 1960; Morton, 1963; Stasek, 1963; Morton & Yonge, 1964; Vokes, 1967). This name is not only the oldest formally applied to the class, but it has the merit of possessing a familiar English cognate, "bivalve," which is meaningful to the layman. Generally, there is little confusion with other bivalve groups such as brachiopods and ostracodes (or even some gastropods) which are not customarily termed bivalves without a qualifying adjective. In any case, the name of the class is not intended to be an anatomical description. If desirable, the vernacular terms "pelecypod" or "lamellibranch" may continue to be employed by those who prefer them to "bivalve."

SUBCLASSES

The function of subclasses of Bivalvia is to provide a few major divisions for convenience in discussion and taxonomic sorting and ultimately to distinguish the trunk lines of phylogenetic descent. The last-named objective cannot be fully attained at the present time. The treatment followed here (Fig. 102) recognizes six major divisions, at least two of which (Palaeotaxodonta, Pteriomorphia) are considered by many paleontologists and neontologists to be more or less natural groupings. The other four are probably artificial. The subclasses are named as follows: 1) Palaeotaxodonta Korobkov, 1954, 2) Cryptodonta Neumayr, 1884, 3) Pteriomorphia Beurlen, 1944, 4) Palaeoheterodonta Newell, 1965, 5) Heterodonta Neumayr, 1884, 6) Anomalodesmata Dall, 1889.

PALAEOTAXODONTA

The Palaeotaxodonta comprise the nuculoids, a compact group characterized by a primitive taxodont hinge and protobranch

DALL, 1913	THIELE, 1934-35		FRANC, 1960		COX, 1960		NEWELL, 1965
PRIONODESMACEA		TAXODONTA	PROTOBRANCHIA	NUCULIDAE NUCULANIDAE MALLETIIDAE	PROTOBRANCHIA	PALAEOTAXODONTIDA	PALAEOTAXODONTA	NUCULOIDA
				SOLEMYIDAE		LIPODONTIDA	CRYPTODONTA	SOLEMYOIDA
						CRYPTODONTIDA		PRAECARDIOIDA
			FILIBRANCHIA	TAXODONTA	PTERIOMORPHIA	EUTAXODONTIDA	PTERIOMORPHIA	ARCOIDA
		ANISOMYARIA		ANISOMYARIA		ISOFILIBRANCHIDA		MYTILOIDA
						PTEROCONCHIDA		PTERIOIDA
						COLLOCONCHIDA		
	EULAMELLIBRANCHIA	SCHIZODONTA	EULAMELLIBRANCHIA	SCHIZODONTA	HETEROCONCHIA	SCHIZODONTIDA	PALAEOHETERODONTA	TRIGONIOIDA
						NAIADIDA		UNIONOIDA
TELEODESMACEA		EXTINCT		EXTINCT		PANTODONTIDA		MODIOMORPHOIDA
		EXTINCT		RUDISTES		PACHYODONTIDA	HETERODONTA	HIPPURITOIDA
		HETERODONTA		HETERODONTA		HETERODONTIDA		VENEROIDA
		ADAPEDONTA		ADAPEDONTA		ASTHENODONTIDA		MYOIDA
ANOMALODESMACEA		ANOMALODESMATA		ANOMALODESMACEA		EUDESMODONTIDA	ANOMALODESMATA	PHOLADOMYOIDA
			SEPTIBRANCHIA			SEPTIBRANCHIDA		

Fig. 102. Comparative classifications of the bivalves. That adapted herein is given in the right-hand column (Newell, n).

ctenidia which function almost solely in respiration. All are soft-bottom detritus-feeders, with representatives of both epifauna and infauna, each with appropriate adaptations. The nuculoids have long been considered to be the most primitive living bivalves, but they are not known to be the most ancient. No direct evidence is found that they gave rise to other radically different morphological types. As Douvillé (1913) and many others have shown, the taxodont hinge of the Arcidae represents a late development quite unrelated to the nuculoids.

CRYPTODONTA

The Cryptodonta (=Palaeoconcha of authors) are an association of convenience for poorly understood, thin-shelled forms without lateral teeth or well-developed cardinal teeth. Most of the families are limited to the early and middle Paleozoic. *Solemya,* a living protobranch of ancient lineage, is classed as a cryptodont until more can be learned about the Paleozoic forms. It differs morphologically from the nuculoids, and the ctenidia are used in feeding as well as respiration. The cryptodonts were considered by Neumayr, Dall, and Douvillé as primitive burrowers ancestral to many later stocks, but the validity of this idea has been demonstrated only in part. Most lack the siphonal gape of deep burrowers, and some of the forms included in the group even have been regarded by some as bivalved crustaceans.

PTERIOMORPHIA

The Pteriomorphia (=fixed, or sedentary, branch of Douvillé) are accepted by many paleontologists as a phylogenetic unit. These are the anisomyarians plus the arcoids and Paleozoic cyrtodonts (Fig. 102). Although they are morphologically diverse, the fossil record suggests continuity and common origins for several of the lines. It is possible, as Cox (1960) has pointed out, that the Mytilacea had a separate origin in the Modiomorphidae, a group of the Palaeoheterodonta. The duplivincular grade of ligament is found in many groups of this subclass, but through parallel trends some of the families have attained the alivincular or parivincular grade of ligament. Characteristically, the Pteriomorphia are members of the epifauna, but a few have adopted a boring habit in firm substrates. Many retain the byssus throughout life, a characteristic of very young bivalves of most other groups.

PALAEOHETERODONTA

The Palaeoheterodonta comprise the early Paleozoic actinodonts, unionaceans, and trigoniaceans. This grouping may be artificial, but the later members are alike in possessing free or incompletely fused mantle margins, an opisthodetic parivincular ligament, and prismatonacreous shells. Posterolateral hinge teeth, where present, originate at the beaks and below the ligament. The actinodonts include the oldest known bivalves (Middle Cambrian, Spain; Vogel, 1962). They may have given rise to the Pteriomorphia, Heterodonta, and possibly other groups (Fig. 103).

HETERODONTA

The Heterodonta differ from the Palaeoheterodonta in possessing nonnacreous shells (complex, or crossed lamellar) and more or less fused, siphonate, mantle margins. Posterolateral teeth, where present, commonly originate some distance behind the beaks and ligament. The ctenidia of living representatives are of the eulamellibranch grade. These animals extend far back into the Paleozoic where they merge gradually with the actinodonts. They nestle or burrow in diverse substrates, and their siphons show appropriate adaptations for depth of penetration beneath the surface.

ANOMALODESMATA

The Anomalodesmata generally are siphonate, burrowing forms with prismatonacreous shells, characteristically with an internal resilium, chondrophores, and a lithodesma. In most groups a hinge plate and teeth are weak or lacking.

ORDERS

The long history of work on bivalve classification has been characterized by repeated revisions based on new evidence and new points of view. Usually, new work has resulted in an emendation of the limits of various taxa. Most authors have believed, as did Cox (1960), that extensive emendation renders the old names obsolete. Simpson (1945, p. 32) has commented on this problem:

> To demand a change of name whenever such a shift is made would result in utmost confusion and duplication of terminology, and to change the author and date would be unjust and would obscure the historical origin of names and concepts. The opposite view might logically demand recognizing as author the first student to use a name in precisely its present sense. In most cases this would mean either that the technical authors of many time-hallowed names would change constantly and would tend to be the latest revisers, or that revisers were honor-bound not to change ranks of groups, which would stultify revision.

The problem of obsolescence and repeated replacement of names does not apply to family-group taxa, because they are legally based on type genera. Consequently, anyone may increase or decrease the scope of these taxa without disturbing their nomenclatural stability. They need not retain, even approximately, the limits suggested by the original author, since they are anchored to a nomenclatural type. Obviously, if knowledge is to expand in taxonomy, *a priori* limits cannot be placed on individual taxa. The use of nomenclatural types for orders is a convenient, elastic, and familiar method of insuring stability of nomenclature, while permitting freedom of individual judgment. It obviates any need for rigidly adhering to original definitions or to the endless dropping of names in consequence of emendation. This device has been in steady use for order-group names in many major groups of invertebrates (e.g., brachiopods, cephalopods, coelenterates, echinoids, trilobites, and others), and the practice of anchoring suborders and orders to genera was used for the bivalves by a few nineteenth century taxonomists, as noted above.

Reference to Figure 102 will show that the ordinal groupings adopted here are essentially those of Cox (1960). The changes in names do not require further comment. The number of orders has been reduced from 15 to 14 by reuniting the Ostreacea

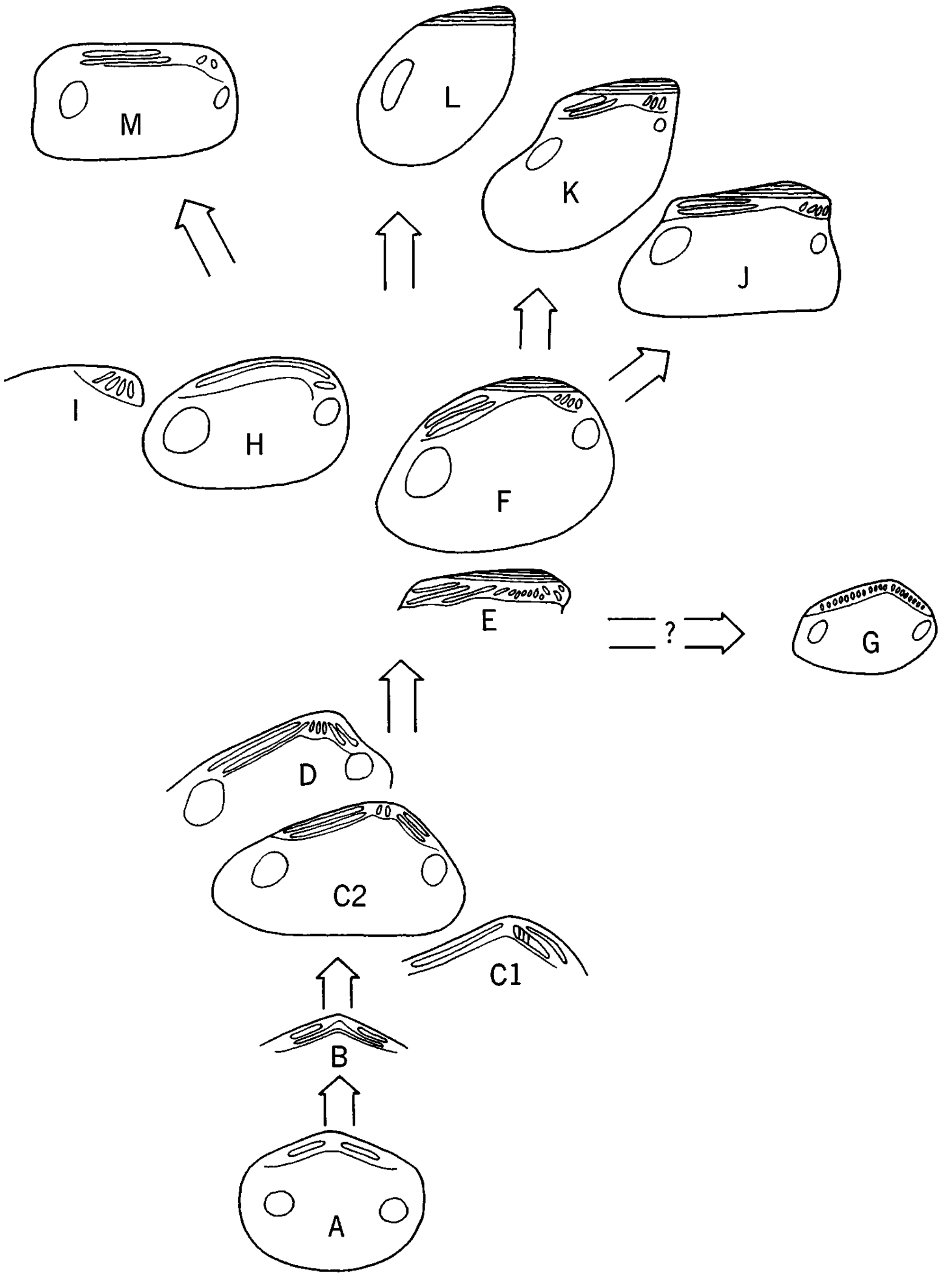

FIG. 103. Conjectural radiation of major groups of bivalves in the Paleozoic (modified from Vogel, 1962). *A, B.* Lamellodontidae, Cambrian. *C1, C2, D.* Hinge types among the Cycloconchidae, Ordovician. *E,F.* Cyrtodontidae, Ordovician. *G.* Nuculoid *(Tancrediopsis)*, Ordovician. *H, I.* Modiomorphidae, Ordovician. *J.* Parallelodontidae, Ordovician. *K.* Pterineidae, Devonian. *L.* Myalinidae, late Paleozoic. *M.* Permophoridae, late Paleozoic.

(Colloconchida) with the Pectinacea and related superfamilies on the basis of morphology and paleontologic evidence of close relationship (Newell, 1960). Several of the orders contain only one or two superfamilies, but their known history and morphological isolation militate against their being combined at present with other groups. An outline of the subclasses and ordinal group taxa follows.

Among the major classes of mollusks the bivalves have been most neglected and no individual in the world today can claim broad familiarity with fossil and living representatives of the entire class. Consequently, it should not be surprising that myriads of morphologic and taxonomic problems await solution. Much divergence of opinion exists among the many authors of this volume on the bivalves and in his organization of materials submitted by them Moore has shown great foresight and skill in respecting and preserving divergent judgments whenever feasible. Some genera appear under two or more families with appropriate explanatory notes. Many others are treated as subjective synonyms because of lack of sufficient evidence of consistent morphologic discrimination. Further investigation will show that many such synonymous genera and subgenera might usefully be revived.

A large majority, perhaps one-half of all Paleozoic genera and early Mesozoic genera (including subjective synonyms), are very poorly understood and require intensive study. Additional knowledge of these fossils will affect phylogenetic theories about the class as a whole. Runnegar's (1966) important morphological studies on Australian Permian desmodonts illustrates the urgency of acquiring precise knowledge of the nature of the fossil record. His work has convinced me of the general integrity of the Pholadomyoida, as herein used, even though the taxonomic distribution of the older genera and families remains somewhat conjectural because of lack of accurate morphological data.

MAJOR DIVISIONS OF BIVALVIA

Class **BIVALVIA** (Bonnani, 1681) Linné, 1758, p. 645.

- Subclass **Palaeotaxodonta.** The nuculoids; taxodont, nacreous or crossed lamellar; equivalved.
  - Order **Nuculoida.** Protobranch taxodonts; Purchon type 1; Stasek type 3; a homogeneous group.
- Subclass **Cryptodonta.** *Solemya* plus Paleozoic cryptodonts; edentulous or nearly edentulous; generally equivalve; probably polyphyletic.
  - Order **Solemyoida.** Solemyidae; homogeneous aragonite ostracum; siphonate, burrowing protobranchs.
  - Order **Praecardioida.** Paleozoic cryptodonts, shell margins not gaping; probably a heterogeneous group.
- Subclass **Pteriomorphia.** Cyrtodonts, arks, most heteromyarians; shell structure, ligament, gills, and stomach variable; commonly byssate in adults; general phyletic unity suggested by the fossil sequence.
  - Order **Arcoida.** Isomyarian filibranchs with crossed-lamellar shells; cyrtodonts and prionodonts; generally equivalve; Purchon type 3; Stasek type 3.
  - Order **Mytiloida.** Anisomyarian, generally equivalve, filibranchs and eulamellibranchs with prismatonacreous shells; Purchon type 3; Stasek type 1; characteristically byssate in adults.
  - Order **Pterioida.** Anisomyarian and monomyarian, mainly pleuroconchs and byssate or cemented in adults; pearl clams, scallops, oysters, filibranchs, eulamellibranchs; nacreous, crossed lamellar, or foliate internally; Purchon types 3 and 4; Stasek type 3.
- Subclass **Palaeoheterodonta.** Early actinodonts, unionaceans, trigoniaceans; prismatonacreous; Purchon type 4; Stasek type 1.
  - Order **Modiomorphoida** Newell, new order. Actinodonts; early Paleozoic precursors of most of the orders of bivalves; teeth radial, poorly differentiated, originating at the beaks; equivalved.
  - Order **Unionoida.** Variable upper Paleozoic and post-Paleozoic nonmarine forms, probably derived from the pre-

ceding; eulamellibranchs; Purchon type 4; Stasek type 1, probably polyphyletic.

Order **Trigonioida.** Trigonal marine shells; laterals or pseudolaterals generally lacking; filibranchs; apparently homogeneous.

Subclass **Heterodonta.** Heterodonts; complex crossed-lamellar eulamellibranchs.

Order **Veneroida.** Active heterodonts with differentiated hinge teeth of which laterals rarely reach beaks in adults; Purchon types 4 and 5; Stasek types, 1, 2, and 3; probably polyphyletic.

Order **Myoida.** Asthenodonts with degenerate hinge, generally with siphons and united mantle margins; Purchon type 5; Stasek type 3; probably polyphyletic.

Order **Hippuritoida.** Pachydonts; mainly attached, extinct forms.

Subclass **Anomalodesmata.** Generally fossorial, with poorly developed cardinal teeth, without laterals; mantle margins united; ligament associated in most primitive forms with internal resilium and lithodesma; internally nacreous.

Order **Pholadomyoida.** Burrowers with primitive hinge; eulamellibranchs and septibranchs; Purchon types 3 and 4; Stasek type 3.

Subclass **Uncertain.**

Order **Conocardioida.** Hinge commonly anchylosed in adults; with marked gape at one end and, in some genera, with a calcareous siphonal extension at the other; shell structures with radial pillars appearing at anticardinal margin as interlocking denticulations; musculature poorly known.

OUTLINE OF CLASSIFICATION

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The following outline of the Bivalvia summarizes taxonomic relationships, geologic occurrence, and numbers of recognized genera and subgenera in each suprageneric group from class to subfamily. A single number refers to genera; where two numbers are given, the second indicates subgenera additional to nominotypical ones.

Main Divisions of Bivalvia

- Bivalvia *(class)* (2169;996). *M.Cam.-Rec.*
  - Palaeotaxodonta *(subclass)* (63;40). *Ord.-Rec.*
    - Nuculoida *(order)* (63;40). *Ord.-Rec.*
      - Ctenodontacea *(superfamily)* (6). *Ord.-Carb.*
        - Ctenodontidae (6). *Ord.-Carb.*
      - Nuculacea *(superfamily)* (15;7). *Ord.-Rec.*
        - Praenuculidae (6). *Ord.-Rec.*
        - Nuculidae (9;7). *Ord.-Rec.*
      - Nuculanacea *(superfamily)* (42;33). *Ord.-Rec.*
        - Malletiidae (22;6). *Ord.-Rec.*
        - Nuculanidae (19;27). *Dev.-Rec.*
      - Isoarcidae (1). *M.Jur.-U.Cret.*
  - Cryptodonta *(subclass)* (20;5). *?U.Cam., L.Ord.-Rec.*
    - Solemyoida *(order)* (3;3). *Dev.-Rec.*
      - Solemyacea *(superfamily)* (3;3). *Dev.-Rec.*
        - Solemyidae (3;3). *Dev.-Rec.*
    - Praecardioida *(order)* (17;2). *?U.Cam., L.Ord.-L.Miss.*
      - Praecardiacea *(superfamily)* (17;2). *?U.Cam., L.Ord.-L.Miss.*
        - Praecardiidae (9;1). *?U.Cam., L.Ord.-L.Miss.*
          - Praecardiinae (5). *?U.Cam., L.Ord.-Dev.*
          - Cardiolinae (3;1). *L.Sil.-L.Miss.*
          - Dexiobiinae (1). *?Sil., L.Miss.*
        - Antipleuridae (7;1). *M.Ord.-Dev.*
          - Antipleurinae (3;1). *Sil.-Dev.*
          - Vlastinae (4). *M.Ord.-Dev.*
        - Butovicellidae (1). *Sil.*
  - Pteriomorphia *(subclass)* (490;191). *L.Ord.-Rec.*
    - Arcoida *(order)* (77;29). *L.Ord.-Rec.*
      - Cyrtodontacea *(superfamily)* (12). *M.Ord.-Dev.*
        - Cyrtodontidae (12). *M.Ord.-Dev.*
      - Arcacea *(superfamily)* (39;20). *L.Ord.-Rec.*
        - Arcidae (12;8). *?Trias., Jur.-Rec.*
          - Arcinae (4;6). *?Trias., Jur.-Rec.*
          - Anadarinae (8;2). *U.Cret.-Rec.*
        - Parallelodontidae (11;6). *L.Ord.-Rec.*
          - Parallelodontinae (4). *L.Ord.-U.Jur.*
          - Grammatodontinae (7;6). *?U.Carb., U.Trias.-Rec.*
        - Cucullaeidae (3;2). *L.Jur.-Cret., Rec.*
        - Noetiidae (13;4). *L.Cret.-Rec.*
          - Noetiinae (5;2). *L. Cret.-Rec.*
          - Stiarcinae (5;1). *U.Cret.-Rec.*
          - Trinacriinae (3;1). *U.Cret.-Eoc.*
      - Limopsacea *(superfamily)* (26;9). *L.Perm.-Rec.*
        - Limopsidae (8;1). *U.Trias.-Rec.*
        - Glycymerididae (10;2). *L.Cret.-Rec.*
          - Glycymeridinae (4;2). *Cret.-Rec.*
          - Arcullaeinae (6). *L.Cret.-U.Cret.*
        - Manzanellidae (3). *Perm.-Rec.*
        - Philobryidae (5;6). *Eoc.-Rec.*
    - Mytiloida *(order)* (64;26). *Dev.-Rec.*
      - Mytilacea *(superfamily)* (56;24). *Dev.-Rec.*
        - Mytilidae (53;24). *Dev.-Rec.*
          - Mytilinae (18;6). *?Perm., Trias.-Rec.*
          - Crenellinae (12;5). *U.Trias.-Rec.*

Lithophaginae (4;7). *?Carb., U.Perm.-Rec.*
Modiolinae (19;6). *Dev.-Rec.*
Mysidiellidae (3). *L.Trias.-U.Trias.*
Pinnacea *(superfamily)* (8;2). *L.Carb.-Rec.*
Pinnidae (8;2). *L.Carb.-Rec.*
Pterioida *(order)* (349;136). *Ord.-Rec.*
Pteriina *(suborder)* (298;127). *Ord.-Rec.*
Ambonychiacea *(superfamily)* (53;8). *?L.Ord., M.Ord.-L.Jur., ?U.Jur.*
Ambonychiidae (22;1). *M.Ord.(Chazy.)-U.Dev., ?L.Miss.*
Myalinidae (21;5). *?L.Dev., L.Miss.-L.Jur., ?U.Jur.*
?Lunulacardiidae (9;2). *L.Ord.-Miss.*
Monopteriidae (1). *L.Penn.-U.Penn., ?L.Perm.*
Pteriacea *(superfamily)* (102;21). *Ord.-Rec.*
Pterineidae (21;3). *Ord.-U.Perm.*
Kochiidae (1). *Dev.*
Pteriidae (11;1). *Trias.-Rec.*
Bakevelliidae (17;2). *Perm.-Eoc.*
Cassianellidae (6). *?Perm., Trias.*
Pergamidiidae (4). *U.Trias.-L.Jur.(Lias.).*
Dattidae (1). *U.Trias.(Rhaet.).*
Inoceramidae (16;9). *L.Perm.-U.Cret., ?Oligo.*
Isognomonidae (8;4). *U.Perm.-Rec.*
Pulvinitidae (3). *U.Jur.-Rec.*
Malleidae (14;2). *Jur.-Rec.*
Pectinacea *(superfamily)* (112;75). *Ord.-Rec.*
Pterinopectinidae (7;3). *U.Sil.-L.Perm. (Leonard.).*
Leiopectinidae (3). *Ord.-L.Dev.*
Aviculopectinidae (24). *U.Dev.-U.Jur.*
Aviculopectininae (16). *L.Miss.-U.Jur.*
Streblochondriinae (4). *Miss.-U.Trias.*
Chaenocardiinae (2). *L.Miss.(Visean)-L.Perm.*
Euchondriinae (2). *U.Dev.-U.Perm.*
Deltopectinidae (1). *L.Perm.*
Pseudomonotidae (1). *L.Carb.-U.Perm.*
Posidoniidae (12;1). *L.Carb.-U.Cret.*
Oxytomidae (7;2). *L.Perm.-U.Cret.*
Entoliidae (4;1). *L.Miss.-U.Cret.*
Pectinidae (31;63). *Trias.-Rec.*
Monotidae (2;1). *U.Trias.*
Buchiidae (8). *U.Trias.-Cret.*
Plicatulidae (3;2). *M.Trias.-Rec.*
Spondylidae (1;2). *Jur.-Rec.*
Terquemiidae (5). *?L.Perm., Trias.-U.Jur., ?Cret.*
?Dimyidae (2). *M.Jur.-Rec.*
Family Uncertain (1). *U.Trias.*
Anomiacea *(superfamily)* (10;11). *?Perm., Cret.-Rec.*
Anomiidae (10;11). *?Perm., Cret.-Rec.*
Limacea *(superfamily)* (21;12). *L.Carb.-Rec.*
Limidae (21;12). *L.Carb.-Rec.*
Ostreina *(suborder)* (51;9). *U.Trias.-Rec.*
Ostreacea *(superfamily)* (51;9). *U.Trias.-Rec.*
Gryphaeidae (22;6). *U.Trias.-Rec.*
Gryphaeinae (6;2). *U.Trias.(Rhaet.)-U.Jur. (Kimmeridg.).*
Pycnodonteinae (4;3). *L.Cret.-Rec.*
Doubtful genus (1).
Exogyrinae (11;1). *M.Jur.(Bajoc.)-Mio.*
Ostreidae (26;3). *U.Trias.-Rec.*
Ostreinae (13;1). *L.Cret.-Rec.*
Lophinae (6;2). *U.Trias.-Rec.*
Doubtful genera (7). *U.Cret., L.Oligo.-Eoc.*
Chondrodontidae (1). *L.Cret.(Alb.)-U.Cret. (Turon.).*
?Lithiotidae (2). *L.Jur.(L.Lias.).*
Palaeoheterodonta *(subclass)* (284;125). *M.Cam.-Rec.*
Modiomorphoida *(order)* (40;2). *M.Cam.-L.Perm., ?U.Perm.*
Modiomorphacea *(superfamily)* (33;2). *L.Ord.-L.Perm., ?U.Perm.*
Modiomorphidae (33;2). *L.Ord.-L.Perm., ?U.Perm.*
Cycloconchacea *(superfamily)* (7). *M.Cam.-U.Dev.*
Cycloconchidae (2). *Ord.*
Lamellodontidae (1). *M.Cam.*
Allodesmatidae (3). *M.Ord.-U.Sil.*
Carydiidae (1). *L.Dev.-U.Dev.*
Unionoida *(order)* (184;105). *?M.Dev., U.Dev.-Rec.*
Archanodontacea *(superfamily)* (2). *U.Dev.-L.Perm.*
Archanodontidae (2). *U.Dev.-L.Perm.*
Anthracosiacea *(superfamily)* (17;1). *?M.Dev., Carb.-Perm., ?Jur.*
Anthracosiidae (4). *Carb., ?Perm.*
?Microdontidae (3). *Perm.*
Palaeomutelidae (2;1). *?U.Carb., Perm.*
?Ferganoconchidae (1). *Jur.*
?Pseudocardiniidae (6). *Jur.*
Family Uncertain (1). *?M.Dev.*
Unionacea *(superfamily)* (159;104). *?Perm., Trias.-Rec.*
Margaritiferidae (1;3). *U.Cret.-Rec.*
Unionidae (133;91). *Trias.-Rec.*
Unioninae (60;40). *Trias.-Rec.*
Quadrulinae (22;9). *L.Cret.-Rec.*
Anodontinae (9;11). *U.Cret.-Rec.*
Alasmidontinae (6;8). *U.Oligo.-Rec.*
Lampsilinae (20;16). *?Trias., L.Oligo.-Rec.*
Hyriinae (16;7). *Cret.-Rec.*
Mutelidae (14;9). *?Trias., Cret.-Rec.*
Etheriidae (3;1). *Plio.-Rec.*
?Desertellidae (1). *L.Cret.(?Alb.).*
?Pachycardiidae (5). *Perm.-U.Trias., ?L.Jur.(Lias.).*
?Actinodontophoridae (2). *Perm.-U.Trias.*
Superfamily and family uncertain (6). *Trias.-Cret.*
Trigonioida *(order)* (60;18). *?M.Ord., Dev.-Rec.*
Trigoniacea *(superfamily)* (60;18). *?M.Ord., Dev.-Rec.*
?Lyrodesmatidae (1). *M.Ord.-U.Ord.*
Myophoriidae (13). *Dev.-U.Trias., ?L.Jur.*
?Scaphellinidae (1). *L.Perm.*

- Trigoniidae (41;18). *M.Trias.-Rec.*
- ?Trigonioididae (2). *L.Cret.-U.Cret.*
- Family Uncertain (2). *Cret.*
- Heterodonta *(subclass)* (1001;582). *M.Ord.-Rec.*
  - Veneroida *(order)* (789;529). *M.Ord.-Rec.*
    - Babinkacea *(superfamily)* (1). *M.Ord.*
      - Babinkidae (1). *M.Ord.*
    - Lucinacea *(superfamily)* (99;38). *Sil.-Rec.*
      - Lucinidae (55;30). *Sil.-Rec.*
        - Lucininae (19;16). *L.Jur.-Rec.*
        - Myrteinae (9;2). *L.Jur.-Rec.*
        - Milthinae (14;8). *Sil.-Rec.*
        - Divaricellinae (7;4). *L.Eoc.-Rec.*
        - Doubtful genera (6). *Mio.-Rec.*
      - Thyasiridae (9;4). *M.Trias.-Rec.*
      - Mactromyidae (13;1). *Dev.-Rec.*
      - Fimbriidae (9). *Carb.-Rec.*
      - Ungulinidae (11;3). *U.Cret.-Rec.*
      - Doubtful genus (1). *Rec.*
      - Cyrenoididae (1). *Rec.*
    - Chamacea *(superfamily)* (3;3). *?U.Cret.-Rec., Paleoc.*
      - Chamidae (3;3). *?U.Cret.-Rec., Paleoc.*
    - Leptonacea *(superfamily)* (99;24). *?Cret., Paleoc.-Rec.*
      - Erycinidae (15;4). *Paleoc.-Rec.*
      - Kelliidae (16;5). *Paleoc.-Rec.*
      - Leptonidae (7;4). *?Cret., Paleoc.-Rec.*
      - Montacutidae (33;5). *Eoc.-Rec.*
      - Galeommatidae (24;6). *U.Eoc.-Rec.*
      - Doubtful genera (4). *Rec.*
    - Chlamydoconchaecea *(superfamily)* (1). *Rec.*
      - Chlamydoconchidae (1). *Rec.*
    - Cyamiacea *(superfamily)* (32;3). *Jur.-Rec.*
      - Cyamiidae (9). *Mio.-Rec.*
      - Turtoniidae (1). *Mio.-Rec.*
      - Sportellidae (13;3). *Jur.-Rec.*
      - Neoleptonidae (9). *Plio.-Rec.*
    - Carditacea *(superfamily)* (74;20). *?Ord., Dev.-Rec.*
      - Permophoridae (19;1). *?Ord., ?Dev., L.Carb.-U.Cret.*
        - Permophorinae (11). *?Ord., ?Dev., L.Carb.-L.Jur.*
        - Myoconchinae (8;1). *?M.Dev., Perm.-U.Cret.*
      - Carditidae (36;16). *Dev.-Rec.*
        - Carditinae (2;1). *Paleoc.-Rec.*
        - Carditamerinae (16;8). *U.Trias.(Carn.)-Rec.*
        - Miodomeridinae (2;2). *Paleoc.-Rec.*
        - Palaeocarditinae (4). *L.Dev.-L.Jur.*
        - Venericardiinae (3;3). *?U.Cret., Paleoc.-Rec.*
        - Carditesinae (5;2). *L.Cret.-Rec.*
        - Thecaliinae (2). *Rec.*
        - Subfamily uncertain (2). *L.Cret.-Mio.*
      - Condylocardiidae (16;3). *Eoc.-Rec.*
        - Condylocardiinae (11;1). *Eoc.-Rec.*
        - Cuninae (5;2). *M.Eoc.-Rec.*
      - Family uncertain (3). *L.Carb.-L.Perm.*
    - Crassatellacea *(superfamily)* (69;28). *Ord.-Rec.*
      - Astartidae (37;22). *?M.Ord., Dev.-Rec.*
        - Astartinae (23;13). *?M.Ord., Dev.-Rec.*
        - Eriphylinae (10;4). *Dev.-Eoc.*
        - Opinae (7;5). *Dev.-U.Cret.*
      - Crassatellidae (15;6). *Dev.-Rec.*
        - Crassatellinae (11;5). *Dev.-Rec.*
        - Scambulinae (4;1). *L.Cret.-Rec.*
      - Cardiniidae (9). *Ord.-Rec.*
      - Myophoricardiidae (3). *Trias.*
      - Hippopodiidae (2). *?Dev., L.Jur.-U.Jur.*
    - Cardiacea *(superfamily)* (66;59). *U.Trias.-Rec.*
      - Cardiidae (23;42). *U.Trias.-Rec.*
        - Cardiinae (8;12). *U.Trias.-Rec.*
        - Trachycardiinae (3;6). *?Eoc., Oligo.-Rec.*
        - Fraginae (4;5). *Oligo.-Rec.*
        - Protocardiinae (4;17). *U.Trias.(Rhaet.)-Rec.*
        - Laevicardiinae (4;2). *Eoc.-Rec.*
      - Lahilliidae (1;1). *U.Cret.-Mio.*
      - Lymnocardiidae (42;16). *Mio.-Rec.*
        - Lymnocardiinae (9;12). *Mio.-M.Plio.*
        - Didacninae (11;2). *L.Plio.(Pont.)-Rec.*
        - Paradacninae (6). *Plio.*
        - Adacninae (10;2). *U.Plio.-Rec.*
        - Pseudocarditinae (1). *Plio.*
        - Subfamily uncertain (5). *Mio.-Plio.*
    - Tridacnacea *(superfamily)* (6;2). *?U.Cret., Tert.-Rec.*
      - Tridacnidae (6;2). *?U.Cret., Tert.-Rec.*
    - Mactracea *(superfamily)* (46;47). *U.Cret.-Rec.*
      - Mactridae (27;46). *U.Cret.-Rec.*
        - Mactrinae (15;37). *U.Cret.-Rec.*
        - Lutrariinae (5;4). *Mio.-Rec.*
        - Pteropsellinae (3;3). *Eoc.-Rec.*
        - Zenatiinae (4;2). *Eoc.-Rec.*
      - Anatinellidae (1). *Rec.*
      - Cardiliidae (3). *?Eoc., Oligo.-Rec.*
      - Mesodesmatidae (15;1). *Eoc.-Rec.*
        - Mesodesmatinae (8;1). *Eoc.-Rec.*
        - Davilinae (2). *Rec.*
        - Erviliinae (5). *Pleist.-Rec.*
    - Solenacea *(superfamily)* (12;5). *L.Cret.-Rec.*
      - Solenidae (2;2). *L.Eoc.-Rec.*
      - Cultellidae (10;3). *L.Cret.-Rec.*
    - Tellinacea *(superfamily)* (71;125). *U.Trias.-Rec.*
      - Tellinidae (26;75). *L.Cret.-Rec.*
        - Tellininae (15;58). *L.Cret.-Rec.*
        - Macominae (11;17). *Eoc.-Rec.*
      - Donacidae (7;13). *U.Cret.-Rec.*
      - Psammobiidae (11;21). *U.Cret.-Rec.*
        - Psammobiinae (10;15). *U.Cret.-Rec.*
        - Sanguinolariinae (1;6). *Mio.-Rec.*
      - Unicardiopsidae (1). *M.Jur.-U.Jur.*
      - Quenstedtiidae (1). *L.Jur.-M.Jur.*
      - Icanotiidae (2). *Cret.(Hauteriv.-Maastricht.).*
      - Scrobiculariidae (2). *Eoc.-Rec.*
      - Semelidae (8;8). *Eoc.-Rec.*
      - Solecurtidae (6;3). *L.Eoc.-Rec.*
        - Solecurtinae (4;3). *L.Eoc.-Rec.*
        - Novaculininae (2). *Rec.*
      - Sowerbyidae (2). *?Trias., U.Jur.*

- Tancrediidae (5;5). *U.Trias.-U.Cret.*
- Doubtful Tellinacea (2). *Permo-Trias.*
- Dreissenacea *(superfamily)* (3;3). *Eoc.-Rec.*
- Dreissenidae (3;3). *Eoc.-Rec.*
- Gaimardiacea *(superfamily)* (5). *Mio.-Rec.*
- Gaimardiidae (5). *Mio.-Rec.*
- Arcticacea *(superfamily)* (58;12). *M.Dev.-Rec.*
- Arcticidae (30;7). *U.Trias.-Rec.*
- Bernardinidae (2). *Rec.*
- Euloxidae (2). *Mio.*
- Kelliellidae (7;1). *Tert.-Rec.*
- Neomiodontidae (6). *L.Jur.-U.Cret.*
- Pollicidae (2). *U.Cret.*
- Ptychomyidae (1;1). *?U.Jur., L.Cret.-U.Cret.*
- Trapeziidae (7;3). *?L.Cret., U.Cret.-Rec.*
- Mecynodontidae (1). *M.Dev.*
- Glossacea *(superfamily)* (18;12). *U.Trias.-Rec.*
- Glossidae (2;6). *Paleoc.-Rec.*
- Dicerocardiidae (8). *U.Trias.-U.Cret.*
- Ceratomyopsidae (2). *M.Jur.-U.Jur.*
- Vesicomyidae (6;6). *Oligo.-Rec.*
- Corbiculacea *(superfamily)* (23;22). *?L.Jur., M.Jur.-Rec.*
- Corbiculidae (19;16). *?L.Jur., M.Jur.-Rec.*
- Pisidiidae (4;6). *?U.Jur, Cret-Rec.*
- Veneracea *(superfamily)* (101;126). *L.Cret.-Rec.*
- Veneridae (95;118). *L.Cret.-Rec.*
- Venerinae (8;6). *M.Eoc.-Rec.*
- Circinae (3;10). *Paleoc.-Rec.*
- Sunettinae (2;2). *Eoc.-Rec.*
- Meretricinae (9;6). *U.Cret.-Rec.*
- Pitarinae (26;36). *L.Cret.-Rec.*
- Samarangiinae (1). *Rec.*
- Dosiniinae (2;11). *U.Cret.-Rec.*
- Cyclininae (5;2). *L.Cret.-Rec.*
- Gemminae (4). *Eoc.-Rec.*
- Clementiinae (4;2). *U.Cret.-Rec.*
- Tapetinae (19;21). *L.Cret.-Rec.*
- Chioninae (12;22). *M.Eoc.-Rec.*
- Petricolidae (3;7). *Eoc.-Rec.*
- Cooperellidae (1;1). *Mio.-Rec.*
- Glauconomidae (1). *Rec.*
- Rzehakiidae (1). *M.Mio.-U.Mio.*
- Myoida *(order)* (88;46). *Carb.-Rec.*
- Myina *(suborder)* (39;31). *Perm.-Rec.*
- Myacea *(superfamily)* (29;27). *U.Jur.-Rec.*
- Myidae (6;7). *Paleoc.-Rec.*
- Corbulidae (17;20). *U.Jur.-Rec.*
- Corbulinae (7;18). *U.Jur.-Rec.*
- Caestocorbulinae (1;1). *L.Cret.-Eoc.*
- Corbulamellinae (1). *Cret.*
- Lentidiinae (1;1). *Paleoc.-Rec.*
- Pachydontinae (2). *Oligo.-Plio.*
- Subfamily uncertain (5). *U.Cret., Oligo.*
- Erodonidae (1). *Eoc.-Rec.*
- ?Pleurodesmatidae (1). *U.Oligo.-Mio.*
- Raetomyidae (2). *Eoc.*
- Spheniopsidae (2). *M.Eoc.-Rec.*
- Gastrochaenacea *(superfamily)* (4;1). *U.Jur.-Rec.*
- Gastrochaenidae (4;1). *U.Jur.-Rec.*
- Hiatellacea *(superfamily)* (6;3). *Perm.-Rec.*
- Hiatellidae (6;3). *Perm.-Rec.*
- Pholadina *(suborder)* (49;15). *?Carb., Jur.-Rec.*
- Pholadacea *(superfamily)* (49;15). *?Carb., Jur.-Rec.*
- Pholadidae (28;7). *?Carb., Jur.-Rec.*
- Pholadinae (7;4). *Cret.-Rec.*
- Martesiinae (16;2). *?Carb., Jur.-Rec.*
- Jouannetiinae (3;1). *U.Cret.-Rec.*
- Xylophagainae (2). *U.Cret.-Rec.*
- Teredinidae (21;8). *?Cret., Paleoc.-Rec.*
- Teredininae (10;2). *Eoc.-Rec.*
- Bankiinae (4;6). *Paleoc.-Rec.*
- Kuphinae (1). *?Eoc., Rec.*
- Subfamily uncertain (6). *U.Cret.-Rec.*
- Hippuritoida *(order)* (129;6). *M.Sil.-U.Cret.*
- Megalodontacea *(superfamily)* (14;3). *M.Sil.-L.Cret.*
- Megalodontidae (14;3). *M.Sil.-L.Cret.*
- Hippuritacea *(superfamily)* (115;3). *U.Jur.-U.Cret.*
- Diceratidae (8). *U.Jur.-L.Cret.*
- Diceratinae (1). *U.Jur.*
- Heterodiceratinae (3). *U.Jur.-L.Cret.*
- Plesiodiceratinae (2). *U.Jur.*
- Epidiceratinae (2). *U.Jur.*
- Requieniidae (8;2). *U.Jur.-U.Cret.*
- Monopleuridae (8). *L.Cret.-U.Cret.*
- Caprotinidae (8). *L.Cret.-U.Cret.*
- Caprinidae (23). *L.Cret.-U.Cret.*
- Hippuritidae (12). *U.Cret.*
- Radiolitidae (39;1). *L.Cret.-U.Cret.*
- Radiolitinae (14;1). *L.Cret.-U.Cret.*
- Biradiolitinae (7). *U.Cret.*
- Sauvagesiinae (7). *L.Cret.-U.Cret.*
- Lapeirousiinae (8). *U.Cret.*
- Subfamily uncertain (3). *U.Cret.*
- Family uncertain (9). *L.Cret.-U.Cret.*
- Anomalodesmata *(subclass)* (113;54). *?L.Ord., M.Ord.-Rec.*
- Pholadomyoida *(order)* (113;54). *?L.Ord., M.Ord.-Rec.*
- Edmondiacea *(superfamily)* (2). *U.Dev.-U.Perm.*
- Edmondiidae (2). *U.Dev.-U.Perm.*
- Pholadomyacea *(superfamily)* (58;8). *?L.Ord., M.Ord.-Rec.*
- Orthonotidae (2). *M.Ord.-M.Dev.*
- Grammysiidae (16;1). *?L.Ord., M.Ord.-U.Perm.*
- Megadesmidae (6;2). *U.Carb.-Perm.*
- Pholadomyidae (25;5). *Miss.-Rec.*
- Burmesiidae (2). *U.Trias.-L.Jur.(Lias).*
- Ceratomyidae (5). *U.Trias.-U.Jur., ?Mio.*
- Myopholadidae (1). *M.Jur.(Bathon.)-L.Cret. (U.Alb.).*
- Pleuromyidae (1). *U.Trias.-L.Cret.*

- Pandoracea *(superfamily)* (27;23). *U.Trias.-Rec.*
  - Pandoridae (1;5). *Oligo.-Rec.*
  - Cleidothaeridae (1). *Mio.-Rec.*
  - Laternulidae (7;2). *U.Trias.-Rec.*
  - Lyonsiidae (5;4). *Eoc.-Rec.*
  - Margaritariidae (1). *Mio.*
  - Myochamidae (2;2). *Mio.-Rec.*
  - Periplomatidae (2;6). *U.Cret.-Rec.*
  - Thraciidae (8;4). *Jur.-Rec.*
- Poromyacea *(superfamily)* (23;17). *Cret.-Rec.*
  - Poromyidae (6;4). *Cret.-Rec.*
  - Cuspidariidae (7;7). *U.Cret.-Rec.*
  - Verticordiidae (10;6). *Paleoc.-Rec.*
- Clavagellacea *(superfamily)* (3;6). *U.Cret. (Turon.)-Rec.*
  - Clavagellidae (3;6). *U.Cret.(Turon.)-Rec.*

Subclass Uncertain (1). *M.Ord.-U.Perm., ?U.Trias.*
- Conocardioida *(order)* (1). *M.Ord.-U.Perm., ?U.Trias.*
  - Conocardiacea *(superfamily)* (1). *M.Ord.-U.Perm., ?U.Trias.*
    - Conocardiidae (1). *M.Ord.-U.Perm., ?U.Trias.*

Bivalve genera uncertainly assigned to families (192).

Class, order, and family uncertain (68).

Genera of doubtfully molluscan affinities (22).

Unrecognizable genera (10).

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SYSTEMATIC DESCRIPTIONS

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CONTENTS

Class BIVALVIA Linné, 1758 (Buonanni, 1681)

[*ex* Vermes Testacea Bivalvia LINNÉ, 1758, p. 645; *nom. correct.* LINNÉ, 1765] [=Acephala CUVIER, 1798; Conchifera LAMARCK, 1818; Pelecypoda GOLDFUSS, 1820; Conchophora GRAY, 1821; Dithyra TURTON, 1822; Lamellibranchia, Lamellibranchiata DE BLAINVILLE, 1824; Elatobranchiata MENKE, 1828; Cormopoda BURMEISTER, 1837; Tropipoda CATLOW & REEVE, 1845; Aglossa LOVÉN, 1848; Elatocephala BRONN, 1862; Anodontoda HAECKEL, 1868; Lipocephala LANKESTER, 1884] [Diagnosis prepared by N. D. NEWELL]

Aquatic, acephalous, passive, and microphagous mollusks characterized by paired lateral shelly valves of conchiolin and calcium carbonate joined at hinge by flexible ligament; shell and ligament secreted by mantle which envelops organs and tissues within bivalved shell; mantle connected with shell submarginally by pallial muscles not present in other mollusks; other shell muscles generally consist of one anterior and one posterior adductor that close valves against opposing stresses within ligament; several small shell muscles activate foot which is variously adapted for creeping, burrowing and secretion of anchorage devices; feeding and respiration are accomplished by more or less symmetrical pair of lateral ctenidia bearing ciliary and mucous systems; fertilization of eggs external, sexes commonly hermaphroditic and protandrous; gut convolute, nephridia paired. *M. Cam.-Rec.*

The origin of the class is shrouded in mystery and the oldest bivalves (Tremadocian and older) give no hint of their derivation. Speculation that they were derived from a monoplacophoran-like ancestor is reasonable but not at all conclusive. Great gaps in the fossil record of many groups probably reflect ineffectual competition with other benthonic organisms, restricted geographic distribution and small population numbers rather than diagenetic destruction of the shells. Gastropods, also with conchiolin-calcareous shells, have a good Cambro-Ordovician record in rocks that rarely show a trace of bivalves.

Extinction of many major groups of competing brachiopods at the end of the Paleozoic Era was followed after a considerable time lapse by a steady evolutionary deployment of bivalves from Late Triassic time until the present. Many living superfamilies are virtually immortal, with known records and very little morphological change in more than 300 or 400 million years. A fascinating exception were the rudists which underwent rapid radiation and were distributed abundantly and widely at low latitudes during the Cretaceous Period. Certain other groups show evolutionary trends but a more prevalent pattern is for a group to appear and vanish abruptly with very little morphologic change.

The class has been singularly successful and apparently is now near the acme of its diversity, suggesting inherent advantages of conservatism, generalized modes of feeding and reproduction, and life in stable habitats.

Subclass PALAEOTAXODONTA Korobkov, 1954

[Diagnosis by N. D. NEWELL]

Characters same as those of order Nuculoida DALL, 1889. *Ord.-Rec.*

Order NUCULOIDA Dall, 1889

[*nom. transl. et correct.* NEWELL, 1965 (*ex* suborder Nuculacea DALL, 1889)] [Diagnosis by N. D. NEWELL]

Shell taxodont, equivalve, with closed margins, isomyarian; nacreous or crossed lamellar; ligament generally amphidetic; gills protobranchiate; foot grooved and reptant, not byssiferous in adults.[1] *Ord.-Rec.*

Superfamily CTENODONTACEA Wöhrmann, 1893

[*nom. transl.* MCALESTER, herein (*ex* Ctenodontidae WÖHRMANN, 1893)] [Materials for this superfamily prepared by A. L. MCALESTER, Yale University]

Shell equilateral, pallial sinus lacking, resilifer absent, cylindrical external ligament posterior to umbones. *Ord.-Carb.*

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[1] The relationships of many poorly understood genera of Recent deep-sea nuculoid bivalves soon will be clarified as a result of anatomical studies nearing completion by H. L. SANDERS, of the Woods Hole Oceanographic Institute, and J. A. ALLEN, of the University of Newcastle upon Tyne, England. Their work suggests that the problematic genus *Pristigloma*, included here in the superfamily Nuculanacea, is more closely related to the Nuculacea. In addition, they have discovered some extremely significant but previously unknown species which exhibit anatomical features and the general shape of nuculoids, but which lack the taxodont dentition found in all other nuculoid bivalves. Pending publication of these important observations, the more traditional assignment of *Pristigloma* and other deep-sea nuculoid genera is retained here.

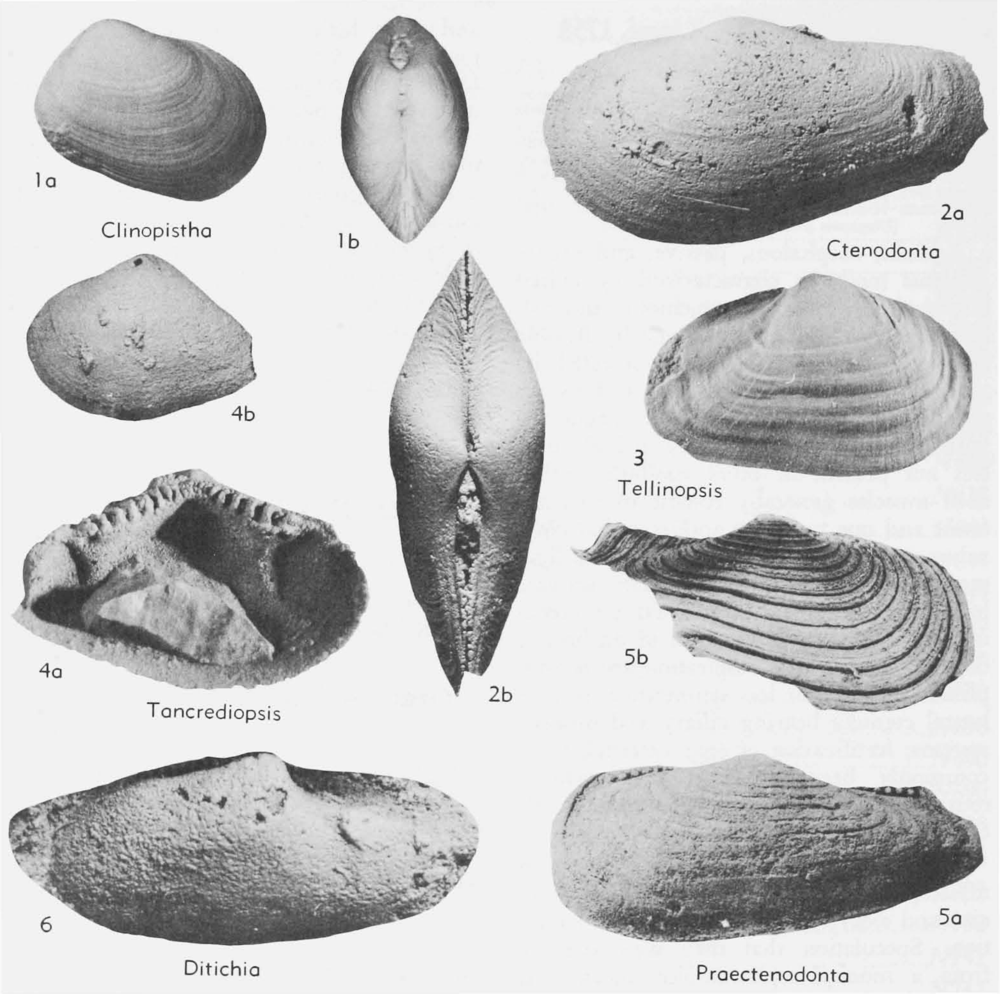

Fig. A1. Ctenodontidae (p. *N*228-*N*229).

Family CTENODONTIDAE Wöhrmann, 1893

Characters of superfamily. *Ord.-Carb.*

Ctenodonta Salter, 1852, p. 64 [**Tellinomya nasuta* Hall, 1847; SD Salter, 1859] [=*Tellinomya* Hall, 1847, p. 151 (obj.) (*non* Agassiz, 1846)]. Very large, elongate, lacking concentric sculpture. *M.Ord.*, N.Am.——Fig. A1,*2*. **C. nasuta* (Hall), Ont.; *2a,b*, LV ext., dorsal view of conjoined valves, ×2 (McAlester, n).

Clinopistha Meek & Worthen, 1870, p. 43 [**C. radiata* var. *levis;* OD] [=*Dystactella* Hall & Whitfield, 1872, p. 192 (type, *Tellinomya subnasuta;* M)] Like *Ctenodonta* but smaller, more elongate anteriorly. *L.Dev.-Carb.*, N.Am.——Fig. A1,*1*. **C. levis*, Carb., USA(Ill.); *1a,b*, RV ext., dorsal view of conjoined valves, ×2 (McAlester, n).

Ditichia Sandberger, 1891, p. 104 [**Leda mira* Beushausen, 1884; OD]. Small, elongate, weak adductor muscle scars. *L.Dev.*, Eu.(Ger.).——Fig. A1,*6*. **D. mira* (Beushausen); LV composite ext.-int. mold, ×4 (McAlester, n).

Praectenodonta Philip, 1962, p. 226 [**Palaeoneilo raricostae* Chapman, 1908; OD] [=*Gotodonta* Soot-Ryen, 1964, p. 502 (type, *Nucula sulcata* Hisinger, 1841; OD)]. Like *Ctenodonta* but with very strong concentric sculpture. *Sil.-L.Dev.*, cosmop.——Fig. A1,*5*. **P. raricostae* (Chapman), Sil., Australia; *5a,b*, LV composite ext.-int. mold, RV ext., ×2 (Philip, 1962).

Tancrediopsis Beushausen, 1895, p. 70 [**Ctenodonta contracta* Salter, 1859; SD Cossmann, 1897]. Like *Ctenodonta,* but with less elongate posterior extremity, some species with fine concentric sculpture. *Ord.,* N.Am.——FIG. A1,*4*. **T. contracta* (SALTER), Ont.; *4a,b,* LV int., ext., ×3, ×2 *(556)*.

Tellinopsis HALL & WHITFIELD, 1869, p. 80 [**Nuculites subemarginata* CONRAD, 1842; OD]. Like *Ctenodonta* but less elongate, with fine radial sculpture. *M.Dev.,* E.N.Am.——FIG. A1,*3*. **T. subemarginata* (CONRAD), USA(N.Y.); RV composite int.-ext. mold showing impression of radial sculpture, ×2 (McAlester, n).

Superfamily NUCULACEA Gray, 1824

[*nom. transl.* DALL, 1889 (*ex* Nuculidae GRAY, 1824)]
[Diagnosis by A. L. MCALESTER]

Truncate posterior extremity, pallial sinus lacking, resilifer present or absent. *Ord.-Rec.*

Family PRAENUCULIDAE McAlester, new family

[Materials for this family prepared by A. L. MCALESTER, Yale University]

Resilifer absent, ligament external. *Ord.-Dev.*

Praenucula PFAB, 1934, p. 234 [**P. dispar expansa*; OD]. Posteriorly truncate, anterior and posterior teeth similar in size and number. *M.Ord.,* Eu. (Czech.).——FIG. A2,*6*. **P. expansa*; *6a,b,* LV and RV (oblique view), int. molds, ×5 (McAlester, n).

Cardiolaria MUNIER-CHALMAS, 1876, p. 107 [**C. barrandei*; OD] [=*Honeymania* MCLEARN, 1918, p. 138 (type, *H. planimarginata;* OD)]. Like *Deceptrix,* but more equilateral and rounded. *Ord.-Sil.,* Eu.-N.Am.——FIG. A2,*1*. **C. barrandei*, Ord., France; LV int. mold, ×2 (McAlester, n).

Deceptrix FUCHS, 1919, p. 79 [**D. carinata*; M] [=*Praeleda* PFAB, 1934, p. 231 (type, *Nucula compar* BARRANDE, 1881, pl. 271; OD)]. Like *Praenucula,* but posterior teeth smaller and more numerous than anterior. *M.Ord.-Dev.,* Eu.——FIG. A2,*5*. **D. carinata,* L.Dev., Ger.; LV int. mold, ×2 (McAlester, n).

Ledopsis BEUSHAUSEN, 1884, p. 91 [**L. rectangularis;* SD MCALESTER, 1968] [=*Pseudoledopsis* MAILLIEUX, 1937, p. 182 (type, *Ledopsis taunica* BEUSHAUSEN, 1895; OD)]. Like *Praenucula,* but with more sharply truncate posterior having strong radial groove. *L.Dev.,* Eu.(Ger.).——FIG. A2,*4*. **L. rectangularis*, LV ext., ×2 (McAlester, n).

Palaeoconcha MILLER, 1889, p. 498 [**P. faberi*; OD]. Rounded, small, anterior and posterior teeth similar in size and number. *U.Ord.,* N.Am.——FIG. A2,*2*. **P. faberi*; *2a,b,* RV int. mold and int.

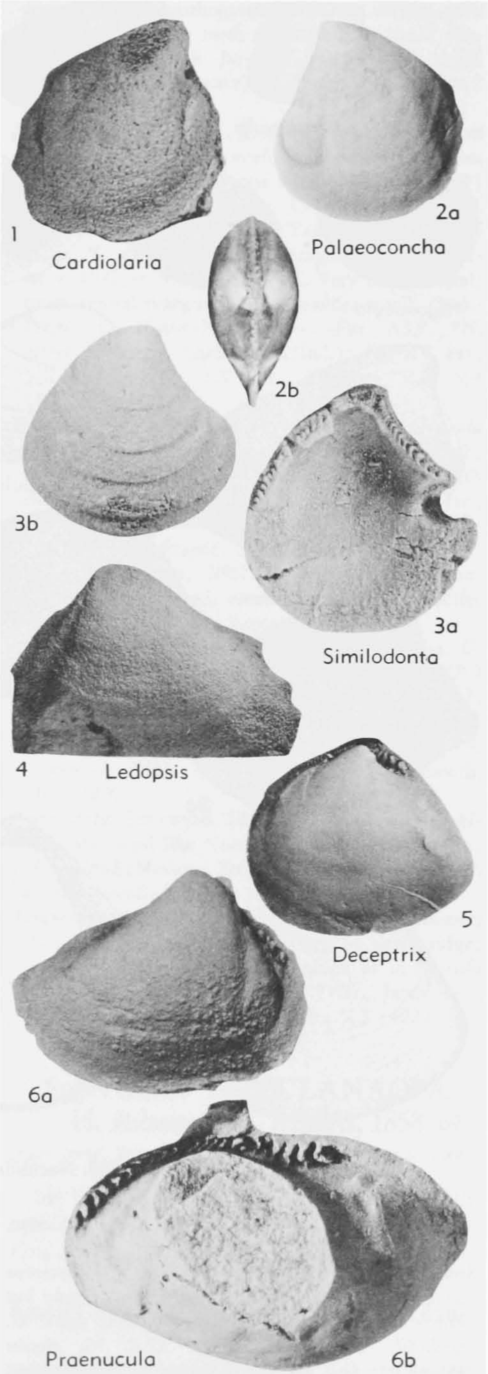

FIG. A2. Praenuculidae (p. *N229-N230*).

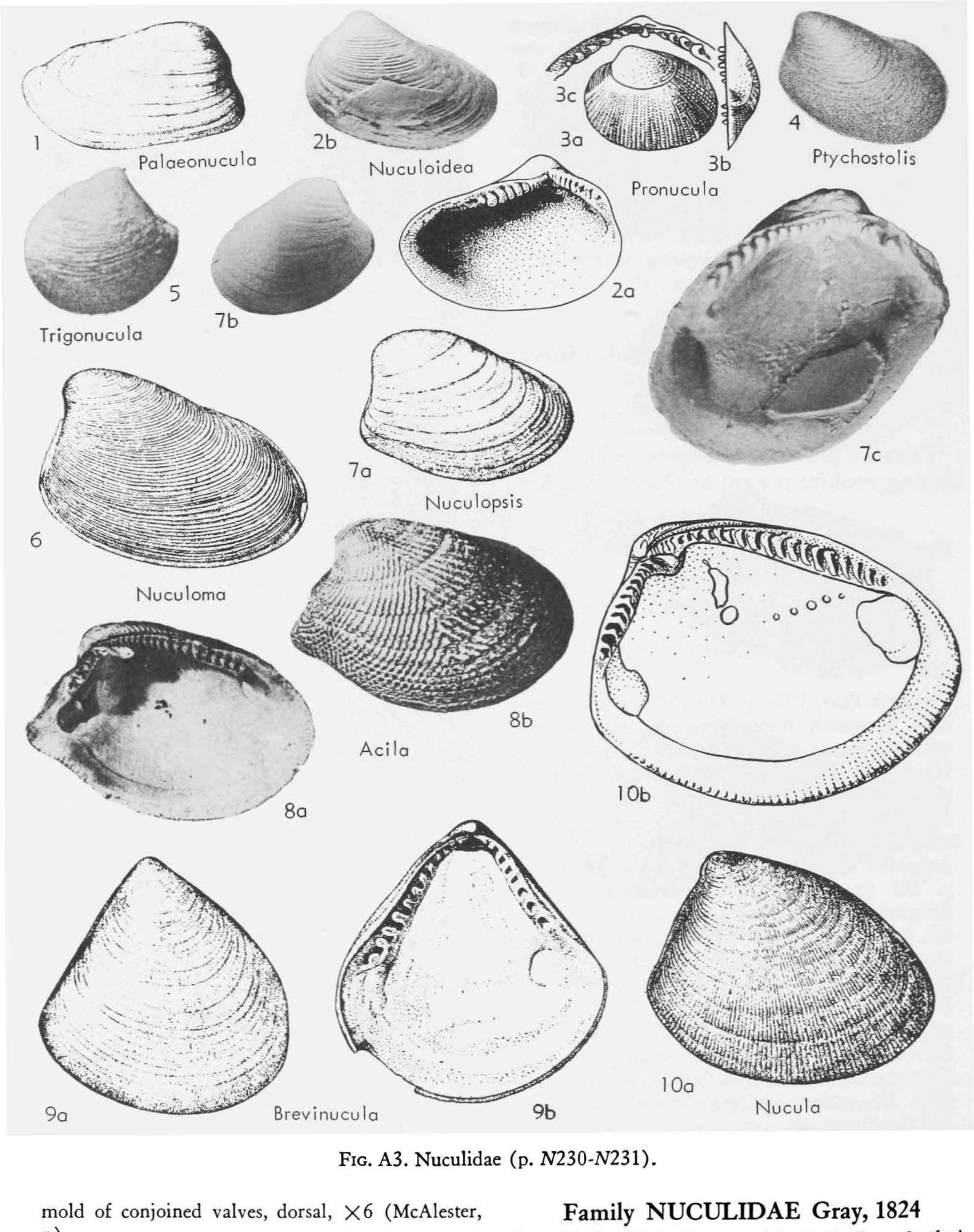

FIG. A3. Nuculidae (p. *N*230-*N*231).

mold of conjoined valves, dorsal, ×6 (McAlester, n).

Similodonta SOOT-RYEN, 1964, p. 498 [**Tellinomya similis* ULRICH, 1892; OD]. Like *Palaeoconcha* but much larger, stronger adductor muscle scars. *U. Ord.-Sil.,* N.Am.-Eu.——FIG. A2,*3*. **S. similis* (ULRICH); *3a,b,* RV int., LV ext., ×2 (McAlester, n).

Family NUCULIDAE Gray, 1824

[Materials for this family prepared by A. M. KEEN, Stanford University]

Shell material nacreous; beaks opisthogyrate; resilifer present; ligament internal. *Ord.-Rec.*

Nucula LAMARCK, 1799, p. 87 [**Arca nucleus*

Linné, 1758; M] [=*Lembulus* Sowerby, 1842, p. 170 (*non Lembulus* Risso, 1826)]. Ovate, normally with polished periostracum. *Cret.-Rec.*, cosmop.

N. (Nucula). Sculpture of radial ribs, inner ventral margin crenate. *U.Cret.-Rec.*, cosmop.——Fig. A3,*10*. **N.* (*N.*) *nucleus* (Linné), Rec., France; *10a,b,* RV ext., LV int., ×5 *(832)*.

N. (Gibbonucula) Eames, 1951, p. 319 [**N.* (*G.*) *corbuliformis* (*non Nucula corbuliformis* Hall & Whitfield, 1869) (=*N.* (*G.*) *neocorbuliformis* Eames, 1955); OD]. Thick-shelled, inflated; surface with coarse concentric and fine radial sculpture; inner ventral margin crenate. *L.Eoc.*, Asia.

N. (Lamellinucula) Schenck, 1944, p. 97 [**Nucula tamatavica* Odhner, 1943; OD]. With strong incised concentric sculpture, weak radial ribs; inner ventral margin crenate. *Eoc.-Rec.*, Eu.-N.Am. S.Am.-Afr.

N. (Leionucula) Quenstedt, 1930, p. 112 [**Nucula albensis* d'Orbigny, 1844; OD] [=*Nuculopsis* Woodring, 1925, p. 14 (*non Nuculopsis* Girty, 1911) (type, *N.* (*Nuculopsis*) *hilli*); *Ennucula* Iredale, 1931, p. 202 (type, *Nucula obliqua* Lamarck, 1819; OD)]. Smooth, resilifer oblique; inner ventral margin smooth. *Cret.-Rec.*, cosmop.

N. (Linucula) Marwick, 1931, p. 49 [**Nucula ruatakiensis* Marwick, 1926; OD]. With fine divaricate radial riblets on lunule and escutcheon. *Mio.*, N.Z.

N. (Pectinucula) Quenstedt, 1930, p. 112 [**Nucula pectinata* Sowerby, 1818; OD]. With strong radial ribs. *Cret.*, Eu.-N.Am.

Acila Adams & Adams, 1858, p. 545 [**Nucula divaricata* Hinds, 1843; SD Stoliczka, 1871]. Sculpture divaricate. *Cret.-Rec.*, N.Am.-S.Am.-Asia.

A. (Acila). With well-defined rostral sinus. *Oligo.-Rec.*, N.Am.-S.Am.-Asia.——Fig. A3,*8*. **A.* (*A.*) *divaricata* (Hinds), Rec., Korea; *8a,b,* LV int., RV ext., ×1 *(833)*.

A. (Truncacila) Grant & Gale (*ex* Schenck, MS), 1931, p. 115 [**Nucula castrensis* Hinds, 1843; OD]. Quadrangular to ovate, without rostral sinus. *L.Cret.-Rec.*, Eu.-N.Afr.-N.Am.-S.Am.-Japan.

Brevinucula Thiele, 1934, p. 786 [**Nucula guineensis* Thiele, 1931; M]. Triangular, short. *Mio.-Rec.*, Afr.-N.Am.——Fig. A3,*9*. **B. guineensis* (Thiele), Rec., W.Afr.; *9a,b,* RV ext., RV int., ×8 *(832)*.

Nuculoidea Williams & Breger, 1916, p. 173 [**Cucullea opima* Hall, 1843; OD]. Resilifer triangular, below inner ends of hinge-teeth series; inner ventral margin microscopically crenate. *Ord.-Dev.*, N.Am.——Fig. A3,*2*. **N. opima* (Hall), Dev., USA(N.Y.); *2a,* RV int., ×1 *(946)*; *2b,* RV ext., ×2 (McAlester, n).

Nuculoma Cossmann, 1907, p. 124 [**Nucula castor* d'Orbigny, 1849; M]. Like *Palaeonucula* but with more strongly opisthogyrate umbones; surface with concentric threads; teeth as in *Nucula*; inner ventral margin smooth. *Jur.*, Eu.-Asia.——Fig. A3,*6*. **N. castor* (d'Orbigny), France; RV ext., ×2 *(832)*.

Nuculopsis Girty, 1911, p. 123 [**Nucula ventricosa* Hall, 1858 (*non Nucula ventricosa* Fleming, 1828) (=*Nuculopsis girtyi* Schenck, 1934); OD] [=*Nuculavus* Chernyshev, 1947, p. 5 (type, *N. minuta*; OD); *Nuculanella* Tasch, 1953, p. 395 (type, *N. piedmontia*; OD); *Stagnnucula* Chernyshev, 1947, p. 9 *(nom. nud.)*]. Very inequilateral; inner ventral margin smooth; resilifer small. *Carb.-Perm.*, Eu.-N.Am.-N.Z.-Asia.——Fig. A3,*7*. **N. girtyi* Schenck, Carb., USA(Ind.); *7a,* RV ext., ×2 *(832)*; *7b,c,* LV ext., RV int., ×2, ×4 (McAlester, n).

Palaeonucula Quenstedt, 1930, p. 110 [**Nucula hammeri* Defrance, 1825; OD]. Inflated, smooth; hinge as in *Nucula* but posterior series of teeth shorter; inner ventral margin smooth. *Trias.-Jur.*, Eu.-Asia-N.Am.——Fig. A3,*1*. **P. hammeri* (Defrance), Jur., France; LV ext., ×1 *(832)*.

Pronucula Hedley, 1902, p. 290 [**P. decorosa;* OD]. Hinge arched, elements separated, resilifer vertical. *U.Oligo.-Rec.*, Australasia.

P. (Pronucula). Inner ventral margin crenate. *U. Oligo.-Rec.*, Australasia.——Fig. A3,*3*. **P.* (*P.*) *decorosa,* Rec.; *3a,b,* RV ext., RV dorsal, ×7; *3c,* RV hinge, enl. *(832)*.

P. (Austronucula) Powell, 1939, p. 220 [**A. schencki*; OD]. Inner ventral margin smooth. *Rec.*, N.Z.

Ptychostolis Tullberg, 1881, p. 14 [**P. nordenskiöldi*; M]. Shell like *Nucula* but with strong lunule. *Jur.*, USSR(Novaya Zemlya).——Fig. A3,*4*. **P. nordenskioeldi,* RV ext., ×1 *(919)*.

Trigonucula Ichikawa, 1949, p. 267 [**T. sakawana*; OD]. Trigonal, escutcheon defined by sharp ridge; sculpture of concentric striae; hinge as in *Nucula* but resilifer not as oblique. *U.Trias.*, Japan.——Fig. A3,*5*. **T. sakawana*; LV ext., ×3 *(422)*.

Superfamily NUCULANACEA H. Adams & A. Adams, 1858

[*nom. transl.* Puri, herein (*ex* Nuculanidae Adams & Adams, 1858)] [Diagnosis by A. L. McAlester]

Shell elongate posteriorly, with or without resilifer, pallial sinus usually present. *Ord.-Rec.*

Family MALLETIIDAE Adams & Adams, 1858

[*nom. correct.* McAlester, herein (*pro* Malletidae Bellardi, 1875, *nom. transl. ex* Mallettinae Adam & Adams, 1858)] [Materials for this family prepared by A. L. McAlester, Yale University]

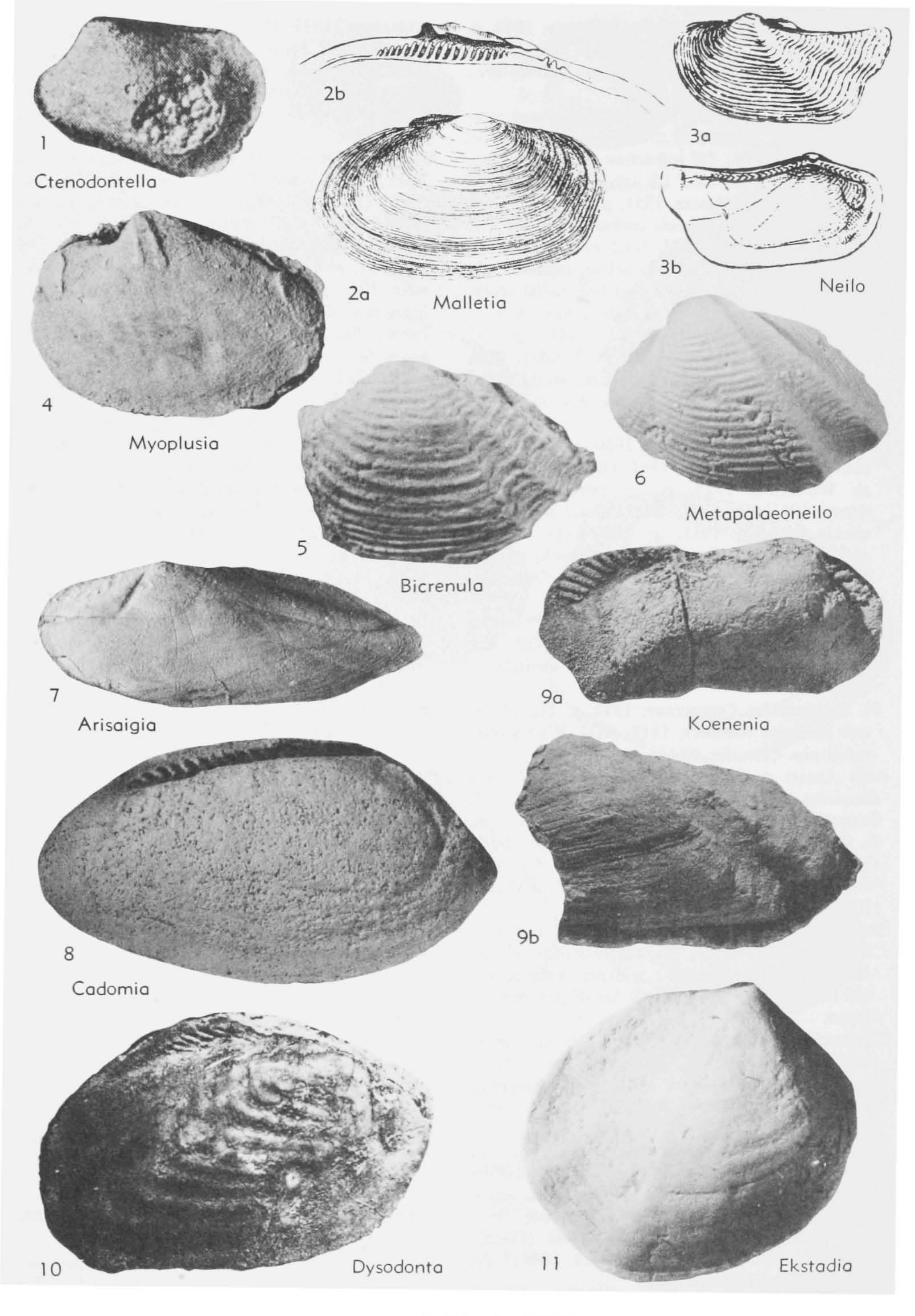

Fig. A4. Malletiidae (p. *N*233).

No resilifer, ligament predominantly external. *Ord.-Rec.*

Malletia des Moulins, 1832, p. 85 [**M. chilensis*; M] [=*Solenella* Sowerby, 1832, p. 197 (type, *S. norrisii;* M); *Ctenoconcha* Gray, 1840, p. 139; *Nucularia* Conrad, 1869, p. 44 (type, *N. papyria;* M); *Pseudomalletia* Fischer, 1886, p. 987 (type, *Yoldia obtusa* Sars, 1872; SD Dall, 1898)]. Thin shell, weak concentric sculpture, elongate, blunt posterior, strong pallial sinus. *Mesoz.-Rec.*, cosmop.

M. (Malletia). Compressed, not rostrate. *Mesoz.-Rec.*, cosmop.——Fig. A4,*2*. **M. (M.) chilensis*, Rec., Chile; *2a,* RV ext., X1; *2b,* LV hinge, enl. (Sowerby, 1842).

M. (Malletiella) Soot-Ryen, 1957, p. 1 [**Malletia pacifica* Dall, 1897; OD]. Compressed, rostrate. *Rec.*, E.Pac.

M. (Minormalletia) Dall, 1908, p. 385 [**M. (M.) arciformis*; SD Finlay, 1926]. Inflated, not rostrate. *Rec.*, E.Pac.

Arisaigia McLearn, 1918, p. 139 [**A. postornata*; OD]. Elongate, radial sculpture on posterior, with posterior radial groove and internal septum. *Sil.*, N.Am.(Nova Scotia).——Fig. A4,*7*. **A. postornata*; LV composite ext.-int. mold, X2 (McAlester, n).

Bicrenula Williams & Breger, 1916, p. 163 [**Palaeoneilo bisulcata* Hall & Whitfield, 1869; SD McAlester, 1968]. Two posterior radial grooves, strong concentric sculpture. *Dev.*, E.N. Am.——Fig. A4,*5*. **B. bisulcata* (Hall & Whitfield), U.Dev., USA(N.Y.); LV composite ext.-int. mold, X4 (McAlester, n).

Cadomia Tromelin, 1877, p. 48 [**C. typa*; M]. Very large, lacking posterior radial groove, weak concentric sculpture. *Ord.*, Eu.(Fr.).——Fig. A4, *8*. **C. typa*; RV composite ext.-int. mold, X1.5 (McAlester, n).

Ctenodontella Khalfin, 1940, p. 262 [**C. macrodiformis*; OD]. Elongate, expanding to greatest height posteriorly. *L.Dev.*, USSR(Sib.).——Fig. A4,*1*. **C. macrodiformis*; LV composite ext.-int. mold, X4 (Khalfin, 1940).

Dysodonta Mansuy, 1913, p. 9 [**D. deprati*; M]. Expanding to greatest height posteriorly, strong concentric sculpture, large blade-shaped posterior teeth. *Sil.*, SE.Asia(N.Vietnam).——Fig. A4,*10*. **D. deprati*; RV composite ext.-int. mold, X1 (Mansuy, 1913).

Ekstadia Soot-Ryen, 1964, p. 501 [**E. tricarinata*; OD]. Rounded, weak surface sculpture, two weak posterior radial grooves. *Sil.*, Eu.(Swed.).——Fig. A4,*11*. **E. tricarinata*; RV ext., X6 (Soot-Ryen, 1964).

Koenenia Beushausen, 1884, p. 72 [**Cucullaea lasii* Roemer, 1843; M]. Very large, posteriorly elongate, strong posterior radial groove. *L.Dev.*, Eu. (Ger.).——Fig. A4,*9*. **K. lasii* (Roemer); *9a,b,* RV int. mold showing dentition and ant. muscle scar, LV cast of post. part ext. mold, X1 (McAlester, n).

Metapalaeoneilo Lamcke, 1934, p. 186 [**Palaeoneilo (M.) baltica*; M]. Equilateral, strong posterior radial groove, strong concentric sculpture, internal septum present. *Sil.*, Eu.(N.Ger.) (Baltic boulders).——Fig. A4,*6*. **M. baltica* (Lamcke); LV ext., X3 (McAlester, n).

Myoplusia Neumayr, 1884, p. 416 [**Leda bilunata* Barrande, 1881; SD McAlester, 1968]. [=*Pseudocyrtodonta* Pfab, 1934, p. 236 (type, *Leda ala* Barrande, 1881; OD)]. Like *Palaeoneilo,* but with much larger and stronger umbonal pedal muscle scars. *M.Ord.*, Eu.(Czech.).——Fig. A4,*4*. **M. bilunata* (Barrande); LV int. mold, X5 (McAlester, n).

Neilo Adams, 1852, p. 93 [**N. cumingii*; M]. Thick shell, strong concentric sculpture, elongate, blunt posterior, strong pallial sinus. *Tert.-Rec.*, cosmop.——Fig. A4,*3*. **N. cumingii,* Rec., N.Z.; *3a,b,* LV ext. and int., X1.5 (Adams, 1852).

Nuculites Conrad, 1841, p. 49 [**N. oblongatus*; SD Miller, 1889] [=*Cleidophorus* Hall, 1847, p. 300 (type, *Nuculites planulata* Conrad, 1841; M); *Cucullella* M'Coy, 1851, p. 50 (type, *Cucullaea antiqua* Sowerby, 1839; SD Beushausen, 1895); *Pyrenomoeus* Hall, 1852, p. 87 (type, *P. cuneatus*; M)]. Like *Palaeoneilo,* but with internal septum. *Ord.-Dev.*, cosmop.——Fig. A5,*7*. **N. oblongatus,* M.Dev., N.Y.; RV composite ext.-int. mold, X1.5 (McAlester, n).

Palaeoneilo Hall & Whitfield, 1869, p. 6 [*nom. conserv.* ICZN (Opinion 215), 1954] [**Nuculites constricta* Conrad, 1842; SD Hall, 1885] [=*Anthraconneilo* Girty, 1911, p. 131 (type, *A. taffiana*; OD); *Anthraconeilopsis* Tasch, 1953, p. 391 (type, *A. kansana;* OD); *Filius* Barrande, 1881, p. 162 (obj. syn. of *Synek* Barrande); *Goniodon* Herrick, 1888, p. 84 (type, *G. ohioensis*; M); *Olegija* Chernyshev, 1948, p. 3 (type, *O. eugenii*; OD); *Straba* Prantl & Růžička, 1954, p. 3 (type, *S. bohemica*; OD); *Strabiella* Prantl & Růžička, 1954, p. 4 (type, *Straba (S.) holynensis*; OD); *Strabina* Prantl & Růžička, 1954, p. 4 (type, *Straba (S.) formosa*; OD); *Synek* Barrande, 1881, p. 162 (type, *S. antiquus*; OD)]. Faint posterior radial groove, concentric sculpture, no internal septum. *Ord.-Mesoz.*, cosmop.——Fig. A5,*9*. **P. constricta* (Conrad), M.Dev., N.Y.; composite ext.-int. molds of both valves (LV below), X1.5 (McAlester, n).

Phaenodesmia Bittner, 1894, p. 188 [**P. klipsteiniana*; SD Diener, 1923]. Like *Palaeoneilo,* but with more tapered posterior. *Trias.*, Eu.——Fig. A5,*2*. **P. klipsteiniana*; *2a,b,* LV ext., dorsal view of both valves, X1 *(58)*.

Prosoleptus Beushausen, 1895, p. 70 [**Nucula lineata* Goldfuss, 1840; OD]. Like *Palaeoneilo,*

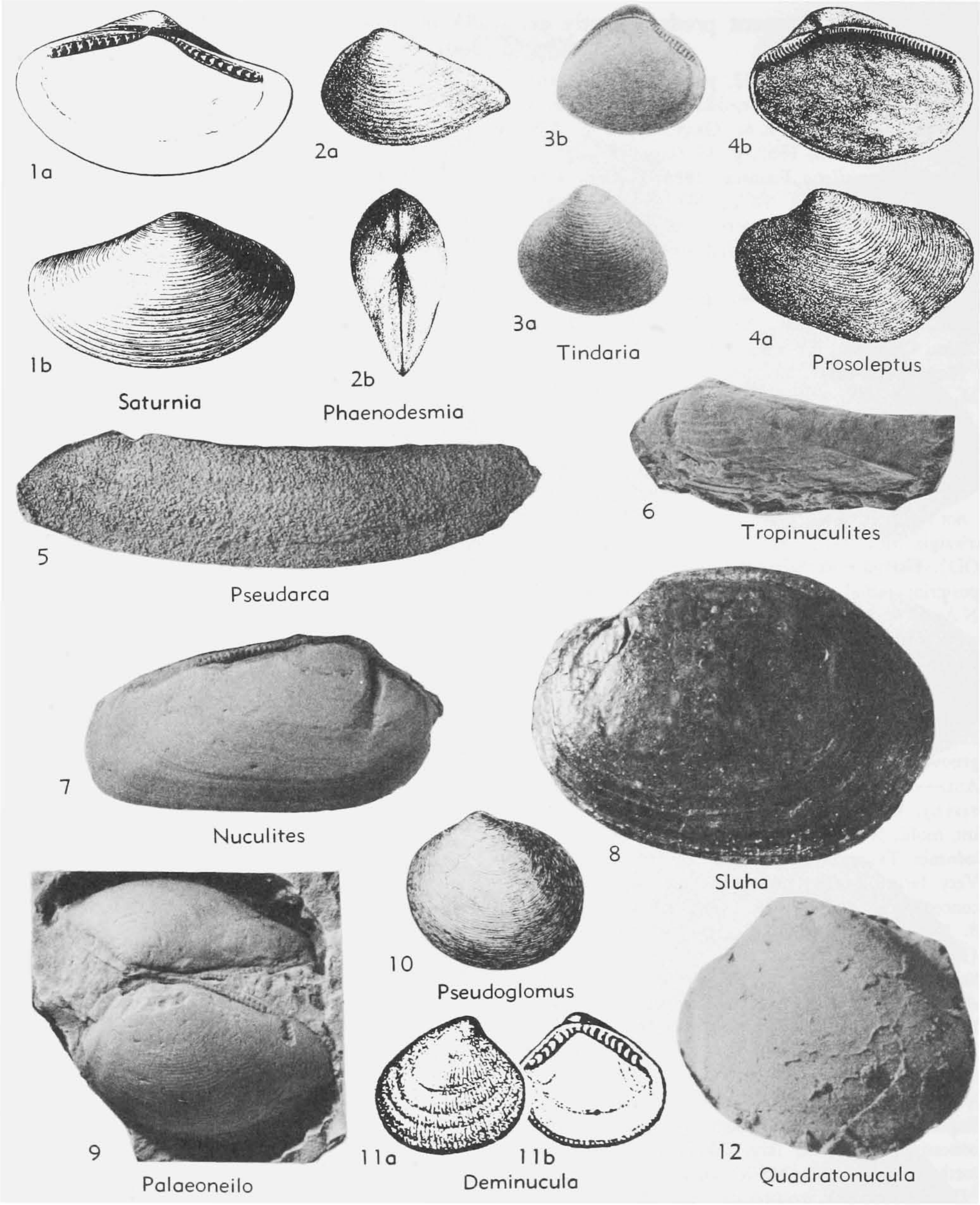

Fig. A5. Malletiidae (p. *N233-N235*).

but with ventral protrusion. *Trias.*, Eu.——A5,*4*. *P. lineata (Goldfuss); *4a,b,* LV ext., RV int., ×1.5 *(58)*.

Pseudarca Tromelin & Lebesconte, 1875, p. 5 [*P. typa; OD] [=*Adranaria* Munier-Chalmas, 1876, p. 105 (type, *A. tromelini*; OD); *Siliquarca* Tromelin & Lebesconte, 1875, p. 5 (obj.)]. Extremely elongate posterior. *Ord.-Dev.*, Eu.——Fig. A5,*5*. *P. typa, Ord., France; LV composite ext.-int. mold, ×1.5 (McAlester, n).

Pseudoglomus Dall, 1898, p. 582 [*Yoldia pompholyx Dall, 1890; OD] [=*Protonucula* Cotton, 1930, p. 223 (type, *P. verconis*; OD)]. Thin shell, weak concentric sculpture, constricted or rounded posterior. *Rec.*, cosmop. (deep oceans).

P. (Pseudoglomus). Rounded, few teeth, slight pallial sinus. *Rec.*, cosmop. (deep oceans).——Fig. A5,*10*. **P. (P.) pompholyx* (Dall), Cuba; LV ext., ×6 (Dall, 1890).

P. (Clencharia) Clarke, 1961, p. 373 [**Tindaria (C.) diaphana;* OD]. Elongate, many teeth, strong pallial sinus. *Rec.*, S.Afr.

Quadratonucula Dickins, 1963, p. 32 [**Q. australiensis*; OD]. Rounded, wide posterior, no surface sculpture. *Perm.*, Australia.——Fig. A5,*12*. **Q. australiensis*; LV ext., ×6 *(263)*.

Saturnia Seguenza, 1877, p. 1178 [**Nucula pusio* Philippi, 1844; M] [=*Austrotindaria* Fleming, 1948, p. 72 (type, *A. wrighti*; OD); *Neilonella* Dall, 1881, p. 126 (type, *Leda (N.) corpulenta;* OD)]. Thick shell, strong concentric sculpture, constricted posterior, strong to weak pallial sinus. *Rec.*, cosmop. (deep oceans).

S. (Saturnia). Not rostrate. *Rec.*, cosmop. (deep oceans).——Fig. A5,*1*. *S. (S.) corpulenta* (Dall), Cuba; *1a,b,* RV int., ext., ×4 *(216)*.

S. (Spinula) Dall, 1908, p. 377 [**Leda (Spinula) calcar*; OD] [=*Bathyspinula* Filatova, 1958, p. 212 *(nom. nud.)*]. Strongly rostrate. *Rec.*, cosmop. (deep oceans).

S. (Tindariopsis) Verrill & Bush, 1897, p. 59 [**Malletia (Tindaria) agathida* Dall, 1889; OD]. Moderately rostrate. *Rec.*, cosmop. (deep oceans).

Sluha Barrande, 1881, p. 159 [**S. expansus*; OD] [=*Praearca* Neumayr, 1891, p. 755 (type, *Arca kosoviensis* Barrande; SD McAlester, 1968); *Servitor* Barrande, 1881, p. 159 (obj.)]. Like *Palaeoneilo*, but rounded, compressed, wider posteriorly. *U.Ord.*, Eu.(Czech.).——Fig. A5,*8*. **S. expansus*; LV composite ext.-int. mold, ×2 (McAlester, n).

Tindaria Bellardi, 1875, p. 28 [**T. arata*; M]. Thick shell, strong concentric sculpture, rounded, weak pallial sinus. *Tert.-Rec.*, cosmop.

T. (Tindaria). Concentric sculpture only. *Tert.-Rec.*, cosmop.——Fig. A5,*3*. **T. (T.) arata*, L. Plio., Italy; *3a,b,* LV ext., int., ×2 *(35)*.

T. (Deminucula) Iredale, 1931, p. 202 [**Nucula praetenta* Iredale, 1924; OD]. Radial and concentric sculpture. *Rec.*, Australia.——Fig. A5,*11*. **T. (D.) praetenta* (Iredale); *11a,b,* LV ext., int., ×4 *(832)*.

Tropinuculites McLearn, 1918, p. 140 [**Nuculites (Orthonota) carinata* Hall, 1860; OD]. Very elongate posterior, with internal septum. *Sil.*, N. Am.(Can.).——Fig. A5,*6*. **T. carinata* (Hall), Nova Scotia; LV composite int.-ext. mold, ×1.5 (McAlester, n).

Family NUCULANIDAE Adams & Adams, 1858

[=Ledidae Adams & Adams, 1858 (obj.)] [Materials for this family prepared by H. S. Puri, Florida Geological Survey]

Resilifer present, ligament partially internal. *Dev.-Rec.*

Nuculana Link, 1807, p. 155 [**Arca rostrata* Chemnitz, 1774; OD (=**Arca pernula* Müller, 1771)] [=*Eptoleda* Iredale, 1939, p. 239 (type, *Leda darwini* Smith, 1884; OD); *Exocholeda* Iredale, 1939, p. 241 *(nom. nud.)*; *Kamaleda* Iredale, 1939, p. 241 *(nom. nud.)*; *Leda* Schumacher, 1817, p. 173 (obj.); *Ledaspina* Marwick, 1931, p. 53 (type, *L. stimulea*; OD); *Monopleura* Philippi, 1887, p. 198 (type, *M. ambigua*; OD); *Perrisonota* Conrad, 1869, p. 98 (type, *P. protexta*; M); *Spineilo* Finlay & Marwick, 1937, p. 17 (type, *Malletia elongata* Marshall, 1917; OD); *Zygonoleda* Iredale, 1939, p. 239 (type, *Z. corbuloides minutalis*; OD)]. Ligament pit narrow, oblique; posterior end produced; with concentric sculpture. *Trias.-Rec.*, cosmop.

N. (Nuculana). Elongate, rostrate, strong concentric sculpture. *Trias.-Rec.*, cosmop.——Fig. A6,*8*. **N. (N.) pernula* (Müller), Eu.; *8a,b,* LV ext., dorsal view of conjoined valves, ×1.5 (Sars, 1878); *8c,* RV hinge, ×5.5 *(938)*.

N. (Borissia) Slodkevich, 1938 [**N. (B.) alferovi;* OD]. Outline as in *Nuculana,* but less inequilateral; with low broad concentric ribs covering median portion of valve. *Mio.?*, USSR (Kamchetka).——Fig. A6,*2*. **N. (B.) alferovi*; *2a,b,* dorsal views of conjoined valves; *2c,* LV ext., ×3 *(848)*.

N. (Costanuculana) Habe, 1951, p. 25 [**N. husamaru* Nomura, 1940; OD]. Shell medium, thick; surface with conspicuous circular furrow on earlier half; later one-third flat and smooth. Hinge teeth, large, few. *Rec.*, Japan.——Fig. A6, *6*. **N. (C.) husamaru* (Nomura); *6a,b,* LV ext., int., ×2 *(365)*.

N. (Costelloleda) Hertlein & Strong, 1940, p. 370 [**N. costellata* Sowerby, 1832; OD]. Shell elongate, with strong concentric sculpture. *Rec.*, N.Am.——Fig. A6,*12*. **N. (C.) costellata* (Sowerby), Calif.; LV ext., ×3 *(403)*.

N. (Jupiteria) Bellardi, 1875, p. 20 [**N. concava* Bronn, 1831; SD Dall, 1898] [=*Teretileda* Iredale, 1929, p. 158 (type, *Nuculana oculata* Iredale, 1925; OD)]. Small, corbuloid, strongly inflated, rostrum blunt and barely ridged; sinus shallow. *U.Cret.-Rec.*, N.Z.-N.Am.-Eu.——Fig. A6,*11*. *N. (J.) oculata* (Iredale), Rec., Australia; LV ext., ×3 *(432)*.

N. (Ledella) Verrill & Bush, 1897, p. 54 [*nom. subst. pro Junonia* Seguenza, 1877, p. 1175 (*non Junonia* Huebner, 1819)] [**Leda messanensis* Seguenza, 1877; SD Verrill & Bush, 1897] [=*Comitileda* Iredale, 1924, p. 181 (type, *Leda miliacea* Hedley, 1902; OD); *Magaleda* Iredale, 1929, p. 158 (type, *Leda inopinata* Smith, 1885; OD)]. Short, with unicarinate rostrum. *Oligo.*, N.Z.-E.Indies; *Mio.-Plio.*, Italy; *Rec.*, cosmop.——Fig. A6,*7*. **N. (L.) messanen-*

sis (SEGUENZA), Rec., N.Am.; LV hinge, ×8 (Verrill & Bush, 1897).

N. (Lembulus) RISSO, 1826, p. 319 [**Lembulus rossianus*; SD GRAY, 1847]. Like *Saccella* but with wider and deeper posterior groove; with diagonal sculpture. *Eoc.-Rec.*, cosmop.——FIG. A6,*3*. **N.* (*L.*) *rossianus* (RISSO), Rec., Medit.; RV ext., ×1 *(789)*.

N. (Politoleda) HERTLEIN & STRONG, 1940, p. 370 [**Nucula polita* SOWERBY, 1832; OD]. Shell

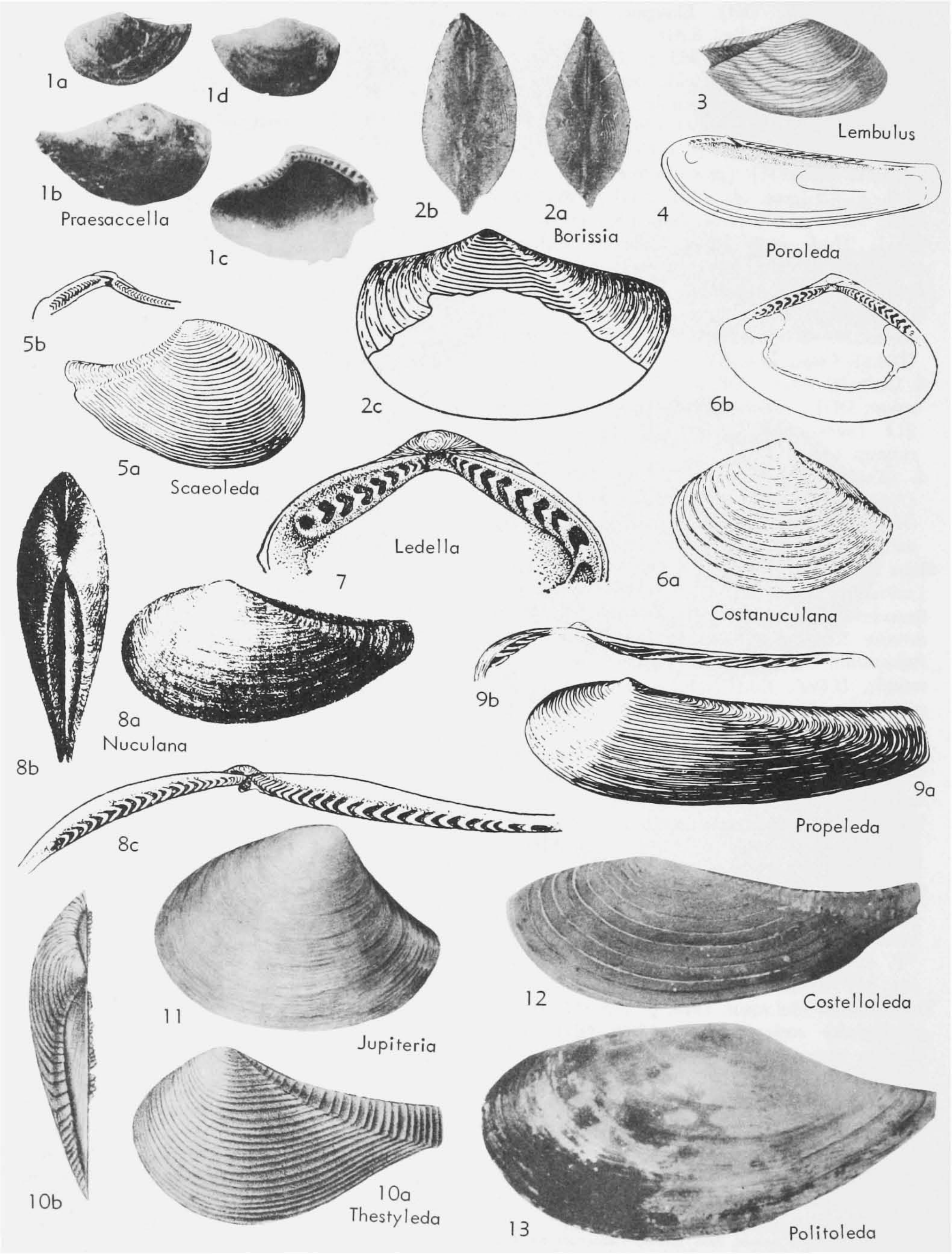

FIG. A6. Nuculanidae (p. *N235-N237*).

elongate, posteriorly pointed; sculpture of very fine concentric growth lines and fine, wavy incised lines on lower half, posteriorly nearly parallel to posterior dorsal margin. _Rec._, trop. Am.——Fig. A6,_13_. *_N. (P.) polita_ (Sowerby); LV ext., ×3 _(403)_.

N. (Poroleda) Tate, 1893, p. 186 [*_Scaphula? lanceolata_ Hutton, 1885; SD Cotton & Godfrey, 1938]. Shell like _Nuculana_ but with an oblique cartilage pit and nearly straight hinge line with longitudinal imbricating teeth. _Eoc.-Rec._, N.Z.——Fig. A6,_4_. *_N. (P.) lanceolata_ (Hutton), Rec.; RV int., ×2 _(398)_.

N. (Praesaccella) Cox, 1940, p. 32 [*_N. (P.) juriana_, OD]. Shell as in _Saccella_ but with entire pallial line, larger and less numerous hinge teeth. _Jur._, India-Eu.(France-Port.).——Fig. A6, _1_. *_N. (P.) juriana_ (Cox), India; _1a_, LV ext., ×2.2, _1b-d_, RV ext., LV int., RV ext., ×4 _(183)_.

N. (Propeleda) Iredale, 1924, p. 181 [*_Leda ensicula_ Angas, 1877; OD] [=_Lamellileda_ Cotton, 1930 (type, _L. typica_; OD)]. Shell sickle-shaped, chondrophore backwardly sloping, hinge thin. _Rec._, Australia.——Fig. A6,_9_. *_N. (P.) ensicula_ (Angas), _9a,b_, LV ext., RV hinge, ×5 _(166)_.

N. (Robaia) Habe, 1958, p. 248 [*_Leda robai_ Kuroda, 1929; OD]. No concentric sculpture, moderately rostrate. _Rec._, Japan.

N. (Rollieria) Cossmann, 1920, p. 82 [_nom. subst. pro Nuculopsis_ Rollier, 1912, p. 64 (_non Nuculopsis_ Girty, 1911); =_Isoleda_ Rollier, 1923, p. 67, _nom. subst. pro Nuculopsis_ Rollier, 1912, and _Isonuculana_ Cox, 1925, p. 124, _nom. subst. pro Isoleda_ Rollier, 1923] [*_Nucula palmae_ Sowerby, 1824; SD Rollier, 1923]. Shell thin, ovate, smooth, without dorsal areas or umbonal ridges; anterior and posterior rows of hinge form very obtuse angle. Pallial line with small sinus. _Jur._, Eu.-India.

N. (Saccella) Woodring, 1925, p. 15 [_nom. subst. pro Ledina_ Sacco, Dec. 1898, p. 26 (_non Ledina_ Dall, April 1898)] [*_Arca fragilis_ Chemnitz, 1784; OD]. Rostrate, rostrum pointed; sculpture of strong concentric rugae; posterior and anterior series of teeth equal; pallial sinus U-shaped. _Tert.-Rec._, cosmop.

N. (Scaeoleda) Iredale, 1929, p. 158 [*_Nucula crassa_ Hinds, 1843; OD]. Shell large, stout, strongly lirate, long-beaked. _Rec._, S.Pac.(Tasmania-Low Isles).——Fig. A6,_5_. *_N. (S.) crassa_ (Hinds), Australia; _5a,b_, RV ext., hinge, ×1.3 _(572)_.

N. (Thestyleda) Iredale, 1929, p. 158 [*_Leda ramsayi_ Smith, 1885; OD]. Rostrate with strong concentric sculpture that curves at rostral sinus. Posterior truncate; often with a keel at inflection of concentric ribs; chondrophore large. _Plio.-Rec._, W.Am.——Fig. A6,_10_. *_N. (T.) ramsayi_ (Smith); _10a,b_, LV ext., dorsal, ×6 _(852)_.

Adrana Adams & Adams, 1858, p. 547 [*_Nucula lanceolata_ Lamarck, 1819; SD Stoliczka, 1871]. Shell thin, compressed, narrow-lanceolate or long-elliptical, nearly equilateral, sculpture oblique. _Eoc.-Rec._, cosmop.——Fig. A7,_2_. _A. taylori_ (Hanley), Rec.; RV ext., ×2 _(383)_.

Costatoleda Roth von Telegd, 1914 (1915), p. 61 [*_Leda (C.) psammobiaeformis_ Roth von Telegd, 1914; OD]. Shell sculptured like _Hilgardia_ but without a well-pronounced rostrum. _Oligo._, Eu. (Hungary).——Fig. A7,_4_. *_C. psammobiaeformis_; _4a,b_, LV ext., dorsal view of conjoined valves, ×1 _(800)_.

Dacryomya Agassiz, 1840, p. 500 [*_Nucula lacryma_ Sowerby, 1824; SD Herrmannsen, 1846, p. 368] [=_Dacryomia_ Gressley, 1838 _(nom. nud.)_]. With chondrophore; inflated, with truncate rostrum, dorsally concave; umbones prominent, opisthogyrous; escutcheon deep, bounded by sharp carinae which divide pallial line or not. _M.Jur._, Eu.——Fig. A7,_1_. *_D. lacryma_ (Sowerby), Eng.; _1a-c_, RV ext., LV ext., LV int., ×2 _(870)_.

Ezonuculana Nagao, 1938, p. 121 [*_Nuculana mactraeformis_ Nagao; OD]. Not nacreous, sculpture concentric, with chondrophore; pallial sinus small to obsolete. _Cret._, Japan.——Fig. A7,_5_. *_E. mactraeformis_ (Nagao), Cret., Japan; _5a,b_, LV int., RV ext., ×2 _(655)_.

Hilgardia Harris & Palmer, 1946, p. 59 [*_Leda multilineata_ Conrad, 1855; OD]. With radial ribs intersecting concentric sculpture as crenulations and nodes. _Eoc._, N.Am.——Fig. A7,_7_. *_H. multilineata_ (Conrad); _7a_, dorsal view of conjoined valves, ×3.5; _7b_, RV int., ×3; _7c_, LV ext., ×2.75 _(389)_.

Ledina Dall, Apr. 1898, p. 580 [_non Ledina_ Sacco, Dec. 1898] [*_Leda eborea_ Conrad, 1860 (_non_ Conrad, 1846) (=*_L. smirna_ Dall, 1898); OD]. Strong, solid arcuate below, ends evenly rounded, valves smooth, equilateral. _?Eoc._, N.Am.——Fig. A7,_3_. *_L. smirna_ Dall; LV ext., ×1 _(387)_.

Lithorhadia Stewart, 1930, p. 37 [*_Leda acala_ Dall, 1898; OD]. Shape of _Nuculana_ but hinge of _Calorhadia_. _Eoc._, cosmop.——Fig. A7,_8_. *_L. acala_ (Dall), N.Am.; LV ext., ×3 _(223)_.

Mesosaccella Chavan, 1946, p. 197 [*_Nucula foersteri_ Müller, 1847; OD]. No ligamental fossettes, ligament external, behind beaks, a depressed widening below beaks foreshadowing the fossette. Outline and sculpture of _Saccella_. _Cret._, Eu.——Fig. A7,_6_. *_M. foersteri_ (Müller); _6a,b_, dorsal view of both valves, RV ext., ×2, ×3 _(650)_.

Paleyoldia Lintz, 1958, p. 108 [*_Yoldia glabra_ Beede & Rogers, 1899; OD]. Compressed, elongate anterior, strong concentric sculpture. _Penn._, USA(Tex.-Okla.Kans.).——Fig. A8,_2_. *_P. glabra_ (Beede & Rogers), Tex.; LV ext., ×2 (McAlester, n).

Phaseolus Monterosato, 1875, p. 4 [**P. ovatus*; OD][=*Silicula* Jeffreys, 1879, p. 573 (obj.)]. Shell small, teeth few, lamelliform, oblique. [Deep-water.] *Rec.,* Atl.-Medit.

Phestia Chernyshev, 1951, p. 9 [**Leda inflatiformis* Chernyshev, 1939; OD] [=*Culunana* Lintz, 1958, p. 106 (type, *Leda bellistriata* Stevens, 1858; OD); *Girtyana* Elias, 1956, p. 127

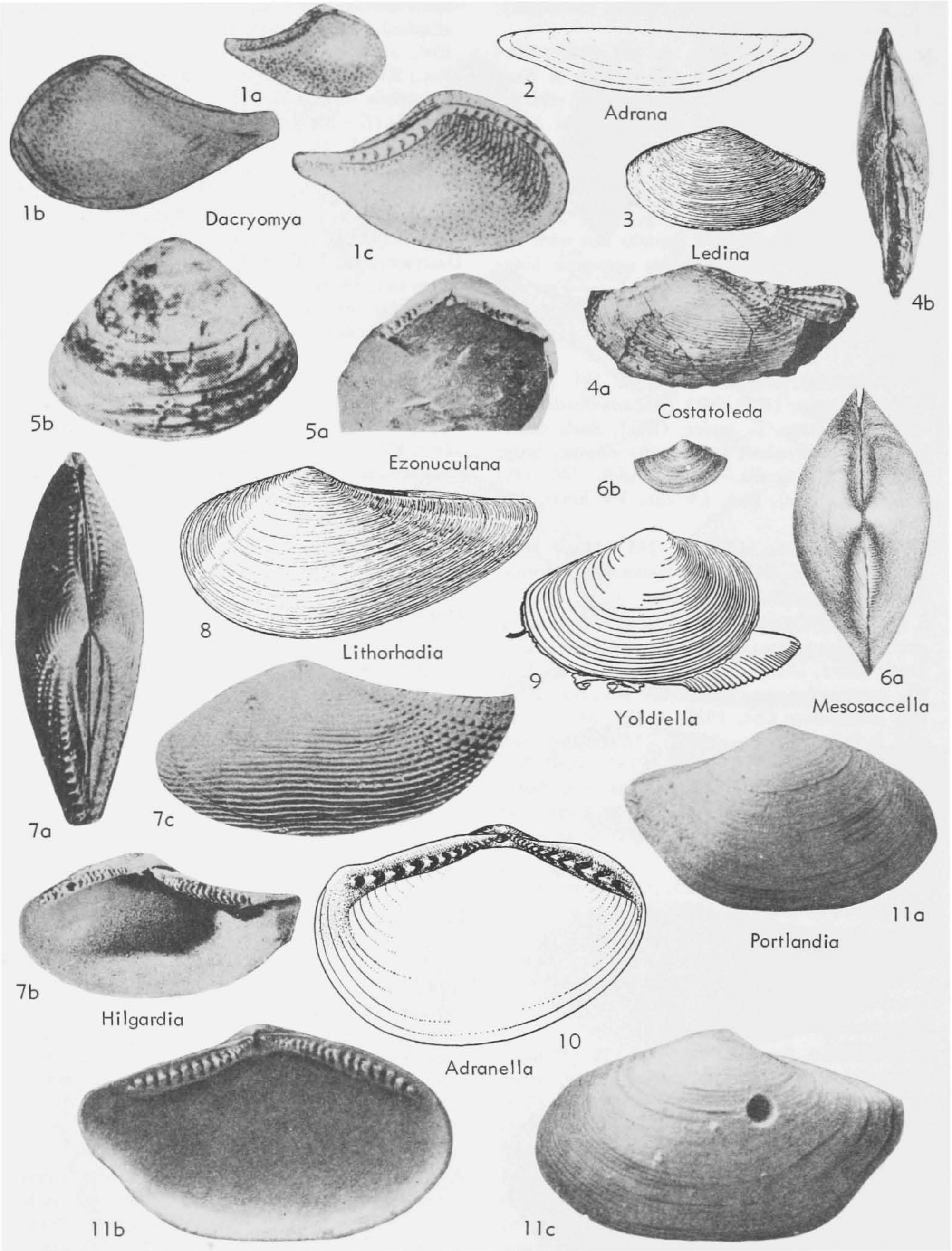

Fig. A7. Nuculanidae (p. *N*237, *N*239),

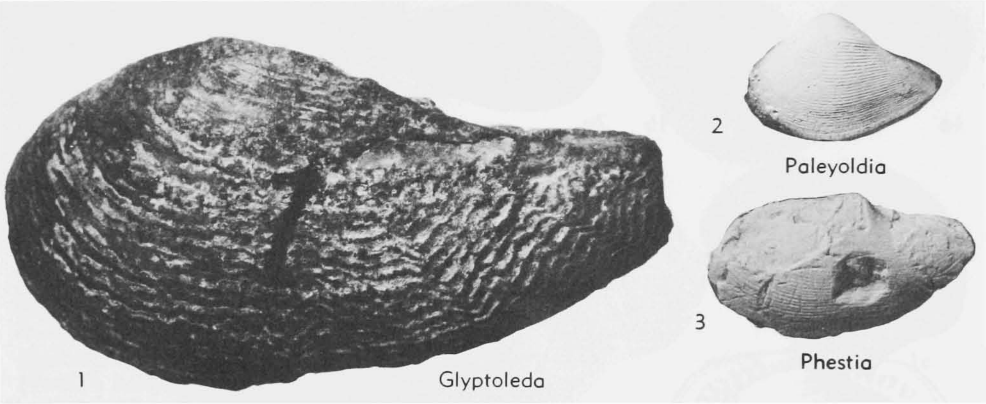

Fig. A8. Nuculanidae (p. *N*238-*N*239).

(type, *G. honessi*; OD); *Nuculochlamys* Paul, 1941, p. 38 *(nom. nud.)*; *Polidevcia* Chernyshev, 1951, p. 25 (type, *Leda karagandensis* Chernyshev, 1941; OD)]. Like *Nuculana,* but with prominent internal ridges. *Dev.-L.Trias.,* cosmop. ——Fig. A8,*3*. **P. inflatiformis* (Chernyshev), U. Carb., USSR; LV ext., ×2 (McAlester, n).

Portlandia Mörch, 1857, p. 93 (ICZN, 1966 (Opinion 769, name no. 1705)] [**Nucula arctica* Gray, 1824; SD ICZN, 1966 (Opinion 769, name no. 2132)] [=*Pseudoportlandia* Woodring, 1925, p. 20 (type, *Leda clara* Guppy, 1873; OD); *Portlandella* Stewart, 1930, p. 61 (type, *Leda rosa* Hanna, 1927; OD)]. Inflated, somewhat rostrate. *Tert.-Rec.,* cosmop.

P. (Portlandia). Posterior end set off by indistinct furrow; pallial sinus deep. *Tert.-Rec.,* cosmop. ——Fig. A9,*4*. **P. (P.) arctica* (Gray), Rec., N.Atl.; RV ext., ×2 (Mossevitch, 1928).——Fig. A7,*11*. *P. (P.) clara* (Guppy), Mio., Jamaica; *11a-c,* RV ext., LV int., ext., ×4 *(1005)*.

P. (Adranella) Verrill & Bush, 1898, p. 858 [**Yoldia (A.) casta* Verrill & Bush, 1898; OD]. Oblong-ovate, compressed, with posterior end broadly rounded, rostrum nearly obsolete. *Rec.,* Carib.——Fig. A7,*10*. **P. (A.) casta* (Verrill & Bush); LV int., ×11 *(938)*.

P. (Hataiyoldia) Kamada, 1962, p. 55 [**Yoldia tokunagai* Yokoyama, 1925; OD]. Like *P. (Portlandia)* but with zigzag surface sculpture. *Mio.,* Japan.

P. (Yoldiella) Verrill & Bush, 1897, p. 55 [**Yoldia lucida* Lovén, 1846; OD]. Small; ligament external; pallial sinus indistinct; mostly in deep water. *Rec.,* E.Am.-W.Am.——Fig. A7,*9*. **P. (Y.) lucida* (Lovén), N.Am.; RV view entire animal, ×5.5 *(937)*.

Pristigloma Dall, 1900, p. 44 [*nom. subst. pro Glomus* Jeffreys, 1876, p. 433 (*non* Gistel, 1848)] [**Glomus nitens* Jeffreys, 1876; M]. Like *Sarepta,* but with more unequal, V-shaped teeth. [Deep oceans]. *Rec.,* cosmop.

Ryderia Wilton, 1830, p. 72 [**Leda renevieri* Oppel; SD Cox, 1936]. Pallial sinus very wide, shallow; shell-shaped like *Nuculana*. Rostrum very long and narrow. *Jur.,* Eu.——Fig. A9,*3*. **R. renevieri* (Oppel), Eng.; *3a-c,* LV ext., dorsal view of both valves, LV ext., ×1*(992)*.

Sarepta Adams, 1860, p. 303 [**S. speciosa*; OD] [=*Ovaleda* Iredale, 1925, p. 248 (type, *Sarepta tellineaformis* Hedley, 1902)]. Rounded, not rostrate, very short hinge. *Rec.,* Indo-Pac.——Fig. A9,*1*. **S. speciosa,* Japan; *1a,b,* LV ext., int., ×3.0 (Adams, 1868).

Veteranella Patte, 1926, p. 158 [**Nuculana (V.) strenua*; OD]. Similar to *Nuculana* but characterized by chevron-shaped ornamentation. *Perm.-Trias.,* Indo-Pac.

V. (Veteranella). Small, oval, posterior not constricted. *U.Trias.,* Indo-China.

V. (Glyptoleda) Fletcher, 1945, p. 298 [**G. reidi*; OD]. Large, elongate, posterior constricted. *Perm.,* Australia.——Fig. A8,*1*. **V. (G.) reidi*; LV ext., ×2 (McAlester, n).

V. (Nucundata) Waterhouse, 1965, p. 641 [**N. undata*; OD]. Similar to *V. (Glyptoleda)* but with less prominent chevron-shaped ornamentation. *Perm.,* N.Z.

Yoldia Möller, 1842, p. 18 [**Y. hyperborea* Torell, 1859 (*pro Y. arctica* Möller, 1842, *non Nucula arctica* Gray, 1824); SD ICZN, 1966 (Opinion 769)] [=*Microyoldia* Verrill & Bush, 1897, p. 56 (type, *Y. regularis* Verrill, 1884; OD); *Tepidoleda* Iredale, 1939, p. 240 (type, *T. lata orion*; OD)]. Elongate-ovate, thin-shelled gaping in most; hinge series subequal; resilium pit large; pallial sinus deep and wide. *Cret.-Rec.,* cosmop.

Y. (Yoldia). Smooth, compressed, pedal gape wide, siphonal gape moderate. *Cret.-Rec.,* cosmop.——

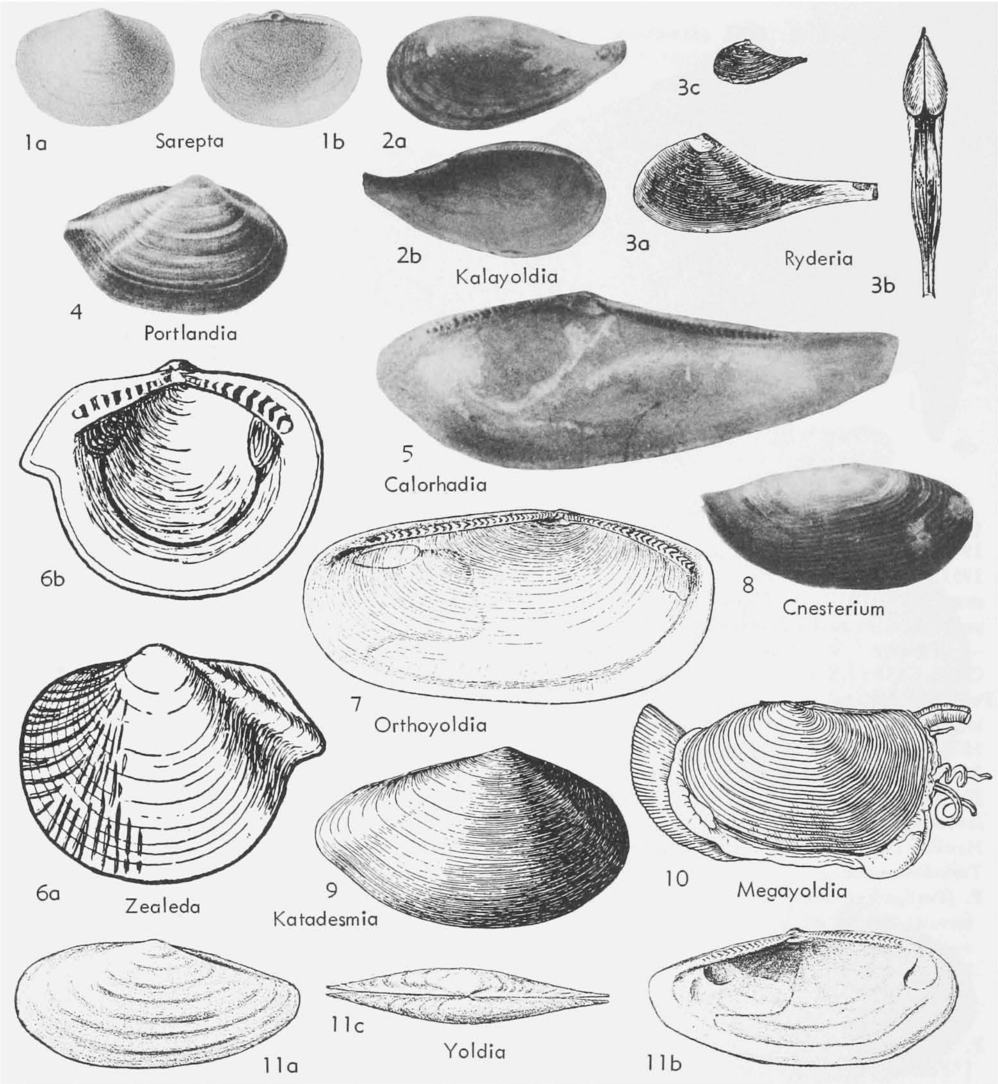

Fig. A9. Nuculanidae (p. *N*239-*N*241).

Fig. A9,*11*. **Y.* *(Y.)* *hyperborea* (Torell), Rec., N.Atl.; *11a-c*, LV ext., int., both valves dorsal, ×1 *(829)*.

Y. (Aeqviyoldia) Soot-Ryen, 1951, p. 6 [**Y. subaequilateralis* Smith, 1875; OD]. Equilateral, slightly rostrate; chondrophore triangular, broad, mantle margins fringed above siphons. *Rec.*, Antarctic(South Shetland I.).

Y. (Calorhadia) Stewart, 1930, p. 37 [**Leda pharcida* Dall, 1898; OD]. With sunken lunule; ligamental pit wide. *Eoc.*, Am.——Fig. A9,*5*. **Y.* *(C.)* *pharcida* (Dall), N.Am.; RV int., ×1.5 *(892)*.

Y. (Cnesterium) Dall, 1898, p. 595 [**Y. scissurata* Dall, 1897 (*pro Nucula arctica* Broderip & Sowerby, 1829, *non* Gray, 1824); OD] [=*Scissula* Dall, 1908, p. 256 (*non* Dall, 1900) (obj.)]. With oblique secondary incised sculpture especially on anterior end. *Rec.*, E.Pac.——Fig. A9,*8*. **Y.* *(C.)* *scissurata*, W.Am.; RV ext., ×1 *(345)*.

Y. (Kalayoldia) Grant & Gale, 1931, p. 128 [**Y. cooperi* Gabb, 1865; OD]. Posterior part of valves short, narrowed, recurved. *Mio.-Rec.*, W.Am.——Fig. A9,*2*. **Y.* *(K.)* *cooperi*, Rec.; *2a,b*, LV ext., int., ×0.5 (Grant & Gale, 1931).

Y. (Katadesmia) Dall, 1908, p. 379 [**Y. (K.) vincula* Dall, 1908; OD]. With well-defined functional opisthodetic ligament. *Rec.*, C.Am.——Fig. A9,*9*. **Y. (K.) vincula*; RV ext., ×3 (Dall, 1908).

Y. (Megayoldia) Verrill & Bush, 1897, p. 55 [**Nucula thraciaeformis* Storer, 1838; OD] [=*Multidentata* Krishtofovich, 1964 (type, *Y. multidentata* Khomenko, 1937; OD)]. Broad, compressed, rostrum indefinite, with posteroventral marginal lobe; chondrophore large, concave, striate within; pallial sinus large; ligament external, strongly developed. *Oligo.-Rec.*, cosmop. ——Fig. A9,*10*. **Y. (M.) thraciaeformis* (Storer), Rec., N.Am.; LV, with animal, ×0.67 (Verrill & Bush, 1897).

Y. (Orthoyoldia) Verrill & Bush, 1897, p. 55 [**Y. scapania* Dall, 1889; OD]. Oblong, blunt or rounded at both ends, without distinct rostrum, no carina; pallial sinus broad; teeth numerous in both series. *Eoc.-Rec.*, Carib.-W.N.Am.——Fig. A9,*7*. **Y. (O.) scapania* Dall, Rec., Brazil; LV int., ×3 (Dall, 1889).

Zealeda Marwick, 1924, p. 25 [**Z. hamata;* OD]. With radial ribs that become divaricate anteriorly; no pallial sinus. *Oligo.-Rec.*, N.Z.——Fig. A9,*6*. **Z. hamata,* Plio., N.Z.; *6a,b,* LV ext., int., ×10 (Marwick, 1924).

Family ISOARCIDAE Keen, new family

[Materials for this family prepared by Myra Keen]

Cordate, inequilateral; shell material nacreous; ligament external. *M.Jur.-U.Cret.*

Isoarca Münster, 1842 [**Isocardia subspirata* Münster, 1837; SD Woodward, 1854] [=*Prionia* Desor & Gressly, 1859 (*non* Huebner, 1819)]. Sculpture decussate to concentrically striate; hinge teeth angled at ends of anterior and posterior series, hinge arched *(673)*. *M.Jur.(Bajoc.)-U.Cret. (Senon.),* Eu.——Fig. A10,*1a*. *I. texata* (Münster), U.Jur., Ger.; RV int., ×1 (Goldfuss).——Fig. A10,*1b,c*. **I. subspirata* (Münster), U.Jur., Ger.; *1b,c,* LV and dorsal views of int. molds, both valves ×1 *(341)*.

Subclass CRYPTODONTA Neumayr, 1884

[*nom. transl. et correct.* Newell, 1965 (*ex* Cryptodonten Neumayr, 1884; unspecified familial group name)] [Diagnosis by N. D. Newell]

Generally equivalve, thin-shelled dimyarian bivalves; hinge plate absent or narrow; ligament external, amphidetic to opisthodetic, generally without nymphs; hinge margin edentulous or taxodont. *?U.Cam., L.Ord.-Rec.*

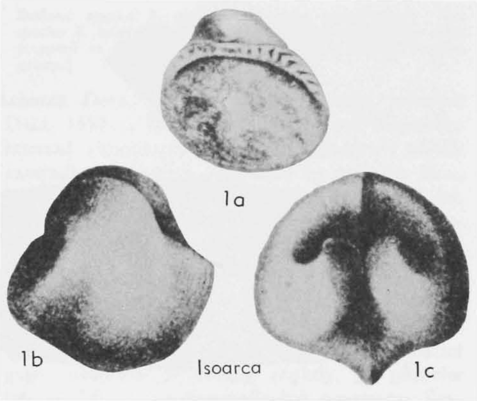

Fig. A10. Isoarcidae (p. *N*241).

A provisional arrangement for diverse, poorly understood, mainly Paleozoic forms.

Order SOLEMYOIDA Dall, 1889

[*nom. transl. et correct.* Newell, 1965 (*ex* suborder Solenomyacea Dall, 1889)] [Diagnosis by N. D. Newell]

Edentulous, anisomyarian, anterior adductor muscle being larger than posterior; shell gaping, with anterior end longer than posterior; shell microstructure homogeneous, aragonitic; gills protobranchiate. *Dev.-Rec.*

Superfamily SOLEMYACEA H. Adams & A. Adams, 1857 (1840)

[*nom. transl.* Dall, 1895 (*ex* Solemyidae Adams & Adams, 1857)] [Materials for this superfamily prepared by L. R. Cox]

Equivalve; oblong or oval, moderately to strongly inequilateral, with umbones toward posterior end; weakly to rather strongly inflated; no anterodorsal area (lunule), escutcheon present in some forms; hinge edentulous; ligament wholly or mainly posterior to beaks, internal or external; dimyarian, pallial line obscure in many forms; ostracum thin, porcelaneous internally; surface smooth or with weak radial ornament; periostracum thick in living forms, projecting (except dorsally) well beyond margins of calcareous part of valves. *Dev.-Rec.*

This superfamily consists only of the family Solemyidae. Its living representatives are protobranchiate, so that in Pelseneer's classification, based on gill structure, the group was placed in the same

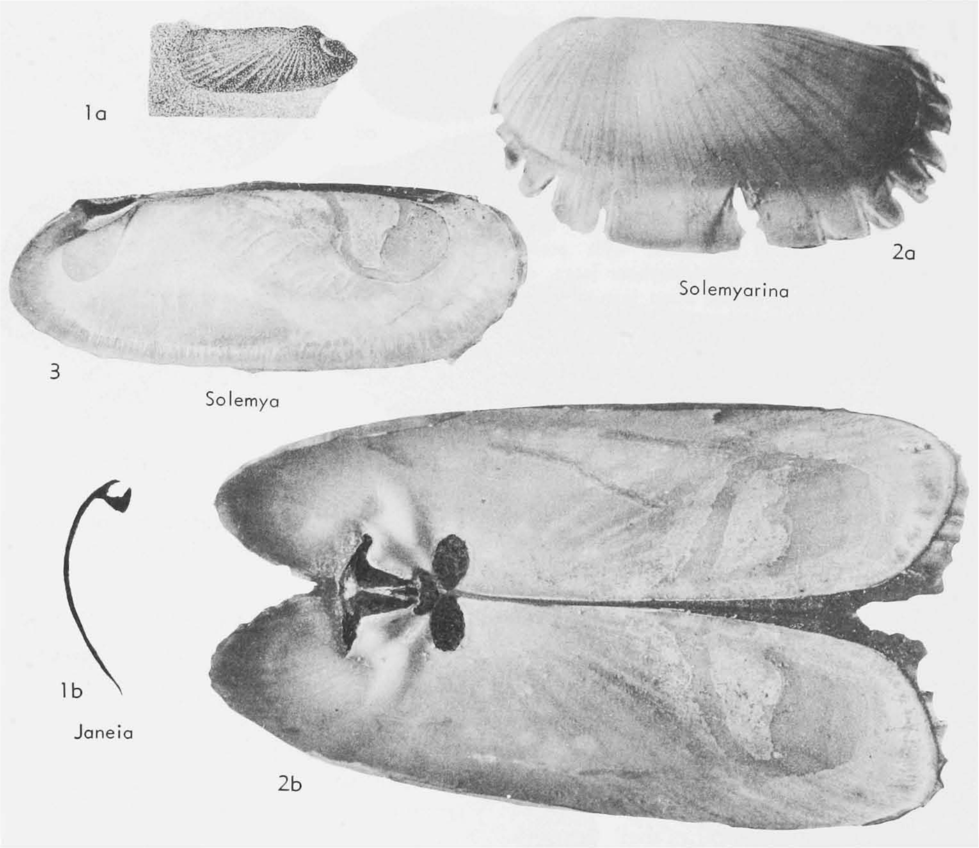

FIG. B1. Solemyidae (p. *N*243).

order as the Nuculacea. The foot is large and adapted for burrowing. When the valves are drawn together their uncalcified (periostracal) fringe can be tucked in between their margins by the action of special muscles. The animal lives buried in the muddy or sandy substratum.

Family SOLEMYIDAE Adams & Adams, 1857 (1840)

[Solemyidae ADAMS & ADAMS, 1857 (*pro* Solenomyadae GRAY, 1840)] [=Solenomyidae VON MARTENS, 1867; Solemyacidae DALL, 1900; Solenomyacidae DALL, 1908] [In accordance with Code Art. 40a,b, this family ranks from 1840 for purposes of priority]

Characters of superfamily. *Dev.-Rec.*

Solemya LAMARCK, 1818, p. 488 [**S. mediterranea* (=**Tellina togata* POLI, 1795, p. 42); SD CHILDREN, 1823] [=*Solenimya* BOWDICH, 1822 *(nom. van.); Solenomya* CHILDREN, 1823 *(nom. van.); Stephanopus* SCACCHI, 1833 (obj.); *Solenymia* SWAINSON, 1840 *(nom. van.)*; *Solenymya* SCHAUFUSS, 1869 *(nom. van.)*]. Elongate-oval or subrectangular, compressed; umbones level with hinge margin, placed well toward posterior end of shell; valve margins with narrow anterior and posterior gapes; ligament wholly or mainly posterior to beaks and located between margin and thick internal chondrophore sloping obliquely downward from beak; posterior adductor scar rather small, anterior scar larger, continued from its posteroventral corner by scar forming narrow band ascending obliquely to and broadening out along dorsal margin, and marking attachment of muscles of integument of visceral mass and (dorsally) of foot;[1] pallial line entire, usually obscure; ornament consisting of irregularly arranged, depressed radial ribs; periostracum polished, consisting of radial sectors alternating in thickness and varying in width according to ribbing of shell; periostracum extends well beyond margins of calcareous part of valves, forming frill which on death of animal cracks along thinner sectors,

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[1] The compiler is grateful to Professor G. OWEN, of Belfast, for confirming the interpretation here given of this characteristic internal scar of *Solemya*.

producing series of rectangular or tongue-like projections separated by fissures (usual condition of Recent museum specimens). [Few fossil forms can be assigned definitely to subgenera, as these are distinguished by internal shell features.] *Dev.-Rec.*, cosmop.

S. (Solemya). Ligament posterior to umbones, only very thin descending strip adhering to shell interior in front of chondrophore, which lacks supporting buttresses. *Rec.*, Medit.-W.Atl. Fossil distribution uncertain.——Fig. B1,*3*. **S. (S.) togata* (Poli), Medit.; LV int., showing ligament (black) with supporting chondrophore, muscle scars, and broken edge of periostracum (along anterodorsal margin), ×2 (Cox, n).

S. (Janeia) King, 1850, p. 177 [**Solemya primaeva* Phillips, 1836, p. 209; OD] [=*Janeira* Tryon, 1884 *(nom. null.)*]. Resembling *S. (Solemya)* in external features and in presence of internal chondrophore; with internal ridge originating at anterior end of chondrophore and diverging from it at acute angle, passing below posterior adductor scar. *Dev.-Perm.*, cosmop.——Fig. B1,*1a*. **S. (J.) primaeva* Phillips, L.Carb., Eng.; LV ext., ×1 *(407)*.——Fig. B1,*1b*. *S. (J.) truncata* (Goldfuss), M.Dev., Ger.; dorsoventral sec. posterior to umbo, showing internal chondrophore, ×2 (W. Quenstedt, 1930).

[The impression of the internal ridge is seen on molds of the type species, which also bear indications of the chondrophore. The latter is well seen in transverse sections of the Devonian species *S. (J.) truncata* (Goldfuss) (Fig. B1,*1b*). It is not possible to say if *Janeia* differed from the subgenera enumerated next in any features of importance.]

S. (Petrasma) Dall, 1908, p. 2 [**Solemya borealis* Totten, 1834, p. 366; OD]. Ligament wholly posterior to umbones; chondrophore with 1 or 2 internal ridges below it. *Plio.*, Japan; *Rec.*, E. Pac.-Japan-W.Atl.-Carib.

S. (Solemyarina) Iredale, 1931, p. 202 [**Solemya velesiana*; OD] [=*Zesolemya* Iredale, 1938 (type, *Solemya parkinsonii* Smith (*ex* Gray, MS); *Solemyaria* Habe, 1951 *(nom. null.)*]. Most of ligament located between chondrophore and dorsal margin, but small part extending anteriorly beyond chondrophore, partly along margin beyond umbo and partly as thin patch reaching downward on interior of valve; internal ridge diverges from chondrophore at acute angle, bounding posterior adductor. *Oligo.*, USA(Ore.-Wash.); *Rec.*, Australia-N.Z.——Fig. B1,*2*. *S. (S.) australis* Lamarck, Rec., Australia; *2a*, RV ext., with frill of cracked periostracum, ×1; *2b*, opened valves, int., showing chondrophore, rib diverging from it, and int. ligament (darkened) with thin oval ant. extension, but foreshortened dorsoventrally, ×2 (both Cox, n).

[The type species of *Solemyarina* has not been figured, but its internal characters have been briefly described by Iredale (1938, Brit. Museum [Nat. History], *Great Barrier Reef Exped. Sci. Rept.* v. 5, no. 6, p. 233). The characters distinguishing it from the better-known New Zealand species *S. parkinsonii* seem unimportant. The species *S. australis* Lamarck, which some authorities have accepted as type species of *Solemya*, also belongs to this group.]

Acharax Dall, 1908, p. 2 [**Solemya johnsoni* Dall, 1891, p. 189; OD]. Like *Solemya* externally; internal chondrophores absent, ligament wholly external, opisthodetic, supported by nymphs. *Mio.*, USA-Japan; *Rec.*, E. Pac.-W. Pac.-Ind. O.-W. Atl. [Probably also fossil from Dev. onward, if considered to include all *Solemya*-like forms with external ligament and without internal rib.]

Adulomya Kuroda, 1931, p. 27 [**A. uchimuraensis*; M]. Relatively large (up to 19 cm. long), elongate, slightly arched, with narrow anterior gape; umbones protruding slightly, at posterior 6th or 7th of length; no radial ornament; ligament external; internal rib running from below beak to posteroventral corner, passing below posterior adductor scar. *Mio.*, Japan.

Order PRAECARDIOIDA Newell, 1965

[Diagnosis by N. D. Newell]

Circular to oval or elongate, shells thin; isomyarian; ligament external, amphidetic or opisthodetic; hinge plate weak or lacking; edentulous, or with interlocking taxodont denticles resembling provinculum of living forms; terminal margins gaping in some forms; pallial line generally entire but with small sinus demonstrated in a few forms. *?U.Cam., L.Ord.-L.Miss.*

Superfamily PRAECARDIACEA Hörnes, 1884

[*nom. transl.* Newell, 1965 (*ex* Praecardiidae Hörnes, 1884)] [Materials for this superfamily prepared by N. D. Newell and Aurèle LaRocque]

Ovate, orthogyre, or prosogyre with prominent beaks; ligament amphidetic or lacking, without nymphs; lunule and escutcheon poorly defined or lacking; musculature unknown. *?U.Cam., L.Ord.-L.Miss.*

Family PRAECARDIIDAE Hörnes, 1884

Shell approximately equivalve; with or without marginal gape; cardinal area broad and flattened to narrow; surface rarely smooth, more commonly radially costate. *?U.Cam., L.Ord.-L.Miss.*

The so-called taxodont dentition in this group may represent a neotenous retention of the provinculum. In some shells the den-

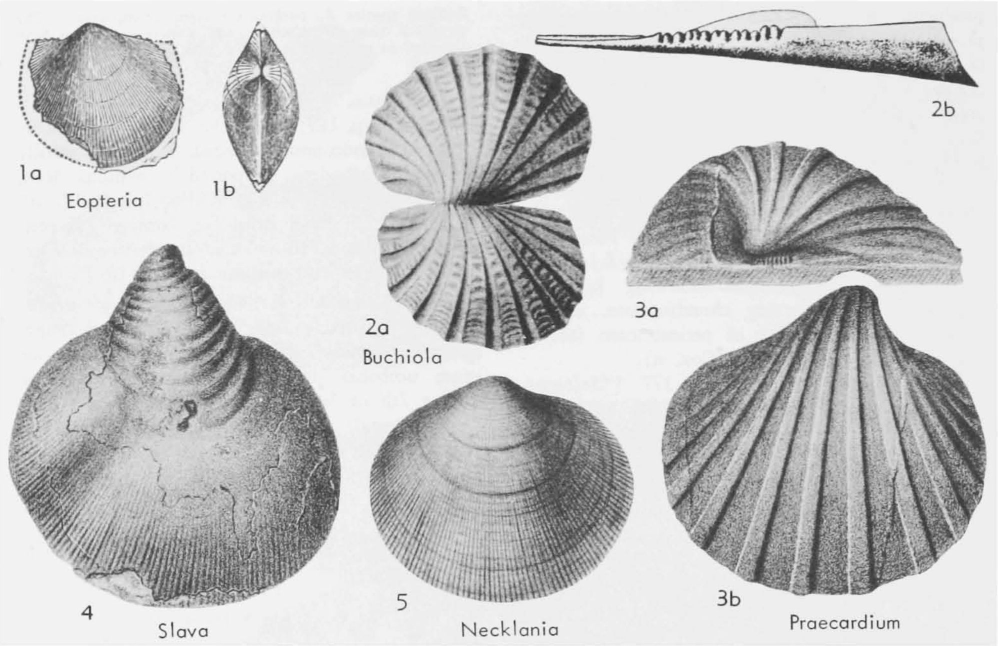


FIG. B2. Praecardiidae (Praecardiinae) (p. *N*244-*N*245).

tition behind and in front of the beaks consists clearly of the interlocking ends of radial ribs.

Subfamily PRAECARDIINAE Hörnes, 1884

[*nom. transl.* NEWELL & LAROCQUE, herein (*ex* Praecardiidae HÖRNES, 1884)]

Equivalve, cardinal area obscure to prominent, few taxodont teeth below beaks. *?U. Cam., L.Ord.-Dev.*

Praecardium BARRANDE, 1881, p. 141 [**P. primulum*; SD RŮŽIČKA & PRANTL, 1960] [=*Silurocardium* LEYMERIE, 1878, pl. B, fig. 4-6 *(nom. oblit.)* (type, *S. barrandei*; SD NEWELL & LAROCQUE, herein); *Gibbopleura* BARRANDE, 1881, p. 81 (type, *G. recumbens*; SD RŮŽIČKA & PRANTL, 1960); *Paracardium* BARRANDE, 1881, p. 137 (type, *P. subharmonicum*; SD NEWELL & LAROCQUE, herein); *Panenka* BARRANDE, 1881, p. 128 (type, *P. robustula*; SD RŮŽIČKA & PRANTL, 1960); *Puella* BARRANDE, 1881, p. 128; *Nevesta, Sponsa* BARRANDE, 1881, p. 133 (obj.); *Pantata* BARRANDE, 1881, p. 135 (type, *P. regens*; SD RŮŽIČKA & PRANTL, 1960); *Pater* BARRANDE, 1881, p. 135 (obj.); *?Paraptyx* CLARKE, 1904, p. 261 (type, *P. ontario*; OD); *Kralovna* BARRANDE, 1881, p. 93 (type, *K. bohemica*; OD); *Regina* BARRANDE, 1881, p. 93 (obj.); *?Praelima* BARRANDE, 1881, p. 144 (type, *P. proaeva*; RŮŽIČKA & PRANTL, 1960; *?Praelucina* BARRANDE, 1881, p. 145 (type, *P. protendens*; SD RŮŽIČKA & PRANTL, 1960); *Pararca* HALL, 1885, p. 429 (type, *P. venusta*; SD S. A. MILLER, 1889); *?Pleurodonta* CONRATH, 1887, p. 49 (type, *P. bohemica*; OD); *Barcinia* SUÑER & COMA, 1959 (type, *Kralovna almerae* BARRANDE, 1881; OD); *Joachymcardium* RŮŽIČKA & PRANTL, 1960, p. 50 (type, *Cardium cunctatum* BARRANDE, 1881; OD)]. Ovoid, evenly ventricose, with distinct but narrow cardinal area; radial costae fine to coarse, rounded, generally but not invariably uniform in size; hinge in best-known species with small, numerous, vertical teeth under beaks, *Sil.*(E_2), Eu.(Boh.-France-Ger.)-*Dev.*, N. Am.(N.Y.-Mich.-Ont.).——FIG. B2,*3*. **P. primulum,* Sil.(E_2), Boh.; *3a,b,* RV cardinal and side views, ×1 *(27)*.

Buchiola BARRANDE, 1881, p. 61 [**Venericardium restrostriatum* VON BUCH, 1832; M] [=*Glyptocardia* HALL, 1885, p. 35 (obj.)]. Differs from *Praecardium* chiefly in being less inflated and in the small number of broad, flat radial costae which are crossed by regularly spaced, up-arched, growth lamellae. *Sil.,* Eu.; *U.Dev.,* Eu.-N.Am.——FIG. B2,*2*. **B. retrostriata* (VON BUCH), U.Dev.(Naples), N.Am.(N.Y.); *2a,* bivalved individual, ext., ×6; *2b,* hinge with denticulations, approx. ×12 *(136)*.

Eopteria BILLINGS, 1865, p. 221 [**E. typica*; OD]. Valves evenly convex, beaks incurved, nearly orthogyre; ventral margin semicircular; hinge about as long as shell length, with subquadrate extremities; valves with slight anterior gape; area obscure or lacking; ornamented with fine costellae. *?U. Cam.* (erratic in *L.Ord.* Levis Sh.), Quebec; *L. Ord.(Beekmantown.),* Quebec-Newf.——FIG. B2, *1. E. richardsoni* (BILLINGS), L.Ord.(Quebec Gr.), St. Antoine, Que.; *1a,* LV ext.; *1b,* dorsal view both valves; both ×1 *(52).*

Necklania RŮŽIČKA & PŘIBYL, 1953, p. 57 [*pro Dalila* BARRANDE, 1881, p. 76 (*non* THOMSON, 1856)] [**Dalila obtusa* BARRANDE, 1881; SD RŮŽIČKA & PRANTL, 1960]. Oval, equivalve, equilateral; umbones generally orthogyre, median, low; beaks short, blunt; surface ornament with numerous radial costae. *U.Sil.*(F_1), Boh.——FIG. B2,*5.* **N. obtusa* (BARRANDE); RV ext., ×0.5 *(27).*

Slava BARRANDE, 1881, p. 154 [**S. bohemica*; SD RŮŽIČKA & PRANTL, 1960] [=*Gloria* BARRANDE, 1881 (obj.); *Tiaraconcha* FRECH, 1891 (obj.)]. Beaks and umbones prominent; surface divided into 2 distinct growth stages by sharply dissimilar convexity and ornamentation; umbones ventricose, ornamented by regular concentric furrows; marginal area of shell less convex, ornamented by fine costellae; hinge short, taxodont, without distinct area. *Sil.,* E.Eu.——FIG. B2,*4.* **S. bohemica,* Sil. (E_2), Boh.; RV ext., ×1 *(27).*

Subfamily CARDIOLINAE Fischer, 1886

[*nom. transl.* NEWELL & LAROCQUE, herein (*ex* Cardiolidae FISCHER, 1886)]

Equivalve; cardinal area prominent; essentially edentulous. *L.Sil.-L.Miss.*

Cardiola BRODERIP in MURCHISON, 1839, p. 617 [**C. interrupta* SOWERBY, 1839, in MURCHISON; SD S. A. MILLER, 1889] [=*?Cardiopsis* MEEK & WORTHEN, 1861, p. 144 (type, *Cardiomorpha radiata* MEEK & WORTHEN, 1860) (*non* DE KONINCK, 1884) (=*Megambonia lyoni* HALL, 1860); *?Salweyia* REED, 1931, p. 298 (type, *S. subobliquata*; OD)]. Ventricose, beaks and umbones prominent, hinge with triangular, flat, divergent cardinal area; surface with coarse radial costae. *U.Sil.(L.Ludlov.)-Dev.,* Eu.-N.Am.; *L. Miss.,* USA.

C. (Cardiola). Ovoid, without posterior wing. *U. Sil.(L.Ludlov.)-Dev.,* Eu.-N.Am.; *L.Miss.,* USA. ——FIG. B3,*4.* **C. (C.) interrupta* (SOWERBY), Sil.(E_2), Boh.; *4a,* LV hinge view; *4b,* same, side view, both ×1 *(27).*

C. (Cardiolopsis) HERITSCH, 1929, p. 46 [**Cardiolopsis typica* STACHE in HERITSCH, 1929; OD]. Differs from *Cardiola, s.s.* in possessing flattened and extended posterior wing. *Sil.,* E.Alps.

?**Euthydesma** HALL, 1885, p. 32 [**Astarte subtextilis* HALL, 1843; M]. Similar to *Cardiomorpha* but with short and regularly rounded anterior end; surface marked by very fine radial costellae producing cancellated appearance. *Sil.(M. Llandov.),* Scot.-*Dev.(Portage),* USA(N.Y.).——FIG. B3,*3.* **E. subtextile* (HALL), Dev.(Portage), USA(N.Y.); LV ext., ×1 *(370).*

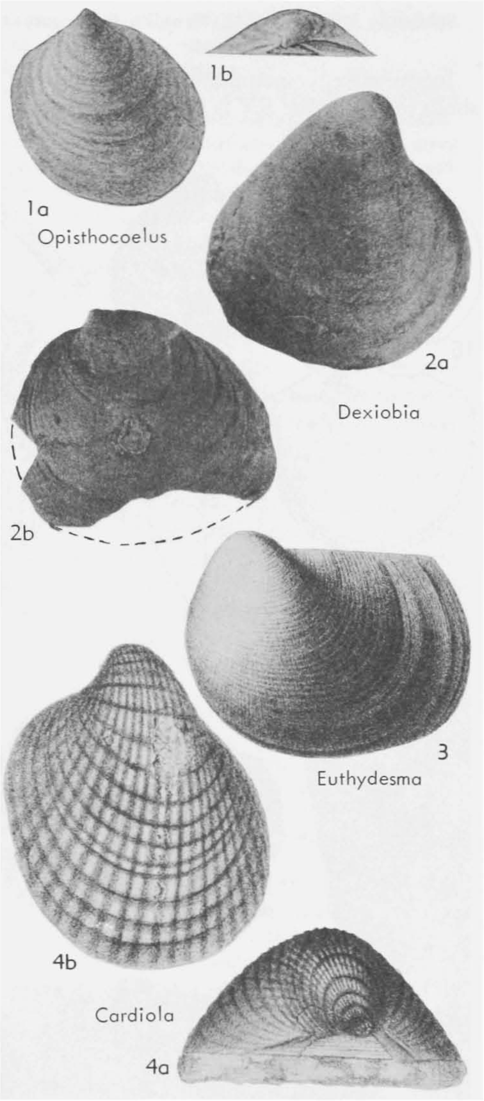


FIG. B3. Praecardiidae (Cardiolinae) *(1, 3-4),* Dexiobiinae) (2) (p. *N*245-*N*247).

Opisthocoelus BEUSHAUSEN, 1895, p. 338 [**O. concentricus*; SD NEWELL & LAROCQUE, herein] [=*?Ontaria* CLARKE, p. 279 (type, *Ungulina suborbicularis* HALL, 1843)]. Ovoid, surface smooth or faintly costellate; interior unknown. *U.Sil.-U. Dev.,* Ger.-Belg.——FIG. B3,*1.* **O. concentricus,* U.Dev., Büdesheim, Ger.; *1a,* RV ext.; *1b,* same, hinge view; both ×2 *(47).*

Subfamily DEXIOBIINAE Newell & LaRocque, new subfamily

Inequivalve, inequilateral, amphidetic shells in which the RV is subtriangular with large umbo and markedly more convex than LV; beaks prosogyre, separated by an edentulous, undefined area. *?Sil., L.Miss.*

Dexiobia WINCHELL, 1863, p. 10 [**Cardiomorpha*

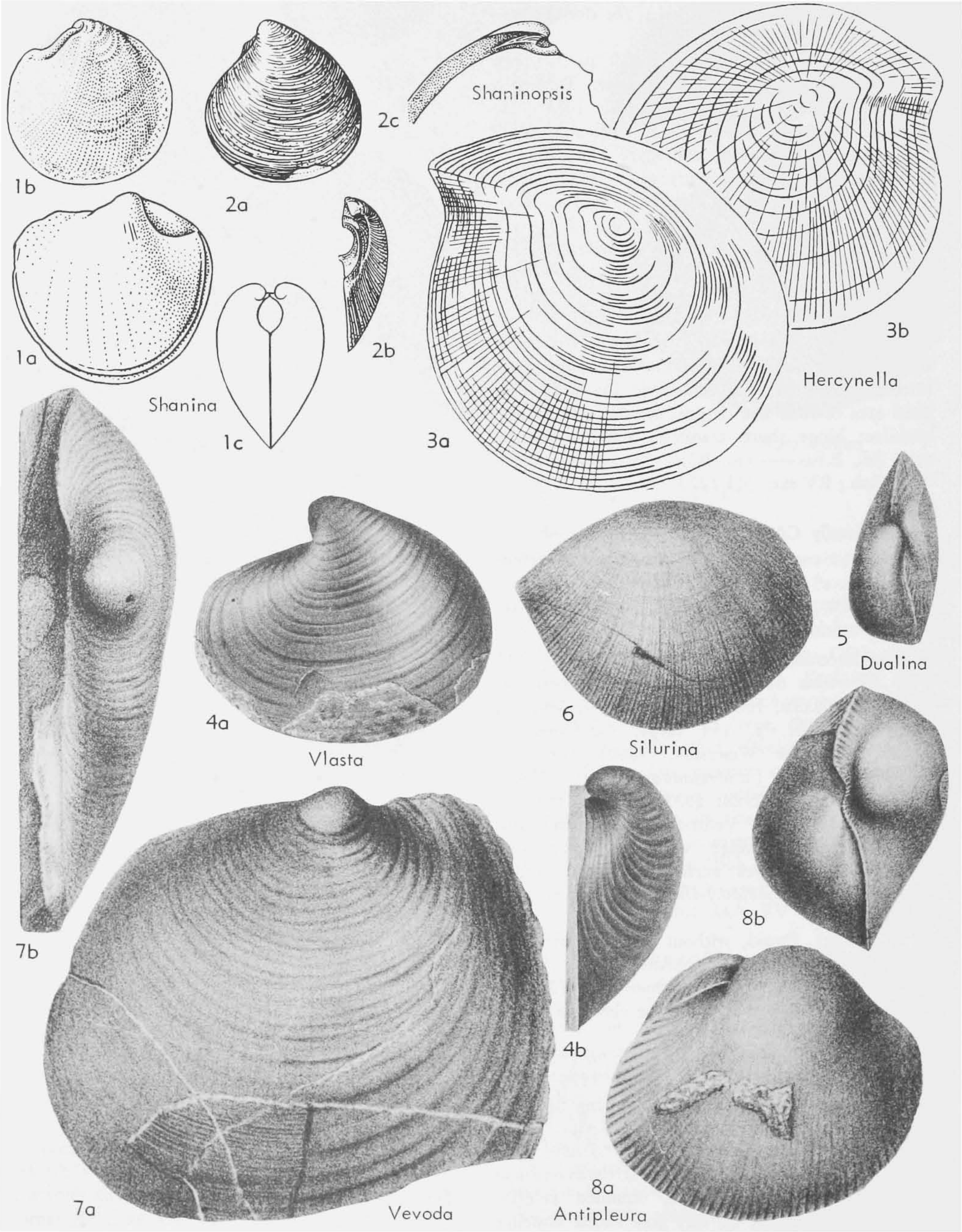


FIG. B4. Antipleuridae (Antipleurinae) *(3,5-6,8)*, (Vlastinae) *(1-2,4,7)* (p. *N*247-*N*248).

ovata Hall, 1858; SD Miller, 1889 (*non* d'Orbigny, 1850) (=**Dexiobia whitei* Winchell, 1863)] [=*Oracardia* Herrick, 1888, p. 41 (type, *O. cornuta*; SD LaRocque & Newell, herein)]. Surface ornamentation of fine radial costellae and irregular concentric wrinkles. *Sil.(E_2)?*, Boh.; *L. Miss.(Kinderhook.)*, C.USA.——Fig. B3,*2*. **D. whitei* (Winchell), L.Miss.(Kinderhook.), USA (Iowa); *2a*, RV ext.; *2b*, LV ext., both ×4 (Driscoll & Hall, 1963).

Family ANTIPLEURIDAE Neumayr, 1891

[*nom. transl.* Dall, 1895 (*ex* Antipleuriden Neumayr, 1891, p. 724)] [Materials for this family prepared by N. D. Newell & Aurèle LaRocque]

Shell equivalve or very inequivalve, ligament probably amphidetic or lacking, without nymphs or differentiated area between beaks; lunule lacking; margin denticulate as interlocking terminations of surface costellae. *M.Ord.-Dev.*

Subfamily ANTIPLEURINAE Neumayr, 1891

[*nom. transl. et correct.* Newell & LaRocque, herein (*ex* Antipleuriden Neumayr, 1891); unspecified familial name]

Shell very inequivalve, commonly costellate. *Sil.-Dev.*

Antipleura Barrande, 1881, p. 18 [**A. bohemica*; M]. Inflated, subcircular, beaks prosogyre; posterior part of shell commonly set off by carina; surface ornamented by uniform costellae. *M.Sil. (E_2)*, Boh.

A. (Antipleura). Beaks about equal in size, large, that of RV lying slightly ahead of LV. *M.Sil. (E_2)*, Boh.——Fig. B4,*8*. **A. (A.) bohemica*; *8a*, right side view of int. mold; *8b*, dorsal view int. mold, showing crenulated shell margin, offset beaks and sinuous hinge; both ×1 *(27)*.

A. (Dualina) Barrande, 1881, p. 77 [**D. comitans*; SD Růžička & Prantl, 1860] [=*Sestra* Barrande, 1881, p. 151 (type, *S. novella*; OD); *Soror* Barrande, 1881, p. 151 (obj.)]. Similar to *Antipleura, s.s.*, but LV appreciably more convex with strongly prosogyre, overhanging beak. *M.Sil.(E_2)*, Boh.——Fig. B4,*5*. **A. (D.) comitans*; dorsal view, ×1 *(27)*.

Hercynella Kayser, 1878, p. 101 [**H. beyrichi*; SD Cossmann, 1895]. Thin, patelloid, with central, subcentral, or submarginal apex at which originates more or less prominent fold extending to front margin of shell; sculpture consisting of radial costellae around shell margin; internal characters unknown. [First considered to be a gastropod, *Hercynella* is now classed as a bivalve because of its resemblance to and association with species of *Silurina.*] *M.Sil.-U.Dev.*, Eu.-USA-Morocco-Australia.——Fig. B4,*3*. *H. nobilis* (Barrande), M.Sil.(E_2), Boh.; *3a,b*, LV ext., RV ext., enl. (Termier & Termier, 1950).

Silurina Barrande, 1881, p. 153 [**S. percalva*; SD Růžička & Prantl, 1960]. Subcircular, with a nasute auricle at the anterodorsal part of the shell; surface with fine costellae; umbones in some species well below dorsal margin; surface with fine costellae. *Sil.(E_2)-Dev.(F_1)*, Boh.——Fig. B4, *6*. **S. percalva*, Sil.(E_2); LV ext., ×1 *(27)*.

Subfamily VLASTINAE Neumayr, 1891

[*nom. transl. et correct.* Dall, 1895 (*ex* Vlastiden Neumayr, 1891)]

Shell thin, ovate, equivalve, beaks elevated, either prosogyre or opisthogyre and incurved; gaping slightly terminally in some genera; hinge margin edentulous or weakly taxodont, arched; flattened cardinal areas and ligament nymphs lacking; valves meeting along hinge line at obtuse angle beneath beaks; surface generally smooth, in some forms marked by concentric furrows with, or without, weak radial costae. *M.Ord.-Dev.*

Vlasta Barrande, 1881, p. 167 [**V. bohemica*; SD Růžička & Prantl, 1960] [=*Jahnia* Růžička & Prantl, 1960, p. 50 (type, *Isocardia bohemica* Barrande, 1881)]. Thin, ovoid to subcircular, tumid, with prominent umbones; gaping at both ends; beaks commonly but not invariably opisthogyre; dentition absent or rudimentary; radial ornamentation very weak or absent. *U.Ord.(Richmond)*, Can.(Ont..); *M.Sil.(E_2)*, Boh.——Fig. B4, *4*. **V. bohemica*, Sil.(E_2), Boh.; *4a,b*, RV side and rear views, both ×0.5 *(27)*.

Shanina Reed, 1915, p. 18 [**S. vlastoides*; M]. Suborbicular, gently convex; beaks subcentral; hinge line thickened behind beaks, sloping downward in front; valves gaping slightly in front of beaks; hinge unknown; interior with faint radiating lines; outer surface with growth lines only. *M. Ord.*, India.——Fig. B4,*1*. **S. vlastoides*, M.Ord. (U.Naugkangyi beds), N.Shan. States, India; *1a*, RV int. mold, ×1.5; *1b*, LV int. mold, ×1; *1c*, restored outline anterior, ×1 *(778)*.

Shaninopsis Isberg, 1934, p. 336 [**S prona*; OD]. Similar to *Shanina*, but without internal radial ribs. *U.Ord.(U.Leptaena Ls.)*, Swed.——Fig. B4, *2*. **S. prona*, U.Ord., Swed.(Kallholn-Dalarna); *2a,b*, LV ext. and ant. views of holotype, showing gape, ×1; *2c*, hinge of same; all ×1.5 *(439)*.

Vevoda Barrande, 1881, p. 166 [**V. expectans*; SD Růžička & Prantl, 1960] [=*Dux* Barrande, 1881 (obj.), p. 166; *Sluzka* Barrande, 1881, p. 160 (type, *S. pulchella*; SD Růžička & Prantl, 1960; OD); *Praeostrea* Barrande, 1881, p. 147 (type, *P. bohemica*; M)]. Subcircular to subelliptical, gaping slightly in front; cardinal line strongly arched; beaks relatively small, prosogyre,

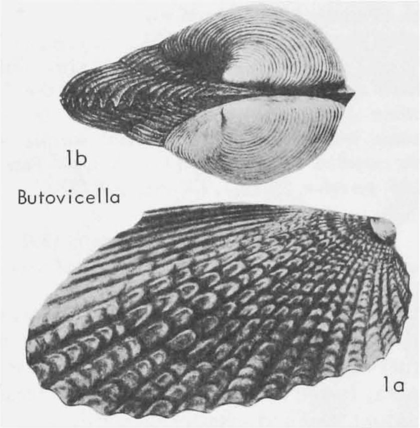


Fig. B5. Butovicellidae (p. *N*248).

swollen, distinct from remainder of shell; surface with both concentric and radial ornamentation, latter weaker. *Sil.*(E_2)*-Dev.*(F_1), Boh.——Fig. B4,*7*. **V. expectans,* Sil.(E_2), Boh.; *7a,* RV ext. showing form, ornamentation, and prominent prodissoconch; *7b,* same, hinge view; both ×1 *(27)*.

Family BUTOVICELLIDAE Kříž, 1965

[Materials for this family prepared by N. D. Newell]

Characters of *Butovicella. Sil.*

Butovicella Kříž, 1965, p. 207 [**Cardiola migrans* Barrande, 1881; M]. Shells small, thin, elongate-ovoid, strongly inequilateral, equivalve, moderately inflated; nepioconch opisthogyre, adult shell prosogyre; sculpture of nodose strong radial ribs; ligament opisthodetic; interior unknown. *Sil.,* Eu.——Fig. B5,*1*. **B. migrans* (Barrande), Kopanina F., *P. nilssoni* Zone, Boh.; *1a,* RV ext., ×5; *1b,* both valves, dorsal, cardinal, ×20 (Kříž, 1965).

Subclass PTERIOMORPHIA Beurlen, 1944

[*nom. transl.* Newell, 1965 (*ex* order Pteriomorphia Beurlen, 1944)] [Diagnosis by N. D. Newell]

Cyrtodonts, arks, anisomyarians, and monomyarians of authors; mainly epifaunal, sedentary forms with free mantle margins, characterized as whole by byssal fixation or cementation generally and tendency for foot and anterior adductor to become reduced or lost in many most specialized genera; some groups secondarily free; duplivincular ligament, unknown in other bivalves, characterizes less specialized Arcacea and several Paleozoic groups (Ambonychiacea, Pterinopectinidae, Pterineidae). [Some superfamilies display convergent and parallel trends in many characters; consequently, a simple morphological diagnosis is not possible.] *L.Ord.-Rec.*

Order ARCOIDA Stoliczka, 1871

[*nom. correct.* Newell, 1965 (*ex* order Arcacea Stoliczka, 1871)] [Materials for this order prepared by N. D. Newell with additions as indicated]

Arks and their near relatives; sedentary, with free or byssate adults; characteristically isomyarian and equivalved with circular to trapezoidal shells; interior shell microstructure crossed-lamellar; gills filibranchiate in living forms; in most groups dorsal margin bears narrow to broad, flat cardinal areas that rise above hinge axis. *L.Ord.-Rec.*

Superfamily CYRTODONTACEA Ulrich, 1894

[*nom. transl.* Newell, 1965 (*ex* Cyrtodontidae Ulrich, 1894)] [Diagnosis by N. D. Newell]

Ovoid, lacking radial ornamentation, slightly prosocline, commonly with prominent umbones and elongate, duplivincular ligament mainly behind beaks; generally with groups of anterior and posterior teeth separated by edentulous area of hinge plate; posterior laterals, where present, parallel to shell margin and mainly behind ligament; anterior teeth commonly arcuate over anterior adductor. *M.Ord.-Dev.*

Family CYRTODONTIDAE Ulrich, 1894

[Materials on this family prepared by Aurèle LaRocque with additions as indicated]

Characters of superfamily. *M.Ord.-Dev.*

Cyrtodonta Billings, 1858 [**C. rugosa*; SD Williams & Breger, 1916] [=*Palaearca* Hall, 1859 (type, *P. ventricosa;* SD LaRocque, herein); *Angellum* Miller, 1878 (type, *A. cuneatum*; OD)]. Cardinal teeth 3, commonly only 2, rarely 4, directed backward, horizontal or nearly so, and not essentially radial. *M.Ord.(St. Peter)-Sil.(Clinton),* N.Am.; *L.Sil.(Llandovery),* Eu.——Fig. C1,*4*. **C. rugosa,* M.Ord.(Trenton.-Blackriv.), near Ottawa, Ont., Can.; *4a,b,* RV ext., showing ornamentation and RV int., ×1 *(51)*.

?Cypricardites Conrad, 1841, p. 51 [**C. curtus*; SD S. A. Miller, 1889]. This genus is presently un-

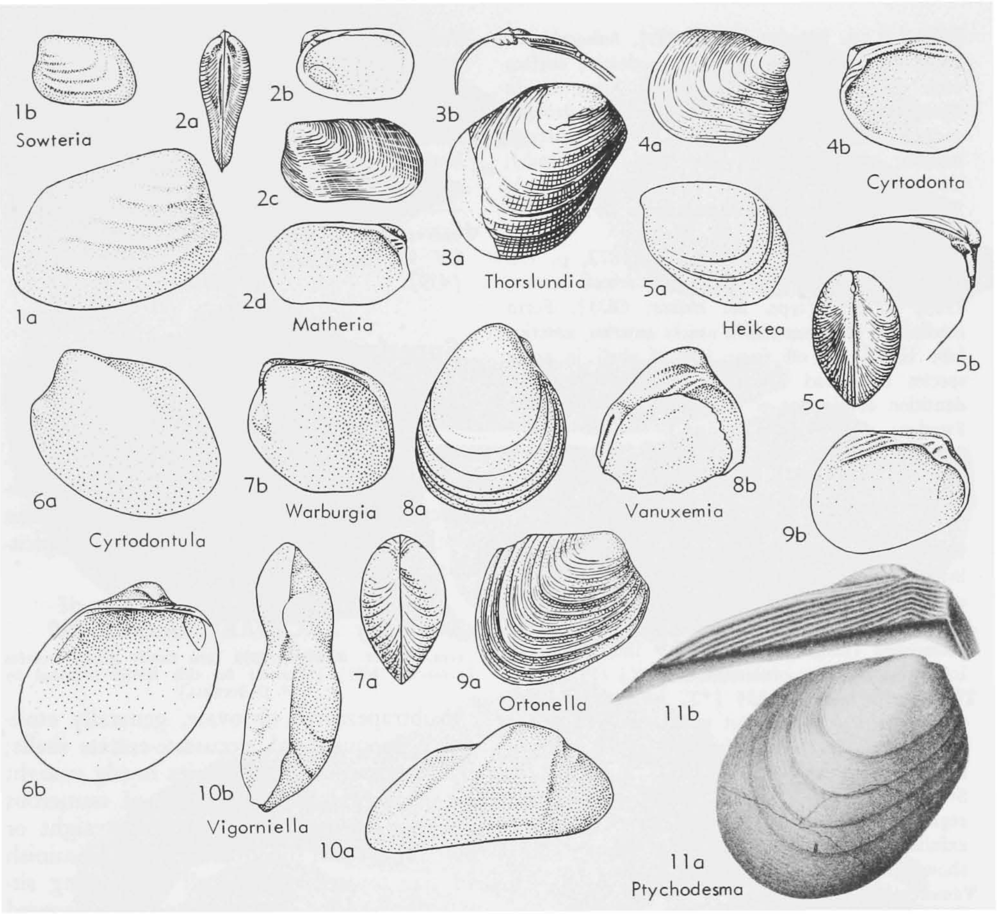


Fig. C1. Cyrtodontidae (p. *N*249-*N*250).

recognizable from available evidence. *U.Ord.*, USA.

Cyrtodontula Tomlin, 1931 [**Whitella obliquata* Ulrich, 1890; OD] [=*Rhynchotropis* Meek, 1872 (type, *R. sterlingensis;* M); *Whitella* Ulrich, 1890 (*non* Spinola, 1850); ?*Bodmania* Miller & Faber, 1894 (type, *B. insultum*; OD)]. Obliquely quadrangular or suboval, more or less ventricose; umbonal ridge and umbones prominent, escutcheon distinct; surface with fine concentric lines and random stronger concentric ridges; 2 to 5 rather oblique folds or teeth in front of beaks, a few posterior lateral teeth. *Ord.(Blackriv.-Richmond.)*, N.Am.; *?Sil.(Niagar.)*, USA(Ind.).——Fig. C1, *6*. **C. obliquata* (Ulrich), U.Ord.(Cincinnati.), USA(Ohio) *(6a)*, Ord., USA(Minn.) *(6b)*; *6a*, LV int. mold, ×1; *6b*, LV int. showing dentition and muscle scars, ×1 *(929)*.

?**Heikea** Isberg, 1934, p. 276 [**H. selecta*; OD]. Similar in form to *Vanuxemia* but inequivalve, RV umbo projecting over that of LV; LV with 1 small cardinal tooth; RV with 1 cardinal socket; without lateral teeth. *M.Ord.-Sil.*, N.Am.-Eu.——Fig. C1,*5*. **H. selecta*, Sil.(U.Leptaena Ls.), Sweden; *5a*, LV ext., ×2; *5b*, LV hinge, ×3; *5c*, both valves dorsal, ×2 *(439)*. [LaRocque & Newell]

?**Matheria** Billings, 1858 [**M. tenera*; OD]. Oblong quadrate or suboval; beaks small, anterior; surface with concentric growth lines; LV with 2 small, divergent cardinal teeth beneath beak; RV with 1 cardinal tooth, no lamellar teeth; ligament external; pallial line simple, obscurely defined. [May belong in Astartidae; see Crassatellacea.] *Ord.(Trenton.)-Sil.(Niagar.)*, N.Am.(Que.-Minn.-Wis.-Ill.).——Fig. C1,*2*. **M. tenera*, Ord.(Trenton.), Blue Point, Que.(Lake St. John); *2a*, both valves dorsal; *2b*, RV int.; *2c*, LV ext.; *2d*; LV int.; all ×1 *(51)*.

Ortonella Ulrich, 1893 (1894) [**Cypricardites* *hainesi* S. A. Miller, 1874; OD]. Subquadrate, beaks anterior, umbonal ridge moderate; surface with concentric lines of growth; hinge as in *Cyrtodonta* but cardinal teeth relatively stronger and immediately under beaks; 2 short posterior lamellar teeth in each valve. *Ord.(Richmond.)*, USA(Ind.).——Fig. C1,*9*. **O. hainesi* (Miller); *9a,* LV ext. showing ornamentation; *9b,* LV int. showing dentition; both ×1 *(929)*.

?**Ptychodesma** Hall & Whitfield, 1872, p. 192 [**P. knappanum*; M] [=?*Macrodesma* Isberg, 1934, p. 277 (type, *M. striata*; OD)]. Form modioloid, umbones small, nearly anterior, anterior lobe broad, set off from rest of shell in some species by broad sulcus; ligament area broad; dentition obsolescent or poorly known. *U.Ord.-Sil,* Sweden; *Dev.,* USA(Ky.-Ind.).——Fig. C1,*11*. **P. knappanum,* M.Dev., USA(Ind.); *11a,* RV ext., ×1; *11b,* LV hinge, ×2 *(379)*. [Newell]

Sowteria Whiteaves, 1908 [**Whitella canadensis* Raymond, 1905; OD]. Subtrapezoidal, beaks anterior, test and dentition unknown; surface of internal molds with strong concentric ridges on anterior 0.7 of shell; postumbonal slope smooth. *Ord.(Chazy.),* Can.(Ont.).——Fig. C1,*1*. **S. canadensis* (Raymond); *1a,b,* RV int. mold, LV int. mold, showing ornamentation, ×1 *(976)*.

Thorslundia Isberg, 1934 [**T. bellistriata*; OD]. Similar to *Cyrtodonta* but with posterior part of hinge plate thickened; surface with radial and concentric ornamentation. *U.Ord.(U.Leptaena Ls.),* Sweden.——Fig. C1,*3*. **T. bellistriata,* Dalarna region (Kallholn); *3a,* RV ext. view of partially exfoliated holotype, ×1; *3b,* RV hinge (holotype) showing dentition, ×2 *(439)*.

Vanuxemia Billings, 1858, p. 186 [**V. inconstans*; SD S. A. Miller, 1889]. Ventricose, oblique, ovate to subcircular; anterior end reduced, posterior broadly rounded; hinge as in *Cyrtodonta,* anterior adductor sharply defined, situated on anterior prolongation of hinge plate. *M.Ord.-U.Ord.,* N.Am.; *U.Ord.(U.Leptaena Ls.),* Sweden.——Fig. C1,*8*. **V. inconstans,* M.Ord., E.Can.; *8a,b,* LV ext., int., ×1 *(51)*. [LaRocque & Newell]

Vigorniella Reed, 1934 [**V. regia*; OD]. Inequivalve, beaks anterior; RV swollen, deep, larger than LV, twisted, carinated, with high incurved beak, depressed posterior area, and broad median transverse sulcus; LV shallow, more or less flattened or concave, with much lower and smaller beak and weaker median sulcus; no external ligamental area. Interior both valves with short, stout, vertical clavicular ridge immediately in front of beaks. *Sil.(Downton., Stage 1,9),* Eng. ——Fig. C1,*10*. **V. regia*; *10a,* RV ext., ×4; *10b,* dorsal view of complete specimen, ×6 *(781)*.

Warburgia Isberg, 1934 [**W. lata*; OD]. Equivalve, thick, hexagonal to oval, beaks anterior; no lunule or area; ligamental area weak; surface concentrically striate. Hinge plate thick; cardinal teeth (number unknown) radially arranged under beak; 1 or 2 short posterior lamellar teeth parallel to hinge margin. *U.Ord.(U.Leptaena Ls.),* Sweden. ——Fig. C1,*7*. **W. lata*; *7a,* dorsal view of both valves showing thickness of shell; *7b,* RV int. with LV int. mold showing ant. muscle scar, ×1 *(439)*.

Superfamily ARCACEA Lamarck, 1809

[*nom. transl.* Gill, 1871 (*ex* family group arcacées Lamarck, 1809] [Diagnosis by N. D. Newell]

Generally trapezoidal, radially ornamented; ligament elongate, generally duplivincular or striate, not confined to median resilifer; periostracum commonly conspicuous. *L.Ord.-Rec.*

Family ARCIDAE Lamarck, 1809

[*nom. correct.* Broderip, 1839 (*pro* family group arcacées Lamarck, 1809)] [Materials for this family prepared by N. D. Newell]

Subtrapezoidal or ovate, generally equivalve, inequilateral, decussate-costate shells; hinge taxodont, dental series nearly straight or slightly arched, consisting of numerous small, more or less transverse, straight or chevron-shaped subequal teeth that diminish in size toward middle, all teeth being situated near hinge axis and radially disposed with respect to point well below beaks; ligament duplivincular, prosodetic, amphidetic, or opisthodetic; without myophoric ridges or shelves. *?Trias., Jur.-Rec.*

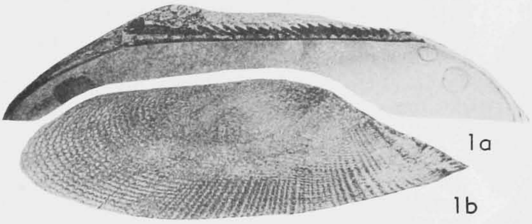
Subfamily ARCINAE Lamarck, 1809

[*nom. transl. et correct.* Stoliczka, 1871 (*ex* family group arcacées Lamarck, 1809)]

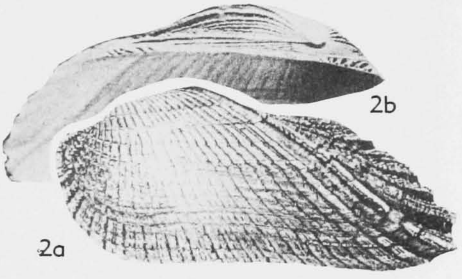
Nestling or rock-boring forms characteristically with byssal gape and commonly corresponding shallow sinus at ventral margin for emergence of byssus; ventral border not crenulate. *?Trias., Jur.-Rec.*

Arca Linné, 1758 [**A. noae*; SD Schmidt, 1818 (ICZN Opinion 189)] [=*Daphne* Poli, 1791 (=*Daphnoderma* Poli, 1795, type, *A. noae*; SD Newell, herein); *Navicula* de Blainville, 1825 (obj.); *Byssoarca* Swainson, 1832 (obj.); *Cibota*

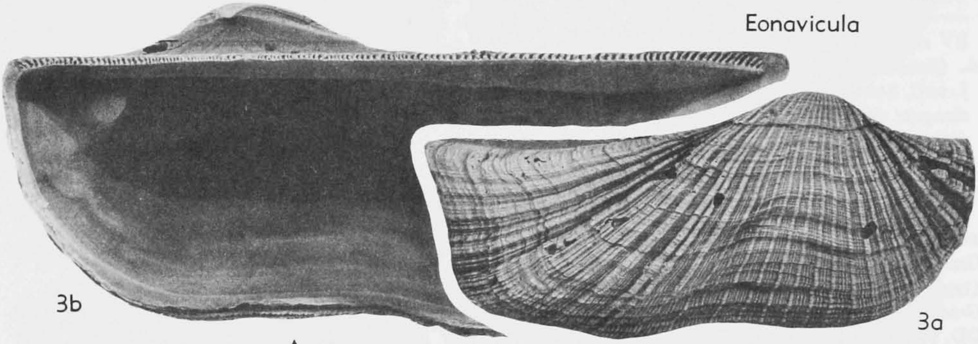
Fig. C2. Arcidae (Arcinae) (p. N252, N254) (facing page).



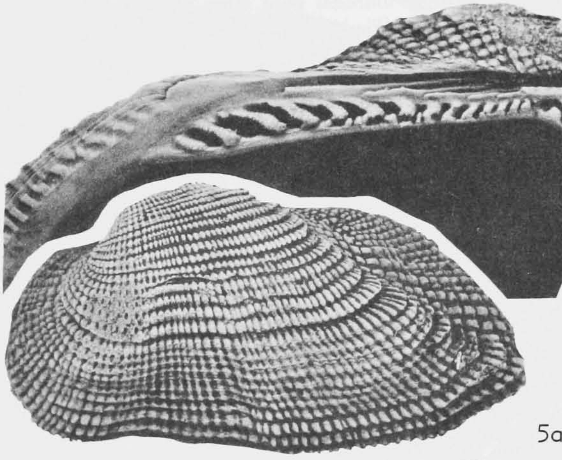
Litharca



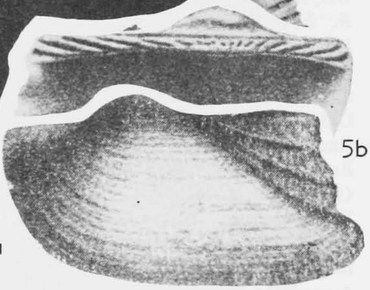
Eonavicula



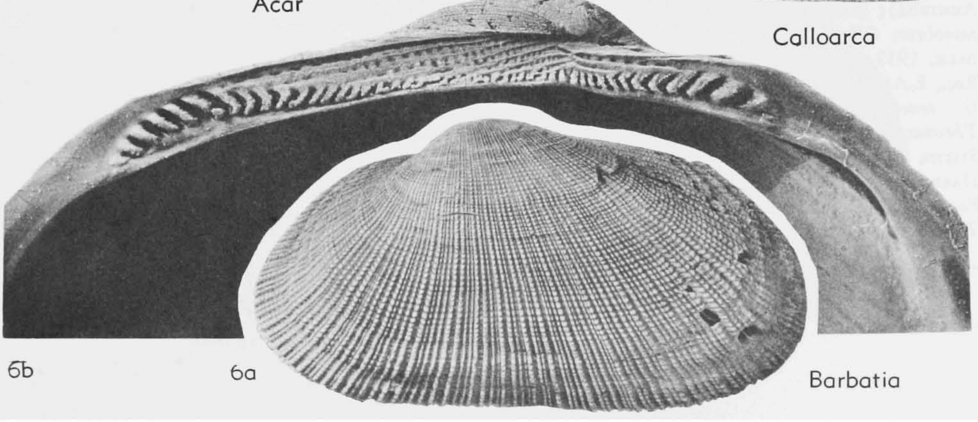
Arca



Acar



Calloarca



Barbatia

Mörch, 1853 (type, *A. noae*; SD Newell, herein); *Arcoptera* Heilprin, 1887 (type, *A. aviculaeformis*); *Mesocibota* Iredale, 1939 (type, *M. luana*)]. Elongate, subtrapezoidal to subrectangular, very inequilateral, commonly expanded or auriculate posteriorly, posterior umbonal carina prominent; cardinal area broad, covered throughout by ligament; dental series long and nearly straight; surface sculpture radial, fine. *M.Jur.-Rec.*

A. (Arca). Teeth small, numerous, transverse across middle of shell, becoming longer and convergent terminally. *U.Cret.-Rec.*, cosmop. in warm waters.——Fig. C2,*3*. **A. (A.) noae*, Rec., Medit.; *3a*, RV ext., ×0.85; *3b*, RV int., ×1.3 (Newell, n).

A. (Eonavicula) Arkell, 1929 [**A. quadrisulcata* J. deC. Sowerby, 1824; OD]. Median teeth more elongate than in *A. (Arca)* converging strongly downward toward point below beaks. *M.Jur.-Rec.*, W.Eu.——Fig. C2,*2*. *A. (E.) trichordis* (de Loriol), U.Jur., Switz.; *2a,b*, LV ext., int., ×1.3 *(20)*.

Barbatia Gray, 1842 [**A. barbata* Linné, 1758; SD Gray, 1857] [=*Modioliformia* Deshayes, 1860 (type, *Arca obliquaria* Nyst, 1847; OD, Eoc., Fr.); *Granoarca* Conrad, 1862 (type, *Arca propatula?*; OD, Mio., USA); *Plagiarca* Conrad, 1875 (type, *B. carolinensis*; OD, U.Cret., N.Car.); *?Soldania* Stephani & Pantanelli, 1878 (type, *Arca mytiloides* Brocchi, 1814; OD, Plio., Italy) (*non* d'Orbigny, 1826); *Savignyarca* Jousseaume, 1891 (type, *S. savignyarca*; OD, Rec., GulfAden); *Asperarca* Sacco, 1898 (type, *Acar nodulosa* Müller, 1776; OD, Rec., Denm.); *Obliquarca* Sacco, 1898 (type, *Arca modioliformis* Deshayes, 1831; OD, Eoc., Italy); *Pugilarca* Marwick, 1928 (type, *B. barneaformis*; OD, Oligo., N.Z.); *Destacar* Iredale, 1936 (type, *Arca metella* Hedley, 1924; OD, Rec., S.Australia); *Abarbatia* Dall, Bartsch & Rehder, 1938, p. 29 (type, *Barbatia oahua*; OD, Rec., Hawaii); *?Hawaiarca* Dall, Bartsch & Rehder, 1928, p. 27 (type, *H. rectangula*; OD, Rec., Hawaii); *?Nipponarca* Habe, 1951, p. 34 (type, *Arca bistrigata* Dunker; OD, Rec., W.Pac.); *Barbarca* Dall, Bartsch & Rehder, 1938 (type, *Calloarca hua*; OD, Rec., Hawaii); *Barbatirus* Iredale, 1939 (type, *B. mimulus*; OD, Rec., E. Australia); *Mimarcaria* Iredale, 1939 (type, *M. saviolum*; OD, Rec., E.Australia); *Miratacar* Iredale, 1939 (type, *Arca wendti* Lamy, 1907; OD, Rec., E.Australia); *Opularca* Iredale, 1939 (type, *O. tenella egenora*; OD, Rec., E.Australia); *Thronacar* Iredale, 1939 (type, *B. corpulenta* Smith, 18??; OD, Rec., N.Australia); *Jacksonarca* Harris & Palmer, 1946 (type, *B. seraperta*; OD, Eoc., Miss.); *Tucetonella* Habe, 1961, p. 112 (type, *Tucetona planacosta*; OD, proposed as a subgenus of *Tucetona*)]. Small, elongate, ovoid, inequilateral, generally equivalve, but rarely RV is slightly smaller than LV; terminations rounded or subangular and slightly expanded; ornamentation costellate, commonly fine. *?Trias.*, *Jur.-Rec.*, cosmop.

B. (Barbatia). Umbonal carina low, rounded, cardinal area low, ligamental grooves closely spaced, costellae numerous, in some forms obsolescent. *?Trias.*, *Jur.-Rec.*, cosmop.——Fig. C2,*6*. **B. (B) barbata* (Linné), Rec., Medit.; *6a,b*, LV ext., int., ×1, ×2 (Newell, n).

B. (Acar) Gray, 1857 [**Arca gradata* Broderip & Sowerby, 1829; SD Woodring, 1925] [=*Vitracar* Iredale, 1939 (type, *V. laterosa*)]. Posterior umbonal carina prominent, extended posteriorly in emargination of shell; cardinal area very narrow, ligament mainly opisthodetic; ornamentation uniform, decussate; adductor scars somewhat elevated. *Paleoc.(Dan.)-Rec.*, Eu.-N.Am.-S.Am.——Fig. C2,*4*. **B. (A.) gradata* (Broderip & Sowerby), Rec., W.Colom.; *4a*, RV ext., ×2.6; *4b*, RV int., ×5.2 (Newell, n).

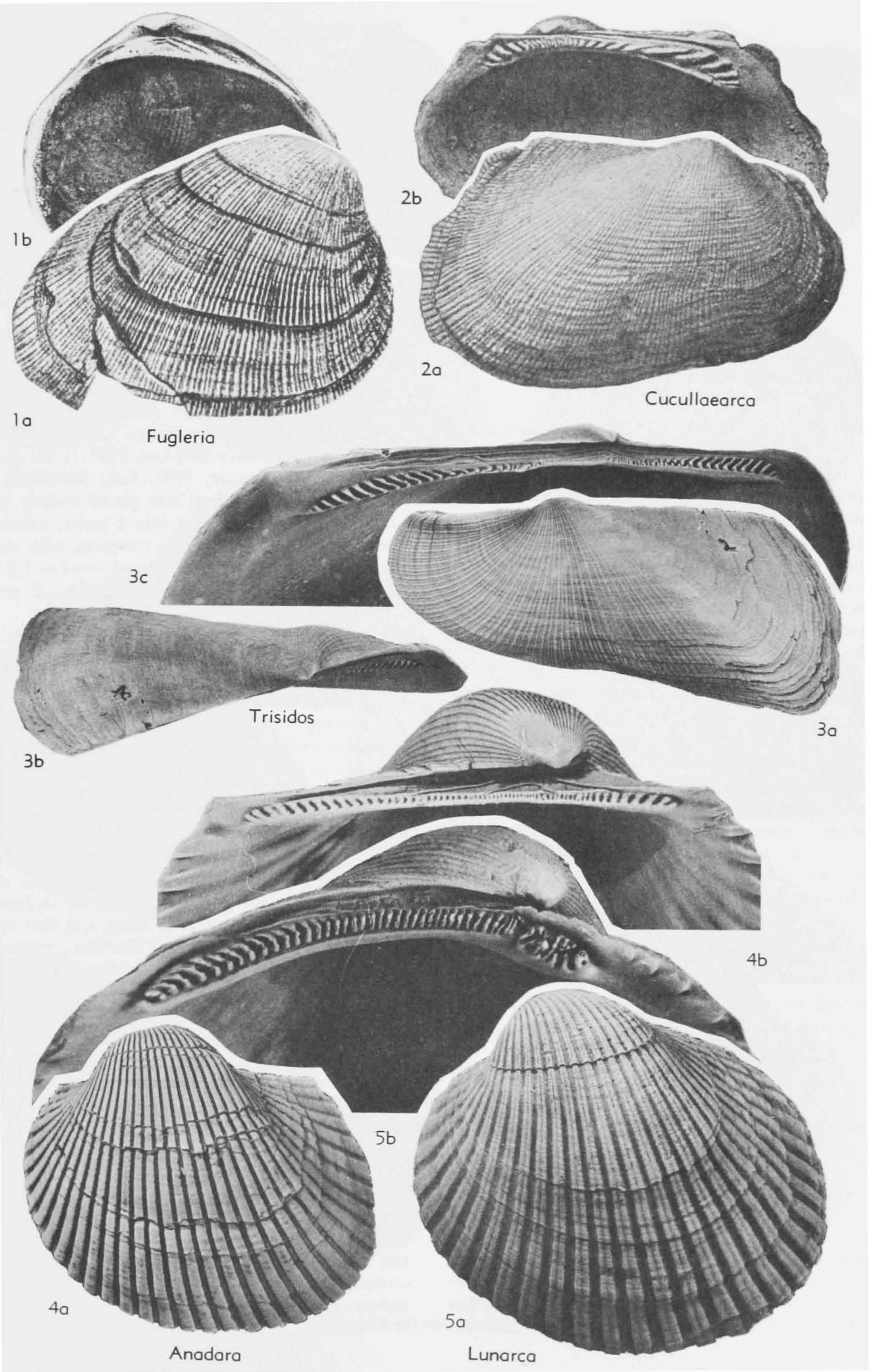
B. (Calloarca) Gray, 1857 [**Byssoarca alternata* Sowerby, 1833; OD]. Similar to *Acar* but costellae very unequal in size, those of posterior umbonal slope large, elevated. *Mio.-Rec.*, N.Am. (Fla.)-C.Am.-NW.S.Am.——Fig. C2,*5*. **B. (C.) alternata* (Sowerby), Rec., Panama; *5a,b*, LV ext., int., ×1.3 *(688)*.

B. (Cucullaearca) Conrad, 1865 [**Byssoarca lima* Conrad, 1847; SD Stoliczka, 1871] [=*Polynema* Conrad, 1875 (type, *B. lintea*, U.Cret., N. Car.)]. Elongate to obliquely subquadrate, subequivalve but generally much distorted, ventral margin deeply sinuated by large byssal gape; cardinal area high, amphidetic; sculpture formed by fine to coarse subequal costae; hinge long, straight, teeth in continuous series in young but in adults divided in middle by long gap, distal teeth conspicuously larger and oblique. *U.Cret.-Rec.*, cosmop. in warm seas.——Fig. C3,*2*. *B. (C.) lintea* (Conrad), U.Cret., SE.USA; *2a,b*, RV ext., int., ×2.25 *(887)*.——Fig. C4,*1*. **B. (C.) lima* (Conrad), Oligo., USA(Miss.); LV ext., ×0.8 (Conrad, 1840).

B. (Fugleria) Reinhart, 1937 [**B. (F.) pseudoillota*; OD]. Ovoid, posterior carina low, rounded; cardinal area and ligament as in *Acar*; ornamentation consisting of uniform costellae. *Plio.*, N.Am.(Fla.-Calif.); *Rec.*, C.Am.——Fig. C3,*1*. **B. (F.) pseudoillota*, Plio., Calif., *1a,b*, RV ext., int., ×1.7 (Reinhart, 1937).

B. (Taeniarca) Olsson, 1965, p. 25 [**B. toaeniata* Dall, 1898; OD]. *Mio.-Plio.*, Ecuador.

Fig. C3. Arcidae (Arcinae) *(1-3)*, (Anadarinae) *(4-5)* (p. N252, N254) (facing page).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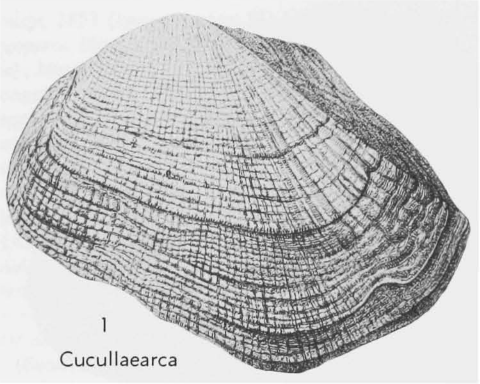

Fig. C4. Arcidae (Arcinae) (p. *N*254).

Litharca Gray, 1892 [**Byssoarca lithodomus* Sowerby, 1833; SD Gray, 1847]. Elongate, cuneiform, subequivalve, strongly inequilateral, posterior end acuminate, carinated, beaks opisthogyre, approximately 0.75 of length behind anterior margin; cardinal area low, ligament prosodetic; sculpture characteristically worn by rock-boring, consisting of fine costellae and concentric threads; ventral margin not corrugated. *Rec.,* Panaman. prov.——Fig. C2,*1*. **L. lithodomus* (Sowerby), Rec., Ecuador; *1a,* RV int., ×5.7; *1b,* RV ext., ×1.1 *(688).*

Trisidos Röding, 1798 [**Arca tortuosa* Linné, 1758; OD] [=*Trisis* Oken, 1815 (obj.); *Parallelopipedum* Mörch, 1850 (obj.); *Epitrisis* Iredale, 1939 (type, *Arca semitorta* Lamarck, 1819, Rec., E. Australia)]. Similar to Arca *(Arca)* but with narrow cardinal area and exhibiting marked torsion around hinge axis. *Eoc.-Rec.,* IndoPac.——Fig. C3,*3*. **T. tortuosa* (Linné), Rec., Philip., *3a,b,* LV ext., dorsal, ×0.75; *3c,* LV hinge, ×1.1 (Newell, n).

Subfamily ANADARINAE Reinhart, 1935

Without byssal gape, adults free or attached by thin byssus; subtrapezoidal, subtrigonal or ovoid, beaks prosogyre; dental series arched *(688, 784). U.Cret.-Rec.*

Anadara Gray, 1847 [**Arca antiquata* Linné, 1758; OD] [=*Anomalocardia* Mörch, 1853 (type, *A. granosa* Linné, 1758, Rec.) (*non Anomalocardia* Schumacher, 1817); *Cara* Gray, 1857 (type, *Arca aviculoides* Reeve, 1844, =*Arca formosa* Sowerby, 1833, Rec., Panama); *Rasia* Gray, 1857 (type, *Arca formosa* Sowerby, 1833, Rec., Panama); *Nemoarca* Conrad, 1869 (type, *N. cretacea,* U.Cret., N.J.); *Pectinatarca* Sacco, 1898 (type, *Arca pectinata* Brocchi, 1814, Mio., Italy); *Diluvarca* Woodring, 1925 (type, *Arca diluvii* Lamarck, 1805, Mio., Eu.); *Tegillarca* Iredale, 1939 (type, *T. granosa bessalis,* Rec., E.Australia); *Esmerarca* Olsson, 1961 (type, *Arca reinharti* Lowe, 1935, Rec., Panama)]. Rotund, moderately heavy, ornamented with strong costae which correspond to interlocking crenulations of shell margins; equivalve in shape and sculpture; cardinal area narrow, elongate; dental series only slightly arched. *U.Cret.-Rec.,* cosmop.

A. (Anadara). Subtrapezoidal; ligament amphidetic; dental series continuous, consisting of similar and uniformly graded teeth. *U.Cret.,* USA (N.J.); *Oligo.-Rec.,* cosmop.——Fig. C3,*4*. **A. (A.) antiquata* (Linné), Rec., Madag.; *4a,* LV ext., ×1.1; *4b,* LV hinge, ×2.25 (Newell, n).

A. (Lunarca) Gray, 1857 [**L. costata*; OD] [=*Argina* Gray, 1842 (type, *Arca pexata* Say, 1821, =*A. campechensis* Gmelin, 1792) (*non Argina* Hübner, 1816); *Mabellarca* Iredale, 1939 (type, *Arca dautzenbergi* Lamy, Rec., E. Australia); *Arginarca* McLean, 1951 (type, *Arca campechensis* Gmelin, 1792, Rec., Gulf Mex.)]. Elongate, ovoid, cardinal area placed entirely behind beaks; teeth divided into 2 series, anterior being short and irregular as compared with posterior series. *Eoc.-Rec.,* widespread.——Fig. C3,*5*. **A. (L.) costata,* Rec., USA(Ala.); *5a,* LV ext., ×1.1; *5b,* LV hinge, ×2.25 (Newell, n).

Bathyarca Kobelt, 1891 [**Arca pectunculoides* Scacchi, 1833; OD] [=*Microcucullaea* Iredale, 1929 (type, *B. perversidens* Hedley, 1907, Rec., S.Australia); *Indacar* Iredale, 1939, p. 261 (type, *Acar pteroessa* Smith, M)]. Ovoid small shells somewhat reduced anteriorly, posterior carina obscure or lacking, umbones situated less than 0.3 back of anterior margin, ornamented with radial costellae and concentric growth lines, ligament area narrow; teeth short, oblique, converging toward point below beaks, divided into anterior and posterior series of slightly longer teeth separated by an elongate edentulous gap, posterior teeth in some forms becoming subparallel to hinge and thus approaching Grammatodontinae. *Eoc.-Rec.,* cosmop. ——Fig. C5,*2*. **B. pectunculoides* (Scacchi), Rec.; RV ext., ×6 (Kobelt, 1891).

Bentharca Verrill & Bush, 1898 [**Macrodon asperula* Dall, 1881; OD]. Similar to *Bathyarca* but extremities quadrate and anterior end of shell is more reduced; teeth not divided or serrated. *Rec.,* Gulf Mex.——Fig. C5,*1*. **B. asperula* (Dall); *1a,b,* LV hinge, RV ext., ×4 *(216).*

Larkinia Reinhart, 1935 [**Anadara larkinii* Nelson, 1870; OD] [=*Grandiarca* Olsson, 1961 (type, *Arca grandis* Broderip & Sowerby, 1829, Rec., Panama)]. Subtrigonal, nearly as high as long, heavy, with prominent, elevated umbones and small beaks, somewhat truncate posteriorly; cardinal area high, ligament amphidetic; costae narrow, steep-sided, smooth or beaded with coarse or scabrous nodes. *?Oligo., Mio.-Rec.,* E.Pac.-Carib.

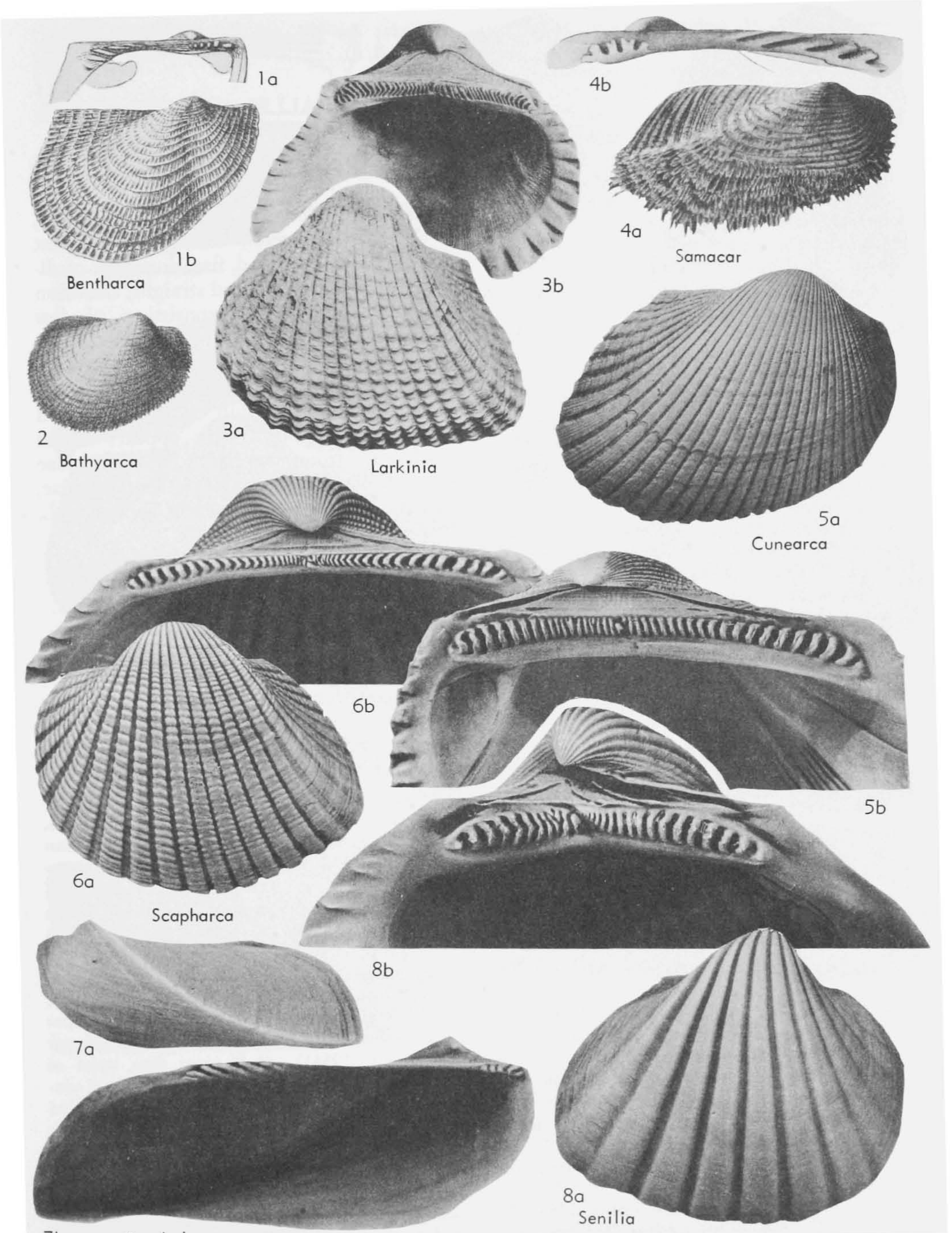

Fig. C5. Arcidae (Arcinae) (p. *N*254, *N*256).

——Fig. C5,*3*. **L. larkinii* (Nelson), Mio., Peru; *3a,b,* LV ext., int., ×0.7 (Olsson, 1932).

Samacar Iredale, 1936 [**Arca strabo* Hedley, 1914 (1915); OD]. Beaks about 0.25 of length back of anterior margin, anterior end rounded, narrow, posterior broad and obliquely truncated; ornamented with low, broad, concentric ridges crossed by faint costellae; hinge with medial edentulous area, anterior teeth short, bifid, and posterior teeth somewhat longer, serrate, obliquely inclined, radial with respect to a point well below beaks. *?Pleist.-Rec.,* Australia.——Fig. C5,*4*. **S. strabo* (Hedley), Rec.; *4a,* RV ext., ×4; *4b,* RV hinge, ×8 *(399).*

Scapharca Gray, 1847 [**Arca inaequivalvis* Bruguière, 1789; OD] [=*Caloosarca* Olsson, 1961 (type, *Andarca rustica* Tuomey & Holmes, 1857, Plio., SE.USA); *Sectiarca* Olsson, 1961 (type, *Anadara (S.) floridana* Conrad, 1869, Rec., Panama)]. Shell relatively thin, moderately convex; valves discordant, LV being larger, its margin overlapping that of RV; dentition as in *Anadara. Oligo.-Rec.,* cosmop.

S. (Scapharca). Elongate, moderately convex, umbones flattened or slightly sulcate; sculpture similar in 2 valves, consisting of smooth or nodose, simple or bifurcating costae, rectangular in cross section and separated by flattened interspaces; cardinal area narrow, elongate; ligament commonly reduced or lacking in front of beaks. *Oligo.-Rec.,* cosmop.——Fig. C5,*6*. **S. (S.) inaequivalvis* (Bruguière), Rec., Malaya; *6a,* LV ext., ×1; *6b,* RV int., ×2 (Newell, n).

S. (Cunearca) Dall, 1898 [**Arca incongrua* Say, 1822; SD Lamy, 1907] [=*Imparilarca* Iredale, 1929 (type, *I. hubbardi,* Rec., Queensl.); *Potiarca* Iredale, 1939 (type, *P. pilula,* Rec., E.Australia)]. Subtrigonal, inflated, with full umbones and small, submedial beaks over high, triangular cardinal area covered completely by amphidetic ligament; sculpture discrepant, costae of LV being larger and more coarsely nodose. *Oligo.-Rec.,* cosmop.——Fig. C5,*5*. **S. (C.) incongrua* (Say), Rec., USA(Fla.); *5a,* RV ext., ×1; *5b,* RV int., ×2 (Newell, n).

?**Scaphula** Benson, 1834 [**S. celox*; SD Benson, 1836]. Subtrapezoidal, elongate, very small smooth shells lacking radial ornamentation over most of surface; posterior umbonal carina high and narrow; teeth numerous, subequal, converging obliquely downward. [Fresh- and brackish-water habitat.] *Rec.,* Burma-India.——Fig. C5,*7*. **S. celox,* India; *7a,* LV ext., ×4; *7b,* LV int., ×6 (Newell, n).

Senilia Gray, 1842 [**Arca senilis* Linné, 1758; SD Gray, 1847]. Similar to *Larkinia* but with extremely prosogyrate beaks, bearing few very broad radial ribs, having more trigonal form, and with oblique interruption in dentition beneath beaks. *Rec.,* W.Afr.——Fig. C5,*8*. **S. senilis* (Linné), Angola; *8a,* RV ext., ×1; *8b,* RV int., ×2 (Newell, n).

Family PARALLELODONTIDAE Dall, 1898

[*nom. subst.* Dall (*pro* Macrodontidae Dall, 1895, invalid name based on junior homonym)] [Materials for this family prepared by N. D. Newell]

Inflated, elongate, nearly equivalve, strongly inequilateral, orthogyre; ligament duplivincular on broad, flat, divergent cardinal areas; hinge long and straight; dentition strongly inequilateral, consisting of few posterior laterals and numerous, generally short, oblique, horizontal, or falcate anterior and medial cardinals. [The phylogeny of this group is difficult to determine and poorly understood. There appears to be gradation from ancestral Cyrtodontidae through Parallelodontidae to Cucullaeidae, and the limits are not clearly defined.] *L. Ord.-Rec.*

Subfamily PARALLELODONTINAE Dall, 1898

[*nom. transl.* Newell, herein (*ex* Parallelodontidae Dall, 1898)]

Byssal gape and corresponding ventral sinus present; valve margins not denticulate; hinge teeth converging toward point slightly above anterior end and ahead of beaks; anterior ends of posterior laterals intersecting dorsal margin of shell. *L.Ord.-U.Jur.*

Parallelodon Meek & Worthen, 1866 [*pro Macrodon* (Lycett) Buckman, 1845 (*non* Schinz, 1822, *nec* Müller, 1842)=*Macrodus* Beushausen 1895 (obj.) (*non* Gray, 1864)] [**Macrodon rugosus* Buckman, 1845] [=*Prorhynchus* Hall, 1884, p. xlviii (type, *Palaeanatina quadratum* Hall, 1883; OD); *Beushausenia* Cossmann, 1897 (obj.) (*non* Maillieux, 1913, =*Maillieuxia* Cossmann, 1920); *?Sufia* Prantl & Ružička, 1955 (type, *S. paradoxa*; OD); *?Mnataia* Prantl & Ružička, 1955 (type, *M. pribyli*; OD); *Palaeocucullaea* Tokuyama, 1960 (type, *Parallelodon monobensis* Nakazawa, 1956)]. Shell more than twice as long as high, some species posteriorly alate; umbones approximately 0.25 of shell length behind anterior extremity; smooth or ornamented with radial ribs; ligament areas broad, with several chevron grooves converging toward beaks; with or without anterior myophoric buttress; hinge long and straight (Driscoll, 1961). *L.Ord.(Tremadoc.)-U.Jur.,* cosmop.——Fig. C6,*1a*. **P. rugosus* (Buckman), M.Jur., Eng.; RV int., ×0.4.——Fig. C6,*1b*. *P. bipartitum* (Roemer), U.Jur., Belg.; LV ext., ×1 *(20).* [=*Glyptarca* Hicks, 1873, p. 48 (type, *G. primaeva;* SD Newell, herein).]

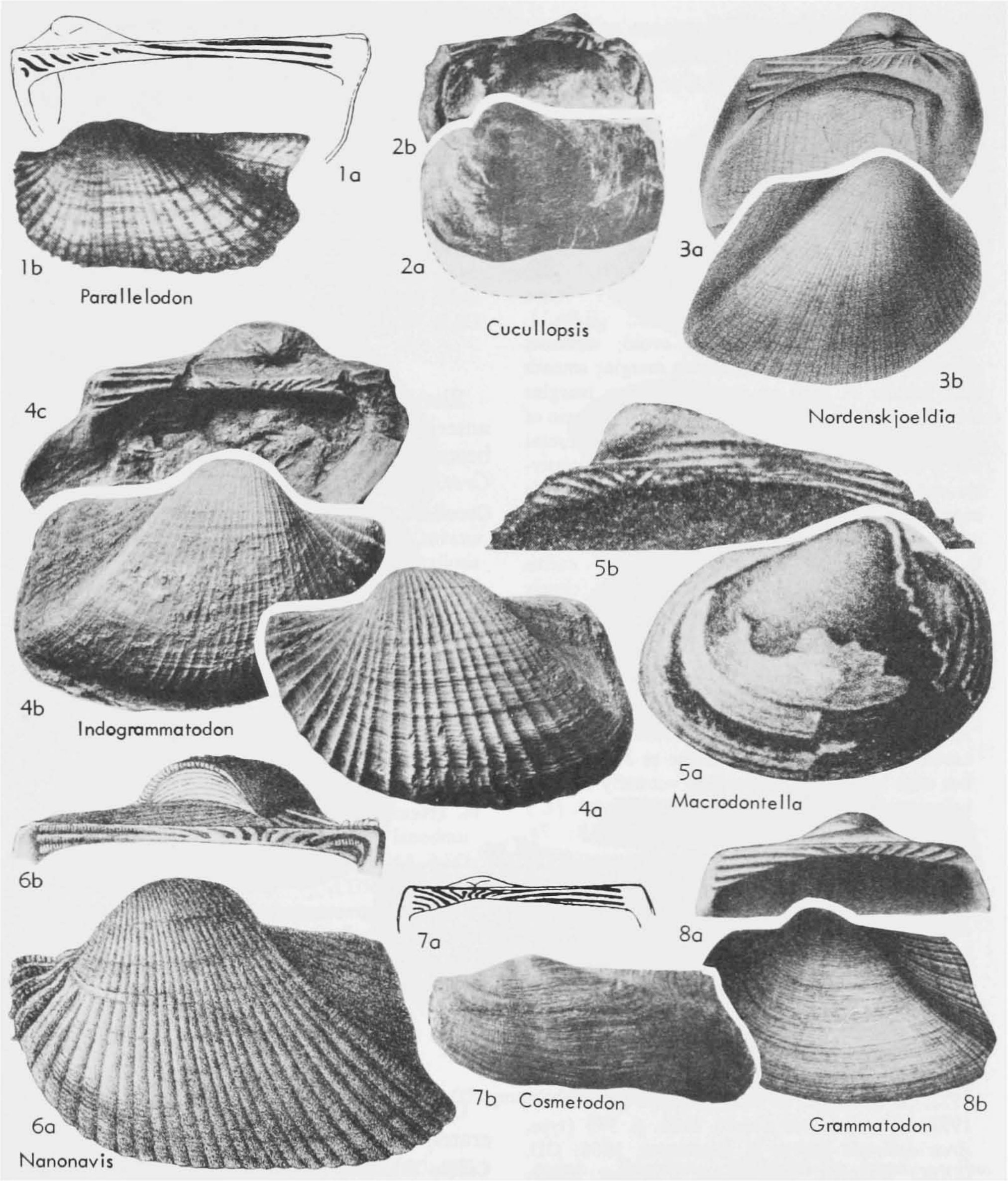

FIG. C6. Parallelodontidae (Parallelodontinae) *(1,5)*, (Grammatodontinae) *(2-4,6-8)* (p. *N*256-*N*258).

?**Carbonarca** MEEK & WORTHEN, 1870 [**C. gibbosa*; OD]. *Penn.*, USA(Ill.).

?**Curvirostrum** BUCKMAN, 1882 [**C. striatum*; OD]. *M.Jur.(Bajoc.)*, Eng.

Macrodontella ASSMANN, 1916 [**M. lamellosa*; OD]. Ovoid, without posterior umbonal carina, surface unornamented; ligament area narrow. *Trias.*, Ger. ——FIG. C6,*5*. **M. lamellosa*, M.Trias., E.Ger., *5a*, RV ext., ×2; *5b*, RV int., ×4 (Assmann, 1916).

Subfamily GRAMMATODONTINAE Branson, 1942

[*nom. transl.* NEWELL, herein (*ex* Grammatodontidae BRANSON, 1942)]

Valve margins closed, without denticulations; hinge teeth converging downward toward point well below beaks so that anterior ends of posterior pseudolaterals intersect ventral margin of hinge plate; shell relatively shorter in several genera with umbones placed relatively farther back than in Parallelodontinae. *?U.Carb., U.Trias.-Rec.*

GRAMMATODON GROUP

Shell trapezoidal, anterior teeth short and not horizontal. *?U.Carb., Jur.-Cret.*

Grammatodon Meek & Hayden, 1861 [**Arca (Cucullaea) inornata* Meek & Hayden, 1859; OD] [=*Pseudomacrodon* Stoll, 1934 (type, *Macrodon pictum,* Callov.-Oxford., E.Eu.)]. Length less than twice height, ovoid; umbones about 0.3 or more back of anterior margin; smooth over middle of shell or costellate; valve margins closed; myophoric buttress lacking; inner margin of hinge plate straight or slightly curved, with several nearly parallel and horizontal posterior pseudolaterals and series of small, generally oblique cardinals converging toward point below beaks. *Jur.-Cret.,* cosmop.

G. (Grammatodon). Posterior umbonal carina commonly well defined and costellae closely spaced. *Jur.-Cret.,* cosmop.——Fig. C6,*8. G. (G.) concinnus* (Phillips), U.Jur., Eu.; *8a,b,* LV int., ext., ×2 *(20).*

G. (Cosmetodon) Branson, 1942 [**Arca keyserlingii* d'Orbigny, 1850; OD] [=*Beushausenia* Arkell, 1930 (*non* Cossmann, 1897, *nec* Maillieux, 1913)]. Externally similar to *Parallelodon* but with hinge teeth converging ventrally to point below umbones. *Jur.,* Eu.——Fig. C6,*7.* **G. (C.) keyserlingii* (d'Orbigny), Oxford, USSR; *7a,* RV int., ×0.5; *7b,* LV ext., ×1 *(20).*

G. (Indogrammatodon) Cox, 1937 [**Cucullaea virgata* J. de C. Sowerby, 1840; OD]. Posterior umbonal ridge poorly defined; costae narrow, widely spaced, coarser on LV. *Jur.,* India-Afr.-SW.Pac.——Fig C6,*4.* **G. (I) virgatus* (Sowerby), M.Jur., India; *4a,b,* LV ext., RV ext., ×2; *4c,* LV int., ×2 *(180).*

G. (Nanonavis) Stewart, 1930 [**Arca carinata* J. Sowerby, 1813; OD] [=*Spinularca* Chavan, 1952, p. 10 (type, *S. cristata* Bigot in Chavan, 1952, M); *Aptolinter* Casey, 1961, p. 575 (type, *Arca aptiensis* Pictet & Campiche, 1866; OD, L.Apt., W.Eu.)]. Trapezoidal, with low, closely spaced costae; umbonal carina sharp, delimiting deeply concave posterodorsal area; hinge plate narrow; teeth serrate, medial and anterior teeth falcate, tangential with dorsal and anterior margins. *Cret.,* USA(Calif.)-Eng.-Japan.——Fig. C6, *6.* **G. (N.) carinata* (Sowerby), Alb., Eng.; *6a,b,* LV ext., hinge, ×2 (Woods, 1899).

G. (Nordenskjoeldia) Wilckens, 1910 [**Arca disparilis* d'Orbigny, 1846 (*non* Reeve, 1844) (=**G. subdisparilis* Nicol, 1954); OD]. Ovoid, with low, closely spaced costae; umbonal carina sharp; teeth not serrate, hinge plate narrow, anterior teeth straight, oblique, becoming anteriorly parallel with anterodorsal margin. *U.Cret.,* India-Madag.——Fig. C6,*3.* **G. (N.) subdisparilis* (Nicol), India; *3a,b,* LV int., RV ext., ×1.5 (Stoliczka, 1891).

?**Cucullopsis** Chao, 1927 [**C. quadrata*; OD]. Shell thick, subquadrate, with height nearly equal to length, umbones prominent and placed well forward, umbonal carina weak and rounded, surface unornamented; several similar, oblique teeth in front and 2 subparallel pseudolaterals behind; ligament area narrow. *U.Carb.(Ural.),* China.——Fig. C6,*2.* **C. quadrata*; *2a,b,* LV ext., int., ×1 *(95).*

CUCULLARIA GROUP

Elongate, radially ribbed shells in which anterior teeth, shorter than posterior teeth, become subparallel with hinge margin. *U. Cret.-Eoc.*

Cucullaria Conrad, 1869 [**Arca heterodonta* Deshayes, 1860; OD]. Ovoid, costate, externally similar to *Barbatia* but with anterior and posterior laterals separated by few small cardinal teeth below beaks. *Eoc.,* France.——Fig. C7,*3.* **C. heterodonta* (Deshayes); *3a,b,* RV ext., hinge, ×0.7 *(259).*

Nemodon Conrad, 1869 [**Arca (Macrodon) eufalensis* Gabb, 1860; OD][=*Gilbertwhitea* Crickmay, 1930 (type, *Arca simillina* Whiteaves, 1879, Jur., B.C.)]. Length about twice height. *U.Cret.,* N.Am.-Asia-Madag.

N. (Nemodon). Costellae closely spaced; posterior umbonal carina distinct. *U.Cret.,* N.Am.——Fig. C7,*6.* **N. (N.) eufalensis* (Gabb); *6a,b,* LV ext., int., ×2 *(951).*

N. (Pleurogrammatodon) Ichikawa & Maeda, 1958 [**P. splendens;* OD]. Inflated, with prominent umbones, costae widely spaced; posterior carina lacking. *U.Cret.,* Japan-Madag.-W.Can. ——Fig. C7,*5.* **N. (P.) splendens,* Japan; *5a,b,* both valves dorsal, LV int., ×0.5 *(424).*

CATELLA GROUP

Ovoid or trapezoidal, small and moderately short. *U.Trias.-Rec.*

Catella Healey, 1908 [**Grammatodon (C.) laticlava*; OD] [=*Cryptochasma* Casey, 1961, p. 567 (type, *Cucullaea ovale*; OD; U.Apt., Eng.)]. Trapezoidal, pterioid, inflated, umbones situated about 0.3 of shell length behind anterior extremity, which is reduced, pointed, and separated from rest of shell by median sulcus; dentition similar to *Grammatodon. U.Trias.-Jur.,* Eurasia.

C. (Catella). Ornamented with concentric rugae or growth lamellae. *U.Trias.(Rhaet.),* Burma; *Jur.,* Sweden.——Fig. C7,*2.* **C. (C.) laticlava,* Rhaet., Burma; *2a,b,* LV ext., hinge, ×1 (Healey, 1908).

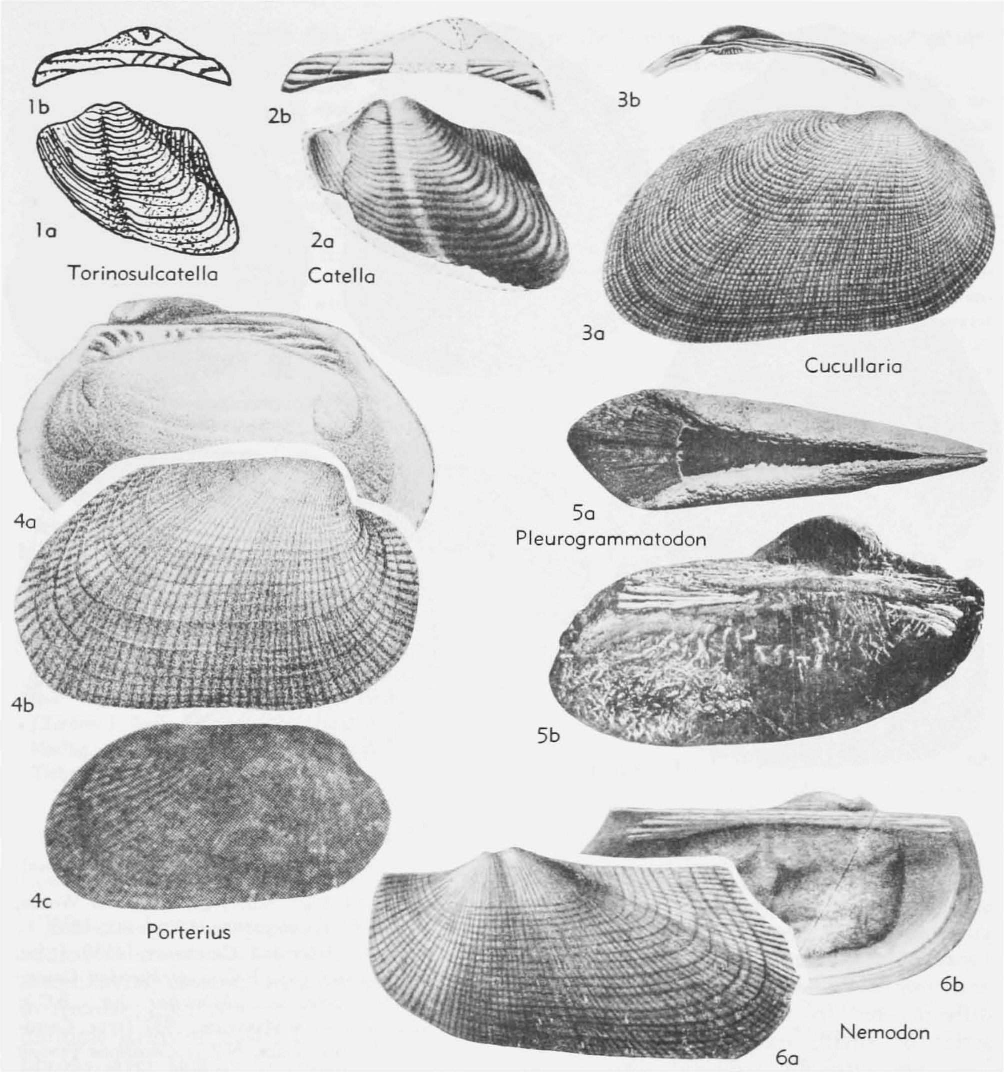

Fig. C7. Parallelodontidae (Grammatodontinae) (p. *N*258-*N*259).

C. (Torinosulcatella) Tamura, 1959 [**C. (T.) kobayashii*; OD]. Ornamented with fine radial costellae. *U.Jur.*, Japan.——Fig. C7,*1*. **C. (T.) kobayashii; 1a,b,* LV ext., hinge, ×2 *(901)*.

Paragrammatodon Nomura & Niino, 1940 [**Pseudogrammatodon pacificus* Nomura & Zinbo, 1934; OD]. Similar to *Porterius* but ornamented with prominent concentric ridges and obsolescent costae. *Rec.*, Japan.

Porterius Clark, 1925 [**Barbatia andersoni* Van Winkle, 1918; OD] [=*Pseudogrammatodon* Arkell, 1930]. Ovoid, costellate, externally similar to *Barbatia* but with posterior lateral teeth and cardinals that converge ventrally as with *Grammatodon*. *Eoc.-Rec.*, NW.USA-Eu.-Japan.——Fig. C7,*4a,b*. *P. adversidentatus* (Deshayes), Eoc., France; *4a,b,* RV int., ext., ×3 *(259)*.——Fig. C7, *4c*. **P. andersoni* (Van Winkle), Oligo., USA (Wash.); RV ext., ×1.5 (Van Winkle, 1918).

Family CUCULLAEIDAE Stewart, 1930

[*nom. transl.* Newell, herein (*ex* Cucullaeinae Stewart, 1930)] [Materials for this family prepared by N. D. Newell]

Ovoid, subtrigonal to subquadrate, smooth or radially costate, heavy shells with nearly median umbones and closed margins; valves of some shells with slight differences in

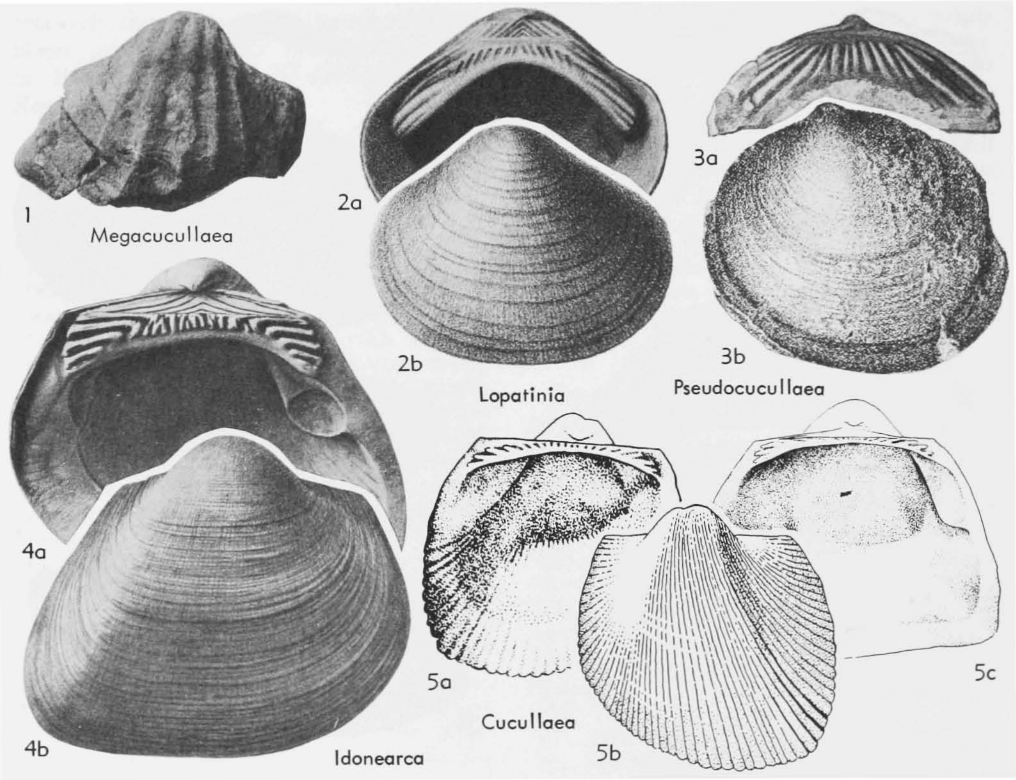

Fig. C8. Cucullaeidae (p. *N*260-*N*261).

ornamentation, LV projecting slightly beyond RV along rear and ventral margins; ligament amphidetic, duplivincular, broad, with few chevron-shaped grooves; teeth well differentiated in adults into intermediate series of small, transverse denticles and long, symmetrically arranged anterior and posterior, commonly crenulated pseudolaterals; teeth of young individuals of some genera converging downward toward point below beaks, at maturity diverging downward, away from beaks; posterior myophoric flange or shell characteristically developed. [Several genera have been based on the form and distribution of the lateral teeth but the phylogenetic significance of these variations is uncertain.] *L.Jur.-Cret., Rec.*

Cucullaea Lamarck, 1801 [**C. auriculifera* (=*Arca cucullata* Röding, 1798, *Arca cucullus* Gmelin, 1791, **?Arca labiata* Solander, 1786); SD Children, 1823] [=*Cucullana* Lichtenstein, 1818 (type, *Arca (C.) cucullus* Gmelin, 1791, Rec., W. Pac.); *Latiarca* Conrad, 1862 (type, *C. gigantea* Conrad, 1830, Eoc., Md.); *Dicranodonta* Woods, 1899 (type, *C. donningtonensis* Keeping, 1883, L. Cret., Eng.); *Ashcroftia* Crickmay, 1930 (type, *A. inversidentata,* Jur., B.C.); *Archaeodon* Crickmay, 1930 (type, *A. phylarchus,* Jur., B.C.); *Cucullastis* Finlay & Marwick, 1937 (type, *Cucullaea (C.) barbara,* Dan., N.Z.); *Cucullona* Finlay & Marwick, 1937 (type, *Cucullaea (C.) inarata,* Dan., N.Z.)]. Subtrigonal, subtrapezoidal to ovoid, heavy shells with rounded posterior umbonal carina, posterior margin obliquely truncated, surface radially ornamented with strong costae; middle series of teeth and crenulations of inner shell margin becoming obsolete in mature and old individuals; pseudolaterals diverging downward in adults. *L.Jur.(Lias.)-Cret.,* Eu.-USA; *Rec.,* IndoPac.

C. (Cucullaea). Subtrigonal to subtrapezoidal short shells, ornamented with moderate to coarse, closely-spaced costae; laterals diverging downward in adults. *Rec.,* IndoPac.——Fig. C8,*5*. **C. (C.) labiata* (Solander), W.Pac.; *5a,b,* LV int., ext., ×3; *5c,* RV int., ×0.5 *(674).*

C. (Idonearca) Conrad, 1862 [**C. tippana* Conrad, 1858 (=*C. capax* Conrad, 1858; **C. vulgaris* Morton, 1830); SD Dall, 1898]. Subtrapezoidal, elongate, with fine, closely spaced radial costellae and subhorizontal lateral teeth. *Jur.-Cret.,* Eu.-USA.——Fig. C8,*4*. **C. (I.) vulgaris* (Morton), Cret., USA; *4a,b,* RV int., ext., ×0.7 *(951).*

Lopatinia Schmidt, 1872 [**L. petschorae* Keyserling, 1846; SD Maury, 1930]. Ovoid, nearly equilateral, with rounded dorsal margin, middle series of teeth gradational with marginal laterals, all diverging downward away from beaks. *Cret.,* USSR-Afr.-S.Am.

L. (Lopatinia). Ornamented with fine costellae. *Cret.,* USSR.——Fig. C8,*2*. *L. (L.) jenisseae* (Lahusen), Sib.; *2a,b,* RV int., LV ext., ×1 (Schmidt, 1872).

L. (Pseudocucullaea) Solger, 1903 [**P. lens*; OD] [=*Eusebia* Maury, 1930 (*non* Duponchel, 1845) (type, *E. stantoni,* Cret., Brazil)]. Surface unornamented. *Cret.,* W.Afr.-S.Am.——Fig. C8, *3*. **L. (P.) lens,* W.Afr.; *3a,b,* RV hinge, LV ext., ×1.5 (Solger, 1903).

Megacucullaea Rennie, 1936 [**Cucullaea kraussi* Tate, 1867 (=*C. cancellata* Krauss, 1850, *non C. cancellata* Phillips, 1829); OD] [=?*Noramya* Casey, 1961, p. 575 (type, *Arca forbesii* Pictet & Campiche, 1866; OD, L.Apt., Eng.)]. Surface ornamented with fine costellae superimposed on few widely spaced radial plications. *U.Jur.(Tithon.),* India; *L.Cret.(Neocom.),* E.Afr.-S.Afr.-Madag.——Fig. C8,*1*. **M. kraussi* (Tate), Tithon., India; RV ext., ×0.5 *(183).*

Family NOETIIDAE Stewart, 1930

[*nom. transl.* Newell, herein (*ex* Noetiinae Stewart, 1930)] [=Noetidae MacNeil, 1937] [Materials for this family prepared by N. D. Newell]

Without byssal gape and mostly free in adults; subtrapezoidal to ovoid, equivalve, inequilateral, costate; dentition generally as in Arcidae; ligament vertically striated with multiple strips of elastic layer imbedded in fibrous layer that is in contact with shell; prosodetic, amphidetic or opisthodetic; myophoric ridge or shelf at inner margin of one or both adductor scars. [Widespread in shallow seas.] *L. Cret.-Rec.*

Subfamily NOETIINAE Stewart, 1930

Ovoid to trigonal, commonly inequilateral with well-developed posterior umbonal ridge and corresponding posterior emargination of shell; ornamentation commonly of primary and intercalated secondary costae, of which latter form principal ribs in adults, inner margin crenulate; ligament elongate and broad, characteristically coextensive with half or more of cardinal area; opisthogyre shells tend to be prosodetic and prosogyre shells opisthodetic. *L.Cret.-Rec.*

Noetia Gray, 1857 [**N. triangularis* (=**Arca reversa* Sowerby, 1833); OD] [=*Noetiella* Thiele & Jaekel, 1931 (type, *N. congoensis,* Rec., E. Atl.)]. Rhomboidal to subtrigonal, heavy shells, produced posteroventrally, beaks opisthogyre, high when situated just anterior to mid-point of hinge, becoming lower when posterior; ornamented with subequal costae, inner margin crenulated posteroventrally; ligament covering most or all of anterior part of cardinal area and part of posterior part of area within cardinal area; teeth radial, chevron-shaped anteriorly and in some species posteriorly, anterior series becoming relatively longer than posterior series in forms with posterior beaks. *L.Cret.-Rec.,* cosmop.

N. (Noetia). Umbonal ridge carinate; radial ribs coarse, simple, not bifurcate over umbonal slope; posterior margin subangular, commonly truncate. *U.Eoc.,* IndoPac.; *L.Mio.-Rec.,* E.Pac.-Carib.——Fig. C9,*3*. **N. (N.) reversa* (Sowerby), Rec., Panama; *3a,b,* RV int., both valves, RV view, ×1 (Maury, 1922).

N. (Eontia) MacNeil, 1938 [**Arca ponderosa* Say, 1822; OD]. Similar to *Noetia* but generally more ovoid and inflated and with coarse bifurcating costae; anterior and posterior dental series subequal; ligament amphidetic. *L.Mio-Rec.,* W. Eu.-W.Atl.-Carib.-E.Pac.——Fig. C9,*7*. **N. (E.) ponderosa* (Say), Rec., USA(Fla.); *7a,b,* LV ext., int., ×1 (MacNeil, 1938).

N. (Incanopsis) Olsson, 1944 [**I. acariformis;* OD][=*Palestinarca* Vokes, 1946 (type, *Trigonarca palestina* Whitfield, 1891, Apt., Lebanon)]. Umbonal ridge carinate; radial ribs numerous, fine, not bifurcate; posterior margin obliquely truncate. *Cret.(Apt.-Senon.),* N.Peru-Lebanon. ——Fig. C9,*2*. **N. (I.) acariformis,* U.Cret., N. Peru; *2a,b,* LV ext., int., ×2 (Olsson, 1944).

Arginopsis MacNeil, 1938 [**Scapharca sullanensis* Woods, 1822; OD] [=*Samanoetia* MacNeil, 1940 (*pro Arginella* MacNeil, 1938) (type, *Arca samanensis* Olsson, 1929, U.Eoc., Peru) (*non Arginella* Forsius, 1926)]. Subovate to subcircular in lateral profile, evenly inflated, umbonal ridge rounded, obscure; beaks strongly prosogyre, situated anteriorly; ornamented with many regular costae; ligament opisthodetic, completely covering posterior part of cardinal area; anterior series of teeth short, chevron-shaped. *U.Eoc.,* Peru.——Fig. C9,*6*. **A. sullanensis* (Woods); *6a,b,* both valves dorsal, RV ext., ×1 (MacNeil, 1938).

Noetiopsis MacNeil, 1938 [**N. woodringi*; OD]. Trigonal, subcarinate, similar to *Noetia,* but with prosogyre beaks situated well forward of midpoint of hinge; ligament opisthodetic. *Eoc.,* Panama.——Fig. C9,*5*. **N. woodringi,* LV ext., ×1 (MacNeil, 1938).

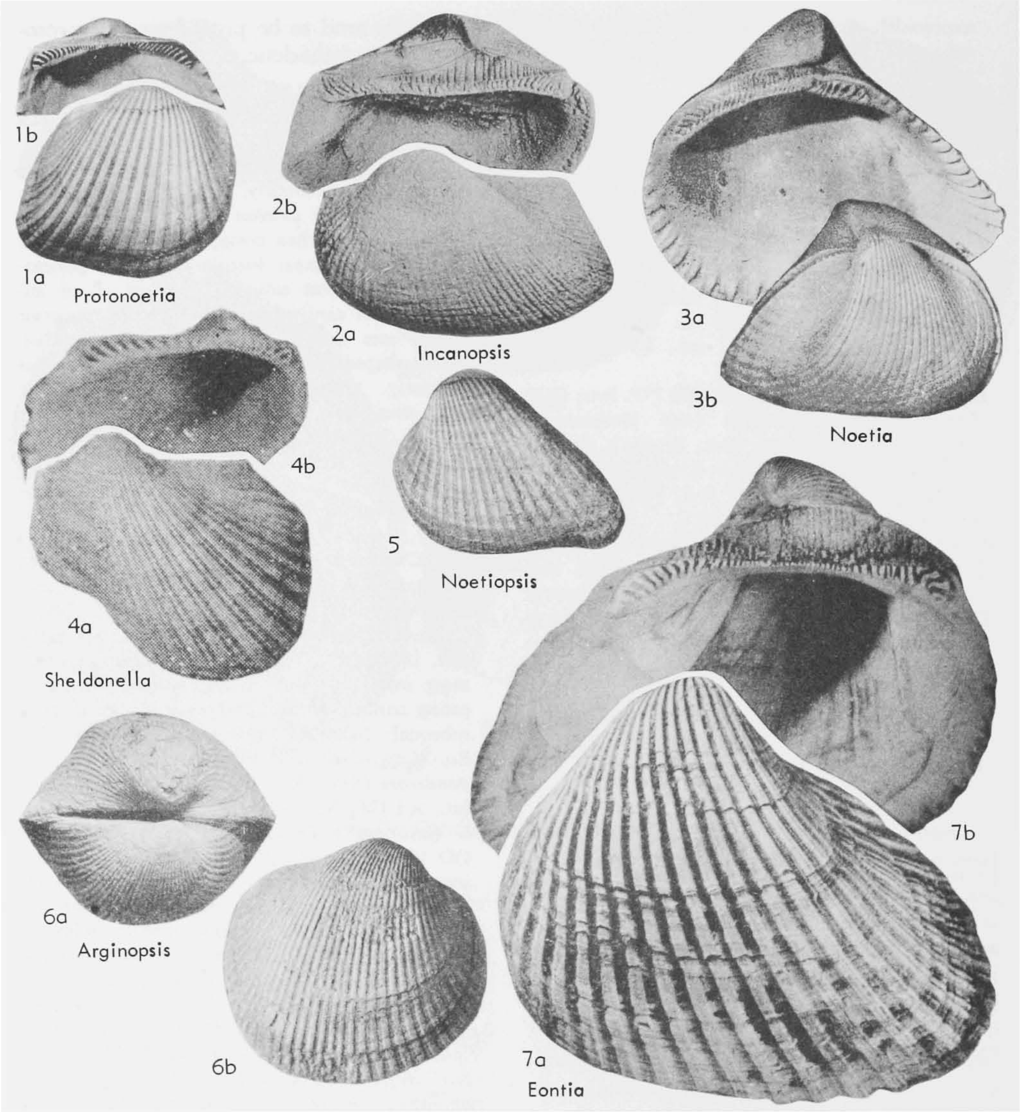

Fig. C9. Noetiidae (Noetiinae) (p. *N*261-*N*262).

Protonoetia MacNeil, 1938 [**Anadara nigeriensis* Newton, 1922; OD]. Subquadrate, inflated, subangular posteroventrally, umbonal ridge subcarinate, beaks nearly central and orthogyre; ornamented with subequal, undivided costae; ligament amphidetic; terminal anterior and posterior teeth chevron-shaped. *M.Eoc.,* W.Afr.(Nigeria).——Fig. C9,*1*. **P. nigeriensis* (Newton); *1a,b,* RV ext., int., ×1 (MacNeil, 1938).

Sheldonella Maury, 1917 [**Noetia (S.) maoica;* OD] [=*Barbatiella* Lamy, 1917 (type, *B. barbatiella,* =*Arca venusta* Dunker, 1852, =*A. lateralis* Reeve, 1844, Rec., IndoPac.); *Didimacar* Iredale, 1939 (type, *D. repenta,* Rec., E.Australia); *Paranoetia* Thiele, 1934 (type, *Arca lateralis* Reeve, 1844, Rec., IndoPac.)]. Elongate, barbatiform, umbonal ridge rounded, beaks moderately high, prosogyre to opisthogyre, situated anteriorly; secondary costae becoming bifurcate marginally in adults. *M.Mio.,* Domin.Repub.; *Rec.,* IndoPac. ——Fig. C9,*4*. **S. maoica,* M.Mio., Domin.Repub.; *4a,b,* LV ext., int., ×3 (MacNeil, 1938).

Subfamily STRIARCINAE MacNeil, 1938

Generally small, ovoid, subequilateral, with submedian umbones, beaks prosogyre

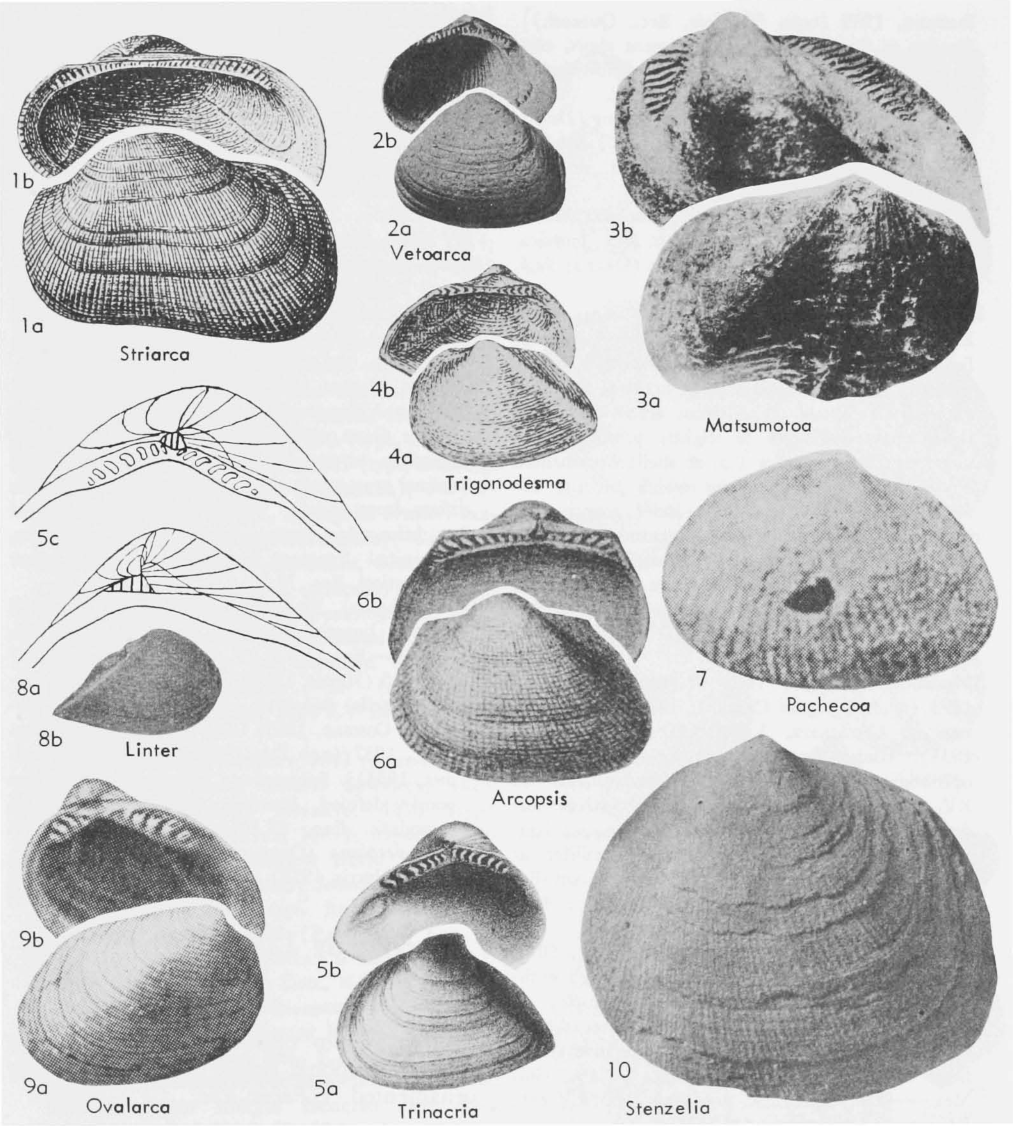

FIG. C10. Noetiidae (Striarcinae) *(1-4,6,9)*, (Trinacriinae) *(5,7,8,10)* (p. *N*263-*N*264).

to slightly opisthogyre; costellate; ligament amphidetic, short to long, bordered by ligament-free cardinal area. *U.Cret.-Rec.*

Striarca CONRAD, 1862 [**Arca centenaria* SAY, 1824; OD] [=*Breviarca* CONRAD, 1872 (type, *Arca saffordi* GABB, 1860; SD STEWART, 1930, U.Cret., Tenn.); *Estellacar* IREDALE, 1939 (type, *E. saga*, Rec., Queensl.); *Galactella* COSSMANN & PEYROT, 1912 (type, *Arca lactea* LINNÉ, 1758, Rec., Medit.)]. *Barbatia*-like costellate shells with relatively long ligament; inner margin of anterior and posterior adductor scars bordered with raised myophoric flange. *U.Cret.-Rec.* USA-Eu.-Australia.——FIG. C10,*1*. **S. centenaria* (SAY), Mio., USA(Md.); *1a,b*, LV ext., RV int., ×2 (Glenn, 1904).

Arcopsis KOENEN, 1885 [**Arca limopsis* KOENEN, 18??; SD REINHART, 1935] [=*Fossularca* COSSMANN, 1887 (type, *Arca quadrilatera* LAMARCK, 1805, *Eoc.*, France); *Gabinarca* IREDALE, 1939 (type, *G. pellita*, Rec., Queensl.); *Mulinarca* IREDALE, 1939 (type, *Barbatia aceraea* MELVILL & STANDEN, 1899, Rec., Queensl.); *Scapularca* COSSMANN & PEYROT, 1912 (type, *Arca scapulina* LAMARCK, 1805, Eoc., France); *Spinearca* IREDALE, 1939 (type, *S. deliciosa*, Rec., Queensl.); *Verilarca*

Iredale, 1939 (type, *V. bivia*, Rec., Queensl.)]. Similar to *Striarca* but with ligament short, confined to shallow, triangular resilifer below beaks. *Paleog.(Dan.)-Rec.*, Eu.-N.Am.-IndoPac.

A. (Arcopsis). Surface costellate. *Paleog.(Dan.)-Rec.*, cosmop.——Fig. C10,*6*. **A. (A.) limopsis* (Koenen), Dan., Denm., *6a,b*, LV ext., int., X4 (Koenen, 1885).

A. (Ovalarca) Woodring, 1925 [**Barbatia ovalina* Dall, 1898; OD]. Surface smooth. *Mio.*, Jamaica. ——Fig. C10,*9*. **A. (O.) ovalina* (Dall); *9a,b*, RV ext., int., X12 *(1005)*.

Matsumotoa Okada, 1958 [**M. japonica*; OD]. Elongate, ovoid, with rounded anterior and obliquely rounded posterior margin, ventral margin medially sinuate; umbonal ridge carinate, bounded anteriorly by broad radial sulcus across middle of shell; beaks orthogyre to slightly prosogyre, situated at about anterior 0.3 of shell; ornamented anteriorly by distinct costae which become obsolescent over posterior area, inner margin not crenulate; dentition cucullaeid, central teeth very short, ventrally convergent, terminal teeth long and slender, subparallel with hinge line; ligament vertically striate. *U.Cret.*, Japan.——Fig. C10,*3*. **M. japonica*; *3a,b*, RV ext., int., X1.25 (Okada, 1958).

Trigonodesma Wood, 1864 [**Arca lissa* Bayan, 1873 (=*A. laevigata* Caillat, 1873, *non* Spengler in Chemnitz, 1784); SD Winckworth, 1934]. Umbonal carina well developed, weakly opisthogyrate, radial sculpture predominant on RV, concentric on LV; posterior muscle scar bordered anteriorly by low myophoric flange; ligament confined to small, triangular resilifer at center of flattened cardinal area. *Eoc.*, N.Am.-Eu. ——Fig. C10,*4*. **T. lissa* (Bayan), Eng.; *4a,b*, LV ext., int., X6 (Wood, 1864).

Vetoarca Stephenson, 1947 [**V. hindsana*; OD]. Beaks prominent, orthogyre, subcentral; shell without radial ornamentation; adductor muscles attached to slightly raised platforms; inner surface within pallial line strongly ribbed; ligament confined to small, triangular resilifer. *U.Cret.*, Gulf Mex.——Fig. C10,*2*. **V. hindsana*; *2a,b*, LV ext., RV int., X2 (Stephenson, 1947).

Subfamily TRINACRIINAE MacNeil, 1937

Small, trigonal to ovoid, with or without weak, subequal, radial ornamentation, strongly inequilateral to subequilateral; ligament restricted to narrow resilifer bounded by small cardinal area, prosodetic, opisthogyre; largest teeth commonly chevron-shaped. [These forms are convergent with the Limopsidae from which they differ in being opisthogyre and in possessing a striated ligament.] *U.Cret.-Eoc.*

Trinacria Mayer, 1868 [**Trigonocoelia crassa* Deshayes, 1860; SD Gardner, 1926]. Opisthogyre, amphidetic to opisthodetic, cardinal area small, indistinct, entirely behind beaks, umbonal ridge broadly rounded; numerous weak costellae; dental series usually interrupted at ligament. *Eoc.*, Eu.-N.Am.——Fig. C10,*5a,b*. **T. crassa* (Deshayes), Paris Basin; *5a,b*, LV ext., int., X4 *(259)*.——Fig. C10,*5c*. *T. media* (Deshayes), Paris Basin; LV hinge, X4 *(570)*.

Linter Stephenson, 1937 [**L. acutata*; OD]. Similar to *Trinacria* but more elongate and with sharp umbonal carina. *U.Cret.*, N.Am.——Fig. C10,*8*. **L. acutata*, USA(Tex.); *8a*, RV hinge, X4 *(570)*; *8b*, RV ext., X4 (Stephenson, 1937).

Pachecoa Harris, 1919 [**Trinacria (P.) cainei*; OD] [=*Halonanus* Stewart, 1930 (type, *Noetia pulchra* Gabb, 1860, Eoc., Tex.)]. Opisthogyre, prosodetic or amphidetic, umbonal ridge weak; cardinal area small, situated entirely behind beaks; differs from *Noetia* in that sculpture consists of few bifurcating costae, inner margin crenulate, and initial ligament groove is oblique, rather than vertical. *Eoc.*, N.Am.

P. (Pachecoa). Elongate-ovoid, cardinal area well defined, ligament elongate, prosodetic. *Eoc.*, SE. USA.——Fig. C10,*7*. **P. (P.) cainei*, S.Car.; LV ext., X5 (Harris, 1919).

P. (Stenzelia) MacNeil, 1954 [**Pectunculus perplanus* Conrad, 1865; OD] [=*Trinacriella* MacNeil, 1937 (*non* Del Guerico, 1913; *nec* Parona, 1933)]. Subquadrate to ovoid, cardinal area poorly defined, ligament short, amphidetic to prosodetic. *Eoc.*, SE.USA.——Fig. C10,*10*. **P. (S.) perplana* (Conrad), USA(Ala.); LV ext., X3.5 (Harris, 1919).

Superfamily LIMOPSACEA Dall, 1895

[Diagnosis by N. D. Newell]

Orbicular to obliquely ovoid, generally without umbonal ridge; smooth or radially ornamented. *L.Perm.-Rec.*

Family LIMOPSIDAE[1] Dall, 1895

[Materials for this family prepared by N. D. Newell]

Small, orbicular to subtrigonal, orthogyre or prosogyre, equilateral to strongly inequilateral, with closed margins; ligament not striated, short, mainly restricted to central

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[1] Note to R. C. Moore from Professor L. W. Grensted at request of W. E. China, ICZN: "The generic ending *-opsis* makes its genitive ὄψεως, *opseos*, and this (as the accent shows) is treated as a dissyllable. The stem therefore is not *-opse* (or Ionic, *-opsi*) but *-ops*. Poeciliopsinae and Macropsidae are therefore quite correct."

triangular resilifer, which may be bordered by smooth uncovered cardinal area; dentition taxodont, radial with respect to point well below beaks, divided into two more or less symmetrical series. [Exhibits some parallelism with Glycymerididae. Convergent with some of the Philobryidae.] *U. Trias.-Rec.*

Limopsis Sassi, 1827 [**Arca aurita* Brocchi, 1814; OD] [=*Trigonocoelia* Nyst & Galeotti, 1835 (obj.); SD Herrmannsen, 1894); *Lunopsis* d'Orbigny, 1850 (type, *Pectunculus hoeninghausii* Müller, 1847, *nom. null.*, Cret., Aachen); *Cnisma* Mayer, 1868 (type, *Pectunculus nuculatus* Lamarck, 1807; M); *Limopsilla* Thiele, 1923, p. 289 (type, *Limopsis pumilio* Smith, 1904; OD); *?Lissarcula* Thiele, 1923, p. 290 (type, *L. australis;* OD); *Loringella* Iredale, 1929 (type, *L. loringi* Angas, 1873; OD) (Rec., E.Australia); *Phrynelima* Iredale, 1929 (type, *Loringella brazieri* Iredale, 1929; OD) (Rec., E.Australia); *Glycilima* Iredale, 1931 (type, *G. paradoxa, nom. nud.*)]. Orbicular, nearly equilateral, commonly with slight forward obliquity. *M.Jur.-Rec.*, cosmop.

L. (Limopsis). Surface without radial ornamentation, inner margins not crenulate. *M.Jur.-Rec.*, cosmop.——Fig. C11,*1*. **L. (L.) aurita* (Brocchi), Plio., Italy; *1a,b*, LV int., ext., ×1 *(222)*.

L. (Pectunculina) d'Orbigny, 1843 (*emend.* Sacco, 1898) [**Pectunculus scalaris* Sowerby, 1825; OD] [=*Cosmetopsis* Roverto, 1898 (type, *Limopsis retifera* Semper, 18??); *Aspalima* Iredale, 1929 (type, *Limopsis erecta* Hedley & Petterd, Rec., S.Australia); *Senectidens* Iredale, 1931 (type, *S. dannevigi*, Rec., E.Australia); *Versipella* Iredale, 1931 (*V. soboles*, Rec., E. Australia); *Limopsista* Finlay & Marwick, 1937 (type, *Limopsis microps*, Dan., N.Z.); *Circlimopa* Iredale, 1939 (type, *C. woodwardi mutanda*, Rec., S.Australia); *Oblimopa* Iredale, 1939 (*O. macgillivrayi actaviva*, Rec., E.Australia)]. Similar to *L. (Limopsis)*, but sculptured with radial costellae; inner margin crenulate. *Cret.-Rec.*, cosmop.——Fig. C11,*7*. **L. (P.) scalaris* (Sowerby), Eoc., Eng.; *7a,b*, RV ext., LV int., ×2 (Wood, 1864).

Empleconia Dall, 1908 [**Limopsis vaginata* Dall, 1891; OD]. Ovoid, strongly oblique, without radial ornamentation; posterior dorsal margin deeply infolded, forming deep, narrow cleft between closed valves. *Rec.*, Bering S., N.Pac.——Fig. C11, *4*. **E. vaginata* (Dall); *4a*, LV ext., ×1.5; *4b*, RV int., ×1 (Dall, 1895).

Hoferia Bittner, 1894 [**Lucina duplicata* Münster, 1838; OD] [=*Arcoptera* Bittner, 1895 (*non* Heilprin, 1887) (type, *A. elegantula*, U. Trias., Alps); *Bittnerella* Dall, 1898; *Elegantarca* Tomlin, 1930 (*nom. subst. pro Arcoptera* Bittner, 1895)]. Ovoid to rhomboid, very inequilateral, umbones and broad cardinal area prominent; without radial sculpture; rounded anterior auricle set off from body of shell by narrow sulcus and byssal notch. *U.Trias.*, Alps.——Fig. C11,*2*. **H. duplicata* (Münster); *2a-c*, RV ext., int., dorsal, ×2 *(58)*.

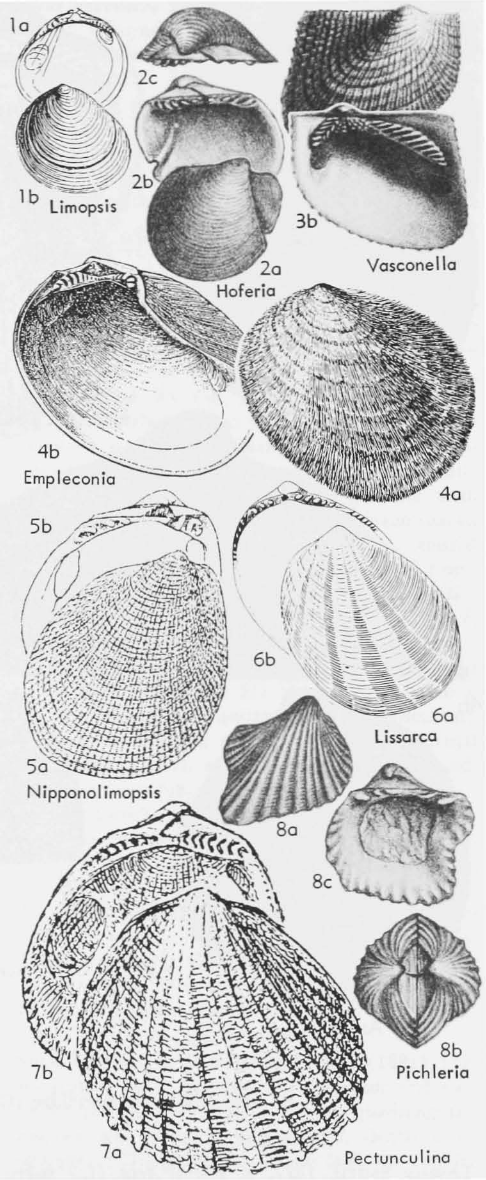

Fig. C11. Limopsidae (p. *N265-N267*).

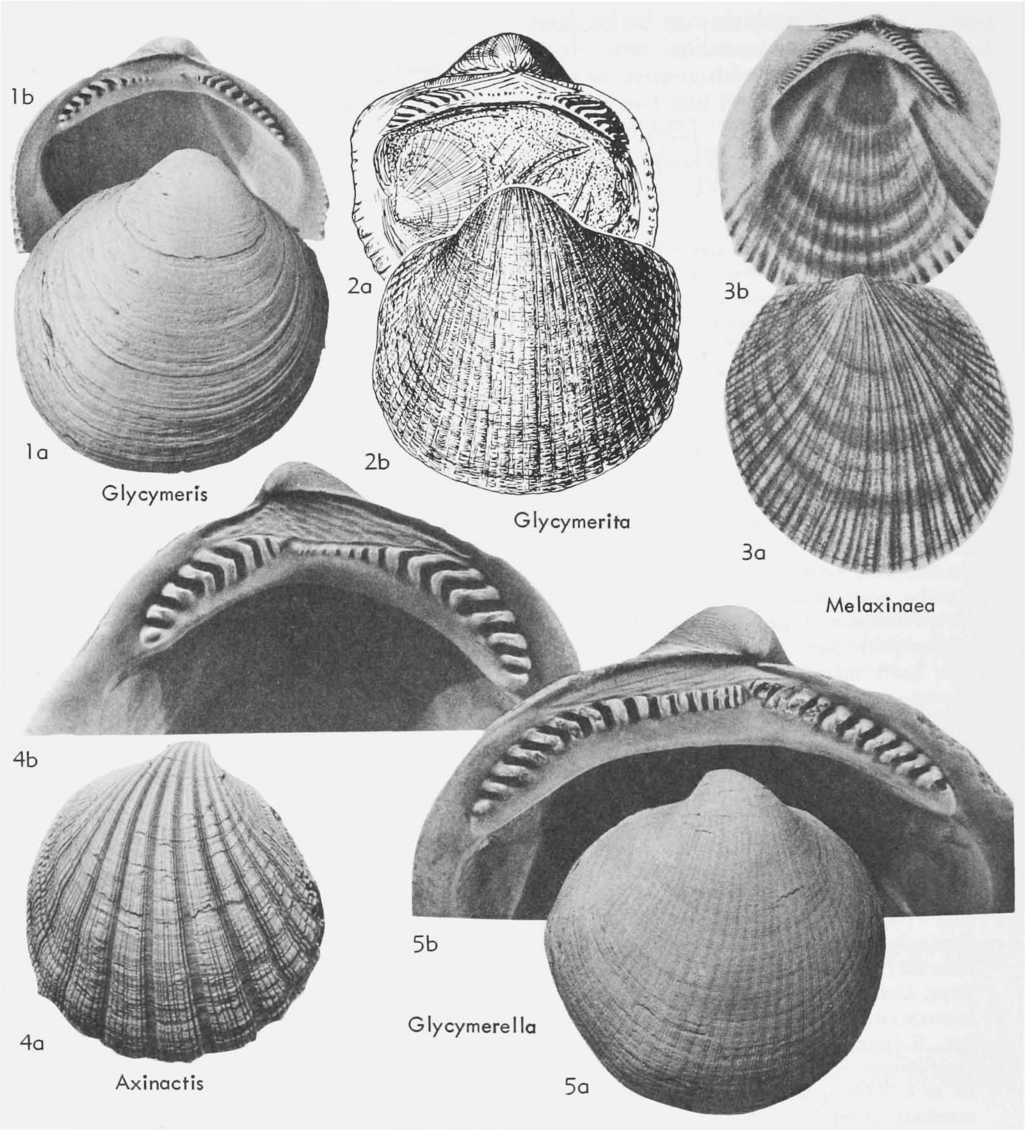

Fig. C12. Glycymerididae (Glycymeridinae) (p. *N*267-*N*268).

Lissarca Smith, 1877, p. 168 [**Arca (L.) rubrofusca*; M] [=*Austrosarepta* Hedley, 1899 (type, *A. picta;* M)]. Shell prosocline, hinge strongly arched, teeth few, with edentulous hiatus in middle, ventral margin crenulate; radial ornamentation obsolescent. *Plio.-Rec.,* SW.Pac.-Antarctic.——Fig. C11,*6*. *L. rubricata* (Tate), S.Australia; *6a,b,* LV ext., RV int., ×10 *(167)*.

Nipponolimopsis Habe, 1951 [**Limopsis nipponica* Yokoyama; OD]. Acuminate-ovoid, inequilateral, with cancellate ornamentation; anterior dental series and adductor somewhat reduced. *Rec.,* Japan.——Fig. C11,*5*. **N. nipponica* (Yokoyama); *5a,b,* RV ext., LV int., ×3 *(365)*.

?**Nucunella** d'Orbigny, 1850, p. 389 [**Stalagmium nystii* Galeotti, 1843; SD Stoliczka, 1871]. *Tert.,* Belg.

Pichleria Bittner, 1894 [**Cucullaea auingeri* Laube, 1865; OD]. Subquadrate, strongly inequilateral, with prominent beaks and broad cardinal area; ornamented by widely spaced costae corresponding to crenulations of margin; rounded posterodorsal auricle set off from body of shell by broad sulcus. *U.Trias.,* Alps.——Fig. C11,*8*. **P. auingeri* (Laube); *8a-c,* RV ext., shell dorsal, RV int., ×3 *(58)*.

?**Vasconella** Boussac, 1911, p. 42 [**Stalagmium aviculoides* d'Archiac, 1850; OD][=*Boussacia*

Cossmann, 1911 (obj.)]. Rhomboidal, strongly inequilateral, with reduced anterior extremity but without anterior sulcus; ornamented by fine intercalating costellae; teeth in 2 series converging ventrally and separated by small triangular, ?duplivincular ligament. *Eoc.,* W.Eu.——Fig. C11,*3*. **V. aviculoides* (d'Archiac), Eoc., France(Biarritz); *3a,b,* RV, ext., int., ×1 (d'Archiac, 1850).

Family GLYCYMERIDIDAE Newton, 1922

[*nom. correct.* Warmke & Abbott, 1961 (*pro* Glycymeridae Newton, 1922] [=Axinaeinae Adams & Adams, 1858; Pectunculidae Gray, 1847 (invalid name, Code Art. 11e, based on *Pectunculus* Lamarck, 1799, *non* Huddesford, 1770)] [Materials for this family prepared by N. D. Newell]

Adults free, not byssate, subtrigonal to subcircular, equivalve, more or less equilateral, heavy shells with submedian, orthogyre, slightly prosogyre or opisthogyre beaks, generally slightly truncate or subangular behind, margins without gape; cardinal area broad, ligament duplivincular, amphidetic or prosodetic, cardinal area with one or more chevron grooves; hinge plate broad, dental series strongly arched, consisting of robust taxodont teeth in anterior and posterior sets that diminish gradually in size toward middle and extremities, teeth transverse or chevron-shaped with angulation pointing toward middle of hinge, radial with respect to point well below beaks, larger teeth commonly crenulate; myophoric buttress or platform commonly developed at front of posterior adductor. *L.Cret.-Rec.*

Subfamily GLYCYMERIDINAE Newton, 1922

[*nom. transl. et correct.* Newell, herein (*ex* Glycymeridae Newton, 1922)]

Orbicular, with or without obscure posterior umbonal carina; smooth or with radial ornamentation, border crenulate. *Cret.-Rec.*

Glycymeris da Costa, 1778 [*non Glycimeris* Lamarck, 1799 (=*Panopea* Ménard, 1807)] [**Arca orbicularis* da Costa, 1778 (=*Arca glycymeris* Linné, 1758); T] [=*Axinaea* Poli, 1791 (type, *Arca pilosa* Linné, 1767, Rec., Atl.); *Axinaeoderma* Poli, 1795 (type, *Arca pilosa* Linné, 1767, Rec., Atl.); *Tuceta* Röding, 1798 (type, *Arca glycymeris* Linné, 1758, Eu.); *Pectunculus* Lamarck, 1799 (*non* Huddesford, 1770) (obj.); *Pectunculopsis* Ebert, 1890 (obj.); *Pseudaxinea* Monterosato, 1892 (type, *Pectunculus violacescens* Lamarck, 1819, Rec., Medit.); *Grandaxinaea* Iredale, 1931 (type, *Glycymeris magnificens* Iredale, 1929, Rec., SW.Pac.); *Veletuceta* Iredale, 1931 (type, *Glycymeris glammeus* Reeve, 1843, Rec., Australia); *Tucetona* Iredale, 1931 (type, *Pectunculus flabellatus* Tennison-Wood, 1878, Rec., S.W. Pac.); *Glycymerula* Finlay & Marwick, 1937 (type, *Axinaea modesta* Angas, 1879, Rec., N.Z.); *Manaia* Finlay & Marwick, 1937; *Tucetilla* Iredale, 1939 (type, *Glycymeris capricornis* Hedley, 1906, Rec., W.Pac.); *Tucetopsis* Iredale, 1939 (type, *Cardium amboinensis* Gmelin, 1791, Rec., W.Pac.)]. Subcircular to subquadrate, beaks orthogyre to opisthogyre, ligament amphidetic, surface smooth or costate, ventral margins internally fluted. *L.Cret.-Rec.,* cosmop.

G. (Glycymeris). Subcircular, subequilateral, with small umbones and beaks; teeth relatively short, transverse, becoming obsolescent medially; surface smooth or costate. *L.Tert.-Rec.,* cosmop.——Fig. C12,*1*. **G. (G.) glycymeris* (Linné), Rec., Medit.; *1a,b,* RV ext., LV int., ×1 (Newell, n).

G. (Glycymerita) Finlay & Marwick, 1937 [**Glycymeris concava* Marshall, 1917; OD]. Subquadrate, posterior subtruncate, with prominently projecting umbones, anterior and posterior teeth moderately elongate, curved or chevron-shaped with convexity directed toward beaks, medial teeth small, transverse, exterior costate. *L.Cret.-Tert.,* Eu.-N.Z.-Calif.——Fig. C12,*2*. **G. (G.) concava* (Marshall), Paleog.(Dan.), N.Z.; *2a,b,* LV int., ext., ×0.7 *(304)*.

Axinactis Mörch, 1861 [**Pectunculus inaequalis* G. B. Sowerby, 1833; SD Hertlein & Strong, 1943]. Orbicular, inequilateral, beaks prominent, opisthogyre; ligament prosodetic; hinge and dental series asymmetrical, somewhat abbreviated behind. *Mio.-Rec.,* trop.Am.

A. (Axinactis). Costae relatively few, large, bearing fine costellae. *Rec.,* Panama.——Fig. C12,*4*. **A. (A.) inaequalis* (Sowerby); *4a,* RV ext., ×1; *4b,* RV int., ×2 (Newell, n).

A. (Glycymerella) Woodring, 1925 [**Arca decussata* Linné, 1758 (=*Pectunpennaceus* Lamarck, 1819)]. Costae numerous, low, bearing fine costellae. *Mio.-Rec.,* trop.W.Atl.——Fig. C12, *5*. **A (G.) decussata* (Linné), Rec.; *5a,* RV ext., ×1; *5b,* LV int., ×2 (Newell, n).

Felicia Mabille & Rochebrune, 1889 (1891) [**F. jousseaumi;* M]. Oblique, with anterior end narrowly rounded, posterior slightly quadrangular; exterior and inner margin smooth; dental series straight. [This genus is said to lack the resilifer of Limopsidae. The size of the holotype (length, 39 mm.) suggests a glycymeridid something like *Peruarca.* Unfortunately, the type species, as far as can be ascertained, has not been illustrated.] *Rec.,* S.Am.(Beagle Channel, Cape Horn).

Melaxinaea Iredale, 1930 [**M. labyrintha;* OD]. Subcircular, compressed, equilateral, with low umbones and inconspicuous orthogyre beaks, ornamented with scabrose costae that become smoother and more numerous distally by intercalation in successive ranks; ligament short and narrow,

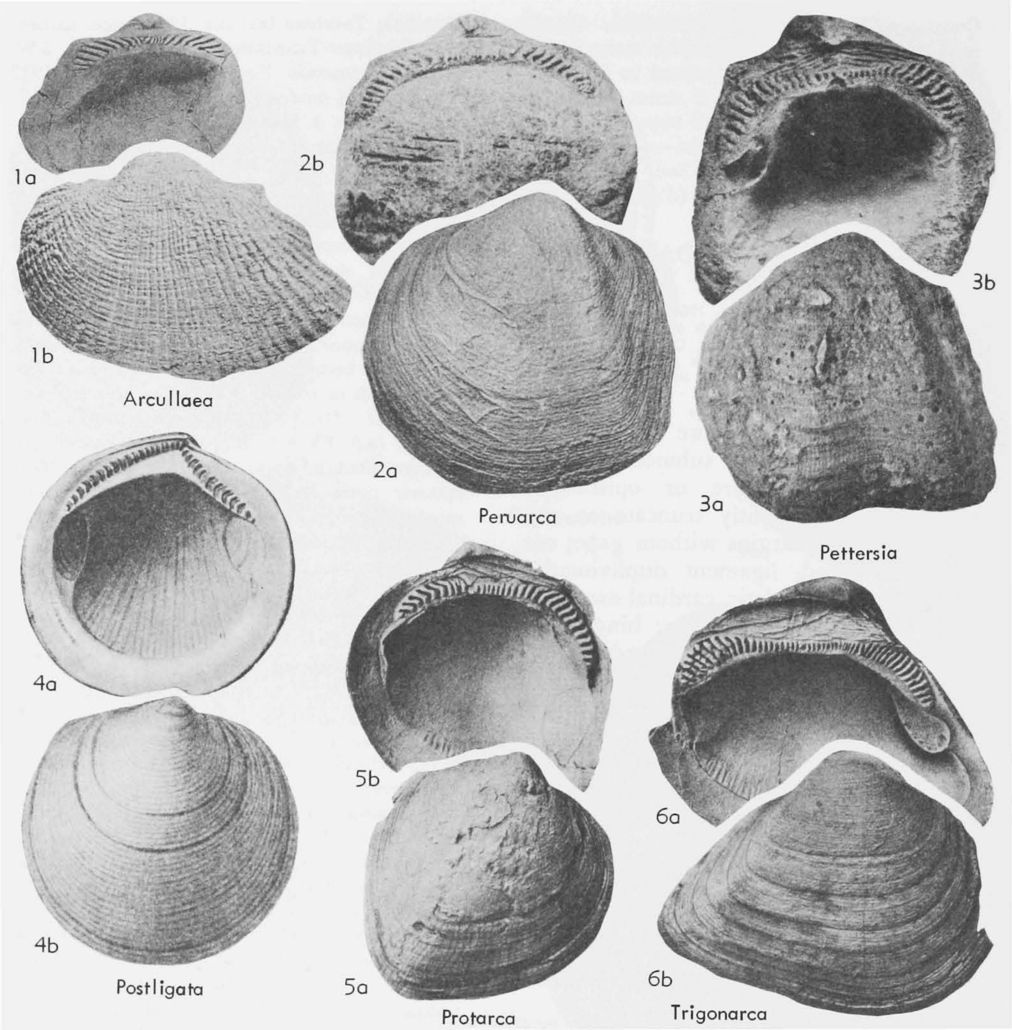

Fig. C13. Glycymerididae (Arcullaeinae) (p. *N*268-*N*269).

amphidetic; teeth similar, chevron-shaped, in 2 series that diverge under beaks at approximately right angle, separated in adult. *Rec.*, W.Pac.——Fig. C12,*3*. **M. labyrintha; 3a,b,* LV ext., int., ×1 (Iredale, 1930).

Subfamily ARCULLAEINAE Newell, new subfamily

Ovoid to subtrigonal, rarely subcircular, inequilateral, beaks central to slightly anterior, with or without rounded posterior umbonal carina; exterior smooth or with more or less obsolescent radial rims, inner margin not crenulate. [This group is externally similar to Cucullaeidae from which it probably was derived but the hinge more closely resembles Glycymerididae.] *L.Cret.-U.Cret.*

Arcullaea Vokes, 1946 [**A. olea*; OD]. Elongate-ovoid, somewhat obliquely truncate behind, radially sculptured with fine costellae which disappear over middle of RV. *L.Cret.*, Lebanon.——Fig. C13,*1*. **A. olea; 1a,* LV int., ×1; *1b,* LV ext., ×3 *(945)*.

Peruarca Olsson, 1944 [**P. pectunculoides*; OD]. Subcircular, truncate behind, posterior umbonal carina well defined, surface without radial costae. *U.Cret.*, Peru.——Fig. C13,*2*. **P. pectunculoides*; *2a,b,* LV ext., RV int., ×0.8 (Olsson, 1944).

Pettersia Nicol, 1953 [**Cardium? abnormalis* Olsson, 1944; OD]. Subtrigonal, rounded, slightly higher than long, with prominent posterior umbonal ridge and broad median sulcus corresponding to ventral sinus, umbones prominent; exterior ornamented with fine costellae. *U.Cret.,* S.Am.(Peru-Colom.).——FIG. C13,*3*. **P. abnormalis* (OLSSON), Peru; *3a,b,* LV ext., RV int., ×1 (Nicol, 1953).

Postligata GARDNER, 1916 [**Glycymeris (P.) wordeni*; OD]. Subcircular, compressed, with low umbones and inconspicuous prosogyre beaks, without radial ornamentation; ligament opisthodetic, elongate, narrow; 2 arcuate series of similar, chevron-shaped teeth forming approximate right angle under beaks, both slightly concave toward front of shell. *U.Cret.,* USA(Md.).——FIG. C13,*4*. **P. wordeni*; *4a,b,* LV int., RV ext., ×4 *(334)*.

Protarca STEPHENSON, 1923 [**P. obliqua*; OD]. Ovoid, with forward obliquity, vertically truncate behind, prosogyrate; surface ornamented with irregular low costae; ligament and dental arch shortened anteriorly. *U.Cret.,* USA(N.Car.).——FIG. C13,*5*. **P. obliqua*; *5a,b,* RV ext., int., ×0.5 *(887)*.

Trigonarca CONRAD, 1862 [**Cucullaea macoensis* CONRAD, 1860; OD]. Subtrigonal, obliquely truncated behind, opisthogyrate, without radial ornamentation; ligament and dental arch shortened and reduced posteriorly. *U.Cret.,* N.Am.-Eu.-S.Afr.-India.——FIG. C13,*6*. **T. macoensis* (CONRAD), USA(Ala.); *6a,b,* RV int., LV ext., ×0.5 *(887)*.

?Family MANZANELLIDAE Chronic, 1952

[=Nuculinidae CHRONIC, 1952; Nucinellidae VOKES, 1956] [Materials for this family prepared by MYRA KEEN and N. D. NEWELL]

Small to minute shells, unornamented, nuculoid in shape, with umbones behind mid-point of dorsal margin; not nacreous; ligament opisthodetic and external; dentition consisting of series of taxodont cardinals below and behind beaks and 1 strongly buttressed anterior lateral in each valve; pallial line entire. [A degree of uncertainty relates to the orientation of these animals, since some authors regard the shells as prosodetic, with posterior lateral teeth.] *Perm.-Rec.*

Manzanella GIRTY, 1909 [**M. elliptica*; OD]. Subquadrate, nearly equilateral, prosogyrate; ligamental furrow elongate; anterior lateral and anterior adductor buttressed from within cavity of valves. *Perm.(San Andres-Kaibab-?Yeso),* SW. USA.——FIG. C14,*3*. **M. elliptica,* ?Yeso F., N. Mex.; *3a,b,* LV int., RV int., ×2 *(338)*.

Huxleyia A. ADAMS, 1860 (Apr.) [**H. sulcata*; M] [=*Cyrilla* A. ADAMS, 1860 (June) (obj.; *pro Huxleyia*); *Diabolica* JOUSSEAUME, 1897 (type, *D. diabolica*; T); *Cyrillista* IREDALE, 1929 (type, *Nuculina concentrica* VERCO, 1907; OD)]. Ligamental fossette large and round, impinging on cardinal area; lateral tooth smaller than in *Nucinella*. *Rec.,* Japan-S. Australia-E. Afr.-W. Am. ——FIG. C14,*1*. **H. sulcata,* Japan; *1a,b,* LV int., ext., ×5 *(365)*.

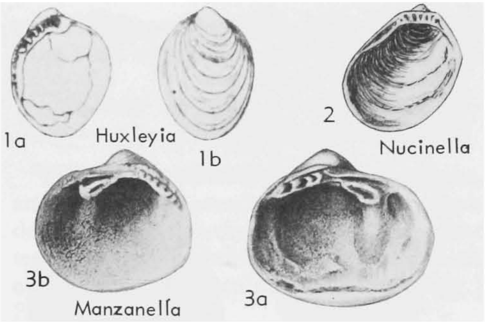

FIG. C14. Manzanellidae (p. *N*269).

Nucinella WOOD, 1851 [**Pleurodon ovalis* WOOD, 1840; SD STOLICZKA, 1870] [=*Pleurodon* WOOD, 1840 (*non* HARLAN, 1831); *Nuculina* D'ORBIGNY, 1844 (*non* PORRO, 1837); *Cyrillona* IREDALE, 1929 (type, *Cyrilla dalli* HEDLEY, 1902; OD); *Neopleurodon* HERTLEIN & STRONG, 1940 (type, *Pleurodon subdolus* STRONG & HERTLEIN, 1937; OD)]. Obliquely ovate, inequilateral, opisthogyrate; ligamental furrow short, narrow; with or without angulate expansions of hinge margins. *Jur.(Hettang.)-Rec.,* Eu.-S.Afr.-E.Afr.-Australia-N. Z.-W.N.Am.-W.Mex.-Carib.——FIG. C14,*2*. **N. ovalis* (WOOD), Plio., Eng.; LV int., ×6 (Wood, 1851).

?Family PHILOBRYIDAE Bernard, 1897

[*nom. transl.* SUTER, 1913 (*ex* Philobryinae BERNARD, 1897)] [Materials for this family prepared by MYRA KEEN]

Small, equivalve, very inequilateral; umbones projecting or with flat cap formed by prodissoconch; shell not nacreous. Ligament internal or only partly external, median or directed backward; short thin byssus between anterior margins of valves; hinge with strong vertical crenulations, with or without marginal teeth or ridges; anterior adductor muscle obsolete in some. *Eoc.-Rec.*

Philobrya CARPENTER, 1872 [*pro Bryophila* CARPENTER, 1864 (*non* TREITSCHKE, 1825)] [**B. setosa* CARPENTER, 1864; M] [=*Philippiella* MARTENS & PFEFFER, 1886 (type, *P. quadrata*; SD DELL, 1964); *Stempellaria* CLASING, 1918 (type, *Avicula magellanica* STEMPELL, 1899; M); *Stempellia* ODHNER, 1921 (*non* LÉGER & HESSE, 1910)]. Mytiliform, surface smooth or nearly so. *Pleist.-Rec.,* N.Am.-S.Pac.-S.Atl.

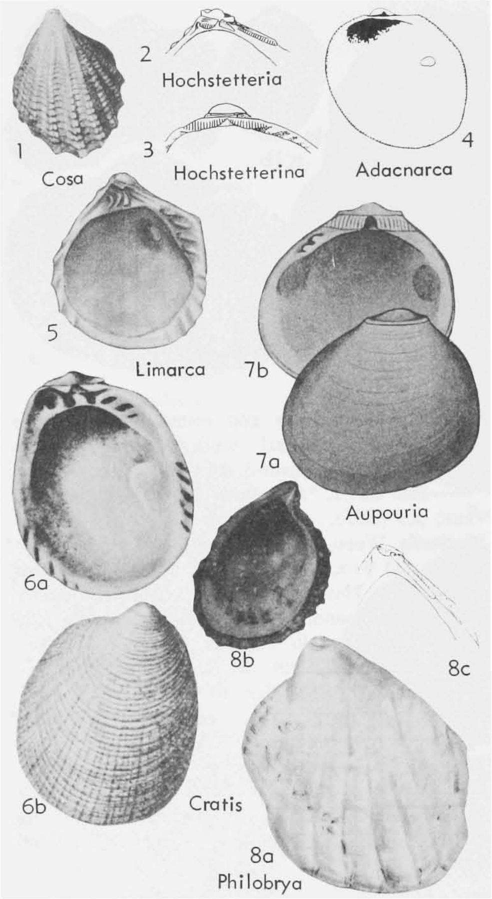

Fig. C15. Philobryidae (p. *N*270).

P. (Philobrya). With flaky periostracum that may or may not be radially marked; hinge area nearly smooth; interior of shell shiny, minutely punctate. *Pleist.-Rec.,* W. N. Am.-S. Afr.-S. Atl.——Fig. C15,*8*. **P. (P.) setosa* (Carpenter), Rec., USA (Calif.); *8a,* LV ext., ×5 (42); *8b,* RV int., ×4 (Keen, n); *8c,* detail of RV hinge, ×16 *(42).*

P. (Adacnarca) Pelseneer, 1903 [**A. nitens*; M]. Rounded, thin, weakly radially striate; hinge margin finely toothed; anterior adductor muscle scar very small. *Rec.,* Antarctic.——Fig. C15,*4*. **P. (A.) nitens* (Pelseneer); LV int., ×4 (Pelseneer, 1903).

P. (Hochstetteria) Vélain, 1877 [**H. aviculoides*; SD Kobelt, 1881] [=*Cosatova* Iredale, 1939 (type, *P. recapitula* Hedley, 1906; OD)]. Embryonal shell prominent; hinge crenulations well marked; ligamental fossette short, triangular. *Rec.,* Medit.-S. Atl.-Australasia.——Fig. C15,*2*. **P. (H.) aviculoides* (Vélain), St. Paul I.; RV hinge, ×16 *(42).*

P. (Hochstetterina) Thiele, 1934 [**Hochstetteria crenella* Vélain, 1877; M] [=*Hochstetteria* auctt.]. Shell margin slightly dentate; hinge cross-striate, teeth wanting. *Rec.,* S.Atl.-S.Pac. ——Fig. C15,*3*. **P. (H.) crenella* (Vélain), N.Z. (Stewart I.); RV hinge, ×20 *(42).*

P. (Micromytilus) Cotton, 1931 [**Myrina crenatulifera* Tate, 1892; SD Cotton & Godfrey, 1940]. Umbo not terminal; hinge teeth series separated by oblique resilifer. *Rec.,* Australia.

P. (Neocardia) Sowerby, 1892 [**N. angulata*; M]. Quadrate, hinge with 1 or 2 marginal crenulations at posterior end; sculpture cancellate. *Rec.,* S.Afr.

P. (Notomytilus) Hedley, 1916 [**Philippiella ruber* Hedley, 1904; OD]. Umbo terminal; hinge plate curved, the somewhat overlapping series of anterior and posterior teeth separated by long, narrow cartilage. *Rec.,* S.Australia.

Aupouria Powell, 1937 [**A. parvula*; OD]. Minute, solid, smooth, hinge with U-shaped resilium and 2 small crenulate teeth anteriorly. *Plio.-Rec.,* N.Z.——Fig. C15,*7*. **A. parvula,* Rec.; *7a,b,* LV ext., RV int., ×15 (Powell, 1937).

Cosa Finlay, 1927 [**Hochstetteria costata* Bernard, 1896; OD]. With well-developed radial ribs. *Eoc.-Rec.,* S.Australia-N.Z.——Fig. C15,*1*. **C. costata* (Bernard), Rec., N.Z. (Stewart I.); LV ext., ×6 *(42).*

Cratis Hedley, 1914 (1915) [**C. progressa*; OD] [=*Denticosa* Iredale, 1930 (type, *Philobrya cuboides* Verco, 1907); OD]. Young stages resembling *Philobrya,* with crenulate hinge and prodissoconch cap; mature shell resembling *Limopsis,* cuboid, reticulately sculptured; cardinal teeth relatively heavy, divaricate. *L.Mio.-Rec.,* N.Z.-Australia.——Fig. C15,*6*. **C. progressa,* Rec., New S.Wales; *6a,b,* RV int., ext., ×7 *(399).*

Limarca Tate, 1886 [**L. angustifrons*; M]. Inequilateral, cartilage pit lanceolate, directed backward; hinge with anterior denticles and long, striate posterior teeth. *U.Eoc.,* S.Australia.——Fig. C15,*5*. **L. angustifrons*; RV int., ×4 (Ludbrook, MS).

Order MYTILOIDA Férussac, 1822

[*nom. correct.* Newell, 1965 (*ex* order Mytillacés Férussac, 1822)] [Diagnosis by N. D. Newell]

Equivalve and very inequilateral; generally byssate and epifaunal throughout life or secondarily burrowing; heteromyarian; ligament opisthodetic and parivincular, greatly extended posteriorly by secondary fusion of mantle edges behind primary ligament; without well-developed siphons, with essentially free mantle margins; shell prismato-nacreous; gills filibranchiate or eulamellibranchiate; pallial line entire. *Dev.-Rec.*

The Pinnidae, secondarily members of the infauna, are usually arbitrarily classed as Pteriacea. They are morphologically isolated but also have much in common with the Mytilacea and there is no paleontological evidence that the Pinnidae were derived from inequivalve ancestors.

Superfamily MYTILACEA Rafinesque, 1815

[*nom. transl. et correct.* Tryon, 1884 (*ex* Mytilidia Rafinesque, 1815)] [Materials for this superfamily prepared by Tron Soot-Ryen with other contributions as indicated]

Equivalve, inequilateral, beaks prosogyre, near anterior end, outer layer of shell consists of fine radially oriented needles, inner layer commonly pearly; ligament opisthodetic, elongate, deep-set, supported by nymphae and connected with valves by calcified resilial ridge which continues to dorsal margin; anterior margin growing over posterior margin below beaks, or radially sculptured lunule is bent inward; hinge margins smooth or with dysodont teeth before, or before and behind ligament; surface usually divided in anterior, median and posterior areas with varying sculpture or color. Anterior adductor small, absent in some, posterior adductor confluent with posterior retractors. Prodissoconch with provinculum, which persists in some species, some with short internal resilium; pallial line simple or with shallow posterior concavity; periostracum usually strong, commonly hirsute; byssiferous. [Marine, brackish or freshwater.] *Dev.-Rec.*

Family MYTILIDAE Rafinesque, 1815

[*nom. correct.* Newell, 1965 (*pro* Mytilidia Rafinesque, 1815)]

Characters of superfamily. *Dev.-Rec.*

Fossil records seem to indicate that *Modiolus*- and *Lithophaga*-like species probably originated in the Silurian or Devonian, as such forms occur early in the Paleozoic strata. *Mytilus*-like species may have evolved from the *Brachidontes* group during the Jurassic. The *Musculus-Crenella* group may possibly be polyphyletic. To bring apparently related forms together the genera are grouped in subfamilies mainly established by Adams & Adams. The contents of these, however, differ somewhat from what was included in them originally.

Subfamily MYTILINAE Rafinesque, 1815

[*nom. transl.* Soot-Ryen, herein (*ex* Mytilidia Rafinesque, 1815)]

Typically mytiliform with anterior beaks, anterior margin usually twisted, with dysodont teeth or interlocking folds, dysodont teeth commonly behind ligament. Smooth or with radial sculpture. [Free-living.] *?Perm., Trias.-Rec.*

Mytilus Linné, 1758, p. 704 [**M. edulis*; SD Gray, 1847, p. 198] [=*Mytulus* Meuschen, 1789 (*nom. null.*); *Mytilarius* Froriep, 1806; *Mytiligenus* Renier, 1807; *Eumytilus* Ihering, 1900]. Wedge-shaped, elongate, beaks terminal, lunule with radiating folds forming dysodont teeth on anterior margin, anterior retractor scar elongate, behind umbo; anterior adductor small but distinct; margins not crenulated, surface smooth or with radial ribs which are not bent dorsalward. *U.Jur.-Rec.*, cosmop.

- **M. (Mytilus).** Resilial ridge pitted; smooth or with radial ribs, margins smooth. [Temperate and boreal seas.] *Plio.-Rec.*, N.Am.-N.Eu.-S.Am.-S.Australia-N.Z.-Kerguelin Is.——Fig. C16,2. **M. edulis*, Rec., France; *2a*, RV ext., ×1 *(89a)*; *2b*, muscle scars, ×1 *(860)*.
- **M. (Crenomytilus)** Soot-Ryen, 1955, p. 23 [**M. grayanus* Dunker, 1853; OD] [=*Mytiloconcha* auctt. (*non* Conrad, 1862)]. Resilial ridge compact, margins minutely serrated. *Oligo.-Plio.*, NW.N.Am., *Rec.*, Japan-Philippines.
- **M. (Pernomytilus)** Rollier, 1914, p. 356 [**M. pernoides* Roemer, 1836; OD]. Thin, concentrically striated or folded, internal characters unknown. *U.Jur.*, Eu.(Ger.).

Antetrichomya Iredale, 1951, p. 348 [**A. problematica;* OD]. Margins crenulated, hinge with large elongate narrow tooth; sculptured by about 20 thickened ribs posteriorly, diverging to more than 40 ventral ribs nearly obsolete medially. *Tert.*, Australia.

Arcomytilus Agassiz in J. Sowerby, 1842, p. 318 [**Mytilus pectinatus* J. Sowerby, 1821 (*non Modiola pectinata* Lamarck, 1819), =*Mytilus subpectinatus* d'Orbigny, 1850; OD]. Wedge-shaped, posteriorly broadly truncate or subtruncate between 2 obtuse ridges. Surface with distinct concentric growth stops and radial striae bending toward dorsal margin and finer unilateral branching striae toward ventral margin which is finely crenulate. *L.Jur. (Lias.)-Eoc.*, Eu.-Afr.——Fig. C16,4. **A. pectinatus* (Sowerby), Kimmeridg., Eng.(Weymouth); RV ext., ×1 (Sowerby, 1821).

Aulacomya Mörch, 1853, p. 53 [**Mytilus magellanicus* Chemnitz, 1785 (=**Mytilus ater* Molina, 1782); SD Ihering, 1900, p. 87]. Mytiliform, anterior adductor absent in larger specimens, an-

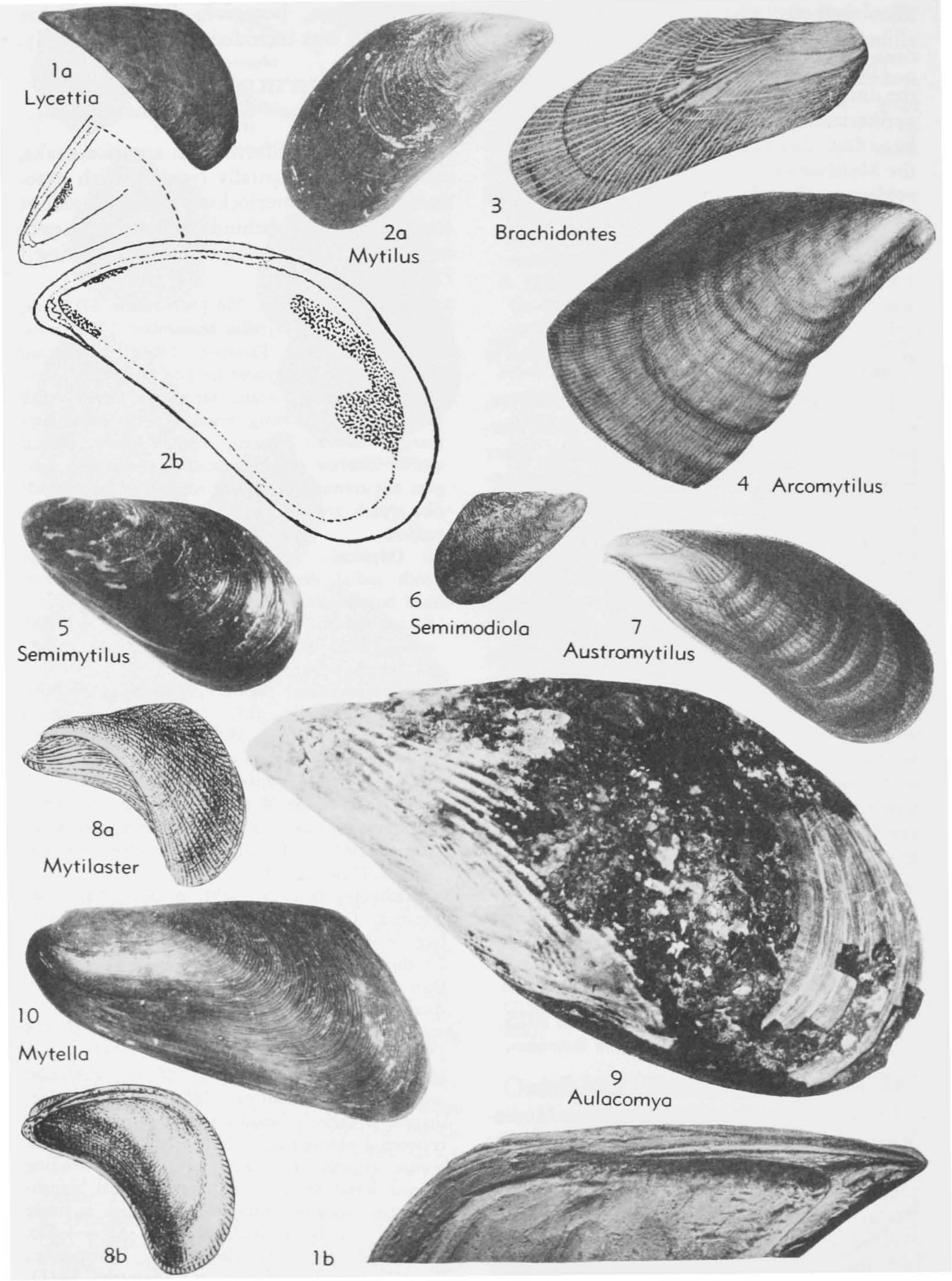

FIG. C16. Mytilidae (Mytilinae) (p. *N*271, *N*273-*N*274).

terior retractor scars elongate, posterior retractors broadly united with adductor; resilial ridge compact; lunule of LV turned inward, forming broad toothlike fold corresponding to depression in RV; surface with more or less distinct radial ribs, margins smooth. *Mio.-Rec.,* S.Am.-S.Afr.-N.Z.——Fig. C16,*9.* **A. ater* (Molina), Rec., Peru; LV ext., ×1 *(860).*

Brachidontes Swainson, 1840, p. 384 [**Modiola sulcata* Lamarck, 1819 (*non* 1805) (=*Mytilus citrinus* Röding, 1798, =**Arca modiolus* Linné, 1767); M] [=*Brachyodontes* auctt.]. Mytiliform, beaks terminal or nearly so, radially sculptured with bifurcating ribs, ligament relatively short, hinge with dysodont teeth before and after ligament. *Jur.-Rec.,* cosmop.

B. (Brachidontes). Umbones subterminal, radial sculpture on ventral part simple or regularly bifurcating. *Jur.-Rec.,* cosmop.——Fig. C16,*3.* **B. (B.) modiolus* (Linné), Rec., USA(Fla.); RV ext., ×1.4 *(728).*

B. (Austromytilus) Laseron, 1956, p. 265 [**Mytilus rostratus* Dunker, 1857; OD]. Hinge usually with 1 tooth in RV and 2 teeth in LV. *Plio.-Rec.,* Australia.——Fig. C16,*7.* **B. (A.) rostratus* (Dunker), Rec., Tasmania, LV ext., ×1 *(783).*

B. (Hormomya) Mörch, 1853, p. 53 [**Mytilus exustus* Linné, 1758; SD Jukes-Browne, 1905, p. 223]. Umbones usually terminal, radial sculpture on ventral part unilaterally bifurcate. *Mio.-Rec.,* N.Am.-Afr.-Pac.O.

?**Coxesia** Mendes, 1952, p. 109 [**C. mezzalirae*; OD]. Shell smooth, sickle-shaped, with pointed terminal umbones, small umbonal septum lies behind beaks; hinge with mytilid type of ligament nymphs; edentulous. *Perm.(Corumbatai),* S.Am. (S.Brazil).——Fig. C17,*1.* **C. mezzalirae*; *1a,b,* LV ext., int., ×2 (Mendes, 1952). [Newell]

Ischadium Jukes-Browne, 1905, p. 223 [**Mytilus hamatus* Say, 1822 (=**Mytilus recurvus* Rafinesque, 1820); OD]. Mytiliform, radial bifurcate sculpture covering whole surface, lunule and anterior margin bent inward, forming 1 or 2 toothlike ridges; resilial ridge compact, ligament relatively short, margins crenulated, anterior adductor absent. *Rec.,* NE.N.Am.

Limnoperna Rochebrune, 1882, p. 102 [**Dreissena siamensis* Morelet, 1866; OD]. Modioliform, small, of variable outline, commonly carinated, beaks slightly behind anterior end, hinge with dysodont teeth before and after ligament, other margins smooth. [Fresh and brackish water.] *Rec.,* E.Asia.

Lycettia Cox, 1937 [**Mytilus lunularis* Lycett, 1857; OD] [=*Cuneolus* Stephenson, 1941 (type, *Dreissena tippana* Conrad, 1858)]. Smooth, falcate, nacreous shells with acute, terminal beaks and sharp carina extending from beaks to posteroventral extremity; without anterior lobation; umbonal cavity covered by small plate or deck which bears elongate radial tooth and furrow on each valve, tooth of RV overlying that of LV; well-defined ligament nymph extending along hinge from near beak to mid-length of flattened area bearing growth rugae. [This genus is strongly convergent with Dreissenidae, from which it differs in nacreous structure of the shell.] *Jur.,* Eng.-India-NE.Afr.; *U.Cret.,* USA(Tex.).——Fig. C16, *1.* **L. lunularis* (Lycett), Inf. Oolite, Eng.; *1a,* LV ext., ×1; *1b,* LV int., ×2 *(182).* [Newell]

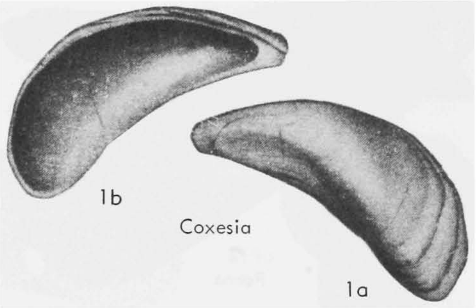

Fig. C17. Mytilidae (Mytilinae) (p. *N*273).

Mauricia Harris, 1919, p. 32 [**Modiola houstonia* Harris, 1895; OD]. Modioliform, thin, concentric growth lines below well-defined umbonal ridge, with broad concentric undulations above it, anterior end radially striated. *Eoc.-Mio.,* N.Am. (USA)-Eu.

Mytella Soot-Ryen, 1955, p. 47 [**Modiola guyanensis* Lamarck, 1819; OD]. Mytiliform to modioliform or elongate, beaks subterminal, anterior margin with or without teeth, resilial ridge pitted, 2 anterior retractor scars; smooth or concentrically striated, rarely finely striated radially. *Mio.-Rec.,* W.N.Am.-S.Am.——Fig. C16,*10.* **M. guyanensis* (Lamarck), Rec., Gulf Calif.; LV ext., ×1 *(860).*

Mytilaster Monterosato, 1883, p. 89 [**Mytilus lineatus* Gmelin, 1780; OD] [=*Mytilidonta* Coen, 1935 (type, *M. paulae*)]. Mytiliform, with varying sculpture from mere concentric growth lines to wavy or divaricate; dysodont teeth after ligament. *Rec.,* Medit.——Fig. C16,*8.* **M. lineatus* (Gmelin); *8a,b,* LV ext., RV int., ×1.5 *(89a).*

?**Peregrinamor** Shoji, 1938 [**P. ohshimi;* OD]. *Rec.,* S. Japan. [Newell]

Perna Retzius, 1788, p. 20 [**P. magellanica* (=**Mya perna* Linné, 1758); SD Soot-Ryen, 1955, p. 29] [*non Perna* Bruguière, 1792; Adams & Adams, 1858] [=*Chloromya* Mörch, 1853; *Mytiloconcha* Conrad, 1862]. Like *Mytilus* but without anterior adductor except in young specimens; lunule bent inward, forming 1 or 2 toothlike ridges, surface and margins smooth. *Eoc.-Rec.,* cosmop.

P. (Perna). Resilial ridge pitted, posterior retractor scars widely separated. *Eoc.-Rec.,* cosmop.(tropic-

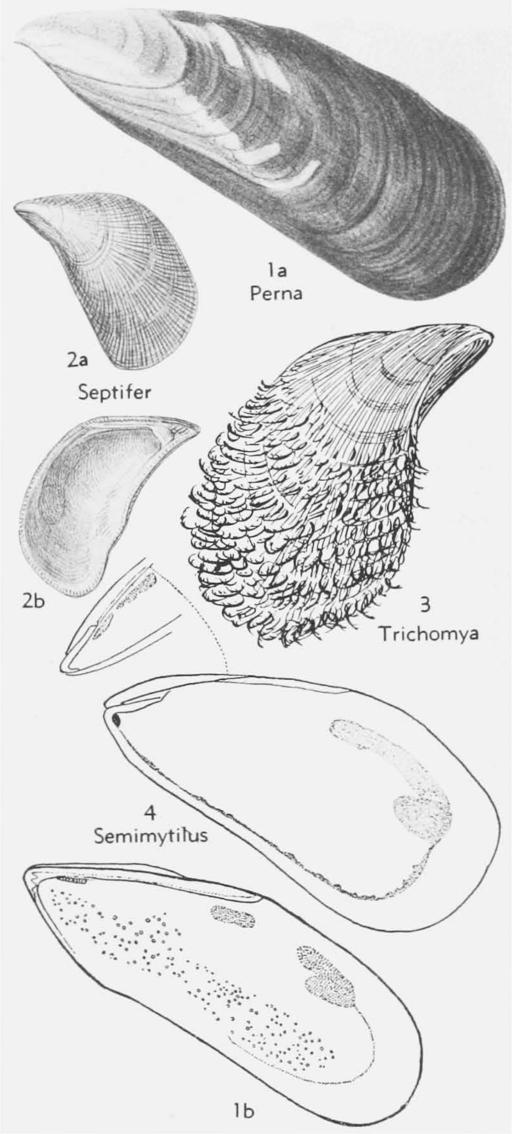

FIG. C18. Mytilidae (Mytilinae) (p. *N*274).

subtropic seas).——FIG. C18,*1*. **P.* *(P.) perna* (LINNÉ), Rec., S.Am.; *1a,* LV ext., ×0.8 *(783)*; *1b,* muscle scars and usual internal pittings, ×0.4 *(860)*.

P. (Choromytilus) SOOT-RYEN, 1952, p. 30 [**Mytilus chorus* MOLINA, 1782; OD]. Resilial ridge compact, posterior retractor scars continuous. *Mio.-Rec.,* Pac.-W.Am.-S.Afr.

Semimodiola COSSMANN, 1887, p. 154 [**Modiola hastata* DESHAYES, 1830; OD]. Modioliform to mytiliform, recurved, keeled; radial striae divaricating and obsolete in middle, margins deeply crenulated. *U.Eoc.,* Eu.——FIG. C16,*6*. **S. hastata* (DESHAYES), Bognor, Eng., RV ext., ×1 (Wood, 1871).

Semimytilus SOOT-RYEN, 1955, p. 25 [**Mytilus algosus* GOULD, 1850; M]. Mytiliform, with nearly terminal beaks, lunule small, circumscribed by fine line, anterior margin without teeth, resilial ridge compact, anterior retractor elongate and separated in middle; surface and margins smooth. *Rec.,* SW.N.Am.-S.Am.——FIG. C16,*5*; C18,*4*. **S. algosus* (GOULD), Peru; C16,*5,* LV ext., ×1.5; C18,*4,* muscle scars, ×1.7 *(860)*.

Septifer RECLUZ, 1848, p. 275 [**Mytilus bilocularis* LINNÉ, 1758; SD STOLICZKA, 1871, p. 366]. Externally similar to *Brachidontes (Brachidontes),* anterior adductor placed on internal septum beneath beaks. *Trias.-Rec.,* cosmop.(tropic, subtropic seas).

S. (Septifer). Radial sculpture strong, margins crenulated. *Trias.-Rec.,* cosmop.——FIG. C18,*2*. **S. bilocularis* (LINNÉ), Rec., IndoPac., *2a,b,* LV ext., int., ×0.8 *(7)*.

S. (Mytilisepta) HABE, 1951, p. 53 [**Tichogonia virgata* WIEGMANN, 1837; OD]. Radial sculpture weak, margins with fine crenulations only. *L. Tert.-Rec.,* Japan.

Trichomya IHERING, 1900, p. 87 [**Mytilus hirsutus* LAMARCK, 1819; OD] [=*Dentimodiolus* IREDALE, 1939 (p. 414) (type, *Dentimodiolus sculptus* IREDALE, 1939)]. Mytiliform with fine radial sculpture, periostracum with serrate hairs. *M.Tert.-Rec.,* W.Pac.——FIG. C18,*3*. **T. hirsuta* (LAMARCK), Rec., S.Australia; RV ext., ×0.5 *(169)*.

Subfamily CRENELLINAE Adams & Adams, 1857

Round to modioliform, beaks more or less behind anterior end, anterior hinge margin thickened and vertically striated or with dysodont teeth, dorsal hinge margin usually finely vertically striated. Surface with radial sculpture commonly absent on median area or rarely smooth. [Free-living, nestling, rarely boring.] *U.Trias.-Rec.*

Crenella BROWN, 1827, pl. 31, fig. 12-14 [**Mytilus decussatus* MONTAGU, 1808; M] [=*Stalagmium* CONRAD, 1833 (type, *Crenella margaritifera* CONRAD, 1833 [?1834]); *Hippagus* LEA, 1833, p. 72 (type, *Hippagus isocardioides* LEA, 1833; M); ?*Myoparo* LEA, 1833 (type, *Mytilus costatus* VON MÜNSTER, 1840); *Nuculocardia* D'ORBIGNY, 1845 (type, *N. divaricata*); ?*Crenellodon* EDWARDS in NEWTON, 1891 (type, *Modiola pulcherrina* ROEMER, 1836)]. Small, round to ovate, rather solid, beaks anterior; hinge thickened and striated, ligament short, sunken, radiating sculpture usually unilaterally bifurcate anteriorly and posteriorly, bifurcate or simple in middle, margins crenulated. ?*Cret., Rec.,* cosmop.——FIG. C19,*8*. **C. decussata* (MONTAGU), Rec., N.Nor.; RV ext., ×10 *(860)*.

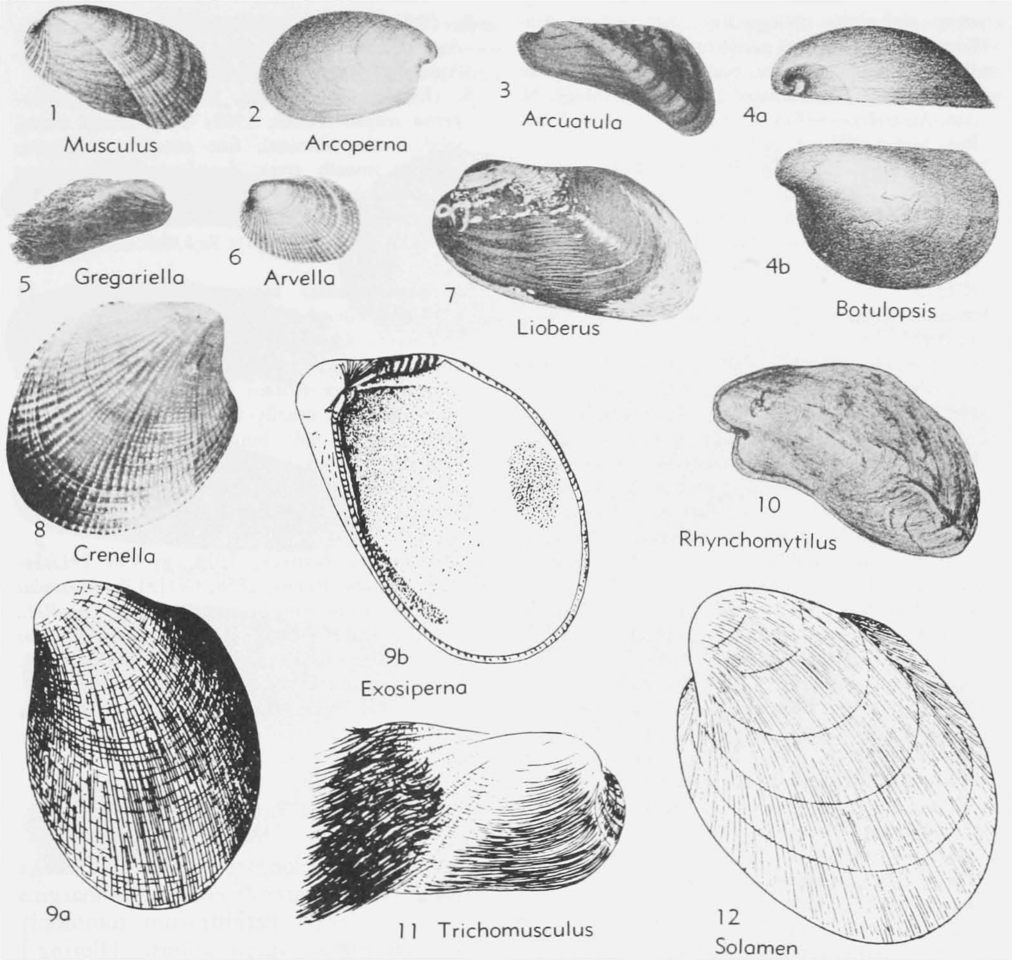

Fig. C19. Mytilidae (Crenellinae) (p. *N*274-*N*276).

Arcoperna Conrad, 1865, p. 140 [**A. filosa*; M]. Oval or oblong, inflated, thin-shelled, beaks terminal; surface with numerous fine striae separated by smooth area near anterior end; hinge with obsolete crenulations or smooth; ligament internal; margins finely crenulated. *Cret.-Eoc., ?Rec.,* N.Eu.-NE.Am.-Afr.——Fig. C19,*2*. **A. filosa,* Eoc., Enterprise F., USA(Miss.); RV ext., ×1 *(151)*.

Arcuatula Jousseaume in Lamy, 1919, p. 173 (*non* Soot-Ryen, 1955) [**Modiola arcuatula* Hanley, 1843; OD] [=*Lamya* Soot-Ryen, 1958]. Modioliform, relatively thin-shelled, hinge with dysodont teeth continued behind ligament, which is long, deep-set on weak nymphae, lunule smooth or radially ribbed, anterior adductor large. *Rec.,* S.Afr.-IndoPac.——Fig. C19,*3*. **A. arcuatula* (Hanley), Philip.; LV ext., ×1 *(783)*.

Arvella Bartsch in Scarlato, 1960, p. 67 [**Mytilus faba* Müller, 1776; OD]. Like *Musculus (Musculus)* but with regular radiating ribs over whole surface, dorsally more or less parallel to margin. *Rec.,* NE.Am.-Greenl.-NE.Asia.——Fig. C19,*6*. **A. faba* (Müller), W.Greenl.; LV ext., ×1 *(450)*.

Botulopsis Reis, 1926, p. 124 [**Botula cassiana* Bittner, 1895; M]. Elongate-ovate, gibbose, dorsal margin straight, beaks terminal, strongly prosogyrous; lunule cordate bounded by well-defined ridge, apparently edentulous. *U.Trias.,* Eu.——Fig. C19,*4*. **B. cassiana* (Bittner), S.Tirol. (St. Cassian); *4a,b,* LV lat., ext., ×1 *(58)*.

Gregariella Monterosato, 1883, p. 90 [**Modiolus sulcatus* Risso, 1826 (=**Modiola opifex* Say, 1825); M] [=*Botulina* Dall, 1889; *Tibialectus* Iredale, 1939, p. 424 (type, *T. otteri*)]. Elongate, inflated, beaks incurved, umbonal keel angulated; radially striated anteriorly and posteriorly where striae end along oblique line, median part concentrically striated, periostracum hairy along umbonal keel; anterior and posterior dysodont teeth, margins crenulated. *Mio.-Rec.,* Medit.-N.Am.-Australia.——Fig. C19,*5*. **G. opifex* (Say), Rec., Medit.; RV ext., ×1 *(89a)*.

Lioberus Dall, 1898, p. 805 [**Modiola castanea* Say, 1822; OD]. Beaks near anterior end, smooth or with obsolete radial sculpture, edentulous, periostracum smooth. *Rec.,* SE.N.Am.——Fig. C19,*7*. **L. castaneus* (Say), USA(Fla.), LV ext., ×2.3 *(728)*.

Musculus Röding, 1798, p. 156 [**Mytilus discors* Linné, 1767; SD Iredale, 1915, p. 485] [=*Modiolaria* Beck, 1838; *Lanistes* Swainson, 1840 (*non* de Montfort, 1810); *Modiolarca* Gray, 1843; *Lanistina* Gray, 1847; *Planimodiola* Cossmann, 1887 (type, *Modiola sulcata* Lamarck, 1805)]. Modioliform, with broadly rounded umbonal keel, posterodorsal part usually separated from remainder of valve by furrow, radiate sculpture separated in middle by concentrically striated area; margins crenulated, dysodont teeth in front and behind ligament. *Jur.-Rec.,* cosmop.

M. (Musculus). Shell rather flat, with broadly rounded umbonal keel, posterior retractors continuous, united with posterior adductor. *Jur.-Rec.,* cosmop.——Fig. C19,*1*. **M. (M.) discors* (Linné), Rec., Denm.; LV ext., ×2 *(450)*.

M. (Propetilus) Iredale, 1937, p. 235 [**Musculus nobilis* Iredale, 1937; OD]. Small, posterior angle pronounced, sculpture very fine, hinge with numerous strong denticles. *Rec.,* S.Pac.

M. (Ryenella) Fleming, 1959, p. 172 [**Mytilus impactus* Hermann, 1782; OD] [=*Modiolarca* Gray, 1843; *Lanistina* Soot-Ryen, 1955 (*non* Gray, 1847)]. Inflated, posterior retractors elongate, fastened along dorsal margin with single branch above posterior adductor. *Mio.-Rec.,* cosmop.

M. (Undatimusculus) Eames, 1951, p. 369 [**Musculus (U.) rakhiensis* Eames, 1951; OD]. Like *Musculus (Musculus)* but umbonal region with coarse concentric folds. *L.Eoc.,* Pak.

Rhynchomytilus Rollier, 1914, p. 355 [**Mytilus studeri* Oppel & Waagen, 1866; OD]. Reniform, gibbose, beaks anterior, inflated and widely projecting beyond rounded and expanded anteroventral corner; fine concentric and radial lines; hinge line smooth or crenulated. *U.Jur.,* Eu.——Fig. C19,*10*. **R. studeri* (Oppel & Waagen), L.Argov., Birmensdorf; LV ext., ×1 *(795b)*.

Solamen Iredale, 1924, p. 198 [**S. rex*; M]. Round to ovate, beaks nearly terminal, sculpture consisting of numerous fine striae separated by smooth areas near anterior end and also commonly dorsally; hinge usually with weak dysodont teeth anteriorly and above and behind ligament, which is short, semi-internal; margins crenulated. *Rec.,* N.Am.-Pac.-Eu.-S.Afr.-Australia(New S.Wales).

S. (Solamen). Thin-shelled, hinge weak. *Rec.,* Australia-W.N.Am.——Fig. C19,*12*. **S. (S.) rex,* Australia(New S.Wales); LV ext., ×2 *(532)*.

S. (Exosiperna) Iredale, 1929, p. 166 [**Arcoperna scapha* Verco, 1908; OD]. Small, ovate, solid, beaks terminal, fine cancellate sculpture without smooth areas, dysodont teeth in front and above ligament, which is deeply sunk, margins crenulated. *Rec.,* S.Australia.——Fig. C19,*9*. **S. (E.) scapha* (Verco); *9a,b,* LV ext., RV int., ×10 *(169)*.

S. (Rhomboidella) Monterosato, 1884, p. 13 [**Modiola rhombea* Berkeley, 1827 (=**Modiola pridaux(i)* Leach, 1815); M]. Small, inflated umbones large, anterior, prodissoconch large, smooth; surface striated by radial diverging and bifurcating ribs usually with narrow smooth area near anterior end; hinge with thickened and vertically striated anterior margin below umbo and vertical striations behind short ligament, margins finely crenulated. *Rec.,* Eu.-NE.N.Am.-S.Afr.-Ind.O.

Trichomusculus Iredale, 1924, p. 196 [**Lithodomus barbatus* Reeve, 1858; OD]. Like *Musculus* but periostracum with branched hairs. *U.Eoc.-Rec.,* N.Z.-Australia.——Fig. C19,*11*. **T. barbatus* (Reeve), Rec., S.Australia; RV ext., ×3.5 *(169)*.

Vilasina Bartsch in Scarlato, 1960, p. 69 [**V. pillula*; OD]. Like *Musculus* but with few weak radial striae anteriorly, otherwise finely concentrically striated. *Rec.,* NE.Asia-NW.N.Am.

Subfamily LITHOPHAGINAE Adams & Adams, 1857

More or less elongate, cylindrical, beaks slightly behind anterior end, hinge margins generally smooth, periostracum commonly with calcareous incrustations. [Boring.] *?Carb., U.Perm.-Rec.*

Lithophaga Röding, 1798, p. 156 [**L. mytuloides* (=*Mytilus lithophagus* Linné, 1780); M] [=*Lithophagus* Megerle von Mühlfeld, 1811; *Lithodomus* Cuvier, 1816; *Lithoglyphus* Sturm, 1821]. Cylindrical, usually tapering posteriorly, beaks near anterior end; smooth or with vertical striae; periostracum strong, commonly covered by calcareous incrustations; ligament deep-set; hinge edentulous; margins smooth. [Boring.] *?Carb., L.Mio.-Rec.,* cosmop.

L. (Lithophaga). Shell with vertical striations, no calcareous incrustations. *?Carb., Rec.,* cosmop.——Fig. C20,*7*. **L. (L.) lithophaga* (Linné), Rec., France; RV ext., ×1 *(89a)*.

L. (Diberus) Dall, 1898, p. 799 [**Modiola plumula* Hanley, 1843; OD] [=*Exodiberus* Iredale, 1939 (type, *Lithophaga calcifer* Iredale, 1939; OD); *Salebrolabis* Iredale, 1939 (type, *Lithophaga divaricalix* Iredale, 1939; OD)]. Two or more posterior sulci with plumelike incrustation distinctly projecting beyond valves. *L.Mio.*, USA(Fla.); *Rec.*, W.N.Am.-IndoPac.——FIG. C20,5. **L. (D.) plumula* (HANLEY), Rec., Costa Rica; LV ext., ×1.2 *(860)*.

L. (Labis) DALL, 1916, p. 405 [**Modiola attenuata* DESHAYES, 1836; M] [=*Doliolabis* IREDALE, 1939, p. 417 (type, *Lithophaga laevigatus instigans* IREDALE, 1939; OD)]. Calcareous incrustations

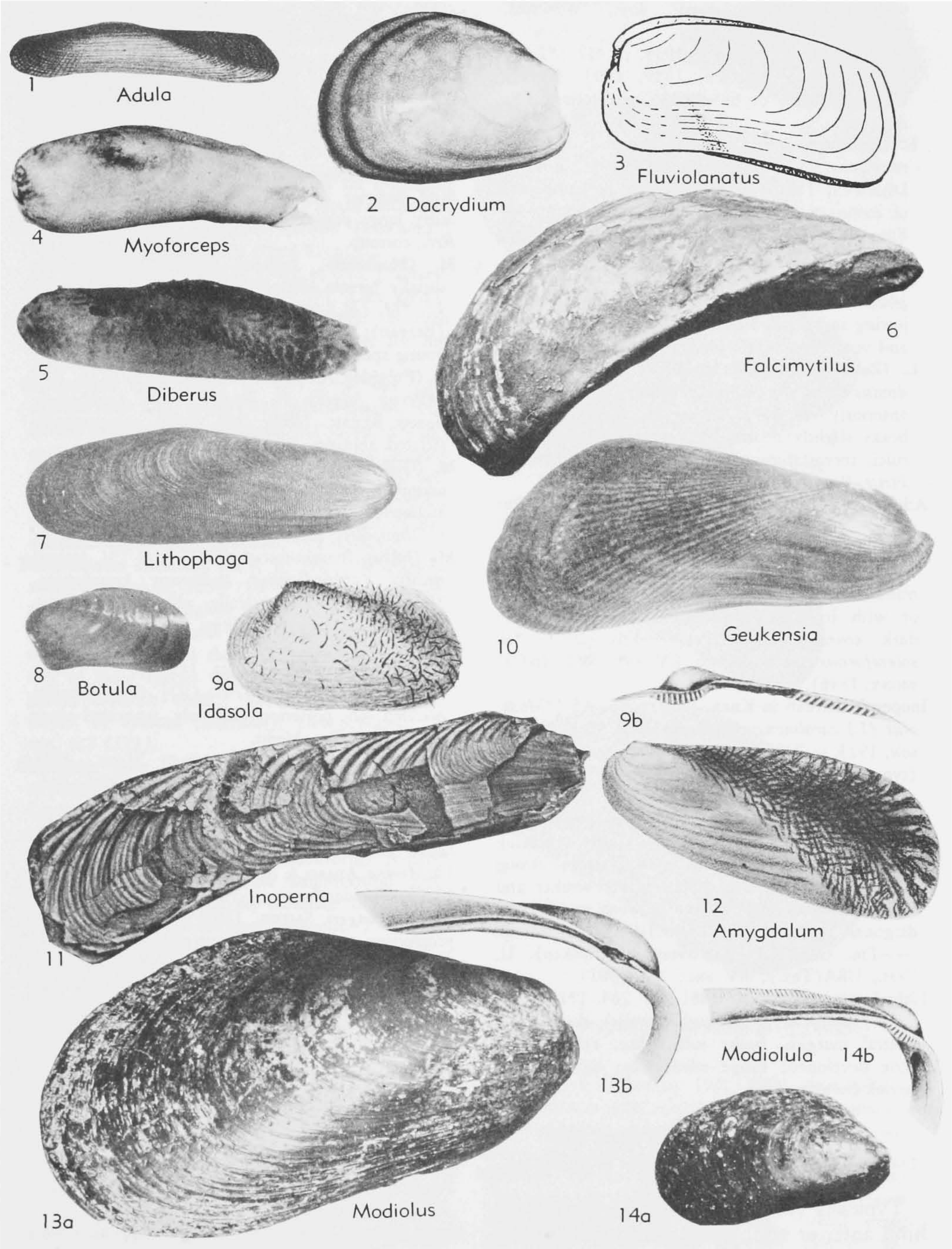

FIG. C20. Mytilidae (Lithophaginae), *(1,4,5,7,11)*, (Modiolinae) *(2-3,6,8-10,12-14)*, (p. *N*276-*N*280).

smooth, long, ending in median spine. *Rec.,* W.N.Am.-Australia.

L. (Leiosolenus) Carpenter, 1856, p. 130 [**Leiosolenus spatiosus* Carpenter, 1856; M]. Calcareous incrustation thin and equally diffused without projecting parts. *Rec.,* W.N.Am.-Australia.

L. (Myapalmula) Iredale, 1939, p. 417 [**Lithophaga dichroa* Iredale, 1939; OD]. Smooth, with very little or no chalky incrustation. *Rec.,* Australia.

L. (Myoforceps) Fischer, 1886, p. 969 [**Modiola caudigera* Lamarck, 1819 (=**Mytilus aristatus* Dillwyn, 1817); M]. Projecting posterior parts of incrustation crossed. *L.Mio.-Rec.,* cosmop.——Fig. C20,*4*. **L. (M.) aristata* (Dillwyn), Rec., C.Am.; LV ext., ×2 *(860)*.

L. (Stumpiella) Soot-Ryen, 1955, p. 93 [**Lithophagus calyculatus* Carpenter, 1856; M]. Projecting incrustation closed behind but with dorsal and ventral openings. *Rec.,* tropic W.N.Am.

L. (Zelithophaga) Finlay, 1927, p. 451 [**Lithodomus trunculus* Gray, 1843; OD]. Shell highest anteriorly, tapering backward, umbones high, beaks slightly behind anterior end, no posterior sulci, incrustation without regular sculpture. *L. Pleist.-Rec.,* N.Z.

Adula Adams & Adams, 1857, p. 517 [**Mytilus soleniformis* d'Orbigny, 1846; M]. Elongate, cylindrical, beaks behind anterior margin, anterodorsal margin thickened, dorsal margin with minute dysodont teeth or smooth, surface smooth or with irregular wrinkles, posterodorsally with dark covering. *Rec.,* Pac.——Fig. C20,*1*. **A. soleniformis* (d'Orbigny); LV ext., ×1 (d'Orbigny, 1846).

Inoperna Conrad in Kerr, 1875. App. A5 [**Modiolus (I.) carolinensis* Conrad, 1875; SD Stephenson, 1923, p. 239] [=*Pharomytilus* Rollier, 1914 (type, *Mytilus plicatus* Sowerby, 1819)]. Narrow, elongate, with nearly parallel dorsal and ventral margins, surface divided by diagonal ridge, part ventral to ridge smooth, that dorsal to it bearing folds which are parallel to growth stages, strong near dorsal margin but split up into weaker and more numerous ones halfway between margin and diagonal ridge. *L.Jur.(U.Lias.)-U.Cret.,* cosmop.——Fig. C20,*11*. **I. carolinensis* (Conrad), U. Cret., USA(Tex.); RV ext., ×1 *(881)*.

Lithodomina Waagen, 1881, p. 264 [**L. typa*; OD]. Elongate, thin, with parallel dorsal and ventral margins, beaks subanterior, anterior end little developed; hinge edentulous; ligament internal. *U.Perm.,* India.

Subfamily MODIOLINAE Keen, 1958

[*nom. transl.* Soot-Ryen, herein (*ex* tribus Modiolini Keen, 1958)]

Typically modioliform, beaks slightly behind anterior end; hinge margin smooth or finely striated vertically; shell surface usually lacking radial sculpture, periostracum commonly hairy. [Free-living, often nestling.] *Dev.-Rec.*

Modiolus Lamarck, 1799, p. 87 [*nom. conserv.* (*pro Volsella* Scopoli, 1777, ICZN pend.)] [**Mytilus modiolus* Linné, 1758; SD Gray, 1847, p. 198] [=*Modiola* Lamarck, 1801; *Perna* Adams & Adams, 1858; *Eumodiolus* Ihering, 1900; *Nudiola* Monterosato, 1917, p. 5 (type, *Modiola adriatica* Lamarck, 1819)]. More or less inflated, rounded anteriorly, umbones obtuse, distinctly behind anterior end; hinge line smooth, ligament fairly long; periostracum commonly hirsute. *Dev.-Rec.,* cosmop.

M. (Modiolus). Inflated, smooth, periostracum usually hirsute. *Dev.-Rec.,* cosmop.——Fig. C20, *13*. **M. (M.) modiolus* (Linné), Rec., Norway (Bergen); *13a,* RV ext., ×1; *13b,* LV hinge of young specimen, ×7 *(450)*.

M. (Fulgida) Jousseaume in Lamy, 1919, p. 318 [**Perna fulgida* H. Adams, 1870 (=*Modiola lignea* Reeve, 1858); M]. Solid, concentrically striated, shining. *Rec.,* RedS.-Ind.O.

M. (Gibbomodiola) Sacco, 1898, p. 41 [**G. taurarcuata;* OD]. Elongately ovate, transversely arcuately gibbous, posteriorly broadly expanded. *U.Oligo.-Rec.,* Medit.

M. (Jolya) Bourguignat, 1877, p. 9 [**J. letourneauxi* (=*Modiolatus stultorum* Jousseaume, 1893); M]. Concentrically plicated anteriorly, hinge wtih elongate anterior ridge. [Estuarine.] *Rec.,* NW.Afr.

M. (Modiolatus) Jousseaume, 1893, p. 192 [**Mytilus plicatus* Gmelin, 1791; OD]. Concentrically plicated on posterior obliquely truncated end. *Rec.,* Ind.O.-Pac.-Medit.

M. (Modiolusia) Yamamoto & Habe, 1958 [**Modiola elongata* Swainson, 1821; OD]. *Rec.,* Japan.

Adipicola Dautzenberg, 1927, p. 274 [**Modiolarca? pelagica* Forbes in Woodward, 1854; M] [=*Myrina* Adams & Adams, 1857 (*non* Fabricius, 1808); *Miridas* Iredale, 1939, p. 425 (type, *Myrina coppingeri* Smith, 1885)]. Elongate, beaks protruding, prosogyre, in front of middle, anterior margin rounded, ventral margin straight, hinge with toothlike process below umbo and more or less obsolete vertical striations in front and behind umbo. *Rec.,* Eu.-S.Afr.-Australia.

Amygdalum Megerle von Mühlfeld, 1811, p. 69 [**A. dendriticum;* M] [=*Modiella* Monterosato, 1884 (type, *Modiola polita* Verrill & Smith, 1880)]. Modioliform, thin, resilial ridge and nymphae very weak; edentulous; surface and margins smooth. [Deep-water.] *Rec.,* cosmop.——Fig. C20,*12*. **A. dendriticum,* W.Indies; LV ext., ×2 *(783)*.

Botula Mörch, 1853, p. 55 [**Mytilus fuscus* Gmelin, 1791; SD Dall, Bartsch, & Rehder, 1938, p. 59] [=*Botulopa* Iredale, 1939, p. 414 (type, *B. silicula infra*)]. Elongate ovate, inflated, beaks terminal, prominent, somewhat coiled; ligament relatively short, dorsal margin with fine vertical striae, other margins smooth. [Warm seas.] *Eoc.-Rec.*——Fig. C20,*8*. **B. fusca* (Gmelin), Rec., Venez.; LV ext., ×2 *(860)*.

Dacrydium Torell, 1859, p. 138 [**?Mytilus vitrea* Holböll in Möller, 1842; M]. Hyaline smooth, beaks anterior; hinge crenulated anteriorly and with vertical striations posteriorly; internal resilium. *Plio.-Rec.*, cosmop.

D. (Dacrydium). Anterior adductor on thickened support; no grooved teeth. *Rec.*, Arctic-Antarctic. ——Fig. C20,*2*. **D. (D.) vitreum* (Holböll), N.Norway; RV ext., ×6 (Soot-Ryen, n).

D. (Quendreda) Iredale, 1936, p. 271 [**Dacrydium fabale* Hedley, 1904; OD]. Like *Dacrydium* but with single grooved tooth on each side of resilium, no thickened support for anterior adductor. *Plio.-Rec.*, Pac.

Falcimytilus Cox, 1937, p. 343 [**Mytilus (F.) suprajurensis* Cox, 1937; OD]. Sickle-shaped, with bluntly pointed terminal beaks and blunt, strongly curved carina which runs from beak to posteroventral corner; edentulous; anterior adductor scar small, situated in umbonal angle. *Jur.*, Eu.-India. ——Fig. C20,*6*. **F. suprajurensis* (Cox), U.Jur. (Kimmeridg.), Eng.; RV ext., ×1 *(182)*.

Fluviolanatus Iredale, 1924, p. 196 [**Modiolarca subtorta* Dunker, 1856 (1857); OD]. Irregularly subquadrangular, slightly twisted, inequivalve, RV overlapping LV, beaks near anterior end; hinge edentulous, ligament short, internal; concentrically and in some species radially striate. [Coastal lagoons, brackish water.] *Rec.*, Australia.——Fig. C20,*3*. *F. amarus* (Laseron), New S.Wales; LV ext., ×3 *(532)*.

Geukensia Poel, 1959, p. 26 [*nom. subst.* (*pro Arcuatula* Soot-Ryen, 1955, *non* Jousseaume in Lamy, 1919; *nec* Gugenberger, 1934)] [**Modiola plicatula* Lamarck, 1819 (=**Modiola demissa* Dillwyn, 1817); OD]. Modioliform, radially ribbed, weaker striations on anteroventral area, margins crenulated but no toothlike crenulations in front or behind deep-set ligament; 2 anterior retractors in and in front of umbonal cavity. *Rec.*, N.Am.——Fig. C20,*10*. **G. demissa* (Dillwyn), Rec., USA(Calif.); RV ext., ×0.7 *(860)*.

Idasola Iredale, 1915, p. 340 [*pro Idas* Jeffreys, 1876 (*non* Mulsant & Verreaux, 1875)][**Idas argenteus* Jeffreys, 1876; M]. Small, thin-shelled, argenteous, with rounded anterior and posterior margins, beaks in front of middle; hinge with vertical striations on thickened anterior margin below umbo and behind the ligament; periostracum thin, with hairlets. *Rec.*, Atl.——Fig. C20,*9*. **I. argentea* (Jeffreys), off Iceland; *9a*, LV ext., ×6.5; *9b*, RV hinge, ×20 *(450)*.

Lecompteus Poel, 1959, p. 13 [**Mytilus ornatus* Münster in Goldfuss, 1837; OD]. Modioliform to mytiliform with complex sculpture of radiating and concentric elements commonly in chevrons. *Jur.-Cret.*, Eu.-Afr.-Asia.

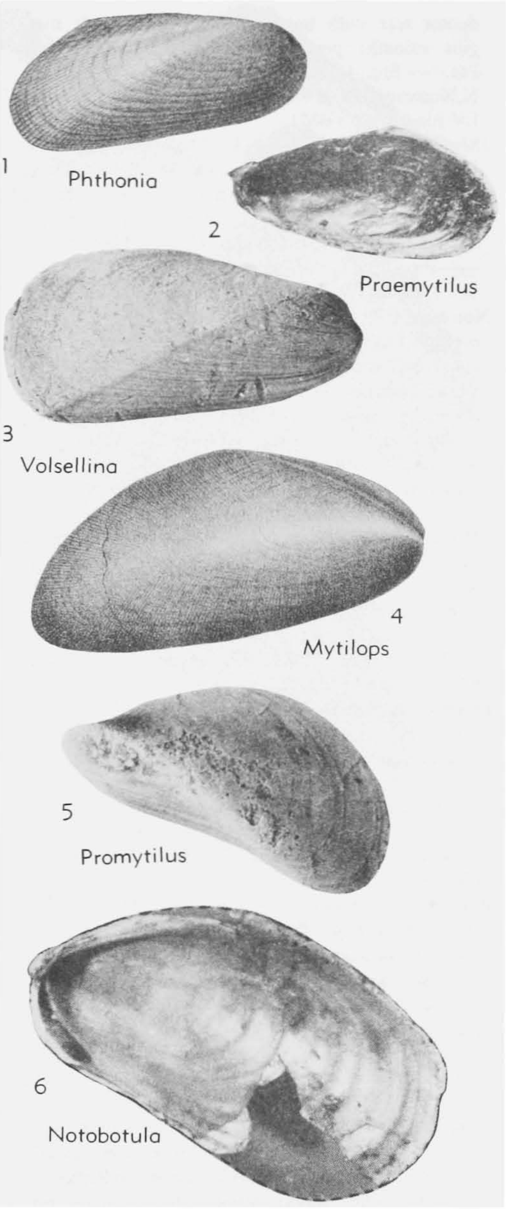

Fig. C21. Mytilidae (Modiolinae) (p. *N*280).

Modiolula Sacco, 1898, p. 41 [**Modiola phaseolina* Philippi, 1844; OD]. Modioliform, hinge with dysodont teeth below umbo and vertical striae above and behind short ligament; anterior adductor scar with buttress-like ridge behind; margins smooth; periostracum hairy. *Rec.*, Eu.-NE. Pac.——FIG. C20,*14*. **M. phaseolina* (PHILIPPI), N.Norway; *14a,* RV ext., ×1 (Soot-Ryen, n); *14b,* LV hinge, ×8 *(450).*

?**Mytilops** HALL, 1883, p. 11 [**Modiola precedens* HALL, 1870; SD S. A. MILLER, 1889]. Similar to *Promytilus* in form but ornamented by outward curving fine costellae that intersect shell margin approximately at right angles. *U.Dev.*, USA(N.Y.). ——FIG. C21,*4*. **M. precedens* (HALL); RV ext., ×1 *(378).* [NEWELL]

Notobotula FLEMING, 1959, p. 170 [**Botula (N.) molina* FLEMING, 1959; OD]. Anterior adductor scar very elongate close above curve of anteroventral margin, raised on thickened step bordered above by buttress-like ridge; hinge margins vertically striated. *L.Pleist.*, N.Z.——FIG. C21,*6*. **N. molina* (FLEMING); RV int., ×3 *(309).*

?**Phthonia** HALL, 1870, p. 70 [**Cypricardites sectifrons* CONRAD, 1842; SD S. A. MILLER, 1889]. Modioliform, with beaks slightly behind anterior extremity; ventral margin nearly straight, diverging only slightly with respect to hinge margin; interior unknown; ornamented by straight or nearly straight costae or costellae. *M.Dev.*, USA (N.Y.).——FIG. C21,*1*. **P. sectifrons* (CONRAD); RV ext., ×1 *(378).* [NEWELL]

Praemytilus ANDERSON & COX, 1948, p. 105 [**Mytilus (P.) strathairdensis*; OD]. Narrowly and obliquely ovate, with rather broad, edentulous, anterior marginal reflection and deep, elongate anterior adductor scar adjoining it. *M.Jur.(Bathon.),* W.Scot.——FIG. C21,*2*. **P. strathairdensis* (ANDERSON & COX), Estheria Sh., Scot. (Strathaird); LV ext., ×1.2 *(16).*

Promytilus NEWELL, 1942, p. 37) [**P. annosus*; OD][=*Pachoya* LUTKEVICH & LOBANOVA, 1956 (type, *P. sicaria*; OD)]. Shell thin, elongate, beaks terminal, anterior lobe small but set off from rest of shell by broad sulcus from beaks to ventral sinuosity; umbonal ridge rounded; hinge line smooth. *Miss.-Perm.*, N.Am.——FIG. C21,*5*. **P. annosus,* South Bend Ls. (U. Missourian), Kans.; holotype, LV ext., ×2 *(666).* [NEWELL]

Stavelia GRAY, 1858, p. 90 [**Mytilus tortus* DUNKER, 1856; OD]. Broad modioliform, commonly distorted, with nearly anterior beaks; edentulous; ligament rather short; periostracum strongly hirsute. *Rec.,* Pac.

Terua DALL, BARTSCH, & REHDER, 1938, p. 57 [**T. pacifica*; OD]. Arcuate, thin, beaks in anterior 4th; hinge edentulous, ligament subinternal, half length of shell, with fine vertical striations behind; margins and surface smooth. *Rec.,* Hawaii.

Volsellina NEWELL, 1942, p. 42 [**Pleurophorus subellipticus* MEEK, 1867; OD]. Thin, elongate, flattened, beaks subterminal, anterior lobe extending slightly ahead of beaks, anterior sulcus obscure, umbonal ridge narrow; edentulous. *Penn.-Perm.,* N.Am.——FIG. C21,*3*. **V. subelliptica* (MEEK), U.Penn.(Willard Sh.), Neb.; RV ext., ×2 *(666).*

Family MYSIDIELLIDAE Cox, 1964

[Materials for this family prepared by L. R. Cox]

Shell medium-sized, ovate or trapezoidal, equivalve or slightly inequivalve, RV larger than LV; dorsal margin straight or arcuate, umbones more or less anterior; no differentiated posterior wing; anterior auricle present or absent; byssal gape probably present in all genera; hinge edentulous; ligament internal, elongated, extending posteriorly in groove from near beak; probably monomyarian; shell structure unknown. *L. Trias.-U.Trias.*

Mysidiella Cox, 1964, p. 44 [*pro Mysidia* BITTNER, 1891, p. 113 (*non* WESTWOOD, 1840)] [**Mysidia orientalis* BITTNER, 1891; OD]. Equivalve, ovate, higher than long, well inflated, with rather prominently protruding, prosogyrous, anterior umbones; no anterior auricles; anterior marginal region reflected below each beak to form deep, narrow lunule, dorsal margin of which is much thickened; lunular margins probably with narrow gape; elongate ligamental ridge below and extending to posterior extremity of dorsal margin; surface smooth except for faint radial striations. *M.Trias.(Ladin.)-U.Trias.(Rhaet.),* Eu.(S.Alps-N. Alps-Hung.-Greece)-Anatolia.——FIG. C22,*1*. **M. orientalis* (BITTNER), U.Trias.(Nor.), Anatolia; *1a-c,* RV ext. and hinge, LV hinge, both ×0.7 (Bittner, 1891-92).

Protopis KITTL, 1904, p. 718 [**Opis (Protopis) triptycha*; M] [=*Joannina* WAAGEN, 1906, p. 390 (type, *J. joannae;* M)]. Subequivalve, trapezoidal, with strongly prosogyrous umbones; strongly inflated diagonally, some species with diagonal keel; with relatively large, sharply pointed anterior auricle not differentiated from body of shell, its margin with byssal gape; ligament in elongate longitudinal groove; surface smooth or with radial ridge on posterodorsal area. *L.Trias. (Werfen.)-U.Trias.(Carn.),* Eu.(S. Alps-Balkans)-Timor.——FIG. C22,*3*. *P. joannae* (WAAGEN), U. Trias.(Carn.), S.Alps; *3a,b,* LV ext. and hinge, ×1 *(950).*

Tommasina Cox, 1964, p. 44 [*pro Mytiliconcha* TOMMASI, 1911, p. 35 (*non* CONRAD, 1862)] [**Mytiliconcha orobica* TOMMASI, 1911; OD] [=*Mytiloconcha* DIENER, 1923 (*non* CONRAD, 1862)]. Probably slightly inequivalve, trapezoidal, longer than high, with anterior, strongly prosogyrous umbones, that of RV protruding prominently, of LV less so; anterior auricle lacking; sharp carina crossing shell diagonally from umbo in each valve; dorsal margin arcuate; ligamental

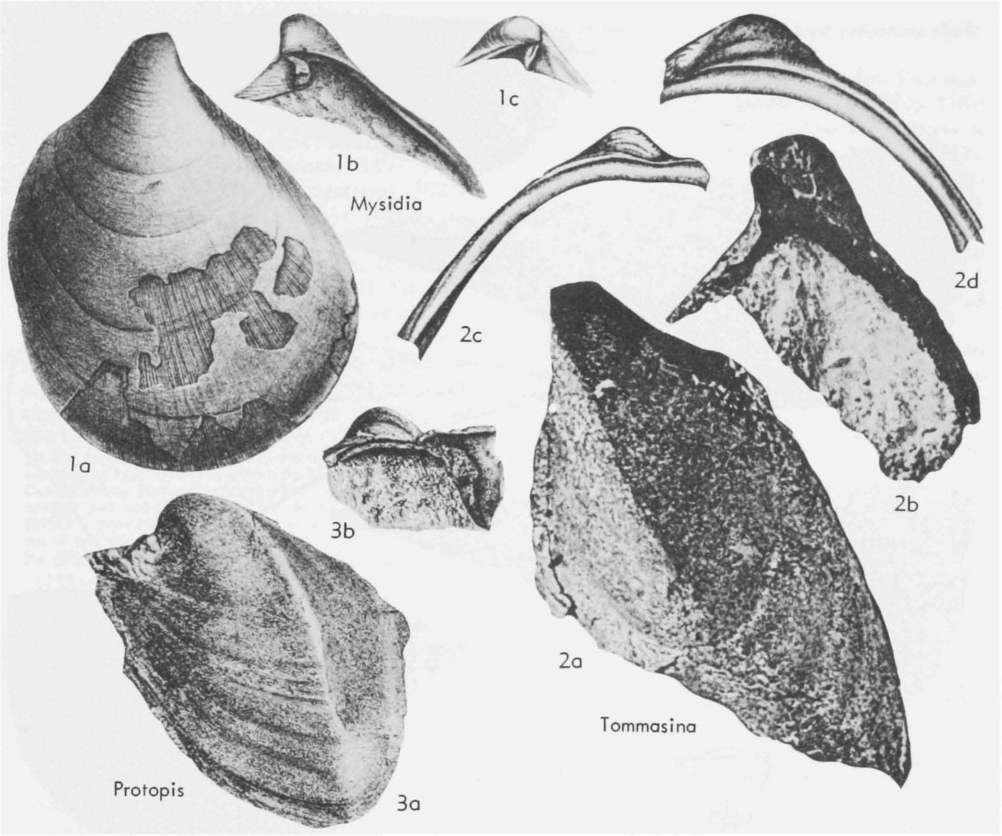

FIG. C22. Mysidiellidae (p. *N*280-*N*281).

groove probably as in *Protopis,* but not yet clearly observed; surface smooth. *U.Trias.(Carn.),* Eu.(S. Alps).——FIG. C22,*2*. **T. orobica* (TOMMASI); *2a,b,* RV ext. and hinge; *2c,d,* LV and RV hinges (reconstr.), all ×1 (Tommasi, 1911).

Superfamily PINNACEA Leach, 1819

[*nom. transl.* NEWELL, 1965 (*ex* Pinnidae LEACH, 1819)] [Materials for this superfamily prepared by L. R. COX and L. G. HERTLEIN]

Medium-sized to large, cuneiform, mytiliform or ham-shaped, mostly equivalve, a few forms distorted and inequivalve; beaks at or near anterior end of long hinge margin; ventral margins with long narrow gape near anterior end for protrusion of bunch of long silky byssal threads; posterior margins gaping in dead shell, living animal capable of closing gape by action of adductor muscles owing to flexible nature of ostracum; dimyarian, with anterior adductor relatively small and placed in anterior angle of shell, and posterior adductor large, situated at or slightly anterior to midlength; hinge edentulous; ligament linear, subinternal, extending along whole length of hinge margin, its posterior part formed by "fusion layer"[1]; some specimens (in *Streptopinna*) with valves completely fused along posterodorsal margin; ostracum with outer layer of prismatic calcite, very thick in some forms, and thin inner nacreous layer absent from part of shell beyond posterior adductors. *L.Carb.-Rec.*

Family PINNIDAE Leach, 1819

Characters of superfamily. *L.Carb.-Rec.*

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[1] See C. M. YONGE, 1953, Roy. Soc. London, Phil. Trans., B, v. 237, p. 343.

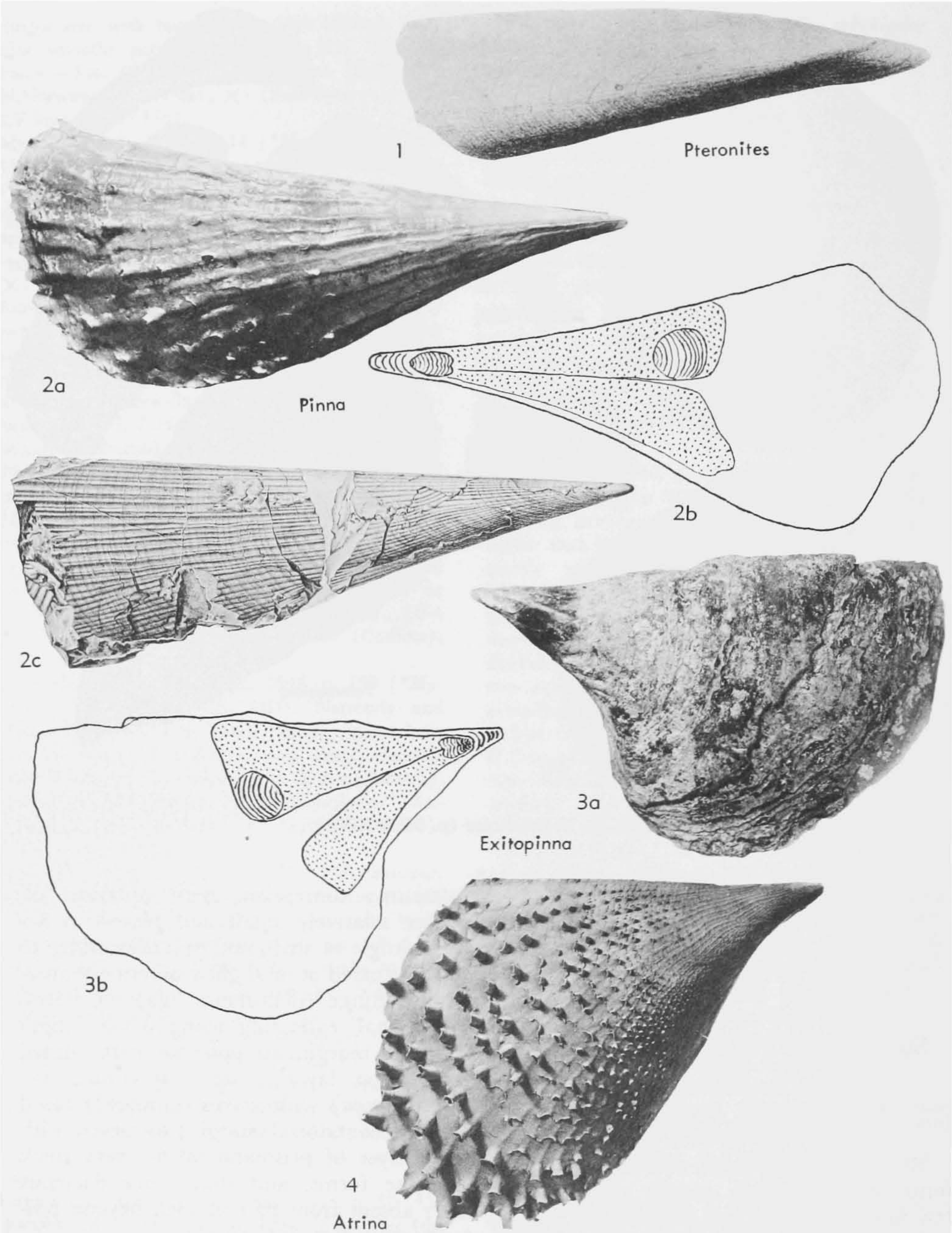

Fig. C23. Pinnidae (p. *N*283).

Most Pinnidae live with the pointed anterior end of the shell buried in soft sediment and the hinge margin and commissure of the valves more or less vertical; the wide posterior end of the shell is exposed. The animal is anchored by the byssus to underlying stones or other objects. The anterior end of the shell may be worn constantly by corrosion and sealed off by a succession of thin partitions, the anterior adductor at the same time migrating in a posterior direction.

Pinna Linné, 1758, p. 707 [**P. rudis*; SD Children, 1823, p. 34] [=*Chimaeroderma* Poli, 1795, p. 259 (type, *Pinna rudis* Linné; SD Cox, herein); *Pinnarius* Duméril in Froriep, 1806 (obj.); *Pinnigenus* Renier, 1807 (suppressed ICZN); *Pinnula* Rafinesque, 1815 (obj.); *Pinnites* von Schlotheim, 1820 (obj.); *Pennaria* Mörch, 1853 (*non* Oken, 1815); *Pinua* Seguenza, 1877 *(nom. null.)*; *Pina* Koch, 1922 *(nom. null.)*]. Equivalve, wedge- to ham-shaped; umbones at extreme anterior end; valves carinate medially, at least in earlier growth stages; mostly with radial ribs, some forms with growth undulations on ventral region; nacre of interior divided medially into two lobes. *L.Carb.-Rec.,* cosmop.

[It has been maintained that *P. muricata* Linné should be accepted as type species of *Pinna* by Linnean tautonymy, as *Concha Pinna* Hasselquist was cited by Linné in its synonymy; but according to Article 68,d,i of the new Code (1961) a pre-Linnean name cited in synonymy should consist of one word only if this rule of typification is to apply.]

P. (Pinna) [=*Chimaera* Poli, 1791 (*non* Linné, 1758); *Sulcatopinna* Hyatt, 1892, p. 341 (type, *P. flexicostata* M'Coy, 1844 =*P. costata* Phillips); *Sulcatipinna* Girty, 1915 *(nom. van.)*; *Quantulopinna* Iredale, 1939, p. 310 (type, *Q. delsa*); *Subitopinna* Iredale, 1939, p. 312 (type, *P. menkei* Reeve, 1858)]. Wedge-shaped, ventral margin straight to concave; median ridge well defined; sculpture of radial ribs or rows of scales. *L.Carb.-Rec.,* fossil forms cosmop., living ones worldwide in tropical or subtropical seas. ——Fig. C23,*2a*. **P. (P.) rudis,* Rec., Barbados; RV ext., ×0.3 (Cox, n).——Fig. C23,*2b*. *P. (P.) atropurpurea* G. B. Sowerby, Rec., S.India; RV interior showing extent of 2 lobes of nacre (stippled), adductor scars, and partitions separating series of loculi at anterior end, ×0.3 *(995)*. ——Fig. C23,*2c*. *P. (P.) costata* Phillips, L. Carb., Belg.; RV ext., ×0.25 (de Koninck, 1885). ——Fig. C23,*3*. *P. (P.) deltodes* Menke, Rec., W.Australia; *3a,* LV ext., *3b,* LV int., showing muscle scars and extent of lobes of nacre (stippled), ×0.3 (Cox, n). [=*Exitopinna* Iredale, 1939 (type, *E. deltodes ultra* Iredale, 1939; OD).]

[Rosewater (1961, Indo-Pacific Mollusca, v. 1, no. 4, p. 197, pl. 150) has shown that the type specimen of Iredale's *Exitopinna* is a stunted, repeatedly broken shell of *Pinna bicolor* Gmelin, 1791 (=*P. rudis* Linné). Therefore, *Exitopinna* is considered to be a junior synonym of *Pinna (Pinna)*.]

P. (Cyrtopinna) Mörch, 1853, p. 51 [**P. incurva* Gmelin, 1791, p. 3366; M]. Long, narrow, slightly curved, very thin; median ridge well defined; radial ribbing weak. *Jur.-Rec.,* fossil forms cosmop., *Rec.,* IndoPac.

P. (Plesiopinna) Amano, 1956, p. 70 [**Plesiopinna atriniformis*; OD]. Wedge-shaped, with median ridge when young, later ham-shaped and irregular; radial ribbing weak. Reported to resemble *Exitopinna* but may be based on deformed shells. *U.Cret.,* Japan.

Atrina Gray, 1842, p. 83 [**Pinna nigra* Dillwyn, 1817, p. 325 (=**P. vexillum* Born, 1778, p. 118); SM Gray, 1847, p. 199] [=*Servatrina* Iredale, 1939, p. 317 (type, *Pinna assimilis* Reeve, 1858)]. Equivalve, ham-shaped, posterior end rounded, no median ridge; smooth or with radial rows of ribs or scales; internal nacre not divided into 2 lobes. *M.Jur.-Rec.,* fossil forms cosmop., *Rec.* in tropical and warm temperate seas.——Fig. C23,*4*. **A. vexillum* (Born), Rec., Philip.Is.; RV ext., ×0.3 (Cox, n).

Curvula Rafinesque, 1819, p. 427 [=*Curvulites* Rafinesque, 1831, p. 4]. Genus without nominal species founded on fossil bivalves of uncertain age from interior of USA. Compared with *Pinna* in description but probably not member of Pinnidae. Subsequently ignored.

Oxisma Rafinesque, 1819, p. 427 [**O. bifida*; M] [=*Oxysma* Herrmannsen, 1847 *(nom. van.)*; *Otysma* Paetel, 1875 *(nom. null.)*]. Unrecognizable from description and subsequently ignored. [Compared with *Pinna* in description but probably not member of Pinnidae. Possibly not a fossil.] [Cox]

Pteronites M'Coy in Griffith, 1844, p. 81 [**P. angustatus*; SD Stoliczka, 1871, p. 388 (specific name wrongly cited as *"angustus"*)] [=*Aviculopinna* Meek, 1864, p. 212 (type, *Solen pinnaeformis* Geinitz, 1848); *Pterinites* Stoliczka, 1871 *(nom. null.)*; *Aviculipinna* Girty, 1904 *(nom. van.)*]. Elongate, cuneiform; umbones set back a short distance from pointed anterior extremity, not protruding above cardinal margin; valves without median carina; radial ornament obscure or lacking; internal characters unknown. *L.Carb.-Perm.,* Eu.-USSR(Sib.)-N.Am.-S.Am.——Fig. C23,*1*. *P. pinnaeformis* (Geinitz), U.Perm.(Zechstein), Ger.; RV ext., ×0.75 (Geinitz, 1861).

Stegoconcha J. Böhm, 1907, p. 148 [**Pinna granulata* J. Sowerby, 1822, p. 65; SD Cox, 1940, p. 133]. Equivalve, large, mytiliform, gibbose, most inflated along rounded ridge passing from umbo to posteroventral corner; height exceeding length; ornament of radial ribs or threads, commonly broken up into granules, and confined to or most conspicuous on dorsal side of ridge; shell moderately thick. *M.Jur.-U.Jur.,* Eu.-Asia-E.Afr.—— Fig. C24,*3*. *S. gmuelleri* (Krenkel), U.Jur.(U. Kimmeridg.), Tanganyika; RV ext., ×0.5 (Cox, n).

Streptopinna von Martens, 1880, p. 318 [**Pinna saccata* Linné, 1758, p. 707; M]. Inequivalve, irregularly twisted or bent, highly variable in form, mytiliform, pteriiform, or elongate-rectangular, but with terminal, pointed umbones; valves commonly fused along posterior part of dorsal margin; ornament of broad radial ribs on dorsal half of valves. *Rec.,* IndoPac.——Fig. C24,*2*. *S. *saccata* (Linné), Muscat, Arabia; *2a,b,* RV ext. views of 2 specimens, showing variability, ×0.5 (Cox, n).

Trichites Voltz in Thurmann, 1833, p. 13 [**T. saussuri*; M] [The earliest publication of *Trichites* (a very old name used by Plot in 1677) as an available generic name has been attributed by

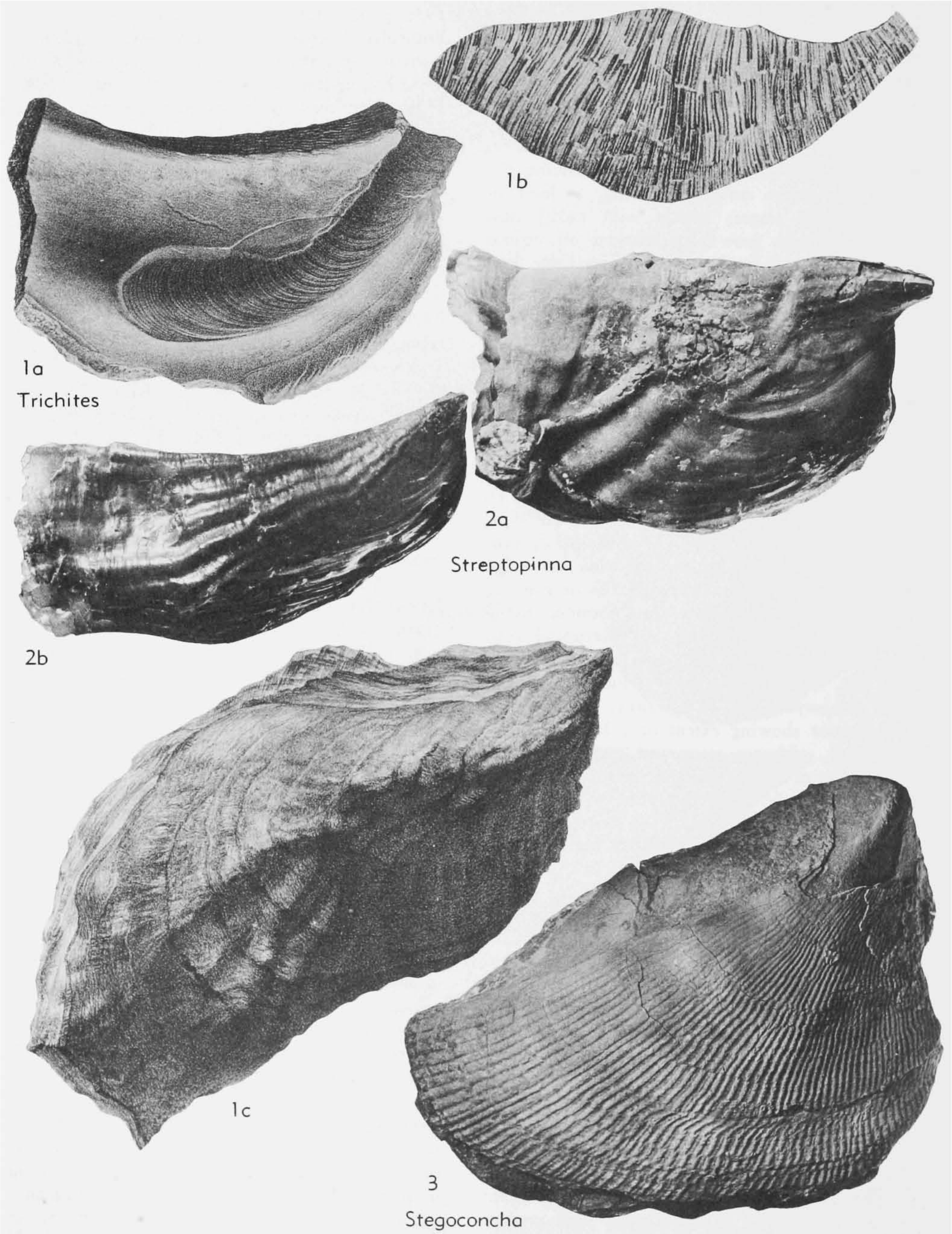

Fig. C24. Pinnidae (p. *N*283-*N*285).

some authors to Deshayes (1832), who, however, published it in the French vernacular form *trichite,* plural *trichites.*] [=*Pinnogena* Bronn, 1836 (no valid nominal species); *Pinnigena* Deshayes, 1839 (obj.); *Pinuigena* Cossmann, 1915 *(nom. null.)*]. Commonly large, irregularly trapeziform or falciform, more or less inequivalve; margins with irregular undulations, closed or with narrow byssal gape; posterior adductor scar deep, much extended in radial direction; surface uneven, some specimens with broad, depressed, bifurcating ribs or with irregular nodosities; shell very thick, composed of fibrous calcite, and commonly found only as fragments. *M.Jur.(Bajoc.)-L. Cret.,* Eu.-Asia-N. Afr.-E. Afr.——Fig. C24,*1a*. *T. seebachi* Böhm, U.Jur.(L.Tithon.), Ger.(Kelheim); RV showing extended adductor scar, ×0.3 (Böhm, 1882).——Fig. C24,*1b*, *T.* sp., U.Jur.(L.Tithon.), Ger.(Kelheim); fragment of test, ×0.7 (Böhm, 1882).——Fig. C24,*1c*. **T. saussuri,* U.Jur.(L.Kimmeridg.), Yonne, Fr.; LV, ×0.5 (Bayle, 1878).

Order PTERIOIDA Newell, 1965

[Diagnosis by N. D. Newell]

Generally inequivalve and pleurothetic; inequilateral or secondarily nearly equilateral; heteromyarian or monomyarian; ligament opisthodetic or amphidetic, alivincular, multivincular or duplivincular, generally extended by secondary fusion layer; prismatonacreous, crossed-lamellar or foliate; pallial line not sinupalliate. *Ord.-Rec.*

Suborder PTERIINA Newell, 1965

[Diagnosis by N. D. Newell]

Adults fixed by byssus through notch in RV, or cemented by RV; byssate throughout much or all of ontogeny; shell microstructure variable; gills filibranch or eulamellibranch. *Ord.-Rec.*

Superfamily AMBONYCHIACEA S. A. Miller, 1877

[*nom. transl.* Newell, 1965 (*ex* Ambonychiidae S. A. Miller, 1877)] [Diagnosis by N. D. Newell]

Strongly inequilateral, triangular, quadrate or trapezoidal, heavy to thin shells with beaks at or near anterior end of hinge; byssal sinus commonly evident; ligament mainly opisthodetic, duplivincular; musculature heteromyarian or monomyarian in adults with posterior adductor placed near or below and behind center of valves; pallial line integripalliate, discontinuous as series of small insertion pits; inner ostracum lamellar aragonite, probably nacreous; outer ostracum prismatic calcite. [Morphologically these shells are intermediate in some respects between the Pterineidae or Cyrtodontidae and the Mytilidae. The last-named family also resembles Modiomorphidae and may have been derived from them rather than from the Ambonychiacea.] *?L.Ord., M.Ord.-L.Jur., ?U.Jur.*

Family AMBONYCHIIDAE S. A. Miller, 1877

[Materials for this family prepared by N. D. Newell & Aurèle LaRocque in consultation with John Pojeta, Jr., Washington, D.C., except as otherwise indicated]

Equivalve, generally prosogyre; hinge teeth few, variable, or apparently absent. [Many genera have been proposed for poorly preserved and poorly prepared specimens. Internal characters of very few of the genera are adequately known. Consequently, external details of form and ornamentation have been stressed.] *M.Ord.(Chazy.)-U.Dev., ?L.Miss.*

Ambonychia Hall, 1847, p. 163 [**A. radiata*; SD Stoliczka, 1871, p. 387] [=*Byssonychia* Ulrich, 1894 (obj.), p. 498; *Eridonychia* Ulrich, 1893 (1895), p. 639 (type, *E. apicalis*; OD)]. Prosocline to slightly opisthocline, orbicular to ovoid shells without anterior lobation; ornamented equally on both valves by simple radial costae; byssal gape generally prominent below beaks; dentition pseudoheterodont, composed of 2 or 3 small radial cardinal teeth in each valve below beaks and few posterior lateral elements located at posterior extremity of hinge margin. *M.Ord.-U.Ord.,* E.N.Am.-Eu.——Fig. C25,*7*. **A. radiata*; M.Ord., USA(N.Y.); *7a,* RV ext., ×1; *7b,* LV int., ×3 *(745)*.

Allonychia Ulrich, 1893 (1895), p. 640 [**Megambonia jamesi* Meek, 1872; OD]. With prominent anterior lobe; ornamented with simple, coarse, radial costae; without posterior wing or discernible byssal gape; hinge unknown. *M.Ord.-U.Ord.,* USA(Ohio Valley).——Fig. C26,*6*. **A. jamesi* (Meek), U.Ord., Ohio; RV int. mold, ×1 *(929)*.

Ambonychiopsis Isberg, 1934, p. 84 [**A. osmundbergensis*; OD] [=*Ambonychia* auctt.]. Beaks terminal; surface with fine radial costellae, cancellate in many shells; without byssal opening; hinge unknown. *M.Ord.(Chazy.)-M.Sil.(Niag.),* N.Am.-Eu.——Fig. C25,*8*. **A. osmundbergensis,* U.Ord.(Boda Ls.), Sweden; *8a,b,* RV ext., dorsal, ×2 *(439)*.

Amphicoelia Hall, 1865 [**A. leidyi*; M]. Without anterior lobe but with prominent anteroventral salient forming obtuse angle with umbonal ridge; beaks terminal; cardinal margin long; ornamentation of costellae or costae, growth varices or concentric undulations; without visible byssal gape; byssal sinus prominent; shell medium to large in size; dentition unknown. *M.Sil.-U.Sil.*, USA.——

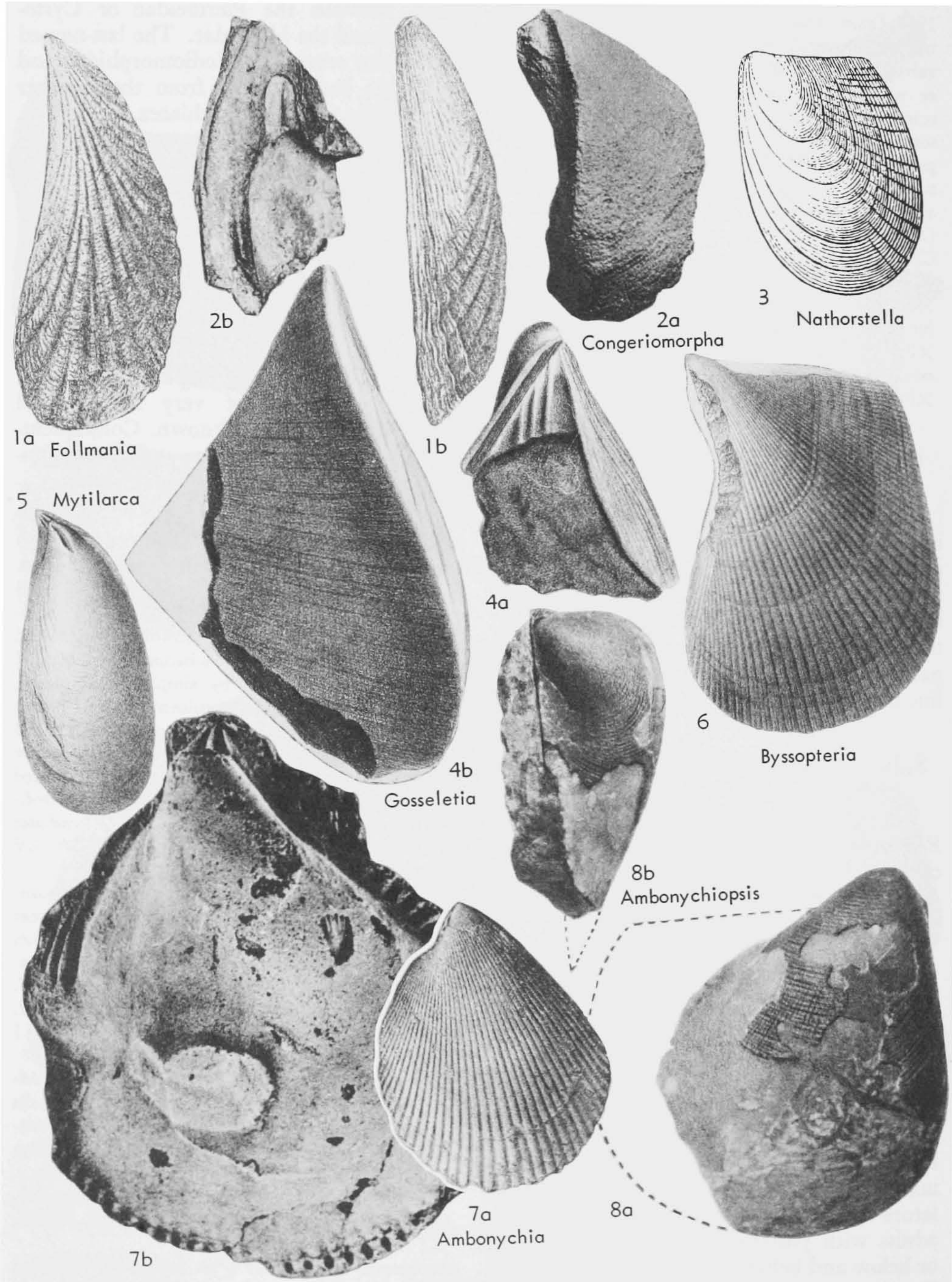

FIG. C25. Ambonychiidae (p. *N*285, *N*287).

Fig. C26,_7_. *_A. leidyi,_ Wis.; LV int. mold, ×1 (Hall, 1865).

Anomalocoelia Isberg, 1934 [*_A. transplicata_; OD]. Similar to _Amphicoelia_ but with shorter anterior end; ligamental area with strong fold. _U.Ord.,_ Eu.——Fig. C26,_1_. *_A. transplicata,_ Boda Ls., Sweden (Dalarna); _1a,_ LV ext. (holotype), ×1; _1b,_ RV hinge (holotype), ×2 _(439)_.

Anomalodonta S. A. Miller, 1874, p. 16 [*_A. gigantea_; SD Miller, 1874, p. 333]. Large, simplicicostate monomyarian upright ambonychiids similar to _Ambonychia_; lacking lateral teeth and with only single poorly developed cardinal tooth in RV. [May be synonymous with _Ambonychia s.s._] _U.Ord.,_ E.N.Am.——Fig. C26,_4_. *_A. gigantea,_ USA(Cincinnati, Ohio); _4a,b,_ LV int., part of RV ext., ×1 _(618)_.

Byssopteria Hall, 1883, p. 4 [*_B. radiata_; M]. Shell erect, superficially like _Ambonychia_ but with multicostate (fasciculate) ornamentation and nasute lobation in front of beaks; hinge unknown. [_Byssopteria_ differs from _Opisthoptera_ in lacking a posterior wing and in having costae rather than costellae.] _U.Dev.(Chemung.),_ USA(Pa.).——Fig. C25,_6_. *_B. radiata;_ LV ext., ×1 _(376)_.

Cleionychia Ulrich, 1892, p. 97 [*_Ambonychia lamellosa_ Whitfield, 1882 (=_A. lamellosa_ Hall, 1862, _A. cancellosa_ Hall, 1861, _nom. null., nom. oblit._); OD] [=_Anoptera_ Ulrich, 1893 (1895), p. 6 (type, _A. miseneri_; M); _?Ambonychinia_ Isberg, 1934, p. 29 (type, _A. undulata_; OD); _Elasmodophora_ Isberg, 1934 (type, _E. acutirostris;_ OD)]. Similar to _Ambonychia,_ but without radial ornamentation or byssal opening; 1 cardinal tooth just under beak in some species, no posterior laterals. _M.Ord.-U.Ord.(Chazy.-Richmond.), ?M.Sil. (Niag.),_ E. N. Am. - Sweden - Norway - Scot.-Ire.-USSR-Korea.——Fig. C26,_3_. *_C. lamellosa_ (Hall), M.Ord.(L.Trenton), USA(Wis.); _3a,b,_ LV int. mold, LV ant., ×1 _(930)_.

?**Congeriomorpha** Stoyanow, 1948 [*_C. andrusovi_; OD]. Modioloid, subtriangular, carinate, with well-defined byssal sinus; depressed umbonal or myophoric platform within beaks, narrow ligamental area; 1 posterior lateral tooth in RV and 2 in LV; cardinal teeth absent. _U.Dev.,_ USA(Ariz.).——Fig. C25,_2_. *_C. andrusovi_; _2a,b,_ LV ext., int., ×2 (Stoyanow, 1948).

?**Enkelbergia** Wedekind in Schindewolf, 1924, p. 274 [*_E. semiglobosa_; M]. Beaks opisthogyre. _U. Dev.(Cheiloceras-Stufe),_ Ger.

Gosseletia Barrois, 1882, p. 273 [*_G. devonica_; SD Follman, 1885]. Subtriangular, beaks terminal, surface without radial ornamentation or byssal gape; umbonal carina prominent; hinge with several oblique cardinals behind beaks and with 2 or 3 posterior laterals below and mainly behind ligament. _L.Dev.-M.Dev.,_ W.Eu.-N.Am.——Fig. C25,_4_. *_G. devonica,_ L.Dev., Spain(Asturias); _4a,b,_ LV hinge int., RV ext., both ×1 (Barrois, 1882).

?**Myalinopterella** Khalfin, 1940, _Dev.,_ USSR (Altai).

Mytilarca Hall & Whitfield, 1869, p. 19 [*_Inoceramus chemungensis_ Conrad, 1842; OD] [=_Plethomytilus_ Hall, 1883, p. 4 (type, _Mytilarca ponderosa_ Hall & Whitfield, 1869; SD S. A. Miller, 1889); _Cyrtodontopsis_ Frech, 1891 (type, _Gosseletia? kayseri_ Frech in Kayser, 1889; SD LaRocque & Newell, herein); _Lophonychia_ Pohl, 1929 (type, _Mytilarca trigonale_ Cleland, 1911; OD)]. Mytiliform, commonly somewhat falcate, with terminal beaks; without radial ornamentation or byssal gape; umbonal carina less pronounced than with _Gosseletia_; few oblique cardinals and 2 or 3 laterals in each valve. _L.Sil. (Brassfield)-U.Dev., ?L.Miss.,_ Eu.-N.Am.——Fig. C25,_5_. *_M. chemungensis_ (Conrad), U.Dev. (Chemung), USA(N.Y.); RV int. mold, ×1 _(377)_.

Nathorstella Kayser, 1901, p. 10 [*_N. semiplicata_; M]. Beaks terminal, mytiliform, without anterior lobation; ornamented with outward curving costae; hinge unknown. _Dev.,_ Ger.-Spitz.

N. (Nathorstella). Subrhombic, costae confined to area behind umbonal ridge. _Dev.,_ Spitz.——Fig. C25,_3_. *_N. (N.) semiplicata,_ Spitz.(Gray Hook); LV ext., ×1 (Kayser, 1901).

N. (Follmannia) Drevermann, 1907, p. 32 [*_Gosseletia pseudalectryonia_ Frech, 1891; M]. Slender, falcate, with coarse, pinnate costae diverging outward from umbonal ridge. _L.Dev.(Coblenz.),_ Ger.——Fig. C25,_1_. *_N. (F.) pseudalectryonia_ (Frech), Coblenz, Rhinel.; _1a,b,_ RV ext., LV ant., ×1 _(323)_.

Opisthoptera Meek, 1872, p. 319 [_pro Megaptera_ Meek & Worthen, 1868 (_non_ Gray, 1846)] [*_Ambonychia casei_ Meek & Worthen, 1866; M] [=_Opistholobata_ Ulrich in Hussey, 1926, p. 165 (type, _O. gouldi_; M)]. Subtriangular, umbones terminal, hinge line very long; surface with numerous radial, bifurcating costae; byssal opening present; hinge said to contain 2 small cardinals in each valve; without posterior laterals. _U. Ord.,_ USA(Ohio Valley); _L.Sil.(Llandov.),_ Scot. ——Fig. C26,_5_. *_O. casei_ (Meek & Worthen), U.Ord.(Cincinnatian), USA(Ky.-Ind.); _5a,_ LV ext.; _5b,_ ant. view int. mold both valves; both ×1 _(929)_.

?**Palaeocardia** Hall, 1865 [*_P. cordiformis_; M]. Beaks large, anterior but not terminal, hinge line short; surface with numerous fine, radial costellae; no byssal opening; dentition unknown. _Sil. (Niagar.),_ USA-Can.——Fig. C26,_2_. *_P. cordiformis,_ USA(Wis.); _2a,_ RV int. mold; _2b,_ post. view int. mold; both ×1 _(374)_.

Paramytilarca Isberg, 1934 [*_P. levis_; OD]. Similar to _Cleionychia_ but with 2 or more posterior laterals and without cardinals. _M.Ord.-U.Ord.,_ Sweden.——Fig. C27,_2_. *_P. levis,_ U.Ord., Boda Ls., Kallholn; _2a,b,_ RV ext., ant., ×2 _(439)_.

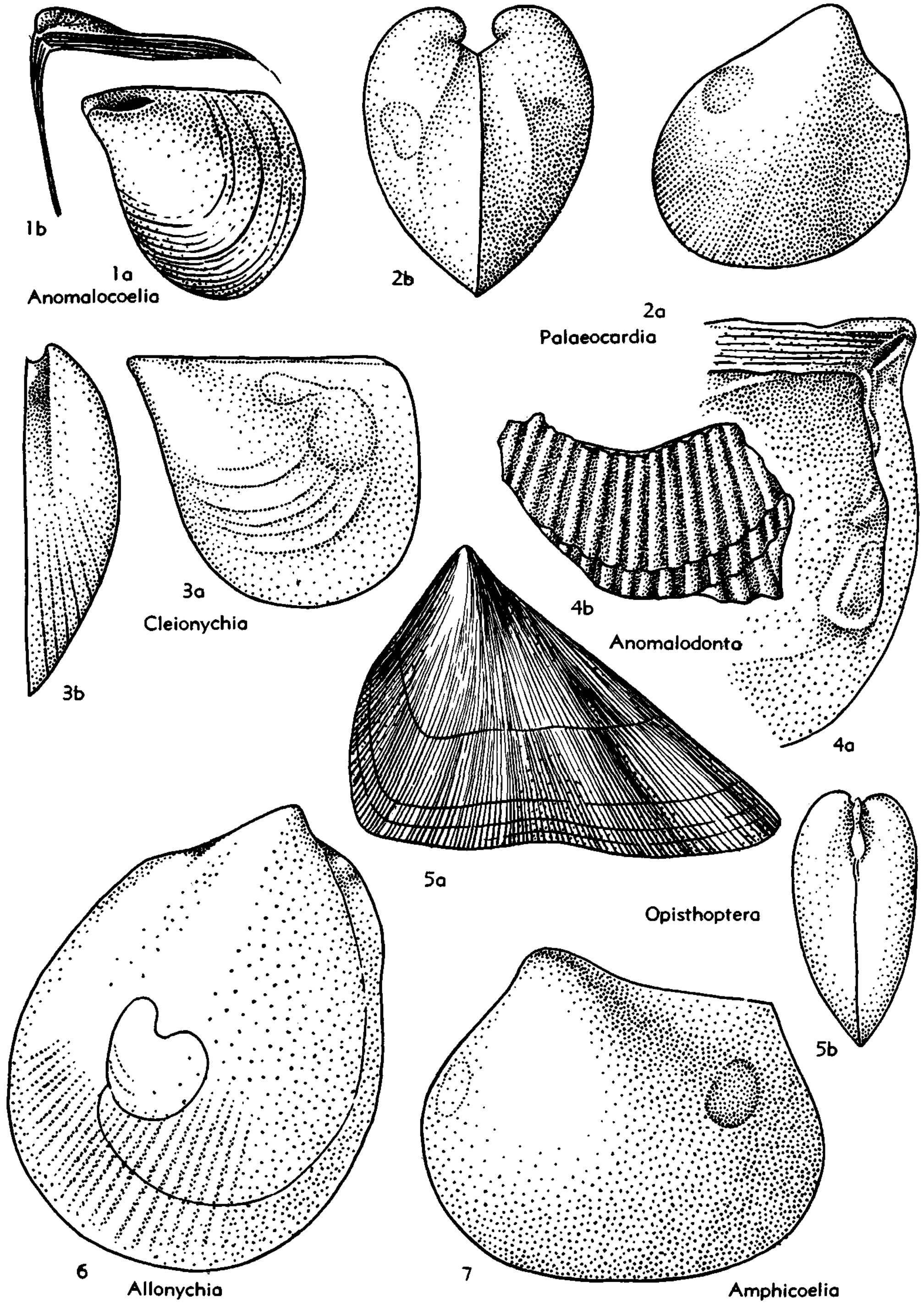

FIG. C26. Ambonychiidae (p. *N*285-*N*287).

?**Pompeckjina** Wedekind in Schindewolf, 1924, p. 275 [**Inoceramus semiorbicularis* Münster; M]. *U.Dev.(Cheiloceras-Stufe),* Ger.

Praeanomalodonta Isberg, 1934, p. 91 [**P. scutulata;* OD]. Similar to *Anomalodonta* but without radial ornamentation. *U.Ord.(Boda Ls.),* Sweden(Dalarna).——Fig. C27,*3*. **P. scutulata,* Kallholn, Sweden; *3a,* LV ext. (holotype); *3b,* LV hinge; both ×2 *(439).*

Psilonychia Ulrich, 1895, p. 648 [**P. perangulata*; OD]. Beaks terminal, pointed; without radial ornamentation; byssal gape small, elongate oval; hinge wide, edentulous. *U.Ord.,* N.Am.——Fig. C27,*4*. **P. perangulata,* USA(Ohio); *4a,b,* LV ext., ant., ×1; *4c,* LV hinge, ×1 *(929).*

Stappersella Maillieux, 1920, p. 144 [**Gosselettia truncata* Roemer, 1844; SD Maillieux, 1937] [=?*Demanetia* Maillieux, 1937, p. 104 (type, *Myalina lodanensis* Frech, 1891; SD LaRocque & Newell, herein)]. Subtrigonal to mytiliform, beaks not quite terminal, without byssal gape, ornamented with coarse, simple costae reflected on internal molds as marginal plicae; hinge as in *Mytilarca* with cardinals and laterals more or less radial with respect to beaks. Some slightly inequivalved individuals said to be edentulous *(Demanetia). L.Dev.,* W.Eu.——Fig. C27,*5*. **S. truncata* (Roemer), U.Coblenz., Ger.(Rhinel.); LV int. mold, ×1 *(323).*

?**Streptomytilus** Kindle & Breger, 1904, p. 452 [**S. wabashensis,* M]. Shell cuneiform, beaks terminal, long, pointed; without radial ornamentation; said to be edentulous and with unstriated ligament area. *M.Sil.(Niagar.),* N.Am.(Ind.-Wis., N.Ont.).——Fig. C27,*1*. **S. wabashensis,* USA (Wabash, Ind.); *1a,b,* LV ext., ant. (holotype), ×1 *(470).*

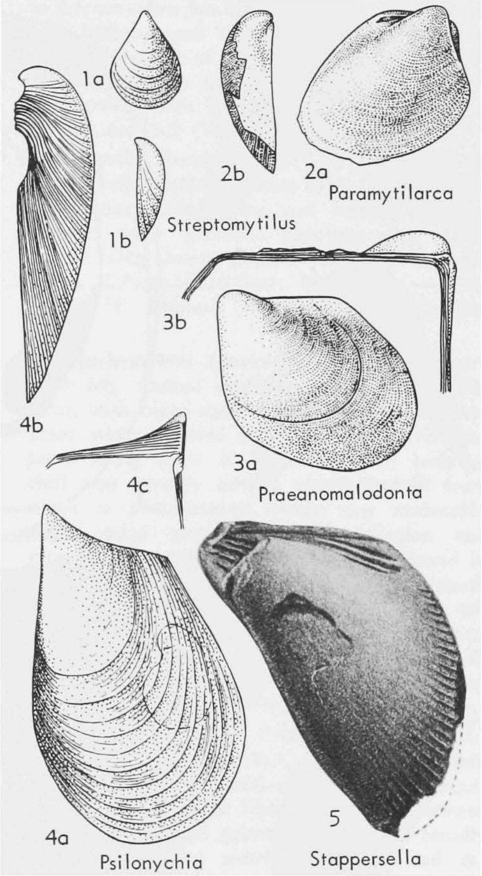

Fig. C27. Ambonychiidae (p. *N*287, *N*289).

Family MYALINIDAE Frech, 1891

[Diagnosis by N. D. Newell] [Materials for this family prepared by N. D. Newell, John Weir, and L. R. Cox, as indicated]

Inequivalved, with RV slightly less convex than LV; edentulous, or with cardinal tooth or boss beneath beak of RV and corresponding furrow in LV; pallial line entire, generally pitted. *?L.Dev., L.Miss.-L. Jur., ?U.Jur.*

MARINE MYALINIDAE

[Materials for this section prepared by N. D. Newell]

Myalina de Koninck, 1842 [**M. goldfussiana*; SD Stoliczka, 1871, p. 366]. Mytiliform shells with nearly terminal beaks, generally unornamented, surface of LV in some species roughened by prominent growth lamellae; RV less convex and commonly slightly smaller than LV; umbonal deck lacking. *L.Miss.-U.Perm.,* cosmop.

M. (Myalina). Thick-shelled species with well-developed anterior lobe, at least on LV; primitive species nearly equivalved with marked prosocline obliquity, advanced species inequivalved, becoming acline or opisthocline and developing posterior auricle. *L.Miss.-U.Perm.,* cosmop.——Fig. C28,*5a*. *M. (M.) copei* (Whitfield), L.Perm.(Moran), USA(Tex.); LV ext., ×0.7 *(666).*——Fig. C28,*5b*. **M. (M.) goldfussiana,* L.Carb.(Visean), Belg.; LV int. showing muscle marks and dental socket, ×1 *(666).*

M. (Orthomyalina) Newell, 1942 [**M. slocomi* Sayre, 1930; OD]. Subquadrate, nearly acline, thick-shelled, without anterior lobation. *M.Penn. (Desmoines.)-Perm.(Wolfcamp.),* USA. —— Fig. C28,*2*. **M. (O.) slocomi* (Sayre), U.Penn. (Virgil.), USA(Kans.); LV int. showing muscle marks and dental socket, ×1 *(666).*

Atomodesma von Beyrich, 1864 [**A. exaratum*; SD Wanner, 1922, p. 63] [=*Maitaia* Marwick,

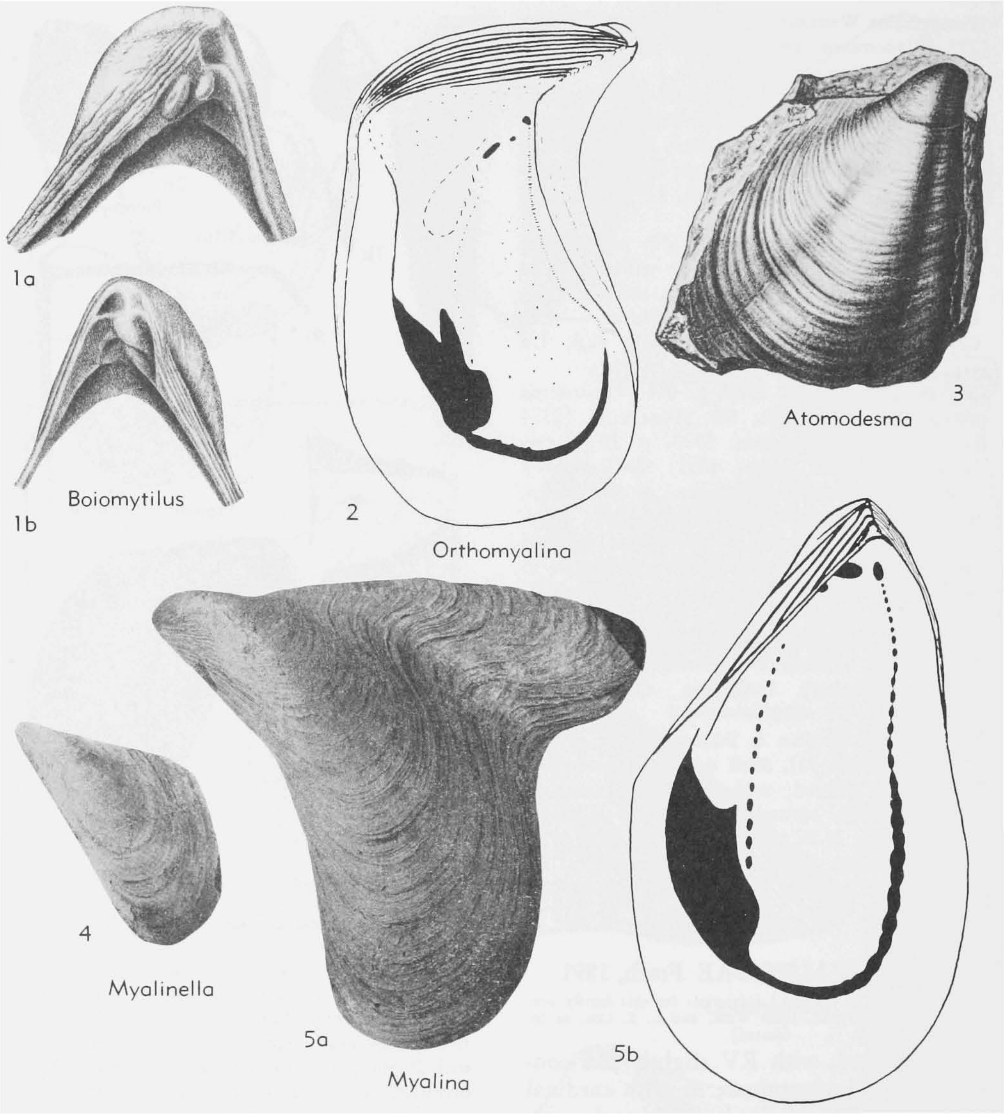

Fig. C28. Myalinidae (marine) (p. *N*289-*N*291).

1934 (type, *M. trechmanni* Marwick, 1934, OD); *Kolymia* Likharev, 1941 (type, *K. inoceramiformis*; OD); *Intomodesma* Popov, 1957 (type, *I. costatum*; OD)]. Prosocline, duplivincular, ovoid shells of inoceramid aspect, with acute, terminal, or nearly terminal beaks, concentric folds, and small, internal umbonal deck or septum; prismatic layer well developed in both valves; lamellar layer thin. *?U.Penn., L.Perm.-U.Perm.,* Australasia-N.Z.-Greenl.(Waterhouse, 1963).——Fig. C28,*3*. **A. exaratum*, Timor (*fide* Dickins, 1956, p. 25); RV ext., ×1 (Wanner, 1922).

?**Aviculomyalina** Assmann, 1916 [**A. lata*; OD]. *M.Trias.(Karchowitz beds),* Pol.(Tarnowitz, Upper Silesia).

?**Boiomytilus** Růžička & Prantl, 1961 [**B. newelli*; OD]. Mytiloid, LV more convex than RV; surface marked by growth lamellae only; 2 small subpyriform teeth separated by socket in LV below beaks, single tooth in RV, lateral teeth apparently lacking; subcircular pit of uncertain function lies immediately ahead of cardinal teeth and small anterior adductor scars occurs just below them, below level of hinge plate; posterior adductor scar large, situated near the posterior margin. _L.Dev._, C.Boh.——Fig. C28,_1_. *_B. newelli_; _1a,b,_ LV and RV hinge, ×1 _(818)_.

Eurydesma Morris, 1845 [*_E. cordatum_; OD] [=_Leiomyalina_ Frech, 1891 (type, _L. antarctica_)]. Acline, heavy, smooth, obliquely oval as viewed laterally, ventricose, with deep, cordate lunule; outer ostracum relatively thick, more than 0.25 thickness of shell. _L.Perm._, Australia-India-S. Afr.-Arg.——Fig. C29,_1_. *_E. cordatum,_ L.Perm., Australia(New S.Wales); _1a-c,_ RV beak, LV beak, RV ext., ×0.7 (Etheridge & Dun, 1910).[1]

Liebea Waagen, 1881 [*_Mytilus squamosus_ Sowerby, 1829; SD Cox, 1936, p. 38]. Shell small, rarely attaining length greater than 2.5 cm.; mytiloid, strongly prosocline, subrhombic; RV relatively smooth and almost imperceptibly less convex than squamose LV; single cardinal tooth of LV overlying single tooth in RV; anterior adductor seated in pit along anteroventral edge of umbonal deck; ligament grooves strongly oblique, 6 or 8 intersecting hinge axis. _Perm._, E.Hemis., widespread. ——Fig. C29,_2_. *_L. squamosa_ (Sowerby), U. Perm.(Zechstein), Ger.; _2a,b,_ hinge view and LV, ×3 (Newell, 1939).

Myalinella Newell, 1942 [*_Myalina meeki_ Dunbar, 1924; OD, p. 60]. Thin-shelled, small strongly prosocline, triangular, with obtuse posterodorsal margins; beaks slender, not lobed; LV only slightly more rugose than RV. _Penn. (Desmoines.)-L.Trias._, Eu.-USA-India-Greenl.—— Fig. C28,_4_. *_M. meeki_ (Dunbar), L.Perm.(Big Blue), USA(Kans.); LV, ×2 _(666)_.

?**Pachymytilus** Zittel, 1881 [*_Mitylus petasus_ d'Orbigny, 1850; SD Cossmann, 1915]. Large, mytiliform, with terminal beaks; test very thick, especially near beaks; exterior smooth or with faint radial striae; anterior marginal region usually reflected, margin forming sinus from deepest point of which groove runs to beak; thick test in anterior angle may bear amorphous, toothlike protuberances. Ligamental area broad, subinternal, usually with single groove for ligament, but in 1 species with about 4 grooves; posterior adductor scar very large. _U.Jur._, Eu.——Fig. C29,_4_. *_P. petasus_ (d'Orbigny), U.Oxford., Yonne, France; RV int., ×0.7 _(1025)_. [Cox]

Posidoniella deKoninck, 1885 [*_Inoceramus vetustus_ Sowerby, 1829; OD]. Ventricose shells of inoceramid aspect without radial ornamentation, anterior auricle, or umbonal deck; prismatic layer thin. _Carb.(Vise.-Namur.)_, Eu.; _Penn.(Pottsville)_, USA.——Fig. C29,_5_. *_P. vetusta_ (Sowerby), L. Carb., Eng.; LV ext., ×1 (Ramsbottom, 1959).

Promyalina Kittl, 1904 [*_P. hindi_; OD]. Similar to _Selenimyalina_ but with somewhat more prominent umbones and with single cardinal tooth in each valve, that of RV overlying tooth of LV. _?U.Perm._, Yugo.; _L.Trias._, cosmop.——Fig. C29, _3_. _P. groenlandica_ (Newell), L.Trias., E.Greenl.; LV int., ext., ×2 (Newell, 1955).

Pseudomyalina Dickins, 1956 [*_P. obliqua_; OD]. Large shells, similar in form to _Septimyalina_ but with weak radial costae and lacking umbonal septum; outer prismatic ostracum very much thicker than inner lamellar ostracum in both valves. _L.Perm.(Coolkilya),_ W.Australia.——Fig. C29,_6_. *_P. obliqua_; LV ext., ×0.5 (Dickins, 1956).

Pseudopachymytilus Krumbeck, 1923 [*_P. timorensis_; M]. Outline pteriiform rather than mytiliform, with hinge margin produced to form posterior wing, rounded at its extremity, and umbones rising above it; beaks terminal; body of shell very strongly inflated along diagonal from umbo to posteroventral corner; test moderately thick; radial ornament absent; reflection and grooving of anterior marginal region, as found in _Pachymytilus_, absent; ligamental area flattened, subinternal, in many forms relatively wide; adductor scars located on platform-like elevations, anterior scar deeply impressed. _L.Jur.(Lias.),_ E. Indies(Timor).——Fig. C29,_7_. *_P. timorensis_; _7a,b,_ LV ext., int., ×1 _(486)_. [Cox]

Selenimyalina Newell, 1942 [*_Myalina meliniformis_ Meek & Worthen, 1866; OD]. Small, strongly prosocline to acline, smooth, nearly equivalve, without anterior lobation; umbones flattened and poorly defined; posterodorsal margin broadly rounded; ligament grooves numerous and extremely fine; dentition similar to _Myalina_ except that single cardinal tooth of RV and corresponding triangular socket of LV are situated on hinge plate which partly covers very shallow umbonal recess. _Penn. (Desmoines.-Virgil.),_ USA.——Fig. C30,_2_. *_S. meliniformis_ (Meek & Worthen), Desmoines., USA(Ill.); LV int., showing muscle marks, ×2 _(666)_.

Septimyalina Newell, 1942 [*_Myalina perattenuata_ Meek & Haydn, 1858; OD]. Prosocline, rhomboidal to falcate, or acline, thick-shelled myalines with slender extended beaks and obsolescent anterior lobe below each beak; both valves smooth or rugose; inequivalved; umbonal cavity covered anterodorsally by broad hinge plate; dentition weak, as in _Myalina_. _L.Carb.(Visean)-L.Perm. (Wolfcamp.),_ USA-W.Eu.——Fig. C30,_1_. *_S. perattenuata_ (Meek & Hayden), U.Penn., USA (Kans.); LV ext., int., ×1 _(666)_.

NONMARINE AND BRACKISH-WATER MYALINIDAE

[Materials for this section prepared by John Weir]

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[1] Bruce Runnegar (pers. commun.) recognizes family Eurydesmidae Reed, 1932 (_recte_ Eurydesmatidae), which he places with Pectinacea. According to his evidence ligament in _Eurydesma_ is not duplivincular and inner ostracum is crossed-lamellar (cf. _Chaenocardia_ and _Pergamidia_).

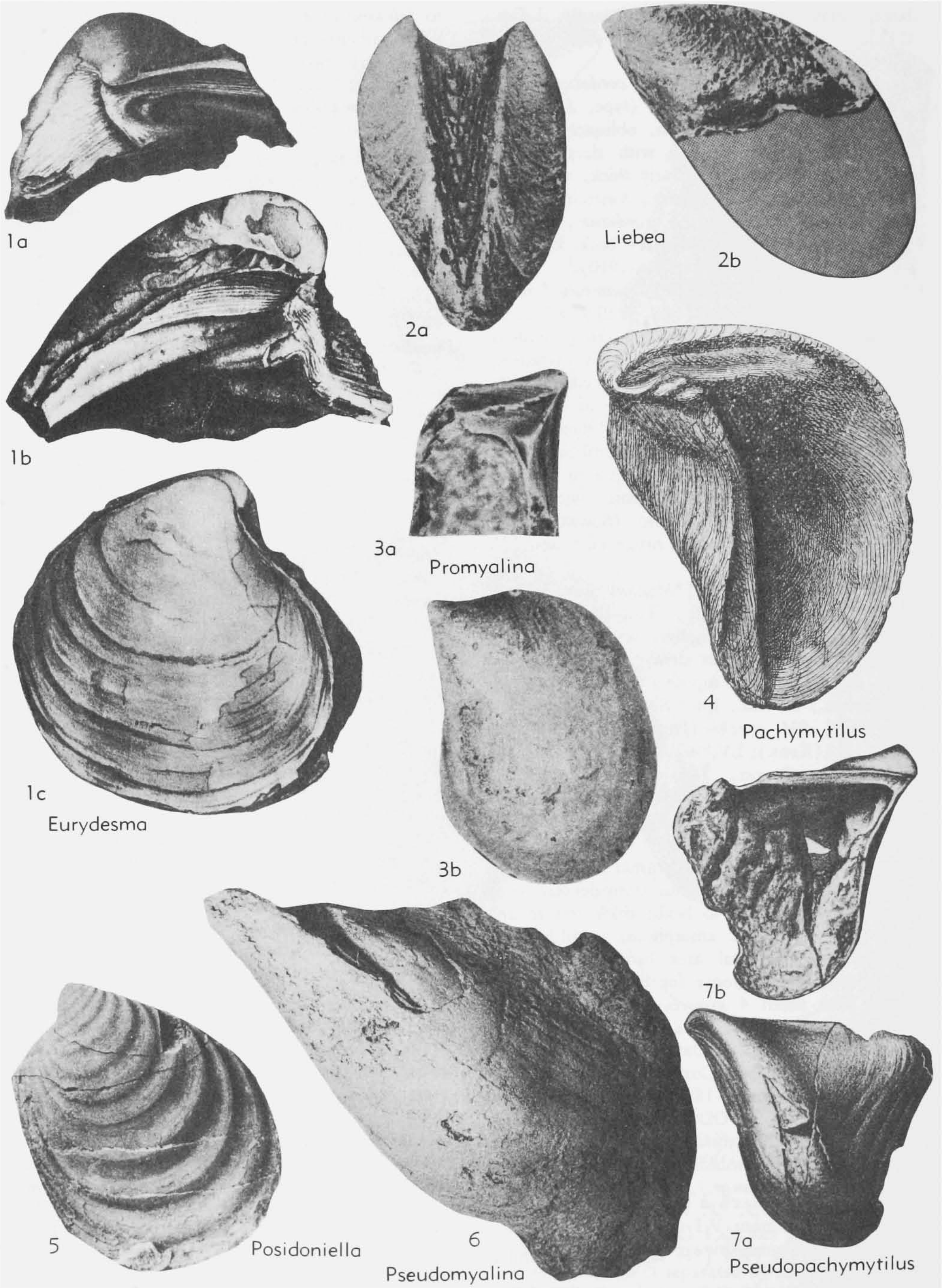
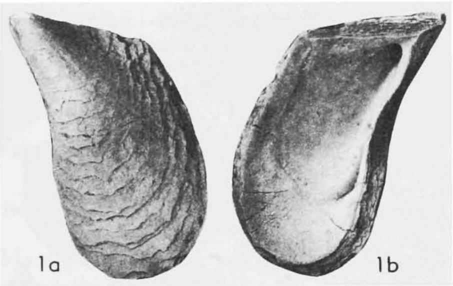


FIG. C29. Mayalinidae (marine) (p. *N*291).

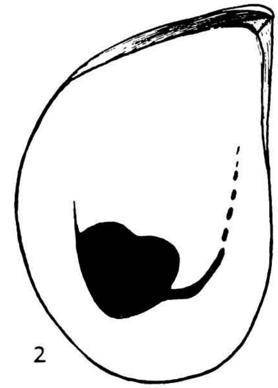
Anthraconaia Trueman & Weir, 1946 (April) [*pro Anthracomya* Salter, 1861 (*non* Rondani, 1856)] [**Anthracomya adamsii* Salter, 1861; OD] [=*Saltermya* Palmer, 1946 (Sept.) (obj.)]. Obliquely subovate, submodioliform or elongate-trapeziform; integripalliate, inequilateral, equivalved (or slightly inequivalved), with straight hinge line; anterior end narrow in subovate and submodioliform species, posterior end expanded, rounded, or truncated (vertically or obliquely), dorsal and ventral margins subparallel in elongate forms; obtuse carinal swelling in some shells runs obliquely from umbo toward posteroventral angle, and wide byssal sinus may occur; umbones not prominent, situated within anterior third of shell. Hinge straight, linear, edentulous; ligament duplivincular, slightly ?amphidetic, inserted as in *Myalina,* in elongated grooves ("striae"), some with no more than 2 in each narrow ligamental area; anterior adductor scar ?semicircular, almost marginal, posterior adductor scar unknown. *U. Carb.(Westphal.-Stephan.),* W.Eu.-USSR(Donetz)-N.Am.(E.Can.).——Fig. C31,*1a.* **A. adamsii* (Salter), U.Carb.(U.Amman.), Eng.; *1a-c,* ?lectotype, LV ext., RV ext., both valves dorsal, ×0.7 *(964b).*——Fig. C31,*1d. A.* sp. cf. *A. fisheri* (Wright), U.Carb.(L.Amman.), Eng.; hinge and ligament grooves, ×2 (Weir, n).

Anthraconauta Pruvost, 1930 [**Unio phillipsii* Williamson, 1836] [=*Anthracomya* Hind, 1895 *(partim)*; *Anthracomya* Davies & Trueman, 1927 *(partim)*]. Equivalved, inequilateral; subovate, cordate or subtriangular, with inconspicuous umbones, straight hinge line and obliquely extended posterior end semielliptical, spatulate or acuminate in outline. Hinge line 50-80 percent of length, forming with straight or curved posterior margin obtuse angle (β), which may be sharp or rounded, never auriculate; dorsal and ventral margins converging toward anterior end which may be quite acute; umbones small, situated well forward but not terminal, rising little or not at all above level of hinge line in type subgenus. Shell substance thin; ornament of concentric growth lines, folds or rugae, subgenera showing in varying degrees radial striation of delicate straight lines probably comprising trace of prismatic or periostracal structure shown through worn periostracum. Internal features unknown. *U.Carb.-Perm.,* cosmop.

A. (Anthraconauta). Like *Naiadites,* but usually smaller, and umbones, situated farther from anterior end, lack proximal spiral twist; carina, byssal sinus and posterior auricle absent; posterodorsal angle (β) not rounded. Shell thin, periostracum well developed. Inflation low (shells usually flattened). Hinge and musculature unknown but probably as in *Naiadites. U.Carb. (Westphal.C.-Stephan.),* W. Eu.-USSR (Donetz); *U.Carb.-Perm.,* USSR(Sib.).——Fig. C31,*2.* **A. (A.) phillipsii* (Williamson), U.Carb.(Morgan.; Westphal. C.), Eng.; LV ext. (type), ×2 (Weir, 1960, in *915*).



Septimyalina



Selenimyalina

Fig. C30. Myalinidae (marine) (p. *N*291).

[Derivative of *Naiadites.* In the Upper Carboniferous-Permian coal basins of Siberia, as a member of an otherwise mainly endemic nonmarine fauna, it proliferated into a large number of forms, some of which are approximately homeomorphous with heterochronous European equivalents *(A. pseudophillipsi, A. phillipsii),* and others have been named as genera by Russian paleontologists. At highest they are probably only of subgeneric rank, and some are so defined below. These subgenera, like *A. (Anthraconauta),* occur at various horizons in the upper Carboniferous and Permian deposits of the Kuznetsk Basin and are doubtless products of variation, although this has still to be confirmed by formal studies of association and variation. ¶Other genera which were endemic to these upper Paleozoic nonmarine deposits of Siberia do not seem to be intimately related to *Anthraconauta*; their internal characters are unknown, but those with straight hinge line and obliquely subovate outline are here, in certain cases (following Khalfin), assigned to the Myalinidae, but with a query. The remainder have not been placed in families by Russian authors, even tentatively.]

A. (Augea) Khalfin, 1950 [**A. ovata*; OD]. Like *Kinerkaella*; inconspicuous umbones forwardly directed at anterior end of shorter hinge line; less elongate diagonally. *U.Carb.-L.Perm.,* USSR (W.Sib.).——Fig. C31,*6.* **A. (A.) ovata,* L. Perm.; RV ext., ×2 (Ragozin, 1955).

A. (Kinerkaella) Khalfin, 1950 [**Parallelodon balakhonskiensis* Ragozin, 1931; OD]. Like *Mrassiella* but more transversely rhomboidal in outline, small, forwardly projecting umbones set nearer to anterior end; concentric rugae and radial striation especially prominent. *U.Carb.,* USSR(W.Sib.).——Fig. C31,*3.* **A. (K.) balakhonskiensis* (Ragozin); LV ext., ×2 (Ragozin, 1955).

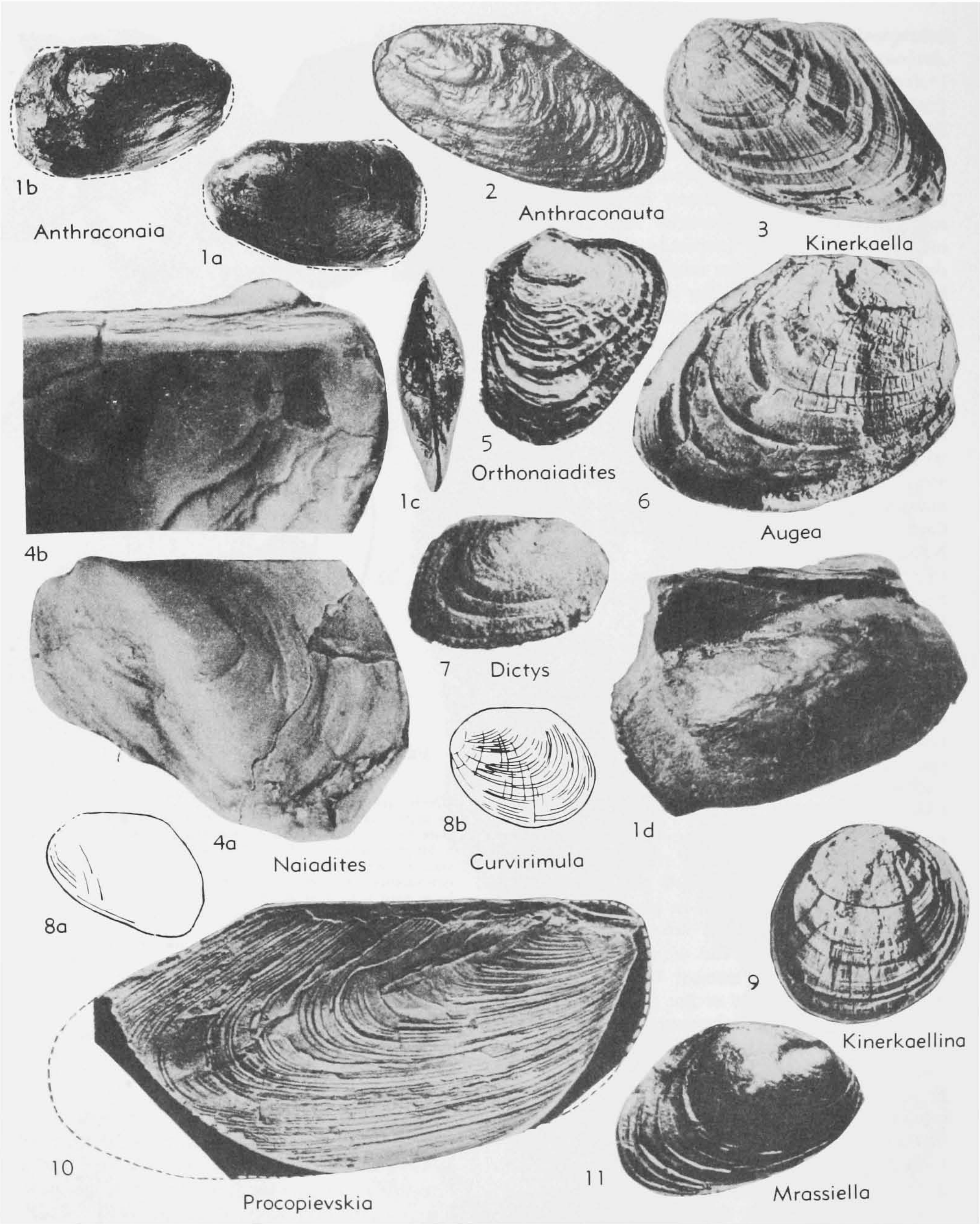


Fig. C31. Myalinidae (nonmarine) (p. *N*293-*N*295).

A. (Mrassiella) Ragozin, 1935 [**M. magniforma*; OD]. Like *A. (Anthraconauta)* but obliquely cordate and more inflated, with rounded margins and angles; small umbones projecting slightly and subcentrally above rather short, straight or gently curved hinge line. *U.Carb.-L.Perm.*, USSR (W.Sib.).——Fig. C31,*11*. **A. (M.) magniforma*, U.Carb.; RV ext., ×1.5 (Ragozin, 1955).

A. (Procopievskia) Ragozin, 1933 [**Anthracomya phillipsii* var. *gigantea* Ragozin, 1931; OD]. Like *Anthraconauta* but larger, with more acute anterior end; posterior extremity obliquely extended, making wide angle between straight dorsal and posterior margins; valves almost flat, umbones situated near anterior end, inconspicuous, not rising above level of hinge line. Periostracum and prismatic layer thin. *L.Perm.*, USSR (W.Sib.).——FIG. C31,*10*. **A. (P.) gigantea* RAGOZIN; RV ext. (outline restored by WEIR), ×1.5 (Ragozin, 1955).

?**Curvirimula** WEIR, 1960 [**Anthracomya belgica* HIND, 1912; OD]. Like *A. (Anthraconauta)* but smaller, with orbicular and elongate-scalene tendencies; posterodorsal angle always rounded, never auriculate; crushed valves (usual condition) showing distinctive system of curved, subradial cracks (in crushed *Anthraconauta* cracks infrequent and straight). *Carb. (U.Dinant.-Amman.)*, W.Eu.; *Carb.(Cumberland.)*, Can.(N.S.).——FIG. C31,*8a*. **C. belgica* (HIND), Namur., Belg.; LV ext. (lectotype), ×2 *(964a)*.——FIG. C31,*8b*. *C. scotica* (ETHERIDGE, JR.), L.Carb.(Oil Shale Gr.), Scot.; LV ext. (holotype, counterpart), ×2 (Weir, n).

?**Dictys** KHAFLIN, 1950 [**D. inflatus*; OD]. Small, inflated shells with inconspicuous umbones; trapeziform (anthraconaiiform), strongly inequilateral, posterior end slightly expanded and truncated. [The slightly convex ventral margin and straight dorsal margin are nearly parallel, but converge toward the rather deep anterior end.] *L. Perm.*, USSR(Sib.).——FIG. C31,*7*. **D. inflatus*; RV ext., ×4 (Ragozin, 1955).

?**Kinerkaellina** KHALFIN, 1950 [**Kinerkaella (K.) imitabilis*; OD]. Small, orthocline-ovate; valves uniformly and gently convex, umbones subcentral, projecting slightly above short hinge line; radial striation irregular. *U.Carb.*, USSR(W.Sib.).——FIG. C31,*9*. **K. imitabilis*; RV ext., ×3.5 (Ragozin, 1955).

Naiadites DAWSON, 1860 [*non Najadites* AMALITSKY, 1892] [**N. carbonarius*; SD HIND, 1894] [=*Anthracoptera* SALTER, 1863]. Like *Myalina* internally, apart from minor differences of anterior musculature resulting from relatively greater length of anterior end in *Naiadites*; modioliform, umbones not terminal. Ligament duplivincular, slightly amphidetic; area narrow, marked by grooves (2 to 7 or 8) of ligamental attachment; LV usually more inflated than RV; wide and shallow byssal sinus present in some; carina (umbonal ridge) of variable curvature, inflation and prominence runs from umbo of 1 or both valves toward posteroventral margin, defining region of maximum inflation and usually large in LV; posterior auricle ("ear" or "wing") may be present. *L.Carb.(Dinant.)*, Scot.; *U.Carb.*, Eu.-N.Am. (*Namur.*, G.Brit., *Westphal. A,B*, W.Eu., USSR, Donetz).——FIG. C31,*4*. **N. carbonarius*, U.Carb., N.Scot.; lectotype, *4a*, LV ext., ×3; *4b*, LV int., showing ant. musculature and duplivincular ligamental area, ×5 *(666)*.

?**Orthonaiadites** KHALFIN, 1950 [**O. triangularis*; OD]. Scalene, orthocline, main diagonal almost coincident with long, straight (or slightly curved) anteroventral margin, which runs almost at right angles to hinge line; antero- and posterodorsal angles rounded, orthogyral umbones projecting slightly; ventral region produced, acutely rounded. *U.Carb.*, USSR(W.Sib.).——FIG. C31,*5*. **O. triangularis;* RV ext., ×3.8 (Ragozin, 1955).

?Family LUNULACARDIIDAE Fischer, 1887

[Materials for this family prepared by N. D. NEWELL & AURÈLE LAROCQUE]

Mainly small shells, equivalve, monomyarian, opisthodetic, with beaks at front of hinge; edentulous; character of ligament unknown. [These forms are similar to Ambonychiidae in many respects but their affinities will remain uncertain until their morphology is better known.] *L.Ord.-Miss.*

Lunulacardium MÜNSTER, 1840, p. 69 [**L. semistriatum*; SD STOLICZKA, 1870] [=*Pinnopsis* HALL, 1843, p. 244 (type, *P. acutirostrum*; SD LAROCQUE & NEWELL, herein); *Chaenocardiola* HOLZAPFEL, 1889, p. 61 (type, *Cardita haliotoidea* ROEMER; SD BEUSHAUSEN, 1895)]. Triangular to elongate oval, thin-shelled, with prominent beaks and long byssal gape. *U.Sil.-L.Carb.*, N.Am.-Eu.

- **L. (Lunulacardium)**. Beaks opisthogyre, shell surface with prominent radial costae. *U.Sil.-L.Carb.*, N.Am.-Eu.——FIG. C32,*1*. **L. (L.) semistriatum*, U.Dev., Ger.; *1a,b*, RV ext., ant., ×2 *(136)*.
- **L. (Honeoyea)** CLARKE, 1904, p. 225 [**H. erinacea*; OD]. Similar to *L. (Lunulacardium)* but radial ornamentation consisting of several ranks of intercalating ribs; anterior and posterior margins commonly spinose. *U.Dev.*, USA(N.Y.)-Ger. ——FIG. C32,*5*. **L. (H.) erinacea*, U.Dev. (Naples), USA(N.Y.); *5a*, LV ext., ×5; *5b,c*, LV ant., post., ×10 *(136)*.
- **L. (Prosochasma)** BEUSHAUSEN, 1895 [**L. pyriforme* MÜNSTER, 1840; SD CLARKE, 1904, p. 228] [=?*Onychocardium* WHITFIELD, 1905, p. 18 (type, *O. portlandicum*; M)]. Similar to *L. (Lunulacardium)* but with smooth or finely costellate surface and short byssal gape. *Dev.*, Ger.-?USA(N.Y.).——FIG. C32,*7*. *L. (P.) bickense* (HOLZAPFEL), L.Dev., Bicken, Ger.; *7a,b*, dorsal and side views; both ×1 *(47)*.

Euchasma BILLINGS, 1865, p. 360 [**E. blumenbachi*; M]. Trigonal, with truncate anterior and slightly gaping front end; posterior end extended slightly in rounded wing; surface ornamented with radial costae; hinge ankylosed?. *L.Ord.*, Can.(Maritime prov.).——FIG. C32,*8*. **E. blumenbachi*, L. Ord., E.Can.; *8a,b*, RV ext., both valves ant., ×1 *(52)*.

Maminka BARRANDE, 1881, p. 106 [**M. comata*; SD LAROCQUE & NEWELL, herein] [=*Matercula* BARRANDE, 1881 (obj.)]. Subtrigonal, with approximately median beaks; anterior end acuminate, truncate, not gaping, bordered by carina; inequivalve, with radial sulcus on either RV or LV; ornamented with radial costae. *Ord.(D$_5$)-Sil.(E$_{1,2}$)*, Boh.——Fig. C32,3. **M. comata,* Sil.(E$_1$); *3a,b,* RV int. mold, ext., ant., *3c,* RV hinge view; all ?×1 *(27).*

Mila Barrande, 1881, p. 106 [**M. complexa*; OD] [=*Dilecta* Barrande, 1881, p. 106 (obj.)]. Subtriangular, with subquadrate posteriorly; slightly inequivalve; beaks terminal with RV beak slightly ahead of LV; beaks terminal; without byssal gape;

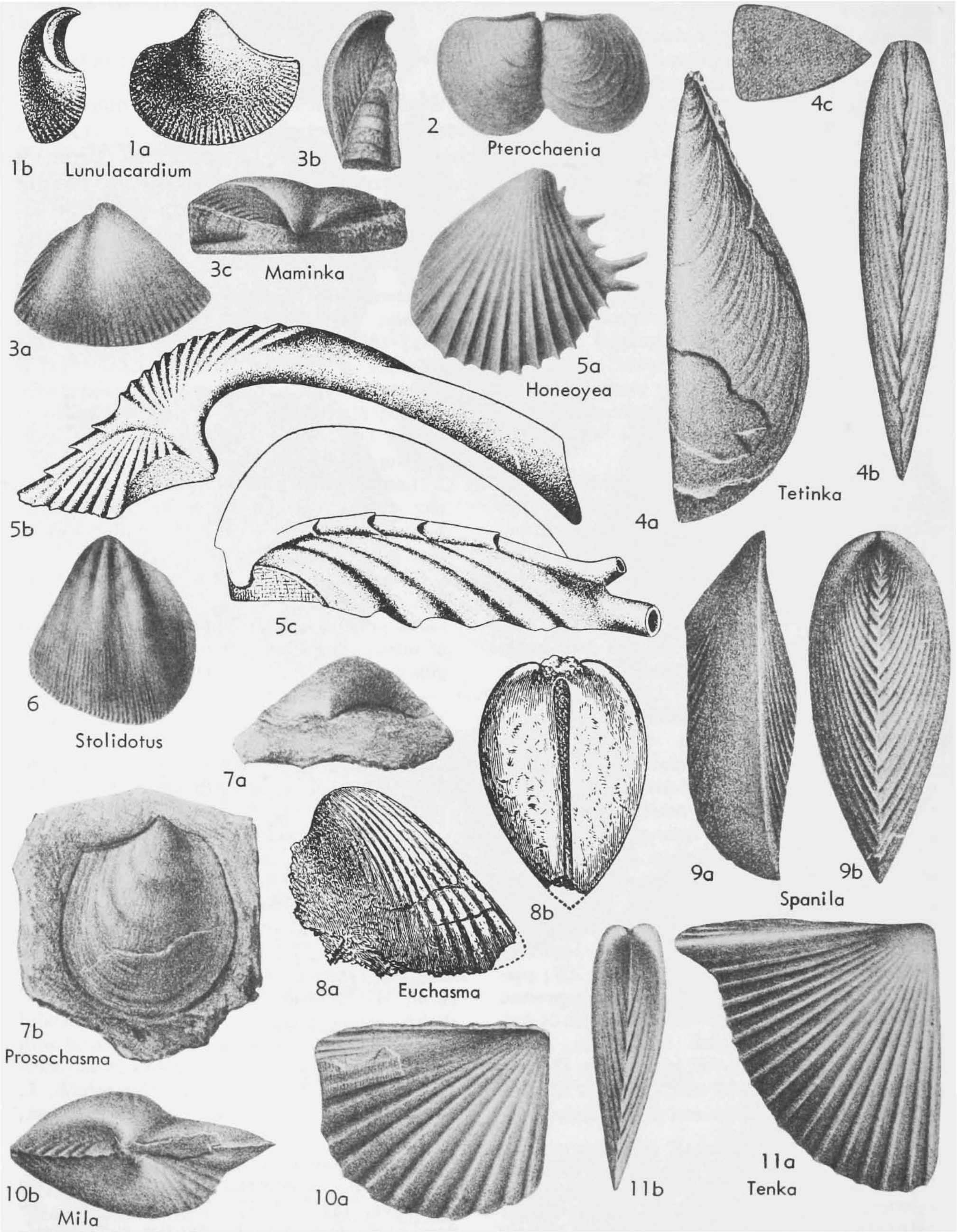


Fig. C32. Lunulacardiidae (p. *N*295-*N*297).

surface with strong radial costae; strong sulcus behind umbonal fold on LV. _Sil.(E_2)-Dev.(F_1)_, Boh.——Fig. C32,_10_. *_M. complexa,_ Sil.(E_2), Dlauha Hora; _10a,b,_ int. mold RV ext. and dorsal views, ×2 _(27)_.

Pterochaenia Clarke, 1904, p. 247 [*_Avicula fragilis_ Hall, 1843; SD Shimer & Shrock, 1944] [=?_Dvorecia_ Růžička, 1949, p. 104 (type, _Avicula contempta_ Barrande, 1881; OD); ?_Joachymia_ Růžička, 1949, p. 102 (type, _Avicula falcata_ Barrande, 1881; OD)]. Similar to _Lunulacardium_ but with internal costellae, small anterior auricle, and prosogyre beaks. _?Sil.(E_2)_, Boh., _M.Dev.-U.Dev._, USA(N.Y.), Timan.——Fig. C32,_2_. *_P. fragilis_ (Hall), U.Dev.(Genesee Sh.), USA(N.Y.); ext. both valves, ×2 _(136)_.

Spanila Barrande, 1881, p. 161 [*_S. discipulus_; SD Růžička & Prantl, 1960] [=_Venusta_ Barrande, 1881 (_non_ Boettger, 1877) (vernacular translation of _Spanila_ (obj.); ?_Patrocardia_ Fischer, 1887, p. 1041 (type, _Hemicardium dimidiatum_ Barrande, 1881, SD Růžička & Prantl, 1960); ?_Conocardiopsis_ Beushausen, 1895, p. 378 (type, _Cardium lyelli_ d'Archiac & de Verneuil, 1842; M)]. Cuneiform, equivalve, with strong anterior carina; strongly truncate anteriorly; lunular depression closed; beaks terminal, pointed, surface with radial costae. [Resembles _Euchasma_ Billings, 1865.] _Sil.,_ Boh.; _?Dev.,_ Ger.——Fig. C32,_9_. *_S. discipulus,_ Sil. (E_{1-2}), Boh.; _9a,b,_ RV lat., both valves ant., ×2 _(27)_.

Stolidotus Hede, 1915, p. 34 [*_S. siluricus_; OD]. Trigonal shells with broad anterior gape; ornamented by fine radial costellae and 3 broad radial furrows that tend to flatten out along margin. _Sil.,_ Sweden.——Fig. 32,_6_. *_S. siluricus,_ Colonus Sh.; LV ext., ×3 (Hede, 1915).

Tenka Barrande, 1881, p. 163 [*_T. bohemica_; OD] [=_Tenuis_ Barrande, 1881, p. 163 (obj.); _Leptynoconcha_ Frech, 1891, p. 249 _(nom. van. pro Tenka)_]. Similar to _Spanila,_ but without carina and with blunt spurlike posterior wing. _Ord.(D_5)-Sil.(E_2),_ Boh.——Fig. C32,_11_. *_T. bohemica,_ Sil. (E_2); _11a,_ RV int. mold; _11b,_ both valves ant.; both approx. ×2 _(27)_.

Tetinka Barrande, 1881, p. 164 [*_T. sagitta_; SD LaRocque & Newell, herein] [=_Amita_ Barrande, 1881, p. 164 (obj.); _Goniophorella_ Frech, 1891, p. 249 _(nom. van. pro Tetinka)_]. Similar to _Spanila_ but without carina; triangular in lateral outline, truncated anteriorly. _Ord.(D_5)-Sil.(E_2),_ Boh., _?Sil.,_ Ger.——Fig. C32,_4_. *_T. sagitta,_ Sil. (E_2), Boh.; _4a,_ RV ext., _4b,_ both valves ant., _4c,_ cross section both valves, cardinal margin to left; all ×2 _(27)_.

Family MONOPTERIIDAE Newell, new family

[Materials for this family prepared by N. D. Newell]

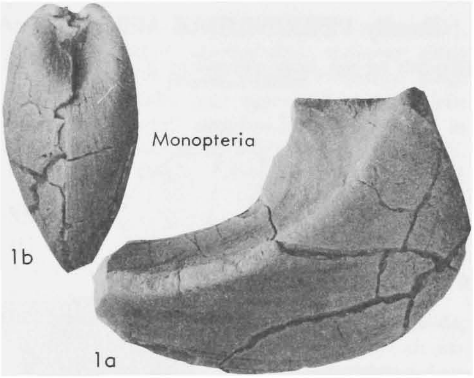


Fig. C33. Monopteriidae (p. _N_297).

Shell form pterioid, equivalve, without radial ornamentation; shell body slender, produced posteriorly in concave arc extending well behind extended rear dorsal wing; prominent umbonal carina reaching from beaks downward and backward in smooth curve, becoming horizontal posteriorly; beaks terminal, small, prosogyre; anterior end truncate, depressed in deep lunule in which are visible one or two interlocking teeth in each valve, those of LV overlying equivalent teeth of RV; ligament as in Myalinidae and Ambonychiidae. _L.Penn.-U.Penn.,_ USA(Midcontinent); _?L.Perm.,_ SW.USA.

Monopteria Meek & Worthen, 1866, p. 20 [*_Gervillia longispina_ Cox; OD]. Characters of family. _L.Penn.-U.Penn., ?L.Perm.,_ USA(Midcontinent-SW.).——Fig. C33,_1_. *_M. longispina_ (Cox), U. Penn., Jacksboro, Tex.; _1a,b,_ RV ext., both valves ant., ×2 (Newell, n).

Superfamily PTERIACEA Gray, 1847 (1820)

[_nom. transl._ Dall, 1894 (_ex_ Pteriidae Gray, 1847; =Aviculidae Goldfuss, 1820)] [Diagnosis by N. D. Newell]

Inequivalve, inequilateral, RV generally less convex than LV, markedly prosocline at least in juveniles with beaks situated well forward; ligament external, opisthodetic, variable otherwise; prismatonacreous or crossed lamellar, endostracum aragonitic, pallial line anteriorly discontinuous; characteristically byssate throughout life with byssal notch in RV at least in juvenile stages. _Ord.-Rec._

Family PTERINEIDAE Miller, 1877

[Materials for this family prepared by N. D. Newell and Aurèle LaRocque]

Inequivalve, LV more convex than RV, orbicular to strongly prosocline, pterioid, commonly with small or obsolescent an-

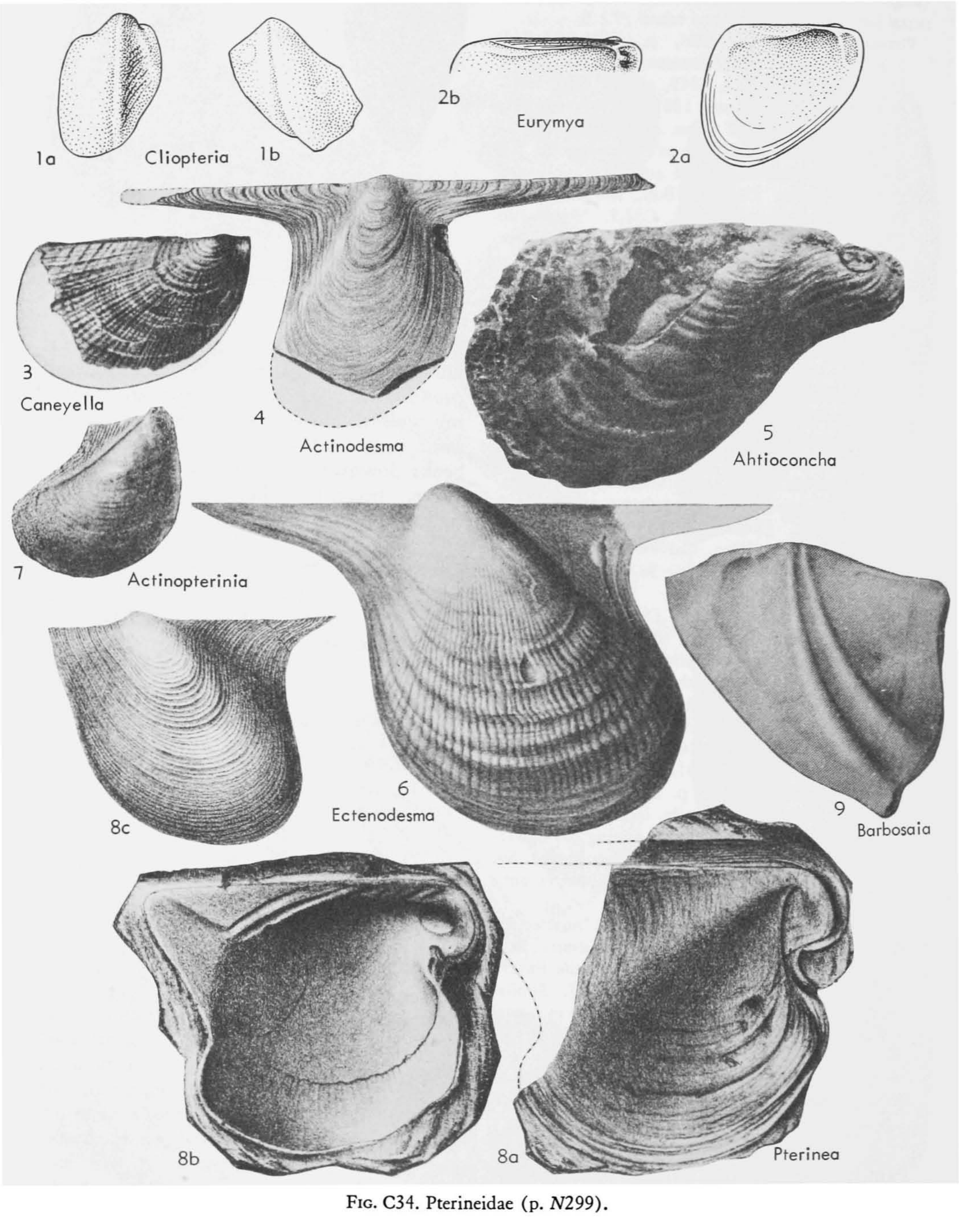


Fig. C34. Pterineidae (p. *N*299).

terior auricles; ligament duplivincular, more or less opisthodetic; heteromyarian or monomyarian, anterior muscles reinforced in several genera by septum or buttress; dentition absent to strong, actinodont or parallelodont, with variable number of small cardinals and commonly posterior laterals diverging from vicinity of beaks. *Ord.-U. Perm.*

Many genera have been based on slight variations in obliquity, form, dentition, and strength of the myophoric buttress. Others are based on supposed stratigraphic or geographic restrictions. Since most are known only from rare or poorly preserved material, it is difficult to evaluate these variations. In comparison with living Pteriidae, many may be of specific rather than generic significance.

Pterinea Goldfuss, 1826, p. 133 [**P. laevis*; SD Stoliczka, 1871] [=*Micropteria* Frech, 1891, p. 80 (type, *Pterinea ventricosa* Goldfuss, 1832; OD); *Caritodens* Foerste, 1910, p. 71 (type, *Pterinea demissa* Conrad, 1842; OD); *Beushausenia* Maillieux, 1913, p. 33 (type, *Pterinea expansa* Maurer, 1886); *Mailleuxia* Cossmann, 1920, p. 137 (*pro Beushausenia* Maillieux, 1913, *non* Cossmann, 1897)]. Upright suborbicular shells without radial ornamentation and possessing a well-developed rounded auricle and well-defined posterior wing. *U.Ord.-L.Dev.*, cosmop.——Fig. C34,*8a,b*. **P. laevis*, L.Dev., Ger.; *8a,b*, RV ext., LV int., ×1 *(323)*.——Fig. C34,*8c*. *P. demissa* (Conrad), U.Ord., USA(Ohio); LV ext., ×1 *(381)*.

Actinodesma Sandberger, 1850 [**A. malleiforme*; M]. Upright pterioid shells with pointed and more or less extended hinge extremities; anterior adductor small or lacking. *L.Dev.-U.Dev.*, Eu.-USA.

A. (Actinodesma) [=*Glyptodesma* Hall, 1883 (type, *G. erectum*; SD Miller, 1889)]. Without radial ornamentation. *L.Dev.-U.Dev.*, Eu.-USA. ——Fig. C34,*4*. **A. (A.) malleiforme*, L.Dev., Ger.; RV ext., ×1 *(323)*.

A. (Ectenodesma) Hall, 1883 [**A. (E.) birostratum*; SD S. A. Miller, 1889; OD] [=*Assellbergsia* Maillieux, 1931 (type, *Avicula obsoleta* Goldfuss, 1826; OD)]. With radial or reticulate ornamentation. *L.Dev.-U.Dev.*, Eu.-USA(N.Y.).——Fig. C34,*6*. **A. (E.) birostratum* (Hall), U.Dev., N.Y.; LV ext., ×1 *(377)*.

Actinopterinia Isberg, 1934, p. 214 [**A. semicircularis*; OD]. Prosocline, smooth, falcate shells similar to *Leptodesma* but lacking(?) anterior auricle. *M.Ord.*, Sweden.——Fig. C34,*7*. **A. semicircularis*, Leptaena Ls., Kullsberg, Sweden; RV ext., ×3 *(439)*.

Ahtioconcha Öpik, 1930, p. 17 [**A. auris*; OD]. Large, ear-shaped, asymmetrical; umbones about 0.3 hinge length behind anterior extremity; hinge line behind umbo bent sigmoidally toward left; posterior expanded, spatulate but not extended in wing; hinge unknown. *Ord.(Kukruse Stage)*, NE. Est.——Fig. C34,*5*. **A. auris*; RV ext., ×1 *(687)*.

?**Alnifia** Termier & Termier, 1950 [**A. clariondi*; M]. *M.Ord.(Llandeil.)*, Morocco.

?**Anderkenia** Khalfin, 1958, p. 163 [**A. ledaemorpha*; OD]. *Ord.*, USSR(Kazakhstan).

?**Barbosaia** Mendes, 1952, p. 70 [**B. angulata*; OD]. Subtriangular, prosocline; shell smooth except for 2 prominent oblique ridges that radiate from beak to posterior extremity. *Perm.(Corumbatai)*, S.Brazil.——Fig. C34,*9*. **B. angulata*; LV ext., ×2 (Mendes, 1952). [Newell]

Caneyella Girty, 1909, p. 32 [**C. richardsoni*; OD]. Elongate-ovoid, with quadrate anterior auricles and obtuse posterior wing; beaks terminal; surface marked by fine costae which divide in fascicles of 2 or 3 ribs becoming weak in some individuals; otherwise similar to *Ptychopteria, s.s. U.Miss.*, S.C.USA-W.USA.——Fig. C34,*3*. **C. richardsoni*, Caney Sh., Okla.; RV ext., ×2 (Girty, 1909).

?**Cliopteria** Williams, 1912, p. 391 [**C. bicostata*; OD]. Nearly equivalve, anterior auricle small, posterior wing lacking; RV with 1 or 2 radiating, rounded, cordlike costae, LV with corresponding furrows; ligament area broad; RV with 2 short anterolaterals and 2 short posterolaterals; LV with 1 strong anterolateral and 1 strong posterolateral; hinge margin with small teeth between laterals. *Sil.(Pembroke)*, USA(Me.).——Fig. C34,*1*. **C. bicostata*; *1a,b*, RV ext., LV int. mold, ×1 *(984)*.

Dolichopteron Maurer, 1886. *L.Dev.*, Ger. Not seen.

?**Eurymya** Ulrich, 1894, p. 512 [**Modiolopsis plana* Hall, 1861; OD]. Subtriangular with broad and winglike posterior and greatly narrowed anterior end; base oblique; hinge line straight; beaks small, situated near anterior extremity; hinge strong; LV with 1 cardinal tooth; RV with corresponding depression; ligamental area broad and longitudinally striated, posterior to beaks. *M.Ord. (Blackriver.-Trenton.)*, USA(Minn.-Ky.).——Fig. C34,*2*. **E. plana* (Hall), Trenton., Minn.; *2a*, LV int., ×1; *2b*, LV hinge, ×2 *(930)*.

Leptodesma Hall, 1883, p. 4 [**L. potens*; SD S. A. Miller, 1889] [=*Cobracephalus* Whidborne, 1897, p. 118 (type, *C. angulosus*; M); *Pterinopsis* Stuckenberg, 1898, p. 37 (type, *P. permocarbonicus*; M); *Cyrtodontarca* Yakovlev, 1903, p. 12 (type, *C. bakewellioides*; OD); *?Pseudobakewellia* Noinsky, 1913, p. 44 *(nom. nud.)*; *Rousseauia* Maillieux, 1920, p. 140 (type, *Avicula pseudocapuliformis* Beushausen in Maillieux, 1920; M); *Pegasella* Caster, 1930, p. 57 (type, *P. ales*; OD); *Peraptera* Dahmer, 1935, p. 651 (type, *P.*

unkelensis; OD); *Dozierella* NEWELL, 1940, p. 282 (type, *Bakewellia gouldii* BEEDE, 1902; OD); *Diodontopteria* LAROCQUE, 1950, p. 288 (type, *D. ehlersi*; OD); *Springeria* ELIAS, 1957, p. 761 (type, *S. matheri*; OD)]. Without radial ornamentation; left umbo more prominent than right; posterior wing commonly well developed; myophoric buttress weak; cardinal teeth few and variable in number. *M.Sil.-U.Perm.*, cosmop.

L. (Leptodesma). Anterior auricle angular and

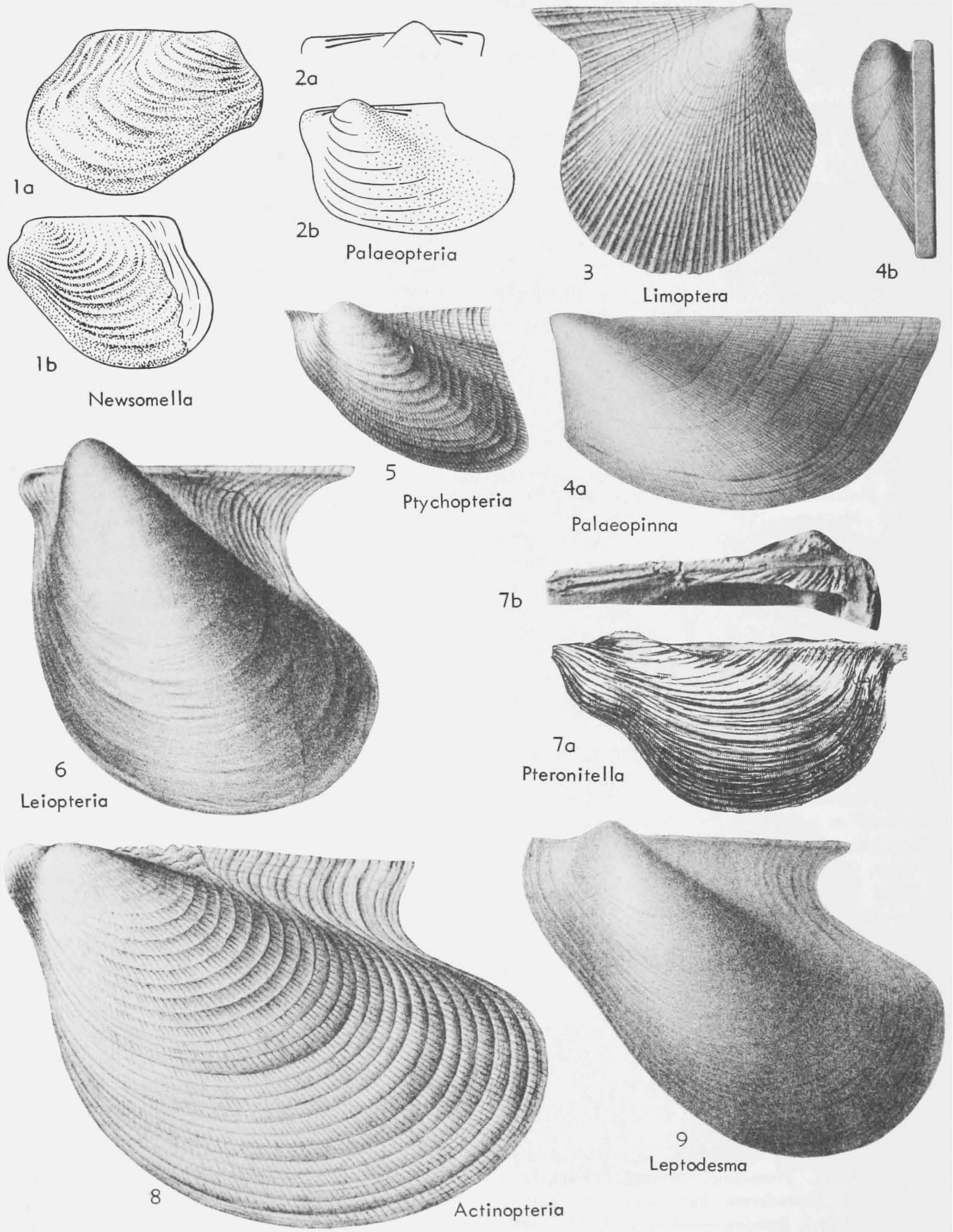


FIG. C35. Pterineidae (p. *N*300-*N*302).

nasute. *M.Sil.-Perm.*, cosmop.——Fig. C35,*9*. **L. (L.) potens*, U.Dev., USA(N.Y.); LV ext., ×1 *(377)*.

L. (Leiopteria) Hall, 1883, p. 4 [**L. dekayi*; SD S. A. Miller, 1889]. Anterior auricle lobate. *M.Sil.-L.Perm.*, cosmop.——Fig. C35,*6*. **L. (L.) dekayi* (Hall), M.Dev., USA(N.Y.); LV ext., ×1 *(377)*.

Limoptera Hall & Whitfield, 1869, p. 15 (see Cooper, 1931) [**Lima macroptera* Conrad, 1838; OD] [=*Myalinodonta* Oehlert, 1881, p. 29 (type, *Avicula normanniana* d'Orbigny, 1847; M); ?*Paropsis* Oehlert, 1888 (type, *P. orbicularis*; M); ?*Klinoptera* Dienst, 1935, p. 388 (type, *K. rhenana*; M)]. Orbicular, with weak to strong radial costae, elongate posterior wing and very small or obsolete anterior auricle; anterior adductor small or lacking in adults. *U.Sil.-M.Dev.*, W.Eu.-USA.——Fig. C35,*3*. **L. macroptera* (Conrad), M.Dev.(Hamilton), USA(N.Y.); RV ext., ×1 *(377)*.

Merismopteria Etheridge, 1892, p. 271 [**Pterinea macroptera* Morris, 1845; OD]. Externally like *Leptodesma (Leiopteria)* without radial ribs; with very thin, high myophoric septum in each valve separating large, elongate, anterior adductor from relatively large pedal retractor muscles, situated behind septum; anterior part of pallial line discontinuous. *Perm.*, Australia-?India.——Fig. C36, *1*. **M. macroptera* (Morris), New S.Wales; *1a,b*, RV and dorsal views of shell; *1c,d*, RV and dorsal views of int. mold; *1e*, LV int. showing ligament area; all latex casts, ×1 (Newell, n).

Newsomella Foerste, 1909, p. 67 [**Rhombopteria (N.) ulrichi;* SD Newell & LaRocque, herein]. Similar externally to *Leiopteria*; ornamented with concentric rugae and on RV with 2 sets of radial costellae crossing each other at angle of about 30 degrees, most conspicuous along umbonal ridge. *M.Sil.(Waldron)*, USA(Tenn.).——Fig. C35,*1*. **N. ulrichi* (Foerste); *1a,b*, RV ext., LV ext., ×1 *(315)*.

?**Palaeopinna** Hall, 1883, p. 4 [**P. flabellum*; SD S. A. Miller, 1889]. Elongate, with small, terminal beaks; truncate anterior margin and broad, posterior region extended in acute, compressed wing; surface ornamented with radial costellae; hinge and RV unknown. *L.Dev.-M.Dev.*, N.Am. ——Fig. C35,*4*. **P. flabellum*, M.Dev.(Oriskany), USA(N.Y.); *4a,b*, LV ext., RV ant., ×0.7 *(377)*.

?**Palaeopteria** Whiteaves, 1897, p. 181 [**P. parvula*; M]. Beaks anterior, surface unknown; hinge with thin laminar teeth on each side of beak, nearly parallel to cardinal margin, 2 anterior and 2 posterior in RV; 2 anterior and 3 posterior in LV; muscle scars unknown. *U.Ord.*, Can.(Man.). ——Fig. C35,*2*. **P. parvula*; *2a*, RV hinge, ×6; *2b*, LV int. mold, ×2 (Whiteaves, 1897).

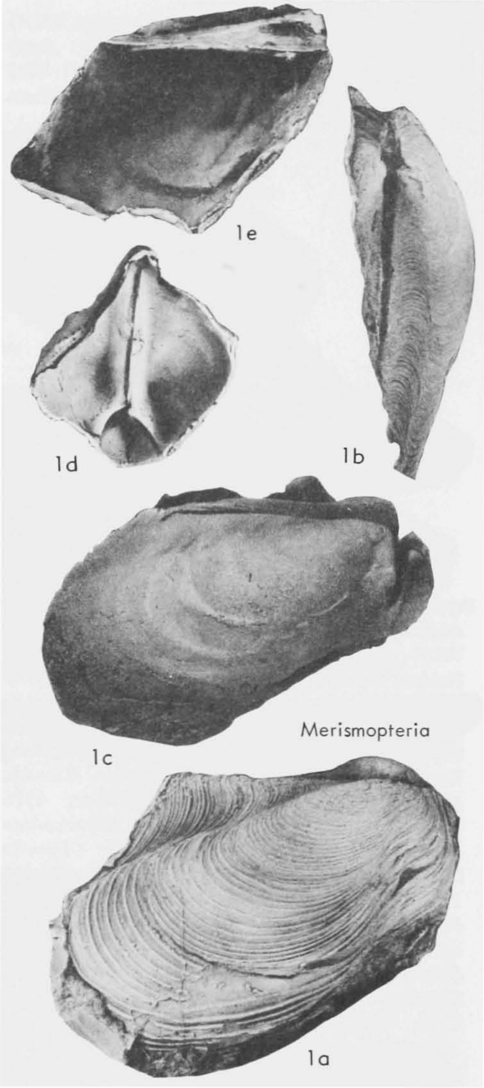


Fig. C36. Pterineidae (p. *N*301).

Pteronitella Billings, 1874, p. 302 [**Avicula retroflexa* Hisinger, 1826 (=*Mytilites retroflexus* Wahlenberg, 1821); M]. Similar externally to *Leptodesma s. s.*, but with arcuate ventral margin and with numerous actinodont teeth. *U.Sil.*, Sweden (Gotl.)-Wales-Can.(N.S.).——Fig. 35,*7*. **P. retroflexa* (Wahlenberg), Ludlov.; *7a*, LV ext. (Wales), ×1; *7b*, LV hinge (Gotl.), ×1 (Walmsley, 1962).

?**Pteronitina** Khalfin, 1958 [**P. aenigmatica*; OD]. *Sil.*, Caradoc., USSR(Kazakhstan).

Fig. C37. Kochiidae (p. N302).

Ptychopteria Hall, 1883, p. 3 [**P. eugenia* (=*P. salamanca* Hall, 1884) (obj.); SD S. A. Miller, 1889] [=*Actinopterella* Williams, 1908 (type, *Pterinea radialis* Clarke, 1907; OD); *Cornellites* Williams, 1908 (type, *Pterinea fasciculata* Goldfuss, 1832; OD); *Tolmaia* Williams, 1908 (type, *Pterinea lineata* Goldfuss, 1863); *Folmannella* Williams, 1908 (type, *Pterinea mainensis* Clarke, 1907; OD); *?Diaphragmella* Etheridge, 1916 (type, *D. merismopteroides*; OD); *Dipterophora* Fuchs, 1920 (type, *D. triculta*; OD); *Oleanella* Caster, 1930 (type, *Ptychopteria expansa* Hall, 1884; OD); *Crassialaria* Dahmer, 1932 (type, *Pterinea quirini* Dahmer, 1931; OD); *Beushausenella* Dahmer, 1935 (type, *B. maillieuxi*; OD) (*pro Pterinea expansa* Frech, 1891); *Augustaia* Růžička, 1949 (type, *Avicula expulsa* Barrande, 1881; OD); *Kodymia* Růžička, 1949 (type, *Avicula dispersa* Barrande, 1881; OD); *Prantliella* Růžička, 1949 (type, *Avicula pallista* Barrande, 1881; OD)]. Strongly prosocline with anterior auricle and posterior wing well developed; LV convex, RV less convex, to flattened or concave; dentition highly variable, actinodont to parallelodont or obsolescent; anterior adductor scar on auricle, small and commonly deep, with or without buttress; radial costae well developed on LV, obsolescent to strong on body of RV. *Sil.-L.Perm.*, cosmop.

P. (Ptychopteria). Anterior auricle obliquely truncated. *U.Dev.*, USA.——Fig. C35,*5*. **P. (P.) eugenia* (Hall), Chemung, N.Y.; LV ext., ×1 *(377)*.

P. (Actinopteria) Hall, 1884, p. xii [**Avicula decussata* Hall, 1843; SD Bassler, 1915] [=*Actinoptera* Hall, 1883 (*non* Rondani, 1861)]. Anterior auricle lobose. *Sil.-Dev.*, cosmop.; *L.Penn.*, USA(Ill.); *L.Perm.*, Australia (New S.Wales).——Fig. C35,*8*. **P. (A.) decussata* (Hall), M.Dev.(Hamilton), USA(N.Y.); LV ext., ×1 *(377)*.

?Family KOCHIIDAE Maillieux, 1931

[*nom. transl.* Newell, herein (*ex* Kochiinae Maillieux, 1931)] [Materials for this family prepared by N. D. Newell]

Shell capuliform, very inequivalve, LV highly convex and narrow, wings small and poorly delimited; RV flat or concave, operculate; dentition obscure or ?lacking; with or without radial ornamentation. *Dev.*, Eu.

Kochia Frech, 1891 [*pro Roemeria* Koch, 1881 (*non* Milne-Edwards & Haime, 1851)] [**Avicula capuliformis* Koch, 1881; OD] [=*Onychia* Sandberger, 1889 (obj.), de Blainville, 1823; *Loxopteria* Frech, 1891 (type, *Avicula dispar* Sandberger, 1889; SD Newell, herein)]. Characters of family. *L.Dev.-U.Dev.*, W.Eu.——Fig. C37,*1*. **K. capuliformis* (Koch), L.Dev.(Siegener Grauwacke), Ger.(Rheinl.); ant., ×1 *(323)*.

Family PTERIIDAE Gray, 1847 (1820)

[*nom. correct.* Meek, 1864 (*pro* Pteriadae Gray, 1847); =Aviculidae Goldfuss, 1820 (*nom. correct.* Gray, 1840, *pro* Aviculae Goldfuss, 1820); name Pteriidae retained in accordance with provisions of Article 40a, of Zool. Code (1961)] [*non* Pteridae Broderip, 1839 (Penny Cyclopedia, v. 14, p. 321), employed for gastropods known as "wing-shells" *(ailées)* such as *Rostellaria, Pterocera, Strombus*] [Materials for this family prepared by L. G. Hertlein & L. R. Cox]

Obliquely ovate to suborbicular, usually with triangular winglike projection bordering each end of straight hinge line; subequivalve to strongly inequivalve, LV usually more inflated; inequilateral, umbones placed well toward anterior end; anterior wing (or auricle) smaller, byssal notch present beneath it in RV; both valves with obtusely triangular cardinal area bearing shallow triangular ligament pit directed posteriorly from beak; dentition variable, teeth (when present) usually short and transverse near beak, elongated posteriorly in longitudinal direction; dimyarian in juvenile stages, monomyarian or with anterior adductor much reduced in adult; posterior adductor impression large; pallial line commonly discontinuous; interior pearly; sculpture variable, relatively smooth forms predominating. *Trias.-Rec.*

Pteria Scopoli, 1777, p. 397 [**Mytilus hirundo* Linné, 1758, p. 706] [=*Avicula* Bruguière, 1792 *(nom. et fig.)*; *Avicula* Cuvier, 1798 (type, *M. hirundo*; SD Kennard, Salisbury & Wood-

Ward, 1931, p. 14); *Glaucus* Poli, 1795; *Glaucoderma* Poli, 1795 (*non* Foster, 1777, *nec* Gmelin, 1791); *Hirundigenus* Renier, 1807 (suppressed ICZN); *Anonica* Oken, 1815 (obj.) (ICZN rejected work); *Austropteria* Iredale, 1931 (type, *A. saltata*; OD); *Magnavicula* Iredale, 1939 (type, *M. bennetti*; OD)]. Obliquely ovate, moderately inflated, slightly inequivalve; elongate

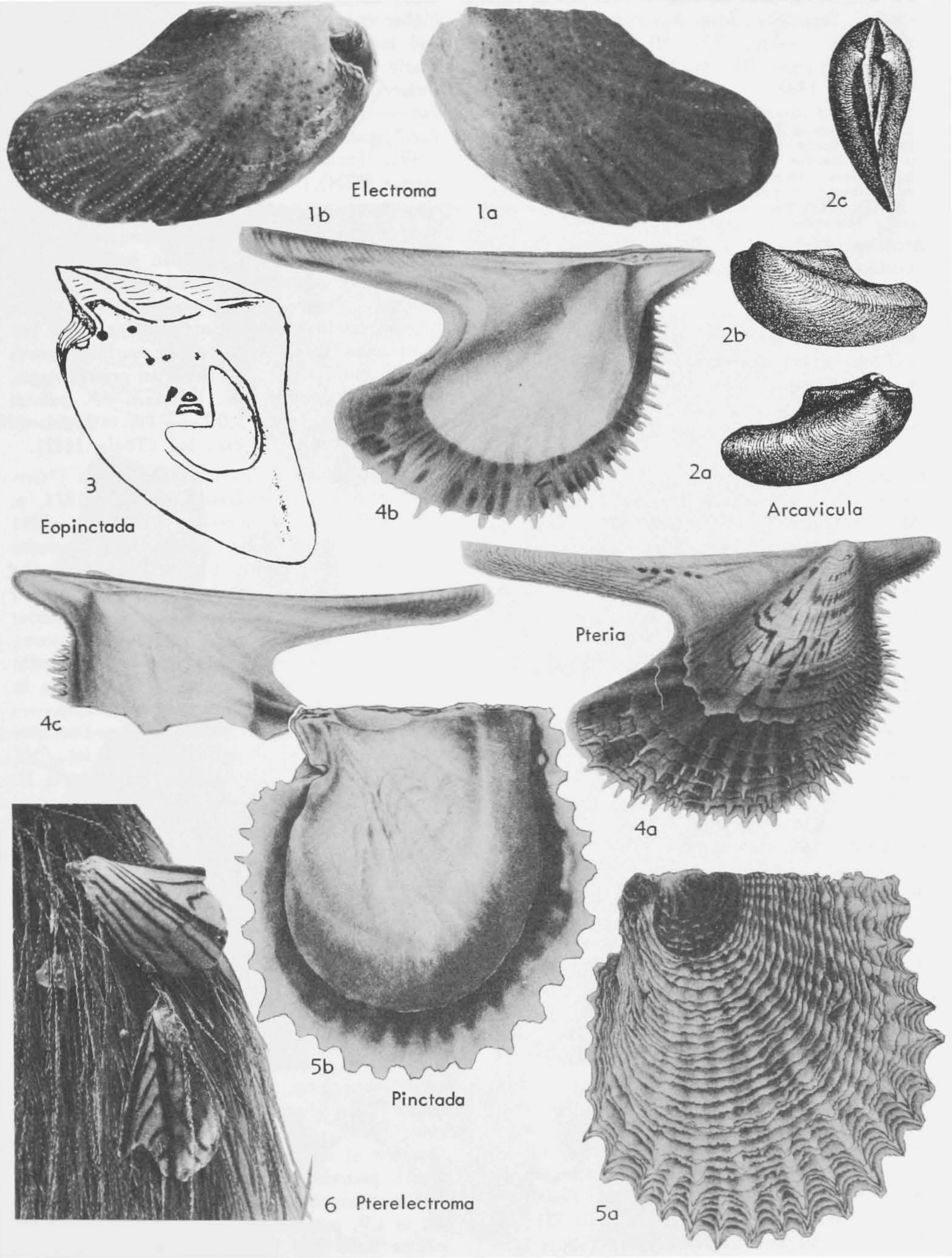


Fig. C38. Pteriidae (p. *N*302-*N*304).

posterior wing commonly present; hinge with 1 or 2 toothlike processes below umbo and longitudinal posterior lamina, absent in some forms; exterior commonly smooth except for growth lines, but with radial rows of lamellar processes in some species. *Trias.-Rec.*, fossil forms cosmop., *Rec.* in warm seas.——Fig. C38,*4*. **P. hirundo* (Linné), Rec., Medit.; *4a-c,* RV ext., LV int., RV int., ×0.7 (Deshayes, 1848).

[*Glaucus* and *Glaucoderma*, both of Poli, 1795, are objective synonyms of *Pteria* in consequence of type designations by Winckworth (1930, *Proc. Malac. Soc. Lond.*, vol. 19, p. 116). *Mytilus hirundo* was stated by Poli on p. 222 of his *Testacea utriusque Siciliae*, vol. 2, to belong to *Glaucus*, although it was not one of the two species (both Limidae) listed under the genus on p. 254. Winckworth's action thus seems permissible.]

Arcavicula Cox, 1964, p. 47 [*pro Arcuatula* Gugenberger, 1934, p. 45 (*non* Lamy, 1919)] [**Avicula arcuata* von Münster, 1836, p. 128; OD]. Small, only slightly inequivalve, with arcuate body, acute to bluntly rounded, undemarcated anterior auricles and obtuse posterior wings; dentition unknown; surface smooth or with radial threads. *M.Trias.-U.Trias.*, Eu.——Fig. C38,*2*. **A. arcuata* (von Münster), U.Trias., S.Alps; *2a,b,* RV, LV, ×3; *2c,* dorsal view, ×3 *(58)*.

Electroma Stoliczka, 1871, p. 391 [**Avicula smaragdina* Reeve, 1857, explan. pl. 12, fig. 45; M] [=*Electrina* von Martens, 1872 (*non* Baird, 1850)]. Elongate, oblique, thin-shelled, more inequivalve than *Pteria*; hinge line short. *U.Cret.-Rec.*, Eu.-SW.Pac.

E. (Electroma). Posterior wing almost lacking. *U.Cret.*, N.Z.; *Rec.*, W.Pac.——Fig. C38,*1*. *E. (E.) smaragdina* (Reeve), Rec., Moluccas; *1a,b,* LV ext., RV ext., ×1 (Cox, n).

E. (Pterelectroma) Iredale, 1939, p. 332 [**Avicula zebra* Reeve, 1857, explan. pl. 11, fig. 36; OD]. Smaller than *E. (Electroma)* with definite posterior wing. *Rec.*, Australia.——Fig. C38,*6*. **E. (P.) zebra* (Reeve); 2 syntypes on algal growth, ×1.3 (Cox, n).

Eopinctada Tamura, 1961, p. 147 [**Pinctada (Eopinctada) matsumotoi*; OD]. Like *Pinctada* but oblique, subtrigonal rather than quadrate, with anteroventral and posterior margins converging to meet at subangular posteroventral extremity; cardinal area broad. *Cret.(Cenoman. or Turon.)*, Japan.——Fig. C38,*3*. **E. matsumotoi*; RV int., ×0.5 (Tamura, 1961).

Pinctada Röding, 1798, p. 166 [**Mytilus margaritiferus* Linné, 1758, p. 704; SD Iredale, 1915, p. 305] [=*Unionium* Link, 1807 (type, *Mytilus margaritiferus* Linné; SD Cox herein); *Margaritiphora* Megerle von Mühlfeld, 1811 (obj.); *Margarita* Leach, 1814 (type, *M. sinensis* Leach, =*Mytilus margaritiferus* Linné); *Margartifera* Schumacher, 1816 (*nom. null.*); *Perlamater* Schumacher, 1817 (type, *P. vulgaris*; SD Cox herein); *Meleagrina* Lamarck, 1819 (obj.); *Margartifera* Schumacher, 1823 *(nom. null.)*; *Pinctadina* de Blainville, 1826 (obj.); *Pentadina, Pintadina* Gray in Griffith's Cuvier, 1834 (obj.); *Margaritifera* Adams & Adams, 1857 (obj.)]. Less oblique and usually thicker-shelled than *Pteria,* subquadrate, commonly slightly higher than long, nearly equivalve; posterior wing and indentation of posterior margin lacking or nearly so; ligamental pit broad; no hinge teeth; surface lamellose. *Mio.-Rec.*, pantrop., espec. Indo-Pac.——Fig. C38,*5*. **P. margaritifera* (Linné), Rec., Japan; *5a,b,* LV ext., RV int., ×0.4 (Cahn, 1949). [=*Margaritifera* Browne, 1789 (suppressed ICZN).]

Pterinella Toula, 1882, p. 31 [**P. petersi*; M]. Very similar to *Pteroperna* but subequivalve, with LV less convex and taller than in that genus; hinge margin much thickened, bearing narrow, elongate, oblique crenulations along its entire length; external grooves of posterior wing less conspicuous than in *Pteroperna*; surface smooth or with radial ribs on LV in earlier growth stages. *L.Cret.*, Balkans.——Fig. C39,*6a,b*. **P. petersi*; *6a,b,* LV ext., int., ×0.7.——Fig. C39,*6c*. *P. crassitesta* Toula; LV ext., ×1 (Toula, 1882).

Pteroperna Morris & Lycett, 1853, p. 16 [**Gervillia costatula* Eudes-Deslongchamps, 1824, p. 131; OD] [=*Pterinoperna* Whitfield, 1891 *(nom. van.)*]. Oblique, bialate, with posterior wing sharply pointed; inequivalve, LV umbo more or less protruding; hinge margin thickened and transversely crenulated anteriorly; posterior wing with up to 4 external longitudinal grooves, lowest of which correspond to internal teeth; radial ribs present on earlier growth stages in some species. *U.Trias.*, Malaya; *Jur.*, cosmop.——Fig. C39,*4a*. **P. costatula* (Eudes-Deslongchamps), M.Jur.(Bathon.), Eng.; RV int., ×1 (Cox, n).——Fig. C39,*4b*. *P. plana* Lycett, M.Jur.(Bajoc.), Eng.; RV ext., ×1 (Cox, n).

Rhaetavicula Cox, 1962, p. 594 [**Avicula contorta* Portlock, 1843, p. 126; OD]. Small, narrow, lunate, strongly prosocline, highly inequivalve, valves probably discordant; LV strongly convex, upcurved posteriorly with twisted appearance, its margins not in one plane; LV umbo narrowly rounded, protruding, anteriorly placed; RV almost flat, probably smaller than LV; posterior wings narrow, elongate, acutely pointed, that of LV flattened and well demarcated from body; left anterior wing small, right anterior auricle small, higher than long, not separated by notch from body of valve; ligament area narrow; body of LV with narrow, unevenly spaced, rounded radial ribs, few of their intervals with secondary radial thread; posterior wing of LV smooth; RV smooth or almost so; elongate posterior lateral tooth present in LV, presence of anterior tooth inconstant; muscle scars and pallial line not observed. *U. Trias. (Rhaet.),* Eu.-Asia-N. Am. (Nev.).——Fig.

C39,2. **R. contorta* (Portlock), Eng.; *2a,* LV ext.; *2b,* RV ext., ×1.5 (Cox, n).

?**Rhynchopterus** Gabb, 1864, p. 31 [**R. obesus*; M]. Trapeziform, oblique, LV with relatively large pointed anterior wing but not alate posteriorly; LV umbo protruding slightly, near middle of hinge margin; RV and hinge structure unknown. *Trias.*, USA(Calif.)-Bear Is.——Fig. C39, *3.* **R. obesus,* M.Trias., USA(Calif.); LV ext., ×1 *(333).*

Somapteria Tamura, 1960, p. 224 [**S. koikensis*; OD]. Rather small, rhomboidal, oblique, longer

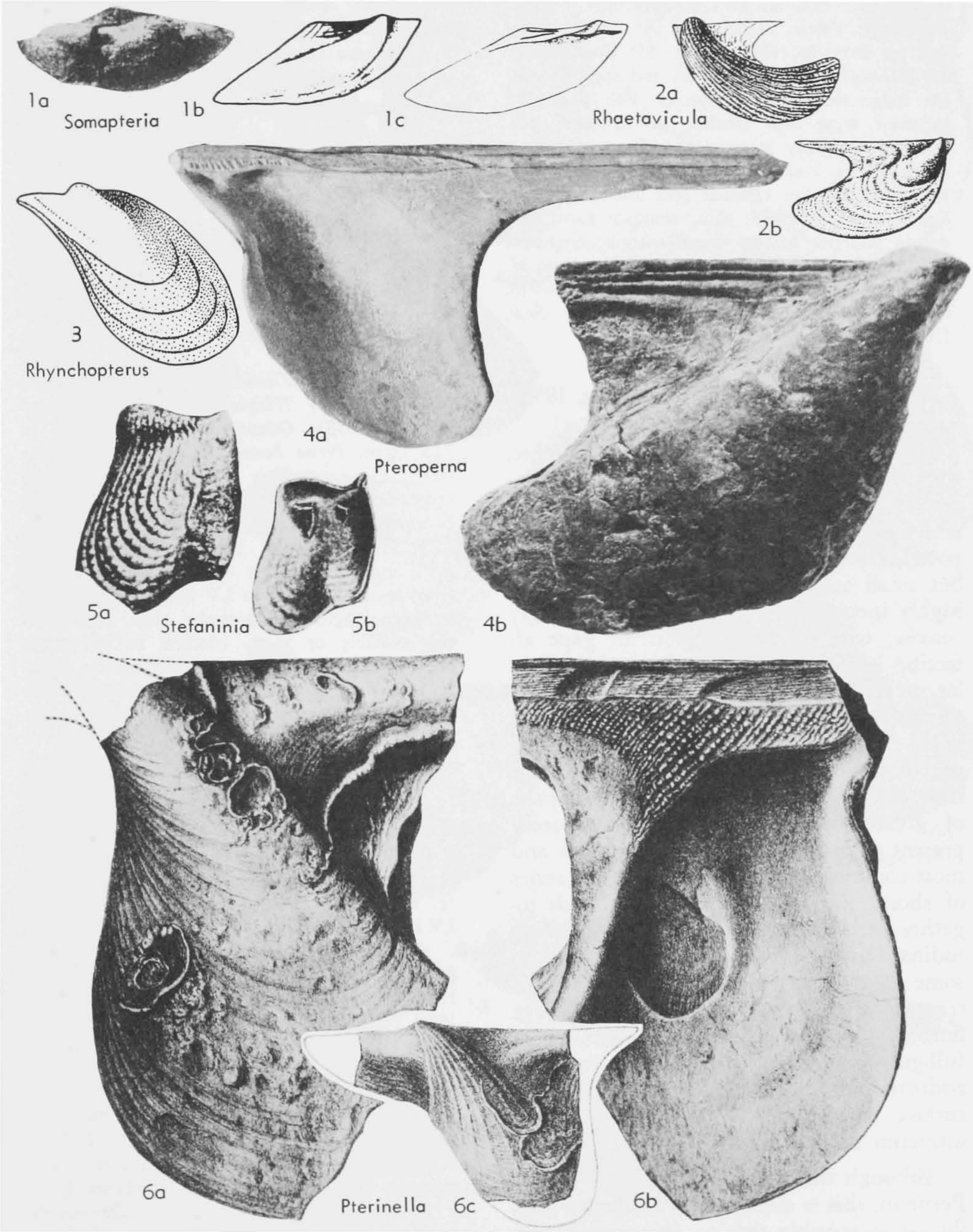


Fig. C39. Pteriidae (p. *N*304-*N*306).

than high, almost equivalve; both valves with obtuse posterior wing and moderately large, pointed anterior wing, not distinctly differentiated from body of shell; umbones protruding only slightly; several short transverse anterior teeth and 2 thin, longitudinal posterior teeth in each valve. *U.Jur.,* Japan.——FIG. C39,*1*. **S. koikensis*; *1a-c,* LV ext., RV ext., LV int., ×1 (Tamura, 1960).

?**Stefaninia** VENZO, 1934, p. 165 [**Gervilleia? ogilviae* BITTNER, 1895, p. 88; SD Cox herein]. Mytiliform, with terminal beak and slightly arcuate hinge margin; type species with ill-defined posterior wing and lobelike anteroventral protuberance; slightly inequivalve, RV more convex (unusual in Pteriidae); anterior margins with slight byssal gape; cardinal area and position of ligament not observed; thin, elongate tooth bordering posterior half of dorsal margin; ornament of concentric ribs notched by radial grooves. *M. Trias.(Ladin.),* Eu.(S.Tyrol-Rhodes).——FIG. C39,*5*. **S. ogilviae* (BITTNER), Rhodes; *5a,b,* LV ext., RV int., ×1 (Venzo, 1934).

Family BAKEVELLIIDAE King, 1850

[Materials for this family prepared by L. R. Cox]

Highly inequilateral, subovate, rhombic, rhomboidal, trapeziform or ensiform Pteriacea, usually with multiple ligamental pits and with hinge teeth; more or less oblique, posteriorly alate or subalate, with or without small anterior auricle; subequivalve to highly inequivalve, with LV more strongly convex; with or without anterior gape affecting both valves, and lacking subauricular notch in RV; ligamental areas flat, external; ligamental pits multiple except in adult *Phelopteria,* extending to lower margin of ligamental area, and usually rather irregularly distributed, with some intervals of greater width than pits; hinge teeth present at least in early growth stages and most commonly consisting of anterior series of short, more or less transverse teeth together with small number of elongate longitudinal teeth on posterior wing, but in some forms numerous, weak, more or less transverse, and extending along entire hinge line, in others tending to obsolescence in full-grown shell; anisomyarian with anterior adductor much reduced, or monomyarian; surface smooth or radially ribbed; inner ostracum nacreous. *Perm.-Eoc.*

Although the type genus appeared in the Permian, this is essentially a Mesozoic family. It is possible that to some extent the various genera here included in it arose independently from the Pteriidae by multiplication of the ligamental pits. *Aviculoperna,* represented by several lower Eocene species, was formerly regarded as a subgenus of *Pteria,* but has the essential features of the Bakevelliidae. A lower Eocene species which has been included in *Gervillia* (*G. eocenica* DESHAYES) is, however, rare and imperfectly known and its ligamental area has not been observed.

Bakevellia KING, 1848, p. 10 [**Avicula antiqua* VON MÜNSTER in GOLDFUSS, 1836, p. 126 (*non* DEFRANCE, 1816) (=**Avicula binneyi* BROWN, 1841, p. 65); OD] [=*Bakewellia* GRUENEWALDT, 1851 (*nom. van.*)]. Small to medium-sized, trapeziform or rhomboidal, not greatly elongated; anterior auricle small to moderately large, posterior wing obtuse or with acutely pointed tip; never strongly inequivalve, anterior gape narrow. *Perm.-Cret.,* cosmop.

B. (Bakevellia) [=*Goniodus* DUNKER, 1848 (*non* AGASSIZ, 1838); *?Plagia* PHILIPPI, 1899 (*non* MEIGEN, 1838); *Odontoperna* FRECH, 1891, p. 215 (type, *Perna bouei* HAUER, 1857, p. 562; OD); *Pseudogervilleia* GILLET, 1922, p. 106 (type, *Gervilleia episcopalis* GILLET; M); *Maizuria* NAKAZAWA, 1959 (type, *B. (M.) kambei*; OD, *L.Trias.,* Kyoto Pref., Japan)]. Typically with small number of short obliquely transverse anterior teeth (1 fewer in LV than in RV) and 1 or more longitudinal posterior teeth, but dentition variable or partly obsolete in full-grown shell in some species; some earlier species anisomyarian, later ones mostly monomyarian; smooth or with weak radial riblets. [*Odontoperna* was thought to be characterized by the absence of longitudinal posterior teeth, but these have now been observed in some specimens of the type species.] *Perm.-Cret.,* cosmop.——FIG. C40,*1a-d*. **B. (B.) binneyi* (BROWN), U.Perm., Eng.; *1a-d,* LV ext., RV ext., LV int. showing adductor scars, dorsal view, all ×1 (King, 1850).——FIG. C40, *1e*. *B. costata* (VON SCHLOTHEIM), M.Trias., Ger.; LV int., ×2 (Credner, 1851).

B. (Bakevelloides) TOKUYAMA, 1959, p. 148 [**Gervillia hekiensis* KOBAYASHI & ICHIKAWA, 1952, p. 76; OD] [=*Neobakevellia* NAKAZAWA, 1959 (type, *Gervillia costata* VON SCHLOTHEIM, 1820; OD, *L.Trias.-M.Trias.,* W.Eu.)]. Like *B. (Bakevellia)* but with several transverse anterior teeth; posterior teeth about 2; monomyarian. *Trias.-Jur.,* Eu.-Asia.——FIG. C40,*3*. **B. (B.) hekiensis* (KOBAYASHI & ICHIKAWA), U.Trias. (Carn.), Japan; RV int., ×1 (Tokuyama, 1959).

Aguilerella CHAVAN, 1951, p. 211 [**Perna kobyi* DE LORIOL, 1901, p. 99; OD] [=*Dentoperna* OKUNEVA, 1960, p. 57 (type, *Perna khudyaevi*

Krimholtz, 1938, p. 272; OD)]. Medium-sized, rhomboidal, mytiliform, height well exceeding length; subequivalve, rather weakly inflated, without protruding umbones; beaks subterminal; anterior teeth 1 or more, short, oblique; posterior teeth narrow, 1 in LV, 1 or 2 in RV; surface

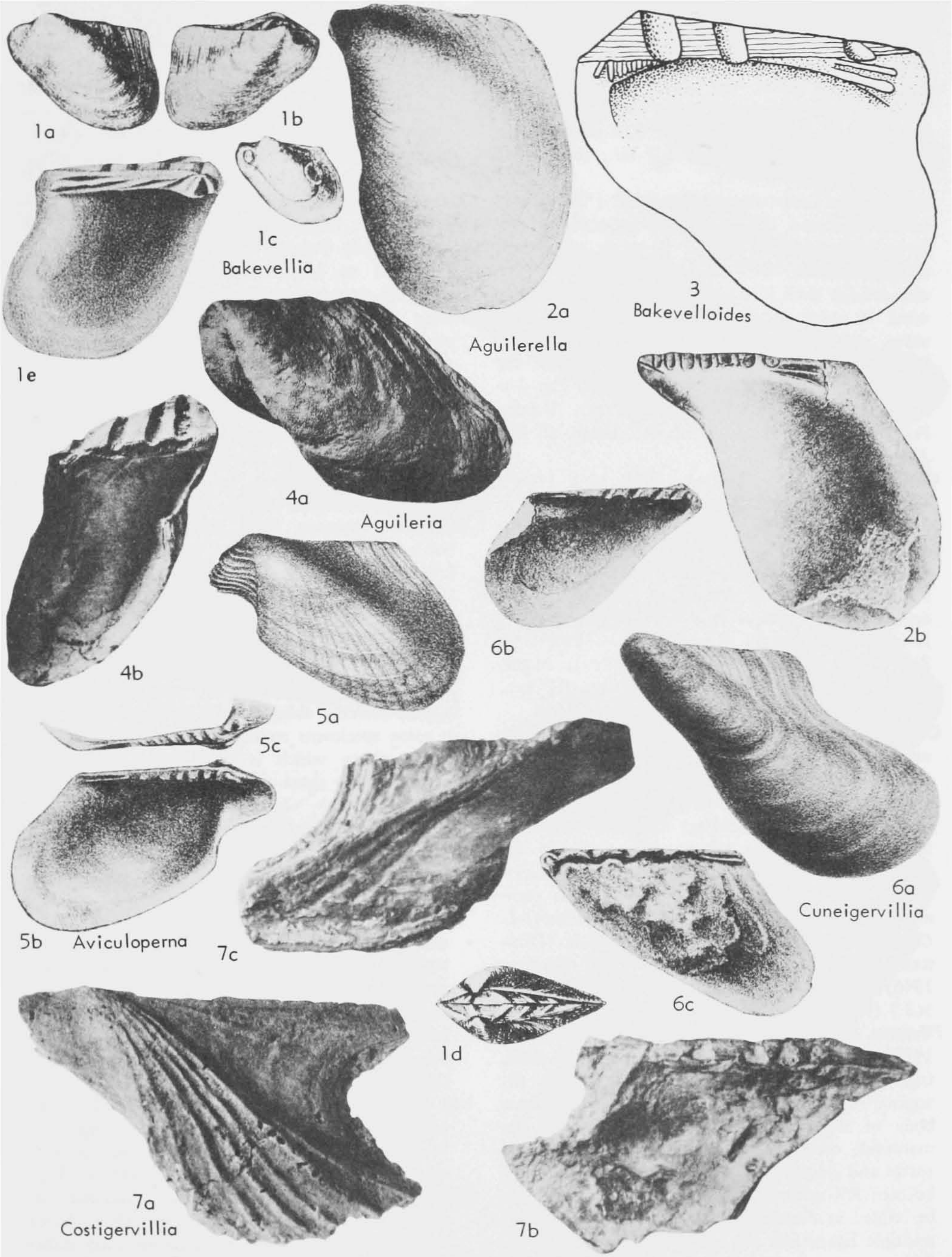


Fig. C40. Bakevelliidae (p. *N*306-*N*308).

smooth. *Jur.(Toarc.-Oxford.),* Eu.-Asia-N. Afr. ——Fig. C40,*2*. **A. kobyi* (de Loriol), Oxford., Switz.; *2a,b,* LV ext., RV int., both ×0.7 (de Loriol, 1901).

Aguileria White, 1887, p. 35 [**A. cumminsi*; OD]. Medium-sized, like *Bakevellia* in shape, subequivalve; hinge teeth not differentiated into anterior and posterior series, but consisting of numerous irregular transverse crenulations. *Cret.,* N.Am.——Fig. C40,*4*. **A. cumminsi,* U.Cret.(Cenoman.), USA(Tex.); *4a,b,* LV ext., LV int., both ×0.7 *(890).*

Aviculoperna Cossmann, 1887, p. 168 [**Perna aviculina* Deshayes, 1864, p. 56; OD]. Small, trapeziform, oblique, with obtuse posterior wing and distally rounded, well-differentiated anterior auricle; anterior teeth 1 in LV, 2 in RV, short, oblique, weak in some forms; posterior teeth 1 in each valve, rather short; LV or both with radial riblets. [Chavan has included a species from the Jurassic of France in this genus.] *Eoc.,* Eu.——Fig. C40,*5*. **A. aviculina* (Deshayes), U.Eoc., France; *5a-c,* LV ext., LV int., RV hinge, all ×2 (Deshayes, 1864).

Costigervillia Cox & Arkell, 1948, p. 9 [**Gervillia crassicosta* Morris & Lycett, 1853, p. 23; OD]. Medium-sized, oblique, bialate, with comparatively long, acute anterior wing; LV of moderate to strong convexity, with strong radial costae; RV flat or almost so, smooth or with weak radial ornament; dentition as in *Bakevellia (Bakevellia). Jur.(Bathon.-Oxford.),* Eng.-France.——Fig. G40, *7*. **C. crassicosta* (Morris & Lycett), M.Jur. (Bathon.), Eng.; *7a-c,* LV ext., LV int., RV ext., all ×1 (Cox, n).

Cuneigervillia Cox, 1954, p. 48 [**Gervillia hagenowii* Dunker, 1846, p. 37; OD]. Rhomboidal or trapeziform, subequivalve, rather feebly inflated, with terminal or subterminal beaks and oblique, cuneiform body not always distinctly separated from obtuse posterior wing; anterior auricle absent or small; earlier growth stages with anterior and posterior teeth as in *Bakevellia,* teeth commonly obsolete in later stages. *L.Jur.(L.Lias.)-L. Cret.,* Eu.——Fig. C40,*6*. **C. hagenowii* (Dunker), L.Lias., Ger.; *6a,* LV ext. ×1 (Dunker, 1846); *6b,c,* young shells, LV int., RV int., both ×2.7 (Philippi, 1897).

?**Euptera** Dartevelle in Dartevelle & Freneix, 1957, p. 65 [**E. zambiensis*; OD]. Medium-sized, trigonal; LV strongly convex, with acutely triangular wings, anterior part well demarcated from body of shell by sinus, posterior less well demarcated; ornament of numerous unequal radial costae and concentric lamellae; hinge structure unknown; RV unknown. [This genus is thought to be related to *Pseudoptera.* It is uncertain whether multiple ligamental pits are present.] *U.Cret.,* W. Afr.

Gervillaria Cox, 1951, p. 49 [**Modiola? alaeformis* J. Sowerby, 1819, p. 93; OD]. Medium-sized to large, highly inequivalve, oblique, bialate; narrow byssal gape present; body of LV strongly inflated, with its umbo rising rather prominently above hinge margin and beak strongly prosogyrous; RV feebly convex, flat or concave; hinge in adult shell with numerous unequal, transverse, somewhat oblique crenulations. *Jur.-Cret.,* Eu.——Fig. C41,*5*. **G. alaeformis* (J. Sowerby), L.Cret., Eng.; *5a,* LV ext., ×0.5; *5b,* RV ext., ×0.5; *5c,* LV int., ×0.7 (Woods, 1905).

Gervillella Waagen, 1907, p. 98 [**Perna aviculoides* J. Sowerby, 1814, p. 147; SD Cox, 1940, p. 112] [=*Gervillela* Gillet, 1922 *(nom. null.)*]. Medium-sized to large, slightly inequivalve, longitudinally elongated, only slightly oblique; posterior wing narrow and obtuse, anterior wing acutely pointed; no byssal gape; dentition consisting of anterior series of 2 to 4 and posterior series of 1 or 2 elongate teeth, all slightly oblique to longitudinal. *Trias.-Cret.,* cosmop.——Fig. C41,*2a*. **G. aviculoides* (J. Sowerby), U.Jur.(Corall.), Eng.; LV ext., ×0.3 (Cox, n).——Fig. C41,*2b*. *G. sublanceolata* (d'Orbigny), L.Cret.(Apt.), Eng.; LV int., ×0.5 (Deecke, 1902).

Gervillia Defrance, 1820, p. 502 [**G. solenoidea (sic)*; SM Defrance, 1824, p. 316] [=*Gervilia* Rang, 1826 *(nom. null.)*; *Gervillea* Fleming, 1828 *(nom. null.)*; *Gervilleia* Rominger, 1846 *(nom. van.)*; *Hydrodaetes* Gistl, 1848 (obj.); *Gervilla* Pethö, 1906 *(nom. null.)*; *Cervilleia* Gillet, 1922 *(nom. null.)*]. Medium-sized, longitudinally elongated, narrow, ensiform, slightly curved, scarcely oblique, with terminal beaks and in some specimens rostrum-like anteroventral projection above which is wide gape of margins; posterior wing short and obtuse. *U.Trias.-U.Cret.,* cosmop.

G. (Gervillia) [=*Gervilliopsis* Whitfield, 1885, p. 73 (type, *Gervillia ensiformis* Conrad, 1858, p. 328; OD); *Dalliconcha* White, 1887, p. 34 (type, *D. invaginata* (=*G. ensiformis*); OD); *Ensigervilleia* Dietrich, 1910, p. 236 (type, *Gervillia silicea* Quenstedt var. *husii*; OD)]. Narrow, unequal transverse crenulations present along each end or all of hinge margin, with elongate longitudinal teeth (1 in RV and 2 in LV) at posterior end. *U.Jur.-Cret.,* cosmop.——Fig. C41,*4*. **G. (G.) solenoidea,* U.Cret.(Senon.), Ger.; *4a,b,* LV ext., LV int., ×1 *(415).*

G. (Cultriopsis) Cossmann, 1904, p. 510 [**G. (Cultriopsis) falciformis*; M] [=*Angustella* Waagen, 1907, p. 98 (type, *Gervillia angusta* von Münster, 1836, p. 122; SD Diener, 1923, p. 97)]. Differing from *Gervillia (Gervillia)* in absence of transverse crenulations along hinge margin; some specimens with rudimentary transverse tooth in anterior angle as well as elongate

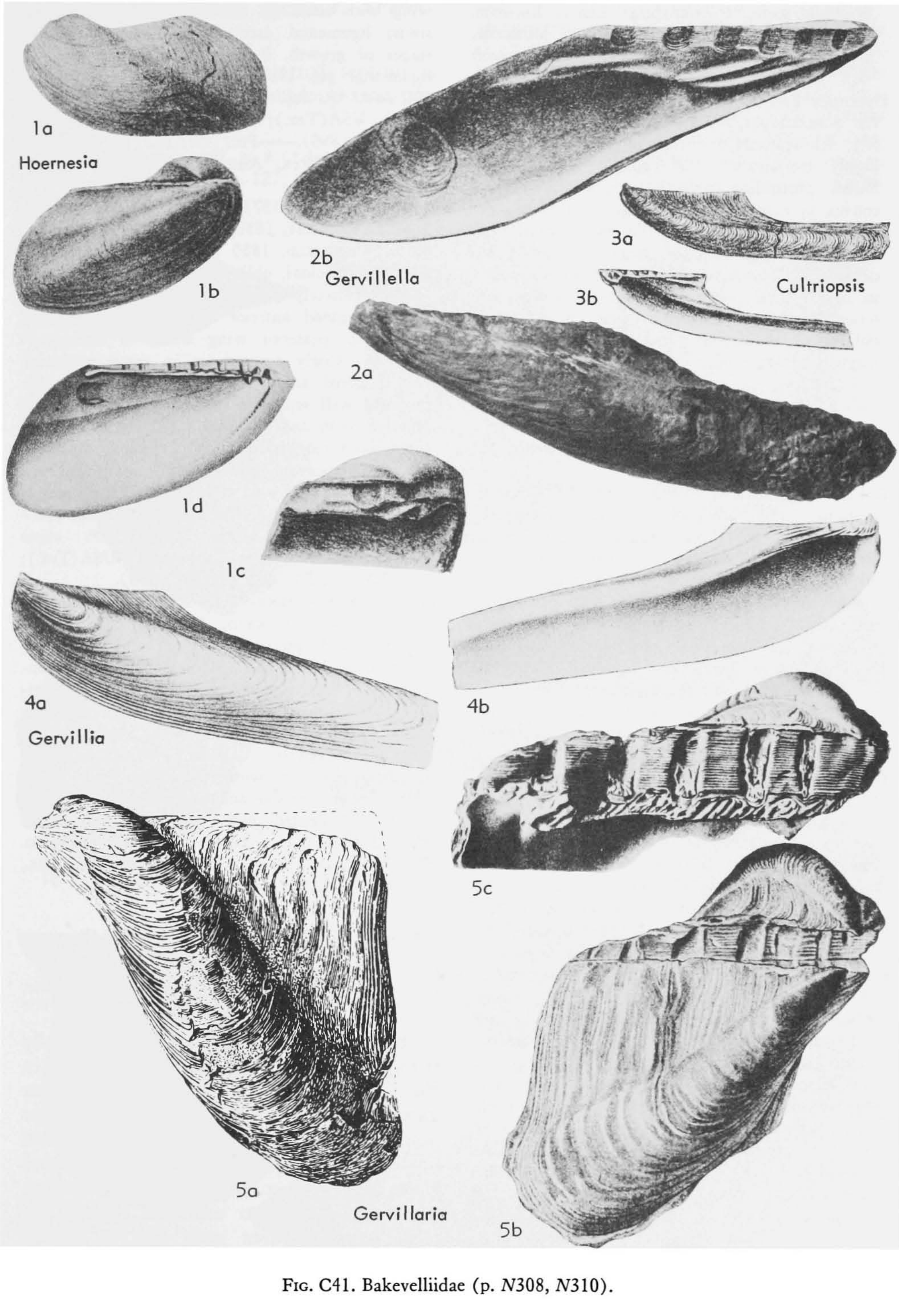


FIG. C41. Bakevelliidae (p. *N*308, *N*310).

posterior teeth. *U.Trias.-L.Jur.(Lias.),* Eu.-Asia.——Fig. C41,*3*. *G. (C.) angusta* von Münster, U.Trias., S.Tyrol; *3a,* LV ext.; *3b,* RV int., both ×1 *(58).*

Hoernesia Laube, 1866, p. 52 [**Mytulites socialis* von Schlotheim, 1823, p. 112; SD Tate, 1868, p. 67]. Elongate-trapeziform, only slightly oblique, highly inequivalve; LV strongly convex, with broad, protruding umbonal region, RV feebly convex to concave; valve margins commonly not in single plane; anterior wing well defined; low internal swelling may correspond to slight radial depression of umbonal region, but septum found in *Septihoernesia* (Cassianellidae) is absent; anterior dentition varying from single large, slightly oblique tooth to series of narrow, oblique ridges; single narrow, elongate tooth on posterior wing. *Trias.-M.Jur.,* Eu.-Asia.——Fig. C41,*1*. **H. socialis* (von Schlotheim), M.Trias., Ger.; *1a-c,* LV ext., RV ext., ant. teeth of LV, all ×1 (Philippi, 1898); *1d,* LV int. showing posterior tooth, ×1 (Credner, 1851).

Kobayashites Hayami, 1959, p. 138 [**K. hemicylindricus*; OD]. Rather small, elongate-rectangular, not oblique; with elongate hinge margin but not alate; beaks subterminal; LV moderately convex, with broadly rounded, slightly protruding umbo and prosogyrous beak; RV almost flat; byssal gape wide; ligamental area narrow, with 4 or more well-separated ligamental pits; each valve with 1 or 2 anterior teeth on hinge plate supported by septum-like thickening below umbo, and weak, elongate posterior tooth; surface smooth. *M.Jur.(Bajoc.),* Japan.——Fig. C42,*3*. **K. hemicylindricus*; LV ext., ×2 *(392).*

Langsonella Patte, 1926, p. 139 [**Gervilleia (Cultriopsis) elongata* Mansuy, 1919, p. 7 *(non Gervillia elongata* Portlock, 1843) (=**Langsonella mansuyi* Cox, 1961; M]. Rather small, elongate, subcylindrical, not oblique, highly inequivalve; LV strongly convex, diagonally carinate, with broad, scarcely protruding umbonal region and large, indistinctly delimited anterior wing; dentition imperfectly known. *Trias.,* Tonkin-Malaya.

Panis Stephenson, 1952, p. 67 [**P. cuneiformis*; OD]. Moderately large, subrectangular, scarcely oblique, high in proportion to length, only slightly inequivalve; umbones not protruding; anterior wings small, bluntly pointed; posterior wings not well demarcated; ligamental area broad, with about 3 unequal ligamental pits; no hinge teeth; surface smooth. *Cret.,* N.Am.-S.Am.——Fig. C42, *2*. **P. cuneiformis,* U.Cret.(Cenoman.), USA (Tex.); *2a,b,* RV int., RV ext., both ×0.7 *(890).*

Phelopteria Stephenson, 1952, p. 68 [**Pteria? dalli* Stephenson, 1936, p. 389; OD]. Medium-sized *Pteria*-like, slightly inequivalve, convexity moderate; anterior wing acutely angular, well demarcated from body in both valves; posterior wing with acute tip but only shallow marginal sinus; ligamental area multivincular in earlier stages of growth, later with one long, shallow ligamental pit. *Cret.,* N.Am.-Eu.-W.Afr.——Fig. C42,*1a-c*. **P. dalli* (Stephenson), U.Cret.(Cenoman.), USA(Tex.); *1a-c,* LV, dorsal view, RV, all ×1 *(890).*——Fig. C42,*1d*. *P. caudigera* (Zittel), U.Cret., Aus.; RV ext., ×1 (Zittel, 1866).

Pseudoptera Meek, 1873, p. 489 [**Avicula anomala* J. de C. Sowerby, 1836, p. 342; OD][=*Pseudopteria* Whitfield, 1880 *(nom. van.)*]. Medium-sized, rhomboidal, oblique, inequivalve; LV with angular, scarcely protruding umbo, rather large, round-margined anterior auricle, much extended downward, posterior wing which is obtuse except for acutely pointed tip in some specimens and diagonal angulation or rib; ligamental pits few and well separated; LV with strong, oblique anterior tooth and elongate, longitudinal posterior tooth, both received between 2 teeth in RV; LV commonly bearing weak radial threads. *Cret.,* Eu.-N.Am.-Japan.——Fig. C42,*4a*. **P. anomala* (J. Sowerby), L.Cret.(Alb.), Eng.; LV ext., ×0.7 (Woods, 1905).——Fig. C42,*4b,c*. *P. viana* (Stephenson), U.Cret.(Cenoman.), USA(Tex.); *4b,c,* LV int., RV int., both ×2 *(890).*

Tenuipteria Stephenson, 1955, p. 110 [**Inoceramus argenteus* Conrad, 1858, p. 329; OD]. Medium-sized, pteriiform, height and length almost equal, highly inequivalve; LV strongly convex, with broadly rounded, well-protruding umbonal region, very small anterior auricle, and undifferentiated posterior wing; RV feebly convex, with small, obtusely angular anterior wing and flattened posterior wing; ligamental pits 3 or more, unequal in size and irregularly spaced; both valves ornamented with weak, unequal radial ribs. *U.Cret.(Owl Creek),* USA(Mo.).——Fig. C42,*5*. **T. argenteus* (Conrad); *5a,b,* LV ext., RV ext., both ×1 (Stephenson, 1955).

Family CASSIANELLIDAE Ichikawa, 1958

[=Paraviculidae Gugenberger, 1935 (family name invalid, not based on generic name)] [Materials for this family prepared by L. R. Cox]

Shell oblique, posteriorly alate, usually strongly inequivalve (but subequivalve in *Burckhardtia*), with or without anterior gape affecting both valves; no subauricular notch; LV strongly convex, with prominent umbo; radial depression, to which internal ridge or septum corresponds, either crossing or lying anterior to umbonal region; external cardinal area with one to several ligamental pits, except apparently in *Reubenia.* Surface smooth or with radial ornament; inner ostracum nacreous. *?Perm., Trias.*

The presence of an internal septum is the chief distinction of this group from the Bakevelliidae.

Cassianella BEYRICH, 1862, p. 9 [**Avicula gryphaeata* VON MÜNSTER, 1836, p. 127; OD] [=*Gryphorhynchus* MEEK, 1864, p. 217 (obj.); *Actinophorus* MEEK, 1864, p. 218 (type, *Avicula decussata* GOLDFUSS, 1836, p. 128; OD)]. Very inequivalve, bialate, usually relatively high, rarely pronouncedly inequilateral or oblique; LV with relatively large, pointed anterior wing, separated from umbonal region by radial depression characteristic of family; marginal sinus below this wing lying in plane almost at right angles to one passing

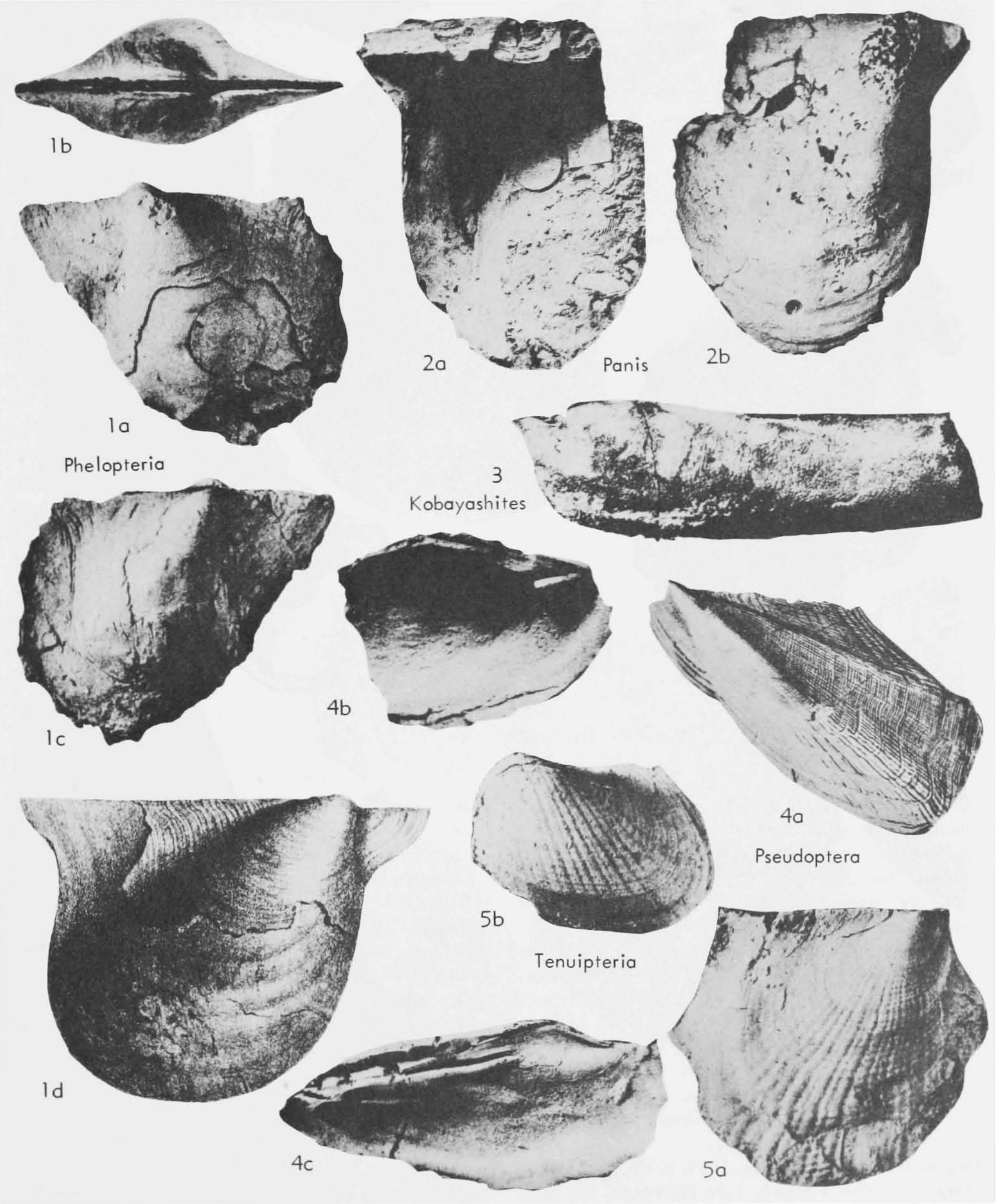


FIG. C42. Bakevelliidae (p. *N*310).

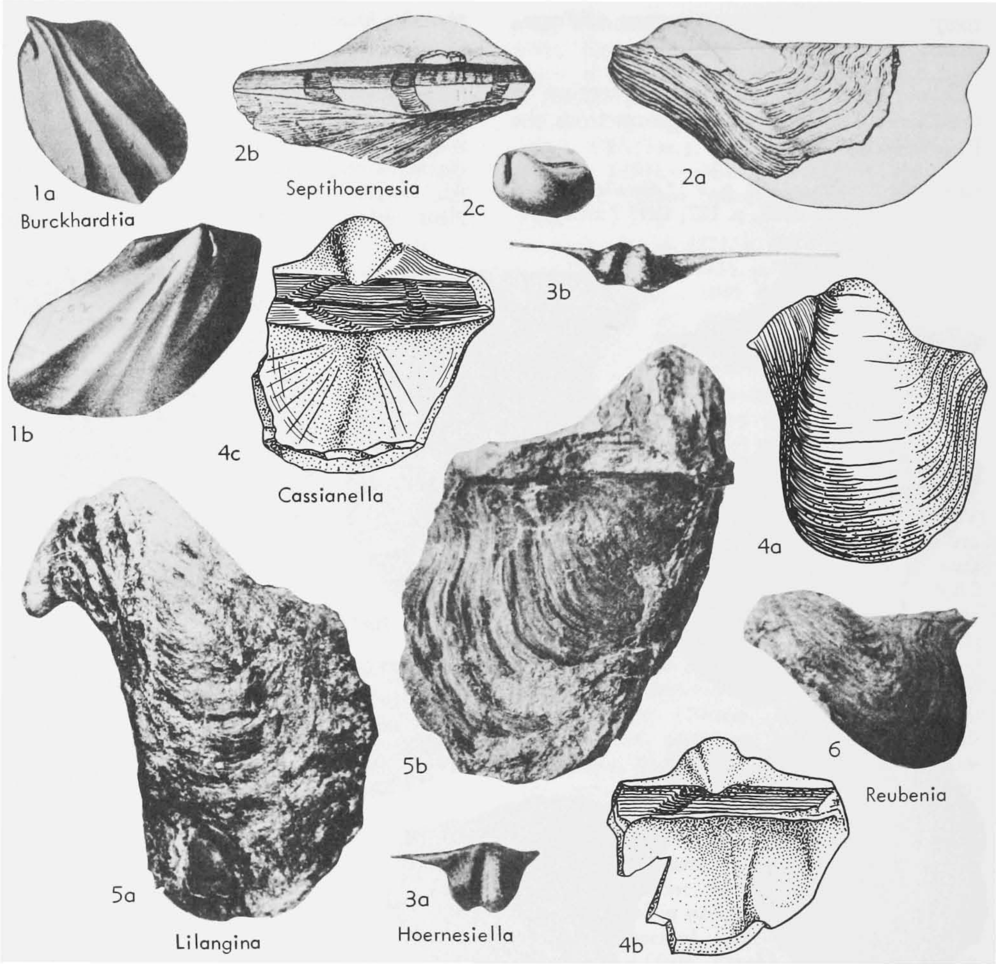


Fig. C43. Cassianellidae (p. *N*312-*N*313).

through hinge margin; RV concave or flat; ligamental pits usually single but some duplicated; few short, transverse subumbonal hinge teeth present together with longitudinal lateral teeth, posterior ones elongate, anterior short; surface smooth or radially ribbed. *?Perm.(Guadalupian), Trias.*, cosmop.——Fig. C43,*4*. *C. beyrichi* Bittner, U.Trias., S.Tyrol; *4a*, LV ext.; *4b*, LV ligamental area with one pit; *4c*, valves in juxtaposition, ligamental areas with 2 pits; all ×1 *(58)*.

Burckhardtia Frech, 1907, p. 334 [**B. boesei*; SD Diener, 1923, p. 34]. Valves equally convex, radially ribbed; wings obtuse. *U.Trias.(Carn.)*, Mex.——Fig. C43,*1*. *B. aguilerae* Frech; *1a,b*, LV, RV, ×1.3 (Frech, 1907).

Hoernesiella Gugenberger, 1934, p. 46 [**H. carinthiaca*; SD Cox herein]. Like *Hoernesia*, but with exceptionally long and acute wings, and with radial depression running vertically from middle of umbonal region to lower margin of body. *U. Trias.(Carn.)*, Carinthia.——Fig. C43,*3a*. **H. carinthiaca*; LV, ×1.——Fig. C43,*3b*. *H. horrida* Gugenberger; LV, ×1 (both Gugenberger, 1934).

Lilangina Diener, 1906, p. 768 [**L. nobilis*; SM Diener, 1908, p. 62]. Like *Septihoernesia*, but with LV umbo very prominent, beak strongly prosogyrous and no anterior wing. *U.Trias. (Carn.)*, Kashmir.——Fig. C43,*5*. **L. nobilis*; *5a,b*, LV, RV, ×0.7 (Diener, 1908).

Reubenia Cox, 1924, p. 61 [**R. hesbanensis*; OD]. Externally like *Septihoernesia*, but with anterior wing much reduced; ligamental area seemingly subinternal. *U.Trias.*, Jordan.——Fig. C43,*6*. **R. hesbanensis*; LV ext., ×1 (Cox, n).

Septihoernesia Cox, 1964, p. 40 [**Gervillia johannisaustriae* Klipstein, 1845, p. 249; OD]. Elongated transversely; radial depression deep, almost on middle of umbonal region; internal septum narrow and prominent, dividing umbonal cavity into 2 chambers; ligamental pits 1-3; LV usually with 2 divergent oblique teeth at anterior end of hinge margin; posterior teeth unknown; surface smooth. *Trias.,* Eu.-Asia.——Fig. C43,*2a,b*. **S. johannisaustriae* (Klipstein), M.Trias.(Ladin.), S.Tyrol; *2a,b,* LV and dorsal view, both ×1 *(58)*.——Fig. C43,*2c*. *S. subglobosa* (Credner), M.Trias.(Muschelkalk), Ger.; LV int. mold, slit representing septum, ×1 (Assmann, 1915).

Family PERGAMIDIIDAE Cox, new family

Shell medium-sized, equivalve to moderately inequivalve with RV more convex, ovate or mytiliform, recalling some Inoceramidae; hinge margin straight, moderately elongate, umbones more or less anterior, no differentiated posterior wing, anterior auricle present or absent, byssal gape present;

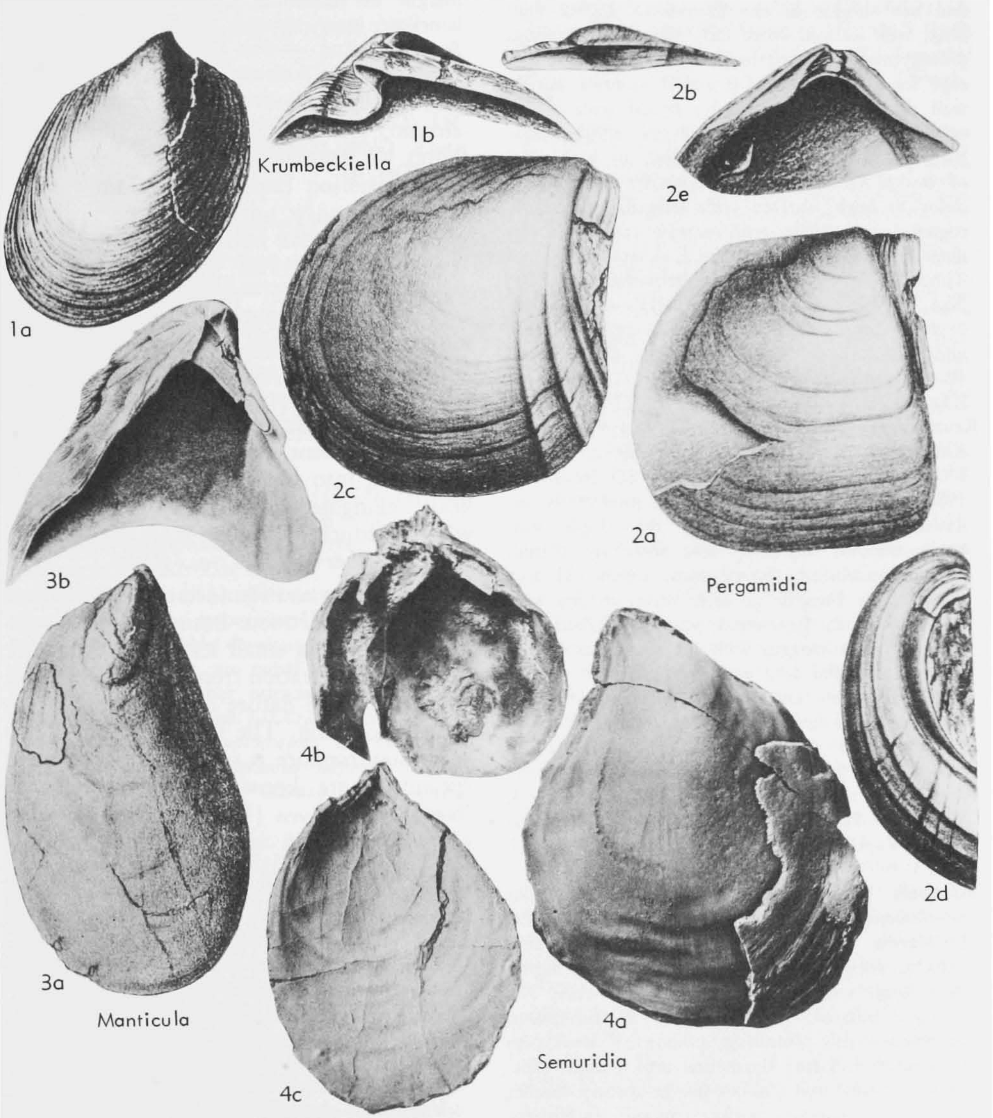


Fig. C44. Pergamidiidae (p. *N*314).

ligamental area triangular, external or subinternal, with single triangular ligamental pit or with no observed pit *(Manticula);* hinge edentulous or with weak posterior lateral tooth *(Semuridia);* monomyarian; shell structure varied, inner nacreous layer observed only in *Semuridia. U.Trias.-L.Jur. (Lias.).*

Pergamidia Bittner, 1891, p. 103 [**P. eumenea*; SD Diener, 1923, p. 135]. Equivalve, subovate, and not oblique or else mytiliform, higher than long, well inflated, with only slightly protruding, prosogyrous umbones; beaks terminally placed except for dorsoventrally extended anterior auricle well demarcated from body; byssal gape correspondingly extended, variable in width; ligamental area subinternal, extending to both sides of beak; ligamental pit triangular, broad, posterior to beak; surface with irregular concentric rugae, some species with narrow radial ribs on anterior region. *U.Trias.(Nor.),* Anatolia-Yunnan-Timor.——Fig. C44,*2a,b.* **P. eumenea,* Anatolia; *2a,b,* RV ext. and hinge, ×0.6 *(56).*——Fig. C44, *2c,d. P. attalea* Bittner, Anatolia; *2c,d,* RV, side and ant. views showing byssal gape, ×0.7 (Bittner, 1892).——Fig. C44,*2e. P. timorensis* Krumbeck, Timor; LV hinge, ×3 *(487).*

Krumbeckiella Ichikawa, 1958, p. 196 [*pro Timoria* Krumbeck, 1924, p. 218 (*non* Kaye, 1919)] [**Timoria timorensis* Krumbeck; SD Ichikawa, 1958, p. 196]. Almost equivalve, moderately inflated, obliquely ovate, longer than high; umbones narrow, more or less anteriorly placed, slightly protruding, prosogyrous; ligamental area of moderate breadth in each valve, mainly posterior to beak; ligamental pit fairly broad, oblique; anterior margin with deep sinus extending below ligamental area and giving rise to sharply margined lunule and earlike projection of hinge margin; lunule broader in RV than in LV, where its margin is affected by byssal gape; surface smooth, but loss of outer layers commonly exposes finely ribbed inner ostracum. *U.Trias.(Nor.),* Timor.——Fig. C44,*1*; **K. timorensis* (Krumbeck), *1a,b,* RV ext., RV hinge region int., ×1 *(487).*

Manticula Waterhouse, 1960, p. 428 [**Mytilus problematicus* Zittel, 1864, p. 28; OD] [=*Maoria* Wilckens, 1927 (*non* Laporte, 1868)]. Inequivalve, roughly mytiliform, higher than long, with completely anterior beaks; RV strongly inflated, grotesquely so in full-grown specimens, with protruding umbo; LV weakly to moderately inflated; ligamental area broad, transversely striated and without pit; no distinct lunule; byssal gape narrow; surface smooth except for irregular concentric folds; ostracum very thick in full-grown specimens. *U.Trias.(Carn.),* N.Z.-N. Caledonia.——Fig. C44,*3.* **M. problematica* (Zittel), N.Z.; *3a,b,* RV ext., RV int., ×0.7 (Wilckens, 1927; *957*).

Semuridia Melville, 1956, p. 116 [**S. jacksoni* (=**Inoceramus dorsetensis* Cox, 1926, p. 183); OD]. Subequivalve, broadly mytiliform, well inflated, with unprotruding, anterior, prosogyrous umbones; anterior auricles small, blunt, with convex outer margin; byssal gape moderate; ligamental area with broad, triangular ligamental pit; weak longitudinal tooth close to posterior end of margin of ligamental area; surface irregularly lamellose; inner ostracum nacreous. *L.Jur.(L.Lias.-Sinemur.),* Eng.——Fig. C44,*4a,b.* **S. dorsetensis* (Cox), Dorset(Charmouth); *4a,b,* RV int. mold (holotype), RV int. showing ligamental area, both ×1 (Cox, n).——Fig. C44,*4c. S. quadrata* Melville, Gloucs.(Stowell Park borehole); LV int., ×1 (Cox, n).

?Family DATTIDAE Healey, 1908

[Materials for this family prepared by L. R. Cox]

Shell small, *Pteria*-like, known only by LV; posterior wing obtuse, no anterior auricle, anterodorsal angle rounded off, with external narrow ligamental area containing 2 ligamental pits, one below beak, other well posterior to it; spoonlike structure also present, possibly a chondrophore, projecting into shell cavity just in front of beak; elongate lateral tooth on posterior wing; adductor muscle scars and pallial line not observed. *U.Trias.(Rhaet.).*

This family was founded on what appears to be the inadequate basis of a single internal mold of a small left valve. Whether it deserves separation from the Bakevelliidae depends on the nature of the spoonlike internal projection. The interpretation of this as a chondrophore is suspect. No additional specimens are known to have been collected.

Datta Healey, 1908, p. 64 [**D. oscillaris*; OD]. Characters of family. *U.Trias.(Rhaet.),* Burma. ——Fig. C45,*1.* **D. oscillaris*; *1a,* LV int. mold, ×2; *1b,* wax squeeze, reproducing features of hinge, ×4.5 (Healey, 1908).

Family INOCERAMIDAE Giebel, 1852

[*nom. transl.* Steinmann, 1903 (*ex* Inoceraminae Zittel, 1881)] [=Sphenoceramidae Heinz, 1932] [Materials for this family prepared by L. R. Cox]

Variously shaped, concentrically lamellose or plicated Pteriacea with multiple ligamental pits; subequivalve to highly inequi-

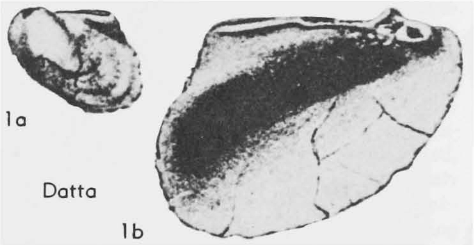


FIG. C45. Dattidae (p. N314).

valve, with LV more convex than RV; radial ribbing present only rarely; commissure plane except where affected by radial ribbing; no anterior gape; posterior wing present or absent; anterior wing usually absent or small; ligamental area with usually numerous regularly arranged ligamental pits which commonly have curved sides and do not indent margins of area; hinge teeth absent except in some *Parainoceramus;* inner ostracum nacreous (but not preserved in many specimens); outer ostracum formed of prismatic calcite. *L.Perm.-U. Cret., ?Oligo.*

Inoceramus J. SOWERBY, 1814, p. 448 [**I. cuvierii;* M, confirmed by ICZN (Opinion 473, 1957)] [=*Catillus* BRONGNIART, 1822 (type, *I. cuvierii* SOWERBY, 1814; SD Cox herein); *Catillum* NILSSON, 1827 *(nom. null.)*]. Subequivalve to strongly inequivalve, ovate, trapeziform or suborbicular; posterior wing variably developed; ligamental area concave transversely; no radial ornament except in *I. (Birostrina);* outer ostracum very thick in some species. *L.Jur.(Lias.)-U.Cret.,* cosmop.

I. (Inoceramus) [=*Haploscapha* CONRAD, 1874 (type, *H. capax,*=*Inoceramus deformis* MEEK, 1871; M); *Cucullifera* CONRAD, 1875 (type, *Haploscapha (Cucullifera) eccentrica*; M); *Neocatillus* FISCHER, 1886 (type, *Inoceramus lamarcki* "BRONGNIART"; OD); *?Athletoceramus, ?Drepanoceramus, ?Euphyoceramus, ?Idioceramus* HEINZ, 1932 (all *nom. dubia*); *Abathoceramus, Alloceramus, Astatoceramus, Aulacoceramus, Callistoceramus, Camptoceramus, Ceratoceramus, Climacoceramus, Cosmioceramus, Cricoceramus, Cycloceramus, Epiceramus, Gnesioceramus, Gonioceramus, Heroceramus, Heteroceramus, Homaloceramus, Inaequiceramus, Megaloceramus, Mimoceramus, Orophoceramus, Orthoceramus, Oxyceramus, Paraceramus, Platyceramus, Pleiaceramus, Proteoceramus, Schizoceramus, Scolioceramus, Smodingoceramus, Striatoceramus, Tethyoceramus, Xenoceramus* HEINZ, 1932 *(nom. nud.)*]. Medium-sized to large, equivalve to moderately inequivalve, feebly to strongly inflated, height exceeding length, not or only slightly oblique; anterior margin not strongly convex or protruding; prominence of LV umbo variable; posterodorsal wing present, more or less flattened, well differentiated from body of valve in some species, undifferentiated in others; surface lamellae more or less regularly spaced; concentric plications variably developed. *L. Jur. (Lias.)-U.Cret.,* cosmop.——FIG. C46,*1a,b.* **I. (I.) cuvierii*; *1a,* Senon., Eng., RV, ×0.5; *1b,* Turon., Eng., ligamental area of LV, ×0.5 (both Woods, 1912).——FIG. C46,*1c. I. (I.) lamarcki* PARKINSON, Turon., Eng.; LV, ×1 (Woods, 1912).

[The great majority of the generic and specific names published by HEINZ in 1932 rank as *nomina nuda,* as they do not comply with the joint requirements of publication with a diagnosis and with the citation of a type species, although some would have been valid had they been published prior to 1930. Some of these names have been used subsequently by HEINZ himself and a few other authors, but only one *(Besairieia)* appears to have acquired validity thereby. Hence the three names introduced by HEINZ which are adopted in this *Treatise* are stated to be those of new genera or subgenera and become valid in view of their publication herein with a cited type species and a diagnosis. In a few cases, when published with a few descriptive words and the citation of a single new nominal species, HEINZ's genera appear to be technically valid, with the species in question the type by monotypy. Unfortunately, in every such case the type species is unrecognizable, and it is necessary to dismiss these generic names as *nomina dubia.*]

I. (Birostrina) J. SOWERBY (*ex* DE LUC, MS), 1821, p. 183 [**I. sulcatus* PARKINSON, 1819; SD Cox herein] [=*Actinoceramus* MEEK, 1864 (obj.); *Taenioceramus* HEINZ, 1932 *(nom. nud.)*]. Small for family, gibbose, inequivalve, tall; hinge margin short, no posterodorsal wing; LV umbo narrow and prominent; beak prosogyrous; broad radial folds present on all or part of surface in some species, other species with concentric ornament only. *Cret.(Neocom.-Cenoman.),* cosmop. ——FIG. C46,*2a.* **I. (B.) sulcatus* PARKINSON, L.Cret.(Alb.), Eng.; LV, ×1 (Woods, 1911). ——FIG. C46,*2b. I. (B.) subsulcatus* WILTSHIRE, L.Cret.(Alb.), Eng.; LV, ×1 (Woods, 1911).

I. (Cataceramus) COX, **n. subgen.,** herein (*ex* HEINZ, *nom. nud.*) [**I. goldfussianus* D'ORBIGNY, 1846, p. 517 (=*I. balticus* BÖHM, 1907, p. 113)] [=*Boehmiceramus, Dimeroceramus, Haploceramus, Selenoceramus* HEINZ, 1932 *(nomina nuda)*]. Medium-sized to large, subequivalve, ovate, length exceeding height, not oblique or only slightly so; umbones broadly rounded, not prominent; hinge line fairly elongate, but no differentiated posterodorsal wing present; concentric plications strong, regular. *U.Cret.(Senon.),* cosmop.——FIG. C46,*4.* **I. (C.) goldfussianus* D'ORBIGNY, (Campan.), Ger.; LV, ×0.5 (Böhm, 1909).

I. (Cremnoceramus) COX, **n. subgen.,** herein (*ex* HEINZ, *nom. nud.*) [**I. inconstans* WOODS, 1912, p. 285 (lectotype, Cox herein designated, WOODS,

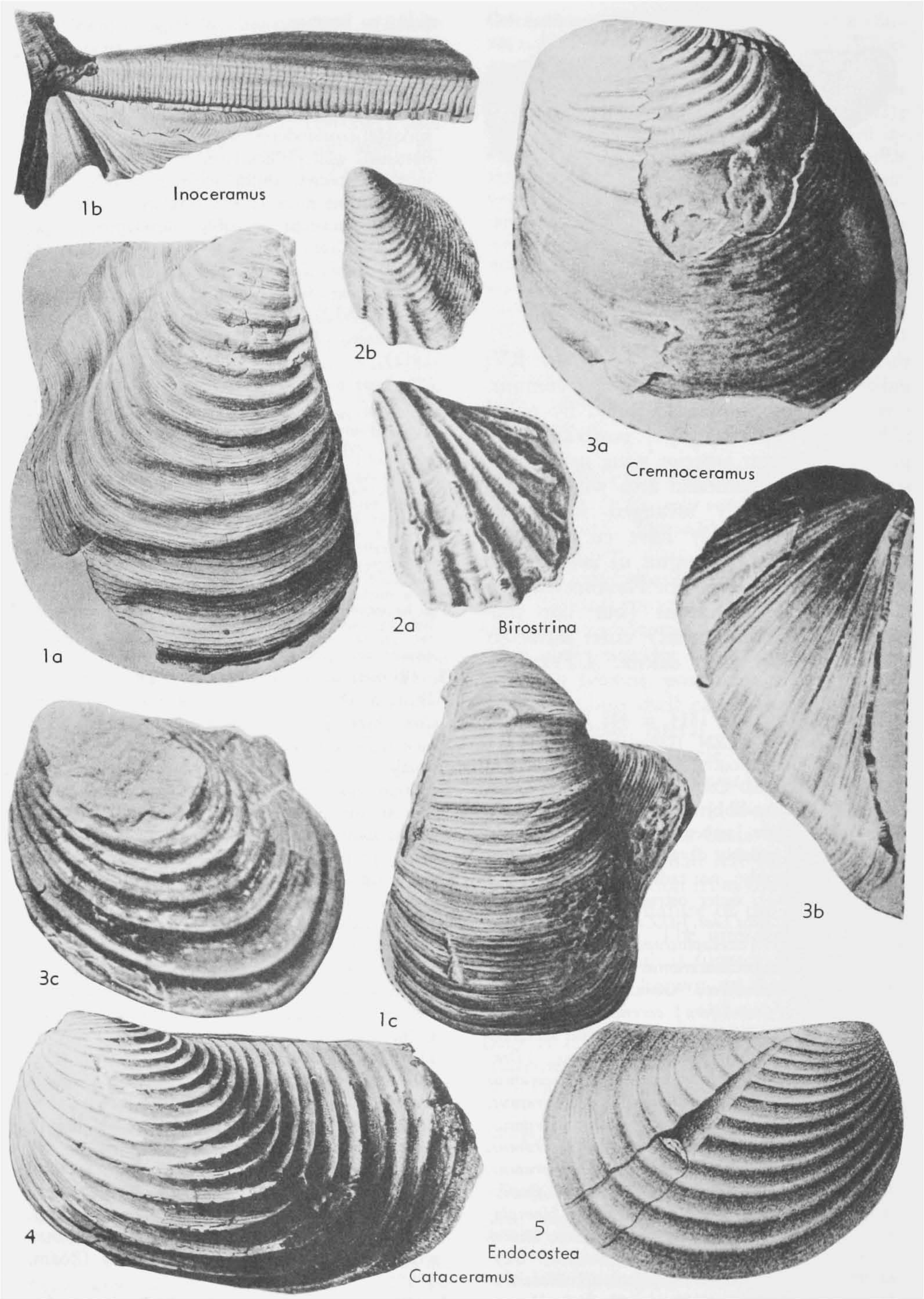


FIG. C46. Inoceramidae (p. *N*315, *N*317).

text-fig. 43[1])] [=*?Acroceramus, ?Alloceramus, ?Bathmoceramus, Cephaloceramus, ?Discoceramus, Gnathonoceramus, ?Madagiceramus, Oncoceramus, Sphaeroceramus, Stenoceramus, Stolleyiceramus, Symboloceramus* HEINZ, 1932 *(nom. nuda); ?Enanticeramus, ?Manoceramus, ?Rhachidoceramus, ?Syngenoceramus, ?Trachyceramus* HEINZ, 1932 *(nom. dubia)*]. Medium-sized, suborbicular to rhombic, slightly to moderately oblique, subequivalve or inequivalve; LV weakly convex in early growth stages, later increasing rapidly in convexity, some specimens with concentric angulation where convexity begins to increase; umbones broadly rounded, not prominent; posterodorsal wing absent or narrow; ornament of irregular concentric rugae and plications. *U.Cret.(Turon.-Senon.)*, cosmop.——FIG. C46,*3a,b*. **I. (C.) inconstans* WOODS, Turon., Eng.; *3a,b*, LV, ×1 (Woods, 1912).——FIG. C46,*3c*. *I. (C.) crassus* PETRASCHEK, Senon., Eng.; LV, ×0.7 (Woods, 1912).

I. (Endocostea) WHITFIELD, 1877, p. 31 [**E. typica*; OD]. Like *I. (Cataceramus)*, but with riblike swelling crossing interior of shell diagonally from posterior side of umbo, forming groove on internal mold. *U.Cret.(Senon.)*, cosmop.——FIG. C46,*5*. **I. (E.) typicus*, N.Am.; RV, part of internal rib broken off and remaining in groove forming its mold, ×1 (Newton & Jenney, 1880).

I. (Haenleinia) J. BÖHM, 1907, p. 317 [**I. flexuosus* HAENLEIN, 1889; SD Cox, herein] [=*Besairieia* HEINZ (1932, *nom. nud.*), 1933 (type, *Haenleinia (Besairieia) besairiei* HEINZ, 1933; M); *Cordiceramus, Cyrtoceramus, Germanoceramus* HEINZ, 1932 *(nom. nud.)*]. Medium-sized, subequivalve, gibbose, ovate, without posterior wing; sinus of posteroventral margin of LV corresponding to radial sulcus of flank; ornament as in *I. (Inoceramus)*. *U.Cret.(Senon.)*, cosmop.——FIG. C47,*1a*. **I. (H.) flexuosus* HAENLEIN, U.Senon., Ger., LV, ×0.7 (Böhm, 1909).——FIG. C47,*1b*. *I. (H.) cordiformis* J. DE C. SOWERBY, L.Senon., Eng., LV, ×0.7 (Woods, 1912).

I. (Mytiloceramus) ROLLIER, 1914, p. 416 [**I. polyplocus* ROEMER, 1857; OD]. Medium-sized, rounded rhombic, slightly oblique, slightly inequivalve; umbones narrowly rounded, not prominent; LV with small anterodorsal wing projecting toward RV; ornament of fairly regular concentric folds. *M.Jur.(Aalen.)*, Eu.-Japan.——FIG. C47,*3*. **I. (M.) polyplocus* ROEMER, Alsace; RV, ×0.7 (Benecke, 1905).

I. (Mytiloides) BRONGNIART, 1822, p. 320 [**Ostracites labiatus* VON SCHLOTHEIM, 1813; M] [=*Mytiloida* BRONGNIART, 1832 *(nom. van.)*; *Mylitoides* CONRAD, 1874 *(nom. null.)*; *Orpheoceramus, ?Citharoceramus, ?Aristoceramus* HEINZ, 1932 *(nom. nud.)*]. Medium-sized, obliquely ovate and elongated, subequivalve, of slight convexity; hinge line short; concentric plications variably developed. *L.Jur.-U.Cret.*, cosmop.——FIG. C47,*4a*. **I. (M.) labiatus* (SCHLOTHEIM), U.Cret.(Turon.), Eng.; LV ×0.5 (Woods, 1911).——FIG. C47,*4b*. *I. (M.) galoi* BÖHM, U.Jur.(Callov.), Argentina; LV, ×1 (Stehn, 1924).

Anopaea EICHWALD, 1861, p. 301 [**Inoceramus lobatus* AUERBACH & FREARS, 1846 (*non* GOLDFUSS, 1836) =**I. brachovi* ROUILLIER, 1849; M]. Medium-sized, subequivalve, elongated, rather pyriform, with low, lobelike anterior region, commonly separated by broad sulcus from rest of shell; no demarcated posterior wing; inflation only moderate; umbones narrow, scarcely protruding; beaks prosogyrous; cordiform lunule present; ligamental pits small and numerous; LV with internal rib below beak; ornament of concentric lamellae and broad plications. *U.Jur.*, Eu.-Indon.-N.Z.——FIG. C47,*2*. **A. brachovi* (ROUILLIER), U.Volgian, USSR; *2a,b*, LV and dorsal views, ×0.5 (Pavlov, 1905).

Aphanaia DE KONINCK, 1877 [**Inoceramus mitchellii* M'COY, 1847; SD NEWELL, 1942]. Ovate to subpyriform, prosogyre, subequivalve, RV slightly less convex than LV; ornament of irregular concentric undulations; lunule shallow, broad and elongate; hinge edentulous, short, without umbonal septum; resilifer pits numerous, closely spaced. *Perm.*, Australia.——FIG. C48,*5*. **A. mitchellii* (M'COY), L.Perm. (Glendon F.), New S.Wales, Australia; *5a*, RV, composite mold, ×0.3; *5b*, RV, latex cast interior of same, ×0.7 (BROWNE and NEWELL, 1966). [NEWELL]

Arcticeramus KOSCHELKINA, 1962, p. 41 [**Inoceramus arcticus* KOSCHELKINA, 1962, p. 72; OD]. Of medium size, inequivalve, LV the more convex and with more protruding umbo; ornament of concentric folds; internal characters unknown. *M.Jur.(Callov.)-U.Jur.(L.Volgian)*, USSR(Sib.).

Inoceramya ULRICH, 1904, p. 134 [**I. concentrica*; M]. Medium-sized, thin-shelled, suborbicular, compressed, probably equivalve; umbones near middle of hinge margin, not protruding; ligamental pits small and numerous, decreasing in size toward ends of hinge margin; internally with riblike swelling which extends obliquely backward from umbo; ornament of regular concentric plications which are absent from posterodorsal region. *Yakutat Formation* (*Mesoz.*, system uncertain), Alaska.——FIG. C48,*5*. **I. concentrica*; *5a*, RV (reconstr.), ×0.7; *5b*, post. part of hinge and internal rib, ×1 (Ulrich, 1904).

Lenella KOSCHELKINA, 1962, p. 31 [**L. tiungensis*; M]. Small to medium-sized, equivalve, mytiliform; posterior wing obtuse, flattened; anterior

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[1] ANDERT (1913) and HEINZ have restricted WOODS' interpretation of *I. inconstans*, but neither has selected a lectotype.

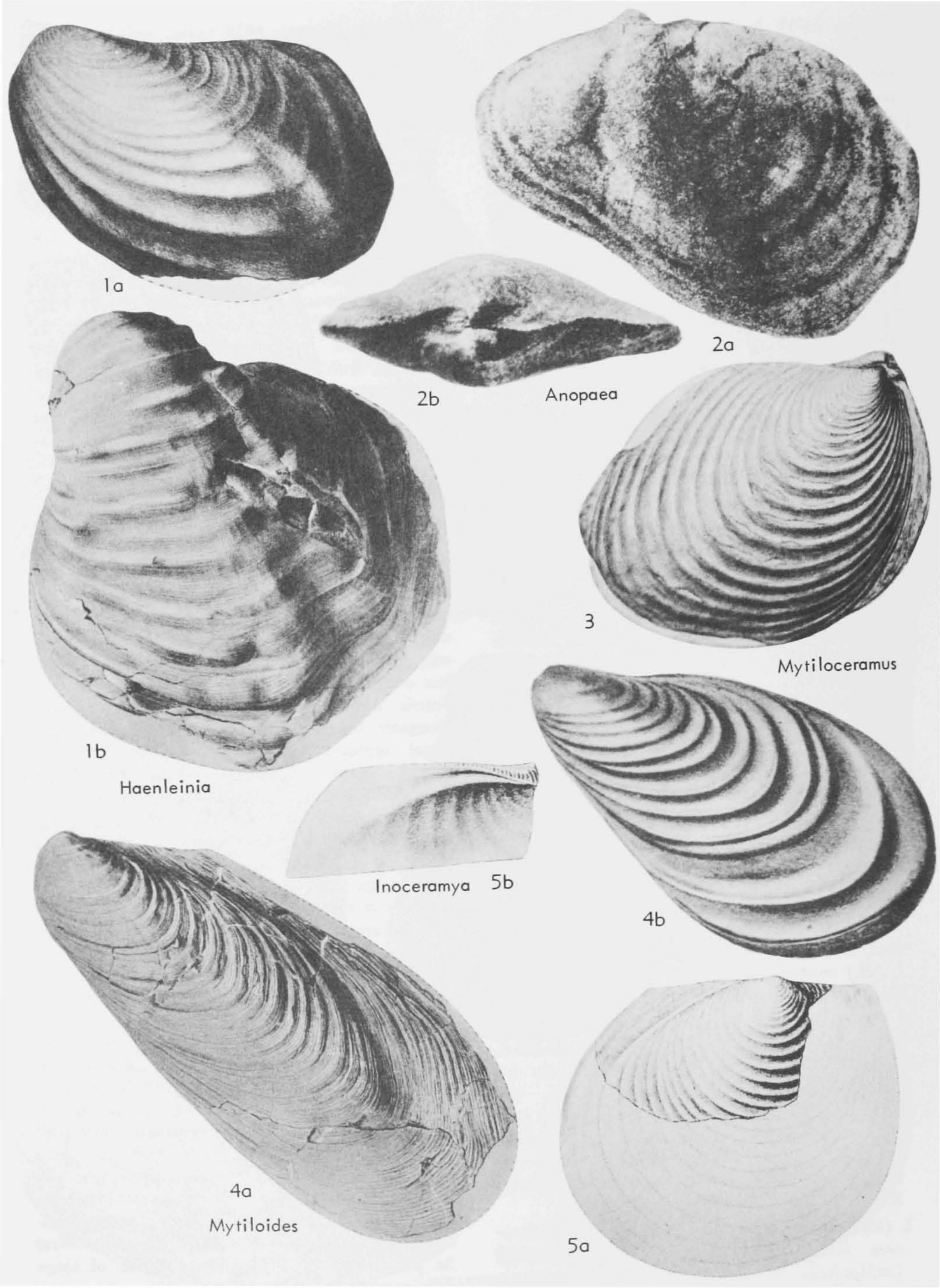

FIG. C47. Inoceramidae (p. *N*317).

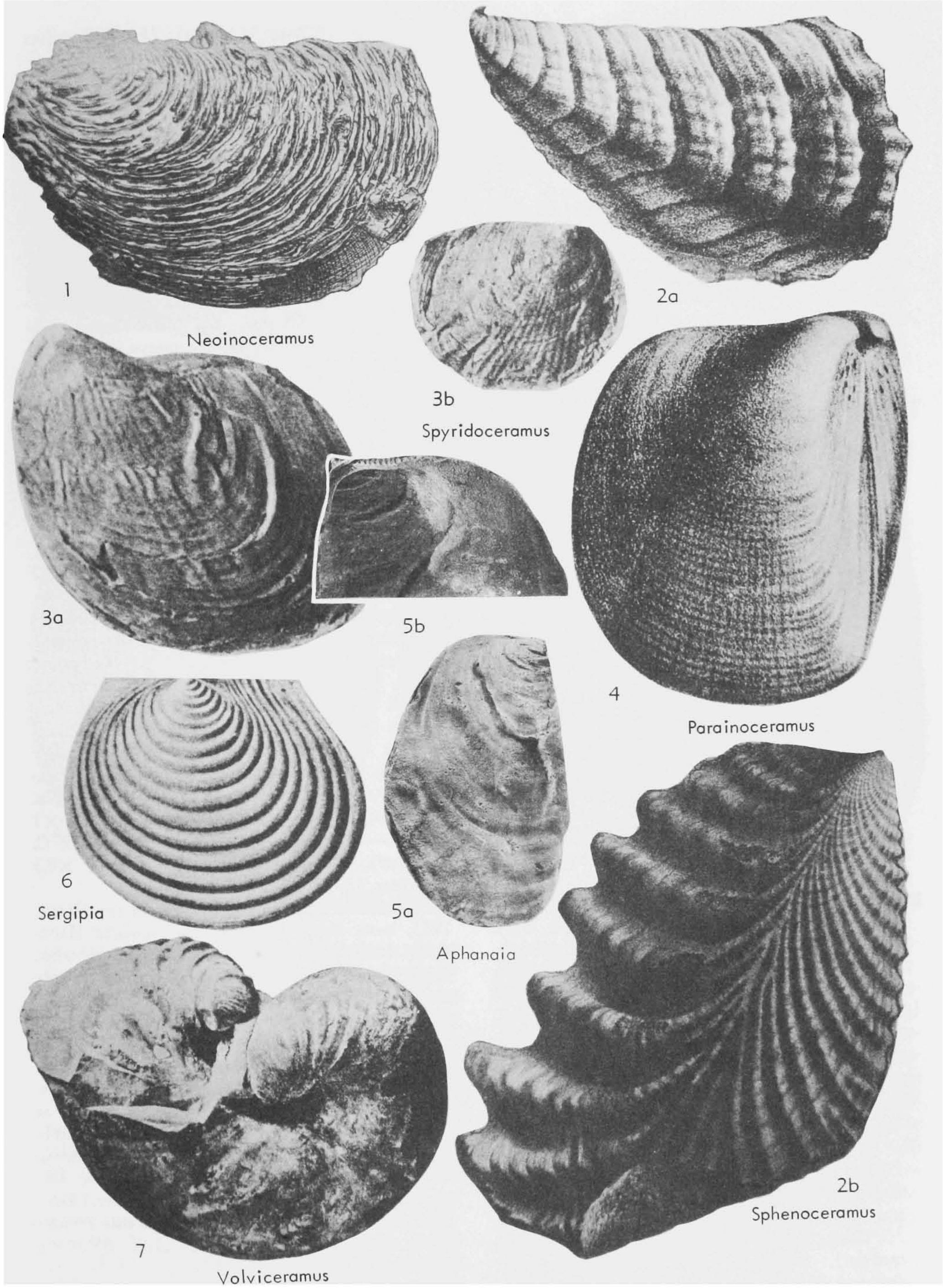

FIG. C48. Inoceramidae (p. *N*317, *N*320-*N*321).

auricle well defined, acute, with byssal sinus below it; ligamental pits few and well separated; shell wall moderately thick; ornament of distant narrow concentric folds with broad posteroventral sinus; small anterior adductor present in early growth stages, later becoming obsolete; pallial line split up into small pits. *L.Jur.(Domer.),* USSR(E. Sib.).

?**Neoinoceramus** Ihering, 1902, p. 134 [**N. ameghinoi*; M]. Large, obliquely ovate, irregular in outline; with relatively short hinge margin and ill-defined anterodorsal and posterodorsal wings; ligamental area and internal characters imperfectly known; ornament of very irregular concentric plications and ridges. *?Oligo.* (base of Patagonian Molasse), Patagonia.——Fig. C48,*1*. **N. ameghinoi*; LV, ×0.4 (Ameghino, 1906).

Parainoceramus Voronetz, 1936, p. 23 [**P. bulkurensis*; SD Cox, 1954, p. 47]. Small to medium-sized, equivalve, of moderate convexity, rectangular or trapeziform, posteriorly subalate; umbones protruding only slightly above hinge margin, beaks subterminal; anterior face of shell more or less impressed; ligamental area flat, pits numerous; short anterior and elongate posterior teeth present in some species, at least in early growth stages; surface smooth or with weak concentric plications. *U.Trias.-Jur.,* cosmop.——Fig. C48,*4*. *P. substriatus* (von Münster), L.Jur.(L.Lias.), Ger.; both valves, ×1 *(341b)*.

Pseudomytiloides Koschelkina, 1963, p. 129 [**Mytiloides marchaensis* Petrova, 1947, p. 130; SD Cox, herein]. Rather small, subequivalve, well inflated, mytiliform; hinge line short, posterior wing virtually absent; no anterior auricle; shell wall thin; ornament of regular closely spaced concentric folds. *L.Jur.(Lias.),* Eu.-Asia.——Fig. C49,*2*. *P. dubius* (J. de C. Sowerby), U.Lias. (Toarc.), Eng.; RV ext., ×1 (BMNH).

Retroceramus Koschelkina, 1957, p. 29 [**Inoceramus retrorsus* Keyserling, 1848, p. 250; OD]. Medium-sized, equivalve, subrhomboidal or obliquely oval; umbones protruding slightly above hinge margin, weakly prosogyrate, beaks not quite terminal; ligament pits closely arranged, alternating in width; small anterior adductor present, pallial line broken up into oval depressions; prismatic layer of shell wall thick, ornament of broad concentric folds. *?U.Trias., L.Jur.(Pliensbach.)-U.Jur.(Kimmeridg.),* cosmop.

R. (Retroceramus) [=*Eoinoceramus* Voronetz, 1961, p. 81 (type, *Inoceramus porrectus* Eichwald, 1871)]. Obliquely oval, broadening in ventral direction; concentric folds regularly arranged. *?U. Trias., L. Jur. (Pliensbach.) - U. Jur. (Kimmeridg.),* cosmop.——Fig. C49,*1a*. **R. (R.) retrorsus* (Keyserling), ?U.Trias., USSR(Olének, Sib.); RV ext., ×1 (von Middendorf).——Fig. C49,*1b,c*. *R. (R.) porrectus* (Eichwald), L.Cret.(Neocom.), USA(Alaska); *1b,c,* both valves (dorsal), RV ext., ×0.7 (Eichwald).

R. (Fractoceramus) Koschelkina, 1957, p. 29 [**Inoceramus formosulus* Voronetz, 1937, p. 18; OD]. Mytiliform; concentric ornament irregular. *M.Jur.,* USSR(Sib.)-Can.

R. (Striatoceramus) Koschelkina, 1959, p. 100 [**Inoceramus vakhrameevi* Koschelkina, 1961, p. 150; SD Koschelkina, 1961]. Irregularly subtriangular; ornament of concentric folds, with narrow radial ribs appearing during growth. *M. Jur.,* USSR(Sib.).

Sergipia Maury, 1925, p. 596 [**Inoceramus (Sergipia) posidonomyaformis*; M]. Thin-shelled, suborbicular, very similar to *Inoceramya,* except that internal riblike swelling has not been observed; ligamental pits minute and numerous. [Like *Inoceramya,* this appears to constitute a link between *Steinmannia* of the Posidoniidae and the Inoceramidae.] *Cret.,* S.Am.(Brazil).——Fig. C48, *6*. **S. posidonomyaformis*; LV ext., ×2 (Maury, 1935).

Sphenoceramus J. Böhm, 1915, p. 183 [**Inoceramus cardissoides* Goldfuss, 1836; SD Vialov *et al.,* 1960, p. 81] [=*Spenoceramus* Böhm, 1922 *(nom. null.)*; *Beloceramus, Cinclidoceramus, Cladoceramus, Dactyloceramus, Dictyoceramus, Eugenoceramus, Euryceramus, ?Helioceramus, Strebloceramus, Thoracoceramus, ?Trochoceramus* Heinz, 1932 *(nom. nud.)*]. *Inoceramus*-like, but tall and trigonal, commonly large, with very narrow, sharply rounded umbo and short hinge margin; equivalve; with radial or obliquely divergent ribbing superposed on concentric plications. *U.Cret.(Senon.),* cosmop.——Fig. C48,*2a*. **S. cardissoides* (Goldfuss), Ger.; LV ext., ×1 *(341b)*.——Fig. C48,*2b*. *S. digitatus* (J. de C. Sowerby), L.Senon., Ger.; RV ext., ×0.3 (Schlüter, 1877).

Spyridoceramus Cox, **new genus,** herein (*ex* Heinz, 1932, *nom. nud.*) [**Inoceramus tegulatus* Hagenow, 1842, p. 559]. Medium-sized, ovate-rhombic, longer than high, inequivalve; LV rather strongly convex with moderately prominent umbo, somewhat resembling a *Pholadomya* valve, RV almost flat; small anterior wing present in both valves; ornament (both valves) of irregular concentric rugae and weak radial riblets; relatively thin-shelled; ligamental area a continuous groove at base of which individual ligamental pits are barely distinguishable. [*Inoceramus argenteus* Conrad is the North American representative of this genus.] *U.Cret.(Campan.),* Rügen (Ger.)-Denmark-N.Am.——Fig. C48,*3*. **S. tegulatus* (Hagenow), Campan., Denm.; *3a,b,* LV, RV, ×1 (Ødum, 1922).

Steinmannia Fischer, 1886, p. 960 [*pro Aulacomya* Steinmann, 1881 (*non* Mörch, 1853)] [**Posidonia bronnii* Voltz, in Zieten, 1833, p. 72; M].

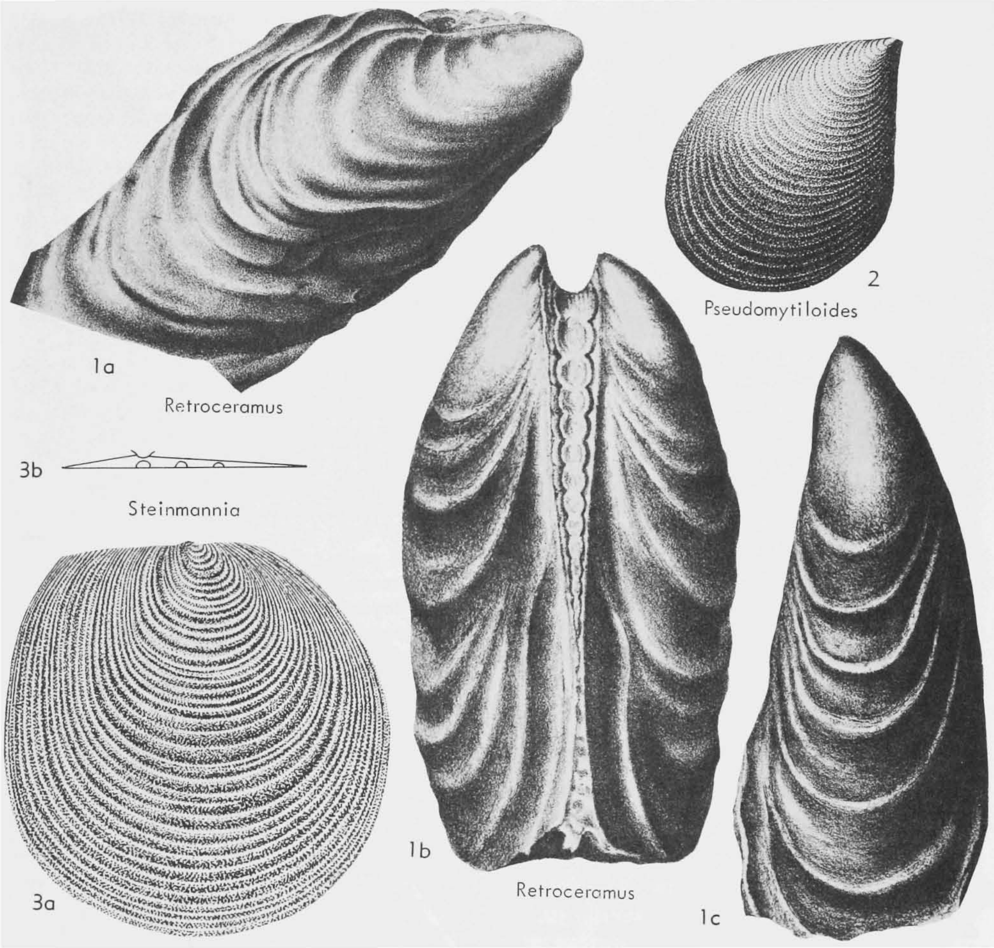

Fig. C49. Inoceramidae (p. *N*320-*N*321).

Suborbicular, not auriculate, equivalve, gibbose (but commonly crushed), thin-shelled, *Posidonia*-like; posterior end with shallow groove running obliquely from beak to posterior margin; ornament concentric ridges and threads; ligamental area narrow, obtusely triangular, extending on both sides of beak and bearing small number (3 or 4) of shallow transverse ligamental pits. *L. Jur. (Toarc.),* Eu.-Asia-N. Afr.-Madag.——Fig. C49,*3*. *S. bronnii (Voltz); *3a,* Eng.(Lincoln), RV, ×1 *(202)*; *3b,* Fr.(Nancy), ligamental area, ×1.4 *(352)*.

?**Turkmenia** Krimholtz, 1936, p. 96 [*T. balkhanensis; M]. Small, trigonally ovate with sharply pointed umbo, posteriorly subalate, longer than high, inequivalve, thought possibly to have grown attached by RV (more convex), to substratum; with narrow ligamental area bearing 4-6 ligamental pits; ornament of broad concentric plications. *L.Cret.(L.Barrem.),* Turkmenia.

Volviceramus Stoliczka, 1871, p. 394 [*Inoceramus involutus J. de C. Sowerby, 1828; OD] [=*?Opsiceramus* Heinz, 1932, p. 17 (type, *Inoceramus rumphii* Böhm, 1924; OD); *?Colpoceramus, ?Condyloceramus, Cymatoceramus, ?Rhadinoceramus, Tactoceramus, ?Xiphoceramus* Heinz, 1932 *(nom. nud.)*]. Large, highly inequivalve, LV coiled in spiral, RV feeble to moderate in convexity; beak directed anteriorly; ornament of concentric plications. *U.Cret.(Senon.),* Eu.-N.Am.——Fig. C48,7. *V. involutus (Sowerby), Senon., Eng.; both valves ant., ×0.7 (Woods, 1912).

Family ISOGNOMONIDAE Woodring, 1925

[=Pernaridia Rafinesque, 1815; Pernadae Fleming, 1828, also Guilding, 1828; Melinidae Stoliczka, 1871; Pernidae Zittel, 1895; Isognomontidae Iredale, 1939] [Materials for this family prepared by L. R. Cox]

Subequivalve to strongly inequivalve, highly to moderately inequilateral, variously shaped but rarely pronouncedly oblique Pteriacea with multiple ligamental grooves but without hinge teeth in adult shell; LV more strongly convex in inequivalve forms, commissure plane or undulating; with or without anterior byssal gape affecting both valves; posterior wing undifferentiated to well defined, anterior auricle present only rarely; ligamental area external, usually flat, ligamental grooves reaching and indenting its lower margin; monomyarian; pallial line commonly discontinuous, broken up into small pits; surface of shell smooth, concentrically lamellose or irregularly undulating; radial ornament absent (except in *Mulletia*); ostracum very thick in most but not all species, inner ostracum nacreous. *U.Perm.-Rec.*

The Isognomonidae appear to have arisen from the Bakevelliidae in Triassic time, losing the *Pteria*-like form characteristic of typical genera of that family. Bernard's work on the ontogeny of the shell in the Recent species *Isognomon ephippium* has shown that hinge teeth are present in the earliest growth stages but soon become obsolete (Fig. C50,*2a-e*). Beginning with a single one, the number of ligamental grooves steadily increases during growth. Living Isognomonidae have much thinner shells than most fossil species.

Isognomon Lightfoot, 1786, p. 41, 52 [**Ostrea perna* Linné, 1767, p. 1149; M] [=*Isognoma* Lightfoot, 1786 (obj.)]. Shell subequivalve, usually higher than long, more or less compressed, of various shapes; umbo directed anteriorly and not protruding above hinge margin; ligamental area broad and flat, scarcely undercut; ligamental grooves numerous, regularly arranged; narrow byssal gape present below beaks, with corresponding reflection of anterior margin. *U.Trias.-Rec.*, cosmop.

I. (Isognomon) [=*Melina* Retzius, 1788, p. 22 (type, *Ostrea ephippium* Linné, 1758, p. 700; SD Herrmannsen, 1847, p. 37); *Perna* Bruguière, 1789 (*non* Retzius, 1788); *Pernigenus* Renier, 1807 (*nom. van.*); *Sutura* Megerle von Mühlfeld, 1811, p. 65 (type, *O. ephippium* Linné; M); *Pernaria* Rafinesque, 1815 (*nom. van.*); ?*Pernomytilus* Rollier, 1914, p. 338 (type, *Mytilus pernoides* Roemer, 1836, p. 89; M); *Aviculoperna* Pchelintsev, 1931 (*non* Cossmann, 1887); *Casteria* Tucker & Wilson, 1933, p. 3 (type, *Pedalion (Casteria) kecia*; OD); *Parviperna* Iredale, 1939, p. 322 (type, *P. perexigua*; OD); *Anisoperna* Iredale, 1939, p. 321 (type, *Perna australica* Reeve, 1858, pl. 3; OD)]. Rhomboidal to pyriform, beak at anterior end of hinge margin, produced and pointing anteriorly; lower part of anterior margin in some species strongly convex and extending well forward of beak, entire anterior margin in other species straight or almost so and inclined so as to form slightly acute angle with hinge margin; hinge margin rather short, posterior wing obtuse and seldom well differentiated; ligamental grooves subequal, intervals between them lying in general plane of ligamental area; surface lamellose. *U.Trias.-Rec.*, cosmop.——Fig. C50,*2a-e*. *I. (I.) ephippium* (Linné), Rec., Mauritius; *2a,b*, RV ext., RV int., ×0.5 (Cox, n); *2c-e*, early ontogenetic stages, showing hinge teeth later obsolete, much enl. *(44)*.——Fig. C50,*2f,g*. *I. (I.) isognomonoides* (Stahl), M.Jur.(Bathon.); *2f*, Switz., RV, ×0.7 (Greppin, 1900); *2g*, Ger., LV ligamental area, ×0.7 *(341b)*.

I. (Hippochaeta) Philippi (*ex* Sangiovanni, MS), 1844, p. 55 [**Perna soldanii* Deshayes in Lamarck, 1836, p. 79 (=**P. maxillata* Lamarck, 1801, p. 134); M] [=*Hypochaeta* Zilch, 1938 (*nom. van.*)]. Large, rhomboidal or rectangular, usually slightly oblique, commonly very thick-shelled; beak terminal, posterior wing not differentiated; without ridge passing from beak to lower extremity of shell; ligamental grooves numerous, narrow and shallow, situated on platforms separated by deep, narrow, furrows; 3 accessory muscle scars present on posterodorsal part of shell interior, aligned obliquely and radially from beak. *Eoc.-Plio.*, cosmop.——Fig. C50,*1*. **I. (H.) maxillatus* (Lamarck), Plio., Italy; *1a*, LV. ext., ×0.5; *1b*, RV dorsal region int. showing ligamental area and accessory scars, ×0.3 (both Cox, n); *1c*, cross section of ligamental area showing deep furrows between ligamental grooves *(L)*, lower figs. corresponding cross section in 2 species of *I. (Isognomon)* (Zilch, 1938).

I. (Isogonum) Röding, 1798, p. 168 [**I. norma* (=**Ostrea isognomum* Linné, 1758, p. 699); T] [=*Pedalion* Dillwyn (*ex* Huddesford, vernac.), 1817, p. 282 (type, *Ostrea isognomon* Linné, 1764, =*O. isognomum* Linné, 1758; T); *Malleoperna* Iredale, 1939, p. 323 (type, *M. intricata*; OD)]. Medium large; tall, narrow, malleiform, rather irregular, with undulating commissure; narrow, moderately elongate posterior wing and small, pointed anterior wing

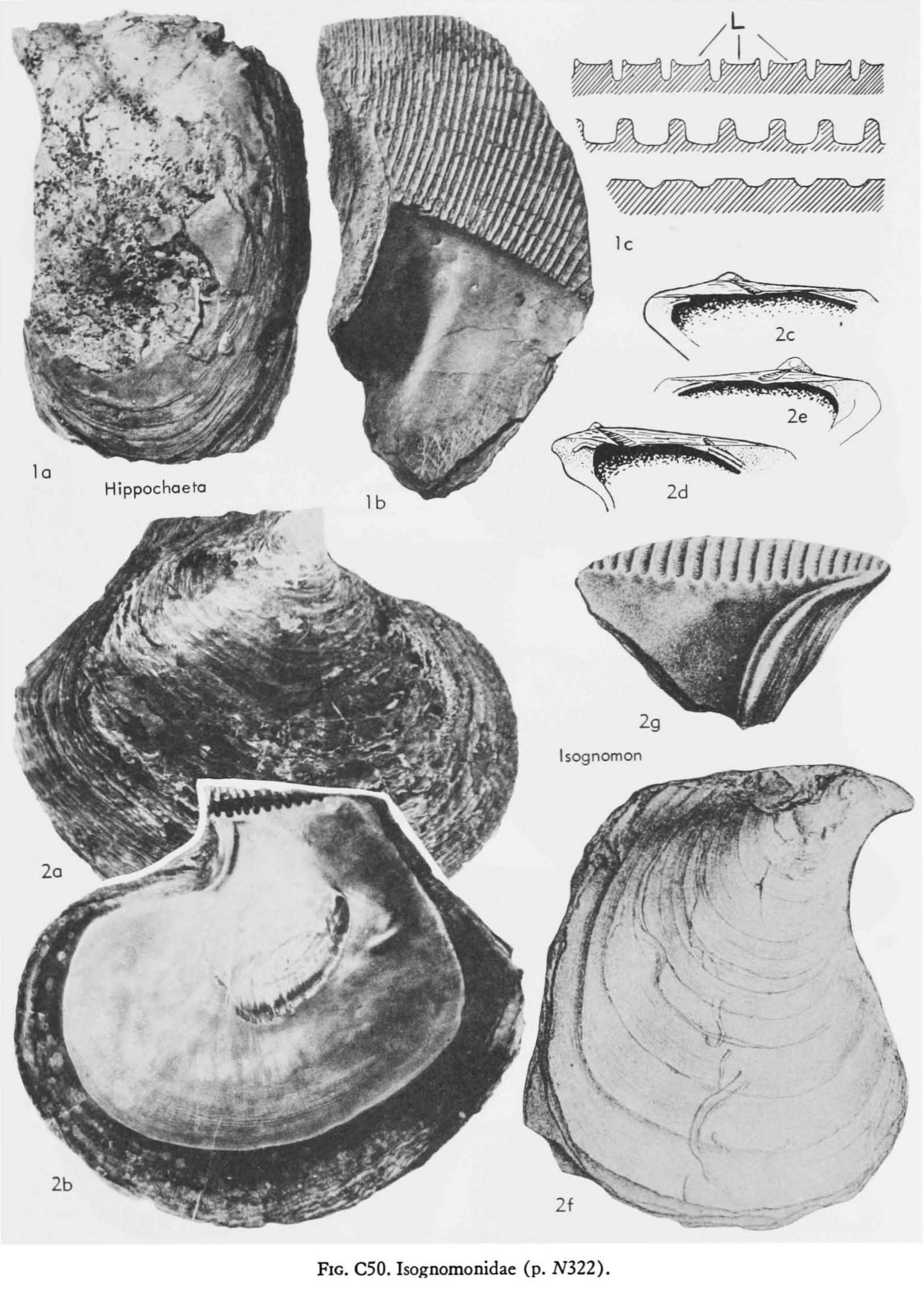

FIG. C50. Isognomonidae (p. *N*322).

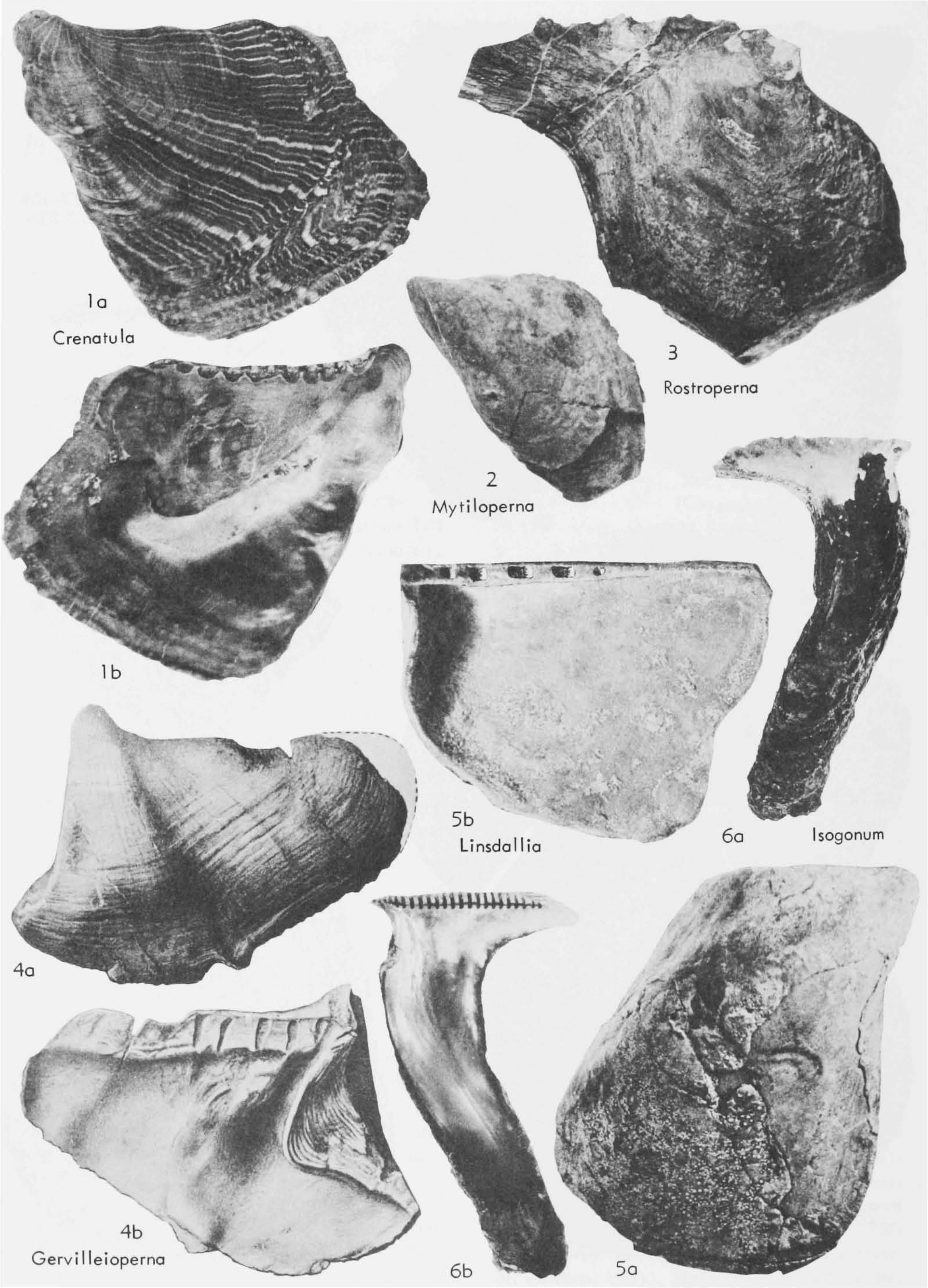

FIG. C51. Isognomonidae (p. *N*323, *N*325-*N*326).

commonly present; relatively thin-shelled for genus; ligamental grooves numerous and narrow, arranged as in *I. (Isognomon). Rec.,* IndoPac.-Australia.——FIG. C51,*6. I. (I.) isognomum* (LINNÉ), Ind.O.; *6a,b,* RV ext., RV int., ×0.3 (Cox, n).

I. (Mytiloperna) VON IHERING, 1903, p. 123 [**Perna americana* FORBES in DARWIN, 1846, p. 266; M] [=*Mytiloperna* ROLLIER, 1914, p. 426 (type, *Perna mytiliformis* SCHLIPPE, 1888, p. 141; SD Cox, herein), proposed independently]. Shell smaller than in other subgenera of *Isognomon,* equivalve, mytiliform, commonly with ridge running from subterminal beak to lower extremity; posterior wing undifferentiated; no distinct byssal gape; ligamental grooves depressed below their intervals as in *I. (Isognomon)* but fewer and more separated. *L.Jur. (Lias.)-U.Jur.,* cosmop.——FIG. C51,*2. I. (M.) murchisonii* (FORBES), M.Jur.(Bathon.), Scot. (Skye); LV ext., ×1.3 (Cox, n).

I. (Rostroperna) Cox, 1961 [**I. (R.) schencki*; OD]. Medium large, slightly inequivalve, resembling *I. (Isognomon)* but with elongate, sharply acute, beaklike posterior wing; ligamental grooves broad, irregular and unequal, with intervals as in *I. (Isognomon). Cret.,* Iran. ——FIG. C51,*3. *I. (R.) schencki*; RV, ×0.5 (Cox, n).

Crenatula LAMARCK, 1803, p. 30 [**C. avicularis*; SD STOLICZKA, 1871, p. 395] [=*Crenatuligenus* RENIER, 1807; *Cranatula* CHILDREN, 1823 *(nom. null.)*; *Dalacia* GRAY, 1825, p. 139 (type, *Crenatula folium* LAMARCK, 1803; M]. Medium-sized, subequivalve, compressed, length exceeding height to varying extent; bialate in earlier growth stages, later irregular in form with anterior wing small and round-margined, posterior wing undifferentiated; thin-shelled, foliaceous; no byssal gape (byssus obsolete); ligamental area narrow, undercut anteriorly; ligamental grooves shallow, semicircular, with relatively narrow intervals; adductor scar dorsally placed; commensal in sponges. *U. Tert.-Rec.,* IndoPac.-Australia-W.S.Am.——FIG. C51,*1. C. picta* (GMELIN), Rec., Red Sea; *1a,b,* LV ext., LV int., ×1 (Cox, n).

Gervilleioperna KRUMBECK, 1923, p. 76 [**G. timorensis*; M]. Large; LV moderately convex, with vertically extended cuneiform body, narrow, prominent umbo, and broad, greatly elongated posterior wing; beak strongly prosogyrous, with well-impressed lunule below it, margin of lunule with narrow byssal gape; RV imperfectly known; ligamental pits few, irregular, relatively narrow, with broader intervals. *L.Jur.(M.Lias.),* Timor.——FIG. C51,*4. *G. timorensis*; *4a,b,* LV ext., LV int., ×0.5 *(486).*

?**Leproconcha** GIEBEL, 1856, p. 67 [**L. paradoxa*; M]. Small, orbicular, externally like *Ostrea,* but with 3 or 4 ligamental pits. *M.Trias.,* Ger.

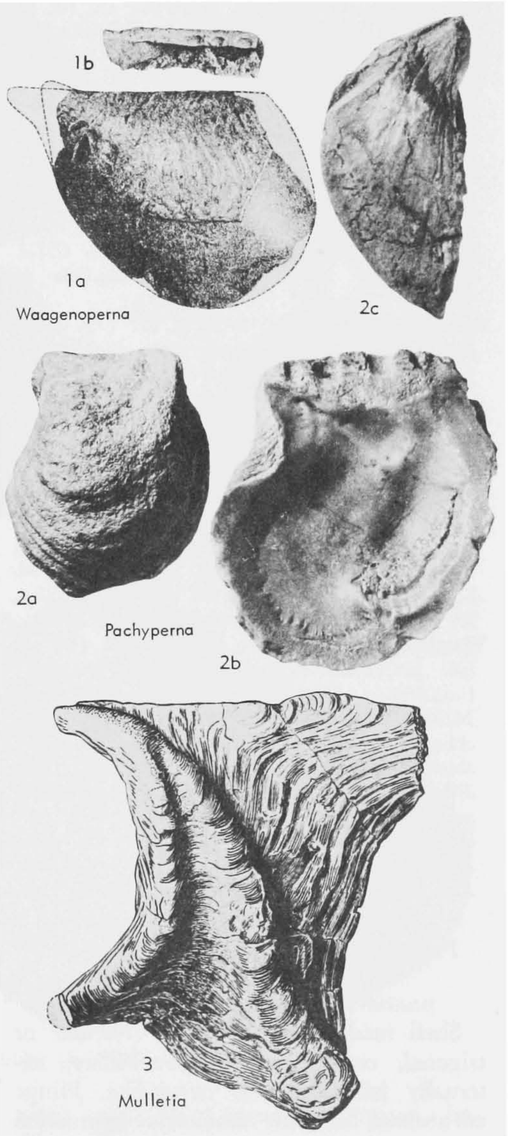

FIG. C52. Isognomonidae (p. *N*326).

Linsdallia COX & ARKELL, 1948, p. 48 [**Perna quadrata* J. DE C. SOWERBY, 1825, p. 149; OD]. Large, strongly inequivalve, broadly trapeziform, longer than high, posteriorly subalate, with relatively wide lunule and broad anterior gape; LV strongly inflated diagonally, with prominent umbo and strongly prosogyrous terminal beak; RV feebly convex; ligamental area rather narrow, well undercut anteriorly; ligamental pits broad, not numerous, irregularly arranged. *M.Jur.(Bajoc.),* Eng.——Fig. C51,*5*. **L. quadrata* (J. de C. Sowerby); *5a,b,* LV ext., RV int., ×0.7 (Cox, n).

Mulletia P. Fischer, 1886, p. 956 [**Perna mulleti* Deshayes in Leymerie, 1842, p. 8; OD]. Quadrangular, thick-shelled, with long attenuated posterior wing; slightly inequivalve; 2 broad, curved, riblike swellings in each valve diverging from umbo to ends of lower margin, where they form prominent projections; between latter valve margins project prominently outward to right; byssal gape narrow. *L.Cret.,* Eu.-S.Am.——Fig. C52,*3*. **M. mulleti* (Deshayes), Apt., Eng.(Isle of Wight); LV, ×0.45 (Woods, 1905).

Pachyperna Oppenheim, 1900, p. 237 [**P. laverdana*; M]. Moderately small, ovate, higher than long, not oblique, subequivalve, strongly convex; shell wall very thick; with small anterior auricle but with no differentiated posterior wing; umbones ill-defined, not protruding; anterior face with broad, shallow lunule but without byssal gape; ligamental area broad, with not more than 5 relatively wide pits; adductor scar large, situated near posterior margin. *Eoc.,* France-N.Italy. ——Fig. C52,*2*. *P. franci* (G. B. Sowerby), M. Eoc., France(Cotentin); *2a,* LV ext., ×0.85; *2b,c,* RV int. and anterior face, ×0.85 (Cox, n).

Waagenoperna Tokuyama, 1959, p. 151 [**Edentula lateplanata* Waagen, 1907, p. 97; OD] [=*Edentula* Waagen, 1907 (*non* Nitzsch, 1820)]. Mytiliform, subequivalve, compressed, oblique, with terminal or subterminal beaks; obsolescent anterior auricle, posterior wing undifferentiated; anterior teeth but no posterior teeth present in young shell, all teeth later obsolete. *U.Perm.-U.Trias.,* Eu.-Asia(Japan).——Fig. C52, *1*. **W. lateplanata* (Waagen), U.Trias., Japan; *1a,b,* LV ext. and ligamental area, ×0.85 *(950)*.

Family PULVINITIDAE Stephenson, 1941

[Materials for this family prepared by L. R. Cox]

Shell medium-sized, ovate, orbicular or trigonal, compressed, not auriculate; externally lamellose and oyster-like. Hinge edentulous, but with rather wide ligamental area in each valve bearing series of narrow, elongate, subparallel, transverse ligamental pits. RV flat or slightly concave, with circular byssal foramen below middle of ligamental area; LV feebly convex; with circular, radially striated byssal (pedal) retractor scar opposite foramen of RV; single adductor scar located medially in each valve; inner ostracum nacreous. *U.Jur.-Rec.*

This family is best known by the type genus, well-preserved specimens of a species of which are found in the Ripley Formation (U.Cret.) of Coon Creek, Tennessee. The discovery of the rare living genus *Foramelina* has confirmed the fact that the foramen in the right valve served for passage of a byssus. In this genus a suture leads from the foramen to the anterior extremity of the ligamental platform, suggesting that the foramen was derived from a byssal sinus by the closing of its margins and its migration inwards. A similar suture has not been observed in the fossil genera. The wide intervals of time that separate the known occurrences of the three genera belonging to this family might suggest that they had evolved independently. The three genera, however, agree so closely in shell morphology that it seems more probable that they are related lineally and that the wide stratigraphical gaps between their recorded occurrences are due to imperfection of the record.

Pulvinites Defrance, 1824, p. 316 [**P. adansoni*; M]. Orbicular or broadly trigonal; adductor scar orbicular, situated in the center of each valve and well separated from foramen or from corresponding byssal muscle scar; lower margin of ligamental area straight. *U. Cret. (Cenoman.-Maastricht.),* France-Lebanon-N.Am.——Fig. C53,*2*. *P. argenteus* (Conrad), Campan.(Ripley), USA(Tenn.); *2a,b,* RV ext., RV int. showing byssal foramen; *2c,d,* LV ext., LV int.; all ×0.7 *(951)*.

Foramelina Hedley, 1914, p. 70 [**F. exempla*; OD]. Trigonal, relatively large; adductor scar smaller than byssal muscle scar and separated from it by about its own breadth; lower margin of ligamental area straight; byssus a dense bundle of threads (not calcified as in *Anomia*). Rec., Australia.——Fig. C53,*3*. **F. exempla*; *3a,b,* RV ext., RV int., ×0.7 *(399)*.

Hypotrema d'Orbigny, 1853, p. 435 [**Pulvinites rupellensis* d'Orbigny, 1850, p. 24; SD Cox, herein]. Taller and narrower than *Pulvinites*; adductor scar in LV touching byssal muscle scar; ligamental area arched. *U.Jur.(Oxford.),* Eu. (France). —— Fig. C53,*1*. **H. rupellense* (d'Orbigny); *1a,* LV int. mold; *1b,* RV int. mold showing foramen; both ×1 (d'Orbigny, 1853; Fischer, 1886).

Family MALLEIDAE Lamarck, 1819

[*nom. correct.* Broderip, 1839 (*pro* Malleacea Gray, 1823)] [=les malléacées Lamarck, 1819 (family name now generally accepted as from this publication in the vernacular); Malleaceae Bronn, 1824; Mallacea Lea, 1833; Vulsellidae Adams & Adams, 1857; Eligmidae Gill, 1871; Stefaniniellidae Tavani, 1939] [Previously Bowdich (1822) and Parkinson (1822) have both used the name Malleaceae for groups of

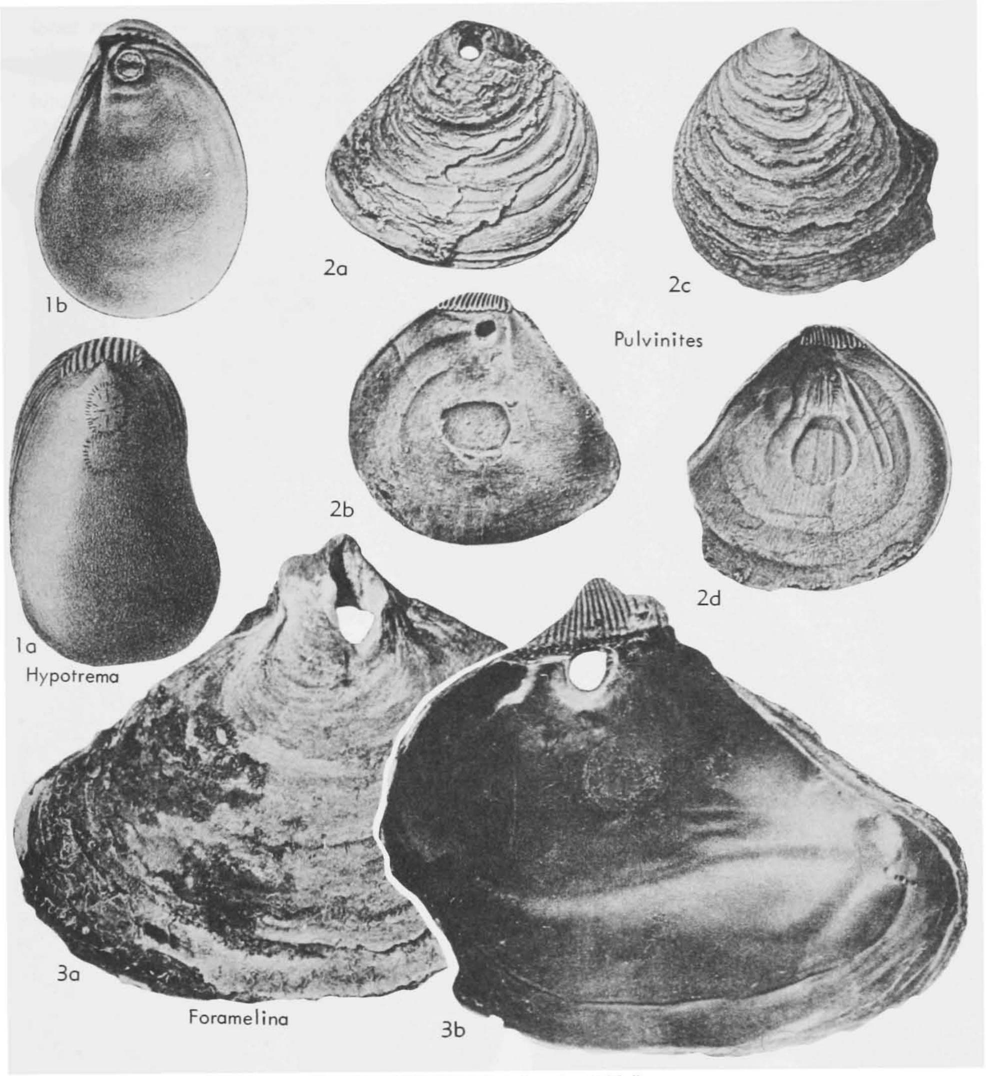

Fig. C53. Pulvinitidae (p. *N*326).

genera (alluded to as "divisions" in the case of the first author) which were virtually equivalent to families although not so termed] [Materials for this family prepared by L. G. Hertlein & L. R. Cox]

Shell subequivalve or inequivalve, irregular in form but not cemented by either valve, with or without byssus; valve margins commonly gaping or irregularly notched posteriorly; ligamental area triangular, internal to external, partly or almost wholly occupied by median triangular pit which is very much like that of *Ostrea,* but in some genera has strongly convex, protruding lower margin; mostly monomyarian in adult stage; inner ostracum nacreous. *Jur.-Rec.*

Malleus Lamarck, 1799, p. 82 [**M. vulgaris* (=**Ostrea malleus* Linné, 1758, p. 699); T] [=*Malligenus* Renier, 1807 (obj., also suppressed ICZN); *Malleolus* Rafinesque, 1815 (obj.); *Tudes* Oken, 1815 (ICZN rejected work) (obj.); *Himantopoda* Schumacher, 1817 (obj.); *Himanthopoda* Latreille, 1825 *(nom. null.)*; *Himotopoda* Paetel, 1875 *(nom. null.)*]. Subequivalve or inequivalve, with body of shell elongated dorsoventrally and not oblique; posterior wing variably developed, anterior wing present or absent; ligamental pit deep, oblique, semiconical, with projecting

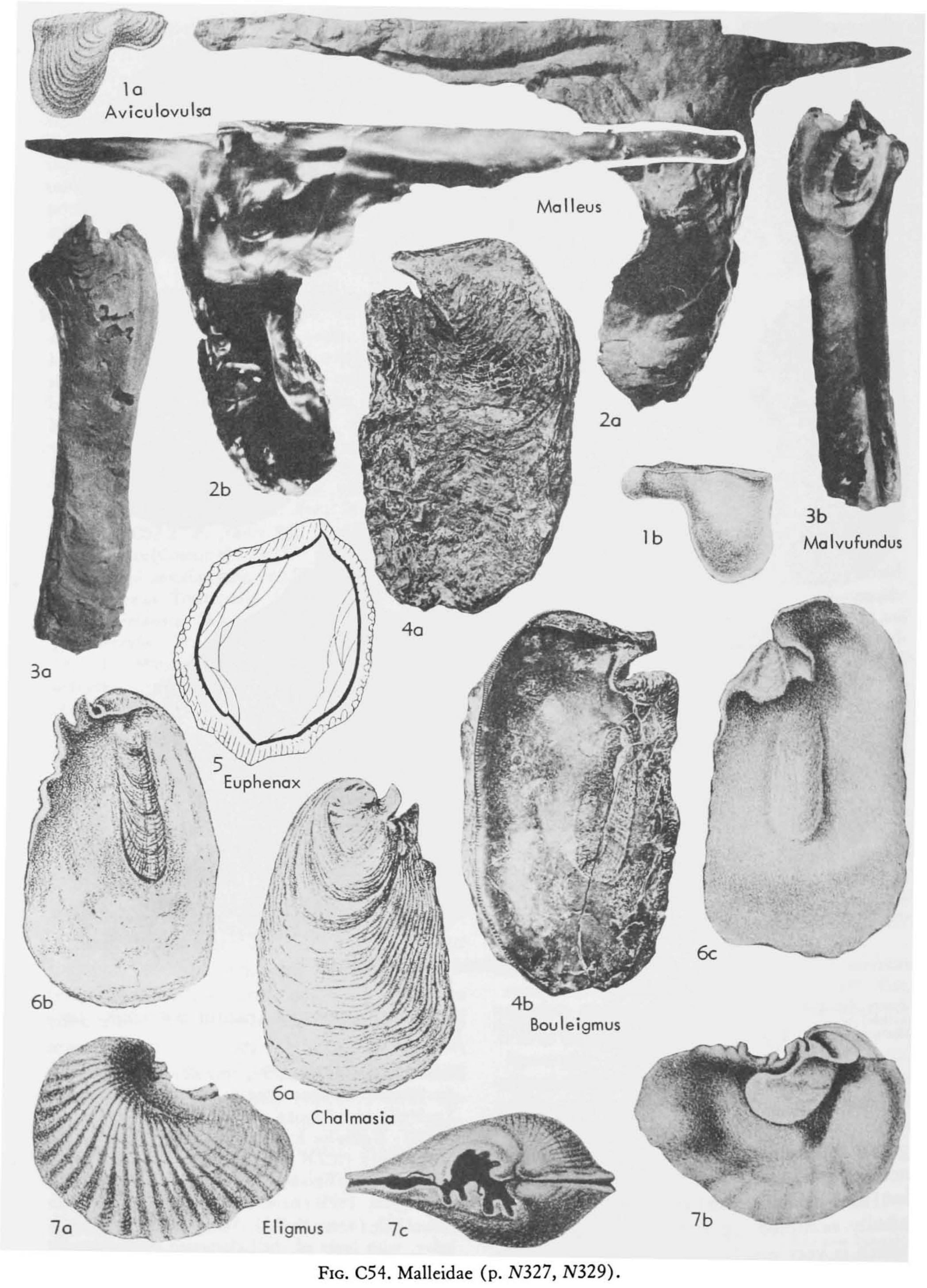

FIG. C54. Malleidae (p. N327, N329).

lower margin; dorsal margin of RV or of both valves deeply notched on anterior side of ligamental area for protrusion of byssus; no true hinge teeth; nacreous lining of shell interior much restricted, its border widely separated from margins of shell especially on body, more ventral part of which bears submedian internal ridge in each valve; muscle scar large, flush, variously shaped; valve margins smooth internally. *Rec.,* IndoPac.-Australia-Medit.

M. (Malleus). Subequivalve, hammer-shaped, with long, narrow, sharply pointed anterior and posterior wings, former commonly at lower level than latter; some species with fine crenellations along inner side of dorsal margin behind and in front of ligamental area; byssal notch narrow; body of shell commonly waved and irregularly lamellose. *Rec.,* IndoPac.——Fig. C54,*2*. **M. (M.) malleus* (Linné), China; *2a,b,* RV ext., int., ×0.5 (Cox, n).

M. (Malvufundus) de Gregorio, 1885, p. 122 [**Ostrea regula* Forskål, 1775, p. 124; SD Cox, herein] [=*Fundella* de Gregorio, 1884, p. 73 (*non* Zeller, 1848) (type, *F. lioyi*; M); *Parimalleus* Iredale, 1931, p. 205 (type, *P. cursator*; OD); *Parvimalleus* Salisbury, 1932 (*nom. null.*); *Brevimalleus* McLean, 1947, p. 70 (*pro Fundella* de Gregorio, 1884, *non* Zeller, 1848)]. Subequivalve or inequivalve; posterior wing short and blunt, anterior wing short or absent; byssal notch commonly relatively broad sinus; no internal crenulations of dorsal margins; earlier growth stages with irregular concentric lamellae. *Rec.,* IndoPac.-Australia-Medit.——Fig. C54,*3*. **M. (M.) regula* (Forskål), Ind.O.; *3a,b,* RV ext., RV int., ×0.5 (Cox, n).

Aviculovulsa Cossmann, 1887, p. 170 [**Avicula macrotis* Deshayes, 1864, p. 48; OD]. Shell small, oblique, resembling *Pteria;* with relatively large anterior ear, separated from body of shell by broad sinus; cardinal area narrow; muscle scar nearly central, transverse, bilobed above; surface concentrically lamellose. *M.Eoc.-U.Eoc.,* Eu.(France).——Fig. C54,*1*. **A. macrotis* (Deshayes), M.Eoc.(Lutet.); *1a,b,* RV ext., RV int., ×3 (Deshayes, 1864).

Bouleigmus Basse, 1933, p. 111 [**B. douvillei*; M]. Known only by RV, which is tall, subrectangular, flat, thick-shelled; umbo narrow, placed and pointing posteriorly, below it, deep notch of posterior margin, with its lower edge transversely wrinkled; muscle scar tall, narrow, flush; margins delicately denticulate internally; surface irregularly lamellose. *U.Cret.,* Madag.——Fig. C54,*4*. **B. douvillei*; *4a,b,* RV ext., RV int., ×0.7 *(31)*.

Chalmasia Stoliczka, 1871, p. 397 [**Vulsella turonensis* Dujardin, 1837, p. 228; OD] [=*Vulsellopsis* Douvillé, 1907, p. 17 (type, *Vulsella caillaudi* Zittel, 1881, p. 40; OD)]. Subequivalve, linguiform; valves gaping posterodorsally, where margins commonly have jagged or rounded projections, of which that closest to ligamental area may extend internally over its tip; ligamental area rather broad; muscle scar tall, narrow, slightly anterior to median with its posterior edge protruding; surface with concentric lamellae or undulations. *U.Cret.(Senon.)-Eoc.,* Eu.(France)-Afr.(Libya-Egypt).——Fig. C54,*6*. **C. turonensis* (Dujardin), U.Cret.(Senon.), France; *6a,b,* LV ext., LV int., ×1 (Fischer, 1886); *6c,* RV int., ×1 (Dujardin, 1837).

Eligmus J. A. Eudes-Deslongchamps, 1856, p. 272 [**E. polytypus*; SD Tate, 1868, p. 67] [=*Beaumontia* J. A. Eudes-Deslongchamps, 1856 (*non* Edwards & Haime, 1851); *Heligmus* Fischer, 1886 *(nom. van.)* (*non* Dujardin, 1845, *nec* Candèze, 1865); *Proheligmus* Cossmann, 1909 (*pro Eligmus* Eudes-Deslongchamps, 1856, *non Eligma* Huebner, 1816)]. Subequivalve, more or less ovate, compressed to moderately inflated, radially costate to varying extent; gaping posterodorsally where margins may also be notched; prominent myophorous platform present on interior of each valve close to ligamental area. *Jur.(Bathon.-Callov.),* Eu.-Asia-N. Afr.-E. Afr.-Madag.——Fig. C54,*7*. **E. polytypus,* Bathon., France; *7a-c,* LV ext., LV int., dorsal view, all ×1 (Eudes-Deslongchamps, 1856).

Euphenax Cox, 1931, p. 177 [**Pseudoheligmus? jamaicensis* Trechmann, 1923, p. 358; OD]. Ovate, moderately to strongly inflated, subequivalve to strongly inequivalve; valve margins closed except (in some specimens) for posterodorsal notch just behind ligamental area; ostracum thick, with cavernous outer layer composed of prismatic cells, compact middle layer, and chambered inner layer; no myophorous platform; exterior with or without radial ribbing. *M.Eoc.,* Jamaica-N.Afr.-Pakistan.——Fig. C54,*5*; C55,*2*. **E. jamaicensis* (Trechmann); C54,*5,* Pak., transv. sec. showing internal chambers, ×1.3 *(173)*; C55,*2a-c,* Somaliland, RV int. and 2 views RV ext., ×1 *(173)*.

Heligmina Douvillé, 1907, p. 109 [**Ostrea uncinata* Lamarck, 1806, p. 164; SD Cox, herein]. Ovate to subtrigonal, slightly higher than long, LV inflated, RV flat, both valves with large rounded sinus of posterodorsal margin extending to region of muscle scar, which is flush and almost median in position; ligamental area acutely triangular; surface concentrically lamellose. *U. Cret.,* Madag., *M.Eoc.-L.Mio.,* Eu.(France).——Fig. C55,*1*. **H. uncinata* (Lamarck), M.Eoc., Paris Basin; *1a,b,* LV int., RV int., ×2 *(273)*.

Heligmopsis Munier-Chalmas in Fischer, 1886, p. 926 [**Ostrea petrocoriensis* Coquand, 1869, p. 92; OD]. Ovate, somewhat elongated dorsoventrally, subequivalve, rather feebly inflated, not gaping, *Lopha*-like, with broad radial ribs producing irregular plications of margin on both sides or on posterior side only; muscle scar elongate, ventrally situated, raised on its posterior side. *U.Cret.(Cenoman.-Coniac.),* Eu.(France); *?Eoc.,* Egypt.——FIG. C55,*3*. **H. petrocoriensis* (COQUAND), Coniac., France.; *3a,b*, LV ext., LV int., ×1 *(273)*.

Nayadina MUNIER-CHALMAS, 1864, p. 99 [**N. heberti*; M] [=*Naiadina* FISCHER, 1886 *(nom. van.)*]. Subequivalve, of various shapes, commonly elongate and inequilateral; valves with or without narrow, simple gape; ligamental area well exposed to exterior, with broad, deeply concave liga-

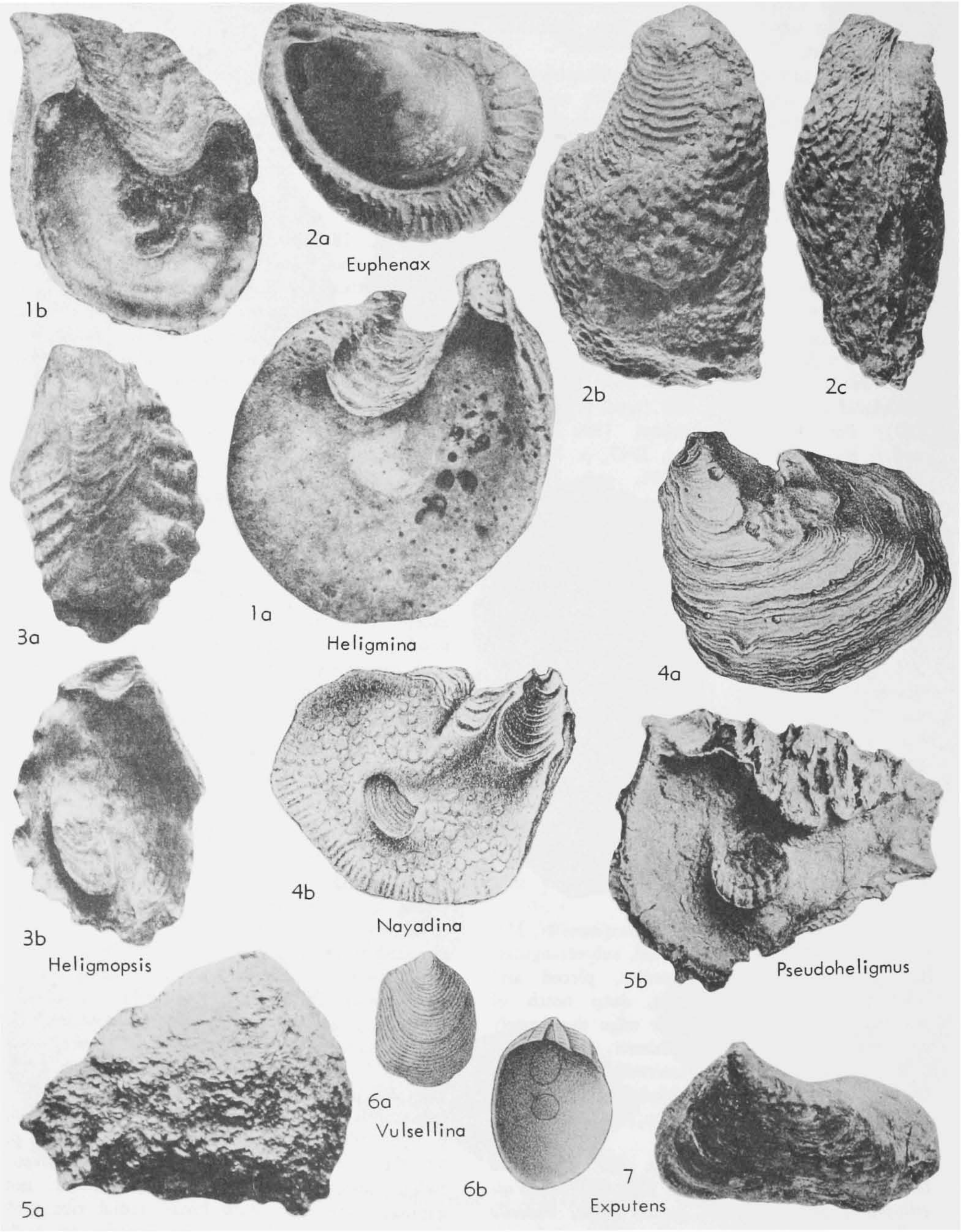

FIG. C55. Malleidae (p. *N*329-*N*332).

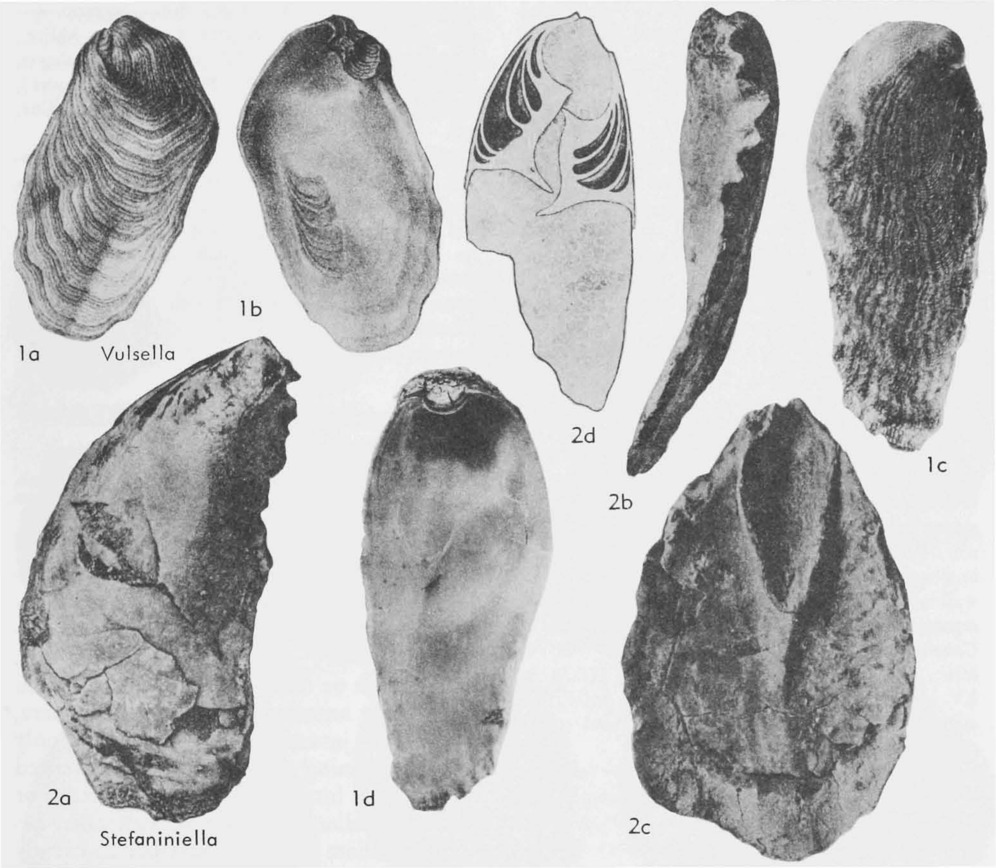

Fig. C56. Malleidae (p. *N*332).

mental pit occupying most of its width; muscle scar (or main scar) placed in relatively ventral position. *U.Cret.(Cenoman.)-M.Eoc.,* Eu.-N.Am.-N.Afr.-SW. Asia.

N. (Nayadina). Rather thick-shelled, more or less lunate, variably elongated; gape of valves narrow and simple or absent; muscle scar rather small, with projecting lower margin; exterior lamellose. *U.Cret.(Cenoman.-U.Senon.),* Eu. (France)-Persia-Madag.-N.Afr.——Fig. C55,*4*. *N. (N.) gaudryi* Thomas & Peron, Cenoman., Tunisia; *4a,b,* LV ext., LV int., ×0.7 (Peron, 1893).

N. (Exputens) Clark, 1934 [**E. llajasensis*; OD]. Elongate, oblong, inequilateral, with posterior end extended; subauriculate anteriorly; valve margins not gaping; umbones commonly pointed and prominent; ligamental area broad, overhanging platform extending posterior from umbones; small anterior adductor scar present in addition to main scar; surface smooth except for well-marked growth lines. *M.Eoc.,* USA-(Calif.)-Carib.(Jamaica).——Fig. C55,*7*. *N. (E.) llajasensis*; LV ext., ×1 *(134)*.

Ostreinella Cossmann in Cossmann & Peyrot, 1914, p. 398 [**Ostrea neglecta* Michelotti, 1847, p. 81; OD]. Shell very small, less than 18 mm. high, thin, fragile, translucent; both valves convex, LV deeper; outline oblique oval, opisthocline at 35 to 60 degrees to hinge line; LV umbo small, pointed, not projecting much above hinge axis, pointing posteriorly and outward, cavity on inside reaches beneath hinge plate up to tip of umbo; commissural shelf of LV exceedingly narrow, distinct only near hinge in few old individuals, rarely with 5 or 6 simple pits on one side; attachment scar generally long and narrow (about 1 by 9 mm.); both valves without radial ribs but with low smooth minor concentric undulations and few smooth appressed growth squamae; ligamental area 1.5 to 2 times longer than high. [Listed by author as subgenus of *Liostrea* (Ostreidae), but Glibert & Van de Poel (1965, p. 6) have pointed out that genus belongs rather in Vulsellidae.] *Oligo.(Tongrian)-Mio.(Tortonian),* S.Eu.(France-Italy).

Pseudoheligmus DOUVILLÉ, 1904, p. 264 [**P. morgani*; M]. Of various shapes, equivalve, with posterior depression in which are long, narrow, simple or bifurcating marginal fissures; muscle scar more or less median in position, on elevated platform as in *Eligmus*; surface with small, convex, quincuncially arranged scales (in type species) or merely irregularly rugose. *U.Cret.(Santon.)-M.Eoc.,* Iran-Eu.(France).——FIG. C55,*5*. *P. trigoniaeformis* (COQUAND), U.Cret.(Santon.), France; *5a,b,* RV ext., RV int., ×1 *(273)*.

Stefaniniella TAVANI, 1939, p. 94 [**S. colosii*; M]. More or less inequivalve, tall, linguiform, oysterlike; with undulating posterior margin but without posterior gape; ligamental pit large, internal or subexternal, hollowed-out spoonlike process representing entire ligamental area and welded to interior of valve by shelly matter continued as ridge below lower extremity of process; muscle scar submedian, with slightly raised margins; anteromedian part of shell wall, including part of wall of ligamental process, divided into chambers separated by thin, curved lamellae. *U.Cret.(U.Cenoman.),* Somaliland.——FIG. C56,*2*. **S. colosii*; *2a,b,* LV direct and post. views, ×0.7; *2c,* LV int. showing large ligamental pit, ×0.7; *2d,* transv. sec. showing chambering of dorsal region of shell, ×1 (Tavani, 1939 & 1942).

Vulsella RÖDING, 1798, p. 156 [**V. major* (=**Mya vulsella* LINNÉ, 1758, p. 671); SD PRASHAD, 1932, p. 88, also ICZN Opinion 325 (1955)] [*Mya vulsella* LINNÉ was not the type species of *Vulsella* by absolute tautonymy, as RÖDING recognized 2 nominal species of *Vulsella (V. major, V. minor)* and included *Mya vulsella* (in part) in the synonymy of both. By placing *Vulsella* on the Official List of Generic Names in Zoology this Opinion has dismissed the objection that etymologically it was a virtual homonym of *Volsella* SCOPOLI, 1777] [=*Vulselligenus* RENIER, 1807 (suppressed ICZN); *Reniella* SWAINSON, 1840, p. 386 (type, *R. dilatata*; M); *Vulcella* D'ORBIGNY, 1846 *(nom. null.)*; *Baphia* "GEVERS" GRAY, 1847, p. 199 (obj.); *Pulsella* WEYENBERGH, 1875 *(nom. null.)*; *Valsella* MARTENS, 1880 *(nom. null.)*; *Abisa* DE GREGORIO, 1884, p. 58 (type, *Vulsella navicula* DE GREGORIO, 1884; SD COX, herein); *Madrela* DE GREGORIO, 1884, p. 62 (type, *Vulsella virginis* DE GREGORIO, 1884; SD COX, herein); *Madrila* FUCHS, 1887 *(nom. null.)*]. Shell elongated dorsoventrally, linguiform, subequivalve, compressed, gaping anteriorly and posteriorly; ears absent or small; muscle scar smaller than in *Malleus,* flush; surface concentrically lamellose, radial ribbing present in some forms; not byssiferous; living forms commonly commensal in sponges. *U.Cret.(Cenoman.)-Rec.,* cosmop.——FIG. C56,*1a,b*. *V. deperdita* LAMARCK, M.Eoc., France; *1a,b,* LV ext., LV int., ×1 (Deshayes, 1832).——FIG. C56,*1c,d*. **V. vulsella* (LINNÉ), Rec., Ind.O.; *1c,d,* LV ext., LV int., ×0.7 (Cox, n).

Vulsellina RAINCOURT, 1876, p. 290 [**V. chaussyensis*; M] [=*Vulsinella* DALTON, 1876 *(nom. null.)*]. Small, subrectangular, flattened; ligamental pit narrow; muscle impression situated very close to ligamental area, and with another small impression below it on adult shells; surface unornamented except for growth rugae. *M.Eoc.(Lutet.),* Eu.(France).——FIG. C55,*6*. **V. chaussyensis*; *6a,b,* RV ext. and int., ×3 *(160)*.

Superfamily PECTINACEA Rafinesque, 1815

[*nom. transl. et correct.* DALL, 1896 (*ex* subfamily Pectenia RAFINESQUE, 1815)] [=Pectinidae FLEMING, 1822; Pectenacea REEVE, 1841] [Superfamily diagnosis prepared by N. D. NEWELL] [Materials on this superfamily prepared by L. G. HERTLEIN, L. R. COX, and N. D. NEWELL]

Adult shells generally orbicular, monomyarian, subequilateral, with winglike extensions of hinge margin (auricles); pleurothetic, with RV underneath when at rest; free, byssate or cemented, with byssal notch below right anterior auricle in most genera, at least in juveniles; sculpture commonly radial, becoming plicate in some advanced forms; main inner layer of shell nacreous or crossed-lamellar aragonite in Paleozoic, becoming foliate calcite in Mesozoic, usually with thin outer prismatic layer, especially in RV; ligament area alivincular, diverging upward in most Paleozoic forms, becoming internal in most post-Paleozoic shells. *Ord.-Rec.*

Family PTERINOPECTINIDAE Newell, 1938

[Materials for this family prepared by N. D. NEWELL]

Prosocline or upright pectinoids with posterior auricle longer and less well differentiated; cardinal areas divergent upward, ligament duplivincular. *U.Sil.-L.Perm.(Leonard.)*.

Pterinopecten HALL, 1883 [**P. undosus*; SD S. A. MILLER, 1889, p. 507]. Orbicular or subrhomboidal shells with intercalating costae; rear auricle poorly differentiated; byssal notch of RV narrow, slitlike. *U.Sil.-U.Dev.,* cosmop.

P. (Pterinopecten). Hinge margin shorter than shell height. *U.Sil.-U.Dev.,* cosmop.——FIG. C57,*6*. **P. (P.) undosus,* M.Dev. (Hamilton), USA (N.Y.); *6a,b,* RV ext., LV ext., ×1 *(376)*.

P. (Fascinewellipecten) Růžička, Prantl & Přibyl, 1959 [**Aviculopecten consolans* Barrande, 1881; OD]. Closely similar to *P. (Newellipecten)* but with fasciate costae. *L.Dev.,* Eu. (Boh.-Ger.).——Fig. C57,*1*. **P. (F.) consolans* (Barrande), Boh.; LV ext., ×1 *(820)*.

P. (Newellipecten) Růžička, Prantl, & Přibyl, 1959 [**Aviculopecten niobe* Barrande, 1881; OD]. Hinge margin longer than shell height. *L.Dev.,* Eu.——Fig. C57,*3*. **P. (N.) niobe* (Barrande), Boh.; LV ext., ×1 *(27)*.

P. (Vertumnia) Hall, 1884 [**Pterinea reversa* Hall, 1883; SD Pohl, 1929, p. 59]. Similar to *P. (Pterinopecten)* but with widely spaced costae and reversed convexity, LV flattened or concave in adults and RV convex. *M.Dev.,* N.Am.(USA).

Anulipecten Růžička, Prantl, & Přibyl, 1959 [**Aviculopecten amicus* Barrande, 1881; OD].

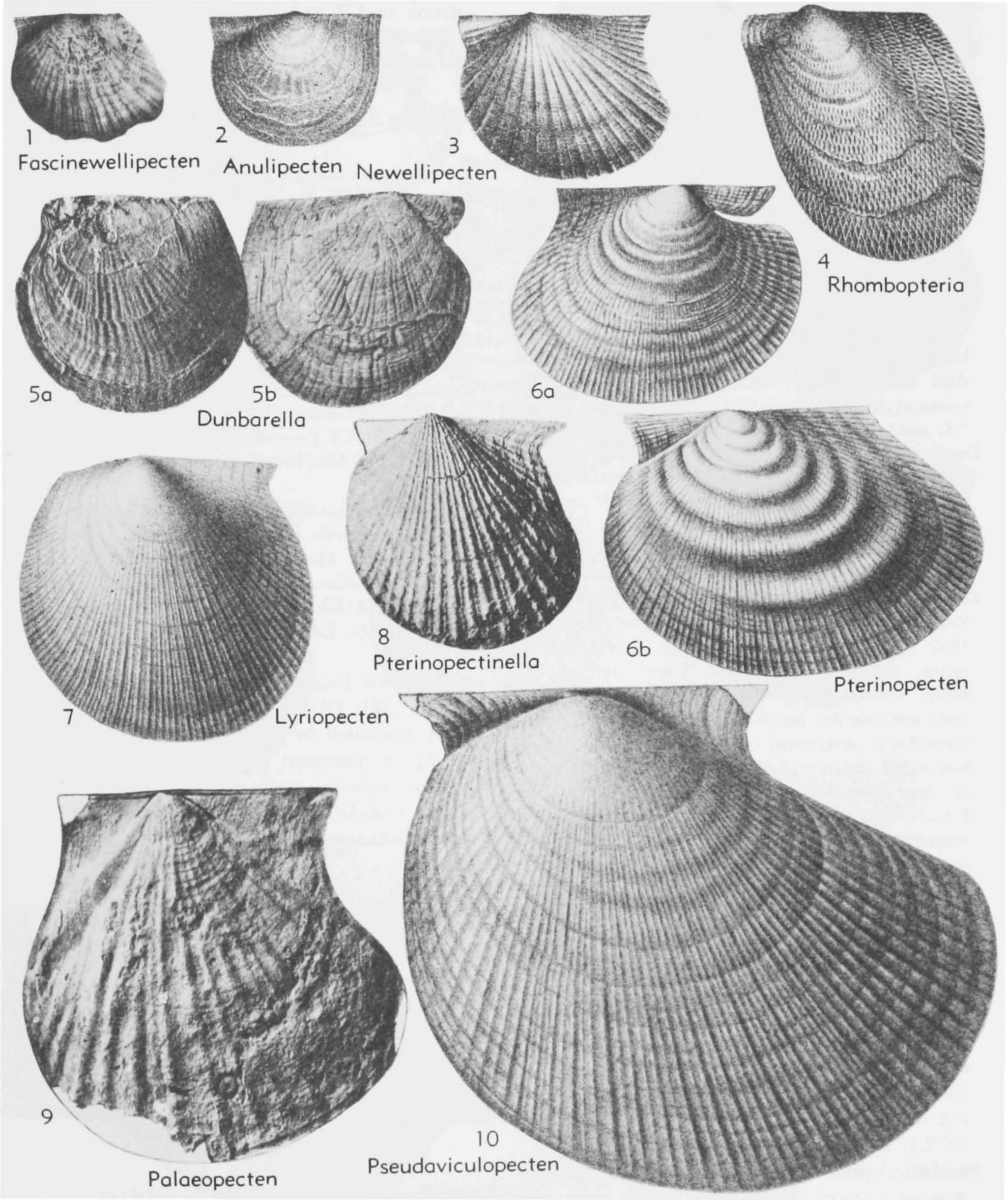

Fig. C57. Pterinopectinidae *(1-3,5-8,10)*; Leiopectinidae *(4,9)* (p. *N*332-*N*334).

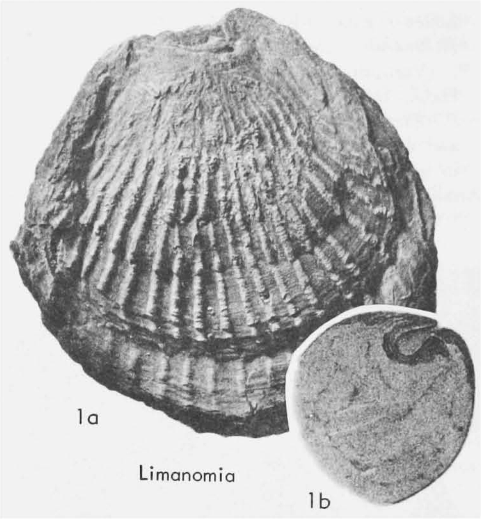

FIG. C58. Pterinopectinidae (p. N334).

Hinge margin longer than shell height; body of shell sculptured by concentric fila; costellae obsolescent or lacking. _L.Dev.,_ Boh.——FIG. C57,_2_. *_A. amicus_ (BARRANDE); LV ext., ×2 _(27)._

Dunbarella NEWELL, 1938 [*_Aviculopecten whitei_ MEEK, 1872; OD]. Similar to _Pterinopecten (Pterinopecten)_ except that costae of RV increase in number by bifurcation. _Miss.-Penn.,_ N.Am.-Eu.——FIG. C57,_5_. *_D. whitei_ (MEEK), Penn. (Virgil.), Neb.; _5a,b,_ LV ext., RV ext., ×2 _(663)._

Limanomia GRAY, 1850, p. 21 [*_L. grayiana_; SD STOLICZKA, 1871, p. 477] [=_Limanomya_ RIGAUX, 1892 _(nom. van.)_]. Suborbicular, subequilateral, acline, with relatively short hinge margin; LV feebly convex, RV flat or slightly concave, with deep subauricular notch, broadening inward; ligamental area unknown; ornament of narrow lamellose radial riblets of 1 or 2 orders of strength, more or less irregularly distributed. _U.Dev.(Frasn.),_ Eu. (N. France)-USSR (Novaya Zemlya). [?Senior subjective synonym of _Lyriopecten_ HALL.].——FIG. C58,_1a_. *_L. grayiana_, France (Boulonnais); LV ext., ×1 (Cox, n).——FIG. C58,_1b_. _L. lincolata_ RIGAUX, France (Boulonnais); subauricular notch in RV, ×1 (Rigaux, 1892). [Cox]

Lyriopecten HALL in S. A. MILLER, 1877 [*_Avicula orbiculata_ HALL, 1843; M] [=_Orbipecten_ FRECH, 1891 (obj.)]. Similar to _Pterinopecten_ except that ornamentation of LV in former is coarser, anterior auricles shorter and byssal notch of RV broadly sinuate. _M.Dev.-U.Dev.,_ N.Am.-Eu.——FIG. C57,_7_. *_L. orbiculatus_ (HALL), M.Dev., USA (N.Y.); LV ext., ×1 _(376)._

Pseudaviculopecten NEWELL, 1938 [*_Monotis princeps_ CONRAD, 1838; OD]. Shells with pronounced forward obliquity, auricles subequal and well differentiated from shell body in both form and ornamentation; sculptured with intercalating costae similar in both valves and transversed by fine fila. _M.Dev.-L.Miss.,_ N.Am.-Eu.——FIG. C57, _10_. *_P. princeps_ (CONRAD), M.Dev.(Hamilton), N.Y.; LV ext., ×1 _(376)._

Pterinopectinella NEWELL, 1938 [*_P. welleri_; OD]. Similar to _Pterinopecten_ but ornamented with coarse, spinose costae which increase by intercalation in LV and by splitting in RV. _U.Miss.-L.Perm.(Leonard.),_ N.Am.-Eu.——FIG. C57,_8_. *_P. welleri,_ U.Penn., Kans.; LV ext., ×1 _(663)._

Family LEIOPECTINIDAE Krasilova, 1959

[Materials for this family prepared by N. D. NEWELL]

Valves prosocline, LV more convex than RV, without well-defined byssal notch or sinus; ligament area narrow, duplivincular; short auricular crura occur internally marginal to the beaks. _Ord.-L.Dev._

Leiopecten KHALFIN, 1940, p. 259 [*_L. rectangularis_; OD]. Surface smooth or ornamented with concentric undulations. _U.Sil.-L.Dev.,_ USSR(Sib., Pribalkhash, Gorny Altae, Karaganda Basin); _L. Dev.,_ USA(N.Y.).——FIG. C59,_1_. *_L. rectangularis,_ L.Dev., Sib.(Pribalkhash), ×2.7 (Krasilova, 1963).

Palaeopecten WILLIAMS, 1913 [*_P. cobscooki_; OD] [=?_Leiopectinella_ KRASILOVA, 1959 (type, _Avicula subequilatera_ HALL, 1859)]. Ornamented by costae or costellae. _U.Sil.,_ USA(Me.); _L.Dev.,_ USA (N.Y.)-USSR(Sib., Pribalkhash).——FIG. C57,_9_. *_P. cobscooki,_ Edmunds F. (Me.); LV ext., ×1 _(985)._

Rhombopteria JACKSON, 1890 [*_Avicula mira_ BARRANDE, 1881; OD]. Rhomboidal, nearly equivalve shells sculptured by 2 sets of fine grooves intersecting in quincunx; posterodorsal angle obtuse; anterior auricles small, sinuate, without byssal notch. _Ord.-Sil.,_ N.Am.-Eu.——FIG. C57,_4_. *_R. mira_ (BARRANDE), Sil., Boh.; LV ext., ×2 _(27)._

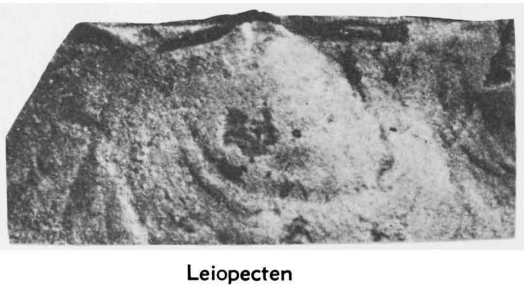

FIG. C59. Leiopectinidae (p. N334).

Family AVICULOPECTINIDAE Meek & Hayden, 1864

[*nom. transl.* S. A. MILLER, 1889 (*ex* Aviculopectininae MEEK & HAYDEN, 1864)] [Materials for this family prepared by N. D. NEWELL with additions by L. R. COX and L. G. HERTLEIN as indicated]

Pectiniform shells in which RV possesses deep byssal notch at least in early ontogeny and is less convex than LV; ligament amphidetic and situated on two flat, diverging interareas, as in *Lima* and *Pinctada*; characteristically with triangular, oblique, subcentral resilifer beneath beak; edentulous, inner shell layer aragonite, nacreous or crossed lamellar; outer layer prismatic or fibrous. *U.Dev.-U.Jur.*

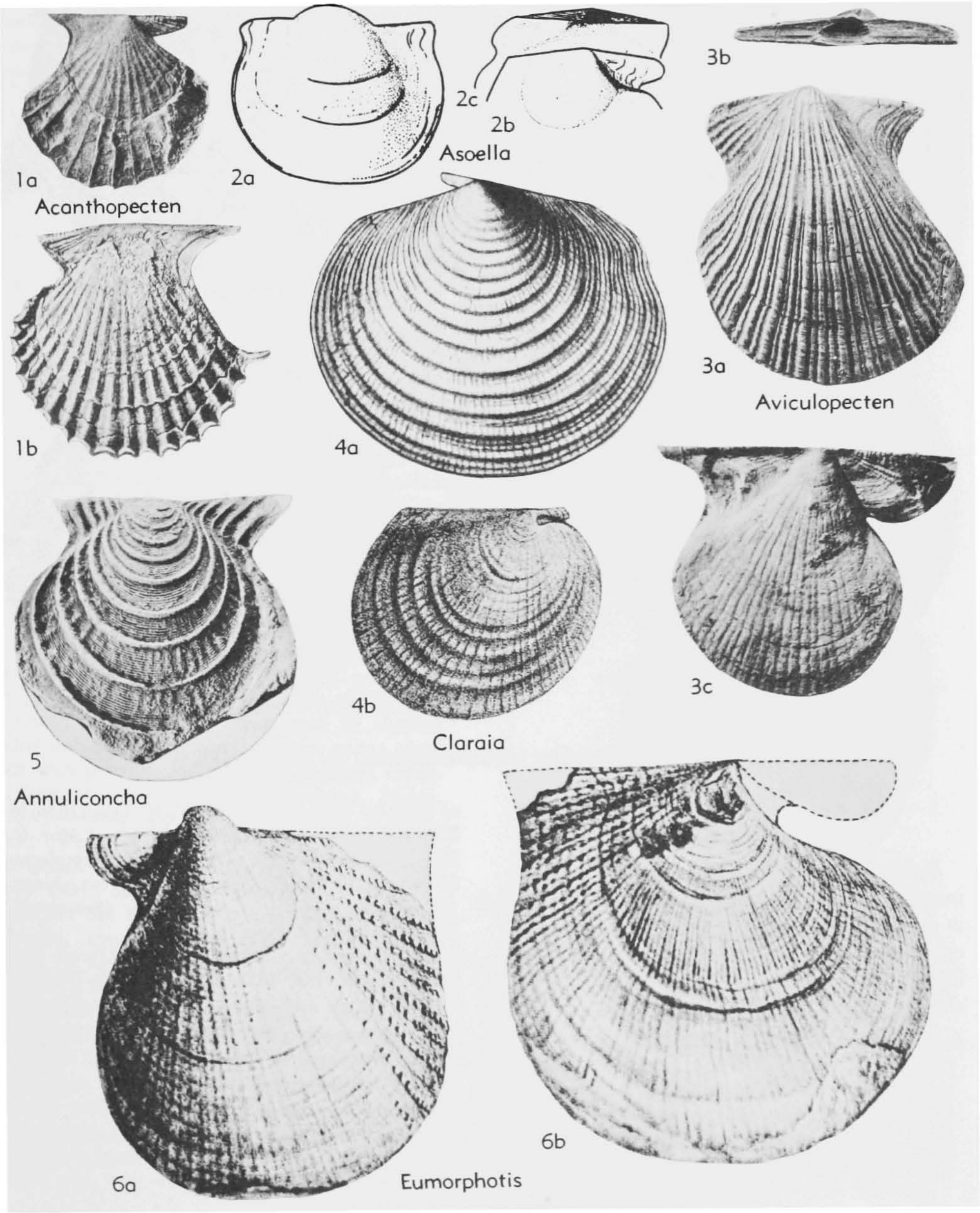

FIG. C60. Aviculopectinidae (Aviculopectininae) (p. *N*336-*N*337).

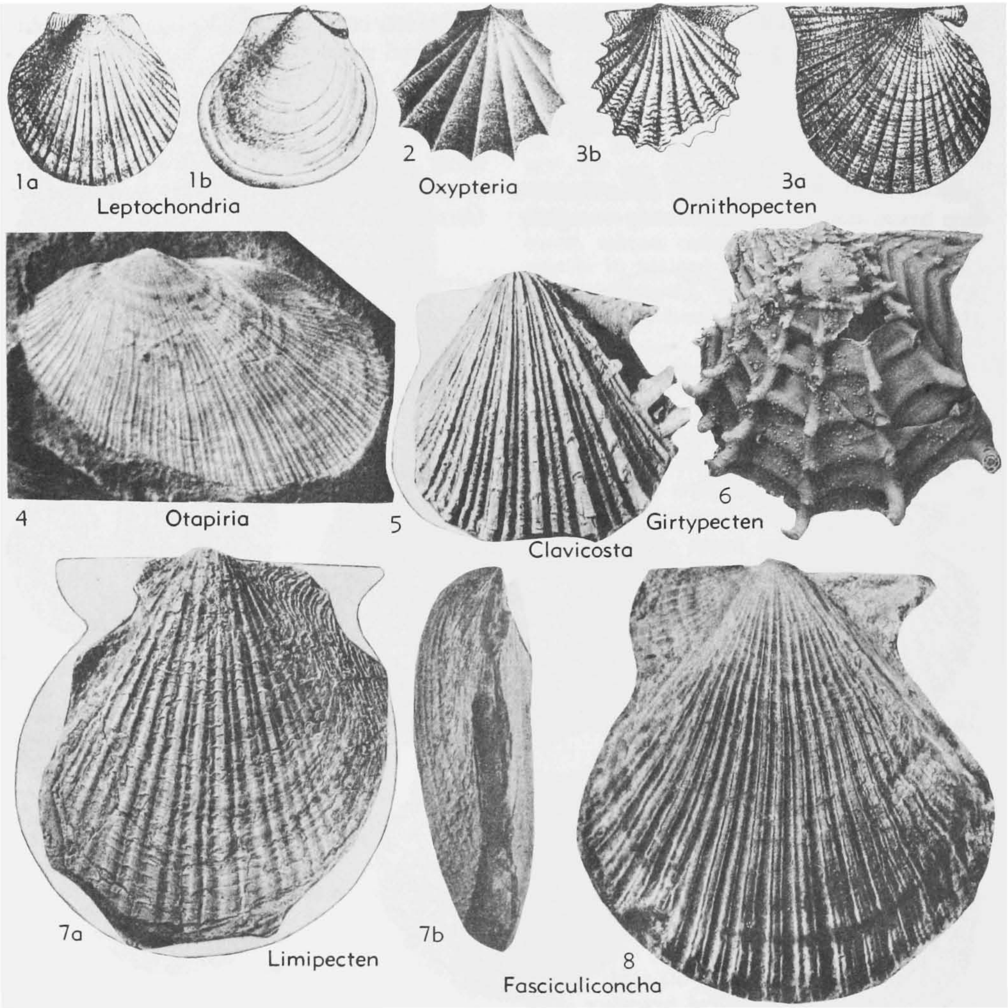

FIG. C61. Aviculopectinidae (Aviculopectininae) (p. *N*337-*N*339).

Subfamily AVICULOPECTININAE
Meek & Hayden, 1864

Prosocline to upright, radially ornamented, shells in which posterior auricle is as long as or longer than anterior; outer ostracum irregularly prismatic in RV, fibrous in LV; inner ostracum nacreous or crossed lamellar. *L.Miss.-U.Jur.*

Aviculopecten M'COY, 1851, p. 171 [**A. planoradiatus*; SD HIND, 1903, p. 66] [=*Limatulina* DE KONINCK, 1885 (type, *Avicula radula* DE KONINCK, 1842; *Heteropecten* KEGEL & DACOSTA, 1951 (type, *Aviculopecten catharinae* REED, 1930)]. Ornamentation radial, increasing on body of shell by intercalation in LV, by bifurcation in RV; RV commonly smaller than left. *L.Miss.-U. Perm.*, cosmop.——FIG. C60,*3a,b*. *A. exemplarius* (NEWELL), U.Penn., Kans.; *3a,b*, LV ext., hinge, ×2.——FIG. C60,*3c*. *A. occidentalis* (SHUMARD), U. Penn., Kans.; RV ext., ×2 *(663)*.

Acanthopecten GIRTY, 1903, p. 417 [**Pecten carboniferus* STEVENS, 1858, p. 261; OD]. Upright, orbicular shells with elongate, slender auricles, of which posterior is only slightly longer than anterior; costae coarse, not increasing in number during later ontogeny, crossed on LV, rarely on RV by regular imbricating growth lamellae which are extended peripherally between costae in short spines. *L.Carb.-U.Perm.*, cosmop.——FIG. C60,*1*.

**A. carboniferus* (Stevens), U.Penn., USA(Neb.); *1a,b,* RV ext., LV ext., ×2 *(663).*

Annuliconcha Newell, 1938, p. 76 [**Aviculopecten interlineatus* Meek & Worthen, 1860, p. 454; OD]. Equivalve, upright, orbicular shells with subequal, acute auricles; ornamented by 2 ranks of concentric, regularly spaced fila; radial ornamentation weak or absent. *L.Miss.-U.Perm.,* cosmop.——Fig. C60,*5.* **A. interlineata* (Meek & Worthen), U.Penn., USA(Ill.); LV ext., ×2 *(663).*

Asoella Tokuyama, 1959, p. 2 [**Eumorphotis (A.) confertoradiata*; OD]. Small (height *ca.* 10 mm.), quadrately suborbicular, almost acline; LV strongly convex, with broadly rounded, projecting umbo; RV feebly convex; wings of LV and right posterior wing subequal, obtuse or slightly acute, not well delimited, marginal sinus below each shallow or absent; right anterior auricle almost as long as posterior wing, subauricular notch relatively shallow; surface with fine radial riblets or smooth. *U.Trias.(Nor.),* Japan.——Fig. C60,*2. A. laevigata* (Tokuyama); *2a-c,* LV ext., dorsal part RV ext., int., all ×6 (Tokuyama, 1959). [Cox]

Claraia Bittner, 1901, p. 568 [**Posidonomya clarae* von Hauer, 1850, p. 112 (*ex* Emmrich, 1844, *nom. nud.*); SD Diener, 1923, p. 38]. Medium-sized, suborbicular, prosocline; LV feebly convex, with narrow, slightly protruding umbo, RV flat or feebly convex; posterior wings obtuse, left anterior wing small, acute, earlike; right anterior auricle small, subauricular notch narrow, widening inward; ornament of irregular concentric folds, and of faint radial costellae in some specimens; small attachment scar usually present. *L.Trias.,* cosmop.——Fig. C60,*4.* **C. clarae* (von Hauer), Werfen beds, S.Tyrol; *4a,* LV ext., ×1 (Wittenburg, 1910); *4b,* RV ext., ×1 *(60).* [Cox]

Clavicosta Newell, 1938, p. 79 [**C. echinata*; OD]. Equivalve, upright, orbicular shells with subequal, acute auricles; ornamented by regular, radial costae of which coarse, spinose costae alternate with pairs of smaller, equal papillose costae. *U. Penn.(Missouri.)-L. Perm.(Wolfcamp.),* N.Am. (USA).——Fig. C61,*5.* **C. echinata,* U.Penn., Tex.; LV ext., ×3 *(27).*

Etheripecten Waterhouse, 1963, p. 193 [**E. striatura*; OD]. Similar to *Aviculopecten* in most characters but RV bears intercalate, rather than bifurcate, costae. *Perm.,* Australia-N.Z.——Fig. C62,*1.* **E. striatura,* U.Perm., N.Z.; *1a,b,* RV ext., LV ext., ×2 *(958).*

Eumorphotis Bittner, 1901, p. 566 [**Pseudomonotis telleri* Bittner, 1898, p. 170; SD Cossmann, 1902, p. 75]. Medium-sized to large, acline or almost so; LV moderately convex, with rather narrow, prominent umbo, RV almost flat; posterior wings obtuse to slightly acute, with marginal sinus broad and shallow; left anterior wing narrow and very distinctly delimited from body of valve by deep sinus, right anterior auricle with narrow, rounded, moderately deep sinus below it, both shorter than posterior wings although not greatly reduced; ornament of radial ribs weaker on RV than on LV, or wanting. *L.Trias.-U.Trias.,* cosmop.——Fig. C60,*6. E. kittli* (Bittner), L. Trias., Dalmat.; *6a,b,* LV ext., RV ext., both ×1 *(60).* [Cox]

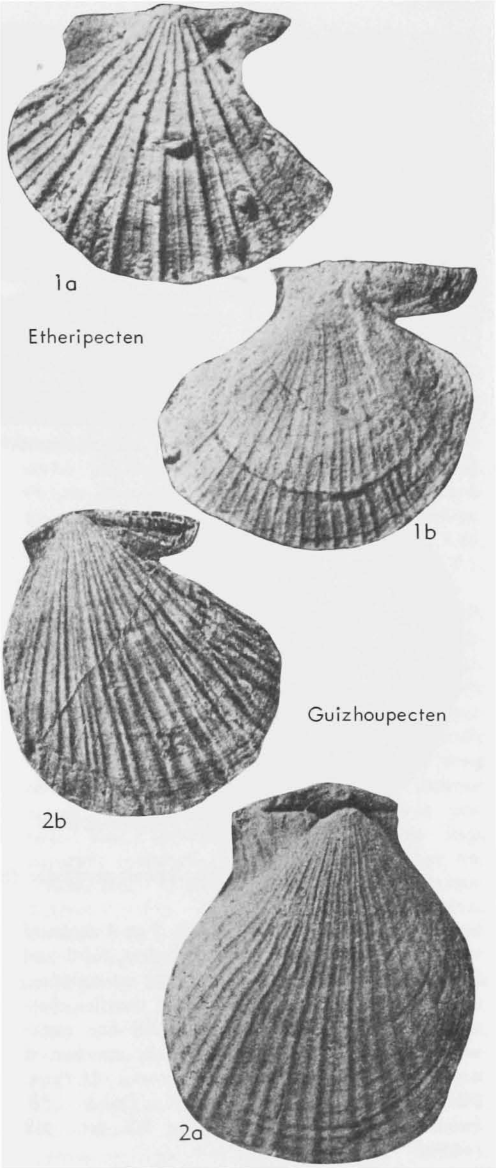

Fig. C62. Aviculopectinidae (Aviculopectininae) (p. *N*337-*N*338).

Fasciculiconcha Newell, 1938, p. 64 [**F. knighti*; OD]. Upright, equilateral shells with subequal

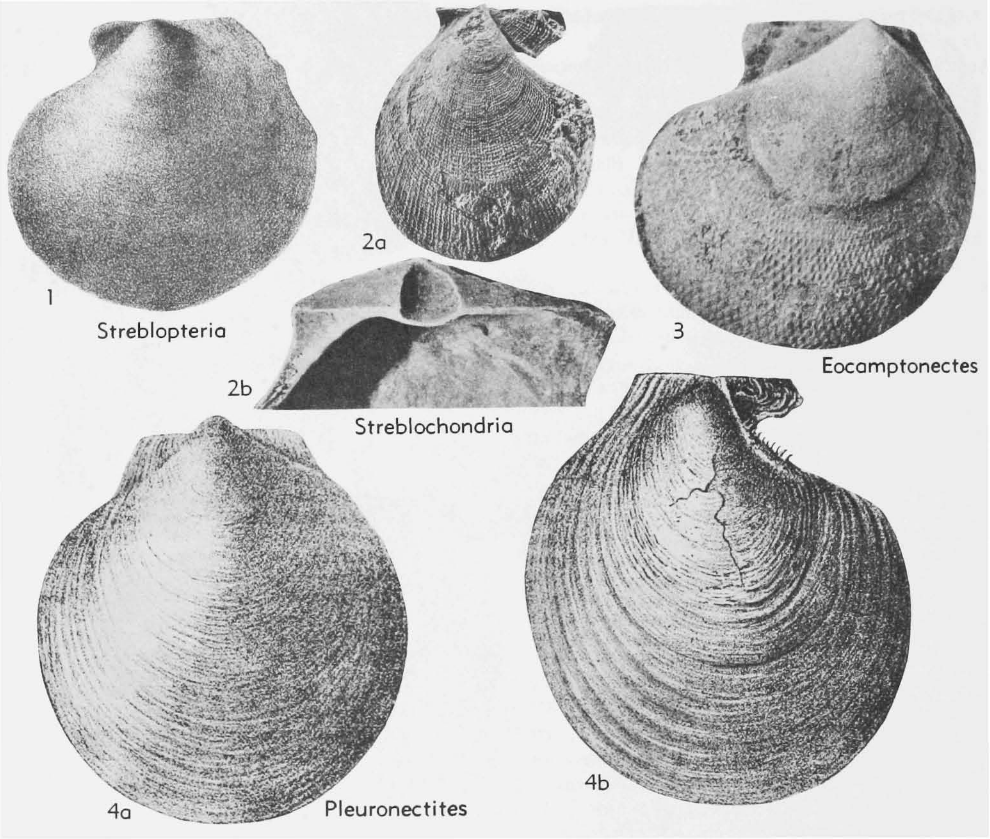

Fig. C63. Aviculopectinidae (Streblochondriinae) (p. *N*339).

auricles; costae of LV arranged in 3 or 4 ranks of which first 2 appear in early ontogeny; third and fourth series introduced later by intercalation, crowding closely to larger costae in bundles characteristic of genus; RV covered with fine costae which increase in number by periodic insertion of new elements. *M.Penn.(Desmoines.)-U.Penn.(Virgil.),* N.Am.(USA).——Fig. C61,*8*. **F. knighti,* U.Penn.(Missouri.), Mo.; LV ext., ×2 *(663).*

Girtypecten Newell, 1938, p. 77 [**Aviculopecten sublaqueatus* Girty, 1908, p. 440; OD]. Suborbicular shells ornamented with coarse, widely spaced costae intersected by similarly spaced concentric ridges; cylindrical, erect spines from intersections of radial and concentric ornamentation. *Perm.(Guadalup.),* USA(Tex.-Wyo.).——Fig. C61,*6*. **G. sublaqueatus* (Girty), Tex.; LV ext., ×2 (Newell, n).

Guizhoupecten Chen, 1962, p. 201 [**G. wangi*; OD]. Shell of *Streblochondria* form, but lacking strong concentric ornamentation; costae of LV intercalate, RV bifurcate; with or without auricular costae, umbonal folds broadly rounded; anterior auricle about twice as long as posterior; resilifer with slight backward obliquity, with additional narrow radial furrow on both anterior and posterior areas of resilifer. *Perm.(Leonard.-Guadalup.),* N.Am.(USA); *Perm.(Wuchiaping),* China.——Fig. C62,*2*. **G. wangi,* U.Perm.(Wuchiaping F.), China; *2a,b,* RV ext., LV ext., ×1 (Chen, 1962).

Leptochondria Bittner, 1891, p. 101 [**Pecten (L.) aeolicus*; M] [=?*Bittnerella* J. Böhm, 1903 (*non* Dall, 1898)]. Small, suborbicular or ovate, acline or slightly prosocline; LV moderately convex, with slightly protruding umbo, RV flat or almost so; beaks near middle of hinge margin; posterior wings and left anterior wing obtuse, indistinctly delimited; below right anterior auricle a deep narrow subauricular notch extending almost to beak; LV with radial riblets of at least 2 orders, new ones arising by intercalation; RV smooth or weakly ribbed; external ligamental area with obtusely triangular pit. [This genus includes some of the small Triassic forms which authors have referred to *"Velopecten."*] *L.Trias.-U.Trias.*, cosmop.——Fig. C61,*1*. *L. tirolica* (Bittner), U. Trias., S.Tyrol; *1a,b,* LV ext., RV ext., both ×3 *(58)*.——Fig. C94,*1*. **L. aeolica* (Bittner), Asia M.; *1a-c,* LV ext., RV ext., hinge, ×1 *(56)*. [Cox, Hertlein]

Limipecten Girty, 1904, p. 721 [**L. texanus*; OD]. Orbicular, robust shells with intercalating costae, those of RV appreciably finer and more numerous than those of LV; fine, concentric ornamentation of imbricating growth lamellae projecting peripherally between costae as short spines. *U.Miss.-L.Perm.(Wolfcamp.),* Eu.-N.Am.——Fig. C61,*7*. **L. texanus,* U.Penn., Tex.; *7a,b,* LV ext., ant., ×1 *(663)*.

Ornithopecten Cox, 1962, p. 596 [**Aviculopecten bosniae* Bittner, 1903, p. 592; OD]. Small, suborbicular, acline to slightly prosocline; left umbo scarcely projecting; posterior wings pointed, more or less acute, not well delimited, marginal sinus below each shallow in most species; left anterior wing and right anterior auricle relatively small, subauricular sinus shallow to moderately deep; ornament of narrow, well-separated radial riblets, any increase of which in either valve is by intercalation, and of concentric lamellae. *M.Trias.-U. Trias.,* Eu.(Bear Is.).——Fig. C61,*3a*. **O. bosniae* (Bittner), M.Trias.(Anis.), Yugosl.; RV ext., ×1.——Fig. C61,*3b*. *O. beneckei* (Bittner), U.Trias.(Carn.), S.Tyrol; LV ext., ×1.6 *(58)*. [Cox]

Otapiria Marwick, 1935, p. 302 [**Pseudomonotis marshalli* Trechmann, 1923, p. 270; OD]. Medium-sized, ovate, rather elongated, prosocline; LV feebly convex, with broad, scarcely protruding umbo, RV flat; posterior wings very obtuse or rounded, without marginal sinus, and quite undemarcated from body of shell; no left anterior wing, anterior and anterodorsal margins meeting in even curve; very small right anterior auricle present, almost overlapped by dorsal part of body; ornament of closely arranged radial riblets. [The general form of the shell and the small size of the auricle suggest affinity with the Monotidae, but the presence (according to Marwick) of a triangular ligamental pit precludes reference to that family.] *U.Trias.(Rhaet.)-U.Jur.(Tithon.),* N.Z. ——Fig. C61,*4*. **O. marshalli* (Trechmann), L. Jur.(L.Lias.); LV, ×1 (Cox, n). [Cox].

?**Oxypteria** Waagen, 1907, p. 93 [**Aviculopecten (O.) bittneri*; M]. Small suborbicular, slightly opisthocline; wings of LV small, obtuse, subequal; ornament of few simple, sharp radial ribs producing scalloped margin; RV unknown. *U.Trias. (Carn.),* Eu.(S.Tyrol).——Fig. C61,*2*. **O. bittneri*; LV ext., ×2 *(950)*. [Cox]

Subfamily STREBLOCHONDRIINAE Newell, 1938

[Streblochondriinae Newell, 1938, p. 80]

Upright to opisthocline, nearly equivalve shells in which hinge line is short and auricles well developed; of these, posterior auricle is shorter than anterior auricle. Outer ostracum radially fibrous in both valves; structure of inner ostracum crossed lamellar. *Miss.-U.Trias.*

Streblochondria Newell, 1938, p. 80 [**Aviculopecten sculptilis* Miller, 1891, p. 92; OD]. Both valves ornamented by numerous intercalating costae crossed by fine regular fila which give latticed aspect to surface ornamentation becoming obsolescent in some species. *Miss.-Perm.,* N.Am.-Eu. ——Fig. C63,*2*. **S. sculptilis* (Miller), U.Penn. (Missouri.), Mo.; *2a,b,* LV ext., hinge, ×1 *(663)*.

Eocamptonectes Newell, **new genus** [**Camptonectes ?papillatus* Girty, 1908, p. 434; OD herein]. Opisthocline, ornamented wth radial curved costellae or rows of papillae arranged in quincunx. *L.Perm.-U.Perm.,* USA(Tex.-Wyo.).——Fig. C63, *3*. **E. papillatus* (Girty), U.Perm.(Capitan F.), Tex.; RV ext., ×4 *(663)*.

Pleuronectites von Schlotheim, 1820, p. 217 [**P. laevigatus*; SD Fischer, 1886, p. 945]. Large, suborbicular, opisthocline; LV moderately convex, with more or less protruding umbo; RV feebly convex, umbo level with hinge margin and pointing anteriorly; wings of LV obtuse, not clearly delimited from body of shell; right posterior wing obtuse, narrow, well delimited; right anterior auricle narrow, only slightly shorter than posterior wing; subauricular sinus moderately deep, narrowly rounded; ctenolium present; surface unornamented. *M.Trias.-U.Trias.,* Eu.(Ger.-France-S.Alps).——Fig. C63,*4*. **P. laevigatus,* M.Trias. (Muschelkalk), Ger.; *4a,b,* LV ext., RV ext., both ×0.7 *(732)*. [Cox]

Streblopteria M'Coy, 1851, p. 170 [**Meleagrina laevigata* M'Coy, 1844; SD Meek & Worthen, 1866, p. 333] [=*Rutotia* de Koninck, 1885 (type, *Pecten hemisphaericus* Phillips, 1836; SD Newell, herein]. Orbicular, smooth shells with gibbous umbones; posterior auricle poorly defined, with obtuse posterodorsal angle. *Miss.-Perm.,* cosmop.——Fig. C63,*1*. **S. laevigata* (M'Coy), holo., L.Carb., Ire.; LV ext., ×1 *(407b)*.

Subfamily CHAENOCARDIINAE S. A. Miller, 1889

[*nom. transl.* Newell, herein (*ex* Chaenocardiidae Miller, 1889, p. 458)]

Ovoid, prosocline to opisthocline shells with obtuse posterodorsal border, obsolescent radial ornamentation; anterior auricle of LV poorly differentiated, that of RV strongly set off, subcircular, with wide, wedge-shaped byssal notch; shell structure crossed lamellar. *L.Miss.-L.Perm.*

Chaenocardia Meek & Worthen, 1869, p. 170 [**C. ovata*; OD]. Shells with prosocline obliquity. *M.Penn.(Desmoines.)*, N.Am.——Fig. C64,*2*. **C. ovata*, M.Penn., Ohio; *2a-c*, LV int., ext., RV ext., ×2 (Newell, n).

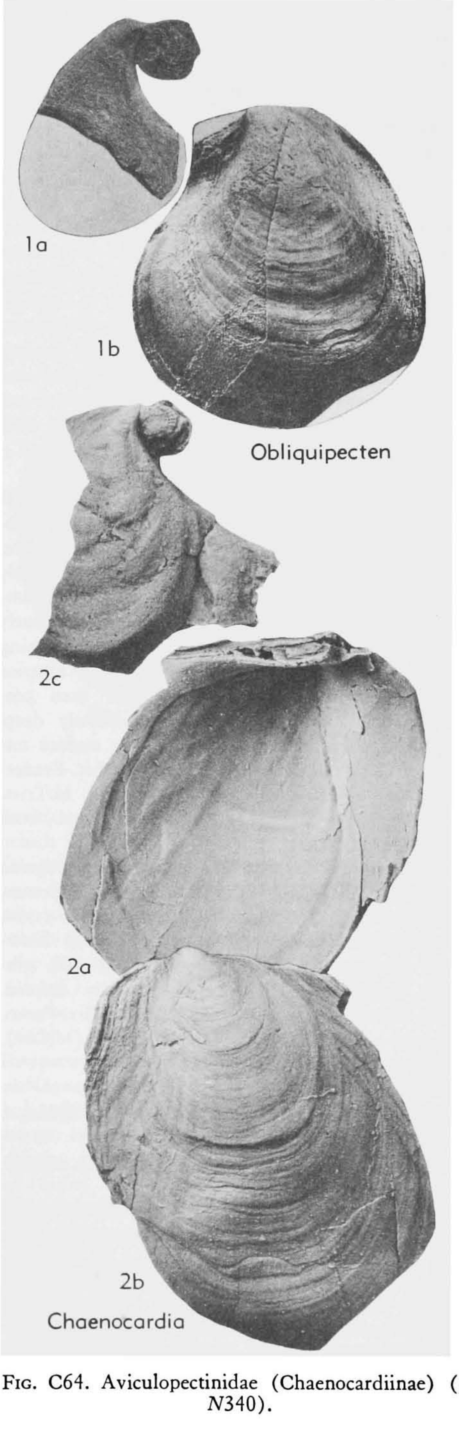

Fig. C64. Aviculopectinidae (Chaenocardiinae) (p. *N*340).

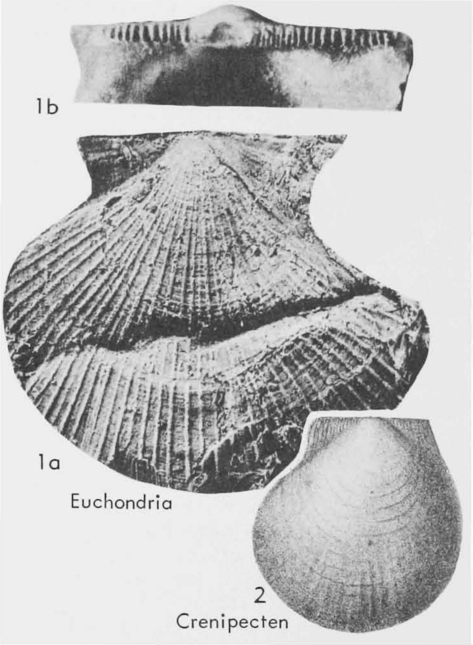

Fig. C65. Aviculopectinidae (Euchondriinae) (p. *N*340-*N*341).

Obliquipecten Hind, 1903, p. 114 [**O. laevis*; M]. Markedly opisthocline, flattened shells, nearly smooth except for few obscure radial costae on anterior part of each valve; hinge margin short, posterior auricle obsolete with very obtuse posterodorsal border. *L.Miss.-L.Perm.*, N.Am.-Eu.——Fig. C64,*1*. **O. laevis*, L.Carb., Eng.; *1a,b*, RV ext., LV ext., ×1 *(663)*.

Subfamily EUCHONDRIINAE Newell, 1938

[*nom. transl.* Newell, herein (*ex* Euchondriidae Newell, 1938, p. 102)]

Small Paleozoic pectinaceans with dorsally divergent cardinal areas bearing closely spaced transverse alternating ridges and furrows. [Transverse grooves were interpreted by Newell (1938) as multiple ligament pits, but it now seems most likely that they represent a neotenous retention of the larval provinculum.] *U.Dev.-U.Perm.*

Euchondria Meek, 1874, p. 445 [**Pecten neglectus* Geinitz; M]. Strongly prosocline, commonly produced posteriorly; hinge with central resilifer, as in *Aviculopecten*; LV ornamented by widely spaced intercalate costae; RV smooth or marked by concentric fila; inner ostracum crossed-lamellar aragonite; outer ostracum calcite with square prisms in RV, apparently structureless in LV. *L.Miss.-U.Perm.*, N.Am.-Eu.-Japan.——FIG. C65,*1a*. **E. neglecta* (GEINITZ), U.Penn., Neb.; LV ext., ×5.——FIG. C65,*1b*. *E. subcancellata* (NEWELL), M.Penn.(Desmoines.), Mo.; RV hinge, ×12 *(663)*.

Crenipecten HALL, 1883, p. xi [**C. crenulatus*; SD S. A. MILLER, 1889]. Shell small, variable in form and ornamentation; hinge as in *Euchondria* except that central resilifer is lacking. *U.Dev.*, USA (N.Y.).——FIG. C65,*2*. **C. crenulatus*; LV ext., ×1 *(377)*.

Family DELTOPECTINIDAE Dickins, 1957

[Materials for this family prepared by N. D. NEWELL]

Pectinoid shells with simple radial plications and flattened cardinal areas without distinct central resilifer, as in Aviculopectinidae, or chevron-shaped ligament grooves characteristic of Pterinopectinidae. Distinct, longitudinal ridges, presumably growth lines, lie on ligament area more or less parallel with hinge axis. Traces of radial lines under beaks recall striated ligament area of certain arcoid genera (e.g., *Striarca, Noetia*). *L.Perm.*

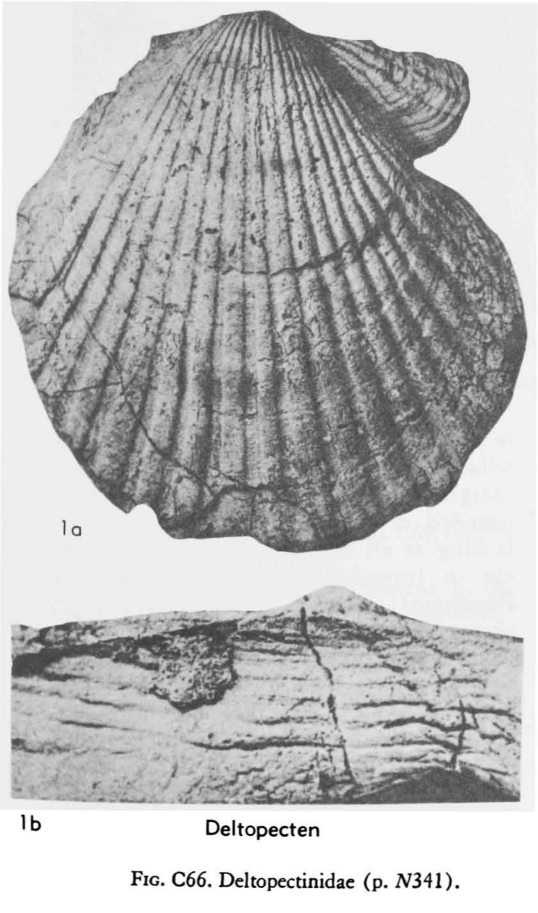

FIG. C66. Deltopectinidae (p. N341).

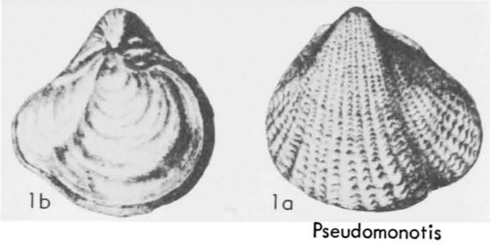

FIG. C67. Pseudomonotidae (p. N341).

Deltopecten ETHERIDGE, JR., 1892, p. 269 [**Pecten illawarensis* MORRIS, 1845 (not figured), p. 277; OD]. Large, orbicular, radially plicate shells with or without fine costae; ligament area striated more or less parallel to hinge axis, resilifers lacking. *L.Perm.(Artinsk.)*, Australia.——FIG. C66,*1*. *D. waterfordi* (DICKINS), Callytharra F.; *1a*, LV ext., ×0.45; *1b*, ligament area, ×2.7 (Newell, n).

Family PSEUDOMONOTIDAE Newell, 1938

[*nom. transl.* NEWELL, herein (*ex* Pseudomonotinae NEWELL, 1938, p. 92)] [=Prospondylidae *(partim)* PCHELINTSEVA, 1960] [Materials for this family prepared by N. D. NEWELL]

Suborbicular to irregular shells with short hinge margin; RV flat or concave and LV moderately to very convex with primitive prosocline rhombic form until relatively advanced ontogenetic stage; posterodorsal margin obtuse, never alate; byssal notch closed in adults as consequence of early degeneration of foot and cementation by umbo of RV; hinge and shell microstructure as in *Aviculopecten*. [Final elimination of the byssal notch in some Permian and Triassic forms led to the genus *Philippiella* WAAGEN and apparently eventually to the true oysters. Many Triassic species formerly classed with *Pseudomonotis* are more appropriately allocated with the Aviculopectinidae.] *L.Carb.-U.Perm.*

Pseudomonotis VON BEYRICH, 1862, p. 10 [**Gryphites speluncarius* VON SCHLOTHEIM, 1820, p. 292; SD STOLICZKA, 1871, p. 389] [=*Eumicrotis*

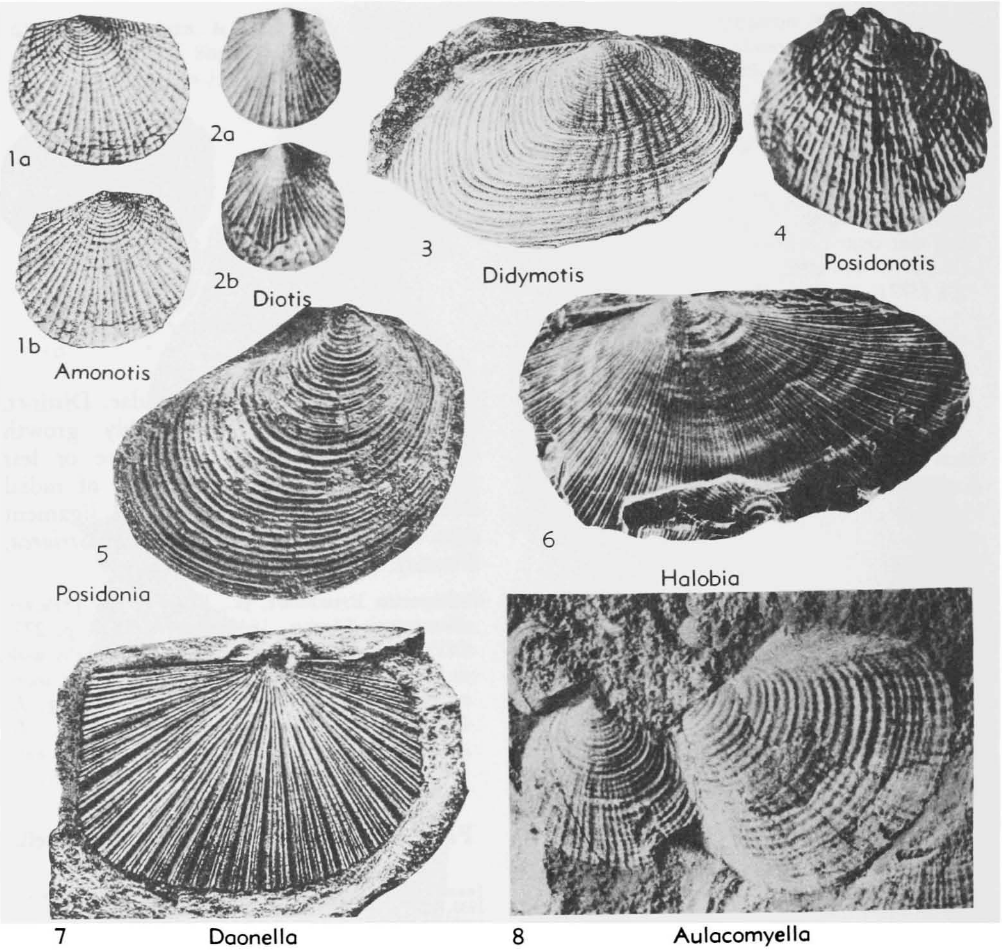

Fig. C68. Posidoniidae (p. *N*342-*N*344).

Meek, 1864 (type, *Monotis hawni* Meek & Hayden, 1958); *Pachypteria* de Koninck, 1885 (type, *Ostrea nobilissima* de Koninck, 1851); *Prospondylus* Zimmermann, 1886 (type, *P. liebeanus*); *Aviculomonotis* Grabau, 1931 (type, *A. mongoliensis*)]. Ornamentation irregular, consisting of radial, intercalate, commonly scabrose costae that are weakly developed or obsolete in some species. *L.Carb.(Visean)-U.Perm.*, widely distributed in northern hemisphere.——Fig. C67, *1.* **P. speluncaria* (von Schlotheim), U.Perm., Eng.; *1a,b*, LV ext., RV ext., both ×1 (King, 1850).

Family POSIDONIIDAE Frech, 1909

[*nom. transl.* Cox & Newell, herein (*ex* Posidoniinae Frech, 1909] [=Halobiidae Kittl, 1912] [Materials for this family prepared by L. R. Cox, with additions by N. D. Newell as indicated]

Ovate, thin-shelled, of low convexity, subequivalve, umbones low, median or anterior to median; ornamented by fine radial costellae or concentric folds or both; hinge margin usually elongate, dorsal angles rounded or obtuse; byssal sinus or notch lacking at all stages in most genera, present in juveniles in some (Carboniferous *Posidonia*); ligament area narrow, rarely observable; hinge edentulous. *L.Carb.-U. Cret.* [Cox & Newell]

Posidonia Bronn, 1828, p. 268 [**P. becheri*; M]. [=*Posidonomya* Bronn, 1834 (obj.)]. Ovate to rhombic shells with concentric undulations; auricles lacking or poorly developed in adults; ovoid shells with umbones submedially situated along short hinge; weakly or not costate; byssal sinus of valves known only in juveniles of Carboniferous forms. Convergent with or ancestral to certain genera included here in the Inoceramidae, from which it differs in ligament structure.

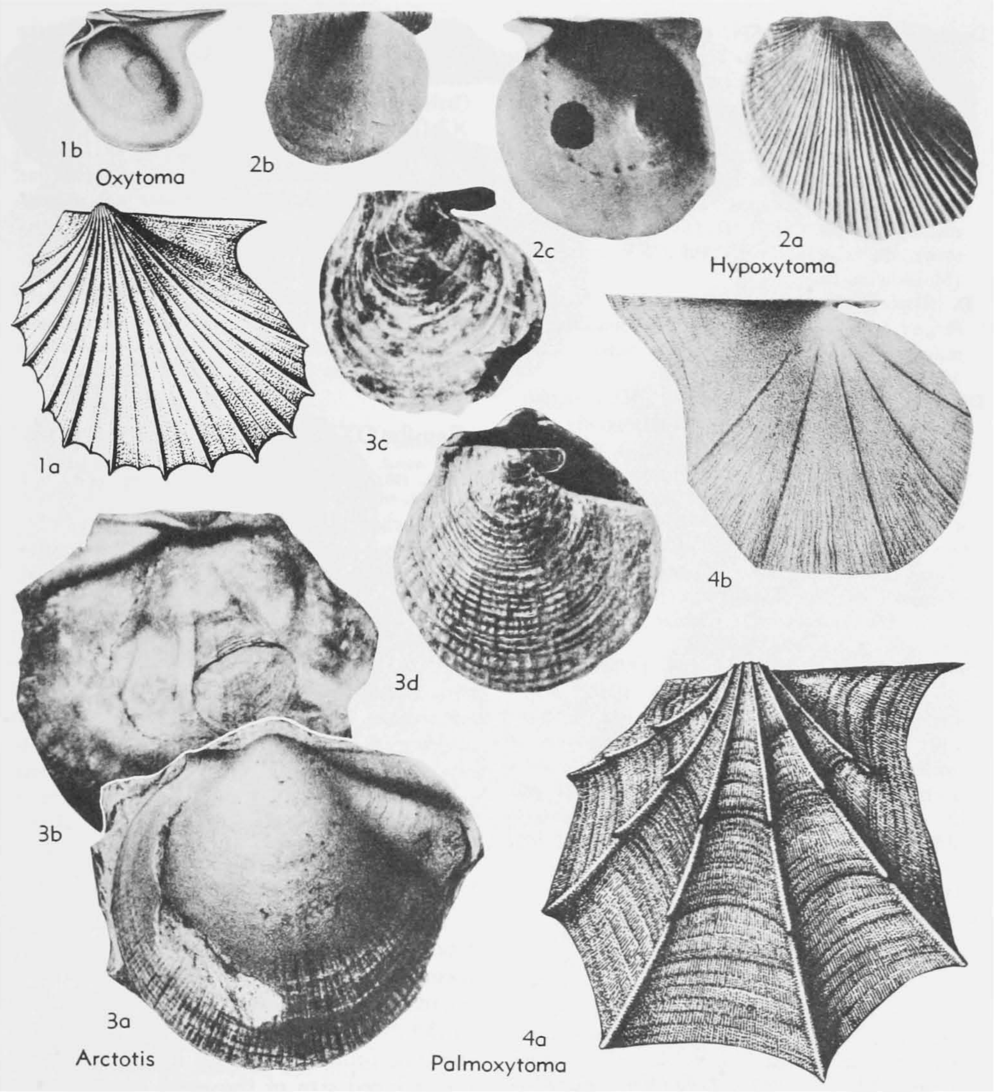

FIG. C69. Oxytomidae (p. *N*344-*N*345).

Some Upper Paleozoic species referred to this genus may belong to *Posidoniella* or *Atomodesma*. *L.Carb.-U.Jur.*, N. Am.-Eurasia-S. Am.-E. Afr.——FIG. C68,*5*. **P. becheri*, L.Carb., Ger.; RV ext., ×1 *(961)*. [NEWELL]

Amonotis KITTL, 1904, p. 736 [**A. cancellaria*; M]. Ovate, almost circular, not oblique; no delimited wings; ornament of narrow concentric folds crossed by weak radial riblets. *U.Trias. (Carn.)*, Eu.(Yugosl.).——FIG. C68,*1*. **A. cancellaria*; *1a,b*, LV ext., RV ext., ×1 (Kittl, 1904).

Aulacomyella FURLANI, 1910, pl. 3 (explan.) [*pro Posidoniella* FURLANI, 1910 (*non* DE KONINCK, 1885)] [**P. problematica*; M]. Resembling *Halobia* in shape and ornament, but lacking delimited anterior wings; externally like *Daonella* but separated from it mainly because of its very different geological age. *U.Jur.(Kimmeridg.)*, Afr. (Somalil.)-Eu.(Dalmat.-Ger.)-S. USA-Mex.-?Japan. ——FIG. C68,*8*. **A. problematica* (FURLANI), Dalmat., RV ext., ×1 (Furlani, 1910).

Bositra DE GREGORIO, 1886, p. 11 [**Posidonia ornati* QUENSTEDT, 1851 (=*Posidonia buchii* RÖMER, 1836; *P. alpina* GRAS, 1852); OD]. Externally like *Posidonia* but with alivincular ligament similar to that of *Pteria*. *Jur.*, Eu. (Jefferies & Minton, 1965).

Daonella Mojsisovics, 1874, p. 5 [**Halobia lommeli* Wissmann, 1841, p. 22; SD Diener, 1923, p. 46]. Like *Halobia* in external characters, but lacking delimited anterior wings; adductor scar subcentral, touched tangentially by 2 internal ridges diverging from the beak. *Trias.*, cosmop.

D. (Daonella). Subovate; ornament of radial riblets commonly grouped in bunches. *Trias.*, cosmop.——Fig. C68,*7*. **D. (D.) lommeli* (Wissman), M.Trias.(Ladin.), Aus.; RV ext., ×1 (Mojsisovics, 1874).

D. (Dipleurites) Kittl, 1912, p. 164 [**Halobia bergeri* Seebach, 1886, p. 7; M]. Semicircular; ornament of numerous very fine radial riblets. *M.Trias.(Muschelkalk)*, Ger.

Didymotis Gerhardt, 1897, p. 178 [**D. variabilis;* M]. Paper-thin, elongate-ovate, posteriorly subtruncate, without delimited anterior wing but with flattened area posterior to beaks, bordered in some specimens by obscure groove; ornament of depressed radial ribs on median part of surface and irregular concentric rugae. *U.Cret.(Turon.-L.Coniac.)*, S.Am.(Colom.-Venez.)-Carib.(Trinidad)-N. Am. (Mex.)-Asia (Japan).——Fig. C68,*3*. **D. variabilis*, L. Coniac., Colom.; RV ext., ×0.7 (Gerhardt, 1897).

Diotis Simonelli, 1884, p. 125 [**Posidonomya janus* Meneghini, 1854, p. 67, M]. Rather small, equilateral, orbicular except for dorsal margins, which are not quite in alignment but meet at umbo in very obtuse angle; anterior margin with broad sinus; ornament of fine radial riblets and (in early growth stages) of narrow concentric folds. *L. Jur. (L. Lias.-M. Lias.)*, Eu.(Italy-Spain).——Fig. C68,*2*. **D. janus* (Meneghini), M.Lias., Italy; *2a,b*, RV ext., LV ext., ×1 (Fucini, 1897).

Enteropleura Kittl, 1912, p. 162 [**Daonella guembeli* Mojsisovics, 1874, p. 8; SD Diener, 1923, p. 52]. Suborbicular, hinge margin relatively short, umbo anteriorly placed, posterior wing more or less clearly delimited; with 2 internal ridges as in *Daonella*, anterior one obscure; ornament of broad concentric folds and obscure radial threads. *M.Trias.(Anis.)-U.Trias.(Nor.)*, Eu.(Alps-Hung.).

Halobia Bronn, 1830, p. 284 [**H. salinarum*; M]. Semicircular or ovate, with long hinge margin; rarely appreciably oblique; anterior wing clearly delimited on each valve, commonly by groove; ornament of closely and irregularly spaced narrow radial threads or grooves and of concentric folds, threads, which in many species are most developed on posterior side, increasing by bifurcation; ligament area striated longitudinally, but rarely observable. *M.Trias.*(chiefly)-*U.Trias.*, cosmop.——Fig. C68,*6*. *H. dilatata* Kittl, U.Trias.(Nor.), Aus.; LV ext., ×0.7 (Kittl, 1912).

Posidonotis Losacco, 1942, p. 11 [**P. dainellii*; M]. Orbicular, equilateral, hinge margin very short for family; wings small but clearly delimited; ornament of narrow radial riblets, increasing by intercalation, and of narrow concentric folds, forming reticulate pattern. *M.Jur.(Aalen.)*, Eu.(Italy).——Fig. C68,*4*. **P. dainellii*; LV ext., ×2 (Losacco, 1942).

Pseudodidymotis Gillet, 1924, p. 75 [**P. lamberti*; OD]. Ovate, moderately inequilateral, prosocline, without delimited wings; umbones not protruding or only slightly; ornament of very fine radial threads. *L.Cret.*, Eu.(France).

Veldidenella Alma, 1926, p. 118 [**V. dieneri*; M]. Very elongate, narrow anteriorly, broad posteriorly; umbo protruding slightly, anteriorly placed, prosogyrous; ornament of closely spaced radial riblets, not arranged in bunches. *U.Trias.*, Eu.(Aus.).

Family OXYTOMIDAE Ichikawa, 1958

[*nom. transl.* Cox, 1961, p. 592 (*ex* Oxytominae Ichikawa, 1958, p. 158)] [Materials for this family prepared by L. R. Cox, with additions by N. D. Newell as indicated]

Suborbicular, subovate or lunate, commonly but not invariably strongly inequivalve, inequilateral; right anterior auricle small, subauricular notch deep; ligamental area external in RV and usually in LV also; more or less oblique ligamental groove present, sloping backward from beak; hinge edentulous or with interlocking protuberances and recesses; pallial line discontinuous, broken up into series of pits; ornament predominantly radial, commonly weaker in RV than in LV; inner ostracum calcitic, with crossed-lamellar structure, outer ostracum of RV prismatic. *L.Perm.-U.Cret.*

This family appears to have been derived from the Aviculopectinidae, from which its members differ in the replacement of a nacreous inner ostracum by a calcitic one, in the discontinuous pallial line, which is of the type found in modern Pteriidae, and in the reduced size of the right anterior auricle.

Oxytoma Meek, 1864, p. 39 [**Avicula muensteri* Bronn, 1830, p. 164 (=*Avicula inequivalvis* J. Sowerby, 1819, p. 78); OD]. Suborbicular and acline to ovate or broadly lunate and prosocline; valves commonly discordant, LV varying in convexity with umbo protruding, RV flat or feebly convex; posterior wing of both valves more or less elongated, sharply pointed, left anterior wing small, subauricular notch deep, acute, with ctenolium; angular projection of shell margin extending on inner side of notch; ligamental area almost parallel with plane of valve margins in LV, almost perpendicular to it in RV; no hinge teeth. *U.Trias.-U.Cret.*, cosmop.

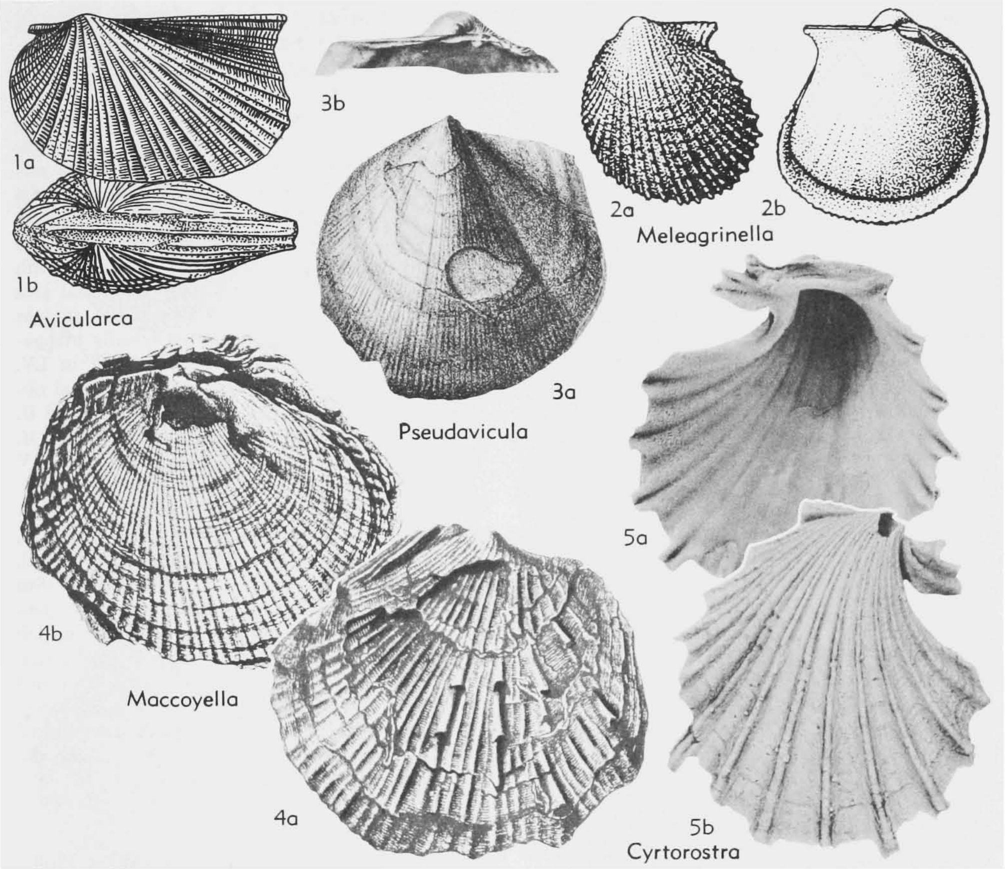

FIG. C70. Oxytomidae (p. *N*346).

O. (Oxytoma). Medium-sized; LV with ribs and riblets commonly 3 orders of strength, primary ribs well separated; only first or first 2 orders present in some specimens; RV smooth or with weak radial threads; adductor scar placed somewhat posteriorly. *U.Trias.-L.Cret.,* cosmop.——FIG. C69,*1*. **O. (O.) inequivalvis* (J. Sowerby), Jur., Eu.; *1a,* LV ext., ×2 (Cox, n); *1b,* RV int., ×2.7 *(341b).*

O. (Hypoxytoma) Ichikawa, 1958, p. 164 [**Avicula danica* Ravn, 1902, p. 11; OD]. Rather small; LV with closely spaced, subequal ribs, absent in earlier growth stages in some specimens; RV smooth; subaurciular notch less deep than in *O. (Oxytoma). L.Cret.-U.Cret.,* cosmop.——FIG. C69,*2a*. *O. (H.) tenuicostata* (Roemer), U.Cret., Ger.; LV ext., ×2.3 (Voight, 1954).——FIG. C69,*2b,c*. **O. (H.) danica* (Ravn), U.Cret., Ger.; *2b,* RV ext., ×5 (Voigt, 1954); *2c,* RV int., ×6.7 *(423).*

O. (Palmoxytoma) Cox, 1961, p. 593 [**Pecten cygnipes* Young & Bird, 1822, p. 235; OD]. Large, orbicular, only slightly prosocline; LV moderately to strongly convex, RV almost flat; LV with small number of narrow, prominent, spinose ribs which are continued by narrow digitations of valve margin and separated by broad, flat intervals which are smooth or bear fine radial striations; ribs increasing by intercalation in some specimens; RV with small number of faint, narrow radial grooves and, in some specimens, fine radial striations; posterior adductor scar more nearly median than in *O. (Oxytoma). L.Jur.(L.Lias.-M.Lias.),* N.Eu.——FIG. C69,*4*. **O. (P.) cygnipes* (Young & Bird), M.Lias., Eng. *(4a)*; France *(4b)*; *4a,* LV ext., ×1 (Cox, n); *4b,* RV ext., ×0.67 (Dumortier, 1869).

Arctotis Bodylevsky, 1960, p. 44 [**Hinnites lenaensis* Lahusen, 1886, p. 4; OD]. Medium-sized, suborbicular or subovate, acline or almost so; LV moderately convex, RV almost flat; posterior wings obtuse, indistinctly delimited, left anterior wing and right anterior auricle shorter than posterior wings, although not greatly reduced; subauricular sinus moderately deep, angular; ligamental area broad, with deep and wide ligamental pit; pallial line discontinuous; ornament of irregularly arranged radial riblets, well developed on LV, weak or absent on RV. *L.Jur.(Lias.)-L.Cret.(Valang.),* USSR(Sib.).——Fig. C69,*3a-c*. **A. lenaensis* (Lahusen), M.Jur.; *3a,* LV ext., ×0.5 (Lahusen, 1886); *3b,c,* RV int., ext., both ×1.1 (Borisiak, 1915).——Fig. C69,*3d*. *A. intermedia* Bodylevsky, U.Jur.(L.Volg.); RV ext., ×2 (Bodylevsky, 1960).

?**Avicularca** von Bubnoff, 1921, p. 281 [**Avicula cardiiformis* von Münster, 1841, p. 78; SD Cox, herein]. Small, ovate, more or less elongate, equivalve, moderately convex, prosocline; umbones broadly rounded, protruding slightly; posterior wing long, acute-tipped, but with only shallow marginal sinus; left anterior wing small, acute; right anterior auricle unknown; rather broad, subhorizontal ligamental area, with very narrow, oblique ligamental pit, present in both valves; ornament (both valves) of radial riblets of 2 or more orders of strength. *U.Trias.,* Eu.(S.Alps).——Fig. C70,*1*. **A. cardiiformis* (von Münster), U.Trias., S.Tyrol; *1a,b,* LV ext., dorsal, ×5 *(58)*.

Cyrtorostra Branson, 1930, p. 44 [**C. varicostata*; OD] [=*Blanfordina* Reed, 1944, p. 312 (type, *B. lunwalensis*); *Prooxytoma* Maslennikov, 1955 (type, *Oxytoma caucasica* Likharev, 1947)]. Suborbicular, acline to opisthocline, prosogyrate; ornamentation equal in the 2 valves, consisting of 2 orders of radial ribs, of which smaller one extends as marginal spines. [Frequently classed with the Mesozoic *Oxytoma*. Probably derived from *Clavicosta* Newell.] *L.Perm.(Leonard.)-U.Perm.,* widely distributed in northern hemisphere.——Fig. C70,*5*. **C. varicostata,* L.Perm. (Phosphoria), Wyo.; *5a,b,* RV int., ext., ×3 *(132)*. [Newell]

Maccoyella Etheridge, Jr., 1892, p. 451 [**Avicula barklyi* Moore, 1870, p. 245; OD] [=*Mimetostreon* Bonarelli & Nágera, 1921, p. 21 (type, *Avicula corbiensis* Moore, 1870; SD Stenzel, 1947, p. 177)]. Medium-sized to large, ovate or suborbicular, irregular in form, acline or slightly prosocline; LV strongly convex, some species with well-incurved umbo; RV flat or feebly convex; posterior wings and left anterior wing obtuse and ill-defined; right anterior auricle small, thick; subauricular notch narrow, oblique, clearly seen only from interior of valve, or possibly absent in some specimens; ligamental area of LV broad and concave, with broad ligamental pit; rather large, amorphous tooth present below or on anterior side of area in some forms; pallial line discontinuous; ornament of radial ribs commonly of 2 or more orders of strength. *?U.Jur.-L.Cret.,* Australia-N.Z.-Patagonia.——Fig. C70,*4*. **M. barklyi* (Moore), *L.Cret.,* Australia; *4a,b,* LV ext., RV ext., both ×0.7 (Etheridge, 1902).

Meleagrinella Whitfield, 1885, p. 71 [**Avicula curta* Hall, 1852, p. 412; SD Cox, 1941, p. 134] [=*Clathrolima* Cossmann, 1908, p. 296 (type, *C. lalmenti*); *Echinotus* Marwick, 1935, p. 301 (type, *Avicula echinata* Smith, 1817)]. Small to medium-sized, orbicular; LV strongly convex, RV flat or feebly convex, valves strongly discordant; usually with small pointed posterior wings but no left anterior wing; right anterior auricle small, with deep, narrow subauricular notch; ligamental area almost in plane of valve margins in LV, at right angles to it in RV; ligamental pit broadly triangular, toothlike protuberance anterior to it in LV, which has narrow, commonly squamose radial riblets; RV smooth or with weak radial riblets. *U.Trias.(Rhaet.)-U.Jur.,* cosmop.——Fig. C70,*2*. *M. echinata* (Smith), M.Jur., Eng.; *2a,b,* LV ext., RV int., ×2 (Cox, n).

Pseudavicula Hudleston, 1890, p. 244 (*ex* Etheridge, Jr., MS) [**Lucina anomala* Moore, 1870, p. 251; M]. Medium-sized, suborbicular or oval, acline, weakly biconvex, LV more inflated than RV although its umbo scarcely protrudes; posterior wings obtuse, indistinctly delimited, no left anterior wing; right anterior auricle small, subauricular notch small but distinct; ligamental area external, that of RV broadest in middle, where wide ligamental pit occurs; no hinge teeth; pallial line discontinuous; ornament of fine radial riblets. *L.Cret.,* Australia.——Fig. C70,*3*. **P. anomala* (Moore); *3a,b,* RV ext., hinge, ×1 *(440)*.

Family ENTOLIIDAE Korobkov, 1960

[Materials for this family prepared by N. D. Newell, with additions by L. G. Hertlein as indicated]

Suborbicular, valves nearly equilateral and equally convex, smooth or with fine radial or concentric sculpture, byssal notch lacking in adults, auricles projecting above hinge margin in LV, hinge line straight in RV, auricular crura present. [This family resembles and may have led to *Amusium.*] *L.Miss.-U.Cret.*

Entolium Meek, 1865 [**Pecten demissus* Phillips, as illustr. by Quenstedt, 1858 (=*Pecten disciforme* Schuebler in Zieten, 1833); OD]. Byssal notch lacking at any stage; margins closed laterally; incised ligamental area usually present and extending parallel to hinge line on each side of ligamental pit; auricular crura present; inner shell layer calcite, foliate; outer layer radially fibrous in both valves. *M.Trias.-U.Cret.,* cosmop. [Hertlein]

E. (Entolium) [=*Protamusium* Verrill, 1897 (obj.); *Protamussium* Paris & Richardson, 1915 *(nom. null.)*; *Protomusium* Stewart, 1930 *(nom. null.)*; *Etolium* McLearn, 1949 *(nom.*

null.)]. Auricles of LV projecting above hinge, commonly as angular wings;[1] smooth *(19b, 19c, 19i, 732c). M.Trias.-U.Cret.,* cosmop.——FIG. C71,*4*. **E. (E.) demissum* (PHILLIPS), M.Jur. (Bajoc.), Ger.; *4a,b,* RV hinge, RV ext., ×1 (Quenstedt, 1858). [=*Entholium* TZANKOV & BONCEV, 1932 *(nom. null.)*.] [HERTLEIN]

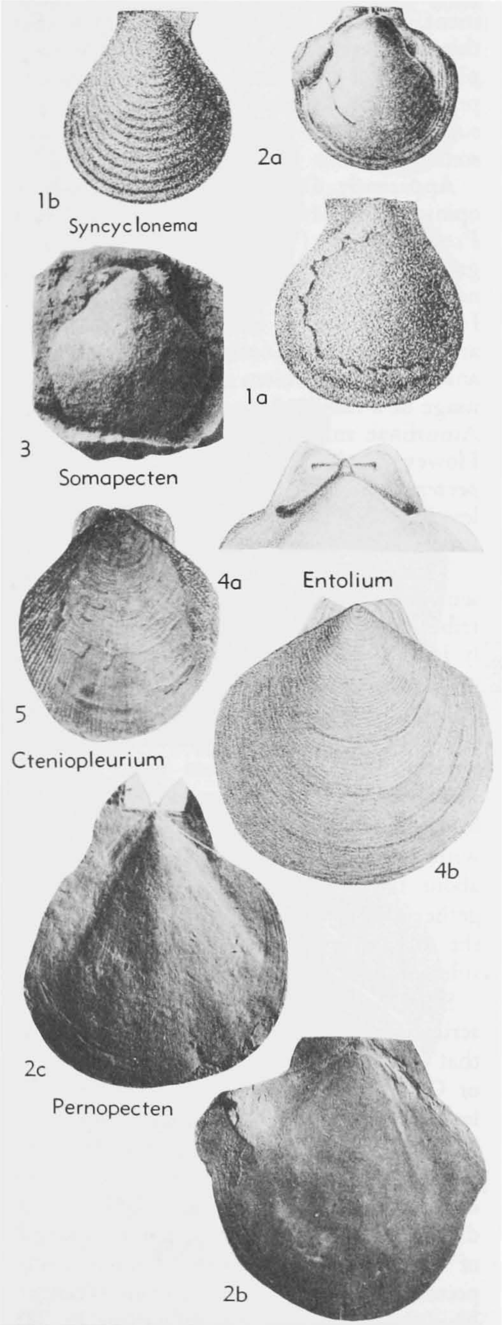

FIG. C71. Entoliidae (p. *N*346-*N*347).

E. (Ctenioplerurium) FELDTMANN, 1951 [**Syncyclonema subreticulatus* FELDTMANN, 1951; OD]. Differs from *Entolium* in that valves are sculptured with fine, usually spinose, radial riblets; byssal notch very slight or lacking. *U.Cret. (M.Senon.),* Australia.——FIG. C71,*5*. **E. (C.) subreticulatum* (FELDTMANN), M.Senon.(Santon.), Australia; RV ext., ×1.5 (Feldtmann, 1951). [HERTLEIN]

Pernopecten WINCHELL, 1865 [**Aviculopecten limaformis* WHITE & WHITFIELD, 1862; OD]. Commonly, but not invariably, truncated behind, interior smooth or ribbed, with gaping front and rear margins; LV distinctly larger than right; byssal notch present in RV of juveniles, obsolete in adults; auricles of LV acuminate; inner ostracum with concentric crossed-lamellar structure, outer ostracum radially fibrous in LV and hexagonal prismatic in RV. *L.Miss.-U.Perm.,* cosmop. ——FIG. C71,*2a*. **P. limaformis* (WHITE & WHITFIELD), L.Miss.(Burlington), Iowa; RV int. mold, ×1 *(377)*.——FIG. C71,*2b,c*. *P. ohioensis* (NEWELL), M.Penn.(Desmoines.), USA(Ohio); LV int., RV ext., ×3 *(663)*. [=*Protoentolium* YANISHEVSKY, 1960 (type, *Pecten sowerbyi* M'COY, 1844; OD)].

?**Somapecten** KIMURA, 1951 [**S. kamimanensis*; OD]. Shell similar to that of *Entolium* but hinge with strong triangular tooth in RV and corresponding socket in LV. [May not be referable to Entoliidae.] *Jur.(?Callov.-Tithon.),* Japan.——FIG. C71,*3*. **S. kamimanensis,* Torinosu Gr.; RV ext., ×1 *(469)*. [HERTLEIN]

?**Syncyclonema** MEEK, 1864 [**Pecten rigida* HALL & MEEK, 1854 *(non* SOWERBY, 1818) [=*Pecten hallii* GABB, 1861); OD] [=*Sincyclonema* MEEK, 1864 (see below); *Sinsyclonema* CONRAD, 1869 *(nom. null.)*; *Syndonema* DALTON, 1878 *(nom. null.)*; *Syncyclomena* CLESSIN, 1878 *(nom. null.)*; *Synclonema* FISCHER, 1886 *(nom. null.)*; *Synciclonema* DE GREGORIO, 1886 *(nom. null.)*; *Synciclomena* DE GREGORIO, 1898 *(nom. null.)*]. Differs from *Entolium* in straight, shorter hinge, in unequal auricles with rounded sinuosity under anterior ones, and in presence of small, rounded concentric ridges on RV *(892)*. [The characters of the type species are not well known and their relationships are uncertain.] *U.Cret.,* N.Am.——FIG. C71,*1*. **S. rigida* (HALL & MEEK), USA (Neb.); *1a,b,* LV ext., RV ext., ×8 *(379)*. [HERTLEIN]

[*Sincyclonema* is rejected as an incorrect original spelling (*Code,* Art. 32a).]

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[1] The right valve of *Entolium* traditionally has been considered to be the one with elevated dorsal wings. However, no evidence based on the adductor muscle impression has been available to indicate which valve is right and which left. Analogy with *Pernopecten* leads me to suspect that the valve with the elevated dorsal wings is the left one. —N. D. NEWELL.

Family PECTINIDAE Rafinesque, 1815

[*nom. correct.* d'Orbigny, 1839 (*pro* Pectenidae Fleming, 1822, *nom. transl. ex* subfamily Pectenia Rafinesque, 1815)] [=Pectinides Bowdich, 1822; Pectinideae Parkinson, 1822; Pectinides "Lam." Bronn, 1824; Pectinides Latreille, 1825; Pectinida Crouch, 1826; Pectinea Menke, 1830] [Materials for this family prepared by L. G. Hertlein]

Shell varying in size, orbicular to oval, valves of some shells equally convex but usually one valve more inflated than other, margins usually, but not invariably closed; umbos central, on either side of which are triangular auricles (ears), anterior one on RV usually with distinct byssal notch or indentation below it; surface smooth or with radial ribs or folds, some species with concentric sculpture of raised lamellae; interior smooth or with fine radial riblets; hinge line straight; external ligament obsolete or nearly so, resilium internal, amphidetic, in triangular pit below umbones; young shells with small taxodont teeth which become obsolete later; cardinal crura or laminae commonly present, diverging from either side of ligamental pit; rounded laminae (auricular crura) present on interior of some shells where auricles join valves; adults monomyarian, with posterior adductor only; free, attached by byssus, or cemented by RV; upper (L) valve, usually more brightly colored; margin of mantle with short filaments and commonly with eyes; dioecious *(256a-e, 732c, 936)*. *Trias.-Rec.*

Although many supraspecific units greatly resemble others in shell structure, their close relationship generally has not been proved. The similarities appear to confirm Philippi's theory of iteration of shell form in this group of mollusks. For this reason it seems best to adopt a conservative course in arranging supraspecific units in groups within the Pectinidae. To define such groups as subfamilies or to separate them as families would imply relationships and distinctions based chiefly on supposition only.

The problem of where the amusiums should be placed in a scheme of classification is one not satisfactorily resolved at the present time. Ridewood, in 1903, proposed the family Amusiidae, based chiefly upon gill structure. On this basis he included *Plicatula* in the family, a decision which almost no one follows because of the obvious conchological differences.

The *Propeamussium* group, having origin in the Mesozoic, has internal ribs but apparently the pattern of the rays, development, auricles, etc., does not suggest that this group gave rise to *Amusium*. The complete lack of any record of typical *Amusium* prior to the Miocene (Aquitanian) might suggest a rather sudden development from some unknown form.

Apparently Cox and North are of the opinion that *Amusium* was derived from *Pseudentolium* (=*Lentipecten*), an Eocene group with smooth shells, a distinct byssal notch, and lacking internal ribs. So far as I know, proof is lacking that *Amusium* arose from this Eocene group. I see no answer to the problem at this time. Possibly usage of a family Amusiidae or a subfamily Amusiinae might be a reasonable solution. However, when groups such as *Amussiopecten* are taken into account, I feel much less inclined to separate the amusiums from the Pectinidae.

This family, at the present time, is represented by about 350 species. These are distributed in all seas but occur most abundantly in shallow, warm waters, such as those of the East Indies, Japan, and Caribbean regions. The various species differ in size, convexity, sculpture, color, and habitat, but iteration and convergence often lead to similarity of form. Some are attached by byssal threads, others lie upon the bottom with the LV uppermost and some can swim about freely by clapping their valves together and ejecting a stream of water from the mantle below the auricles, first on one side and then on the other.

Several thousand species have been described as fossils. Davies (1934) pointed out that species occurring in strata of Eocene or Oligocene age rarely exceed 50 mm. in length. Much larger specimens occur in Mesozoic sediments as well as in those of post-Oligocene age. *Pecten (Amussiopecten) dregeri* von Teppner, from strata of middle Miocene age in Austria, attains a length of 240 mm. The largest known living pecten is *P. caurinus* Gould from Wrangell Narrows, Alaska, with valves up to 288 mm. long and 198 mm. high (Grau, 1959).

The author of this portion of the *Treatise* wishes to acknowledge the aid and advice of Dr. K. F. North, who generously permitted free access to his manuscript containing the results of a comprehensive study of the supraspecific units of the Pectinidae. Acknowledgment also is made to Mr. Gilbert Grau for aid and advice.

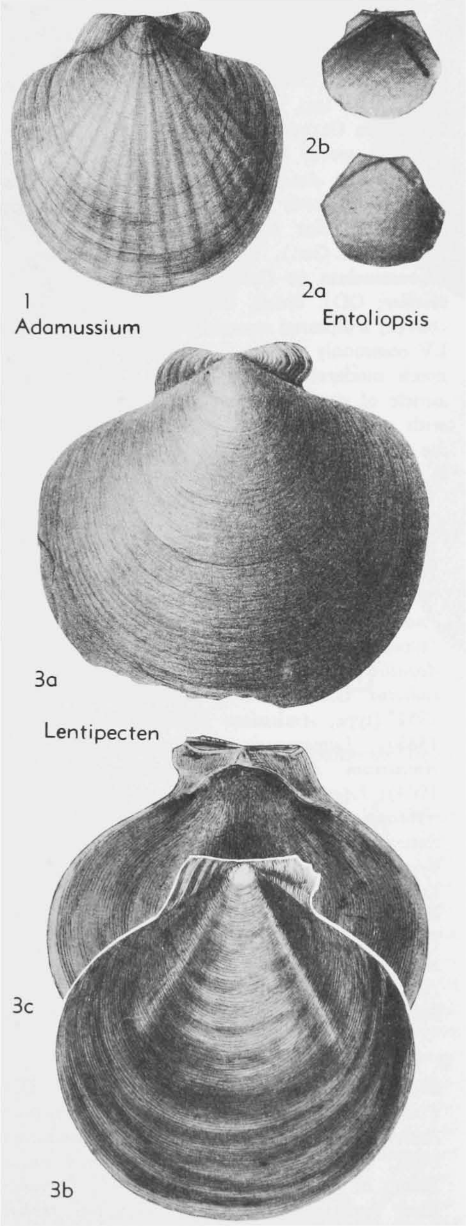

Fig. C72. Pectinidae (Lentipecten Group) (p. N349).

LENTIPECTEN GROUP

Usually small, rounded, valves gaping anteriorly and posteriorly; byssal notch present; usually smooth but some with radial folds or microscopic striae; hinge similar to that of *Amusium* but with fewer cardinal crura. *L.Eoc.-Rec.*

Lentipecten Marwick, 1928 [**Pecten hochstetteri* Zittel, 1864; OD]. Differing from *Entolium* in that valves usually gape laterally, in presence of distinct byssal notch and in that outer margin of RV anterior auricle is rounded; hinge similar to *Amusium* but with fewer cardinal crura (13). *L.Eoc.-U.Plio.*, Eu.-Asia-N.Z.

L. (Lentipecten) [=*Pseudentolium* Cox, 1948 (type, *Pecten corneus* J. Sowerby, 1818)]. Valves suborbicular in outline, smooth. *L.Eoc.-U.Plio.*, Eu.-N.Z.——Fig. C72,*3a*. **L. (L.) hochstetteri* (Zittel), L.Mio.(Hutchinson), N.Z.; RV ext., ×1 (Zittel, 1864).——Fig. C72,*3b,c*. *L. (L.) corneus* (Sowerby), Eoc., Eng.; *3b,c*, RV ext., int., ×0.7 (J. Sowerby, 1818).

L. (Entoliopsis) Eames, 1951 [**Amusium (Entoliopsis) uniradiatum*; OD]. Differs from *Lentipecten* in that anterior portion of interior of each valve bears radial ridge not extending to umbo or ventral margin; 1 auricular ridge delimiting each auricle internally on right and 2 ridges corresponding to each of these on LV. *L.Eoc.*, Asia(Pak.).——Fig. C72,*2*. **L. (E.) uniradiatus* (Eames); *2a*, LV ext., ×3; *2b*, LV int., ×3 *(288)*.

Adamussium Thiele, 1934 [**Pecten colbecki* E. A. Smith, 1902; OD]. Rounded, thin, gaping anteriorly and posteriorly, corrugated with shallow radial folds and bearing microscopic radial striae; right anterior ear rounded, shallow byssal notch beneath it. *Rec.*, Antarctic.——Fig. C72,*1*. **A. colbecki* (Smith); RV ext., ×0.5 (E. A. Smith, 1902).

AMUSIUM GROUP

Disc-shaped forms, smooth to finely sculptured externally, interior with radial riblets. [Genera may have been derived from different groups.] *Jur.-Rec.*

Amusium Röding, 1798 [**Ostrea pleuronectes* Linné, 1758; SD Herrmannsen, 1846] [=*Anusium* Gray, 1826 *(nom. null.)*; *Pleuronectes* Bronn, 1831 (*non* Linné, 1758); *Pleuronectia* Swainson, 1840 (type, *P. laevigata* Swainson, 1840,=*Ostrea pleuronectes* Linné, 1758); *Pleuronopecten* Tucker-Rowland, 1938 (*pro Pleuronectia*); *Amussium* Herrmannsen, 1846 *(nom. van.)*]. Fairly large, thin, valves slightly convex and gaping along margins below auricles; trace of byssal notch present; internal lirae commonly in pairs; hinge with pair of short ridges diverging from shallow ligamental pit and extending toward margins; auricular crura present *(256a-e)*. *L.Mio.-Rec.,* tropic-subtropic.——Fig. C73,*1*. **A. pleuronectes* (Linné), Rec., IndoPac.; *1a,* RV ext., ×1; *1b,* RV int., ×1 *(7c)*.

Korobkovia Glibert & van de Poel, 1965, p. 10 [**Pecten woodi* Nyst, 1861 (*non* 1853); OD]. Differs from *Amusium* in lacking ribs in interior of RV, and from *Lentipecten* in presence of fine ribs in interior of LV. *U.Mio.(Auvers.),* Eu. (Belg.-Neth.-Ger.).

Propeamussium de Gregorio, 1884 [**Pecten (P.) ceciliae*; OD]. Small, thin, valves nearly equally convex; sculptured externally with concentric lines, LV commonly with radial striae or riblets; byssal notch moderately deep to slight; right anterior auricle of some shells with radial riblets; interior with radial riblets which usually extend to middle or to margin. *L.Jur.-Rec.,* cosmop.

P. (Propeamussium) [=*Propeamusium* Dall, 1886 *(nom. van.)*; *Propreamusium* Jackson, 1890 *(nom. null.)*; *Paramusium* Verrill, 1897 (type, *Amusium dalli* E. A. Smith, 1885); *Paramussium* de Gregorio, 1898 *(nom. null.)*; *Propeannessium* Cossmann & Pisarro, 1906 *(nom. null.)*; *Occultamussium* Korobkov, 1937 (type, *Pecten semiradiatus* Mayer, 1861); *Pseudopalliorum* Oyama, 1944 (type, *Pecten interradiatus* Gabb, 1869); *Flavamussium* Oyama, 1951 (type, *Amussium caducum* E. A. Smith, 1885); *Luteamussium* Oyama, 1951 (type, *Amussium sibogai* Dautzenberg & Bavay, 1904); *?Actinopecten* Bonarelli, 1951 (type, *A. ripidopsis* Bonarelli, 1951)]. Valves rather flattened, usually gaping along lateral margins; byssal notch slight; internal ribs extend about halfway (farther in some) to margin *(256a-e, 802)*. *L.Jur.-Rec.,* cosmop.——Fig. C73,*3a*. **P. (P.) ceciliae* (de Gregorio), Mio., Sicily; RV ext., (type) (imperfect, auricles lacking), ×1 (de Gregorio, 1898).——Fig. C73,*3b*. *P. (P.) anconitanum* (Foresti), L.Mio., Italy; RV ext., ×1.5 *(256e)*.

P. (Parvamussium) Sacco, 1897 [**Parvamussium duodecimlamellatum* Bronn, 1831; OD] [=*Variamussium* Sacco, 1897 (type, *Amussium cancellatum* E. A. Smith, 1885); *Parviamussium* Dall, 1898 *(nom. null.)*; *Variopecten* Sacco, Broili in Zittel, 1924 *(nom. null.)*; *Ctenamusium* Iredale, 1929 (type, *Amusium thetidis* Hedley, 1902); *Glyptamusium* Iredale, 1939 (type, *Amusium torresi* E. A. Smith, 1885); *Graptamussium* Oyama, 1944 (type, *P. torresi*

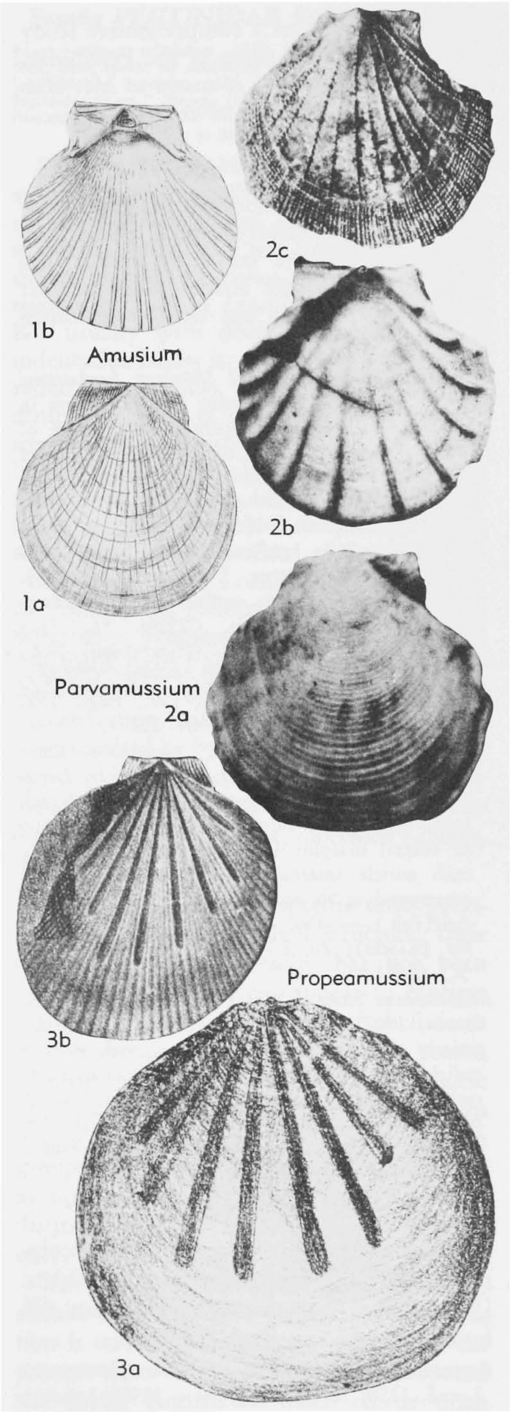

Fig. C73. Pectinidae (Amusium Group) (p. *N*349-*N*351).

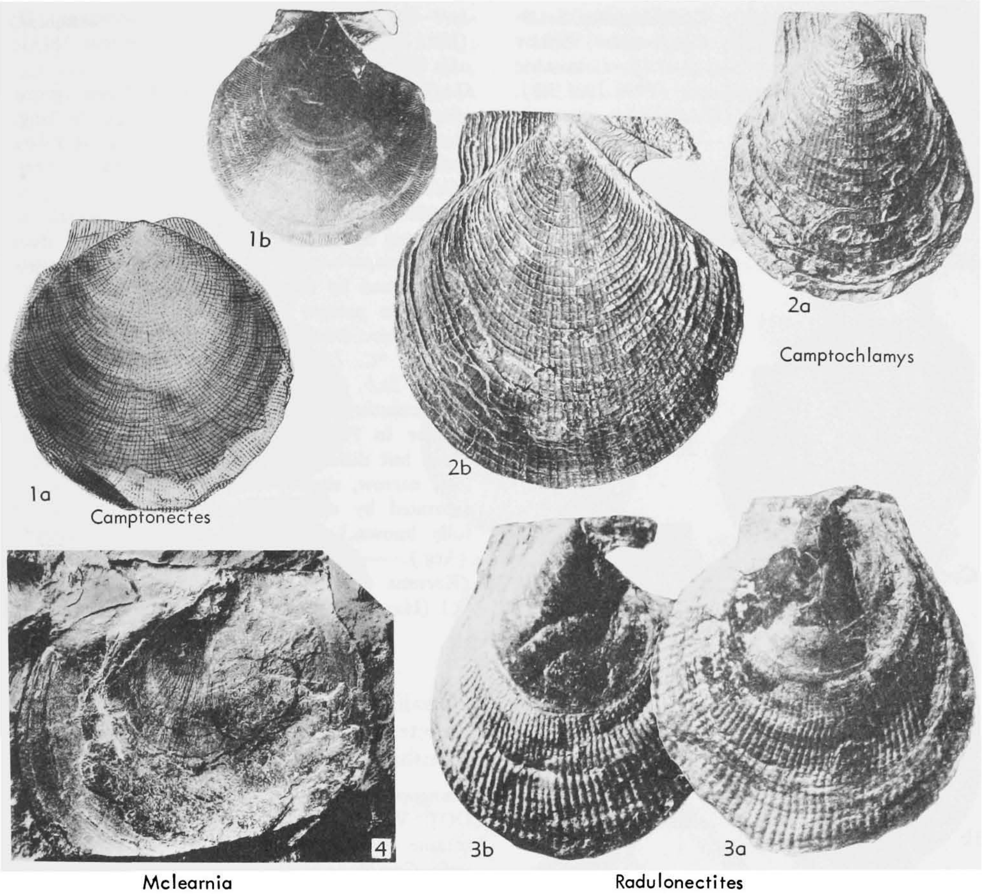

Fig. C74. Pectinidae (Camptonectes Group) *(1-3)*; Group Uncertain *(4)* (p. *N*351-*N*352).

E. A. Smith, =*Amussium torresi* E. A. Smith, 1885); *Squamamussium* Oyama, 1944 (type, *Amusium squamigerum* E. A. Smith, 1885, =*Amussium squamigerum* E. A. Smith, 1885); *Xenamussium* Oyama, 1944 (type, *Pecten hoskynsi* Forbes, 1844); *Bathyamussium* Oyama, 1951 (type, *Amussium jeffreysi* E. A. Smith, 1885); *Micramussium* Oyama, 1951 (type, *Ctenamusium siratama* Oyama, 1951) *Polynemamussium* Habe, 1951 (type, *Pecten intuscostatus* Yokoyama, 1920)]. Differs from *P. (Propeamussium)* in its usually more rounded shape, lacking lateral gape, in presence of well-developed byssal notch, and in that internal ribs extend to or almost to margin; differs from *Cyclopecten* in possessing internal ribs *(821a,b)*. *U.Cret.-Rec.*, cosmop.——Fig. C73,*2a,b*. _*P. (P.) duodecimlamellatum_ (Bronn), Mio., Italy; *2a*, RV ext., ×4; *2b*, RV int., ×4 (Depéret & Roman, 1928).——Fig. C73,*2c*. *P. (P.) felsinum* (Foresti), Plio., Italy; LV ext., ×4 *(256e)*.

CAMPTONECTES GROUP

Left valve more convex than right; smooth, or with strong *Camptonectes* (divaricate striae) sculpture; large byssal notch present. *?Trias., L.Jur.-U.Cret.*

Camptonectes Agassiz in Meek, 1864 [_*Pecten lens_ J. Sowerby, 1818; SD Stoliczka, 1871]. Exterior sculptured with fine, oblique, divergent, curved, crenulated, commonly punctate striae and concentric lines, or raised laminae *(19b, 19c, 19i)*. *L.Jur.-U.Cret.*, cosmop.

C. (Camptonectes) [=*Campstonectes* von Tepp-

NER, 1922 *(nom. null.)*; *Campitonectes* SALISBURY, 1939 *(nom. null.)*; *Camponectes* VYALOV & KOROBKOV, 1939 *(nom. null.)*]. Concentric sculpture of fine growth lines *(19b, 19c, 19i)*. *L. Jur. (U. Lias.)-U. Cret. (Maastricht.),* cosmop. ——FIG. C74,*1*. **C. (C.) lens* (J. SOWERBY), U. Jur., Eng.; *1a,* LV ext., ×1 (Sowerby, 1818); *1b,* RV ext., ×1 *(19b)*.

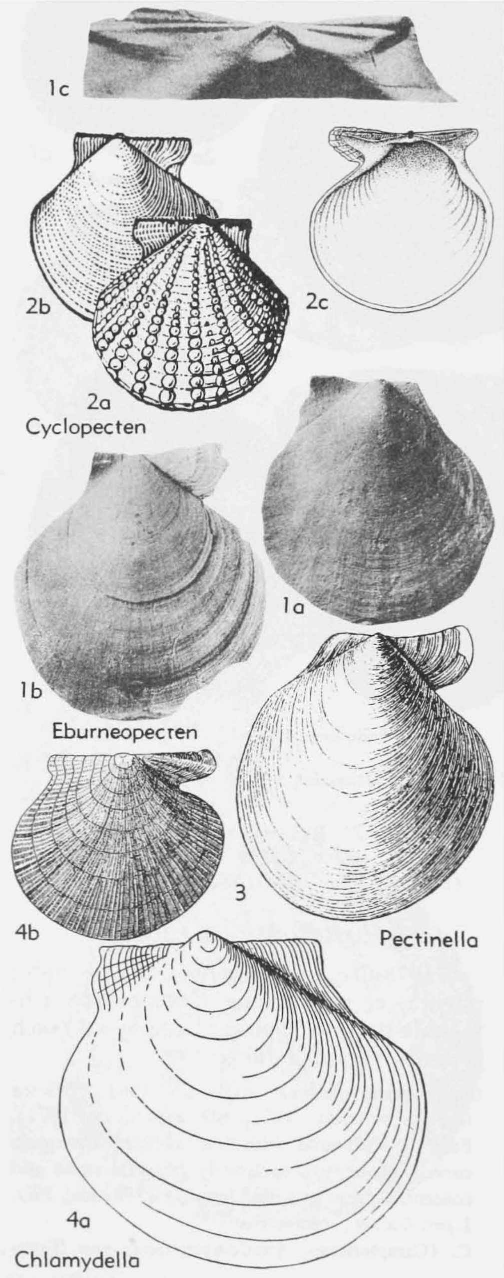

FIG. C75. Pectinidae (Eburneopecten Group) (p. *N352-N354*).

C. (Boreionectes) ZAHAROV, 1965 [**Pecten cinctus* SOWERBY, 1823; OD]. Orbicular, hinge line long, byssal notch well developed; exterior of valves smooth except for concentric grooves. *Cret. (Valangin.),* USSR(Sib.).

C. (Camptochlamys) ARKELL, 1930 [**Pecten intertextus* ROEMER, 1839; OD]. Differing from *C. (Camptonectes)* in that weak radial riblets are crossed by concentric laminae giving rise to reticulate pattern of sculpture *(19b, 19c, 19i)*. *Jur. (Bajoc.-Portland.),* G. Brit. (Eng.).——FIG. C74,*2*. **C. (C.) intertextus* (ROEMER), *U.Jur.,* Eng.; *2a,b,* LV ext., RV ext., ×0.5 *(19b)*.

?**Radulonectites** HAYAMI, 1957 [**R. japonicus*; OD]. Similar to *Pleuronectites* in general shell characters but differing in that it is sculptured with low, narrow, slightly wavy radial ribs which are separated by narrow grooves. [Relationship not fully known.] *?Trias.,* Eu.; *L.Jur.,* Japan-S.Am. (Arg.).——FIG. C74,*3*. **R. japonicus,* L.Jur. (Kuruma Gr.), Japan; *3a,b,* LV ext., RV ext., ×1 (Hayami, 1957).

EBURNEOPECTEN GROUP

Small, thin; interior without radial riblets; ctenolium present in some shells. Relationships not fully known. *U.Cret.-Rec.*

Eburneopecten CONRAD, 1865 [**Pecten scintillatus;* OD]. Valves not gaping, nearly smooth except for minute radial striae, some forms *(Micronectes)* with *Camptonectes* sculpture and with fine concentric grooves; anterior auricle larger, with radial sculpture; hinge with cardinal crura; with or without auricular crura *(256d)*. *U.Cret.,* Japan; *Eoc.-Oligo.*; E.N.Am.

E. (Eburneopecten) [=*Eburnopecten* DE GREGORIO, 1898 *(nom. null.)*; *Euburneopecten* TUCKER-ROWLAND, 1838 *(nom. null.)*]. Smooth except for fine lines of growth and microscopic divaricating radial striae generally restricted to marginal areas; auricular crura present on type species *(256d)*. *Eoc.-Oligo.,* E. N.Am.——FIG. C75,*1*. **E. scintillatus* (CONRAD), Eoc., USA(Miss.); *1a,b,* LV ext., RV ext., ×2; *1c,* RV hinge, ×5 *(389)*.

E. (Micronectes) ICHIKAWA & MAEDA, 1958 [**Micronectes bellaturus*; OD]. Differs from *Eburneopecten s.s.* in presence of fine, widely spaced, incised, concentric grooves on valves and in lacking auricular crura. Relationships not well known. *U.Cret.,* Japan.

Ciclopecten SEGUENZA, 1877 [**C. peloritanus*; OD]. Small, thin, with concentric folds, apparently with radiating striae externally. Characters not fully known. *Plio.,* Italy.

Cyclopecten Verrill, 1897 [**C. pustulosus* Verrill, 1893 (=*Pecten pustulosus* Verrill, 1893); SD Sykes, Smith, & Crick, 1898]. Small, thin, not gaping, RV flexible and upturned at margin in some forms; sculptured with concentric lamellae on one valve and radial riblets or rows of pustules on other, or both valves smooth; auricles well delimited; cardinal crura single, commonly feebly developed, hinge generally bearing vertical transverse striae; byssal notch large, but few or no pectinidial teeth. *Mio.-Rec.*, cosmop.

C. (Cyclopecten) [=*Cycopecten* de Gregorio, 1898 *(nom. null.)*; *Cyclochlamys* Finlay, 1926 *(nom. null.)* (type, *Pecten transenna* Suter, 1913)]. RV with concentric lamellae or nearly smooth, LV with radial rows of arched scales or pustules *(936)*. *Mio.-Rec.*, cosmop.——Fig. C75, *2a,b*. **C. (C.) pustulosus*, Rec., N.Foundl.; *2a,b*, LV ext., RV ext., ×2 *(936)*.——Fig. C75,*2c*. *C. (C.) simplex* Verrill, Rec., W.Indies; RV int., ×8 *(936)*.

C. (Chlamydella) Iredale, 1929 [**C. favus* Hed-

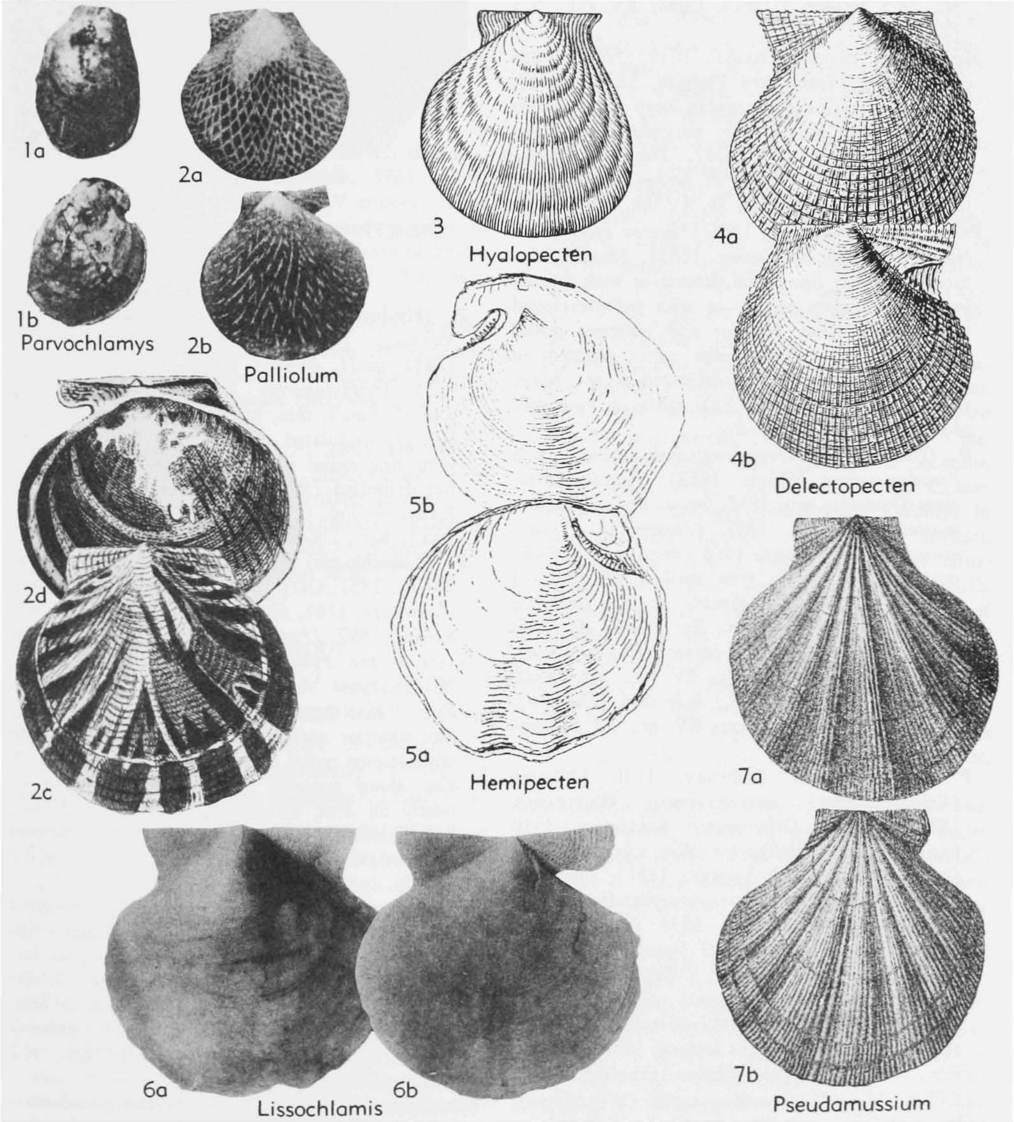

Fig. C76. Pectinidae (Eburneopecten Group) (p. *N*354-*N*355).

Ley, 1902; OD]. Differs from *C. (Cyclopecten)* in elongated (anteroposterior) form and in that RV is sculptured with fine radial riblets separated by raised scales, LV with fine concentric raised lines *(802). Rec.,* Australia.——Fig. C75,*4.* **C. (C.) favus* Hedley; *4a,b,* LV ext., RV ext., ×13 *(397).*

C. (Pectinella) Verrill, 1897 [**Pecten (Pseudamusium) sigsbei* Dall, 1886 (=*Pseudamusium sigsbeei* Dall, 1886); OD]. Auricles unequal and oblique; surface of valves smooth except for growth lines *(936). Rec.,* Carib.——Fig. C75,*3.* **C. (P.) sigsbeei* (Dall), Cuba; RV ext., ×3 *(216).*

Hemipecten Adams & Reeve, 1849 [**H. forbesianus;* M] [=*Semipecten* Fischer, 1886 (obj.)]. Attached inequivalve, irregular, deep byssal notch and ctenolium, only slightly auriculated posteriorly; hinge edentulous *(936). Plio.-Rec.,* Indo-Australia.——Fig. C76,*5.* **H. forbesianus,* Rec., E. Indies; *5a,* RV ext., ×1.5; *5b,* RV int., ×1.5 *(7c).*

Palliolum Monterosato, 1884 [**Pecten incomparabilis* Risso, 1826; SD Crosse, 1885]. Small, sculptured with very fine radial threads or with threads forming reticulate pattern or with well-developed threads only along anterior and posterior dorsal margins, sculpture of opposite valves different in some species; posterior ear delimited or not; hinge with 1 pair of small cardinal crura on each side of ligamental pit. *U.Eoc.-Rec.*

P. (Palliolum) [=*Pseudamussium* auctt. (*non Pseudamussium* Mörch, 1853); *Pseudoammussium* Gemmellaro, 1887 *(nom. null.)*; *Pseudamusium* Verrill, 1897 *(?emend.)*; *Pseudomuseum* B. L. Clark, 1918 *(nom. null.)*; *Palliorum* Oyama, 1944 *(nom. null.)*]. Sculpture of nearly obsolete radial threads or fine reticulate pattern *(793, 892). ?Eoc., Rec.,* Medit.-Afr.——Fig. C76,*2a,b.* **P. (P.) incomparabile* (Risso), Rec., Medit.; *2a,b,* LV ext., RV ext., ×2 *(89a).*——Fig. C76,*2c,d. P. (P.) hybridum* (Gmelin), Rec., W.Afr.; *2c,d,* LV ext., RV int., ×1 (Chemnitz, 1795).

P. (Delectopecten) Stewart, 1930 [**Pecten (Pseudamusium) vancouverensis* Whiteaves, 1893; OD] [=*Deletopecten* Salisbury, 1930 *(nom. null.)*; *Similipecten* Winckworth, 1932 (type, *Pecten similis* Laskey, 1811); *Arctinula* Thiele, 1934 (type, *Pecten groenlandicum* Sowerby); *Aretinula* Neave, 1939 *(nom. null.)*; *Catillopecten* Iredale, 1939 (type, *Pecten murrayi* E. A. Smith, 1885)]. Differs from *Hyalopecten* in that undulations are subdued or lacking and sculpture commonly develops reticulate pattern or may be almost lacking *(892). U.Eoc.-Rec.,* W.N.Am.-Japan-N.Eu.-Australia.——Fig. C76,*4.* **P. (D.) vancouverense* (Whiteaves), Rec., Vancouver I., Can.(B.C.); *4a,b,* LV ext., RV ext., ×5 (Dall, 1921).

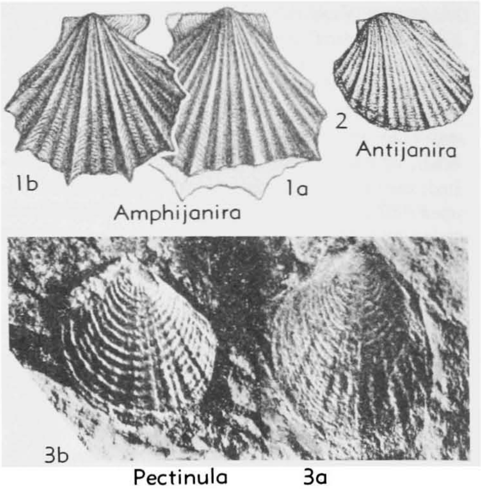

Fig. C77. Pectinidae (Antijanira Group) (p. *N*355).

P. (Hyalopecten) Verrill, 1897 [**H. undatus* Verrill, 1885 (=*Pecten undatus* Verrill, 1885) (=*H. dilectus* Verrill & Bush, 1897); OD] [=*Hylopecten* Stewart, 1930 *(nom. null.)*]. Small, thin, hyaline; valves nearly equal, strongly undulated concentrically and sculptured with fine radial striae; posterior auricle on RV not delimited *(936). L.Mio.-Rec.,* E.Atl.-W.Atl.-E.Pac.——Fig. C76,*3.* **P. (H.) undatum* (Verrill), Rec., USA(Mass.); LV ext., ×1.5 *(936).*

P. (Lissochlamis) Sacco, 1897 [**Pecten excisus* Bronn, 1831; OD] [=*Pyxis* Foresti, 1877 (*non* Chemnitz, 1784, *non* Bell, 1827); *Lissochlamys* Sacco, 1897 *(?emend.)*; *Pixis* Ugolini, 1906 (errore *pro Pyxis* Meneghini in de Stefani, 1878); *Pyxio* von Teppner, 1922 (errore *pro Pyxis* "Meneghini")]. LV convex, RV nearly flat; anterior auricle longer than posterior, both with strong radial riblets which are variable in size along anterior and posterior portions or nearly all over valves *(821a,b). U.Mio.-L.Plio.,* Italy-France.——Fig. C76,*6.* **P. (L.) excisum* (Bronn), L.Plio., *6a,b,* LV ext., RV ext., ×0.7 *(821a).*

P. (Parvochlamys) Sacco, 1904 [**Parvochlamys oolaevis*; OD]. Somewhat ovoid in shape, sculptured only with radiating riblets on upper lateral areas; right anterior auricle short. [Relationship not well known *(821a,b).*] *M.Mio. (Helvet.),* Italy.——Fig. C76,*1.* **P. (P.) oolaevis* (Sacco); *1a,* LV ext., ×4; *1b,* RV ext., ×3 (Sacco, 1904).

Pseudamussium Mörch, 1853 [**Pecten pseudamussium* Chemnitz, 1784 (=*Pecten septemradiatus* Müller, 1776); ICZN] [=*Pseudamussium* Klein, 1753 (pre-Linnean); *Peplum* Bucquoy, Dautzenberg & Dollfus, 1889 (type, *Ostrea clavata* Poli, 1795); *Platipecten* Monterosato, 1889 (type, *Pecten subclavatus* Cantraine, 1835)]. Small, RV more convex than LV, hinge lines short, auricles unequal; entire valve sculptured with radial riblets of variable strength and whole folded into several broad radial corrugations *(802, 892). M.Mio.,* Iran; *U.Mio.-Rec.,* Eu.; *Rec.,* E.Pac.——Fig. C76, *7. *P. septemradiatum* (Müller), Plio., Sicily; *7a,b,* LV ext., RV ext., ×1 (Philippi, 1900).

ANTIJANIRA GROUP

Approximately every third or fourth rib larger than others, sculpture of radial ribs and concentric imbrications; reticulate as in *Pectinula. U.Trias.-L.Jur.*

Antijanira Bittner, 1901 [**Pecten (A.) hungaricus*; M] [=*Antijanirula* Bittner, 1901 *(nom. null.)*]. RV flat or nearly so, LV convex; about every third radial rib of LV raised (similar to *Neithea*); lanciform area mostly in front of beaks. *U.Trias.,* Eu.(Hung.).——Fig. C77,*2. *A. hungarica* (Bittner); LV ext., ×1 *(61).*

Amphijanira Bittner, 1901 [**Pecten janirula* Bittner, 1895; OD]. Differs from *Antijanira* in that both valves are convex. *U.Trias.,* Eu.(Hung.).——Fig. C77,*1. *P. janirula* (Bittner); *1a,b,* LV ext., RV ext., ×3 *(58).*

Pectinula Leanza, 1943 [**P. cancellata*; OD]. Small, auricles smooth and differentiated from shell by groove; sculpture reticulate; convexity of valves and hinge characters unknown. [Relationship unknown.] *L.Jur.(M.Lias.),* S.Am.(Arg.).——Fig. C77,*3. *P. cancellata*; *3a,b,* LV ext., RV ext., ×1.5 (Leanza, 1943).

CHLAMYS GROUP

Both valves convex, LV usually more than RV; with large byssal notch below right anterior ear; sculpture of radial elements fine to coarse, commonly crossed by concentric imbricating lamellae. *Trias.-Rec.*

Chlamys Röding, 1798 [*non* Koch, 1801] [**Pecten islandicus* Müller, 1776; SD Herrmannsen, 1847]. Higher than long or rounded, commonly somewhat oblique; LV usually more convex but in some species valves nearly equally convex; auricles clearly delimited, usually large; byssal notch large; ctenolium usually present; sculpture of radial (usually stronger) and concentric elements, with scalelike spines commonly developed at their junctions, especially on LV but some shells nearly smooth; interspaces of many forms with intercalaries in adult; margin usually scalloped; cardinal crura variable in number and size. *Trias.-Rec.,* cosmop.

C. (Chlamys) [=*Clamys* Leach, 1815 *(nom. null.)*; *Chalmys* Dollfus & Dautzenberg, 1886 *(nom. null.)*; *Actinochlamys* Rovereto, 1898 (type, *Chlamys virgulata* Rovereto, 1898); *Myochlamys* von Ihering, 1907 (obj.) (*pro Chlamys* Bolten, 1898, *non* Koch, 1801); *Chlamydina* Cossmann, 1907 (obj.) (*pro Myochlamys* von Ihering, 1907, *non* Fairman, 1876); *Zygochlamys* von Ihering, 1907 (type, *Pecten geminatus* G. B. Sowerby, 1896); *Belchlamys* Iredale, 1929 (type, *Pecten aktinos* Petterd, 1886); *Mimachlamys* Iredale, 1929 (type, *Pecten asperrimus* Lamarck, 1819); *Scaeochlamys* Iredale, 1929 (type, *Pecten lividus* Lamarck, 1819); *Talochlamys* Iredale, 1929 (type, *Chlamys famigerator* Iredale, 1925); *Veprichlamys* Iredale, 1929 (type, *Chlamys perillustris* Iredale, 1925); *Coralichlamys* Iredale, 1939 (type, *C. acroporicola*)]. Usually higher than long, anterior auricle longer than posterior one; sculpture of numerous, generally grooved or striated and spinose, radial ribs; inner margin commonly with rounded, grooved, weak riblets; cardinal crura weak or nearly obsolete *(19b,c,i). Trias.-Rec.,* cosmop.——Fig. C78,*5. *C. (C.) islandica* (Müller), Rec., N.Atl.; *5a,* LV ext., ×0.5 (Gould, 1870); *5b,* RV ext., ×0.2 *(829).*

C. (Aequipecten) Fischer, 1886 [**Ostrea opercularis* Linné, 1758; M] [=*Amoebea* Fontannes, 1878 (*non* Ehrenberg, 1830) (type, *Pecten amoebus* Fontannes, 1878); *Aequipectus* Cossmann, 1910 *(nom. null.)*; *Aequivalvis* Jekelius, 1915 *(nom. null.)*; *Equipecten* B. L. Clark, 1929 *(nom. null.)*]. Differs from *Chlamys* in more rounded outline, nearly equal auricles, smaller byssal notch, fewer, usually not bifurcating radial ribs, and flattened, marginally pointed internal riblets near margin; pair of cardinal crura and auricular denticles (or weak auricular crura) present *(19b,c,i, 219).* [Probably polyphyletic.] *?U.Jur., L.Cret.-Rec.*——Fig. C78, *7. *C. (A.) opercularis* (Linné), Rec., France; RV ext., ×0.7 (Chenu, 1844). [=*Merklinia* Sobetsky, 1960 (type, *Pecten asper* Lamarck, 1819).]

C. (Anatipopecten) Hertlein, 1936 [**Pecten anatipes* Morton, 1833; OD]. About 5 rounded radial ribs which with interspaces are radially threaded; byssal notch small; hinge with coarse cardinal crura *(802). Oligo.-Plio.,* N.Am.——Fig. C78,*2. *C. (A.) anatipes* (Morton), Oligo. (Vicksburg F.), USA(Miss.); *2a,* LV ext., ×1 (Cooke, 1926); *2b,* RV ext., ×2 *(802).*

C. (Annachlamys) Iredale, 1939 [**Pecten leopardus* Reeve, 1853; OD]. Differs from *Equichlamys* in narrower, more numerous ribs and in lacking radial threads. *Mio.-Rec.,* Eurasia (Tethyan)-Australia.——Fig. C78,*6a,b. C. (A.) kuhnholtzi* (Bernardi), Rec., New Caledon.; *6a,b,* RV ext., portion LV int., ×0.6 (Bernardi, 1860).——Fig. C78,*6c*. *C. *(A.) leopardus* (Reeve), Rec., Australia; LV ext., ×0.42 (Reeve, 1853).

C. (Antipecten) Cossmann & Peyrot, 1914 [**C. sacyi*; OD]. RV nearly flat, LV convex; auricles very large, hinge line oblique *(793)*. *Mio.(Burdigal.-Helvet.)*, Eu.(France).——Fig. C78,*3*. **C. (A.) sacyi*, Burdigal.; *3a,b*, LV, RV ext., ×0.7 (Cossmann & Peyrot, 1914).

C. (Argopecten) Monterosato, 1899 [**Pecten solidulus* Reeve, 1853; OD] [=*Plagioctenium* Dall, 1898 (type, *Pecten ventricosus* Sowerby,

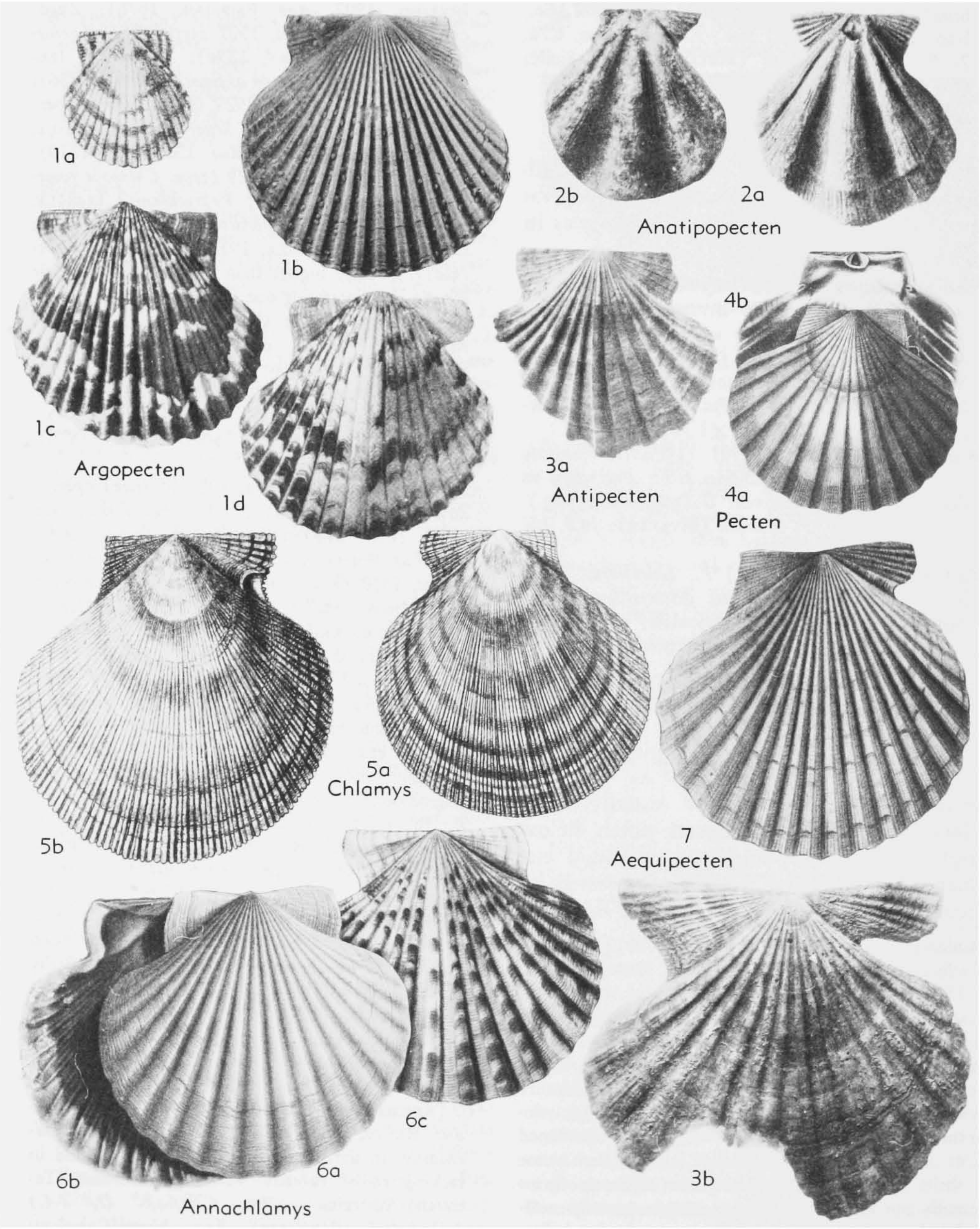

Fig. C78. Pectinidae (Chlamys Group) (p. *N*355-*N*357).

1842, _nom. nov. pro Pecten tumidus_ Sowerby, 1835, _non_ Dujardin, 1832, _nec_ Hartmann in Zieten, 1833, =_P. circularis_ Sowerby, 1835); _Plagiopecten_ G. D. Hanna, 1924 _(nom. null.)_; _Plagiopectenium_ Stewart, 1930 _(nom. null.)_; _Haumea_ Dall, Bartsch & Rehder, 1938 (type, _H. juddi_); _Corymbichlamys_ Iredale, 1939 (type, _Chlamys corymbiatus_ Hedley, 1909); _Volachlamys_ Iredale, 1939 (type, _Pecten cumingii_ Reeve, 1853)]. Differs from _Aequipecten_ in more highly and nearly equally inflated valves, lacking secondary radial riblets and with larger auricles; concentric sculpture in looped lamellae; with tendency to oblique growth in adult stage _(256a-e)_. _L.Mio.-Rec.,_ cosmop. (tropic, subtropic, warm temperate).——Fig. C78,_1a_. *_C. (A.) solidula_ (Reeve), Rec., ?loc.(unknown); _1a,_ LV ext., ×1 (Reeve, 1853).——Fig. C78,_1b_. _C. (A.) gibba_ (Linné), Rec.; _1b,_ LV ext., ×1 (Perry & Schwengel, 1940).——Fig. C78,_1c,d_. _C. (A.) circularis_ (Sowerby) (type of _Plagioctenium_), Rec., Gulf Calif.; _1c,d,_ LV ext., RV ext., ×0.7 (Arnold, 1906).

C. (Athlopecten) Marwick, 1928 [*_Pecten athleta_ Zittel, 1864; OD]. Large; RV with low rounded radial ribs, LV with twice as many ribs which are narrower, paired, and imbricated; hinge almost smooth _(593)_. _M.Oligo.,_ N.Z.——Fig. C79,_4_. *_C. (A.) athleta_ (Zittel); LV ext., ×0.3 (Zittel, 1864).

C. (Cryptopecten) Dall, Bartsch & Rehder, 1938 [*_C. alli_; OD] [=_Gloripallium_ Iredale, 1939 (type, _Ostrea pallium_ Linné, 1758)]. Major ribs and interspaces sculptured with radial riblets covered with fluted scales; cardinal crura present; _Mio.-Rec.,_ IndoPac.——Fig. C79,_1a_. *_C. (C.) alli,_ Rec., Hawaii; _1a,b,_ LV ext., RV ext., ×1.5 (Dall, Bartsch & Rehder, 1938).——Fig. C79,_1c_. _C. (C.) pallium_ (Linné) (type of _Gloripallium_), Rec., W.Pac.; LV ext., ×0.5 _(124)_.

C. (Duplipecten) Marwick, 1928 [*_Pecten waihaoensis_ Suter, 1914; OD]. Equivalve, gaping; auricles subequal, byssal notch well developed but no ctenolium; RV almost smooth, LV sculptured with faint, well-spaced radial ribs _(593)_. _L.Eoc.-M.Eoc.,_ N.Z.——Fig. C79,_5_. *_C. (D.) waihaoensis_ (Suter), M.Eoc. (Barton.); _5a,b,_ LV ext. (lectotype), RV ext., ×0.7 (Suter, 1917).

C. (Equichlamys) Iredale, 1929 [*_Pecten bifrons_ Lamarck, 1819; OD]. LV more convex than RV, auricles nearly equal, byssal notch small, ctenolium nearly obsolete in adult stage; with 7 to 9 ribs which grade into broad flattened folds of shell, whole covered with fine radial threads; interior with radial ridges corresponding to major ribs. _L.Plio.-Rec.,_ W.Pac.——Fig. C79,_3_. *_C. (E.) bifrons_ (Lamarck), Rec., Australia; _3a,b,_ LV ext., RV ext., ×0.4; _3c,_ RV int., ×0.4 (Chenu, 1844).

C. (Flexopecten) Sacco, 1897 [*_Ostrea flexuosa_ Poli, 1795; OD] [=_Glabropecten_ Sacco, 1897; _Lissopecten_ Verrill, 1897 (type, _Ostrea hyalina_ Poli, 1795); _Proteopecten_ Monterosato, 1899 (type, _Pecten proteus_ Solander in Dillwyn, 1817); _Flexipecten_ Oppenheim, 1903 _(nom. null.)_]. Rounded, RV more convex than LV; several rather broad, plicate, radial ribs, hinge with single pair of cardinal lamellae on each side of ligamental pit _(821a,b)_. _M.Mio.(Helvet.)-Rec.,_ Medit.; _Plio.,_ Iran; _Quat.,_ E.Afr.——Fig. C79,_2_. *_C. (F.) flexuosa_ (Poli), Rec., Medit.; _2a,b,_ RV ext., LV ext., ×1 (Chenu, 1844).

C. (Hilberia) von Teppner, 1922 [*_Pecten söllingensis_ von Koenen, 1868; OD]. RV more arched than LV, auricles large; radial ribs numerous, fine, those on RV wider than on LV _(793, 906)_. _Eoc.-M.Mio.(Helvet.),_ N.Eu.——Fig. C80,_1_. *_C. (H.) soellingensis_ (von Koenen), M.Oligo., Ger.; _1a,b,_ LV ext., RV ext., ×0.7 (von Koenen, 1868).

C. (Juxtamusium) Iredale, 1939 [*_J. oblectatum_; OD]. Thin, compressed, equivalve, gaping slightly at sides; auricles unequal; sculpture of fine radial striae, nearly obsolete on LV, crossed by microscopic concentric striae; internal margin, only, ribbed. _Rec.,_ Australia.——Fig. C80,_4_. *_C. (J.) oblectata_ (Iredale); _4a,b,_ LV ext., RV hinge, ×1.5 _(437)_.

C. (Kaparachlamys) Boreham, 1965 [*_Pecten hectori_ Hutton, 1873; OD]. Resembles _C. (Placopecten)_ but probably derived from _Phialopecten_. _Plio. (Opoitian Waitotaran-L.Nukumaruan),_ N.Z.

C. (Leochlamys) MacNeil, 1967 [*_C. (L.) tugidakensis_; OD]. Differs from _C. (Chlamys)_ in longer anterior auricle, deep, broad byssal notch, and coarse, usually spinose ribs. _?Jur.-Cret.,_ W. Eu.; _Mio.,_ ?Alaska-W.Can.-Japan-Medit.-E.Atl.; _Plio.,_ Alaska-Sakhalin-Japan-Pak.-Eng.; _Pleist.-Rec.,_ Japan-?Eng.

C. (Leptopecten) Verrill, 1897 [*_Pecten monotimeris_ Conrad, 1837; OD]. Small, thin, very oblique, shell corrugated to form broad radial folds; cardinal crura small, hinge plate crossed by fine transverse grooves _(219, 936)_. _Mio.-Rec.,_ N.Am.-S.Am.——Fig. C80,_2_. *_C. (L.) monotimeris_ (Conrad); Rec., Calif.; _2a,b,_ LV ext., RV ext., ×1.5 (Oldroyd, 1924).

C. (Lyropecten) Conrad, 1862 [*_Pallium estrellanum_ Conrad, 1856; SD Dall, 1898] [=_Lyropectin_ Conrad, 1863 _(nom. null.)_; _Liropecten_ Gabb, 1869 _(nom. null.)_]. Large, thick, nearly equivalve, some shells with concentric undulations; auricles nearly equal, byssal notch well developed; radial ribs undivided, entire surface covered with radial striae; hinge with 2 or 3 pairs of coarse cardinal crura _(219)_. _L.Mio.-M.Plio.,_ E. Pac.-?W.Atl.——Fig. C80,_3a-c_. *_C. (L.) estrellana_ (Conrad), U.Mio., USA(Calif.); _3a,b,_ LV ext., LV int., ×0.5; _3c,_ RV ext., ×0.6 (Arnold, 1906).——Fig. C80,*3d*. *C*. *(L.) crassicardo* (Conrad), U.Mio., USA(Calif.); RV ext., ×0.3 (Arnold, 1906).

C. (Macrochlamis) Sacco, 1897 (June) [**Ostrea latissima* Brocchi, 1814; OD] [=*Macrochlamys* Sacco, 1897 (Dec.) (*non Macrochlamys* Benson, 1832) (obj.); *Oopecten* Sacco, 1897 (type, *Pecten rotundatus* Lamarck, 1819); *Machrochlamys* de Gregorio, 1898 *(nom. null.)*; *Gigantopecten* Rovereto, 1899 (*pro Macrochlamys* Sacco, 1897, *non* Benson, 1832) (obj.); *Inaequipecten* Ugolini, 1906 (type, *Pecten tournali* de Serres, 1829); *Grandipecten* Cossmann & Peyrot, 1914 (*pro Machrochlamys* Sacco, 1897, *non* Benson, 1832) (obj.)]. Differs from *C*. *(Lyropecten)* in that the LV usually more convex than RV (but this character variable), byssal notch shallower and cardinal crura weaker

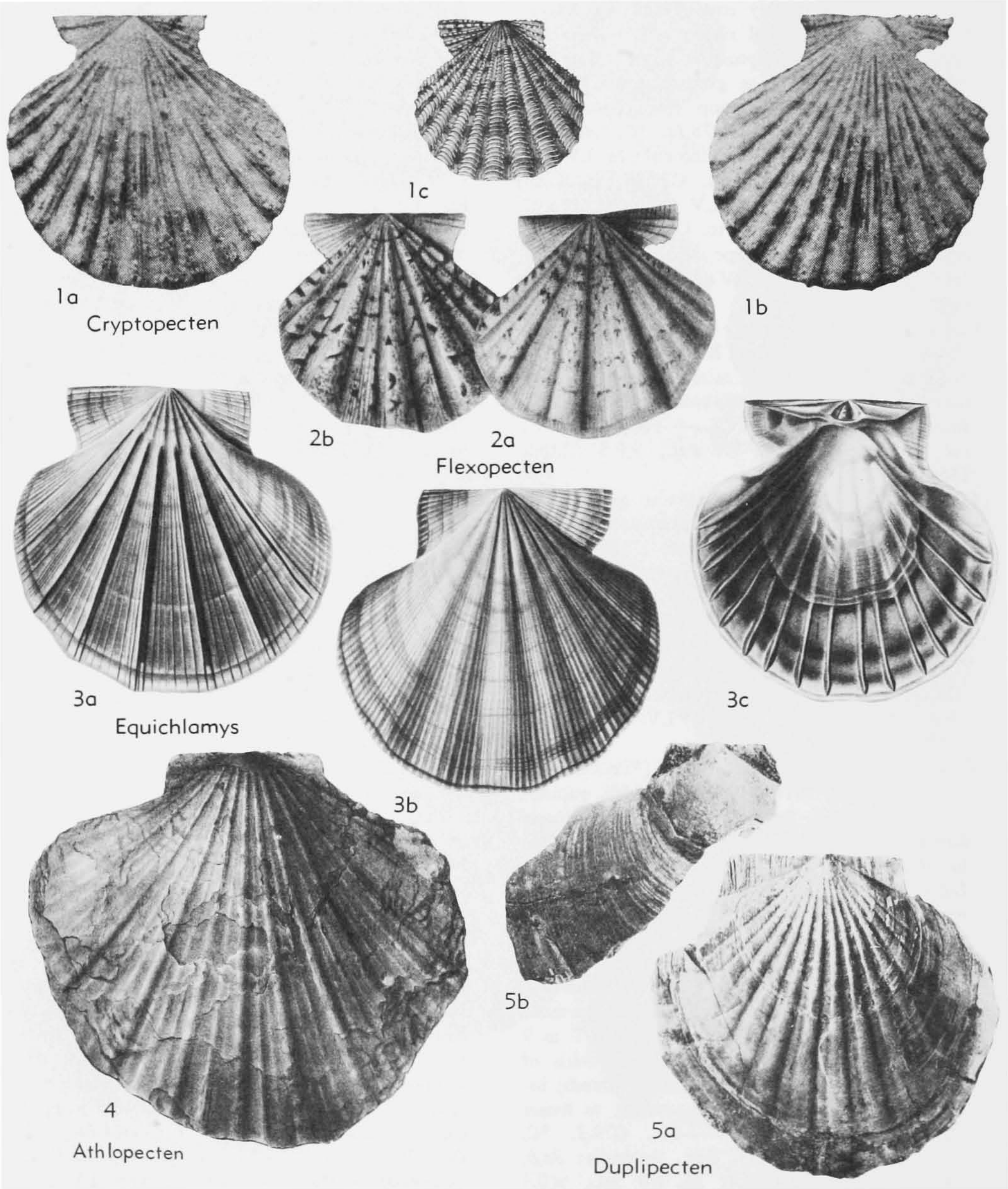

Fig. C79. Pectinidae (Chlamys Group) (p. *N*357).

(821a,b). Oligo.(Tongr.)-Plio., Eurasia(Tethyan); *?Mio., Plio.,* W.Atl.——Fig. C81,*1.* **C. (M.) latissima* (Brocchi), Plio.(Ast.), Italy; *1a,b,* LV ext., RV ext., ×0.3; *1c,* RV int., ×1 *(821a).*

C. (Manupecten) Monterosato, 1889 [**Ostrea pes-felis* Linné, 1758; SD Sacco, 1897] [=*Felipes* Locard in Carus, 1889]. Elongated (beak to base); with few coarse, elevated radial ribs which, with interspaces, are sculptured by numerous, small riblets; cardinal margin of some shells strongly crenulated with tubercles *(821a,b). M. Mio.(Helvet.)-Rec.,* Medit.——Fig. C82,*2.* **C. (M.) pesfelis* (Linné), Rec.; *2a,b,* LV ext., LV int., ×0.5 (Chenu, 1844).

C. (Mixtipecten) Marwick, 1928 [**Pecten (Aequipecten) amuriensis* Woods, 1917; OD] [=*Mixtopecten* Tucker-Rowland, 1938 *(nom. null.)*]. Small, RV almost flat, left convex, auricles large, byssal notch deep; RV with few weak radial ribs at extremities, LV having many narrow, primary ribs with secondaries in interspaces

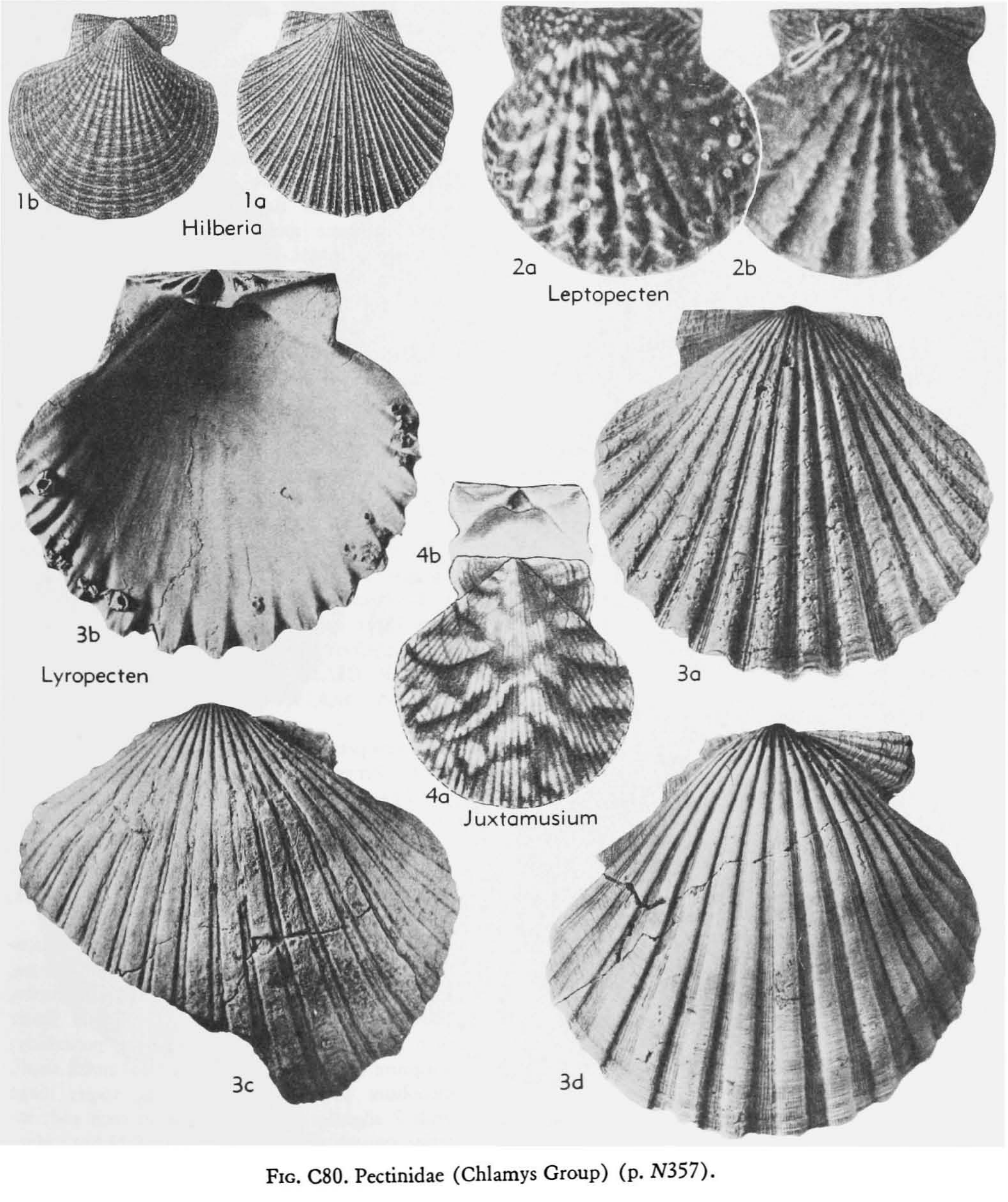

Fig. C80. Pectinidae (Chlamys Group) (p. *N*357).

(593). U.Cret., N.Z.——Fig. C82,*3.* **C. (M.) amuriensis* (Woods), Pirapauan; *3a,b,* LV ext., RV ext., ×1.5 (Woods, 1917).

C. (Miyagipecten) Masuda, 1952 [**M. matsumoriensis*; OD]. Differs from *C. (Placopecten)* in that RV has only concentric sculpture, radial sculpture on LV weak; in stronger cardinal crura, and in lacking ctenolium in young stage. *M.Mio.,* Japan.——Fig. C82,*4.* **C. (M.) matsumoriensis* (Masuda); *4a,* LV ext., ×0.5 (53); *4b,* RV ext.,-×0.5 (Masuda, 1952).

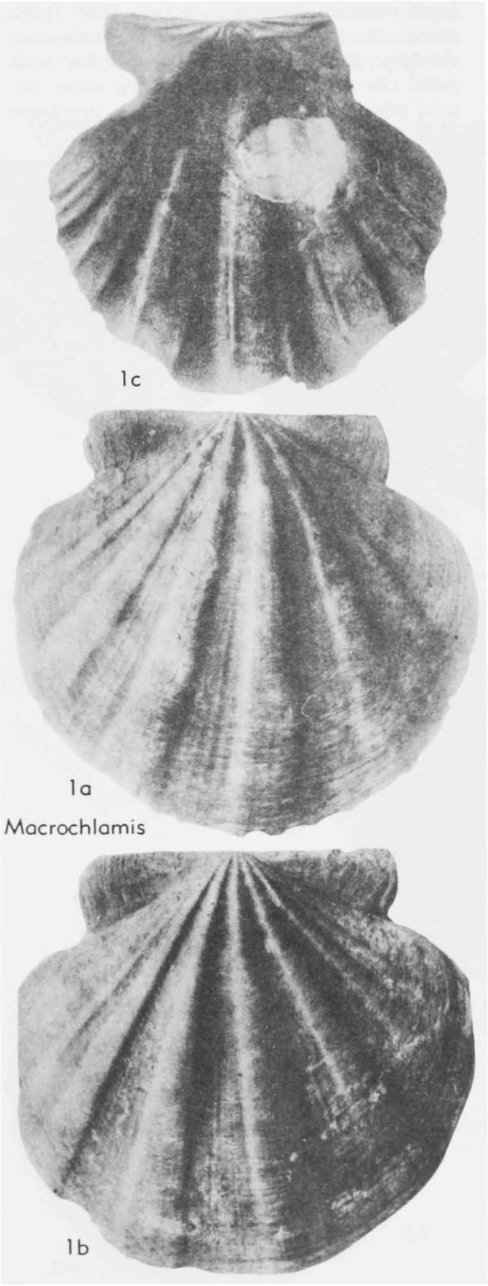

Fig. C81. Pectinidae (Chlamys Group) (p. *N*358).

C. (Nanaochlamys) Hatai & Masuda, 1953 [**Pecten notoensis* Yokoyama, 1929; OD]. Differs from *C. (Swiftopecten)* in having more numerous, bifid ribs, shorter anterior ear, and more rounded outline. *M.Oligo.-Mio.,* Japan.——Fig. C82,*1.* **C. (N.) notoensis* (Yokoyama); *1a,b,* RV ext., LV ext., ×0.8 (Hatai & Masuda, 1953).

C. (Nodipecten) Dall, 1898 [**Ostrea nodosa* Linné, 1758; OD] [=*Nodopecten* Olsson, 1914 *(nom. null.)*; *Neodipecten* von Teppner, 1922 *(nom. null.)*]. Differs from *C. (Lyropecten)* in that ribs are intermittently nodose (hollow nodes) and posterior auricle is smaller than anterior; ctenolium well developed; imbricated surface layer in some species very marked *(219). M.Mio.-Rec.,* E.Atl.-W.Atl.; *Plio.-Rec.,* W.N.Am. ——Fig. 41,*1.* **C. (N.) nodosa* (Linné), Rec., W.Atl.(off Fla.); *1a,* LV, ×0.45; *1b,* RV, ×0.45 (Chenu, 1844).

C. (Pacipecten) Olsson, 1961 [**Pecten tumbezensis* d'Orbigny, 1846; OD]. Differs from *C. (Leptopecten)* in its more equilateral form, presence of auricular crura, and thicker shell. *U.Mio.-Rec.,* E.Pac.——Fig. C82,*6.* **C. (P.) tumbezensis* (d'Orbigny), Rec., off Peru; *6a,b,* LV ext., RV ext., ×1 *(688).*

C. (Pethopecten) Hertlein, 1936 [**Pecten (Chlamys) szerémensis* Pethö, 1896; OD]. Shell oblique, hinge line short; sculpture of about 10 broad round corrugated ribs which on dorsal area bear short spines, interspaces with fine, spinose riblets. *Cret. (Cenoman.-Senon.),* Eu. (Hung.). ——Fig. C82,*5.* **C. (P.) szeremensis* (Pethö), U.Senon.; *5a,b,* RV ext., LV ext., ×0.7 (Pethö, 1906).

C. (Phialopecten) Marwick, 1928 [**Pecten triphooki* Zittel, 1864; OD]. Differs from *C. (Sectipecten)* in its flatter RV and more numerous, narrower ribs which form radial ridges rather than folds of shell *(593). L.Plio.-M.Plio.,* N.Z.——Fig. C82,*7.* **C. (P.) triphooki* (Zittel), L.Plio.; *7a,* LV ext., ×0.5 (Marwick, 1948); *7b,* RV ext., ×0.5 (Zittel, 1864).

C. (Placopecten) Verrill, 1897 [**Pecten clintonius* Say, 1824; OD] [=?*Nipponopecten* Masuda, 1962 (type, *Pecten akihoensis* Matsumoto, 1930)]. Large, compressed, RV slightly flatter than LV, gaping both anteriorly and posteriorly; sculpture of fine radial riblets; byssal notch small, ctenolium present only in young stage; hinge with 2 slightly divergent crura on each end; interior smooth *(936). L.Mio.-Rec.,* E.N.Am.; *Mio.,* ?Japan.——Fig. C83,*4.* **C. (P.) clintonia*

(SAY); *4a,* LV ext., Mio., USA(Md.), ×0.4 (Glen, 1904); *4b,* RV ext., Mio., USA(Va.), ×0.4 (Tucker-Rowland, 1938).

C. (Radiopecten) STEPHENSON, 1941 [**Pecten weeksi* STEPHENSON, 1941; OD]. Valves slightly convex, LV (upper) more so than RV; auricles

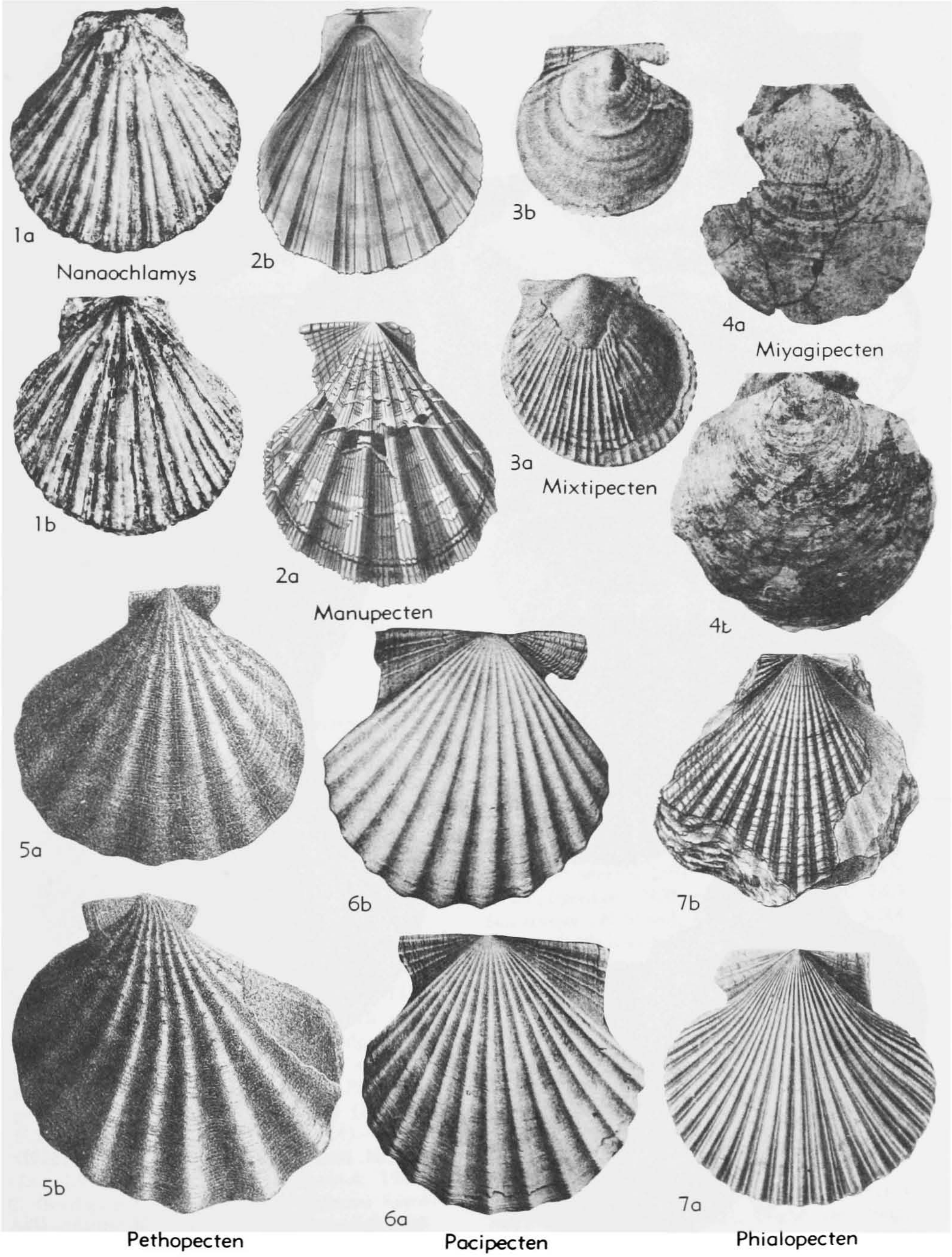

FIG. C82. Pectinidae (Chlamys Group) (p. *N*359-*N*360).

subequal; about 5 or 6 broad, rounded ribs on RV, entire surface grooved, giving rise to about 30 radial ribs, those on LV narrow and sharp. *U. Cret.(Senon.),* E. N. Am.-Eu.——FIG. C83,*3*.

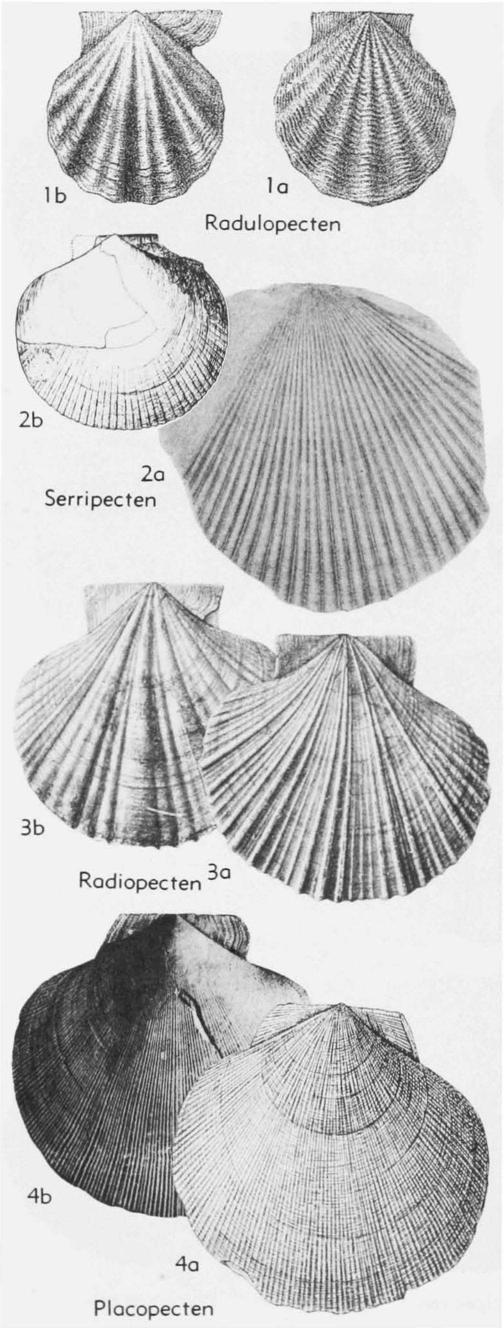

FIG. C83. Pectinidae (Chlamys Group) (p. *N*360-*N*363).

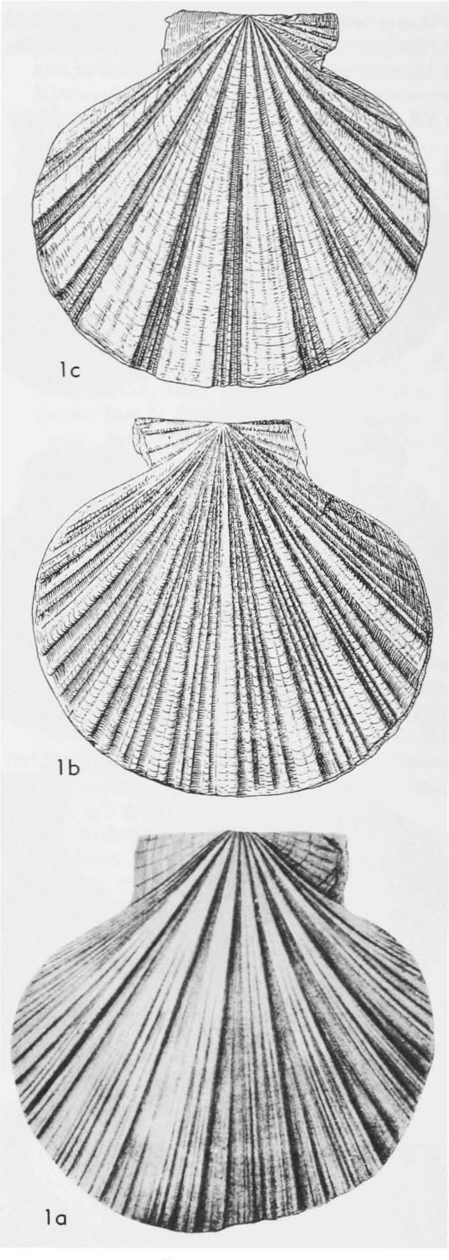

FIG. C84. Pectinidae (Chlamys Group) (p. *N*363).

**C. (R.) weeksi* (STEPHENSON), Maastricht., USA (Tenn.); *3a,b,* LV ext., RV ext., ×0.7 *(951)*.

C. (Radulopecten) ROLLIER, 1911 [**Pecten hemicostatus* MORRIS & LYCETT, 1853; OD]. LV flatter than RV, which bears 5 pairs of twinned ribs,

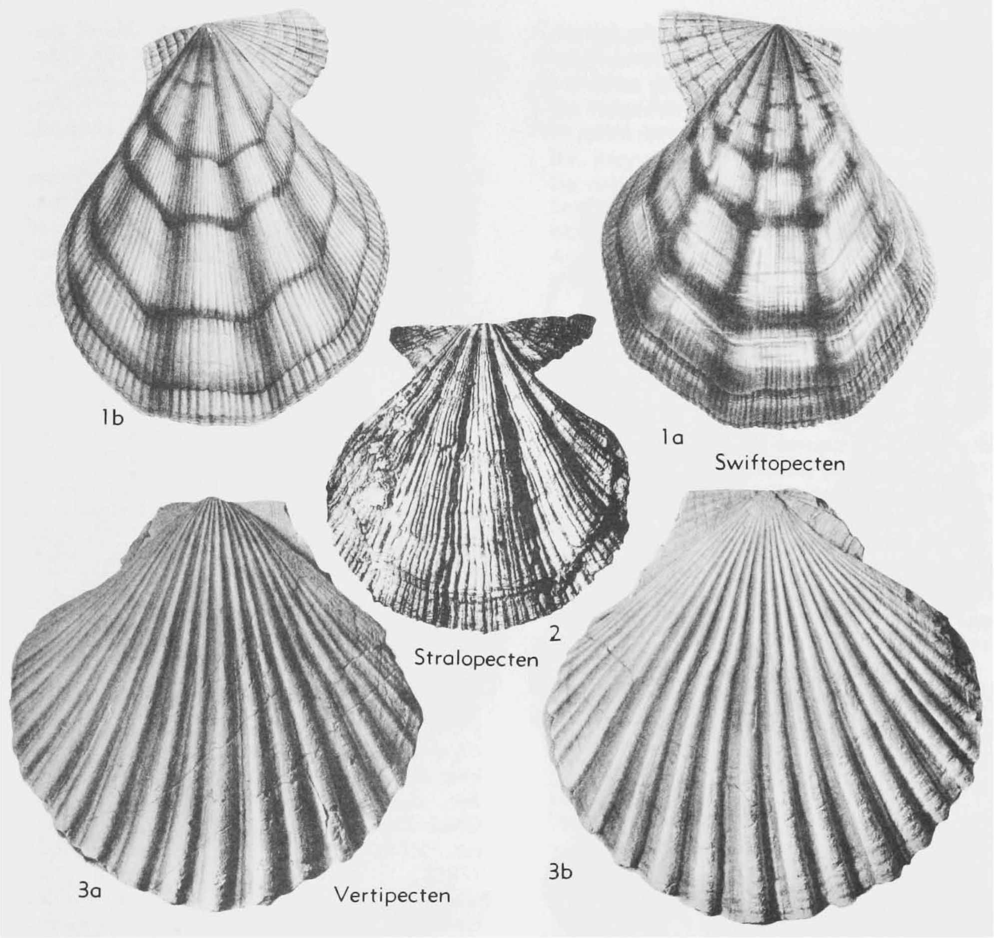

Fig. C85. Pectinidae (Chlamys Group) (p. *N*363-*N*364).

LV with 5 squamose ribs corresponding to sulci of opposite valve *(193)*. *Jur.(Bajoc.-Tithon.)*, Eurasia(Tethyan).——Fig. C83,*1*. **C. (R.) hemicostata* (Morris & Lycett), Bathon., Eng.; *1a,b*, LV ext., RV ext., ×1 (Philippi, 1900).

C. (Sectipecten) Marwick, 1928 [**Pecten wollastoni* Finlay, 1926 (=*P. sectus* Hutton, 1873, *non* Goldfuss, 1833; OD]. Byssal notch moderately developed, no ctenolium; sculpture of about 8 radial folds, radially grooved and with riblets in interspaces *(593)*. *U.Mio.-M.Plio.*, N.Z. ——Fig. C84,*1a*. **C. (S.) wollastoni* (Finlay), U.Mio.; RV ext., ×0.5 (Suter, 1914).——Fig. C84,*1b,c*. *C. (S.) allani* (Marwick), M.Tert.; *1b,c*, LV ext., RV ext., ×0.5 (Marwick, 1927).

C. (Serripecten) Marwick, 1928 [**Pecten hutchinsoni* Hutton, 1873; OD] [=*Janupecten* Marwick, 1928 (type, *Pecten uttleyi* Marwick, 1924)]. RV more convex than LV; auricles subequal; radial sculpture of numerous, sharp, scaly ridges and threads *(593)*. *L.Eoc.(Mangaorapan)-L.Plio.(Opoitian)*, N.Z.——Fig. C83,*2a*. **C. (S.) hutchinsoni* (Hutton), U.Oligo.; RV ext., ×0.4 (Suter, 1914).——Fig. C83,*2b*. *C. (S.) uttleyi* (type of *Janupecten*); LV ext., ×0.6 (Marwick, 1924).

C. (Stralopecten) Tucker-Rowland, 1938 [**Pecten ernestsmithi* Tucker, 1931; OD]. Differs from *Anatipopecten* in larger size, larger triangular auricles, and wider byssal notch; cardinal crura obsolete in adult. *Mio.-Plio.*, E.N.Am.——Fig. C85,*2*. **C. (S.) ernestsmithi* (Tucker), Plio., USA(N.C.); RV ext., ×0.4 (Tucker-Rowland, 1938).

C. (Swiftopecten) Hertlein, 1936 [**Pecten swiftii* Bernardi, 1858; OD]. Higher than long, nearly equivalve, auricles nearly equal and with well-developed byssal notch and ctenolium in adult; 4, 5 or more folded radial ribs (paired in some shells), thickened where crossed by concentric undulations, commonly with nodes at intersections on LV, entire surface with coarse radial striae and microscopic tessellations; hinge with strong cardinal crura, 1 on each side of ligamental pit. *M.Mio.-Rec.,* Japan; *M.Mio.-Pleist.,* USA(Alaska); *U.Mio.-M.Plio.,* USA(Calif.).——Fig. C85,*1.* **C. (S.) swiftii* (Bernardi), Rec., Japan; *1a,b,* LV ext., RV ext., ×0.5 (Bernardi, 1858).

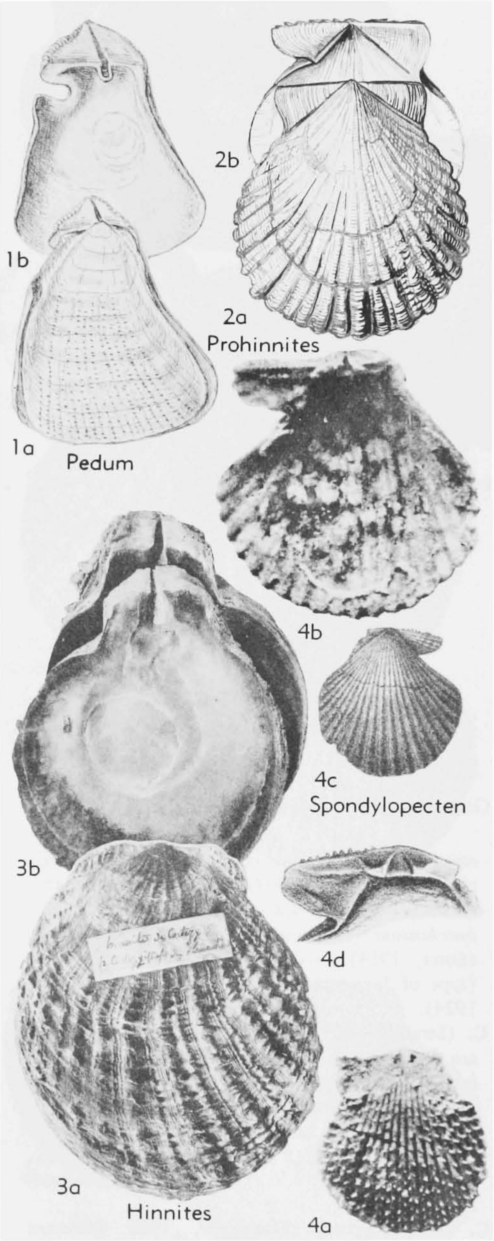

Fig. C86. Pectinidae (Hinnites Group) (p. *N*364-*N*365).

C. (Vertipecten) Grant & Gale, 1931 [**Pecten bowersi* Arnold, 1906; OD]. Differs from *Athlopecten* in that ribs of LV are not paired and about every 3rd one is elevated above others. *L.Oligo.-L.Mio.,* W.N.Am.-Japan.——Fig. C85,*3.* **C. (V.) bowersi* (Arnold), L.Mio., USA (Calif.); *3a,b,* LV ext., RV ext., ×0.4 (Arnold, 1906, mod.).

HINNITES GROUP

Free in early growth stages, resembling *Chlamys,* later cemented to substrate at RV umbo and developing irregular form, some resembling *Spondylus (Spondylopecten).* [Relationships poorly known, probably polyphyletic.] *M.Jur.(Bajoc.)-Rec.*

Hinnites Defrance, 1821 [**H. corteysii* (=*Ostrea crispa* Brocchi, 1814); SD Gray, 1847] [=*Hinnita* Férussac, 1822 (obj.) *(nom. van.)*; *Hinnus* S.Wood in Gray 1826 (type, *Lima gigantea* Gray, 1825); *Hynnites* Herrmannsen, 1847 (obj.) *(nom. van.)*]. Free in early stages similar to *Chlamys* but later attached by RV which becomes irregular *(793).* [Probably polyphyletic.] *U.Eoc.-Rec.,* cosmop. (tropic-warm temperate).——Fig. C86,*3.* **H. crispa* (Brocchi), Plio., Italy; *3a,* LV ext., ×0.5; *3b,* LV int. and RV hinge, ×0.3 *(793).*

Pedum Lamarck, 1799 [**Ostrea spondyloidea* Gmelin, 1790; SD Schmidt, 1818] [=*Pedinus* Rafinesque, 1815 *(nom. nud.)*]. Wedge-shaped, compressed, lower valve flat, deeply sinuated near hinge; hinge toothless, ligament partially external in open groove similar to that of *Spondylus*; young like *Chlamys*; permanently attached, commonly embedded in masses of corals. *Rec.,* IndoPac.——Fig. C86,*1.* **P. spondyloideum* (Gmelin); *1a,* LV ext., ×1.5; *1b,* RV int., ×1.5 *(7c).*

Prohinnites Gillet, 1922 [**Hinnites leymerii* Deshayes in Leymerie, 1842; SD Ebersin, 1960]. Similar to *Hinnites* but without obvious relationship. *L. Cret. (Valangin.-Apt.),* Eu.-Mex.-S.Am.——Fig. C86,*2.* **P. leymerii* (Deshayes), Neocom., France; *2a,b,* LV ext., RV hinge, ×1 *(124b).*

Spondylopecten Roeder, 1882 [**Pecten (S.)* cf. *erinaceus* Buvignier, Roeder, 1822 (=*Pecten (Chlamys) roederi* de Loriol, 1901); M] [=*Plesiopecten* Munier-Chalmas in Fischer, 1886 (type, *Pecten subspinosus* von Schlotheim, 1820); *Cardinopecten* Rollier, 1904 (type, *Pecten erinaceus* Buvignier, 1852; SD Hertlein, herein)]. Sculptured with number of strong, usually rounded radial ribs, those of LV spinose in some species; byssal notch deep; cardinal area of RV with narrow median groove (similar to *Spondylus*) which continues to ligamental pit; hinge of RV with 2 prominent thick teeth (1 each side of ligamental pit) which fit into corresponding sockets in LV. [Apparently some species are attached to tip of RV. Restricted to reef facies.] *Jur.(Bajoc.-Tithon.)*, Eu.-Asia(India).——Fig. C86,*4*. **S. roederi* (de Loriol), Oxford. (*4a,b*, France; *4c,d*, Switz.); *4a*, LV ext., ×2; *4b*, RV int., ×2 (Roeder, 1882); *4c*, RV ext., ×1.5; *4d*, RV hinge, ×2 (Loriol, 1901).

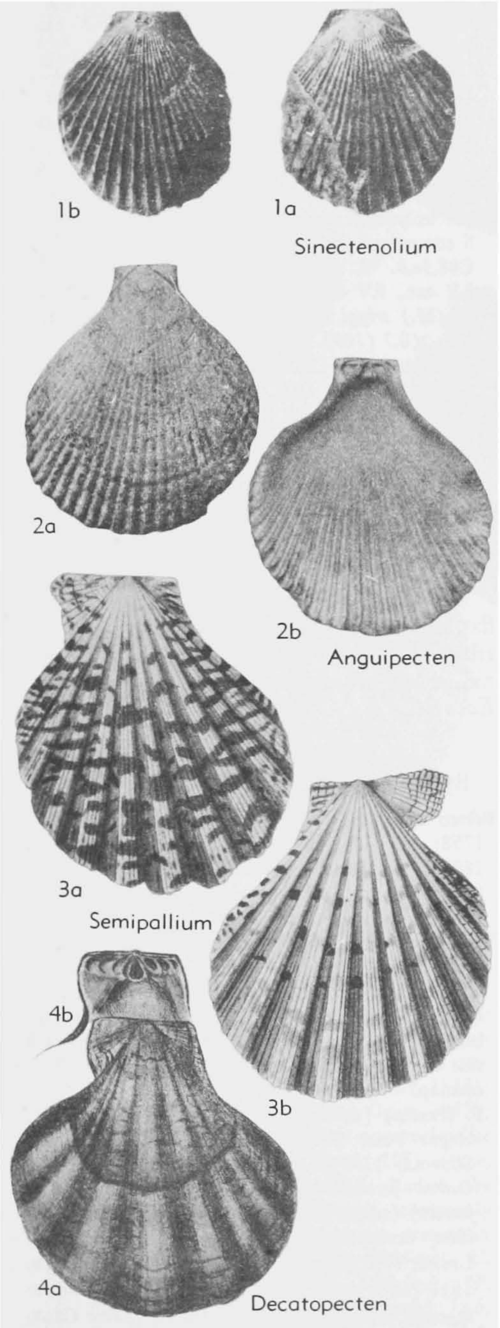

Fig. C87. Pectinidae (Decatopecten Group) (p. *N365-N366*).

DECATOPECTEN GROUP

RV more convex than LV, usually with few ribs; hinge generally short. *?Paleoc., Mio.-Rec.*

Decatopecten Rüppel in Sowerby, 1839 [**Pecten plica* Linné, 1758 (=*Ostrea plica* Linné, 1758); M] [=*Decadopecten* Swainson, 1840 (type, *Pecten plicata* Sowerby, 1839, *errore pro P. plica* Sowerby, 1839, *non P. plicata* J. de C. Sowerby, 1829, *nom. van.*)]. Elongate orbicular, flattish, auricles subequal, byssal notch very small or lacking, no ctenolium; ribs radially striated; hinge short, with few strong, nearly transverse crura. *?Paleoc., Mio.-Rec.*, W.Pac.-Ind.O.

[Swainson (1840) published the name *Decadopecten* (an invalid subsequent spelling) attributed to Rüppel (1839), citing as the sole included species "*D. plicata* Sow. Man. f. 172," which is evidently a misspelling of Sowerby's *Pecten plica* as recorded for his Fig. 172. Confusion is introduced further by the existence of *Pecten plicata* J. de C. Sowerby, 1829, as the name of a different species (*non Pecten plicatus* Chemnitz, 1784).]

D. (Decatopecten) [=*Pallium* Martini, 1774 (nonbinominal); *Pallium* Schumacher, 1817 (*non* Schröter, 1802); *Dentipecten* Gray, 1847 (obj.)]. Longer than high, with about 6 finely grooved costae formed by corrugations of shell; byssal notch very small. *L.Plio.-Rec.*, IndoPac. ——Fig. C87,*4*. **D. (D.) plica* (Linné), Rec.; *4a,b*, LV ext., RV hinge, ×1 (Sowerby, 1839).

D. (Anguipecten) Dall, Bartsch & Rehder, 1938 [**A. gregoryi*; OD]. Differs from *D. (Decatopecten)* in its vertically elongated form and more numerous, finer ribs. *Mio.-Rec.*, IndoPac. ——Fig. C87,*2*. **D. (A.) gregoryi* (Dall, Bartsch & Rehder), Rec., USA(Hawaii); *2a*, LV ext., ×0.7; *2b*, LV int., ×0.7 (Dall, Bartsch & Rehder, 1938).

D. ? (Sinectenolium) Eames & Cox, 1956 [**S. douglasi*; OD]. Small, thin, ears obtusely triangular; radially ribbed, margin fluted; no byssal notch or ctenolium. Hinge unknown. *Paleoc.*, Iran.——Fig. C87,*1*. **D. (S.) douglasi* (Eames & Cox); *1a,b*, RV ext., LV ext., ×1 (Eames & Cox, 1956).

Semipallium Jousseaume, 1928 [**Pecten tigris* Lamarck, 1819; OD]. Oblique elongate, apical angle usually less than 90°; RV more convex than LV; auricles unequal or nearly equal, hinge line rather short, byssal notch moderately well de-

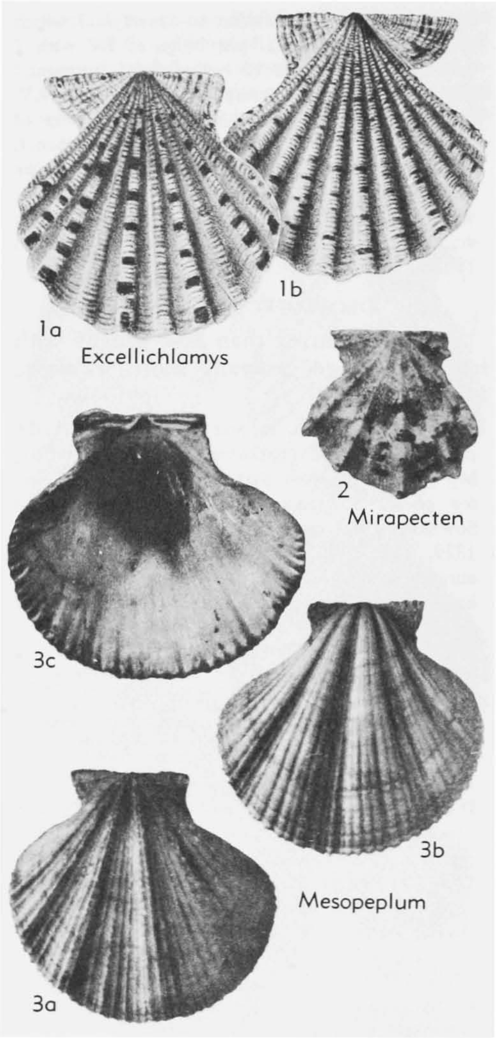

Fig. C88. Pectinidae (Decatopecten Group) (p. *N*366).

veloped; several compound ribs usually not bifurcating; hinge as in *Chlamys,* or with weak cardinal crura. *Mio.-Rec.,* IndoPac.

S. (Semipallium) [=*Pera* Chemnitz, 1784 (nonbinominal); *Bractechlamys* Iredale, 1939 (type, *B. evecta*); *Complicachlamys* Iredale, 1939 (type, *C. wardiana*); *Comptopallium* Iredale, 1939 (type, *C. pauciplicatum*)]. Several compound ribs, not bifurcating. *Mio.-Rec.,* IndoPac.——Fig. C87,*3*. **S. (S.) tigris* (Lamarck), Rec.; *3a,b,* LV ext., RV ext., ×0.7 (Chenu, 1844).

S. (Excellichlamys) Iredale, 1939 [**Pecten spectabilis* Reeve, 1853; OD]. Small to medium-sized, auricles large, unequal; sculpture of raised rounded ribs separated by deep interspaces, those on LV alternating in height. *Mio.,* Fiji; *Plio.-Rec.,* IndoPac.-N.Australia.——Fig. C88,*1*. **S. (E.) spectabile* (Reeve), Rec., Japan; *1a,b,* LV ext., RV ext., ×1 (Dunker, 1882).

S. (Mesopeplum) Iredale, 1929 [**M. caroli*; OD] [=*Notochlamys* Cotton, 1930 (type, *Chlamys anguineus* Finlay, 1927 =*Pecten undulatus* Sowerby, 1847, *non* Nilsson, 1827); *Dendopecten* Hertlein, 1936 (type, *Pecten dendyi* Hutton, 1902)]. Suborbicular; ctenolium present in young, obsolete in adult; sculptured with 5 compound ribs. *M.Mio.-Rec.,* Australia.——Fig. C88,*3a,b*. **S. (M.) caroli* (Iredale), Rec.; *3a,b,* LV ext., RV ext., ×0.7 *(437)*.——Fig. C88,*3c*. *S. (M.) triggi* (Cotton & Godfrey), Rec.; RV int., ×0.7 *(169)*.

S. (Mirapecten) Dall, Bartsch & Rehder, 1938 [**M. thaanumi*; OD]. Small, thin, with several radial ridges bearing hollow spines; hinge finely transversely denticulated. *U.Mio.-Rec.,* C.Pac.-W. Pac.——Fig. C88,*2*. **S. (M.) thaanumi* (Dall, Bartsch & Rehder), Rec., USA(Hawaii); LV ext., ×1.5 (Dall, Bartsch, & Rehder, 1938).

PECTEN GROUP

RV decidedly convex, LV gently convex, flat, or concave; auricles nearly equal; radial ribs fairly broad usually; hinge with cardinal crura or almost lacking armature. *U. Eoc.-Rec.*

Pecten (Pecten) Subgroup

Byssal notch very shallow. *U.Eoc.-Rec.*

Pecten Müller, 1776 [**Ostrea maxima* Linné, 1758; SD Schmidt, 1818] [=*Pectinium* Link, 1807 (type, *P. maximum,* =*Ostrea maxima* Linné, SD Hertlein, herein); *Pectinigenus* Renier, 1807 (obj.); *Pectinites* von Schlotheim, 1820 (*non* Gesner, 1758; *nec* Gmelin, 1793); *Pectenus* Rafinesque, 1815 *(nom. nud.)*]. Radial ribs well developed and on RV usually wider than interspaces, radially striate, grooved, or nearly smooth; hinge with cardinal crura extending from each side of ligamental pit *(256a-e, 732c)*. *U.Eoc.-Rec.,* cosmop.

P. (Pecten) [=*Vola* Klein, 1753 (pre-Linnaean); *Argus* Poli, 1791 (*non* Bohadsch, 1761; *nec* Scopoli, 1777); *Argoderma* Poli, 1795 (type, *Ostrea jacobaea* Linné, 1758, SD Hertlein, herein) (refers to shell of *Argus* Poli, 1791); *Pallium* Schröter, 1802 (type, *Pecten maximus* Linné, 1758); *Pandora* Megerle von Mühlfeld, 1811 (obj.) (*non* Lamarck, 1799); *Janira* Schumacher, 1817 (*non* Leach, 1814); *Janera* Gray, 1847 *(nom. null.)*; *Vola* Mörch, 1853 (*non* Mulsant, 1850); *Argodesma* Paetel, 1875

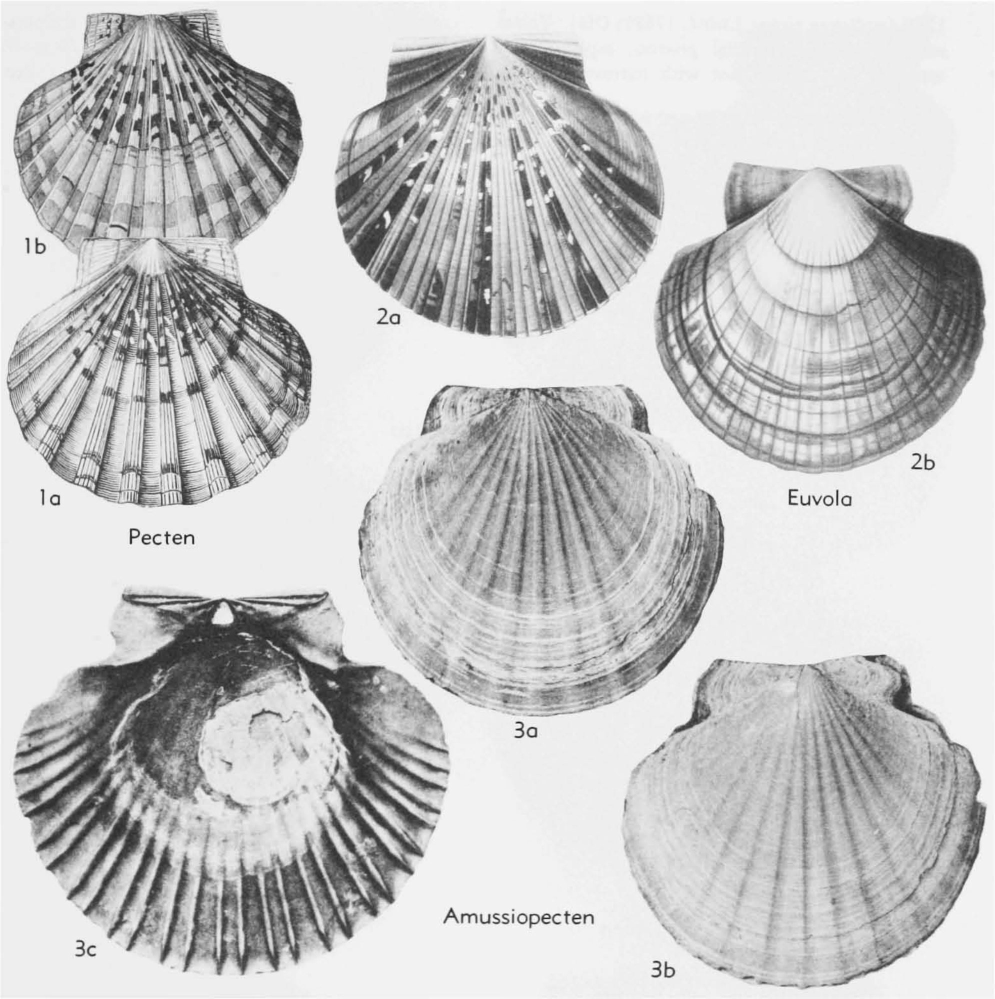

FIG. C89. Pectinidae (Pecten Group—Pecten (Pecten) Subgroup) (p. *N*366-*N*368).

(nom. null.); *Deperetia* von Teppner, 1922 (type, *Pecten cristatocostatus* Sacco, 1897); *Heritschia* von Teppner, 1922 (type, *Pecten aduncus* Eichwald, 1830); *Jaworskia* von Teppner, 1922 (type, *Pecten grandis* Sowerby, 1828); *Philippia* von Teppner, 1922 (*non* Gray, 1847); *Notovola* Finlay, 1926 (*Pecten novaezelandiae* Reeve, 1852); *Serratovola* Habe, 1951 (type, *Pecten tricarinatus* Anton, 1839)]. Radial ribs well developed, usually flat-topped, commonly radially striated or grooved; concavity present in many shells on LV umbonal area *(256a-e)*. *U.Eoc.-Rec.,* N.Eu.-Medit.——Fig. C89,*1a,b*. **P. (P.) maximus* (Linné), Rec., Eng.Channel; *1a,b,* LV ext., RV ext., ×0.25 *(124b)*.——Fig. 78,*4*. *P. (P.) jacobaeus,* Rec., Medit.; *4a,b,* RV ext., LV int., ×0.2 (Brown, 1844).

P. (Amussiopecten) Sacco, 1897 [**Pecten burdigalensis* Lamarck, 1809; OD] [=*Amusiopecten* Oppenheim, 1903 *(nom. null.)*; *Amussyopecten* Foldvári, 1929 *(nom. null.)*]. Differs from *Flabellipecten* in its nearly obsolescent radial ribs with correspondingly stronger internal radial riblets similar to *Amusium*; cardinal margin of hinge commonly more angulated with high angulated auricles *(256a-e, 821a,b)*. *U.Oligo. (Chatt.) - U.Mio. (Torton.),* Eurasia (Tethyan)-Medit.; *L.Mio.,* N.Am.(Calif.)-E.Indies-E.Afr.; *L.Mio.-M.Mio.,* Iran; *M.Mio.,* S.Am.(Venez.); *U.Mio.* or *L.Plio.,* Japan.——Fig. C89,*3*. **P. (A.) burdigalensis* (Lamarck), L.Mio.(Burdigal.), France; *3a,b,* LV ext., RV ext., ×0.5 *(256d)*; *3c,* RV int., ×0.5 (Cossmann & Peyrot, 1914).

P. (Euvola) Dall, 1898 [**Pecten ziczac* Linné, 1758 (=*Ostrea ziczac* LINNÉ, 1758); OD]. Valves smooth except for radial grooves, especially on umbonal portion; interior with narrow, rounded riblets corresponding to exterior radial sculpture. *Oligo.-Rec.,* Carib.; *Plio.,* Gulf Calif. *(19i)*.——FIG. C89,*2*. **P. (E.) ziczac* (LINNÉ), Rec.,

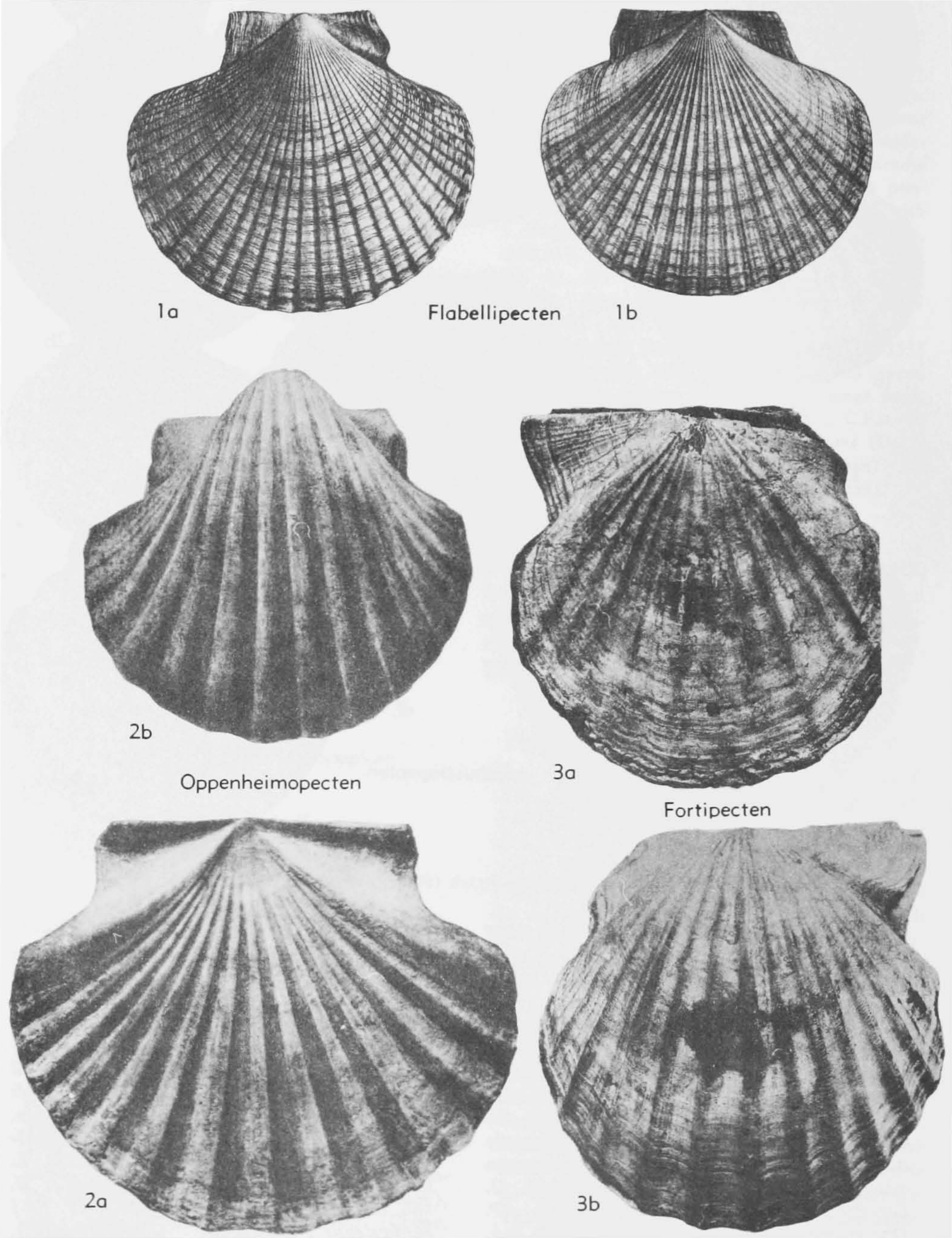

FIG. C90. Pectinidae (Pecten Group—Pecten (Pecten) Subgroup) *(1-2)*, (Pecten Group—Pecten (Patinopecten) Subgroup) *(3)* (p. *N*369-*N*371).

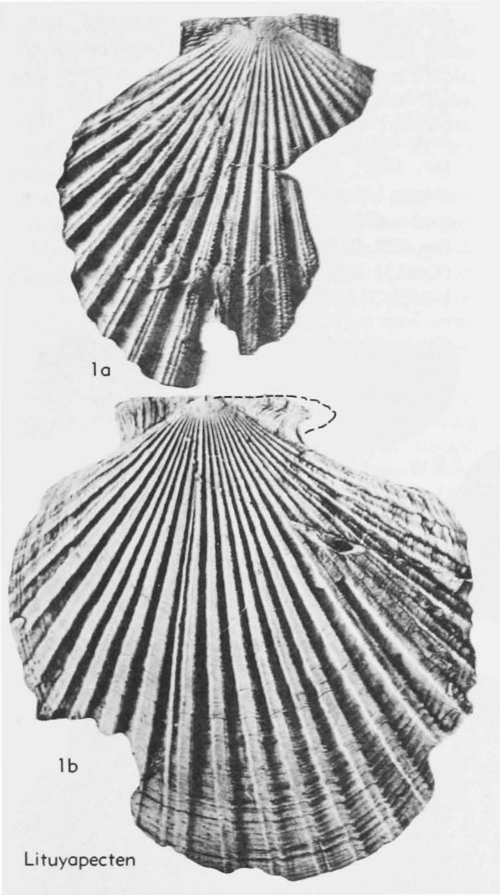

FIG. C91. Pectinidae (Pecten Group—Pecten (Patinopecten) Subgroup) (p. *N*371).

Carib.; *2a,b,* LV ext., RV ext., ×0.4 (Chenu, 1844).

P. (Flabellipecten) SACCO, 1897 [**Ostrea flabelliformis* BROCCHI, 1814; OD]. Differs from *P. (Pecten)* in convex umbonal area of LV, gently arched RV, usually depressed radial ribs and smaller auricles *(256a-e, 821a,b). L.Mio. (Aquitan.)-U.Plio.(Calabr.),* Eurasia (Tethyan); *M.Mio.-Rec.,* SE. USA-W. USA-Panama.——FIG. C90,*1.* **P. (F.) flabelliformis* (BROCCHI), U.Plio. (Piacenz.), Italy; *1a,* RV ext., ×0.6; *1b,* LV ext., ×0.5 (Goldfuss, 1835).

P. (Oppenheimopecten) VON TEPPNER, 1922 [**P. subbenedictus* FONTANNES, 1878; OD] [=*Convexopecten* TUCKER-ROWLAND, 1938 (type, *Pecten josslingi* SMITH, 1847); *Oppenheimia* ROGER, 1939 *(nom. null.)*]. RV very strongly convex (beak strongly incurved and overhanging that of LV), ribs rounded to subrectangular, auricles squarely terminated; LV flat to concave, ribs

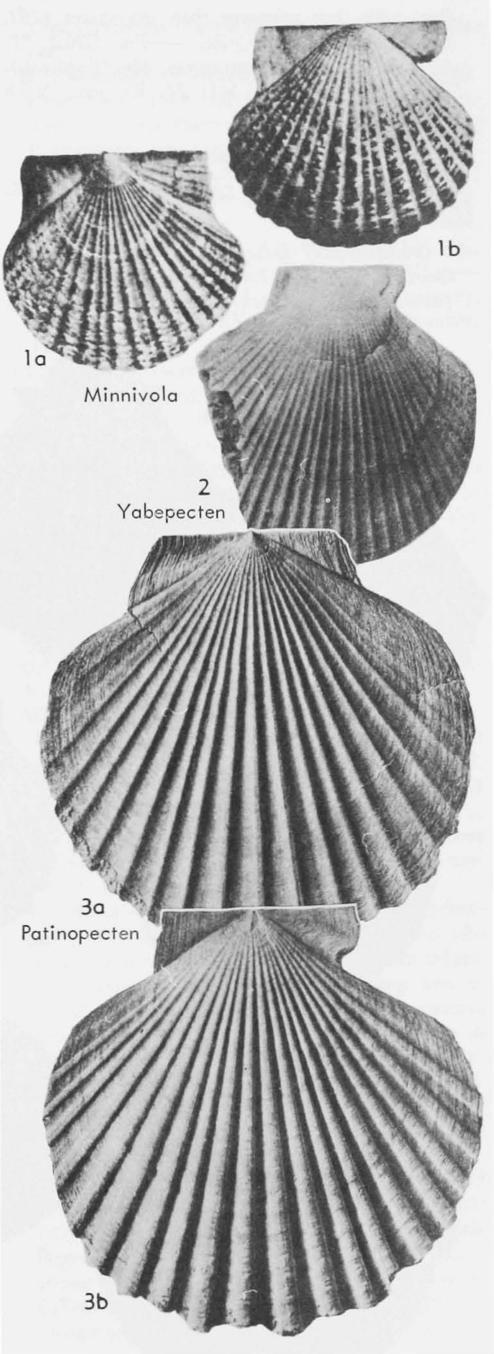

FIG. C92. Pectinidae (Pecten Group—Pecten (Patinopecten) Subgroup) (p. *N*370-*N*371).

low, wide, but narrower than interspaces *(793, 906). L.Mio.(Aquitan.)-Rec.*——FIG. C90,*2*. **P. (O.) subbenedictus* FONTANNES, Mio.(Burdigal.), France; *2a,* LV ext., ×1; *2b,* RV ext., ×0.8 *(256a).*

Pecten (Patinopecten) Subgroup

Byssal notch deep, cardinal crura weak. *U.Oligo.-Rec.*

P. (Patinopecten) DALL, 1898 [**Pecten caurinus* GOULD, 1850; OD] [=*Platinopecten* DALL, 1914 *(nom. null.)*; *Blanckenhornia* VON TEPPNER, 1922 (type, *Pecten oweni* ARNOLD, 1906, =*Pecten lohri* HERTLEIN, 1928); *?Masudapecten* AKIYAMA, 1962 (type, *Patinopecten masudai* AKIYAMA, 1962)*; ?Kotorapecten* MASUDA, 1962 (type, *Pecten kagamianus* YOKOYAMA, 1923); *?Mizuhopecten* MASUDA, 1963 (type, *Pecten yessoensis* JAY, 1857; OD)]. Large round, gently convex valves, LV nearly flat; radial ribs sulcate in some species *(219). U.Oligo.-Rec.,* N.Pac.-NE.Pac.——FIG. C92,*3*. **P. (P.) caurinus* GOULD, Plio., USA (Calif.); *3a,b,* LV ext., RV ext., ×0.5 (Arnold, 1906).

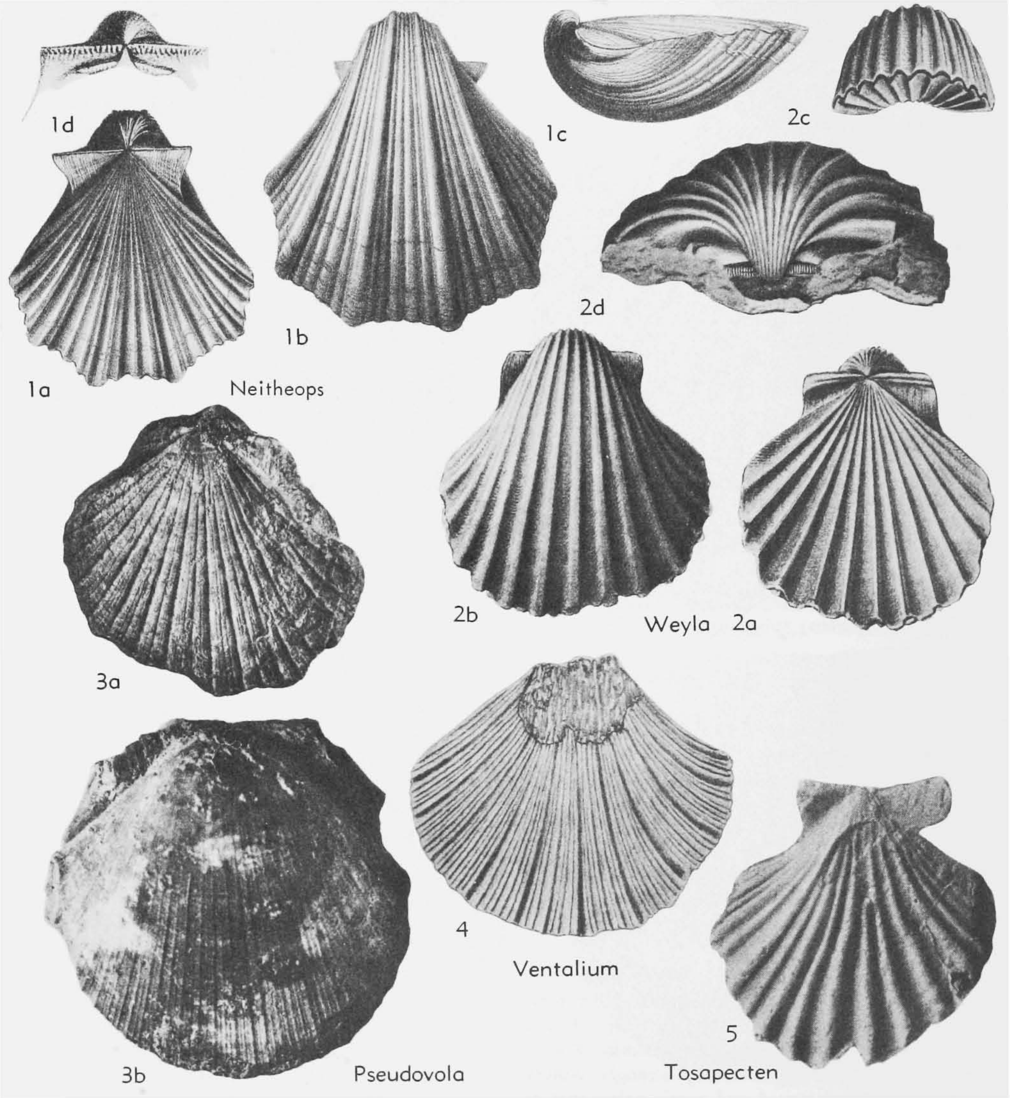

FIG. C93. Pectinidae (Neithea Group) (p. *N*371).

P. (Fortipecten) Yabe & Hatai, 1940 [**P. takahashii* Yokoyama, 1930; OD]. Shell thick, umbo of RV overhanging that of LV; ribs coarse, simple; auricles very large. *L.Plio.-M.Plio.,* Japan-Alaska. ——Fig. C90,*3*. **P. (F.) takahashii* Yokoyama, Japan; *3a,* LV ext., ×0.4 (71, mod.); *3b,* RV ext., ×0.4 (Yabe & Hatai, 1940).

P. (Lituyapecten) MacNeil, 1961 [**P. (L.) lituyaensis*; OD]. Differs from *Patinopecten* in possessing 1 to several rows of frill-like flanges on ribs (rounded to flat-topped) of LV. *U.Oligo.* or *L.Mio.,* USA(Alaska); *Plio.,* USA(Calif.)-Mex. (Baja Calif.).——Fig. C91,*1*. **P. (L.) lituyaensis,* Plio., Alaska; *1a,* LV ext., ×0.39; *1b,* RV ext., ×0.25 (MacNeil, 1961).

P. (Minnivola) Iredale, 1939 [**Minnivola isomeres*; OD]. Differs from *P. (Euvola)* in having deep byssal notch below right anterior auricle; ctenolium present. *M.Mio.-Plio.,* Iran-W.Pak.; *Rec.,* Australia-Philip.——Fig. C92,*1*. **P. (M.) isomeres* (Iredale), Rec., Australia; *1a,b,* LV ext., RV ext., ×1 (Eames & Cox, 1956).

P. (Yabepecten) Masuda, 1963, p. 149 [**Pecten tokunagai* Yokoyama, 1911; OD]. Differs from *Patinopecten* in shallower byssal notch of RV and more numerous, rounded, radial ribs. *Plio.,* Japan.——Fig. C92,*2*. **P. (Y.) tokunagai* (Yokoyama), RV ext., ×0.9 (Masuda, 1963).

NEITHEA GROUP

RV more convex than LV; byssal notch usually slight but may be well developed; hinge commonly with coarse cardinal crura or denticles, entire hinge vertically striated in many species. *U.Trias.-Cret., ?L.Eoc.*

Neithea Drouet, 1825 [**Pecten aequicostatus* Lamarck, 1819; SD Chenu, 1862] [=*Neithaea* Gray, 1840 *(nom. null.)*; *Neitea* d'Orbigny, 1846 *(nom. null.)*; *Mithea* Anderson, 1902 *(nom. null.)*; *Neitha* Preston, 1925 *(nom. null.)*; *Meithea* Stewart, 1930 *(nom. null.)*; *Nerithea* Grant & Gale, 1931 *(nom. null.)*]. Equal or nearly equal radial ribs, or with 4 to 6 raised radial ribs separated by 3 or 4 smaller ones or with radial striae; auricles equal or anterior one larger, shallow byssal notch present; hinge with two diverging, transversely striated cardinal teeth, 1 on each side of ligamental pit, and two lamellae corresponding to each of these on LV; rows of small denticles along interior upper margin of auricles *(892)*. *Cret. (Neocom.-Senon.),* cosmop. *?L.Eoc.,* Switz.

N. (Neithea) [=*Aequineithea* Hayami, 1960 (obj.)]. Numerous radial ribs equal or nearly equal in size. *Cret.(Neocom.-Senon.),* cosmop.

N. (Neithella) Hayami, 1960 [**Janira wrightii* Shumard, 1860; OD]. Sculpture of 4 or 5 prominent radial ribs; anterior auricle much larger than posterior one (which is only slightly developed)]. *Cret. (Neocom.-Turon.),* Eu.-E.N.Am.-Madagascar.

N. (Neitheops) Stewart, 1930 [**Neithea grandicosta* Gabb, 1869; OD] [=*Rogeria* von Teppner, 1922 (*non* Emery, 1894)]. Sculpture of 5 or 6 prominent ribs commonly separated by 3 or 4 smaller ones. *Cret. (Valangin.-Maastricht.), ?L.Eoc.,* Switz., cosmop.——Fig. C93,*1a-c*. *N. (N.) quinquecostata* (Sowerby), Cenoman., France; *1a-c,* LV view of both valves, RV ext., both valves ant., ×0.7 (d'Orbigny, 1847).——Fig. C93,*1d*. *N. (N.) phaseola* (d'Orbigny), Cenoman., France; RV hinge, ×1 (d'Orbigny, 1847).

?**Ventalium** de Gregorio, 1930 [**V. insignis*; OD]. Flattish, fan-shaped, sculptured with minute radial riblets; about 10 deep, radiating sulci, each of which separates groups of about 6 to 8 riblets; hinge unknown. [Type imperfect, characters not fully known but considered by de Gregorio to be related to *Pecten*.] *L.Jur.(Lias.),* Sicily.——Fig. C93,*4*. **V. insignis*; RV ext., ×0.7 (de Gregorio, 1930).

Weyla J. Böhm, 1922 [**Pecten alatus* von Buch, 1835; OD]. RV very highly convex, byssal sinus slight; hinge with 1 or 2 pairs of cardinal laminae, striated vertically. *U.Trias.-M.Jur.,* N.Am.-S.Am.-N.Afr.-Medit.

W. (Weyla) [=*Parapecten* Crickmay, 1930 (type, *P. ntlakapamuxanus*)]. Both valves sculptured with coarse radial costae. *L.Jur.(Lias.),* N.Am.-S.Am.-N.Afr.-Medit.——Fig. C93,*2*. **W. (W.) alata* (von Buch), Peru *(2a-c)*, Arg. *(2d)*; *2a-c,* LV view of both valves, RV ext., both valves ventral, ×0.5 (Steinmann, 1929); *2d,* RV umbonal view showing hinge, ×0.7 *(445)*.

W. (Pseudovola) Lissajous, 1923 [**P. depéreti*; OD]. RV sculptured with about 100 radial ribs of which about one-fourth are higher than others, all crossed by concentric striae giving rise to reticulate pattern; LV flattish, slightly concave near beak, sculptured with about 15 radial ribs in interspaces of which about 6 smaller riblets occur, 1 higher than others, all crossed by concentric imbrications. *M.Jur.(Bathon.),* France.——Fig. C93,*3*. **W. (P.) depereti* (Lissajous); *3a,* LV ext., ×1; *3b,* RV ext., ×1.5 (Lissajous, 1923).

W. (Tosapecten) Kobayashi & Ichikawa, 1949 [**Pecten (Velopecten) suzukii* Kobayashi, 1931; OD]. RV convex, LV nearly flat; anterior auricle larger and with byssal notch well developed; strong radial ribs differ in arrangement on valves. *U.Trias.,* Japan.——Fig. C93,*5*. **W. (T.) suzukii* (Kobayashi); RV ext., ×1 (Kobayashi, 1931).

PSEUDOPECTEN GROUP

LV of many shells nearly as convex as RV; distinct byssal notch present. *U.Trias.-M.Jur.*

Pseudopecten Bayle, 1878 [**Pecten aequivalvis* J. Sowerby, 1816; M]. Nearly equivalve; about 15 or 16 radial ribs which are nearly smooth or with spines on RV. *L.Jur.-M.Jur.,* Eu.-S.Am.-E.Indies.

P. (Pseudopecten). Radial ribs on RV smooth or some with spines *(732c). L.Jur.(Sinemur.-Domer.),* Eu.——Fig. C94,*5a,b*. **P. (P.) aequivalvis* (J. Sowerby), Eng.; *5a,b*, LV, RV, ×0.4 (Chenu, 1944).

P. (Echinopecten) Brasil, 1895 [**Pecten barbatus* J. Sowerby, 1819; OD]. RV generally flatter than LV and bearing long, depressed spines. *Jur. (Hettang.-Bajoc.),* Eu.-S.Am.——Fig. C94,*3*. **P. (E.) barbatus* (J. Sowerby), Inf. Oolite, Eng.; RV ext., ×1 (Sowerby, 1819).

Indopecten Douglas, 1929 [**Pecten clignetti* Krumbeck, 1913 (=*Pecten (Aequipecten) clignetti* G. Böhm, 1906, *nom. nud.*); OD]. RV moderately convex; valves corrugated to form 5 or 6 rounded radial folds, some bearing secondary riblets, smooth or with rows of knobs or tubercles at regular intervals; shallow byssal notch present;

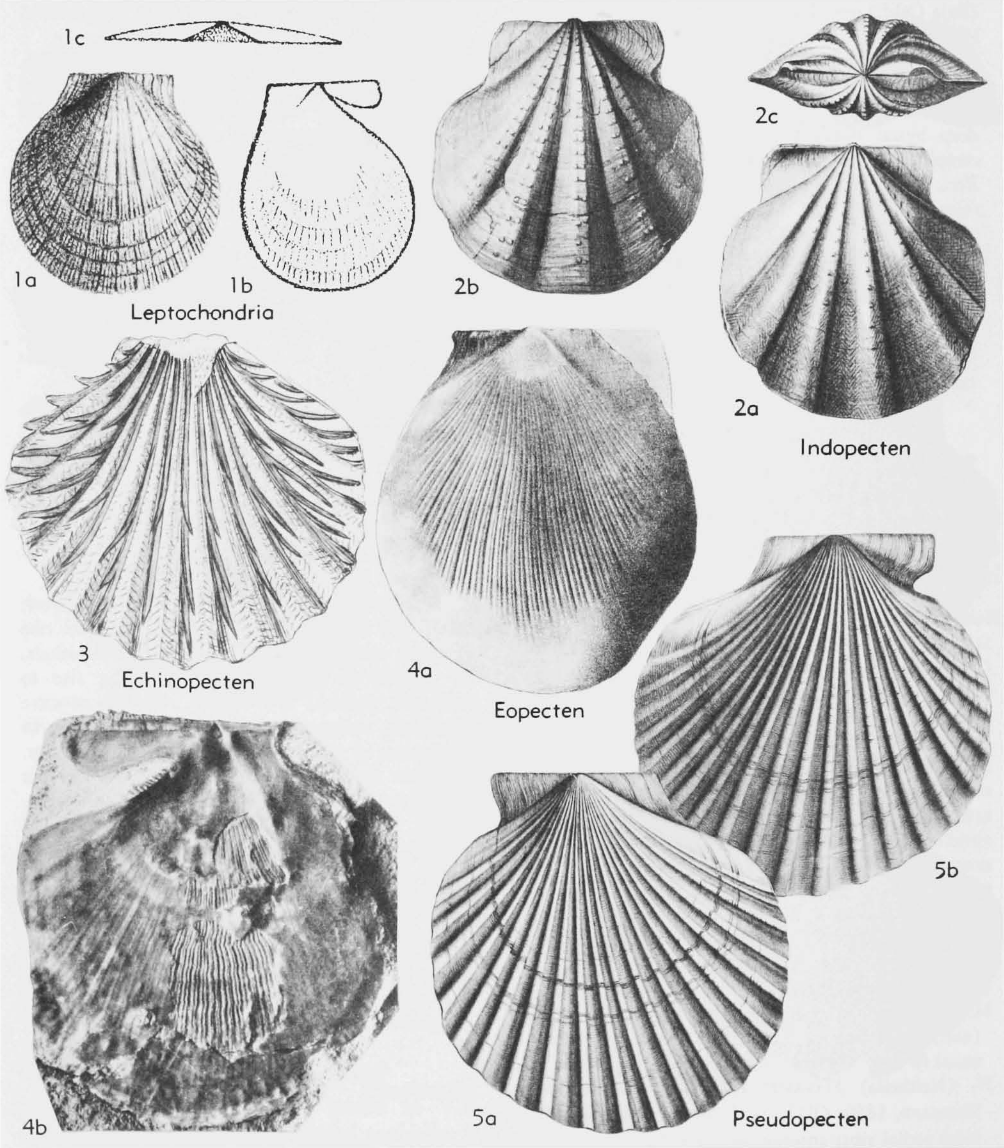

Fig. C94. Pectinidae (Pseudopecten Group) *(2-3,5)*; Aviculopectinidae (Aviculopectininae) *(1)*; Group Uncertain *(4)* (p. *N338*, *N372-N373*).

interior structure of LV with series of regular zigzag lines. [Relationships not well known.] *U.Trias.(U.Nor.),* E.Indies.——Fig. C94,*2*. **I. clignetti* (Krumbeck), *2a-c,* LV ext., RV ext., both valves umbonal views, ×0.7 (Krumbeck, 1913).

GROUP UNCERTAIN

Eopecten Douvillé, 1897, p. 203 [**Hinnites tuberculatus* Goldfuss, 1836 (*errore pro Spondylus tuberculosus* Goldfuss, 1836; OD] [=*Velata* Quenstedt, 1856 (*non* Griffith & Pidgeon, 1834, obj.; *Velopecten* Philippi, 1899 (*pro Velata* Quenstedt, 1856 (*non Velates* Montfort, 1810); *Velatopecten* Rollier, 1906 *(nom. van.)*]. Medium-sized to large, acline, more or less irregular in outline at all stages of growth, some specimens irregularly puckered or with allomorphic ornament; inequivalve, with LV convex and RV flat or concave, with indications of having grown attached at umbo; left anterior wing large, indistinctly demarcated, right anterior auricle elongate, deep subauricular notch with ctenolium below it; posterior wing rather small; RV with narrow, obtusely triangular cardinal area with deep narrowly triangular pit below beak corresponding to internal resilium, corresponding features of LV uncertain; interior of RV in some specimens with blunt oblique internal ridge originating near resiliifer; ornament of radial ribs of 2 or 3 orders of strength increasing by implantation. *L.Jur.(Lias.)-L.Cret.(Alb.),* cosmop.——Fig. C94,*4a*. **E. tuberculosus* (Goldfuss), M.Jur., Ger.; LV ext., ×0.5 *(341b)*.——Fig. C94,*4b*. *E. abjectus* (Phillips), M.Jur., Inf. Oolite, Eng. (Dorset.), RV int., ×0.7 *(184)*.

?**Mclearnia** Crickmay, 1930, p. 45 [**M. mclearni*; OD]. Large, suborbicular, subequilateral, not pronouncedly inequivalve; posterior wing obtuse, not clearly delimited from body of shell; right anterior auricle narrow, more elongate than posterior wing, with deep sinus below it; resilium pit deep, triangular, subcentral, no evidence of crura; adductor scar unknown; pallial line split up into small depressions dorsally, but with its anterior and posterior branches meeting below resilium pit; *Chlamys*-like ornament of radial riblets impressed on interior in early growth stages, ornament apparently lacking in later stages. [Needs further investigation.] *L.Cret.,* Can.(B.C.).——Fig. C74,*4*. **M. mclearni*; RV int., ×0.5 (Crickmay, 1930).

Family MONOTIDAE P. Fischer, 1887

[*nom. transl.* Kittl, 1912, p. 166 (*ex* Monotinae P. Fischer, 1887, p. 95)] [Materials for this family prepared by L. R. Cox]

Thin-shelled, of feeble to moderate convexity, subequivalve or distinctly inequi-

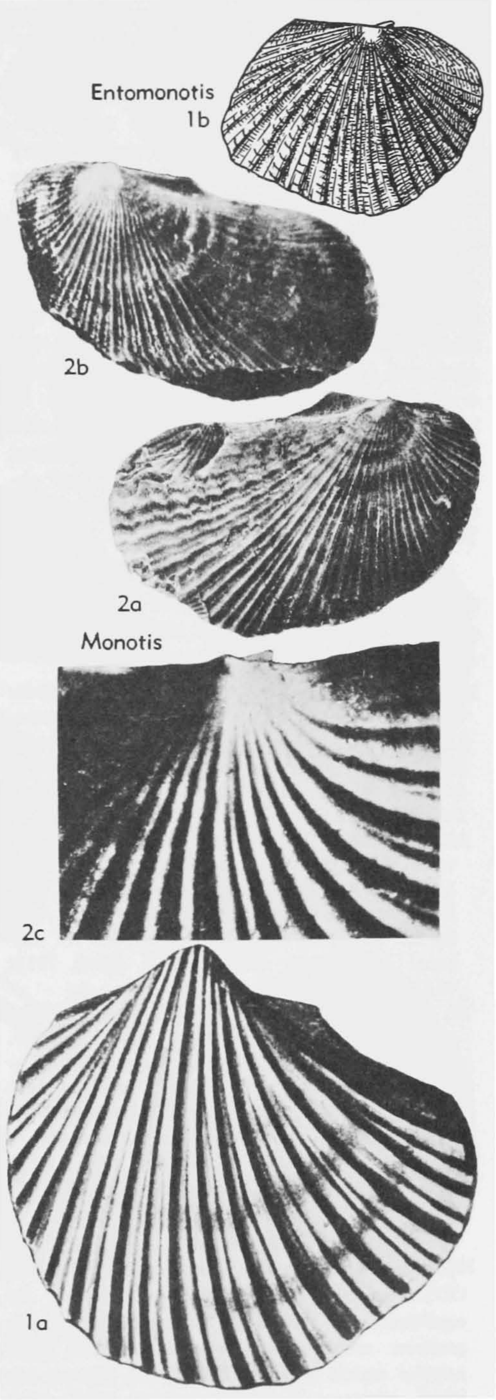

Fig. C95. Monotidae (p. *N*374).

valve, with RV flatter, obliquely ovate, prosocline, inequilateral, obtusely subalate posteriorly, posterior wing (except in *Pleuromysidia*) more or less distinctly demarcated from body of shell in both valves; LV without distinct anterior wing, its anterodorsal margin evenly rounded; very small, commonly uptilted right anterior auricle present, but hidden from view in many specimens by dorsal part of body of valve; subauricular notch narrow, deep; hinge edentulous; ligamental area external, forming narrow, inequilateral triangle entirely posterior to beaks, longitudinally striated and (in *Monotis*) with single, shallow, wide ligamental pit; ornament similar in both valves, consisting usually of radial ribs which increase by intercalation, but absent in some specimens; muscle scars not observed; original shell structure unknown. *U. Trias.*

The presence of the right anterior auricle distinguishes this family from the Halobiidae; the small size of this auricle from the Aviculopectinidae.

Monotis Bronn, 1830, p. 284 [**Pectinites salinarius* von Schlotheim, 1820, p. 230; SD Hermannsen, 1852, p. 86)]. Hinge line of moderate length; posterior wing more or less distinctly demarcated in both valves; right anterior auricle uptilted. *U.Trias.,* cosmop.

M. (Monotis). Subequivalve to slightly inequivalve; right anterior auricle very small. *U.Trias.,* Aus.-Yugosl.(Dalmat.)-Sicily.——Fig. C95,*2*. **M. (M.) salinaria* (von Schlotheim), Nor., Aus.; *2a,* LV ext., ×1; *2b,* RV ext., ×1; *2c,* LV umbonal region with auricle, ×3.3 (Kittl, 1912; *423*).

M. (Entomonotis) Marwick, 1935, p. 298 [**Monotis richmondiana* Zittel, 1864, p. 26 (as **M. salinaria,* var.); OD]. All specimens distinctly inequivalve, with LV well inflated; right anterior auricle larger than in *M. (Monotis). U. Trias. (Nor.),* N.Z.-N.Caledon.-Indon.-Japan-Spitz.-USSR (Crimea-E.Sib.-Cauc.)-?Iran-Mex.-W.S.Am.-W.N.Am.——Fig. C95,*1*. **M. (E.) richmondiana* (Zittel), N.Z.; *1a,* LV ext., ×1; *1b,* RV ext., ×0.7 (Frech, 1908; *596*).

?**Pleuromysidia** Ichikawa, 1954, p. 52 [**P. dubia*; OD]. Subequivalve, well inflated, strongly inequilateral and prosocline; hinge line very short; posterior wings obtuse, scarcely defined; right anterior auricle small, as in *Monotis,* but not uptilted, ornament weak, of close-set radial striae. *U.Trias.(Carn.),* Japan.

Family BUCHIIDAE Cox, 1953

[Buchiidae Cox, 1953, p. 6] [=Aucellidae Fischer, 1887 (*nom. transl.* Lahusen, 1897, *ex* Aucellinae Fischer, 1887); suppressed by ICZN Opinion 492 (1957)] [Materials for this family prepared by L. R. Cox]

Shell obliquely ovate, with relatively short hinge margin and posterior wings absent or obtuse and ill-demarcated; height most commonly well exceeding length; usually more or less inequivalve, with LV more gibbose, but equivalve in *Pseudaucella*; right anterior auricle well demarcated, with deep, acute subauricular sinus in most genera and extending out of plane of valve margins toward LV in some forms; ligamental area triangular and external or subexternal in both valves, with single shallow ligamental pit; no hinge teeth; ornament lacking or of concentric ribs, with subordinate radial threads in a few forms; ostracum entirely calcitic. *U.Trias.-Cret.*

Buchia Rouillier, 1845, p. 289 [**Avicula mosquensis* von Buch, 1844, p. 537; M] [=*Aucella* Keyserling, 1846 (suppression confirmed by ICZN Opinion 492); *Ancella* Stoliczka, 1866 *(nom. null.)*; *Anaucella* Pchelintseva, 1955 (type, *Aucella bronni* Lahusen, 1888 (*non* Rouillier, 1848)]. Strongly prosocline, height well exceeding length; highly inequivalve, LV strongly convex with more or less prominently projecting umbo and prosogyrous beak, RV flat to feebly convex with its umbo scarcely projecting; right anterior auricle concave tonguelike process which is not in alignment with hinge margin but extends toward LV and rests in socket in its cardinal area in front of beak; cardinal area an inequilateral triangle of moderate breadth in each valve, with shallow ligamental pit directed backward from beak, pit of LV with raised margins; ornament of concentric ridges or ribs, with subordinate radial threads in some species. (The differences between the type species of *Anaucella* (not yet renamed) and typical *Buchia* appear not to be of more than specific importance. Pchelintseva, however, also included in *Anaucella* the Triassic species *"Lima" ussuriensis* Voronetz; this probably should be made the type of a new genus which may not belong to the Buchiidae.] *M.Jur.(Aalen.)-L.Cret.,* cosmop., most abundant in boreal regions; *U.Jur.-U.Cret.(Maastricht.),* Ind.O.(Madag.)-USSR. —— Fig. C96,*1a,b*. **B. mosquensis* (von Buch), U.Jur.(L.Volg.), USSR; *1a,b,* LV ext., RV view of both valves, ×1 (Lahusen, 1888).——Fig. C96,*1c,d*. *B. subovalis* (Pavlov), U.Jur.(L.Volg.), USSR; *1c,d,* RV ext., int., ×1, ×2, showing auricle (Pavlov, 1907).——Fig. C96,*1e*. *B. keyserlingi* Lahusen, L.Cret.

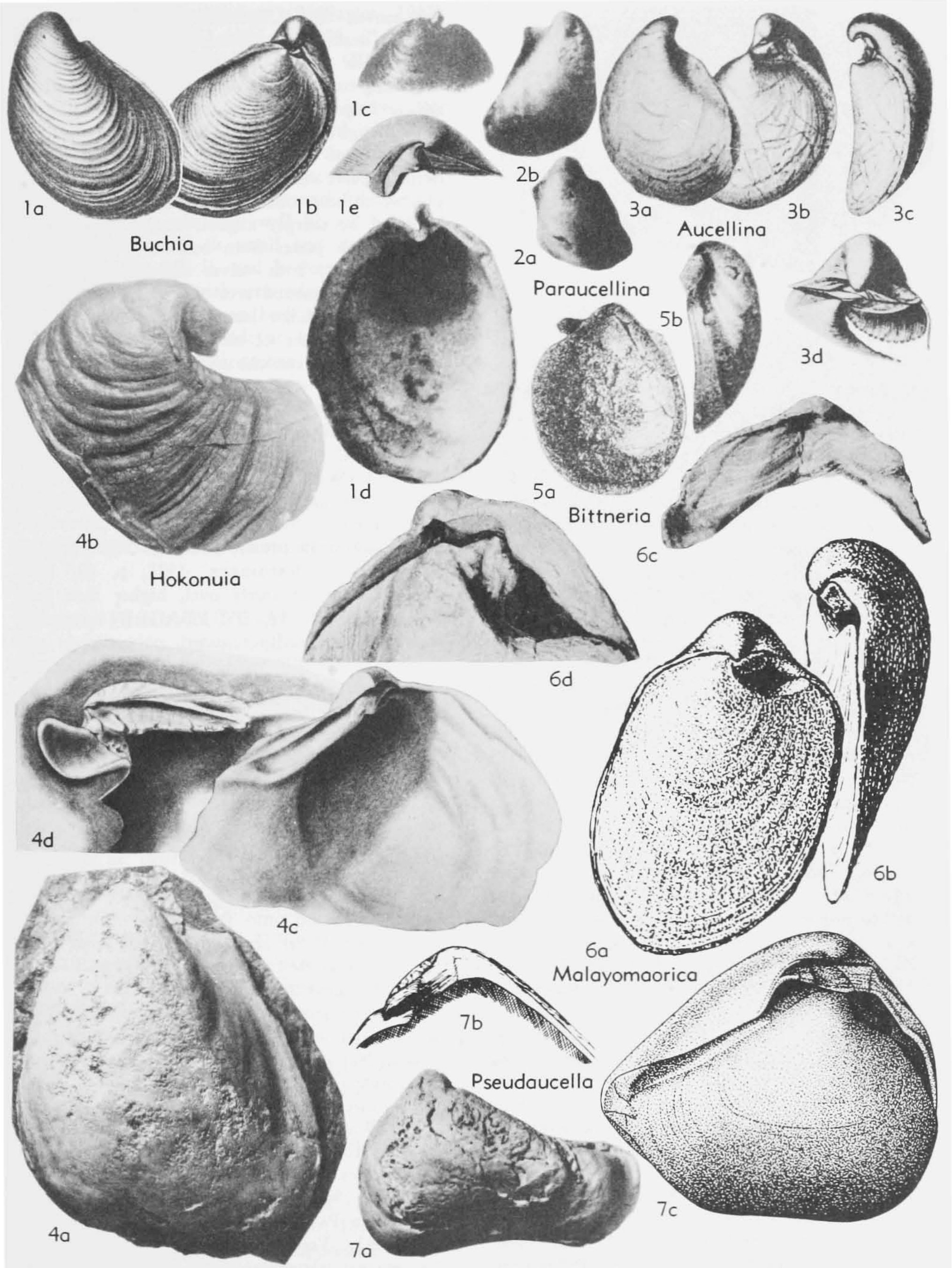

FIG. C96. Buchiidae (p. *N*374, *N*376-*N*377).

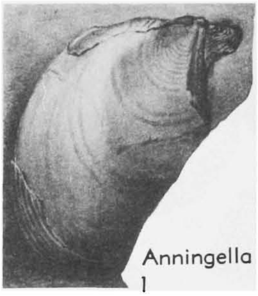

FIG. C97. Buchiidae (p. *N*376).

(L.Neocom.), USSR; dorsal view RV showing auricle and ligamental pit, ×2 *(747)*.

Anningella Cox, 1958, p. 44 [*pro Anningia* Cox, 1936 (*non* BROOM, 1927)] [**Anningia carixensis* Cox, 1936, p. 468; OD]. Known only by RV, which is ovate, higher than long, almost acline, flattened in earlier growth stages, later moderately convex; anterior auricle projecting prominently, lying in plane of valve margins, its lower margin strongly sinuate but not forming side of deep notch; ornament of concentric growth imbrications. *L.Jur.(L.Lias.)*, Eng.——FIG. C97,*1*. **A. carixensis* (Cox); RV ext., ×1.3 *(178)*.

Aucellina POMPECKJ, 1901, p. 365 [**Avicula gryphaeoides* J. DE C. SOWERBY, 1836, p. 335 (*non* SEDGWICK, 1828) (=*Inoceramus coquandianus* D'ORBIGNY, 1846, p. 505); SD MARWICK, 1939, p. 463]. Resembling *Buchia,* except that RV is always almost flat and its anterior auricle is in alignment with hinge margin, with cardinal area extending to its extremity; subauricular notch extending almost to beak; ctenolium present. *Cret.(Apt.-Turon.)*, Eu.-Caucasus-Australia-Patag.-Antarctic.——FIG. C96,*3*. *A. coquandiana* (D'ORBIGNY), Alb., Ger. *(3a-c)*; Eng. *(3d)*; *3a-c,* LV ext., RV and ant. views of both valves, all ×1 *(747)*; *3d,* Eng.; RV ant. auricle and cardinal area, ×3 (Woods, 1905).

?**Bittneria** BROILI, 1904, p. 168 [**Avicula? efflata* BROILI, 1904, p. 167; M]. Higher than long, prosocline; LV strongly convex, with well-protruding umbo; RV unknown; LV posterior wing quite undemarcated but small anterior wing well defined, separated from body of valve by deep sinus; surface smooth. *U.Trias.*, Eu.(S.Tyrol.).——FIG. C96,*5*. **B. efflata* (BROILI); *5a,b,* LV ext. and ant. views, ×1 *(950)*.

Hokonuia TRECHMANN, 1918, p. 202 [**H. limaeformis*; SD DIENER, 1923, p. 118] [=*Nuggetia* WILCKENS, 1927, p. 29 (type, *N. morganiana,* =*H. limaeformis*); M]. Large, prosocline, gibbose, slightly inequivalve, commonly irregular in form, especially anteriorly; LV well inflated, with prominent umbo and strongly prosogyrous beak; RV less convex than LV, with strongly prosogyrous, angular beak; posterodorsal region obtusely angular in each valve; left anterior wing ill-defined, extending only slightly beyond beak, right anterior auricle large, nearly parallel-sided, extending almost at right angles to hinge line so as to project into cavity of other valve below its hinge margin; deep, angular subauricular notch present, its margin, which bears ctenolium, lying in narrow lunule bordered by sharply angular and strongly curved ridge which passes from beak to projecting anterior margin; both valves with broad, concave, triangular ligamental area posterior to beak, area bearing 2 toothlike longitudinal ridges in some specimens; surface of shell unornamented except for irregular concentric undulations. *U.Trias.(Carn.)*, N.Z.——FIG. C96,*4*. **H. limaeformis*; *4a,* LV ext., ×0.7 (Cox, n); *4b,* dorsal ant. part of RV showing auricle and ridge bordering lunule, ×0.7 (Cox, n); *4c,* LV int. showing ligamental area, ×1 (Waterhouse, 1961); *4d,* RV int. showing auricle and ligamental area, ×1 (Waterhouse, 1961).

Malayomaorica JELETZKY, 1963, p. 149 [**Aucella malayomaorica* KRUMBECK, 1923, p. 65; OD]. Medium-sized, obliquely oval, higher than long, strongly inequivalve, LV moderately to strongly convex with broadly rounded, only slightly protruding umbo, RV feebly convex; hinge margin short, posterior wings obtuse, not clearly demarcated; left beak well removed from anterior end of hinge line; left anterior wing well developed in some specimens, almost absent in others; right anterior auricle relatively large, bent towards LV, with wide notch beneath it; ligamental area of LV broad, almost in plane of valve margins, longitudinally striated, with its lower margin indented by deep transverse furrow originating below beak, and with irregular anterior toothlike bulge which fits into interior of right anterior auricle; ligamental area of RV with ridge which fits into transverse furrow of LV; ornament of subimbricate growth lamellae crossed by radial threads, best seen on LV, small tubercles or spines at points of intersection. *U.Jur.(Kimmeridg.)*, Indonesia-N.Z.——FIG. C96,*6*. **M. malayomaorica* (KRUMBECK), E.Celebes *(6a,b)*, N.Z. *(6c,d)*; *6a,b,* viewed from right side and from ant. end, ×1.5 (Wandel, 1936); *6c,* ligamental area of LV, showing furrow and bulge; *6d,* dorsal region of both valves juxtaposed, RV in front; both ×2 (Jeletzky, 1963).

Paraucellina PAVLOV, 1907, p. 89 [**P. krasnopolskii;* M)]. Very thin and fragile; LV strongly convex, trigonally ovate, slightly prosocline; umbo prominent, beak almost at middle of hinge margin; left anterior wing well defined, its outer angle approximately right angle; ligamental area narrow; RV unknown. *U.Cret.(Cenoman.)*, USSR. ——FIG. C96,*2*. **P. krasnopolskii*; *2a,b,* LV viewed from side and front, ×2 (Pavlov, 1907).

Pseudaucella Marwick, 1926, p. 305 [**Aucella? marshalli* Trechmann, 1923, p. 269; OD]. Rather small subequivalve, well inflated, variable in shape but commonly subtrigonal, longer than high; beaks at about anterior third of length, orthogyrous; hinge margin very short; posterodorsal region with broad, well-impressed escutcheon; ventral margin commonly with broad sinus; anterior margin extending well beyond right anterior auricle, which is small and narrow, with acute sinus beneath it, and projects over LV to some extent; ligamental area relatively wide, extending almost equally on both sides of beak in LV; ligamental pit broad; at top of ligamental area, in LV, horizontal groove anterior to beak apparently received upper margin of right anterior auricle; ligamental area of RV apparently extending on to lower part of auricle. *L.Jur.(U.Lias.)*, N.Z.-N.Caledonia.——Fig. C96,7. **P. marshalli* (Trechmann), N.Z.; *7a,* LV, ×1 (Cox, n); *7b,* RV ligamental area and anterior auricle, ×2.7 (Marwick, 1926); *7c,* specimen with valves displaced, showing LV ligamental area, ×2.7 (Cox, n).

Family PLICATULIDAE Watson, 1930

[*nom. transl.* Iredale, 1939 (*ex* Plicatulinae Watson, 1930)] [Materials for this family prepared by L. R. Cox and L. G. Hertlein]

Small to medium-sized, oval, orbicular or subtrigonal, mostly subequilateral, commonly somewhat irregular in outline, usually rather compressed; inequivalve to subequivalve, valve margins closed, byssal notch lacking; auricles small or absent; RV attached at umbo or by larger area of its surface; monomyarian, with adductor scar relatively small, suborbicular or irregular in shape; cardinal area small or absent, not differing appreciably in size in the two valves when present; resilium deeply sunk in triangular pit; hinge typically with isodont crura, 2 in each valve; surface concentrically lamellose and usually with irregular radial costae, costellae or threads; shell structure as in Spondylidae. Separated from that family mainly on grounds of soft anatomy. *M.Trias.-Rec.*

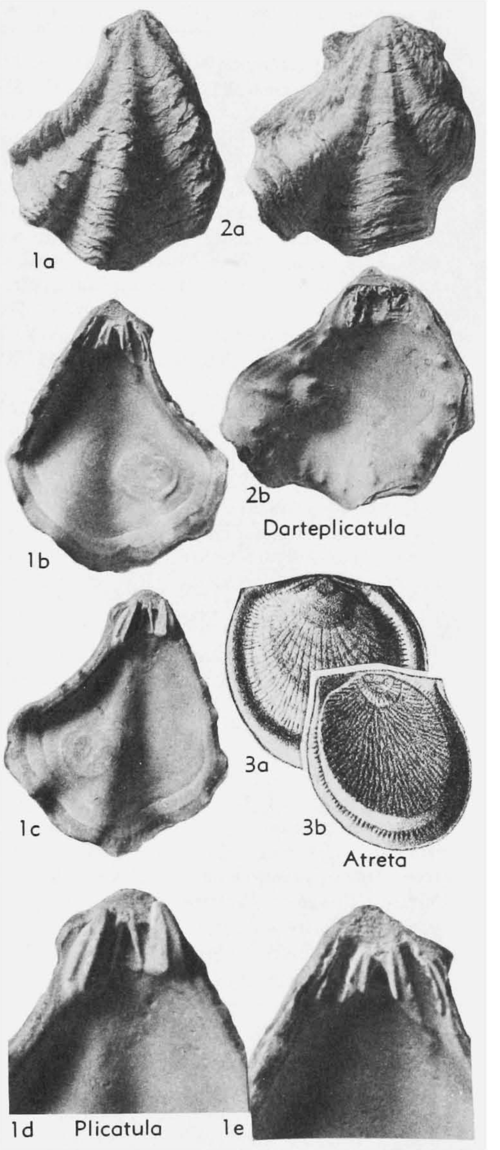

Fig. C98. Plicatulidae (p. *N*377-*N*388).

Plicatula Lamarck, 1801, p. 132 [**Spondylus plicatus* Linné, 1758; SD Schmidt, 1818] [=*Plicatuligenus* Renier, 1807 (suppressed ICZN); *Micatula* Carpenter, 1859 *(nom. null.); Plycatula* Monterosato, 1877 *(nom. null.)*]. Small to medium-sized, subequivalve or with RV usually more convex; attachment area small to moderately large; cardinal area small; resilium pit acutely triangular; crura straight, narrow, prominent, narrowly divergent, crenulated, those in RV adjacent to resilium pit; in addition, sides of pit in LV formed by raised ridges simulating 2nd pair of crura; adductor scar situated in relatively posterior position. *M.Trias.(Ladin.)-Rec.,* Eu.-Afr.-N.Am.-Indon.

[Many authors have considered *P. gibbosa* Lamarck to be synonymous with the Linnean species *Spondylus plicatus,* but according to H. Dodge (1952, *Bull. Am. Mus. Nat. Hist.*, v. 100, p. 127) "this identification cannot be supported."]

P. (Plicatula) [=*Harpax* Parkinson, 1811, p. 221 (type, *H. parkinsoni* Bronn, 1824, p. 52; SD, M); ?*Ostrenomia* Conrad, 1872, p. 216 (type, *O. carolinensis*; M); *Plicatulopecten* Neumann, 1907, p. 104 (type, *Plicatulopecten boehmi*; SD Cox, herein)]. Auricles absent or ill-defined; most species with radial ornament, which may range from fine costellae to broad costae, and with imbricating growth lamellae; short spines present in many forms. *M.Trias.(Ladin.)-Rec.*; fossil forms cosmop., *Rec.*, trop. only.——Fig. C98,*1*. *P. (P.) marginata* Say, Mio., USA(Va.); *1a,b*, LV ext., int., *1c*, RV int., all ×1; *1d,e*, RV and LV hinge, ×2 (Cox, n).

P. (Darteplicatula) Freneix & Gorodiski, 1963, p. 35 [**P. polymorpha* Bellardi, 1854, p. 197; OD]. With more or less distinct auricles; ornament of broad radial costae and submicroscopic radial striation; interior with tubercles or short costae near margin. *Eoc.-L.Mio.*, Eu.-N.Afr.-W. Afr.-N.Am.——Fig. C98,*2*. **P. (D.) polymorpha*, Eoc., S.Nigeria; *2a,b*, RV ext., LV int., ×1.1 (Cox, n).

P. (Pseudoplacunopsis) Bittner, 1895, p. 215 [**Pseudoplacunopsis affixa*; OD]. Orbicular, not auriculate, compressed, RV flatter than LV, some specimens attached by almost its entire surface; ornament of fine radial threads. *U.Trias.*, Eu.-Jordan-Indon.

Atreta Étallon, 1862, p. 192 [**Ostrea blandina* d'Orbigny, 1850, p. 375; SD Cox, 1964, p. 45] [=*Diploschiza* Conrad, 1866, p. 77 (type, *D. cretacea*); *Cyclostreon* Eichwald, 1868, p. 406 (type, *Ostrea plicatuloides* Leymerie, 1851, p. 195; M); *Dimyopsis* Bittner, 1895, p. 219 (type, *Ostrea intusstriata* Emmrich, 1853, p. 377; M)]. Small, orbicular; RV shallowly bowl-shaped with flattened rim, attached by greater part of its surface and bearing internal divaricating or anastomosing riblets ending in some species as transverse crenulations of rim; LV flat or almost so, with concentrically lamellose exterior; resilium pit very small; crura short and thin, rarely observable; adductor scar obscure. *U.Trias.(Carn.)-U.Cret.(Campan.)*, Eu.-N.Am.——Fig. C98,*3*. **A. blandina* (d'Orbigny), U.Jur.(Oxford.), France (Jura); *3a,b*, RV int., RV int., ×2 (de Loriol, 1904).

Saintiopsis Sacco, 1898, p. 11 [**Plicatula laevis* Sacco, 1898 (*ex* Bellardi MS.)]. Small, suborbicular to subquadrate, subalate, thin-shelled, smooth; RV broadly adherent, flat, LV feebly convex; hinge structure as in *Plicatula* but crura widely divergent. *Plio.*, Italy.

[The type species, attributed to Bellardi, appeared as a *nom. nud.* in faunal lists long before its description by Sacco.]

Family SPONDYLIDAE Gray, 1826

[Materials for this family prepared by L. G. Hertlein & L. R. Cox]

Small to (mostly) medium-sized, orbicular or oval, gibbous, inequivalve, RV usually more convex; nearly equilateral, pectiniform, closed, with byssal notch lacking, slightly auriculate; attached at umbo or by larger area of surface of RV; monomyarian, with large, subcircular, posteriorly placed adductor scar; cardinal area amphidetic, much larger on attached valve, where it commonly forms acute triangle; ligament alivincular, resilium deeply sunk in triangular pit; hinge taxodont in early stage, with isodont crura, two in each valve, in adult stage, those in RV adjacent to resilium pit, sculpture of irregular radial costellae, commonly spinose; inner layers of ostracum aragonitic but not nacreous, outer layer calcitic, lamellar. *Jur.-Rec.*

While the outer shell layer is relatively persistent in this family, as in the Pectinidae, the inner layer, including the hinge crura, may disappear in fossilization. Hence many fossil specimens, such as those from the Upper Cretaceous upon which the genus *Dianchora* was founded, appear to be edentulous.

Spondylus Linné, 1758, p. 690 [**S. gaederopus*; SD Schmidt, 1818, p. 61] [=*Spondyligenus* Renier, 1807 (suppressed ICZN); *Gaideropa* Deshayes, 1832, p. 163 (obj.); *Spondilus* Verany, 1846 (*nom. null.*); *Spodylus* Nagao, 1934 (*nom. null.*)]. Characters of family. *Jur.-Rec.*, W.Pac.-IndoPac.-Medit.

S. (Spondylus) [=*Dianchora* J. Sowerby, 1815, p. 183 (type, *D. striata*; SD Cox, herein); *Podopsis* Lamarck, 1819, p. 194 (type, *P. truncatus*; SD Cox, herein); *Pachytos* Defrance, 1825, p. 207 (type, *Plagiostoma spinosa* J. Sowerby, 1814, p. 177; SD Herrmannsen, 1847, p. 188); *Pachytes* Hoeninghaus, 1830 (*nom. van.*); *Pachyta* Menke, 1830 (*nom. van.*); *Pachytus* Agassiz, 1846 (*nom. van.*); *Pachites* d'Orbigny, 1846 (*nom. null.*); *Diachora* Desmarest, 1859 (*nom. null.*); *Eleutherospondylos* Dunker, 1882 (type, *Spondylus regius* Linné; SD Cox, herein); *Lanilda* Iredale, 1939, p. 373 (type, *Spondylus ducalis* Roeding, 1798, p. 194; OD); *Sponvola* Iredale, 1939, p. 379 (type, *S. ella*)]. Well inflated, mostly with strong radial sculpture, many forms spiny or foliaceous; cardinal area of RV large, triangular; crural teeth short, heavy, smooth or with weakly crenulated edges. *Jur.-Rec.*, fossil forms cosmop., *Rec.*, pantropic.——Fig. C99,

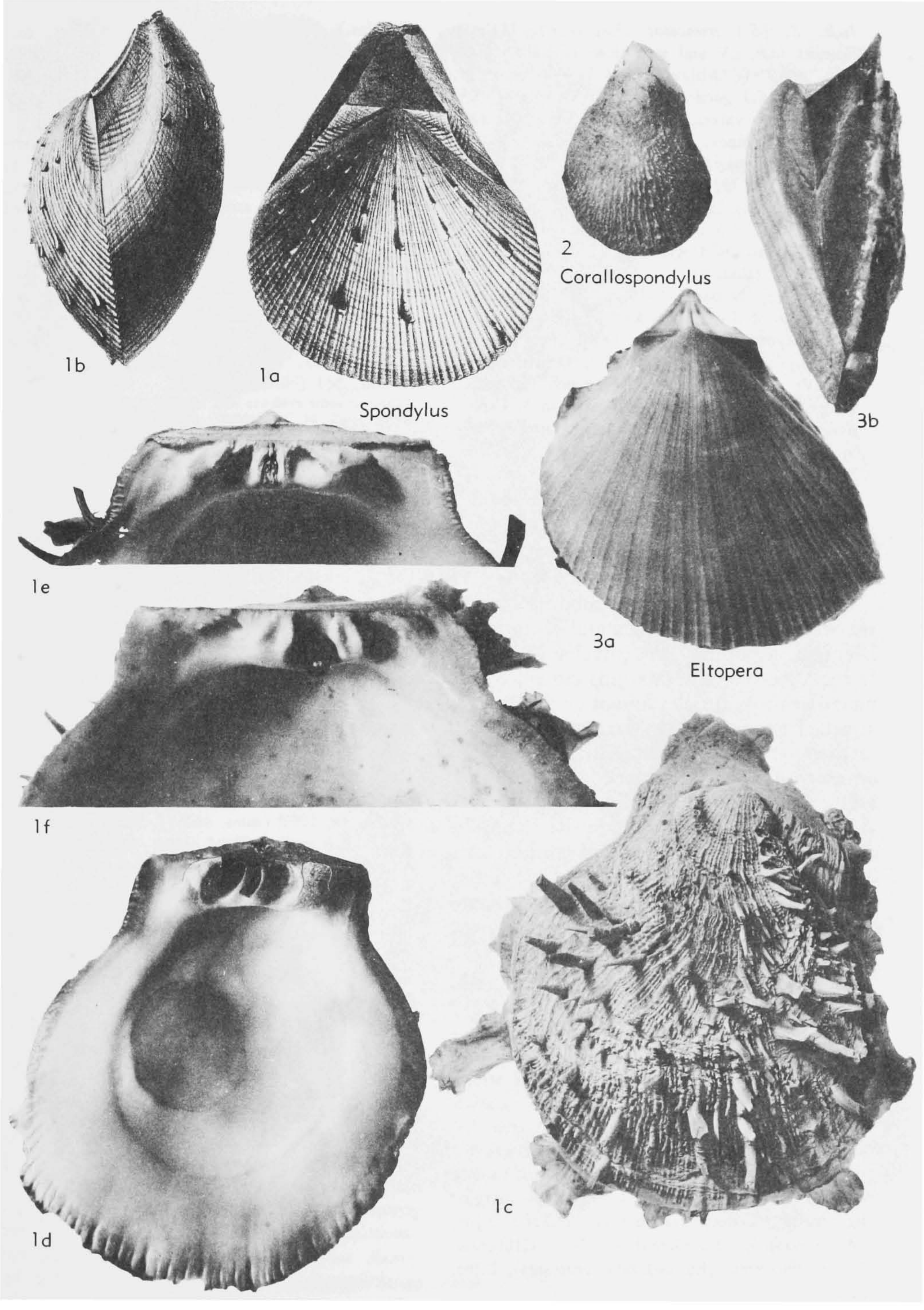

Fig. C99. Spondylidae (p. *N*378, *N*380).

1a,b. S. (S.) truncatus (Lamarck), U.Cret., France; *1a,b,* LV and ant. views of both valves, both ×0.7 (d'Orbigny, 1843-7).——Fig. C99, *1c-f. *S. (S.) gaederopus,* Rec., Medit.; *1c,* LV view of both valves, ×1; *1d,* LV int., ×1; *1e,f,* LV and RV hinge, ×1 (all Cox, n).

S. (Corallospondylus) Monterosato, 1917, p. 2 [**S. gussonii* O. G. Costa, 1829, p. xli; M]. Small, terebratuloid, with delicately spinose radial costellae. *Oligo.-Rec.,* Medit.——Fig. C99,*2. *S. (C.) gussonii* Costa, Rec.; LV view of both valves, ×2 (Cox, n).

S. (Eltopera) Iredale, 1939, p. 377 [**S. fortior* (as subsp. of *S. pacificus* Reeve, 1856, based on its holotype, expl. pl. 1); OD]. Less inflated than *S. (Spondylus),* attached by entire surface of RV; cardinal area of RV much elongated; radial ornament more delicate than in *S. (Spondylus)*; crural teeth small, rather widely separated. *Rec.,* W.Pac.-IndoPac.——Fig. C99,*3. *S. (E.) pacificus,* Lord Hood I.; *3a,b,* ext., LV facing observer, and end view, both ×1 (Cox, n).

Family TERQUEMIIDAE Cox, 1964

[Materials for this family prepared by L. R. Cox]

Small to medium-sized, suborbicular or subovate, mostly subequilateral, commonly irregular in outline; subequivalve to strongly inequivalve, valve margins closed, byssal notch lacking; auricles absent or ill-defined; attached at umbo or by larger area of surface of RV[1]; monomyarian; each valve typically with well-developed cardinal area with median ligamental pit which is triangular in shape or at least has dorsally converging sides; no internal resilium pit; crura absent[2]; surface with irregular radial costae, costellae, or threads, spinose in some forms; original shell structure unknown. *?L.Perm., Trias.-U.Jur., ?Cret.*

Terquemia Tate, 1867, p. 395 [*pro Carpenteria* Eudes-Deslongchamps, 1860 (*non* Gray, 1858)] [**Carpenteria pectiniformis* Eudes-Deslongchamps, 1860, p. 130; SD Stoliczka, 1871, p. 443]. Moderately large, oyster-like, with strong radial ribs, not auriculate; RV strongly convex with medium-sized to large attachment area, LV almost flat to moderately convex; cardinal area of moderate breadth, longitudinally extended, usually not triangular but truncated by its upper margin; ligamental pit deep and narrow. *U.Trias.-U.Jur. (Kimmeridg.),* Eu.-Greenl.——Fig. C100,*3a,b. *T. pectiniformis* (Eudes-Deslongchamps), L.Jur. (M.Lias.), France(Calvados); *3a,b,* RV ext., int., ×1 (Eudes-Deslongchamps, 1860).——Fig. C100, *3c. T. ostreiformis* (d'Orbigny), U.Jur.(U. Oxford.), France(Jura); RV cardinal area, ×0.7 *(550).*

Enantiostreon Bittner, 1901, p. 70 [**E. hungaricum*; SD Diener, 1923, p. 128]. Similar to *Terquemia* in form and strongly costate ornament, but with cardinal area triangular, less elongated longitudinally and with relatively broader ligamental pit. *?U.Perm.,* Japan; *L.Trias.(Scyth.)-U. Trias. (Rhaet.),* Eu. (Ger.-N. Alps-S. Alps-Hung.-Spain)-China.——Fig. C100,*5a. *E. hungaricum,* U.Trias.(Rhaet.), Bavaria; RV ext., ×0.7 (Frech, 1907).——Fig. C100,*5b. E. cristadifforme* (von Schlotheim), M.Trias.(Muschelkalk), L.Silesia; LV int., ×1 (Noetling, 1880).

[There is some evidence that Middle Triassic (Muschelkalk) species such as "*Ostracites*" *cristadifformis* von Schlotheim, which have been included in *Enantiostreon,* may be attached by LV or RV indifferently (cf. Seilacher, 1954, *Neues Jahrb. Geol. Paläont., Monatsh.,* v. 4, p. 173, who refers these forms to the ostrean genus "*Alectryonia,*" = *Lopha*).]

?Gerlus de Gregorio, 1930, p. 21 [**Placunopsis hystrix* Gemmellaro, 1875, p. 64; M]. Small to medium-sized, subtrigonal to orbicular, not auriculate; attached valve strongly convex, free valve flat or concave; ornament of narrow beaded costellae with broader intervals; internal characters unknown. *U.Trias.,* Sicily.——Fig. C100,*1. *G. hystrix* (Gemmellaro); *1a-c,* RV ext., LV ext., RV lat., ×1 (Gemmellaro, 1875).

Newaagia Hertlein, 1952, p. 275 [*pro Philippiella* Waagen, 1907 (*non* Pfeiffer, 1886)] [**Spondylus obliquus* von Münster, 1841, p. 74; SD Diener, 1923, p. 124, for *Philippiella*] [=*Lucasiella* Cossmann, 1909 (*non* Banks, 1900); *Philipiella* Cossmann, 1909 *(nom. null.)*]. Small to medium-sized; RV well inflated, with moderately large attachment area, LV flat to feebly convex; anterior and posterior wings small but distinct; cardinal area elongated longitudinally, obtusely triangular; ligamental pit narrow, triangular; ornament of spinose radial ribs, recalling that of *Spondylus. ?L.Perm., U.Trias.(Carn.),* USA(Tex.)-Eu.(Ger.-N.Alps-S.Alps)-Asia(Iran).——Fig. C100,*2a,b, N. noetlingi* (Frech), M.Trias.(Muschelkalk), U.Silesia; *2a,b,* LV and RV ext., ×1 (Frech, 1907).——Fig. C100,*2c. *N. obliqua* (von Münster), M. Trias.(Ladin.), S.Tyrol; LV int., ×1 *(58).*

?Placunopsis Morris & Lycett, 1853, p. 5 [**P. fibrosa* Laube, 1867, p. 16 (=*P. jurensis* (*non* Roemer sp.) Morris & Lycett; ICZN pend.] [=*Placunopis* Meek, 1873 *(nom. null.)*; *?Holocraspedum* Cragin, 1893, p. 190 (type, *Ostrea anomiaeformis* Roemer, 1852, p. 75; M)]. Rather small, suborbicular or ovate, subequilateral, not auriculate; lower valve (?RV) flat, attached by almost its entire surface when evidence of attachment exists, specimens with smaller attachment

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[1] See note with *Enantiostreon,* however.

[2] See note on *Placunopsis,* however.

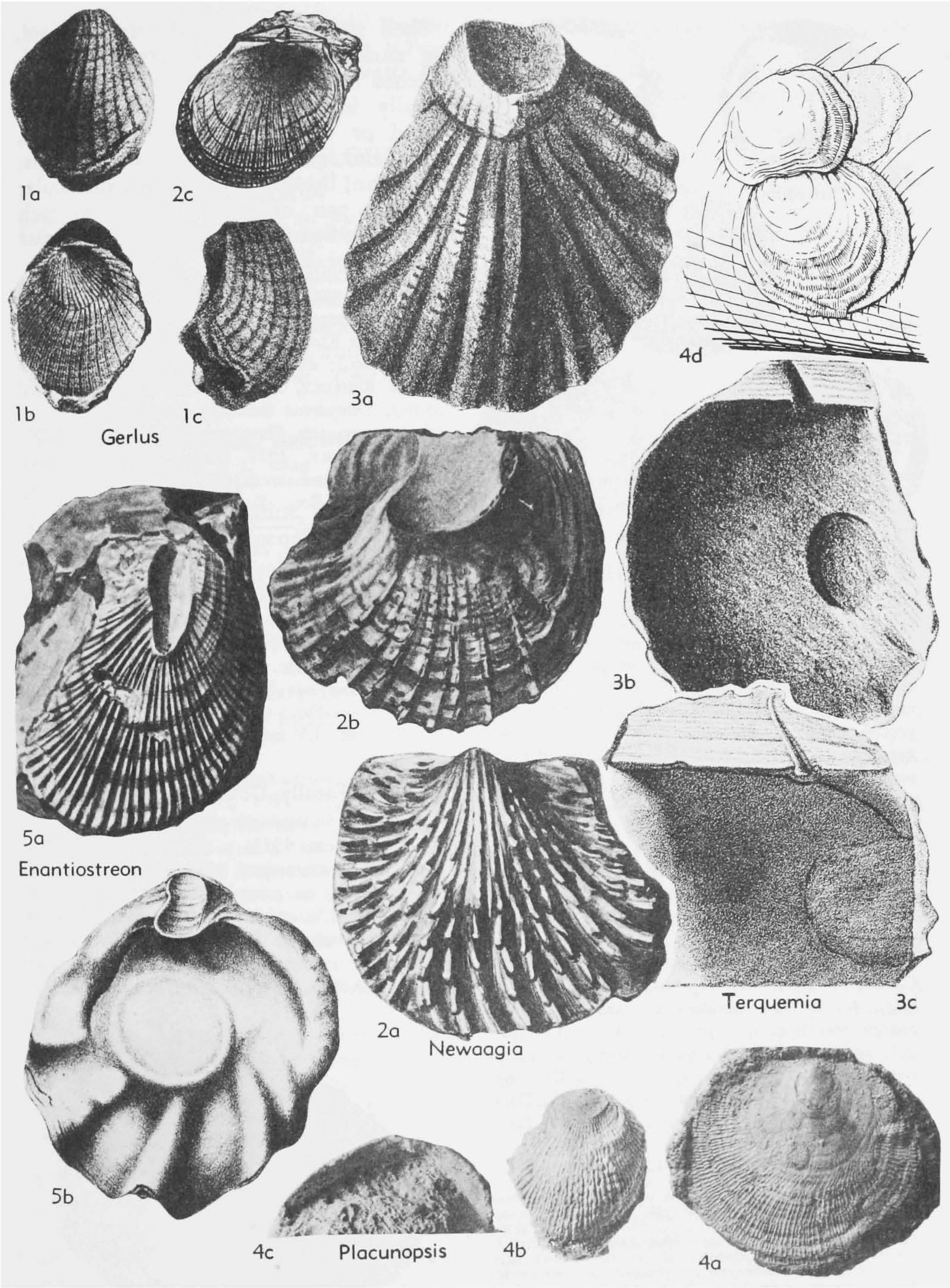

FIG. C100. Terquemiidae (p. *N*380, *N*382).

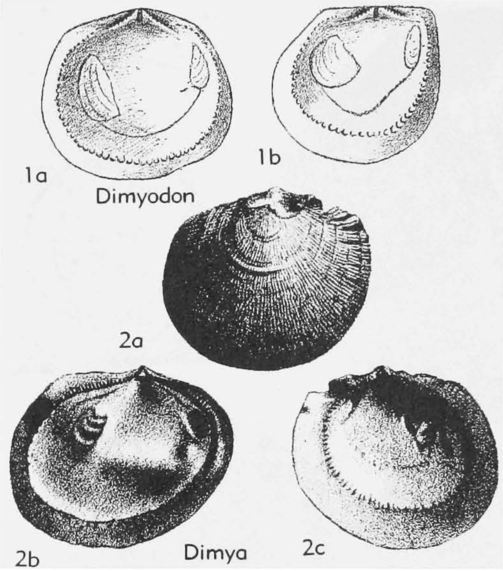

Fig. C101. Dimyidae (p. N382).

areas rare or wanting; upper valve almost flat to strongly inflated, with distinct, not quite marginal umbo, some specimens with allomorphic sculpture derived from shells to which lower valve had grown attached; adductor scar relatively large, not quite median in position; no well-defined cardinal area, ligamental pit or chondrophore; an uneven thickening along the hinge margin may have been cardinal area; irregular transverse ridge or swelling, function of which is uncertain, occupies umbonal cavity of free valve; crura typically absent (note 1); ornament of irregular radial threads, barely visible in some species, well developed in others; ostracum foliaceous. *M.Trias.-U.Cret.(Maastricht.),* cosmop. (note 2).——Fig. C100,*4a-c.* **P. fibrosa* (Laube), M.Jur.(Bathon.), Eng.; *4a,* flat but presumed LV ext., ×1; *4b,c,* convex specimen, also presumed to be LV ext., ×1, and int. of hinge region, arrow pointing to swelling in umbonal cavity, ×2.3 (all Cox, n). ——Fig. C100,*4d. P. plana* (Giebel), M.Trias. (Muschelkalk), Ger.; specimens sessile on *Lima* shell, ×1.3 (Seilacher, 1954).

[(1) Seilacher (1954, *Neues Jahrb. Geol. Paläont., Monatsh.,* v. 4, p. 168, fig. 3) has illustrated the interior of 4 attached valves of *"Placunopsis" matercula* (Quenstedt) from the Lower Muschelkalk, each with a single oblique ridge anterior to the beak. No comparable structure has been observed in any other species. (2) Certain species from the Pennsylvanian of the USA which have been referred to *Placunopsis* are probably pseudomonotids (N. D. Newell, *in litt.*).]

Family DIMYIDAE P. Fischer, 1886

[=Dimyacidae auctt.] [Materials for this family prepared by L. R. Cox and L. G. Hertlein]

Shell small, thin, suborbicular or oval, not auriculate, rather compressed, closed, attached by RV, which is less convex; externally lamellose, some species radially ribbed or striated; interior porcelaneous, with faint radial ridges in some forms; dimyarian; ligament an internal, alivincular resilium; pair of cardinal crura in each dimyarian; ligament an internal, alivincular valve. *M.Jur.-Rec.*

Dimya Rouault, 1850, p. 470 [**D. deshayesiana*; OD] [=*Dymya* Rouault, 1850 *(nom. nud.), Margariona* Kobelt (*ex* Dall, MS), 1882 (genus without sp.); *Deuteromya* Cossmann, 1903 (*pro Dimya* Rouault, *non* Menke, 1830, subordinal name), *Dimyarina* Iredale, 1936, p. 269 (type, *Dimya corrugata* Hedley, 1902, p. 309; OD); *Dymia* Noszky, 1939 *(nom. null.)*]. Cardinal crura short and weak; posterior adductor scar bilobed. *Eoc.-Rec.,* Eu.-Carib.-Indon.-Australia-N. Z.-IndoPac.-E.Pac.——Fig. C101,*2.* **D. deshayesiana,* Eoc., France; *2a,b,* RV ext., int., LV int., ×1.7 (Rouault, 1850).

Dimyodon Munier-Chalmas in Fischer, 1886, p. 937 [**D. schlumbergeri*; OD] [=*Dimyodus* Wöhrmann, 1894 *(nom. van.)*]. Cardinal crura prominent, elongate, transversely striated; posterior adductor scar not bilobed. *M.Jur.(Bathon.),* Eu. (France).——Fig. C101,*1.* **D. schlumbergeri*; *1a,b,* LV int., LV int., ×3.4 *(305).*

Family UNCERTAIN

[Materials for this family prepared by L. R. Cox]

Oretia Marwick, 1953, p. 62 [**O. coxi*; OD]. Large to medium-sized, obliquely ovate, hinge margin short, no posterior wing; RV more inflated than LV, with well-protruding, anterior, slightly prosogyrous umbo, shallow lunule, and very small transverse anterior auricle with wide notch beneath it; hinge probably edentulous, liga-

Fig. C102. Family uncertain (p. N382-N383).

ment unknown; surface with coarse, irregular concentric folds; ostracum relatively thin. *U.Trias. (Carn.),* N.Z.——FIG. C102,*1*. **O. coxi;* RV, ×0.7 (Cox, n).

Superfamily ANOMIACEA Rafinesque, 1815

[*nom. transl. et correct.* GILL, 1871 (*ex* family Anominia RAFINESQUE, 1815)] [Materials for this superfamily prepared by MYRA KEEN]

Monomyarian, anterior adductor muscle obsolete; gills filibranchiate; hinge lacking true teeth but with central ligament supported in some by ridges (crura); inner layer of shell lustrous. *?Perm., Cret.-Rec.*

Family ANOMIIDAE Rafinesque, 1815

[*nom. correct.* H. ADAMS & A. ADAMS, 1858 (*pro* family Anominia RAFINESQUE, 1815)] [=Placunidae GRAY, 1842]

Shells irregular in outline, mostly sessile, slightly to markedly inequivalve. Byssus present in young stages, later modified in most to become pluglike, horny, passing through embayment or foramen in lower valve (normally RV). Adductor muscle scar subcentral, with one or more pedal and byssal retractor muscle scars above it, best seen on LV, opposite to foramen. *?Perm., Cret.-Rec.*

Anomia LINNÉ, 1758 [**A. ephippium;* SD SCHMIDT, 1818] [=*Echion* POLI, 1791 (type, *A. caepa* LINNÉ = *A. ephippium*; SD KEEN, 1959); *Echionoderma* POLI, 1795 (obj.), SD KEEN, 1959; *Fenestella* RÖDING, 1798 (obj.), SD WINCKWORTH, 1945; *Operculella* MONTEROSATO, 1915 (type, *O. operculata*; *nom. nud.*) (*?non* REICHENBACH, 1828)]. Shell thin, partially attached, foramen in RV, LV with 3 muscle scars on central area. *?Perm., Cret.-Rec.,* Eu.-Afr.-AsiaM.-N.Am.-Australia-N.Z.

A. (Anomia). Surface sculptured with radial striae; byssal retractor muscle scars 3, subequal; foramen of moderate size. *?Perm., Cret.-Rec.,* Eu.-Afr.-Asia-N.Am.——FIG. C103,*4*. **A. (A.) ephippium,* Rec., Eu.; *4a,b,* RV ext., LV int., ×0.5 (Keen, n).

A. (Paraplacuna) OPPENHEIM, 1892 [**A. gregaria* BAYAN, 1870; M]. Lower retractor scar partly coalesced with adductor scar; sculpture somewhat reticulate. [In brackish-water beds.] *Eoc.,* Eu.——FIG. C103,*1*. **A. (P.) gregaria* BAYAN, Hung.; *1a-c,* LV ext., int., RV int., ×0.7 *(691)*.

A. (Patro) GRAY, 1850 [**A. elyros* (=**A. australis* GRAY, 1847; M)] [=*Patros* GRAY, 1850 *(nom. null.)*]. Byssal foramen small, 2 retractor scars smaller than lower (adductor) scar. *Rec.,* Australia.

A. (Prismatro) MARWICK, 1948 [**A. undata* HUTTON, 1885; OD]. Shell lacking radial striae; RV thick, prismatic. *Plio.,* N.Z.

Carolia CANTRAINE, 1838 [**C. placunoides*; M] [=*Hemiplacuna* GRAY, 1850 (type, *H. rozieri* GRAY, 1850; M)]. Compressed-orbicular, byssal foramen small to wanting; adductor scar without accessory retractor scars. *Eoc.-Mio.,* N.Afr.-N.Am.-S.Am.

C. (Carolia). Surface radially striate; byssal foramen nearly closed in adult; resilium received by chondrophore in lower valve. *Eoc.,* N.Afr.-Carib.——FIG. C103,*9*. **C. (C.) placunoides,* Egypt; *9a-b*; RV int., LV hinge, ×0.5 *(1026)*.

C. (Parinomya) OLSSON, 1928 [**C. (P.) parinensis*; OD]. Sculpture radial, with prickles and fimbriations; foramen persistent in adult. *Eoc.,* W.S.Am.-India.

C. (Wakullina) DALL, 1896 [**C. (W.) floridana*; OD]. Smooth, byssal foramen obsolete, resilium of upper valve on diverging crura. *Oligo.-Mio.,* E.N.Am.

Enigmonia IREDALE, 1918 [*nom. subst. pro Aenigma* KOCH in MARTINI & CHEMNITZ, 1846 (*non* NEWMAN, 1836)] [**Anomia rosea* GRAY, 1825 (=**A. aenigmatica* HOLTEN, 1803); OD]. Shell extremely thin, adapted to sessile attachment on mangrove roots. *Eoc.-Rec.,* Eu.-IndoPac.——FIG. C103,*2*. **E. aenigmatica* (HOLTEN), Rec., Philip. Is.; *2a-c,* LV ext., int., RV ext., ×1 *(1009)*.

?**Hemiplicatula** DESHAYES, 1861 [**Placuna solida* DESHAYES in MELLEVILLE, 1843; M] [=*Semiplicatula (nom. null.)*]. Small, compressed, smooth, crura thick, resembling teeth; muscle scar sunken, submarginal. *Eoc.,* Eu.——FIG. C103,*7*. **H. solida* (DESHAYES in MELLEVILLE), France; *7a-c,* RV ext., int., LV int., ×5 (Deshayes, 1861).

?**Isomonia** DAUTZENBERG & FISCHER, 1897 [**Monia alberti* DAUTZENBERG & FISCHER, 1896; M]. Dorsal margin with auricles as in Pectinidae but without any byssal notch; upper retractor muscle scar large, coalesced with lower and with adductor scar. *Rec.,* Medit.——FIG. C103,*10*. **I. alberti* (DAUTZENBERG & FISCHER); *10a,b,* LV ext., int., ×1 (Dautzenberg & Fischer).

Paranomia CONRAD, 1860 [**Placunanomia (P.) saffordi* (=**Placuna scabra* MORTON, 1834); SD STOLICZKA, 1871] [=*Paronomia* GARDNER, 1916 *(nom. null.)*]. Byssal foramen closed in adult; one retractor scar in either valve; sculpture of spinose radial riblets. *U.Cret.,* E.N.Am.——FIG. C103,*8*. **P. scabra* (MORTON), USA(Tenn.), *8a-c,* RV int., LV int., ext., ×0.7 *(951)*.

Placuna LIGHTFOOT, 1786 [**Anomia placenta* LINNÉ, 1758; SD SCHMIDT, 1818] [=*Placenta* PHILIPSSON, 1788, *ex* RETZIUS MS (obj.; T); *Ephippium* RÖDING, 1798 (type, *E. polonicum* = *Anomia sella* GMELIN, 1791 ?=*Placenta quadrangula* PHILIPSson, 1788; SD Dall, 1898); *Sellaria* Link, 1807 (type, *S. anglicana* = *Anomia sella* Gmelin, 1791; SD Keen, 1959); *Placunema* Stoliczka, 1871 (type, *Anomia sella* Gmelin, 1791; OD)]. Outline of shell regularly orbicular to saddle-shaped, mostly compressed; resilium buttressed by

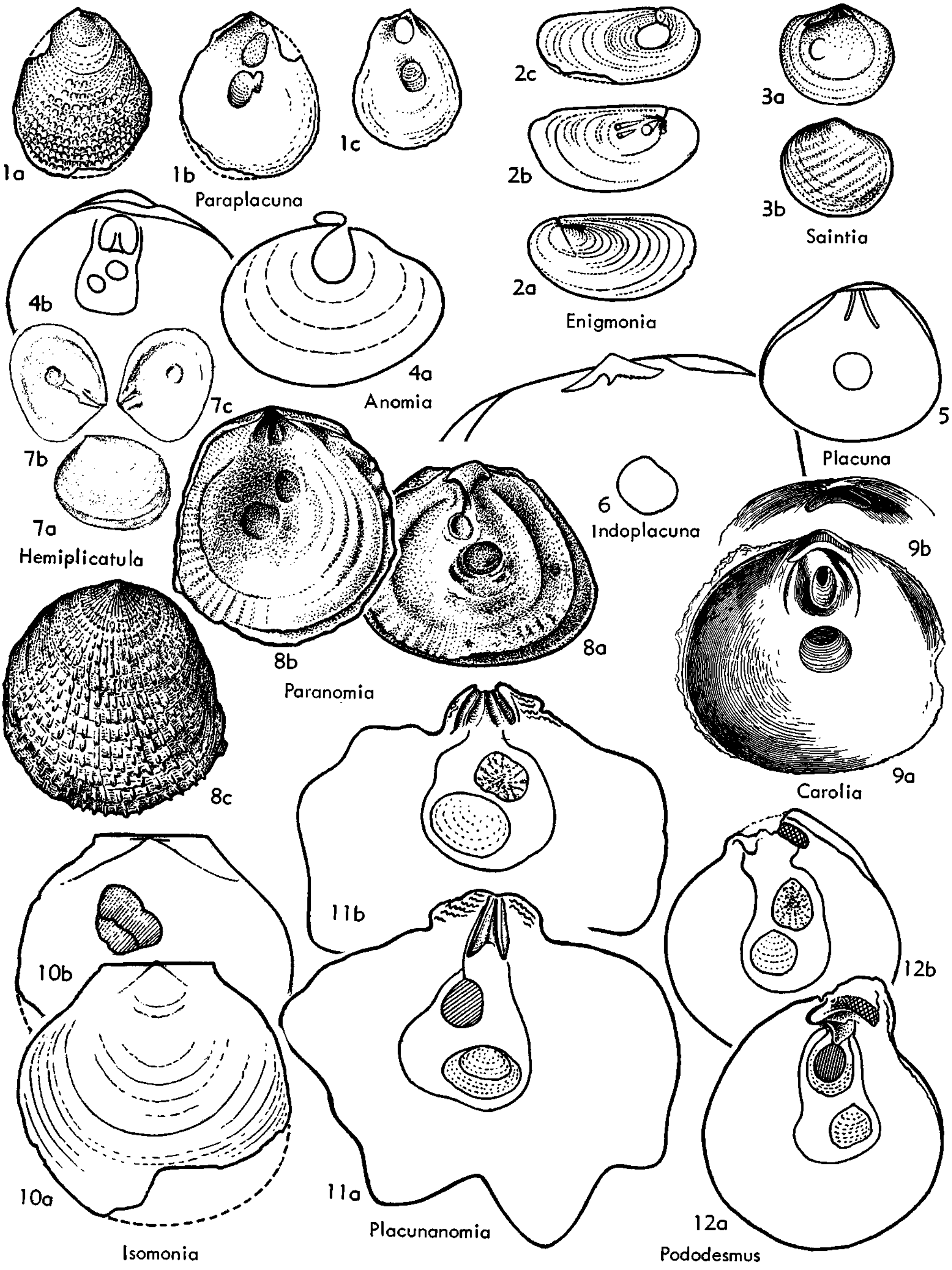

Fig. C103. Anomiidae (p. *N*383-*N*385).

long ridges or crura; not sessile. *Eoc.-Rec.,* Eu.-IndoPac.-Asia-N.Afr.

P. (Placuna). Flattened, crura widely diverging; central cavity small. *Oligo.-Rec.,* Eu.-IndoPac.——Fig. C103,*5*. **P. (P.) placenta* (Linné), Rec., Ceylon; RV int., ×0.25 *(242)*.

P. (Indoplacuna) Vredenburg, 1924 [**P. (I.) sindiensis*; SD Keen, 1959]. Resilifer bent sharply; primary crural ridges supplemented by less divergent secondary pair. *L.Mio.-M.Mio.,* S.Eu.-N.Afr.-Asia.——Fig. C103,*6*. **P. (I.) sindiensis,* India; RV int., ×0.5 *(242)*.

P. (Pseudoplacuna) Mayer, 1877 [**Pseudoplacuna helvetica* Mayer, 1877; M]. Internal cavity larger, valves more inflated than in *P. (Placuna)*. *M.Eoc.,* Eu.

Placunanomia Broderip, 1832 [**P. cumingii*; M] [=*Placumonya, Placunanomya* Whitfield, 1885 *(nom. null.)*; *Placuanomia* Olsson, 1961 *(nom. null.)*]. With about 3 strong radial plications; byssal foramen obsolete in adult; interior with 1 retractor scar. *Mio.-Rec.,* E.N.Am.-W.C.Am.-W.N.Am.——Fig. C103,*11*. **P. cumingii,* Rec., W.C.Am.; *11a,b,* RV int., LV int., ×0.5 (Stanford Univ. specimen).

Pododesmus Philippi, 1837 [**P. decipiens* (=**Placunanomia rudis* Broderip, 1834); M]. Sculpture of irregular corrugations; shell attached, byssal foramen large, small, or even obsolete; LV with 1 large and radially striate byssal retractor scar. *?Oligo., Mio.-Rec.,* N.Am.-S.Am.-Eu.-Australia.

P. (Pododesmus). Foramen small to partially or entirely closed outside. *Mio.-Rec.,* Japan-N.Am.-S.Am.——Fig. C103,*12*. **P. (P.) rudis* (Broderip), Rec., E.S.Am.; *12a,b,* RV int., LV int., ×0.5 (Stanford Univ. specimen).

P. (Heteranomia) Winckworth, 1922 [**Anomia squamula* Linné, 1758; OD]. Muscle scars small; gills U-shaped. *Rec.,* Eu.

P. (Monia) Gray, 1850 [**Anomia zelandica* Gray in Dieffenbach, 1843; SD Kobelt, 1881] [=*Monica* Coen, 1933 *(nom. null.)*]. Byssal retractor scar large; foramen of moderate to large size. *?Oligo., Mio.-Rec.,* N.Z.-N.Am.-Eu.

P. (Tedinia) Gray, 1853 [**T. pernoides*; M]. Byssal foramen obsolete in adult; resilium elevated on pedestal-like chondrophore. *Rec.,* W.N.Am.

?**Saintia** Raincourt, 1877 [**S. munieri*; OD]. Hinge with 2 bifid crura and central denticle; adductor scar large, circular, excentric; retractor scars not evident. *Eoc.(Cuis.),* Eu.——Fig. C103, *3*. **S. munieri,* France; *3a,b,* LV int., ext., ×1 *(772)*.

Superfamily LIMACEA Rafinesque, 1815

[*nom. transl.* Newell, herein (*ex* Limidae Rafinesque, 1815)] [Diagnosis by N. D. Newell]

Characters of Limidae. *L.Carb.-Rec.*

Family LIMIDAE Rafinesque, 1815

[*nom. correct.* d'Orbigny, 1846 (*pro* family Limaridia Rafinesque, 1815)] [=Radulidae Adams & Adams, 1858] [Materials for this family prepared by L. R. Cox and L. G. Hertlein]

Shell usually equivalve (slightly inequivalve in one subgenus), moderately to *Ctenostreon*), ovate, orbicular or subtrigonal, most commonly higher than long, many forms somewhat extended obliquely in anteroventral direction (i.e., opisthocline); typically biauriculate but with anterior auricle reduced or absent in some forms and posterior wing or auricle usually obtuse and commonly ill-differentiated from body of shell; triangular cardinal area with shallow triangular ligament pit present in both valves, umbones well separated; many forms with anterior gape close to or well separated from hinge margin and some with posterior gape also, gapes affecting both valves equally; hinge edentulous or with weak teeth of taxodont type; monomyarian, adductor scars rather obscure in most forms; surface smooth or with radial ornament, concentric ornament very rare; ostracum with outer calcitic layer and middle and inner layers of non-nacreous aragonite. [Some Recent forms capable of swimming by flapping of valves, with valve margins disposed vertically; some constructing protective nest with byssus threads.] *L.Carb.-Rec.*

Lima Bruguière, 1797, pl. 206 [**L. alba* Cuvier, 1797 (=*Ostrea lima* Linné, 1758, p. 699); M, Cuvier, 1797, p. 421] [=*Mantellum* Röding, 1798 (obj.); *Limigenus* Renier, 1807 (suppressed ICZN); *Limaria* Rafinesque, 1815 (*non* Link, 1807); *Glaucion* Oken, 1815 (obj.); *Radula* Mörch, 1853 (*non* Gray, 1847)]. Subtrigonal, higher than long, with rather short hinge margin; auricles relatively well differentiated, anterior one slightly the smaller; anterior umbonal ridge not strongly marked; inflation only moderate; gapes of valve margins only slight; hinge edentulous or with weak denticles near ends of hinge margin; ornament of scaly radial ribs. *Jur.-Rec.,* cosmop.

[Although the year 1798 is usually cited as that of the publication of Cuvier's *Tableau élémentaire de l'histoire naturelle des animaux,* the title page of which bears the date "An 6," it is evident from an entry in the *Journal typographique et bibliographique,* Paris, Ann. 1, no. xi, p. 81, that its actual date of publication was prior to Dec. 24, 1797. Even then, however, it is most probable that it appeared later than Bruguière's plate illustrating *Lima* in *Encyclopédie méthodique.*——¶Only the bare generic name *Lima* appeared in Bruguière's plate illustrating a series of shells, so that to decide what species to take as type it is necessary to apply Article 69, a, ii, of the International Code. This Article does not make it clear whether it is applicable only if the generic name *and its author* are cited in the earliest publication in which nominal species are referred to the genus. The present contributors consider that, although Cuvier did not state that the genus *Lima,* in which he included the single nominal species *Lima alba* (=*Ostrea lima* Linné), was the genus which Bruguière has founded rather than a supposedly new one, it may be reasonably assumed that it was Bruguière's genus because (1) Cuvier omitted to mention the authors' names of most of the genera which he cited, including many which Linné had founded in 1758; (2) Cuvier and Bruguière both worked in Paris and maintained close touch with each other; and (3) it is highly improbable that two different authors would independently and in the same year have conceived the idea not only of erecting the same new zoological genus, but also of applying the same name *Lima* to it.——¶Vokes (1963, *Tulane Studies in Geology,* v. 1, p. 75) has argued that the fixing of *Ostrea lima* as type species of *Lima* Bruguière should be attributed to Lamarck (1801, *Système des animaux sans vertèbres,* p. 136), but here again there is no mention of Bruguière by name. The references given by Lamarck, however, include one to the plate in the *Encyclopédie méthodique* in which Bruguière established the genus *Lima.*]

L. (Lima) [=*Austrolima* Iredale, 1929, p. 165 (type, *L. nimbifer*; *Australima* Cotton, 1931 *(nom. null.)*]. Inequilateral, oblique, equivalve; some species with weak denticles in dorsal angles. *Jur.-Rec.,* cosmop.——Fig. C104,*3.* **L. (L.) lima* (Linné), Rec., Philip. Is.; *3a,* LV ext.; *3b,* LV int. of hinge region, both ×1 (Cox, n).

L. (Meotolima) Oyama, 1943, p. 36 [**L. (M.) ogasawarana*; OD]. Subequilateral; slightly inequivalve, LV more inflated than RV and with wider ligament area. *Eoc.,* Japan.

Acesta Adams & Adams, 1858, p. 558 [**Ostrea excavata* Fabricius, 1779, p. 368; M]. Large, thin-shelled, ovate, inequilateral, ventricose, with moderate byssal gape; anterior umbonal ridge ill-defined; anterior auricle reduced; cardinal area mainly posterior to beak, ligament pit broad, curved. [Now in cold waters or at great depths.] *U.Jur.-Rec.,* cosmop.

A. (Acesta) [=*Callolima* Bartsch, 1913, p. 235 (type, *Lima (Callolima) rathbuni* Bartsch)]. Ornament of superficial radiating riblets, commonly strongest laterally and grading into fine striae on median portion of valves. *U.Jur.-Rec.,* cosmop.——Fig. C104,*2.* **A. (Acesta) excavata* (Fabricius), Rec., Norway; LV ext., ×0.5 (Cox, n).

A. (Costellacesta) Kauffman, 1964, p. 95 [**Lima (Costellacesta) riddlei*; OD]. Anterior auricle absent; byssal gape lanceolate, extended; entire surface bearing narrow rounded riblets of equal strength, with intervals each occupied by 1 to 6 weak subequal threads. *U.Cret.(Maastricht.),* E. N.Am.

A. (Plicacesta) Vokes, 1963, p. 90 [**Lima smithi* G. B. Sowerby, 1888, p. 207; OD]. With radial ribbing more strongly developed on middle of valves than laterally and affecting whole thickness of test. *Eoc.-Rec.,* Japan-USA(Calif.).——Fig. C104,*1.* **A. (Plicacesta) smithi* (G. B. Sowerby), Rec., Japan; LV ext., ×0.7 (Oyama, 1943).

Antiquilima Cox, 1943, p. 179 [**Lima antiquata* J. Sowerby, 1818, p. 25 (=**Chamites succinctus* von Schlotheim, 1813, p. 72); OD]. Obliquely ovate, rather compressed; anterior umbonal ridge absent except near umbo; anterior auricle large and well differentiated, its gaping margin extended downward; teeth lacking; ornament of rather sinuous radial riblets of 2 or more orders of strength and of irregularly spaced growth rugae. *Jur.(Lias.-Bajoc.),* cosmop.——Fig. C104, *4.* **A. succincta* (von Schlotheim), L.Jur.(L. Lias.), Ger.; LV, ×1 (Quenstedt, 1856).

?**Aviculolima** E. Philippi, 1900, p. 622 [**A. jaekeli*; OD]. Body of shell recalling that of *Pteria,* but obliquely elongated in anterior instead of posterior direction; posterior wing acutely pointed, anterior wing rounded; cardinal area wide, with broad, posteriorly directed ligament pit. [Known only by LV.] *M.Trias.(L.Muschelkalk),* Eu.(Ger.).——Fig. C105,*1.* **A. jaekeli*; *1a,b,* LV, ×1 *(732).*

Badiotella Bittner, 1890, p. 94 [**B. schaurothiana* Bittner, 1895, p. 201; SM Bittner, 1895]. Small, trigonally orbicular, highly inequilateral, with sharp, backward-pointing umbones; anterodorsal outline straight or gently arched, coinciding with umbonal ridge which borders concave lunule; no anterior auricle, posterior auricle very small or absent; cardinal area broad, with narrow median ligament pit; LV with small tooth below each end of hinge margin, fitting into recess in RV; ornament of radial ribs. *M.Trias.(Ladin.),* S. Tyrol.——Fig. C105,*2.* **B. schaurothiana* Bittner; *2a-c,* RV ext., int., end view, all ×2; *2d,* ligament area, ×3.3 *(58).*

[As originally published, *Badiotella* must be considered as a genus proposed validly but without an included nominal species, as the specimens on which it was founded were compared to *Spirifer spuria* von Münster, a brachiopod, and were not distinguished under the specific name *schaurothiana* until 1895.]

Ctenoides Mörch, 1853, p. 56 [**Ostrea scabra* Born, 1778, p. 96; SD Stoliczka, 1871, p. xxii] [=*Divaricolima* Rovereto, 1898, p. 153 (type, *Lima eximia* Giebel, 1864); *Ptenoides* Smith, 1904 *(nom. null.)*]. Ovate to subtrigonal, subequilateral, high in proportion to length, somewhat compressed, with well-developed byssal gape bordered by liplike reflections of margins; no umbonal ridges; auricles well differentiated, subequal or anterior one slightly larger, with gaping margin extended downward; cardinal area narrow; hinge with moderately strong lateral teeth; sculpture of rounded radial riblets, divaricating ventrally and bearing fine scales. *U.Jur.(Tithon.)-Rec.,* cosmop.——Fig. C105,*5.* **C. scabra* (Born), Rec., W.Indies; *5a,b,* RV ext., RV int.; *5c,* anterior view bivalve shell showing gape, all ×1 (Cox, n).

Ctenostreon Eichwald, 1862, p. 374 [**Ostracites pectiniformis* von Schlotheim, 1820, p. 231; M] [=*Ostreopecten* Quenstedt, 1867 (obj.); ?*Pseudoctenostreon* Burckhardt, 1930 (no nomi-

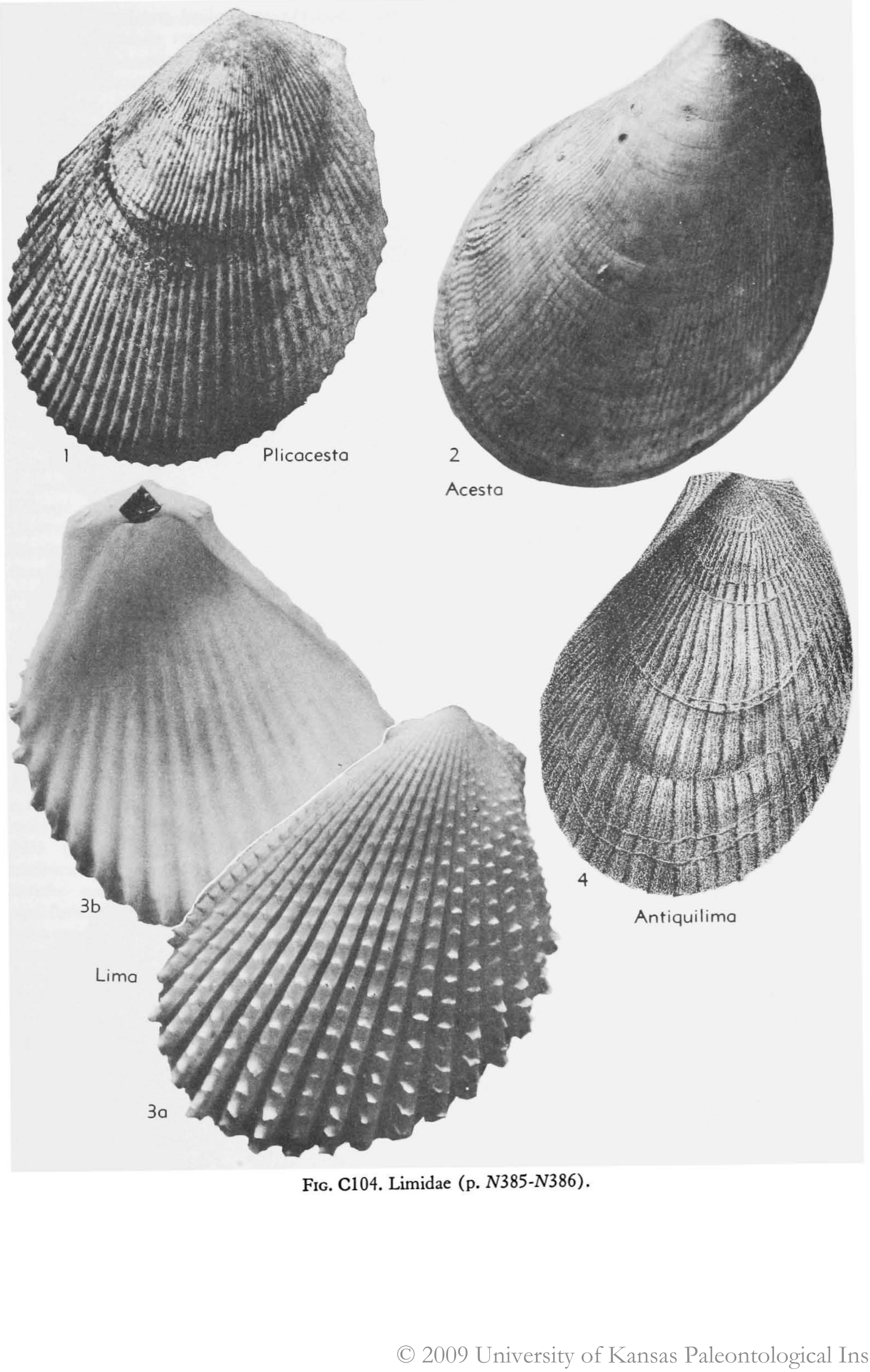

Fig. C104. Limidae (p. *N*385-*N*386).

nal species)]. Large, thick-shelled, suborbicular, irregular in outline, rather compressed; auricles large, anterior one usually smaller; gape of anterior margins wide and extended in earlier growth stages, later closing; cardinal area broad; adductor scar well marked; ornament of broad, rounded, squamose or spinose radial ribs. *L.Jur.(Lias.)-L. Cret.(Neocom.),* cosmop.——Fig. C105,6. **C.*

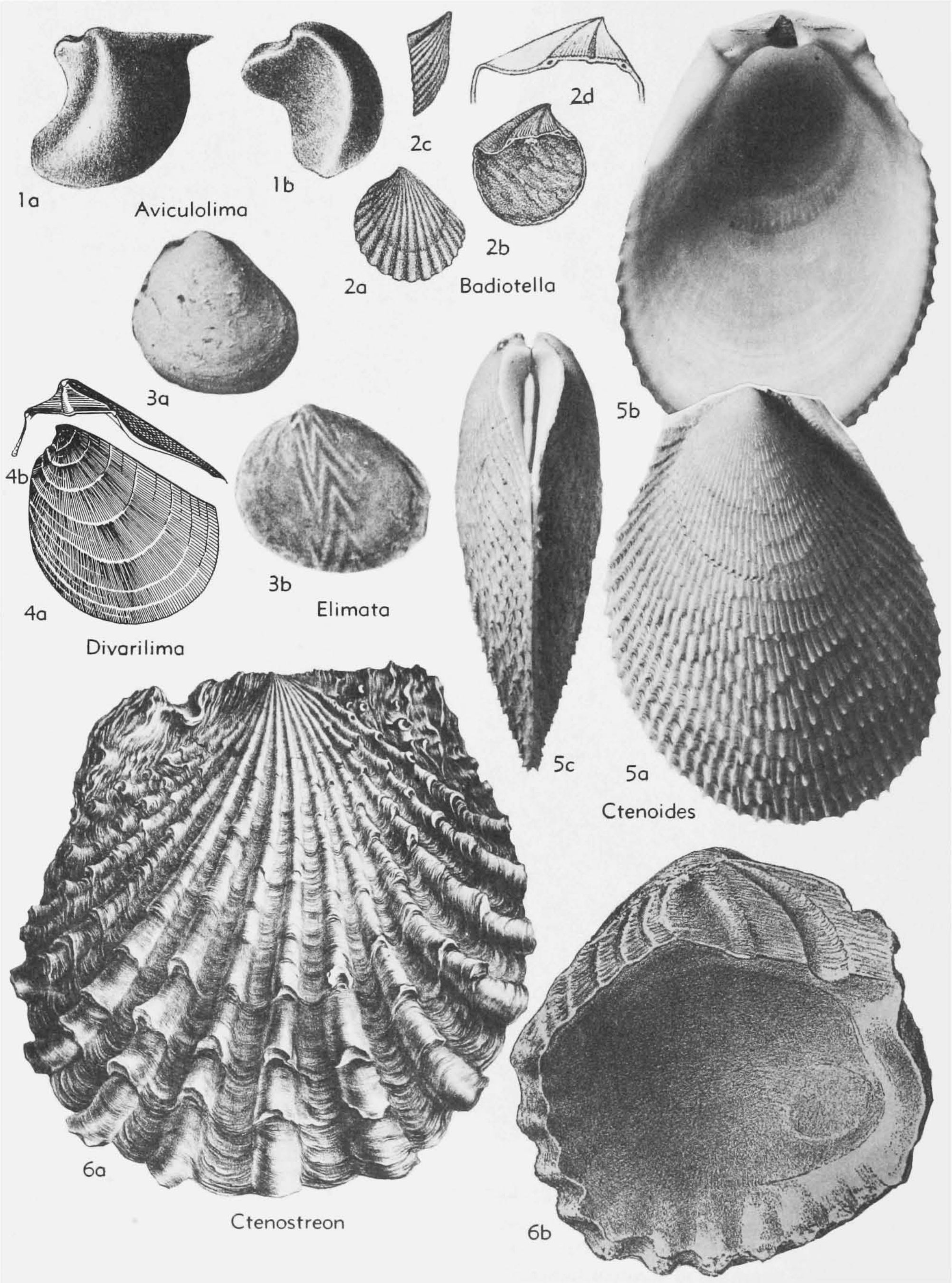

Fig. C105. Limidae (p *N*386, *N*388-*N*389).

pectiniformis (VON SCHLOTHEIM), M.Jur.(Bajoc.); *6a* (Ger.), LV ext., X0.5 *(341b)*; *6b* (France, Calvados), RV int., X0.7 *(732)*.

Divarilima POWELL, 1958, p. 72 [**Lima sydneyensis* HEDLEY, 1904, p. 200; OD]. Very small, trigonally ovate, strongly inequilateral, with sharp, backward-pointing umbones; anterodorsal outline almost straight, extended, coinciding with well-marked umbonal ridge bordering concave lunule; auricles very small; cardinal area with rather narrow median ligament pit; hinge edentulous; ornament of radial riblets interrupted by growth lamellae at irregular intervals. *Rec.*, E. Australia-Kermadek Is.——FIG. C105,*4*. **D. sydneyensis* (HEDLEY), NewS.Wales; *4a,b*, RV, hinge, X3.7 *(396)*.

Elimata DICKENS, 1963 [**E. guppyi*; OD]. Suboval shells with poorly developed auricles; surface smooth save for faint growth lines. *L.Perm.-U. Perm.*, W. Australia-W. Eu.-Greenl.-SW. USA.——FIG. C105,*3a*. **E. guppyi*, L.Perm.(Poole Ss.), W. Australia; LV ext., X3 *(263)*.——FIG. C105,*3b*. *E. permiana* (NEWELL), U.Perm., Cape Stosch F., E.Greenl.; *3b*, LV ext., X3 (Newell, 1955). [NEWELL]

?**Gryphellina** NEWELL, 1940 [**Capulus sellardsi* BEEDE, 1907; OD]. RV ventricose, gibbous, with protuberant and strongly overhanging prosogyrous beak; somewhat opisthocline, auricles small and rounded, with poorly defined byssal sinus; body of shell cancellated with intersecting costellae and fila; hinge comparable to that of *Lima*; LV unknown. *L.Perm.(Whitehorse)*, SW.USA.——FIG. C106,*2*. **G. sellardsi* (BEEDE), Dozier Dol., Tex.; *2a*, LV ext., X2; *2b*, LV hinge, enl. *(665)*. [NEWELL]

Limaria LINK, 1807, p. 157 [**L. inflata* (=**Ostrea tuberculata* OLIVI, 1792, p. 120); SD WINCKWORTH, 1930, p. 116] [=*Mantellum* MÖRCH, 1853 (*non* RÖDING, 1798)]. Small to small medium-sized, ovate, without umbonal ridges; auricles small, subequal; cardinal area almost equilateral, ligament pit broad; hinge edentulous; ostracum thin. *Eoc.-Rec.*, cosmop. [=*Winckworthia* GLIBERT & VAN DE POEL, 1965, p. 49 (obj.).].

[This species, originally described by the nonbinominal author CHEMNITZ, was named binominally by LAMARCK and LINK independently in 1807, LAMARCK's *Lima inflata* having priority. In 1791, however, GMELIN had assigned the name *Ostrea inflata* to a distinct species of Limidae and, although this already bore the name *Ostrea bullata* BORN (1778), its subsequent inclusion in *Lima* rendered the species of LAMARCK and LINK a secondary homonym. OLIVI's *Ostrea tuberculata* may be revived for *Lima inflata* LAMARCK.]

L. (Limaria) [=*Promantellum* IREDALE, 1939, p. 385 (type, *P. parafragile*); *Submantellum* OLSSON & HARBISON, 1953, p. 60 (type, *Lima orbignyi* LAMY, 1833, =*L. angulata* SOWERBY, 1844, *non* VON MÜNSTER, 1841)]. Somewhat oblique, rather strongly inflated with wide posterior gape and narrower anterior gape well separated from hinge margin; ornament of narrow radial riblets. *Mio.-Rec.*, cosmop.——FIG. C106,*10*. **L. (L.) tuberculata* (OLIVI), Rec., Malta; *10a*, LV, side view; *10b*, posterior view; *10c*, anterior view of bivalve shell showing gapes, all X1 (Cox, n).

L. (Limatulella) SACCO, 1898, p. 16 [**Lima loscombii* G. B. SOWERBY, 1820, explan. *Lima* fig. 4; OD]. Like *L. (Limaria)* but without appreciable gapes; ornament of weak unequal radial riblets. *Eoc.-Rec.*, Eu.——FIG. C106,*4*. **L. (L.) loscombii* (G. B. SOWERBY), Rec., Scot.; *4a*, LV ext., *4b*, posterior view bivalve shell, both X1.4 (Cox, n).

L. (Mantellina) SACCO, 1904, p. 148 [**Mantellum (Mantellina) inoceramoides*; OD]. Small, delicate, concentrically crenulated. *Mio.(Helvet.)*, Italy.

L. (Stabilima) IREDALE, 1939, p. 390 [**S. tadena*; OD]. High in proportion to length, subequilateral, scarcely oblique; ornament of jagged radial riblets with broader intervals. *Rec.*, E. Indies-Australia.——FIG. C106,*5*. **L. (S.) tadena*, Australia(Moreton Bay); RV ext., X1 (Cox, n).

Limatula WOOD, 1839, p. 235 [**Pecten subauriculata* MONTAGU, 1808, p. 63; SD GRAY, 1847, p. 200] [=*Cystigenus, Cystia* RENIER, 1807 (suppressed ICZN); *Limacula* GRAY, 1840 *(nom. null.)*; *Limula* D'ORBIGNY, 1846 *(nom. null.)*; *?Linatulina* HERRICK, 1889 *(nom. null.)*]. Small, oval, subequilateral, relatively high, strongly inflated, without umbonal ridges; auricles small, subequal; margins not gaping; hinge edentulous; sculpture of fine radial riblets, most conspicuous toward center of valves and absent from posterior end. *Trias.-Rec.*, cosmop.——FIG. C106,*6*. *L. gibbosa* (J. SOWERBY), M.Jur.(Bajoc.), Eng.(Dorset); LV, X1 (Cox, n).

Limea BRONN, 1831, p. 623 [**Ostrea strigilata* BROCCHI, 1814, p. 571; M] [=*Limaea* GRAY, 1847 *(nom. van.)*]. Small, suborbicular or ovate, not gaping; sculpture of radial ribs which crenate margin; cardinal area narrow; hinge with series of short denticles on each side; adductor impression subcentral. *M.Trias.-Rec.*, cosmop.

L. (Limea). Obliquely ovate, umbones prominent; ornament of numerous very weak costae; teeth narrow, oblique, unequal, located in angles at ends of hinge margin; ligament pit relatively large. *Mio.-Rec.*, Eu.——FIG. C106,*7*. **L. (L.) strigilata* (BROCCHI), Mio., Austria; *7a,b*, RV ext., RV int., X10 *(411)*.

L. (Eolimea) Cox, **new subgenus**, herein [**Lima margineplicata* KLIPSTEIN, 1845,[1] p. 248]. Trigonally ovate, inequilateral, rather weakly inflated; ornament of broad, transversely lamellose, rounded radial costae; teeth transverse, extending along whole hinge margin except below relatively large

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[1] KLIPSTEIN, A. VON, *Beiträge zur geologischen Kenntniss der östlichen Alpen*. Giessen.

ligament pit. *M.Trias.(Ladin.),* Eu.(S.Tyrol). ——Fig. C106,*1.* **L. (E.) margineplicata* (Klipstein); *1a,b,* RV ext. and dorsal view, ×4; *1c,* hinge teeth, ×6 (Bittner, 1896).

L. (Escalima) Iredale, 1929, p. 165 [**Limea acclinis* Hedley, 1905, p. 46; OD]. Obliquely ovate, entire surface with weak angular costae; teeth and ligament pit as in *L. (Limea). Rec.,*

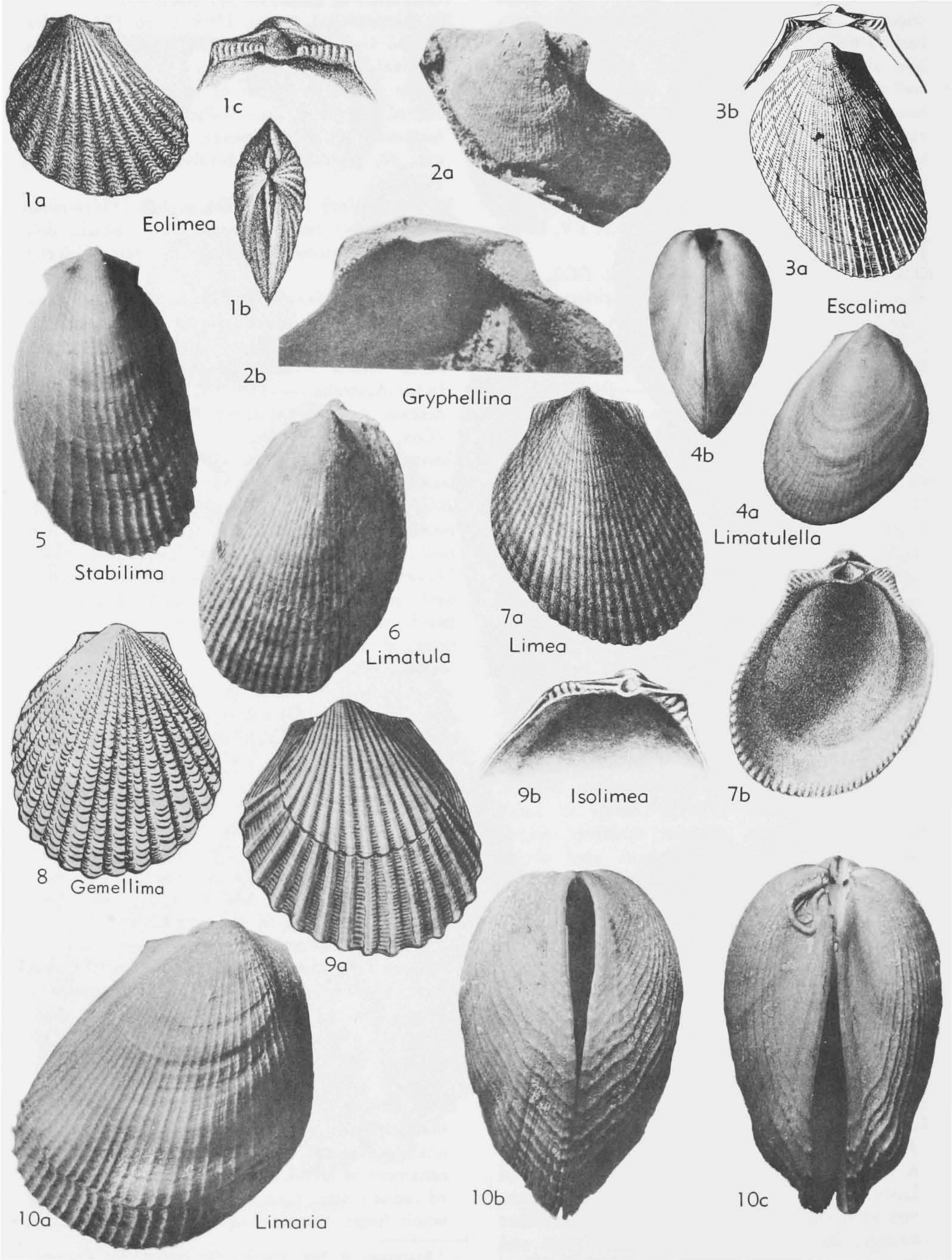

Fig. C106. Limidae (p. *N*389-*N*391).

Australia.——Fig. C106,*3*. **L. (E.) acclinis* Hedley, NewS.Wales; *3a,* RV, ext., ×3.4; *3b,* hinge line, ×4.6 (Hedley, 1905).

L. (Gemellima) Iredale, 1929, p. 166 [**Limea austrina* Tate, 1886, p. 73; OD]. Sculpture of fairly coarse lamellose ribs with narrow intervals; hinge denticles minute, transverse, extending along whole hinge margin; ligament pit small. *Rec.,* Australia.——Fig. C106,*8*. **L. (G.) austrina* Tate, S.Australia; LV ext., ×5.4 *(169).*

L. (Isolimea) Iredale, 1929, p. 166 [**Limea parvula* Verco, 1908, p. 345; OD]. Suborbicular; sculpture of relatively small number of strong costae with broad intervals; teeth and ligament pit as in *L. (Limea). Rec.,* Australia.——Fig. C106,*9*. **L. (I.) parvula* Verco, S.Australia; *9a,b,* RV ext., RV int., ×10 (Verco, 1908).

L. (Notolimea) Iredale, 1924, p. 194 [**Lima australis* Smith, 1891, p. 444; OD]. Suborbicular, strongly costate; teeth small, numerous, transverse, extending along whole hinge margin; ligament pit small. *U.Oligo.-Rec.,* Australia-N.Z. ——Fig. C107,*4*. **L. (N.) australis* (Smith), Rec., off Sydney, New S.Wales; RV ext., ×4 (Smith, 1891).

Mysidioptera Salomon, 1895, p. 117 [**M. ornata*; SD Diener, 1923, p. 111] [=*Misidioptera* Reis, 1926 *(nom. null.)*]. Ovate to suborbicular; posterodorsal margin rather elongated, posterior wing not clearly demarcated from body, anterior auricle absent or small; no anterior umbonal ridge; cardinal area inequilateral, ligament pit directed posteriorly from beak; small byssal gape present in some if not in all species. *L.Trias.-U.Trias.,* cosmop.

M. (Mysidioptera) [=*Latemaria* Wilckens, 1909, p. 220 (type, *Mysidioptera kittlii* Bittner, 1895); *Pseudolucina* Wilckens, 1909, p. 207 (type, *Mysidioptera cassiana* Bittner, 1895)]. Acline or opisthocline; anterior auricle absent or small; surface smooth or with radial striae or ribs. *L.Trias.-U.Trias.,* cosmop.——Fig. C107,*7*. *M. (M.) incurvostriata* (Gümbel), U.Trias., S.Tyrol; *7a,b,* RV ext. and cardinal area, ×1 *(58).*

M. (Pseudacesta) Waagen, 1907, p. 113 [**M. (Pseudacesta) dieneri*; M]. Ovate, prosocline, smooth, with very distinct anterior auricle. *U. Trias.,* Eu.(S.Tyrol).

Palaeolima Hind, 1903, p. 38 [**Pecten simplex* Phillips, 1836, p. 212; SD Cox, 1952, p. 48]. Small, obliquely ovate, opisthocline, length commonly slightly exceeding height, inflation moderate; beaks near middle of moderately long hinge margin; auricles obtuse; no distinct umbonal ridge; cardinal area (observed in Triassic but not yet in Paleozoic forms) as in typical Limidae; surface smooth or with radial ribs, grouped in pairs or bunches in some species. Differs very little from *Plagiostoma,* but size is invariably small and umbonal ridge and lunule are absent. *L.Carb.-U.Trias.,* Eu.-Asia-N.Am.——Fig. C107,*2*. *P. footei* (Waagen), Perm., Salt Range, Pakistan; RV ext., ×3.3 (Waagen, 1887).

Plagiostoma J. Sowerby, 1814, p. 175 [**P. giganteum*; SD Stoliczka, 1871, p. xxii] [=*Plagiostomatites* Krueger, 1823 (obj.); *Plagiostomata* Berthold, 1827 *(nom. van.)*; *Plagiastoma* Coquand, 1880 *(nom. null.)*; *?Anomalolima* Philippi, 1900, p. 635 (type, *Lima maxima* d'Archiac, 1837); *?Anomalolina* Cossmann, 1901 *(nom. null.)*]. Medium-sized to large, obliquely ovate, opisthocline, length commonly slightly exceeding height, inflation moderate to strong; beaks more or less anterior to middle of moderately long cardinal area; ligament pit broad; auricles obtuse; anterior umbonal ridge well defined, with excavated lunule in front of it; marginal gapes small or absent; edentulous or with 1 or 2 broad, longitudinally directed teeth in each dorsal angle; surface smooth, radially striated, or with weak ribs commonly with punctate intervals. *M.Trias.-U. Cret.,* cosmop.——Fig. C107,*8*. **P. giganteum,* L.Jur.(L.Lias.), Eng.; *8a,* RV ext., *8b,* LV cardinal area and lunule, ×0.75 *(202).*

Pseudolimea Arkell in Douglas & Arkell, 1932, p. 161 [**Plagiostoma duplicata* J. de C. Sowerby, 1827, p. 114; OD] [=*Limoarca* von Münster, 1832, p. 421 (genus without nominal species, name never adopted); *Limnoarca* Paetel, 1875 *(nom. null.)*]. Rather small, gibbose, obliquely ovate to orbicular; anterior umbonal ridge ill-defined; beaks near middle of moderately long cardinal area; ligament pit broad; hinge commonly with slightly oblique teeth occupying dorsal angles, but many specimens edentulous; ornament of angular ribs, commonly with thread in each interval. *Trias.-U.Cret.,* cosmop.——Fig. C107,*3*. *P. hettangiensis* (Terquem), L.Jur.(L.Lias.), S. Switz.; *3a,b,* RV ext., RV int., ×1.3 (von Bistram, 1903).

Regalilima Cox, 1943, p. 177 [**Lima oolitica* Lycett, 1857, p. 126; OD]. Large, trapeziform, inequilateral, without anterior auricle; anterior umbonal ridge well developed and extended, with flattened area in front of it; cardinal area broad; anterior gape wide; ornament of broad flat ribs, obscure in some specimens. *M.Jur.(Bajoc.),* Eng. ——Fig. C107,*6*. **R. oolitica* (Lycett); *6a,* RV ext., ×0.5; *6b,* RV, ant. end showing gape, ×0.67 *(185).*

?**Roncania** de Gregorio, 1896, p. 107 [**R. prima*; M]. Founded on small trigonally ovate shell with broad radial ribs, some divaricating; tentatively included in Limidae by its author, but systematic position uncertain. *U.Eoc.,* N.Italy.

Serania Krumbeck, 1923, p. 218 [**S. seranensis*; M]. Narrowly ovate, very inequilateral and oblique; anterior umbonal ridge well defined and extended, with flattened region in front of it, descending steeply to margin; no anterior auricle, posterior wing not demarcated from body; fold within anterior area delimiting lunule-like depression, margin of which forms deep byssal gape; cardinal area with broad ligament pit, wholly posterior to beak; ornament of irregular concentric folds. *U.Trias.*, E.Indies(Ceram).——FIG. C107,*1*. **S. seranensis*; RV, *1a*, side view, *1b*, dorsal view showing cardinal area and byssal gape, both ×1 *(486)*.

Tirolidia BITTNER, 1895, p. 202 [**Lima (Tirolidia)*

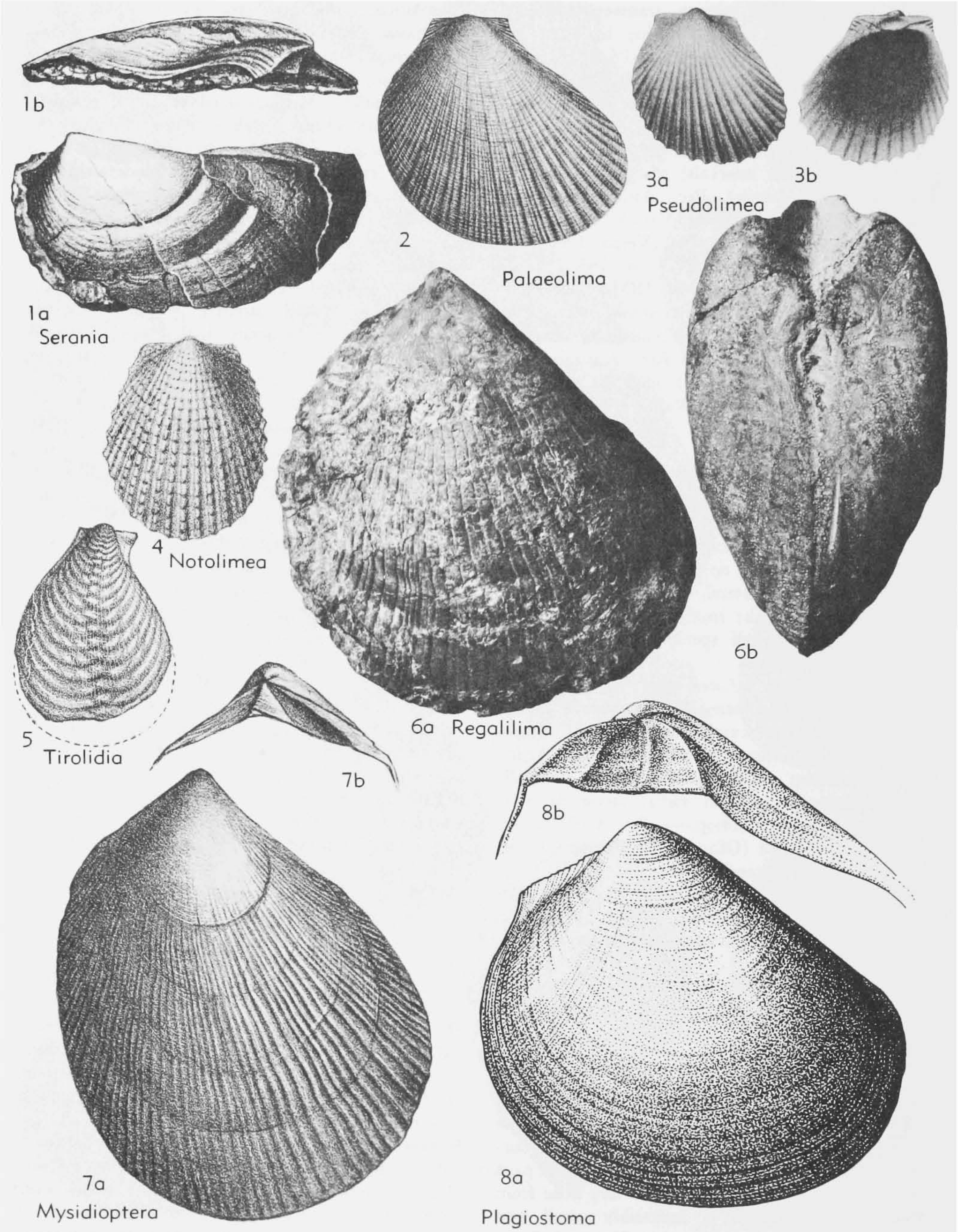

FIG. C107. Limidae (p. *N*391-*N*393).

haueriana; SD Diener, 1923, p. 118]. Subtrigonal, only slightly inequilateral, with relatively short hinge margin and narrowly rounded, slightly protruding umbo; auricles small, well differentiated, anterior one acute at tip; inflation rather weak; gape of valves slight; cardinal area imperfectly known; surface with discontinuous subconcentric ribs, or smooth. *M.Trias.-U.Trias.*, Eu.(S.Alps).——Fig. C107,*5*. *T. cassiana* Bittner, M.Trias.(Ladin.); RV, ×2 *(58)*.

Suborder OSTREINA Férussac, 1822

Because completion of systematic descriptions for taxa of this suborder was delayed too long for placement here, they are assigned out-of-sequence position (*see* Part N, Volume 3).

Subclass PALAEOHETERODONTA Newell, 1965

[Diagnosis by N. D. Newell]

Equivalve, with closed margins and, where preserved, prismatonacreous shells; ligament amphidetic or opisthodetic, external and parivincular; dentition generally consisting of few teeth more or less radial and divergent from umbonal region, striated in some genera, rarely becoming taxodont in few genera (certain Unionoida); where lateral teeth occur, they originate below beaks and are not separated from cardinals by edentulous interval, as in Heterodonta. [These forms include the actinodonts (earliest known Bivalvia), Trigonioida and Unionoida. They lead in various lines to the Pteriomorphia, Heterodonta, and possibly to the Mytiloida early in the Paleozoic.] *M.Cam.-Rec.*

Order MODIOMORPHOIDA Newell, new order

[=Actinodonta Douvillé, 1912; Actinodontoida Newell, 1965] [Diagnosis by N. D. Newell]

Extinct Paleozoic marine ovoid bivalves; shell microstructure unknown; generally unornamented, otherwise possessing characters of subclass. [This somewhat heterogeneous, poorly understood assemblage is grouped together for convenience. Clearly it includes ancestral radicals of many major lines.] *M.Cam.-L.Perm., ?U.Perm.*

Superfamily MODIOMORPHACEA Miller, 1877

[*nom. transl.* Newell, 1965 (*ex* Modiomorphidae S. A. Miller, 1877)] [Materials for this superfamily prepared by Aurèle LaRocque & N. D. Newell]

Elongate, isomyarian or slightly anisomyarian, with anterior, but not terminal beaks; edentulous(?) or possessing a few posterior laterals and differentiated subumbonal cardinals. [This superfamily anticipates and strongly resembles certain Unionacea, Mytilacea and Carditacea, but differs especially in that the laterals originate below the beaks and essentially extend to the posterior extremity of the hinge under the ligament.] *L.Ord.-L.Perm., ?U.Perm.*

Family MODIOMORPHIDAE S. A. Miller, 1877

[=Modiolopsidae Fischer, 1887]

Shell subovate with or without radial ornamentation, opisthodetic, without extended posterior wing, more or less modioloid in form, commonly, but not invariably expanded posteriorly, with anterior lobe ahead of umbones and commonly with umbonal ridge or carina extending obliquely backward from umbones to posteroventral region; anterior adductor generally small, deeply impressed, in many shells reinforced by bordering buttress; posterior adductor relatively large, ovoid; anterior laterals absent, cardinals and posterior laterals may or may not be present. [It has been claimed but not satisfactorily demonstrated that some of these forms are edentulous. Some resemble Mytilacea and may represent ancestors of that group.] *L.Ord.-L.Perm., ?U. Perm.*

Modiomorpha Hall & Whitfield, 1869, p. 72 [**Pterinea concentrica* Conrad, 1838; SD Hall, 1885] [=*Palanatina* Hall & Whitfield, 1870 (type, *P. typa*; OD); *Dechenia* Spriestersbach, 1915, p. 70 (type, *D. rhenana*; SD LaRocque & Newell, herein); *Spriestersbachia* Maillieux, 1930, p. 62 (*nom. van. pro Dechenia* Spriestersbach, 1915)]. Mesial ventral sinus and oblique preumbonal sulcus distinct; LV with 1 large wedge-shaped tooth; RV with corresponding socket; without laterals *(159)*. *M.Sil.-L.Perm.*,

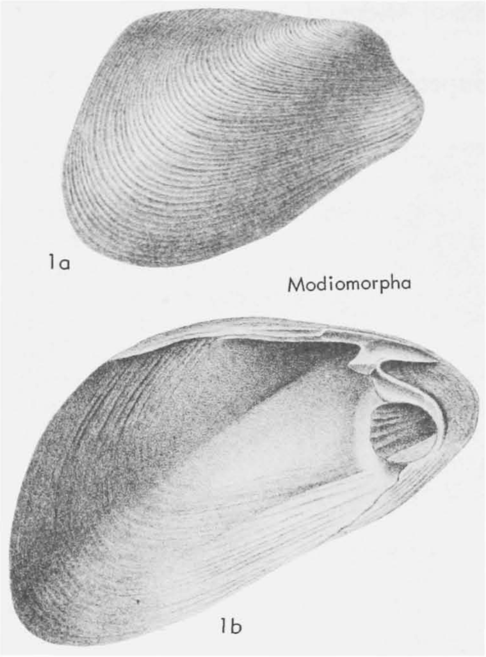

FIG. D1. Modiomorphidae (p. *N*393-*N*394).

widely distributed.——FIG. D1,*1*. **M. concentrica* (Conrad), M.Dev., USA(N.Y.); *1a,b*, RV ext., LV int., ×1 (Hall, 1884).

?**Aristerella** Ulrich, 1894, p. 524 [**A. nitidula*; OD]. Inequivalve, LV smaller; small, subovate, moderately convex; no lateral furrow; without radial costae; hinge thin and apparently without teeth; ligament parivincular?; otherwise similar to *Whiteavesia*. *M.Ord.(Blackriv.)-Miss.*, USA (Mo.).——FIG. D2,*6*. **A. nitidula*, Ord.(Trenton.), USA(Minn.); *6a*, RV int. mold; *6b*, dorsal view of molds showing inequality of valves; both ×4.5 *(930)*.

Byssodesma Isberg, 1934, p. 199 [**B. ulrikae*; OD]. Similar to *Modiomorpha* but with lunule and ?without hinge teeth. *U.Ord.*, Sweden.——FIG. D2,*5*. **B. ulrikae*, Boda Ls., Dalarna; *5a*, RV (holotype), ×2; *5b*, hinge of same, ×3 *(439)*.

Callodonta Isberg, 1934, p. 212 [**C. monilifera*; OD]. Equivalve, higher posteriorly; beaks anterior, prosogyre; without radial ornamentation; hinge with 6 cardinal teeth, anterior one pointed, others blunt. *U.Ord.*, Sweden.——FIG. D2,*4*. **C. monilifera*, Boda Ls., Dalarna region, *4a*, LV (holotype), ×3; *4b*, LV hinge, ×6 *(439)*.

Colpomya Ulrich, 1894, p. 522 [**C. constricta*; M]. Subrhomboidal, elongate, widest posteriorly; beaks anterior but not terminal; umbonal ridge strongly convex; hinge plate straight, thick in front of beaks, thinner behind them; RV with 1 tubercle, LV with corresponding depression and strong process partly fitting into depression in front of tubercle of RV. *M.Ord.(Blackriv.)-Sil.(U. Medin.)*, E.N.Am.——FIG. D2,*7*. **C. constricta*, Ord.(Trenton.), USA(Ky.); *7a*, LV int.; *7b*, RV ext.; both ×1 *(930)*.

?**Cymatonota** Ulrich, 1893, p. 661 [**C. typicalis*; OD] [=*Chaenodomus* Ulrich, 1894, p. 477 (obj.); *Endodesma* Ulrich, 1894, p. 525 (type, *E. cuneatum*; OD); *Physetomya* Ulrich, 1893, p. 693 (type, *P. acuminata*; OD); *Psiloconcha* Ulrich, 1894, p. 530 (type, *P. grandis*; OD)]. Elongate, with subparallel dorsal and ventral margins; beaks about one-fourth distance from front end; ends rounded; umbonal ridge rounded; with broad lateral sulcus and commonly ventral sinus; surface essentially smooth, without radial ornamentation; posterior adductor larger than the anterior. *U.Ord.*, E.N.Am.——FIG. D3,*8*. **C. typicalis*, USA(Ohio); LV ext., ×1 *(929)*.

Dceruska Barrande, 1881, p. 77 **D. primula*; M]. Small, modioloid, without lunule, escutcheon or radial ornamentation; musculature and hinge unknown. [This genus requires restudy before it can be evaluated.] *Ord.(D3)*, Eu.(Boh.).

?**Dipleurodonta** Isberg, 1934, p. 197 [**D. pulchella*; OD]. Externally similar to *Eurymya* and *Eurymyella*, but without posterior wing; cardinals unknown; 2 long and thin posterior lateral teeth parallel to shell margin. *U.Ord.(Richmond.)*, N. Am.-Sweden(Boda Ls.).——FIG. D2,*3*. **D. pulchella*, Sweden(Dalarna region); *3a*, RV int. mold; *3b*, LV ext.; both ×3 *(439)*.

Ectenocardiomorpha Isberg, 1934, p. 188 [**E. elongata*; OD]. Similar to *Eurymyella* but without posterior wing and with strongly marked postumbonal ridge; differs from *Dipleurodonta* in lacking lamellar teeth. *U.Ord.*, Sweden.——FIG. D2,*1*. **E. elongata*, Boda Ls., Dalarna region; *1a*, LV ext. (holotype); *1b*, LV hinge, both ×3 *(439)*.

?**Eurymyella** Williams, 1912, p. 382 [**E. shaleri*; OD]. Subtriangular, narrow in front, subalate behind; umbonal ridge rounded and moderately elevated, without mesial depression; hinge plate very narrow at ends and without lamellar teeth, fairly strong under beaks where cardinal tooth occurs in each valve. *Sil.(Pembroke, Eastport)*, USA(Maine).——FIG. D2,*2*. **E. shaleri*; RV ext., ×1 *(984)*.

Goniophora Phillips, 1848, p. 264 [**Cypricardia cymbaeformis* Sowerby, 1839; OD] [=?*Digoniomya* Whidborne, 1897, p. 116 (type, *D. elegans*; M); *Mytilomorpha* Hind, 1899 (obj.); ?*Naiadopsis* Mendes, 1952, p. 111 (type, *N. lamellosus*; OD)]. Equivalve, rhomboidal to trapezoidal; beaks anterior, curved inward and forward; strong umbonal carina from beaks to posterobasal angle;

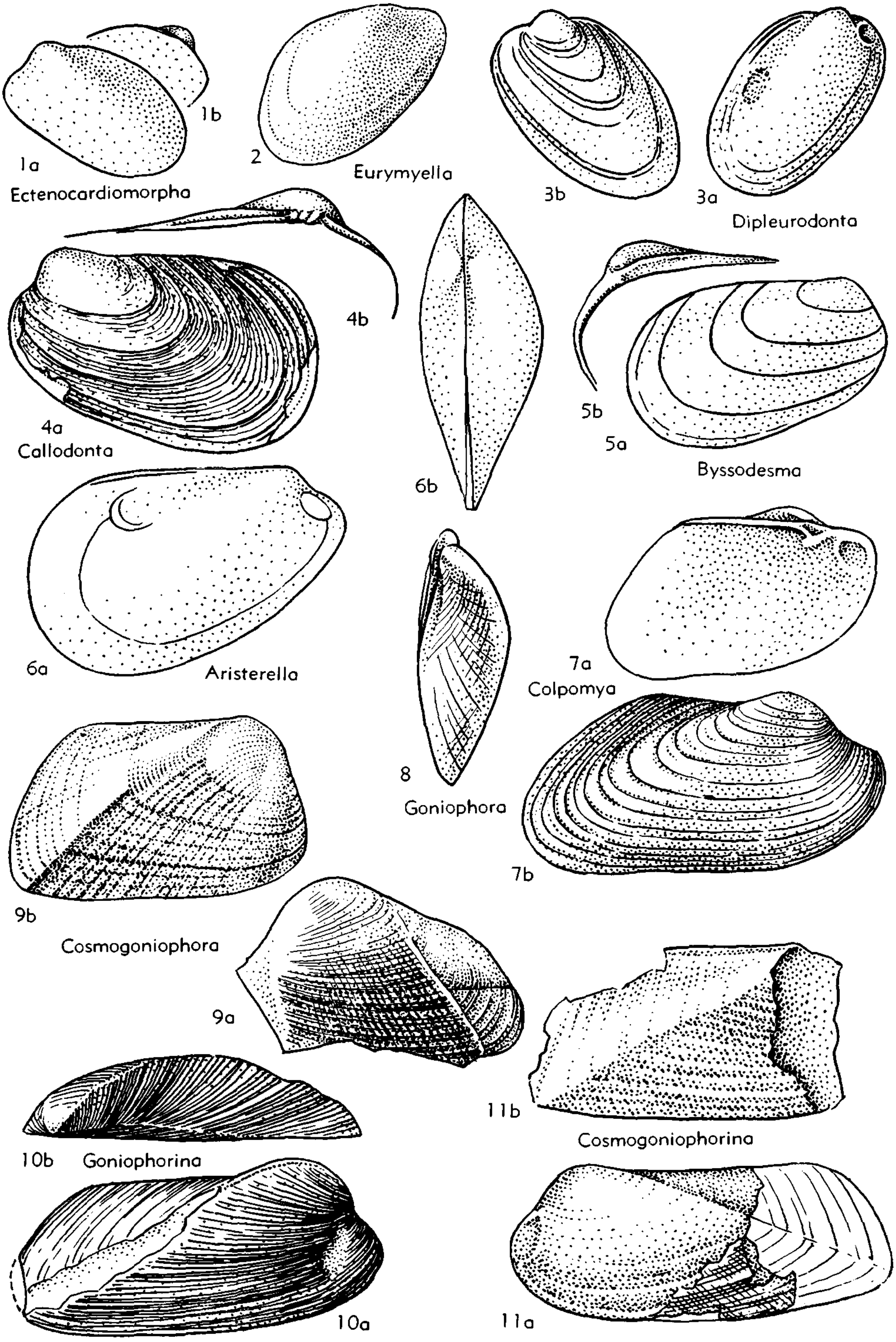

FIG. D2. Modiomorphidae (p. *N*394, *N*396-*N*397).

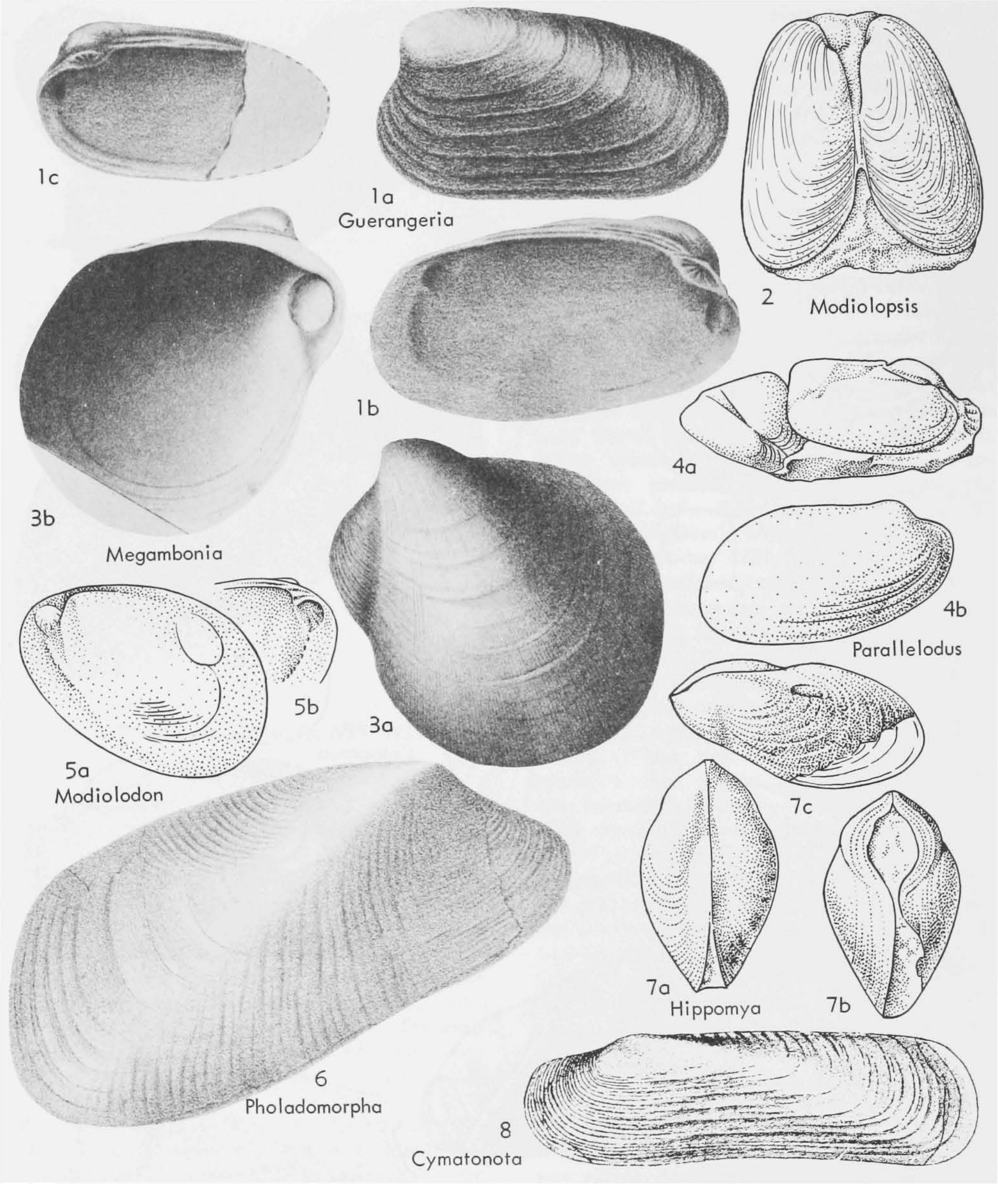

FIG. D3. Modiomorphidae (p. *N397-N398*).

dentition weak; LV in some species with 1 oblique tooth; anterior adductor deeply impressed and with a strong myophoric buttress behind it. *L. Ord.-L.Perm.*, cosmop.

G. (Goniophora). Without radial costae. *Ord. (Trenton.)-L.Perm.*, cosmop.——FIG. D2,*8*. **G. (G.) cymbaeformis* (Sowerby), Sil.(U.Ludlow), Eng.; RV ant., ×1 (Sowerby in Murchison, 1839).

G. (Cosmogoniophora) McLearn, 1918 [**G. bellula* Billings, 1874; OD]. With radial costae. *L.Ord.(Tremadoc.)*, Arg.-*Dev.*, N.Am.——FIG. D2,*9*. **G. (C.) bellula* (Billings), Sil.(Stonehouse F.), N.S.(Arisaig); *9a,b*, LV ext., RV ext., both ×1.0 *(564)*.

Goniophorina Isberg, 1934 [**G. volvens*; OD]. Similar to *Goniophora* but without teeth. *U.Ord.*, Sweden; *L.Perm.*, SW.USA.

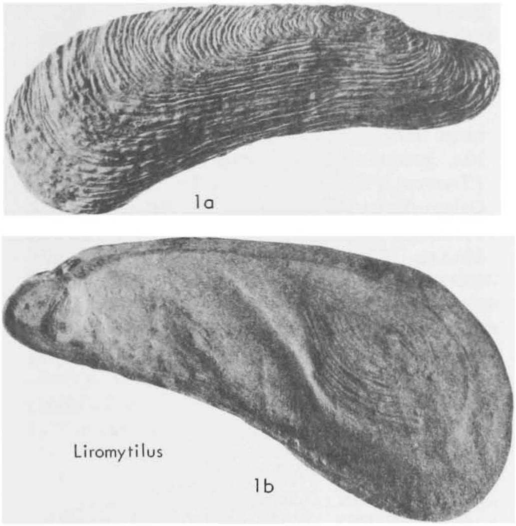

FIG. D3A. Modiomorphidae (p. *N*397).

G. (Goniophorina). Without radial costae. *U.Ord.-L.Perm.*——FIG. D2,*10*. **G. (G.) volvens,* U.Ord. (Boda Ls.), Sweden(Dalarna region); *10a,b,* RV ext. and dorsal (holotype), ×2 *(439).*

G. (Cosmogoniophorina) ISBERG, 1934 [**G. (C.) carinata*; OD]. With radial costae. *U.Ord.,* Sweden.——FIG. D2,*11*. **G. (C.) carinata,* Boda Ls., Dalarna region; *11a,* LV ext. (holotype), ×3; *11b,* RV int. mold, ×2 *(439).*

Guerangeria OEHLERT, 1880 (1881) [**G. davousti*; M]. Elongate, subquadrate, with anterior beaks; lacking escutcheon and lunule or radial ornamentation; somewhat similar superficially to *Cypricardinia*; single prominent cardinal tooth in RV marked by strong radial grooves, with corresponding socket in LV; well-defined posterior lateral tooth and socket in RV. *L.Dev.,* W.Fr.——FIG. D3,*1*. **G. davousti,* near Brulon; *1a,b,* LV ext., int., ×3; *1c,* RV int., ×3 (Oehlert, 1881).

?**Hippomya** SALTER, 1864, p. 299 [**H. ringens*; OD]. Modioliform, without radial ornamentation or posterior wing; large byssal gape with thickened rim in front of byssal sulcus. *Ord.,* Eng.——FIG. D3,*7*. **H. ringens,* Budleigh Salterton, Eng.; *7a,b,* dorsal and ventral view of both valves, ×0.7; *7c,* LV lat. view, ×0.7 *(823).*

?**Liromytilus** LAROCQUE, 1950, p. 294 [**Modiomorpha attenuata* WHITEAVES; OD]. Surface with strong concentric ridges; umbones inconspicuous, not terminal, situated in anterior one-sixth of shell; anterior adductor small, posterior scar large, occupying more than one-half of posterior part of shell, bounded anteriorly by raised ridge; 2 small pyramidal cardinal teeth just in front of right umbo; lateral teeth and dentition of LV unobserved. *M.Dev.,* Can.(Manitoba).——FIG. D3A,*1*. **L. attenuata* (WHITEAVES); *1a,b,* ×0.5 (LaRocque). [LAROCQUE]

Megambonia HALL, 1859, p. 12 [**Pterinea cardiiformis* HALL, 1843; OD]. Ventricose, upright, with strongly defined anterior lobation; surface with fine radial costellae; hinge short, with distinct lateral tooth and groove near posterior cardinal angle of each valve. *Sil.(?Arisaig),* Can. (N.S.); *M.Dev.,* USA(N.Y.).——FIG. D3,*3*. **M. cardiiformis* (HALL), Dev. (Onondaga), N.Y.; *3a,b,* LV ext., LV int., both ×1 *(379).*

Modiolodon ULRICH, 1894 (June 16), p. 521 [**Modiolopsis oviformis* ULRICH, 1890; OD] [*non ?Modiolodon* NECHAEV, 1894 (probably published late in year) (type, *Clidophorus pallasi oblongus* GOLOWKINSKY, 1868; OD)]. Similar to *Modiolopsis,* but with 1 to 3 oblique cardinal teeth in each valve. *M.Ord.-U.Ord.,* N.Am.; *Sil.(Llandov.),* Scot.; *?U.Perm.,* USSR(Krasnowidowo, Volga R.). ——FIG. D3,*5*. **M. oviformis* (ULRICH), Ord. (Trenton.), USA(Ky.); *5a,b,* LV int. mold and cast, ×1 *(930).*

Modiolopsis HALL, 1847, p. 157 [**Pterinea modiolaris* CONRAD, 1838; M] [=*Orthodesma* HALL & WHITFIELD, 1875, p. 93 (type, *O. rectum*; OD); *Orthonotella* MILLER, 1882, p. 117 (type, *O. faberi*; M); *?Sphenolium* S. A. MILLER, 1889, p. 513 (type, *S. cuneiforme*; OD); *Corallidomus* WHITFIELD, 1895, p. 493 (type, *C. concentricus*; M); *Lithobia* KOKEN, 1902, p. 132 (type, *L. atava*; M); *Modiodesma* ULRICH, 1924 (obj.)]. Edentulous; without marked lateral sulcus or ventral

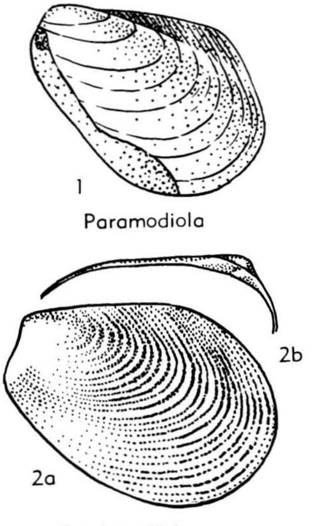

FIG. D4. Modiomorphidae (p. *N*398-*N*399).

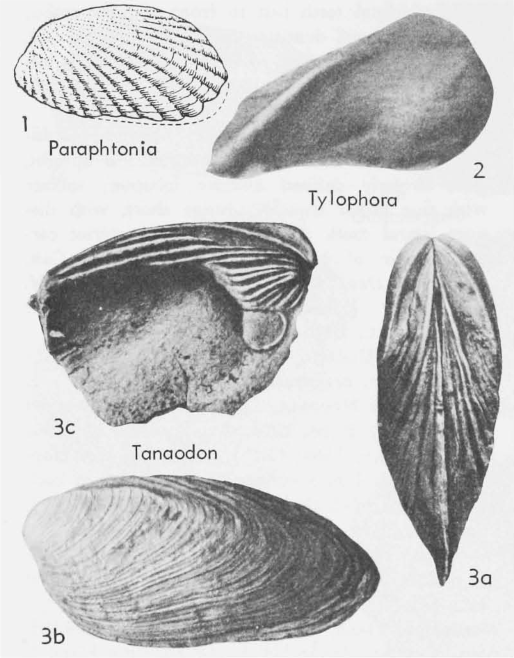

FIG. D5. Modiomorphidae (p. *N*398-*N*399).

sinus; radial ornamentation lacking. *M.Ord.-U. Ord.,* cosmop.——FIG. D3,*2*. **M. modiolaris* (CONRAD), U.Ord., USA(N.Y.); both valves ext., *ca.* ×0.8 *(931)*.

Parallelodus BRANSON, 1909 [**P. obliquus*; OD]. Similar to *Whiteavesia,* but RV with 1 anterior tooth and 1 posterior tooth, LV with 2 anterior teeth and 2 posterior teeth; teeth long and nearly parallel to hinge line. *M.Ord.(Blackriv.),* USA (Mo.).——FIG. D3,*4*. **P. obliquus*; *4a,* 2 specimens showing dentition; *4b,* RV ext.; all ×1 *(82)*.

Paramodiola ISBERG, 1934, p. 163 [**P. glabra*; OD]. Similar to *Modiomorpha* but with beaks low, anteriorly undifferentiated from front lobe of shell; edentulous. *M.Ord.,* Sweden.——FIG. D4,*1*. **P. glabra,* Kullsberg Ls., Dalarna region; lat. view of holotype, ×3 *(439)*.

Paraphtonia KHALFIN, 1958, p. 182 [**P. imitabilis*; OD]. Externally similar to *Modiomorpha* but ornamented with coarse radial ribs. *M.Ord.,* USSR (Sib.).——FIG. D5,*1*. **P. imitabilis*; LV ext., ×1 (Khalfin, 1958).

Pholadomorpha FOERSTE, 1914, p. 279 [**Modiolopsis pholadiformis* HALL, 1851; OD (=*Sedgwickia? divaricata* HALL & WHITFIELD, 1875)]. Similar to *Whiteavesia* except that costae are coarse and divaricate with respect to umbonal ridge. *U.Ord.,* USA(Ohio-N.Y.)-Can.(Quebec).——FIG. D3,*6*. **P. pholadiformis* (HALL), Quebec; RV ext., ×1 *(381)*.

Prolobella ULRICH, 1894, p. 532 [**P. striatula*; OD]. Obliquely acuminate-ovate; beaks anterior but not terminal; anterior end of shell lobed; surface with concentric and radial ornamentation; hinge thin, apparently without teeth; short clavicle-like process just in front of beaks. *M.Ord. (Trenton.),* E.N.Am.——FIG. D6,*1*. **P. striatula,* Galena Dol., USA(Minn.); LV ext., ×1 *(930)*.

?**Pyanomya** MILLER, 1881, p. 318 [**P. gibbosa* MILLER, 1881; M]. Externally similar to *Modiomorpha*; interior unknown. *U.Ord.,* Ohio.

?**Radiatodonta** DAHMER, 1921, p. 245 [**R. goslariensis*; OD]. Like *Modiomorpha* but with several short, steep-sided cardinal teeth, converging above in front of beak. *L.Dev.,* Eu.(Ger.).——FIG. D6,*6*. **R. goslariensis,* Oberharzer Kahleberg Ss., near Drecktalskopf; LV int. mold, ×1 *(211b)*.

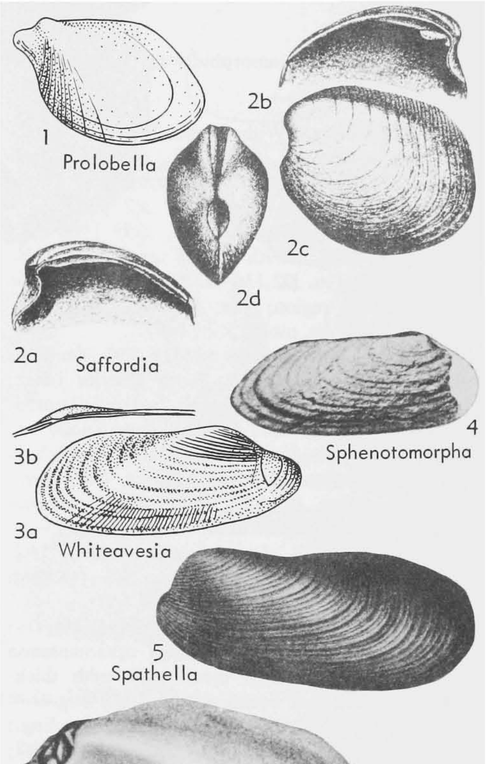

FIG. D6. Modiomorphidae (p. *N*398-*N*399).

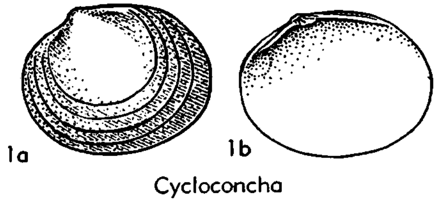

FIG. D7. Cycloconchidae (p. *N*399).

Redonia ROUAULT, 1851, p. 362 [**R. deshayesiana;* SD FISCHER, 1886]. Similar to *Modiomorpha* but attenuated posteriorly and with 2 posterior laterals in RV and 1 in LV. [Assigned also to Carditacea which it somewhat resembles excepting for fact that the posterior lateral teeth originate at beaks instead of behind the ligament. Placed in a separate family Redoniidae BABIN, 1966, but the distinction from Modiomorphidae appears to be insignificant.] *Ord. (Llandeil.),* Eu. (France-Boh.-Spain)-N.Afr.——FIG. E44,*4*. **R. deshayesiana,* Brittany; *4a,b,* LV int., RV int., ×1; *4c,d,* LV and RV hinges, enl.(Chavan, n).

?Saffordia ULRICH, 1894, p. 625 [**S. ventralis*; OD]. Subovate; beaks anterior; without radial ornamentation; lunule and escutcheon; hinge plate thin; LV with 1 horizontal wedge-shaped cardinal tooth and 1 slender lateral tooth extending from the beak; RV with cardinal socket and 1 lateral furrow. *M.Ord.-U.Ord.,* E.Can.-NE.USA.——FIG. D6,*2*. **S. ventralis,* U.Ord., USA(Minn.); *2a,* RV hinge; *2b,* LV hinge; *2c,* LV; *2d,* ant. view; all ×1 *(929).*

Semicorallidomus ISBERG, 1934, p. 175 [**S. whitfieldi*; OD]. Similar to *Modiolopsis* but less elongate; LV with depression under umbo, probably to receive tooth in RV. *U.Ord.,* Sweden.——FIG. D4,*2*. **S. whitfieldi,* Boda Ls., Dalarna region; *2a,* LV ext. (holotype), ×3; *2b,* LV hinge, ×5 *(439).*

Spathella HALL, 1885, p. xxxiii [**S. typica*; OD]. Transversely subcylindrical, anterior end short, narrowly rounded; beaks subanterior, small; umbonal slope rounded or subangular; surface with concentric ornamentation only. Interior unknown. *U.Dev.-Miss.,* N.Am.-Eu.——FIG. D6,*5*. **S. typica,* U.Dev., USA(N.Y.); LV, ×1 *(379).*

Sphenotomorpha WILLIAMS & BREGER, 1916, p. 233 [**S. rigidula*; OD]. Similar to *Modiomorpha* but with straight, horizontal or slightly declining hinge line; no mesial depression. *L.Dev.,* USA(Maine)-Brazil.——FIG. D6,*4*. **S. rigidula,* Chapman Ss.; RV ext., ×1 *(986).*

?Tanaodon KIRK, 1927, p. 1 [**T. louderbacki*; M] [=*Neoactinodonta* HEIDECKER, 1959, p. 3 (type, *N. amygdalina*; M)]. Beaks terminal; lunule small, escutcheon large, well defined; ventral profile convex; without radial ornamentation; hinge plate broad, traversed by many oblique teeth below the ligament, with or without cross striations, teeth becoming progressively longer and parallel with posterior margin of shell. *M.Dev.,* E.Australia-China.——FIG. D5,*3*. **T. louderbacki,* M.Dev., Tung Kou Distr., Szechuan, China; *3a-c,* dorsal view both valves; LV ext., LV int., all ×0.7 *(473).*

Tylophora DAHMER, 1936, p. 23 [**Goniophora convoluta* DREVERMANN; M]. Similar to *Goniophora* but ornamented with fine radial costellae; hinge unknown. *L.Dev.,* Eu.(Ger.).——FIG. D5,*2*. **T. convoluta* (DREVERMANN), L.Coblenz.; RV ext., ×1 *(213).*

Whiteavesia ULRICH, 1893 (1895), expl. pl. 56 [*nom. subst. pro Actinomya* ULRICH, 1894 (*non* MAYER, 1870)] [**Modiolopsis cincinnatiensis* HALL & WHITFIELD, 1875; OD]. Lateral sulcus and ventral sinus absent, interior marked by fine radial ridges which may reflect fine external ornamentation; hinge edentulous(?). *M.Ord.-U.Ord.,* E.N.Am.-ArcticN.Am.——FIG. D6,*3*. **W. cincinnatiensis* (HALL & WHITFIELD), U.Ord., USA(Ky.); *3a,* RV int. mold; *3b,* RV hinge; both ×1 *(929).*

Superfamily CYCLOCONCHACEA Ulrich, 1884

[*nom. transl.* NEWELL, herein (*ex* Cycloconchidae ULRICH, 1884)] [Diagnosis by N. D. NEWELL]

Ovoid, more or less isomyarian shells with submedian (never terminal) beaks; lacking radial ornamentation; dentition consisting of few elongate teeth below beaks increasing in length toward anterior and posterior margins of hinge. *M.Cam.-U.Dev.*

Family CYCLOCONCHIDAE Ulrich, 1884

[Materials for this family prepared by AURÈLE LAROCQUE & N. D. NEWELL]

Amphidetic, with median cardinals and laterals in front of and behind beaks; those of RV stronger than those of LV. *M.Ord.-U.Ord.*

Cycloconcha S. A. MILLER, 1874 [**C. mediocardinalis*; M]. Subcircular, with 2 or 3 cardinal teeth near middle of hinge and well-differentiated, long, lateral tooth in front and behind beaks. *M.Ord.-U.Ord.,* USA(Ohio).——FIG. D7,*1*. **C. mediocardinalis,* U.Ord.; *1a,b,* LV ext., RV int., ×1.25 *(615).*

Actinodonta PHILLIPS, 1848, p. 225 [**A. cuneata*; M]. Elongate-ovate, smooth, with somewhat extended posteroventral extremity; beaks located 0.25 to 0.3 behind anterior extremity; anterior

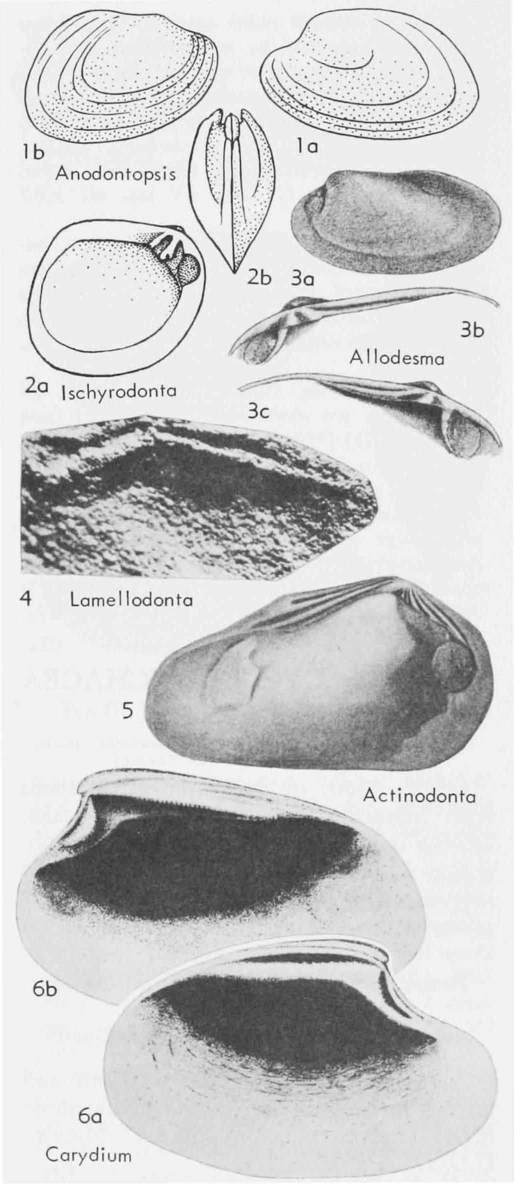

FIG. D8. Cycloconchidae *(5)*; Lamellodontidae *(4)*; Allodesmatidae *(1-3)*; Carydiidae *(6)* (p.*N*399-*N*400).

adductor circular, somewhat smaller than posterior, reinforced posteriorly by buttress; dentition consisting of about 9 radial teeth on broad hinge plate, teeth short medially and longer marginally; anterior muscle scar strongly impressed, smaller than posterior scar. *M.Ord.*, G.Brit.——FIG. D8,*5*. **A. cuneata*, Llandeil., LV int., ×1 *(735)*.

Family LAMELLODONTIDAE Vogel, 1962

[Materials for this family prepared by N. D. NEWELL]

Subequilateral, amphidetic, with one or two subequal, noncrenulate lateral teeth in front of and behind beaks, in some shells joining medially in obtuse apex; cardinal teeth lacking. *M.Cam.*

Lamellodonta VOGEL, 1962, p. 216 [**L. simplex*; M]. Ovoid to subcircular, with centrally situated beaks. *M.Cam.*, Spain.——FIG. D8,*4*. **L. simplex*, Zaragoza; RV hinge, ×10 *(943)*.

Family ALLODESMATIDAE Dall, 1895

[Materials for this family prepared by AURÈLE LAROCQUE & N. D. NEWELL]

Beaks near anterior end; surface without radial ornamentation; isomyarian; one or two posterior lateral teeth in each valve, or lacking; anterior laterals lacking or short; one or two cardinals in each valve; anterior adductor with strong posterior myophoric ridge. [Some genera of this family resemble certain Modiomorphidae and Carditidae.] *M.Ord.-U.Sil.*

Allodesma ULRICH, 1894, p. 617 [**Modiolopsis subelliptica* ULRICH, 1892; OD]. Elongate elliptical; hinge with 1 or 2 posterior lateral teeth in each valve; RV with 2 and LV with 1 cardinal tooth; anterior lateral teeth short or lacking; pallial line simple. *M.Ord.*, NE.USA-E.Can.——FIG. D8, *3*. **A. subellipticum* (ULRICH), Galena Dol., USA (Minn.); *3a*, LV int. mold, ×2; *3b,c*, RV and LV hinge, ×4 *(930)*.

Anodontopsis M'COY, 1851, p. 53 [**A. angustifrons*; OD] [=?*Orthodontiscus* MEEK, 1871, p. 298 (type, *Anodontopsis? milleri*; OD)]. Ovoid to subtrigonal; LV with 1 slender posterior lateral and 1 shorter anterior lateral tooth; RV with 2 posterior laterals and 1 shorter anterior lateral tooth. *Sil.(U.Ludlov.)*, G.Brit.——FIG. D8,*1*. **A. angustifrons*, Eng.(Kendal); *1a,b*, LV ext., RV ext., ×1 (Sedgwick & M'Coy, 1854).

?Ischyrodonta ULRICH, 1890 [**I. truncata*; OD]. Short or elongate, thick-shelled; hinge straight or slightly arcuate, wide and strong; RV with 1 strong cardinal tooth; LV with 2 strong cardinals; no laterals. *U.Ord.*, E.N.Am.——FIG. D8,*2*. **I. truncata*, Cincinnatian, USA(Ohio); *2a*, LV int.; *2b*, int. bivalved specimen; both ×1 *(926)*.

Family CARYDIIDAE Haffer, 1959

[Materials for this family prepared by N. D. NEWELL]

Shell isomyarian, strongly inequilateral, opisthodetic, with prosogyre beaks approximately 0.3 behind front margin; one posterior lateral tooth in each valve below ligament; anterior dentition consisting of single curved, crenulated lateral tooth or single radially furrowed cardinal tooth; teeth of LV underlying those of RV. *L. Dev.-U.Dev.*

Carydium Beushausen, 1895, p. 154 [**C. gregarium;* SD Wolf, 1930, p. 46]. Shell ovoid to subtrigonal, tapering posteriorly; without radial ornamentation; anterior dentition variable, ranging from simple denticulate lateral tooth to radially furrowed tubercle. *L.Dev.-U.Dev.,* Eu.(Ger.-Belg.). ——Fig. D8,*6*. **C. gregarium,* L.Dev.(Singhofen), Ger.; *6a,b,* LV int., RV int., ×4 (Haffer, 1959).

Order UNIONOIDA Stoliczka, 1871

[*nom. correct.* Weir, herein (*pro* order Unionacea Stoliczka, 1870)] [Diagnosis by John Weir]

Inequilateral, equivalved or subequivalved, flatly compressed to globular shells, varying in outline from nearly circular to elongate and rodlike (or with symmetry destroyed by attachment in one Recent family); but commonly ovate, elliptical, trigonal or trapeziform, ranging in length from 20 mm. to large forms of 300 mm. Beaks prosogyrous, relatively small, flat, and inconspicuous; or moderately large and prominent, with capacious cavities, giving good upstanding molds in fossils. Lunule and escutcheon absent, or only feebly defined. Periostracum well developed, smooth and thin in Recent forms, but tough and resistant (in post-Pleistocene, and possibly older, fossils it is sometimes the only part preserved). Ornament of simple growth lines, supplemented (in some Unionacea only) by ribs or knobs, which may be spinose. Ligament external, opisthodetic. Internally shells are nacreous in Unionacea, and possibly also in some older taxa; integripalliate, isomyarian or subisomyarian, anterior retractor of foot commonly forming conspicuous circular or reniform scar above and behind anterior adductor. Dentition, when present, may consist only of one or two more or less subumbonal teeth situated transversely on hinge plate or forming groups of strong teeth (normally two in LV and one in RV) based on short dental fulcra situated in front of umbo, and supplemented (Unionacea only) by elongate, lamellar posterior teeth (commonly two in LV and one in RV) below ligament and subparallel to hinge line. Anomalous dentition of pseudotaxodont character in Palaeomutelidae (Anthracosiacea). Mantle edges in living forms united only between branchial and anal orifices. *?M.Dev., U. Dev.-Rec.*

This possibly heterogeneous order provides a convenient grouping of the Unionacea with certain older cryptogenic groups of *Unio*-like and *Anodonta*-like bivalves, which, except for some Pachycardiidae, shared with the Unionacea a preference for nonmarine environments. Despite the great variability of shell outline and dentition which makes concise diagnosis of genera and higher taxa exceedingly difficult, all have in common a certain combination of shell characters which, if not highly distinctive (hence their previous association with the Cardiniidae and other families), at least imparts a certain homogeneity of morphic character to the assemblage. In the Unionacea and Anthracosiacea shell form is greatly influenced by ecologic station *(285)*, a factor which, added to the innate variability of the population at a given station or geologic horizon, contributes to the difficulty of classification.

No palaeontological evidence indicates that these superfamilies had a common origin. Those of the upper Paleozoic apparently lacked the nacreous condition that distinguishes the later Unionacea (or conditions of fossilization have destroyed all evidence of it), and while most Unionacea, like older forms, have simple growth lines as the only surface sculpture, others develop a more elaborate ornament of ribs, tubercles, or spinous excrescences that never are found in the Anthracosiacea and Archanodontacea.

Dentition is normally present, but certain taxa are characteristically edentulous (Anodontidae, ?Archanodontacea), and in others the anodont condition occurs in individuals as an aspect of variation in the hinge apparatus. The characteristic lamellar posterior "lateral" teeth that occur commonly in the Unionacea are not found in the Anthracosiacea. These teeth underlie the ligamental nymphs, at least proximally, and in this respect are not strictly homologous with the analogous teeth of Heterodonta.

The pseudotaxodont dentition of the Palaeomutelidae is unique. In the series of irregular teeth ranged along the hinge one or more below the umbo may acquire special prominence, and the whole series may be reduced to a few large, irregular teeth on a short and broadened hinge plate.

The very large bivalves of the Upper Devonian and Carboniferous that are now accorded superfamily rank as Archanodontacea have apparently no ancestral or other intimate relationship with the later-appearing but in part contemporaneous (or homotaxial) Anthracosiacea. A considerable gap in time separates their latest representative in the Pennsylvanian and the earliest *Unio* of the Triassic and a still greater interval before the appearance of unequivocal *Anodonta,* which the earliest (Devonian) archanodonts, especially, so much resemble in outline. The *Unio*-like *Neamnigenia* of the Permian of Siberia may represent a link. Unfortunately, as in *Archanodon,* its hinge is unknown. It occurs in a highly endemic fossil fauna whose other bivalve genera all became extinct before the end of the Permian; accordingly, *Neamnigenia* is unlikely to be the earliest recorded unionid, directly ancestral to species in the Triassic rocks of other regions (East Africa, North America, etc.) that are commonly referred to *Unio.* Its relations (if any) to the earlier and more *Anodonta*-like *Archanodon* are equally doubtful.

It is unknown whether any of these extinct genera possessed the glochidium or lasidium larvae of the Recent Unionacea.

Superfamily ARCHANODONTACEA
Weir, new superfamily

[Materials for this superfamily prepared by John Weir]

Very large, sporadically thick shells (to 22 cm. in length), inequilateral, integripalliate, isomyarian, varying somewhat in outline and proportions, but in general transversely subelliptical, anodontiform, with inconspicuous depressed umbones situated at about 0.1 to 0.2 of length from anterior end. Straight hinge line extending posteriorly for half (or rather more) of postumbonal length, making obtuse angle with obliquely inclined posterior margin. Ventral margin gently convex, straight, or slightly curved in wide but shallow sinus; hinge apparently edentulous; one or two lamellar ridges (claustra) radiating from umbo in posterior or posteroventral direction over inner dorsal surface of valves in at least one species, but lacking articular function. Posterior adductor scar unknown; anterior adductor situated close in front of umbo near dorsal margin, may unite with adjacent insertions of anterior retractor and anterior umbonal retentor muscles to form large composite scar of oval or reniform outline. *U.Dev.-L.Perm.*

The Archanodontacea are a cryptogenic group of very large *Anodonta*-like freshwater shells of the upper Paleozoic. Sporadic occurrences of them are known from the Upper Devonian (Up. Old Red Ss.) of Ireland *(Archanodon, s.s.)* and USA *(Amnigenia)*, Lower Carboniferous of England *(Archanodon, s.l.)* and Pennsylvanian of Nova Scotia *(Asthenodonta)*. Upper Devonian forms lived somewhat gregariously as communities of rather variable shells. At present it is possible to define neither the trends nor the limits of their variation, but differences between the Irish *"Anodonta" jukesi* Forbes and the American *Amnigenia catskillensis* Hall may be no more than specific or subspecific.

These considerations probably apply also to Carboniferous forms, of which altogether only four or five nearly complete specimens are known. The sparse material suggests that these were larger and more elongate than shells of the Upper Devonian belonging to the group, but again this difference may be no more than specific. The generic separation of the latest member of *Asthenodonta* was based on a misinterpretation of the anterior muscle complex. Excellent plaster casts of type material supplied by the Geological Survey of Canada show clearly that the structure called "ligamental fulcrum" by Whiteaves, and misrepresented in his figure, is an integral dorsal part of the scar of a very large anterior muscle complex, and probably represents the combined insertions of the anterior retractor and anterior umbonal retentor muscles, situated adjacent to and coalescing with the scar of the adductor. A similar, if

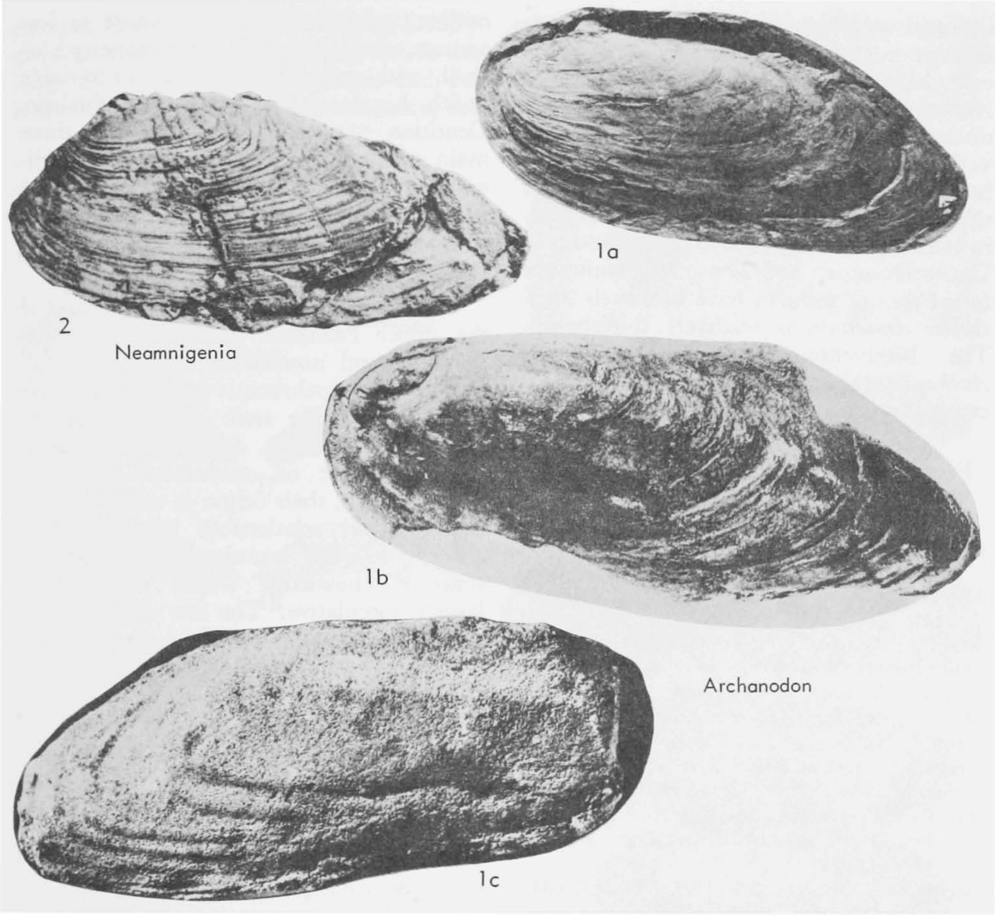

Fig. D9. Archanodontidae (p. *N*404).

less emphatic, division of the anterior muscle scar with smaller dorsal component, possibly representing only the anterior retractor, is shown in one of Hall's figures of the smaller Devonian species *Amnigenia catskillensis*. With the elimination of the "ligamental fulcrum" as a special structure, the justification of a separate genus *Asthenodonta* disappears.

Claustra have been figured only in the American forms referred to *Amnigenia*. It would be premature to say that they are absent in the others.

In view of the foregoing considerations there seems to be no alternative, in the present state of knowledge, to regarding *Amnigenia* and *Asthenodonta* as subjective synonyms of *Archanodonta*, a conclusion which does not rule out the possibility of resurrecting these names for subgenera or genera if new material reveals unsuspected structural differences.

It is improbable that these *Anodonta*-like shells of the upper Paleozoic belong to the Unionacea. Apart from the gap in time that separates them from the earliest *Anodonta* (Eoc.) and *Unio* (Trias.), it is unlikely that they had evolved the elaborate mechanism of larval dispersal that characterizes Recent Unionacea. Otherwise it is difficult to explain the sporadic nature of their heterochronous occurrences. Had such an efficient mechanism of distribution been available, the thick-shelled *Archanodon westoni* of the Pennsylvanian of Nova Scotia might have been expected to yield fossils in the homotaxial deposits of the USA and in the much-explored Westphalian coal measures of Britain and western Europe, but none has been found. It is not easy, however, to formulate a diagnosis of *Archanodon* that would emphasize morphic distinctions from *Anodonta*. The Pennsylvanian *Archanodon westoni* appears to have been thick-shelled (WHITEAVES records a thickness of 9 mm. anteriorly, and 12 mm. in one fragment). On the other hand, the Upper Devonian and Lower Carboniferous forms do not seem to have had such thick shells. *Anodonta* is relatively thin-shelled. The heterochronous homeomorphy of *Archanodon* and *Anodonta* must be accepted.

Family ARCHANODONTIDAE Weir, new family

Characters of superfamily. *U.Dev.-L. Perm.*

Archanodon HOWSE, 1878 [**Anodonta jukesi* FORBES, 1853; OD] [=*Amnigenia* HALL, 1885 (type, *Cypricardites catskillensis* VANUXEM, 1842); *Asthenodonta* WHITEAVES, 1893 (type, *A. westoni*)]. Characters of superfamily. *Dev.(Up.Old Red Ss.)*, Ire.-Eng.; *U.Dev.*, USA; *L.Carb.*, Eng.; *Penn.*, N.Scot.——FIG. D9,*1a*. **A. jukesi* (FORBES), Up. Old Red Ss., Ire.; LV ext., ×0.4 (Weir, n).——FIG. D9,*1b*. *A. westoni* (WHITEAVES), Penn., N.Scot.; LV ext., ×0.4 (Weir, n).——FIG. D9,*1c*. *A.* sp., L.Carb., Eng.; RV ext., ×0.4 (Weir, n).

Neamnigenia KHALFIN, 1950 [**N. beljanini*; OD]. Large *Unio*-like shells; umbones obtuse, not prominent. Posterior end narrow, not expanded; posterior margin acutely rounded at its extremity, obliquely inclined above at very obtuse angle to straight hinge margin, which attains length of 0.5 to 0.8 length of shell. Ventral margin gently convex, without great subumbonal depth. Anterodorsal margin rather long and straight. [Nonmarine.] *L.Perm.*, USSR(Sib.).——FIG. D9,*2*. *N. longa* (BETEKHTINA); LV ext., ×1 (Ragozin, 1955).

Superfamily ANTHRACOSIACEA Amalitsky, 1892

[*nom. transl.* WEIR, herein (*ex* Anthracosiidae AMALITSKY, 1892)] [Materials for this superfamily prepared by JOHN WEIR except as recorded otherwise]

Upper Paleozoic nonmarine bivalves of moderate size (rarely attaining 90 mm. in length, and averaging less than half this), dimyarian (isomyarian or subisomyarian), integripalliate. Shells highly variable in outline and inflation. Hinge more or less arcuate, according to the relative length of shell, with definite hinge plate of variable width. Ligament parivincular, opisthodetic. Dentition variable, but comprising three main categories, 1) with one or two cardinal teeth in one or both valves, rarely more; 2) irregularly pseudotaxodont; 3) teeth absent. *?M.Dev., Carb.-Perm., ?Jur.* (especially *U.Carb.*).

The fresh-water or nonmarine bivalves of the upper Paleozoic (excluding Archanodontacea and nonmarine Myalinidae) fall into two heterochronous groups which are here given family rank as Anthracosiidae and Palaeomutelidae. Although much work has been done on constituent genera of these families, their origin is unknown and their mutual relationship uncertain. Discussion of these questions in the present state of knowledge would therefore be largely speculative. The few relevant facts and views are mentioned in discussion of each family, and possibility that the superfamily now proposed may be heterogeneous must be borne in mind. The nonmarine environments of the families were very different, typical Anthracosiidae having been essentially inhabitants of paralic marshes, and less fully continental than the Permian Paleomutelidae. Nevertheless, in the absence of evidence from phylogeny, these families have in common a number of characters which make possible their provisional combination in the Anthracosiacea, thus conveniently maintaining the association of the Upper Carboniferous genera *Carbonicola* and *Anthracosia* with Permian *Palaeanodonta* and *Palaeomutela* favored by AMALITSKY (13), COX (1932, 1936) and ZITTEL's *Grundzüge* (1924), while facilitating future taxonomic redistribution by according separate family rank to the Carboniferous and Permian genera on the basis of distinctive dental patterns.

Palaeanodonta presents special difficulties. The name was proposed by AMALITSKY for certain forms of the Permian of the Oka-Volga basin, which he had previously assigned to *"Najadites."* The type species, by original designation, is *Unio castor* EICHWALD, whose sole figure, representing an external view of an open shell (Fig. D10,*3*) gives no clue to hinge structure, nor is the hinge mentioned in the diagnosis and description. As interpreted by AMALITSKY, the genus may be diphyletic, the Russian species falling naturally into two distinct groups of probably different origin: 1) small shells, some demonstrably edentulous, with opis-

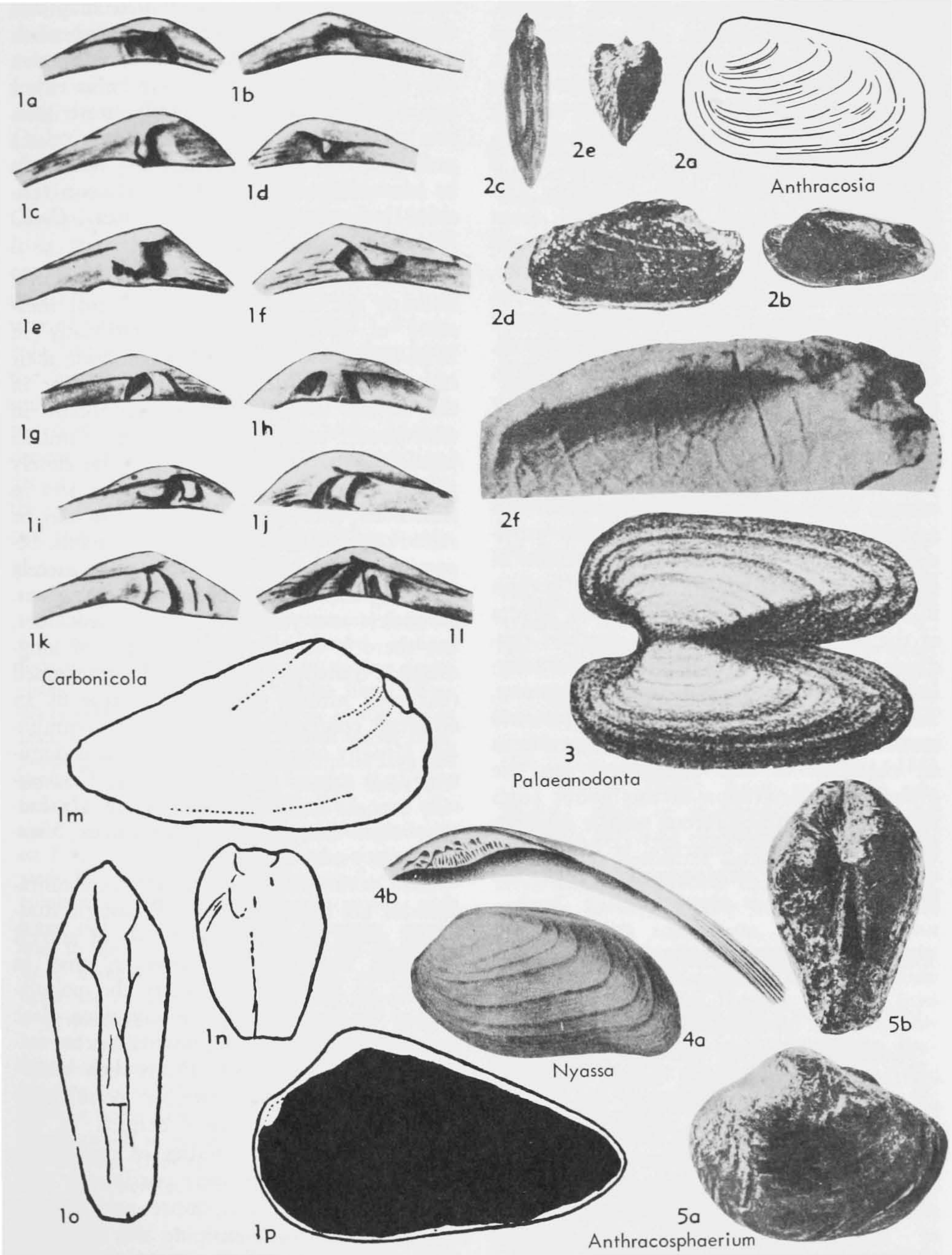

FIG. D10. Anthracosiidae *(1-3,5)*; Family Uncertain *(4)* (p. *N*407, *N*411).

thodetic ligament, and externally like the type species (or plausible variants of it), and 2) relatively large, elongate edentulous forms like *"Najadites" verneuili,* which has, at least on the inner dorsal margin of the LV, two long, narrow parallel grooves, separated by a slender ridge. Doubtless these are opposed to but do not interlock with corresponding features in the other valve. A hinge margin of this kind may be interpreted as an extremely narrow ligamental area of duplivincular type. It is found also in certain early *Naiadites (N. obesus),* and also in *Anthraconaia,* from which the Permian *"Najadites" verneuili* may have evolved, through certain elongate, posteriorly narrowed forms that characterize the later stages of the Westphalian and the Stephanian in Europe. Group 2) is excluded from the present definition of *Palaeanodonta.* It is not known if *Unio castor* Eichwald (type species of *Palaeanodonta*) possesses hinge features of this kind; more probably, like some plesiotypes, it is edentulous, with opisthodetic ligament. On this assumption I include *Palaeanodonta* provisionally in the Anthracosiidae, by reason of its general external similarity to certain forms of the typical Carboniferous genera of the family and because the anodont condition occurs sporadically in the characteristically unstable hinges of these genera. The undoubtedly very different environment of *Palaeanodonta* may be regarded as an objection to this assignment, on the ground that derivation of this genus from forms of the Carboniferous paralic marches is unlikely. If this objection is valid, then the origin of *Palaeanodonta,* as of the Palaeomutelidae, is cryptic.

Family ANTHRACOSIIDAE Amalitsky, 1892

[*emend.* Trueman & Weir, 1946] [=Carbonicolidae Cox, 1932 *(partim)*]

Shells equivalve or subequivalve, highly variable, but commonly ovate, elliptical, subtriangular or suborbicular in outline; hinge line gently arcuate. Circular anterior adductor scar deeply impressed, slightly smaller in area than shallow oval posterior scar and situated near margin within angle of usually well-defined, subtriangular frontal lobe; anterior retractor muscle situated above and close to anterior adductor, its impression visible on internal molds as small single or double scar on crest of umbonal ridge. Dentition variable, usually consisting of one subumbonal tooth (in both valves, or in one only), which may not reach edge of hinge plate, but two teeth may occur in each valve, or in one valve only (single tooth, which may be in either valve, fitting between); rarely more than two teeth (maximum four, of low relief) present in each valve, and hinge plate may be edentulous. Lunule and escutcheon variable, but usually feebly defined. *Carb., ?Perm.*

These inhabitants of Carboniferous forest swamps are common fossils in coal measures of Westphalian age, especially in Britain, which may well have been their center of dispersal. At many horizons in the British coal measures they occur in enormous numbers, forming "mussel bands" in which the shells may be closely packed in *lumachelles* of up to six feet in thickness. Individual mussel bands may be remarkably widespread and continuous, becoming stratal indices of more than merely local importance in coal-mining operations. Doubtless many cases are thanatocoenoses, but there is usually little evidence of long-distance transport, and it has been assumed that each affords a reliable sample of an adjacent, contemporaneous, living community. Usually one anthracosiid genus is dominant in a mussel band, commonly *Carbonicola* or *Anthracosia,* but locally *Anthracosphaerium;* nonmarine Myalinidae (*Naiadites,* etc.) may also occur.

Like nonmarine Myalinidae, the Anthracosiidae are highly variable. Biometric studies of shells from mussel bands at several horizons have shown, however, that in respect of certain parameters the population of the genus studied in any given place is homogeneous, and represents a cross section of a chronospecies. From such homogeneous but highly variable populations morphospecies have been defined in the past, before detailed studies of association variation and ecology were possible, or considered necessary; and, more recently, for convenience in systematizing this taxonomically intractable family, thus rendering it of stratigraphical value as the basis of the fruitful scheme of zonal subdivision now generally applied to the British coal measures.

Nothing definite is known of the origin of the family. The parivincular ligament and relatively small size of the anterior adductor may be consistent with derivation from some mytilacean, but not from the duplivincular Myalinidae. This would separate *Carbonicola* from *Anthraconaia* [*Anthracomya*], which were classified together as Unionidae by WHEELTON HIND and as Cardiniidae in the ZITTEL textbook (1913). It is true that elongate, so-called anthraconaioid forms occur in the lower coal measures of England, apparently as products of variation in populations of *Carbonicola*, but it is not known whether they have the hinge of true *Anthraconaia*; nor has such a variation relationship yet been detected between *Carbonicola* and *Anthraconaia s.s.* (the *adamsi-salteri-modiolaris* group). Provisionally it is better to refer the elongate "anthraconaioids" of the lower coal measures to *Carbonicola* with a query.

Anthracosia KING, 1856 [**A. beaniana*; OD]. Shell transversely subovate, elliptical, or elongate subtriangular, some with obliquely truncate posterior end; umbones low, strongly incurved, inclined forward and downward, giving in varying degree characteristic tilt to umbonal growth lines. Hinge plates beveled on their free edges, giving rise in internal molds to prominent median dorsal ridge. Postumbonal portion of each hinge plate long and narrow; anterior subumbonal portion short and broad, deflected ventrally at obtuse angle to posterior portion, and usually carrying single tooth on 1 or both valves. Dorsally and posteriorly to tooth (or dental cavity) and at anterior end of opisthodetic, parivincular ligament groove, each hinge plate bears conspicuous triangular groove with its apex contiguous to umbo. [In apposition these triangular grooves doubtless enclosed a ligamental structure, which may have grown from a persistent juvenile resilium.] Anterior lobe of internal mold compressed and strongly demarcated from rest of mold by vertical or inclined ridge descending ventrally from each umbo behind anterior adductor scar; sides of mold behind anterior lobe nearly parallel in dorsal view. *Carb.(Westphal. B)*, W.Eu.-USSR(Donetz).——FIG. D10,*2a*. **A. beaniana*, Eng., neotype (ICZN pend.); LV ext., ×1 *(915)*.——FIG. D10,*2b-e*. *A. aquilina* (J. DE C. SOWERBY); *2b,c*, int. mold LV, both valves dorsal, ×1; *2d,e*, lectotype (ICZN pend.), RV, both valves ant., ×1 *(915)*.——FIG. D10,*2f*. *A.* sp. aff. *A. atra* (TRUEMAN), Scot.; hinge, ×2 *(915)*.

Anthracosphaerium TRUEMAN & WEIR, 1946 [**Carbonicola exigua* DAVIES & TRUEMAN, 1927; OD] [=*Carbonicola* HIND, 1894 *(partim)*; *Carbonicola* DAVIES & TRUEMAN, 1927 *(partim)*]. Suborbicular or subovate, inflated, equivalved, with gibbous, contiguous umbones. Internal characters unknown. *U.Carb.(Westphal. A, B)*, W.Eu.-USSR (Donetz).——FIG. D10,*5*. **A. exiguum* (DAVIES & TRUEMAN), Eng.(?Westphal. B), *5a,b*, holotype LV lat., both valves dorsal, ×1 *(915)*.

Carbonicola M'COY, 1855 [**Unio acutus* J. SOWERBY, 1813; SD DAVIES & TRUEMAN, 1927] [=*Carbonicola* HIND, 1894 *(partim)*; *Carbonicola* DAVIES & TRUEMAN, 1927 *(partim)* (*non* AMALITSKY, 1892)]. Like *Anthracosia*, but umbones erect, in most shells unequal in height, and umbonal growth lines usually not tilted. Hinge line curved, rarely straight behind umbo; hinge plates deep, forming continuous arc without marked division into anterior and posterior portions as in *Anthracosia*; 1 subumbonal tooth on one or both valves, or 2 in some, rarely more; or edentulous. Outline of internal mold in dorsal plan forming double wedge; beaks of mold prominent and divergent, its median dorsal ridge weak; anterior lobe not compressed and demarcated from rest of mold as in *Anthracosia*. *Carb.* (especially *U.Carb.*) *(Namur.-Westphal. A)*, W.Eu.-USSR(Donetz).——FIG. D10,*1a-l*. *C.* sp. aff. *C. pseudorobusta* (TRUEMAN), Scot.; *1a-l*, hinges, LV's on left and unpaired, ×1 *(565)*.——FIG. D10,*1m-p*. **C. acuta* (J. SOWERBY), Eng.; *1m-o*, lectotype (a mold; RV lat., both valves ant., dorsal), ×1; *1p*, same, LV, with shell restored, ×1 *(915a)*.

?**Palaeanodonta** AMALITSKY, 1895 [**Unio castor* EICHWALD, 1895] [=*Palaeanodonta* AMALITSKY, 1891 *(nom. nud.)*; *Najadites* AMALITSKY, 1892 (*non* DAWSON, 1860)]. Small, transversely subelliptical, ovate or rhomboidal, elongated and somewhat attenuated posteriorly, posterior extremity narrower (measured dorsoventrally) than anterior lobe and regularly rounded, truncated or pointed. Umbones slightly inflated, distinct but not prominent, approximate, situated at about 0.25 of length from anterior end. Anterior lobe defined by well-marked lunular hollow; indefinite carina may be present, running obliquely from umbo to posteroventral extremity; hinge edentulous; hinge line gently curved or straight; ligament opisthodetic in narrow furrow. *Perm.*, USSR-S.Afr.-E.Afr.-Burma-Norway.——FIG. D10,*3*. **P. castor* (EICHWALD), USSR; both valves, ×2 (Eichwald, 1855-61).

?Family MICRODONTIDAE Weir, new family

Small, equivalved, isomyarian, integripal-

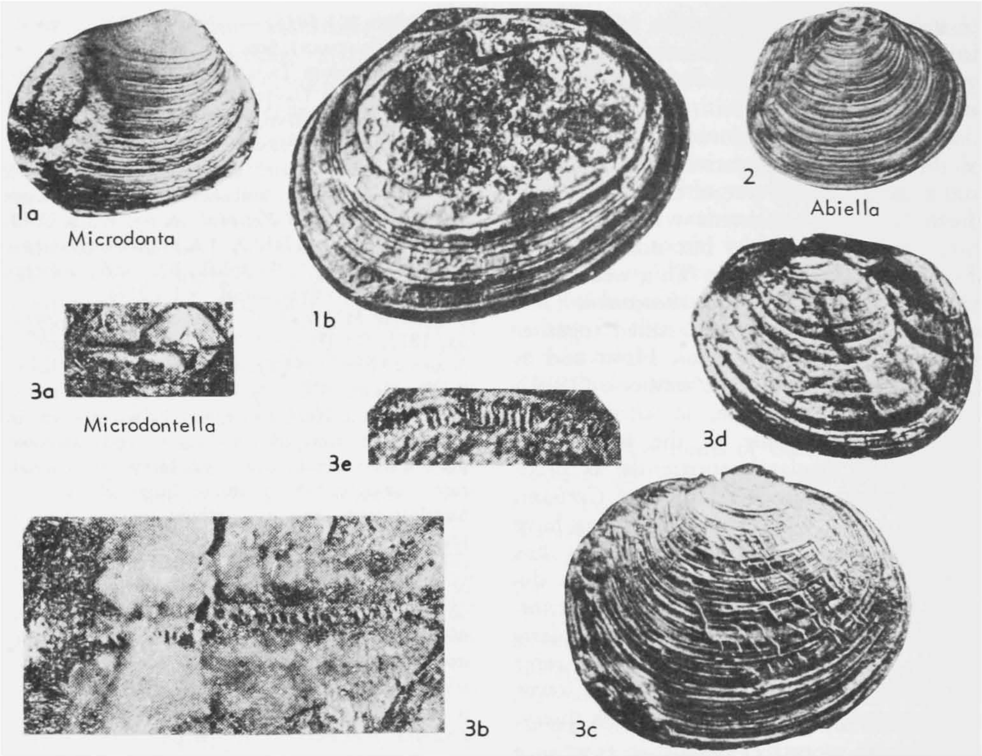

FIG. D11. Microdontidae (p. *N*408-*N*409).

liate shells with parataxodont (microdont) dentition, consisting of irregular denticles arranged in uninterrupted series along hinge, or edentulous. Suborbicular, transversely subelliptical in outline, with straight or nearly straight hinge line; or subnuculoid with slightly curved hinge line. Nonmarine. *Perm.*

In their usually crushed condition some of these shells have an external resemblance to *Posidonia* [*Posidonomya*], to which they were referred by their first describer, T. RUPERT JONES (1901), but from which they differ in all internal characters. They have been referred by Russian paleontologists to three genera, of which one, *Abiella,* is apparently edentulous, but the other two have in common a distinctive microdont dentition consisting of minute and somewhat irregular denticles arranged in taxodont fashion as an uninterrupted arc close to the dorsal margin, the teeth radiating from a point near the center of a valve.

In the commonly crushed condition of these fossils it is, according to Russian authors, not always easy to discriminate the genera, and different species have been assigned now to one genus, now to another. However few constituent taxa may ultimately be involved, these shells of distinctive dentition seem to constitute a homogeneous group which, isolated and endemic to the Kuznetsk Basin, may usefully be accorded family rank. Affinities are uncertain, but they may have originated, by degeneration of the hinge, from marine ctenodonts, which have taxodont teeth of normal size. *Abiella* is a homeomorph of the Lower Namurian *Edmondia punctatella* (JONES), recently reinvestigated by R. B. WILSON, who sustains its reference to *Edmondia. Abiella* probably belongs to the same family as the associated microdont genera, in which the hinge precludes their inclusion in the Edmondiidae.

Microdonta KHALFIN, 1950 [**Palaeomutela microdonta* KHALFIN, 1939; OD]. Nuculoid; valves convex; hinge margin gently curved, microdont.

Perm., USSR(Sib.).——Fig. D11,*1a*. **M. microdonta* (Khalfin); RV ext., ×2.5.——Fig. D11,*1b*. *M. astartellaeformis* (Fedotov); RV int. showing part of microdont hinge, ×6 (Ragozin, 1955).

Abiella Ragozin, 1933 [**Posidonomya concinna* Jones, 1901; SD Ragozin, 1955]. Like *Microdontella,* but apparently lacking microdont dentition; straight anterior and posterior parts of short hinge line meeting in wide angle at umbo. *Perm.,* USSR(Sib.).——Fig. D11,*2*. **A. concinna* (Jones); RV ext., ×3 (Ragozin, 1955).

Microdontella Lebedev, 1944 [**M. problematica*; OD[1]]. Like *Posidonia* in outline but microdont, with more tumid umbones in uncrushed shells and gently curved hinge line. *U.Perm.,* USSR (Sib.).——Fig. D11,*3a,b*. **M. problematica*; *3a,* dorsal view showing tumid umbones, ×3; *3b,* same, showing microdont dentition, ×10 *(536)*.——Fig. D11,*3c,d*. *M. subovata* (Jones); *3c, LV* (cast of ext.), ×4; *3d,* RV (impression), ×4 (Ragozin, 1955).——Fig. D11,*3e*. *M. tomiensis* (Ragozin); microdont hinge "greatly enlarged" *(536)*.

?Family PALAEOMUTELIDAE Weir in Vokes, 1967

[=Anthracosidae *(sic)* Amalitsky, 1892 *(partim)*; Carbonicolidae Cox, 1932 *(partim)*]

Small shells of variable shape, mainly triangular-subovate or trapeziform, attaining maximum length of 35 to 40 mm., but usually less than 20 mm.; equivalved, inequilateral, integripalliate, subisomyarian; scar of posterior adductor suboval, anterior pyriform or lunate. Dorsally to anterior adductor scar and close to it small circular scar of anterior retractor muscle of foot; small semilunate scar close to and behind anterior adductor scar represents another pedal muscle (?anterior protractor). Umbones prominent and triangular in short triangular or subovate shells, inconspicuous in longer rhomboidal or trapezoidal forms. Hinge line arcuate in shorter shells but in longer ones may be subangulate below umbo and nearly straight posteriorly; ligament external, opisthodetic. Hinge plate of variable width bears transverse or obliquely inclined, higher irregular teeth of varying number, which may be prominent and even massive below umbo, or defined merely by numerous irregular grooves running more or less transversely, but in some shells anastomosing to form roughly reticulate pattern over parts of hinge plate. Shell sculpture consisting of growth lines only. *?U.Carb., Perm.*

The distinctive dentition, comprising numerous highly variable and irregular teeth in both valves, is pseudotaxodont. Single teeth of series in either or both valves may acquire prominence ("cardinal teeth," cf. *Carbonicola* Amalitsky, 1892, *non* M'Coy, and *Anthracosia* Amalitsky, 1892, *non* King), but only as an aspect of variation, associated with fewer teeth, that culminates in the hinge of *Oligodon.*

Wöhrmann thought that *Palaeomutela* was derived from the marine genus *Palaeoneilo,* and, more recently, Chernyshev assigned it to the Ctenodontidae. Both these views imply that dentition was primarily taxodont, which seems unlikely. Amalitsky and Cox placed *Palaeomutela* in the Anthracosiidae (Carbonicolidae), but in view of distinctive hinge morphology and the cryptic origin of the genus it seems better to make it the type of a new family Palaeomutelidae, which I assign provisionally to the Anthracosiacea for convenience rather than from conviction of affinity, although it may well have been derived from more typical members of the superfamily.

Palaeomutela Amalitsky, 1892 [**P. verneuilli*; SD Weir, herein] [Amalitsky invalidly designated both *P. verneuili* and *P. keyserlingi* as type species of the genus. He also described and figured specimens of *Palaeomutela (s.l.)* as *Carbonicola* (*non* M'Coy, 1855) and *Anthracosia* (*non* King, 1856)] [=*?Palaeopleiodon* Amalitsky, 1891; *Rectodontia* Chernyshev, 1943]. Characters of family. Hinge plate with irregular, pseudotaxodont dentition extending over whole arc of dorsal margin, or with teeth reduced in number and restricted to shortened, subumbonal hinge plate. *Perm.,* Eu.(USSR)-S.Afr.-E.Afr.

- **P. (Palaeomutela).** Pseudotaxodont dentition extending over whole arc of dorsal margin. *Perm.,* Eu.(USSR)-S.Afr.-E.Afr.——Fig. D12,*2a-c*. **P. (P.) verneuili,* U.Perm., USSR; *2a,b,* LV int. molds, ×1; *2c,* LV ext., ×1.——Fig. D12,*2d,e*. *P. (P.) keyserlingi,* U.Perm., USSR; *2d,* LV ext., ×1; *2e,* hinge, enl. *(13)*.
- **P. (Oligodon)** Amalitsky, 1892 [**O. geinitzi*; SD Weir, herein] [Amalitsky invalidly designated both *O. geinitzi* and *O. zitteli* as type species of *Oligodon*]. Ovate-elliptical; teeth as in *P. (Palaeomutela),* but fewer, massive and carried subumbonally on short, broad hinge plate

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[1] Ragozin (1955) cited *Posidonomya subovata* Jones, 1901, as the "typical species," doubtless regarding *M. problematica* subjectively as a junior synonym.

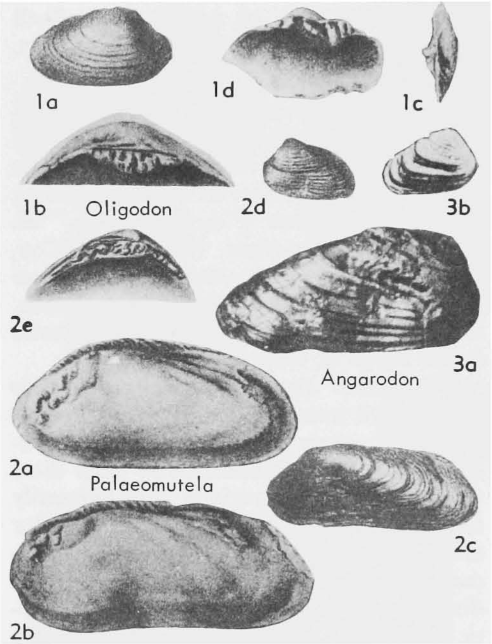


Fig. D12. Palaeomutelidae (p. *N*409-*N*410).

which may be projecting and linguiform. *U. Perm.*, Eu.(USSR).——Fig. D12,*1a,b*. **P. (O.) geinitzi*; *1a*, RV ext., ×1; *1b*, hinge, enl.——Fig. D12,*1c,d*. *P. (O.) zitteli*; *1c*, dorsal view of projecting hinge plate, ×1; *1d*, hinge, enl. *(13)*.

?**Angarodon** Ragozin, 1935 [**A. ḳumsassiensis*; OD]. Trigonal, inequilateral, valves evenly swollen. Shallow median sulcus runs obliquely from umbones to ventral margin; umbones, rather massive and broad-based, form obtuse angle of triangle; other angles always rounded. Hinge line probably short. Internal characters unknown. Nonmarine. *U.Carb.*, USSR(W.Sib.).——Fig. D12,*3*. **A. ḳumsassiensis, 3a,b*, 2 casts RV ext., ×1.5 (Ragozin, 1955).

?Family FERGANOCONCHIDAE
Martinson, 1956

[Materials for this family prepared by L. R. Cox; its assignment to Anthracosiacea doubted by Weir]

Shell small to small-medium in size, ovate or oblong, umbones at or anterior to mid-length; inflation weak to moderate; dentition, where known, consisting of very weak, scarcely perceptible, lamelliform anterior and posterior lateral teeth, about two in each valve; no cardinal teeth; muscle scars, pallial line, and position of ligament not observed; surface unornamented except for growth lines and rugae; ostracum thin. [Fresh-water.] *Jur.*

Ferganoconcha Chernyshev, 1937, p. 18 [**F. sibirica*; SD Lumkevich *et al.*, 1960, p. 99]. Shell 12 to 30 mm. long when full-grown, ovate, subequilateral, inflation very weak; umbones broadly rounded, not at all or very little protruding; hinge line slightly arcuate; hinge structure as defined for family; growth rugae relatively coarse. *L. Jur.-U. Jur.*, USSR(Sib.)-C.Asia-E.Asia.——Fig. D13,*1*. **F. sibirica*, M.Jur., E.Sib.; RV ext., ×1 (Martinson, 1956).

?Family PSEUDOCARDINIIDAE
Martinson, 1961

[Materials for this family prepared by L. R. Cox]

Shell small to medium-sized, ovate or oblong, obliquely truncated posteriorly, inequilateral, with umbones anterior to mid-length, moderately inflated; most species with posterior diagonal ridge; dentition consisting of anterior and posterior series of elongated lateral teeth, respectively more or less parallel to adjacent dorsal margin, and without any intervening transverse or "cardinal" teeth; muscle scars, pallial line, and position of ligament unobserved; surface unornamented except for growth rugae. [Freshwater.] *Jur.*

Pseudocardinia Martinson, 1959, p. 33 [**P. submagna*; OD]. Shell small to medium-sized, known species not exceeding 42 mm. in length, oblong, short to moderately elongate, with posterior end slightly truncated obliquely; umbones broadly rounded, moderately protruding; posterior diagonal ridge usually present; RV with 2 anterior and 2 posterior lateral teeth, separated by sockets each receiving single corresponding tooth of LV;

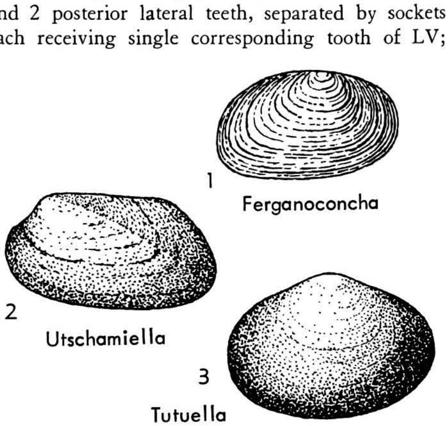


Fig. D13. Ferganoconchidae *(1)*; Pseudocardiniidae *(2,3)* (p. *N*410-*N*411).

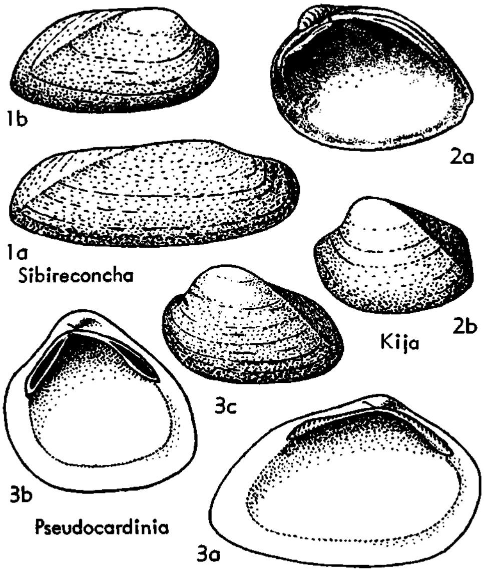


FIG. D14. Pseudocardiniidae (p. *N*410-*N*411).

RV teeth have rounded transverse ridges, to which grooves in dental sockets of LV correspond; anterior laterals not extending beyond beaks. *M.Jur.(Aalen.-Bathon.),* C.Asia.-E.Asia.——FIG. D14, *3a.* **P. submagna,* Bajoc., E.Tien-Shan; LV int., ×1 (Martinson, 1959).——FIG. D14,*3b. P. carinata* (MARTINSON), Bajoc., E.Tien-Shan; RV int., ×0.9 (Martinson, 1959).——FIG. D14,*3c. P. jeniseica* MARTINSON, Bajoc., Chulimo-Yenisei basin, C.Asia; LV ext., ×1 (Martinson, 1961).

Kija LEBEDEV, 1958, p. 73 [**K. tjazhinensis*; OD]. Shell small, known species not exceeding 17 mm. in length, ovate, short to well elongated, obliquely truncated posteriorly; umbones protruding slightly; most species with posterior diagonal ridge; RV with 2 or 3 anterior and 2 or 3 posterior, transversely grooved lateral teeth, separated by sockets which receive corresponding teeth of LV; anterior laterals extending posteriorly well beyond beaks, posterior laterals distant from latter, occupying posterodorsal angle. *M.Jur.-U.Jur.,* C.Asia.——FIG. D14,*2a.* **K. tjazhinensis,* U.Jur., Chulimo-Yenisei basin; RV int., ×3.3 (Lebedev, 1958).——FIG. D14,*2b. K. kibetenensis* LEBEDEV, U.Jur., same region; LV ext., ×3.3 (Lebedev, 1958).

Okribella KAKHADZÉ, 1942, p. 77 [**O. elliptica*; OD]. Shell to 24 mm. long, ovate, length nearly twice height, inequilateral, inflation moderate; umbones broadly rounded, not protruding, at about anterior third of length; hinge edentulous; growth lines irregular, moderately coarse; adductor scars very dorsally placed, narrow, anterior one deep, posterior shallow. *M.Jur.(Bathon.),* USSR (Georgia).

?**Sibireconcha** LEBEDEV, 1958, p. 69 [**S. lankoviensis*; OD]. Shell small, known species not exceeding 22 mm. in length, oblong, much elongated, strongly inequilateral, obliquely truncated posteriorly; umbones broad, not protruding; weak posterior diagonal ridge present; dentition unknown. *M.Jur.,* USSR(W.Sib.-E.Sib.-Transbaikal)-China.——FIG. D14,*1a.* **S. lankoviensis,* C.Asia (Chulimo-Yenisei basin); RV ext., ×1.4 (Lebedev, 1958).——FIG. D14,*1b. S. anodontoides* (CHERNYSHEV), same region; RV ext., ×1.2 (Lebedev, 1958).

?**Tutuella** RAGOZIN, 1938, p. 106 [**T. chachlovi*; SD LUMKEVICH *et al.,* 1960, p. 99]. Shell about 10 to 20 mm. long when full-grown, ovate, subequilateral, more strongly convex than *Ferganoconcha* and with more protruding umbones; hinge line straight; dentition unknown; growth lines inconspicuous. *L.Jur.-M.Jur.,* USSR(Sib.)-C.Asia-E.Asia.——FIG. D13,*3.* **T. crassa* RAGOZIN, M.Jur., Chulimo-Yenisei basin, C.Asia; LV ext., ×1 (Lebedev, 1958).

?**Utschamiella** RAGOZIN, 1938, p. 138 [**U. tungussica*; SD LUMKEVICH *et al.,* 1960, p. 99]. Shell about 10-20 mm. long when full-grown, oblong, strongly inequilateral, with unprotruding, prosogyrous umbones placed near anterior end; inflation moderate; obtuse angulation commonly runs from umbo to posteroventral angle of shell; dentition unknown. *L.Jur.-M.Jur.*(mainly *Lias.*), USSR (Sib.)-C.Asia-E.Asia.——FIG. D13,*2.* **U. tungussica,* L.Jur.(Lias.), Sib.(Tungusska basin); LV ext., ×1.5 (Ragozin, 1938).

Family UNCERTAIN

?**Nyassa** HALL & WHITFIELD, 1869 [**N. arguta*; OD] [=*Modioconcha* HALL & WHITFIELD, 1869; *nom. oblit.* (obj.)]. Equivalve, beaks anterior, transversely elongate or subelliptical. Beaks small, appressed; hinge long, arcuate, with numerous irregular cardinal teeth under the beak and 1 to 4 elongate lamellar teeth; ligament external. Surface with concentric growth lines and in some species obscure radii and a weak sulcus. *M.Dev.,* N.Am.-Eu.(Ger.).——FIG. D10,*4.* **N. arguta,* USA (N.Y.); *4a,* ext. LV, showing ornamentation, ×1; *4b,* hinge RV, showing dentition, greatly enl. (Hall, 1885). [LAROCQUE]

Superfamily UNIONACEA
Fleming, 1828

[*nom. transl.* THIELE, 1934 (*ex* Unionidae FLEMING, 1828)] [*pro* Naiadacea AUCTT. (invalid family-group lacking type genus)] [Materials for this superfamily prepared by FRITZ HAAS, except as otherwise recorded]

Shell mostly equivalve and isomyarian except where modified by attachment, mainly nacreous, with prismatic layer and heavy periostracum; beaks commonly with ornamentation; dentition, wherever present, usually consisting of somewhat rugose cardinal and posterior lamellar teeth. [Exclusively fresh-water habitat with larval stage parasitic in fish.] *?Perm., Trias.-Rec.*

The fresh-water bivalves classed together in the Unionacea are distinguished by the porcelain-white to bluish or purple-tinted pearly layer of their shells, rather variable nature of dentition or lack of hinge teeth, various structures of the soft parts, and characters of larval development. Variability of the shells due to ecologic modifications gives rise to many problems in classification.

SHELL CHARACTERS

Unionacean shells range in outline from nearly circular to elongate rodlike shapes and in thickness from flatly compressed forms to subglobular. Some shells are less than one inch (25 mm.) in length and others more than one foot (300 mm.). The shell is composed of three layers: a horny organic external covering of conchiolin, the **periostracum,** which is smooth, yellow-brown or black-brown, and commonly marked by color bands that radiate from the beak; a **prismatic calcareous layer**; and forming the hinge teeth and interior, a **nacreous layer** of calcium carbonate with lamellar structure consisting chiefly of aragonite. These layers together range from paper-thin to a thickness of about 15 mm. Names commonly applied to parts of unionacean shells, and not corresponding to those used by other clams, are indicated in Fig. D15. Although the surface of some shells is smooth or merely shows growth lines, that of others is partly or entirely wrinkled or ribbed, and there may be knobs, tubercles, or even spinose projections; commonly these surface features of the shell form a pattern that is fairly definite and constant within limits of an individual genus or species.

The **hinge** varies greatly in the Unionacea. Shells having well-defined dentition are characterized by prominent cardinals beneath and somewhat in front of the beaks accompanied by less conspicuous long, lamellar ridges (regarded by many investigators as modified cardinal teeth not homologous with the laterals of heterodonts) behind the beaks. This dentition normally consists of two cardinals and two posterior lamellar teeth on the left valve matching sockets between the teeth of the opposed valve, but there is much deviation from this. The teeth project from a widened portion of the dorsal shell margin **(hinge plate),** which persists in the toothless space between cardinals and lamellar teeth. The cardinal teeth are relatively persistent; those which are very slender commonly are supported by a strengthening deposit **(fulcrum).** The posterior lamellar teeth tend to be reduced and in many forms to disappear. Some shells have very imperfect dentition (Alasmidontinae) or none at all (Anodontinae) other than lamellar ridges close to the dorsal margin; such ridges (termed **claustra**) are not homologous with the teeth of other Unionacea. A type of hinge found in a few genera (e.g., *Pseudodon, Leguminaia*) tentatively classed among Unionacea is distinguished by several short rounded projections along the dorsal margin of the shell near the beaks, but no hinge plate or fulcrum is present. Still another type, which is observed in the generally edentulous Mutelidae, is marked by crenulations along the hinge line, superficially resembling taxodont dentition.

Inside the shell, the **beak cavities** may be capacious and deep or small and shallow. Muscle impressions (anterior and posterior adductors) lack special importance, but that of the pallial muscle is marked by an entire **pallial line** in most shells or by one with a slight sinus in some mutelid (Fig. D15,*C*).

Shells belonging to genera of the Margaritiferidae, Unionidae, and Mutelidae are bilaterally symmetrical, owing to the upright (orthothetic) position in which they are held, partly embedded in bottom sediment. Among the Etheriidae, however, a free-moving early life is followed by attachment of one of the valves lying on its side (pleurothetic) like an oyster, and because the lower valve becomes larger and deeper, symmetry of the shell vanishes. Exceptionally, as in *Arconaia* and *Arcidopsis* of the Unionidae, the youthful symmetrical stage is followed by sideward bending of the valves or twisting of the shell around its axis in such manner that it can no longer stand upright but comes to rest on its side with one valve larger than the other.

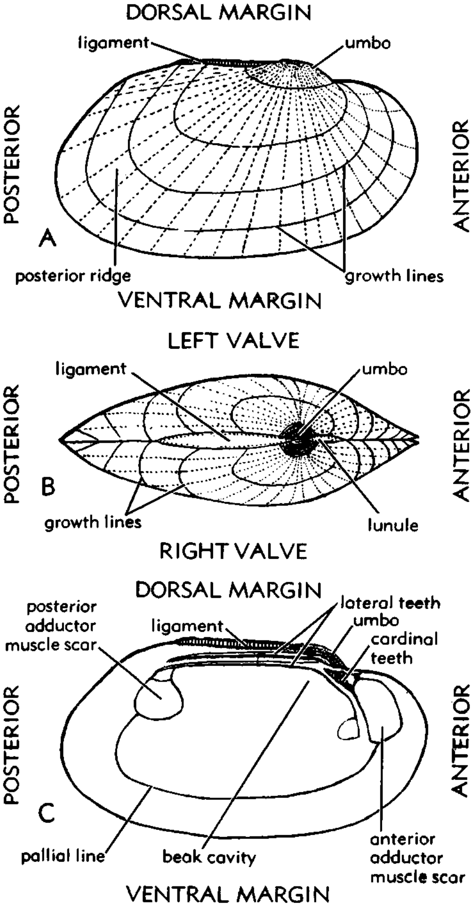


FIG. D15. Morphological features of unionacean shells (*A-C*, exterior, dorsal, interior) (after Baker).

LARVAL STAGE

All known Unionacea, after hatching from fertilized eggs, pass through a larval stage (generally termed glochidium, but in the Mutelidae called lasidium). First development of the larva occurs in a brood pouch (marsupium) of the parent, consisting of space between pairs of gills. The glochidia develop within their egg membranes and feed almost exclusively on the egg yolk. After a time, the larvae are expelled and further growth then becomes dependent on chance contact with a fish, to which the glochidium fixes itself by a sticky thread and by hooks on its valves. As a cyst-inclosed parasite in the flesh of the fish, it draws nourishment from its host until it grows into a minute complete clam, when it pierces the skin of the fish and drops to the bottom of whatever stream, pond, or lake is being traversed by its free-swimming carrier. Obviously, this curious adaptation in larval development, which distinguishes the Unionacea from other pelecypods, is extremely important as means of dispersal.

ECOLOGIC INFLUENCE ON SHELL CHARACTERS

Study of unionacean assemblages living in different environments serves to demonstrate the existence of variations in shell characters that may be correlated with the nature of physical surroundings. Size, shape, and color of the surficial conchiolin layer all may be affected. The shells of members of this group living on a hard bottom generally are shorter and rounder than those found in mud or soft sand. Individuals collected from lake-bottom sediment show a tendency to have shortened and thickened anterior areas associated with produced and somewhat compressed posterior regions. Shells of Unionacea from small streams are less swollen generally than corresponding shells in rivers. Also, the same species may be represented by smooth shells in small streams and by populations with more or less strongly sculptured shells in large streams and lakes. Prevailingly, shell surfaces marked by tubercles and ridges characterize river and lake environments.

Variations that reflect ecological factors must not be overlooked in study of the classification of Unionacea, for otherwise erroneous conclusions as to the taxonomic significance of divergent or convergent shell characters are invited. Owing to the ecological plasticity and the rapidity and wide range of dispersal of these fresh-water clams by fish-borne larvae, a single generation may produce offspring that on reaching maturity differ notably from parent forms. This is strikingly illustrated by comparing the completely sculptured shells of some unionids in large eastern African lakes with taxonomically equivalent smooth shells in streams that empty into these lakes.

CLASSIFICATION

Arrangement of the varied hosts of Unionacea, distributed throughout the world and having a range from ?Triassic or Jurassic to Recent, offers great difficulty to the taxonomist who aspires to recognize and define phylogenetically significant assemblages of varying magnitude. Characters of the soft parts, such as union of mantle lobes, completeness of siphons, adaptation of gill spaces as marsupia, nature of the foot and musculature all aid in recognizing relationships among living forms but mostly have little value for work on fossils. Chief shell characters judged to be useful for classification include general form (with attention given to effects of sessile existence), features of the beak region (denoting nature of the immature shell), ligament, dentition, muscle scars, and pallial markings. Evidence of the high degree of developmental plasticity of the unionacean shell and the certainty that many gaps in knowledge limit the understanding of modern forms, not to mention fossils, indicate the difficulty of formulating a satisfactory natural classification not yet achieved in this group. The only all-inclusive study of fossil Unionacea so far published is by Sandberger (1870-75) long before most of the genera were established. Later workers have been concerned with Recent forms alone or with assemblages of various regions. The Zittel (1913) textbook on invertebrate fossils mentions only 13 unionacean genera, mostly without characterizations: these are divided among three families (Unionidae, Mutelidae, Etheriidae). Only very recently a system of the Unionacea for both Recent and fossil forms has been published by Modell (1942); it lists practically all the genera and subgenera of the superfamily known at that time.

The following section of the *Treatise* on Unionacea recognizes 150 genera and 112 subgenera (223 units excluding nominotypical subgenera); these are grouped in four families, one of which (Unionidae) is divided into six subfamilies.

LITERATURE ON UNIONACEA

As well may be expected, a vast literature pertains to Recent and fossil unionacean bivalves. Only a selected fraction can be cited in the general reference list. Here it may be useful to make note of more important works in a few classical groups, as follows.

Comprehensive general works on Recent Unionacea. Here may be included nos. *140, 354, 496, 497, 535, 538, 845, 846, 862-869* of the reference list.

Regional monographs on Recent Unionacea. For North America, nos. *144, 147, 328;* Central America, nos. *306, 359, 588;* South America, nos. *359, 694, 702;* Europe, nos. *798, 969;* India, nos, *389, 756;* China, no. *405;* Africa, nos. *142, 362, 538, 589;* Australia, nos. *168, 434.*

Comprehensive monograph on fossil Unionacea. No. *824.*

Regional works on fossil Unionacea. For North America, no. *401;* Europe, nos. *86, 87, 411, 881, 968;* China, no. *686.*

Family MARGARITIFERIDAE Haas, 1940

[Validated family-group name, ICZN, 1957 (Opinion 495, p. 293)] [=Margaritaninae Ortmann, 1910 (suppressed by ICZN, 1957, Opinion 495, p. 290)]

Shell equivalve, mostly compressed; umbonal sculpture (if present) comprising two angular unjoined hooks; beak cavities shallow, posterior lamellar teeth tending to be reduced. Gills without water tubes, partly free posteriorly, with incomplete diaphragm, marsupium occupying all four gills. *U.Cret.-Rec.*

Margaritifera Schumacher, 1816, p. 7 [valid emendation of *Margartifera* Schumacher, 1816 (ICZN, 1957, Opinion 495, p. 289)] [**Mya margaritifera* Linné, 1758, p. 671; M] [=*Margaritana* Schumacher, 1817, p. 123 (obj.); *Margatifera* Schumacher, 1823, p. 6 *(nom. van. pro Margartifera)*; *Damalis* Leach, 1847, p. 272]. Characters of family. *U.Cret.-Rec.,* Eu.-N.Am.-Asia.

M. (Margaritifera). Shell heavy, thick, compressed, without posterior lamellar teeth. *U.Cret.-Rec.,* Eu.-N.Am.-E.Asia.——Fig. D16,*3*. **M. (M.) margaritifera* (Linné), Rec., Eu.; *3a,b,* LV ext., RV int., ×0.5 (after *497*).

M. (Cumberlandia) Ortmann, 1912 [**Unio monodonta* Say, 1829; OD]. Elongate-arcuate,

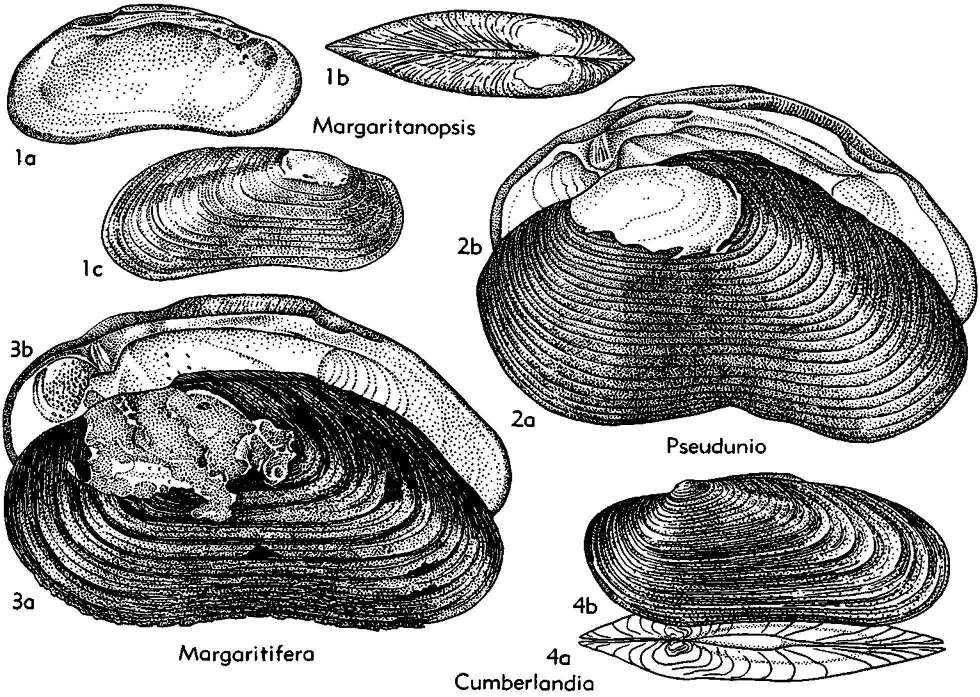


FIG. D16. Margaritiferidae (p. *N*414-*N*415).

thin; lamellar teeth weak, poorly defined. Continuous laminar septa between gills, running obliquely forward. *Rec.,* N.Am.——FIG. D16,*4*. **M. (C.) monodonta* (SAY); *4a,b,* both valves dorsal, LV ext., ×0.5 (after *497*).

M. (Margaritanopsis) HAAS, 1910 [**Unio laosensis* LEA, 1863; OD]. Elongate, compressed, kidney-shaped; cardinals and posterior lamellar teeth with long interdental area. *Rec.,* SE.Asia.——FIG. D16,*1*. **M. (M.) laosensis* (LEA); *1a-c,* LV int., both valves dorsal, RV ext., ×0.5 (after *534*).

M. (Pseudunio) HAAS, 1910 [*pro Potodoma* HERRMANNSEN, 1947 (*non* MEIGEN, 1800)] [**Unio sinuata* LAMARCK, 1819 (=**Unio auricularius* SPENGLER, 1793); OD]. Shell ear-shaped, heavy, thick; with cardinals and posterior lamellar teeth. *Eoc.-Rec.,* Eu.-N.Am.——FIG. D16,*2*. **M. (P.) auricularia* (SPENGLER), Rec., Eu.; *2a,b,* LV ext., RV int., ×0.5 (after *497*).

Family UNIONIDAE Fleming, 1828

Equivalve (nacreous, with thick periostracum), beaks generally sculptured and commonly with remnant of larval shell; beak cavities deep, hinge mostly with two cardinals and two posterior lamellar teeth in LV and single cardinal and lamellar tooth in RV. Gills with water tubes, marsupium occupying all four gills or outer pairs only, diaphragm complete. *Trias.-Rec.*

Subfamily UNIONINAE Fleming, 1828

[*nom. transl.* THIELE, 1934 (*ex* Unionidae FLEMING, 1828)]

Umbonal sculpture mostly concentric. Marsupium occupying all four gills or outer pairs only. *Trias.-Rec.*

Unio PHILIPSSON, 1788 [**Mya pictorum* LINNÉ, 1758; SD TURTON, 1831 (ICZN, 1957, Opinion 495, p. 289)] [=*Limnaea* POLI, 1791 (obj.); *Limnaeoderma* POLI, 1795; *Uniigenus* RENIER, 1807; *Lymnium* OKEN, 1815 (rejected, ICZN, Opinion 417); *Unionea* RAFINESQUE, 1815; *Mysca* TURTON, 1822; *?Margarita* LEA, 1836 (*non* LEACH, 1819); *Myisca* L. AGASSIZ, 1846; *Chondrostea* GISTEL, 1848; *?Margaron* LEA, 1852; *Nodularia* CONRAD, 1853; *Nodularidia* COCKERELL, 1901]. Posterior slope generally distinct, coarse ridges on umbo looped or broken, remainder of shell smooth, periostracum with or without rays. Marsupium occupying whole length of outer gill pairs. [Fossil species of *Unio* described from North America are generally forms with complete hinge

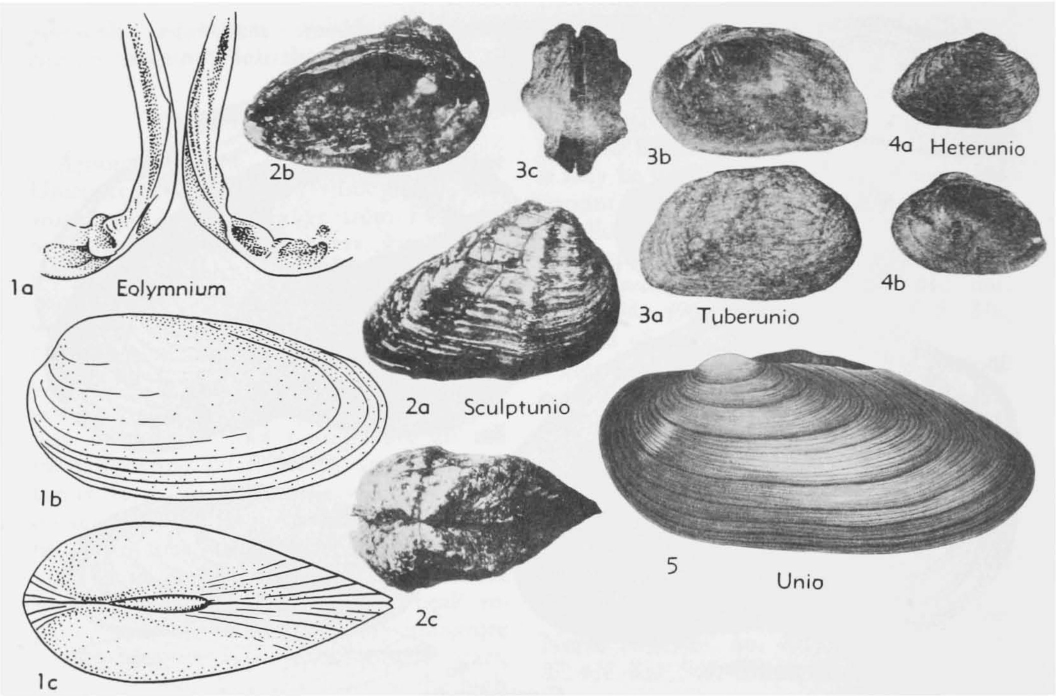


Fig. D17. Unionidae (Unioninae) (p. *N*415-*N*416).

and are distinct from the palearctic *Unio* defined here.] *Trias.-Rec.,* Eu.-Asia-Afr.-USSR.

U. (Unio). Gills subequal, foot fairly well developed. *Trias.-Rec.,* Eu.-Asia-Afr.——Fig. D17, *5.* **U. (U.) pictorum* (Linné), Rec., Eu.; LV ext., ×0.7 (after *497*).

U. (Eolymnium) Prashad, 1919 [**Unio terminalis* Bourguignat, 1852; OD]. Inner gills broader than outer pair, branchial aperture high, foot poorly developed. *Rec.,* Eu.(E.Medit.).——Fig. D17,*1.* **U. (E.) terminalis* Bourguignat; *1a-c,* hinges, LV ext., both valves dorsal, ×1 (after Bourguignat).

The three following subgenera are known to me only through Lindholm's short description; it seems appropriate, hence, to retain them at this place, where their author had them.

U. (Heterunio) Lindholm, 1932 [**U. exquisitus*; OD]. Shell with apical sculpture consisting of concentrically arranged, short or interrupted ridges which may cover half of disc; inflated and mostly so in the middle of well-defined posterior ridge. *M.Plio.,* USSR(SW.Sib.).——Fig. D17,*4.* **U. (H.) exquisitus*; *4a,b,* RV ext., int., ×0.7 (after *543*).

U. (Sculptunio) Lindholm, 1932 [**U. bituberculosus* Martens, 1874; OD]. Shell characterized by 2 rows of knobs which radiate from beaks. *M.Plio.,* USSR(SW.Sib.).——Fig. D17,*2. U. (S.) bituberculosus trigonoides* Lindholm; *2a-c,* RV ext., int., both valves dorsal, ×0.7 (after *543*).

U. (Tuberunio) Lindholm, 1932 [**U. uniserialis*; OD]. Upper half of disc rather strongly granulate, wrinkled; row of 4 to 5 larger knobs on posterior slope. *M.Plio.,* USSR(SW.Sib.).——Fig. D17,*3.* **U. (T.) uniserialis*; *3a-c,* RV ext., int., both valves ant., ×0.7 (after *543*).

Acuticosta Simpson, 1900 [**Unio sinensis* Lea, 1868; OD]. Solid, inflated, pointed behind, produced at center of base, in one species with distinct, nodulated posterior ridge; beaks full, their radial sculpture strong, zigzag; cardinals rather low, ragged, lamellar teeth obliquely ridged and granular. *Rec.,* China.——Fig. D18,*3.* **A. sinensis* (Lea); *3a-d,* LV ext., RV int., LV int., both valves dorsal, ×0.8 (Haas).

Afroparreysia Haas, 1936 [**Parreysia lobensis* Frierson, 1913; OD]. Ovoid, lenticular; beaks very far forward, with deep internal cavities; sculpture narrowly zigzag, extending over entire disc, commonly reduced to wavy folds; hinge with long interdental interval, cardinals nearly normal to lamellar teeth. *Rec.,* W.Afr.(Cameroons).——Fig. D18,*1.* **A. lobensis* (Frierson); *1a,b,* LV ext., RV int., ×1 (Frierson).

Arcidopsis Simpson, 1900 [**Unio footei* Theobald, 1876; OD]. Elongate, with dorsal and ventral

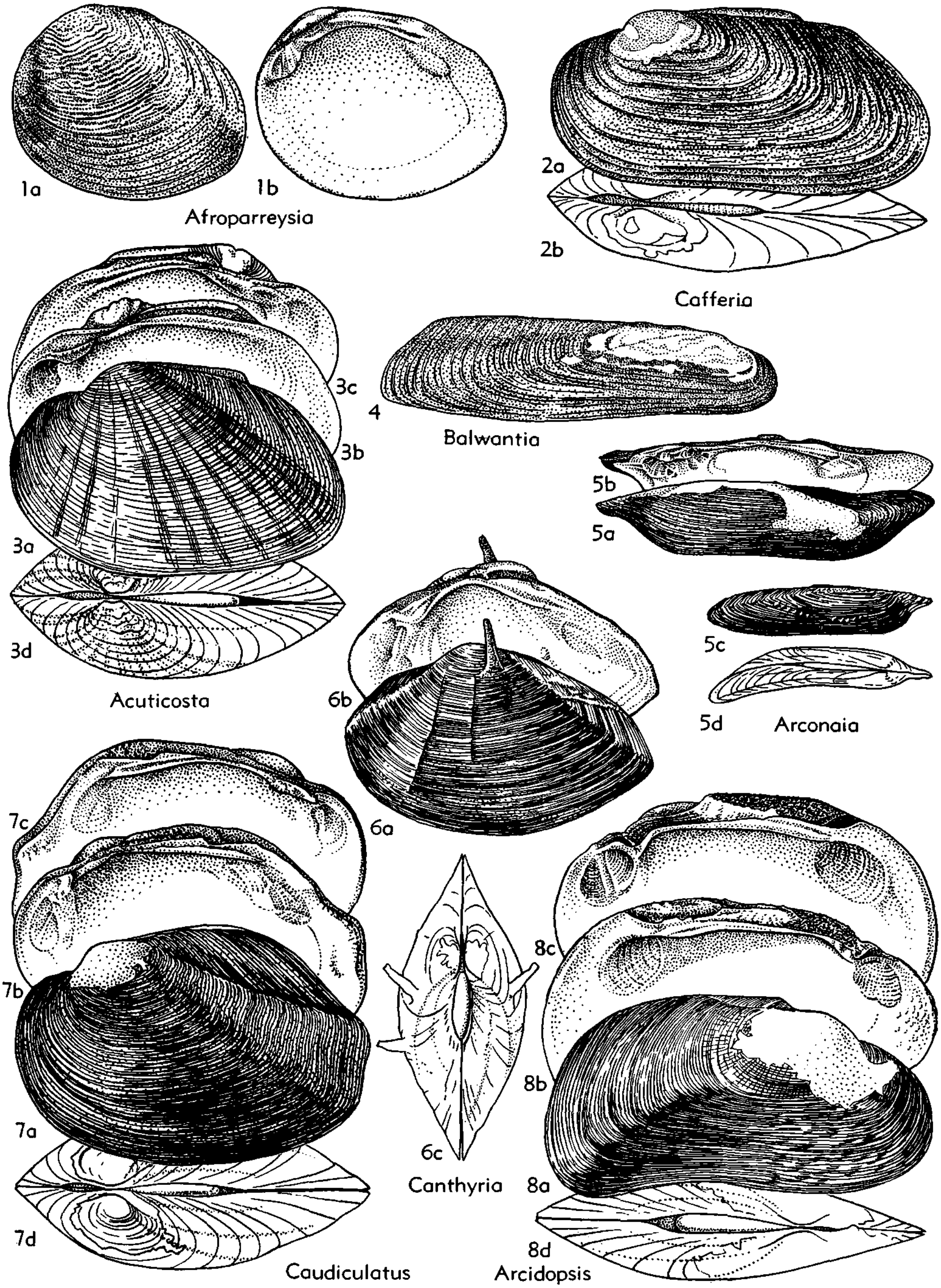


FIG. D18. Unionidae (Unioninae) (p. *N*416, *N*418, *N*420).

margins nearly straight and parallel, short, low, rather compressed and rounded in front, high, long, obliquely and roundedly truncate and inflated behind; posterior slope ill-defined, full; periostracum black, disc with fine concentric and radial ridges; cardinals strong, short, supported by strong, riblike fulcrum, lamellar teeth very remote, short. *Rec.,* India.——Fig. D18,*8*. **A. footei* (Theobald); *8a-d,* RV ext., LV int., RV int., both valves dorsal, ×0.75 (Haas).

Arconaia Conrad, 1865 [**Unio lanceolata* Lea, 1856; OD]. Elongated into pointed projections at both ends, thick-shelled, twisted on axis or almost straight but generally having posterior end curved to right or left; posterior slope distinct, beaks low, with shallow cavities; hinge with strong, triangular and serrated cardinals and rather thick, long, almost straight lamellar teeth. *Tert.-Rec.,* E.Asia.——Fig. D18,*5*. **A. lanceolata* (Lea), Rec.; *5a-d,* LV ext., RV int., RV ext., both valves dorsal, ×0.3 (Haas).

Balwantia Prashad, 1919 [**Anodonta soleniformis* Benson, 1836; OD]. Elongate, soleniform, thin, narrower in front, gaping at anterior base and behind; posterior slope low, not well defined; beaks low; hinge line narrow, toothless but for vestiges of marginal lamellae. Foot large, muscular, adapted for burrowing. *Rec.,* E.India.——Fig. D18,*4*. **B. soleniformis* (Benson); RV ext., ×0.3 *(384)*.

Caelatura Conrad, 1853 [**Unio aegyptiaca* Cailliaud, 1826; OD] [=*Pharaonia* Bourguignat, 1880; *?Reneus* Rochebrune, 1888; *?Renatus* Rochebrune, 1904; *Horusia, Jaronia* Pallary, 1924]. Elliptical, generally thin, short and rounded in front, long and high behind, pointed or rounded, mostly somewhat produced at posteroventral margin; beaks not prominent, with sculpture consisting of zigzag generally pustulate ridges, commonly extending to disc which may bear rays; cardinals long, thin, bladelike, lamellar teeth normal. *U.Plio.-Rec.,* Afr.

C. (Caelatura). Short, mostly elliptical or ovate, inflated; anterodorsal margin not steeply descending; beaks inflated, full, with sculpture of W-shaped bluntly pustulate folds. *U.Plio.-Rec.,* Afr. ——Fig. D19,*7*. **C. (C.) aegyptiaca* (Cailliaud), Rec.; *7a-c,* LV ext., both valves dorsal, hinges, ×0.8 *(497)*.

C. (Brazzaea) Bourguignat, 1885 [**B. anceyi*; OD] [=*Bruzzaea* Paetel, 1890; *Brazzea* Germain, 1909]. Thin, translucent, wine-colored, elliptical, greatly inflated, with small posterodorsal wing and high double posterior ridge; beaks apparently smooth, compressed, but umbones full; anterodorsal margin of RV projecting slightly above LV; hinge edentulous, ending abruptly in front at deep lunule. *Rec.,* Afr.——Fig. D19,*8*. **C. (B.) anceyi* (Bourguignat); LV ext., ×0.7 *(74)*.

C. (Grandidieria) Bourguignat, 1885 [**Unio burtoni* Woodward, 1859; OD] [=*Ruellania* Bourguignat, 1885]. Small, oval, rounded or rhomboidal, heavy, much inflated; beaks high with zigzag wrinkles which become finely nodulose and sulcate on disc, especially in front and behind; hinge line curved; cardinals short, deeply cleft, lamellar teeth short, somewhat curved. *Pleist.-Rec.,* E.C.Afr.——Fig. D19,*1*. **C. (G.) burtoni* (Woodward), Rec.; *1a-c,* RV ext., int., LV int., ×1 (Pilsbry & Bequaert).

C. (Kalliphenga) Haas, 1936 [**Unio ruellani* Bourguignat, 1883; OD]. Small, obliquely rhomboidal; beaks prominent; dorsal margin straight; all teeth of hinge heavy; periostracum black to green, as if coated with lacquer, densely rayed; nacre rosy, with metallic iridescence. *Rec.,* E.Afr.(L.Victoria)-C.Afr.——Fig. D19,*3*. **C. (K.) ruellani* (Bourguignat); *3a-c,* RV ext., int., LV int., ×1 (Haas).

C. (Kistinaia) Haas, 1936 [**C. shoutedeni*; OD]. Quadrangular, inflated and truncate, short in front, long, submedianly produced and truncate behind; beaks prominent, with W-shaped ridges; posterior ridge distinct; cardinals strong, lamellar teeth thin. *Rec.,* C.Afr.——Fig. D19,*2*. **C. (K.) shoutedeni*; *2a-d,* LV ext., RV int., LV int., both valves dorsal, ×1 (Haas).

C. (Laevirostris) Simpson, 1900 [**Unio stagnorum* Dautzenberg, 1890 (=**Pharaonia bourguignati* Rochebrune, 1886); OD]. Rounded lens-shaped or irregularly quadrangular, thin, compressed; anterodorsal margin descending steeply, posterior margin long and high; beaks not prominent, with sculpture reduced to few isolated tubercles; cardinals long, bladelike, lamellar teeth slightly curved, at angle with cardinals; areola and posterior slope commonly corrugated. *Rec.,* C.Afr.——Fig. D19, *4*. **C. (L.) bourguignati* (Rochebrune); *4a-c,* RV ext., int., LV int., ×1 (Pilsbry & Bequaert).

C. (Mweruella) Haas, 1936 [**Unio mweruensis* E. A. Smith, 1908; OD]. Anteriorly short, rounded truncate, posteriorly long and pointed, much compressed, with greatest depth near dorsal margin; disc sculptured with folds zigzag near beaks becoming gradually wavy toward center; posterior slope covered with fan-shaped folds radiating from posterior ridge; cardinals long, bladelike when young, thicker and somewhat ragged when old. *Rec.,* C.Afr.——Fig. D19,*6*. **C. (M.) mweruensis* (Smith); *6a-d,* LV ext., int., RV int., both valves dorsal, ×1 (Haas).

C. (Rhytidonaia) Haas, 1936 [**C. graueri* Haas, 1927; OD]. Elongate, irregularly quadrangular, thick, ventral margin almost straight, posterodorsal margin high; beaks not prominent; entire disc sculptured wtih ridges which are W-shaped near beaks and wavy over mature shell; cardinals thickened throughout ontogeny. *Rec.,* C.Afr.——Fig. D19,*5*. **C. (R.) graueri* Haas; *5a-d,* LV

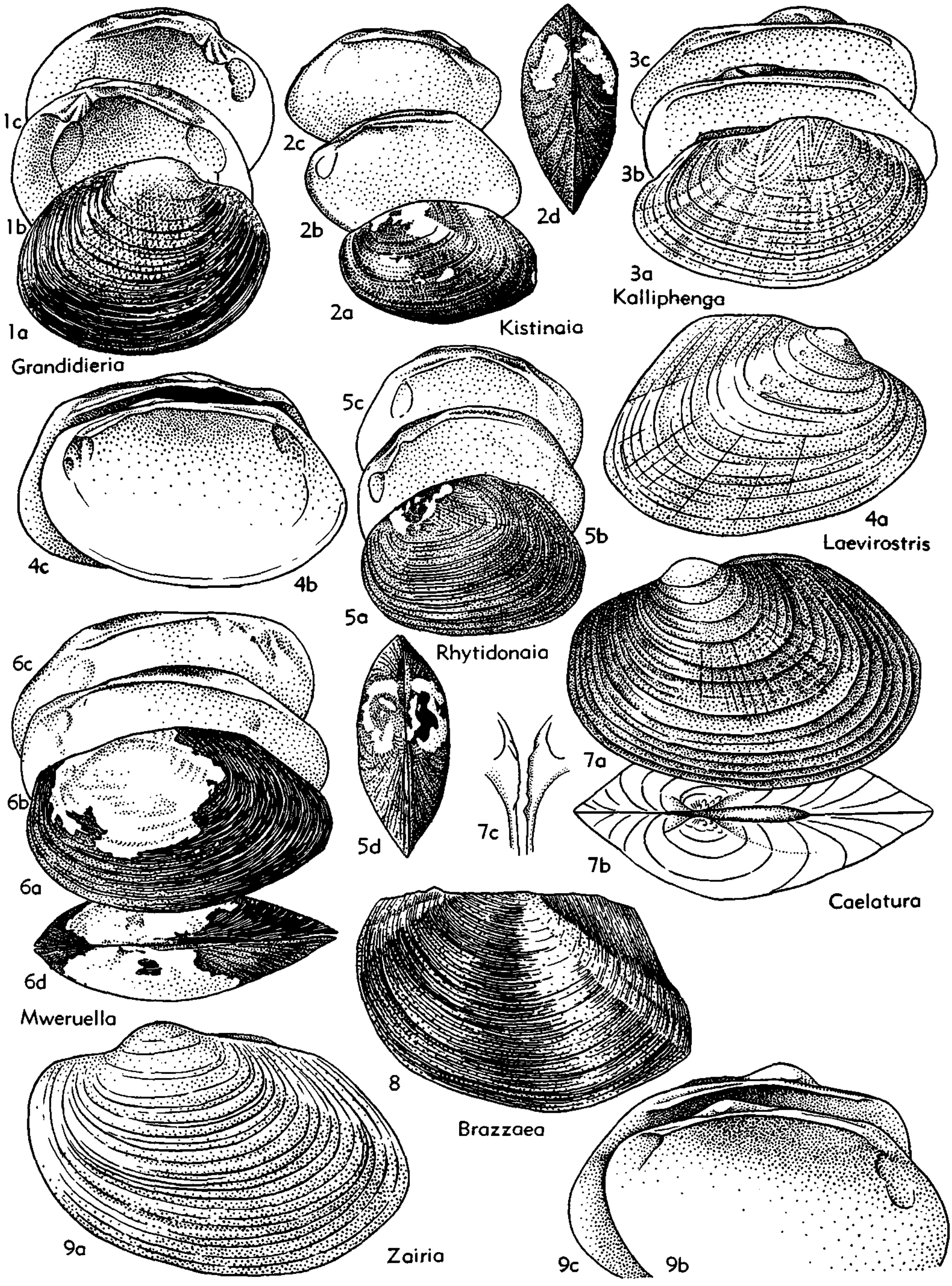


Fig. D19. Unionidae (Unioninae) (p. *N*418, *N*420).

ext., RV int., LV int., both valves dorsal, ×1 (Haas).

C. (Zairia) Rochebrune, 1886 [*Zairia elegans;* SD Pilsbry & Bequaert, 1927] [=*Zaira* Simpson, 1900]. Elongate-ovate or elliptical, thin, with dorsal margin rather straight; beaks prominent, sculptured only on extreme tips with weak, W-shaped tuberculate; cardinals long, bladelike, lamellar teeth almost straight, meeting cardinals under beaks at very low angle. *Rec.,* W.Afr.——Fig. D19,*9.* **C. (Z.) elegans* (Rochebrune); *9a,b,* LV ext., RV int., LV int., ×1 (Pilsbry & Bequaert).

Cafferia Simpson, 1900 [**Unio caffer* Krauss, 1848; OD]. Elongated, elliptical, or rhomboid, rather solid; beaks full, ornamented with corrugated zigzag ridges, corrugations commonly extending over entire disc; periostracum yellowish to black, rayless; hinge typical, its elements rather strong. *Pleist.-Rec.,* S.Afr.——Fig. D18,*2.* **C. caffra* (Krauss), Rec.; *2a,b,* LV ext., both valves dorsal, ×0.75 *(497).*

Canthyria Swainson, 1840 [**Unio spinosus* Lea, 1836; OD]. Spinose, inflated, suboval, with high, rather sharp posterior ridge; disc smooth; hinge typical of family, sharply curved at center. *Rec.,* N.Am.——Fig. D18,*6.* **C. spinosa* (Lea); *6a-c,* LV ext., RV int., both valves dorsal, ×0.5 *(497).*

Caudiculatus Simpson, 1900 [**Unio caudiculatus* Martens, 1866; OD]. Oval, inflated, slightly winged posteriorly, with deep furrow above posterior margin; cardinals short, low, widely separated from lamellar teeth. *Rec.,* W.Pac.(Borneo).——Fig. D18,*7.* **C. caudiculatus* (Martens); *7a-d,* LV ext., RV int., LV int., both valves dorsal, ×0.8 (Haas).

Chamberlainia Simpson, 1900 [**Unio hainesianus* Lea, 1856; OD] [=*Simpsonia* Rochebrune, 1904]. Large, very massive in front, less so behind, round obovate, with low posterior slope winged in young shells; beaks low but full; periostracum yellowish green in young, blackish brown in old shells, rayed; ligament hidden by symphynoty of dorsal wing; cardinals blunt, low, breaking into denticles in old shell, lamellar teeth very short, thick, remote; interdental interval very long, partly covered by periostracum; umbonal cavities moderately deep, nacre purplish, highly iridescent. *Rec.,* SE.Asia.——Fig. D20,*5.* **C. hainesiana* (Lea); *5a-d,* LV ext., RV int., LV int., both valves dorsal, ×0.3 (Haas).

Contradens Haas, 1913 [**Unio contradens* Lea, 1838; OD] [=*Schizocleithrum* Haas, 1913]. Oval, elongate, short and rounded in front, longer behind; beaks not prominent, mostly inflated, sculptured with wavy wrinkles which may extend over disc; hinge normal, cardinals compressed or bladelike; auxiliary tooth above cardinal of RV; posterior cardinal of LV small to obsolescent; lamellar teeth long, somewhat curved; interdental interval narrow, smooth. *Pleist.-Rec.,* SE.Asia-Indon.

C. (Contradens). Sculpture restricted to tips of beaks. *Pleist.-Rec.,* SE.Asia.——Fig. D20,*4.* **C. (C.) contradens* (Lea), Rec.; *4a-c,* LV ext., RV int., both valves dorsal, ×0.7 (Haas).

C. (Sprickia) Modell, 1942 [**Unio verbeeki* Martens, 1897; OD]. Sculpture extending over most or all of disc. *Rec.,* SE.Asia-Indon.——Fig. D20,*6.* **C. (S.) verbeeki* (Martens); *6a-c,* LV ext., RV int., LV int., ×1 (Haas).

Ctenodesma Simpson, 1900 [**Unio borneensis* Issel, 1874; OD] [=*Cristadens, Christadens* Simpson, 1914]. Subtrapezoid to subelliptical, rather thin, compressed; posterior slope poorly defined; beaks low, ornamented by densely zigzag ridges which become finely corrugated or nodulose over disc; cardinals of varying shape, showing tendency to break up into denticles. *Rec.,* W.Pac.(Borneo).——Fig. D20,*1.* **C. borneense* (Issel); *1a-d,* LV ext., RV int., LV int., both valves dorsal, ×0.8 (Haas).

Cucumerunio Iredale, 1934 [**Unio novae-hollandia* Gray, 1834; OD] [=*Cucumaria* Conrad, 1853 (*non* de Blainville, 1830; *nec* Lesson, 1831); *Cucumeria* Simpson, 1900 *(nom. null)*; *?Aparcthyria, ?Quaesithyria* Iredale, 1943]. Elongate, trapezoid, widest behind, thickest in front; disc covered posteriorly with irregular nodules which radiate somewhat from posterior ridge; cardinals not well developed, small, with tendency to break into denticles; lamellar teeth feeble. *Rec.,* Australia.——Fig. D20,*3.* **C. novaehollandiae* (Gray); *3a,b,* RV ext., both valves dorsal, ×0.3 *(497).*

Cuneopsis Simpson, 1900 [**Unio celtiformis* Heude, 1874; OD]. Heavy, elongate, wide in front, tapering to a point behind, commonly twisted on axis; beaks high, anterior, ornamented by radiating lines of nodules; cardinals immediately under beaks, short, lamellar teeth granularly striated, very long. *U.Mio.-Rec.,* E.Asia.——Fig. D20,*2.* **C. celtiformis* (Heude), Rec.; *2a-d,* RV ext., LV int., RV int., both valves dorsal, ×0.6 (Haas).

Diaurora Cockerell, 1903 [*pro Aurora* Simpson, 1900 (*non* Ragonot, 1887; *nec* Sollas, 1888)] [**Unio auroreus* Heude, 1883; OD]. Small, ovate, subinflated, rather solid, with high, small beaks and strong, corrugated sculpture which extends over half of disc; periostracum fulvous, with green rays; cardinals conical, truncate, lamellar teeth normal; nacre orange. *Rec.,* China.——Fig. D21,*8.* **D. aurorea* (Heude); *8a,b,* LV ext., int., ×1 (Zilch).

Elliptio Rafinesque, 1819 [**Unio nigra*; OD] [=*Eurynia* Rafinesque, 1820; *Cunicula* Swainson, 1840; *Curricula* Gray, 1847; *Eurinia* Conrad, 1853; *Rurynea* Paetel, 1875; *Eurynaia* Frierson, 1927]. More or less elongate; beaks placed well back of anterior end, not prominent,

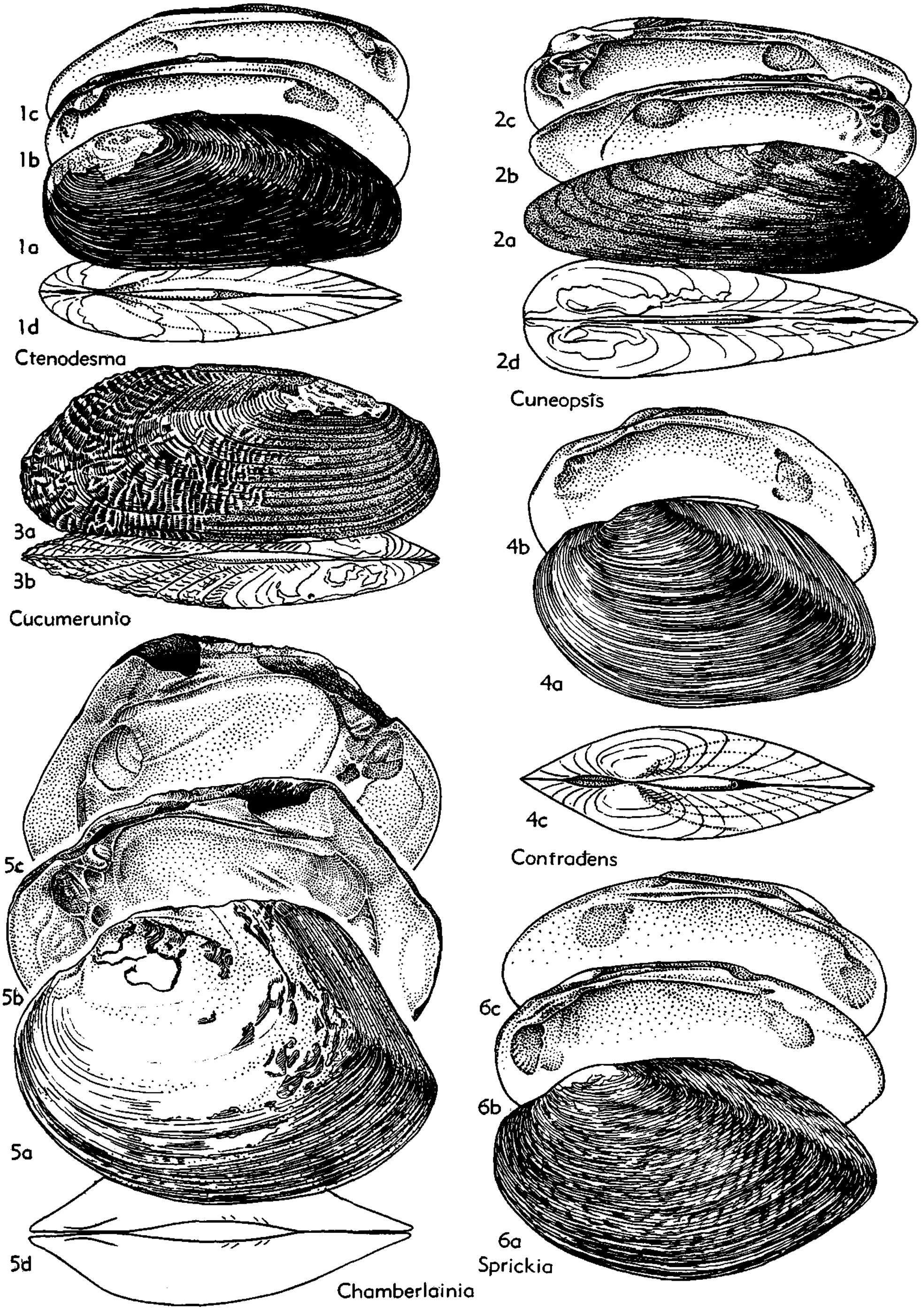


FIG. D20. Unionidae (Unioninae) (p. *N*420).

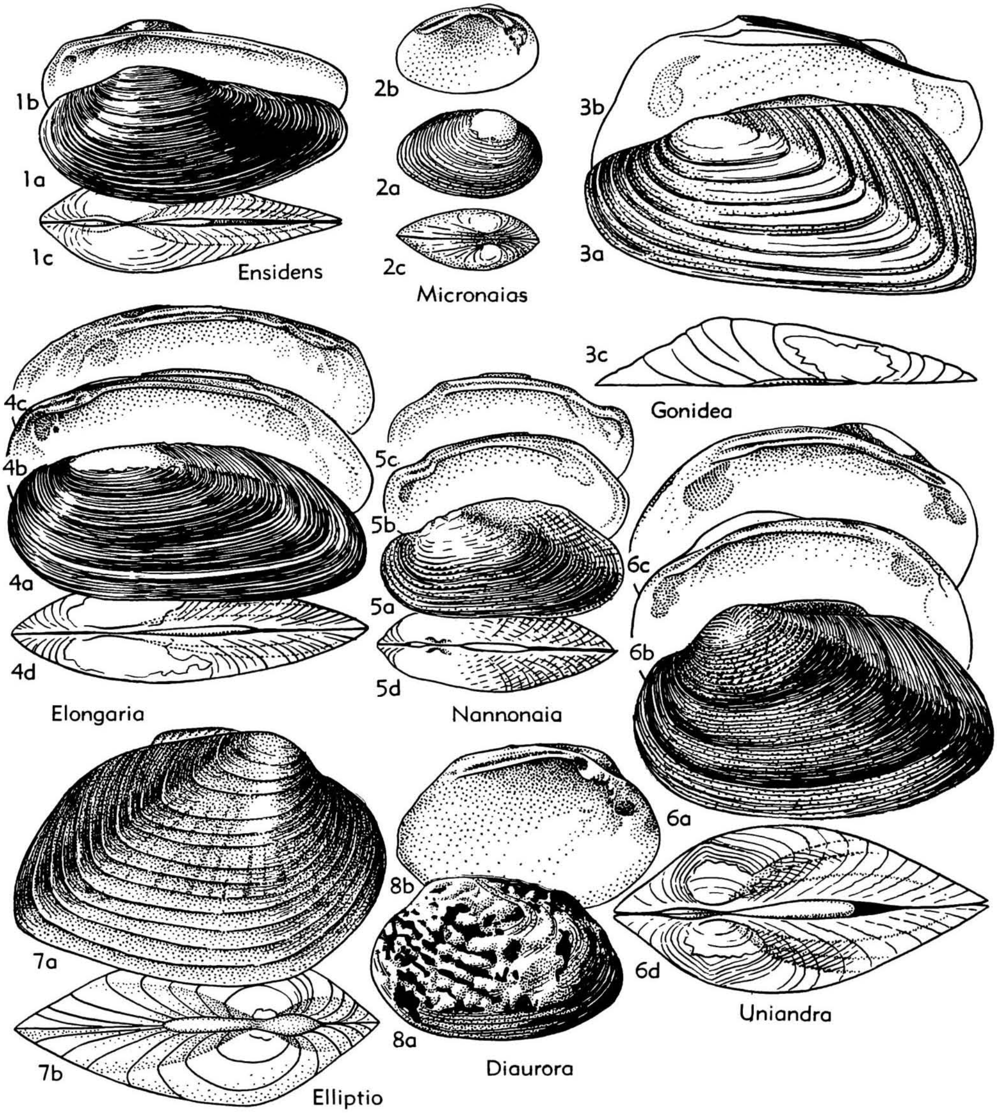


Fig. D21. Unionidae (Unioninae) (p. *N*420, *N*422-*N*423).

covered by few rather strong ridges parallel to growth lines or forming double loops; hinge typical of family. [Cretaceous species referred to *Elliptio* may belong to *Protelliptio* Russell.] *?U.Cret., Rec.,* N.Am.-?Eu.

E. (Elliptio). Rhomboid or oval, usually more or less biangulate behind; disc without sculpture. *?U.Cret., Rec.,* N.Am.——Fig. D21,7. *E. (E.) crassidens* (Lamarck), Rec.; *7a,b,* RV ext., both valves dorsal, ×0.5 *(497).*

E. (Micronaias) Simpson, 1900 [**Unio aratus* Lea, 1843; OD]. Small, oval; whole disc strongly and closely ridged concentrically; beaks rather prominent; hinge typical of family, all teeth curved. *Rec.,* C.Am.——Fig. D21,2. **E. (M.) aratus* (Lea); *2a-c,* RV ext., LV int., both valves dorsal, ×1 *(535).*

Elongaria Haas, 1913 [**Unio orientalis* Lea, 1840; OD]. Elongate, narrow, rather solid; beaks not prominent; posterior slope low, indistinctly defined; periostracum smooth or with low wrinkles which radiate from umbonal region; preumbonal region somewhat impressed as seen dorsally; hinge normal, cardinals long, lamelliform; without fulcrum; interdental interval long and narrow, lamellar teeth long, almost straight, beak cavities shallow. *Pleist.-Rec.,* W.Pac.(Java-Borneo).

E. (Elongaria). Long, narrow, thick, somewhat inflated; beaks low, not prominent; disc smooth; cardinals broadly lamelliform. *Pleist.-Rec.,* Java.——FIG. D21,*4*. **E. (E.) orientalis* (LEA), Rec.; *4a-d,* LV ext., RV int., LV int., both valves dorsal, ×0.7 (Haas).

E. (Nannonaia) HAAS, 1913 [**Unio trompi* DROUËT & CHAPER, 1892; OD]. Small, long, narrow, thin, rather inflated; beaks lower than posterior dorsal margin, projecting above anterior one; disc with fine wrinkles on rear end; cardinals thin, bladelike. *Rec.,* W.Pac.(Borneo).——FIG. D21,*5*. **E. (N.) trompi* (DROUËT & CHAPER); *5a-c,* LV ext., RV int., LV int., both valves dorsal, ×1 (Haas).

Ensidens FRIERSON, 1911 [**Unio ingallsianus* LEA, 1852; OD]. Ovate or elongate, pointed behind, thin obese; beaks prominent, smooth or sculptured with faint, concentric zigzag ridges; posterior slope low, ill-defined; hinge with thin, bladelike cardinals and long, almost straight, thin lamellar teeth; without buttress-supporting cardinals. *Rec.,* SE. Asia.

E. (Ensidens). Elongate, pointed behind, beaks without sculpture. *Rec.,* SE.Asia.——FIG. D21,*1*. **E. (E.) ingallsianus* (LEA); *1a-c,* LV ext., RV int., both valves dorsal, ×0.7 (Haas).

E. (Uniandra) HAAS, 1912 [**Unio inaequalis* ROCHEBRUNE, 1882; OD]. Ovate, hardly pointed behind; beaks prominent, sculptured by concentric zigzag ridges; posterior slope compressed. *Rec.,* SE.Asia.——FIG. D21,*6*. **E. (U.) inaequalis* (ROCHEBRUNE); *6a-d,* LV ext., RV int., LV int., both valves dorsal, ×1 (Haas).

Gonidea CONRAD, 1857 [**Anodonta randalli* TRASK, 1855 (**Anodonta angulata* LEA, 1838); OD] [=*Limnobasilissa* HANNIBAL, 1912]. Elongate subtriangular, much narrowed in front, wide behind, inflated, usually with high posterior ridge; beaks sharp but not high, sculptured with few, strong, concentric ridges; hinge with or without rudimentary cardinal and lamellar tooth in each valve. *Mio.-Rec.,* N.Am.——FIG. D21,*3*. **G. angulata* (LEA), Rec.; *3a-c,* LV ext., int., dorsal, ×0.8 *(140)*.

Haasodonta MCMICHAEL, 1956 [**Hyridella fannyae* JOHNSON, 1948; OD]. Subquadrate, much inflated, shell thin, compressed in front, swollen behind, particularly along greatly expanded posterior ridge; posterior dorsal margin winged; periostracum brown; hinge line straight, long; cardinals and laterals elongate, lamellar. *Rec.,* N. Guinea.——FIG. D22,*1*. **H. fannyae* (JOHNSON); *1a-c,* RV int., LV ext., both valves dorsal, ×0.7 (McMichael).

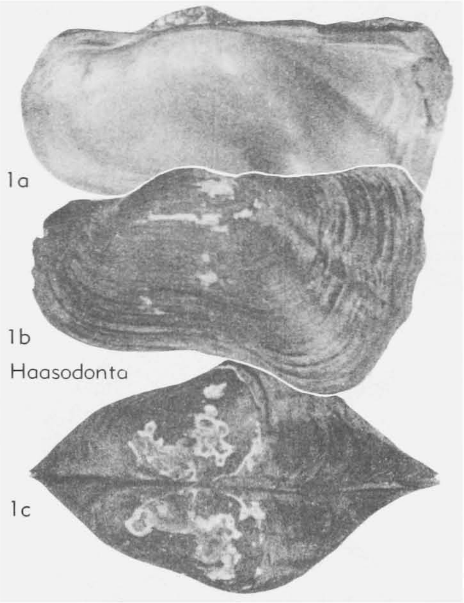


FIG. D22. Unionidae (Unioninae) (p. N423).

Heudeana FRIERSON, 1922 [**Unio murinus* HEUDE, 1883; OD]. Elliptical, somewhat moderately solid; beaks little prominent, sculptured with widely undulating ridges; cardinals thin, bladelike, lamellar teeth short, straight, almost touching cardinals; fulcrum very narrow. *Rec.,* China.——FIG. D23,*3*. **H. murina* (HEUDE); *3a,b,* LV ext., RV int., ×0.5 (Haas).

Hyriopsis CONRAD, 1853 [**Unio delphinus* GRUNER, 1841 (*non* SPENGLER, 1793) (=**Hyriopsis bialata* SIMPSON, 1900); OD] [=*Limnoscapha* LINDHOLM, 1932]. Large, compressed, heavy, rhomboid-elliptical, low in front, high behind, commonly produced posteroventrally, winged dorsally; beaks low, compressed, sculpture consisting of numerous wavy ridges nearly parallel with growth lines, some extending over part of disc; periostracum greenish or brownish, with few rays; cardinals oblique to interdental interval, separating into denticles in old shell, with auxiliary cardinals; lamellar teeth long, somewhat curved, vertically striated in old shell, with lower auxiliary in some RV's; interdental interval long, narrow, curved. *Oligo.-Rec.,* Eu.-E.Asia-SE.Asia.——FIG. D23,*2*. **H. bialata* SIMPSON, Rec., Eu.; LV ext., ×0.5 (Haas).

Inversidens HAAS, 1911 [**Unio brandti* KOBELT, 1879; OD]. Rounded elliptical; 2 cardinals and 1 posterior lamellar teeth on LV, 1 cardinal and 2 posterior lamellar teeth on RV. *Rec.,* Japan.——FIG. D23,*4*. **I. brandti* (KOBELT); *4a-d,* LV ext.,

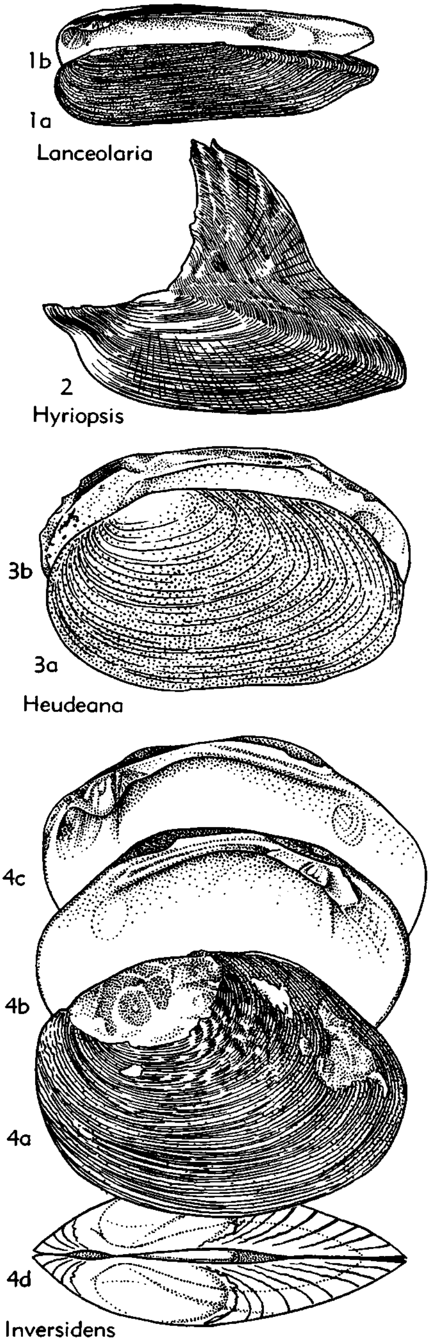


Fig. D23. Unionidae (Unioninae) (p. *N*423-*N*424).

int., RV int., both valves dorsal, ×1 (after Haas).

Lamellidens Simpson, 1900 [**Unio marginalis* Lamarck, 1819; OD]. Elongate, elliptical, pointed behind; beaks with curved radiating ridges which may be zigzag-shaped and concentric, reaching about halfway from beaks, and fading out gradually; periostracum smooth, shiny, dark, almost rayless; cardinals compressed, elongated; lamellar teeth long. *Mio.-Rec.,* E.Indies.——Fig. D24,*4*. **L. marginalis* (Lamarck), Rec.; *4a,b,* LV ext., both valves dorsal, ×0.8 *(497)*.

Lanceolaria Conrad, 1853 [**Unio grayanus* Lea, 1834; OD] [=*Cylindrica* Simpson, 1900; *Pericylindrica* Tomlin, 1930]. Very inequilateral sword-shaped, extended and pointed behind, bent to right or left in some, posterior slope well defined, beaks low, periostracum rayed in immature forms; cardinals short, lamellar teeth very long. *Plio.-Rec.,* E.Asia.——Fig. D23,*1*. **L. grayana* (Lea), Rec.; *1a,b,* LV ext., RV int., ×0.3 (after Haas).

Lastena Rafinesque, 1820 [**Anodonta lata* Rafinesque, 1820; OD] [=*Hemistena* Rafinesque, 1820; *?Flexiptis* Rafinesque, 1831; *Odatelia* Rafinesque, 1832; *Lostena* Gray, 1847; *Stenelasma* Herrmannsen, 1849; *Hemilastena* L. Agassiz, 1852; *Lastenes* Desmarest, 1859; *?Sayunio* de Gregorio, 1914]. Elongate, very inequilateral, wide and rounded-truncate in front, pointed behind; posterior slope low, with 2 or 3 posterior ridges; beaks low, sculptured with few coarse, irregular, longitudinal folds; periostracum shining, commonly rayed; hinge consisting of imperfect cardinal in each valve and in some forms vestiges of lamellar teeth. *Rec.,* N.Am.——Fig. D24,*2*. **L. lata* (Rafinesque); *2a,b,* LV ext., both valves dorsal, ×0.7 *(497)*.

Leguminaia Conrad, 1865 [**Monocondylaea mardinensis* Lea, 1864; OD] [=*Legumenaia* Tryon, 1884; *Seguminaia* Paetel, 1890]. Rhomboid to elliptical, slightly biangulate behind, posterior ridge faint, double; beaks anterior, sculptured with fine, concentric ridges which tend to form 2 rounded loops; periostracum almost or completely without rays; hinge without fulcrum, teeth arising immediately from dorsal margin of shell, single cardinal in each valve, that of LV under beak, in RV in front of beak; dorsal side of teeth commonly covered with periostracum; beak cavities shallow. *Rec.,* SE.Eu.-SC.Eu.-SW.Asia(Iraq-Syria).

L. (Leguminaia). Rather solid, beaks rather full; cardinals strong, with slight 2nd cardinal in LV of some forms. *Rec.,* SW.Asia(Iraq).——Fig. D25,*4*. **L. (L.) mardinensis* (Lea); *4a-c,* RV ext., LV int., both valves dorsal, ×0.6 *(535)*.

L. (Microcondylaea) Vest, 1866 [**Anodonta uniopsis* Lamarck, 1819; OD] [=*Microcondylus* Drouët, 1879]. Decidedly inequilateral, elongate, subrhomboid to elliptical, compressed, rather

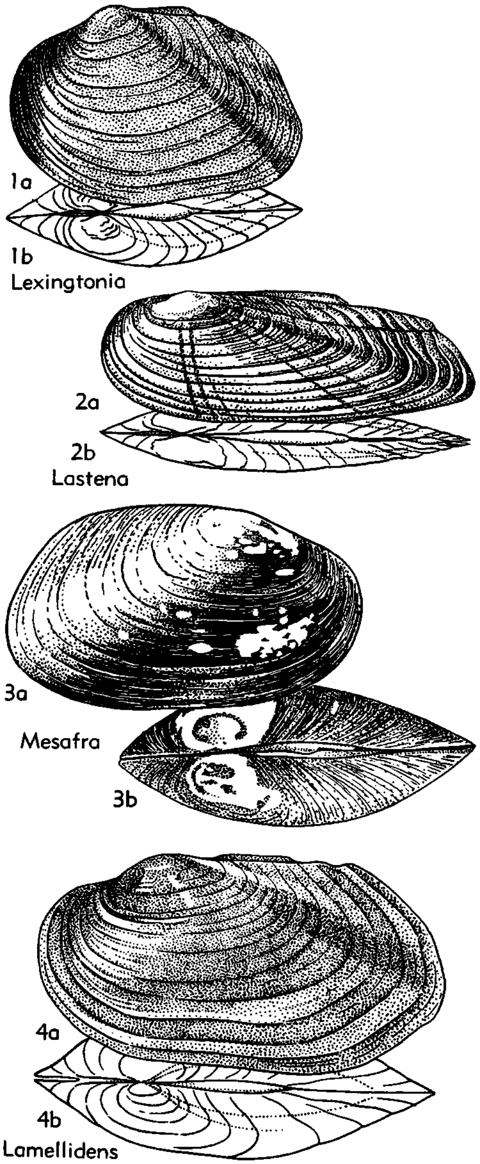


FIG. D24. Unionidae (Unioninae) (p. *N*424-*N*425).

thin, with low beaks; 1 cardinal in each valve, very compressed. *Rec.,* SE.Eu.-SC.Eu.——FIG. D25,*2*. **L. (M.) uniopsis* (LAMARCK); *2a-c,* LV ext., RV int., both valves dorsal, ×0.7 *(497).*

L. (Pseudodontopsis) KOBELT, 1913 [**Unio euphraticus* BOURGUIGNAT, 1853; OD]. Thin, broadly elliptical or rhomboid, rather compressed; beaks subcentral with tendency to shift forward during growth; 1 cardinal in each valve, very compressed. *Rec.,* SW.Asia(Iraq).——FIG. D25,*3*. **L. (P.) euphratica* (BOURGUIGNAT); *3a-c,* LV ext., RV and LV hinges, both valves dorsal, ×0.7 *(481).*

L. (Pseudoleguminaia) GERMAIN, 1911 [**Pseudodon chantrei* LOCARD, 1883; OD]. Subelliptical, somewhat inflated, rather thin, almost transparent; beaks near center, rather full, sculptured with irregular undulations; periostracum bright, yellowish-brown; cardinals very obtuse, rather prominent and thick. *Rec.,* SW.Asia(Syria).——FIG. D25,*1*. **L. (P.) chantrei* (LOCARD); *1a-c,* LV int., RV int., LV ext., ×0.7 (Locard).

Lexingtonia ORTMANN, 1914 [**Unio subplanus* CONRAD, 1837; OD] Subquadrate or subtrapezoidal, beaks slightly elevated, well behind anterior extremity; beak sculpture consisting of 6 to 8 rather crowded subconcentric ridges, which form indistinct rounded angle on posterior ridge; periostracum brownish, wtih rather indistinct continuous rays; hinge teeth well developed, nacre white to pink. *Rec.,* N.Am.——FIG. D24,*1*. **L. subplana* (CONRAD); *1a,b,* LV ext., both valves dorsal, ×1 *(497).*

Mesafra HAAS, 1936 [**Caelatura mesafricana* PILSBRY & BEQUAERT, 1927; OD]. Ventricose, elongate-ovoid, thin; beaks full, not prominent, with sculpture consisting of crowded ribs that radiate from tips; hinge teeth thin, bladelike, cardinals short; periostracum lusterless, silky, olive green. *Rec.,* C.Afr.——FIG. D24,*3*. **M. mesafricana* (PILSBRY & BEQUAERT); *3a,b,* RV ext., both valves dorsal, ×1 (Haas).

Nephronaias FISCHER & CROSSE, 1893 [**Unio plicatulus* CHARPENTIER, 1856; OD] [=*Leptonaias, Simonaias, Caenonaias, Graptonaias* FISCHER & CROSSE, 1893]. Oblong to elliptical, that of male showing tendency to become kidney-shaped with age, female usually having posterior inflation; surface concentrically sculptured, beaks low, ornamented with faint broken ridges tending to fall into 2 rounded loops; umbonal cavities rather deep; hinge with generally somewhat compressed ragged cardinals and with obliquely ridged posterior lamellar teeth. *Rec.,* C.Am.-N.Am.

N. (Nephronaias). Elliptical. *Rec.,* C.Am.——FIG. D26,*4*. **N. (N.) plicatula* (CHARPENTIER); *4a-c,* RV ext., LV int., both valves dorsal, ×2 *(497).*

N. (Elliptoideus) FRIERSON, 1927 [**Unio sloatianus* LEA, 1840; OD]. Marsupium occupying all 4 gills. *Rec.,* N.Am.——FIG. D26,*2*. **N. (E.) sloatiana* (LEA); RV ext., ×1 *(497).*

N. (Martensnaias) FRIERSON, 1927 [**Unio rubicundus* MARTENS, 1900; OD]. Oblong, solid, with well-developed posterior slope; beaks high, anteriorly placed (2.5 of length); disc marked by strong concentric sulci, and posterior slope with radial plications; cardinals strong, crenu-

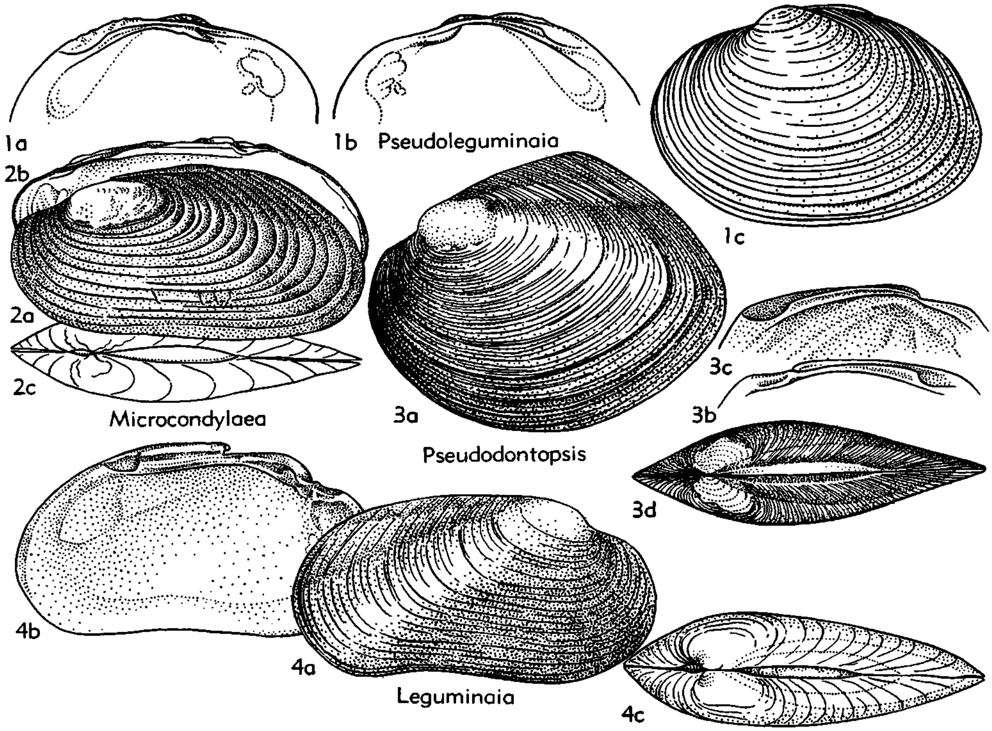


Fig. D25. Unionidae (Unioninae) (p. N424-N425).

lated, lamellar teeth strongly curved; nacre purple. *Rec.*, C.Am.——Fig. D26,*1*. **N. (M.) rubicunda* (Martens); *1a,b,* LV ext., int., ×0.5 *(588)*.

N. (Nephritica) Frierson, 1927 [**Unio poeyanus* Lea, 1857; OD]. Very similar to *Popenaias* but more cylindrical, having greatest diameter behind middle, scarcely diminishing anteriorly. *Rec.*, C.Am.——Fig. D26,*5*. **N. (N.) poeyana* (Lea); *5a-c,* RV ext., LV int., both valves dorsal, ×0.8 *(535)*.

N. (Popenaias) Frierson, 1927 [**Unio popeii* Lea, 1857; OD]. Elongate, especially in front; teeth compressed, sharp. *Rec.*, N.Am.——Fig. D26,*3*. **N. (P.) popeii* (Lea); *3a-c,* RV ext., LV int., both valves dorsal, ×0.8 *(535)*.

N. (Reticulatus) Frierson, 1927 [**Unio reticulatus* Simpson, 1900; OD]. Elliptical, solid, inflated; surface covered with fine, concentric ridges and having delicate, radiating furrows which cut sulcations and form them into loops. *Rec.*, C.Am. ——Fig. D26,*6*. **N. (R.) reticulata* (Simpson); RV ext., ×1 *(845)*.

N. (Sphenonaias) Fischer & Crosse, 1893 [**Unio liebmanni* Philippi, 1847; OD] [=*Barynaias* Fischer & Crosse, 1893]. Solid, somewhat trapezoid in shape; cardinal teeth heavy. *Rec.*, C.Am. ——Fig. D26,*7*. **N. (S.) liebmanni* (Philippi); *1a,b,* LV ext., RV int., both valves dorsal, ×0.5 *(497)*.

Nippononaia Suzuki, 1941 [**Unio ryoseḳiana*; OD]. Subelliptical, medium-sized, with many acute V-shaped ridges centering on line from beak to middle of ventral margin which is finely crenulate. *L.Cret.*, Japan.——Fig. D27,*3*. **N. ryoseḳiana* (Suzuki); LV ext., ×1 (after *896*).

Nitia Pallary, 1924 [**Unio teretiusculus* Philippi, 1847; OD]. Heavy, inflated, elongate, slender, with almost straight and parallel dorsal and ventral margins; beaks slightly prominent; periostracum thick, grayish, feltlike; beaks with zigzag ridges which become wavy wherever they extend over part of disc; cardinals short, heavy; lamellar teeth long, slender. *Rec.*, C.Afr.-NE.Afr.——Fig. D27,*1*. **N. teretiuscula* (Philippi); *1a-c,* LV ext., both valves dorsal, hinges, ×1 *(497)*.

Oxynaia Haas, 1913 [**Unio jourdyi* Morlet, 1886; OD]. Elongate, rounded in front, pointed behind, beaks prominent, with zigzag ridges on oldest part, posterior slope low; cardinals stout, lamellar

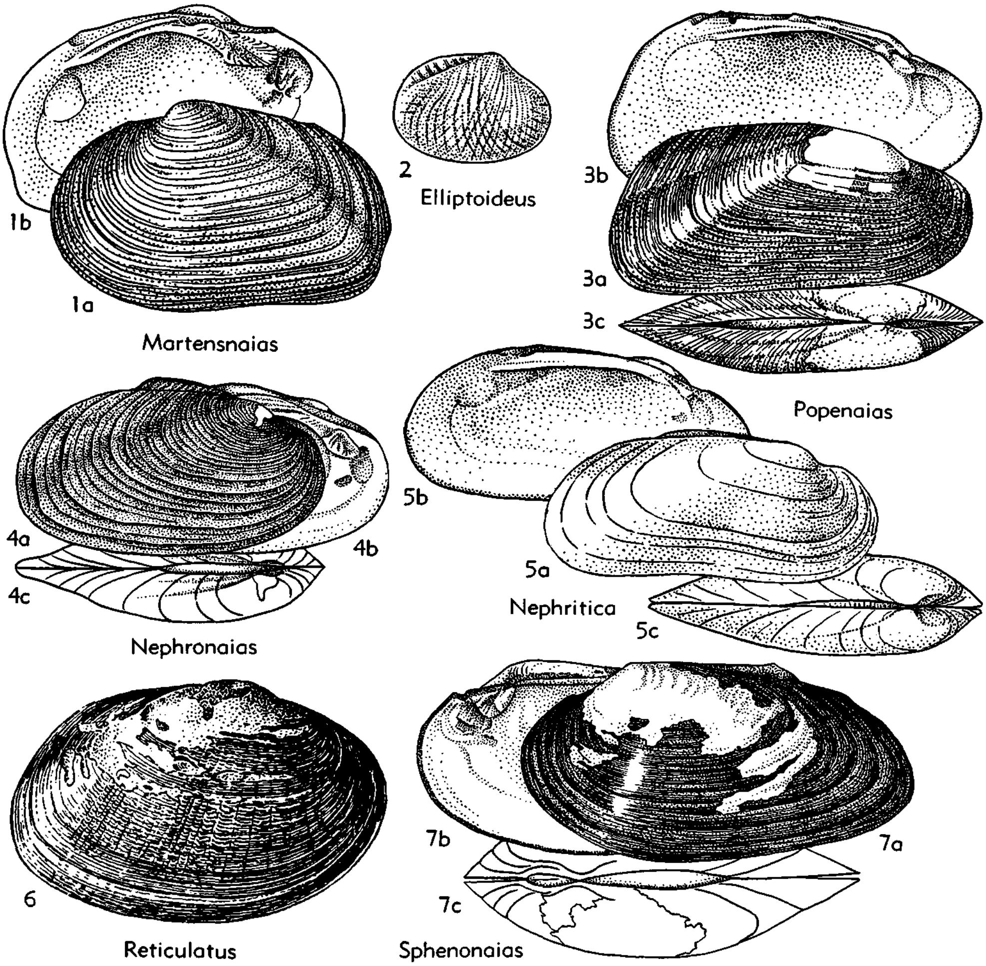


Fig. D26. Unionidae (Unioninae) (p. *N*425-*N*426).

teeth, slender. *Rec.*, SE.Asia.——Fig. D27,*4*. *O. jourdyi (Morlet); *4a-c*, LV ext., RV int., both valves dorsal, ×1 (after Haas).

Palindonaia Modell, 1950 [*Unio solandri J. de C. Sowerby, 1826; OD]. Small, elongate, oval or rectangular, rather compressed; beaks low, posterior ridge faint, indistinct sculpture on beaks and posterior slope; cardinals small, flat. *Cret.(Gosau)-Eoc.*, Eu.——Fig. D27,*2*. *P. solandri emszti* Modell, Cret., Eu.; RV ext., ×1 *(632)*.

Paranodonta Kobayashi & Suzuki, 1936 [*P. ôtai; OD]. Elliptical to subovate, very thick, highly convex; beaks near center; disc smooth except for growth lines; cardinals almost rudimentary, laterals absent. *U.Jur.(Naktong Wakino Ser.)*, Japan.——Fig. D27,*5*. *P. otai; RV ext., ×1 *(479)*.

Parreysia Conrad, 1853 [*Unio multidentatus Philippi, 1847; OD]. Heavy, inflated, rounded to subrhomboid, with full, high, radially zigzag ribs on beaks, sculpture commonly extending over disc; periostracum smooth, bright, rayed; hinge normal, cardinals heavy, ragged or vertically striate, lamellar teeth short, in some shells duplicated in RV; cavity of beaks rather deep. *Mio.-Rec.*, S.Asia-C.Afr.

P. (Parreysia). Shell with center of ventral region swollen; beak sculpture strong, with central ridges generally united at their lower points to form chevron-shaped markings. *Mio.-Rec.*, S.Asia.——Fig. D28,*2*. *P. (P.) corrugata* (Mueller), Rec.; *2a,b*, RV ext., LV int., ×1 *(497)*.

P. (Nyassunio) Haas, 1936 [*Unio nyassaensis Lea, 1864; OD]. Rounded triangular to quadrangular, old specimens elongate and descending

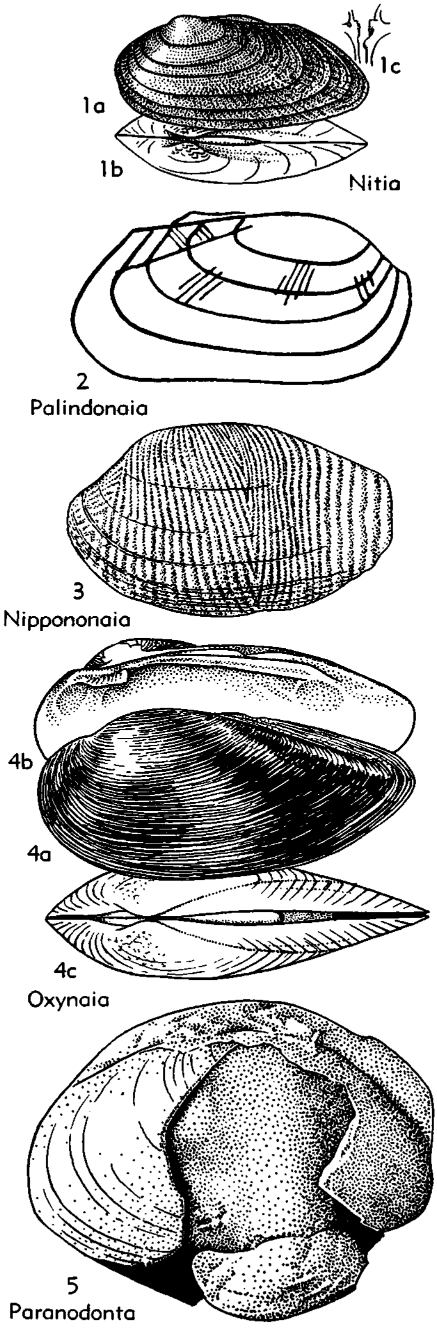


Fig. D27. Unionidae (Unioninae) (p. *N*426-*N*427).

behind, solid; beaks very prominent, sculpture consisting of sharply bent zigzag wrinkles reduced to isolated waves in old specimens; posterior slope concave, posterior ridge distinct, showing as furrow within; hinge heavy, cardinals serrate, compressed, standing at angle with short lamellar teeth. *Rec.,* C.Afr.——Fig. D28,*1.* **P. (N.) nyassaensis* (Lea); *1a-d,* LV ext., RV int., LV int., both valves dorsal, ×0.5 (Haas).

P. (Radiatula) Simpson, 1900 [**Unio crispisulcatus* Benson, 1862; OD] [=*Indonaia* Prashad, 1918]. Triangularly oval, beaks little inflated, entire surface of disc covered with radiating or zigzag-shaped or divaricate ridges separated into nodules by concentric sulcations. *Mio.-Rec.,* S. Asia.——Fig. D28,*6.* **P. (R.) crispisculata* (Benson), Rec.; LV ext., ×0.8 *(384).*

Physunio Simpson, 1900 [**Unio gravidus* Lea, 1856; OD]. Irregularly obovate, thin, narrowed in front, produced at posterior base; posterior slope high, winged, excavated, posterior ridge distinct; beaks inflated, with deep cavities, tips sculptured with zigzag folds; disc smooth, periostracum yellowish or brownish green; hinge normal, cardinals elongate, compressed, lamellar teeth short, somewhat curved, auxiliary tooth added in each valve in old specimens. *Rec.,* SE.Asia-Java.

P. (Physunio). Generally very ventricose, not symphynote; beak cavities deep. *Rec.,* SE.Asia-Indon.(Java).——Fig. D28,*5.* **P. (P.) gravidus* (Lea); *5a-d,* RV ext., LV int., RV int., both valves dorsal, ×0.5 (Haas).

P. (Lens) Simpson, 1900 [**Unio eximius* Lea, 1860; OD]. Sublenticular, not symphynote; umbonal cavities compressed. *Rec.,* SE.Asia.——Fig. D28,*8.* **P. (L.) eximius* (Lea); *8a-c,* RV ext., int., both valves dorsal, ×0.8 (Haas).

P. (Velunio) Haas, 1914 [**Unio velaris* Sowerby, 1868; OD]. Compressed, symphynote; beaks incurved forward. *Rec.,* SE.Asia.——Fig. D28,*7.* **P. (V.) velaris* (Sowerby); LV ext., ×1 (Haas).

Plethobasus Simpson, 1900 [**Unio aesopus* Green, 1827 (=**Obliquaria cyphya* Rafinesque, 1820); OD]. Large, irregularly oval, inflated, abruptly swollen at posterior base; beaks subanterior, rather high, having few strong ridges which curve upward behind and row of tubercles extending from beaks to postbasal area; hinge normal, cardinals rough, triangular; cavities of beaks not deep; front part of shell heavy, rear part much thinner. *Pleist.-Rec.,* N.Am.——Fig. D28,*3.* **P. cyphyus* (Rafinesque), Rec.; *3a,b,* LV ext., both valves dorsal, ×0.7 *(497).*

Pleurobema Rafinesque, 1820 [**Unio mytiloides* Rafinesque, 1820; SD Herrmannsen, 1846]. Heavy, triangular to rhomboid, umbonal region prominent; beaks subanterior or anterior, incurved, pointing forward; beak sculpture coarse, consist-

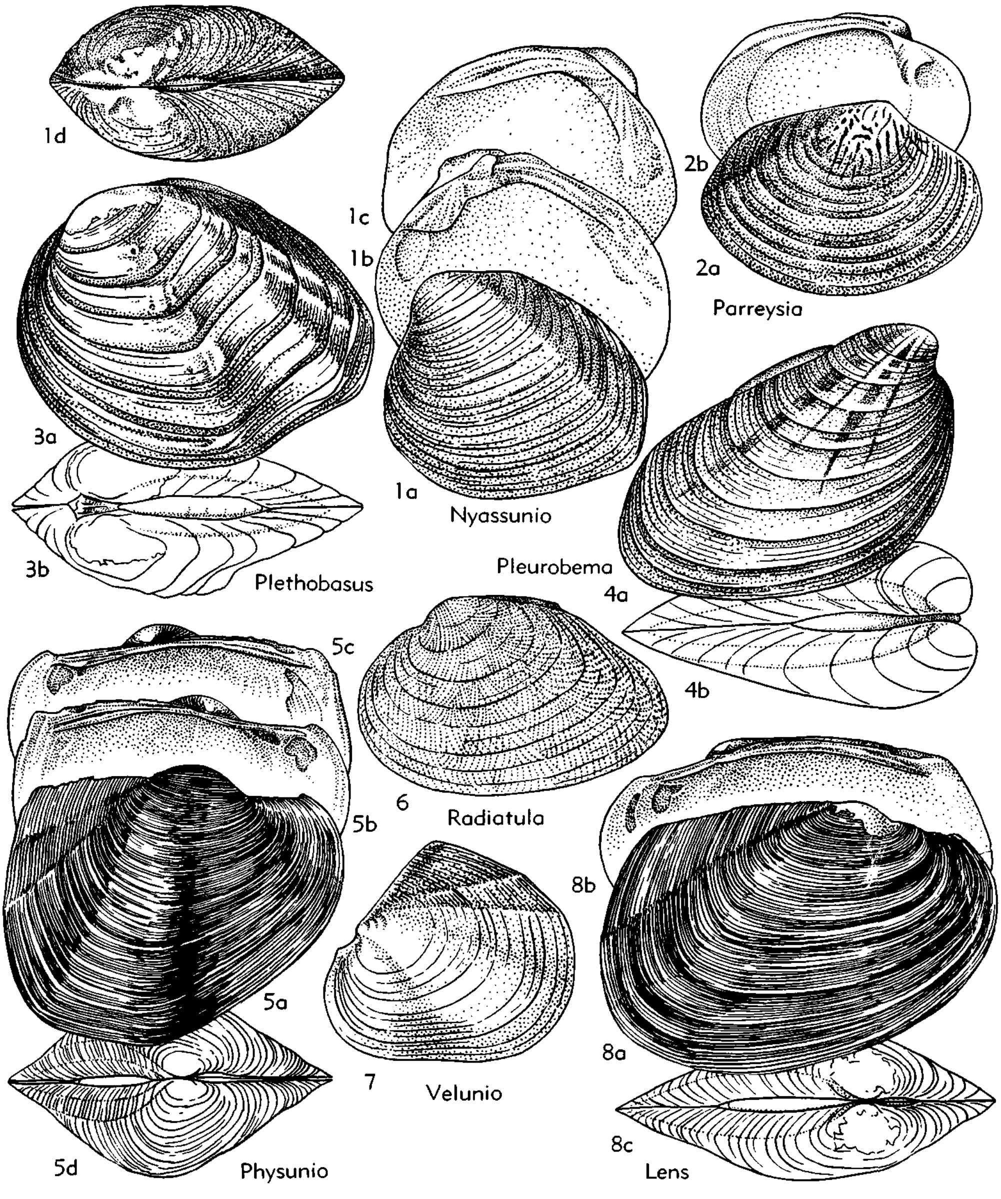


FIG. D28. Unionidae (Unioninae) (p. *N*427-*N*429).

ing of few irregular, commonly discontinuous ridges which curve upward posteriorly; posterior slope low, posterior ridge low and rounded; periostracum commonly with rays which show tendency to break into square spots; hinge rather strong, cardinals triangular, ragged, lamellar teeth almost reaching cardinals, auxiliary lateral below that of RV. *U.Cret.-Rec.*, N.Am.——FIG. D28,*4*. **P. mytiloides* (RAFINESQUE), Rec.; *4a,b*, RV ext., both valves dorsal, ×0.75 *(497)*.

Plicatounio KOBAYASHI & SUZUKI, 1936 [**P. naktongensis*; OD]. Moderately convex, subelliptical to subtriangular; umbones large, located at or slightly ahead of middle; several strong subcrenate plications radiate from umbonal region to posteroventral margin; anterior cardinal tooth relatively

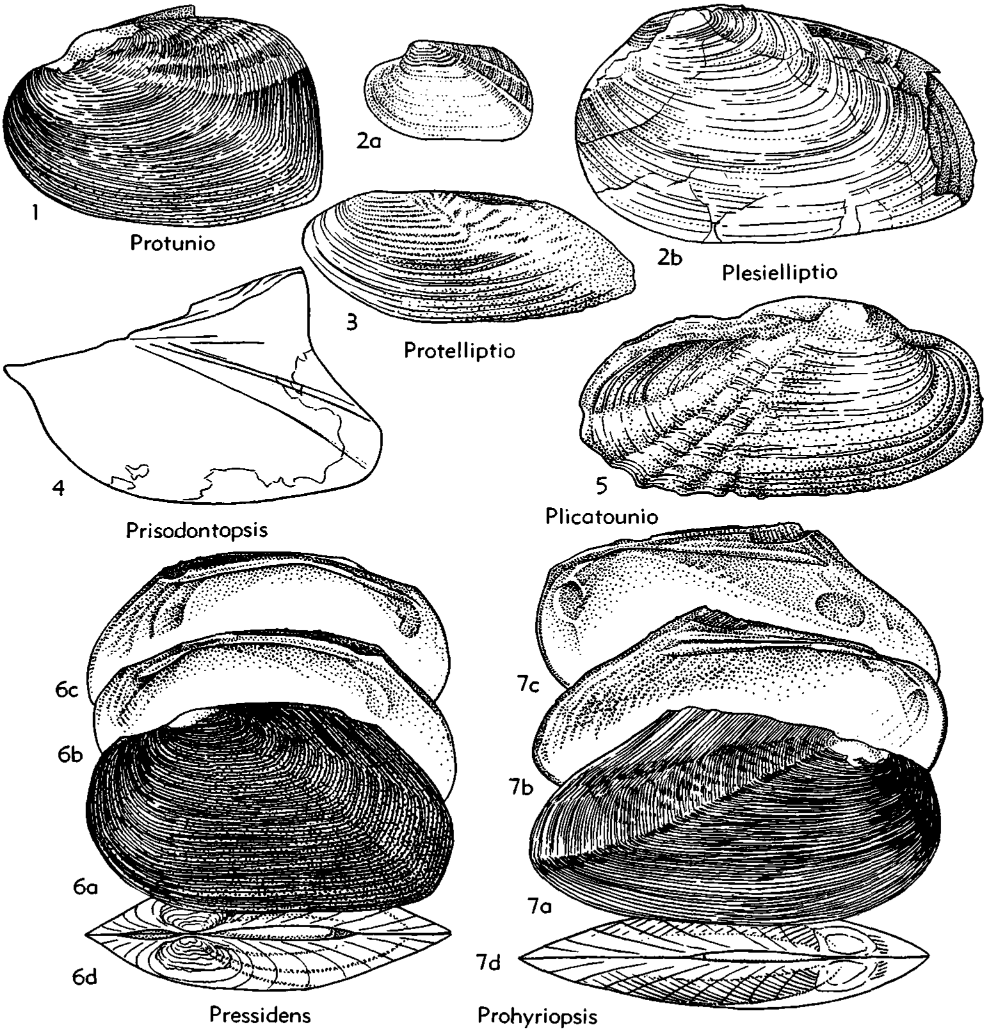


Fig. D29. Unionidae (Unioninae) (p. *N*429-*N*431).

long and regularly crenulate; posterior cardinal prominent, noncrenulate; anterior adductor scar more strongly impressed than posterior. *U.Jur.*, Manchuria-Japan; *U.Cret.*, N.Afr.(Fr.Sudan).——Fig. D29,*5*. **P. naḳtongensis*, U.Jur., Japan; RV ext., ×0.75 *(479)*.

Pressidens Haas, 1900 [**P. moellendorffi*; OD]. Oval, thin, somewhat compressed; beaks low, their sculpture consisting of concentric undulating wrinkles, or entirely absent; posterior slope high; hinge consisting of one long compressed cardinal and of one long low lateral in each valve. *Rec.*, W.Pac.(Borneo).——Fig. D29,*6*. **P. moellendorffi*; *6a-d*, LV ext., RV int., LV int., both valves dorsal, ×0.75 (Haas).

Prisodontopsis Tomlin, 1928 [*pro Pseudavicula* Simpson, 1900 (*non* Etheridge, 1892)] [**Unio (Metaptera) johnstoni* E. A. Smith, 1893; OD]. With well-developed anterior and posterior dorsal wings; posterior margin of posterior wing deeply incurved; beaks low, full; cardinals elongate, slightly corrugated, 1 in LV, 2 in RV; lamellar teeth long, straight, thin and prominent, 2 in LV, 1 in RV. *Rec.*, C.Afr.——Fig. D29,*4*. **P. johnstoni* (Smith); LV ext., ×1 (Pilsbry & Bequaert).

Prohyriopsis Haas, 1914 [**Unio stolatus* Martens, 1900; OD]. Elongate, very inequilateral, somewhat symphynote, produced and slightly truncate behind, thin, compressed; posterior slope high, compressed in middle, wtih distinct posterior ridge close to which slope shows slightly wavy folds; ligament hidden; cardinals compressed, at angle with dorsal margin, lamellar teeth long and straight. *Rec.,* W.Indon.(Sumatra).——Fig. D29, *7*. **P. stolata* (Martens); *7a-d,* RV ext., LV int., RV int., both valves dorsal, ×0.75 (Haas).

Protelliptio Russell, 1934 [**Unio biornatus* Russell, 1932; OD]. Medium-sized, elongate-ovoid; beaks low, sculptured with numerous regular concentric or double-looped plications; 2 somewhat divergent lines directed posteroventrally. *L.Cret.-Paleoc.,* N.Am.

P. (Protelliptio). Concentric plications on beak extending on to disc and posterior loop weakly developed; 2 narrowly divergent, posterodorsal lines may be present; posterodorsal surface usually marked by radiating, upcurved plications similar to those of *Lasmigona*; umbonal ridge poorly developed. *L.Cret.,* N.Am.——Fig. D29,*3*. **P. (P.) biornatus* (Russell); LV ext., ×0.8 *(807)*.

P. (Plesielliptio) Russell, 1934 [**Unio priscus* Meek & Hayden, 1867; OD]. Narrowly to broadly ovoid; beaks sculptured with a few fine, close-set plications, concentric or double-looped, and having 2 slightly divergent, straight or gently curved lines directed posteroventrally, without posterior radiating ornamentation; other shell characters as in *Elliptio*. *U.Cret.-Paleoc.,* N.Am. ——Fig. D29,*2*. **P. (P.) priscus* (Meek & Hayden), Paleoc. (Ft. Union F.); *2a,* LV ext., ×0.75; *2b,* LV ext., ×1 *(604)*.

Protunio Haas, 1913 [**Unio messageri* Bavay & Dautzenberg, 1901; OD]. Ovate rhombic, solid, rounded in front, truncate behind; beaks prominent, ornamented by undulating ridges which extend over upper half of disc; cardinal of RV low, sulcate above, posterior cardinal of LV identical, anterior narrow; compressed, lamellar teeth long, slightly curved, thicker behind; interdental interval rather long, wide, smooth. *Rec.,* SE.Asia. ——Fig. D29,*1*. **P. messageri* (Bavay & Dautzenberg); LV ext., ×1 (Haas).

Pseudodon Gould, 1844 [**Anodon inoscularis* Gould, 1844; OD] [=*Pseudodus* Morgan, 1885]. Ovate to elliptical, very inequilateral; beaks low, ornamented by W-shaped wrinkles which gradually become undulate with age; posterior slope mostly high, well defined, ornamented in some; periostracum dark brown or black, rayless in mature specimens; teeth unsupported by buttress arising immediately from margin of shell; 1 blunt, mostly blade-shaped cardinal in each valve, in some species with vestiges of another cardinal or of lamellar teeth; umbonal cavities shallow. *Plio.-Rec.,* E.Asia-SE.Asia.

P. (Pseudodon). Ellipsoid, rather thick, ventricose, with distinct posterior slope which may be alate and may be crossed by wrinkles; cardinals heavy, rounded above. *Rec.,* China-SE.Asia.——Fig. D30,*3*. **P. (P.) inoscularis* (Gould); *3a,b,* RV ext., LV int., ×0.75 (Haas).

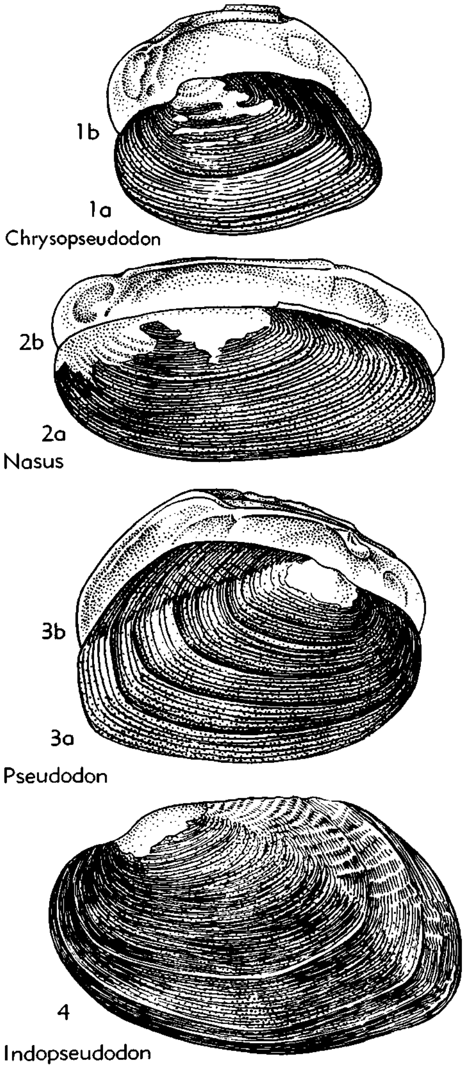


Fig. D30. Unionidae (Unioninae) (p. *N*431-*N*432, *N*434).

P. (Bineurus) Simpson, 1900 [**Unio mouhoti* Lea, 1863; OD]. Elongate, rhomboid, thin, rounded in front, widely and indistinctly biangulate behind; with 2 or more raised ridges on posterior slope which may be transversely wrinkled; disc ornamented by fine irregular concentric grooves; cardinals smooth, compressed. *Rec.,* SE.Asia.——Fig. D31,*2*. **P. (B.) mouhoti* (Lea); *2a-c,* LV ext., RV int., both valves dorsal, ×0.7 (Haas).

P. (Cosmopseudodon) Haas, 1920 [**P. resupina-*

tus MARTENS, 1902; OD]. Elongate, rather thick, with well-defined triangular posterior slope; beaks low, sculptured with V-shaped folds which gradually smooth distally into undulating wrinkles; disc of juvenile shells sculptured with curved folds; cardinals thick, low. *Rec.,* SE.Asia.——FIG. D31,*4.* **P.* (*C.*) *resupinatus* MARTENS; *4a-c,* LV ext., RV int., both valves dorsal, ×0.7 (Haas).

P. (Chrysopseudodon) HAAS, 1920 [**P. aureus* HEUDE, 1885; OD]. Small, rhomboid, solid, in-

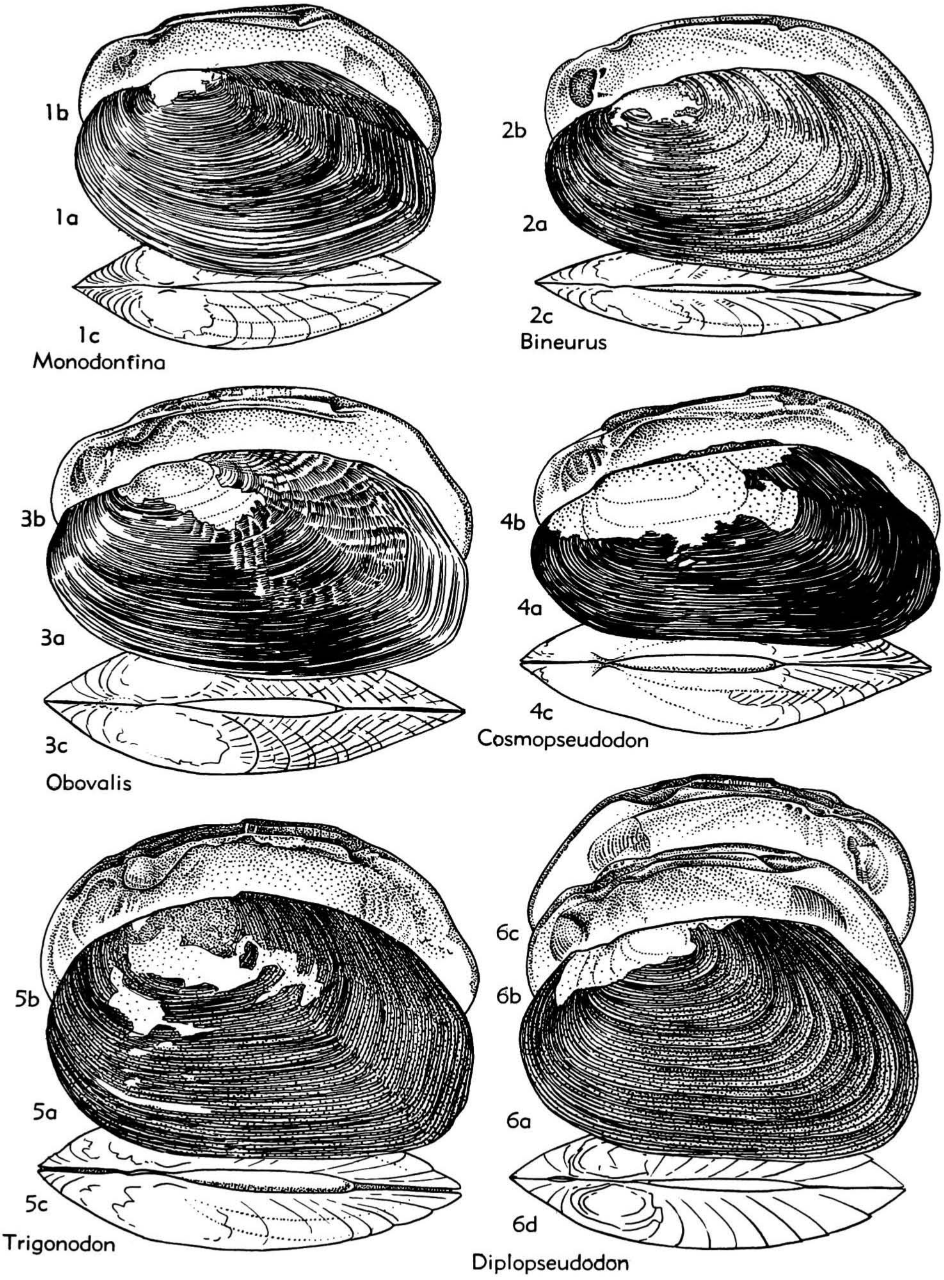


FIG. D31. Unionidae (Unioninae) (p.*N*431-*N*432, *N*434).

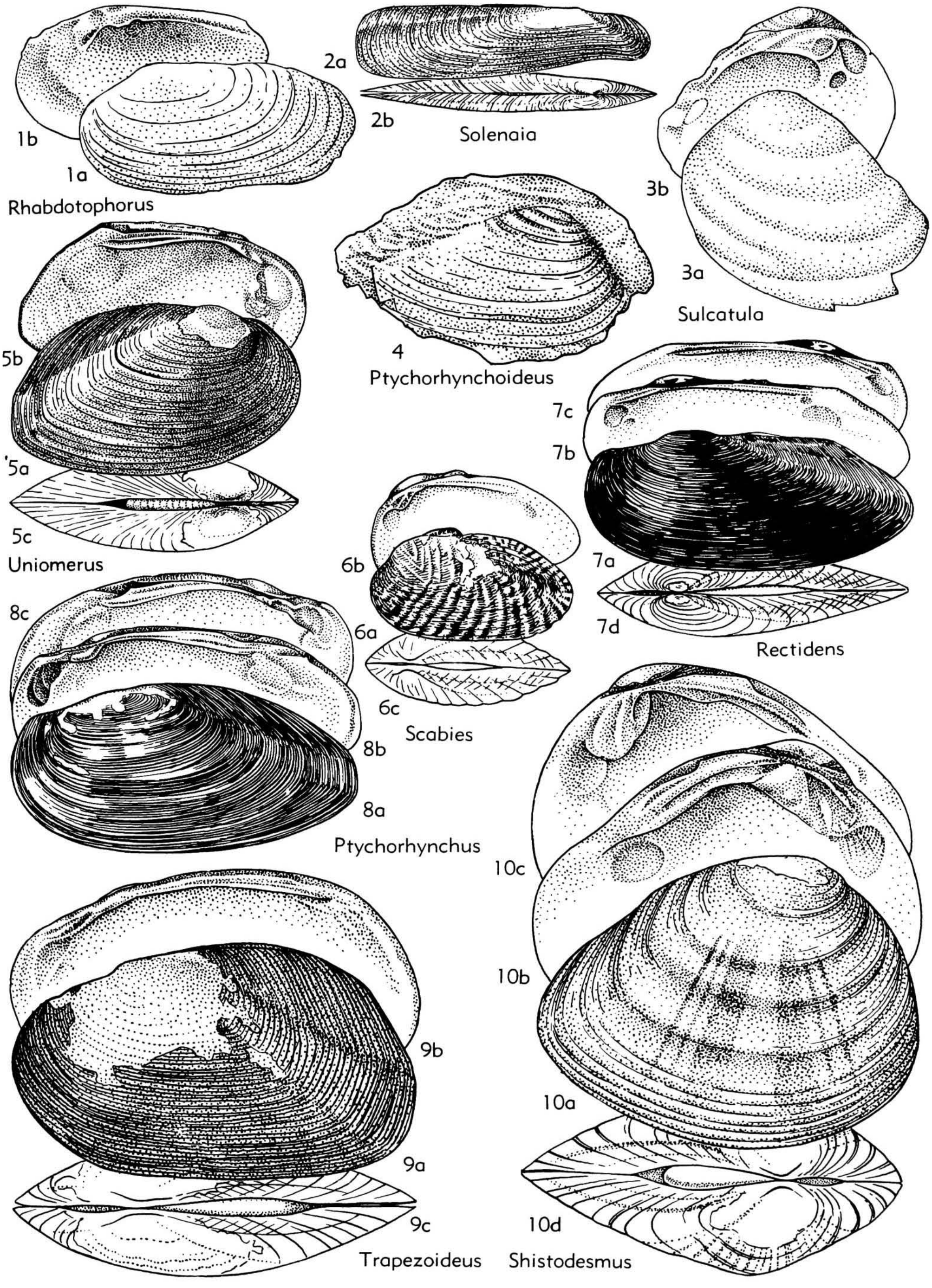


Fig. D32. Unionidae (Unioninae) (p. *N*434-*N*435).

flated; beaks rather central, prominent, with concentric wrinkles; posterior slope wide, concave, with folds over upper half; 1 cardinal in each valve. *Rec.,* China.——FIG. D30,*1*. **P. (C.) aureus* HEUDE; *1a,b,* LV ext., RV int., ×1 (Haas).

P. (Diplopseudodon) HAAS, 1920 [**P. crassus* DROUËT, 1892; OD]. Elongate rhomboid, comparatively high, thick, inflated; anterior end short and low, posterior long and high with distinct posterior slope; 2 cardinals in RV and 1 in LV. *Rec.,* W.Pac.(Borneo).——FIG. D31,*6*. **P. (D.) crassus* DROUËT; *6a-d,* LV ext., RV int., LV int., both valves dorsal, ×0.7 (Haas).

P. (Indopseudodon) PRASHAD, 1922 [**Anodon salwenianus* GOULD, 1884; OD]. Characterized by considerable length and strong, plicate sculpture on alate posterior slope. *Rec.,* SE.Asia. (Burma).——FIG. D30,*4*. **P. (I.) salwenianus* (GOULD); LV ext., ×0.75 (Haas).

P. (Monodontina) CONRAD, 1853 [**Margaritana vondembuschiana* LEA, 1840; OD] [=*Suborbiculus* SIMPSON, 1900]. Rounded, compressed, anterior slope low, posterior high, alate, symphinote when young; 1 smooth tooth parallel to dorsal margin in each valve. *Rec.,* SE.Asia.——FIG. D31,*1*. **P. (M.) vondembuschiana* (LEA); *1a-c,* LV ext., RV int., both valves dorsal, ×0.5 (Haas).

P. (Nasus) SIMPSON, 1900 [**Monocondylaea nankingensis* HEUDE, 1874; OD]. Very elongate, low, moderately thick, somewhat inflated; posterior very low, rounded or roundly truncate; beaks not prominent, of unknown sculpture; cardinals compressed, high, blunt. *Rec.,* China. ——FIG. D30,*2*. **P. (N.) nankingensis* (HEUDE); *2a,b,* LV ext., RV int., ×0.8 (Haas).

P. (Obovalis) SIMPSON, 1900 [**Pseudodon loomisi* SIMPSON, 1900; OD]. Elongate-ovate, thin, moderately inflated, with low posterior slope; V-shaped folds branching out from posterior ridge, crossing posterior slope and neighboring portion of disc; periostracum dark; with 1 high, triangular cardinal and vestiges of 1 lamellar tooth in each valve. *Rec.,* Japan.——FIG. D31,*3*. **P. (O.) loomisi* SIMPSON; *3a-c,* LV ext., RV int., both valves dorsal, ×0.75 (Haas).

P. (Trigonodon) CONRAD, 1865 [**Monocondylaea crebristriata* ANTHONY, 1863; OD]. Solid, compressed, rhomboid; disc irregularly and finely concentrically wrinkled; cardinals triangular, heavy, showing auxiliary tooth in each valve. *Plio.-Rec.,* SE. Asia (Burma)-Indon. (Java).——FIG. D31,*5*. **P. (T.) crebristriatus* (ANTHONY), Rec.; *5a-c,* LV ext., RV int., both valves dorsal, ×0.75 (Haas).

Ptychorhynchoideus MODELL, 1931 [**P. gümbeli*; OD]. Small or medium-sized, elongate-ovate; beaks not prominent, their sculpture concentric with distinct angles posteriorly, less distinctly angulate anteriorly, central part mostly elevated; hinge imperfectly known, cardinals short, flat, lamellar teeth rather short; disc smooth except for folds crossing posterior slope. *U.Oligo.,* Eu.——FIG. D32,*4*. **P. guembeli*; RV ext., ×1 *(629)*.

Ptychorhynchus SIMPSON, 1900 [**Unio pfisteri* HEUDE, 1874; OD]. Elongate elliptical, round in front, pointed behind, heavy, slightly inflated, with low posterior slope which is crossed by slightly curved, parallel folds above; beaks low, ornamented by zigzag wrinkles; cardinals low, more or less elongate, lamellar teeth moderately long, wide, commonly granulose; umbonal cavities shallow. *Rec.,* China.——FIG. D32,*8*. **P. pfisteri* (HEUDE); *8a-c,* LV ext., RV int., LV int., ×0.75 (Haas).

Rectidens SIMPSON, 1900 [**Unio prolongatus* DROUËT, 1893; OD]. Very elongate, inequilateral; beaks full, displaying sculpture of concentric undulating ridges; posterior slope distinct, almost carinate, posterior ridge mostly high, with fine, parallel folds; periostracum indistinctly rayed; cardinals thin, elongate. *Pleist.-Rec.,* SE.Asia.——FIG. D32,*7*. **R. prolongatus* (DROUËT), Rec.; *7a-d,* LV ext., RV int., LV int., both valves dorsal, ×0.5 (Haas).

Rhabdotophorus RUSSELL, 1935 [**R. gracilis*; OD]. Ovoid, elongate; beaks well in advance of midlength, unornamented except by fine, curved costae on postumbonal slope which sweeps backward and upward, commonly interrupted by heavier growth lines; hinge plate narrow; 2 wedge-shaped cardinals on LV, 1 peglike tooth on RV; lamellar teeth slender and posteriorly placed, probably 2 on LV and 1 on RV; anterior adductor scar with dendritic pattern. *U.Cret.,* N.Am.——FIG. D32,*1*. **R. gracilis*; *1a,b,* LV ext., RV int., ×1 (Russell).

Scabies HAAS, 1911 [**Unio scobinatus* LEA, 1856; OD]. Elongate elliptical, V-shaped tuberculate ridges on most of shell; right posterior lamellar tooth with auxiliary tooth beneath posterior extremity. *Rec.,* E.Asia.——FIG. D32,*6*. **S. scobinata* (LEA); *6a-c,* LV ext., RV int., both valves dorsal, ×1 (after Haas).

Shistodesmus SIMPSON, 1900 [**Unio lampreyanus* BAIRD & ADAMS, 1867; OD] [=*Shistodesma* SIMPSON, 1900; *Schistodesmus* HAAS, 1914]. Heavy, triangular, inflated, beaks high; surface of disc marked by strong broad, concentric ridges; periostracum lustrous, greenish-yellow, commonly with discontinuous green rays; posterior ridge tending to be spinose, especially in young specimens; RV with high, triangular, vertically furrowed cardinal of LV narrow, posterior cardinal high, thick, situated under beak, upper lamellar tooth straight and low, lower tooth curved and high; fulcrum very strong and wide; umbonal cavities deep, compressed, right one opened by gap in the interdental interval. *Rec.,* China.——FIG. D32,*10*. **S. lampreyanus* (BAIRD & ADAMS); *10a-d,* RV ext., LV int., RV int., both valves dorsal, ×1 (Haas).

Solenaia CONRAD, 1869 [**Mycetopus emarginatus* LEA, 1860; OD]. Very elongate, soleniform, falcate, rather thin, narrower and rounded in front with upper anterior portion strongly sulcate, gaping at anterior base and behind, with strong posterior ridge which ends below posterior extremity; beaks low, sculptured by looped concentric ridges; periostracum rayless; dentition consists of vestiges of 1 or more lamellar teeth in each valve; pallial line with distinct posterior sinus. *?Cret., Rec.,* China-SE.Asia.——FIG. D32,*2*. **S. emarginata* (LEA), Rec.; *2a,b,* RV ext., both valves dorsal, ×0.3 *(535)*.

Sulcatula LEROY, 1940 [**S. tungurensis*; OD]. Externally like *Shistodesmus*; general outline oblong, not pointed at the posterior extremity; cardinal tooth of RV strong, rounded below, bordered above by small socket and behind, close to lamellar tooth, by large one; lamellar tooth long and bevelled; cardinal of LV gently tapering posteriorly and joining long bifid lamellar tooth, limited anteriorly by rounded and thin cardinal. *U.Mio.,* China.——FIG. D32,*3*. **S. tungurensis*; *3a,b,* LV ext., int., ×0.75 *(539)*.

Trapezoideus SIMPSON, 1900 [**Unio foliacea* GOULD, 1843; OD]. Trapezoid, compressed, with low posterior slope and low beaks which are concentrically sculptured by zigzag ridges; disc somewhat concentrically sulcate; hinge with elongate cardinals. *Rec.,* S.Asia-SE.Asia.——FIG. D32,*9*. **T. foliaceus* (GOULD); *9a-c,* LV ext., RV int., both valves dorsal, ×1 (Haas).

Uniomerus CONRAD, 1853 [**Unio tetralasmus* SAY, 1830; SD HAAS, herein (all of 8 species included by CONRAD in *Uniomerus,* none designated as type species, are synonyms or varieties of *Unio tetralasmus* SAY)] [=*Unionerus* UTTERBACK, 1915 *(nom. null.)*]. Shell trapezoid, with almost parallel dorsal and ventral margins; beaks sculptured with 10 to 15 curved, rather strong concentric ridges sweeping upward posteriorly and drawing close together; hinge typical, teeth compressed. *Rec.,* N.Am.——FIG. D32,*5*. **U. tetralasmus* (SAY); *5a-c,* RV ext., LV int., both valves dorsal, ×0.5 (Lea).

Unionea HAAS, 1955 [**Unic fabagina* DESHAYES & JULLIEN, 1874; OD] [=*Unionella* HAAS, 1913 (*non* ETHERIDGE, 1888)]. Small, ovate-rhomboidal, very short in front, obliquely truncate behind, solid, heavy; beaks prominent, inflated, bearing very pointed zigzag wrinkles which may extend over entire disc; posterior ridge distinct, prominent; cardinals low, triangular or compressed, lamellar teeth short, strong, straight, including strong auxiliary lamellar tooth under that of RV; interdental interval long, smooth, ascending posteriorly. *Rec.,* SE.Asia.——FIG. D33,*2*. **U. fabagina* (DESHAYES & JULLIEN); *2a-c,* LV ext., RV int., both valves dorsal, ×1 (Haas).

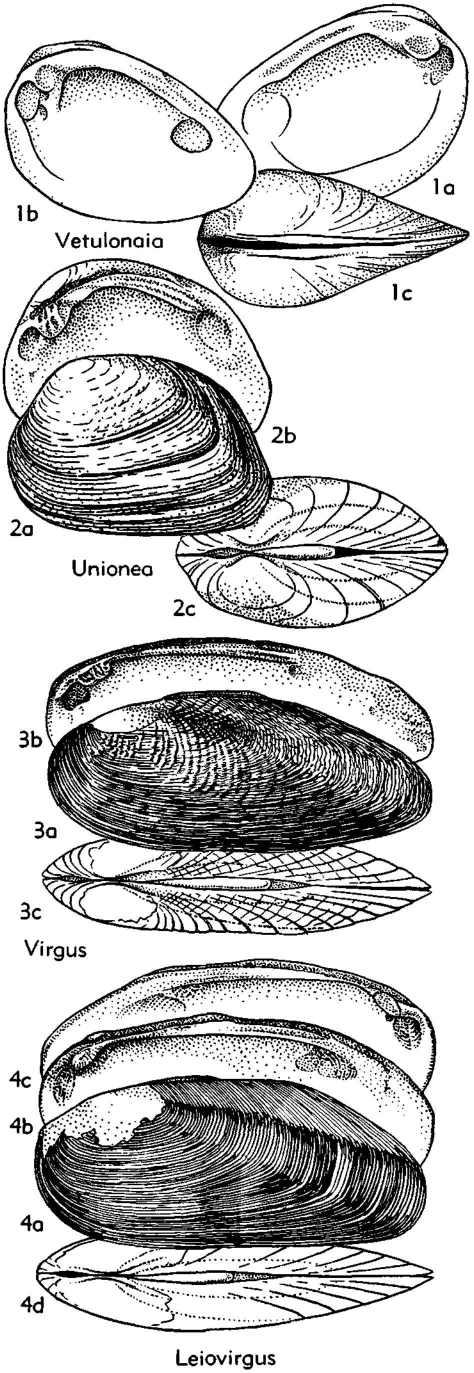


FIG. D33. Unionidae (Unioninae) (p. *N*435-*N*436).

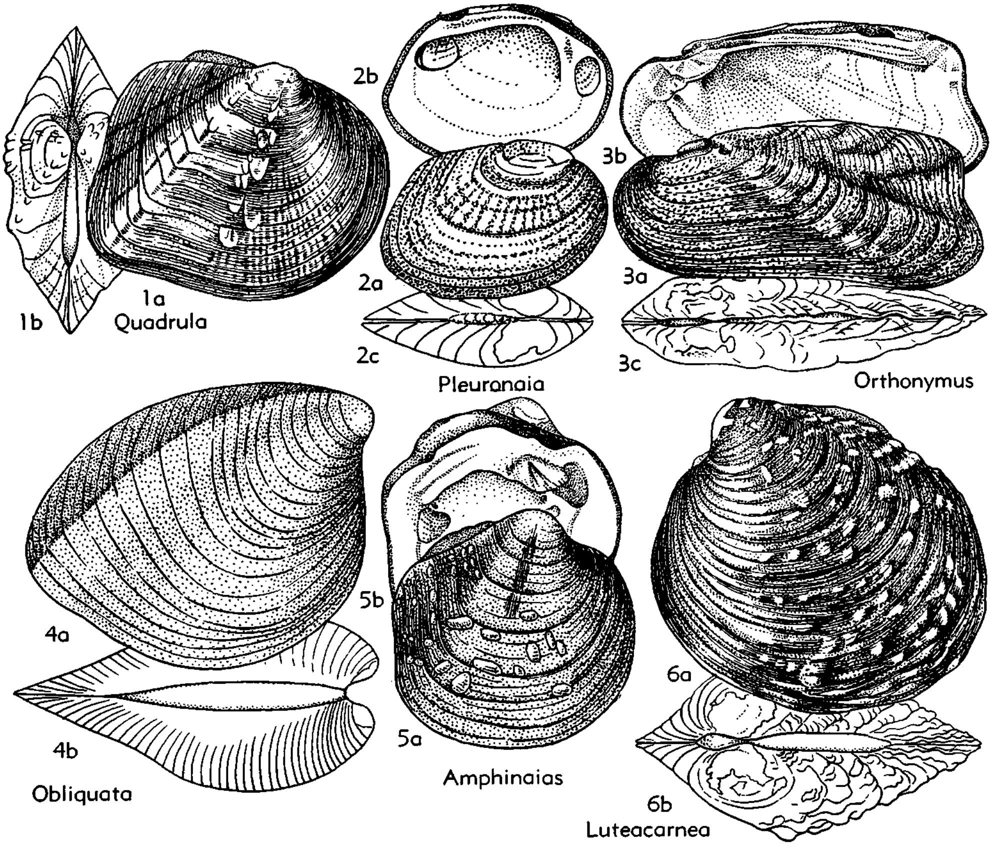


FIG. D34. Unionidae (Quadrulinae) (p. *N*436).

Vetulonaia BRANSON, 1935 [**V. whitei*; OD] [=*Vetulonaea* HOLT, 1942]. Beaks nearly terminal, LV with 2 lamellar teeth, cuneiform cardinal tooth above triangular socket; RV with single lamellar tooth below triangular socket; umbonal region marked by concentric wrinkles, ventral area posterior to beaks marked by radial undulations. *?Jur.*, N.Am.—FIG. D33,*1*. **V. whitei*; *1a-c,* LV int., RV int., both valves dorsal, ×0.7 *(79)*.

Virgus SIMPSON, 1900 [**Unio beccarianus* TAPPERONE CANEFRI, 1883; OD]. Rather solid, elongate, compressed, rounded in front, nearly straight below; posterior slope low, smooth or sculptured; cardinals small, solid, generally 2 in each valve; interdental interval long and narrow, lamellar teeth rather long, straight. *Rec.*, N.Guinea.

V. (Virgus). Solid, sculptured with parallel folds which begin at posterior ridge and branch out over posterior slope and adjacent region of disc. *Rec.*, N.Guinea.——FIG. D33,*3*. **V. (V.) beccarianus* (TAPPERONE CANEFRI); *3a-c,* LV ext., RV int., both valves dorsal, ×0.7 (Haas).

V. (Leiovirgus) HAAS, 1912 [**Unio misoolensis* SCHEPMAN, 1896; OD] [=*Nesonaia* HAAS, 1912]. Elongate, very short in front, long behind; beaks low, sculptured with radial folds; disc smooth. *Rec.*, N.Guinea(Misool I.).——FIG. D33,*4*. **V. (L.) misoolensis* (SCHEPMAN); *4a-d,* LV ext., RV int., LV int., both valves dorsal, ×0.8 (Haas).

Subfamily QUADRULINAE Haas, 1929

Shell mostly heavy, high, squarish to triangular; beaks full, ornamented with V- or W-shaped folds which commonly extend over entire disc, degenerating in some into rows of tubercles; hinge heavy, angular; shell shape commonly subject to sexual dimorphism. Marsupium occupying all four gills. *L.Cret.-Rec.*

Quadrula RAFINESQUE, 1820 [**Obliquaria quadrula* RAFINESQUE, 1820; SD HERRMANNSEN, 1847] [=*Theliderma* SWAINSON, 1840; *Telederma*

Paetel, 1875]. Triangular, quadrangular or rhomboid, inflated; beaks rather prominent, sculptured generally with few coarse, irregular, subparallel ridges which form knobs or tubercles where they cross posterior ridge; disc smooth or sculptured; periostracum usually dull, rayless or only feebly rayed; hinge normal, hinge plate flat, wide; cardinals heavy, ragged, lamellar teeth rather short, lower auxiliary one in some RV's. *Pleist.-Rec.,* N.Am.

Q. (Quadrula). Rounded to rhomboid, solid, pustulose, equal in both sexes; beaks sculptured with few coarse, subparallel ridges; anterior end rounded or subtruncate, base commonly arcuate, posterior end truncate, high, angled above; beak cavities rather deep. *Pleist.-Rec.,* N.Am.——Fig. D34,*1*. **Q. (Q.) quadrula* (Rafinesque), Rec.; *1a,b,* RV ext., both valves dorsal, ×0.75 *(497)*.

Q. (Amphinaias) Crosse & Fischer, 1894 [**Unio couchianus* Lea, 1860; OD] [=*Bullata* Frierson, 1927 (*non* Jousseaume, 1875); *Pustulosa* Frierson, 1927]. Round quadrate, truncate behind, full, angled back of ligament; beaks high with few coarse ridges swollen at posterior ridge; disc mostly pustulose, but may be smooth or corrugated; periostracum commonly with broad and faint green ray; hinge massive. *Rec.,* N.Am.——Fig. D34,*5*. **Q. (A.) couchianus* (Lea); *5a,b,* RV ext., LV int., ×0.7 *(497)*.

Q. (Luteacarnea) Frierson, 1927 [**Quadrula striata* Rafinesque, 1820; OD] [=*Striata* Frierson, 1927 (*non* O. Boettger, 1878)]. Oboval, thick inflated, concentrically ridged, ridges being pustulose in places. Soft parts yellow. *Rec.,* N. Am.——Fig. D34,*6*. **Q. (L.) striata* Rafinesque; *6a,b,* LV ext., both valves dorsal, ×0.7 *(497)*.

Q. (Obliquata) Frierson, 1927 [**Obliquaria (Scalenaria) obliquata* Rafinesque, 1820; OD] [=?*Scalenaria* Rafinesque, 1820]. Subtriangular, rather inflated, heavy; beaks very anterior, high, full, turned forward over conspicuous lunule; truncate in front, more or less pointed behind; with radial depression behind and parallel to posterior ridge; hinge massive, cardinals radial; beak cavities deep, compressed. *Rec.,* N.Am.——Fig. D34,*4*. **Q. (O.) obliquata* (Rafinesque); *4a,b,* RV ext., both valves dorsal, ×0.7 *(497)*.

Q. (Orthonymus) L. Agassiz, 1852 [**Unio cylindricus* Say, 1816; OD]. Quadrate rhomboid, with radial furrow on posterior slope; whole surface except anterior end generally pustulose, that of posterior slope commonly wrinkled; umbonal region high; periostracum lustrous, with pattern of triangular spots or chevron-shaped lines; hinge strong, in some with auxiliary 3rd lamellar tooth in RV; umbonal cavities deep, compressed, *Rec.,* N.Am.——Fig. D34,*3*. **Q. (O.) cylindrica* (Say); *3a-c,* LV ext., RV int., both valves dorsal, ×0.5 *(497)*.

Q. (Pleuronaia) Frierson, 1927 [**Unio barnesianus* Lea, 1838; OD]. Subtriangular to almost elliptical, solid; beaks high, full; posterior ridge strong, curved or subangular; cardinals small, including auxiliaries, also with auxiliary lamellar teeth; beak cavities shallow. *Rec.,* N.Am.——Fig. D34,*2*. **Q. (P.) barnesiana* (Lea); *2a-c,* RV ext., LV int., both valves dorsal, ×1 *(535)*.

Amblema Rafinesque, 1819 [**A. costata* Rafinesque, 1832; SD Rafinesque, 1832] [=*Bariosta* Rafinesque, 1832; *Crenodonta* Schlueter, 1838; *Baryosta* L. Agassiz, 1846]. Heavy, with prominent beaks; surface usually sculptured with oblique folds, posterior slope generally having smaller radial plications which curve up behind; periostracum brown to black. *L.Cret.-Rec.,* N.Am.-C.Am.

A. (Amblema). Rounded to subrhomboid; radial plications usually strong, oblique, though in some discs may be almost unornamented or slightly sculptured concentrically. *L.Cret.-Rec.,* N.Am.-C.Am.——Fig. D35,*5*. **A. (A.) plicata costata* Rafinesque, Rec.; *5a,b,* LV ext., both valves dorsal, ×0.5 *(497)*.

A. (Plectomerus) Conrad, 1853 [**Unio dombeyana* Valenciennes, 1827; SD Frierson, 1927] [=?*Gonamblus* Rafinesque, 1831]. Rhomboidal, inflated with high posterior ridge; beak sculpture coarse, irregular corrugations swollen to nodules on posterior ridge; disc sculptured on posterior half with oblique ridges, which may be corrugated, and with strong corrugations on posterior slope; beak cavities moderately deep, nacre purple. *Rec.,* N.Am.——Fig. D35,*3*. **A. (P.) dombeyana* (Valenciennes); *3a,b,* LV ext., both valves dorsal, ×0.7 *(497)*.

A. (Psorula) Haas, 1930 [**Quadrula rudis* Simpson, 1900; OD]. Round to rounded quadrangular, ventricose to quite compressed; beaks prominent, with deep, commonly quite compressed cavities; umbonal sculpture of many crowded, wavy, concentric wrinkles gradually passing into concentric pustulose or granular sculpture of disc on which very conspicuous, cord-like zones of growth are visible; nacre white to violet. *Rec.,* C.Am.——Fig. D35,*2*. *A. (P.) salinarum* Haas; *2a-c,* LV ext., RV int., LV int., ×0.4 (Haas).

Cokeria Marshall, 1916 [**C. southalli*; OD]. Subquadrangular, rather thin, ventricose, gaping in front; rounded and narrow in front, perpendicularly truncate and high behind; beaks high, incurved, sculptured with 4 concentric ridges, which become elevated posteriorly; pronounced furrow extending from beak to lower 3rd of posterior margin; in RV with 2 thin cardinals and 1 thin high lamellar tooth; 2 lamellar teeth in LV. [Based on a unique individual, hence doubtful; perhaps an abnormality of *Quadrula (Quadrula) undulata* (Barnes).] *Rec.,* N.Am.——Fig. D35,9. **C. southalli*; *9a,b,* RV ext., int., ×0.75 *(580).*

Costanaia MacNeil, 1935 [**C. arciformis*; OD]. Subquadrate, much inflated, posterior margin perpendicularly truncated, nearly straight, ventral margin arcuate; beaks high, anterior, with fine

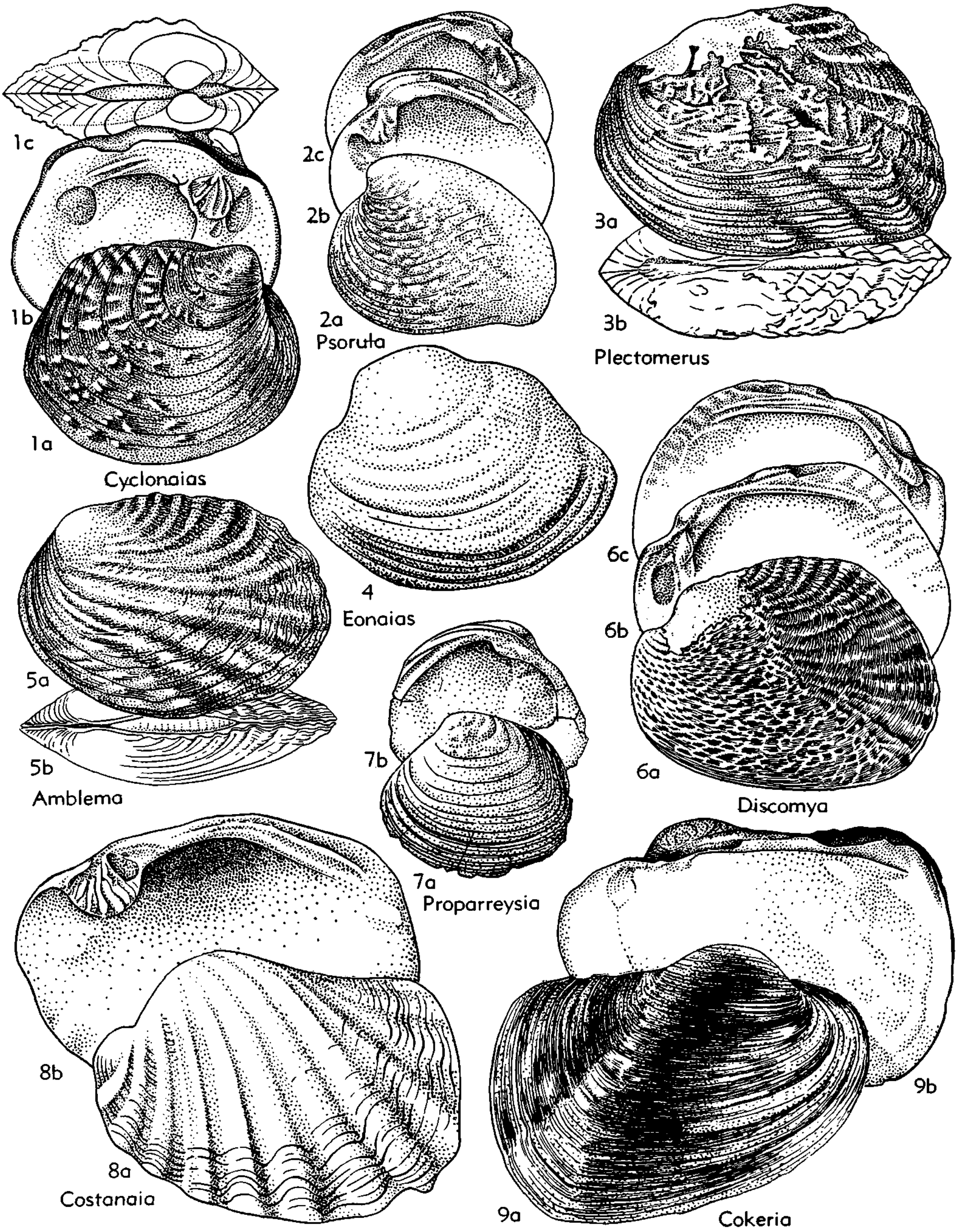


Fig. D35. Unionidae (Quadrulinae) (p. *N*437-*N*439, *N*441-*N*442).

concentric undulations, pointing down umbonal ridge as raised chevrons; surface sculptured with 12 to 15 radial ribs which intersect shell margin at deep crenulations; hinge margin long, arcuate; cardinals deeply furrowed, lamellar teeth short and feeble. *Mio.,* N.Am.——FIG. D35,*8*. **C. arciformis*; *8a,b,* LV ext., RV int., ×0.75 *(568)*.

Cyclonaias PILSBRY, 1922 [**Obliquaria tuberculata* RAFINESQUE, 1820; OD] [=*Rotundaria* AGASSIZ, 1852 (*non* RAFINESQUE, 1820)]. Rounded or quadrate; beaks prominent, curved inward and forward over strongly marked lunule, their sculpture consisting of 20 to 30 fine, irregular, broken, somewhat concentric corrugations which gradually blend with regular sculpture; posterior 0.6 of shell tuberculate; beak cavities deep, compressed, nacre violet. *Pleist.-Rec.,* N.Am.——FIG. D35,*1*. **C. tuberculata* (RAFINESQUE), Rec.; *1a-c,* RV ext., LV int., both valves dorsal, ×0.5 *(497)*.

Discomya SIMPSON, 1900 [**Unio radulosus* DROUËT & CHAPER, 1892; OD]. Round or rhomboidal, compressed, almost lens-shaped, heavy, short and narrowly rounded in front, wide and roundly truncate behind; beaks low, their sculpture unknown; posterior slope very low and compressed; shell sculpture covering entire disc, consisting on anterior half of 2 intersecting systems of elongated knobs which meet nearly at right angles to form meshwork, while on posterior half are cordlike folds which curve upward, some with bifurcation; massive hinge plate, cardinals short, heavy, lamellar teeth short, almost at right angles with cardinals from which they are separated by wide, smooth, ascending interdental interval; beak cavities deep, compressed. *Rec.,* W.Pac.(Borneo).——FIG. D35,*6*. **D. radulosa* (DROUËT & CHAPER); *6a-c,* LV ext., RV int., LV int., ×0.75 (Haas).

Eonaias MARSHALL, 1929 [**E. reynosenica*; OD]. Beaks with numerous V-shaped loops, which are nearly regularly spaced and nested into each other, V's pointing toward ventral margin; posterior areas with fine ribs running from posterior ridge to margin. *Plio.,* N.Am.——FIG. D35,*4*. **E. reynosenica*; LV ext., ×1 (Marshall).

Fusconaia SIMPSON, 1900 [**Unio trigonus* LEA, 1831 (=subsp. of *U. undatus* BARNES, 1823); OD] [=?*Lintoxia* RAFINESQUE, 1820; ?*Lyntoxia* L. AGASSIZ, 1846, *Fusconia* FRIERSON, 1927]. Rounded, elliptical, rhomboid, or triangular with beaks high and full, curved inward and forward, sculptured with few coarse, parallel ridges which curve upward behind; periostracum dark, disc not sculptured; hinge plate of moderate width, cardinals strong, nacre white, salmon or purple. *Pleist.-Rec.,* N.Am.-C.Am.——FIG. D36,*2*. **F. undata trigona* (LEA), Rec.; *2a-c,* RV ext., LV int., both valves dorsal, ×0.4 *(497)*.

Lamprotula SIMPSON, 1900 [**Chama plumbea* CHEMNITZ, 1795; OD] [=*Gibbosula* SIMPSON, 1900]. Rounded, subquadrangular, or triangular, heavy, inflated, with high beaks; beak with few coarse, concentric ridges which form double loops; disc generally covered with coarse nodules or knobs; periostracum gray to black, lustrous; hinge massive, all teeth vertically striated, lower auxiliary lamellar tooth in RV; cavity of beaks deep, compressed. *Oligo.-Rec.,* E.Asia-Japan.

L. (Lamprotula). Rounded or subquadrangular, with beaks near anterior end. *Oligo.-Rec.,* E.Asia-Japan.——FIG. D37,*5*. **L. (L.) plumbea* (CHEMNITZ); *5a,b,* LV ext., int., ×0.5 *(497)*.

L. (Parunio) PING, 1931 [**Parunio crassus*; OD]. Rounded ovoid with anterior beaks, ventrally curved; surface commonly with ridges or rows of nodules parallel to growth lines; hinge massive, lamellar teeth above and parallel to cardinals. *Plio.-Rec.,* E.Asia.——FIG. D37,*2*. **L. (P.) crassa* (PING), Plio.; *2a,b,* LV ext., int., ×0.5 *(738)*.

Loxopleurus MEEK, 1871 [**Unio belliplicatus*; OD]. Subquadrangular, very inflated, with almost central high beaks; surface sculptured with about 6 broad, subparallel folds originating at or near beaks and corresponding to crenulations of the ventral and posterior margins. *U.Cret.,* N.Am.——FIG. D36,*5*. **L. belliplicatus* (MEEK); LV ext., ×0.75 *(569)*.

Megalonaias UTTERBACK, 1915 [**Unio heros* SAY, 1829 (=**U. giganteus* BARNES, 1823); OD] [=*Magnonaias* UTTERBACK, 1915]. Large, heavy, subrhomboid, moderately inflated; posterior slope rather high ribbed with coarse, regular undulations originating in umbonal region; beaks low, sculptured with coarse double-looped corrugations which extend as nodules to posterior ridge and as zigzag ridges over umbonal region to upper portion of disc; periostracum black; cardinals heavy, lamellar teeth long and straight, extending near to cardinals. *Rec.,* N.Am.-C.Am.——FIG. D36,*9*. **M. gigantea* (BARNES), Rec.; LV ext., ×0.3 (Conrad).

Megalonoidea MACNEIL, 1935 [**M. porcata*; OD]. Large, subquadrate, inflated; beak sculpture of semiconcentric, doubly looped undulations in youngest stage, but in adult of heavy diagonal posterior plications originating at anterior side of umbonal chevrons and smaller plications set at conspicuous angle with large ones; cardinals fairly heavy, lamellar teeth long and arcuate; ventral border of shell slightly scalloped by external ribs. *Mio.,* N.Am.——FIG. D37,*1*. **M. porcata*; RV ext., ×0.5 *(568)*.

Pliconaias MARSHALL, 1929 [**P. popenoei*; OD]. Subquadrate; beaks with wavy concentric undulations, each posteriorly completed by fine straight threadlike rib running across posterodorsal area

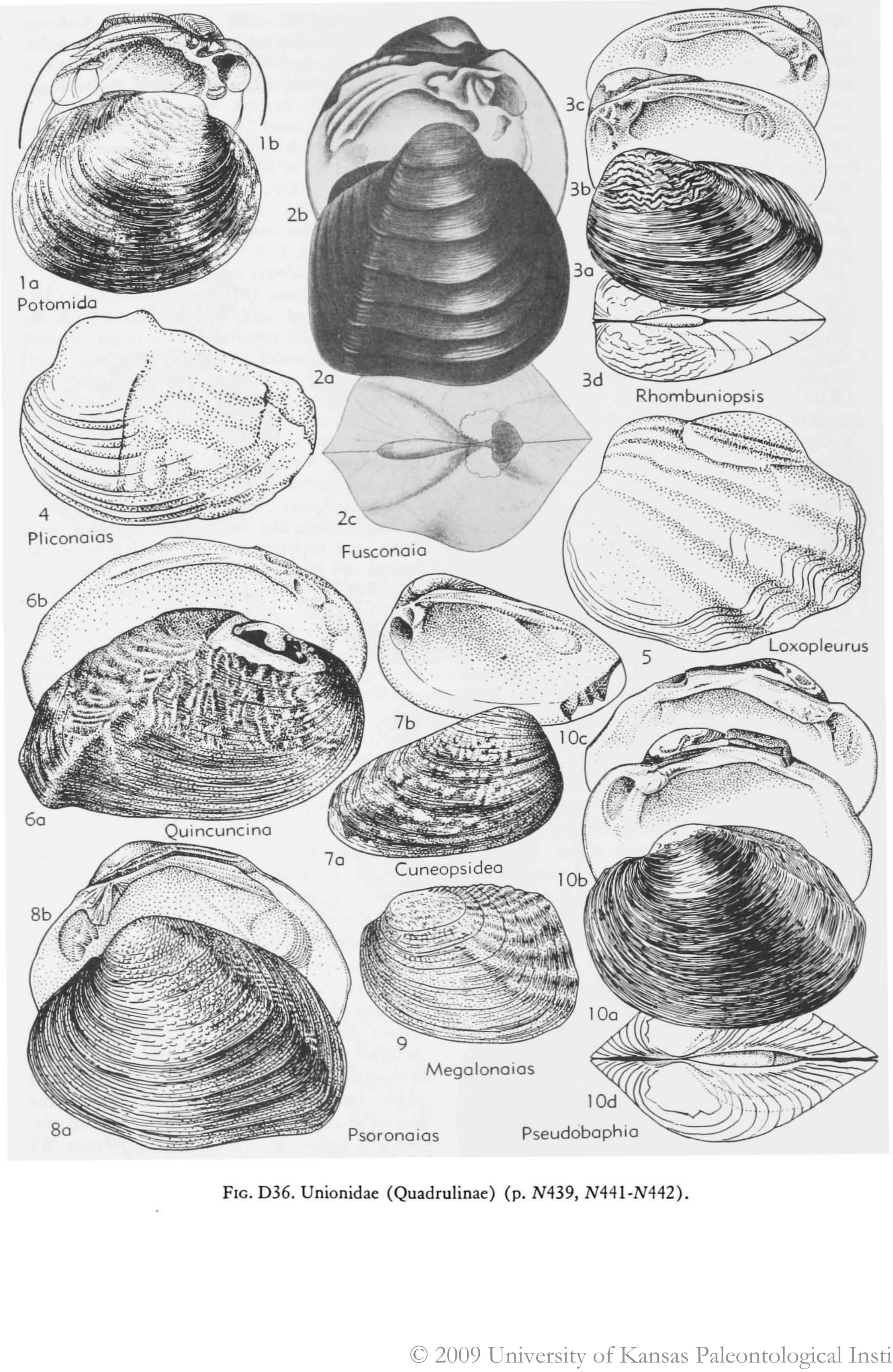


FIG. D36. Unionidae (Quadrulinae) (p. *N*439, *N*441-*N*442).

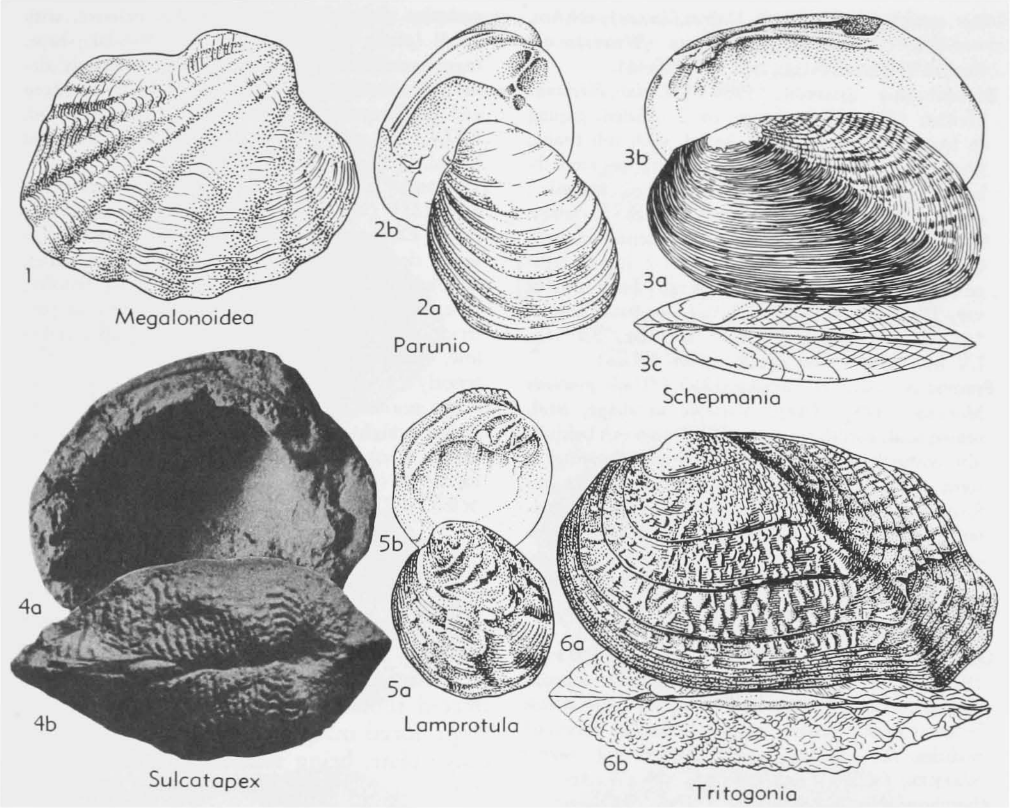


FIG. D37. Unionidae (Quadrulinae) (p. *N*439, *N*442).

toward beak; anteriorly undulations nearly fade out but are indistinctly completed by faint ribs curving toward beak; posterior portion of shell with several rude plications running obliquely across surface with pattern found in plicate North American naiads. *Plio.*, N.Am.——FIG. D36,*4*. **P. popenoei*; LV ext., ×0.7 *(584)*.

Potomida SWAINSON, 1840 [**Unio corrugata* (=**Unio semirugatus* LAMARCK, 1819); OD] [=*Potamida* L. AGASSIZ, 1846; *Psilunio, Rytia* STEFANESCU, 1896; *Sabbaia* COSSMANN, 1897; *Rhombunio* GERMAIN, 1911; *Migranaia* HANNIBAL, 1912]. Rounded rhomboid, moderately heavy, subinflated, round and short in front, wide and roundly truncate behind; beaks high, full with numerous, fine subparallel wavy ridges which may extend well over disc as rows of knobs or nodules; cardinals moderately massive, lamellar teeth commonly curved slightly; beak cavity rather deep. [Under lacustrine conditions (e.g., Hungarian and Rumanian *Pliocene*) the shells are more elongate wedge-shaped and the beaks anterior; the cardinals and lamellar teeth may be parallel to each other, strongly remindful of American and of East Asiatic quadruline.] *Oligo.(John Day)-Rec.*, Eu.-?E.Asia.

P. (Potomida). Rounded, narrow in front, wide behind; beaks submedian, covered by numerous subparallel wavy ridges, mostly not extending to disc; hinge moderately heavy. *Oligo.(John Day)-Rec.*, Eu.-?E.Asia.——FIG. D36,*1*. **P. (P.) littoralis semirugata* (LAMARCK), Rec., Eu.; *1a,b*, RV ext., LV int., ×1 (Ellis).

P. (Cuneopsidea) WENZ, 1928 [*pro Iridea* STEFANESCU, 1896 (*non* SWAINSON, 1840)] [**Unio sculptus* BRUSINA, 1874; OD]. Elongate to wedge-shaped, beaks placed well forward, anterior end steeply descending; sculpture of subparallel wavy ridges and on greater portion of disc, of knobs and nodules; hinge massive, cardinals and lamellar teeth parallel. *Pleist.*, E.Eu.——FIG. D36,*7*. **P. (C.) sculpta* (BRUSINA); *7a,b*, RV ext., int., ×0.5 *(967)*.

Proparreysia PILSBRY, 1921 [**Unio percorrugata* WHITFIELD, 1903; OD]. Small, quadrate; surface in younger specimens with very strong corrugation extending over half of disc, front half of shell unsculptured; hinge strong, cardinals high, lamellar teeth strongly bent. *U.Cret.(Lance),* N.Am. ——FIG. D35,*7*. **P. percorrugata* (WHITFIELD); *7a,b,* RV ext., LV int., ×1 (Whitfield).

Pseudobaphia SIMPSON, 1900 [**Unio biesianus* HEUDE, 1877; OD]. Large, oval, inflated, gaping in front and behind, rather heavy, with full beaks; posterior extremity biangular; periostracum smooth, brownish, rayed; cardinal of RV large, irregular, situated behind pit and in front of beak; 2 remote lamellar teeth, poorly defined, interdental interval with numerous denticles; LV with 2 large cardinals and 2 remote, indistinct laterals; beak cavities very large and deep. *Rec.,* E.Asia.——FIG. D36,*10*. **P. biesiana* (HEUDE); *10a-d,* LV ext., RV int., LV int., both valves dorsal, ×0.5 (Haas).

Psoronaias CROSSE & FISCHER, 1893 [**Unio psoricus* MORELET, 1851; OD]. Variable in shape, oval, subtrigonal, cordiform, or rather drawn out behind; disc covered with small tubercles and showing in some folds posteriorly; cardinal of RV thick and furrowed, behind thin, compressed auxiliary; lamellar teeth rather short, forming obtuse angle with cardinals and separated from them by narrow, straight interdental interval. *Rec.,* C.Am.——FIG. D36,*8*. **P. psorica* (MORELET); *8a,b,* LV ext., RV int., ×0.6 *(306)*.

Quincuncina ORTMANN, 1922 [**Q. burkei* WALKER, 1922; OD]. Sculptured, beak sculpture subconcentric and followed on disc by zigzag ridge which becomes locally broken into quincuncially arranged nodules. *Rec.,* N.Am.——FIG. D36,*6*. **Q. burkei* WALKER; *6a,b,* RV ext., LV int., ×1 (Walker).

Rhombuniopsis HAAS, 1920 [**Unio (Cuneopsis) tauriformis* FULTON, 1906; OD]. Oval to subtriangular, heavy; beaks nearly anterior, inflated, their sculpture consisting of undulate folds; beak cavities deep; hinge consisting of heavy, low cardinals and short, strong lamellar teeth with distinct angle between these elements. *Pleist.-Rec.,* E.Asia.——FIG. D36,*3*. **R. tauriformis* (FULTON), Rec.; *3a-d,* LV ext., RV int., LV int., both valves dorsal, ×1 (Haas).

Schepmania HAAS, 1912 [**Unio nieuwenhuisi* SCHEPMAN, 1892; OD]. Elongate, rounded in front and behind, rather high and heavy, beaks not prominent; posterior slope crossed by parallel folds originating at posterior ridge and curving up toward dorsal margin; hinge normal for family, cardinals low and stout, lamellar teeth low and short; interdental interval long and smooth. *Rec.,* W.Pac.(Borneo).——FIG. D37,*3*. **S. nieuwenhuisi* (SCHEPMAN); *3a-c,* LV ext., RV int., both valves dorsal, ×0.75 (Haas).

Sulcatapex YEN, 1945 [**S. cretaceus*; OD]. Trapezoidal to subtriangular in outline, inflated, heavy, with prominent umbones and strong ligament trace; beaks near anterior end, slightly incurved and sculptured with broad, radiating wrinkles together with coarse, subregularly concentric ridges; posterior slope well marked; hinge massive, with broad plate; cardinals of subrhomboidal shape, ragged and heavy; lamellar teeth moderately developed, more or less impressed; muscle scar deep and of irregular shape. *L.Cret.,* N.Am.——FIG. D37,*4*. **S. cretaceus*; *4a,b,* LV int., both valves dorsal, ×1 *(1011)*.

Tritogonia L. AGASSIZ, 1852 [**Unio verrucosus* SAY, 1834 (=**Unio tuberculatus* BARNES, 1823); OD]. Elongate rhomboid, heavy with strong posterior slope, obliquely truncated behind in males, somewhat compressed and rounded in females; base incurved, whole disc of female, except posterior wing, covered with pustules; beaks rather low, bearing irregular, subparallel ridges posteriorly curved upward; periostracum dark olive; hinge normal, hinge plate narrow, lamellar teeth long, straight, near cardinals; cavity of beaks rather deep. *Rec.,* N.Am.——FIG. D37,*6*. **T. verrucosa* (SAY); *6a,b,* LV ext., both valves dorsal, ×0.5 *(497)*.

Subfamily ANODONTINAE Ortmann, 1910

Shell thin to medium thick, of variable shape; hinge either toothless or with short posterior lamellar elements which cannot be homologized with those of previously treated subfamilies since they arise directly from dorsal margin of shell and not from a hinge plate, being sometimes termed "claustra," in contrast to "lamellar teeth" or "laterals." Beak sculpture consists of concentric, wavy ridges. Marsupium pad-shaped, occupying entire outer gills; fully developed glochidia kept within marsupium over winter; a special device for oxygen supply of glochidia within the gills has been developed, the so-called lateral (or Ortmann's) water tubes. *U.Cret.-Rec.*

Anodonta LAMARCK, 1799 [**Mytilus cygneus* LINNÉ, 1758, *nom. conserv.*] [=*Glochidium* RATHKE, 1797; *Anodontigenus* RENIER, 1807; *Cista* HUEBNER, 1810; *Anodon* OKEN, 1815; *Anodontes* CUVIER, 1817; *Edentula, Lipodonta* NITZSCH, 1820; *Anodonte* FISCHER VON WALDHEIM, 1823; *Onodon* PARTINGTON, 1836-37; *Anodontina* SCHLUETER, 1853; *Colletoperum* BOURGUIGNAT, 1881; *Pteranodon* L. FISCHER, 1886; *Euanodonta* WESTERLUND, 1890; *Nayadina* DE GREGORIO, 1914; *Anodota* PETRBOK, 1930; *Collopterum* BÉDÉ, 1932; *Euphrata* PALLARY, 1933]. Irregularly elliptical, thin, flattened to inflated, uncommonly winged slightly behind; beak sculpture consisting of parallel ridges, usually doubly looped, becoming slightly nodulose on loops; surface smooth, periostracum lustrous; hinge reduced to thin margins of shell, curved, but some in lacustrine habitats with traces of claustra; accompanied by symphynoty of posterior wing (*Colletopterum* phase). *U.Cret.-Rec.,* worldwide in northern hemisphere.

A. (Anodonta). Beak subcentral, moderately strong posterior ridge and dorsal wing, surface smooth except for growth lines. *U.Cret.-Rec.,* holarctic. ——FIG. D38,*3*. **A.* (*A.*) *cygnea* (LINNÉ), Rec.; LV ext., ×0.25 (*497*).

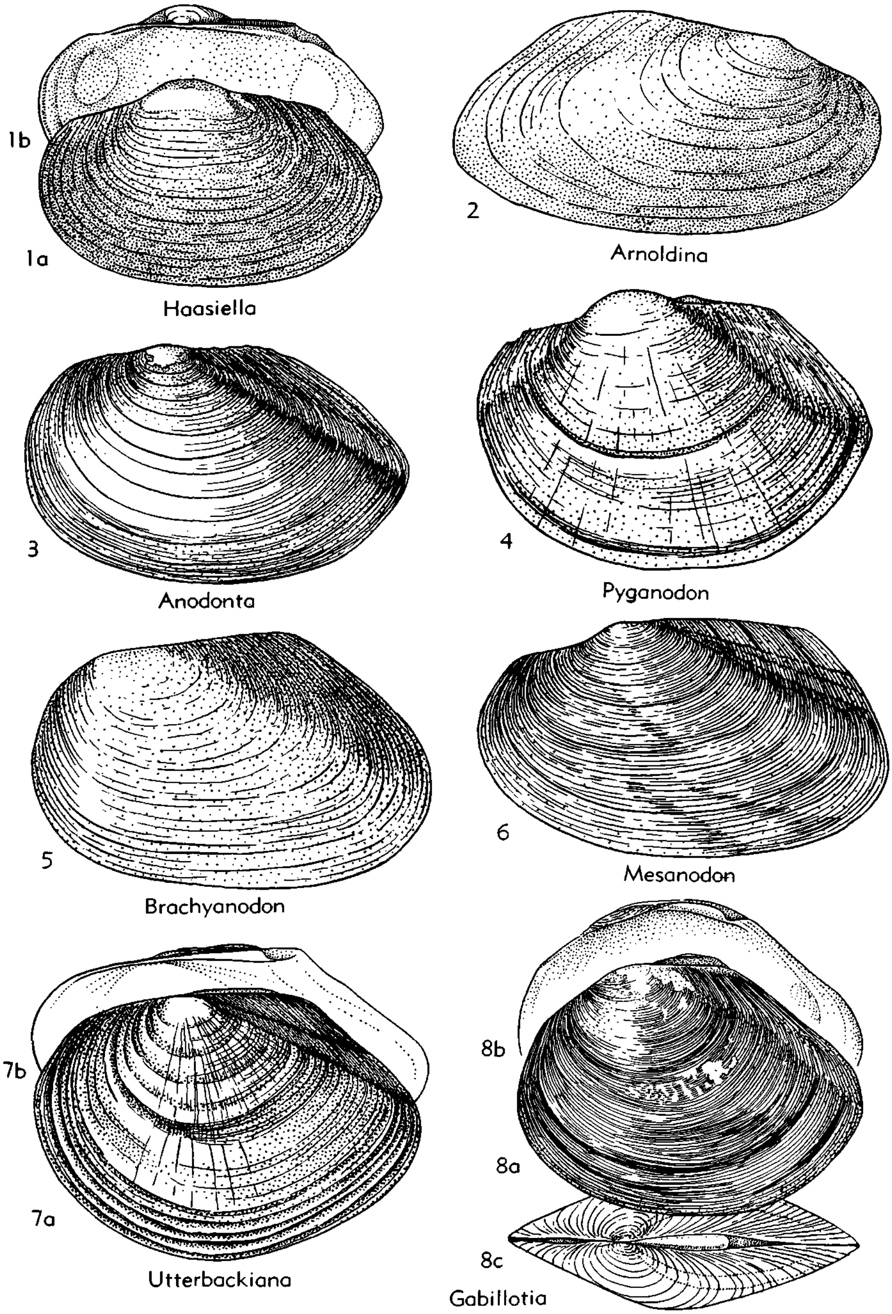


FIG. D38. Unionidae (Anodontinae) (p. *N*442-*N*444).

A. (Arnoldina) Hannibal, 1912 [**A. dejecta* Lewis, 1875; OD]. Elongate-elliptical, broader behind; beaks not prominent, their sculpture consisting of numerous irregular ridges which tend to become doubly looped and nodulose. *Pleist.-Rec.,* USA(Calif.).——Fig. D38,*2.* **A. (A.) dejecta* Lewis, Pleist.; RV ext., ×0.7 *(386).*

A. (Brachyanodon) Crosse & Fischer, 1893 [**A. chapalensis* Crosse & Fischer, 1892 (=**A. coarctata* Anton, 1839); SD Thiele, 1934]. Short, beaks anteriorly situated, not prominent, dorsal margin ascending behind beaks. *Rec.,* C.Am.——Fig. D38,*5.* **A. (B.) coarctata* Anton; LV ext., ×1 *(497).*

A. (Gabillotia) Servain, 1890 [**A. pseudodopsis* Locard, 1883; SD Simpson, 1900]. Large, moderately thick, slightly compressed, subrhomboid, gaping behind; beaks low, with fine, broken, concentric sculpture; hinge line very short, edentulous, invaded by periostracum. *L.Plio.(U. Maeot.)-Rec.,* SE. Eu.-SW. Asia (Syria).——Fig. D38,*8.* **A. (G.) pseudodopsis* Locard, Rec.; *8a-c,* LV ext., RV int., both valves dorsal, ×0.4 *(481).*

A. (Haasiella) Lindholm, 1925 [**A. arcaeformis* Heude, 1877; OD]. Very inflated, with beaks almost central. Glochidium without hook or filament. *Rec.,* E.Asia.——Fig. D38,*1.* **A. (H.) arcaeformis* Heude; *1a,b,* LV ext., RV int., ×0.5 *(405).*

A. (Liouvillea) Bédé, 1932 [**A. pallaryi*; OD]. Hinge with feeble "cardinals" and 2 claustra in RV, and with single claustrum in LV [Doubtful subgenus; good figure unavailable.] *Rec.,* N.Afr.

A. (Mesanodon) Crosse & Fischer, 1893 [**A. lurulenta* Morelet, 1849; SD Thiele, 1934]. Subrhomboid or ovoid, thin, inflated, with well-developed low dorsal wing; beaks low, sharp, their sculpture unknown; periostracum green or olive. *Rec.,* C.Am.——Fig. D38,*6.* **A. (M.) lurulenta* Morelet; LV ext., ×1 *(306).*

A. (Pyganodon) Crosse & Fischer, 1893 [**A. globosa* Lea, 1841; SD Frierson, 1927]. Large, oval, thin, inflated; beaks submedian, full and rather high, with looped and nodulose sculpture; periostracum lustrous bluish-green. *Rec.,* C.Am. ——Fig. D38,*4.* **A. (P.) globosa* Lea; LV ext., ×0.4 *(306).*

A. (Utterbackiana) Frierson, 1927 [**A. suborbiculata* Say, 1831; OD] [=*Utterbachia, Utterbackia,* F. C. Baker, 1927]. Large compressed, suborbicular, somewhat produced near middle of base, rounded in front, bluntly pointed behind; beaks flattened, bearing few irregular ridges, generally broken into nodules, or only corrugated; posterior ridge distinct; disc smooth, periostracum delicately rayed near beaks. *Rec.,* N.Am.——Fig. D38,*7.* **A. (U.) suborbiculata* Say; *7a,b,* LV ext., RV int., ×0.3 *(140).*

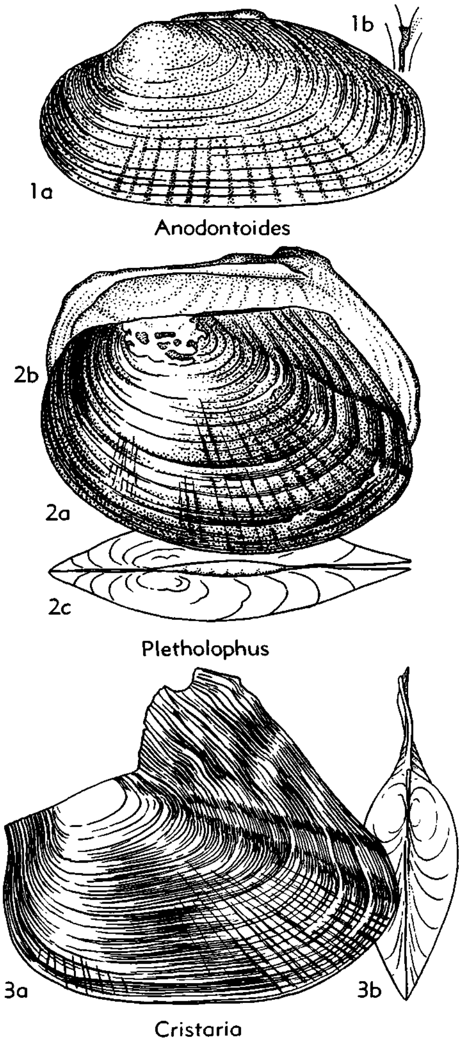


Fig. D39. Unionidae (Anodontinae) (p *N*444-*N*446).

Anodontoides Simpson, 1898 [*pro Anodontopsis* Simpson, 1898 (*non* M'Coy, 1851)] [**Anodonta ferussaciana* Lea, 1834; OD]. Elliptical, inflated, thin, some constricted at center of base; beaks rather full, with few coarse, subparallel, concentric ridges, curved up abruptly toward rear, superimposed on fine radiating ridges; periostracum smooth, shining, commonly rayed; hinge line slightly curved in front of beaks, edentulous or with rudimentary claustra. *Pleist.-Rec.,* N.Am.——Fig. D39,*1.* **A. ferussacianus* (Lea), Rec.; *1a,b,* LV ext., hinges, ×0.75 *(497).*

Cristaria Schumacher, 1817 [*pro Dipsas* Leach, 1814 (*non* LAURENTI, 1768)] [**Dipsas plicatus* LEACH, 1815; OD] [=*Barbala* Museum Callonnianum, 1797, *nom. nud.*; *Appius* MENKE, 1830; *Dianisotis* RAFINESQUE, 1831; *Dipsada* CUVIER, 1834; *Dipsax* VOIGT, 1834; *Dipsus* GRAY, 1835; *Dionisotis* FÉRUSSAC, 1835; *Barbata* SOWERBY, 1839; ?*Craspedodonta* KUESTER, 1842; *Cleone* GISTEL, 1848; *Dypsas* KOBELT, 1880; *Crassitesta,*

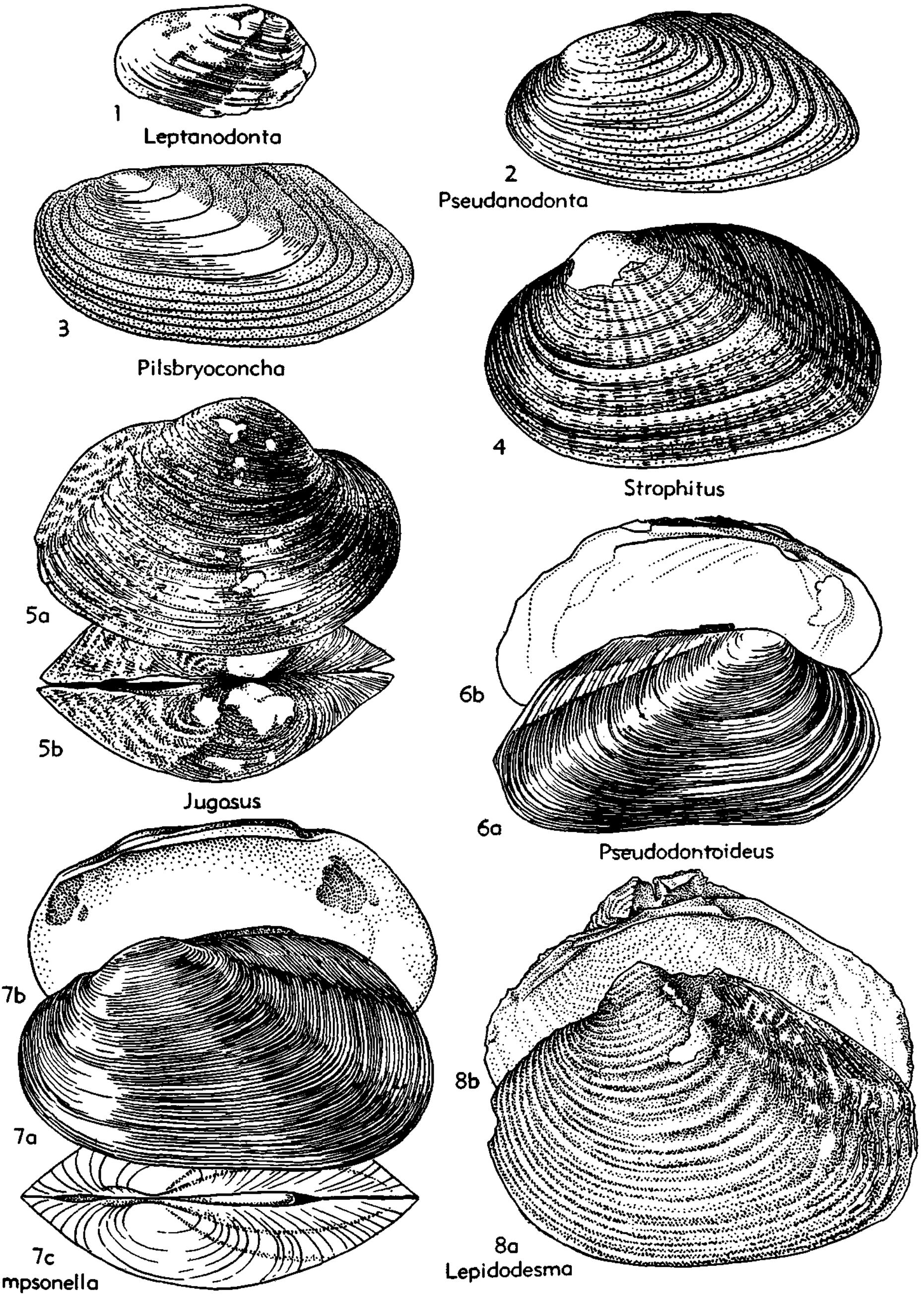


FIG. D40. Unionidae (Anodontinae) (p. N446).

Clione Simpson, 1900]. Mostly thin, elliptical, winged posteriorly and symphynote; beaks rather low, sculptured with fine, somewhat doubly looped ridges at first, and later with coarse, low concentric ridges, nearly parallel with growth lines; periostracum smooth, commonly rayed; hinge with anterior claustrum wanting or vestigial and with elongate remote posterior claustrum in each valve. *Tert.(Mieken Ser.)-Rec.,* E.Asia-Japan.

C. (Cristaria). Large, thin, thicker in front, strongly winged posteriorly, with 2 rows of plications on posterior slope. *Tert.-Rec.,* E.Asia-Japan.——Fig. D39,*3*. **C. (C.) plicata* (Leach), Rec.; *3a,b,* LV ext., both valves dorsal, ×0.3 *(140)*.

C. (Pletholophus) Simpson, 1900 [**Symphynota discoidea* Lea, 1834; OD]. Short, elliptical, lenticular, with compressed beaks sculptured with low, wide, concentric ridges; weakly winged, pointed posteriorly; claustra very weak or wanting. *Rec.,* E.Asia-SE.Asia.——Fig. D39,*2*. **C. (P.) discoidea* (Lea); *3a-c,* LV ext., RV int., both valves dorsal, ×1 *(497)*.

Lepidodesma Simpson, 1900 [**Unio languilata* Heude, 1874; OD]. Large, thin, inflated, with 2 high and sharp posterior ridges; beaks very high and full, with sculpture of cordlike ridges following growth lines and extending over whole shell; with row of radiating nodules on middle of disc and another stronger one on posterior ridge; ligament very large, covered with concentric scales; 2 anterior claustra in LV; 1st elongate, and with 2 long, posterior claustra, higher having edge reflexed upward; an anterior and posterior claustrum in RV; periostracum scaly, folded into hinge. *U.Plio.-Rec.,* E.Asia.——Fig. D40,*8*. **L. languilatum* (Heude), Rec.; *8a,b,* LV ext., RV int., ×0.4 *(405)*.

Leptanodonta Wenz, 1927 [**Dreissenomya unionides* Wenz, 1927 (*non* Fuchs, 1870) (=**Leptanodonta rumana* Wenz, 1941); OD]. Small, thin, rounded trapezoidal, compressed with small, low beaks; dorsal margin straight, sloping anteriorly, anterior margin subangular, ventral and dorsal margins straight, almost parallel, posterior margin somewhat produced; hinge edentulous.*L.Plio.(U.Maeot.),* Eu.(Rumania).——Fig. D40,*1*. **L. rumana;* Wenz; RV ext., ×1 *(966)*.

Pilsbryoconcha Simpson, 1900 [**Unio exilis* Lea, 1839; OD]. Elongate, elliptical, thin, compressed, with low posterior wing, narrow and rounded in front, pointed behind, with almost parallel dorsal and ventral margins, latter expanded posteriorly; beaks low, compressed, sculptured with coarse, irregularly concentric and doubly looped undulations; periostracum smooth, yellowish to brown, faintly rayed in some; hinge edentulous, but commonly with vestiges of faint, compressed claustrum in front of beaks. *Rec.,* SE.Asia-Indon.——Fig. D40,*3*. **P. exilis* (Lea); LV ext., ×0.6 (Haas).

Pseudanodonta Bourguignat, 1877 [**Anodonta complanata* Rossmaessler, 1835; SD Westerlund, 1902] [=*Pseudoanodonta* Picaglia, 1893; *Pseuanodonta* Kennard & Woodward, 1926]. Elongate, compressed, thin, short and rounded in front, long and bluntly pointed behind, with ventral margin gently curved, expanded posteriorly, and dorsal margin almost straight, ascending posteriorly; incipient posterior wing; beaks low, sculptured with 3 to 5 tuberculate ridges; surface smooth, green, hinge edentulous. *Rec.,* Eu.——Fig. D40,*2*. **P. complanata* (Rossmaessler); LV ext., ×0.7 *(798)*.

Simpsonella Cockerell, 1903 [*pro Dalliella* Simpson, 1900 (*non* Cossmann, 1895)] [**Anodonta purpurea* Valenciennes, 1833; OD]. Subtrapezoidal, thin, inflated, with low posterior slope and full beaks bearing sculpture of zigzag ridges which develop into angular protracted ridges on posterior slope; surface smooth; hinge generally toothless, but in some with single vestigial cardinal and equally vestigial, short, low, thin claustrum in each valve; beak cavities moderately deep. *Rec.,* Philip.——Fig. D40,*7*. **S. purpurea* (Valenciennes); *7a-c,* LV ext., RV int., both valves dorsal, ×1 (Haas).

Strophitus Rafinesque, 1820 [**Anodonta undulata* Say, 1816; OD] [=*Strophites* Deshayes, 1832; *Strophilus* Gray, 1847; *Strophites* Desmarest, 1859]. Elliptical to rhomboid, inflated, moderately heavy, pointed or biangular behind, with low posterior slope; beaks full, sculpture consisting of few strong, concentric ridges, which curve sharply upward behind; surface smooth or plicate on posterior slope; periostracum lustrous, rayed in some; hinge line incurved in front of beaks, hinge nearly edentulous except for vestigial compressed anterior claustrum in each valve; posterior claustra rarely present. *Rec.,* N.Am.

S. (Strophitus). Smooth. *Rec.,* N.Am.——Fig. D40,*4*. **S. (S.) undulatus* (Say); LV ext., ×1 (Sowerby).

S. (Jugosus) Simpson, 1914 [**S. wrightianus* Walker, 1901; OD]. Dorsal slope strongly plicate subradially; claustra unusually strong. *Rec.,* N.Am.——Fig. D40,*5*. **S. (J.) wrightianus* Walker; *5a,b,* RV ext., both valves dorsal, ×0.9 (Walker).

S. (Pseudodontoideus) Frierson, 1927 [**Margaritana alabamensis* Lea, 1861; OD] [=*Pseudodontideus* Thiele, 1934]. Beak sculpture consisting of few strong ridges parallel with growth lines; general surface with irregular, concentric sculpture; anterior claustra feeble, low, smooth; posterior claustra obsolescent or absent. *Rec.,* N.Am.——Fig. D40,*6*. **S. (P.) alabamensis* (Lea); *6a,b,* RV ext., LV int., ×0.5 *(140)*.

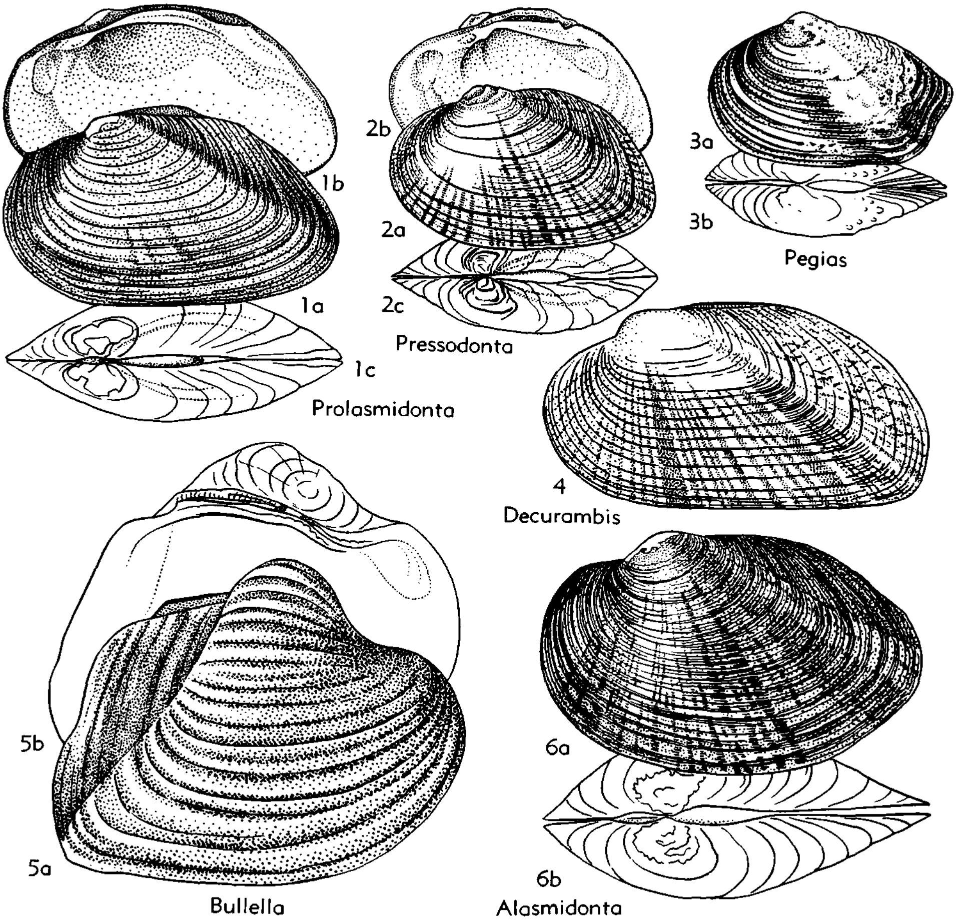


FIG. D41. Unionidae (Alasmidontinae) (p *N*447-*N*448).

Subfamily ALASMIDONTINAE Frierson, 1927

Oval to subrhomboid, compressed to inflated, thin to thick, with low to high posterior slope; beaks with tuberculate double-looped sculpture of strong ridges; disc smooth or with radiating tubercles originating at beaks; hinge incomplete, with anterior obsolescent posterior claustra. Marsupium filling entire outer gills. *U.Oligo.-Rec.*

Alasmidonta SAY, 1818 [*pro Monodonta* SAY, 1816 (*non* LAMARCK, 1801)] [**Monodonta undulata* SAY, 1816; OD] [=*Alasmodonta* SAY, 1819; *Alasmodon* THOMSON, 1820; *Alasmisodonta* DE BLAINVILLE, 1825; *Amblasmodon* RAFINESQUE, 1831; ?*Anadontina* SCHLUETER, 1838; *Uniopsis, Hemidon, Hemiodon* SWAINSON, 1840; *Anelasmodon* L. AGASSIZ, 1846; *Anelasmodonta* HERRMANNSEN, 1846; *Alasmesodonta* GRAY, 1847; *Alasmedonta* GRAY, 1847; *Unionopsis* MEEK, 1876]. Ovate-rhomboid, solid, inflated, with high posterior slope, beaks high, full, with strong, concentric or double-looped sculpture; periostracum lustrous, rayed; 2 anterior claustra in LV and 1 in RV, posterior claustra wanting or imperfect; cavity of beaks deep. *Pleist.-Rec.*, N.Am.

A. (Alasmidonta). Ovate-rhomboid, heavy, inflated, shining, with very strong, generally concentric beak sculpture; anterior claustra solid, low, somewhat radially ridged, posterior claustra short, imperfect or wanting; beak cavities deep, compressed. *Pleist.-Rec.*, N.Am.——FIG. D41,*6*. **A.* (*A.*) *undulata* (SAY), Rec.; *6a,b,* LV ext., both valves dorsal, ×0.8 (Haas, n).

A. (Bullella) SIMPSON, 1900 [**Margarita* (*Margaritana*) *arcula* LEA, 1836; OD]. Thin, greatly inflated, somewhat triangular, with high, sharp posterior slope; beaks very full, with very strong concentric sculpture, extending well on to disc; anterior claustra reflexed, compressed. *Rec.,* N. Am.——FIG. D41,*5*. **A. (B.) arcula* (LEA); *5a,b,* RV ext., LV int., ×1 *(140).*

A. (Decurambis) RAFINESQUE, 1831 [**Alasmodonta scriptum* RAFINESQUE, 1831 (=**Alasmidonta marginata* SAY, 1818); OD] [=*Decarambis* PAETEL, 1875; *Rugifera* SIMPSON, 1900]. Elongate rhomboid, inflated, surface with brilliant rays which commonly break into a dappled or splashed color pattern; posterior slope slightly corrugated; hinge imperfect, posterior claustra wanting. *Rec.,* N.Am.——FIG. D41,*4*. **A. (D.) marginata* SAY; LV ext., ×0.8 *(343).*

A. (Pegias) SIMPSON, 1900 [**Margarita (Margaritana) fabula* LEA, 1836; OD] [=*Pegias* ORTMANN, 1921]. Irregularly subovate, with posterior end greatly elevated above base line, and obliquely truncated below; posterior ridge present; shells of females with posterior ridge better developed and posterobasal truncation more oblique; anterior claustra rather heavy, posterior claustra lacking. *Rec.,* N.Am.——FIG. D41,*3*. **A. (P.) fabula* (LEA); *3a,b,* LV ext., both valves dorsal, ×1 *(497).*

A. (Pressodonta) SIMPSON, 1900 [*pro Calceola* SWAINSON, 1840 (*non* LAMARCK, 1799)] [**Unio calceolus* LEA, 1830; OD]. Rhomboid, with posterior slope low and rounded; periostracum generally with unbroken rays; beak sculpture slightly corrugated; teeth compressed. *Rec.,* N.Am.——FIG. D41,*2*. **A. (P.) calceola* (LEA); *2a-c,* LV ext., RV int., both valves dorsal, ×1 (Walker).

A. (Prolasmidonta) ORTMANN, 1914 [**Unio heterodon* LEA, 1830; OD]. Posterior claustra in reversed position, 2 in RV and 1 in LV; beak sculpture moderately heavy, ridges forming angle on posterior ridge, and slight sinus in front of it; shells of females slightly swollen in region of posterior ridge. *Rec.,* N.Am.——FIG. D41,*1*. **A. (P.) heterodon* (LEA); *1a-c,* LV ext., RV int., both valves dorsal, ×1 *(497).*

Arcidens SIMPSON, 1900 [**Alasmidonta confragose* SAY, 1829; OD]. Moderately thick, inflated, subrhomboidal, with high, full beaks with strong sculpture of irregular corrugations which fall into 2 loops, ridges at base swollen into knobs that continue out in 2 radiating rows on disc; in front and behind beaks are many fine, radial plications, posterior of which follow zigzag course; periostracum dark olive, lustrous; anterior claustra elongate, compressed, 2 in LV and 1 in RV, posterior claustra reduced to numerous indistinct uneven vestiges; beak cavities deep. *Pleist.-Rec.,* N.Am.——FIG. D42,*3*. **A. confragosus* (SAY), Rec.; RV ext., ×0.8 (Walker).

Arkansia ORTMANN & WALKER, 1912 [**A. wheeleri*; OD]. Moderately thick, subrotund to subovate, or subrhomboidal, inflated; disc sculptured with irregular, oblique folds, which may be indistinct; beak sculpture poorly developed, consisting of 2 or 3 double-looped ridges with loops slightly swollen or tuberculose, disappearing toward disc and not merging with its sculpture; hinge well developed, with strong anterior claustra, very strong projection on interdental interval of LV, and with well developed, strong but rather short posterior claustra. *Rec.,* N.Am.——FIG. D42,*4*. **A. wheeleri*; RV ext., ×0.8 (Walker).

Lasmigona RAFINESQUE, 1831 [**Alasmodonta rugosa* BARNES, 1823 (=**Alasmodonta costata* RAFINESQUE, 1820); OD] [=*Elasmogona* L. AGASSIZ, 1846; *Elasmogena* HERRMANNSEN, 1852]. Rhomboid, compressed or inflated posteriorly; beaks low, compressed, bearing sculpture of double-looped ridges, and commonly with radiating ridges in front and behind; anterior claustra heavy or reduced, posterior claustra obsolescent. *Pleist.-Rec.,* N.Am.

L. (Lasmigona). Subrhomboid, compressed, corrugated behind; periostracum lustrous; posterior claustra weakly developed, sloping diagonally downward and backward; cavities of beaks shallow. *Pleist.-Rec.,* N.Am.——FIG. D42,*5*. **L. (L.) costata* (RAFINESQUE); *5a-c,* LV ext., RV int., both valves dorsal, ×0.4 *(497).*

L. (Platynaias) WALKER, 1918 [**Symphinota compressa* LEA, 1829 (=**Unio viridis* RAFINESQUE, 1820); OD]. Shell smooth subsolid, shining, rayed; beak sculpture sharply double-looped; claustra delicate, posterior ones compressed, moderately developed. *?Rec.,* N.Am.——FIG. D42,*2*. **L. (P.) viridis* (RAFINESQUE); *2a-c,* LV ext., RV int., both valves dorsal, ×0.3 *(497).*

L. (Pterosyna) RAFINESQUE, 1831 [**Alasmodonta complanata* BARNES, 1823; OD] [=*Complanaria, ?Megadomus* SWAINSON, 1840; *Pterosygna* SIMPSON, 1900]. Large, ovate-rhomboid, inflated in postbasal region; beaks compressed, with sculpture of sharp strong double loops; periostracum dark, obscurely rayed; claustra heavy. *Rec.,* N. Am.——FIG. D42,*6*. **L. (P.) complanata* (BARNES); *6a-c,* LV ext., RV int., both valves dorsal, ×0.3 *(497).*

L. (Sulcularia) RAFINESQUE, 1831 [**Alasmodonta badia* RAFINESQUE, 1820; OD] [=*Alasminota* ORTMANN, 1914]. Moderately thick, beak sculpture rather strong, doubly looped; periostracum brownish, somewhat rayed; anterior claustra delicate, posterior claustra nearly or entirely wanting. *Rec.,* N.Am.——FIG. D42,*1*. **L. (S.) badia* (RAFINESQUE); *1a,b,* LV ext., both valves dorsal, ×1 *(497).*

Simpsonaias FRIERSON, 1914 [**Alasmidonta ambigua* SAY, 1825; OD] [=*Simpsoniconcha* FRIERSON, 1914]. Small, elongate elliptical, rounded in front and behind, slightly incurved ventrally; beaks rather sharp but not full, ornamented by fine parallel ridges which are looped in middle and open behind; periostracum brownish, rayless; hinge imperfect, with simple irregular anterior claustrum in each valve, posterior claustra obsolescent or lacking; anterior end of shell thickened. *Rec.,* N.Am.——Fig. D43,*1.* **S. ambigua* (Say); RV ext., ×1 (Walker).

Vanderschliea Modell, 1943 [**Unio ḳolasii* Modell, 1931; OD]. Elongate, with nearly parallel dorsal and ventral margins; beak sculpture an anterior shallow loop which curves up and ends in rounded loop; hinge rather strong, complete, 2 anterior and 1 posterior claustra in LV, those of RV being narrow; beak cavities shallow. *U. Oligo. (Cyrenen.-Mergel.),* C.Eu.——Fig. D43,*2.* **V. ḳolasii* (Modell); *2a,b,* LV ext., RV int., ×1 *(631).*

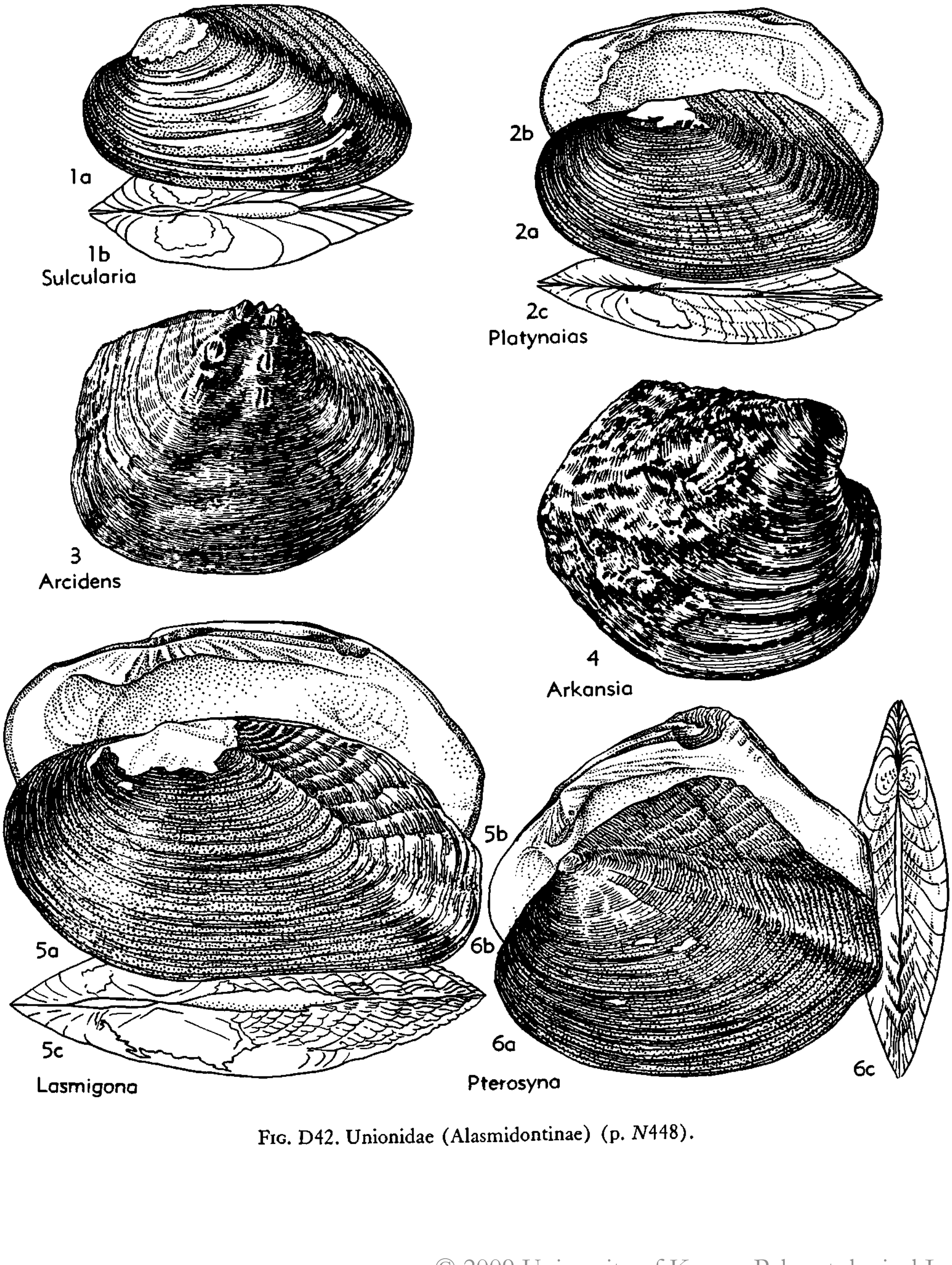


Fig. D42. Unionidae (Alasmidontinae) (p. *N*448).

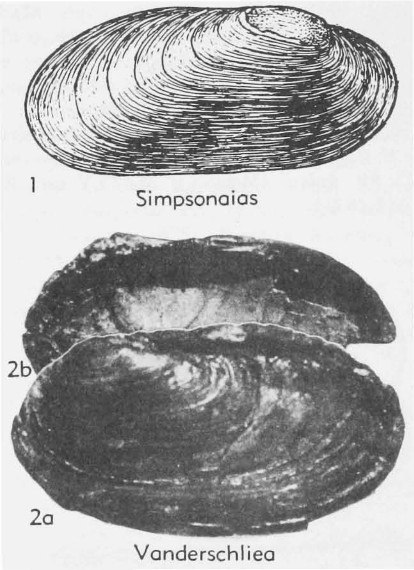


Fig. D43. Unionidae (Alasmidontinae) (p. *N*448-*N*449).

Subfamily LAMPSILINAE Ortmann, 1912

Shell generally thin and without sculpture on disc; periostracum generally lustrous and rayed; hinge complete, interdental interval never flat, but smooth and rounded. [Most Lampsilinae show sexual dimorphism of the shell to a greater or lesser extent. The marsupium occupies only the posterior part of the outer gills, the marsupial portion being differentiated even when not occupied.] *?Trias., L.Oligo.-Rec.*

Lampsilis Rafinesque, 1820 [**Unio ovatus* Say, 1823; SD Herrmannsen, 1846] [=*Aeglia* Swainson, 1840]. Oval to elliptical, generally smooth, usually without posterior ridge; periostracum mostly smooth, lustrous, commonly rayed; sculpture obsolete or with double-looped parallel ridges, posterior loop open behind; hinge normal, but auxiliary cardinal may occur in RV; female shell with strong inflation and dilatation in postbasal region, producing posterior truncation of shell. *?Trias., L.Oligo.-Rec.,* N.Am.-C.Am.

L. (Lampsilis). Weak posterior ridge, beak raised above straight dorsum, narrow rays. *?Trias., L. Oligo.-Rec.,* N.Am.-C.Am.——Fig. D44,*5*. **L. (L.) ovata* (Say), Rec.; *5a,b,* RV ext., both valves dorsal, ×0.6 *(497)*.

L. (Cyrtonaias) Crosse & Fischer, 1893 [**Unio berlandieri* Lea, 1857; OD] [=*Cyrtonais* Frierson, 1927]. Oval or subtetragonal, heavy; beaks generally full; disc smooth or concentrically striated. *Rec.,* N.Am.-C.Am.——Fig. D44,*3*. **L. (C.) berlandieri* (Lea); RV ext., ×0.5 *(535)*.

L. (Delphinonaias) Crosse & Fischer, 1893 [**Unio delphinulus* Morelet, 1849; OD]. Very compressed, posterodorsal margin raised into high wing; cardinals compressed. *Rec.,* C. Am.——Fig. D44,*9*. **L. (D.) delphinulus* (Morelet); RV ext., ×0.7 *(306)*.

L. (Disconaias) Crosse & Fischer, 1893 [**Unio discus* Lea, 1838; OD]. Large, oval or subtrigonal, very much compressed, concentrically striated; cardinals strong, lamellar teeth very long and furrowed. *Rec.,* N.Am.(Mex.).——Fig. D44, *4*. **L. (D.) discus* (Lea); *4a,b,* LV ext., both valves dorsal, ×0.3 *(497)*.

L. (Mesonaias) Crosse & Fischer, 1893 [**Unio explicatus* Morelet, 1849; OD]. Transverse oval, high, beaks not prominent; disc smooth or concentrically striated; cardinals oblique, compressed. *Rec.,* C.Am.——Fig. D44,*2*. **L. (M.) explicata* (Morelet); *2a,b,* LV ext., RV int., ×0.4 *(306)*.

L. (Ortmanniana) Frierson, 1927 [**Unio carinatus* Barnes, 1823; OD]. Heavy, very elliptical, moderately inflated; periostracum yellowish-green, broadly rayed; beaks not prominent, sculpture fine, restricted to tips; cardinals rather small, stumpy; female shell not greatly swollen in postbasal region. *Rec.,* N.Am.——Fig. D44,*7*. **L. (O.) carinata* (Barnes); *7a-c,* RV ext., LV int., both valves dorsal, ×0.5 *(497)*.

L. (Phyllonaias) Crosse & Fischer, 1893 [**Unio paludosus* Morelet, 1849; OD]. Flat, posterodorsal margin high, forming rudimentary wing; cardinals mostly compressed. *Rec.,* C.Am.——Fig. D44,*8*. **L. (P.) paludosa* (Morelet); *8a,b,* LV ext., RV int., ×0.7 *(306)*.

L. (Venustaconcha) Frierson, 1927 [**Unio venustus* Lea, 1838; OD] [=*Venusta* Frierson, 1927 (*non* O. Boettger, 1877, *nec* Barrande, 1881)]. Elliptical, slightly inflated, pointed behind; beak sculpture doubly looped, rear loop open behind in some; periostracum dull, rayed, with wavy lines, generally arranged in bands; female shell only slightly swollen at posterior base, behind which is slight sinus. *Rec.,* N.Am.——Fig. D44, *6*. **L. (V.) venusta* (Lea); RV ext., ×1 *(535)*.

L. (Villosa) Frierson, 1927 [**Lampsilis villosus* Wright, 1898; OD]. Small, obovate, inflated; beaks rather high, sculptured with fine, parallel ridges arranged in double loop, that in front being large and rounded, that behind small and rather pointed below; periostracum varying from smooth to somewhat clothlike, always showing green tints when seen through transmitted light, indistinctly rayed; greatest height of shell just behind center, greatest diameter just in front of center or behind beaks; hinge teeth compressed.

Rec., N.Am.——Fig. D44,*1*. *L. *(V.) villosa* Wright; RV ext., ×1 (Simpson).

Actinonaias Crosse & Fischer, 1893 [*Unio *sapotalensis* Lea, 1841; OD]. Elliptical to rhomboid, heavy, somewhat inflated; beaks low, their sculpture not known; surface smooth; periostracum lustrous, with divided rays; cardinals short, heavy. *Pleist.-Rec.,* N.Am.(Mex.).——Fig. D45,*2*. *A. *sapotalensis* (Lea), Rec.; RV ext., ×0.8 *(535)*.

Carunculina Simpson, 1900 [*Unio *texasensis* Lea, 1857; OD] [=?*Toxolasma* Rafinesque, 1831; ?*Toxelasma* L. Agassiz, 1847]. Small, inflated, obovate, rather solid; periostracum thick, lusterless, almost rayless, clothlike; beak sculpture consisting

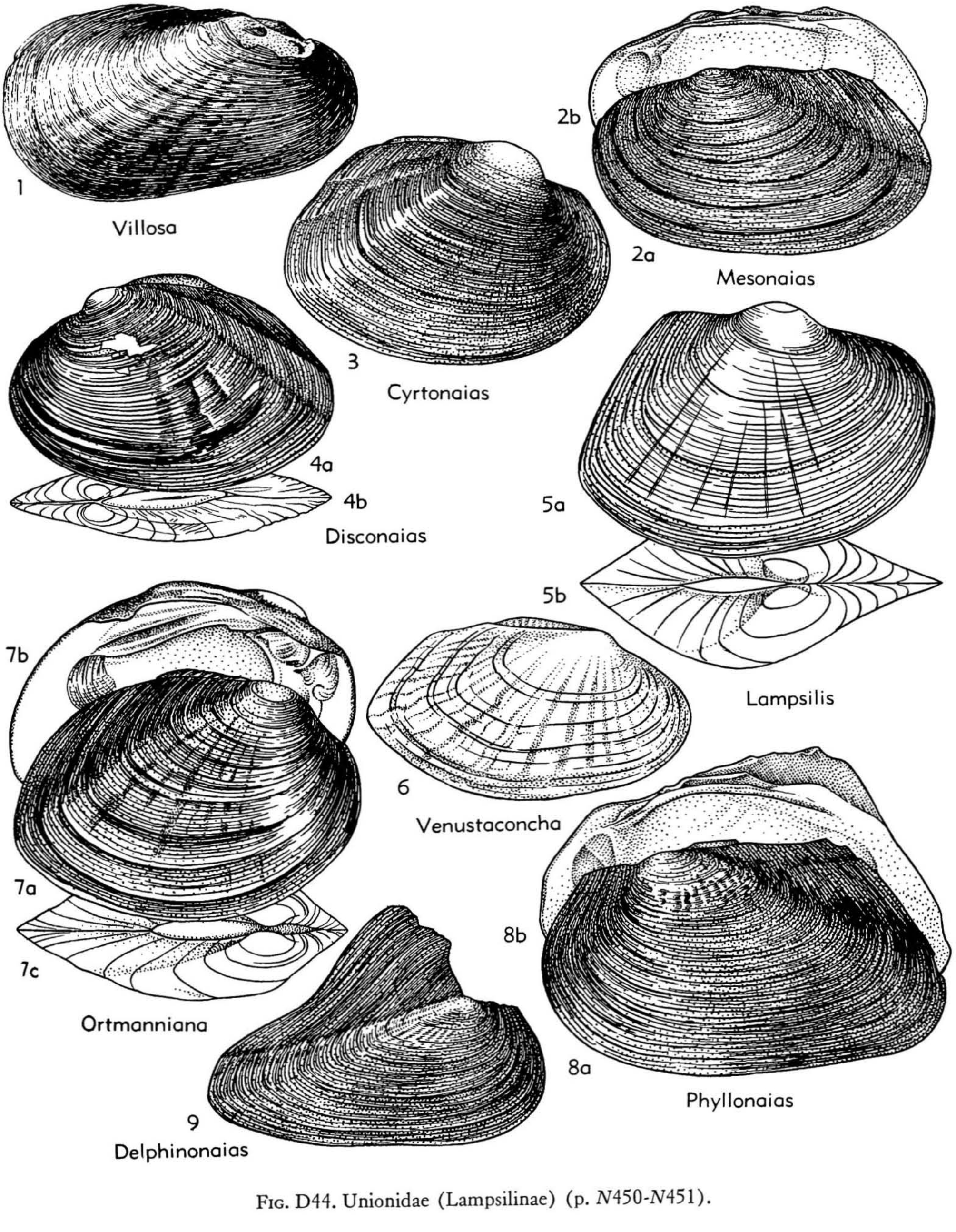


Fig. D44. Unionidae (Lampsilinae) (p. *N*450-*N*451).

of rather strong, concentric ridges which usually form 1 single rounded loop in front and are strongly curved upward behind; cardinals compressed, mostly reflexed upward; male shell somewhat pointed behind, female shell truncated obliquely on posterior base. *Rec.,* N.Am.——Fig. D45,*1.* **C. parva texasensis* (Lea); *1a,b,* RV ext., LV int., ×1 *(535).*

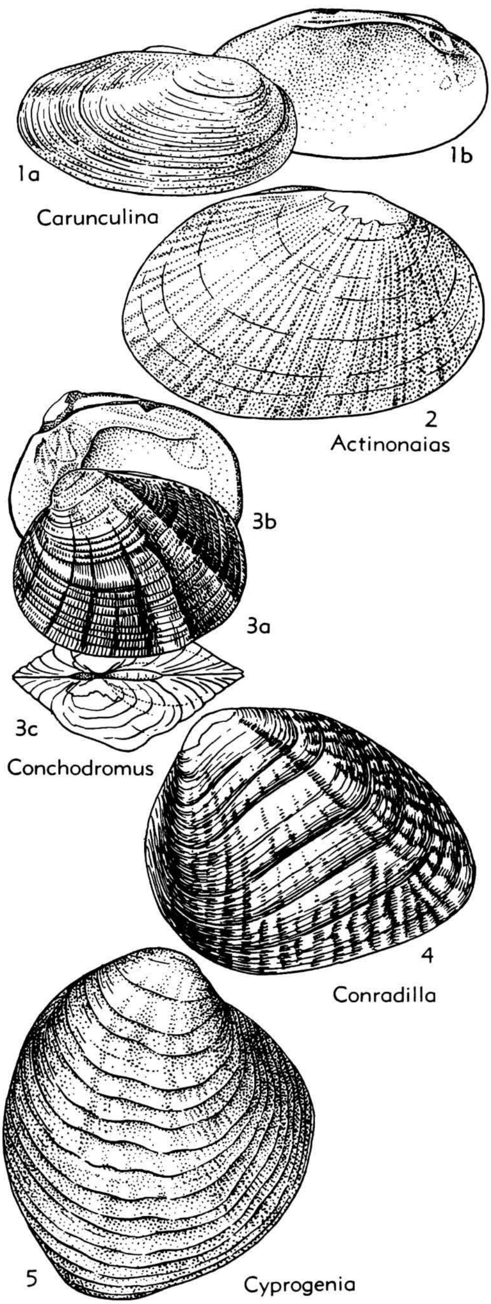


Fig. D45. Unionidae (Lampsilinae) (p. *N*451-*N*452).

Conchodromus Haas, 1930 [*pro Dromus* Simpson, 1900 (*non* Selby, 1840)] [**Unio dromus* Lea, 1834; OD]. Heavy, rounded-triangular; beaks very anterior, rather high, with sculpture of fine ridges running parallel with growth lines, furrows between ridges interrupted at distinct posterior ridge, row of humps running down from beaks to center of ventral margin, otherwise shell sculptured by irregular concentric ridges; periostracum marked by wavy, radial fine lines or maculations; hinge plate wide, cardinals triangular, small, low, lamellar teeth short, low; cavity of beaks deep and compressed. *Rec.,* N.Am.——Fig. D45,*3.* **C. dromus* (Lea); *3a-c,* LV ext., RV int., both valves dorsal, ×0.5 *(497).*

Conradilla Ortmann, 1921 [**Unio caelatus* Conrad, 1834; OD] [=?*Lemiox* Rafinesque, 1831]. Subtriangular to ovate, solid; beaks sculpture almost absent, consisting of few feeble double-looped ridges; periostracum dark, feebly rayed with undulating lines; hinge teeth heavy, lamellar teeth club-shaped, truncate behind; female shell swollen in posterobasal region, swelling irregularly ridged in some. *Rec.,* N.Am.——Fig. D45,*4.* **C. caelata* (Conrad); LV ext., ×1 (Reeve).

Cyprogenia L. Agassiz, 1852 [**Unio irroratus* Lea, 1830 (=**Obovaria stegaria* Rafinesque, 1820); OD] [=*Crypogenia* Fischer, 1886]. Heavy, inflated, rounded triangular, mostly biangular behind; umbonal region flattened, beaks curved inward and forward, sculptured faintly with double-looped ridges; sculpture of disc nodular, radially wrinkled or lachrymose; periostracum shining, with delicate dark mottling on light background; hinge plate wide, flat, cardinals long, triangular, lamellar teeth short, obliquely striated; cavity of beaks not deep. *Rec.,* N.Am.——Fig. D45,*5.* **C. stegaria* (Rafinesque); RV ext., ×1 *(535).*

Dysnomia L. Agassiz, 1852 [**Obliquaria flexuosa* Rafinesque, 1820; OD] [=*Epioblasma* Rafinesque, 1831; *Disnomia* Bielz, 1869; *Dysonomia* Paetel, 1890; *Epilobasma* Simpson, 1900]. Shell of males with posterior and central radiating ridge, that of females with great produced inflation which is continuation of central ridge. *Rec.,* N.Am.

D. (Dysnomia). Shell of males with wide, flattened space between central and posterior ridges, that of females with produced inflation but little behind center of base. *Rec.,* N.Am.——Fig. D46, *4.* **D. (D.) flexuosa* (Rafinesque); *4a,b,* ♂ RV ext., ♀ RV ext., ×0.5 (Walker).

D. (Capsaeformis) Frierson, 1927 [**Unio capsaeformis* Lea, 1834; OD]. Male shells but little inflated or compressed, rounded into postbasal flap. *Rec.,* N.Am.——Fig. D46,*5.* **D. (C.) cap-*

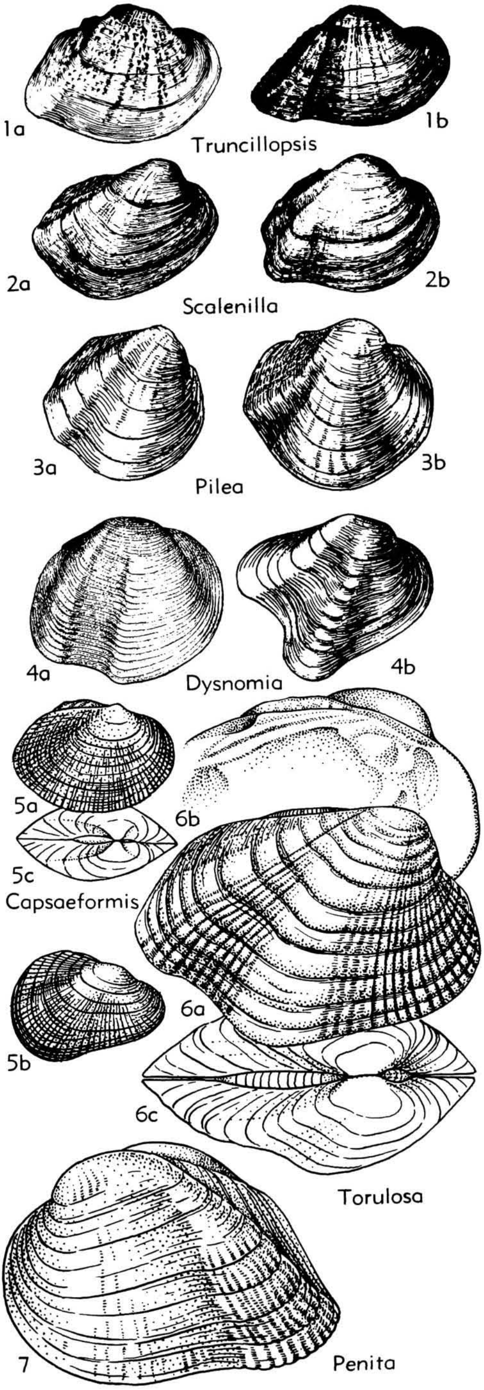


FIG. D46. Unionidae (Lampsilinae) (p. *N*452-*N*453).

saeformis (LEA); *5a-c,* ♂RV ext., ♀RV ext., both valves dorsal, ×0.5 *(497).*

D. (Penita) FRIERSON, 1927 [**Unio penitus* CONRAD, 1834; OD]. Somewhat quadrate, not sharply truncate behind; swelling of female in front of posterobsasal point and rounded below. *Rec.,* N.Am.——FIG. D46,*7*. **D. (P.) penita* (CONRAD); LV ext., ×1 (Reeve).

D. (Pilea) SIMPSON, 1900 [**Unio personatus* SAY, 1829; OD]. Male shell with wide shallow, radiating depression in front of posterior ridge, those of females with rounded, foliaceous swelling at posterior base. *Rec.,* N.Am.——FIG. D46,*3*. **D. (P.) personata* (SAY); *3a,b,* ♂RV ext., ♀RV ext., ×0.5 (Walker).

D. (Scalenilla) ORTMANN & WALKER, 1922 [**Unio sulcatus* LEA, 1830; OD]. Male shell with wide radiating shallow depression in front of posterior ridge; that of female with small well-defined radial postbasal swelling. *Rec.,* N.Am.——FIG. D46,*2*. **D. (S.) sulcata* (LEA); *2a,b,* ♂RV ext., ♀RV ext., ×0.5 (Walker).

D. (Torulosa) FRIERSON, 1927 [**Amblema torulosa* RAFINESQUE, 1820; OD]. Shell of male with median and posterior radiating ridges, both usually nodose; postbasal expansion of female rounded, large, thin, placed far back. *Rec.,* N. Am.——FIG. D46,*6*. **D. (T.) torulosa* (RAFINESQUE); *6a-c,* RV ext., LV int., both valves dorsal, ×0.7 *(535).*

D. (Truncillopsis) ORTMANN & WALKER, 1922 [**Truncilla triqueter* RAFINESQUE, 1820; OD]. Greatly inflated, sharply truncate posteriorly; inflation of female shell at extreme posterobasal point. *Rec.,* N.Am.——FIG. D46,*1*. **D. (T.) triquetra* (RAFINESQUE); *1a,b,* ♂RV ext., ♀RV ext., ×0.5 (Walker).

Friersonia ORTMANN, 1912 [**Lampsilis iridella* PILSBRY & FRIERSON, 1908; OD]. Subelliptical, without distinct posterior ridge; disc unsculptured; beak sculpture consisting of 6 to 8 ridges, later ones being distinctly double-looped and interrupted in middle; periostracum greenish-yellow rayed; sexual dimorphism of shells not marked. *Rec.,* N.Am.(Mex.).——FIG. D47,*6*. **F. iridella* (PILSBRY & FRIERSON); *6a,b,* LV ext., RV int., ×1 (Pilsbry & Frierson).

Glebula CONRAD, 1853 [**Unio rotundata* LAMARCK, 1819; OD]. Short, elliptical, biangularly pointed behind, heavy, much inflated, with low posterior ridge; beaks compressed, their sculpture not known; periostracum brownish, clothlike; hinge plate very narrow, cardinals split, in each valve, into many (up to 12) irregularly radiating, compressed, granular processes; lamellar teeth short, remote; cavity of beaks shallow; shell of females swollen at posterior base. *Rec.,* N.Am.——FIG. D47,*7*. **G. rotundata* (LAMARCK); *7a,b,* LV ext., both valves dorsal, ×0.8 *(497).*

Leptodea RAFINESQUE, 1820 [**L. leptodon*; OD]

[=*Lasmonos* Rafinesque, 1831; *Monelasmus* L. Agassiz, 1846; *Monelagmus* Paetel, 1875; *Pareptera* Frierson, 1914]. Elongate elliptical, compressed, rather thin, pointed behind; beaks low, their sculpture feeble, with postdorsal wing in young shells and some with vestiges of anterior wing; shell gaping ventrally in front and behind; hinge very imperfect, cardinals commonly wanting, lamellar teeth faint or absent. *Rec.,* N.Am. ——Fig. D47,*4*. **L. leptodon*; *4a-c,* LV ext., RV int., both valves dorsal, ×0.5 *(497)*. [=*Paraptera* Ortmann, 1911.]

Ligumia Swainson, 1840 [**Unio recta* Lamarck, 1819; OD] [=*?Potamilus, ?Potamila* Rafinesque, 1818; *?Sintoxia* Rafinesque, 1820; *Ligumea* Swainson, 1840; *?Syntoxia* L. Agassiz, 1847;

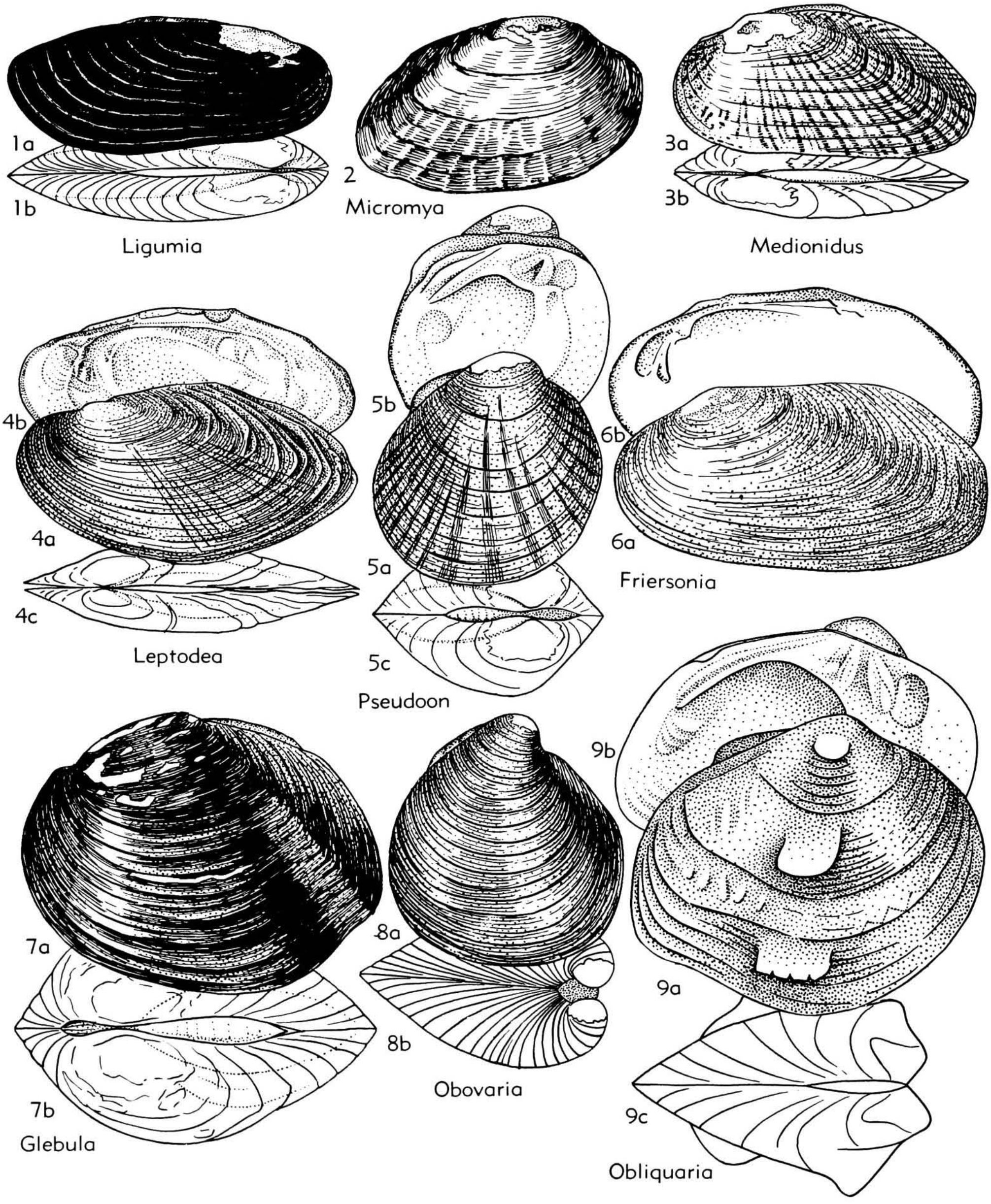


Fig. D47. Unionidae (Lampsilinae) (p. *N*453-*N*455).

Legumia L. Agassiz, 1852; *Ligumina* Philippi, 1853; *?Syntonia* Schaufuss, 1869; *?Syntoina* Paetel, 1875]. Somewhat elongate, smooth, inflated, moderately heavy, sharply pointed behind; female shell much produced at posterior base; periostracum very lustrous, feebly rayed; beaks low, marked with very delicate regular sculpture, posterior loop commonly open behind; cardinals smooth, mostly compressed. *Pleist.-Rec.,* N.Am.——Fig. D47,*1*. **L. recta* (Lamarck), Rec.; *1a,b,* RV ext., both valves dorsal, ×0.3 *(497)*.

Medionidus Simpson, 1900 [**Unio conradianus* Lea, 1834; OD]. Elongate, arcuate in adults, rather inflated, dorsal slope (and adjoining portion of disc in some) wrinkled; beak sculpture of rather fine ridges in 2 loops, anterior rounded, posterior somewhat angular; periostracum lustrous with green rays and irregular spots; cardinals small, massive, more or less roughened, lamellar teeth rather short, remote, slightly curved and club-shaped; shell of females slightly swollen just behind middle of base. Marsupium occupying central posterior portion of outer gills. [*Unio senectus,* from the Paleocene, originally referred to *Medionidus,* is now considered to belong to *Rhabdotophorus.*] *Rec.,* N.Am.——Fig. D47,*3*. **M. conradianus* (Lea); *3a,b,* LV ext., both valves dorsal, ×1 *(497)*.

Micromya L. Agassiz, 1852 [**Unio fabalis* Lea, 1831; OD]. Small to medium, triangular-oval or subelliptical, not very long or much pointed behind; beak sculpture double-looped, commonly obsolete, posterior loop tending to be open; inner edge of the mantle in front of branchial opening of females with row of rather irregular, larger and smaller papillae, reaching not quite to middle of lower margin. *Rec.,* N.Am.——Fig. D47,*2*. **M. fabalis* (Lea); RV ext., ×1 (Walker).

Obliquaria Rafinesque, 1820 [**O. (Quadrula) reflexa*; OD] [=*Oblicaria* d'Orbigny, 1846]. Inflated, solid, oval, pointed behind, with row of large longitudinal knobs running from beaks to center of base; posterior ridge well developed, space between it and row of tubercles somewhat excavated; posterior slope corrugated; beaks prominent, incurved, pointing forward, their sculpture strong and consisting of 4 or 5 heavy parallel ridges low in front, curving upward behind; cardinals strong, ragged, lamellar teeth short, nearly straight; male and female shells essentially alike. *Pleist.-Rec.,* N.Am.——Fig. D47,*9*. **O. reflexa*, Rec.; *9a-c,* RV ext., LV int., both valves dorsal, ×1 *(497)*.

Obovaria Rafinesque, 1819 [**Unio retusa* Lamarck, 1819; SD Simpson, 1900]. Short, oval, rounded or retuse, solid, inflated, thicker in front; beaks high, sculptured with very faint irregular nodulose ridges which tend to fall into 2 loops, posterior commonly open behind; periostracum dull, silky, or clothlike, rarely rayed; cardinals massive, lamellar teeth short, club-shaped. *Pleist.-Rec.,* N.Am.

O. (Obovaria). Shell retuse to oval, short; beaks high, central; cardinals rarely parallel with lamellar teeth; cavity of beaks deep, subcompressed; nacre bluish-white or purple. *Pleist.-Rec.,* N.Am.——Fig. D47,*8*. **O. (O.) retusa* (Lamarck), Rec.; *8a,b,* RV ext., both valves dorsal, ×0.6 *(497)*.

O. (Pseudoon) Simpson, 1900 [**Unio ellipsis* Lea, 1828 (=**Amblema olivaria* Rafinesque, 1819); OD] [=*Actionaias* Ortmann, 1925]. Elliptical, inflated, heavy, that of males pointed behind; periostracum dark, rayless or feebly rayed; beaks anterior, cardinals short or somewhat elongated, massive, tending to be parallel lamellar teeth; nacre silvery. *Rec.,* N.Am.——Fig. D47,*5*. **O. (P.) olivaria* (Rafinesque); *5a-c,* RV ext., LV int., both valves dorsal, ×0.75 *(497)*.

Pachynaias Crosse & Fischer, 1893 [**Unio spheniopsis* Morelet, 1849; OD] [=*Arotonaias* Martens, 1900; *Ptychoderma* Simpson, 1900]. Triangularly ovate or rounded, heavy, with tolerably well-marked posterior ridge; surface marked by strong, irregular concentric sulcae; beaks small, rather prominent, sculptured with fine, irregular, broken ridges which are somewhat double-looped, front loop larger and more rounded; periostracum olive to tawny, wrinkled, feebly rayed in some; hinge plate narrow, cardinals compressed, ragged, lamellar teeth short, slightly curved, obliquely striated; female shells produced in postbasal region. *Rec.,* C.Am.——Fig. D48,*6*. **P. spheniopsis* (Morelet); LV ext., ×1 *(306)*.

Plagiola Rafinesque, 1819 [**Unio securis* Lea, 1829 (=**Obliquaria depressa* Rafinesque, 1820); OD] [=*Plagiolopsis* Thiele, 1934]. Heavy, elongate triangular, more inflated posteriorly in females, with concentrically striate posterior ridge; beaks high, sculptured with fine parallel double-looped ridges, anterior loop rounded, posterior angular; cardinals ragged, lamellar teeth club-shaped, more or less straight; cavity of beaks moderate. *Pleist.-Rec.,* N.Am.——Fig. D48,*4*. **P. depressa* (Rafinesque), Rec.; *4a-c,* RV ext., LV int., both valves dorsal, ×1 *(535)*.

Proptera Rafinesque, 1819 [**Unio alatus* Say, 1825; SD Herrmannsen, 1846] [=*Megaptera* Rafinesque, 1820; *Symphynota* Lea, 1829; *Naidea, Lymnadea, Lymnadia* Swainson, 1840; *Symphinota* Villa, 1841; *Limnadea* L. Agassiz, 1846; *Noidea* Schaufuss, 1869; *Symphionota, Symphyonota* Philippi, 1853]. Rather large, gaping at anterior base and edge of dorsal slope, winged along dorsal region, at least when young; where present, beak sculpture feeble, consisting of anterior and posterior loops, former commonly wanting, latter somewhat rarely nodulose; periostracum clothlike when young, rayless or feebly rayed; teeth compressed, cardinals usually imperfect or wanting, laterals remote; nacre purplish. *Pleist.-Rec.,* N.Am.——FIG. D48,5. **P. alata* (SAY), Rec.; *5a,b,* RV ext., LV int., ×0.4 *(497).*

Ptychobranchus SIMPSON, 1900 [**Unio fasciolaris* HILDRETH, 1828; OD]. Elliptical to triangular, heavy, umbonal region rather elevated; beak sculpture of discontinuous ridges, double-looped in some; hinge normal, cardinals low, rather small, lamellar teeth club-shaped, remote; cavities of beaks shallow. *U.Oligo.(Cyrenen.-Mergel.)-Rec.,* C.Eu.-N.Am.

P. (Ptychobranchus). Triangular, some arcuate when old; posterior slope rounded, well developed; periostracum usually with wavy fine rays or broken, radiating bands, which tend to form

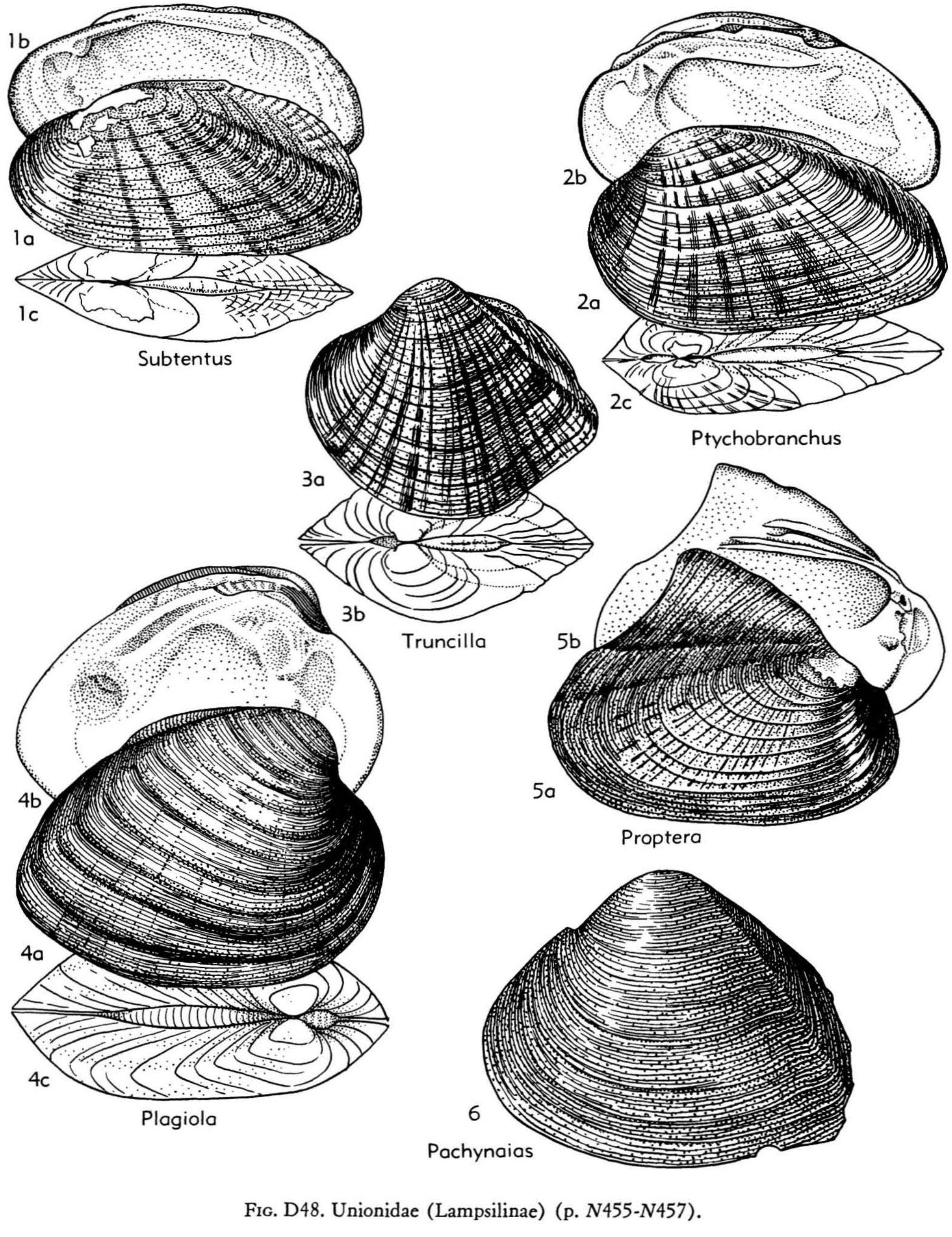


FIG. D48. Unionidae (Lampsilinae) (p. *N*455-*N*457).

square spots. *U.Oligo.(Cyrenen.-Mergel.)-Rec.*, C. Eu.-N.Am.——Fig. D48,*2*. **P. (P.) fasciolaris* (Hildreth), Rec., C.Eu.; *2a-c*, LV ext., RV int., both valves dorsal, ×0.5 *(497)*.

P. (Subtentus) Frierson, 1927 [**Unio subtentus* Say, 1825; OD]. Elongate elliptical, only slightly inflated, with ill-defined posterior ridge and posterior slope strongly wrinkled; periostracum bright, with broken rays which may form irregular patches but usually develop into square spots; shell of female slightly inflated behind middle of base. *Rec.*, N.Am.——Fig. D48,*1*. **P. (S.) subtentus* (Say); *1a-c*, LV ext., RV int., both valves dorsal, ×0.8 *(497)*.

Truncilla Rafinesque, 1820 [**T. truncata*; SD Herrmannsen, 1849] [=*Amygdalonaias* Crosse & Fischer, 1893]. Inflated at posterior slope, posterior ridge sharp and well defined; area of beaks flattened but not compressed, beak sculpture delicate, somewhat broken and double-looped, anterior loop rounded, posterior loop sharp below; periostracum lustrous, with pattern of broken or arrow-shaped rays; hinge delicate, on narrow plate, cardinals rather compressed, high, ragged; female shell slightly swollen at posterior base. *Pleist.-Rec.*, N. Am.——Fig. D48,*3*. **T. truncata*, Rec.; *3a,b*, LV ext., both valves dorsal, ×0.6 *(497)*.

Subfamily HYRIINAE Ortmann, 1911

[This family-group name, based on a junior synonym of *Prisodon*, is retained in accordance with provisions of the Zoological Code (1961), Art. 40]

Shell of variable shape high rounded to long narrow; beak sculpture invariably radial, ranging from restricted to tips and poorly developed to extended over most of disc and well developed; hinge normal, well developed, cardinals tending to become divided radially; anal opening closed above and marsupium occupying only inner gills. *Cret.-Rec.*

Prisodon Schumacher, 1817 [**P. obliquus*; SD Simpson, 1896] [=*Triquetra* Klein, 1753 (*nom nud.*, pre-Linnean); *Hyria* Lamarck, 1819; *Hyri.* de Blainville, 1821; *Ilyiria* Fleming, 1822; *Prysodon* Stefanescu, 1896; *Hyriana* Simpson, 1900]. Aviculiform, solid, somewhat inflated; with well-developed posterior ridge beneath excavated area, generally incurved from its posteroventral extremity to end of posterodorsal wing; posterior slope wtih row of radial plications; disc concentrically sculptured and having delicate radiating lirae throughout, so that surface is finely reticulate; beaks full, not elevated, their sculpture not seen; periostracum yellowish-green, bronze or brownish, lustrous; hinge narrow under beaks, widening in front and behind; LV with 2 elongate compressed cardinals which tend to separate into denticles, and 2 vertically granulostriate lamellar teeth; RV with 2 or more similar cardinals and single lamellar tooth; beak cavities not deep. *Mio.-Rec.*, S.Am.——Fig. D49,*1*. **P. obliquus*, Rec.; LV ext., ×0.4 (Sowerby).

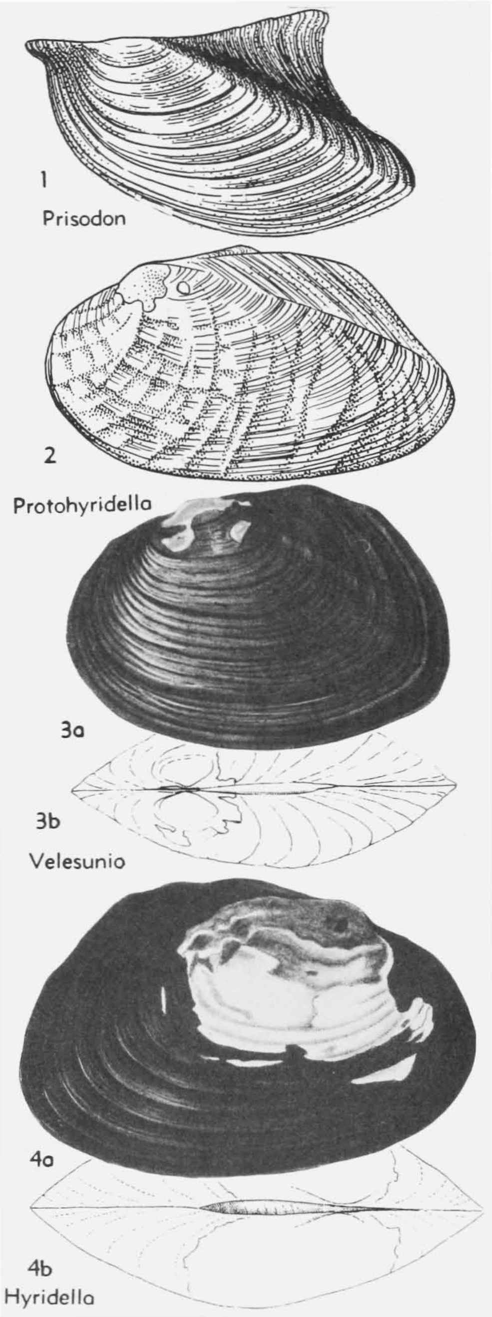


Fig. D49. Unionidae (Hyriinae) (p. *N*457, *N*460-*N*461).

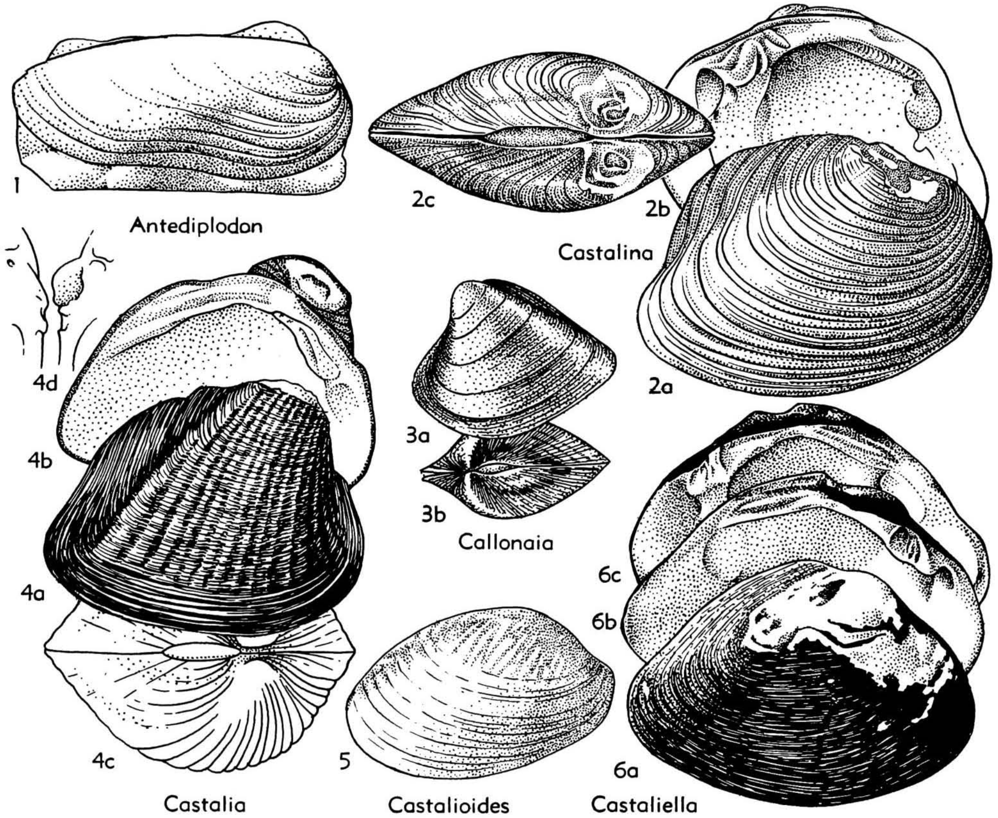


FIG. D50. Unionidae (Hyriinae) (p. *N*458-*N*460).

Antediplodon Marshall, 1929 [**Unio dumblei* Simpson, 1896; OD]. Characterized by elongate form, abrupt anterior end, and especially by sculpture of the beaks, which consists of several fine, radiating ribs. *Plio.,* USA(Tex.).——Fig. D50,*1*. **A. dumblei* (Simpson); RV ext., ×0.8 *(584)*.

Callonaia Simpson, 1900 [**Castalia duprei* Recluz, 1843; OD]. Triangular, thin, inflated, with very high, full beaks apparently devoid of sculpture; shell truncated above; very high, sharp posterior ridge extending to base; anterior end somewhat pointed above, rounded below; ligament very short; disc nearly smooth but somewhat sulcate anteriorly; periostracum bright greenish-yellow, lustrous; hinge line arched, teeth high, compressed; 2 cardinals in each valve, side by side and interlocking; 1 lamellar tooth in RV and 2 in LV, granular and vertically striate; beak cavities very deep, not compressed. *Rec.,* S.Am.(Brazil).——Fig. D50,*3*. **C. duprei* (Recluz); *3a,b,* LV ext., both valves dorsal, ×0.5 (Sowerby).

Castalia Lamarck, 1819 [**C. ambigua*; OD] [=*Tetraplodon* Spix, 1827]. Triangular, heavy, inflated, with high sharp posterior ridge, behind which margin is distinctly truncate; beaks very full and high, sculpture radial or with 1 or 2 pairs of central ribs coalescing below, whole extending over disc as strong ridges; periostracum thick, dark, dull; hinge line arched, all teeth vertically ridged; 1 strong compressed cardinal in LV, 2 in RV, all in front of beaks, behind which lie denticles; 1 lamellar tooth in RV and 2 in LV; beak cavities deep, not compressed. *Rec.,* S.Am.——Fig. D50,*4*. **C. ambigua*; *4a-d,* RV ext., LV int., both valves dorsal, hinges, ×1 *(497)*.

Castaliella Simpson, 1900 [**Castalia sulcata* Krauss, 1849; OD]. Subtriangular, greatly inflated, moderately heavy and strongly sulcate; beaks high, radiately sculptured; posterior ridge well defined, sharp; periostracum reddish chestnut; hinge margin narrow, arched; 2 vertically striated cardinals in RV, 3 in LV, side by side; 1 granular lamellar tooth in RV and 2 in LV; beak cavities deep, not compressed; nacre purple. *Rec.,* NE.S.Am.——Fig. D50,*6*. **C. sulcata* (Krauss); *6a-c,* RV ext., LV int., RV int., ×0.8 (Haas).

Castalina Ihering, 1891 [**C. martensi*; OD].

Somewhat triangular, sides slightly flattened, heavy, with strong posterior ridge, subtruncate posterior slope rising almost to wing above; beaks full, high, with radial sculpture; disc covered by weak irregular, concentric sulci, posterior slope generally plicate or corrugated; periostracum thick, blackish, rayless; hinge plate arched, wide; cardinals radially divided in each valve, with 2 to several denticles; 2 vertically or obliquely striate lamellar teeth in LV and 1 in RV; beak cavities deep. *Rec.,* S.Am.——Fig. D50,*2*. **C. martensi*; *2a-c,* RV ext., int., both valves dorsal, ×0.8 *(427)*.

Castalioides Marshall, 1934 [**C. laddei*; OD]. Shell with strong sculpture of radial ribs, several of innermost pairs arranged to form very long V's; ribs crossing anterior and posterior slopes forming divaricate pattern with radial ribs. *Pleist.,*

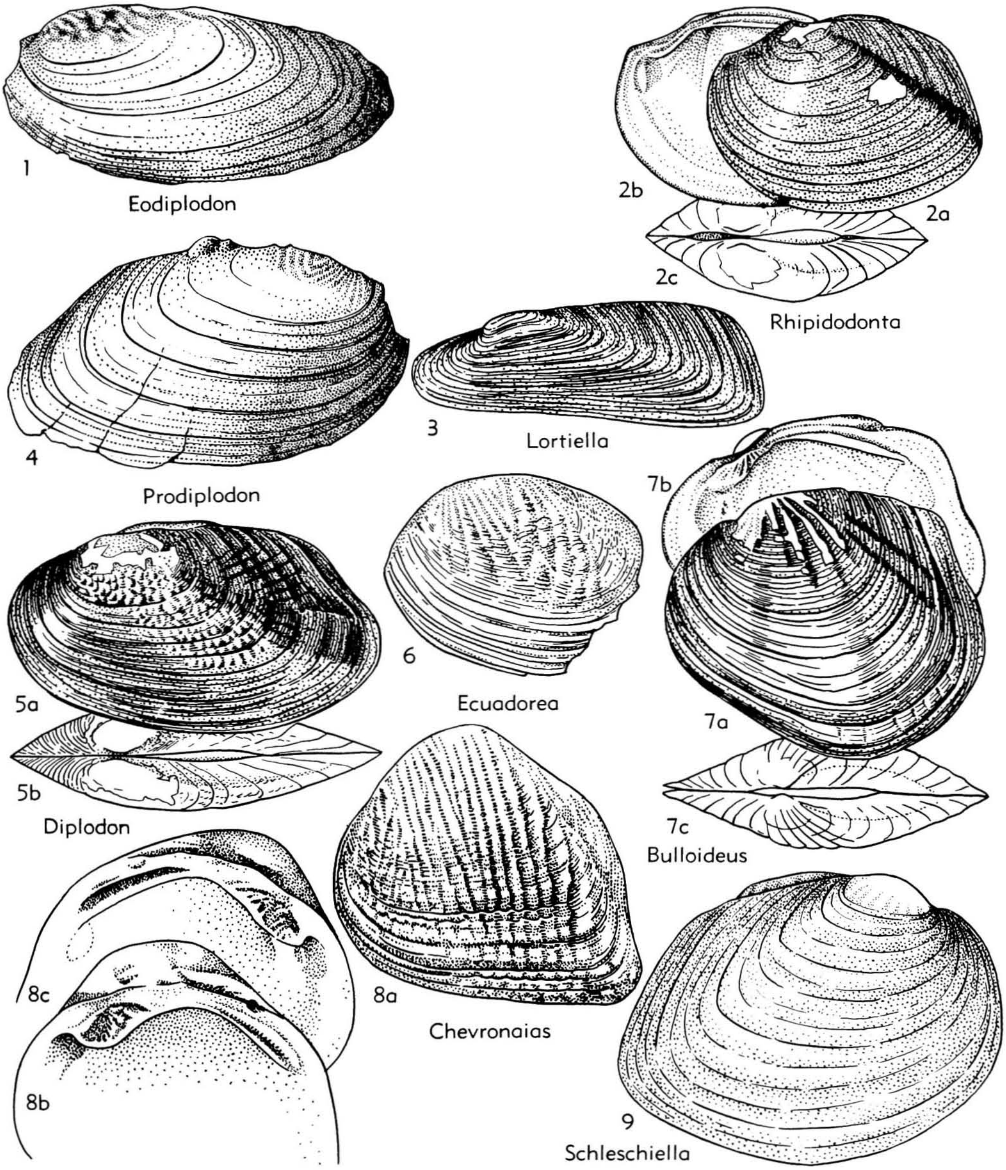


Fig. D51. Unionidae (Hyriinae) (p. *N*460-*N*461).

S.Am.(Venez.).——FIG. D50,*5*. **C. laddei*; RV ext., ×1 *(586)*.

Chevronaias OLSSON & WURTZ, 1951 [**C. colombiana*; OD]. Small, solid, subrhomboidal, bearing strong umbonal angle that divides flattened, depressed, subtruncated posterior slope from disc; hinge as in *Triplodon*; right cardinals low, with deep intervening socket having frilled, minutely pustulate sides; surface of disc with inset chevron-like folds radiating from beaks and spreading over posterior slope; shell cavity deep. *Rec.*, S.Am. (Colom.).——FIG. D51,*8*. **C. colombiana; 8a-c,* LV ext., RV int., LV int., ×1 *(690)*.

Diplodon SPIX, 1827 [**D. ellypticum*; OD] [=*Iridella* SWAINSON, 1840]. Elliptical, rounded, elongate or trapezoidal, with rather low radially sculptured beaks, ridges usually curved and approaching one another below; posterior ridge low or scarcely developed; surface concentrically sculptured, broken in some into fine nodules or corrugations; periostracum dull, rayless; hinge with 2 compressed cardinals (one in front of other) and 2 compressed lamellar teeth in LV; beak cavities shallow. *Cret.-Rec.*, N.Am.-S.Am.

D. (Diplodon). Unbroken ridges covering whole beaks. *Cret.-Rec.*, N.Am.-S.Am.——FIG. D51,*5*. **D. (D.) ellypticus,* Rec.; *5a,b,* LV ext., both valves dorsal, ×1 *(497)*.

D. (Bulloideus) SIMPSON, 1900 [**Unio bulloides* LEA, 1859; OD]. Thin, rounded, inflated, truncate behind and slightly so before, with rather sharp posterior ridge and dorsal wing; beaks full, subcentral, rather high, regularly radially sculptured; periostracum smooth, olive-bronze; cardinals compressed, commonly splitting into denticles, 2 in RV and 1 in LV, 2 lamellar teeth in LV and 1 in RV. *Rec.*, S.Am.——FIG. D51,*7*. **D. (B.) bulloides* (LEA); *7a-c,* LV ext., RV int., both valves dorsal, ×1 *(497)*.

D. (Rhipidodonta) MÖRCH, 1853 [**Unio paranensis* LEA, 1834; OD] [=*Cyclomya* SIMPSON, 1900]. Obovate to suborbicular, narrow in front, produced just behind center of base, generally slightly pointed behind, with very low posterior ridge and slight dorsal wing behind; beaks high, marked by irregular radial ribs; hinge line strongly arched, curved behind and incurved in front of beaks; lower right cardinal largest, commonly subdivided. *Tert.(Guanabanas)-Rec.*, S. Am.——FIG. D51,*2*. **D. (R.) paranensis* (LEA), Rec.; *2a-c,* LV ext., RV int., both valves dorsal, ×0.8 *(497)*.

D. (Schleschiella) MODELL, 1950 [**Unio burroughianus* LEA, 1834; OD], Heavy, short, oval or subsquarish to elongate rectangular, with distinct posterior ridge; beaks rather full, with regularly radiating, widely separated, sharp ridges; cardinals compressed, rough, usually subdivided in each valve, lamellar teeth curved, compressed. *Rec.*, S.Am.——FIG. D51,*9*. **D. (S.) burroughianus* (LEA); RV ext., ×0.8 *(535)*.

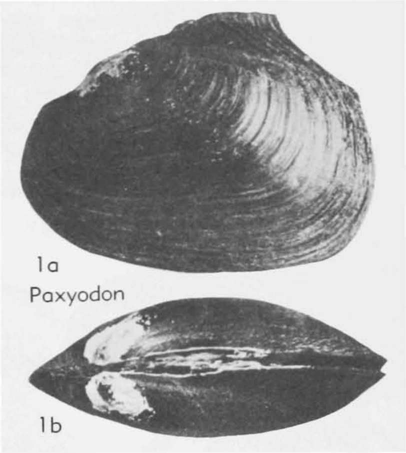


FIG. D52. Unionidae (Hyriinae) (p. N461).

Ecuadorea MARSHALL & BOWLES, 1932 [**E. bibliana*; OD]. Beaks with radial sculpture similar to that of *Diplodon* and *Prisodon*; radial ribs arranged in a V-pattern, each V nesting in succeeding one; posterodorsal area crossed obliquely by several plicae to the margin. *?Plio., Rec.*, S.Am.——FIG. D51,*6*. **E. bibliana,* ?Plio.; LV ext., ×1 *(587)*.

Eodiplodon MARSHALL, 1928 [**E. gardnerae*; OD]. Beaks with very coarse, nearly direct radial undulations, some of which are broken up into nodules; close to tip of beak each pair of undulations unites into V, but later ones become nearly direct, not forming V. *Tert.*, S.Am.(Peru).——FIG. D51,*1*. **E. gardnerae*; LV ext., ×0.8 *(583)*.

Hyridella SWAINSON, 1840 [**Unio australis* LAMARCK, 1819 (=*Unio napeonensis* CONRAD, 1840); OD] [=*Propehyidella* COTTON & GABRIEL, 1932]. Elongate elliptical to short ovoid or subrhomboid; beaks rather low, sculpture consisting of curved, generally nodulose ridges, which approach each other below but usually remain separated by smooth area; surface almost smooth, or slightly nodose; periostracum rayless; teeth rather delicate, compressed, somewhat rudimentary in some. *Rec.*, Australia-N.Guinea-N.Z.

H. (Hyridella). Solid, similar to *H. (Velesunio)*, but ornamented in juveniles by divaricate, irregular wrinkles, becoming gradually smooth in adults; periostracum lustrous, smooth; hinge teeth well developed. *Rec.*, Australia.——FIG. D49,*4*. **H. (H.) australis* (LAMARCK); *4a,b,* RV ext., both valves dorsal, ×0.7 *(497)*.

H. (Lortiella) IREDALE, 1934 [**Mycetopus rugatus* SOWERBY, 1868; OD]. Elongate, thin, narrow, produced and rounded in front, acuminately lengthened and winged behind, ventral margin nearly straight; posterior ridge rounded, posterior area flattened; growth lines heavy; teeth thin, delicate, lamellar teeth elongate, cardinals small, tending to disappear, 2 in RV when young, only 1 in adult. *Rec.,* Australia.——Fig. D51,*3*. **H. (L.) rugata* (Sowerby); LV ext., ×0.5 (Sowerby).

H. (Protohyridella) Cotton & Gabriel, 1932 [**Unio glenelgensis* Dennant, 1898; OD]. Solid, subrhomboidal, subdepressed, rather produced posteriorly; indistinct rib extending from beak to posteroventral margin divides surface into anterior corrugated disc and posterior smooth area; beaks not prominent; hinge teeth well developed. *Rec.,* Australia.——Fig. D49,*2*. **H. (P.) glenelgensis* (Dennant); LV ext., ×0.75 *(168)*.

H. (Velesunio) Iredale, 1934 [**Unio balonnensis* Conrad, 1850 (=**Unio ambiguus* Philippi, 1847); OD]. [=*Microdontia* Tapparone-Canefri, 1883; *Hyridella* Cotton & Gabriel, 1932 (*non* Swainson, 1840); *Westralunio, Alathyria, Centralhyria, Hyridunio, Rugoshyria* Iredale, 1934]. Shape variable, beak sculpture not strong, consisting of broken, nodulose ridges curving toward each other below, generally with smooth space between, restricted to umbonal area. *Rec.,* Australia-N. Guinea-N. Z.——Fig. D49,*3*. **H. (V.) ambigua* (Philippi), *3a,b,* LV ext., both valves dorsal, ×0.8 *(497)*.

Paxyodon Schumacher, 1817 [**P. ponderosus* (=**Mya syrmatophora* Gronovius, 1781); OD] [=*Pachyodon* de Blainville, 1825; *Paxydonta* Deshayes, 1832]. Medium-sized, subtriangular, aviculiform, alate before and behind, solid, inflated, with well-developed posterior ridge which becomes sharp edge near beaks; area above ridge deeply excavated; surface of entire shell smooth excepting very fine and crowded incremental striae; beaks full, low, their sculpture not seen, cavities moderately deep; periostracum, rather dull, hinge margin long, straight, narrow, cardinals compressed, reaching from beaks almost to anterior margin, 2 in RV, 1 in LV, where commonly shorter and weaker auxiliary cardinal occurs under normal one; lamellar teeth long, reaching from beaks almost to posterior margin, 1 in RV, 2 in LV; all teeth somewhat vertically and granularly striate; small radially arranged denticles between cardinals and lamellar teeth occur under beaks. *Rec.,* S.Am.——Fig. D52,*1*. *P. alatus* (Sowerby); *1a,b,* LV ext., both valves dorsal, ×0.8 (Ortmann).

Prodiplodon Marshall, 1928 [**P. singewaldi*; OD]. Beak sculpture resembling that of *Diplodon* and *Prisodon,* consisting of several V-shaped undulations, larger ones embracing smaller, and other undulations on anterior and posterior umbonal areas, each pair of which, if continued, would form another V in the series. *Tert.,* S.Am. (Peru); *Plio.,* S.Am.(Venez.).——Fig. D51,*4*. **P. singewaldi,* Tert., Peru; RV ext., ×0.8 *(583)*.

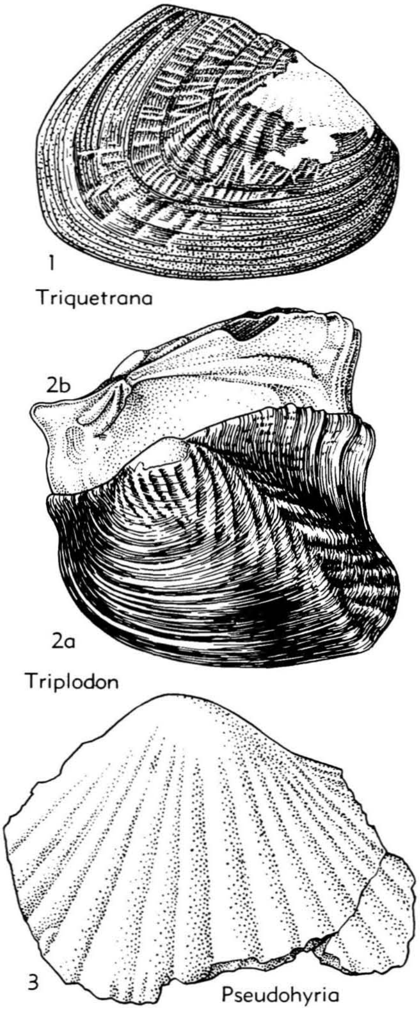


Fig. D53. Unionidae (Hyriinae) (p. *N*461-*N*463).

?**Pseudohyria** MacNeil, 1936 [**P. gobiensis*; OD]. Subquadrate, rounded anteriorly, somewhat angulate posteriorly, broadly arcuate ventrally; beaks about central, prominent, their sculpture unknown; surface sculptured with well-defined slightly elevated radial ribs that enlarge posteriorly and crenulate margin deeply; shell thicker in front than behind; cardinals moderately heavy, elongate, double in RV and single in LV, bounded anteriorly by impressed adductor scar; lamellar teeth not well known, apparently short and curved; ligament short. *Cret.,* Asia(Inner Mongol.).

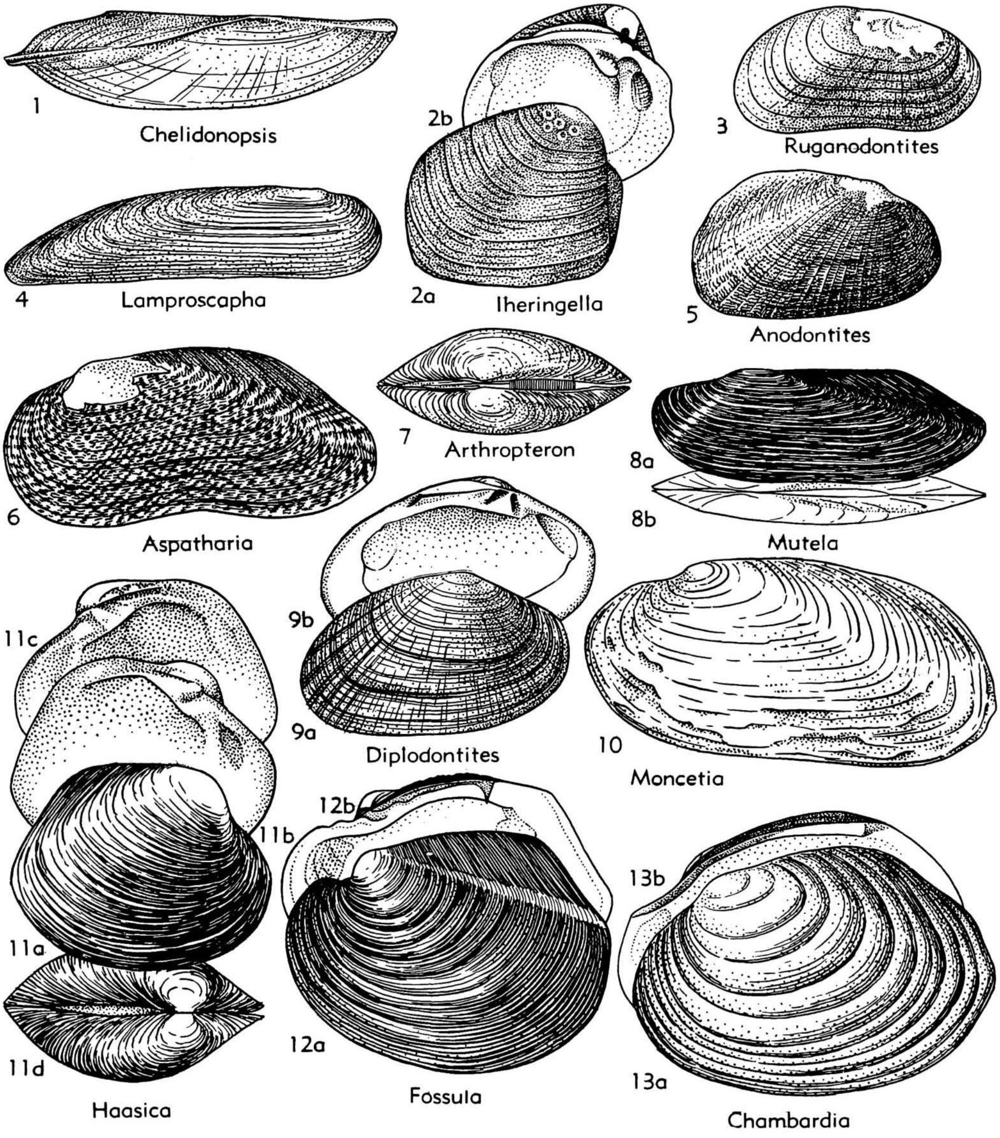


Fig. D54. Mutelidae (p. *N*463-*N*464).

——Fig. D53,*3*. **P. gobiensis*; RV ext., ×1 *(569)*.

Triplodon Spix, 1827 [**T. rugosum*; OD] [=*Niäa* Lea, 1836; *Naia* Swainson, 1840; *Niaea* Mörch, 1853; *Harmandia* Rochebrune, 1881]. Subrhomboidal, heavy, slightly inflated, narrower and winged in front, with posterodorsal wing; posterior slope commonly double; beaks with strong, nearly radial sculpture, central ribs coalescing below, whole continuing as strong, radial, and zigzag ridges over most of disc; periostracum thick, greenish when young, brownish or blackish when old; 2 or more short, compressed cardinals in each valve, becoming subdivided into denticles; 1 lamellar tooth in RV and 2 in LV. *Tert.-Rec.*, S.Am.

T. (Triplodon). Posterodorsal wing well developed. *Tert.-Rec.*, S.Am.——Fig. D53,*2*. **T. (T.) rugosus*, Rec.; *2a,b*, LV ext., RV int., ×0.5 (Sowerby).

T. (Triquetrana) Simpson, 1900 [**Unio stevensi* Lea, 1871; OD]. Compressed, with feebly developed posterior wing. *Rec.*, S.Am.——FIG. D53,*1*. **T.* (*T.*) *stevensi* (LEA); RV ext., ×0.8 *(535)*.

Family MUTELIDAE Swainson, 1840

Shell mostly unsculptured; beaks smooth or faintly corrugated, without well-defined remains of embryonic shell; hinge with cardinals only or edentulous, few with secondary taxodont dentition; nacre soft, richly tinted, pallial line rarely with slight posterior sinus. Labial palps large, anal and superanal openings not separated; mantle generally closed behind into separate branchial and anal siphons; marsupium occupying inner gills; lasidium larva composed of three segments, median one bearing single shell. *?Trias., Cret.-Rec.*

Mutela SCOPOLI, 1777 [**Mytilus dubius* GMELIN, 1791; OD] [=*Purpurina* FÉRUSSAC, 1826; *Spatha* LEA, 1838; *Calliscapha* SWAINSON, 1840; *Mutelina* BOURGUIGNAT, 1885; *Utela* MOORE, 1898; *Pseudomutela* SIMPSON, 1900]. Elongate, oblong to subtriangular, smooth, with low, unornamented beaks; posterior ridge rounded; periostracum moderately glossy, rayless; hinge straight, commonly with faint vestiges of denticles. *Cret.-Rec.*, Afr.-?Eu.

M. (Mutela). Posterior ridge low and smooth. *Cret.-Rec.*, Afr.——FIG. D54,*8*. **M.* (*M.*) *dubia* (GMELIN), Rec.; *8a,b*, LV ext., both valves dorsal, ×0.5 *(140)*.

M. (Chelidonopsis) ANCEY, 1887 [**Chelidonura arietina* ROCHEBRUNE, 1886 (=**Spatha hirundo* MARTENS, 1881); OD] [=*Chelidonura* ROCHEBRUNE, 1886 (*non* A. ADAMS, 1850); *Chelidoneura* GERMAIN, 1908]. Elongate, thin, gaping on anterior basal part, winged anteriorly along dorsal margin; posterior ridge acute, developing distally into tube; marked internally by deep furrow. *Rec.*, Afr.——FIG. D54,*1*. **M.* (*C.*) *hirundo* (MARTENS); RV ext., ×0.5 (Pilsbry & Bequaert).

M. (Moncetia) BOURGUIGNAT, 1885 [**Moncetia anceyi*; OD] [=*Monoetia* PAETEL, 1890]. Oblong, with blunt ends, very much compressed and flattened; periostracum dull; hinge with single blunt tuberculose cardinal tooth in RV; beak sculpture unknown. *Rec.*, Afr.——FIG. D54,*10*. **M.* (*M.*) *anceyi* (BOURGUIGNAT); LV ext., ×1 (Bourguignat).

Anodontites BRUGUIÈRE, 1792 [**A. cristata*; OD] [=*Patularia* SWAINSON, 1840; *Glabaris* GRAY, 1847; *Haplothaerus* CONRAD, 1847; *Euryanodon* CROSSE & FISCHER, 1894; *Styganodon* MARTENS, 1900; *Pachyanodon, Scolianodon* MARTENS, 1900; *Anodontites* MARSHALL, 1925; *Glabris* PRASHAD, 1932]. Rounded to elongate, inflated, moderately heavy; beaks full, smooth, periostracum smooth or clothlike, rarely rayed faintly; hinge edentulous, hinge line straight or slightly curved; lunule distinct and large. *Tert.-Rec.*, S.Am.-C.Am.

A. (Anodontites). Rounded to elliptical; posterior ridge low or wanting. *Tert.-Rec.*, S.Am.-C.Am. ——FIG. D54,*5*. **A.* (*A.*) *cristatus*, Tert.; RV ext., ×0.5 (Marshall).

A. (Lamproscapha) SWAINSON, 1840 [**Anodon ensiformis* SPIX, 1827; SD HERRMANNSEN, 1846] [=*Virgula* SIMPSON, 1900]. Moderately heavy to heavy, very elongate, straight to falcate, rounded in front, pointed behind at posterior base, where high, sharply defined posterior ridge ends and above which it is somewhat truncated; beaks low; periostracum green to olive. *Rec.*, S.Am.——FIG. D54,*4*. **A.* (*L.*) *ensiformis* (SPIX); RV ext., ×0.4 *(140)*.

A. (Ruganodontites) MARSHALL, 1931 [**A. colombiensis* MARSHALL, 1921; OD]. Elongate, thick, usually somewhat falcate, with broad, shallow depression running from beaks to middle of ventral margin; periostracum thick, microscopically striate radially, much wrinkled, as also is underlying calcareous portion of shell; wrinkles obscurely divided into narrow, gradually widening rays extending from beaks to margin; nacre greenish-livid. *Rec.*, S.Am.——FIG. D54,*3*. **A.* (*R.*) *colombiensis*; RV ext., ×0.8 *(585)*.

Aspatharia BOURGUIGNAT, 1885 [**Margaritana vignouana* BERNARDI, 1859 (=**Anodonta rugifera* DUNKER, 1858); OD]. Oblong or oval; hinge plate essentially edentulous, abruptly terminated behind by deep triangular escutcheon but commonly low, blunt, toothlike prominence under beak of LV. *Pleist.-Rec.*, Afr.

A. (Aspatharia). Elongate, rhomboid, somewhat compressed, with full rounded posterior ridge from which curved rows of fine broken corrugations radiate; periostracum dark olive, wrinkled, rayless; beaks marked by corrugations that diverge as very broad inverted V's; hinge edentulous, in some shells with low, slightly elevated ridge in LV in front of beak; nacre bluish-green. *Rec.*, Afr.——FIG. D54,*6*. **A.* (*A.*) *rugifera* (DUNKER); LV ext., ×0.8 (Reeve).

?**A. (Arthropteron)** ROCHEBRUNE, 1905 [**A. ouassouloui*; OD]. Oval, smooth, moderately convex; lunule large, narrowly lanceolate; beak sculpture unknown. [Subgenus of dubious validity.] *Rec.*, Afr.——FIG. D54,*7*. **A.* (*A.*) *ouassouloui;* both valves dorsal, ×0.7 (Rochebrune).

A. (Chambardia) BOURGUIGNAT, 1890 [**C. letourneuxi*; SD HAAS, 1957] [=*Spathella* BOURGUIGNAT, Dec. 1885 (*non* T. HALL, Nov. 1885); *Spathopsis* SIMPSON, 1900; *Leptospatha* ROCHEBRUNE & GERMAIN, 1904; *Mitriodon* ROCHEBRUNE, 1904]. Long elliptical, compressed; beaks rather low, with short, concentric waves; surface smooth or rarely with corrugations on or near posterior slope; lunule narrow, its border slightly higher in RV; faint compressed tooth in front of beak in LV hinge fitting into depression in RV; beak cavities shallow. *Pleist.-Rec.,* Afr.——Fig. D54,*13. A. (C.) rubens* (Lamarck), Rec.; *13a,b,* LV ext., RV int., ×0.4 *(140).*

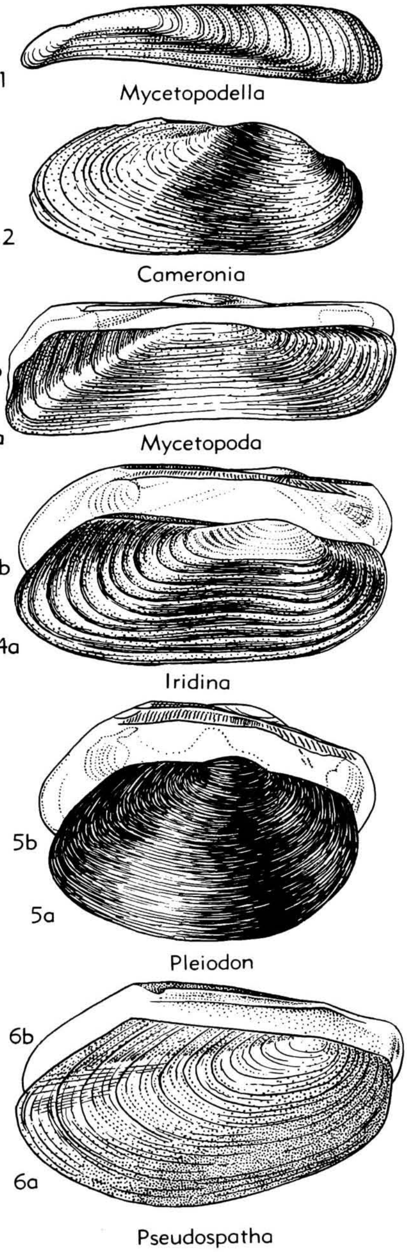


Fig. D55. Mutelidae (p. *N464-N466*).

Diplodontites Marshall, 1922 [**D. cookei*; OD]. Elliptical, moderately thick; beaks elevated; lunule triangular; periostracum clothlike, dull, yellowish-olive, with 10 radiating, greenish stripes on posterodorsal area; hinge with hinge plate; RV with 3 cardinals, anterior tooth strongest, posterior poorly differentiated; LV with 3 cardinals, anterior almost obsolete, middle triangular and very large, posterior long and low; socket between 1st and 2nd cardinal very deep. *Rec.,* S.Am.——Fig. D54, *9. *D. cookei*; *9a,b,* RV ext., LV int., ×1 *(581).*

Fossula Lea, 1870 [**Monocondylaea fossiculifera* d'Orbigny, 1835; OD] [=*Fossicula* Marshall, 1925]. Obovate, inflated, heavy, with rather high beaks and low posterior ridge; periostracum olive-brown, somewhat smooth, slightly rayed in some; hinge with irregular tooth in LV under beak, followed posteriorly by cavity and 2 irregular teeth separated by cavity under beak of RV; teeth and cavities somewhat pitted and partly covered with brown periostracum. *Rec.,* S.Am.——Fig. D54,*12. *F. fossiculifera* (d'Orbigny); *12a,b,* LV ext., RV int., ×0.5 *(140).*

Haasica Strand, 1932 [**Plagiodon balzani* Ihering, 1893; OD] [=*Marshalliella* Haas, 1932 (*non* Kieffer, 1913; *nec* Poppius, 1914)]. Externally like *Monocondylaea*; hinge plate with high narrow cardinal in RV, separated from low denticle behind by cuneiform groove; preumbonal callosity in RV, divided from high narrow tooth by narrow deep furrow which extends under beak; beak cavities deep, somewhat compressed. *Rec.,* S.Am.——Fig. D54,*11. *H. balzani* (Ihering); *11a-d,* RV ext., LV int., RV int., both valves dorsal, ×1 (Haas).

Iheringella Pilsbry, 1893 [**Plagiodon isocardioides* Lea, 1856; OD] [=*Plagiodon* Lea, 1856 (*non* Dumeril, 1841)]. Solid, inflated, rounded to subtriangular, with posterior ridge; beaks high, curved inward and forward, without sculpture; periostracum dull olive, clothlike; hinge teeth imperfectly developed, nodose or broken into denticles, irregular tooth in LV under beak, bifid in some and 2 in RV wtih intervening socket under beak. *Rec.,* S.Am.——Fig. D54,*2. *I. isocardioides* (Lea); *2a,b,* RV ext., LV int., ×1 *(497).*

Iridina Lamarck, 1819 [**I. exotica*; OD] [=*Platiris* Lea, 1838; *Platyris* L. Agassiz, 1846; *Eufira* Gistel, 1848; *?Iridella* Conrad, 1853; *Euphira* Paetel, 1875]. Heavy, oblong or oval, with strongly developed hinge plate set with many short taxodont teeth. *?Cret.,* S.Am.(Brazil); *U.Plio.* or *Pleist.-Rec.,* ?S.Am.-Afr.

I. (Iridina). Elongate; teeth small and very numerous throughout length of heavy hinge plate which bears low prominence under beak of LV. *Rec.,* Afr.——Fig. D55,*4. *I. (I.) exotica*; *4a,b,* RV ext., LV int., ×0.3 *(140).*

I. (Cameronia) Bourguignat, 1879 [**Iridina spekei* Woodward, 1859; OD]. Oblong, hinge

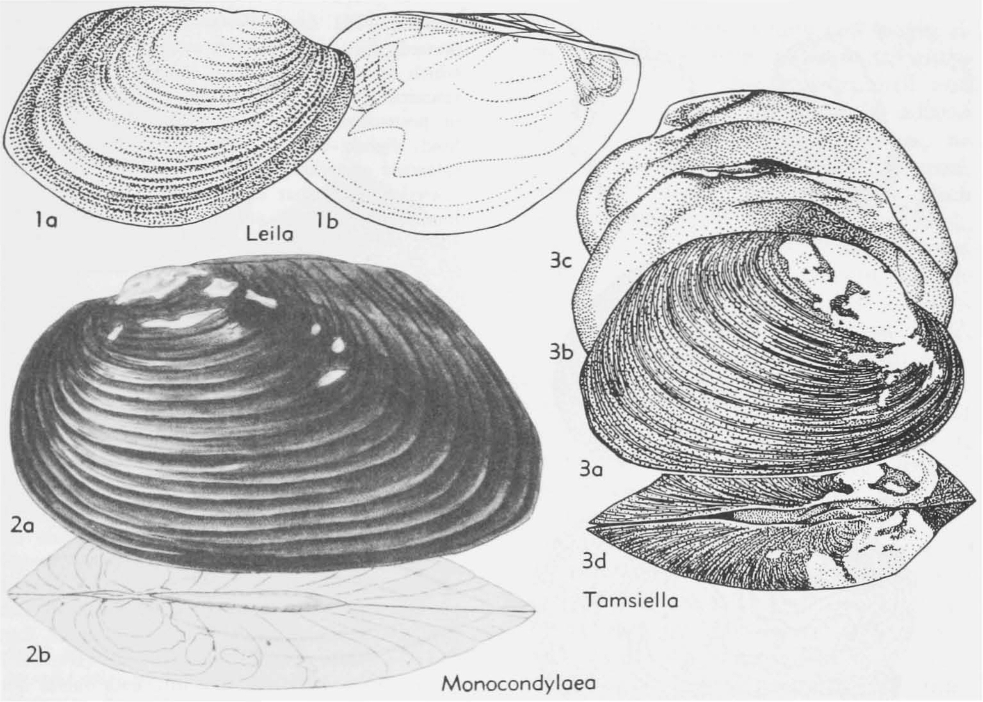


FIG. D56. Mutelidae (p. *N*465-*N*466).

plate constricted under beaks, teeth weak or obsolete anteriorly. *Rec.,* Afr.——FIG. D55,*2*. **I. (C.) spekei* WOODWARD; RV ext., ×0.3 (Pilsbry & Bequaert).

I. (Pleiodon) CONRAD, 1834 [**Pleiodon macmurtrei* (=**Iridina ovata* SWAINSON, 1832); OD] [=*Pleodon* SWAINSON, 1840; *Pliodon* L. AGASSIZ, 1846]. Oval, teeth and hinge plate strongly developed in front of beaks. *?Cret.,* S.Am.(Brazil); *U.Plio.* or *Pleist.-Rec.,* Afr.-?S.Am.——FIG. D55,*5*. **I. (P.) ovata* SWAINSON, Rec.; *5a,b,* RV ext., LV int., ×0.3 *(140)*.

Leila GRAY, 1840 [**Anodonta blainvilleana* LEA, 1834; OD] [=*Columba* LEA, 1834 (*non* LINNÉ, 1758)]. Large, obovate, inflated, with straight dorsal margin produced into slight wings before and behind, bluntly pointed posteriorly and somewhat truncate above, with faint posterior ridge; beaks smooth, full; periostracum olive, generally smooth; hinge edentulous; beak cavities rather shallow; pallial line commonly showing slight posterior sinus. *Rec.,* S.Am.——FIG. D56,*1*. **L. blainvilleana* (LEA); *1a,b,* RV ext., LV int., ×0.6 *(140)*.

Monocondylaea D'ORBIGNY, 1835 [**M. paraguayana*; OD] [=*Aplodon* SPIX, 1827 (*non* RAFINESQUE, 1818); *Monocondyla* GRAY, 1840; *Monocondylea* D'ORBIGNY, 1844; *Monocondylus* MORELET, 1866; *Monocondyloia* PAETEL, 1875; *Moncondylaea* CLESSIN, 1876; *Spixoconcha* PILSBRY, 1893]. Rounded to ovate, rather heavy with low posterior ridge; periostracum dull olive-green to olive-brown, clothlike; hinge with 2 irregular teeth under beak in LV and 2 in RV, interlocking with those of LV, all being somewhat tuberculate. *Tert.-Rec.,* S.Am.——FIG. D56,*2*. **M. paraguayana,* Rec.; *2a,b,* LV ext., both valves dorsal, ×0.8 *(140)*.

Mycetopoda D'ORBIGNY, 1835 [**M. soleniformis*; OD] [=*Mycetopus* D'ORBIGNY, 1840]. Thin, elongate, truncate posteriorly, with low, posterior ridge and rather flat, smooth or slightly concentrically wrinkled beaks; periostracum smooth, lustrous, pale greenish-yellow or brownish, rayless; hinge line long, straight, edentulous or showing faint traces of fine denticles beneath the nacre; beak cavities shallow. Foot very long, developed at lower end into head or button. *?Trias., Rec.,* N. Am.-S.Am.——FIG. D55,*3*. **M. soleniformis,* Rec.; *3a,b,* RV ext., LV int., ×0.3 *(140)*.

Mycetopodella MARSHALL, 1927 [**Mycetopus falcatus* HIGGINS, 1868; OD]. Very elongate, falcate, wide behind, narrow in front, abruptly descending, with swelling at anterior end; broad radial

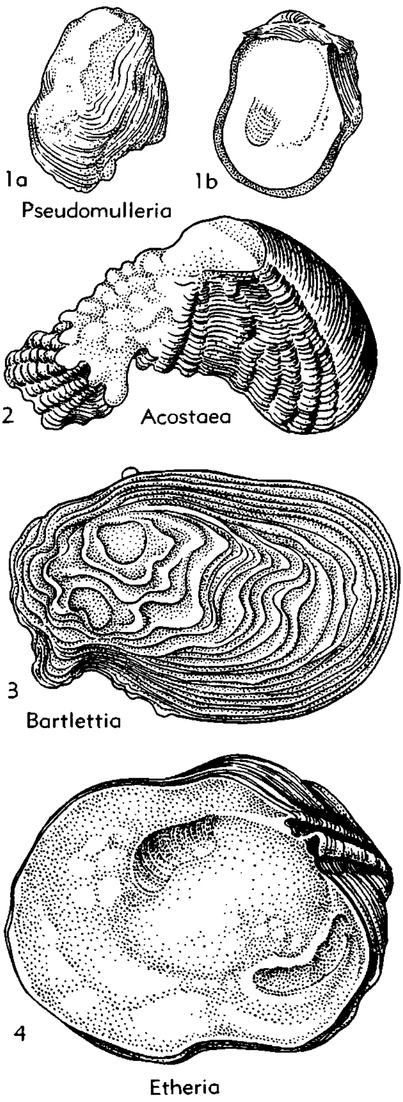


FIG. D57. Etheriidae (p. *N*466-*N*467).

constriction from anteriorly situated beaks to ventral margin; hinge edentulous, nearly straight except in front of beaks at lunule where it is slightly excavated; ligament very long; posterior ridge sharp, anterior ridge much more pronounced; periostracum dull, with numerous fine radiating striae, about 90 in 1 mm. *Rec.,* S.Am.——FIG. D55,*1*. _*M. falcata_ (Higgins); LV ext., ×0.5 *(582).*

Pseudospatha Simpson, 1900 [_*Spatha tanganyicensis_ E. A. Smith, 1880; OD] [=*Burtonia* Bourguignat, 1883 (*non* Bonaparte, 1850)]. Compressed, thin, oblique, with straight dorsal margin which ends in small wing in front and behind; rounded and cut away at anterior base, produced in posterobasal region, gaping in front and behind, slightly twisted on its axis and usually bent sideward posteriorly; with low, commonly double posterior ridge that ends in biangulate point behind; beaks situated anteriorly, compressed, sculptured with faint irregular concentric ridges which continue over shell and at beaks commonly are rather sharply pustulose; periostracum yellowish-brown, delicately rayed in some; hinge rudimentary, one or more faint, compressed cardinals and single lamellar tooth in each valve; nacre coppery or purple, commonly rayed. *Rec.,* Afr.——FIG. D55,*6*. _*P. tanganyicensis_ (Smith); *6a,b,* RV ext., LV int., ×0.55 (E. A. Smith).

Tamsiella Haas, 1931 [_*Monocondylaea tamsiana_ Dunker, 1858; OD]. Resembles *Monocondylaea*; hinge without hinge plate; low cardinal in RV bordered behind by shallow furrow which terminates at beak; adjoining part of dorsal margin thickened callosity; shallow groove in LV in front of beak, followed under beak by feeble denticle which is bordered behind by shallow furrow. *Rec.,* S.Am.——FIG. D56,*3*. _*T. tamsiana_ (Dunker); *3a-d,* LV ext., RV int., LV int., both valves dorsal, ×1 (Haas).

Family ETHERIIDAE Swainson, 1840

Shell nacreous, regular and free when young (orthothetic), becoming irregular, attached by surface of one valve when adult (pleurothetic); shell substance foliaceous or lamellar, covered by thick, olive-colored, commonly deciduous periostracum; hinge edentulous; anterior adductor muscle in some forms reduced. Foot obsolete in adults. *Plio.-Rec.*

Etheria Lamarck, 1807 [_*E. semilunata_ Lamarck, 1807; SD Swainson, 1840 (=_*E. elliptica_ Lamarck, 1807)] [=*Etheriigenus* Renier, 1807; *Aetheria* Oken, 1818; *Etherea* Schweigger, 1820; *Ethaeria* L. Agassiz, 1839]. Irregular, inequivalve, adherent by beak and tubular prolongations of one of valves; substance of shell foliaceous; hinge margin curved, edentulous; ligament external, tortuous, partially sunk in groove in dorsal margin of attached LV. *Plio.-Rec.,* Afr.-Ind.O. (Madag.).——FIG. D57,*4*. _*E. semilunata,_ Rec.; LV int., ×0.4 (Sowerby).

Acostaea d'Orbigny, 1851 [_*Mulleria lobata_ Férussac, 1823; OD] [=*Mulleria* Férussac, 1823 (*non* *Müllera* Leach, 1814); *Muelleria* Philippi, 1853; *Acostea* Gray, 1854; *Eumulleria* Anthony, 1907].

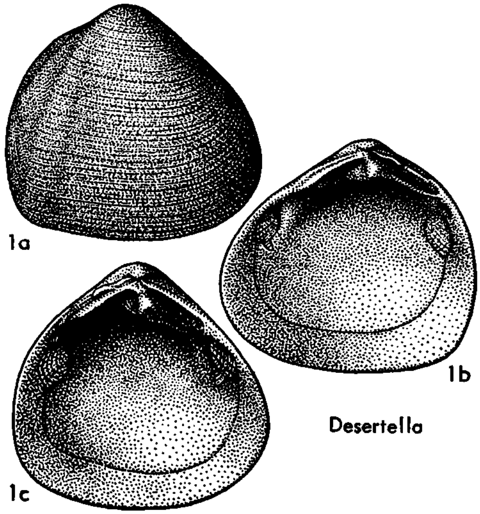


FIG. D58. Desertellidae (p. *N*467).

Shell of adults irregular, heavy, inequivalve, attached only by RV; periostracum thick; beaks elongate; ligament in marginal groove; young shell regular, free, shaped like *Anodontites.* Both anterior and posterior adductor muscles in young free, anterior adductor obsolete in adult attached state. *Rec.,* S.Am., India.

A. (Acostaea). With narrow, anterior projection including embryonic shell. *Rec.,* S.Am.——FIG. D57,*2*. **A. (A.) lobata* (FÉRUSSAC); RV ext., ×0.6 (Sowerby).

A. (Pseudomulleria) ANTHONY, 1907 [**Mulleria dalyi* E. A. SMITH, 1898; OD] [=*Pseudomülleria* PILSBRY, 1911]. Irregularly quadrate, without decided anterior projection; anterior adductor muscle obsolete. *Rec.,* India.——FIG. D57,*1*. **A. (P.) dalyi* (SMITH); *1a,b,* RV ext., LV int., ×0.5 (E. A. Smith).

Bartlettia A. ADAMS, 1866 [**Etheria stefanensis* MORICAND, 1856; OD] [=*Bartelletia* PAETEL, 1875; *Rochanaia* MORRETES, 1945]. Solid, elongate, loosely attached or not at all; beaks low, shell surface with irregular rough zones of growth, with triangular escutcheon behind strong ligament, latter marginal and not sunk in groove. *Rec.,* S.Am.——FIG. D57,*3*. **B. stefanensis* (MORICAND); LV ext., ×0.5 (Sowerby).

?Family DESERTELLIDAE Dechaseaux, 1946

[Materials for this family prepared by L. R. Cox]

Shell medium-sized, equivalve, subequilateral, subtrigonal, but with posterior end high and subtruncate; length and height almost equal; blunt diagonal ridge delimiting relatively narrow posterior area; shell wall thick; umbones moderately well inflated and incurved, slightly opisthogyrous; no lunule or escutcheon; ligament external, opisthodetic; nymph short and thick. Each valve with two teeth diverging from beak, LV anterior and RV posterior almost equal in size, very stout and prominent, bluntly pointed, received in deep recesses; LV posterior and RV anterior also almost equal, less prominent than other two, each elongated and close to margin, and each received in recess between major tooth of opposite valve and margin adjacent to it; dentition of valves thus appearing identical when interior of shell is viewed; adductor scars subequal, placed rather dorsally, posterior ones almost superficial, each with small accessory scar above it, anterior one slightly impressed, each with low buttress-like thickening of shell wall on its posterior side in some specimens, and small accessory scar on its posteroventral side; pallial line entire. Surface with fine concentric striae. Original shell structure (whether nacreous or not) unknown. [Habitat nonmarine.] *L.Cret.(?Alb.).*

Desertella MUNIER-CHALMAS in HAUG, 1905 [**D. foureaui*; M]. Characters of family. *L.Cret.,* N. Afr.——FIG. D58,*1*. **D. foureaui*, Fort Flatters, N.Afr.(Alg.); *1a-c,* RV ext., RV int., LV int., ×1.3 (Cox, n).

?Family PACHYCARDIIDAE Cox, 1961

[Materials for this family prepared by L. R. Cox]

Ovate, trapeziform or cuneiform, inequilateral, equivalve, of weak to moderately strong convexity; ligament external, opisthodetic. Subumbonal ("cardinal") teeth strong to more or less obsolete, not more than two in each valve; posterior "laterals" always present, although weak in some forms, extending in more typical genera below nymph almost to beak, anterior "laterals" present or absent; adductor scars subequal, pallial line simple; interior of shell originally nacreous in some, possibly in all, genera. Surface smooth or (rarely) with concentric ornament. [Fresh-water, brackish-water and marine.] *Perm.-U.Trias., ?L. Jur.(Lias.).*

The more typical genera of this family were formerly included in the Cardiniidae, but they are not true heterodonts like *Cardinia*. Evidence of an originally nacreous interior has been found in specimens of *Trigonodus*.

Pachycardia Hauer, 1857 [**P. rugosa*; OD] [=*Pacycyardia* Mojsisovics, 1879 *(nom. null.)*]. Medium-sized, cuneiform, strongly inequilateral, well inflated, some specimens subrostrate and weakly carinate posteriorly; umbones prominent, well incurved, strongly prosogyrous; lunule wide, cordiform, distinctly bordered; no escutcheon; ligament external. LV with stout, triangular main cardinal tooth separated by broad recess from weaker, variable anterior cardinal close to lunular margin; and with elongate posterior lateral which is parallel to margin and projects rather prominently near its posterior end; RV with stout, variable, commonly grooved, anteriorly placed cardinal and elongate posterior lateral which extends to below beak and is received in recess above lateral of other valve. Surface smooth. [Brackish-water or marine.] *M.Trias.-U.Trias.*, Eu.(S.Alps-Balkans).——Fig. D59,*3*. **P. rugosa*, U.Trias.(Carn.); *3a,b*, Yugo.; LV ext., LV int., ×1 *(950)*; *3c*, S.Tyrol, RV int., ×1 (Broili, 1904).

?**Cardinioides** Kobayashi & Ichikawa, 1952 [**C. japonicus*; OD]. Medium-sized, trigonally ovate, more or less inequilateral; moderately inflated, some forms with weak posterodorsal carination; no lunule or escutcheon. LV with large, irregularly triangular, commonly grooved, mesially placed cardinal tooth and short, remote posterior lateral; RV with 2 weak, widely divergent cardinal teeth, bordering recess for main tooth of other valve, and posterior lateral which originates below hinge plate and increases in strength posteriorly. Surface smooth except for growth threads. [Marine.] *?Perm.*, N.Afr.; *U.Trias.(Carn.)-L.Jur.(Lias.)*, Japan.——Fig. D59,*5*. *C. varidus* Hayami, Lias., Japan; *5a-c*, LV ext., LV int., RV int., ×1 (Hayami, 1957 and Cox, n).

Kidodia Cox, 1936 [**K. stockleyi*; OD]. Small, elongate-ovate, inequilateral, of feeble convexity. No cardinal teeth; LV with thin posterior lateral tooth occupying posterodorsal corner, RV with thin anterior lateral; between each of these teeth and dorsal margin is narrow, elongate recess for reception of projection of margin of opposite valve. [Fresh-water.] *Perm.(Karroo* or *Gondwana)*; E. Afr.-S.Am.(Arg.).——Fig. D59,*2*. **K. stockleyi*, Tanganyika; *2a,b*, RV int., LV int., ×2.2 *(178)*.

Trigonodus Sandberger in Alberti, 1864 [**T. sandbergeri*; SD Stoliczka, 1871]. Medium-sized, ovate to trapeziform, strongly inequilateral, moderately inflated; no lunule or escutcheon; ligament external, but rather submerged in some species. LV with stout, triangular, commonly grooved, main cardinal tooth separated by broad recess from anterodorsal margin (where presence of weak anterior cardinal is inconstant) and with 2 thin, elongate posterior laterals; RV with stout, triangular, commonly grooved, anteriorly placed cardinal tooth and elongate posterior lateral which is received in recess between 2 laterals of other valve; some species with internal radial buttress which passes from umbo to anterior side of posterior adductor scar. Surface smooth or concentrically ridged. [Brackish-water or marine.] *M.Trias.-U.Trias.*, Eu.-Asia-N. Am.-N. Z.——Fig. D59,*4a,b*. **T. sandbergeri*, U.Trias.(Lettenkohle), Ger.; *4a,b*, LV int., RV int., from wax impressions, ×1 (Sandberger, 1864).——Fig. D59,*4c,d*. *T. carniolicus* Bittner, U.Trias.(Carn.), Yugo.; LV ext., LV int., ×1 *(950)*.——Fig. D59,*4e*. *T. problematicus* (Klipstein), U. Trias. (Carn.), Yugo.; RV int., ×1 *(950)*.

Unionites Wissmann, 1841 [**U. muensteri*; OD] [=*Anoplophora* Alberti, 1864 (*non* Hope, 1840); *Uniona* Pohlig, 1880 (type, *U. leuckarti*, =*Venulites donacinus* von Schlotheim, 1820; SD Cox, 1961); *Anodontophora* Cossmann, 1897 (*pro Anoplophora* Alberti) (type, *Myacites fassaensis* Wissmann in Münster, 1841; SD Stoliczka, 1871); *Anaplophora* Healey, 1908 *(nom. null.)*; *Anoplophoria* Zeller, 1908 *(nom. null.)*; *Unionina* Diener, 1923 *(nom. null.)*; *Anodonthophora* Parona, 1928 *(nom. null.)*]. Small, ovate rectangular or trapeziform, inequilateral, of feeble to moderate convexity; lunule and escutcheon present or absent; ligament external, opisthodetic; nymphs not prominent. Subumbonal teeth, if distinguishable at all, usually weak and amorphous, one in each valve; anterior laterals usually absent; one distinguishable in RV in some forms; weak, elongate posterior lateral present in both valves, extending almost to beak, that of LV formed by lamina projecting from margin; shorter and more remote lateral may occupy posterodorsal angle of valves; some species with weak internal radial buttress on posterior side of anterior adductor scar. Surface smooth. [Brackish-water or marine.] *L. Trias.-U.Trias.*, Eu.-Asia-Arctic O.(Spitz.-Bear I.)-N.Z.——Fig. D59,*1a-c*. **U. muensteri*, U.Trias. (Carn.), S.Tyrol; RV ext., RV hinge, LV hinge, all ×1 *(58)*.——Fig. D59,*1d*. *U. rectus* (Gümbel), U.Trias.(Carn.), N.Tyrol; RV int., ×1.3 *(1001)*.

?Family ACTINODONTOPHORIDAE
Newell, new family

[Material for this family prepared by N. D. Newell]

Shell elongate to subelliptical; beaks prosogyre, located about one-fourth of shell length from anterior margin; lunule and escutcheon distinct; surface smooth or ornamented with radial costae, and (in some) with concentric undulations; ligament external, opisthodetic, nymphs elongate; anterior adductor stout, strongly impressed, with myophoric buttress, posterior adductor impression larger, shallow; pedal retractor

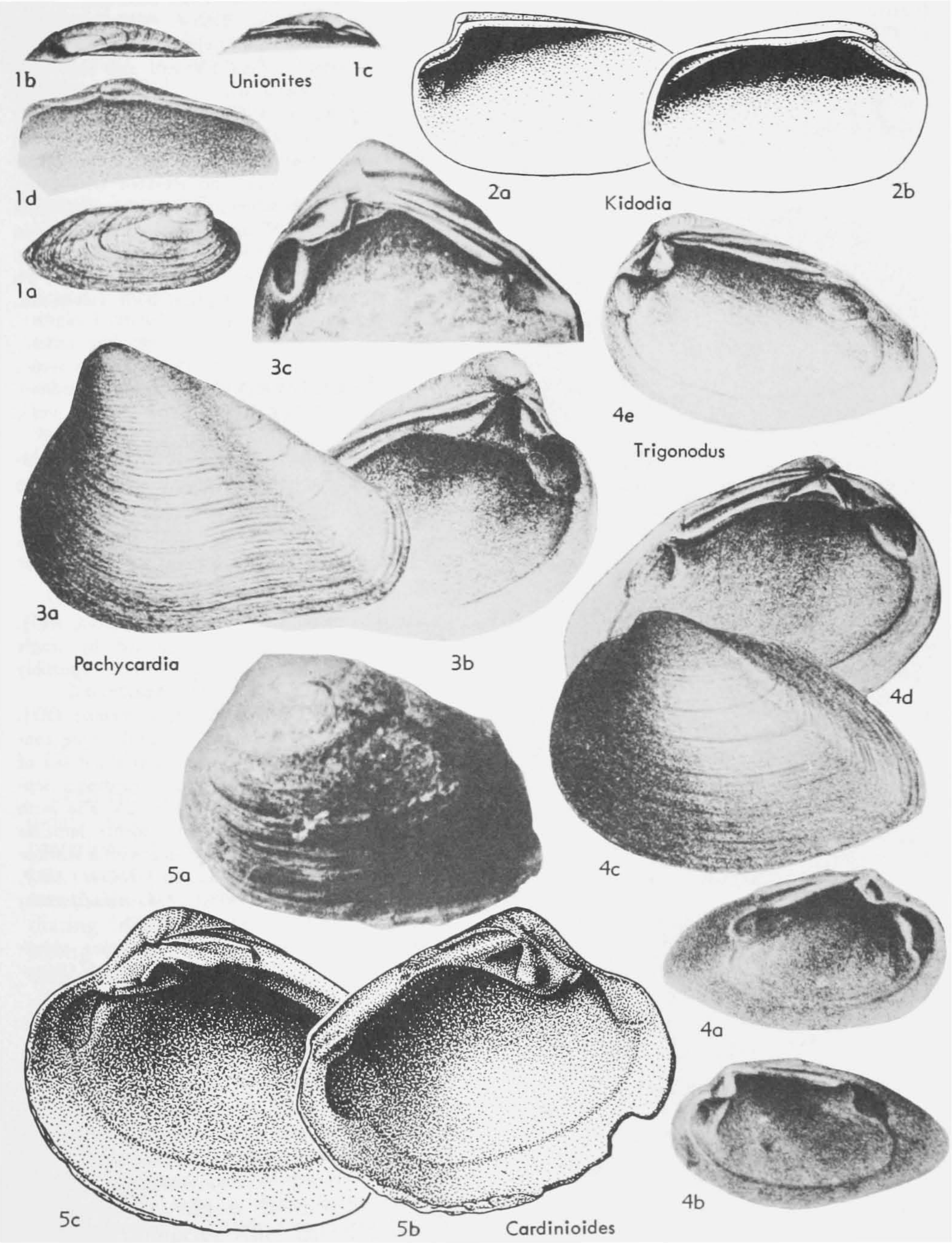


Fig. D59. Pachycardiidae (p. N468).

scar deep, situated just behind buttress, cardinal teeth numerous, elongate, radiating from beaks; one or more strong lateral teeth in each valve, that of the RV lying in deep furrow below lateral tooth of LV. *Perm.-U.Trias.*

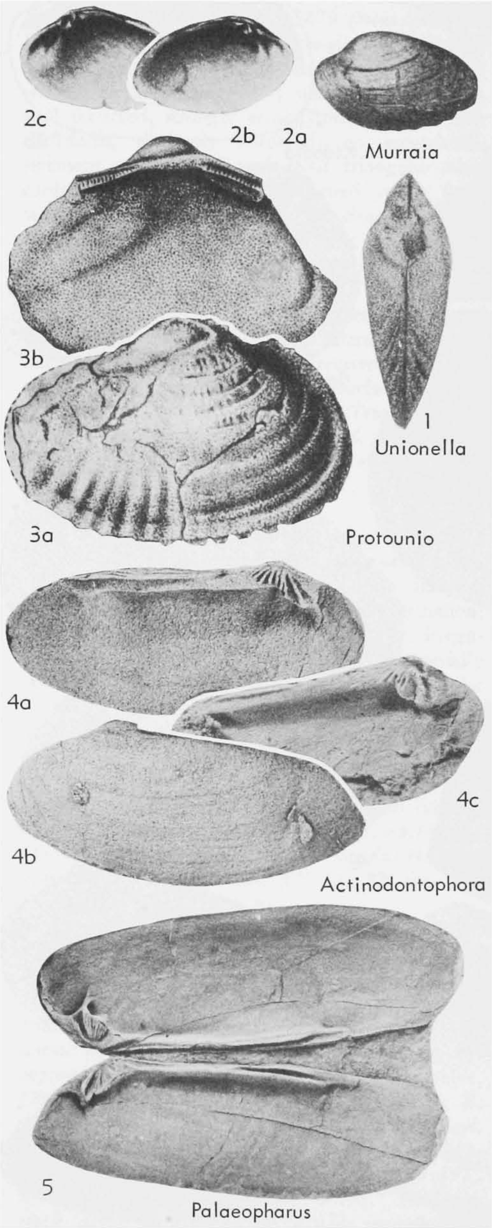


FIG. D60. Actinodontophoridae *(4-5)*; Family Uncertain *(1-3)* (p. *N*470-*N*471).

Actinodontophora ICHIKAWA, 1951, p. 327 [**A. katsurensis*; OD]. With several radial cardinals anterior elements of which are relatively long and massive, grading posteriorly to short and thin; anterior tooth of cardinal series occurring in RV. *Perm.*, Japan.——FIG. D60,*4*. **A. katsurensis*, Kanakura F.; *4a*, latex replica int. (holotype), ×1; *4b,c*, latex replicas LV ext. and int., ×1; (Nakazawa & Newell, n).

Palaeopharus KITTL, 1907, p. 34 [**P. scheii*; SD DIENER, 1915, p. 229]. Similar to *Actinodontophora*, but first and last teeth of cardinal series relatively massive, long and elevated with intervening denticles bundled in single broad pseudocardinal tooth in LV and corresponding socket in RV. *U.Trias.*, Bear Is.(Arctic)-Ellesmereland-Japan. ——FIG. D60,*5*. *P. paucicostatus* NAKAZAWA, N_3 Nabae F., Japan; latex replica, both valves, int. molds, ×1 (Nakazawa, n).

Superfamily and Family UNCERTAIN

Some fossil pelecypods of doubtful relationships, apparently distantly related to the Unionacea, are included here. Since they are known by their original descriptions, the authors' diagnoses are either quoted or given in a somewhat condensed form.

Bisulcus HITCHCOCK, 1865 [**B. undulatus*; OD]. Continuous paired grooves separated by single ridge, as trail of fresh-water bivalve (possibly primitive unionid). *Trias.*, USA(Mass.).

Murraia RUSSELL, 1932 [**M. naiadiformis*; OD]. Small thin, slightly gaping, LV slightly more convex than RV; beaks broad, placed at about 0.3 of shell length; RV with 2 divergent cardinals, separated by deep subtrigonal socket; LV also with 2 cardinals, anterior more prominent; lamellar teeth apparently lacking; pallial line with a shallow sinus. [May not be a unionacean.] *L.Cret.(Alb.)*, N.Am.(Can.).——FIG. D60,*2*. **M. naiadiformis*; *2a-c*, LV ext., int., RV int., ×1 *(807)*.

Nakamuranaia SUZUKI, 1943 [**Leptesthes chingshanense* GRABAU, 1923; OD]. *L.Cret.*, N.China-S.Korea. [NEWELL]

?Protounio MARTINSON, 1953 [**P. cardiiformis*; OD]. Shell big, oval, obese, with thick valves; umbo wide, almost always situated centrally, turned slightly forward and inside, sloping in some; posterior half of shell low-ribbed, hardly visible, ribs running radially from above to below, almost vanishing on anterior half of shell, radial ribs crossed by fine, hardly visible concentric striation which is more obvious toward edge of shell; some specimens without trace of radial ribbing; hinge peculiarly schizodont, hinge line curved, cardinal teeth absent; 2 laterals in

LV both in front and behind umbo, teeth showing fine perpendicular striation; 1 lateral in RV (?both in front and behind umbo); anterior laterals shorter and thicker than posterior ones; ventral margin scalloped, interior face covered by mother-of-pearl. *U.Cret.,* Asia(Mongol.).——FIG. D60,*3.* **P. cardiiformis*; *3a,b,* RV ext., LV int., ×0.8 *(590).* [Considered by Cox to be a synonym of *Trigonioides.*]

?Trisulcus HITCHCOCK, 1865 [**T. laqueatus*; OD]. Like *Bisulcus* but with 3 grooves separated by ridges which may show slight protuberances. *Trias.,* USA(Mass.).

Unionella ETHERIDGE, 1888 [*non Unionella* HAAS, 1913] [**U. bowralensis,* 1888; OD]. Quadrangular to irregularly trapeziform, equivalve, inequilateral; umbones depressed and continuous, eroded; ligament external; anterior adductor impression single, bounded posteriorly by oblique ridge; posterior adductor impression single and inconspicuous; supplementary umbonal muscular scar pitlike, either forming circular line or clustered; pallial line simple. *U.Trias.(Wianamatta Ser.),* New S. Wales.——FIG. D60,*1.* **U. bowralensis*; both valves, dorsal, ×1 *(299).*

Order TRIGONIOIDA Dall, 1889

[*nom. correct.* NEWELL, 1965 (*ex* order Trigoniacea DALL, 1889)] [Diagnosis by N. D. NEWELL]

Characters of superfamily Trigoniacea. *?M.Ord., Dev.-Rec.*

Superfamily TRIGONIACEA Lamarck, 1819

[*nom. transl.* DALL, 1900 (*ex* "les trigonées" LAMARCK, 1819] [Diagnosis by L. R. COX]

Shell equivalve; trigonal; ovate or rhomboidal; posteriorly truncate or subtruncate; posterior slope carinate or subcarinate; surface smooth or ornamented; ligament external, short, opisthodetic. Hinge teeth radiating from beak; left valve typically with strong median tooth and weaker one on each side; right valve typically with two main teeth received in recesses between those of left; additional and weaker teeth may be present, however, or some of teeth mentioned may be obsolete; adductor scars small, placed close to hinge teeth, anterior scar in each valve bordered on its inner side in many forms by buttress which passes under adjacent tooth or part of hinge plate; more rarely, similar buttress may border posterior adductor scar; pallial line entire except in Scaphellinidae; ostracum nacreous. [This diagnosis does not apply to the Trigonioididae, reference of which to the superfamily is very doubtful.] *?M.Ord., Dev.-Rec.*

Authorities have differed in their application of BERNARD's hinge teeth notation to shells of this superfamily. While DOUVILLÉ has regarded all teeth as cardinals, the three main ones of the left valve being (from rear to front) *4b, 2* and *4a,* and the two main teeth of the right valve *3b* and *3a,* ODHNER has suggested that they include homologues of laterals (Fig. D61). It has been decided not to adopt any system of tooth notation in the present account. Several well-known monographs are devoted to members of this superfamily, particularly the family Trigoniidae, and allusion may be made to certain descriptive terms which have come into fairly general use. The ridge which passes diagonally from the umbo to the posteroventral corner in each valve is termed the "marginal carina," the main part of the surface lying anterior to it, the "flank," and the part behind it, the "area." Dorsally, the area may be separated from the escutcheon (if present) by a second ridge, the "escutcheon carina."

The anatomical characters are known only in *Neotrigonia,* the sole surviving genus of the superfamily, and are referred to briefly under the family Trigoniidae.

?Family LYRODESMATIDAE Ulrich, 1894

[Materials for this family prepared by N. D. NEWELL & AURÈLE LAROCQUE]

Shell small, subtrigonal, rounded in front, acuminate posteriorly and commonly obliquely truncate; umbonal fold rounded or carinate; beaks small; hinge plate semicircular, with several angular, crenulated teeth radiating more or less symmetrically from beneath the beak. *M.Ord.-U.Ord.*

Lyrodesma CONRAD, 1841, p. 51 [**L. planum*; M] [=*?Lyronucula* FISCHER, 1886, p. 987 (type, *Lyrodesma gallicum* MUNIER-CHALMAS, 1876; M] [=*?Pseudaxinus* SALTER, 1864 (type, *Anodontopsis securiformis* M'COY, 1851)]. Anterior surface smooth; postumbonal slope with faint radial costellae; sinupalliate. *M.Ord.-U.Ord.,* E.N.Am.-Eu. ——FIG. D62,*1. L. acuminatum* (ULRICH), M. Ord., USA(Cannon Falls, Minn.); *1a,b,* RV ext., LV int., ×2; *1c,* RV hinge, ×3 *(929).*

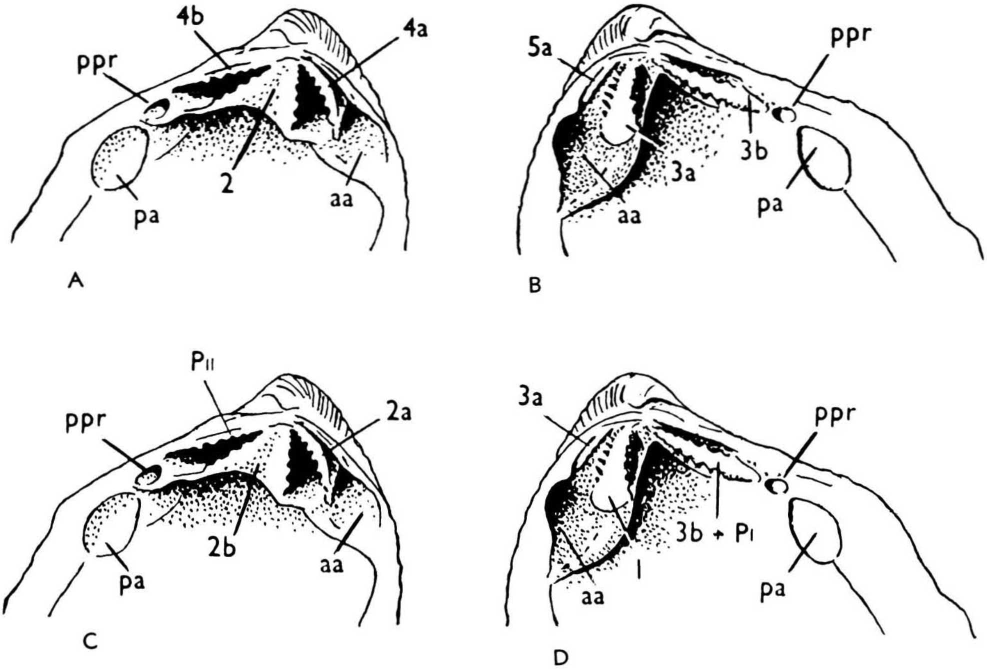


FIG. D61. *Trigonia* sp., showing alternative interpretations of trigoniacean dentition in terms of Bernard notation.

A,B, DOUVILLE's interpretation (more usual).
C,D. ODHNER's interpretation.
Teeth of left valve: *(A) 4b, 2, 4a; (C) PII, 2b, 2a.*
Teeth of right valve: *(B) 3b, 3a, 5a; (D)* 3*b* + *PI, 1, 3a.* [Explanation: *aa,* ant. adductor muscle scar; *pa,* post. adductor muscle scar; *ppr,* post. pedal retractor muscle scar.]

Family MYOPHORIIDAE Bronn, 1849

[*nom. correct.* Cox, 1951 (*pro* Myophorieae BRONN, 1849)]
[Materials for this family prepared by L. R. Cox]

Shell small to moderate in size, quadrate, ovate or subtrigonal, mostly diagonally carinate and posteriorly truncate; beaks usually but not always prosogyrous. Main tooth of left valve directed posteriorly, simple or bilobed; two main teeth of right valve asymmetrically disposed, posterior one narrower and more elongate; these teeth may be smooth or transversely striated, but less strongly than in Trigoniidae; an additional and weaker tooth may be present on one or both sides of main tooth in left valve, and in right valve third, relatively weak tooth may lie anterior to two mentioned; anterior myophorous buttress present in some forms, its impression forming groove on internal molds; pallial line entire. Surface of shell smooth, or bearing radial or concentric, but only rarely oblique, costae; ornament of flank and posterior area similar in most but not all genera. *Dev.-U.Trias., ?L.Jur.*

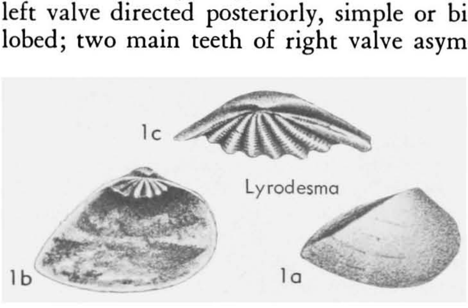


FIG. D62. Lyrodesmatidae (p. *N*471).

Myophoria BRONN in ALBERTI, 1834, p. 54 [**Trigonellites vulgaris* VON SCHLOTHEIM, 1820, p. 192; SD HERRMANNSEN, 1847, p. 80] [=*Trigonellites* VON SCHLOTHEIM, 1820 (*non* PARKINSON, 1811); *Cryptina* DESHAYES in BOUÉ, 1835, p. 47

(type, *C. raibeliana*); *Trigonella* Hehl, 1842 (*non* Conrad, 1837); *Miophoria* Boni, 1935 *(nom. null)*]. Trigonally ovate, very inequilateral, diagonal or marginal carina pronounced; no escutcheon; flank with one to few narrow radial ribs, impersistent in some specimens, with smooth, commonly shallowly concave interspaces; area smooth or with impersistent ribs; left valve with median tooth strong, simple or obscurely bifid, anterior tooth moderately strong, marginal, and posterior tooth obscure; right valve with strong, triangular anterior tooth, bifid in some forms, but posterior tooth obscure; main teeth smooth or transversely striated, striation confined to umbonal end in some specimens; myophorous buttress well developed. *L.Trias.-U.Trias.,* Eu.-Asia-N.Afr.——Fig. D63,*1*. **M. vulgaris* (von Schlotheim), M. Trias.(Muschelkalk), Ger.; *1a,b,* RV ext. and int., ×2; *1c,* LV int., ×2 (Hohenstein, 1913).

Costatoria Waagen, 1906, p. 393 [**Donax costata* Zenker, 1833, p. 55; SD Nakazawa, 1960, p. 52]. Trigonally ovate to rhomboidal, moderately inequilateral; marginal carina more or less pronounced; escutcheon defined but small; flank with number of prominent, unevenly spaced radial ribs and smooth or concentrically striated interspaces; area smooth or with weak radial ribs; left valve with median tooth strong and simple, anterior tooth moderately strong, short, and posterior tooth thin, elongate, and marginal; right valve with anterior and posterior teeth moderately strong, subequal; sides of teeth transversely grooved in larger species; myophorous buttress present. *L.Perm.,* USA(Tex.-Wyo.); *U.Perm.,* Japan-Eu. (Alps); *L.Trias.-U.Trias.,* cosmop.——Fig. D63, *3a*. *C. goldfussi* (Alberti), M.Trias.(Muschelkalk), Ger., LV ext., ×3.3 (Hohenstein, 1913). ——Fig. D63,*3b,c*. *C. whateleyae* (von Buch), U.Trias., S.Tyrol; *3b,c,* RV ext. and int., ×1.6 *(58)*.

?**Cytherodon** Hall & Whitfield, 1873 [**Nuculites appressus* Conrad, 1842; M]. Form and musculature similar to *Rhenania* and *Schizodus,* posteriorly obliquely truncate and posteroventrally acute, with well-defined, narrow umbonal carina; hinge poorly known, consisting of few cardinal teeth. *M.Dev.,* N.Am.(Ohio-Va.).

Eoschizodus Cox, 1951, p. 369 [*pro Kefersteinia* Neumayr, 1891, p. 788 (*non* Quatrefages, 1865)] [**Megalodus truncatus* Goldfuss, 1837, p. 184] [=?*Curtonotus* Salter, 1863, p. 494 (*non* Stephens, 1827); ?*Cyrtonotus* Fischer, 1886, p. 996 (*non* Lucas, 1844)]. Subtrigonal to ovate, smooth, subequilateral to strongly inequilateral, subtruncate or rounded posteriorly; umbones prosogyrous or orthogyrous; marginal carina well defined in some species, absent in others; no escutcheon; left valve with triangular, simple or bilobed median tooth, anterior tooth of moderate strength and posterior tooth narrow, marginal; right valve with anterior tooth stoutly triangular and posterior tooth elongate; teeth not striated; myophorous buttress absent or indistinct. *Dev.-Perm.,* cosmop.——Fig. D63,*4*. **E. truncatus* (Goldfuss), Dev., Ger.; *4a,b,* LV ext. and int. hinge, ×1; *4c,* RV int. hinge, ×1 *(47)*.

Gruenewaldia Wöhrmann, 1889, p. 215 [**Cardita decussata* von Münster, 1837, p. 185; M] [=*Elegantinia* Waagen, 1906, p. 393 (obj.); *Trigomyophoria* Kobayashi, 1954, p. 66 (obj.)]. Rhomboidal, gibbose, very inequilateral, sharply truncate posteriorly; marginal carina prominent, commonly wide and blunt, with deep depression in front of it and corresponding sinus of ventral margin; escutcheon moderate in width, bordered by prominent carina; flank and area ornamented with concentric ridges, most closely spaced on area and antecarinal depression; radial riblets also present on flank in some species; left valve with simple, triangular median tooth, its apex separated by gap from margin in some specimens, anterior tooth short but only slightly weaker than median tooth, and posterior tooth obscure; right valve with strong tuberculiform or triangular anterior tooth and more elongate posterior tooth, fused together at proximal end in some specimens; teeth with strong transverse grooving; myophorous buttress inconspicuous. *M.Trias.-U.Trias.,* Eu.-Asia-Bear Is. ——Fig. D63,*2*. **G. decussata* (von Münster), U. Trias., S.Tyrol; RV ext., ×1.5 *(58)*.

Hefteria Dahmer, 1948, p. 125 [**Cardinia carinata* Roemer, 1855, p. 125; OD]. Oblong, elongate; marginal carina sharp and prominent, sigmoidal; flank ornamented with narrow, sharp, regular concentric costae; hinge teeth simple, arranged as in *Eoschizodus,* and with right posterior tooth well developed. *L.Dev.,* Eu.(Ger.).

Heminajas Neumayr, 1891, p. 789 [**Myophoria fissidentata* Wöhrmann, 1889, p. 213; M]. Elongate-ovate, inequilateral, tapering and truncated posteriorly; marginal carina weak; surface smooth; left valve with widely triangular median tooth, grooved in some specimens, anterior tooth strong and well separated from margin, and posterior tooth thin and elongate; right valve with 3 well-defined teeth, most anterior of which is short and stout, median strong and grooved in some specimens, and posterior very thin and elongate; myophorous buttress present. *L.Trias.-U.Trias.,* Eu. (Aus.-Hung.).——Fig. D63,*10*. **H. fissidentata* (Wöhrmann), U.Trias., Aus.; *10a,b,* LV ext. and int., ×1; *10c,* RV int., ×1 (Arthaber, 1905; *1002*).

?**Liotrigonia** Cox, 1952, p. 53 [**Trigonia lingonensis* Dumortier, 1869, p. 275; OD]. Trigonally ovate, slightly inequilateral, larger than typical Myophoriidae; umbones prominent, sharply rounded, beaks orthogyrous; marginal carina well marked, coinciding with most inflated part of valve; area slightly concave, smooth, escutcheon

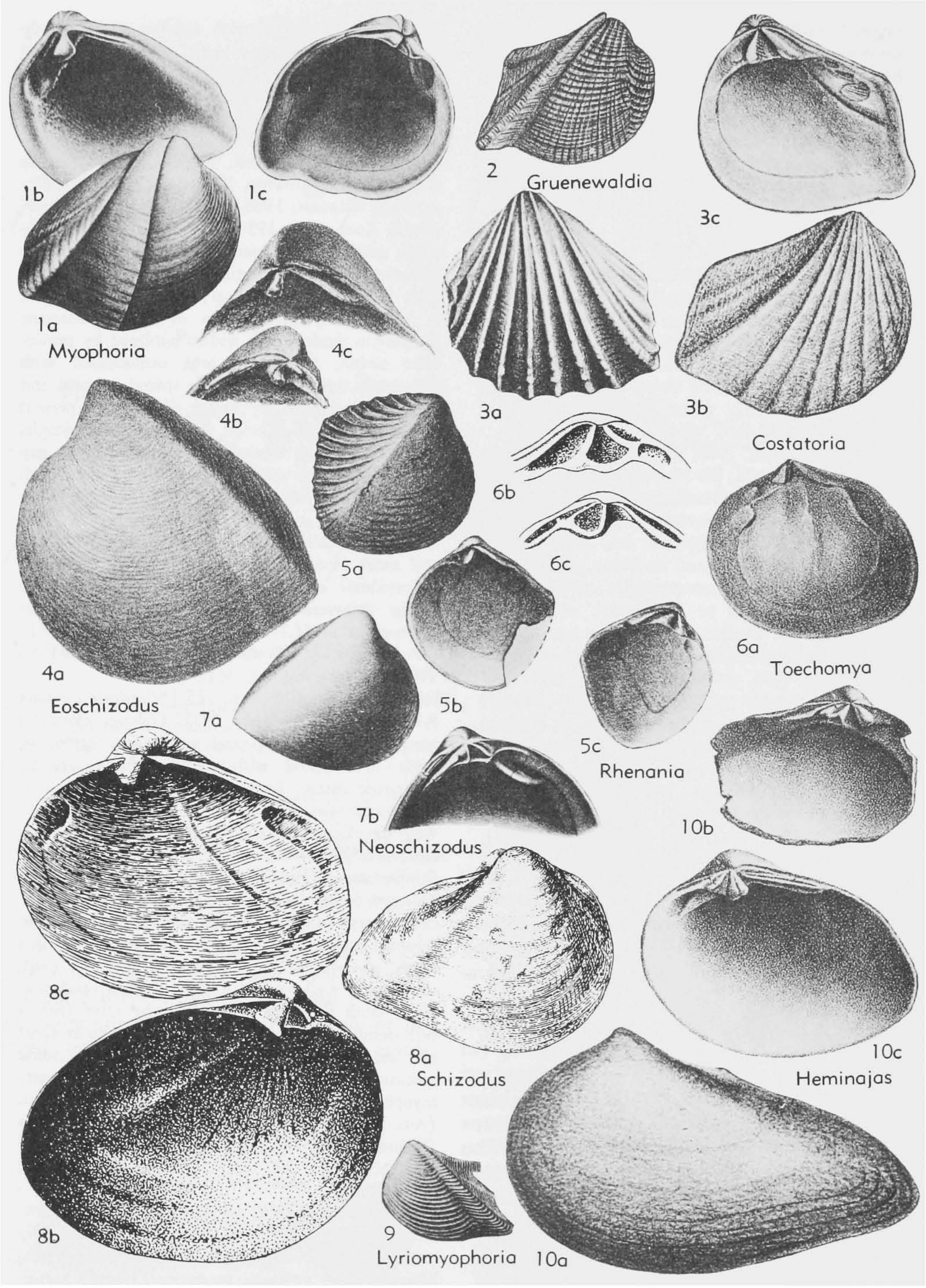


FIG. D63. Myophoriidae (p. *N*472-*N*473, *N*475-*N*476).

wide, depressed; flank evenly convex, smooth except for narrow, irregular, subconcentric wrinkles mostly confined to its anterior part; left valve with strong triangular median tooth having concave lower margin, weaker anterior tooth, each transversely grooved on side facing other, and thin posterior tooth fused with nymph; dentition of right valve unknown; myophorous buttress well-developed. *L. Jur. (M. Lias.),* Eu.(France)-Eng.-USSR(E.Sib.).——Fig. D64,*1.* **L. lingonensis* (Dumortier); *1a,* LV ext., Eng., ×1 *(554)*; *1b,* LV int., France, ×1 (Dumortier, 1869).

Lyriomyophoria Kobayashi, 1954, p. 66 [**Lyriodon elegans* Dunker, 1849, p. 15; OD]. Outline and concentric ornament as in *Gruenewaldia,* but less gibbous, with marginal carina not prominent and with depression in front of it correspondingly shallow; no radial ornament. *Perm.-U.Trias.(Rhaet.),* Eu.-Asia-N.Afr.-N.Z.——Fig. D63,*9.* **L. elegans* (Dunker), M.Trias.(Muschelkalk), Ger.; ×1 (Assmann, 1916).

Neoschizodus Giebel, 1855, p. 35 [**Lyrodon laevigatum* Goldfuss, 1837, p. 197; SD Stoliczka, 1871, p. xx] [=*Leviconcha* Waagen, 1906, p. 393 (type, *Lyrodon ovatum* Goldfuss, 1837, p. 197); *Tropiphora* Waagen, 1906, p. 393 (type, *Lyrodon laevigatum* Goldfuss; SD Cox, herein); *Okunominetania* Ichikawa, 1954, p. 62 (type, *Neoschizodus (O.) okunominetaniensis*); *Middalaya* Dickens, 1956 (type, *M. johnstonei*)]. Shape, smooth surface, and dentition as in *Eoschizodus,* except that main teeth may be transversely striated; myophorous buttress well developed. *L.Perm.-U.Trias.,* cosmop.——Fig. D63,*7.* **N. laevigatus* (Goldfuss), M.Trias.(Muschelkalk), Ger.; *7a,b,* RV ext., LV int., ×2, ×2.7 (Hohenstein, 1913).

Rhenania Waagen, 1907, p. 149 [**Myophoria schwelmensis* Beushausen, 1895, p. 132; SD Cox, herein] [=*Rhenania* Waagen, 1906, p. 393 *(nom. nud.)*]. Small, quadrate or oblong; umbones terminal or subterminal; marginal carina nearly straight; area relatively large, with curved, oblique ridges; flank smooth or with concentric rugae; left valve with simple, broadly triangular median tooth; anterior and posterior teeth subequal and moderately strong; right valve with stout anterior tooth, widely divergent from thin, elongate, marginal posterior tooth; myophorous buttress absent. *Dev.,* Eu.(Ger.).——Fig. D63,*5.* **R. schwelmensis* (Beushausen), Givet.; *5a,b,* RV ext. and int., ×2; *5c,* LV int., ×1 *(47).*

Schizodus de Verneuil & Murchison, 1844, p. 505 (*ex* King, MS) [**Axinus obscurus* J. Sowerby, 1821, p. 12; SD de Verneuil, 1845, p. 308] [=*?Leptodomus* M'Coy in Griffith, 1844, p. 66 (*non* Schoenherr, 1843); *Prisconaia* Conrad, 1867, p. 10 (type, *P. ventricosa*); *Axinopsis* Tate, 1868, p. 412 (*pro Schizodus* "King," *non Schizodon* Waterhouse, 1842); *?Niobe* de Koninck, 1885, p. 77 (*non* Angelin, 1851); *?Protoschizodus* deKoninck, 1885, p. 125 (*pro Niobe* deKoninck); *Schizodon* Cossmann, 1912 *(nom. van.)*; *?Protoschizodon* Cossmann, 1912 *(nom. van.)*]. Ovate or trigonally ovate, subequilateral to strongly inequilateral, obliquely truncated and in some forms attenuated posteriorly, smooth; umbones usually feebly prosogyrous, more rarely opisthogyrous; marginal carina rounded off; no escutcheon; left valve with strong, bilobed median tooth, anterior tooth small and marginal, and posterior tooth obsolete or almost so; right valve with single stout, forward-directed tooth, posterior tooth being obsolete; no myophorous buttress. *Carb.-Perm.,* cosmop.——Fig. D63,*8a.* **S. obscurus* (Sowerby), U.Perm., Eng.; RV ext., ×1.——Fig. D63,*8b,c.* *S. harii* Miller, Penn., USA(Mo.); *8b,c,* LV int., RV int., ×1 (Miller, 1892; Beede, 1900).

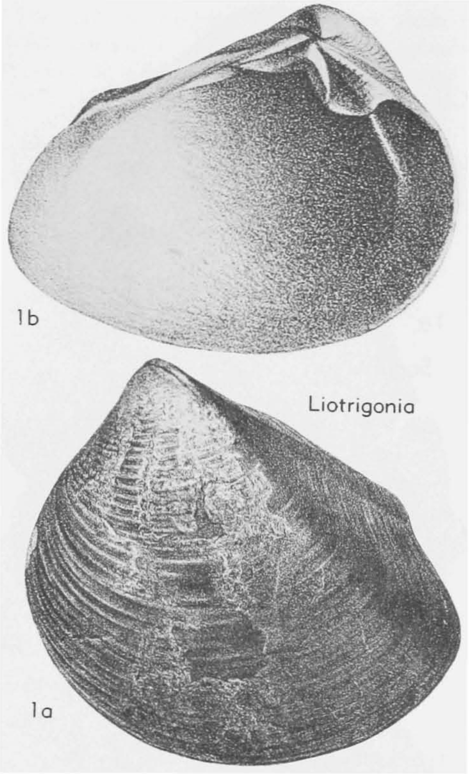


Fig. D64. Myophoriidae (p. *N*473, *N*475).

Toechomya Clarke, 1899, p. 96 [**Schizodus transversus* Beushausen, 1884, p. 95; SD Cox, 1951, p. 368]. Smooth, ovate, only slightly inequilateral, subtruncate posteriorly, not carinate; umbones orthogyrous; hinge plate present in both valves; left valve with simple, narrowly triangular

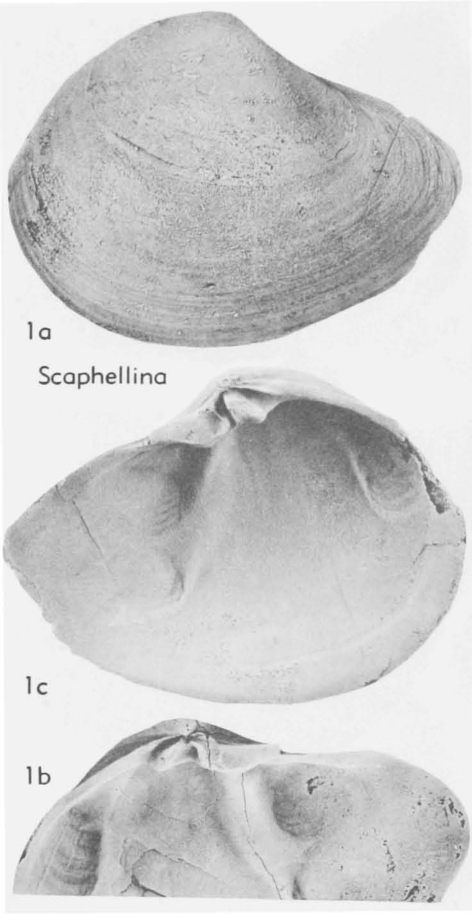


Fig. D65. Scaphellinidae (p. *N*476).

median tooth, separated by broad sockets from thin anterior tooth and obscure, thin, elongate posterior tooth adjacent to margin; right valve with stoutly triangular, anteriorly directed subumbonal tooth separated by narrow furrow from thin anterior tooth and by triangular socket from elongate posterior tooth which is parallel to and separated by narrow socket from margin; myophorous buttresses, posterior stronger, bordering 2 adductor scars. *M.Dev.*, Eu.——Fig. D63,*6*. **T. transversa* (Beushausen), M.Dev., Ger.; *6a*, LV int. mold, ×1 *(46)*; *6b,c*, LV and RV hinge teeth, enlarged *(135)*.

?Family SCAPHELLINIDAE Newell & Ciriacks, 1962

[Scaphellinidae Newell & Ciriacks, 1962, p. 4] [Materials for this family prepared by N. D. Newell]

Ovoid, opisthogyrate, opisthodetic shells with obscure escutcheon but lacking lunule; with strong myophoric buttress in front of posterior adductor; adductor scars deeply impressed, anterior adductor slightly smaller than posterior, higher than wide; dentition (A)(R)*010101*/(L)*101010*(P) consisting of three cardinal teeth and three sockets in each valve, of which posterior tooth of RV and corresponding socket of LV are rudimentary and not visible on worn valves; lateral teeth absent; median tooth as in many trigoniaceans, broad, distally notched and gable-shaped; floor of median socket deeply notched. [As in the Myophoriidae, the anterior cardinal tooth in these forms is in the LV, contrary to the situation in heterodonts, in which the anterior cardinal tooth characteristically is in the RV.] *L. Perm.*

Scaphellina Newell & Ciriacks, 1962, p. 4 [**S. bradyi* (=*Schizodus concinnus* C. C. Branson, 1930); OD]. Gibbous, heavy, about 0.25 to 0.3 longer than high, unornamented; lateral profile broadly rounded anteriorly, somewhat attenuated and slightly gaping posteriorly; beaks depressed, situated slightly ahead of mid-point of hinge. *L. Perm. (Kaibab, Park City)*, N.Am.——Fig. D65, *1*. **S. concinna* (Branson), Park City, USA (Wyo.), *1a*, RV ext., ×1.1; *1b,c*, RV and LV int., ×1.1 (Newell, n).

Family TRIGONIIDAE Lamarck, 1819

[*nom. Latine redditum* Gray, 1823 (as "Trigoniana") *et correct.* King, 1850, *pro* "les trigonées" Lamarck, 1819 (examination of literature has led to conclusion that "general acceptance" has been accorded to Lamarck's publication of the family name in the French vernacular as establishing him as founder of the family (International Code, Art. 11 (e)iii] [Materials for this family prepared by L. R. Cox]

Shell usually larger than in Myophoriidae, highly variable in shape and ornament; umbones most commonly opisthogyrous, but orthogyrous or prosogyrous in a few groups; escutcheon usually present; area and flank differentiated and differently ornamented in most genera; flank ornament generally concentric or oblique, but radial in some forms; median tooth of left valve broad, grooved, strongly concave to deeply emarginate below; posterior left weak or obscure, marginal; anterior left of moderate strength; right valve with two subequal and more or less symmetrically divergent teeth not borne on hinge plate, and with very obscure anterior marginal tooth in some species; two main teeth of right valve and sides of left valve teeth against which they fit bear strong transverse ridges (*Praegonia* FLEMING is an exception); anterior myophorous buttresses well developed; pallial line entire; Recent forms filibranchiate; mantle lobes free; nonbyssiferous. *M.Trias.-Rec.*

The family Trigoniidae as now interpreted coincides with the single genus *Trigonia* of older authors. The genus was divided by some into several sections, of which the Costatae, Clavellatae, Undulatae, Scaphoideae, Glabrae, and Scabrae were the most important. Latterly numerous genera, mostly even more restricted than these

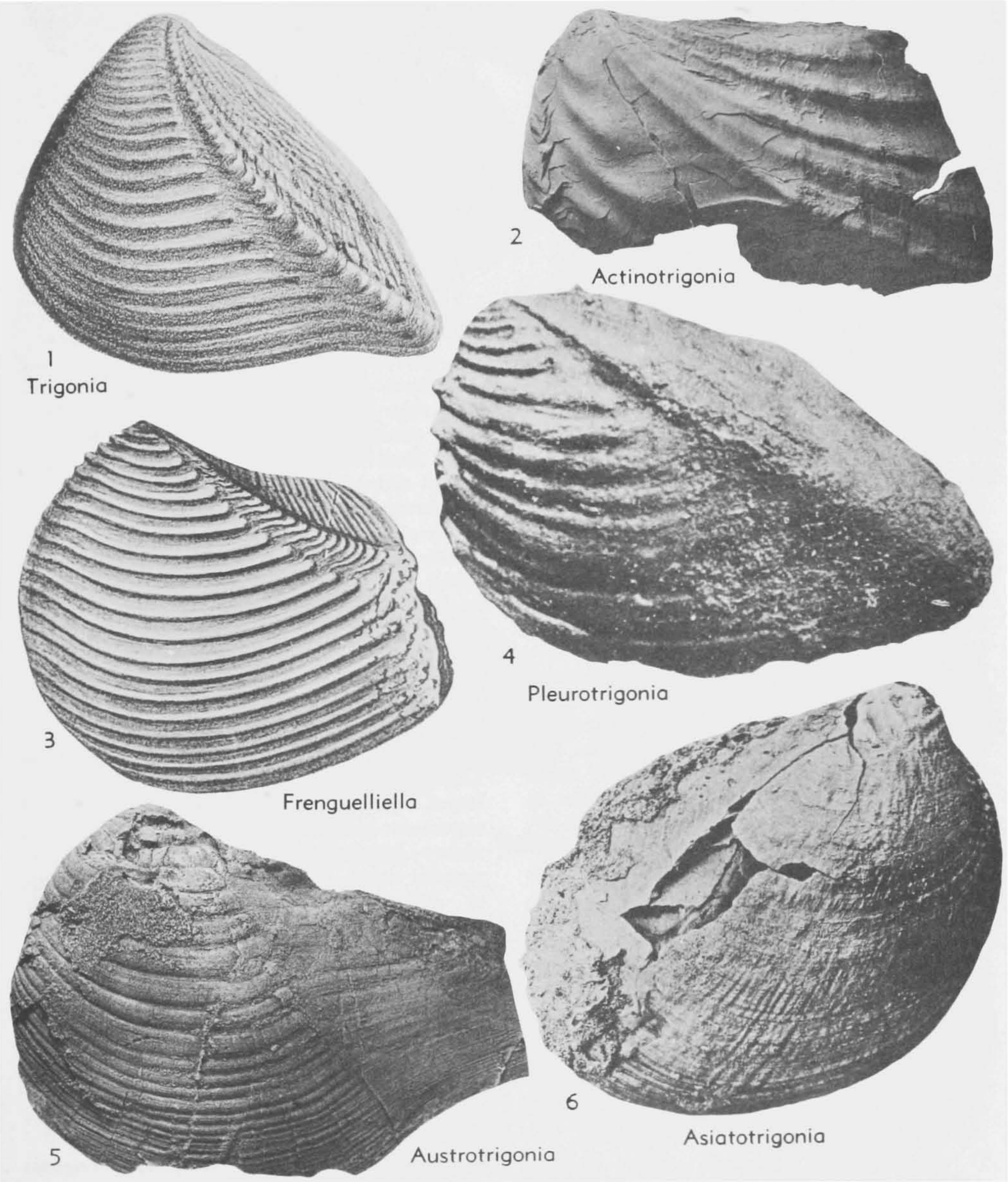


FIG. D66. Trigoniidae (p. *N*478).

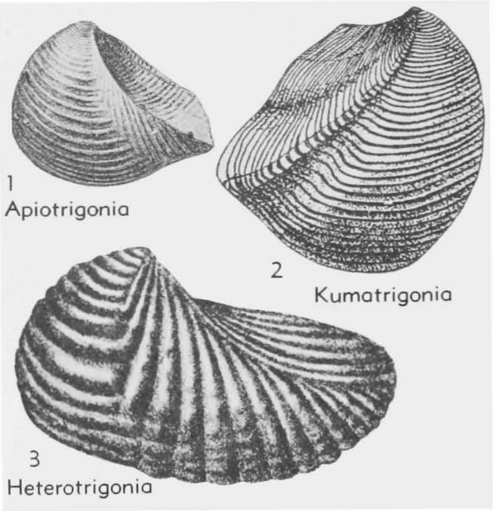


Fig. D67. Trigoniidae (p. *N*478, *N*480).

sections, have come to be recognized. A few authors have divided the family into subfamilies, but these are not adopted in the present work.

Trigonia Bruguière, 1789, p. xiv [**Venus sulcata* Hermann, 1781, pl. 4, fig. 9; ICZN Opinion 327 (1955)] [=*Lyridon* J. de C. Sowerby, 1823 (obj.); *Lyriodon* Bronn, 1834 *(nom. van.)*; *Lyrodon* Goldfuss, 1837 *(nom. van.)*]. Trigonal to trigonally ovate; marginal carina prominent, serrated, escutcheon carina obtuse; escutcheon smooth or transversely ridged; flank (except in a Triassic representative) with continuous concentric costae. *M.Trias.-U.Cret.*, cosmop.

T. (Trigonia). Trigonal, umbones prominent; area wide, bipartite, radially costate; flank costate (except in a Triassic representative), ends of costae commonly separated from marginal carina in left valve or in both by smooth radial space. *M. Trias. (Anis.)-U. Cret. (Cenoman.),* cosmop.——Fig. D66,*1*. **T. (T.) sulcata* (Hermann), L.Jur. (Toarc.), France(Alsace); LV ext., ×0.7 (Bayle, 1878).

T. (Frenguelliella) Leanza, 1942, p. 164 [**T. inexspectata* Jaworski, 1915, p. 377; OD]. Trigonally ovate, umbones less prominent than in *T. (Trigonia)*; area without radial ornament, transversely ridged, smooth in later growth stages in some species. *L. Jur. (Lias.) - U. Cret. (Senon.),* cosmop.——Fig. D66,*3*. **T. (F.) inexspectata* Jaworski, L.Jur.(Domer.), Arg.; LV ext., ×1 (Jaworski, 1916).

T. (Kumatrigonia) Tamura, 1959, p. 213 [**Frenguelliella (Kumatrigonia) tanourensis*; OD]. Like *T. (Frenguelliella)*, but taller and more trigonal, and with each transverse ridge of area connected with flank costa. *U.Trias.,* Japan.——Fig. D67,*2*. **T. (K.) tanourensis* (Tamura); RV ext., ×1.5 *(901)*.

T. (Latitrigonia) Kobayashi in Kobayashi & Tamura, 1957; p. 36 [**Latitrigonia pyramidalis* Kobayashi & Tamura, 1957; OD]. Rather small, subquadrate, with wide, mostly smooth area occupying almost half of surface in some species; flank costae widespaced, each thickened at its posterior end to form a node in some forms. *M.Jur.-U.Jur.,* Japan.

T. (Pleurotrigonia) van Hoepen, 1929, p. 33 [**Trigonia blanckenhorni* Newton, 1909, p. 40; OD]. Elongate, strongly inequilateral; umbo depressed; escutcheon carina obscure, marginal carina rounded off after mid-growth; area wide, smooth except for radial threads in earliest growth stages; flank costae rounded, absent from narrow anterior face set at right angles to commissure. *L.Cret.(Alb.),* S.Afr.——Fig. D66,*4*. **T. (P.) blanckenhorni* Newton; LV ext., ×1 *(785)*.

Actinotrigonia Cox, 1963, p. 49 [**A. bathurstensis*; OD]. Oblong, strongly inequilateral; umbones not protruding, slightly opisthogyrous; escutcheon ill-defined; marginal carina well-marked but obtuse ridge; area very broad, ornamented with small number of radial ridges with broader intervals; flank with broad, smooth, shallow antecarinal depression to which sinus of ventral margin corresponds, rest of its surface bearing broad, depressed, oblique rounded ribs. *U.Cret. (Cenoman.),* Bathurst I., N.Australia.——Fig. D66,*2*. **A. bathurstensis*; LV ext., ×1 (Cox, n).

Agonisca Fleming, 1963, p. 843 [**A. corbiensis*; OD]. Rather small for family, trigonally ovate, with low prosogyrous beaks; lacking marginal carina and area; ornament of irregular concentric folds; hinge as in *Praegonia. M.Trias.(Ladin., Kaihikuan)*, N.Z.

Apiotrigonia Cox, 1952, p. 59 [**Trigonia sulcataria* Lamarck, 1819, p. 64; OD]. Strongly inequilateral, pyriform or subovate; marginal and escutcheon carinae obscure except near umbo; area narrow; posterior part of flank with nearly vertical, rounded costae, anterior part with subconcentric or only slightly oblique costae. *Cret.(Alb.-Maastricht.)*, Eu.-Asia-W.N.Am.

A. (Apiotrigonia). Relatively small, pyriform, with rather prominent umbo; escutcheon with transverse ribbing, area smooth; anterior series of flank costae simple or tuberculate, occupying greater part of surface. *Cret.(Alb.-Maastricht.),* Eu.-Asia-W.N.Am.——Fig. D67,*1*. *A. (A.) pennata* (J. Sowerby), L.Cret.(Alb.), Eng.; LV ext., ×1 *(554)*.

A. (Heterotrigonia) Cox, 1952, p. 63 [**Trigonia diversicostata* Whiteaves, 1876, p. 68; OD]. Less tapering than *A. (Apiotrigonia)*; area with few

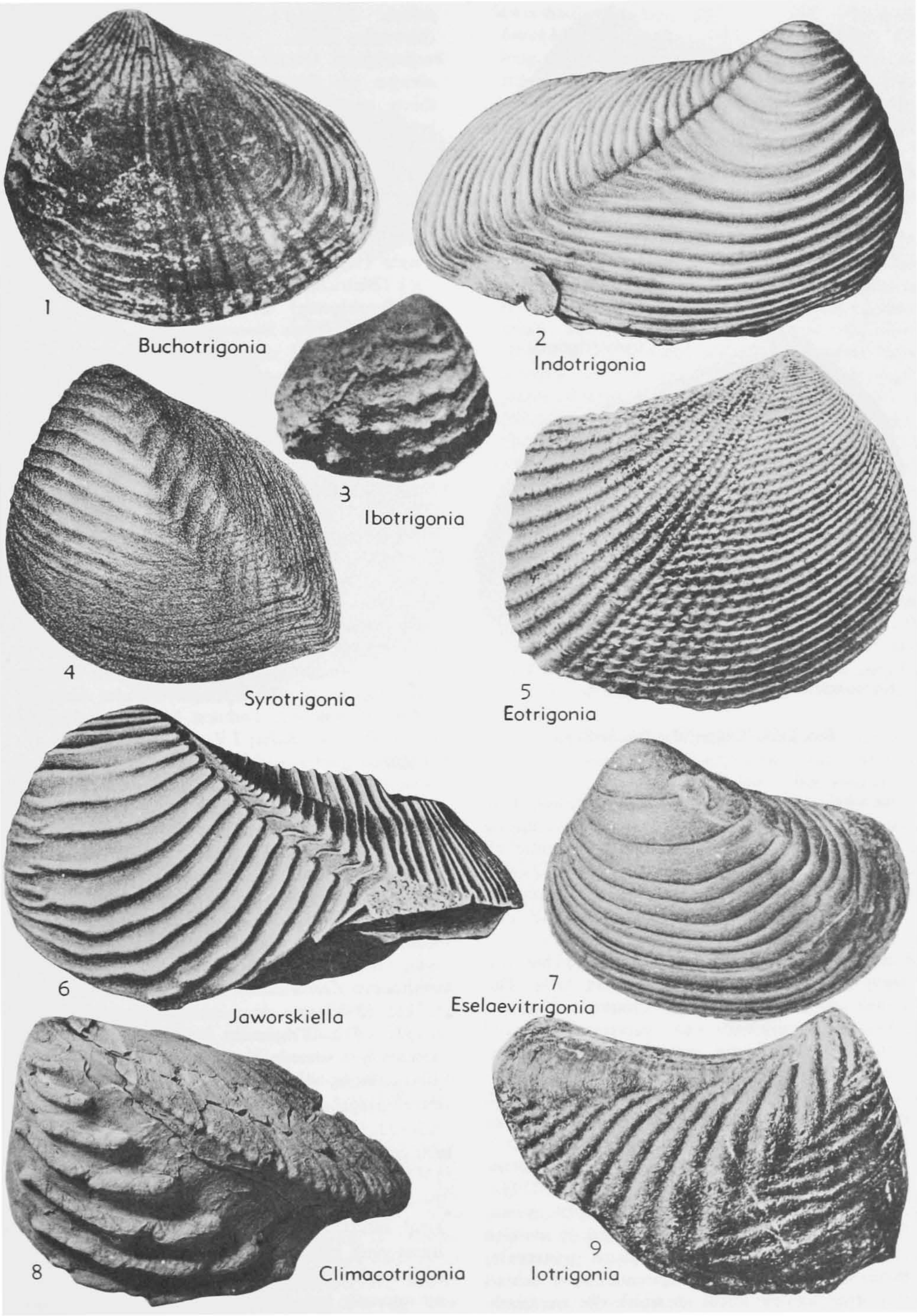


Fig. D68. Trigoniidae (p. *N*480-*N*481).

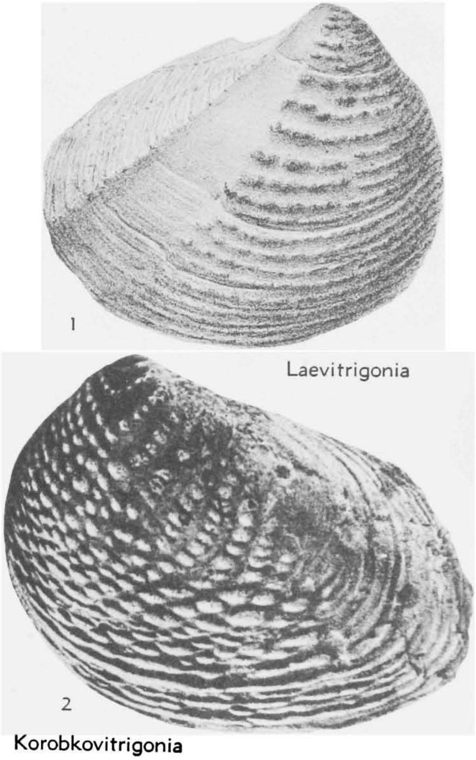


FIG. D69. Trigoniidae (p. N481).

rounded radial ribs; flank costae broader than in *A. (Apiotrigonia)*, anterior series occupying smaller proportion of surface and becoming almost obsolete in later growth stages. *U.Cret.*, B.C.-Japan.——FIG. D67,*3*. **A. (H.) diversicostata* (WHITEAVES), Haida F., B.C.; LV ext., ×1 (Whiteaves, 1876).

Asiatotrigonia COX, 1952, p. 63 [**Trigonia sultanuisi* ARCHANGELSKI, 1916, p. 32; OD]. Obliquely ovate, not tapering or truncated posteriorly, strongly inequilateral; no carinae; area and escutcheon undefined; posterior region unornamented; flank smooth except for few obscure V-shaped costae near umbo and more or less radial, irregular, narrow wrinkles present on its anterior part in later growth stages. *U.Cret.(Cenoman.)*, Turkestan.——FIG. D66,*6*. **A. sultanuisi* (ARCHANGELSKI); RV ext., ×0.7 (Archangelski, 1916).

Austrotrigonia SKWARKO, 1963, p. 33 [**A. prima*; OD]. Very inequilateral, broad and gently rounded anteriorly, produced and attenuated posteriorly; flank with low irregular concentric ribs, behind it a broad shallow sulcus on which ribs are faintly continued; area narrow, with growth lines only. *L.Cret.(Neocom.)*, Australia.——FIG. D66,*5*. **A. prima*, N.Terr.; LV ext. (holotype), ×0.7 (Skwarko, 1963).

Buchotrigonia DIETRICH, 1938, p. 97 [**Trigonia abrupta* VON BUCH, 1838, p. 65; M]. Trigonal, short; area wide, transversely ribbed in early growth stages, later smooth; flank with narrow, nontuberculate costae discrepantly or obliquely arranged. *L.Cret.-U.Cret.*, S.Am.-Spain-Syria-N.Z.

B. (Buchotrigonia). Marginal carina ill-defined except in early growth stages. *L.Cret.-U.Cret.*, S.Am.-Spain-N.Z.——FIG. D68,*1*. **B. (B.) abrupta* (VON BUCH), L.Cret., Colombia; LV ext., ×1 (Dietrich, 1938).

B. (Syrotrigonia) COX, 1952, p. 61 [**B. (S.) fraasi*=**Trigonia libanotica* VOKES, 1942, p. 168; OD]. Marginal carina prominent, broad antecarinal depression in front of it; flank with slightly oblique costae which bend up steeply at edge of depression and cross it. *L.Cret.(Apt.)*, Syria.——FIG. D68,*4*. **B. (S.) libanotica* (VOKES); LV ext., ×1 (Noetling, 1886).

Climacotrigonia COX, 1963, p. 50 [**C. dailyi*; OD]. Trapeziform, strongly inequilateral; umbones orthogyrous, not protruding; no escutcheon; marginal carina a prominent ridge; area flat, broad, unornamented except for growth rugae; flank with broad, smooth antecarinal depression with corresponding sinus of ventral margin, and with rest of its surface bearing small number of very prominent, slightly irregular and oblique, round-topped ribs with rather broader intervals. *U.Cret.(Cenoman.)*, Bathurst I., N.Australia.——FIG. D68,*8*. **C. dailyi*; LV ext., ×1 (Cox, n).

Eotrigonia COSSMANN, 1912, p. 26 [**Trigonia semiundulata* M'COY, 1866=**T. subundulata* JENKINS, 1865, p. 362; OD]. Rather small, oblong; marginal carina obtuse, marked by rounded costa; area rather wide, bearing several radial costae with delicate serrations; flank ornamented with narrow costae which are slightly oblique to concentric, sloping down toward marginal carina. *L.Eoc.-Mio.*, Australia.——FIG. D68,*5*. **E. subundulata* (JENKINS), Oligo., Australia; RV ext., ×2 *(161)*.

Geratrigonia KOBAYASHI in KOBAYASHI & MORI, 1954, p. 171 [**Trigonia hosourensis* YOKOYAMA, 1904, p. 11; OD]. Trigonally ovate; marginal carina obtuse; area smooth, bipartite; flank with narrow, subconcentric, nontuberculate costae which are rather irregular, particularly in early growth stages. *L.Jur.(L.Lias.)*, Japan.

Ibotrigonia KOBAYASHI in KOBAYASHI & TAMURA, 1957, p. 38 [**I. masatanii* KOBAYASHI & TAMURA, 1957; OD]. Rather small, roundly trigonal; marginal carina irregularly serrated; area smooth or transversely ridged and with median carina; flank with small number of subconcentric costae, broken up unevenly into tubercles. *M.Jur.*, Japan.——FIG. D68,*3*. **I. masatanii* KOBAYASHI & TAMURA; RV ext., ×2 (Kobayashi & Tamura, 1957).

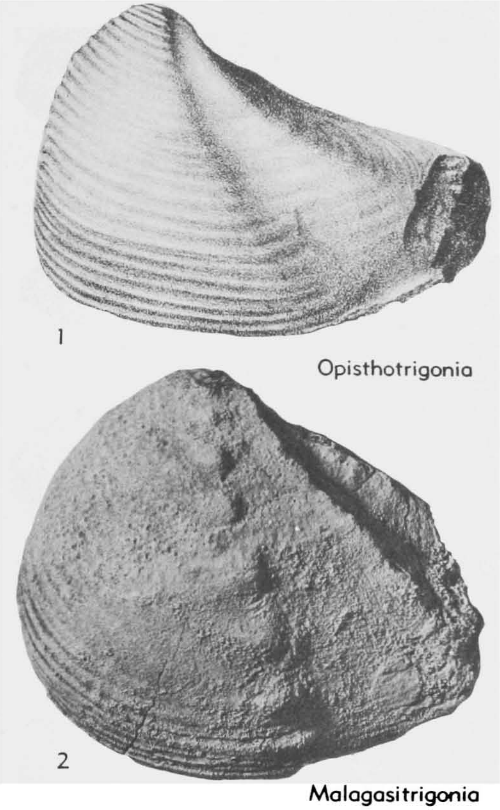


FIG. D70. Trigoniidae (p. *N*481, *N*485).

Indotrigonia DIETRICH, 1933, p. 30 [**Trigonia smeei* J. DE C. SOWERBY, 1840, expl. pl. 61; OD]. Oblong, elongate, strongly inequilateral, with rather prominent umbo; marginal and escutcheon carinae ill-defined, escutcheon not impressed; area convex, with rather coarse, irregular transverse ridges and with radial threads in earliest growth stages; flank with rounded concentric costae which are discontinuous in some specimens and are more depressed and rounded than in *Trigonia*. *U.Jur.(Oxford.)-L.Cret.(Neocom.),* India-E.Afr.——FIG. D68,*2*. **I. smeei* (SOWERBY), U.Jur. (Oxford.), India(Kutch); RV ext., ×0.7 (Kitchin, 1903).

Iotrigonia VAN HOEPEN, 1929, p. 6 [**I. crassitesta*; OD]. Elongate, ovate or sublunate, strongly inequilateral; umbones prominent; marginal and escutcheon carinae rounded off; area smooth, with median groove; flank costae belonging to 2 series, which in earlier or in all growth stages meet in an acute, down-pointing V. *L.Cret.-U.Cret.,* S.Afr.-Asia-S.Am.-Australia-N.Z.-Antarctic.——FIG. D68, *9*. *I. haughtoni* (RENNIE), L.Cret.(Neocom.), S. Afr.; RV ext., ×0.7 *(785)*.

Jaworskiella LEANZA, 1942, p. 166 [**Trigonia burckhardti* JAWORSKI, 1914, p. 299; OD]. Oblong, strongly inequilateral; marginal carina well marked; area with strong transverse ridges, flank with narrow, more or less sinuous, simple costae which are subconcentric except near their well-upcurved posterior end. *L.Jur.(M.Lias.)-U.Jur.,* S. Am.-Port.——FIG. D68,*6*. **J. burckhardti* (JAWORSKI), L.Jur.(Lias.), Arg.; LV ext., ×0.7 (Jaworski, 1915).

Korobkovitrigonia SAVELIEV, 1958, p. 99 [**K. korobkovi*; OD]. Ovate to suborbicular, unelongated, commonly oblique; no distinct marginal carina; area with small tubercles in earlier growth stages, later with coarse growth rugae only; flank with 2 series of steep, oblique, tuberculate costae meeting in V's except in later growth stages, where anterior or both series may be replaced by irregularly arranged tubercles or coarse rugae. *Cret.(Barrem.-Turon.),* C.Asia-Spain-Port.-Alg.-S. Am.——FIG. D69,*2*. **K. korobkovi,* L.Cret.(Alb.), C.Asia(Mangyshlak); LV ext., ×0.85 (Saveliev, 1958).

Laevitrigonia LEBKÜCHNER, 1932, p. 35 [**Trigonia gibbosa* J. SOWERBY, 1819, p. 61; OD] [=*Laevitrigonia* DEECKE, 1925 *(nom. nud.)*]. Ovate, inequilateral; smooth, shallow antecarinal depression usually present; flank, if not almost smooth, ornamented with weak, irregularly spaced concentric costae commonly broken up into pustules, or with oblique rows of pustules. *L.Jur.(Lias.)-U.Cret.,* cosmop.

L. (Laevitrigonia). Marginal and escutcheon carinae ill-defined except near umbo; antecarinal depression usually well marked, but obscure or absent in a few species; area of moderate width, with median groove, smooth except for growth lines. *L.Jur.(Lias.)-U.Jur.(Tithon.),* Eu.-Asia-E. Afr.——FIG. D69,*1*. **L. (L.) gibbosa* (J. SOWERBY), U.Jur.(Portland.), Eng.; RV ext., ×0.85 *(554)*.

L. (Eselaevitrigonia) KOBAYASHI & MORI, 1954, p. 161 [**Trigonia meridiana* WOODS, 1917, p. 6; OD]. Antecarinal depression with ill-defined borders, marginal and escutcheon carinae rounded off; flank costae well separated, not broken up into pustules, continued across antecarinal depression and area; area with radial costellae in early growth stages. *U.Jur.(Tithon.)-U.Cret. (Turon.),* India-N.Z.——FIG. D68,*7*. **L. (E.) meridiana* (WOODS), U.Cret.(Turon.), N.Z.; LV ext., ×1 (Woods, 1917).

L. (Malagasitrigonia) COX, 1963, p. 51 [**L. (M.) collignoni*; OD]. Antecarinal depression broad, smooth, bordered posteriorly by series of large tubercles; marginal and escutcheon carinae sharp and prominent; area narrow, smooth, strongly convex; flank costae weak, mostly narrow, irregular. *L.Cret.,* Madag.——FIG. D70,*2*. **L. (M.) collignoni*; LV ext., ×1 (Cox, n).

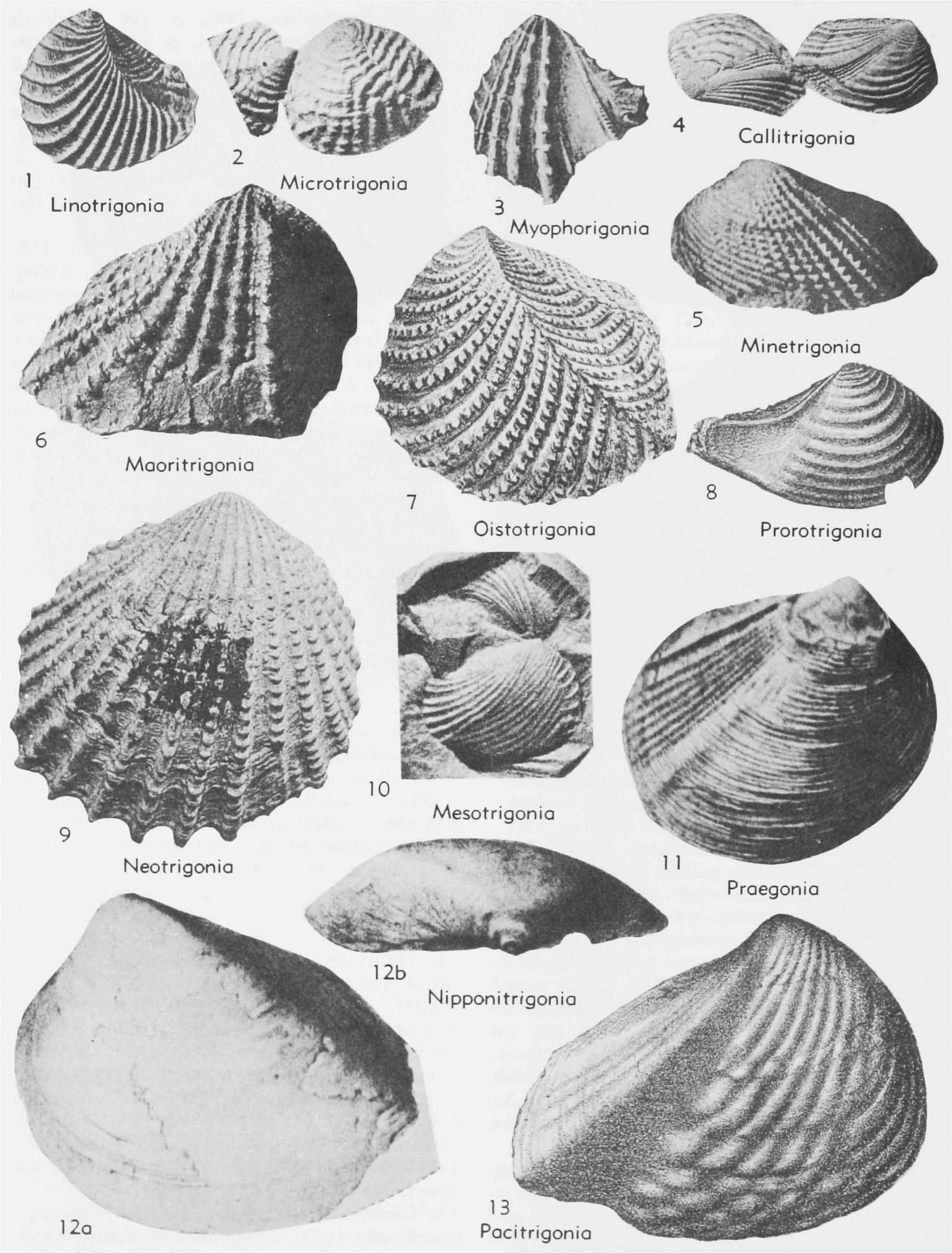
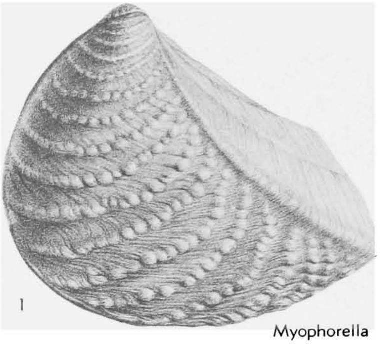
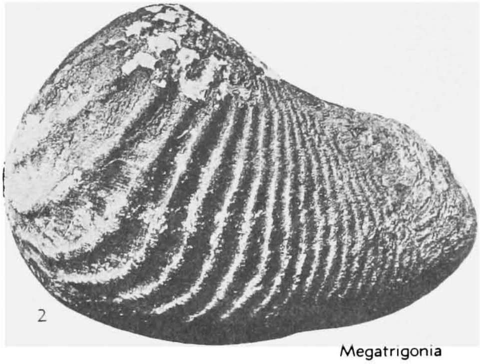


Fig. D71. Trigoniidae (p. *N*483, *N*485).



Myophorella



Megatrigonia

FIG. D72. Trigoniidae (p. *N*483, *N*485).

Linotrigonia VAN HOEPEN, 1929, p. 15 [**L. linifera*; OD]. Trigonal to suborbicular, more or less compressed; marginal and escutcheon carinae obtuse; area wholly or partly ornamented with oblique costae, each of which corresponds to and diverges in chevron-like manner from one on flank; flank with steeply inclined, smooth or nodose costae. *U.Jur.-U.Cret.,* cosmop.

L. (Linotrigonia). Umbo protruding slightly; oblique costae of area commonly confined to early growth stages; flank costae relatively wide-spaced. *U.Jur.-U.Cret.,* cosmop.——FIG. D71,*1*. *L. (L.) elegans* (BAILY), L.Cret.(Alb.), S.Afr.; LV ext., ×2 (Woods, 1906).

L. (Oistotrigonia) COX, 1952, p. 60 [**Trigonia spinosa* PARKINSON, 1811, p. 176; OD]. Suborbicular or oval; umbones depressed; posterior end and area relatively wide; oblique costae usually present on all or most of area; flank costae close-spaced in most species, transversely crenulated, or bearing small sharp tubercles commonly continued by transverse ridges on sides of costae. *L.Cret.-U.Cret.,* cosmop.——FIG. D71,*7*. **L. (O.) spinosa* (PARKINSON), L.Cret.(Alb.), Eng.; LV ext., ×1 *(554)*.

Maoritrigonia FLEMING, 1962, p. 3 [**Myophoria nuggetensis* TRECHMANN, 1918, p. 210; OD]. Trigonal, with prominent umbo; escutcheon impressed, with tuberculate radial ornament; marginal carina tuberculate; area with median groove and fine trellised ornament; flank with narrow antecarinal depression and dominant, unevenly spaced, tuberculate radial costae and weak concentric lamellae. *U.Trias.(Carn.-Nor.),* N.Z.-N. Caledonia.——FIG. D71,*6*. **M. nuggetensis* (TRECHMANN), N.Z.; RV ext., ×1 (Cox, n).

Megatrigonia VAN HOEPEN, 1929, p. 3 [**M. obesa*; OD]. Large, pyriform; marginal and escutcheon carinae absent except near umbo; area narrow, smooth; escutcheon deep, smooth; flank with steeply sloping, mostly oblique, rounded costae, of which those on its anterior half are broad and well separated but those on its posterior half narrow and close. *U.Jur.(Tithon.)-L.Cret.,* S.Afr.-E. Afr.-India-S.Am.——FIG. D72,*2*. **M. obesa,* L. Cret.(Neocom.), S.Afr.; LV ext., ×0.45 (van Hoepen, 1929).

Mesotrigonia FRENEIX, 1958, p. 165 [**M. tarameahensis*; OD]. Small, oval, only slightly inequilateral, with scarcely protruding umbones; marginal and escutcheon carinae inconspicuous, formed by rounded radial ribs of same strength as several present on area; posterior part of flank with closely spaced, narrow, oblique ribs, anterior part with more distant subconcentric ribs; all ribs finely tuberculate. *U.Cret.(Senon.),* N.Caledonia.——FIG. D71,*10*. **M. tarameahensis*; RV and LV ext., ×1 (Freneix, 1958).

Microtrigonia NAKANO, 1957, p. 116 [**M. amanoi*; OD]. Small, suborbicular; marginal carina indistinct, area with transverse costae; flank with concentric costae on umbonal region, later with 2 series of tuberculate costae, anterior ones oblique, posterior radial. *U.Cret.(Maastricht.),* Japan.——FIG. D71,*2*. **M. amanoi,* RV and LV ext., ×2 (Nakano, 1957).

Minetrigonia KOBAYASHI & KATAYAMA, 1938, p. 187 [**Trigonia hegiensis* SAEKI, 1925, p. 35; OD]. Trigonally ovate; umbo broad, depressed; marginal carina very obtuse, escutcheon carina sharp; escutcheon and area with fine trellised ornament, area also with median furrow; flank with numerous intersecting radial and concentric costae, of which former are more strongly developed on its posterior half, with small tubercles present at their intersections. *U.Trias.,* Japan-B.C.-S.Am.——FIG. 71,*5*. **M. hegiensis* (SAEKI), Japan; LV ext., ×1.5 (Kobayashi & Ichikawa, 1952).

Myophorella BAYLE, 1878, expl. pl. 120 [**M. nodulosa* BAYLE=**Trigonia nodulosa* LAMARCK, 1801, p. 117; SD CRICKMAY, 1932, p. 458]. Trigonally ovate to oblong, strongly inequilateral; marginal carina obtuse; escutcheon shallow; area bipartite, variously ornamented; flank bearing rows of tubercles or tuberculate costae which are usually oblique but subconcentric in some species. *L.Jur.(Lias.)-L.Cret.,* cosmop.

[CRICKMAY designated *M. nodulosa* BAYLE (*non* LAMARCK)

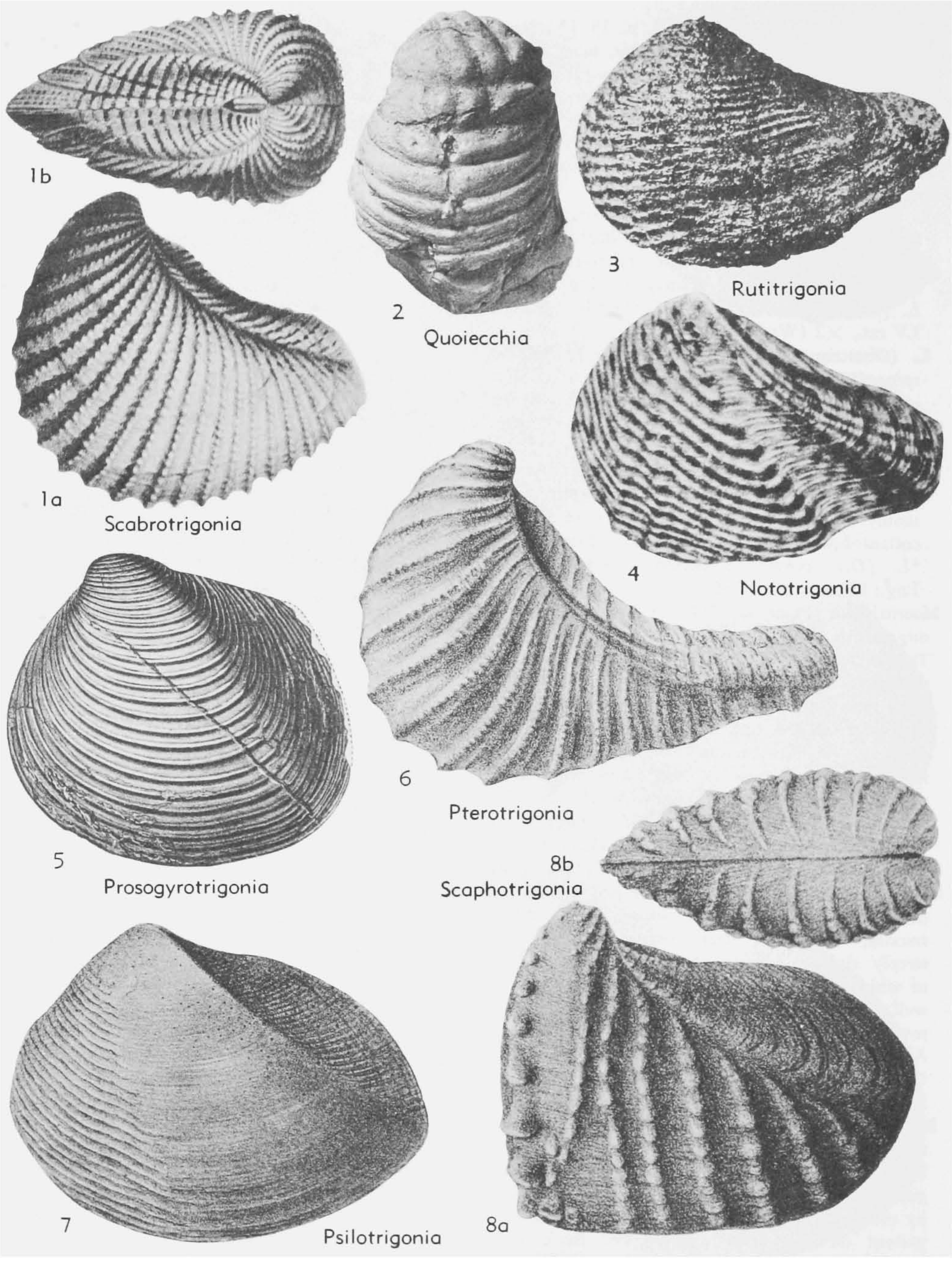


Fig. D73. Trigoniidae (p. *N*485-*N*487).

as type. Some authors have stated that BAYLE's figures do not represent the Lamarckian species, but FAVRE, who has figured LAMARCK's type, has shown that it belongs to the species represented by figs. 1, 2 and 6 of BAYLE.]

M. (Myophorella) [=*Haidaia* CRICKMAY, 1930, p. 51 (type, *Trigonia dawsoni* WHITEAVES, 1878, p. 154); *Scaphogonia* CRICKMAY, 1930, p. 51 (type, *S. argo*); *Scaphitrigon* CRICKMAY, 1930, p. 50 *(nom. null.)*; *Clavotrigonia* LEBKÜCHNER, 1932, p. 38 (type, *Trigonia clavellata* J. SOWERBY, 1815,=*T. clavellata* TOWNSEND, 1813, p. 441); *Clavitrigonia* LEANZA, 1942, p. 162 (type, *T. clavellata* J. SOWERBY, 1815; *Promyophorella* KOBAYASHI & TAMURA, 1955, p. 96 (type, *Myophorella (Promyophorella) sigmoidalis*)]. Area transversely ridged or smooth, without radial ornament; escutcheon smooth; flank costae uninterrupted throughout growth in some species, discontinuous and broken up anteriorly in later growth stages in others. *L.Jur.(M.Lias.)-L.Cret. (Neocom.),* cosmop.——FIG. D72,*1*. **M. (M.) nodulosa,* U.Jur.(Oxford.), France; LV ext., ×0.45 (Bayle, 1878).

M. (Pseudomyophorella) NAKANO, 1961, p. 85 [**Pseudomyophorella savelievi*; OD]. Like *M. (Myophorella)* except that area bears radial ribs. *U.Jur.(?Oxford.),* C.Asia(W.Turkmenia).

Myophorigonia COX, 1952, p. 52 [**Myophoria paucicostata* JAWORSKI, 1922, p. 126; OD] [=*Myophoriogonia* KOBAYASHI, 1954 *(nom. null.)*]. Relatively small, unelongated; marginal carina sharp; escutcheon narrow or absent; area flat or concave, smooth or transversely ridged; flank with strong, unevenly arranged radial costae and subordinate concentric costae confined in some forms to its anterior part. *U.Trias.-M.Jur.(Bajoc.),* Peru-Mex.-BearIs.-Eng.——FIG. D71,*3*. **M. paucicostata* (JAWORSKI), U.Trias., Peru; LV ext., ×2 *(446)*.

Neotrigonia COSSMANN, 1912, p. 25 [**Trigonia pectinata* LAMARCK, 1819, p. 63; OD]. Rather small, trigonally ovate; entire surface bearing tuberculate radial costae, of which 2 coincide with obtuse angles representing marginal and escutcheon carinae; escutcheon not impressed. *Oligo.-Rec.,* Australia.——FIG. D71,*9*. **N. pectinata* (LAMARCK), Rec.; RV ext., ×1 *(161)*.

Nipponitrigonia COX, 1952, p. 53 [**Trigonia kikuchiana* YOKOYAMA, 1891, p. 363; OD]. Trigonally ovate, short, subequilateral to moderately inequilateral; marginal carina obtuse, rounded off in later growth stages; area smooth, escutcheon undefined; flank with weak concentric costae which in later growth stages fade away entirely or persist only on its anterior side. *U. (?M.) Jur.-U.Cret. (Cenoman.),* Japan.——FIG. D71,*12*. **N. kikuchiana* (YOKOYAMA), L.Cret.; *12a,b,* LV ext., lat. and hinge views, ×1 (Yehara, 1915).

Nototrigonia COX, 1952, p. 62 [**Trigonia cinctuta* ETHERIDGE, 1902, p. 28; OD]. Pyriform, elongate, posteriorly subrostrate; escutcheon carina well defined, escutcheon unimpressed; area narrow, radially ribbed; flank with a broad antecarinal depression; remainder of its surface with rounded costae. *L.Cret.,* Australia.

N. (Nototrigonia). Antecarinal depression smooth; flank costae moderately oblique, rather sinuous. *L.Cret.,* S.Australia.——FIG. D73,*4*. **N. (N.) cinctuta* (ETHERIDGE); LV ext., ×1 (Etheridge, 1902).

N. (Callitrigonia) COX, 1963, p. 51 [**N. (C.) twidalei*; OD]. Small; marginal carina broad rounded rib; antecarinal depression of right valve but not of left with fine tuberculate radial riblets; flank costae almost concentric. *L.Cret.,* NW. Queensland.——FIG. D71,*4*. **N. (C.) twidalei*; RV ext., RV ext., ×1 (Cox, n).

Opisthotrigonia COX, 1952, p. 62 [**Trigonia retrorsa* KITCHIN, 1903, p. 57]. Elongate, very inequilateral, with narrow, prominent, strongly opisthogyrous umbones and subrostrate posterior extremity; marginal carina well defined, at least near umbo; area narrow, smooth; flank with broad, smooth or transversely ridged antecarinal depression, remainder of its surface with rather irregular, mostly subconcentric costae. *U.Jur.(Tithon.),* India-E.Afr.——FIG. D70,*1*. **O. retrorsa* (KITCHIN), India(Cutch); LV ext., ×1 (Kitchin, 1903).

Pacitrigonia MARWICK, 1932, p. 507 [**P. sylvesteri*; M]. Oblong, strongly inequilateral, marginal carina rounded off in later growth stages; flank with broad, smooth antecarinal depression, rest of its surface bearing broad, irregular undulations which may be broken up into elongated pustules, oblique in early growth stages but later almost concentric; area smooth or with radial ribs confined to earlier growth stages. *U.Cret.(U.Senon.),* S. Am.-N. Z. —— FIG. D71,*13*. *P. hanetiana* (D'ORBIGNY), Chile; RV ext., ×1 (Moericke, 1895).

Praegonia FLEMING, 1962, p. 2 [**P. coombsi*; OD]. Ovate, with low prosogyrous umbones; without marginal carina but with area defined by change in ornament; escutcheon carina sharp, escutcheon narrow, impressed; flank with weak, rounded concentric threads, area with radial riblets; main tooth of left valve weak, ungrooved. *M.Trias. (Ladin.),* N.Z.——FIG. D71,*11*. **P. coombsi;* RV ext., ×1 (Fleming, 1962).

Prorotrigonia COX, 1952, p. 57 [**Trigonia seranensis* KRUMBECK, 1923, p. 211; OD]. Elongate-pyriform, attenuated and subrostrate posteriorly; marginal carina not defined; flank with concentric costae which do not reach smooth posterior area. *U.Trias.,* Ceram.——FIG. D71,*8*. **P. seranensis* (KRUMBECK); RV ext., ×1 *(486)*.

Prosogyrotrigonia KRUMBECK, 1924, p. 244 [**P. timorensis*; M]. Evenly ovate, strongly inequilateral, beaks prosogyrous; marginal carina absent, border of area marked only by change in ornament; anterior part of flank with fairly regular concentric costae, posterior part with weaker and more numerous concentric ridges. *U.Trias.*, Timor-Indochina.——Fig. D73,5. **P. timorensis*, Timor; LV ext., ×0.7 *(487)*.

Psilotrigonia Cox, 1952, p. 53 [**Trigonia beesleyana* Lycett, 1874, p. 91; SD]. Ovate, compressed; umbones broad, depressed; marginal carina well defined but obtuse; no escutcheon; area wide, slightly concave, with curved oblique striations; flank with thin, slightly oblique wrinkles on its anterior third but otherwise smooth. *M.Jur.*

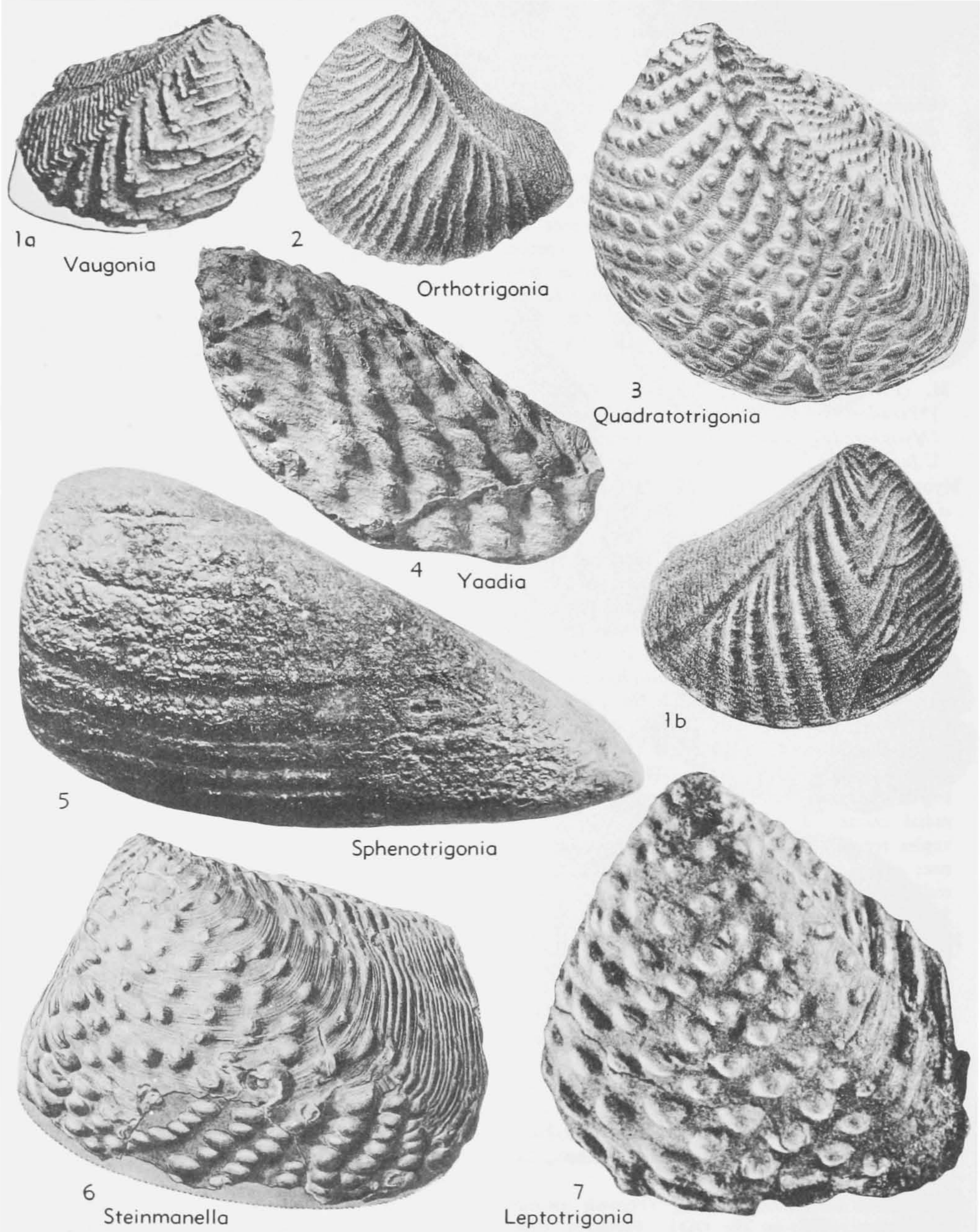


Fig. D74. Trigoniidae (p. *N*487-*N*488).

(Bajoc.)-U.Cret., Eng.-Italy-N. Afr.-India-Japan.——FIG. D73,*7.* **P. beesleyana* (LYCETT), M.Jur. (Bajoc.), Eng.; LV ext., ×1 *(554).*

Pterotrigonia VAN HOEPEN, 1929, p. 9 [**P. cristata*; OD]. Club-shaped, gibbous, with narrow, elevated, strongly opisthogyrous umbones; marginal and escutcheon carinae ill-defined except near umbo; area very narrow, smooth or transversely ridged, strongly curved, with upward-facing concavity; escutcheon wide, well impressed near umbo, with transverse costellae; flank with steep, oblique, simple or tuberculate costae; internal radial ridge coinciding approximately with middle of area. *U.Jur.(Tithon.)-U.Cret.,* cosmop.

P. (Pterotrigonia) [=*Acanthotrigonia* VAN HOEPEN, 1929, p. 14 (type, *Trigonia shepstonei* GRIESBACH, 1871, p. 66); *Notoscabrotrigonia* DIETRICH, 1933, p. 331 (type, *Trigonia tocaimaana* LEA, 1840, p. 256); *Pisotrigonia* VAN HOEPEN, 1929, p. 20 (type, *P. salebrosa*); *Ptilotrigonia* VAN HOEPEN, 1929, p. 22 (type, *P. lauta*); *Rinetrigonia* VAN HOEPEN, 1929, p. 22 (type, *Lyrodon ventricosa* KRAUSS, 1850, p. 456)]. Posterior end attenuated and commonly rostrate. *U.Jur. (Tithon.)-U.Cret.,* cosmop.——FIG. D73,6. *P. (P.) caudata* (AGASSIZ), L.Cret.(Apt.), Eng.; LV ext., ×1 *(554).*

P. (Scabrotrigonia) DIETRICH, 1933, p. 330 [**Trigonia scabra* LAMARCK, 1819, p. 63; OD]. Posterior end broader than in *P. (Pterotrigonia)* and not rostrate; costellae of escutcheon continued over area and forming chevrons with flank costae. *U.Cret.(Cenoman.-Maastricht.),* cosmop.——FIG. D73,*1.* **P. (S.) scabra* (LAMARCK), U. Cret.(Cenoman.), France; *1a,b,* LV ext., hinge view of both valves, ×0.7 (d'Orbigny, 1843-47).

?Quoiecchia CRICKMAY, 1930, p. 51 [**Q. aliciae*; OD]. Rather small, oval, higher than long, without differentiated area or escutcheon; umbo directed anteriorly?; broad, rounded, almost radial folds, crossed by concentric grooves, present until mid-growth, when they are replaced by concentric folds. *L.Cret.,* B.C.——FIG. D73.*2.* **Q. aliciae*; holotype, ?LV, ×2 (Cox, n).

Rutitrigonia VAN HOEPEN, 1929, p. 31 [**R. peregrina*; OD]. Pyriform to ovate; marginal and escutcheon carinae ill-defined except near umbo; area narrow, smooth; flank or its anterior part with thin, rather flexuous, subconcentric costae. *U.Jur.(Tithon.)-U.Cret.,* cosmop.——FIG. D73,*3.* **R. peregrina,* L.Cret., S.Afr.; LV ext., ×1 (van Hoepen, 1929).

Scaphotrigonia DIETRICH, 1933, p. 330 [**Trigonia navis* LAMARCK, 1819, p. 64; OD]. Trigonally ovate, with narrow, prominent umbones; marginal and escutcheon carinae ill-defined except in earlier growth stages; area with median furrow and at first transversely ridged, later smooth; escutcheon smooth; anterior end of shell broadly flattened in plane almost at right angles to commissure and bearing subhorizontal costae terminating in tubercles at angulation limiting flattened surface, this angle being separated by narrow, smooth zone from posterior part of flank, which bears steep, mostly tuberculate costae. *L. Jur.(U.Lias.),* Eu.; *M.Jur.?(Callov.),* USA(Calif.).——FIG. D73,*8.* **S. navis* (LAMARCK), L.Jur. (U.Lias.), France(Alsace); *8a,b,* LV ext., ant. view of both valves, ×0.7 *(9).*

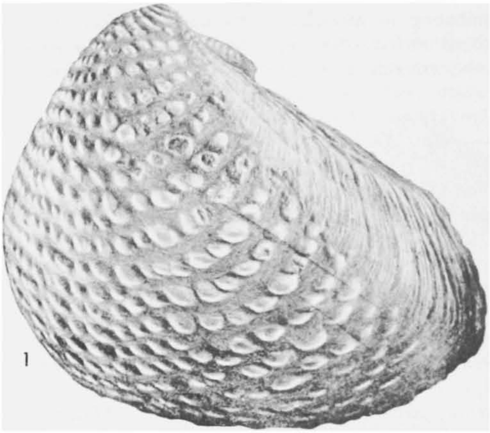
Sphenotrigonia RENNIE, 1936, p. 365 [**Trigonia (Sphenotrigonia) frommurzei*; OD]. Elongate-cuneiform, with obtuse, terminal, prosogyrous umbones; marginal and escutcheon carinae absent except in early growth stages; area smooth; flank with broad, irregular undulations. *L.Cret.(Neocom.),* S.Afr.——FIG. D74,*5.* **S. frommurzei*; LV ext., ×0.7 *(785).*

Steinmanella CRICKMAY, 1930, p. 50 [**Trigonia holubi* KITCHIN, 1908, p. 103; OD] [=*Steinmannella* KOBAYASHI & AMANO, 1955 *(nom. van.)* (*non Steinmannella* WELTER, 1911); *Steinmanaea* CRICKMAY, 1962 (*pro Steinmanella*)]. Oblong to suborbicular; marginal carina rounded off or indistinct; area with median groove and with or without transverse ridges; escutcheon with transverse tuberculate ridges; most of flank ornamented with oblique tuberculate costae. *L.Cret.-U.Cret.,* S.Afr.-S.Am.-W.N.Am.-Japan.

S. (Steinmanella) [=*Transitrigonia* DIETRICH, 1933, p. 331 (type, *Trigonia transitoria* STEINMANN, 1881, p. 260); *?Packardella* KOBAYASHI & AMANO, 1955 *(nom. nud.)*]. Oblong to subtrigonal; area with strong irregular transverse ridges, invading posteroventral part of flank in some species; flank costae concentric near umbo, but oblique and tuberculate on most of surface, where they are either all continuous or become broken up and irregular anteriorly and ventrally. *L.Cret.,* S.Afr.-S.Am.-W.N.Am.——FIG. D74,*6.* **S. (S.) holubi* (KITCHIN), L.Cret.(Neocom.), S.Afr.; LV ext., ×0.7 (Kitchin, 1908).

S. (Litschkovitrigonia) SAVELIEV, 1958, p. 97 [**Trigonia litschkovi* MORDVILKO, 1953, p. 341; OD]. Like *S. (Steinmanella),* but early growth stages with costae which have V-shaped bend and extend across area, later stages commonly with tuberculate costae more densely arranged; area smooth or transversely ridged. *L.Cret. (Valangin.-Apt.),* C.Asia.——FIG. D75,*1.* *S. (L.) ovata* (LITSCHKOV), L.Cret.(Hauteriv.), Mangyshlak; LV ext., ×0.6 (Saveliev, 1958).

S. (Setotrigonia) KOBAYASHI & AMANO, 1955, p. 206 [**S. (Setotrigonia) shinoharai*; OD]. Suborbicular; area short, indistinctly delimited from flank; flank costae broken up into segments of varying lengths and continued on area as narrow, wavy transverse ridges. *U.Cret.(Campan.),* Japan.



Litschkovitrigonia

FIG. D75. Trigoniidae (p. N487).

S. (Yeharella) KOBAYASHI & AMANO, 1955, p. 200 [**Trigonia japonica* YEHARA, 1923, p. 10; OD]. Flank costae commonly broken up in later growth stages into irregular elongated protuberances instead of into rounded tubercles; area without transverse ridges. *M.Cret.-U.Cret.,* Japan-USA (Calif.).

Vaugonia CRICKMAY, 1930, p. 53 [**V. veronica*; OD]. Trigonally ovate, short; escutcheon and marginal carinae well defined; area bipartite, transversely ridged; simple or tuberculate V-shaped costae present on flank up to varying stage of growth, angle of V's situated in relatively posterior position; remainder of flank with rather irregular costae. *L.Jur.(L.Lias.)-U.Jur.(Portland.),* cosmop.

V. (Vaugonia) [=*Hijitrigonia* KOBAYASHI in KOBAYASHI & MORI, 1955, p. 85 (type, *Vaugonia (Hijitrigonia) genticulata* KOBAYASHI & MORI; OD)]. Flank with V-shaped costae persisting to relatively late growth stage, and with costae on its anteroventral region only slightly oblique to concentric and usually more numerous than steep costae on its posteroventral region. *L.Jur.(L. Lias.)-U.Jur.(Portland.),* cosmop.——FIG. D74, *1a.* **V. (V.) veronica,* M.Jur., B.C.; RV ext., ×1 (Crickmay, 1930).——FIG. D74,*1b. V. (V.) literata* (YOUNG & BIRD), L.Jur.(U.Lias.), Eng.; RV ext., ×1 *(554).*

V. (Orthotrigonia) COX, 1952, p. 56 [**Trigonia duplicata* J. SOWERBY, 1819, p. 63; OD]. Relatively small; V-shaped costae confined to earlier growth stages, remainder of flank with rather irregular, mostly steep costae, bifurcating anteriorly in some specimens. *L.Jur.(L.Lias.)-U.Jur. (Kimmeridg.),* cosmop.——FIG. D74,*2.* **V. (O.) duplicata* (SOWERBY), M.Jur.(Bajoc.), Eng.; LV ext., ×1 *(554).*

Yaadia CRICKMAY, 1930, p. 50 [**Y. lewisagassizi*; OD]. Quadrate, ovate or trigonal, not elongated; marginal carina obtuse, commonly nodose; escutcheon narrow, tuberculate; area more or less distinctly bipartite, tuberculate or with transverse or oblique ridges; flank with oblique rows of large tubercles. *L.Cret.-U.Cret.,* cosmop.

Y. (Yaadia). Strongly inequilateral, obliquely ovate; area tubercles large, transversely elongated; flank tuberculate anteriorly and posteriorly, with narrow intervening smooth zone. *L.Cret.,* B.C. ——FIG. D74,*4.* **Y. (Y.) lewisagassizi*; rubber squeeze prepared from holotype, distorted LV ext. mold, ×0.7 (Cox, n).

Y. (Leptotrigonia) SAVELIEV, 1958, p. 105 [**Quadratotrigonia (Leptotrigonia) craveciae*; OD]. Trigonal, with prominent angular umbones; tubercles on area variable, commonly replaced by transverse ridges in later growth stages; flank costae uninterrupted. *L.Cret.(Barrem.)-U. Cret.(Turon.),* C.Asia.——FIG. D74,*7.* **Y. (L.) craveciae* (SAVELIEV); L.Cret.(Apt.), W.Turkmenia; LV ext., ×1 (Saveliev, 1958).

Y. (Quadratotrigonia) DIETRICH, 1933, p. 331 [**Trigonia nodosa* J. DE C. SOWERBY, 1826, p. 7; OD]. Subquadrate, strongly inequilateral; tubercles on area variable in size and arrangement, commonly replaced by transverse rugae in later growth stages; flank ornament uninterrupted. *L. Cret.-U.Cret.,* cosmop.——FIG. D74,*3.* **Y. (Q.) nodosa* (SOWERBY), L.Cret.(Apt.), Eng.; LV ext., ×0.7 *(554).*

?Family TRIGONIOIDIDAE Cox, 1952

[Materials for this family prepared by L. R. Cox]

Shell of medium size, ovate to subtrigonal, subequilateral to moderately inequilateral, variably elongated; umbones orthogyrous or almost so; posterior carina absent or confined to the neighborhood of umbo; ornament consisting of radial or oblique, rounded ribs; transversely crenulated posterior lateral teeth present, anterior laterals and cardinals present or absent; pallial line entire. *L.Cret.-U.Cret.*

Japanese authors include this family in the Trigoniacea, although KOBAYASHI has suggested that the unionid genus *Nipponaia* may have been descended from *Trigonioides*. Cox has advocated reference of the family to the Unionacea and MARTINSON originally regarded *Protounio* as a unionid.

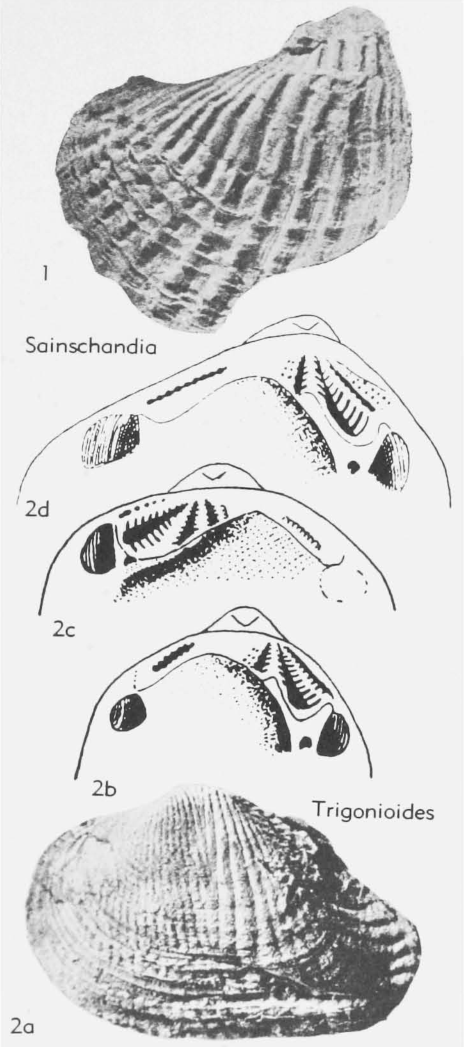


Fig. D76. Trigonioididae (p. *N*489).

Trigonioides Kobayashi & Suzuki, 1936, p. 248 [**T. kodairai*; OD] [=*Hoffetrigonia* Suzuki, 1940, p. 229 (type, *Trigonioides kobayashi* Hoffet, 1937)]. Shell form as defined for family; flank ornamented with steeply inclined ribs which converge ventrally so as to form acute V's on median part of shell, ribs of posterior series being generally thicker; both extremities of shell or only posterior one bearing less steeply sloping, oblique ribs; ventral margin crenulated internally; hinge plate well developed, widening anteriorly; hinge teeth, all of which bear regular transverse crenulations, consisting of narrow posterior lateral in right valve, well separated from beak and received in recess between 2 teeth projecting from hinge plate in left valve, and of anterior series of radially disposed teeth, 3 or 4 in each valve, extending from below beak to anterior end of hinge plate, subumbonal ones relatively short, more anterior ones broad and elongated; adductor scars small, subequal, dorsally placed, anterior one with small accessory scar just behind it. [Fresh and brackish waters.] *L.Cret.-U.Cret.,* Japan-Laos-Korea-Manchuria.——Fig. D76,*2a*. **T. kodairai,* L.Cret., S.Korea; LV ext., ×1.5 *(479)*.——Fig. D76,*2b,c*. *T. matsumotoi* Kobayashi & Suzuki, U. Cret.(Turon.), Japan; *2b,c,* LV int., RV int., ×1 (Ota, 1959).——Fig. D76,*2d*. *T. kobayashi* Hoffet, U.Cret.(Senon.), Laos; LV int., ×1 (Ota, 1959).

Sainschandia Martinson, 1957, p. 287 [**S. sculpturensis*; SD Martinson, 1961, p. 209]. Subtrigonal, subtruncate anteriorly, with prominent, anteriorly placed, orthogyrous umbones; ornament consisting of strong rounded ribs which form a single radially arranged series, crossed in later growth stages by concentric ridges; hinge devoid of short subumbonal teeth but with elongate, transversely crenulated anterior and posterior laterals. *U.Cret.(Cenoman.-Turon.),* SE. Mongolia. ——Fig. D76,*1*. **S. sculpturensis,* Cenoman.; RV ext., ×1 (Martinson, 1957).

Family UNCERTAIN

Classification of the following genera, based on species (questionably referred to *Trigonia*), is uncertain.

Anopisthodon R. A. Philippi, 1899, p. 74 [**Trigonia? obesa*; M]. Founded on imperfect internal mold possibly referable to Trigoniidae, but said to lack impressions of posterior cardinal teeth. *Cret.,* S.Am.(Chile).

Aulacopleurum R. A. Philippi, 1899, p. 94 [**Trigonia? trapezoidea*; SD Cox herein]. Based on imperfect internal molds probably not all congeneric and all of very doubtful affinities with Trigoniidae. *Cret.,* S.Am.(Chile).