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VOLUMES ALREADY PUBLISHED

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VOLUMES 1 AND 2 (OF 3)

Part N. MOLLUSCA 6 (Bivalvia), xxxviii+952 p., 6198 fig., 1969.
VOLUMES IN PREPARATION (1969)

Part A. INTRODUCTION.
Part B. PROTISTA 1 (Chrysomonadida, Coccolithophorida, Charophyta, Diatomacea, etc.).
Part J. MOLLUSCA 2 (Gastropoda, Streptoneura exclusive of Archaeogastropoda, Euthyneura).
Part M. MOLLUSCA 5 (Coleoidea).
Part T. ECHINODERMATA 2 (Crinoidea).
Part X. ADDENDA, INDEX.
Part F (supplement). Coelenterata (Anthozoa Rugosa).
Part G (revision). Bryozoa.
Part L (revision). Ammonoidea.
Part V (revision). Graptolithina.

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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 Paleooecology (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 Opikina).

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), obriena (not O'Briena), terranovae (not terra-novae), nunezi (not Nuñez), Spironema rectum (not Spironema recta, because generic name is neuter, not feminine); among genus-group names, Broggeria (not Brøggeria), Obrienia (not O'Brienia), McCookites (not McCookites); among family-group names, Oepikidae (not Opiukidae), 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 Graphiadactylis); among family-group names, Graphiodactyliidae (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-
Authorized 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 ambiguа* (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 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 *Endocerida* (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., *nud*.) and others. Thus we may recognize the preceding numbered groups as follows: 1) *nomina iniolata* (sing., *nomen iniolatum*, abbr., *iniol*.), 2) *nomina perfecta* (*nomen perfectum*, nom. perf.), 3) *nomina imperfecta* (*nomen imperfectum*, nom. imperfl.), 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 publica-
tion 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. Poteriocrinoidae 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, Störmerella, Römerina, Westgärda; family name, Rüžičkiniidae. 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 Cyrtosphirifer; Fusarchaias Reichel, 1949, without definitely fixed type species (=Fusarchaias Reichel, 1952, with F. bermudesi 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 oblitata (nomem 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 oblitata, respectively. Each of these groups may include both available and unavailable names, but the latter can well be ignored. Names considered to possess availability conduct 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 Pentagonopentalonalis 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.); Cymatophyllum Lang, Smith & Thomas, 1940 (nom. van.).]

Stichophyama Pomez, 1872 [*Manon turbinatum Römer, 1841; SD Rauff, 1893] [=Stichophyama Vosmaer, 1885 (nom. null.); Sticophyama Moret, 1924 (nom. null.).]

Stratophyllum Smyth, 1933 [*S. tenue] [=Ethmoplaex Smyth, 1939 (nom. van. pro Stratophyllum); Stratophyllum Lang, Smith & Thomas, 1940 (nom. van. pro Stratophyllum Smyth) (non Stratophyllum 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)].


Pentagonopentalonalis 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 Styliniaceae d'Orbigny, 1851)*

**Superfamily ARCHAEOCTONOIDEA Petrunkevitch, 1949**

*nom. transl. Petrunkevitch, 1955 (ex Archaeoctonidae Petrunkevitch, 1949)*

**Superfamily CRIOCERATITIDAE Hyatt, 1900**

*nom. transl. Wright, 1952 (ex Crioceratitiidae 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 Streptelasmatae Nicholson, 1889, nom. imperf.)*]

**Family PALAEOSCORPIIDAE Lehmann, 1944**

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

**Family AGLASPIDIDAE Miller, 1877**

[nom. correct. Stormer, 1969 (pro Aglaspididae Miller, 1877, nom. imperf.)*]

**Superfamily AGARICICAE Gray, 1847**

[nom. correct. Wells, 1956 (pro Agaricioidae Vaughan & Wells, 1943, nom. transl. ex Agaricidae 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 ARIETITTIDAE Hyatt, 1874**

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

**Family STEPHANOCERATIDAE Neumays, 1875**

[nom. correct. Fischer, 1882 (pro Stephanoceratinae Neumays, 1875)* 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 disintering 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 unwise to 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 Gorgon­acea, Milleporina, Rugosa, Scleractinia, Stromatoporoida, Phalangida).

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, Na­tilida, 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 Homonym­my 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 long­established 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 CORYNEXOCHIDAE 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 term (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 Orthoida 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 Shimaniskiy & Zhuravleva, 1961, nom. transl. ex order Endoceridae Teichert, 1933)]

Order ENDOCERIDA Teichert, 1933
[nom. correct. Teichert, 1964 (pro order Endoceridea Teichert, 1933)]

Suborder ENDOCERINA Teichert, 1933
[nom. correct. Teichert, 1964 (pro suborder Endoceracea Schindewolf, 1935, nom. transl. ex order Endoceridea 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 biological 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 biological 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.

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 Mysterium Schrammen, 1936 (ref. 40, p. 60) (non Roger, 1862)] [*Mysterium 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. anticosiensis; SD Lindström, 1883*] (=*Columnopora* Nicholson, 1874; *Houghtoninia* Rominger, 1876).

**Staurocyclus** 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? favisosa* 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 (=*Grapholithus Bryonoides* Hall, 1858)].

**ABBREVIATIONS**

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

**Abbreviations**

<table>
<thead>
<tr>
<th>Abbreviations</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aarsber., Aarsberetning</td>
<td>ant., anterior</td>
</tr>
<tr>
<td>Abhandl., Abhandlung(en)</td>
<td>append., appendix</td>
</tr>
<tr>
<td>Abstr., Abstract</td>
<td>approx., approximately</td>
</tr>
<tr>
<td>Abt., Abteilung</td>
<td>Apsheron., Apsheronian</td>
</tr>
<tr>
<td>aff., affinis (related to)</td>
<td>Apt., Aptian</td>
</tr>
<tr>
<td>afhandl., afhandling</td>
<td>Aquitan., Aquitanian</td>
</tr>
<tr>
<td>Afr., Africa, -an</td>
<td>Arbeit., Arbeiten</td>
</tr>
<tr>
<td>Ala., Alabama</td>
<td>Arch., Archipelago, Archives, Archivos</td>
</tr>
<tr>
<td>Alb., Albion</td>
<td>Arg., Argentina</td>
</tr>
<tr>
<td>Alg., Algeria</td>
<td>Argov., Argovian</td>
</tr>
<tr>
<td>Am., America, -an</td>
<td>Ariz., Arizona</td>
</tr>
<tr>
<td>Amman., Ammanian</td>
<td>art., article</td>
</tr>
<tr>
<td>Anis., Anisian</td>
<td>Artinsk., Artinskian</td>
</tr>
<tr>
<td>Astart., Astartian</td>
<td>Atl., Atlantic</td>
</tr>
<tr>
<td>Auctt., auctorum (of authors)</td>
<td>Auct., Auctor</td>
</tr>
<tr>
<td>Aus., Austria</td>
<td>Auvers., Auversian</td>
</tr>
<tr>
<td>Av., attached valve</td>
<td>Avd., Avedingen</td>
</tr>
<tr>
<td>Bajoc., Bajocian</td>
<td>Barrem., Barremian</td>
</tr>
<tr>
<td>Barton., Bartonian</td>
<td>Bathon., Bathonian</td>
</tr>
</tbody>
</table>

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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 des Sciences de Paris, Comptes Rendus, Mémoires.


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.


Acta Musei Nationalis Pragae (see Národního Musea v. Praze, Sborník).


Akademie der Wissenschaften und der Literatur zu Mainz, mathematisch - naturwissenschaftlichen Klasse, Abhandlungen. Wiesbaden.

[K.] Akademie der Wissenschaften zu Wien, mathematische-naturwissenschaftliche Klasse, Denkschriften; Sitzungsberichte.

Akademiya Znanosti Umitnosti. Ljubljana.


Akademiya Nauk SSSR, Institut Paleontologicheskikh, Trudy (Paleontologicheskaya Seriya); Paleontologicheskii Zhurnal; Zoologicheskiy Zhurnal. Moskva.


Allan Hancock Pacific Expedition, Reports. Los Angeles.

American Association for the Advancement of Science, Proceedings; Publications. Washington, D.C.


American Journal of Science. New Haven, Conn.

American Malacological Union, Pacific Division, Reports. Buffalo.


American Museum of Natural History, Bulletins; Novitates; Memoirs. New York.


Anales del Instituto de Biología Universidad de Mexico. Mexico City.


Annals and Magazine of Natural History. London.
Annuario Museo Zoologico Università Napoli (Italia).
Archiv für Biontologie (Gesellschaft Naturforschender Freunde). Berlin.
Archiv für Molluskenkunde. Frankfurt.
Archives de Biologie. Paris.
Archives Néerlandaises de Zoologie. Leiden.
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.
Australian Museum, Memoirs; Records. Sydney.
Australian Zoologist. Sydney.
Bayerische Akademie der Wissenschaften, mathematisch-physikalische Klasse, Abhandlungen; Sitzungsberichte. München.
Biological Society of Washington, Proceedings.
Bombay Natural History Society, Journals.
Boston Society of Natural History, Memoirs; Occasional Papers; Proceedings.
British Association for the Advancement of Science, Reports. London.
British Museum (Natural History), Bulletins; Scientific Reports. 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, 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.
Canadian Field Naturalist, Transactions. Ottawa. (Formerly Ottawa Naturalist, 1887-1919.)
Canadian Naturalist and Geologist. Montreal.
Carnegie Institution of Washington, Papers; Publications; Department Marine Biology. Washington, D.C.
Centennial and Bicentennial Congress of Biology, Proceedings. Singapore.
[Králířovské] Česká Společnost Nauk, Třída Matematicko-Fyzikální; Věstník; Rozpravy. Praha.
Charlesworth’s Magazine of Natural History. London.
Chemical Society of Japan, Bulletins; Journals. Tokyo.
Chicago Academy of Sciences, Bulletins; Transactions.
Cincinnati, Quarterly Journals of Science.
Cincinnati Society of Natural History, Journals.
Conchological Club of Southern California, Minutes. Los Angeles.
Connecticut Academy of Arts and Sciences, Memoirs; Transactions. New Haven, Conn.
Czechoslovakia, Státntí Geologický Ústav, Rozpravy; Sborník. Praha.
Danish Biological Station, Reports of, to the Board of Agriculture. København.
K. Danske Videnskabernes Selskabs, Matematisk-Fysiske, Oversigt over Förhandlingar; Skrifter. København. (Académie Royale des Sciences et des lettres de Danemark, Mémoires.)
Denison University, Scientific Laboratories, Bulletins; Journals. Granville, Ohio.
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K. Preussische Geologische Landesanstalt, Abhandlungen; Jahrbuch. Berlin (From 1880-1905, K. Preussische Geologische Landesanstalt und Bergakademie). (See Geologisches Jahrbuch.)


Public Museum, Bulletins. Milwaukee, Wis.


Quarterly Review of Biology. Baltimore, Md.


Resultat: IV de Norske Statsunderstøttede Spitsbergenexplor. Oslo.


Revista de Agricultura Comercio, y Trabajo. Habana.

Revista del Museo de La Plata.

Revista de la Sociedad Malacológica Carlos de la Torre. Habana.


Revue de Zoologie et de Botanique Africaines. Bruxelles.

Royal Physical Society of Edinburgh, Proceedings.


Royal Society of Edinburgh, Memoirs; Proceedings; Transactions.

Royal Society of London, Philosophical Transactions; Proceedings.

Royal Society of New Zealand, Proceedings; Transactions. Wellington.

Royal Society of South Africa, Transactions. Cape town.


San Diego Society of Natural History, Memoirs; Transactions.

Schweizerische Paläontologische Gesellschaft, Abhandlungen; Zurich.


Senckenbergiana Lethaea (Senckenbergische Naturforschende Gesellschaft Wissenschaftliche Mitteilungen) ["Lethaea" added to title, 1954]. Frankfurt.

Senckenbergische Naturforschende Gesellschaft, Abhandlungen. Frankfurt.


Serviço Geológico e Mineralógico do Brasil, Ministério da Agricultura, Indústria e Comércio, Boletim; Monografias. Rio de Janeiro.

Siboga Expedition, Monographs. Leiden.

Siebengreubliche Vereins für Naturwissenschaften in Herrmannstadt, Verhandlungen und Mitteilungen. Smithsonian Contributions to Knowledge. Washington, D.C.

Smithsonian Miscellaneous Collections. Washington, D.C.

Sociedad Geológica de Portugal, Boletin. Oporto.

Società Geologica Italiana, Bolletini; Memorie. Roma.

Società Malacologica Italiana, Bollettini. Pisa.


Société d'Emulation de la Provence, Marseille, Mémoires.

Société des Études Scientifiques d'Angers, Bulletin.


Société Géologique du Nord, Annales; Mémoires. Lille.


Société d'Histoire Naturelle de Paris, Mémoires.


Société Impériale des Naturalistes de Moscou, Bulletin (see Moskovskoe Obschestvo Ispytatelei Prirody).

Société Impériale des Naturalistes de St.-Pétersbourg. Leningrad.

Société Linéenne de Bordeaux, Actes; Bulletin d'Histoire Naturelle.

Société Linnéenne de Normandie, Bulletin; Mémoires. Caen.


Société des Naturalistes de Varsovie, Comptes Rendus. Tashkent.

Société Neuchâteloise Sciences Naturelles, Mémoires.

Société Paléontologique de la Russie, Annaire. Leningrad.

Société Paléontologique de la Suisse, Mémoires (see Schweizerische Paläontologische Gesellschaft). Zurich.


Société de Physique et d'Histoire Naturelle de Genève, Comptes Rendus; Mémoires.

Société Royale Malacologique de Belgique, Annales; Mémoires. Bruxelles.


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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 publica-
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.

**Stratigraphic Divisions**

Generally Recognized Divisions of Geologic Column

<table>
<thead>
<tr>
<th>Europe</th>
<th>North America</th>
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<tr>
<td><strong>ROCKS OF CENOZOIC ERA</strong></td>
<td><strong>ROCKS OF CENOZOIC ERA</strong></td>
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<tr>
<td><strong>NEOGENE SYSTEM</strong></td>
<td><strong>NEOGENE SYSTEM</strong></td>
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<tr>
<td>Pleistocene Series (including Recent)</td>
<td>Pleistocene Series (including Recent)</td>
</tr>
<tr>
<td>Pliocene Series</td>
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</tr>
<tr>
<td>Miocene Series</td>
<td>Miocene Series</td>
</tr>
<tr>
<td><strong>PALEOGENE SYSTEM</strong></td>
<td><strong>PALEOGENE SYSTEM</strong></td>
</tr>
<tr>
<td>Oligocene Series</td>
<td>Oligocene Series</td>
</tr>
<tr>
<td>Eocene Series</td>
<td>Eocene Series</td>
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<tr>
<td>Paleocene Series</td>
<td>Paleocene Series</td>
</tr>
<tr>
<td><strong>ROCKS OF MESOZOIC ERA</strong></td>
<td><strong>ROCKS OF MESOZOIC ERA</strong></td>
</tr>
<tr>
<td><strong>CRETACEOUS SYSTEM</strong></td>
<td><strong>CRETACEOUS SYSTEM</strong></td>
</tr>
<tr>
<td>Upper Cretaceous Series</td>
<td>Gulfian Series (Upper Cretaceous)</td>
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<td>Maastrichtian Stage</td>
<td>Navarroan Stage</td>
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<tr>
<td>Campanian Stage</td>
<td>Tayloran Stage</td>
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<td>Santonian Stage</td>
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<td>Coniacian Stage</td>
<td>Woodbianian (Tuscaloosan) Stage</td>
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<tr>
<td>Turonian Stage</td>
<td>Comanchean Series (Lower Cretaceous)</td>
</tr>
<tr>
<td>Cenomanian Stage</td>
<td>Washitan Stage</td>
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<tr>
<td>Lower Cretaceous Series</td>
<td>Fredericksburgian Stage</td>
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<tr>
<td>Albion Stage</td>
<td>Trinitian Stage</td>
</tr>
<tr>
<td>Aptian Stage</td>
<td>Coahuilan Series (Lower Cretaceous)</td>
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<td>Barremian Stage</td>
<td>Nuevoleonian Stage</td>
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<td>Durangoan Stage</td>
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<td>Berriasian Stage</td>
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<td>Aptian Stage</td>
<td></td>
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<tr>
<td><strong>JURASSIC SYSTEM</strong></td>
<td><strong>JURASSIC SYSTEM</strong></td>
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<tr>
<td>Upper Jurassic Series</td>
<td>Upper Jurassic Series</td>
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<td>Portlandian Stage</td>
<td>Portlandian Stage</td>
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<td>Kimmeridgian Stage</td>
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<td>Oxfordian Stage</td>
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<td>Middle Jurassic Series</td>
<td>Middle Jurassic Series</td>
</tr>
<tr>
<td>Callovian Stage (or Upper Jurassic)</td>
<td>Callovian Stage (or Upper Jurassic)</td>
</tr>
<tr>
<td>Bathonian Stage</td>
<td>Bathonian Stage</td>
</tr>
<tr>
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  Givetian Stage
  Couvinian Stage

Lower Devonian Series
  Emsian Stage
  Siegenian Stage
  Gedinnian Stage

SILURIAN SYSTEM
  Ludlow Stage
  Wenlock Stage
  Llandovery Stage

ORDOVICIAN SYSTEM
  Ashgill Stage
  Caradoc Stage
  Llanvirn Stage
  Arenig Stage
  Tremadoc Stage

CAMILIAN SYSTEM
  Upper Cambrian Series
  Middle Cambrian Series
  Lower Cambrian Series

EOCAMBRIAN SYSTEM
ROCKS OF PRECAMBRIAN AGE

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.

Erian Series (Middle Devonian)
  Taghanican Stage
  Tioughniogan Stage
  Cazennovian Stage

Ulsterian Series (Lower Devonian)
  Onesquethawan Stage
  Deerparkian Stage
  Helderbergian Stage

SILURIAN SYSTEM
  Cayugan Series
    Includes age equivalents of middle and upper Ludlow (in New York)

Niagaran Series
  Includes age equivalents of upper Llandovery, Wenlock, and lower Ludlow (in New York)

Medinan Series
  Includes age equivalents of lower and middle Llandovery (in New York)

ORDOVICIAN SYSTEM
  Cincinnatian Series (Upper Ordovician)
    Richmondiian Stage
    Maysvillian Stage
    Edenian Stage
  Champlainian Series (Middle Ordovician)
    Mohawkian Stage
    Trentonian Substage
    Blackriveran Substage
    Chazy Stage

Canadian Series (Lower Ordovician)

CAMPBRIAN SYSTEM
  Croixian Series (Upper Cambrian)
    Trempealeauan Stage
    Franconian Stage
    Dresbachian Stage
  Albertan Series (Middle Cambrian)
  Waucoban Series (Lower Cambrian)

EOCAMBRIAN SYSTEM
ROCKS OF PRECAMBRIAN AGE

RAYMOND C. MOORE

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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]

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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.
Bivalvia—General Features

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 Linne 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.

---

\(^1\)The name Pelecypoda was derived from the Greek words πέλεκυς, axe, and πόδος, 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
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). Hiattella 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
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

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**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).**
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. N16). 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 proboscidcs, 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. 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).

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).
Morphology of Soft Parts—Mantle and Siphons

N11

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 Erycinae are commensals 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 Comford (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 extensible 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. N14).

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.
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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, Anomidae, Arcidae, Trigonidiidae, 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, Donaciidae, 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 Modolarca, Dreissena, the Pholadidae, Teredinidae, Verticordiidae, Lynciidae, 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).

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
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(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

![Diagram of foot and byssus](image-url)
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.

Byssally attached Pteriomorphia include most Mytilacea, Pteriacea, Anomiacea, the Pinnacea, and many Pectinacea and Limalacea. 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* [My-
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tilidae] 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, disklike "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., Area 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 Trigonacea, 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
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-
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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.

- outer labial palp (right side)
- outer labial palp (left side)
- inner labial palp (right side)
- inner labial palp (left side)
- descending lamella of outer demibranch
- ascending lamella of outer demibranch
- outer labial palp
- inner demibranch
- mouth
- eye
- foot
- byssus

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, extensible 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
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 pseudo-feces. They are most commonly ejected

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).

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).
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-
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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 Bennett 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 diomyarian 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.

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-
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-

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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.
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 protothoraxs 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 mantle edge.

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, de-oxygenated blood black (62).
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) ...
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 incumbent water.

Fig. 27. Nervous system of Nucula (69).
Fig. 29. Reproductive system of *Entodesma saxicola* (BAIRD), Recent, California; visceral mass viewed from right side after removal of right ctenidium, X2 (191).

Fig. 30. Dissection showing soft parts of *Mytilus edulis* LINNÉ, X1.3 (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 Cox (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 spermatzoa 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 spermatzoan) 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. Cox 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 spermatzoa 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

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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. N58) to open them. Fundamentally they are two in number and are designated, according to their positions, as the anterior and posterior adductors. Their
Bivalvia—General Features

Fig. 33. Bivalve musculature.—1. *Zirfaea crispata* (Linné) showing attachments of anterior adductor and accessory muscles, ×1.5 (Purchon, 1955).—2. *Donax vitatus* (Da Costa) showing cruciform and other muscles in relation to various anatomical features, ×2 (190).

The 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 antero-posterior 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*, *Hiastella*, and members of the Pholadidae) they are capable of contracting alter-
nately, 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; Ig, 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.]
somayarian, 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."
Morphology of Soft Parts—Musculature

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.

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. 36. Mya truncata LINNÉ, interior of right valve showing muscle attachments of mantle along pallial line, ×0.7. Pallial sinus at right (Wood, 1857).
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 embryd 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
Morphology of Soft Parts—Musculature

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 equinale 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 Pinnaidae 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 Linne 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. 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).
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 nonbysiferous 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., Spatula) visceral attachment muscles leave two impressions, a rather large, crescentic one behind the anterior adductor and a smaller, more elongated one in a mediiodorsal 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, equivale, 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, X1.4 (Nuttall, n).
Fig. 41. Bivalve shell morphology.—1. *Chlamys* (*Nodipecten*) *nodosa* (Linne), Recent, off Florida, equi- valve, 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. N78) 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 equivale 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., Araa, 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. N94), 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 X0.7 (Cox, n).
Fig. 43. Shapes of bivalve shells, illustrating terms commonly used to describe them, all X1 except 14 (from British Museum (Natural History), British Mesozoic Fossils, British Caenozoic Fossils).

margin in most forms lacking a cardinal area (p. N103). 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.\(^1\)

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1. In *Glossus* it actually faces ventralward.

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 Linne, 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 above-mentioned 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-
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 (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. N60-N62).

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 Pectinidæ, 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.
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 anterodorsal 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 orifice 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

![Diagram of bivalve shell structures](image)

**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, X1.
—2. *Chlamys* sp., Rec.; 2a, RV showing partly calcified resilium; 2b, after removal of resilium, X2.
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 teeth interlock that there will 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 this 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

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... 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

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. N46) 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 resilifer.¹ Chondrophore is an alternative term for a projecting resilifer. 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

¹ Also known as resilifer.

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**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, X1.---4. Lutraria angustior PHILIPPI, Rec., E.Atl. and Medit.; LV with resilifer on prominent hinge plate, X0.7 (from 157a).---5. Mya arenaria LINNÉ, Pleist. and Rec., Arctic; N.Atl., N.Pac.; 5a, oblique view of strong chondrophore of LV, X0.5; 5b, same, transverse section (from 157a).---6. Eucyra eburnea (Wood-MASON & ALCOCK), Rec., Ind.O.; 6a,b, RVs, lithodesma or ossiculum missing and present, X3.3; 6c, both valves in juxtaposition, X2.7; 6d, transverse section.---7. Offaeesma angasi (CROSE & FISCHER), Rec., N.Z., with spoon-shaped chondrophore mounted on strong posterior supporting buttress or clavicle; 7a, both valves of broken specimen, X2.3; 7b, section; 7e, LV, X3. [Explanation: ant, anterior; ca, cardinal tooth; ch, chondrophore; hp, hinge plate; lat, lateral tooth; oss, ossiculum or lithodesma; post, posterior; r, resilium; rf, resilifer.]
Morphology of Hard Parts—Internal Structures of Hinge

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, δόντων, 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 “-odont” names that have been proposed for major taxa are included in the list on p. N118.

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 κτενόν, small comb) and the secondary type as pseudoctenodont (Fig. 44,2).

An uneven series of small transverse teeth simulating taxodont teeth occurs in the non-marine 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).
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 ἀφεός, 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 παχύς, 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
Morphology of Hard Parts—Internal Structures of Hinge

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 iuò, 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 resilifer 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 resilifer, 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 dio, 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 I 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 resilifer, 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 I, and when its distal end persists as an anterior lateral tooth, this lamella is designated as A1 (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 DOUVILLE. 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, Al, All, 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, A1' is the socket that receives A1).

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
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:

\[
\begin{array}{cccccc}
A1 & AII & 3a & 3b & PI & PIII \\
AII & 2a & 2b & 4b & PII & (PIV)
\end{array}
\]

or \(A1, AII, 3a, 1, 3b, PI, PIII/AII, 2a, 2b, 4b, PII, (PIV)\).

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 \(A1\) 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:

\[
\begin{array}{cccccc}
A1 & AII & 3a & (1) & 3b & (5b) & PI & (PIII) \\
AII & (2a) & 2b & 4b & PII & (PIV)
\end{array}
\]

or \(A1, AII, 3a, (1), 3b, (5b), PI, (PIII) / AII, (2a), 2b, 4b, PII, (PIV)\).

Attempts have been made by DOUVILLE 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. DOUVILLE 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. DOUVILLE's application of cardinal hinge tooth notation to the Unionidae, (e.g., 5a, 3a, 3b/4a, 2a, 2b, 4b, 4b, has not met with general acceptance. [See Addendum (p. N908) for more on bivalve dental notation.]

**TRANSPOSED HINGES**

There are many recorded cases where certain hinge teeth of the two valves are

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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 *Permaphorus 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.

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**

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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, Anomidiidae; 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, Mytilimera, 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
Morphology of Hard Parts—Ligament

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 distinguish 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 and Mytilus (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 postlarval ligament 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. Alivinicular amphidetic ligament comparable to primary ligament (e.g., *Limopsis*).—B. Alivinicular ligament intermediate in form between amphidetic and opisthodetic.—C. Opisthodetic ligament placed directly between valve margins (e.g., *Myltilus* (=tr., Table 1).—D. Opisthodetic parivinicular 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. Duplivinicular 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. Multivinicular 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 *Area*, 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 resilifer 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 *Mysilus* (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.

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<th>Placement</th>
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<th>Fusion</th>
<th>Layer</th>
<th>Lamellar Layer</th>
<th>Fibrous Layer</th>
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**HETERODONTA**

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<tr>
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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
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 metaphlax 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-
Morphology of Hard Parts—Supplementary Structures

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 Martesiiinae 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.

PALLETS OF TEREDINIDAE

Pallets, which are peculiar to the Tere dinidae, 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.
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, X1.—2. Grammatomya pulcherrima (Deshayes), Recent, Indian Ocean, anterior part of shell with diagonal ribs and posterior part with radial ribs, X1.7.—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 terebid, *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

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

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

and irregular, X2.—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, X2.—5. *Mactra* (*Tumbeziconcha*) thracoides (Adams & Reeve), Rec., Peru, surface with excentric undulations, X1.3.—6. *Chlamys* (*Nodpecten*) nodosus (Linne), 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, X1.3.—7. *Gafrarium* sp., Pleist., E.Indies, surface with divaricate ribs interrupted by concentric or commarginal grooves, X2.—8. *Semipecten tigris* (Lamarck), Rec., E.Indies, with reticulate honeycombed surface on which main sculpture consists of radial ribs bearing secondary riblets, X4.—9. *Donax punctatusstriatus* Hanley, Rec., trop.W.Am., showing pitted (punctate) radial grooves, X2.

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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
are remarkable for the radial, wavy, or zigzag ribs which are present on their earlier-formed growth stages only. In some Trigonidae 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).
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 pseudolaevaeis (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 Pleuropectinctes 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.]

**INEQUIVALE 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; 1ab, ×0.5 (Nuttall, n).—2. *Corbula caloosae* Dall, Pleist. (Caloosahatchie), Florida (Dall).—3. *Hemimetis* sp. aff. *H. plicata* (Valenciennes), Neog., E. Indies; 3ab, ×1.](https://example.com/fig60.png)
Morphology of Hard Parts—Structure of Shell Wall

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, *Neithia* 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 Cuspidaridae 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.

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. 122, 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
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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 Böggild. 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, Trigonacea, 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 Böggild'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 prodissococonj 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:

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<th>Trace Elements in Bivalve Shells (in parts per million)</th>
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<td><strong>Element</strong></td>
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<td><strong>Average</strong></td>
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1 For all Bivalvia examined.

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
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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 122). 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.

Young 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 different 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). 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 antero-posterior 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 antero-posterior 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. 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

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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.
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 shell...
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 dimensions) 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

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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.
Bivalvia—General Features

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 (Linne), Rec., E. Atl.--2. Chione reticulata (Linne), Rec., E. Atl.--3. Cardium orbita G. B. Sowerby, Rec., E. Atl.--4. Corbis fimbriata (Linne), Rec., E. Atl.

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 considerable complexity, but he showed that the form of a bivalve shell in which the valve bones (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 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).

In shells with almost orthogyrate umbones and valves (e.g., Meretrix, Glycymeris) 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.

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°.
Orientation and Axes

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. 126), 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).
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).
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 $180^\circ$ 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

![Diagram of Bivalve Shell Geometry](image_url)

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, bellerophonid 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. N88).
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 *Area*, 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., *Ceratomyra, 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 (Peronacea) plana*) one umbo is known to penetrate the other. In any case, it is prob-
able 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.]

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. *Callicus 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* LINNE, Rec., E.Atl.; 2a, prodissoconch and early subsequently formed shell; 2b,c, anatomy at young and late larval stages.
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,
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 prodissococonch I, having been originally applied to the complete larval shell, this earlier stage has been termed by Werner (followed by other authors) the prodissococonch I, commonly abbreviated to “prod. I.” It is virtually the same as the protostracum of Bernard. The size of the prodissococonch 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 prodissococonch I and of a newly added zone of mantle-secreted shelly matter, the prodissococonch II, on which distinct growth lines are visible. It slowly loses the D-like form of prodissococonch 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 prodissococonch, etc.
Ontogeny

EMBRYONIC AND LARVAL DEVELOPMENT IN FRESH-WATER BIVALVES

Fresh-water bivalves belonging to the family Dreissenidae have a free-swimming sponding stages of planktotrophic larval shells and can be distinguished by an experienced worker. It is believed that examination of the prodissococonchs of fossil bivalves, when well enough preserved, will throw light upon the mode of early development.

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.

Prodissococonch II is ill-defined or absent in larval shells that have undergone lecithotrophic development, but stages I and II are both distinguishable on the prodissococonch of forms in which development to the bottom stage has been direct. They differ, however, in appearance from the corre-
larval life and pass through trophophore 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

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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 Nucula, 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 Malleita, on the other hand, several of the earliest-formed teeth are at first straight and longitudinal. In Nucula and Malleita 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
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 Bernhard 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 Wragley'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, equiva
dle 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 den
tition.

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

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**Fig. 84.** Bivalve ontogeny—changes in shell char
acters during and after metamorphosis (Nuttall, n).
—1. *Plicatula filamentosa* Conrad, Eoc. (Clai
born.), Ala., showing early (nepioconch) and inter
mediate (mesoconch) growth forms, ×2.—2.

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*Echinochama arcinella* (Linæ), Rec., E.Atl., umbo
of left valve with preserved nepionic shell, ×17
(from Odhner, 1919).—3. *Hinnites crispus* (Broc
cchi), Plio., Italy; 3a,b, changes from early
pectiniform to later oyster-like shape, ×1.

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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 noncommittal term when referring to scars of muscles of uncertain function).

**accline.** 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, *Area*. 
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 crus (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 paliobranchial 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 Anomidae 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.)
concholin. Material (protein) of which periostrosum and organic matrix of calcareous parts of shell are composed.
convexity. Degree of inflation.
**Bivalvia—General Features**

coriculoid type. Heterodont dentition with 3 cardinal teeth in each valve, middle one of RV occupying median position below beaks. Formerly termed cyrenoid type.
corset. 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-lamelar. 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).
ectenodont. With numerous short hinge teeth transverse to margin (applied to certain groups of early origin only).
cetenolium. 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.
denticate. Small rounded toothlike protuberance.
dentication. 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.
dissocnoch. 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).
duplilvincular. 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, Area.
dysodont. With small weak teeth close to beaks (as in some Mytilacea).
edentulous. Lacking hinge teeth.
edmarginate. With margin interrupted by notch or sinus.
ensiform. Shaped like genus Ensis, with outline resembling curved sword.
etire. 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.
equivale. 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. Protrusable 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 funnels plates. Transverse laminae in wall of radiolitid lower valve, inclined downward funnel-wise toward axis and combining with radial laminae to produce cellular structure.  
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.  
homeomyarian. 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* (Linne, 1758).]  
hypoplax. Elongate accessory plate extending along posterior end of ventral margin in some Pholadidae.  
hypostacum. 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.  
inequivale. 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 incumbent.  
inner (layer of) ligament. Same as fibrous ligament.  
tegetipalliate. With pallial line devoid of sinus.  
tegetr线下列. Longitudinal band on surface of lower valve of radiolitid rudist, separating 2 bands designated as siphonal bands.  
tegetodentum. Shelly plate present in some Unionidae bridging space between pseudocardinal and lateral teeth.  
teget space. Depression between adjacent costae or other linear surface elevations.  
teget interval. Same as teget space 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.  
isode. With small number of symmetrically arranged hinge teeth; examples, *Spondylus, Plicatula*.  
homeomyarian. 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 dентition 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 posterodorsal 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 umbral region in some Pholadidae.
metapla. 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.
momyarian. 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.
myoophore. 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.
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 umbral 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).
opisthoge. Curved so that beaks point in posterior direction (term applied to umbones).
orbicular. Circular.
orthoclone. 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.
ortogyrate. 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.
oraculum. Term used in 2 senses: 1) outer part of calcareous wall of shell, secreted at mantle edge
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(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 (com­
marginal over radial elements of ornament).

pachyodont. With heavy, blunt, amorphous teeth.

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 hippocritids.

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

prodissoconch 2. Later-formed part of prodissoconch, secreted by mantle edge.

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

prosocoeious. 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.

protoplast. Same as prodissoconch 1.

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).

pseudocrenodont. 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.

pseudoxodont. With numerous irregular short hinge teeth transverse to hinge margin and known to be unrelated to ctenodont and pseudo- ctenodont forms.

punctate. With pinprick-like depressions.

punctum (pl., puncta, never punctae). Pinprick-like depression of surface.

quadrate. Square, or almost so.
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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.

resilifer (or resilifier). 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.

scallop ed. 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.

counture. 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.

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 protruberance of surface of shell.

spirogyrate. Coiled protruberance of surface of shell.

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 umbal 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. 121-122). 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 Modiolloides [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 "calcarea-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 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
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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.

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.

Fig. 86. Reconstruction of the phylogeny of early Paleozoic bivalves suggesting relationship of Lamellodonta to main groups (after Vogel, 176).

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 Sarsden. 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 Dotville 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 Llandeiliian 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 Llandeiliian beds in
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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 (*Gres 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. 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 *Paracyclus* in the Upper Ordovician of Scotland. Among the crypodonts are some genera (*Rhitymeya, 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* [*Modiolopsidea*].

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 duplivelicular 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 (*Pracardiidae, Paracardiium, 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 crypodont 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*, *Edmondiiidae*, *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. *Paralleledodon*, 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 Trigonacea, 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 *Proscocelus*. Finally, certain genera which, like *Cypriocardia* 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*, *Cypriocardella*, *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 *Entoliun* 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 *Pachyteria*, 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 *Asartella*, in which the hinge teeth are very similar to those of modern members of the Astartidae. Finally, Carboniferous crypto­dents with the shell form of permanent burrowers, such as *Chaeonomya*, *Solenomorpha*, *Wilkingia*, and *Sanguinolites*, approach some of the later Anomalodesmata very closely. *Wilkingia* and *Chaeonomya* 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 *Praenudulomya* are here accepted as members of the Pholadomyidae, although it is not known if they were sinupalliate. The Australian Permian is noteworthy for the oc-
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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 *Dzonella*. 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 *Lopa* includes the species *L. montiscaprilis* (*Klipsch*), 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*, *Mysidoptera*, 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 Conchoelasma, 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 Palaeocardiata) 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 Carditidae 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 (Homomysa, Pachymysa (Areomysa), and, more rarely, Pholadomya), and also of Pleurommysa. 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 Trigonidae, Ostreidae, Limidae, and Pholadomyidae. Among the Arcidae 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 Areca, and Barbatia make their appearance. Mytilidae are usually abundant, and include radially ribbed forms (Areomysa, 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 spines, was evidently adapted for life recumbent on the sea floor. Among the oysters, byphaeate 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-Liasic 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 northwest 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 import-
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ance 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 *Philadomya*, *Homomya*, *Gonio­mya*, *Pleuromyia*, *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 *Neithia*, 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 *Pterotrignia*, 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 *Cardiidae*, missing during the Jurassic, reappeared. Among the burrowers *Panopea* replaced the usually smaller *Pleuromyia*.

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** Douville, 1913 (42, p. 438, as "actinodontides"). Introduced for group of lower Paleozoic bivalves of undefined taxonomic rank characterized by more or less longitudinally extended, divergent teeth on both sides of beaks. Accepted as suborder of order Taxodonta and scope extended by Dechaseaux (38, p. 266).


**Ammobranchida** 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.

**Anidombyaria** 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 Steimann (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, Poladacea. 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.


**Ashekamella** 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).

**Aulolamellibranchiata** 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 Pteriomorpha and consisting only of the Ostreae.

**Cryptodonta** Neumayar, 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 Douville (1912), who, however, had merely cited the generic name *Ctenodona* Salter. Adopted for suborder of order Teleodesmacea 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, Iso cardiacea.

**Cycrina** Stenzel, Krause & Twining, 1957 (156, p. 133). Proposed for 1 of 2 suborders of order Heterodonta. Equivalent to "cyrenoid type" of Bernard.

**Cycnodonta** Korobkov, 1954 (85, p. 56, 141). Proposed for 1 of 3 suborders of order Heterodonta. Equivalent to "cyrenoid type" of Bernard.
Desmodonta Neumayr, 1883 (III, 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, "Anatinae," Mactridae, "Paphidae" [Mesodesmatidae], "Glycimeridae," ?Solenidae. Name latinized by Fischer (1886).

Dinymaria 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 Hermannsen (1846).

Diogenodonta Dall, 1895 (34, p. 538). Proposed for group of order Teleodesmacea defined as "latterals usually 1 or 2, and cardinals 3 or less." Contents, Cypricardiacea, Astartacea, Cyrenacea, Carditacea, Chamacea, Rudistacea, 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).


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, "Submulyacea," "Conchacea," Myacea, Pholadacea, "Anatinae." Name latinized by Cooke (1895).


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, Trigonidae, Name latinized by Cooke (1895).

Folioibranchia Menegaux, 1889 (103, p. 142, as "folioibranches"). Proposed for 1 of 4 major taxa into which bivalves are divided on basis of gill characters; in this group (same as "protoibranchiés" of Pelseneer) each demibranch consists of row of simple flattened leaflets. Contents, Nuculacea, Solemyacea. Name latinized by Perrier (1897).

Gastrodeutia 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.

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.


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 as Heterodonta 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.

Integrippaliata d'Orbigny, 1843 (120, p. 14, as "integropaléales"). One of 2 suborders into which order "orthoconques" is divided. Name latinized as "Integrippalìa" by Woodward (1854) and as "Integrippaliata" by Zittel (1881).

Isodonta Dall, 1895 (34, p. 524). Proposed for group in order Prionodesmacea to include Pectinacea and Anomacea. Name based on adjective "isodonte" introduced by Fischer (1886, p. 936).

Isolibranchia 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.

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Lucinodonta Korobkov, 1954 (85, p. 56, 81). Proposed for 1 of 3 suborders of order Heterodonta. This and the Astarterodonta correspond to the “lucinoid type” of Bernard.

Macrocioliobranchia 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.

Microcioliobranchia 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 taxa of bivalves, characterized by single adductor muscle. Name latinized by Geinitz (1845).

Oligodonta March, 1912 (101, p. 113). Proposed for 1 of 6 orders into which Bivalvia are divided. Contents, Arcacea.


Palaeobranchia Iredale, 1939 (74, p. 232). One of 7 orders into which subclass Prionodemascea is divided and consisting of Solemyidae. See also Lipodonta.

Palaeoconchae D’Orbigny, 1843 (120, p. 14, as “orthocoques”). 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).


Prionodonta MacNeill, 1937 (98, p. 457). Proposed as suborder of order Filibranchia, to include Cyrtodontacea, Parallelodontaceae, Glycymeridacea, and Arcacea. Dall (32, 34) had introduced term “prionodont” in same sense as “taxodont” but had not given it Latin form or systematic status.


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 divisions of order Heterodonta and consisting of forms with Bernard’s “cyrenoid type” of dentition.

Pracheterodonta Douville, 1912 (41, p. 1680, as “préhétérodontes”). Proposed for a group of undefined taxonomic status, consisting of myophoriids, trigoniids and “préastartidés” (Prosocolus, Dentellia, Megalodon, Palaeocardita, etc.). Accepted as order and name latinized by Davies (1935).


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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, Cardiacea, Cardiacea, Chamacea, Tridacnacea, Leptonacea?, Lucinacea, Isocardiaea?, Veneracea, Rudista?.

Teledonta Dall, 1895 (24, p. 551). Proposed for group belonging to order Teleodesmacea characterized by "most perfected type of modern teeth." Contents, Veneracea, Tellinacea, Solenacea, Mactracea.

Acknowledgments

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FORM, FUNCTION, AND EVOLUTION

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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, thanatocoenotic 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 neon to logic 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 co-attached 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 Cymatona (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. Areuatula (ribbed modiolid); also Pinna and Atrina (not shown).

1-2,5,7,9,12. Closely attached forms.—1. Areuatula, also smooth-shelled Modiolus s.s. (on rock).


2-4,8,10-11. Fissure-dwellers.—2. Some Pinctada.

——3. Some Chlamys.—4. Some Barbatia, usually not nesting.—8. Lima.—10. Some Arca, rare and usually not nesting.—11. Iso gnomon (e.g., 1. radiatus).


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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 anatomy, 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)
Introduction—Concepts and Methodology

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 bioecoenotic 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). Stašek (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). Stašek 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” (Stašek, 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, richthofenid 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 "jack-knife 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., \textit{Cyrtodonta}, \textit{Cycloconcha}, \textit{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 \textit{Pinctada}, Mesozoic-Cenozoic \textit{Pteria}, Silurian-Mississippian \textit{Leiopteria}, Devonian \textit{Cornellites}, \textit{Limoptera}, Ordovician-Pennsylvanian \textit{Pterinea}), Mesozoic-Cenozoic Isognomonidae, Cretaceous Inoceramidae, the Pectinidae (living \textit{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 vestigial.
genetic 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-in-take 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 de-
pended 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, subequivalve 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 Pelseen (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 sig-
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 posterocentral 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 equivalent to moderately inequivalve and only slightly inflated, with maximum convexity umbalonal 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* (*Pseudo-

monotidae*?), Jurassic *Gervillia* (Isognomonidae), certain Triassic monotids, possibly late Paleozoic Aviculopectinidae (*Pseudavicul opecten, Aviculopecten*), Silurian-Mississippian Leiopteria (*Pterineidae*) and Devonian *Pterinea* and *Cornellites* (*Pterineidae*) belong to this form group.

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,
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. *Pinetada* 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 sub-equivalve 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. *Leptopesten*, 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 pteriform 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 byssus 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 vertically 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 incumbent 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 flatting 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 attach-
ment 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-umbro 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 mytioids 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* s.s. 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 *Pinetada* 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.

*Pinicada* 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 *Pinicada* 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 *Pinicada 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, *Pinicada 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 Pinetada 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, Pinetada 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 sub-ovate, 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 nesting 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 dorso-centrally. 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, anomiioids, 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 Pinetada). Though distantly related, these bivalves

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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: opisthoclione), 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 Pinactada, 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 Pinactada 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 Pinactada 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 (Wall, 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 semixposed 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 (Hinmites), 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 subtidal 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 equivalent 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 which 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.

Various 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 hav-
ing 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 *Barretta* 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 together 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 *Thyrastyron* 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 proscocline or opisthoclinal 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 with 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 (Arkins, 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 subequate, 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. Abyssal 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 Lucinidae). 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, Propeamusium, 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 occu-
pied 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 opisthoclinal 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, subtrangular, 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 midshell 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 subtrangular 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 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 Poteta, 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 in 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 Malleia and Solemya to attain their normal burrowing depth, as shown.

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nearly identical in the vertical burrowing, sessile filter-feeders \textit{Solen} and \textit{Ensis}, as it is in the horizontal burrowing, vagrant deposit-feeder \textit{Solemya} (Fig. 90). Even more significantly, both \textit{Solemya} and \textit{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., \textit{Dinocardium}, \textit{Laec­vicardium}) and Veneridae (\textit{Gemma}) char­acterize this group. \textit{Nucula} is the most simi­lar detrital-feeding protobranch. Deeper­burrowing 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. \textit{Mya} and \textit{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 \textit{Cardium}; wedge-shaped, moder­ately convex \textit{Donax}; ovate moderately convex \textit{Macoma}; and elliptical, very slightly inflated \textit{Tellina}. Mechanical penetration tests on the shells indicated that the ease of burrowing decreased in the following order: \textit{Tellina}, \textit{Donax}, \textit{Macoma}, and \textit{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 \textit{Tellina} deepest and \textit{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 \textit{Cardium} and \textit{Gemma} would con­stitute the shallowest zone, followed in order by geometric forms represented by: 1) \textit{Mercenaria}, 2) \textit{Astarte} or \textit{Crassatella}, 3) elon­gate \textit{Macrocrista}, 4) \textit{Mya} or \textit{Panope}, 5) \textit{Tagelus}, and 6) \textit{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 \textit{Cardium}, \textit{Macoma}, and \textit{Tellina} burrowed to the depth of the shell in similar times (\textit{Cardium} slightly slower), \textit{Tellina} being aided by its streamlined shape, \textit{Cardium} and \textit{Macoma} by their rocking motion during burrowing. \textit{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 protothoracic 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 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 bur-
rowing 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 within 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 equivalue and subequivalue 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 commisural 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. Weller (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
Functional Morphology of Shell

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 withstand current 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 consti-
stitutes 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 interpretive studies define the precise function of individual dental units, to date much neglected. As a locking device, the taxodont, schizodont, cycloodont, 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, Asartidae, 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.

**LIGAMENTS**

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 Trueeman (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 on the adult shell or in embryonic stages; 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 or 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
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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 posterointerally, 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 anterointervenal 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. Poye, 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-bysal 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-bysal retractor normally lies directly opposed to the direction of byssal extension, the optimum position for efficient operation. Once the position of the pedal-bysal 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-bysal retractor and main (posterior) pedal retractor are side by side in the postero-dorsal corner of the shell and projection of the byssus is anteroventral. In Isognomon (Fig. 34,A) projection of the byssus is dorso-anterior 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 Lucinacea 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). [Explanations: 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 incumbent channel, re-entrant 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.]

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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 ligamenta I 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
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-

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**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 Molluscs).

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 ostrata ostrata* 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.

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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 non-siphonate 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 particlesorting 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 incurrent currents and sort particles at the mouth of the incurrent channel. The smaller, more rounded posterior adductor muscle is defined by an insertion area mid-posteriorly 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 incident 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 incident 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 incident 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. 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-
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.
Comparative Ecology

Table 1.—Communities, Biotic Association of Mollusks, and Environmental Characteristics Summarized for Living Thyasira. Families Arranged in Order of Number of Recorded Molluscan Associations.

<table>
<thead>
<tr>
<th>ASSEMBLAGE</th>
<th>4-50</th>
<th>15-100</th>
<th>11-140</th>
<th>25-550</th>
<th>30-550</th>
<th>100+</th>
<th>200-600</th>
<th>200-780</th>
<th>300+</th>
</tr>
</thead>
<tbody>
<tr>
<td>SUBSTRATE</td>
<td>clay, sandy clay, soft clay, silty clay, soft shale, soft mud</td>
<td>clay, soft, soft mud</td>
<td>clay, soft, soft mud</td>
<td>soft, soft mud</td>
<td>soft, soft mud</td>
<td>soft, soft mud</td>
<td>soft, soft mud</td>
<td>soft, soft mud</td>
<td>soft, soft mud</td>
</tr>
<tr>
<td>TEMPERATURE</td>
<td>cool</td>
<td>cool</td>
<td>cool</td>
<td>cold</td>
<td>cold</td>
<td>negative</td>
<td>cold</td>
<td>cold</td>
<td>cold</td>
</tr>
<tr>
<td>PRODUCTIVITY</td>
<td>low</td>
<td>low</td>
<td>low</td>
<td>low</td>
<td>low</td>
<td>low</td>
<td>low</td>
<td>low</td>
<td>low</td>
</tr>
</tbody>
</table>

Commonly Associated Molluscan Genera

- **Bivalvia - Total**: 11
- **Nuculidae**: Nucula
- **Semelidae**: Syndeomya
- **Nuculanidae**: Nuculana
- **Asartidae**: Astarte
- **Pectinidae**: Pecten
- **Arcticidae**: Arctica
- **Lamellidae**: Lucina
- **Cuspisaridae**: Cuspisarida
- **Hiatellidae**: Hiatella
- **Tellinidae**: Tellina
- **Arcticidae**: Arcticodium
- **Cardiidae**: Cardium
- **Corbulidae**: Corbula
- **Myidae**: Mya
- **Limidae**: Lima
- **Mytilidae**: Mytilus
- **Geodonta**: Geodonta

**Gastropoda - Total**: 0

**Scaphopoda - Total**: 0

**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...

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Localities, with pulses in southern migration of *Thyasira*
- First pulse—Zones of *B. sp.* (weak flank ribs) — *B. obtusus*
- Second pulse—Zones of *B. asperiformis* — *B. perplexus*
- Third pulse—Zone of *B. scotti*

**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 | D709 | D714 | D1012 | D1216 | D1410 | D1684 | D1866 | D1899 | D2286 | D2326 | D3532 | D3993 | D4162 | D4742 | D9779 | 10666 | 10666 | 229838 |
|----------------|----|-----|------|------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
| LITHOLOGY      | sh | sh  | sh   | sh   | sh    | sh    | sh    | sh    | sh    | sh    | sh    | sh    | sh    | sh    | sh    | sh    | sh    | sh    | sh    | sh    | sh    | sh    |
| ASSEMBLAGE      | H  | H   | D    | D    | D     | D     | D     | D     | H     | H     | H     | H     | H     | H     | H     | H     | H     | H     | H     | H     | H     | H     |
| BIVALVIA        | 1  | 3   | 6    | 2    | 3     | 3     | 4     | 4     | 3     | 2     | 1     | 2     | 3     | 1     | 1     | 4     | 2     | 2     | 3     | 1     | 1     | 2     | 2     | 5     | 4     |
| Thyasira        | R  | R   | C    | C    | R     | R     | C     | R     | C     | R     | R     | C     | R     | R     | R     | C     | R     | R     | C     | R     | R     | R     | R     | R     |
| *Inoceramus     | -  | -   | R    | R    | -     | -     | C     | -     | -     | C     | -     | -     | C     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     |
| Lucina          | -  | R   | R    | R    | C     | C     | R     | C     | C     | C     | C     | C     | C     | C     | C     | C     | C     | C     | C     | C     | C     | C     | C     | C     |
| *Cymbopleura    | -  | -   | -    | -    | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     |
| Pteria          | -  | -   | -    | -    | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     |
| "Ostrea"        | -  | -   | R    | R    | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     |
| *Nucula         | -  | -   | -    | -    | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     |
| 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     |
| Aporrhais?      | -  | -   | -    | -    | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     |
| Lunatia?        | -  | -   | -    | -    | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     |
| CEPHALOPODA     | 2  | 2   | 3    | 3    | 4     | 4     | 3     | 2     | 5     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     |
| *Baculites      | C  | C   | C    | C    | C     | C     | C     | C     | C     | C     | C     | C     | C     | C     | C     | C     | C     | C     | C     | C     | C     | C     | C     | C     |
| *Hoplocerasites| R  | R   | R    | R    | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     |
| *Didymoceras   | -  | -   | C    | C    | C     | C     | C     | C     | C     | C     | C     | C     | C     | C     | C     | C     | C     | C     | C     | C     | C     | C     | C     | C     |
| *Didymoceras   | -  | -   | -    | -    | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     |
| *Oxybeloceras   | -  | -   | R    | R    | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     |
| *Anapachydiscus| -  | -   | -    | -    | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     |
| *Placenticeras | -  | -   | -    | -    | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     |
| *Menulites      | -  | -   | -    | -    | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     |
| *Scaphites      | -  | -   | -    | -    | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     |
| *Eutrephoceras  | -  | -   | -    | -    | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     |
| SCAPHOPODA      | 0  | 0   | 0    | 0    | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0     |
| Dentalium       | -  | -   | -    | -    | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     | -     |
| MOLLUSKS—TOTAL  | 5  | 10  | 5    | 6    | 7     | 7     | 6     | 9     | 4     | 4     | 4     | 3     | 3     | 3     | 3     | 4     | 2     | 2     | 5     | 4     | 3     | 5     | 2     | 6     | 3     | 8     |

*Extinct genus

[Explanations. Lithology: ic, ironstone concretions (siderite-limonite); lc, limestone concretions, usually argillaceous; s, shaly; sc, siderite concretions; sh, shale, usually dark, noncalcareous, thin-beded; ss, sandstone, usually fine- to medium-grained, argillaceous; T, Tepee Butte limestone masses, irregular light-colored argillaceous limestone bodies.

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 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 1 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 Linicinae (*Axinopsida, Lucina, Myrtea—*all similarly adapted, like *Thyasira*, to the environment), Nuculanidae (*Nuculana, Portlandia*), Nuculidae (*Nucula*), Semelidae (*Abra* or *Syndosmya, Theora*), Astariidae (*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 *Cuspida* and *Arca, Turniella* and *Apornhais* 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).](image-url)
single occurrence (including *Thyasira*), yielding an average of 4.6 genera (and species) per occurrence. This is comparable with the restricted 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...
Phylogeny, Evolution, and Interpretation

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 with reduction in size of the posterior fold.

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 microhabitats 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 correlated 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.
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

By NORMAN D. NEWELL

[The American Museum of Natural History and Columbia University] [Chapter revised and slightly expanded from American Museum Novitates, no. 2206, 1965, 25 p.]

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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.

ACKNOWLEDGMENTS

In this work I have been aided by grants from the National Science Foundation; by Dr. Harold E. Vokes, who placed an early draft of his comprehensive catalogue of pelecypod genera at our disposal (Vokes, 1967,72); by Drs. L. R. Cox and Myra Keen, Prof. C. M. Yonge, Dr. C. R. Stasek, and all of the collaborators of this volume who have from time to time given generously of their encyclopedic knowledge. Very special thanks are expressed to my wife, Valerie Zirkle Newell, for her indispensable aid in many phases of my work on Treatise Bivalvia.

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 Linne. 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 Linne (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. Linne (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 Douville (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 Douville 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 prismatonicreous shells; oysters possess prismaticfoliacious 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.

Douville'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 Douville 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 Douville. Unfortunately, Davies' work did not incorporate many pre-Tertiary forms, nor will his classification accommodate them.

Douville 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 Douville 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-
problems 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

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**Table 1**

<table>
<thead>
<tr>
<th>Anomalodesmacea</th>
<th>Teleodesmacea</th>
<th>Eulamellibranchia</th>
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<tr>
<td>Poromyacea</td>
<td>Myacea</td>
<td>Adesmacea</td>
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<td>Anatinacea</td>
<td>Natadacea</td>
<td>Ostreacea</td>
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<td>Pinnidace</td>
<td>Trigonidacea</td>
<td>Limidae</td>
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<tr>
<td>Pteridacea</td>
<td>Actinodontaec</td>
<td>Mytilacea</td>
</tr>
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<td>Douville</td>
<td>Nuculacea</td>
<td>Sedentary Branch</td>
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<td>Pelseneer</td>
<td>Normal Branch</td>
<td>Palaeoconna</td>
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<tr>
<td>Pelsoeneur</td>
<td>Dall</td>
<td>Burrowing Branch</td>
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**Fig. 101.** Schematic comparison of classification of DALL and DOUVILLE (based in part on geologic history), with the “horizontal” classification of PELSNEER based mainly on ctenidial grade (Newell, n).
### TABLE 1. SOME CHARACTERISTICS OF EXTANT BIVALVE SUPERFAMILIES

<table>
<thead>
<tr>
<th>Subclasses and Superfamilies</th>
<th>Gill Grade</th>
<th>Gill Cilia</th>
<th>Stomach Type</th>
<th>Labial Palps</th>
<th>Shell Microstructure</th>
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Superfamilies not represented by extant bivalves include the following:

- Cycloconchaacea
- Cyrodonchaacea
- Edmondopathacea
- Hippuripatadaceae
- Shell microstructure complex, varying with families
- Megalodontacea
- Modiomorphacea
- Praeconchacea
- 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 Douville 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 eulamellibranchiate gills (Pinnidae, Limidae, Ostreidae) 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 Douville is shown in Figure 101.

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.
Classes—Subclasses—Orders

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 Douville'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 Golffuss, 1820, and Lamellibranchiata (or Lamellibranchiia) 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, Pteriomorpha) 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) Pteriomorpha Beurlen, 1944, 4) Palacoheterodonta 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
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 DOUVILLE (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 DOUVILLE 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 DOUVILLE) 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 Mesiomorphidae, a group of the Paleoheterodonta. 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. Char-
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 prismatonicreous 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 Pteriomorpha, 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 prismatonicreous 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.
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**

<table>
<thead>
<tr>
<th>Class</th>
<th>Subclass</th>
<th>Order</th>
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<tbody>
<tr>
<td><strong>BIVALVIA</strong></td>
<td><strong>Palaeotaxodonta</strong></td>
<td>Nuculoida</td>
</tr>
<tr>
<td><strong>Palaeoheterodonta</strong></td>
<td><strong>Pachymorpha</strong></td>
<td>Modiomorphoida</td>
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<tr>
<td></td>
<td><strong>Cryptodonta</strong></td>
<td>Unionoida</td>
</tr>
<tr>
<td></td>
<td><strong>Pteriomorphia</strong></td>
<td>Arcoida</td>
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<td></td>
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<td>Mytiloida</td>
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<tr>
<td></td>
<td></td>
<td>Pterioida</td>
</tr>
</tbody>
</table>

(Class 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 equivaive; 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 equivaive; Purchon type 3; Stasek type 3.

Order **Mytiloida**. Anisomyarian, generally equivaive, 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, unionaceans, trigoniaceans; prismatonacreous; Purchon type 4; Stasek type 1.

Order **Unionioidea**. 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**

By LAVON MCCORMICK and R. C. MOORE

[University of Kansas]

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.
Modiolinae (19;6). Dev.-Rec.
Mysidiidae (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.
Ambonychidae (22;1). M.Ord.(Chazy.)-U.Dev., ?L.Miss.
?Lunulacardiidae (9;2). ?Ord.-Miss.
Pteriaceae (superfamily) (102;21). Ord.-Rec.
Pteriinae (21;3). Ord.-U.Perm.
Kochiidae (1). Dev.
Pteriidae (11;1). Trias.-Rec.
Bakevelliidae (17;2). Perm.-Eoc.
Pergamidiidae (4). U.Trias.-L.Jur.(Lias.).
Duttidae (1). U.Trias.(Rhaet.).
Pectinacea (superfamily) (112;75). Ord.-Rec.
(Leonard.).
Leiopectinidae (3). Ord.-L.Dev.
Streblorochostraci (4). Miss.-U.Trias.
Chaenocardiiidae (2). L.Miss.(Visean)-L.Perm.
Deltostreblidae (1). L.Perm.
Pseudomonotoidea (1). L.Carb.-U.Perm.
Posidonoidae (12;1). L.Carb.-U.Cret.
Oxytomidae (7;2). L.Perm.-U.Cret.
Entolidae (4;1). L.Miss.-U.Cret.
Pectinidae (31;63). Trias.-Rec.
Motonidae (2;1). U.Trias.
Buchiidae (8). U.Trias.-Cret.
Plicatulidae (3;2). M.Trias.-Rec.
Spondylidae (1;2). ?Jur.-Rec.
Family Uncertain (1). U.Trias.
Ostreacea (superfamily) (51;9). U.Trias.-Rec.
Gryphaeidae (22;6). U.Trias.-Rec.
(Kimmeridg.).
Trigoniidae (41;18), M.Trias.-Rec.
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.
Myrtea (9;2), L.Jur.-Rec.
Mytilinae (14;8), Sil.-Rec.
Divaricellinae (7;4), L.Eoc.-Rec.
Doubtful genera (6), Mio.-Rec.
Thyasiridae (9;4), M.Trias.-Rec.
Mactromyidae (13;5), M.Ord.-Rec.
Montacutidae (33:5), Mio.-Rec.
Sportellidae (13;3), Mio.-Rec.
Chamidae (3;3), Mio.-Rec.
Chlamydoconchacea (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.
Myconchidae (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.
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.
Eriphylinae (10;4), Dev.-Eoc.
Opinae (7;5), Dev.-U.Cret.
Crassatellinae (15;6), Dev.-Rec.
Crassatellinae (11;5), Dev.-Rec.
Scambulinae (4;1), L.Cret.-Rec.
Cardiniidae (9), Ord.-Rec.
Myopohoricardiidae (3), Trias.
Cardiacea (superfamily) (66;59), U.Trias.-Rec.
Cardiidae (23;42), U.Trias.-Rec.
Cardiidae (8;42), U.Trias.-Rec.
Trachycardiidae (3;6), ?Eoc., Oligo.-Rec.
Fragunae (4;5), Oligo.-Rec.
Protocardinnae (4;17), U.Trias.(Rhaeti.)-Rec.
Laevicardiidae (4;2), Eoc.-Rec.
Lahillidae (1;1), U.Cret.-Mio.
Lynnocardidae (42;16), Mio.-Rec.
Lynnocardinae (9;12), Mio.-M.Plio.
Didacninae (11;2), L.Plio.(Pont.)-Rec.
Paradacninae (6), Plio.
Adacninae (10;2), U.Plio.-Rec.
Pseudocardinnae (1). Plio.
Subfamily uncertain (5), Mio.-Plio.
Tridacnidae (6;2), ?U.Cret., Tert.-Rec.
Mactracea (superfamily) (46;47), U.Cret.-Rec.
Mactridae (27;46), U.Cret.-Rec.
Mactridae (15;37), U.Cret.-Rec.
Lutrarinae (5;4), Mio.-Rec.
Pteropollinae (3;3), Eoc.-Rec.
Zenatinae (4;2), Eoc.-Rec.
Anatinellinae (1), Rec.
Mesodesmatinae (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.
Macoma (11;17), Eoc.-Rec.
Donaciidae (7;13), U.Cret.-Rec.
Psammobiiidae (11;21), U.Cret.-Rec.
Psammobiiidae (10;15), U.Cret.-Rec.
Sanguinolariinae (1;6), Mio.-Rec.
Unicardiopsidae (1), M.Jur.-L.Jur.
Questdidiidae (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.
Novaculinidae (2), Rec.
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Pandoridae (1;5). Oligo.-Rec.
Cladothaeidae (1). Mio.-Rec.
Laternulidae (7;2). U.Trias.-Rec.
Lyonsiidae (5;4). Eoc.-Rec.
Margaritariidae (1). Mio.-Rec.
Myochamidae (2;2). Mio.-Rec.
Periplomatidae (2;6). U.Cret.-Rec.
Thraciidae (8;4). Jur.-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.
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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Class, Order, and Family Uncertain
Genera of Doubtfully Molluscan Affinities
Unrecognizable Genera
REFERENCES
Class BIVALVIA Linné, 1758
(Buonanni, 1681)

[ex Verneus Testarea Bivalvia Linne, 1758, p. 645; nom. corr. (Couper, 1798); Conchifera Lamarck, 1818; Pelecypoda Goldfuss, 1820; Conchophora Gray, 1821; Diaphyla Turton, 1822; Lamellibranchia, Lamellibranchia de Blainville, 1824; Elatobranchiata Menke, 1825; Ctenopoda Borkhausen, 1837; Tropopoda Catlow & Reeve, 1845; Aglossa Lovén, 1848; Elatocephala Bronn, 1862; Anodontoda Haecker, 1868; Lipoccephala Lancaster, 1884) [nom. transl. et correct. Wohrmann, 1893]

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 (Tremado­rous; gut convolute, nephridia paired.CRET. Rec.

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 Nuculacea, 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.

Subclass PALAEOTAXODONTA
Korobkov, 1954

[Diagnosis by N. D. Newell]

Characters same as those of order Nuculoida Dall, 1889. Ord.-Rec.

Order NUCULOIDEA Dall, 1889
[nom. transl. et correct. Newell, 1965] [Diagnosis by N. D. Newell]

Shell taxodont, equivelar, with closed margins, isomyarian; nacreous or crossed lamellar; ligament generally amphidetic; gills protobranchiate; foot grooved and reptant, not byssiferous in adults. Ord.-Rec.

Superfamily CTENODONTACEA
Wöhmann, 1893
[nom. transl. McAlester, herein (ex Ctenodontidae Wöhmann, 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.
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, X2 (McAlester, n).

Clinopistha Meeek & 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(lll.; 1a,b, RV ext., dorsal view of conjoined valves, X2 (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, X4 (McAlester, n).

Praectenodonta Philip, 1962, p. 226 [*Palaeonoelas raricostae Chapman, 1908; OD] [=Gonodonta 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., X2 (Philip, 1962).

Tancrediopsis Beushausen, 1895, p. 70 [*Cteno­
donta 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., X3, X2 (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, X2 (McAlester, n).

Superfamily NUCULACEA 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, X5 (McAlester, n).

Cardiolaria Munier-Chalmas, 1876, p. 107 [*C. barrandeii; 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. barrandeii, Ord., France; LV into mold, X2 (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, X2 (McAlester, n).

Ledopsis Beuhsaunen, 1884, p. 91 [*L. rectangularis; SD McAlester, 1968] [=Pseudoledopsis Mailleux, 1937, p. 182 (type, Ledopsis taunica Beuhsaunen, 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., X2 (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.

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mold of conjoined valves, dorsal, ×6 (McAlester, n).

**Similodonta** SooT-REYn, 1964, p. 498 [*Tellinomyia similis* Ulrich, 1892; OD]. Like *Palaeoncula* 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).

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**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 [*Area nucleus*]
Nuculoida—Nuculanacea

Linné, 1758; M [≡Lambulia 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. (Gibsonnucula) 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. (Linucula) MARWICK, 1931, p. 49 [*Nucula ruatkienisis MARWICK, 1926; OD]. With fine divericate radial ribs on lunule and escutcheon. Mio., N.Z.


Nuculoidea WILLIAMS & BREGER, 1916, p. 173 [*Cucullaea 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.-Eo.-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 CHERNYHEV, 1947, p. 5 (type, N. minutus); OD). Nuculanella TASH, 1953, p. 395 (type, N. pinedontia); OD). Nuculavus CHERNYHEV, 1947, p. 9 (nom. nud.). Very inequilateral; inner ventral margin smooth; resilifer small. Car. -Perm., Eu.-N.Am.-N.Afr.—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).


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).


Ptychosotolis TULLBERG, 1881, p. 14 [*P. nordensioidi; M]. Shell like Nucula but with strong lunule. Jur., USSR (Novaya Zemlya).—Fig. A3,4. *P. nordensioidi, 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. Post, 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 Mallettidae BELLARD, 1875, nom. transl. ex Mallettinae ADAMS & ADAMS, 1858)]
[Materials for this family prepared by A. L. McALESTER, Yale University]
Fig. A4. Malletiidae (p. N233).
No resilifer, ligament predominantly external. Ord.-Rec.

Malletia des Moulines, 1832, p. 85 [*M. chilensis; M] [=Solenella Sowerby, 1832, p. 197 (type, S. norrisii; M)]; Ctenodonta Gray, 1840, p. 139; Nuculaia 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., cosmol.

M. (Malletia). Compressed, not rostrate. Mesoz.-Rec., cosmol.—Fig. A4,2. *M. chilensis*, Rec., Chile; 2a, RV ext., X1; 26, LV hinge, enl. (Sowerby, 1842).


M. (Minormalletia) Dall, 1908, p. 385 [*M. (M.) arciformis; SD Finlay, 1926*]. Inflated, not rostrate. Rec., E.Pac.

Arisagia 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 Khalin, 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 (Khalin, 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).


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 dentine and ant. muscle scar, LV cast of post. part ext. mold, X1 (McAlester, n).

Metapalaconeilo 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).

Myoplisia Neumayr, 1884, p. 416 [*Leda bilunata Barrande, 1881; SD McAlester, 1968*]. [=Pseudocyrtodonta Pfaff, 1934, p. 236 (type, Leda ala Barrande, 1881; OD)]. Like Palaconeilo, 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., cosmol.—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)]; Cuculleta M'Coy, 1851, p. 50 (type, Cuculleta antiqua Sowerby, 1839; SD Beushausen, 1895); Pyrenomoeus Hall, 1852, p. 87 (type, P. cuneatus; M). Like Palaeoneilo, but with internal septum. Ord.-Dev., cosmol.—Fig. A5,7. *N. oblongatus, M.Dev., N.Y.; RV composite ext.-int. mold, X1.5 (McAlester, n).

Palaconeilo Hall & Whitfield, 1869, p. 6 [*nom. conserv. ICZN (Opinion 215), 1954*] [*Nuculites restricta Conrad, 1842; SD Hall, 1885*] [=Anthraconeilo 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 Syneke Barrande); Goniodon Herrick, 1888, p. 84 (type, G. ohiensis; M); Oligjea Chernyshev, 1948, p. 3 (type, O. engenii; OD); Straba Prantl & Różička, 1954, p. 3 (type, S. bohemia; OD); Strabilia Prantl & Różička, 1954, p. 4 (type, Straba (S.) holynensis; OD); Synek Barande, 1881, p. 162 (type, S. antiquus; OD). Faint posterior radial groove, concentric sculpture, no internal septum. Ord.-Mesoz., cosmol.—Fig. A5,9. *P. restricta (Conrad), M.Dev., N.Y.; composite ext.-int. molds of both valves (LV below), X1.5 (McAlester, n).

Phaenodensia Bittner, 1894, p. 188 [*P. klipesteiniiana; SD Diener, 1923*]. Like Palaconeilo, but with more tapered posterior. Trias., Eu.—Fig. A5,2. *P. klipesteiniiana; 2a,b, LV ext., dorsal view of both valves, X1 (58).

Prosoleptus Beushausen, 1895, p. 70 [*Nucula lineata Goldfuss, 1840; OD*]. Like Palaconeilo,
but with ventral protrusion. Trias., Eu.—A5,4.

*P. lineata* (GolDFuss); 4a,b, LV ext., RV int., X 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.—

**Pseudoglonomus** 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).


Fig. A5,10. *P. (P.) pompholyx (DALL), Cuba; LV ext., X6 (Dall, 1890).


Quadratonicula DICKINS, 1963, p. 32 [*Q. australiensis; OD]. Rounded, wide posterior, no surface sculpture. *Perm., Australia.—Fig. A5,12.

Saturnia SEGUENZA, 1877, p. 1178 [*Nucula pusio PHILIPPI, 1844; M] [=Austrotnudaria 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., X4 (216).

S. (Spinula) DALL, 1908, p. 377 [*Leda (Spinula) calcata; OD] [=Bathy-spinula FILATOV, 1958, p. 212 (nom. nud.)]. Strongly rostrate. *Rec., cosmop. (deep oceans).


Sulha BARRANDE, 1881, p. 159 [*S. expansus; OD] [=Pracarca NeumaY, 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, X2 (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; 2a,b, LV ext., int., X2 (35).


Tropinculites 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, X1.5 (McAlester, n).

Family NUCULANIDAE Adams & ADAMS, 1858

[=Ledidae ADAMS & ADAMS, 1858 (obj.)] [Materials for this family prepared by H. S. POM, Florida Geological Survey]
N236  Bivalvia—Palaeotaxodonta

sis (Seguenza), Rec., N.Am.; LV hinge, X8 (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., X1 (789).

N. (Politoleda) Hertlein & Strong, 1940, p. 370 [*Nucula polita Sowerby, 1832; OD]. Shell

Fig. A6. Nuculanidae (p. N235-N237).
Nuculoida—Nuculanacea

N237

colution, 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., X3 (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., X2 (398).

N. (Praesaecella) Cox, 1940, p. 32 [*N. (P.) juriiana, OD]. Shell as in Saccella but with entire pallial line, larger and less numerous hinge teeth. *N. [India-Eu.(France-Port.)].—Fig. A6, 1a-c. *N. (P.) juriiana (Cox), India; 1a, LV ext., X2.2, 1b-d, RV ext., LV int., RV ext., X4 (183).

N. (Propeleda) Iredale, 1924, p. 181 [*Leda ensicula Angas, 1877; OD] (=Lamellileda Cotton, 1930 (type, L. typica; OD)). Shell sickleshaped, chondrophore backwardly sloping, hinge thin. Rec., Australia.—Fig. A6.9. *N. (P.) ensicula (Angas), 9a,b, LV ext., RV hinge, X5 (166).


N. (Rolleria) Cossmann, 1920, p. 82 [*nom. subst. pro Nuculopsis Rullier, 1912, p. 64 (non Nuculopsis Girty, 1911)]; *Isoleda Rullier, 1923, p. 67, nom. subst. pro Nuculopsis Rullier, 1912, and Ionoleda Cox, 1925, p. 124, nom. subst. pro Isoleda Rullier, 1923) [*Nucula palmae Sowerby, 1824; SD Rullier, 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. *N. [Jur., Eu.-India].


N. (Scealeda) 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, X1.3 (572).

N. (Thestyleda) Iredale, 1929, p. 158 [*Leda ramayi 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.) ramayi (Smith); 10a,b, LV ext., dorsal, X6 (852).

Adrina 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., X2 (383).

Costatoleda Roth von Teleog, 1914 (1915), p. 61 [*Leda (C.) psammobiaeformis Roth von Teleog, 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, X1 (800).

Dacyrynya Agassiz, 1840, p. 500 [*Nucula lacryma Sowerby, 1824; SD Herrmannsen, 1846, p. 368] (=Dacyromia 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., X2 (870).

Ezoniculana Nagao, 1938, p. 121 [*Nucula 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., X2 (635).

Hilgardia Harris & Palmer, 1946, p. 59 [*Leda multilinata Conrad, 1855; OD]. With radial ribs intersecting concentric sculpture as crenulations and nodes. Eoc., N.Am.—Fig. A7.7. *H. multilinata (Conrad); 7a, dorsal view of conjoined valves, X3.5; 7b, RV int., X3; 7c, LV ext., X2.75 (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., X1 (387).

Lithorhadia Stewart, 1930, p. 37 [*Leda acula Dall, 1898; OD]. Shape of Nuculana but hinge of Calorhidia. Eoc., cosmop.—Fig. A7.8. *L. acula (Dall), N.Am.; LV ext., X3 (223).

Mesosciela Chayvan, 1946, p. 197 [*Nucula joerstleri Muller, 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. joerstleri (Muller); 6a,b, dorsal view of both valves, RV ext., X2, X3 (650).

Paleylodia Lintz, 1958, p. 108 [*Voldia 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., X2 (McAlester, n).
**Phascolus** 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

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**Fig. A7. Nuculanidae** (p. N237, N239),
Nuculoida—Nuculanacea  N239

Fig. A8. Nuculanidae (p. N238-N239).

(type, G. honessi; OD); Nuculochlamys Paul, 1941, p. 38 (nom. nud.); Polidevcia CHERNYSH, 1951, p. 25 (type, Leda karagandensis CHERNYSH, 1941; OD). Like Nuculana, but with prominent internal ridges. Dev.-L.Trias., cos mop.

FIG. A8,3. *P. inflatiformis (CHERNYSHEV), U. Carb., USSR; LV ext., X2 (McAlester, n).

Portlandia MORCH, 1857, p. 93 (ICZN, 1966 (Opinion 769, name no. 2132)) [*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.


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.


Sarepta ADAMS, 1860, p. 303 [*S. speciosa; OD] [=Ovaleda IREDALE, 1925, p. 248 (type, Sarepta tellineiformis HEDLEY, 1902)]. Round, not rostrate, very short hinge. Rec., Indo-Pac.—Fig. A9,1. *S. speciosa, Japan; 1a,b, LV ext., int., X3.0 (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. (Glyptoleda) FLETCHER, 1945, p. 298 [*G. reidi; OD]. Large, elongate, posterior constricted. Perm., Australia.—Fig. A8,1. *V. (G.) reidi; LV ext., X2 (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 MOLLER, 1842, p. 18 [*Y. hyperborea TORELL, 1859 (pro Y. arctica MOLLER, 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.

**Ryderia**

**Kalayoldia**

**Bivalvia—Cryptodonta**

**Yaldia**

**Sarepta**

**Portlandia**

**Nuculanidae** (p. N239-N241).

**Fig. A9.1.** *Y. (Y.) hyperborea* (Torell), Rec., N.Atl.; 11a-c, LV ext., int., both valves dorsal, ×1 (829).

**Y. (Acqiyoldia)** Soo-Ryen, 1951, p. 6 [*Y. subaequilateralis* Smith, 1875; OD]. Equilateral, slightly rostrate; chondrophore triangular, broad, mantle margins fringed above siphons. Rec., Antarctic (South Shetland Is.).

**Y. (Colorhadiia)** 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. (Cnestarium)** 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, recurred. 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 KHOMEŃKO, 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, Plp., 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 angles at ends of anterior and posterior series, hinge arched (673). M.Jur.(Bajoc.-)U.Cret. (Senon.), Eu.—Fig. A10,1a. 1. 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 equivalent, thin-shelled dimyarian bivalves; hinge plate absent or narrow; ligament external, amphidetic to opisthodetic, generally without nympha; hinge margin edentulous or taxodont. ?U.Cam., L.Ord.-Rec.

Order SOLEMYOIDA DALL, 1889
[nom. transl. et correct. NEWELL, 1965 (ex suborder Solemyacea 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 SOLEYMACAEA

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...
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 Solenomyidae GRAY, 1840)] (=Solenomyidae von Martens, 1867; Solemyidae DALL, 1900; Solemonidae DALL, 1908) [In accordance with Code Art. 40a,b, this family ranks from 1840 for purposes of priority]

Characters of superfamily. Devo.-Rec.

SOLEMYA LAMARCK, 1818, p. 488 [*S. mediterranea (=*Tellina togata PALL, 1795, p. 42); SD CHILDREN, 1823] [=Solenimya BOWDICII, 1822 (nom. van.); Solenomya CHILDREN, 1823 (nom. van.); Stephanopus SACCCHI, 1833 (obj.); Solenymia SWAINSON, 1840 (nom. van.); Solenymya SCHAF-Fuss, 1869 (nom. van.)]. Elongate-oval or sub-rectangular, 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; 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,
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.At/. Fossil distribution uncertain.—Fig. BI,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] [=Janeia 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. BI,1a. S. (f.) primaeva Phillips, L.Carb., Eng.; LV ext., ×1 (407).—Fig. BI,1b. S. (f.) truncata (Goldfuss), M.Dev., Ger.; dorsal-ventral 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. (f.) truncata (Goldfuss) (Fig. BI,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. Pli., Japan; Rec., E. Pac.-Japan-W. Atl.-Carib.

S. (Solemyarina) Iredale, 1931, p. 202 [*Solemya veleatiana; OD] [=Zeolemya veleatiana, 1938 (type, Solemya parkinsonii Smith (ex Gray, MS); Solemyarina 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. BI,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. Rep. 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.]

Adolomya 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 PRAECARDIOIDEA 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 sinuses 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 Atiké Larocque]

Ovate, orthogryre, or prosogryre 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 PRAECAARDIIDAE Hörnes, 1884

Shell approximately equivaleval; 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 neotenic retention of the provinculum. In some shells the den-
Fig. B2. Praecardiidae (Praecardiinae) (p. N244-N245).

Subfamily PRAECARDINAE 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. obl.)] (type, S. barrandi; 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.); ?Parapyx Clarke, 1904, p. 261 (type, P. ontario; OD); Kralovna Barrande, 1881, p. 93 (type, K. bohemica; OD); Regina Barrande, 1881, p. 93 (obj.); ?Praelimna 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 Sùner & Coma, 1959 (type, Kralovna almeriae 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), Eu.(Boh.-France-Ger.)-Dev., N. Am.(N.Y.-Mich.-Ont.).---Fig. B2,3. *P. primulum, Sil.(E2), 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.K. 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 X1 (52).

Necklania Růžička & Pěšek, 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.), Boh.—Fig. B2,S. *N. obtusa (BARRANDE); RV ext., X0.5 (27).

Slava BARRANDE, 1881, p. 154 [*S. bohemica; SD Růžička & PRANTL, 1960] (=Gloria BARRANDE, 1881 (obj.); Tieraconcha 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,t. *S. bohemica, Sil. (Ea), Boh.; RV ext., X1 (27).

Subfamily CARDIOLINAE Fischer, 1886
[nom. transl. NEWELL & LAROCQUE, herein (ex Cardioliidae 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 MEER & WORTHEN, 1861, p. 144 (type, Cardiomorpha radiata MEER & 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.(Ea), Boh.; 4a, LV hinge view; 4b, same, side view, both X1 (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 HALLO, 1843; M]. Similar to Cardiomorpha but with short and regularly rounded anterior end; surface marked by very fine radial costellae producing cancelled appearance. Sil.(M.)

FIG. B3, Praecardiidae (Cardioliidae) (1, 3-4), Dexiobiinae (2) (p. N245-N247).

Llandov.), Scot.-Dev.(Portage), USA(N.Y.)—Fig. B3,3. *E. subtextile (HALL), Dev.(Portage), USA(N.Y.); LV ext., X1 (370).

Opisthocoeus BEUHSAUSEN, 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., Budesheim, Ger.; 1a, RV ext.; 1b, same, hinge view; both X2 (47).

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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., LMiss.*

**Dexiobia** WINCHELL, 1853, p. 10 [*Cardiomorpha

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Fig. B4. Antipleuridae (Antipleurinae) (3,5-6,8), (Vlastinae) (1-2,4,7) (p. N247-N248).
Family ANTIPLEURIDAE Neumayr, 1891

Shell very inequivalve, commonly costellate. Sil.-Dev.

Subfamily ANTIPLEURINAE Neumayr, 1891

Shell inequivalve, commonly costellate. Sil.-Dev.

Antipleura Barrande, 1881, p. 18 [*A. bohemia; M]. Inflated, subcircular, beaks prosogyre; posterior part of shell commonly set off by carina; surface ornamented by uniform costellae. M.Sil. (Ea), Boh.

A. (Antipleura). Beaks about equal in size, large, of RV lying slightly ahead of LV. M.Sil. (Ea), Boh.—Fig. B4.8. *A. (A.) bohemia; 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.t., but LV appreciably more convex with strongly prosogyre, overhanging beak. M.Sil. (Ea), Boh.—Fig. B4.5. *A. (D.) comitans; dorsal view, ×1 (27).

Hercynella Kayser, 1878, p. 101 [*H. beyrichi; SD Cossmann, 1885]. Thin, patellid, 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. (Ea), Boh.; 3a,b, LV ext., RV ext., enl. (Termier & Termier, 1950).

Silurina Barrande, 1881, p. 153 [*S. percalva; SD Růžička & Prantl, 1960]. Subicular, 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.(Ea)-Dev. (Fia), Boh.—Fig. B4.6. *S. percalva, Sil.(Ea); LV ext., ×1 (27).

Subfamily VLASTINAE Neumayr, 1891

Shell thin, ovate, equivaleve, 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 nympha 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. bohemia; SD Růžička & Prantl, 1960] [=lahnia Růžička & Prantl, 1960, p. 50 (type, Isocardia bohemia 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.(Ea), Boh.—Fig. B4.4. *V. bohemia, Sil.(Ea), 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. B4.7. *S. vlastoides, M.Ord. (N.Auakangyi 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.(Kalholn-Dalarna); 2a,b, LV ext. and ant. views of holotype, showing gape, ×1; 2c, hinge of same; all ×1.5 (439).

Yevoda 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); Praecordrea Barrande, 1881, p. 147 (type, P. bohemia; M)]. Subicular to subelliptical, gaping slightly in front; cardinal line strongly arched; beaks relatively small, prosogyre,
swollen, distinct from remainder of shell; surface with both concentric and radial ornamentation, latter weaker. *Sil.(Ez)-Dev. (Fr.), Boh.*—Fig. B4,7. *V. expectans, Sil.(Ez), Boh.; 7a, RV ext. showing form, ornamentation, and prominent prodissoconch; 7b, same, hinge view; both X1 (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 ostiophone, adult shell prosogyre; sculpture of nodose strong radial ribs; ligament opisthodetic; interior unknown. *Sil., Eu.—Fig. B5,1. *B. migrans (Barrande), Kopanina F., P. nilsoni Zone, Boh.; 1a, RV ext., ×5; 1b, both valves, dorsal, cardinal, X20 (Kříž, 1965).*
recognizable from available evidence. U.Ord., USA.

_Cyrtodontula_ **Tomlin**, 1931 [*Whitella obliquata Ulrich, 1890; OD] [=Rhynchohotropis 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. obliqua*ta (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; umbonal ridge and umbones prominent, escutcheon distinct; 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
hainesii 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. Cl,9. *O. hainesii (Miller); 9a, LV ext. showing ornamentation; 9b, LV int. showing dentition; both ×1 (929).

**Psychodessa** Hall & Whitfield, 1872, p. 192 [*P. knappanum; M* [=?Macrodessa 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; denticition obsolescent or poorly known. U.Ord.-Sil, Sweden; Dev., USA(Ky.-Ind.).—Fig. Cl,11. *P. knappanum, M.Dev., USA(Ind.); 11a, RV ext., ×1; 11b, LV hinge, ×2 (379). [Newell]

**Sowerzia** 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. Cl,1. *S. canadensis (Raymond); 1a,b, RV int. mold, LV int. mold, showing ornamentation, ×1 (976).

**Thorshuldia** 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. Cl,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. Cl,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. Cl,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. Cl,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 Lamarrk, 1809)] [Diagnosis by N. D. Newell]

Generally trapezoidal, radially ornamented; ligament elongate, generally duplivanicular or striate, not confined to median resilier; periostracum commonly conspicuous. L.Ord.-Rec.

**Family ARCIDAE Lamarck, 1809**

[nom. correct. Broderip, 1839 (pro family group arcacées Lamarrk, 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 radically disposed with respect to point well below beaks; ligament duplivanicular, 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 Lamarrk, 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. nose; SD Schmidt, 1818 (ICZN Opinion 189)] [=Daphne Poli, 1791 (Daphnoderma Poli, 1795, type, A. nose; SD Newell, herein); Naucula de Blainville, 1825 (obj.); Byssarca Swainson, 1832 (obj.); Clbeta

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Fig. C2. Arcidae (Arcinae) (p. N252, N254) (facing page).
A. (Area). Teeth small, numerous, transverse across middle of shell, becoming longer and convergent terminally. U.Cret.-Rec., cosmom, in warm waters. —Fig. C2,3. *A. (A.) noae, Rec., Medit.; 3a, RV ext., ×0.85; 3b, RV int., ×1.3 (Newell, n).

B. (Eonavicula) Arkell, 1929 [*A. quadriangularata J. & C. Rec., W.Eu.—Fig. C2,2. A. (E.) trichordis (de Loriol), U.Jur., Switz.; 2a, b, LV ext., ×1.3 (20).

Barbatia Gray, 1842 [*A. barbata Linné, 1758; SD Gray, 1857] [=Modioliformia Deshayes, 1860 (type, Arca obliquaria Nyst, 1847; OD, Eoc., Fr.); Granocara Conrad, 1862 (type, Arca protopulita; OD, Mio., USA); Plagiocara Conrad, 1875 (type, B. carolinensis; OD, U.Cret., N.Car.); ?Soldaniana Stephani & Pantanelli, 1878 (type, Arca mytiloides Brocchi, 1814; OD, Plio., Italy) (non D'Orbigny, 1826); Savignyarea Jouseaume, 1891 (type, S. savignyarea; OD, Rec., Guféaden); Asperarca Sacco, 1898 (type, Acar nodulosa Muller, 1776; OD, Rec., Denn.); Obliquarca Sacco, 1898 (type, Arca modioliformis Deshayes, 1831; OD, Ecc., Italy); Pugilarca Marwick, 1928 (type, B. barneaformis; OD, Oligo., NZ.); Destacar Iredale, 1936 (type, Arca metella Hedley, 1924; OD, Rec., S.Australia); Abarbatia Dall, Bartsch & Rehder, 1938, p. 29 (type, Barbatia oahu; OD, Rec., Hawaii); ?Hauaiarca Dall, Bartsch & Rehder, 1928, p. 27 (type, H. rectangula; OD, Rec., Hawaii); ?Nipponarea Habe, 1951, p. 34 (type, Arca bistrigata Dunker; OD, Rec., W.Pac.); Barbarcarca Dall, Bartsch & Rehder, 1938 (type, Calloarca hina; OD, Rec., Hawaii); Barbaturea Iredale, 1939 (type, B. mimulus; OD, Rec., E. Australia); Mimarcara Iredale, 1939 (type, M. saviolium; OD, Rec., E.Australia); Miraactar 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, 1872; OD, Rec., N.Australia); Jackonarca Harris & Palmer, 1946 (type, B. seraperita; OD, Ecc., Miss.); Tucetonea Habe, 1961, p. 112 (type, Tucetona planocasta; OD, proposed as a subgenus of Tucetona)]. Small, elongate, ovoid, inequilateral, generally equivalent, but rarely RV is slightly smaller than LV; terminations rounded or subangular and slightly expanded; ornamentation costellate, commonly fine. ?Trias., Jur.-Rec., cosmom.

B. (Barbatia). Umbonal carina low, rounded, cardinal area low, ligamental grooves closely spaced, costellae numerous, in some forms obsolescent. ?Trias., Jur.-Rec., cosmom.—Fig. C2,6. *B. (B.) barbata (Linné), Rec., Medit.; 6a, b, LV ext., int., ×1, ×2 (Newell, n).

B. (Acar) Gray, 1857 [*A. gradata Broderip & Sowerby, 1829; SD Woodward, 1925] [=Viracar Iredale, 1939 (type, V. lateroarea)]. 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.Colum.; 4a, RV ext., ×2.6; 4b, RV int., ×5.2 (Newell, n).

B. (Calloarca) Gray, 1857 [*Byssoarea alternata Sowerby, 1833; SD]. 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., ×1.3 (688).

B. (Cucullaeacrca) Conrad, 1865 [*Byssoarea lima Conrad, 1847; SD Stolticzk, 1871] [=Polyema Conrad, 1875 (type, B. limnea, U.Cret., N. Car.)]. Elongate to obliquely subquadrate, sub- equivalent but generally much distorted, ventral margin deeply sinuated by large byssal gape; cardinal area high, amphidetic; sculpture formed by fine to coarse subequa 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., cosmom. in warm seas.—Fig. C3,2. B. (C.) limnea (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 Acur; 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).


Fig. C3. Arcinac (Arcinac) (1-3), (Anadarinac) (4-5) (p. N252, N254) (facing page).
Litharca Gray, 1892 [*Byssoraca 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 amphidetic; 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 (Linne, 1758; OD) [=Triis Oken, 1815 (obj.); Parallelolipipedum Möhrch, 1850 (obj.); Epitrisis Iredale, 1939 (type, Arca semitora 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 (Linne), 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 Linne, 1758; OD] [=Anomalocardia Mörch, 1853 (type, A. granosa Linne, 1758, Rec.) (non Anomalocardia Schumacher, 1817); Cara Gray, 1857 (type, Arca aviculoides Reeve, 1844, =Arca formosa Sowerby, 1833, Rec., Panama); Razia Gray, 1857 (type, Arca formosa Sowerby, 1833, Rec., Panama); Nemoarea Conrad, 1869 (type, N. cretacea, U.Cret., N.J.); Pectinatunaca Sacco, 1898 (type, Arca pectinata Brocchi, 1814, Mio., Italy); Diluvarca Woodring, 1925 (type, Arca diluvis Lamarck, 1805, Mio., Eu.); Tegillarca Iredale, 1939 (type, T. granosa bessalis, Rec., E.Australia); Eimera 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 (Linne), Rec., Madag.; 4a, LV ext., ×1.1; 4b, LV hinge, ×2.25 (Newell, n).

Bathyarca Kobelt, 1891 [*Arca pectunculoides Scacchi, 1833; OD] [=Microcucullacea Iredale, 1929 (type, B. pereisides Hedley, 1907, Rec., S.Australia); Indacar Iredale, 1939, p. 261 (type, Arca pteroessa Smith, M.J.)]. 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 exterimities 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 larkinia 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. N254, N256).
---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 mediad edentulous area, anterior teeth short, bifid, and posterior teeth somewhat longer, serrate, obliquely inclined, radial with respect to a point well below beaks. ?Pleist.-Recc., Australia.—Fig. C5,4. *S. strabo* (Hedley), Rec.; 4a, RV ext., ×4; 4b, RV hinge, ×8 (399).

**Scapharca** Gray, 1847 [*Arca inaequivalvis* Bruguère, 1789; OD] [=Calosarca Olsson, 1961 (type, *Anadara rustic* Tuomet & Holmes, 1857, Pls., SE.USA); *Sectharca* 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; denticles 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 interstices; cardinal area narrow, elongate; ligament commonly reduced or lacking in front of beaks. Oligo.-Rec., cosmop.—Fig. C5,6. *S. (S.) inaequivalvis* (Bruguère), Rec., Malaya; 6a, LV ext., ×1; 6b, RV int., ×2 (Newell, n).

**S. (Cunearia)** Dall, 1898 [*Arca incongrua* Say, 1822; SD Lam., 1907] [=Imparlarca Iredale, 1929 (type, *I. hubbardi*, Rec., Queensl.); *Potiarca* Iredale, 1939 (type, *P. pilula*, Rec., E.Australia)]. Subtripodal, 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 denticles 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 equivalent, strongly inequilateral, orthogyre; ligament duplicinacular on broad, flat, divergent cardinal areas; hinge long and straight; denticles strongly inequilateral, consisting of few posterior laterals and numerous, generally short, oblique, horizontal, or falcate anterior and medial cardinal areas. [The phylogeny of this group is difficult to determine and poorly understood. There appears to be gradation from ancestral Cyrtodontidae through Paralleloodontidae to Cucullaeidae, and the limits are not clearly defined.] L. Ord.-Rec.

**Subfamily PARALLELODONTINAE** Dall, 1898

[nom. transl. Newell, herein (ex Paralleloodontidae Dall, 1895)]

Byssal gape and corresponding ventral sinus present; valve margins not denticate; 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 & Wortman, 1866 [pro Macrodon (Lycett) Buckman, 1845 (non Schinz, 1822, nec Müller, 1842) =Macrodontus Beushausen 1895 (obj.) (non Gray, 1845)]. [*Macrodontus rugosus* Beushausen, 1845] [=Prorhynchus Hall, 1884, p. xviii (type, Palaeonatina quadratum Hall, 1883; OD); *Beushausenia* Cossmann, 1897 (obj.) (non Maillieux, 1913, =Maillieuxia Cossmann, 1920)]; ?Sufia Prantl & Ruzička, 1955 (type, *S. paradoxa*; OD); ?Mnataia Prantl & Ruzička, 1955 (type, *M. pribyi*; OD); Palaeocucullaea Tokuyama, 1960 (type, Parallelododon 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).]
Subfamily GRAMMATODONTINAE 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 Parallelodonta. ?U.Carb., U.Trias.-Rec.

GRAMMATODON GROUP


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. (Cosmetodon) Branson, 1942 [*Arca keyserlingii d'Orbigny, 1850; OD] [=Beuthausenia Arkell, 1930 (non Cossmann, 1897, nec Mailleux, 1913)]. Externally similar to Paralodontus 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., X0.5; 7b, LV ext., X1 (20).

G. (Indogrammatodon) Cox, 1937 [*Cucullaea virgata J. de C. Sowerby, 1840; OD]. Posterior umbral ridge poorly defined; costae narrow, widely spaced, coarser on LV. Jur., India-Afr.-SW.Pac.—Fig C6.4. *G. (1) virgatus (Sowerby), M.Jur., India; 4a,b, LV ext., RV ext., X2; 4c, LV int., X2 (180).

G. (Nanonavis) Stewart, 1930 [*Arca carinata J. Sowerby, 1813; OD] [=Spinulacea Chavan, 1952, p. 10 (type, S. cristata Bigot in Chavan, 1952, M); Aptolitinae, 1961, p. 575 (type, Arca apienia Pictet & Campiche, 1866; OD, L.Apt., W.Eu.)]. Trapezoidal, with low, closely spaced costae; umbal carina sharp, delimiting deeply concave posterocontinental 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, X2 (Woods, 1899).

G. (Nordenskjoeldia) Wilckens, 1910 [*Arca disparilis d'Orbigny, 1846 (non Reeve, 1844) (=G. subdispilis Nicol, 1954; OD)]. Ovoid, with low, closely spaced costae; umbal 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.) subdispilis (Nicol), India; 3a,b, LV int., RV ext., X1.5 (Stoliczka, 1891).

?Cucullopsis Chao, 1927 [*C. quadrata; OD]. Shell thick, subquadrat, 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., X1 (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, X0.7 (259).


N. (Nemodon). Costellae closely spaced; posterior umbral carina distinct. U.Cret., N.Am.—Fig. C7.6. *N. (N.) eufalensis (Gabb); 6a,b, LV ext., int., X2 (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., X0.5 (424).

CATELLA GROUP

Ovoid or trapezoidal, small and moderately short. U.Trias.-Rec.

Catella Healey, 1908 [*Grammatodon (C.) laticlava; OD] [=Cryptoehasma 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; dentication 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, X1 (Healey, 1908).
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 Cucullacinae 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
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.]

*C. (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.); Latiarea Conrad, 1862 (type, C. gigantea Conrad, 1830, Eoc., Md.); Dicranodonta Woods, 1899 (type, D. 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.-Cret., 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., X3; 5c, RV int., X0.5 (674).

C. (Idonearea) Conrad, 1862 [*C. tippana Conrad, 1858 (=C. capax Conrad, 1858; *C. vulgaris Morton, 1830); SD Dall, 1898]. Sub-

Fig. C8. Cucullaeidae (p. N260-N261).
trapezoidal, elongate, with fine, closely spaced radial costellae and subhorizontal lateral teeth. *Jur.-Cret.*, *C.* (1.) *vulgaris* (MORTON), *Cret.*, *USA*; 4a,b, RV int., ext., ×0.7 (951).

**Lopatina** SCHMIDT, 1872 [*L. peshchorea 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.*, USR-Afr.-S.Am.

**L. (Lopatina)**. Ornamented with fine costellae. *Cret.*, *USSR*-fig. C8,2. L. (L.) *jenisseae* (LAHUSEN), *Sib.*; 2a,b, RV int., LV ext., ×1 (Schmidt, 1872).


**Family NOETIIDAE** Stewart, 1930

[nom. transl. NEWELL, herein (ex Noetini STEWART, 1930)] [=Noetiidae MACNEIL, 1937] [Materials for this family prepared by N. D. NEWELL]

Without byssal gape and mostly free in adults; subtrapezoidal to ovoid, evolute, 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; prosodic, amphidetic or opisthodetic; myophoric ridge or shelf at inner margin of one or both adductor scars. [Widespread in shallow seas.] *L. Cret.-Rec.*

**Subfamily NOETINAE** 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 opisthogyre 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 posterovertrally, beaks opisthogyre, high when situated just anterior to mid-point of hinge, becoming lower when posterior; ornamented with subequal costae, inner margin crenulated posterovertrally; 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. (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.—fig. C9,7. *N. (E.) ponderosa* (SAY), Rec., Panana; 3a,b, RV int., both valves, RV view, ×1 (MAURY, 1922).


**Arginopsis** MACNEIL, 1938 [*Scapharca sullanensis* WOODS, 1822; OD] [=Samaoneia MACNEIL, 1940 (pro Arginella MACNEIL, 1938) (type, *Arca sullanensis* OLSON, 1929, U.Eoc., Perum (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).

Protonoetia MacNeil, 1938 [*Anadara nigeriensis Newton, 1922; OD]. Subquadrate, inflated, subangular posteroventrally, umbonal ridge subcarnate, 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., X1 (MacNeil, 1938).


Subfamily STRIARCINAE MacNeil, 1938

Generally small, ovoid, subequilateral, with submedian umbones, beaks prosogyre
Striarca CONRAD, 1862 [*Arca centenaria SAY, 1824; OD] [=Breviarea CONRAD, 1872 (type, Arca saffordi GABB, 1860; SD STEWART, 1930, U.Cret., Tenn.); Estellacar IREDALE, 1939 (type, E. saga, Rec., Queens.).] ; Galactella CossMANN & PEYROT, 1912 (type, Arca lactea LINNE, 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.—

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., Queens.); Multinarca IREDALE, 1939 (type, Barbatia aceracea MELVILL & STANDEN, 1899, Rec., Queens.); Scapularca CossMANN & PEYROT, 1912 (type, Arca scapulina LAMARCK, 1805, Eoc., France); Spinearca IREDALE, 1939 (type, S. deliciosa, Rec., Queens.).] ; Verilarca

Fig. C10. Noetiidae (Striarcinae) (1-4,6,9, (Trinacriinae) (5,7,8,10) (p. N263-N264).
Iredale, 1939 (type, V. bivia, Rec., Queensl.). Similar to Siuracea 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. (4.) limopsis (Koenen), Dan., Denm. 6a,b, LV ext., int., ×4 (Koenen, 1885).

A. (Ovalarea) Woodring, 1925 [*Barbatia ovalina Dall, 1898; OD]. Surface smooth. Mio., Jamaica.—Fig. C10.9. *A. (O.) ovalina (Dall); 9a,b, RV ext., int., ×12 (1005).

Matsumotoa Okada, 1958 [*M. japonica; OD]. Elongate, ovoid, with rounded anterior and obliquely rounded posterior margin, ventral margin mediately 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 obsolete posteriorly, inner margin not crenulate; dentition cuneated, 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., ×1.25 (Okada, 1958).

Trigonodesma Wood, 1864 [*Arca lissa BAYAN, 1873 (=A. laevigata CAIiALLAT, 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., ×6 (Wood, 1864).

Vetourca 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., ×2 (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, prosodic, 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 [*Trigonocelia crassa Deshayes, 1860; SD GARDNER, 1926]. Opisthogyre, amphidetic to opisthocochetic, 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., ×4 (259).—Fig. C10.5c. T. media (Deshayes), Paris Basin; LV hinge, ×4 (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, ×4 (570); 8b, RV ext., ×4 (Stephenson, 1937).

Pachecoa Harris, 1919 [*Trinacria (P.) cainei; OD] [=Halonanus STEWART, 1930 (type, Noelia pulchra GABb, 1860, Eoc., Tex.)]. Opisthogyre, prosodic 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, prosodic. Eoc., SE. USA.—Fig. C10.7. *P. (P.) cainei, S.Car.; LV ext., ×5 (Harris, 1919).

P. (Stenzelia) MacNeil, 1954 [*Pectunculus perplanus CONRAD, 1865; OD] [=Trinaciella MACNEIL, 1937 (non DEL GUERICO, 1913; nec PARONA, 1933)]. Subquadrate to ovoid, cardinal area poorly defined, ligament short, amphidetic to prosodic. Eoc., SE.USA.—Fig. C10.10. *P. (S.) perplana (CONRAD), USA(Ala.); LV ext., ×3.5 (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 LIMOPSIDAE1 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

1 Note to R. C. MOORE FROM PROFESSOR L. W. GRENSTED AT REQUEST OF W. E. CHINA, ICZN: "The generic ending -ops means its generic -ops, opsins, and this (as the accent shows) is treated as a dissyllable. The stem therefore is not -ops (or Ionic, -opis) but -opi. Poecilopleuridae and Macropsidae are therefore quite correct."
triangular resilifer, which may be bordered by smooth uncovered cardinal area; denticion 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); **Cnima** 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); **Prynhelma** Iredale, 1929 (type, *Loringella brasieri* Iredale, 1929; OD) (Rec., E.Australia); **Glycilima** Iredale, 1931 (type, *G. paradoxa*, *nom. nud.*).

Orbicular, nearly equilateral, commonly with slight forward obliquity. M./ur.-Ree., cosmop.---FIG. C11,1. *L. (L.) aurita* (Brocchi), Plio., Italy; 1a,b, LV int., ext., X1 (222).

**L. (Pectunculina)** d’Orbigny, 1843 (emend. Sacco, 1898) [*Pectunculus scalaris* Sowerby, 1825; OD] [=Cosmetopsis Rovert, 1898 (type, *Limopsis retifera* Semper, 1872)]; **Aspalima** Iredale, 1929 (type, *Limopsis erecteda* Hedley & Petterd, Rec., S.Australia); **Senectidens** Iredale, 1931 (type, *S. dannesi*, Rec., E.Australia); **Versipella** Iredale, 1931 (V. soboles, Rec., E. Australia); **Limopsista** Finlay & Markwick, 1937 (type, *Limopsis microps*, Dan., N.Z.); **Circlimopa** Iredale, 1939 (type, *C. woodwardi mutanda*, Rec., S.Australia); **Oblimopa** Iredale, 1939 (O. magillierayi actaviva, Rec., E.Australia). Similar to *L. (Limopsis)*, but sculptured with radial costellae; inner margin crenulate. Cret.-Ree., cosmop.---Fig. C11,7. *L. (P.) scalaris* (Sowerby), Eoc., Eng.; 7a,b, RV ext., LV int., X2 (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., X1.5; 4b, RV int., X1 (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,

1985). 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, X2 (58).

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**Glycymeridae (Glycymeridinae)** (p. N267-N268).

**Lissarca** SMITH, 1877, p. 168 [*Arca (L.) rubrofusca; M] [=Astropleura HEDLEY, 1899 (type, A. pecta; 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 aviculoideae d’ARCIAC, 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, d'uplicivulinar ligament. *Eoc., W.Eu.—*Fig. C11,3. *P. aviculoides (d'Archiac), Eoc., France(Biarrritz); 3a,b, RV, ext., int., X1 (d'Archiac, 1850).

**Family GLYCIMERIDIDAE** Newton, 1922

* nom. correct. Warncke & Abbott, 1961 (pro Glycimeridae Newton, 1922) [=Axisedinae Adams & Adams, 1858; Pe-tunctilingidae Gray, 1847 (invalid name, Code Art. 16, based on *Pectunculus Lamark*, 1799, non Hudsdesford, 1770)].

Materials for this family prepared by N. D. Newell.

Adults free, not byssate, subtrigonal to subcircular, equivale, 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 d'uplicivulinar, 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 GLYCIMERIDINAE** Newton, 1922

* nom. transl. et correct. Newell, herein (ex Glycimeridae Newton, 1922).*

Orbicular, with or without obscure posterior umbonal carina; smooth or with radial ornamentation, border crenulate. Cret.-Rec.

**Glycimeris** da Costa, 1778 [non *Glycimeris Lamark*, 1799 (=Panopea Ménard, 1807)].


G. *Glycimeris*. Subcircular, subequilateral, with small umbones and beaks; teeth relatively short, transverse, becoming obsolete medially; surface smooth or costate. L.Terti.-Rec., cosmop.—*Fig. C12,1. *G. (G.) glycymericis (Linné), Rec., Medit.; 3a,b, RV ext., LV int., X1 (Newell, n). G. (Glycymelisa) Finlay & Markwick, 1937 [*Glycymelisa 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.-Terti., Eu.-N.Z.-Calif.—*Fig. C12,2. *G. (G.) concava (Marshall), Paleog.(Dan.), N.Z.; 2a,b, LV int., X0.7 (304).

**Axinaeis** Mörch, 1861 [*Pectunculus inaequilis 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. (*Axinaeis*). Costae relatively few, large, bearing fine costellae. Rec., Panama.—*Fig. C12,4. *A. (A.) inaequilis (Sowerby); 4a, RV ext., X1; 4b, RV int., X2 (Newell, n).

A. (*Glycymelisa*) Woodring, 1925 [*Arca decussata Linné, 1758 (=Pectuncunaeoccus Lamark*, 1819)]. Costae numerous, low, bearing fine costellae. Mio.-Rec., trop.W.Alt.—*Fig. C12, 5. *A. (G.) decussata (Linné), Rec.; 5a, RV ext., X1; 5b, LV int., X2 (Newell, n).

**Melaxinaeis** 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,
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., X1 (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 lessobsolete 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., X1; 1b, LV ext., X3 (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., X0.8 (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 corre-
sponding to ventral sinus, umbones prominent; exterior ornamented with fine costellae. U.Cret., S.Am.(Peru-Colom.).—Fig. C13,5. *P. abnormalis (Olsson), Peru; 3a,b, LV ext., RV int., ×1 (Nicol, 1953).

Postiglata 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. C13,6. *N. sulcata, Japan; 1a,b, LV int., RV ext., ×4 (334).

Protarca STEPHENSON, 1923 [*P. obliqua; OD]. Ovoid, with forward obliquity, vertically truncate behind; prosogyre; surface ornamented with irregular low costae; ligament and dental arch shortened anteriorly. U.Cret., USA(N.Car.).—Fig. C13,7. *P. obliqua; 5a,b, LV ext., int., ×0.5 (887).

Trigonarca CONRAD, 1862 [*Cucullaea macoensis Conrad, 1860; OD]. Subtrigonal, obliquely truncate 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
[=Nucolinidae Chronic, 1952; Nucinellidae Vokes, 1956]
[Materials for this family prepared by MYRA KEEN and N. D. NAWELL]

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 cardinal teeth between anterior margins of valves; hinge internal or only partly external, median or 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.

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. C14,1. *M. elliptica, ?Yeso F., N. Mex.; 3a,b, LV int., RV ext., ×2 (328).

Huxleyia A. Adams, 1860 (Apr.). [*H. sulcata; M] [=Cyrilla A. Adams, 1860 (June) (obj.; pro Huxleyia); Diabolica Jousseaume, 1897 (type, D. diabolica; T); Cyrillona 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. C14,2. *N. ovalis (Wood), Plio., Eng.; LV int., ×6 (Wood, 1851).

?Family PHILOBRYIDAE Bernard, 1897
[nom. transl. SUTTER, 1913] (ex Philobryinae Bernard, 1897)]
[Materials for this family prepared by MYRA KEEN]

Small, equivaleve, 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.
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., X5 (42); 8b, RV int., X4 (Keen, n); 8c, detail of RV hinge, X16 (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., X4 (Pelseneer, 1903).

P. (Hochstetteria) Vélain, 1877 [*H. aviculoides; SD Kobelt, 1881] [=Cosatavia Iredale, 1939 (type, P. recapitula Hedley, 1906; OD)]. Embryonal shell prominent; hinge crenulations well marked; ligamental fossette short, triangular. Rec., Medit.-S. Atl.-Australia.—Fig. C15.2.

*P. (H.) aviculoides (Vélain), St. Paul I.; RV hinge, X16 (42).

P. (Hochstetterina) Thiele, 1934 [*Hochstetteria crenella Vélain, 1877; M] [=Hochstetteria aviculoides]. 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, X20 (42).

P. (Micromytilus) Cotton, 1931 [*Myrina crenatilis] 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., X15 (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., X6 (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., X7 (399).

Limarca Tate, 1886 [*L. angustijrons; M]. Inequilateral, cartilage pit lanceolate, directed backward; hinge with anterior denticles and long, striate posterior teeth. U.Eoc., S. Australia.—Fig. C15.5. *L. angustijrons; RV int., X4 (Ludbrook, MS).

Order MYTILOIDA Ferussac, 1822

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 pris-
mato-nacreous; gills filibranchiate or eulamellibranchiate; pallial line entire. Dev.-Rec.

The Pinnidae, secondarily members of the infauna, are usually arbitrarily classified 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 invariable ancestors.

Superfamily MYTILACEA Rafinesque, 1815

[nom. transl. et correct. Tryon, 1884 (ex Mytilidida Raffinesque, 1815)] [Materials for this superfamily prepared by Tryon Soot-Ryen with other contributions as indicated]

Equivale, 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 nymphæa 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 provilucum, 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, 1905 (pro Mytilida 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 Mytilidida 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.]

Mytilus Linne, 1758, p. 704 [*M. edulis; SD Gray, 1847, p. 198] [=Mytilus Meichen, 1789 (nom. null.); Mytilarius Froire, 1806; Mytiligenus Renier, 1807; Envitilus 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.] Plb.-Rec., N.Am.-N.Eu.-S.Am.- S.Australia-N.Z.-Kerguelin Is.———Fig. CI6,2. [*M. edulis, Rec., France; 2a, RV ext., X1 (89a); 2b, muscle scars, X1 (860)].


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 Modiolia 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. CI6,4. [*A. pectinatus (Sowerby), Kimmeridge, Eng.(Weymouth); RV ext., X1 (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. N271, N273-N274).
terior retractor scars elongate, posterior retractor 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 cirrhus* Röding, 1798, *=Arca modiolus* Linné, 1767); M] [=Brachyodontes suctt.]. 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). Umbo 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. Flio.-Rec., Australia.—Fig. C16.7. *B. (A.) rostratus* (Dunker), Rec., Tasmania, LV ext., ×1 (783).


*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*; a,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 tooth-like 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* Lyckett, 1857; OD] (=Cuneolus Stephenson, 1941 (type, Dreissena tippiana Conrad, 1858)]. Smooth, calcareous shells with acute, terminal beaks and sharp carina extending from beaks to postero-ventral extremity; without anterior lobation; um- boonial cavity covered by small plate or deck which bears elongate radial tooth and furrow on each valve, tooth of RV overlapping 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* (Lyckett), Inf. Oolite, Eng.; 1a, LV ext., ×1; 1b, LV int., ×2 (182). [NEWELL]

**Mauricia** Harris, 1919, p. 32 [*Modiola houstonia* Harris, 1895; OD]. Modioliform, thin, concentric growth lines below well-defined umboonal ridge, with broad concentric undulations above it, anterior end radially striated. Eoc.-Mio., N.Am. (USA)-Eu.

**Myella** 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 divericar; dysodont teeth after ligament. Rec., Medit.—Fig. C16.8. *M. lineatus* (Gmelin); a,b, LV ext., RV int., ×1.5 (89a).

**Peregrinamor** Shoji, 1938 [*P. oshimii*; OD]. Rec., S.Japan. [NEWELL]

**Perna** Retzius, 1788, p. 20 [*P. magellanica* (=*Mya perna* Linné, 1758); SD Soot-Ryen, 1955, p. 29] (non *Perna Bruguire*, 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 tooth-like ridges, surface and margins smooth. Eoc.-Rec., cosmop.

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., X1.5; C18.4, muscle scars, X1.7 (860).

Septifer Recluz, 1848, p. 275 [*Mytilus bicornis 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. bicornis (Linné), Rec., IndoPac., 2a,b, LV ext., int., X0.8 (7).

S. (Mytilisepta) Habe, 1951, p. 53 [*Tichogonia virgata Wiegmann, 1837; L]. 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., X0.5 (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, nesting, 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); ?Myoparia Lea, 1833 (type, Mytilus constans von Münster, 1840); Nuculocaria d’Orbigny, 1845 (type, N. divaricata); ?Crenellodon Edwards in Newton, 1891 (type, Modiola pulcherrina Römer, 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., X10 (860).
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., X1 (151).

Arcuatula Joussaeume 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., X1 (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., X1 (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., X1 (58).

Gregariella Montenosato, 1883, p. 90 [*Modiolus sulcatus Risso, 1826 (=Modiola opifex Say, 1825); M] [=Botulina Dall, 1889; Tibialecτus Iredale, 1939, p. 424 (type, T. otteri)]. Elongate, inflated, beaks incurved, umbonal keel angulated; radially striated anteriorly and posteriorly where
strae end along oblique line, median part con-
centrally striated, periostracum hairy along um-
bonal keel; anterior and posterior dysodont
teeth, margins crenulated. Mio.-Rec., Medit.-N.
Am.-Australia.—Fig. C19.5. *G. opifex (Say),
Rec., Medit.; RV ext., X1 (89a).
Lioberus DALL, 1898, p. 805 [*Modiola castanea
Say, 1822; OD]. Beaks near anterior end, smooth
or with obsolete radial sculpture, edentulous, perio-
stracum smooth. Rec., SEN.Am.—Fig. C19.7.
*L. castaneus (Say), USA(FLa.), LV ext., X2.3
(728).
Musculus RÖDING, 1798, p. 156 [*Mytilus discors
LINNÉ, 1767; SD IREDALE, 1915, p. 485]
 [=Modiolara BECK, 1838; Lanistes SWAINSON,
1840 (non DE MONTFORT, 1810); Modiolarca Gray,
1843; Lanistina Gray, 1847; Planimodiola CosS-
MANN, 1887 (type, Modiola sulcata LAMARCK,
1805)]. Modioliform, with broadly rounded um-
bonal keel, postero-dorsal part usually separated
from remainder of valve by furrow, radiate sculptu-
re separated in middle by concentrically striated
area; margins crenulated, dysodont teeth in front
M. (Musculus). Shell rather flat, with broadly
rounded umbonal keel, posterior retractors con-
tinuous, united with posterior adductor. Jur.-Rec.,
cosmom.—Fig. C19.1. *M. (M.) discors (LINNÉ),
Rec., DENM.; LV ext., X2 (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 elon-
gate, fastened along dorsal margin with single
branch above posterior adductor. Mio.-Rec.,
cosmom.
M. (Undatimusculus) EAMES, 1951, p. 369 [*Mus-
culus (U.) rakhienlis EAMES, 1951; OD]. Like
Musculus (Musculus) but umbonal region with
course concentric folds. L.Eoc., Pak.
Rhynchomytilus ROLLIER, 1914, p. 355 [*Mytilus
studi Oppel & WAGEN, 1866; OD]. Reniform,
gibbose, beaks anterior, inflated and widely pro-
jecting beyond rounded and expanded antero-
ventral corner; fine concentric and radial lines;
hinge line smooth or crenulated. U.Jur., Eu.—
Fig. C19.10. *R. studeri (OPPEL & WAGEN),
L. ARGOV., BIRMENSDORF; LV ext., X1 (795b).
Solamen IREDALE, 1924, p. 198 [*S. rex; M]. Round
to ovate, beaks nearly terminal, sculpture consist-
ing 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-N. Am.—Fig. C19.12. *S. (S.) rex,
Australia (New S.Wales); LV ext., X2 (352).
S. (Exosiperna) IREDALE, 1929, p. 166 [*Aro-
perna scapha VERCO, 1908; OD]. Small, ovate,
round, beaks terminal, fine cancellate sculpture
without smooth areas, dysodont teeth in front
and above ligament, which is deeply sunk, mar-
gins crenulated. Rec., S.Australia.—Fig. C19.9.
*S. (E.) scapha (VERCO); 9a,b, LV ext., RV int.,
X10 (169).
S. (Rhomboideilla) MONTEROSATO, 1884, p. 13
[*Modiola rhombes BERKELEY, 1827 (=*Modiola
priduix(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 [*Litho-
domus barbatus REEVE, 1858; OD]. Like Muscul-
s but periostracum with branched hairs. U.Eoc.-Rec.,
N.Z.-Australia.—Fig. C19.11. *T. barbatus
(REEVE), Rec., S.Australia; RV ext., X3.5 (169).
Vilasina BARTSCH in SCARLATO, 1960, p. 69 [*V.
pillula; OD]. Like Musculus but with few weak
radial striae anteriorly, otherwise finely cen-
trically 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.]
Lithophaga RÖDING, 1798, p. 156 [*L. mytiloides
(=*Mytilus littoralis LINNÉ, 1780); M]
 [=Lithophagus MEGERLE VON MÜHLEFELD, 1811,
Lithodomus CUVIER, 1816; Lithogyphus 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
dentulous; margins smooth. [Boring.] ?Carb.,
L. Mio.-Rec., cosmom.
L. (Lithophaga). Shell with vertical striations,
—Fig. C20.7. *L. (L.) lithophaga (LINNÉ),
Rec., France; RV ext., X1 (89a).
L. (Diberus) DALL, 1898, p. 799 [*Modiola
plumula HANLEY, 1843; OD] [=Exodelberus IRE-
DALE, 1939 (type, Lithophaga calcifer IREDALE,
1939; OD); Salebrolobis IREDALE, 1939 (type,
Lithophaga divaricatax IREDALE, 1939; OD)].
Two or more posterior sulci with plumeliine in-
Mytiloida—Mytilacea

Crustation distinctly projecting beyond valves. *L. Miio., USA (Fla.); Rec., W.N.Am.-IndoPac.*

**FIG. C20.** *L. (D.) plumula (Hanley), Rec., Costa Rica; LV ext., X 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

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*Fig. C20. Mytilidae (Lithophaginae), (1,4,5,7,11), (Modiolinae) (2-3, 6, 8-10, 12-14), (p. N276-N280).*

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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 evenly diffused without projecting parts. Rec., W.N.Am.—Australia.

L. (Myapalmula) Soott-Ryen, 1955, p. 93 [*Modiolina cauligera Lamarck, 1819 (=Mytilus arista Lillwyn, 1817); M]. Projecting posterior parts of incrustation crossed. L.Mio.—Rec., cosmop.—Fig. C20,4. *L. (M.) arista (Dillwyn), Rec., C.Am.; LV ext., ×2 (860).

L. (Stumpiella) Soott-Ryen, 1955, p. 517 [*Mytilus soleniformis d’Orbigny, 1846; M]. Elongate, thin, with parallel dorsal and ventral margins, 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 denticulate teeth or smooth, surface smooth or with irregular wrinkles, posterodorsally with dark covering. Rec., Pac.—Fig. C20,7. *A. soleniformis (d’Orbigny); LV ext., ×1 (d’Orbigny, 1846).

Inoperna Conrad in Kerr, 1875. App. A5 [*Modiola (1) carolinaeensis 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. carolinaeensis (Conrad), U.Cret., USA(Tex.); RV ext., ×1 (881).

Lithodoma Waagen, 1881, p. 264 [*L. typi; 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. Soott-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 nesting.] Dev.—Rec.

Modiolus Lamarck, 1799, p. 87 [nom. conserv. (pro Volutella Scopoli, 1777, ICZN pend.)] [*Mytilus modiolus Linne, 1758; SD Gray, 1847, p. 198] (=Modiolus Lamarck, 1801; Perna Adams & Adams, 1858; Eumodiolus HERING, 1900; Nodiola Monterosato, 1917, p. 5 (type, Modiola adriatica Lamarck, 1819)]. More or less inflated, rounded anteriorly, umbones obsolete, 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 (Linne), 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., Red.S.—Ind.O.

M. (Gibbomodiola) Sacco, 1898, p. 41 [*G. taur-arcuata; OD]. Elongately ovate, transversely acuminate gibbous, posteriorly broadly expanded. O.Oligo.—Rec., Medit.


Adipolina Dautzenberg, 1927, p. 274 [*Modiola? pelagica Forbes in Woodward, 1854; M] (=Myrina Adams & Adams, 1857 (non Fabricius, 1808); Miridae Iredale, 1939, p. 425 (type, Myrina cockingeri 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 Mühldorf, 1811, p. 69 [*A. dendriticum; M] (=Modiola Monterosato, 1884 (type, Modiola polita Verrill & Smith, 1880)]. Modioliform, thin, residual 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 Gme-
Mytiloida—Mytilacea

Lin, 1791; SD Dall, Bartsch, & Rehder, 1938, p. 59 [Botula 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 Müller, 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 suborta 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 Lam, 1919; nec Gugenerberger, 1934)] [*Modiola plicatula Lamarck, 1819 (= Modiola demissa Dillwyn, 1817); OD]. Moioliform, radially ribbed, weaker striations on anteroventral area, margins crenulated but no toothlike crenulations in front or behind deep-set ligament; 2 anterior retractor 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, argentous, 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. argenteus (Jeffreys), off Iceland; 9a, LV ext., ×6.5; 9b, RV hinge, ×20 (450).

Lecompteus Poel, 1959, p. 13 [*Mytilus ornatus


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 ad-
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ductor 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., x1 (Soot-Ryen, n); 14b, LV hinge, x8 (450).

?Mytilopsis 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., x1 (378). [NEWELL]

Notobotula FLEMING, 1959, p. 170 [*Botula (N.) molina FLEMING, 1959; OD]. Anterior adductor scar very elongate close above curve of antero-ventral 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., x3 (309). [NEWELL]

Praemytilus ANDERSON & COX, 1948, p. 105 [*Mytilus (P.) strathairdensis (CONRAD); OD]. Narrowly and obliquely ovate, with rather broad, 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., x1.2 (16).

Promytilus NEWELL, 1942, p. 37 [*P. annosus; OD | ≡ Pachoya LIUTKEVICH & 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 Is. (U. Missourian), Kans.; holotype, LV ext., x2 (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 MEEEK, 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 (MEEEK), U.Penn. (Willard Sh.), Neb.; RV ext., x2 (666).

Family MYSIDIELLIDAE Cox, 1964

[MATERIALS FOR THIS FAMILY PREPARED BY L. R. COX]

Shell medium-sized, ovate or trapezoidal, equivalent 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 Mysida BITTNER, 1891, p. 113 (non WESTWOOD, 1840)] [*Mytiloconcha orientalis BITTNER, 1891; OD]. Equivalent, 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. (Carn.); U.Trias. (Rhaet.), Eu. (Alps-Hung.-Greece); U. Trias. (U. Carn.); U. Trias. (Rhaet.), Eu. (S. Alps-Hung.-Greece)-Anatolia.—Fig. C22,1. *M. orientalis (BITTNER), U.Trias. (Nor.), Anatolia; 1a-c, RV ext. and hinge, LV hinge, both x0.7 (Bittner, 1891-92).

Protopis KITTTL, 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 posterior dorsal 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, x1 (950).

Tommasina Cox, 1964, p. 44 [*pro Mystilloconcha TOMMASI, 1911, p. 35 (non CONRAD, 1862)] [*Mystilloconcha orobica TOMMASI, 1911; OD] [= Mystilloconcha 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
Mytiloida—Pinnacea


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 X 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 equivalent, a few forms distorted and inequivalent; 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 mid-length; 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 posterior dorsal 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.*

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 Linneé, 1758**, p. 707 [*P. rudis*; SD Children, 1823, p. 341] [=Chimaeroderma Poli, 1795, p. 259 (type, Pinna rudis Linneé; SD Cox, herein); Pinnarius Düménil in Ftorièf, 1806 (obi.-); Pinnigenus Renier, 1807 (suppressed ICZN); Pinnula Rafinesque, 1815 (obi.); Pinnites von Schlotheim, 1820 (obi.); Pennaria Mörch, 1853 (non Oken, 1815); Pinu Seguenza, 1877 (nom. null.); Pina Koch, 1922 (nom. null.).] Equivalve, wedge-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 Linneé should be accepted as type species of *Pinna* by Linnean tautonomy, as Concha hasselqui HASSELQUIST, 1820 is cited by Linneé 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, p. 707 (non Linneé, 1758); Sulcatopinna Hyatt, 1892, p. 341 (type, P. flexicostata M'Coy, 1844 =P. costata Phillips); Sulcatapinna Girty, 1915 (nom. van.); Quantulopinna Iredale, 1939, p. 310 (type, Q. delia); Subitopinna Iredale, 1939, p. 312 (type, P. meneki 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). [=Eixtopinna Iredale, 1939 (type, E. deltodes ultra Iredale, 1939; OD).]

[Rorwater (1961, Indo-Pacific Mollusca, v. 1, no. 4, p. 197, pl. 150) has shown that the type specimen of Iredale's *Eixtopina* is a stunted, repeatedly broken shell of Pinna bucalor Gmelin, 1791 (=E. rudis Linneé). Therefore, *Eixtopinna* is considered to be a junior synonym of *Pinna (Pinna).*]


**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 *Exotopinna* 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. *P. vexillum* (Born), Rec., Philip.Is.; RV ext., ×0.3 (Cox, n).

**Curvula** Rafinesque, 1819, p. 427 [Curviulites 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.

**Oxysma** 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 Meer, 1864, p. 212 (type, Solen pinnaeformis Geinitz, 1848); Pteronites Stoliczka, 1871 (nom. null.); Aviculo­pinna 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.Perms.(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 posteroverentral 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. granulata (Krenkel), U.Jur.(U. Kimmeridg.), Tanganyika; RV ext., ×0.5 (Cox, n).

**Streptopinna** von Martens, 1880, p. 318 [*Pinna saccata Linneé, 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
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. N283-N285).
some authors to Deshayes (1832), who, however, published it in the French vernacular form *trichites*, plural *trichites*.) [=Pinnigona Bronn, 1836 (no valid nominal species); Pinnigona Deshayes, 1839 (obj.); Pinigona 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 nodules; 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. seebachii Böhm, U. (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. saussurii*, U. Jur. (L. Kimmeridg.), Yonne, Fr.; LV, ×0.5 (Bayle, 1878).

**Order PTERIOIDA Newell, 1965**

[Diagnosis by N. D. Newell]

Generally inequivalve and pleurothetic; inequivalve or secondarily nearly equilateral; heteromyarian or monomyarian; ligament opisthodetic or amphidetic, alivincular, multivincular or duplivincular, generally extended by secondary fusion layer; prismatoostracum, 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. transd. Newell, 1965 (ex Ambonychiidae S. A. Miller, 1877)] [Diagnosis by N. D. Newell]

Strongly inequivalve, 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 Cytrodontidae 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 & Aurélie Larocque in consultation with John Poyta, Jr., Washington, D.C., except as otherwise indicated]

Equivalent, 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 Stoliceka, 1871, p. 387] [=Byssonychia Ulrich, 1894 (obj.), p. 498; Eridonychia Ulrich, 1893 (1895), p. 639 (type, *E. apicalis*; OD)]. Prosocline to slightly opisthodetic, 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 [*Megamsonia 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. osumbergensis*; 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. osumbergensis*, 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. N285, N287).
Anomalodonta S. A. MILLER, 1874, p. 16

Byssopteria HALL, 1883, p. 4

Cleionychia ULRICH, 1892, p. 97

Gosseletia BARROIS, 1882, p. 273

Mytilarca HALL & WHITFIELD, 1869, p. 19

Myalinopterella KHALFIN, 1940, Dev., USSR (Alta).

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 LA ROQUE & 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., Pl.Mist., 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. semipliicata; OD]. 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.) semipliicata, 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.; 1ab, RV ext, LV ant., ×1 (323).

Opisthoptera MEEK, 1872, p. 319 [*pro Megaptera MEEK & WORTHEN, 1868 (non GRAY, 1846); OD]. [*Ambonychia casei MEEK & WORTHEN, 1866; M] [=Opisthobolata ULRICH in HUSEY, 1926, p. 165 (type, O. Gouldi; OD)]. Subangular, 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. (Llandover.), 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; OD]. Beaks large, anterior but not terminal, hinge line short; surface with numerous fine, radial costae; no byssal opening; dentition unknown. Sil. (Niag.), USA-Can.—Fig. C26,2. *P. cordiformis, USA(Wis.); 2a, RV int. mold; 2b, post. view int. mold; both ×1 (374).

Paramylarca 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., Kalholn; 2a,b, RV ext., ant., ×2 (439).
Pterioda—Pteriina—Ambonychiacea

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 X2 (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., X1; 4c, LV hinge, X1 (929).

Stappersella Mailleux, 1920, p. 144 [*Goselettia truncata Roemer, 1844; SD MAILLEUX, 1937] [=?Demanetia Mailleux, 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, X1 (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), X1 (470).

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. goldjussiana; 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 acinal 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., X0.7 (666).—Fig. C28,5b. *M. (M.) goldjussiana, L.Carb.(Visean), Belg.; LV int. showing muscle marks and dental socket, X1 (666).

M. (Orthomyalina) Newell, 1942 [*M. slocomi Sayre, 1930; OD]. Subquadrate, nearly acinal, 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, X1 (666).

Atomodesma von Beyrich, 1864 [*A. exaratum; SD Wanner, 1922, p. 63] [=Maitaia Marwick, 1945, p. 115 (type, Myalina exarata Roemer, 1844; SD MARWICK, 1939)]. Thick-shelled, nearly acinal, with prominent anterior lobe; RV less than LV; not differing in any essential way from Myalina.
1934 (type, M. trechmanni Marwick, 1934, OD); Kolymia Lilharev, 1941 (type, K. inoceramiformis; OD); Intomodesma Porov, 1957 (type, I. costatum; OD). Prosocl ine, 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 layers thin. U.Penn., L.Perm.-U.Perm., Australasia-N.Z.-Greenl. (Waterhouse, 1963).—Fig. C28,3. *A. exaratum*, Timor (fide Dickens, 1956, p. 25); RV ext., X1 (Wanner, 1922).


?Boiomytilus Rožička & 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 occur 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, x1 (818).

**Eurydesma** **Morris, 1845** [*E. cordatum*; OD] [=Leiotymalina Frech, 1891 (type, L. antarctica)]. Acline, heavy, smooth, obliquely ovate 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., x0.7 (Etheridge & Dun, 1910).  

**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 umbal deck; ligament grooves strongly oblique, 6 or 8 intersecting hinge axis. Perm., E.Hemis., widespread. —Fig. C29.2. *L. squamosa* (Sowerby), U.Perm. (Big Blue), USA (Kans.); LV ext., X2 (666).

**Myalinella** **Newell, 1942** [*Myalina meeki** Dunbar, 1924; OD, p. 60]. Thin-shelled, small strongly prosocline, triangular, with obtuse posterior margins; beads 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, x2 (666).

**Pachymytilus** **Zittel, 1881** [*Mysilus petaxus** 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 protruberances. 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. petaxus* (D'Orbigny), U. Oxford., Yonne, France; RV int., x0.7 (1025). [Cox]

**Posidoniella** **deKoning, 1885** [*Inoceramus vetus-tus* Sowerby, 1829; OD]. Ventricose shells of inoeceramid aspect without radial ornamentation, anterior auricle, or umbonal deck; prismatic layer thin. Carb. (Vise.-Namur.), Eu.; Penn. (Pottsville), USA.—Fig. C29.5. *P. vetus-tus* (Sowerby), L. Carb., Eng.; LV ext., x1 (Ramsbottom, 1959).

**Promyalina** **Kittl, 1904** [*P. hindsii*; 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. 3. P. groenlandica (Newell), L.Trias., E.Greenl.; LV int., ext., x2 (Newell, 1955).

**Pseudomyalina** **Dickens, 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. (Cookydia), W. Australia.—Fig. C29.6. *P. obliqua*; LV ext., x0.5 (Dickens, 1956).

**Pseudopachymytilus** **Krumbeek, 1923** [*P. timoren-sis*; 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 fromumbo 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. timoren-sis*; 7a, b, LV ext., int., x1 (486). [Cox]

**Selenimyalina** **Newell, 1942** [*Myalina melini-formis** Meek & Worthen, 1866; OD]. Small, strongly prosocline to acline, smooth, nearly equi­valved, 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 fromumbo 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. Penn. (Desmoines.-Virgil.), USA.—Fig. C30.2. *S. melini-formis* (Meek & Worthen), Desmoines, USA (Ill.); LV int., showing muscle marks, x2 (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. (Viscan.)-L.Perm. (Wolfcamp.), USA-W.Eu.—Fig. C30.1. *S. perattenuata* (Meek & Hayden), U.Penn., USA (Kans.); LV ext., int., x1 (666).

**NONMARINE AND BRACKISH-WATER MYALINIDAE**

[Materials for this section prepared by John Weak]

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Fig. C29. Mayalinidae (marine) (p. N291).
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 homeomorphic with heterochronous European equivalents (A. pseudophilippii, A. philippii), 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. (Anthraconaula), 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 Anthraconaula; their internal characters are unknown, but those with straight hinge line and obliquely subovate outline are here, in certain cases (following Khalfín), assigned to the Myalinae, but with a query. The remainder have not been placed in families by Russian authors, even tentatively.


A. (Kinerkaella) Khalfín, 1950 [*Parallelodon balakhonskienissi Ragozin, 1931; OD]. Like Mrassella 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.) balakhonskienissi (Ragozin); LV ext., X2 (Ragozin, 1955).
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.Perms., USSR (W.Sib.).—Fig. C31,11. *A. (M.) magniforma, U.Carb.; RV ext., X1.5 (Ragozin, 1955).

A. (Procopievskia) RAGOZIN, 1933 [*Anthracoma phillipi 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. Perio-
stracum and prismatic layer thin. *L. Perm., USSR (W.Sib.).—Fig. C31,10. *A. (P.) gigantea Ragozin; RV ext. (outlined restored by Weir), ×1.5 (Ragozín, 1955).

?Curvirima Weir, 1960 [*Anthracoma bellica HIND, 1912; OD]. Like *A. (Anthracoma) 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 Anthracoma casts infrequent and straight). *Carb. (U. Dinant.-Amman.)., W. Eu.; *Carb. (Cumberland.), Can. (N.S.).—Fig. C31,8a.

*C. bellica (Hind), Namur., Belg.; LV ext. (lectotype), ×2 (964a).—Fig. C31,8b. *C. scoticà (Etheridge, Jr.), L.Carb. (Oil Shale Gr.), Scot.; LV ext. (holotype, counterpart), ×2 (Weir, n).

?Dictys Kahlfin, 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).


Naiadites Dawson, 1860 [non Naiadites 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 umb 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, Donetsk).—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).

?Orthoaiadites Kahlfln, 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, orthogyrval 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 & Àurel Larocque]

Mainly small shells, equinvalve, monomyarian, opisthodetic, with beaks at front of hinge; edentulous; character of ligament unknown. (These forms are similar to Ambonychidae in many respects but their affinities will remain uncertain until their morphology is better known.) *L.Ord.-Miss.

Lunulocardium Münster, 1840, p. 69 [*L. semi­striatum; SD Stoliczka, 1870] [=Pinnopis Hall, 1843, p. 244 (type, *P. acutirostrum; SD Larocque & Newell, herein); Chaenocardia Holzapfel, 1889, p. 61 (type, Cardita haliotoidae 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. (Honeyoea) Clark, 1904, p. 225 [*E. erinacea; OD]. Similar to L. (Lunulocardium) 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, LV int., LV ant., post., ×10 (136).

L. (Prososchisma) Beushausen, 1895 [*L. pyiforme Münster, 1840; SD Clarke, 1904, p. 228] [=?Onychocardium Whitfield, 1905, p. 18 (type, *O. portlandicum; M)]. Similar to L. (Lunulocardium) but with smooth or finely costellate surface and short byssal gape. *Dev., Ger.—USA (N.Y.).—Fig. C32,7. *L. (P.) buckeni (Holzapfel), L.Dev., Bicken, Ger.; 7a,b, dorsal and side views; both ×1 (47).

Euchasma Billings, 1865, p. 360 [*E. blumenbachii; 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. blumenbachii, L. Ord., E.Can.; 8a,b, RV ext., both valves ant., ×1 (52).

Maminke 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; in-
equivalve, with radial sulcus on either RV or LV; ornamented with radial costae. Ord. (D1) - Sil. (E1, s), Boh. — Fig. C32, 3. *M. comata, Sil. (E1); 3a, b, RV int. mold, ext., ant., 3c, RV hinge view; all ? X 1 (27).

*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;
surface with strong radial costae; strong sulcus behind umbalonal fold on LV. Sil.(E.)-Dev.(F.,)

*Avicula fragilis* HALL, 1843; SD SHIMER & SHROCK, 1944

=?*Divorceia Růžička, 1949, p. 104 (type, *Avicula contempta BARRANDE, 1881; OD); ?Joachymia Růžička, 1949, p. 102 (type, *Avicula jalacata BARRANDE, 1881; OD).* Similar to *Lunulacardium* but with internal costellae, small anterior auricle, and prosogyre beaks. Sil.(E.), Boh.; M.Dev.-U.Dev., USA(N.Y.); Timan.—Fig. C32.10. *M. complexa, Sil.(E.),

*Dlauha Hora; 10a,b, int. mold RV ext. and dorsal views, X2 (27).

*Pterochaenia* CLARKE, 1904, p. 247 [*Avicula fragilis* HALL, 1843; SD SHIMER & SHROCK, 1944]

=?*Duorecia Růžička, 1949, p. 104 (type, *Avicula contempta BARRANDE, 1881; OD); ?Joachymia Růžička, 1949, p. 102 (type, *Avicula jalacata BARRANDE, 1881; OD).* Similar to *Lunulacardium* but with internal costellae, small anterior auricle, and prosogyre beaks. Sil.(E.), Boh.; M.Dev.-U.Dev., USA(N.Y.); Timan.—Fig. C32.2. *P. fragilis (HALL), U.Dev.(Genese Sh.), USA(N.Y.); ext. both valves, X2 (136).

*Spanila* BARRANDE, 1881, p. 161 [*S. discipulus; SD Růžička & PRANTL, 1960] =*Venusta BARRANDE, 1881 (non BOETTGER, 1877) (vernacular translation of *Spanila* (obj.); ?Pariocardia FISCHER, 1887, p. 1041 (type, *Hemicardium dimidiatum BARRANDE, 1881, SD Růžička & PRANTL, 1960); ?Conocardiopsis BEUSHAUSEN, 1895, p. 378 (type, *Cardium lyelli d'ARCHIAC & de VERNEUL, 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.,a), Boh.; 9a,b, RV lat., both valves ant., X2 (27).

*Stolidotus* Hede, 1915, p. 34 [*S. siluricus; OD*]. Trigonal shells with broad anterior gap; ornamented by fine radial costellae and 3 broad radial furrows that tend to flatten out along margin. Sil., Sweden.—Fig. C32.6. *S. siluricus, Colonius Sh.; LV ext., X3 (Hede, 1915).

*Tenka* BARRANDE, 1881, p. 163 [*T. bohemica; OD*] =*Tenuis BARRANDE, 1881, p. 163 (obj.); *Lep­tnynoconcha FRECH, 1891, p. 249 (nom. van. pro *Tenka*). Similar to *Spanila*, but without carina and with blunt spurious posterior wing. Ord.(D,)-Sil.(E.,) Boh.—Fig. C32.11. *T. bohemica, Sil. (E.,); 11a, RV int. mold; 11b, both valves ant., both approx. X2 (27).

*Tetinka* BARRANDE, 1881, p. 164 [*T. sagitta; SD LeROQUE & 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,)-Sil.(E.,) Boh., ?Sil., Ger.—Fig. C32.4. *T. sagitta, Sil. (E.,) Boh.; 4a, RV ext., 4b, both valves ant., 4c, cross section both valves, cardinal margin to left; all X2 (27).

Family MONOPTERIIDAE Newell, new family

[Materials for this family prepared by N. D. NEWELL]
Family PTERINEIDAE Miller, 1877

[Materials for this family prepared by N. D. Newell and Aurelie LaRocque]

Inequivalve, LV more convex than RV, orbicular to strongly prosocline, pteroid, commonly with small or obsolescent an-
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); Caridens 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 suborbiculo­shells 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., X1 (323).—Fig. C34,8c. P. demissa (Conrad), U.Ord., USA(Ohio); LV ext., X1 (381).

Actinodesma Sandberger, 1850 [*A. malleiforme; M]. Upright pterioid shells with pointed and more or less extended hinge extremities; anterior aductor small or lacking. L. Dev.—U. Dev., Eu.-USA.


A. (Ectenodesma) Hall, 1883 [*A. (E.) bifrostra­tum; SD S. A. Miller, 1889; OD] [=Ar­sellbergia 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.) bifrostra­tum (Hall), U. Dev., N.Y.; LV ext., X1 (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, Leptana Ls., Kullsberg, Sweden; RV ext., X3 (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., X1 (687).

Alnia Terriër & Terriër, 1950 [*A. clari­ondii; M]. M. Ord. (Llandeilo), Morocco.

Anderkenia Kahlfin, 1958, p. 163 [*A. leda­emorpha; OD]. Ord., USSR(Kazakhstan).

Barbossia 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., X2 (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 Psychopterina, s.s. U. Miss., S.C. USA-W. USA.—Fig. C34,3. *C. richardsoni, Caney Sh., Okla.; RV ext., X2 (Girty, 1909).

Cliptopteria Williams, 1912, p. 391 [*C. bicosta­tata; OD]. Nearly equivalent, 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. (Pembrooke), USA(Me.).—Fig. C34,1. *C. bicosta­tata; 1a,b, RV ext., LV int. mold, X1 (984).


Eurymya Ulrich, 1894, p. 512 [*Modiolopsis plana Hall, 1881; 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., X1; 2b; LV hinge, X2 (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. permorcar­bonicus; M); Cyriontarcara Yakovlev, 1903, p. 12 (type, C. bakewellioides; OD); ?Pseudobakewelli­ella 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. ala­t; OD); Peristera Dahmer, 1935, p. 651 (type, P.
unkelensis; OD); Dozierella Newell, 1940, p. 282 (type, Bakewellia gouldii Beebe, 1902; OD); Diodontopteria Laroque, 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.Perms., cosmop. L. (Leptodesma). Anterior auricle angular and

Fig. C35. Pterineidae (p. N300-N302).
nasute. *M.Sil.-Perm., cosmop.*—Fig. C35,9. *L. (L.) potens, U.Dev., USA(N.Y.); LV ext., X1 (377).

L. (Leiopteria) Hall, 1883, p. 4 [*L. dekayi; SD S. A. Miller, 1889]. Anterior auricle lobate. *M.Sil.-L.Perms., cosmop.*—Fig. C35,6. *L. (L.) dekayi (Hall), M.Dev., USA(N.Y.); LV ext., X1 (377).

Limoptera Hall & Whitfield, 1869, p. 15 (see Cooper, 1931) [*L. macroptera Conrad, 1838; OD] [=Myalinodonta Ohlert, 1881, p. 29 (type, *Avicula normanniana* d’Orbigny, 1847; M)]; ?Paropus Ohlert, 1888 (type, *P. orbiculavis*; 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., X1 (377).

Merismopteria Etheridge, 1892, p. 271 [*Pterinea macroptera Morris, 1845; OD]. Externally like *Leptodesma* (Leiopteria) without radial ribs; with very thin, high myopphoric 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, X1 (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,l. *N. ulrichi (Foerste); 1a,b, RV ext., LV ext., X1 (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., X0.7 (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, X6; 2b, LV int. mold, X2 (Whiteaves, 1897).

Pteronitella Billings, 1874, p. 302 [*Avicula retroflexa Hisinger, 1826 (=Mytilites retroflexus Wahlberg, 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 (Wahlberg), Ludlov.; 7a, LV ext. (Wales), X1; 7b, LV hinge (Gotl.), X1 (Walmshy, 1962).

Family KOCHIIDAE Maullieux, 1931
[nom. transl. Newell, herein (ex Kochiidae MAULLIEUX, 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 & HAIMÉ, 1851)] [*Avicula capuliformis Koch, 1881; OD] [=Onychia sandbergeri, 1889 (obj.), DE BLAINVILLE, 1823; oxopteria Frech, 1891 (type, A. 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., X1 (323).

Family PTERIIDAE Gray, 1847 (1820)
[nom. correct. MEER, 1864 (pro Pteridae Gray, 1847); =Aviculidae Goldfuss, 1830 (nom. correct. Gray, 1840, pro Aviculae Goldfuss, 1820)]; name Pteridae retained in accordance with provisions of Article 40a, of Zoöl. Code (1961) [pro Pteridae Broderip, 1839 (Penny Cyclopedia, v. 14, p. 321), employed for gastropods known as "wing-shells" (ailles) such as Rosellaria, Pterocera, Stombus] [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; subequivale 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 ostensibly 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; dymarian in juvenile stages, monomyarian or with anterior adductor much reduced in adult; posterior adductor impression large; pallial line common; shell often 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 COVIER, 1798 (type, M. hirundo); SD KENNARD, SALISBURY & WOOD-MENDELSOHN, 1914]. Anterior auricle lobose. Sil.-Dev., cosmop.; L.Penn., USA(III.); L.Perm., Australia (New S.Wales).—Fig. C35.8. *P. (A.) decussata (HALL), M.Dev.(Hamilton), USA(N.Y.); LV ext., X1 (377).

Ptychopteria HALL, 1883, p. 3 [*P. eugenia (=P. salamanka HALL, 1884) (obj.); SD S. A. MILLER, 1889] [=Actinopterella WILLIAMS, 1908 (type, Pterinea radialis CLARKE, 1907; OD); Cornellites WILLIAMS, 1908 (type, P. fasciculata GOLDFUSS, 1832; OD); Tolmaia WILLIAMS, 1908 (type, P. lineata GOLDFUSS, 1863); Polmannella WILLIAMS, 1908 (type, P. mainensis CLARKE, 1907; OD); ?Diaphragmella ETHERIDGE, 1916 (type, D. merismopteroides; OD); Dipterophora FUCHS, 1920 (type, D. trigula; OD); Oleanella CASTER, 1930 (type, Ptychopteria expansa HALL, 1884; OD); Crassialaria DAHMER, 1931 (type, B. maillieuxi; OD) (pro Ptychopteria expansa FRECH, 1891); Augustaita ROZIČKA, 1949 (type, Avicula expulsa BARRANDE, 1881; OD); Kodymia ROZIČKA, 1949 (type, Avicula dispersa BARRANDE, 1881; OD); Pranitiella ROZIČKA, 1949 (type, Avicula pallista BARRANDE, 1881; OD)]. Strongly proscline with anterior auricle and posterior wing well developed; LV convex, RV less convex, to flattened or concave; umbones to strong on body of RV. Sil.-L.Perm., cosmop.


P. (Actinopteria) HALL, 1884, p. xii [*Avicula decussata HALL, 1843; SD BASSLER, 1915] [=Actinopterella WILLIAMS, 1883 (non RONDANI, 1861)]. Anterior auricle lobose. Sil.-Dev., cosmop.; L.Penn., USA(III.); L.Perm., Australia (New S.Wales).—Fig. C35.8. *P. (A.) decussata (HALL), M.Dev.(Hamilton), USA(N.Y.); LV ext., X1 (377).
Pterioida—Pteriina—Pteriacea

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. N302-N304).
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 lamellae processes in some species. Trias.-Rec., fossil forms cosmop., Rec. in warm seas.—FIG. C38,4. *P. hirundo* (Linneé), Rec., Medit.; 4a-c, RV ext., LV int., RV int., ×0.7 (Deshayes, 1848).

[Glacica and Glacocerda, both of Polz, 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 Polz on p. 222 of his Tectacea utrincipse Sicilae, vol. 2, to belong to Glacica, although it was not one of the two species (both Limidae) listed under the genus on p. 259. Winckworth's action thus seems permissible.]

Arcavicular Cox, 1964, p. 47 [pro Arcaviculara Gugen­ berger, 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 teeth. 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 or less 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) matsutomi]; OD]. Like Pinctada but oblique, subtriangular 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. matsutomi*; RV int., ×0.5 (Tamura, 1961).

Pinctada Röding, 1798, p. 166 [*Mytilus margaritiferus* Linneé, 1758, p. 704; SD Iredale, 1915, p. 305] [=Unionium Link, 1807 (type, Mytilus margaritiferus Linneé; SD Cox herein); Margaritiphora Meegerle von Mühlfeld, 1811 (obj.); Margaritifera Leach, 1814 (type, M. sinensis Leach, =Mytilus margaritiferus Linneé); Margaritifera Schumacher, 1816 (nom. null.); Perlamer Schumacher, 1817 (obj., P. vulgaris; SD Cox herein); Meleagrina Lamarck, 1819 (obj.); Margaritifera Schumacher, 1823 (nom. null.).] Pinctada de Blainville, 1826 (obj.); Pentadina, Pentadina 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 equivelar; posterior wing and indentation of posterior margin lacking or nearly so; ligamental pit broad; no hinge teeth; surface lamelllose. Mio.-Rec., pantrop., espec. Indo-Pac.—FIG. C38,5. *P. margaritifera* (Linneé), Rec., Japan; 5a,b, LV ext., RV int., ×0.4 (Cahn, 1949). [=Margaritifera Browne, 1789 (pressed ICZN).]

Pterinella Toula, 1882, p. 31 [*P. peteri*; M]. Very similar to Pteroperna but subequivelar, 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. C39,4a. *P. peteri*; 6a,b, LV ext., int., ×0.7.—FIG. C39,6c. P. crassitesta Toula; LV ext, ×1 (Toula, 1882).

Pteroperna Morris & Lyckett, 1853, p. 16 [*Gervillia costatula* Eudes-Deslongchamps, 1824, p. 131; OD] [=Pterinoperna Whiffen, 1891 (nom. van.)]. Oblique, binate, with posterior wing sharply pointed; inequivelar, 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 Lyckett, M. Jur.(Bajoc.), Eng.; RV ext., ×1 (Cox, n).

Rhaetavicular Cox, 1962, p. 594 [*Avicula contorta* Portlock, 1843, p. 126; OD]. Small, narrow, lunate, strongly prosocline, highly inequivelar, 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 inconsistent; 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).

*Rhynchopterous 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

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**Fig. C39. Pteriidae (p. N304-N306).**
than high, almost equiivalve; both valves with oblique posterior wings, 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; ia-c, LV ext., RV int., X 1 (Tamura, 1960).

Stefaninia Venzo, 1934, p. 165 [*Gervilleia? ogilvae BITTNER, 1895, p. 88; 5 Cox herein].

Mytiliform, with terminal beak and slightly acuminate hinge margin; type species with ill-defined posterior wing and lobe-like anteroventral pro-tuberance; slightly inequivalve, RV more convex (unusual in Pteriidae); anterior margins with slight byssal gape; cardinal area and position of ligamental area 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. ogilvae (BITTNER), Rhodes; 5a,b, LV ext., RV int., X 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 subaltalate, 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 subarticular notch in RV; ligamental areas flat, external; ligamental pits multiple except in adult Phelopertia, 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 obsceneness 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. Aviculo-perna, represented by several lower Eocene species, was formerly regarded as a sub-genus 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.

Bakevella King, 1848, p. 10 [*Avicula antiqua von MÜNSTER in GOLDFUES, 1836, p. 126 (non DEFRAINE, 1816) (=*Avicula binneyi Brown, 1841, p. 65); OD] (=Bakevella GRIESEL, 1851 (nom. van.)]. Small to medium-sized, trapeziform or rhomboidal, not greatly elongated; anterior auricle small to moderately large, posterior wing oblique or with acutely pointed tip; never strongly inequivalve, anterior gape narrow. Perm.-Cret., cosmop.

B. (Bakevella) [=Goniodus Dunker, 1848 (non AGASSIZ, 1838); ?Plagia PHILIPPI, 1899 (non MEIGEN, 1838); Odontoperne FRECH, 1891, p. 215 (type, *Perna bouei HAUSER, 1857, p. 562; OD); Psodynamavilla GILLET, 1922, p. 106 (type, *Gervilleia episcopalis GILLET; M); Maissuri NAKAZAWA, 1959 (type, *B. (M.) kambeti; 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 dentication variable or partly obsolete in full-grown shell in some species; some earlier species anisomyarian, later ones mostly monomyarian; smooth or with weak radial ribs. [Odontoperne 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.; ia-d, LV ext., RV ext., LV int. showing adductor scars, dorsal view, all X 1 (King, 1850).—[Fig. C40,1e. B. costa (von SCHLOTHEM), M.Trias., Ger.; LV int., X2 (Credner, 1851).


Aquilera Chavan, 1951, p. 211 [*Perna kobyi DE LORIOL, 1901, p. 99; OD] (=Dentoperne OKUNIWA, 1960, p. 57 (type, Perna khudyaevi...
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. Bakevelliiidae (p. N306-N308).**
smooth. Jur.(Toarc.-Oxford.), Eu.-Asia-N. Afr. ——Fig. C40.2. *A. kobyi (de LORIOL), Oxford., Switz.; 2a,b, LV ext., RV int., both \( \times 0.7 \) (de LORIOL, 1901).

Agulinaria 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 \( \times 0.7 \) (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 ribs. [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 \( \times 2 \) (Dehaysy, 1864).

Costigervilia COX & ARKELL, 1948, p. 9 [*Gervillia crassicosta MORRIS & LYCETT, 1853, p. 23; OD]. Medium-sized, oblique, bivalve, 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. C40, 7. *C. crassicosta (Morris & Lycett), M.Jur. (Bathon.), Eng.; 7a-c, LV ext., LV int., RV ext., all \( \times 1 \) (Cox, n).

Cuneigervilia COX, 1954, p. 48 [*Gervillia hagenowii DUNKER, 1846, p. 37; OD]. Rhomboidal or trapeziform, subequivalve, rather falciform, 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. \( \times 1 \) (Dunker, 1846); 6b,c, young shells, LV int., RV int., both \( \times 2.7 \) (Philippi, 1897).

Euptera DARTEVELLE in DARTEVELLE & FRENEX, 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 Pseudopecta. 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, bivalve; 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., \( \times 0.5 \); 5b, RV ext., \( \times 0.5 \); 5c, LV int., \( \times 0.7 \) (Woods, 1905).

Gervillella WAAGEN, 1907, p. 98 [*Perna aviculoides J. Sowerby, 1814, p. 147; SD Cox, 1940, p. 112] [=Gervillella 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., \( \times 0.3 \) (Cox, n).— —Fig. C41.2b. G. sub лицаelata (s'orbigny), L.Cret.(Apt.), Eng.; LV int., \( \times 0.5 \) (Deecke, 1902).

Gervillia DEFRANCE, 1820, p. 502 [*G. solenoidea (sic); SM Defrance, 1824, p. 316] [=Gervilia RANG, 1826 (nom. null.); Gervilla Fleming, 1828 (nom. null.); Gervillia Rominger, 1846 (nom. van.).] Hydrodaetes GISTL, 1848 (obj.); Gervilla PETHÖ, 1906 (nom. null.); Gervillia 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) [=Gervillioptis WHITFIELD, 1885, p. 73 (type, Gervilla ensiformis CONRAD, 1858, p. 328; OD); Dalliconna WHITE, 1887, p. 34 (type, D. insignitaria (=G. ensiformis); OD); Ensigervillia DIELICH, 1910, p. 236 (type, Gervilla silicea QUESNEDT var. hasti; OD).] Narrow, unequal transverse crenulations present among divergent ends of hinge margin, with elongate longitudinal teeth (1 in RV and 2 in LV) at posterior end. L.Jur.-Cret., cosmop.——Fig. C41.4. *G. (G.) solenoidea, U.Cret.(Senon.), Ger.; 4a,b, LV ext., LV int., \( \times 1 \) (415).

G. (Cultriopsis) COSSMANN, 1904, p. 510 [*G. (Cultriopsis) falciformis; M] [=Angustella WAAGEN, 1907, p. 98 (type, Gervilla angusta VON MÜSTER, 1836, p. 122; SD DIENER, 1923, p. 97)]. Differing from Gervilla (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. N308, N310).
——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 [*Mystilites 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 *Septothyroesia* (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 protrudingumbo and prosogyrous beak; RV almost flat; byssal gape wide; ligamental area narrow, with 4 or more well-separated ligamental valves; each valve with 1 or 2 anterior teeth on hinge plate supported by septum-like thickening belowumbo, 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 Gervilleia elongata Portlock, 1843) (=Langsonella mansuyi Cox, 1961; M].* Rather small, elongate, subcylindrical, not oblique, highly inequivalve; LV strongly convex, diagonally cuneate, with broad, scarcely protruding umbonal region and large, indistinctly delimited anterior wing; denticion imperfectly known. *Trias., Tonkin-Malaya.*

**Panis** STEPHENSON, 1952, p. 67 [*P. cunei/armis;* OD]. Moderately large, subcylindrical, 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. cunei/armis*, U.Cret.(Cenoman.), USA (Tex.); 2a,b, RV int., RV ext., both ×0.7 (890).

**Phleopteria** STEPHENSON, 1952, p. 68 [*Pteriopsis dalli STEPHENSON, 1936, p. 389; OD]. Medium-sized *Pteriopsis*-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 multivinicular 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,ld. *P. candigerus* (Zittel), U.Cret., Aus.; RV ext., ×1 (Zittel, 1866).

**Pseudoptera** MEEK, 1873, p. 489 [*Aviculo anomala* J. de C. SOWERBY, 1836, p. 342; OD] (=*Pseudooptera* WHITFIELD, 1880 [nom. van.]). Medium-sized, rhomboidal, oblique, inequivalve; LV with angular, scarcely protrudingumbo, rather large, round-marginined anterior auricle, much extended downward, posterior wing which is obtruse except for acutely pointed tip in some specimens and diagonal angulation orrib; 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, pteriform, 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); 5ab, 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 *Burckhardia*), with or without anterior gape affecting both valves; no subauricular notch; LV strongly convex, with prominentumbo; 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 orna-
The presence of an internal septum is the chief distinction of this group from the Bakevelliidae.

*Cassianella* BEYRICHT, 1862, p. 9 (*Avicula gryphaeata* von Münster, 1836, p. 127; OD) [=*Gryphorrhynchus* 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
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 X 1 (38).

**Burckhardtia** Frech, 1907, p. 334 [*B. boesoi; 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, X1.3 (Frech, 1907).

**Hoernesia** 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, X1.—**Fig. C43,3b. *H. horrida Gugenberger; LV, X1 (both Gugenberger, 1934).

**Lilangina** Diener, 1906, p. 768 [*L. nobilis; SD 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, X0.7 (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., X1 (Cox, n).

**Septihoernesia** Cox, 1964, p. 40 [*Geraillia johannisaustriae Klapstein, 1845, p. 249; OD]. Elongated transversely; radial depression deep, almost
Family PTEROIDIDA COX,
new family

Shell medium-sized, equi-valve 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;
ligamental area triangular, external or subinternal, with single triangular ligamental pit or with no observed pit (Manticlea); 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.), N.Z.-N.Carn.

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, X0.6 (56).—Fig. C44, 2c.d. P. attalea BITTNER, Anatolia; 2c.d, RV, side and ant. views showing byssal gape, X0.7 (Bittner, 1892).—Fig. C44,2e. P. timorensis KRUMBECK, Timor; LV hinge, X3 (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., X1 (487).

Manticlea 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., X0.7 (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 lamelllose; 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 X1 (Cox, n).—Fig. C44,4e. S. quadrata Melville, Gloucs.(Stowell Park borehole); LV int., X1 (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, X2; 1b, wax squeeze, reproducing features of hinge, X4.5 (Healey, 1908).

Family INOCERAMIDAE Giebel, 1852

[nom. transl. STEINMANN, 1903 (ex Inoceramidae Zittel, 1881)] [=Sphenoceramidae HEINZ, 1932] [Materials for this family prepared by L. R. Cox]

Variously shaped, concentrically lamelllose 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); Catillus Nilsson, 1827 (nom. null.)]. Subequal 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) [=Haploscala Conrad, 1874 (type, H. capax, =Inoceramus deformis Meek, 1871; M); Cucullifera Conrad, 1875 (type, Haploscala (Cucullifera) eccentrica; M); Neocatillus Fischer, 1886 (type, Inoceramus lamarcki "Brongniart"; OD); ?Athletoceramus, ?Drepanoceramus, ?Euphyoceramus, ?Idioceramus Heinz, 1932 (all nom. dubia); Abathoceramus, Allosceramus, Asiaticoceramus, Aulacoera m, Callistoceramus, Camptoceramus, Cerato ceramus, Climacoceramus, Coscinoceramus, Cric coceramus, Cycloceramus, Epiceramus, Gnesioceramus, Goniceramus, Heroceramus, Heteroceramus, Homaloceramus, Inaequiceramus, Megaloceramus, Mimos ceramus, Moreoceramus, Orhopoceramus, Orthoceramus, Oxy ceramus, Paraceramus, Platyceramus, Pleiaceramus, Proto ceramus, Schizoceramus, Scolo cerasamus, Smodingoceramus, Striatoceramus, Tethyoceras mus, Xenoceramus Heinz, 1932 (nom. nud.)]. Medium-sized to large, equivalent 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; postero dorsal 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. C46,1ab. *I. (1.) cuvierii; 1a, Senon., Eng., RV, X 0.5; 1b, Turon., Eng., ligamental area of LV, X 0.5 (both Woods, 1912).—Fig. C46,lc. I. (1.) lamarcki Parkinson, Turon., Eng.; LV, X 1 (Woods, 1912).

[The great majority of the generic and specific names published by Heinz in 1932 rank as nomina nudae, 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 (Bastoria) 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 postero dorsal 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.-Senonian.), cosmop.—Fig. C46,2a. *I. (B.) sulcatus Parkinson, L.Cret.(Alb.), Eng.; LV, X1 (Woods, 1911).—Fig. C46,2b. I. (B.) subsulcatus Wiltshire, L.Cret.(Alb.), Eng.; LV, X 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, Dimerocephalus, Haplo ceramus, Selenoceramus Heinz, 1932 (nomina nudae)]. Medium-sized to large, subequal to, ovate, length exceeding height, not oblique or only slightly so; umbones broadly rounded, not prominent; hinge line fairly elongate, but no differentiated postero dorsal wing present; concentric plications strong, regular. U.Cret.(Senon.), cosmop.—Fig. C46,4. *I. (C.) goldfussianus d'Orbigny, (Campan.), Ge.; LV, X 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. N315, N317).
text-fig. 43] [=?Acroceramus, ?Alloceramus, ?Bahmoceras, Cephalceras, ?Discoceras, Gnathoceras, ?Madagicaeramus, Onoco-
eramus, Sphaeroceras, Stenoceras, Stolley-
eramus, Symboloceras, Heinz, 1932 (nom.
uda); ?Enticeramus, ?Manoceramus, ?Rha-
chidoceras, ?Syngeneroceramus, ?Trachyce-
eramus 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 con-
centric angulation where convexity begins to in-
crease; umbones broadly rounded, not prominent;
postero-dorsal wing absent or narrow; orna-
ment of irregular concentric rugae and plica-
tions. U.Cret. (Turon.-Senon.), cosmop.–Fig.
C46,3a,b. *I. (C.) inconstans Woods, Turon.,
Eng.; 3a,b, LV, ×1 (Woods, 1912).–Fig.
C46,3e. I. (C.) inconstans Petraschek, Senon.,
Eng.; LV, ×0.7 (Woods, 1912).
I. (Endococstea) Whitefield, 1877, p. 31 [*E.
typica; OD]. Like I. (Cataceramus), but with
ribble swelling crossing interior of shell diago-
nally 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 remain-
ing in groove forming its mold, ×1 (Newton &
Jenney, 1880).
I. (Haenleinia) J. Böhm, 1907, p. 317 [*I. flexu-
sus Haenlein, 1889; SD Cox, herein] [=Besai-
riea Heinz (1932, nom. nud.), 1933 (type, Haen-
leinia (Besaieriea) besairei Heinz, 1933; M);
Cordiceramus, Cyrtoceras, Germanoceramus
Heinz, 1932 (nom. nud.)]. Medium-sized, sub-
equivalve, gibbose, ovate, without posterior wing;
sinus of posteroventral margin of LV corres-
poding to radial sulcus of flank; ornament as in I.
(Inoceramus). U.Cret. (Senon.), cosmop.–Fig.
Ger., LV, ×0.7 (Böhm, 1909).–Fig. C47,1b.
I. (H.) cortiformis J. de C. Sowerby, L.Senon.,
Eng., LV, ×0.7 (Woods, 1912).
I. (Mytiloideceramus) Rollier, 1914, p. 416 [*I.
polyplocus Roemer, 1857; OD]. Medium-sized,
rounded rhombic, slightly oblique, slightly ine-
equivalve; umbones narrowly rounded, not prominent;
LV with small antero-dorsal wing project-
ing toward RV; ornament of fairly regular
concentric folds. M.Jur. (Aalen.), Eu.-Japan.–
Fig. C47,3. *I. (M.) polyplocus Roemer, Alsace;
RV, ×0.7 (Bencèce, 1905).
I. (Mytiloides) Bronniart, 1822, p. 320 [*Ostra-
citites labiatus von Schlotheim, 1813; M]
[=Mytiloides Bronniart, 1832 (nom. van.)]

Mytiloides Conrad, 1874 (nom. null.); Orphe-
eramus, ?Citharoceramus, ?Aristoceras,
Heinz, 1932 (nom. nud.)]. Medium-sized, ob-
liquely ovate and elongated, subequivalve, of
slight convexity; hinge line short; concentric
placations 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.)
galoii Böhm, U.Jur. (Call.,), Argentina; LV,
×1 (Stehn, 1924).
Anopacea Eichwald, 1861, p. 301 [*Inoceramus
lobatus Auërbach & Frears, 1846 (non Gold-
fuss, 1836) =*I. brachovi Rouillard, 1849; M].
Medium-sized, subequivalve, elongated, rather 
pyriform, with low, lobelike anterior region, com-
monly separated by broad sulcus from rest of
shell; no demarcated posterior wing; inflation
only moderate; umbones narrow, scarcely pro-
truding; beaks prosogyre; cordiform lunule
present; ligamental pits small and numerous; LV
with internal rib below beak; ornament of con-
centrill lamellae and broad plications. U.Jur.,
Eu.-Indon.-N.Z.—Fig. C47,2. *A. brachovi
(Rouillard), U.Volgan, USSR; 2a,b, LV and
dorsal views, ×0.5 (Pavlov, 1905).
Aphania de Koninck, 1877 [*Inoceramus mitchel-
lii M'Coy, 1847; SD Newell, 1942]. Ovate to
subpyriform, prosogyre, subequivalve, RV slightly
less convex than LV; ornament of irregular con-
centric undulations; lunule shallow, broad and
elongate; hinge edentulous, short, without um-
bonal septum; resilifer pits numerous, closely
spaced. Perm., Australia.—Fig. C48,5. *A.
mitchelli (M'Coy), L.Perim. (Glendon F.), New
S.Wales, Australia; 5a, RV, composite mold,
×0.3; 5b, RV, latex cast interior of same, ×0.7
(Brownie and Newell, 1966). [Newell]
Arcticeraus Koschelkina, 1962, p. 41 [*Ino-
eramus arcticus M'Coy, 1847, p. 72; OD]. Of
medium size, inequivalve, LV the more con-
 vex and with more protruding umbo; ornament
of concentric folds; internal characters unknown.
M.Jur.-U.Jur.-U.Volgan, USSR (Sib.).
Inoceramus Ulrich, 1904, p. 134 [*I. concentrica;
M]. Medium-sized, thin-shelled, suborbicular,
compressed, probably ovate; umbones near middle of hinge margin, not protruding; liga-
mental 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 postero-dorsal
region. Yakutat Formation (Mesoz., system un-
certain), Alaska.—Fig. C48,5. *I. concentrica;
5a, RV (reconst.), ×0.7; 5b, post. part of hinge and
internal rib, ×1 (Ulrich, 1904).
Lenella Koschelkina, 1962, p. 31 [*L. tiungensi-
M]. Small to medium-sized, equivale, mytili-
form; posterior wing obtuse, flattened; anterior

2 ANDER.T (1913) and Heinz have restricted Woods' interpre-
tation of I. inconstans, but neither has selected a lecto-
type.
Fig. C47. Inoceramidae (p. N317).
Fig. C48. Inoceramidae (p. N317, N320-N321).
N320 Bivalvia—Pteriomorpha

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 HERING, 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. bulkuriensis; SD Cox, 1954, p. 47]. Small to medium-sized, subovate, of moderate convexity, rectangular or trapeziform, posteriorly subulate; 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. (L. lias.), Eu.-Asia.—Fig. C49,2. P. dubius (J. DE C. SOWERBY), U. lias. (Toarc.), Eng.; RV ext., ×1 (BMNH).

Retrococeramus KOSCHELKINA, 1957, p. 29 [*Inoceramus retroversus KEYSERLING, 1848, p. 250; OD]. Medium-sized, subequivalve, subrhomboidal or obliquely oval; umbones protruding slightly above hinge margin, weakly protracted, 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. ju. (Pliensbach.) - U. ju. (Kimmeridg.), cosmop.—Fig. C49,1a. *R. (R.) retroversus (KEYSERLING), ?U. trias., USSR (Olenek, 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. (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) posidonomaformis; M]. Thin-shelled, suborbicular, very similar to Inocerama, except that internal riblike swelling has not been observed; ligamental pits minute and numerous. (Like Inocerama, this appears to constitute a link between Steinmannia of the Posidoniidae and the Inoceramidae.) Cret., S. Am. (Brazil).—Fig. C48,6. *S. posidonomaformis; LV ext., ×2 (Maury, 1935).

Sphenoceramus J. BÖHM, 1915, p. 183 [*Inoceramus cardissoides GOLDFUS, 1836; SD VIALOV et al., 1960, p. 81] [=Sphenoceramus BÖHM, 1922 (nom. null.); Beloceramus, Cinclidoceramus, Cladoceramus, Dactyloceramus, Dictyoceramus, Eugenoceramus, Euryceramus, Helioceramus, Sterbroceramus, Thoracoceramus, ?Thoracoceramus 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. (L. lias.), 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-robic, 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 argentatus CONRAD is the North American representative of this genus.] U. cret. (Campan.), Rügen (Ger.)-Denmark-N. Am.—Fig. C48,2. *S. tegulatus (Hagenow), Campan., Denn.; 3a,b, LV, RV, ×1 (Odling, 1922).

Steinmannia FISCHER, 1886, p. 960 [*pro Aulacomya STEINMANN, 1881 (non MöRCH, 1853)] [*Posidonnia bronni VOLTZ, in ZIETEN, 1833, p. 72; M].

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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. bronni (VOLTZ); 3a, Eng.(Lincoln), RV, X1 (202); 3b, Fr.(Nancy), ligamental area, X1.4 (352).

*Turkmenia Krimholz, 1936, p. 96 [*T. balkhanensis; M]. Small, trigonally ovate with sharply pointed umbo, posteriorly subulate, longer than high, inequivalve, thought possibly to have grown attached by RV (more convex), to substratum; with narrow ligamental area bearing 4-6 liga-

mental 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 rumphi 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., X0.7 (Woods, 1912).

**Family ISOGNOMONIDAE** Woodring, 1925
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; radial ornament absent (except in *Melitina*); ostracum very thick in most but not all species, inner ostracum nacreous. U.Perm.-Rec.

The *Isognomidae* 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 Bruguère, 1789 (non Retzius, 1788); Pernigenus Renier, 1807 (nom. van.); Sutura Meegerle 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); *Acticulopera Phchelintsev, 1931 (non Cossmann, 1887); Casteria Tucker & Wilson, 1933, p. 3 (type, *Pedalion (Casteria) keci*; OD); *Parviperna Iredale, 1939, p. 322 (type, *P. perplexia*; 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. (1.) *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. C50,2g. I. (1.) *isognomonoides* (Stahl), M.Jur. (Bathon.); 2f, Switz., RV, ×0.7 (Greppin, 1900); 2g, Ger., LV ligamental area, ×0.7 (34hl).

I. (Hippochaeta) Philippi (ex Sangiovanni, MS), 1844, p. 55 [*Perna soldanii Deshayes in Lamarck, 1836, p. 79 (=P. maxillata Lamarck, 1801, p. 134); M] (=*Hippochaeta 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 postero dorsal 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. (Isognomon) Röding, 1798, p. 168 [*I. norma (=*Ostrea isognomon Linné, 1758, p. 699); T] (=*Pedalion Dillwyn (ex Hudsford, vernac.), 1817, p. 282 (type, *Ostrea isognomon Linné, 1764, =O. isognomon 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

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Fig. C50. Isognomonidae (p. N322).
Fig. C51. Isognomonidae (p. N323, N325-N326).
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; *Crenatula* 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.

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**Pterioida—Pteriina—Pteriacea**

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**Fig. C52. Isognomonidae (p. N326).**
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, irregular lamellae and oyster-like. Ligamental area straight; byssus a dense bundle of threads (not calcified as in Anomia). Hypotremata d'Orbigny, 1853, p. 435 [*Pulvinites rugellensis 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. rugellense (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 malleacea Lamarck, 1819 (family name now generally accepted as from this publication in the vernacular); Malacoceracea Brongn., 1824; Malacea Lea, 1833; Vulsellideae Adams & Adams, 1857; Eligmiidae Gill, 1871; Stefaniniellidae TAYLOR, 1939] [Previously Bowdich (1822) and Parkinson (1822) have both used the name Malacacea for groups 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 byssus 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. C52,3. *P. mulleti (DESHAYES), Apt. Eng. (Isle of Wight); LV, ×0.45 (Woods, 1905).

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; 3ab, RV ext., RV int., ×0.7 (951).
Pterioida—Pteriina—Pteriacea

a 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.); Himantopoda ПаE­TEL, 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.-Australia-Medit.

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); Parimalleusiredale, 1931, p. 205 (type, P. curator: OD); Purimalleus Salisbury, 1932 (non. null.); Bressimalleus 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).

Aviculovula 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 lamelllose. M.Eoc.-U.Eoc., Eu. (France).—Fig. C54,I. *A. macrotis (Deshayes), M.Eoc.(Lutet.); 1a,b, RV ext., RV int., ×3 (Deshayes, 1864).

Bouleignimus Basse, 1933, p. 111 [*B. douvilliei; 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 denticate internally; surface irregularly lamelllose. U.Cret., Madag.—Fig. C54,4. *B. douvilliei; 4a,b, RV ext., RV int., ×0.7 (31).

Chalmasia Stoliczka, 1871, p. 397 [*Vulzella turonensis DuJardin, 1837, p. 228; OD] [=Vulselfellopsis Douvillé, 1907, p. 17 (type, Vulzella 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).

Elignimus J. A. Eudes-Deslongchamps, 1856, p. 272 [*E. polytypus; SD Tate, 1868, p. 67] [=Beaumontia J. A. Eudes-Deslongchamps, 1856 (non Edwards & Haim, 1851); Heligmus Fischer, 1886 (nom. van.) (non DuJardin, 1845, nec Candéze, 1865); Proheligmus Cossmann, 1909 (pro Elignimus Eudes-Deslongchamps, 1856, non Elignia 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 lamelllose. 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).

Helignopsis Munier-Chalmas in Fischer, 1886, p. 926 [*Ostrea petrocinensis 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. petrociensis (COQUAND), Coniac., France.; 3a,b, LV ext., LV int., X1 (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. N329-N332).*
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., X0.7 (Peron, 1893).

N. (Exputens) CLARK, 1934 [*E. ilajasensis; 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.) ilajasensis; LV ext., X1 (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, opisthoclinc 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. mor-
gani; M]. Of various shapes, equivale, with posterior
depression in which are long, narrow, sim-
ple or bifurcating marginal fissures; muscle scar
more or less median in position, on elevated plat-
form as in *Eligmus*; surface with small, convex,
quinquincially arranged scales (in type species)
or merely irregularly rugose. *U.Cret.* (Santon.)-M.
Eoc., Iran-Eu. (France).--Fig. C55,5. *P. trig-
oniaformis* (Coquand), *U.Cret.* (Santon.), France;
5a,b, RV ext., RV int., X1 (273).

**Stefaniniella** Tavani, 1939, p. 94 [*S. colossii; M].
More or less inequivalve, tall, linguiform, oyster-
lke; with undulating posterior margin but with­
out posterior gape; ligamental pit large, internal
or subexternal, holl owed-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. co-
lossii; 2a,b, LV direct and post. views. X0.7; 2c,
LV int. showing large ligamental pit, X0.7; 2d,
transv. sec. showing chambering of dorsal region
of shell, X1 (Tavani, 1939 & 1942).

**Vulsella** Röding, 1798, p. 156 [*V. major (=*Mya
vulsella Linné, 1758, p. 671); SD Prasad, 1932,
p. 88, also ICZN Opinion 325 (1955)] [Mya
vulsella Linné was not the type species of Vul-
sella by absolute tautonymy, as Röding recog-
nized 2 nominal species of Vul-
sella (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 Vol-
sella Scopoli, 1777] [=Vulselligenus Renier, 1807
(suppressed ICZN); Reniella Swainson,
1840, p. 386 (type, *R. dilatata; M); Vul-
sella d'Orbigny, 1846 (nom. null.); Baphia "Gevers"
Gray, 1847, p. 199 (obj.); Pulsella Weyenbergh,
1875 (nom. null.); Valsella Martinès, 1880 (nom.
null.); Abisa de Gregorio, 1884, p. 58 (type,
Vulsella nasicida de Gregorio, 1884; SD Cox,
herein); Madrela de Gregorio, 1884, p. 62 (type,
Vulsella virgins de Gregorio, 1884; SD Cox,
herein); Madrela Fuchs, 1887 (nom. null.). Shell
elongated dorsoventrally, linguiform, subequivale,
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 byssi-
ferous; living forms commonly commensal in
sponges. *U.Cret.* (Cenoman.)-Rec., cosmop.—
Fig. C56,1a,b. *V. deperditia LAMARCK, M.Eoc.,
France; 1a,b, LV ext., LV int., X1 (Deshayes,
1832).—Fig. C56,1c,d. *V. vulsellina (Linné),
Rec., Ind.O.; 1c,d, LV ext., LV int., X0.7 (Cox,
R.).

**Vulsellina** Raincourt, 1876, p. 290 [*V. chaussyen-
sis; M] [=Vulsinella Dalton, 1876 (nom.
null.)]. Small, subrectangular, flattened; ligamental
pit narrow; muscle impression situated very close
to ligamental area, and with another small im-
pression below it on adult shells; surface un-
ornamented except for growth ruge.

**Superfamily PECTINACEA** Rasinesque, 1815

[nom. transl. et correct. Dall, 1896 (ex subfamily Pectenia
Rafinesque, 1815)] [Pectenidae Fleming, 1822; Pectenaceae
Reeve, 1841] [Superfamily diagnosis prepared by N. D.
Newell] [Materials on this superfamily prepared by L. G.
Herklehn, L. R. Cox, and N. D. Newell]

Adult shells generally orbicular, mono-
varian, subequilateral, with winglike ex-
tensions of hinge margin (auricles); pleuro-
thetic, 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 pos-
terior auricle longer and less well differ-
entiatied; cardinal areas divergent upward,
(Leonard.).

**Pterinopecten** Hall, 1883 [*P. undosus; SD S. A.
Miller, 1889, p. 507]. Orbicular or subhomb-
oideal shells with intercalating costae; rear auricle
poorly differentiated; byssal notch of RV narrow,

**Pterinopecten** (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., X1 (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., X1 (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., X1 (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. N332-N334).
Hinge margin longer than shell height; body of shell sculptured by concentric fila; costellae obsolete 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* 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 Altai, Karaganda Basin); L.Dev., USA (N.Y.)—Fig. C57,1. *L. rectangularis*, L.Dev., Sib. (Pribalkhash), ×2.7 (Krasilova, 1963).

**Palaecten** WILLIAMS, 1913 [*P. cobscooki*; OD] [=?Leiopectinella Krasilova, 1959 (type, Aviculopecten 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 [*Aviculo mira* BARRANDE, 1881; OD]. Rhomboidal, nearly equivaleve 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).
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 Pinetada; 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. N336-N337).
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, X2.—Fig. C60,3c. A. occidentalis (Shumard), U. Penn., Kans.; RV ext., X2 (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.
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.-UPerm., cosmop.—Fig. C60.5. *A. interlineata (Meek & Worthen), U.Penn., USA (Ill.); LV ext., ×2 (663).

Asella 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, procholine; 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).


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. kittii* (Bittner), L. Trias., Dalmat.; 6a,b, LV ext., RV ext., both ×1 (60). [Cox]

Fasciculiconcha Newell, 1938, p. 64 [*F. knighti; OD]. Upright, equilateral shells with subequal
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., X2 (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., X2 (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., X1 (Chen, 1962).

**Leptochondria** BITTNER, 1891, p. 101 [*Pecten (L.) aelicus; M] [=?Bittnerella J. BOHM, 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. triolina (BITTNER), U. Trias., S.Tyrol; 1a,b, LV ext., RV ext., both \( \times 3 \) (58).—Fig. C94,1. *L. aulica (BITTNER), Asia M.; 1a-c, LV ext., RV ext., hinge, \( \times 1 \) (36). [Cox, HERTLEIN]


*Limpepecten* Cox, 1962, p. 596 [*Aviculopecten bosniae BITTNER, 1903, p. 592; OD*]. Small, suborbicular, acine to slightly prosocline; leftumbo 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., \( \times 1 \).—Fig. C61,3b. O. beneckeii (BITTNER), U. Trias.(Carn.), S.Tyrol; LV ext., \( \times 1.6 \) (38). [Cox]

*Ooturia* 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, \( \times 1 \) (Cox, n). [Cox]

*Oxyperia* 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., \( \times 2 \) (950). [Cox]

Subfamily STREBLOCHONDRIINAE Newell, 1938

[Upright to opisthocline, nearly equivalent 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.*]

**Strebrochondria** 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, \( \times 1 \) (663).

**Eocamponecetes** Newell, new genus [*Camponecetes? papillatus GITRY, 1908, p. 434; OD herein*]. Opisthocline, ornamented with radial curved costellae or rows of papilae arranged in quincunx. *L. Perm.-U. Perm., USA(Tex.-Wyo.).—Fig. C63,3. *E. papillatus* (GITRY), U.Perm.(Capitan F.), Tex.; RV ext., \( \times 4 \) (663).

**Pleuronecetes** 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, nearly 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 \( \times 0.7 \) (732). [Cox]

**Strebropteria** M'Coy, 1851; p. 170 [*Meleagrina laeavigata* M'Coy, 1844; SD MEEK & WORTHEN, 1866, p. 333] [=Kutotia de Koninck, 1885 (type, Pecten hermanni) PHILLIPS, 1836; SD NEWELL, herein]. 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 peripherically between costae as short spines. *U. Miss.-L.Perm.(Wolfsamp.), Eu.-N.Am.—Fig. C61,1. *L. textanus, U.Penn., Tex.; 7a,b, LV ext., ant., \( \times 1 \) (663).

**Pterioida—Pteriina—Pectinacea** N339

Subfamily CHAENOCARDINAE S. A. Miller, 1889

[*nom. transl. NEWELL, herein (ex CHAENOCARDINAE MILLER, 1889, p. 458)*]

Ovoid, prosocline to opisthocline shells with obtuse postero-dorsal 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. *Miss.-L. Perm.*
**Obliquipecten** Hind, 1903, p. 114 [*O. laevis; M*]. Markedly opisthodine, 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 posterdorsal border. L.Miss.-L.Per., N.Am.-Eu.-Fig. C64,1. *O. laevis, L.Carb., Eng.; la,b, RV ext., LV ext., X1 (663).

**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., X5.—Fig. C65.1b. E. subcancellata (Newell), M.Penn.(Desmoines.), Mo.; RV hinge, X12 (663).

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 arcoïd genera (e.g., Striarca, Noetia). *LPerm.

Deltopecten Etheridge, Jr., 1892, p. 269 [*Pecten illawarrensis 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., X0.45; 1b, ligament area, X2.7 (Newell, n).

Family PSEUDOMONOTIDAE Newell, 1938


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. Posidonidae (p. N342-N344).

**Family POSIDONIIDAE** Frech, 1909

[**nom. transl.** Cox & Newell, herein (ex Posidoniidae 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, sub-equivalve, 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.
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., X1 (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; 1ab, LV ext., RV ext., X1 (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., X1 (Furlani, 1910).

**Bositra** DE GREGORIO, 1886, p. 11 [*Posidonia ornata* 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).
Bivalvia—Pteriomorphia

Daonella Mojsisovics, 1874, p. 5 [*Halobia lom-meli 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 (Wiss-man), 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 sub-truncate, 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.).—Fig. C68.3. *D. variabilis, L.Coniac., Colom.; RV ext., ×0.7 (Gerhardt, 1897).

Diotis Simonelli, 1884, p. 125 [*Posidonotomya 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; 2×, 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.(Norn.), 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 situated longitudinally, but rarely observable. M.Trias.(chiefly)—U.Trias., cosmop.—Fig. C68.6. *H. dilataata Kittl, U.Trias. (Nor.), Aus.; LV ext., ×0.7 (Kittl, 1912).

Posidonotis Losacco, 1942, p. 11 [*P. daieielli; 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. dainelli; 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).

Veldidennella Alma, 1926, p. 118 [*V. dieneri; M]. Very elongate, narrow anteriorly, broad posteriorly; umbo protruding slightly, anteriorly placed, prosocline; ornament of closely spaced radial riblets, not arranged in bunches. U.Trias., Eu.(Aus.).

Family OXYTOMIDAE Ichikawa, 1958

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 [*Aviculo muenserti Bronn, 1830, p. 164 (=Aviculo inequivalvis J. Sowerby, 1819, p. 78); OD]. Suborbicular and acine 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.Cret.—U.Cret., cosmop.
(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.; la, LV ext., X2 (Cox, n); lb, RV int., X2.7 (34lb).

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; subauricular notch less deep than in O. (Oxytoma). L.Cret.-U.Cret., cosmop.—Fig. C69,2a. O. (H.) tenuicostata (Roemer), U.Cret., Ger.; LV ext., X2.3 (Voigt, 1954).—Fig. C69,2b-e. *O. (H.) danica (Ravn), U.Cret., Ger.; 2b, RV ext., X5 (Voigt, 1954); 2c, RV int., X6.7 (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. Lias.-M. Lias.), N.Eu.—Fig. C69,4. *O. (P.) cygnipes (Young & Bird), M.Lias., Eng. (4a); France (4b); 4a, LV ext., X1 (Cox, n); 4b, RV ext., X0.67 (Dumontier, 1869).

Arctotis Bodlevsky, 1960, p. 44 [*Hinnites lenensis 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.)

**C.** (Valang.) USSR(Sib.).—Fig. C69,3a-c.

* C. * a. * lenaensis* (Lahusen), M.Jur.; 3a. LV ext., ×0.5 (Lahusen, 1886); 3b-c, RV int., ext., both ×1.1 (Borisisk, 1915).—Fig. C69,3d. A. * intermedia* Bodyslevskiy, U.Jur.(L.Volg.); RV ext., ×2 (Bodyslevskiy, 1960).

t *Avicularca* von Burnoff, 1921, p. 281 [*Avicula cardiformis* von Münster, 1841, p. 78; SD Cox, herein]. Small, ovate, more or less elongate, equi-

valve, moderately convex, prosocline; umbones broadly rounded, protruding slightly; posterior wing long, acute, but tipped, with only shallow marginal sinus; left anterior wing small, acute; right anterior auricle unknown; rather broad, sub-

horizontal 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. cardiformis* (von Münster), U.Trias., St.Tyroli; 1a,b, LV ext., dorsal, ×5 (58).

**Cytorostra** Branson, 1930, p. 44 [*C. varicostata*; OD] [=Blanfordina Reed, 1944, p. 312 (type, B. luswalensis)]; Prooxytoma Maslennikov, 1955 (type, Oxyma caucasica Likharev, 1947)]. Sub-

orbicular, acrline to opisthoclinc, 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 Oxyma. 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 (122). [Newell]

**Maccoyella** Etheridge, Jr., 1892, p. 451 [*Avicula barkliyi* Moore, 1870, p. 245; OD; Etolium existing by Quenstedt, 1858 (=Pecten disciforme Schubler 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.-L.Cret., Russia.

—Fig. C70,4. *M. barkliyi* (Moore), L.Cret., Australia; 4a,b, LV ext., RV ext., both ×0.7 (Etheridge, 1902).

**Meleagrinella** Whitefield, 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 protruberance anterior to it in LV, which has narrow, commonly square radial riblets; RV smooth or with weak radial riblets. U.Trias.(Rhau.)—U.Jur., cosmop.—Fig. C70,2. *M. echinata* (Smith), M.Jur., Eng.; 2a,b, LV ext., RV int., ×2 (Cox, n).

**Pseudavicula** Huldsch, 1890, p. 214 (ex Etheridge, Jr., MS) [*Lucina anomala* Moore, 1870, p. 251; M]. Medium-sized, suborbicular or oval, acrline, 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, sub-

auricular 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 Schubler 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.); Protamusium Paris & Richardson, 1915 (nom. null.); Prosamusium Stewart, 1930 (nom. null.); Entolium McLearne, 1949 (nom. null.); E. Meek, 1865]
null.)]. Auricles of LV projecting above hinge, commonly as angular wings;* smooth (19b, 19c, 19i, 732c). M.Trias.-U.Cret., cosmop.—Fig. C71.f. *E. (E.) demissum (PHILLIPS), M.Jur.

(E. Cteniopleurium) FELDTMANN, 1951 [*Syncyclonema subreticulatum 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 [*Avericuloppecten 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 YANISHESKY, 1960 (type, Pecten sowerbyi M'Coy, 1844; OD)].

iSomapecten 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] [=Syncyclonema MEEK, 1864 (see below); Sincyclonema CONRAD, 1869 (nom. null.); Syndonema DALTON, 1878 (nom. null.); Syncyclonema CLessis, 1878 (nom. null.); Syncloclonema FISCHER, 1886 (nom. null.); Syncyclonema DE GREGORIO, 1886 (nom. null.); Syncyclonema DE GREGORIO, 1898 (nom. null.)]. Differs from Entolium in that valves are sculptured with round 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, RV ext., ×8 (379). [HERTLEIN]

[Syncyclonema is rejected as an incorrect original spelling (Code, Art. 32a).]

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

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 umboines; 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 Pseudotollium (=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 Amusipecten 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 (Amusipecten) 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.

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 [*Pincta hochstetteri Zittel, 1864; OD]. Differing from EntoIium 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 carneus 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.e. L. (L.) cornus (Sowerby), Eoc., Eng.; 3b,e, 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 pleuronecetes Linneé, 1758; SD Herrmannsen, 1846] [=Amusium Gray, 1826 (nom. null.); Pleuronecetes Bronn, 1831 (non Linneé, 1758); Pleuronecetia Swainson, 1840 (type, P. laevigata Swainson,

Fig. C72. Pectinidae (Lentipecten Group) (p. N349).
N350 Bivalvia-Pteriomorphia


1840, Ostrea pleuroneetes Linné, 1758; Pleuronoepecten Tucker-Rowland, 1938 (pro Pleuronecta); Amusium Herrmansen, 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. pleuroneetes* (Linné), Rec., IndoPac.; 1a, RV ext., X1; 1b, RV int., X1 (7c).

Korobkova 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 *Lenticpecten* 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./ur.-Rec., cosmop.

P. (Propeamussium) de Gregorio, 1884 [*Pecten (P.) ceciliae*; OD]. Propeamussium Jackson, 1890 (nom. null.); Paramusium Verrill, 1897 (type, *Amusium dalli* E. A. Smith, 1885); Paramusium de Gregorio, 1898 (nom. null.); Propeamussium Cossmann & Pisarro, 1906 (nom. null.); Occultamusium Korobkov, 1937 (type, *Pecen semiradiatus* Meyer, 1861); Pseudopallium Oyama, 1944 (type, *Pecten interradiatus* Gabb, 1869); Flavamusium Oyama, 1951 (type, *Amusium caducum* E. A. Smith, 1885); Luteamusium Oyama, 1951 (type, *Amusium sibogai* Dautzenberg & Bavay, 1904); ?Actinopepten Bonarelli, 1951 (type, *A. rapidopsis* 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./ur.-Rec., cosmop.—Fig. C73,3a. *P. (P.) ceciliae* (de Gregorio), Mio., Sicily; RV ext., (type) imperfect, auricles lacking), X1 (de Gregorio, 1898).—Fig. C73,3b. *P. (P.) anconitanum* (Foresti), L.Mio., Italy; RV ext., X1.5 (256e).

P. (Parvamussium) Sacco, 1897 [*Parvamusium duodeclamellatum* Bronn, 1831; OD] [*Variamusium Sacco, 1897 (type, *Amusium cancellatum* E. A. Smith, 1885); Parsiammusium Dall, 1898 (nom. null.); Variopepten Sacco, Broili in Zittel, 1924 (nom. null.); Ctenamusium Iredale, 1929 (type, *Amusium thetidis* Hedley, 1902); Glyptamusium Iredale, 1939 (type, *Amusium torrei* E. A. Smith, 1885); Graptamusium Oyama, 1944 (type, *P. torrei*).
E. A. SMITH, \textit{Amussium torresi} E. A. SMITH, 1885); \textit{Squamamussium} OYAMA, 1944 (type, \textit{Amussium squamigerum} E. A. SMITH, 1885); \textit{Xenamussium} OYAMA, 1944 (type, \textit{Pecten hokynski} FORBES, 1844); \textit{Bathyamussium} OYAMA, 1951 (type, \textit{Amussium jeffreysi} E. A. SMITH, 1885); \textit{Micramussium} OYAMA, 1951 (type, \textit{Ctenamusium siratama} OYAMA, 1951) \textit{Polynemamus­ius} HABE, 1951 (type, \textit{Pecten intuscostatus} YOKOYAMA, 1920). Differs from \textit{P. (Propeamus­ius)} 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 \textit{Cytelpecten} in possessing internal ribs (82a,b). V.Cret.-Rec., cosmop. ——Fig. C73,2a,b. \textit{P. (P.) duodecimlamellatum} (BRONN), Mio., Italy; 2a, RV ext., \(\times 4\); 2b, RV int., \(\times 4\) (Depéret & Roman, 1928). ——Fig. C73,2c. \textit{P. (P.) felsinum} (FORESTI), Plio., Italy; LV ext., \(\times 4\) (256c).

**CAMPTONECTES GROUP**

Left valve more convex than right; smooth, or with strong \textit{Camptonectes} (divaricate striae) sculpture; large byssal notch present. ?Trias., \textit{L.Jur.-U.Cret}.

\textit{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, 19t). \textit{L.Jur.-U.Cret.}, cosmop.

\textit{C. (Camptonectes)} [\textit{Campstonectes} von TEP­
N352 Bivalvia—Pteriomorpha


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FIG. C74.1. *C. (C.) lens* (J. Sowerby), U. Jur., Eng.; 1a, LV ext., ×1 (Sowerby, 1818); 1b, RV ext., ×1 (19b).

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. (Campotonectes) in that weak radial ribs 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 ribs; ctenolium present in some shells. Relationships not fully known. U. Cret.—Rec.

Eburnepecten Conrad, 1865 [*Pecten scintillatus*; OD]. Valves not gaping, nearly smooth except for minute radial striae, some forms (Micronectes) with Campotonectes 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. (Eburnepecten) [=Eburnepecten De Gregorio, 1898 (nom. null.); Eburnepecten Tucker-Rowland, 1838 (nom. null.)]. Smooth except for fine lines of growth and microscopic diverging 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).


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) [=Cyclopecten 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., X2 (936).—Fig. C75, 2c. C. (C.) simplex Verrill, Rec., W. Indies; RV int., X8 (936).

C. (Chlamydella) Iredale, 1929 [*C. javus Hed-
ley, 1902; OD]. Differs from C. (Cyclopecten) in elongated (anteroposterior) form and in that RV is sculptured with fine radial ridges formed 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 sigsbei DALL, 1886); OD]. Auricles unequal and oblique; surface of valves smooth except for growth lines (936). Rec., Carib.—Fig. C75,3. *C. (P.) sigsbei (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 (7ε).

Palliolium 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. (Palliolium) [=Pseudamusium auct. (non Pseudamusium Möhrch, 1853); Pseudamusium Gemellaro, 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.) incomparable (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 (Chenmitz, 1795).

P. (Deletopecten) Stewart, 1930 [*Pecten (Pseudamusium) vancouerenis Whiteaves, 1893; OD] (=Deletopecten Salisbury, 1930 (nom. null.); Similarpecten Winckworth, 1932 (type, Pecten similis Laskey, 1811); Arcticula Thiele, 1934 (type, Pecten groenlandicum Sowerby); Arcticula 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.) vancouerenis (Whiteaves), Rec., Vancouver I., Can.(B.C.); 4a-b, LV ext., RV ext., ×5 (Dall, 1921).

Fig. C77. Pectinidae (Antijanira Group) (p. N355).

P. (Hyalopecten) Verrill, 1897 [*H. undatus Verrill, 1885 (=Pecten undatus Verrill, 1885) (=H. dillectus Verrill & Bush, 1897); OD] [=Hyalopecten 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. (Lissoclamlis) Sacco, 1897 [*Pecten excisus BRONN, 1831; OD] (=Pyxis Foresti, 1877 (non Chemnitzz, 1784, non Bell, 1827); Lissoclamlis Sacco, 1897 (?emend.); Pixis Ugolini, 1906 (error pro Pyxis Meneghini in de Stefani, 1878); Pyxio von Teppner, 1922 (error pro Pyxis "Meneghini"). LV convex, RV nearly flat; anterior auricle longer than posterior, both with strong radial ridges which are variable in size along anterior and posterior portions or nearly all over valves (821a,b). U.Mio.-L.Plio., Italy.—Fig. C76,6. *P. (L.) excisum (BRONN), L.Plio., 6a-b, LV ext., RV ext., ×0.7 (821a).

P. (Parvochlamys) Sacco, 1904 [*Parvochlamys olaevis; OD]. Somewhat ovoid in shape, sculptured only with radiating ridges on upper lateral areas; right anterior auricle short. [Relationship not well known (821a,b).] M.Mio. (Helvet'), Italy.—Fig. C76,1. *P. (P.) olaevis (Sacco); 1a, LV ext., ×4; 1b, RV ext., ×3 (Sacco, 1904).

Pseudamusium Möhrch, 1853 [*Pecten pseudamusium Chemnitzz, 1784 (=Pecten septemradiatus Müller, 1776); ICZN] (=Pseudamusium Klein,
Pterioida—Pteriina—Pectinacea

N355

1753 (pre-Linnean); *Peplum Bucquoy, Dautzenberg & Dollfus, 1889* (type, *Ostrea clavata* Poli, 1795); *Platipecten Montessorato, 1889* (type, *Pecten subclavatus* Cantraine, 1835). Small, RV more convex than LV, hinge lines short, auricles unequal; entire valve sculptured with radial ribs of variable strength and whole folded into several broad radial corrugations (802, 892). *M.Mio., Iran; U.Mio.—Rec.*  

**ANTIJANIRA GROUP**

Approximately every third or fourth rib larger than others, sculpture of radial ribs and concentric imbrications; reticulate as in *Pectinula. U.Trias.—LJur.*

**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 *Nieithaea*); lanciform area mostly in front of beaks. *U.Trias., Eu.(Hung.).*—Fig. C77,2. *A. hungarica* (Bittner). LV ext., RV 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* Möller, 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.); Chlamys 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 akinos* Petter, 1886); Mimachlamys Iredale, 1929 (type, *Pecten asperimus* Lamarck, 1819); Scaechlamys Iredale, 1929 (type, *Pecten lividus* Lamarck, 1819); Talochlamys Iredale, 1929 (type, *Chlamys famigerata* Iredale, 1925); Veprichlamys Iredale, 1929 (type, *Chlamys perullaris* Iredale, 1925); Coralichlamys Iredale, 1939 (type, *C. acroporcola*). 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 ribs; 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. (Acqueipecten) Fischer, 1886 [*Ostrea opercularis* Linné, 1758; M] [=Amoeoba 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 ribs 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. (Anatippecten) Hektlein, 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. (Anachlamys) Iredale, 1939 [*Pecten leoparulus* 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.) kuhnholzii* (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, 1815)]

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Fig. C78. Pectinidae (Chlamys Group) (p. N355-N357).
C. (Equichlamys) IREDALE, 1929 [*Pecten bifrons LAMARCK, 1819; OD]. More convex than RV, auricles nearly equal, byssal notch small, ctenoidal ridges 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. (Lepipecten) VERRILL, 1897 [*Pecten monomorthis 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.) monomorthis (CONRAD); Rec., Calif.; 2a,b, LV ext., RV ext., ×1.5 (Oldroyd, 1924).

C. (Lyropecten) CONRAD, 1862 [*Pallium estrellanum CONRAD, 1856; SD DALL, 1898] [=Liropecten CONRAD, 1863 (nom. null.)]; Liropecten GABB, 1869 (nom. null.)]. Large, thick, nearly oblique, shelf 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.AtI. — 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.); Gigantopsis 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. N357).
C. (Manupecten) Monterosato, 1889 [*Ostrea pes-felis Linné, 1758; SD Sacco, 1897] [=Fellipes 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.) pes-felis (Linné), Rec.; 2a,b, LV ext., LV int., X0.5 (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. N357).
(593). \textit{U.Cret.}, N.Z.—Fig. C82,3. *C. (M.) amuriensis* (Woods), Pirapauan; 3a,b, LV ext., RV ext., $\times 1.5$ (Woods, 1917).

\textbf{C. (Miyagipecten)}\footnote{Masuda, 1952} [*\textit{M. matsumoriensis}; OD]. Differs from \textit{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. \textit{M.Mio.}, Japan.—Fig. C82,4. *C. (M.) matsumoriensis* (Masuda); 4a, LV ext., $\times 0.5$ (53); 4b, RV ext., $\times 0.5$ (Masuda, 1952).

\textbf{C. (Nanaochlamys)} Hatai & Masuda, 1953 [*\textit{Pecten notoensis} Yokoyama, 1929; OD]. Differs from \textit{C. (Swiftopecten)} in having more numerous, bifid ribs, shorter anterior ear, and more rounded outline. \textit{M.Oligo.-Mio.}, Japan.—Fig. C82,1. *C. (N.) notoensis* (Yokoyama); 1a,b, RV ext., LV ext., $\times 0.8$ (Hatai & Masuda, 1953).

\textbf{C. (Nodipecten)} Dall, 1898 [*\textit{Ostrea nodosa} Linné, 1758; OD] [*\textit{Nodopecten Olsson, 1914 (nom. null.); Neodipecten von Teppner, 1922 (nom. null.)}. Differs from \textit{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). \textit{M. Mio.-Rec.}, E.Atl.-W.Atl.; \textit{Plio.-Rec.}, W.N.Am.—Fig. 41,1. *C. (N.) nodosa* (Linné), Rec., W.Atl.(off Fla.); 1a, LV, $\times 0.45$; 1b, RV, $\times 0.45$ (Chenu, 1844).

\textbf{C. (Pacipecten)} Olsson, 1961 [*\textit{Pecten tumbezensis} d'Orbigny, 1846; OD]. Differs from \textit{C. (Leptopecten)} in its more equilateral form, presence of auricular crura, and thicker shell. \textit{U.Mio.-Rec.}, E.Pac.—Fig. C82,6. *C. (P.) tumbezensis* (d'Orbigny), Rec., off Peru; 6a,b, LV ext., RV ext., $\times 1$ (688).

\textbf{C. (Pethoepecten)} Hertlein, 1936 [*\textit{Pecten (Chlamys) szeremensis} 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. \textit{Cret. (Cenoman.-Senon.)}, Eu. (Hung.).—Fig. C82,5. *C. (P.) szeremensis* (Pethö), U.Senon.; 5a,b, RV ext., LV ext., $\times 0.7$ (Pethö, 1906).

\textbf{C. (Phialopecten)} Marwick, 1928 [*\textit{Pecten tripodii} Zittel, 1864; OD]. Differs from \textit{C. (Sectipecten)} in its flatter RV and more numerous, narrower ribs which form radial ridges rather than folds of shell (593). \textit{L.Plio.-M.Plio.}, N.Z.—Fig. C82,7. *C. (P.) tripodii* (Zittel), L.Plio.; 7a, LV ext., $\times 0.5$ (Marwick, 1948); 7b, RV ext., $\times 0.5$ (Zittel, 1864).

\textbf{C. (Placopecten)} Verrill, 1897 [*\textit{Pecten clintonius} Say, 1824; OD] [*\textit{=?Nipponopecten Masuda, 1962 (type, \textit{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). \textit{L.Mio.-Rec.}, E.N.Am.; \textit{Mio.-?Japan}.—Fig. C83,4. *C. (P.) clintonia*
Pterioida—Pteriina—Pectinacea

(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. N359-N360).
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.

*C. (R.) weeksi (Stephenson), Maastricht, USA (Tenn.); 3a,b, LV ext., RV ext., X0.7 (951).

C. (Radulopecten) Rollier, 1911 [*Pecten hemi-costatus Morris & Lycey, 1853; OD]. LV flatter than RV, which bears 5 pairs of twinned ribs,
LV with 5 squamose ribs corresponding to sulci of opposite valve (193). *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 Anatipecten 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. (Swiftpecten) HERTLEIN, 1936 [*Pecten swiftii BERNARDI, 1858; OD]. Higher than long, nearly equivalent, auricles nearly equal and with well-developed byssal notch and ctenolium in
N364 Bivalvia-Pteriomorphia

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., x0.5 (Bernardi, 1858).

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., x0.4 (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 Deprance, 1821 [*H. corteysii (=Ostrea crispa Brocchi, 1814); SD Gray, 1847] [=Hinnita FéruSSac, 1822 (obj.); Hinus 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., x0.5; 3b, LV int. and RV hinge, x0.3 (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., x1.5; 1b, RV int., x1.5 (7c).

Prohinnites Gillet, 1922 [*Hinnites leymieri 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. leymieri (Deshayes), Neo-com., France; 2a,b, LV ext., RV hinge, x1 (124b).

Spondylopecten Roeder, 1882 [*Pecten (S.) cf. erinaceus Buvignier, Roeder, 1822 (=Pecten (Chlamys) roederi de Loria, 1901); M] [=Pleiopecten Munier-Chalmas in Fischer, 1886 (type, Pecten subspinosus von Schlotheim, 1820); Cardinopecten Rollier, 1904 (type, Pecten erinaceus Buvignier, 1852; SD Hertlein, herein)]. Sculp-

Fig. C86. Pectinidae (Hinnites Group) (p. N364-N365).
tured 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).

**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 Decatopecten (an invalid subsequent spelling) attributed to Rüppel (1839), citing as the sole included species “D. plicula Sow. Man. t. 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. C87. *S. (M.) triggi (Cotton & Godfrey), Rec.; RV int., ×1.5 (Dall, Bartsch, & Rehder, 1938).


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., Indo Pac.-N. Australia.——Fig. C88.1. *S. (E.) spectabiles (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); Dendopedecten Hertlein, 1936 (type, Pecten dendyi Hutton, 1902)]. Suborbicular; ctenolium present in young, obsolete in adult; sculptured with 5 compound ribs. Mio.-Rec., Australia.——Fig. C88.3a,b. *S. (M.) caroli (Iredale), Rec.; 3ab, LV ext., RV ext., ×0.7 (437).——Fig. C88.3c. S. (M.) thaanumi (Iredale), Rec.; RV int., ×0.7 (169).

S. (Mirapecten) Dall, Bartsch & Rehder, 1938 [*M. thaunumi; 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.) thaunumi (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.); Pectinities von Schlotheim, 1820 (non Gesner, 1758; nec Gmelin, 1793); Pecten 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-Linnæan); Argus Poli, 1791 (non Bohadsch, 1761; nec Scopoli, 1777); Argorodera 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 Lamark, 1799); Janira Schumacher, 1817 (non Leach, 1814); Janera Gray, 1847 (nom. null.); Vola Mörch, 1853 (non Mulsant, 1850); Argodesma Paetel, 1875

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Pterioida—Pteriina—Pectinacea

Pecten

Amussiopecten

Euvola

Fig. C89. Pectinidae (Pecten Group—Pecten (Pecten) Subgroup) (p. N366-N368).

P. (Amussiopecten) SACCO, 1897 [*Pecten burdigalensis LAMARCK, 1809; OD] [=Amussiopecten OPPENHEIM, 1903 (nom. null.); Amussiopecten FOLDVÁRI, 1929 (nom. null.)]. Differs from Flabellipecten in its nearly obsolescent radial ribs with correspondingly stronger internal radial ribs 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., X0.5 (256d); 3c, RV int., X0.5 (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.,


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Fig. C91. Pectinidae (Pecten Group—Pecten (Patinopecten) Subgroup) (p. N371).

Carib.; 2a,b, LV ext., RV ext., X0.4 (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., X0.6; 1b, LV ext., X0.5 (Goldfuss, 1835).

P. (Oppenheimiopecten) 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. N370-N371).
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., X1; 2b, RV ext., X0.8 (256a).

**Pecten (Patinopecten) Subgroup**

Byssal notch deep, cardinal crura weak.

_U.Oligo.-Rec._

**P. (Patinopecten) DALL, 1898** [*Pecten caurinus GOULD, 1850; aD] [=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); ?Masuhopecten 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., X0.5 (Arnold, 1906)._
Pterioida—Pteriina—Pectinacea

N371

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.) lityyaensis; OD]. Differs from Patipecten in possessing 1 to several rows of flange-like ridges on ribs (rounded to flat-topped) of LV, U.Oligo, or L.Mio., USA (Alaska); Pl., USA (Calif.-Mexc. (Baja Calif.). — Fig. C91,1. *P. (L.) lityyaensis, Pl., Alaska; 1a, LV ext., ×0.39; 1b, RV ext., ×0.25 (MacNeil, 1961).

P. (Minnivola) Iredale, 1939 [*Minnivola isomer; OD]. Differences from P. (Euvala) in having deep byssal notch below right anterior auricle; ctenolium present. M.Mio.-Pl., Iran-W.Pak.; Rec., Australia-Philip. — Fig. C92,1. *P. (M.) isomer (Iredale), Rec., Australia; 1a, LV ext., ×1 (Eames & Cox, 1956).

P. (Yabepecten) Masuda, 1963, p. 149 [*Pecten tokunagai YOKOYAMA, 1911; OD]. Differs from Patipecten in shallower byssal notch of RV and more numerous, rounded, radial ribs. Pl., 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 Drolet, 1825 [*Pecten aequicostratus LAMARCK, 1819; SD Chenu, 1862] [=Neitheaea Gray, 1840 (nom. null.); Neithea d’ ORBIGNY, 1846 (nom. null.); Mitthea ANDERSON, 1902 (nom. null.); Neitha PRESTON, 1925 (nom. null.); Neitha STEWART, 1930 (nom. null.); Nerithaea 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 RV; rows of small denticles along interior upper margin of auricles (392). Cret. (Neocom.-Senon.), cosmop. ?L.Eoc., Switz.

N. (Neitheea) [=Aequicostraea HAYAMI, 1960 (obj.)]. Numerous radial ribs equal or nearly equal in size. Cret. (Neocom.-Senon.), cosmop.

N. (Neitheya) HAYAMI, 1960 [*Janira wrighii 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 Tepper, 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).

Ventualium de GREGORIO, 1930 [*V. insignis; OD]. Flattish, fan-shaped, sculptured with minute radial ribs; about 10 deep, radiating sulci, each of which separates groups of about 6 to 8 ribs; 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).


W. (Weyla) [=Parapecten CRICKMAY, 1930 (type, P. nilakapamuxanus)]. 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. deperti; 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; RV flattish, slightly concave near beak, sculptured with about 15 radial ribs in interspaces of which about 6 smaller ribs occur, 1 higher than others, all crossed by concentric imbrications. M.Jur. (Bathon.), France. — Fig. C93,3. *W. (P.) deperti (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 aequalisvis 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.) aequalisvis (J. Sowerby), Eng.; 5a,b, LV, RV, X0.4 (Chenu, 1944).


Indopecten Douglas, 1929 [*Pecten clignetti Krumbeck, 1913 (=Pecten (Echinpecten) 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. clignetii (Krumbeck), 2a-c, LV ext., RV ext., both valves umbonal views, X0.7 (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, aclinic, 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 resilifer; 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., X0.5 (341b). — Fig. C94.4b. E. abjectus (Phillips), M. Jur., Inf. Oolite, Eng. (Dorset.), RV int., X0.7 (184).

?Mcelearnia Crickmay, 1930, p. 45 [*M. mcelearnii; 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 ribs 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. mcelearnii; RV int., X0.5 (Crickmay, 1930).

Family MONOTIDAE P. Fischer, 1887
[nom. transl. Kittle, 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-

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**Fig. C95. Monotidae (p. N374).**
Family BUCHIIDAE Cox, 1953

[Buchidae 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 equivalent 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 keyserlingi, 1846 (suppression confirmed by ICZN Opinion 492); Aucella Stoliczka, 1866 (nom. null.); Anaucella Pchelintseva, 1955 (type, Anaucella 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" usuriensis Voronez; this probably should be made of the type of a new genus which may not belong to the Buchiidae.) M.Jur.-U.Cret. (Maastricht.); cosmop., most abundant in boreal regions; U.Jur.-U.Cret. (Maastricht). Ind.O. (Madag.)-USSR. — Fig. C96, 1ab. *B. mosquensis (von Buch), U.Jur. (L.Volg.), USSR; 1a, 1b, 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.

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. (Entomotis) 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 (Frehch, 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.
Fig. C96. Buchiidae (p. N374, N376-N377).
Aucella Anningia carixensis

N376 Bivalvia—Pteriomorphia

Aucellina POMPECK, 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 Broilli, 1904, p. 168 [*Avicula? efflata Broilli, 1904, p. 167; M]. Higher than long, prosocline; LV strongly convex, with well-protruding umbo; RV unknown; LV posterior wing quite undermarked 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 (Broilli); 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.Trias. (Kimmeridg.), Indonesia—N.Z.—Fig. C96,6. *M. malayomaorica (Krumbeck), E.Celebes—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).

Paracellina 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

Fig. C97. Buchiidae (p. N376).
viewed from side and front, ×2 (Pavlov, 1907). *Pseudacella* 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; posterdorsal region with broad, well-pressed 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 Plicateulidae** Watson, 1930

[ nom. transl. IREDALE, 1939 (ex Picateulinae Watson, 1930)]

[Materials for this family prepared by L. R. Cox and L. G. HERTELEIN]

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.*

Plicateulina LAMARCK, 1801, p. 132 [*Spondylus plicatus* LINNÉ, 1758; SD SCHMIDT, 1818] [≡Plicateuligenus RENIER, 1807 (suppressed ICZN); Micatula CARPENTER, 1859 (nom. null.); Plicateula 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*,]

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); *Plicatula* NEUMANN, 1907, p. 104 (type, *Plicatulopsis boehmi*; SD Cox, herein). Auricles absent or ill-defined; most species with radical 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, I. 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. (Darteplicata) 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. *Euc.-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. (Pseudoplacuncops) BITTNER, 1895, p. 215 [*Pseudoplacuncops 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.

Atleta ÉTALLON, 1862, p. 192 [*Ostrea blandina d’ORBIGNY, 1850, p. 375; SD Cox, 1964, p. 45*] [=Dipschiza CONRAD, 1866, p. 77 (type, *D. cretacea*); Cyclostreon EICHWALD, 1868, p. 406 (type, *Ostrea plicatuloides* LEYMerie, 1851, p. 195; M); Dimploschiza 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.)—Fig. C98, 4. *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, subulate, 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. HERTELIN & 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. gaedersopus*; 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. SOWELL, 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. SOWELL, 1814, p. 177; SD HERMMANNSEN, 1847, p. 188); *Pachytos hoeninghaus* 1830 (nom. van.); *Pachyta MENKE, 1830 (nom. van.); Pachytus AGASSIZ, 1846 (nom. van.); Pachytes d’ORBIGNY, 1846 (nom. null.); Dianchora DESMAREST, 1859 (nom. null.); Eleutherospondylus DUNKER, 1882 (type, *Spondylus regius* LINNÉ; SD Cox, herein); L. IREDALE, 1939, p. 373 (type, *Spondylus duclais roeding* 1798, p. 194; OD); *Ponovala* 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.
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.) gaedopus, Rec., Medit.; 1e, LV view of both valves, ×1; id, LV int., ×1; 1f, LV and RV hinge, ×1 (all Cox, n).


S. (Elopera) Iredale, 1939, p. 377 [*S. foriior (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 LV 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,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 RV1; 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 absent2; 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.

1 See note with Enantiostreon, however.
2 See note on Placunopsis, however.
Fig. C100. Terquemiidae (p. N380, 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; 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 umbalon 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., X1; 4b,c, convex specimen, also presumed to be LV ext., X1, and int. of hinge region, arrow pointing to swelling in umbalon cavity, X2.3 (all Cox, n).—FIG. C100,4d. P. plana (Giebel), M.Trias. (Muschelkalk), Ger.; specimens sessile on Lima shell, X1.3 (Seilacher, 1954).

Family DIMYIDAE P. Fischer, 1886

Shell small, thin, subbicular or oval, not auriculate, rather compressed, closed, attached by RV, which is less convex; externally lamelllose, 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.); Deuteryyma Cossmann, 1903 (pro Dimya Rouault, non Menke, 1830, subordinal name), Dimyarinia Iredale, 1936, p. 269 (type, Dimya corrugata Hedley, 1902, p. 309; OD); Dymia Noskzy, 1939 (nom. null.).] Cardinal crura short and weak; posterior adductor scar bilobed. Eoc.-Rec., Eu.-Carib.-Indo.-Australia-N. Z.-IndoPac.-E.Pac.—FIG. C101,2. *D. deshayesiana*, Eoc., France; 2a,b, RV ext., int., LV int., X1.7 (Rouault, 1850).

*Dimyodon* Munier-Chalmas in Fischer, 1886, p. 937 [*D. schlumbergeri; OD*] [=Dimyodus Wohrmann, 1894 (nom. van.).] Cardinal crura prominent, elongate, transversely striated; posterior adductor scar not bilobed. M.Jur.-Rec., Eu. (France).—FIG. C101,1. • D. schlumbergeri; 1a,b, LV int., LV int., X3.4 (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-
Superfamily ANOMIACEA
Rafinesque, 1815

Family ANOMIIDAE Rafinesque, 1815

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 Linne, 1758 [*A. ephippium; SD Schmidt, 1818] [=Echion Poli, 1791 (type, A. caeca Linne = A. ephippium; SD Keen, 1959); Echi noderm Poli, 1795 (obj.), SD Keen, 1959; Fenestrella Roding, 1798 (obj.), SD Winckworth, 1945; Operculata 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., Eur.-Afr.-AsiaM.-N.Am.-Aus tria-N.Z.


A. (Paraplatina) 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. C103,4. *A. (A.) ephippium, Rec., Eu.; 4a-b, RV ext., LV int., ×0.5 (Keen, n).


A. (Prismato) Marwick, 1948 [*A. undata Hut ton, 1885; OD]. Shell lacking radial striae; RV thick, prismatic. Plio., N.Z.

Caralia CantraINE, 1838 [*C. placunoides; M] [=Hemiplacuna Gray, 1850 (type, H. rozi reri 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. (Caralia). 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.) perina nsis; OD]. Sculpture radial, with prickles and fimbriations; foramen persistent in adult. Eoc., W.S.Am.-India.


Enigmia Iredale, 1918 [*nom. subst. pro Aenigma Koch in Martini & Che nmitz, 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 Melvilleville, 1843; M] [=Semic plicatula (nom. null.)]. Small, compressed, smooth, crura thick, resembling teeth; muscle scar sunken, submarginal. Eoc., Eu.—Fig. C103,7. *H. solida (Deshayes in Melvilleville), France; 7a-c, RV ext., int., LV int., ×5 (Deshayes, 1861).

?Isomonia Daunzzenberg & Fischer, 1897 [*Monia alberti Daunzzenberg & 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 (Daunzzenberg & Fischer); 10a-b, LV ext., int., ×1 (Dau znzzenberg & Fischer).

Paranomia Conrad, 1860 [*Placunanaonomia (P.) saufordi (=Placuna scabra Morton, 1834); SD Stoliczka, 1871] [=Paronomia Gardner, 1916 (nom. null.)]. Bysial foramen closed in adult; one retractor scar in either valve; sculpture of spinose radial ridbles. U.Cret., E.N.Am.—Fig. C103,8. *P. scabra (Morton), USA (Tenn.), 8a-c, RV int., LV ext., ×0.7 (1931).

Placuna Lightfoot, 1786 [*Anomia placenta Linne, 1758; SD Schmidt, 1818] [=Placenta Philipsson, 1788, ex Retzius MS (obj.; T); Ephippium Roding, 1798 (type, E. polonicum = Anomia sella Gmelin, 1791) = Placenta quadrangula Philipson, 1788].
N384 Bivalvia—Pteriomorpha

SON, 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


P. (Placuna). Flattened, crura widely diverging; central cavity small. Oligo.-Rec., Eu.-IndoPac. —Fig. C103,5. *P. (P.) placenta (Linne), Rec., Ceylon; RV int., X0.25 (242).

P. (Indoplacuna) Vredenburg, 1924 [*P. (I.) sindiensis; SD Keen, 1959]. Resilifer bent sharply; primary crural ridges supplemented by less divergent secondary pair. Mio.-M.Mio., S.Eu.-N.Afr.-Asia.—Fig. C103,6. *P. (I.) sindiensis, India; RV int., X0.5 (242).


Placunamia Broderip, 1832 [*P. cumingii; M]. [=Placunonya, Placunamia Whitlefield, 1885 (nom. null.); Placunamia Olsson, 1961 (nom. null.)]. With about 3 strong radial plications; byssal foramen obsolete in adult; interior with 1 retracor scar. Mio.-Rec., E.N.Am.-W.C.Am.-W.N.Am.—Fig. C103,11. *P. cumingii, Rec., W.C.Am.; 1a,b, RV int., LV int., X0.5 (Stanford Univ. specimen).

Pododesmus Philippi, 1837 [*P. decipiens (=*Placunamia 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 retracor scar. 0Oligo., 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.; 1a,b, RV int., LV int., X0.5 (Stanford Univ. specimen).


P. (Tedinia) Gray, 1853 [*T. pernoide; M]. Byssal foramen obsolete in adult; resilium elevated on pedal-like chordophore. Rec., W.N.Am.

P. (Saintia) Raincourt, 1877 [*S. munieri; OD]. Hinge with 2 bifid crura and central denticle; adductor scar large, circular; excentric; retracor scars not evident. Eoc.(Cuis.), Eu.—Fig. C103, 3. *S. munieri, France; 3a,b, LV int., ext., X1 (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 Limarididae Rafinesque, 1815)] [=Radulidae Adams & Adams, 1858]

Materials for this family prepared by L. R. Cox and L. G. Hertlein.

Shell usually equivale (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., opisthoclinc); typically biauricular but with anterior auricle reduced or absent in some forms and 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 calctic layer and middle and inner layers of non-nacreous argonite. [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 Bruguëre, 1797, pl. 206 [*L. alba Cuvier, 1797 (=Ostrea lima Linne, 1758, p. 699); M. Cuvier, 1797, p. 421] [=Mantellum Röding, 1798 (obj.); Limigenus Renier, 1807 (suppressed ICZN); Limaria Rafinesque, 1815 (non Link, 1807); Glaucium 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. 1ur.-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. 34, 1797. Even then, however, it is most probable that it appeared later than Broderip's plate illustrating Lima in Encyclopédie méthodique.—Only the bare generic name Lima appeared in Broderip'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. 

Badiotella BITTNER, 1890, p. 94 [*B. schaurothiana BITTNER, 1895, p. 201; SM BITTNER, 1895]. Small, trigonally orbicular, highly inequilateral, with sharp, backward-pointing umbones; antero-dorsal 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; 2ac, 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 Spirea sparva 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] (Divariculoma ROVERETO, 1898, p. 153 (type, Lima eximia GIEBEL, 1864); Ptenoides SMITH, 1904 ([nom. null.])). Ovate to subtrigonal, sub-equilateral, high in proportion to length, somewhat compressed, with well-developed byssal gape bordered by liriate 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 ribs, denticulating ventrally and bearing fine scales. U.Jur.(Tithon.)-Rec., cosmom.—Fig. C105,5. *C. scabra (Born), Rec., W.Indies; 5ab, 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] (=Ostrepecten QUENSTEDT, 1867 (obj.); ?Pseudocenostreon BURKHARDT, 1930 (no nomi-
FIG. C104. Limidae (p. N385-N386).
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.*
peciniformis (von Schlotheim), M.Jur.(Bajoc.); 6a (Ger.), LV ext., ×0.5 (341b); 6b (France, Calvados), RV int., ×0.7 (732).

Divarilina 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, ×3.7 (396).

Elinata Dickens, 1963 [*E. guppyi*; OD]. Sub-oval 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.(Poole Ss.), W. Australia; LV ext., ×3 (263).—**Fig. C105,3b.** *E. perniana* (Newell), U.(Perm., Cape Stosch F., E.Greenl.); 3b, LV ext., ×3 (Newell, 1955). [*Newell.*]

?Gryphellina Newell, 1940 [*Capulus sellardsi Beede, 1907; OD]. RV ventricose, gibbous, with protuberant and strongly overhanging prosogyrous beak; somewhat opisthochline, auricles small and rounded, with poorly defined byssal sinus; body 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., ×2; 2b, LV hinge, enl. (665). [*Newell.*]

Limaria Link, 1807, p. 157 [*L. inflata (=*Ostrea tuberculata* Oliv., 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 Gilbert & Van de Poel, 1965, p. 49 (obj.).]

This species, originally described by the nonbinomial author Chemnitz, was named binomially by Lamarck and Link independently in 1807. LAMARCK'S *Lima inflata* having priority. In 1791, however, Gilkein had assigned the name *Ostrea inflata* to a distinct species of Limidae and, although this already bore the name *Ostrea bulbula* Born (1778), its subsequent inclusion in *Lima* rendered the species of Lamarck and Link a secondary homonym. Olivii's *Ostrea tuberculata* may be revived for *Lima inflata* Lamarck. [*L. (Lima).* Obliguely 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.) striatula* (Brocchi), Mio., Austria; 7a,b, RV ext., RV int., ×10 (411).

L. (Lima) [=Promantellum Iredale, 1939, p. 385 (type, *P. parafragile*); Submantellum Olson & Harrison, 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* (Oliv.), Rec., Malta; 10a, LV, side view; 10b, posterior view; 10c, anterior view of bivalve shell showing gapes, all ×1 (Cox, n).

L. (Limatulaella) 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 ×1.4 (Cox, n).

L. (Mantellina) Sacco, 1904, p. 148 [*Mantellum (Mantellina) inosiceroamoides*; OD]. Small, deli­cate, concentrically crenulated. *Mio.(Helvet.),* Italy.

L. (Stabilina) 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., ×1 (Cox, n).

Limatula Wood, 1839, p. 235 [*Pecten subauriculata Montagu, 1808, p. 63; SD Gray, 1847, p. 200] [=Cystigenus, Cyista Rentier, 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. gibosa* (J. Sowerby), M.Jur.(Bajoc.), Eng.(Dorset); LV, ×1 (Cox, n).

Limea Bronn, 1831, p. 623 [*Ostrea striatula* Brocchi, 1814, p. 571; M] [=Limacea Gray, 1847 (nom. van.)]. Small, subbouricular 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). Obliguely 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.) striatula* (Brocchi), Mio., Austria; 7a,b, RV ext., RV int., ×10 (411).

L. (Eolimea) Cox, new subgenus, herein [*Lima margineplicata* Klipstein, 1845, 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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— Fig. Cl06, 1. *L. (E.) margineplicata* (Klipstein); 1a,b, RV ext. and dorsal view, X 4; 1c, hinge teeth, X 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. Cl06. Limidae (p. N389-N391).
Pterioida—Pteriina—Limacea

N391

Australia.—Fig. C106.3. *L. (E.) acclinis HEDLEY, NewS.Wales; 3a, RV, ext., X3.4; 3b, hinge line, X4.6 (Hedley, 1905).

L. (Gemellima) IREDALE, 1929, p. 166 [*Limea australis 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.) australis TATE, S.Australia; LV ext., X5.4 (169).

L. (Isolima) 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; 3a,b, RV ext., RV int., X10 (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., X4 (Smith, 1891).

Mysidiopera SALOMON, 1895, p. 117 [*M. ornata; SD DIENER, 1923, p. 111*] [=Mysidiopera REIS, 1926 (nom. null.)]. Ovate to suborbicular; posterior dorsal 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. *M.Trias.-U.Trias.*, cosmop.

M. (Mysidiopera) [=Latemaria WILCKENS, 1909, p. 220 (type, Mysidiopera kitiili BITTNER, 1895); Pseudolimnea WILCKENS, 1909, p. 207 (type, Mysidiopera cassiana BITTNER, 1895)]. Acine or opisthocline; anterior auricle absent or small; surface smooth or with radial striae or ribs. *M.Trias.-U.Trias.*, cosmop.—Fig. C107.7. *M. (M.) incurvostriata (GÖMBEL), U.Trias., S.Tyrol; 7a,b, RV ext. and cardinal area, X1.5 (58).

M. (Pseudacesta) WAAGEN, 1907, p. 113 [*M. (Pseudacesta) dieneri; M*]. Ovate, proosoline, smooth, with very distinct anterior auricle. U.Trias., Eu.(S.Tyrol).

Palaeolina 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 Plagiotoma, but size is invariably small and umbonal ridge and lunule are absent. U.Carb. *P.Trias., Eu.-Asia-N.Am.—Fig. C107.2. P. footiei (WAAGEN), Perm., Salt Range, Pakistan; RV ext., X3.3 (Waagen, 1887).

Plagiostoma J. SOWERBY, 1814, p. 175 [*P. giganteum; SD STOLICZKA, 1871, p. xxii*] [=Plagiostomatites KRUEGER, 1823 (obj.); Plagitostomatina BERTHOLD, 1827 (nom. van.)]. Plagiostoma COQUAND, 1880 (nom. null.)? Anomalolimina COSSMAN, 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, X0.75 (202).

Pseudolimnea ARKELL in DOUGLAS & ARKELL, 1932, p. 161 [*Plagiostoma duplicata J. DE C. SOWERBY, 1827, p. 114; OD*] [=Limoarca VON MÖNSTER, 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. *M.Trias.-U.Cret.*, cosmop.—Fig. C107.3. *P. hettangienis (TERQUEM), L.Jur.(L.Lias.), Switz.; 3a,b, RV ext., RV int., X1.3 (von Bistrum, 1903).

Regaliliminea COX, 1943, p. 177 [*Lima oolithica 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. oolithica (LYCETT); 6a, RV ext., X0.5; 6b, RV, ant. end showing gape, X0.67 (185).

S. 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 KREMBECK, 1923, p. 218 [*S. serenensis; 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 X1 (486).

Tirolidia BITTNER, 1895, p. 202 (*Lima (Tirolidia)

Fig. C107. Limidae (p. N391-N393).
Modiomorphoida—Modiomorphacea

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. 2107, T. cassiana BITTNER, M.Trias.(Ladin.); RV, ×2 (58).

Suborder OSTREINA Ferussac, 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, prismatic orconcentric 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.]


Superfamily MODIOMORPHACEA Miller, 1877

[nom. transl. NEWELL, 1965 (ex Modiomorphidae S. A. Miller, 1877)] [Materials for this superfamily prepared by Aurel 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.]


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.]


Modiomorpha HALL & WHITFIELD, 1869, p. 72 [*Pterinea concentrica CONRAD, 1838; SD HALL, 1885] [=Palanatina HALL & WHITFIELD, 1870 (type, P. typa; OD); Dechenia SPIESTERSBACH, 1915, p. 70 (type, D. rhenana; SD LaRoque & Newell, herein); Spiestersbachia MAILLIEUX, 1930, p. 62 (nom. van. pro Dechenia SPIESTERSBACH, 1915)]. Mesial ventral sinus and oblique preumbonal sulcus distinct; LV with 1 large wedge-shaped tooth; RV with corresponding socket; without laterals (159).
widely distributed.—Fig. D1,1. *M. concentrata* (Conrad), M.Dev., USA (N.Y.); 1a, RV ext., LV int., X1 (Hall, 1884).

**Aristella 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 Whitealelia. M.Ord. (Blackrill) -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 X3 (439).

**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), X2; 5b, hinge of same, X3 (439).

**Callodonta Isberg**, 1934, p. 212 [*C. monilijera*; 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. monilijera*, Boda Ls., Dalarna region; 4a, LV (holotype), X3; 4b, LV hinge, X6 (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. (Blackrill) -Sil. (U. Medin.), E.N.Am.—Fig. D2,7. *C. constricta*, Ord. (Trenton), USA (Ky.); 7a, LV int.; 7b, RV ext.; both X1 (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). 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., X1 (929).

**Deceruska 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, LV ext.; 3b, RV ext.; both X3 (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 X3 (439).

**Eurymyella Williams**, 1912, p. 382 [*E. shaleri*; OD]. Subtriangular, narrow in front, subulate 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., X1 (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. N394, N396-N397).
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., X1 (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 X1.0 (564).

Goniophorina Isberg, 1934 [*G. volvens; OD]. Similar to Goniophora but without teeth. U.Ord., Sweden; L. Perm., SW.USA.
M. (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. davoustii; OD]. Elongate, subquadrature, 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. davoustii, near Brulon; 1a,b, LV ext. int., ×3; 1c, RV int., ×3 (Oehlert, 1881).

†Hippomyla 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, ×0.75; 7c, LV lat. view, ×0.7 (823).

†Liomytilus Lacroque, 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 (Lacroque).

Megambonia Hall, 1859, p. 12 [*Pterinea cardiformis 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. cardiformis (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]. Similar to Modiolopsis, but with 1 to 3 oblique cardinal teeth in each valve. M. Ord.-U.Ord., N. Am.; Sil. (?Llandover), 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. atawa; M); Modiodesma Ulrich, 1924 (obj.)]. Edentulous; without marked lateral sulcus or ventral...
Paraphonia

Tylophora


sinus; radial ornamentation lacking. M.Ord.-U. Ord., cosmop.—FIG. D3,2. *M. modiolaris (Conrad), U.Ord., USA(N.Y.); both valves ext., ca. X0.8 (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 X1 (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, Kullberg Ls., Dalarna region; lat. view of holotype, X3 (439).


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).
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 Barin, 1966, but the distinction from Modiomorphidae appears to be insignificant.] Ord. (Llandeilo), Eu. (France-Boh.-Spain)-N.Afr.—Fig. E44,4. *R. deshayesiana, Whitfield; 4a,b, LV int., RV int., X1; 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 X1 (929).

Semicorallidomus Isberg, 1934, p. 175 [*S. whitefieldi; 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. whitefieldi, Boda Ls., Dalarna region; 2a, LV ext. (holotype), X3; 2b, LV hinge, X5 (439).

Spathella Hall, 1885, p. xxxii [*S. typica; OD]. Transversely subcyindrical, 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, X1 (379).

Sphenotomompha 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., X1 (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 pro-

file 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 Dist., Szechuan, China; 3a-c, dorsal view both valves; LV ext., LV int., all X0.7 (473).

Tylophora Dummer, 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., X1 (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 X1 (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 LaRoque & 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., X1.25 (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
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 Aurele 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.Cam.-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.Cam.*, 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*, Cincinnati, 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 pos-

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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).
Unionoida

Order UNIONOIDA Stoliczka, 1871
[nom. correct. WEB, herein (pro order Unionacea STOLICZKA, 1870)] [Diagnosis by JOHN WEB]

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; integipalliate, isomyarian or subsomyarian, 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) 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 Archaenodontacea.

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) Anthracosiacae. 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 (clastra) 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 (Annigenia), 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" jukesii FORBES and the American Annigenia 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 "ligamenta I fulcrum" by WHITEAVES, and misrepresented in his figure, is an integral dorsal part of the scar of a very large anterior muscle complex. Excellent plaster casts of type material supplied by the Geological Survey of Canada show clearly that the structure called "ligamenta I fulcrum" by WHITEAVES, and misrepresented in his figure, is an integral dorsal part of the scar of a very large anterior muscle complex. Excellent plaster casts of type material supplied by the Geological Survey of Canada show clearly that the structure called "ligamenta I fulcrum" by WHITEAVES, and misrepresented in his figure, is an integral dorsal part of the scar of a very large anterior muscle complex.
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 Westphal-
ian 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


*Archanodon* Howse, 1878 [*Anodonta jukesi* Forbes, 1853; OD] [=Amnigenia Hall, 1885 (type, Cypricardites catskillensis Vanuxem, 1842); *Asthendonota* Whiteaves, 1893 (type, *A. westoni*)]. Characters of superfamily. *Dev.(Up.Old Red St.), Ire.-Eng.; *U.Dev., USA; L.Carb., Eng.; Penn., N.Scot. — Fig. D9,la. *A. jukesi* (Forbes), Up. Old Red St., Ire.; LV ext., ×0.4 (Weir, n). — Fig. D9,lb. *A. westoni* (Whiteaves), Penn., N.Scot.; LV ext., ×0.4 (Weir, n). — Fig. D9,lc. *A. sp., L.Carb., Eng.; RV ext., ×0.4 (Weir, n).

*Neamnigenia* Khalfin, 1950 [*N. beljani; 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. Antero-dorsal margin rather long and straight. [Non-marine.] *L.Per., USSR(Sib). — Fig. D92. *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 *Grundziige* (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*uschwald, 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-
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 Palaecomutelidae, is cryptic.

Family ANTHRACOSIIDAE Amalitsky, 1892
[emend. TRUEMAN & WEB, 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 umbalinal 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 anthracosid 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...
Unionoida—Anthracosioidea

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 duplilinxal Myaliniidae. This would separate Carbonicola from Anthraconaia [Anthracomya], which were classified together as Unionoidea by WHEWELTON HIND and as Cardiniidae in the Zittel textbook (1913).

It is true that elongate, so-called anthraconaoidal 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 Anthracosia; nor has such a variation relationship yet been detected between Carbonicola and Anthraconaia (the adami-olderi-modiolaris group). Provisionally it is better to refer the elongate “anthraconaoids” of the lower coal measures to Carbonicola with a query.

Anthracosia KINO, 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 doublet 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., X1 (915).—Fig. D10,2b-c. A. aquilina (J. DE C. SOWERBY); 2b-c, int. mold LV, both valves dorsal, X1; 2d, lectotype (ICZN pend.), RV, both valves ant., X1 (915).—Fig. D10,2f. A. sp. aff. A. atra (TRUEMAN), Scot.; hinge, X2 (915).

Anthracosphaerium TRUEMAN & WEIR, 1946 [*Carbonicola exigua Davies & Trueeman, 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, holotype LV lat., both valves dorsal, X1 (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, X1 (565).—Fig. D10,1m-p. *C. acuta (J. SOWERBY), Eng.; 1m-o, lectotype (a mold); RV lat., both valves ant., dorsal), X1; 1p, same, LV, with shell restored, X1 (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, X2 (EICHWALD, 1855-61).

?Family MICRODONTIDAE Weir, new family

Small, equivalved, isomyarian, integripal-
Hinge, or edentulous. Suborbicular, transversely subelliptical in outline, with straight or nearly straight hinge line; or sub nuculoid 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 re-investigated 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.
UNIONOIDEA—ANTHRACOSIAECA

Perm., USSR (Sib.)—Fig. D11,la. *M. microdonta* (KHALFIN); RV ext., X2.5.—Fig. D11,lb. *M. astartellaformis* (FEDOTOV); RV int. showing part of microodont hinge, x6 (Ragozin, 1955).

Abiella RAGOZIN, 1933 [*Posidonomya concinna* JONES, 1901; SD RAGOZIN, 1955]. Like Microdonelia, but apparently lacking microodont 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., x3 (Ragozin, 1955).

Microdonelia LEBEDEV, 1944 [*M. problematica*; OD]. Like Posidonia in outline but microodont, with more tumid umbones in uncrushed shells and gently curved hinge line. UPerm., USSR (Sib.).—Fig. D11,3a,b. *M. problematica*; 3a, dorsal view showing tumid umbones, x3; 3b, same, showing microodont dentition, x10 (536).—Fig. D11,3c,d. *M. subovata* (JONES); 3c, LV (cast of ext.), x4; 3d, RV (impression), x4 (Ragozin, 1955).—Fig. D11,3e. *M. tomiensis* (RAGOZIN); microdont hinge "greatly enlarged" (536).

?Family PALAEOMUTELIDAE

Weir in Vokes, 1967

[=Anthracosia (sic) AMALITSKY, 1892 (pariim); Carbonicicolidae Cox, 1932 (pariim)]

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, in-equilateral, integripalliate, subisomyarian; scar of posterior adductor suboval, anterior angular-subovate or trapeziform, attaining maximum length of 35 to 40 mm., but pyriform or lunate. Dorsally to anterior adductor scar of posterior adductor muscle of foot; 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.

WOHRMANN 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 (Carbonicicolidae), 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 superfamly.

Palaeomutela AMALITSKY, 1892 [*P. verneuilli*; SD Weir, herein] [AMALITSKY invalidly designated both P. verneuilli and P. keyserlingi as type species of the genus. He also described and figured specimens of Palaeomutela (s.d.) 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.) verneuilli*, U.Perm., USSR; 2ab, LV int. molds, X1; 2c, LV ext., X1.—Fig. D12,2d,e. *P. (P.) keyserlingi*, U.Perm., USSR; 2d, LV ext., X1; 2e, hinge, enl. (13).

P. (Oligodon) AMALITSKY, 1892 [*O. geinitzi*; SD Weir, herein] [AMALITSKY invalidly designated both O. geinitzi and O. zittelli 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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N410 Bivalvia—Palaeoheterodonta


which may be projecting and linguiform. U. Perm., Eu.(USSR).—Fig. D12,1a,b. *P. (O.) geinitzii; 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).


?Family FERGANOCONEIDAE
Martinson, 1956

[Materials for this family prepared by L. R. Cox; its assignment to Anthracosiasiæa 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. Ferganoconchiidae (1); Pseudocardiiniidae (2,2) (p. N410-N411).
RV teeth have rounded transverse ridges, to which grooves in dental sockets of LV correspond; anterior laterals not extending beyond beaks. *P. submagna*, Bajoc., E. Tien-Shan; LV int., X 1 (Martinson, 1959).—*P. carcinata* (MARTINSON), Bajoc., E. Tien-Shan; RV int., X0.9 (Martinson, 1959).—*P. jeniseica* MARTINSON, Bajoc., Chulimo-Yenisei basin, C. Asia; LV ext., X 1 (Martinson, 1961).

**Kija** LEBEDEV, 1958, p. 73 [*K. tjazhinensis*; OD]. Shell small, known species not exceeding 17 mm. in length, oblong, much elongated, strongly inequilateral, obliquely truncated posteriorly; umbones broad, not protruding; weak posterior diagonal ridge present; dentition unknown. *L.Jur.*-M.*Jur.*, USSR (Georgia).—*K. tjazhinensis*, U. Juras., Sib. (Tungusska basin); RV ext., X1.5 (Ragozin, 1938).

**Nyassa** HALL & WHITFIELD, 1869 [*N. arguta*; OD] [=Modioconcha HALL & WHITFIELD, 1869; nom. obl. (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.).—*N. arguta*, USA (N. Y.); 4a, ext. LV, showing ornamentation, X1; 4b, hinge RV, showing dentition, greatly enl. (Hall, 1885). [LAROCQUE]

**Superfamily UNIONACEA** Fleming, 1828

[nom. transl. THIELE, 1934 (ex Unionidae Flem., 1828)] [pro Naiadacea Auctt. (invalid family-group lacking type genus)] [Materials for this superfamilly prepared by FRITZ HAAS, except as otherwise recorded]

Shell mostly equivalent 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.]

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. DIS. 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, Leguminia**) 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 **Arclidopsis** 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.
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. Prevailing, 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 taxo-
nomically 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, denticion, 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 characters: these are divided among three families (Unionidae, Mutelidae, Etheridae). 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 nomenclatural 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)] [=Margaritinae ORTMANN, 1910 (suppressed by ICZN, 1957, Opinion 495, p. 290)]

Shell equivaleve, mostly compressed; umbal 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.


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., X0.5 (after 497).

M. (Cumberlandia) ORTMANN, 1912 [*Unio monodonta SAY, 1829; OD]. Elongate-arcuate,
thin; lamellar teeth weak, poorly defined. Continuous laminar septa between gills, running obliquely forward. Rec., N.Am.—Fig. D16.1. *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

[non 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 Linne, 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; Myisca Turton, 1822; ?Margarita Lea, 1836 (non Leach, 1819); Myisca L. Agassiz, 1846; Chondroseta Gistel, 1848; ?Margaron Lea, 1852; Nodularia Conrad, 1853; Nodularia 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
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 (Linne), Rec., Eu.; LV ext., X0.7 (after 497).

U. (Eolymnium) Prashad, 1919 [*Unio terminalis Bourguignon, 1852; OD]. Inner gills broader than outer pair, branchial aperture high, foot poorly developed. Rec., Eu.(E.Medit.).—Fig. D17,1. *U. (E.) terminalis Bourguignon; 1a-c, hinges, LV ext., both valves dorsal, X1 (after Bourguignon).

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., X0.7 (after 543).

U. (Sculptunio) Lindholm, 1932 [*U. bituberculatus Martens, 1874; OD]. Shell characterized by 2 rows of knobs which radiate from beaks. M.Plio., USSR(SW.Sib.).—Fig. D17,2. U. (S.) bituberculatus trigonoides Lindholm; 2a-c, RV ext., int., both valves dorsal, X0.7 (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., X0.7 (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, X0.8 (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., X1 (Frierson).

Arcidopsis Simpson, 1900 [*Unio footei Theobald, 1876; OD]. Elongate, with dorsal and ventral...
Fig. D18. Unionidae (Unioninae) (p. N416, N418, N420).
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 fulcra, 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).

**Balwanita** 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 (324).

**Caelatura** Conrad, 1853 [*Unio aegyptiaca Cailliaud, 1826; OD*] [=Pharaonia Bourguignat, 1880; *Renetus 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; antero-rectal margin not steeply descending; beaks inflated, full, not 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] [=Brazzaea Paetel, 1890; Brazzaeae German, 1909]. Thin, translucent, wine-colored, elliptical, greatly inflated, with small postero-dorsal wing and high double posterior ridge; beaks apparently smooth, compressed, but umboes full; antero-rectal 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, 1889 (=Pharaonia bourguignati Rochebrune, 1886); OD]. Rounded lens-shaped or irregularly quadrangular, thin, compressed; antero-dorsal 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; arcola 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 muerensis* 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.) muerensis* (Smith); 6a-d, LV ext., int., RV int., both valves dorsal, ×1 (Haas).

C. (Rhytidonia) Haas, 1927 [*C. graueri* Haas, 1927; OD]. Elongate, irregularly quadrangular, thick, ventral margin almost straight, postero-dorsal margin high; beaks not prominent; entire disc sculptured with 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
ext., RV int., LV int., both valves dorsal, $\times 1$ (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, blade-like, 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., $\times 1$ (Pilsbry & Bequaert).

Cafferia Simpson, 1900 [*Unio caffer Krauss, 1848; OD]. Elongated, elliptic, or rhomboid, rather solid; beaks full, ornamented with corrugated zig-zag 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, $\times 0.7$ (497).

Canthyria Swainson, 1840 [*Unio spinosus Lea, 1836; OD]. Spinose, inflated, suboval, with high, rather sharp posterior ridge; disc smooth; hinge typical, its elements rather strong. Pleist.-Rec., S.Afr.—Fig. D18,6. *C. spinosa (Lea); 6a-c, LV ext., RV int., both valves dorsal, $\times 0.5$ (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, $\times 0.8$ (Haas).

Chamberlainia Simpson, 1900 [*Unio hainesianus Lea, 1856; OD] [=Simponia 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 symphony 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, $\times 0.3$ (Haas).

Contradens Haas, 1913 [*Unio contradens Lea, 1838; OD] [=Schizoeothyrum 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 blade-like; 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, $\times 0.7$ (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., $\times 1$ (Haas).

Ctenodesma Simpson, 1900 [*Unio borneensis Issel, 1874; OD] [=Crissadens, Chrisadens 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, $\times 0.8$ (Haas).

Cucumerunio Iredale, 1934 [*Unio novae-hollandia Gray, 1834; OD] [=Cucumaria Conrad, 1855 (non de Blainville, 1830; nec Lesson, 1831); Cucumaria Simpson, 1900 (nom. null); ?Aparcthyria, ?Quaectica 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, $\times 0.3$ (497).

Cuneopsis Simpson, 1900 [*Unio celiiformis 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. celiiformis (Heude), Rec.; 2a-d, RV ext., LV int., RV int., both valves dorsal, $\times 0.6$ (Haas).

Diaurora CockereIl, 1903 [pro Aurora Simpson, 1900 (non Ragionot, 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., $\times 1$ (Zilch).

Elliptio Rafinesque, 1819 [*Unio nigra; OD] [=Eurynia Rafinesque, 1820; Cunicula Swainson, 1840; Curricula Gray, 1847; Eurypia Conrad, 1853; Rurynea Paetel, 1875; Euryphia Frierson, 1927]. More or less elongate; beaks placed well back of anterior end, not prominent,
Fig. D20. Unionidae (Unioninae) (p. N420).
 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.

E. (Nannonaia) Haas, 1913 [*Unio trompi Drouët & Chapier, 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).

E. (Elongaria). Long, narrow, thick, somewhat inflated; beaks low, not prominent; disc smooth; cardinals broadly lamelliform.

E. (Nannonaia) Haas, 1913 [*Unio trompi Drouët & Chapier, 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.(Java-Borneo).

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.


Gonidea CONRAD, 1857 [*Anodonta randalli Trask, 1855 (*Anodonta angulata LEA, 1838); OD] [*Anodonta angulata HANNIBAL, 1912]. Ellongate subtriangular, much narrowed in front, wide behind; 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., LV int., dorsal, X0.5 (140).

Haasodonta McMICHAEL, 1956 [*Hyridella fannyae JOHNSON, 1948; OD]. Subsquare, 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, X0.7 (McMichael).

Heudana FRIERSON, 1922 [*Unio murrinus 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. murrinus (HEUDE); 3a,b, LV ext., RV int., X0.5 (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., X0.5 (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,
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, × 1 (after Haas).

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 RAINFESQUE, 1820; OD] [=Hemistena RAFINESQUE, 1820; ?Flexiptis RAFINESQUE, 1831; Odatelia RAFINESQUE, 1832; Lostena GRAY, 1847; Stenelasma HERMANNSEN, 1849; Hemilastena L. AGASSIZ, 1852; Lastenes DESMAREST, 1859; ?Sayanio 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 (533).

L. (Microcondylaea) Vest, 1866 [*Anodonta uniopsis LAMARCK, 1819; OD] [=Microcondylus DEQUET, 1879]. Decidedly inequilateral, elongate, subrhomboid to elliptical, compressed, rather...
thin, with low beaks; 1 cardinal in each valve, very compressed. Rec., SW.Asia(Iraq).—Fig. D25.3. 
*L. (P.) euphratica (BOURGIGNAT); 3a-c, LV ext., RV and LV hinges, both valves dorsal, ×0.7 (491).

L. (Pseudoleguminaias) GERMANN, 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, with rather indistinct continuous rays; hinge teeth well developed, nacre white to pink. Rec., N.Am.—Fig. D24.1. *L. subplanus (CONRAD); 1a,b, LV ext., both valves dorsal, ×1 (497).

Mesafra HAAS, 1936 [*Caelatura mesaficana PILSBRY & BEQUAERT, 1927; OD]. Ventricle, 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. mesaficana (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 sloati-anus LEA, 1840; OD]. Marsupium occupying all 4 gills. Rec., N.Am.—Fig. D26.2. *N. (E.) sloati-anus (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-
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).

Nippononiaa Suzuki, 1941 [*Unio ryosekiana; 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. ryosekiana (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.
teeth, slender. Rec., SE. Asaia.—Fig. D27, 4. *O. jurdyi (Morlet); 4a-c, LV ext., RV int., both valves dorsal, X1 (after Haas).

Palindonaia Morlet, 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 emszi Morlet, Cret., Eu.; RV ext., X1 (632).

Paranodonta Kobayashi & Suzuki, 1936 [*P. otai; 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., X1 (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, P. (P.) corregrata (Muller), Rec.; 2a,b, RV ext., LV int., X1 (497).

P. (Nyassunio) Haas, 1936 [*Unio nyassaensis Lea, 1864; OD]. Rounded triangular to quadrangular, old specimens elongate and descending
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, X0.5 (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.) crispisulcata (BENSON), Rec.; LV ext., X0.8 (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, X0.5 (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., LV int., both valves dorsal, X0.8 (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., X1 (Haas).

Plethobasus SIMPSON, 1900 [*Unio aesopus GREEN, 1827 (=*Obliquaria cyphya RAFAINESQUE, 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. cyphus (RAFINESQUE), Rec.; 3a,b, LV ext., both valves dorsal, X0.7 (497).

Pleurobema RAFAINESQUE, 1820 [*Unio mystiloides RAFAINESQUE, 1820; SD HERRMANNSEN, 1846]. Heavy, triangular to rhomboid, umbonal region prominent; beaks subanterior or anterior, incurved, pointing forward; beak sculpture coarse, consist-
Unionoida—Unionacea

Fig. D28. Unionidae (Unioninae) (p. N427-N429).

Regular 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

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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, with distinct posterior ridge.
Unionoida—Unionacea

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., 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 posterodorsally. 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 posterodorsally, 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 messengeri 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. messengeri (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. (Cosmopseudodon) HAAS, 1920 [*P. resupina-
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.N431-N432, N434).
Fig. D32. Unionidae (Unioninae) (p. N434-N435).
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.) auratus HEUDE; 1a,b, LV ext., RV int., ×1 (Haas).

P. (Diplosuedodon) HAAS, 1920 [*P. crassus DROUÉT, 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 DROUÉT; 6a-d, LV ext., RV int., LV int., both valves dorsal, ×0.7 (Haas).

P. (Indopsuedodon) PRAHASH, 1922 [*Anodon saluenius G. OULD, 1884; OD]. Characterized by considerable length and strong, plicate sculpture on alate posterior slope. Rec., SE.Asia. (Burm.)—Fig. D30.4. *P. (L.) saluenius (GOULD); LV ext., ×0.75 (Haas).

P. (Monodontina) CONRAD, 1853 [*Margaritifera vondembuschiana LEA, 1840; OD] [=Subborealis SIMPSON, 1900]. Rounded, compressed, anterior slope low, posterior high, alate, symphinite 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 [*Monocyclaidea nankensis 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.) nankensis (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 [*Monocyclaidea crebristriatus 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 (Burm.)-Indon. (Java).—Fig. D31.5. *P. (T.) crebristriatus (ANTHONY), Rec.; 5a-c, LV ext., RV int., both valves dorsal, ×0.75 (Haas).

Psychorhynchus simsonii, 1900 [*Unio pfiisteri 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. pfiisteri (HEUDE); 8a-c, LV ext., RV int., LV int., ×0.75 (Haas).

Rectidens SIMPSON, 1900 [*Unio prolongatus DROUÉT, 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 (DROUÉT), 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 mid-length, 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).

Scabes 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. scobinatus (LEA); 6a-c, LV ext., RV int., both valves dorsal, ×1 (after Haas).

Shistodesmus SIMPSON, 1900 [*Unio lampryanus 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; fulcra very strong and wide; umbonal cavities deep, compressed, right one opened by gap in the interdental interval. Rec., China.—Fig. D32.10. *S. lampryanus (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 sulcated, 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** Leroj, 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. V.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 sulcated; 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 tetralsmus 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 tetralsmus Say)] [=Uniomerus 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. tetralsmus* (Say); 5a-c, RV ext., LV int., both valves dorsal, ×0.5 (Lea).

**Unionea** Haas, 1955 [*Unio fabagina Deshayes & Jullien, 1874; OD] [=Unionella Haas, 1913 (non Etheridge, 1888)]. Small, ovate-rhomboideal, 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).
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, X0.7 (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.—Fig. D33,3. *V. (V.) beccarianus (Tapperone Canefri); 3a-c, LV ext., RV int., both valves dorsal, X0.7 (Haas).

V. (Leiovirgus) Haas, 1912 [*Unio misoolensis Scheepman, 1896; OD] [=Nesonia 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 (Scheepman); 4a-d, LV ext., RV int., LV int., both valves dorsal, X0.8 (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
Q. (Quadula). 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. *Unio* (A.) couchianus (LEA, 1860; OD) [=Bullata FRIERSON, 1927 (non JOUSSEAUME, 1875); Pustulosa FRIERSON, 1927]. Round, truncate, quadrate 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. D34.1. *Q. (O.) quadrala (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, truncate, quadrate 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. (Lutacarnea) FRIERSON, 1927 [*Quadula striata RAFINESQUE, 1820; OD] [=Striata FRIERSON, 1927 (non O. BOETTGER, 1878)]. Obovate, 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. AGASSI, 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; umbal region high; periostracum lustrous, with pattern of triangular spots or chevron-shaped lines; hinge strong, in some with auxiliary 3rd lamellar tooth in RV; umbal 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. (Pleuromyia) FRIERSON, 1927 [*Unio barnesiensis 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.) barnesiensis (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. AGASSI, 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.—Fig. D35.5. *A. (A.) plicata costata RAFINESQUE, Rec.; 5a,b, LV ext., both valves dorsal, ×0.5 (497).

A. (Plecaenesis) JORDAN, 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. (Psebula) HAAS, 1930 [*Quadula radul Simpson, 1900; OD]. Round to rounded quadrangular, ventricose to quite compressed; beaks prominent, with deep, commonly quite compressed cavities; umbral 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. southali; 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...
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 feebly. *Mio., N.Am.—Fig. D35.8. *C. arci-

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. *Lamprotula (RAFINESQUE), Rec.; LV ext., LV int., X 0.5 (568).

Disconya SIMPSON, 1900 [*Unio radulosis DROUET & 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 cord-like 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. *E. reynosina; LV ext., X 0.75 (Haas).

Eonoaias MARSHALL, 1929 [*E. reynosina; OD]. Beaks with numerous V-shaped loops, which are nearly regularly spaced and nested into each other, Vs pointing toward ventral margin; posterior areas with fine ribs running from posterior ridge to margin. *L. N.Am.—Fig. D35.4. *E. reynosina; LV ext., X 1 (Marshall).

Fusconaias SIMPSON, 1900 [*Unio trigonous LEA, 1831 (=subsp. of U. undatus BARNES, 1823); OD] [=?Linitoxia RAFINESQUE, 1820; ?Lyntoxia L. AGASSIZ, 1846, Fusconia FRIESEN, 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. *L. N.Am.-C.Am.—Fig. D36.2. *F. undata trigonous (LEA), Rec.; 2a-c, RV ext., LV int., both valves dorsal, X 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., X 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. *L. (P.) crassa (PING), Plio.; 2a,b, LV ext., X 0.5 (738).

Loxo pleurus MECK, 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 (MECK); LV ext., X 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., X 0.3 (Conrad).

Megalonoida MACNEIL, 1935 [*M. porcata; OD]. Large, subquadrature, 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., X 0.5 (568).

Piconaias MARSHALL, 1929 [*P. popenoei; OD]. Subquadrature; beaks with wavy concentric undulations, each posteriorly completed by fine straight threadlike rib running across postero dorsal area.
Fig. D36. Unionidae (Quadrulinae) (p. N439, N441-N442).
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., X0.7 (584).

**Potomida** SWAINSON, 1840 [*Unio corrugata* (=*Unio semirugatus* LAMARCK, 1819); OD] [=Potamida L. AGASSIZ, 1846; Psilunio, Rytia STEFANESCU, 1896; Sabbia Cossmann, 1897; Rhombunio GERMAIN, 1891; 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. (F.) littoralis semirugata* (LAMARCK), Rec., Eu.; la,b, RV ext., LV int., X1 (Ellis).

**P. (Cuncopsisa)** WENZ, 1928 [*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., X0.5 (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, lamel-
lar teeth strongly bent. U.Cret.(Lance), N.Am. ——Fig. D35,7. *P. perccorragata (WHITFIELD); 7a,b, RV ext., LV int., ×1 (Whitfield).

**Pseudaphia** SIMPSON, 1900 [*Unio biesianus HEUDE, 1877; OD]. Large, oval, inflated, gaping in front and behind, rather heavy, with full beads; 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).

**Psoronia** CROSE & FISCHER, 1893 [*Unio psoricus MORELET, 1851; OD]. Variable in shape, oval, subtriangular, 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).

**Rhombuniospis** 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).

**Scheepmania** HAAS, 1912 [*Unio nieuwenhuii SCAPEMAN, 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. nieuwenhuii (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).

**Tritongonia** 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 incurred, 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 cygnus LINNÉ, 1758, nom. conserv.] [=Glochidium RATHKE, 1797; Anodontigenus RENIER, 1807; Cista HUEBER, 1810; Anodon OKEN, 1815; Anodontes CUVIER, 1817; Edentula, Lipodonta NITSCHE, 1820; Anodontes FISCHER VON WALDHEIM, 1823; Onodon PARTINGTON, 1836-37; Anodontina SCHLUETER, 1853; Colletotherium BOURGUIGNAT, 1881; Pteranodon L. FISCHER, 1886; Eunodonta WESTERLUND, 1890; Nayadina de GREGORIO, 1914; Anodota PETROK, 1930; Colleterium BÉDIÉ, 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.


—Fig. D38.3. *A. (A.) cygnea (LINNÉ), Rec.; LV ext., X0.25 (497).
N444 Bivalvia—Palaeoheterodonta

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. Maerot.)-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] (=Uutterbachia, Utterbachia, 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 (149).

Anodontoides SIMPSON, 1898 [pro Anodontopsis SIMPSON, 1898 (non M'Coy, 1851)] [*Anodontia 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,
Unioidea—Unionacea

1814 (non Laurenti, 1768)] [*Dipsas plicatus Leach, 1815; OD] [=Barbala Museum Callonianum, 1797, nom. nud.; Appius Menke, 1830; Dianisotis Rafinesque, 1831; Dipsada Cuvier, 1834; Dipsax Voigt, 1834; Dipsus Gray, 1835; Dionisotis Féruссac, 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. (Miken Sel.) - 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, X0.3 (140).

C. (Pletholus) 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, X1 (497).

**Lepidodesma Simpson, 1900 [*Unio languitata 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; ligmement 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 scally, folded into hinge. **U. Plio. Rec., E. Asia.**

*Fig. D40.8. *L. languitatum (Heude), Rec.; 8a,b, LV ext., RV int., X0.4 (405).

**Leptonadonta Wenz, 1927 [*Dreissenomya unioides Wenz, 1927 (non Fuchs, 1870) (= Leptonadonta 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. Maec.). Eu. (Rumania).**

*Fig. D40.1. *L. rumana; Wenz; RV ext., X1 (966).

**Pilsbryconcha 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., X0.6 (Haas).

**Pseudanodonta Bourguignat, 1877 [*Anodonta complanata Rossmaessler, 1835; SD Westerlund, 1902] (= Pseudoanodonta Picaglia, 1893; Paeanodonta 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., X0.7 (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, X1 (Haas).

**Sphrophitus Rafinesque, 1820 [*Anodonta undulata Say, 1816; OD] (= Strophites Deshayes, 1832; Strophites Gray, 1847; Strophites Desmaest, 1859).** Elliptical to rhomboideal, 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. (Sphrophitus). Smooth. **Rec., N. Am.**

*Fig. D40.4. *S. (S.) undulatus (Say); LV ext., X1 (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, X0.9 (Walker).

**S. (Pseudodonticoides) Frierson, 1927 [*Margaritana alabamensis Lea, 1861; OD] (= Pseudodonticoides 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 obsolete or absent. **Rec., N. Am.**

*Fig. D40.6. *S. (P.) alabamensis (Lea); 6a,b, RV ext., LV int., X0.5 (140).
Subfamily ALASMI DONTINAE 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] [=Alasmidonta Say, 1819; Alasmodonta Thomas, 1820; Alasmidonta de Blainville, 1825; Amphalamdon Rafinesque, 1831; ?Anodontina Schulteter, 1838; Uniopsis, Hemidon, Hemiodon Swainson, 1840; Anelasmodonta don L. Agassiz, 1846; Anelasmodonta Herrman sen, 1846; Alasmidonta Gray, 1847; Alasmidonta Gray, 1847; Unionopsis Meek, 1876]. Oval-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.--FIG. D41,6. *A. (A.) undulata (Say), Rec.; 6a, b, LV ext., both valves dorsal, X 0.8 (Haas, n).

A. (Bullella) Simpson, 1900 [*Margarita (Margaritana) arcuca 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., \( \times 1 \) (140).

A. (Decurambis) Rafinesque, 1831 [*Alasmidonta scripta Rafinesque, 1831 (=Alasmidonta marginata Say, 1818); OD] [=Decurambis 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., \( \times 0.8 \) (343).

A. (Pegias) Simpson, 1900 [*Margaria (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, \( \times 1 \) (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, B, LV ext., RV int., both valves dorsal, \( \times 1 \) (Walker).

A. (Prolasmodonta) Ortman, 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, \( \times 1 \) (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 show 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., \( \times 0.8 \) (Walker).

Arkansia Ortman & Walker, 1912 [*A. wheeleri; OD]. Moderately thick, subrounded 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., \( \times 0.8 \) (Walker).

Lasmigona Rafinesque, 1831 [*Alasmidonta rugosa Barnes, 1823 (=Alasmidonta costata Rafinesque, 1820); OD] [=Elasmogona L. Agassiz, 1846; Elasmogona 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); 3a-c, LV ext., RV int., both valves dorsal, \( \times 0.3 \) (497).

L. (Platynaisia) Walker, 1918 [*Symphinita 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, \( \times 0.3 \) (497).

L. (Pterosyna) Rafinesque, 1831 [*Alasmidonta complanata Barnes, 1823; OD] [=Complanaria, ?Megadomus Swainson, 1840; Pterosyna 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, \( \times 0.3 \) (497).

L. (Sulcularia) Rafinesque, 1831 [*Alasmidonta badia Rafinesque, 1820; OD] [=Alasmiptormann, 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, \( \times 1 \) (497).

Simpsonaias Frierison, 1914 [*Alasmidonta ambigua Say, 1825; OD] [=Simpsoniconcha Frierison, 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. ambiguа (SAY); RV ext., X1 (Walker).

Vanderschlieca Modell, 1943 [*Unio kolasi 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. kolasi (Modell); 2а,b, LV ext., RV int., X1 (631).

Fig. D42. Unionidae (Alasmidontinae) (p. N448).
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 Hermannsen, 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, X 0.6 (497).

L. (Cyrtonaias) Crosse & Fischer, 1893 [*Unio berlandieri Lea, 1857; OD] [=Cyrtonaias Frier­ son, 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., X 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., X 0.7 (306).

L. (Disconaias) Crosse & Fischer, 1893 [*Unio discus Lea, 1838; OD]. Large, oval or sub-trigonal, 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, X 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., X 0.4 (306).

L. (Orunanniana) Frier­ son, 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, X 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., X 0.7 (306).

L. (Venustaconcha) Frier­ son, 1927 [*Unio venusta­ tus Lea, 1838; OD] [=Venusta Frier­ son, 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., X 1 (533).

L. (Villosa) Frier­ son, 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.
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.

Carunculina Simpson, 1900 [*Unio texensis Lea, 1857; OD*] [*Toxolasma Rafinesque, 1831; ?Toxelasma L. Agassiz, 1847*]. Small, inflated, obovate, rather solid; periostracum thick, lusterless, almost rayless, clothlike; beak sculpture consisting...
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 some-
what pointed behind, female shell truncated obliquely on posterior base. Rec., N.Am.—Fig. D45,1. *C. parva texensis* (Lea); 1a,b, RV ext., LV int., X1 (535).

**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, X0.5 (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., X1 (Reeve).

**Cyprogenia** L. Agassiz, 1852 [*Obovaria stegaria* Rafinesque, 1820; OD] [=*Crypogenia* Fischer, 1886]. Heavy, inflated, rounded triangular, mostly triangular 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 motting 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., X1 (535).

**Dysnomia** L. Agassiz, 1852 [*Obliquaria flexuosa* Rafinesque, 1820; OD] [=*Epilobasma* Rafinesque, 1831; *Dysnomia* Biez, 1869; *Dysnomia* 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., X0.5 (Walker).

D. **(Capsaeformis)** Frieron, 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-
saeformis (LEA); 5a-c, δ RV ext., ϕ RV ext., both valves dorsal, X0.5 (497).

D. (Penita) FRIERSON, 1927 [*Unio penitus CONRAD, 1834; OD]. Somewhat quadrate, not sharply truncate behind; swelling of female in front of posterobasal point and rounded below. Rec., N.Am.——Fig. D46.7. *D. (P.) penita (CONRAD); LV ext., X1 (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, δ RV ext., ϕ RV ext., X0.5 (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, δ RV ext., ϕ RV ext., X0.5 (Walker).

D. (Torulosa) FRIERSON, 1927 [*Amblema torulosa RAFFINESQUE, 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 (RAFFINESQUE); 6a-c, RV ext., LV int., both valves dorsal, X0.7 (535).

D. (Truncillosis) ORTMANN & WALKER, 1922 [*Truncilla triqueter RAFFINESQUE, 1820; OD]. Greatly inflated, sharply truncate posteriorly; inflation of female shell at extreme posterobasal point. Rec., N.Am.——Fig. D46.1. *D. (T.) triqueter (RAFFINESQUE); 1a,b, δ RV ext., ϕ RV ext., X0.5 (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., X1 (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, X0.8 (497).

Leptodea RAFFINESQUE, 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.

Ligumia Swainson, 1840 [*Unio recta Lamarck, 1819; OD] [=Potamilus, Potamila Rafinesque, 1818; Sintoxia Rafinesque, 1820; Ligumea Swainson, 1840; Syntoxia L. Agassiz, 1847; Medianidus

Legumia L. Agassiz, 1852; Ligumina Philippi, 1853; Syntonia Schaeffer, 1869; Symptonia 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, X0.3 (497).

Medionidus Simpson, 1900 [*Unio conradiatus* 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. conradiatus* (Lea); 3a,b, LV ext., both valves dorsal, X1 (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., X1 (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., both valves dorsal, X1 (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, X0.6 (497).

O. (Pseudoon) Simpson, 1900 [*Unio elliptis* Lea, 1828 (=*Amblyea olivaria* Rafinesque, 1819); OD] [=Actionaia 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, X0.75 (497).

Pachyniaes Crosse & Fischer, 1893 [*Unio spheno­topsis* Morelet, 1849; OD] [=Acanthasaurus Martin, 1900; Ptychodroma 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. spheno­topsis* (Morelet); LV ext., X1 (306).

Plagiola Rafinesque, 1819 [*Unio securus* Lea, 1829 (=*Obliquaria depressa* Rafinesque, 1820); OD] [=Plagiolopsis Theile, 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, X1 (535).

Proptera Rafinesque, 1819 [*Unio alatus Say, 1825; SD Herrmannsen, 1846] [=Megalptera Rafinesque, 1820; Symphy­tona Lea, 1829; Noidea, Lymnaea, Lymnaida Swainson, 1840; Symphynota Villa, 1841; Limnacea L. Agassiz, 1846; Noidea Schaeffer, 1869; Symphynota, Symphytona 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 feebly, 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. *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

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**Fig. D48. Unionidae (Lampsilinae) (p. N455-N457).**
square spots. *U. Oligo.* (Cyrenena-Mergel.)-Rec., C.Eu.-N.Am.—Fig. D48,2. *P. (P.) fasciolaris* (Hildreth), Rec., C.Eu.; 2ae-c, LV ext., RV int., both valves dorsal, X 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); la-c, LV ext., RV int., both valves dorsal, X 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, X 0.6 (497).

**Subfamily HYRIINAE** Ortmann, 1911

This family-group name, based on a junior synonym of *Pristodon*, 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.

**Pristodon** Schumacher, 1817 [*P. obliquus*; SD Simpson, 1896] [=Triquetra Klein, 1753 (nom. nud., pre-Linnean); Hyria Lamarck, 1819; Hyria de Blainville, 1821; Hyria 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 with 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., X 0.4 (Sowerby).

**Fig. D49. Unionidae (Hyriinae) (p. N457, N460-N461).**
Antediplodon Marshall, 1929 [*Unio dumbeii 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. dumbeii (Simpson); RV ext., X0.8 (584).

Callonaia Simpson, 1900 [*Castalia duprei Reclus, 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 (Reclus); 3a,b, LV ext., both valves dorsal, X0.5 (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, X1 (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., N.E.S.Am.—Fig. D50,6. *C. sulcata (Krauss); 6a-c, RV ext., LV int., RV int., X0.8 (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.,

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**Fig. D51. Unionidae (Hyriinae) (p. N460-N461).**
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 Spik, 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 ridges. Beaks with radial sculpture similar to that of Diplodon and Prisodon; radial ribs arranged in a V-pattern, each V nesting in succeeding one; posterior dorsal area crossed obliquely by several plicate to the margin. Rec., S.Am.—Fig. D51,6. *E. bibiana; ?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. Rec., S.Am.—Fig. D51,7. *E. gardnerae; LV ext., ×0.8 (583).

Hyridella Swainson, 1840 [*Unio australis Lamarck, 1819 (=Unio napeonensis Conrad, 1840); OD] [=Propehyridella Cotton & Gabriel, 1932]. Elongate elliptical to short ovoid or subrhomboid; beaks rather low, sculpture consisting of curved, generally nodulate 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. (Veleunio), but ornamented in juveniles by divericate, 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. (Lottiella) 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, subhomboidal, 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.) ambiguus* (Philippi), 3a,b, LV ext., both valves dorsal, ×0.8 (497).

**Paxyodon** Schumacher, 1817 [*P. ponderosus* (= *Mya symmatophora* Gronovius, 1781); OD] [=Pachydon de Blainville, 1825; Paxydonta Dehays, 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 striae; 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); Pliol., S.Am.(Venez.).—Fig. D51,4. *P. singewaldi*, Tert., Peru; RV ext., ×0.8 (583).

**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.).
Chelidonopsis

Lamproscapha

Iheringella

Ruganodontites

Anodontites

Arthropteran

Aphantaria

Diplodontites

Fossula

Haasica

Chambardia


---Fig. D53.3. *P. gobiensis; RV ext., ×1 (569).

Triplodon Spix, 1827 [*T. rugosum; OD] [=Niaa Lea, 1836; Naia Swainson, 1840; Niaea Morch, 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. (Triquetra) Simpson, 1900 [*Unio stevensii Lea, 1871; OD]. Compressed, with feebly de-
developed posterior wing. Rec., S.Am.—Fig. D53, 1. *T. (T.) stevensi (Lea); RV ext., ×0.8 (535).

Family MUTEILIDAE 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 supernal openings not separated; mantle generally closed behind into separate branchial and anal siphons; marsupium occupying inner gills; lasidium larva commonly closed behind into separate posterior sinus. Labial palps large, anal and branchial and anal siphons; marsupium opposed of three segments, median one bearing single shell. ?Trias., Cret.-Rec.

Mutela Scopoli, 1777 [*Mytilus dubius Gmelin, 1791; OD] [=Purpura Férussac, 1826; Spatha Lea, 1838; Calliscapha Swainson, 1840; Mutelina Bourguignat, 1885; Utela Moore, 1898; Pseudo­mutela Simpson, 1900]. Elongate, oblong to sub-triangular, smooth, with low, unornamented beaks; posterior ridge rounded; periostracum moderately developed posterior ridge and above which it is somewhat truncated; beaks low; periostracum green to olivine. Rec., S.Am.—Fig. D54,5. *A. (A.) cristatus, Tert.; RV ext., ×0.5 (Marshall).

A. (Lamproscapha) Swainson, 1840 [*Anodonta 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, microscopic­ially 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 (385).

Aspatharia Bourguignat, 1885 [*Margarianna vignonana 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. ouassouloni; OD]. Oval, smooth, moderately convex; lunule large, narrowly lanceolate; beak sculpture unknown. [Subgenus of dubious validity.] Rec., Afr.—Fig. D54,7. *A. (A.) ouassouloni; both valves dorsal, ×0.7 (Rochebrune).

A. (Chambardia) Bourguignat, 1890 [*C. leturneutxi; SD Haas, 1957] [=Spathella Bourguignat, Dec. 1885 (non T. Hall, Nov. 1885); Spathopsis Simpson, 1900; Leptostapha Rochebrune & Germain, 1904; Miroyodon 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. *A. (C.) rubens* (LAMARCK), Rec.; 13a,b, LV ext., RV int., ×0.4 (140).

**Diplodontites** MARSHALL, 1922 [*D. cookei*; OD]. Elliptical, moderately thick; beaks elevated; lunule triangular; periostracum clothlike, dull, yellowish-olive, with 10 radiating, greenish stripes on posterosdorsal 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 with 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, 1858; Platyris L. AGASSIZ, 1846; Eufira GISTEL, 1848; ?Irida 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. (1.) *exotica*; 4a,b, RV ext., LV int., ×0.3 (140).

II. (Cameronia) BOURGUIGNAT, 1879 [*Iridina spekei* WOODWARD, 1859; OD]. Oblong, hinge
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] [=Pleiodon Swainson, 1840; Pleiodon 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 Linne, 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] [=Apidon Spix, 1827 (non Rafinesque, 1818); Monocondyla Gray, 1840; Monocondylea d'Orbigny, 1844; Monocondylus Morelet, 1866; Monocondyloia Paetel, 1875; Monocondyloan 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
Etheria, 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 biangular 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, 1. *P. tanganyicensis* (Smith); 6a,b, RV ext., LV int., ×0.55 (E. A. Smith).

Tamsiella Haas, 1931 [*Monocoelylae tamsiana Dunker, 1858; OD*. Resembles *Monocoelylae*; 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 Ferussac, 1823; OD*] (=*Mulleria Ferussac, 1823 (non Mullera Leach, 1814); Multeria Philippi, 1853; Acostea Gray, 1854; Eumulleria Anthony, 1907].
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 (FÉRUSSAI); RV ext., ×0.6 (Sowerby).

A. (Pseudomulleria) ANTHONY, 1907 [*Mulleria dalyi E. A. SMITH, 1898; OD] [=Pseudomulleria PILSBRY, 1911]. Irregularly quadrate, without decided anterior projection; anterior adductor muscle obsolete. Rec., India.—Fig. D57.1. *A. (P.) dalyi (SMITH); la,b, RV ext., LV int., ×0.5 (E. A. Smith).

Bartelletia A. ADAMS, 1866 [*Etheria stefanensis MORICAND, 1856; OD] [=Bartelletia PARTEL, 1875; Rochania 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, equivalent, subequilateral, subtrigonal, but with posterior end high and subtruncated; length and height almost equal; blunt diagonal ridge delimiting relatively narrow posterior area; shell wall thick; umbones moderately well inflated and incurred, 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-CHALMERS in HAUG, 1905 [*D. foureaui; M]. Characters of family. L.Cret., N. Afr.—Fig. D58.1. *D. foureaui, Fort Flatters, N.Afr.(Alg.); la-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, equivalent, 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 naacreous interior has been found in specimens of Trigonodus.

Pachycardia HAUER, 1857 [*P. rugosa; OD] [=Pachycardia Mojsisovics, 1879 (nom. null.)]. Medium-sized, cuneiform, strongly inequilateral, well inflated, some specimens subcylindrical 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 anterodorsal margin (where presence of weak anterior cardinal is constant) 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, =Venuilites donacinius VON SCHLOTHEIM, 1820; SD Cox, 1961); Anodontophora COSMANN, 1897 (pro Anoplophora ALBERTI) (type, Myacites jas-saniis Wissmann in Münster, 1841; SD StolizkA, 1871); Anaplophora HEALEY, 1908 (nom. null.); Anaplophoria ZELLER, 1908 (nom. null.); Unionina DIENER, 1923 (nom. null.); Anodontophora PARONA, 1928 (nom. null.)]. Small, ovate rectangular or trapeziform, inequilateral, of feeble to moderate convexity; lunule and escutcheon present or absent; ligament external, ophisthodetic; nympha 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 postero-dorsal 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 oral-
mented 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.*

**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), X1; 4b-c, latex replicas LV ext. and int., X1; (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 pseudo-cardinal tooth in LV and corresponding socket in RV. *U.Trias., Bear Is.(Arctic)-Ellesmereland-Japan.*—Fig. D60,5. *P. paucicostatus* Nakazawa, N.; Nabae F., Japan; latex replica, both valves, int. molds, X1 (Nakazawa, n).

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**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., X1 (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. bowralensis; family & eardiiformis; 3a,b, order Trigoniacea DALL, LAROCQUE

Unionella ETHERIDGE, 1888 [*U. bowralensis; OD]. Quadrangular to irregularly trapeziform, equivale, 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. bowralensis; both valves, dorsal, \( \times 1 \) (299).

Order TRIGONIOIDA Dall, 1889 [nom. correct. NEWELL, 1965 (ex order Trigoniacea DALL, 1889)] [Diagnosis by N. D. NEWELL]


Superfamily TRIGONIOacea Lamarck, 1819 [nom. transl. DALL, 1900 (ex "les trigonees" LAMARCK, 1819) [Diagnosis by L. R. COX]

Shell equivale; 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 DOUVILLE 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 & AURELE LABOUCHE]

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 MCCoy, 1851)]. Anterior surface smooth; postumbonal slope with faint radial costellae; sinapalliate. M.Ord.-U.Ord., E.N.Am.-Eu.——Fig. D62, l. \( \times 1 \), 2, 3 (929).
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.

Myophoria Bronn in Alberti, 1834, p. 54 [*Trigonellites vulgaris von Schlotheim, 1820, p. 192; SD Hermannsen, 1847, p. 80] [=Trigonellites von Schlotheim, 1820 (non Parkinson, 1811); Cryptina Deshayes in Boué, 1835, p. 47]
Trigonoiida—Trigonacea

(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; myophyrous buttress well developed. L.Trias.—U.Trias., Eu.—Asia.—N.Afr.—Fig. D63,1. *M. vulgaris (von Schlotheim), M. Trias. (Muschelkalk), Ger.; 1a,b, LV ext. and int., X 2; 1c, LV int., X 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; myophyrous buttress absent or indistinct. V.S.(Tex.—Wyo.); L.Perm., cosmop.—Fig. D63,4. *E. truncatus (Goldfuss), Dev., Ger.; 4a,b, LV ext. and int. hinge, X 1; 4c, RV int. hinge, X 1 (47).

Gruenewaldia Wörnmann, 1889, p. 215 [*Cardita decussata von Münster, 1837, p. 185; M] [=Elephantinia 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; myophyrous buttress inconspicuous. M.Trias.—U.Trias., Eu.—Asia—Bear Is.—Fig. D63,2. *G. decussata (von Münster), U. Trias., S.Tyrol; RV ext. and int., X 1.5 (58).

Hefteria Dahmer, 1948, p. 125 [*Cardina 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 *Eschizodus*, and with right posterior tooth well developed. L.Dev., Eu.(Ger.).

Heminajas Neumayr, 1889, p. 789 [*Myophoria fusetidens Wörnmann, 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; myophyrous buttress present. L.Trias.—U.Trias., Eu.—(Aust.—Hung.).—Fig. D63,10. *H. fusetidens (Wörnmann), U. Trias., Aus.; 10a,b, LV ext. and int., X 1; 10c, RV int., X 1 (Arthaber, 1905, 1002).

?Liotrigonia Cox, 1952, p. 53 [*Trigonia lingosensis Dumortier, 1869, p. 275; OD]. Trigonally ovate, slightly inequilateral, larger than typical Myophoridae; umbones prominent, sharply rounded, beads orthogyrous; marginal carina well marked, coinciding with most inflated part of valve; area slightly concave, smooth, escutcheon...
Fig. D63. Myophoriidae (p. N472-N473, N475-N476).
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., x1 (554); 1b, LV int., France, x1 (Dumortier, 1869).
Neoschizodus GIEBEL, 1855, p. 35 [*Lyrodon laevigatum GOLDFUSS, 1837, p. 197; SD STOLICZKA, 1871, p. xx] [=Levecica 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. johnstoni)]. 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., x2, x2.7 (Hohenstein, 1913).
Rhenania WAAGEN, 1907, p. 149 [*Myophoria schwelmensis BEUHAUSEN, 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., Eng. (Ger.).—Fig. D63,5. *R. schwelmensis (BEUHAUSEN), Givet.; 5a,b, RV ext. and int., x2; 5c, LV int., x1 (47).
Schizodus DE VERNEUIL & MURCHISON, 1844, p. 505 (ex KING, MS) [*Axinus obsculus ]. SOWERBY, 1821, p. 12; SD DE VERNEUIL, 1845, p. 308] [=?Leptodomus MCCoy in GRIFFITH, 1844, p. 66 (non SCHOENHERR, 1843); Prisciona ConRAD, 1867, p. 10 (type, P. ventricosa); Axiolinopsis TATE, 1868, p. 412 (pro Schizodus “King,” non Schizodon WATERHOUSE, 1842); ?Niobe de

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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 sub-umbonal 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 (BEUHSAUSEN), 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 redditus GRAY, 1823 (as “Trigoniana”) et correct. KING, 1850, pro “les trigonces” 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 an-
terior 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...
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, pI. 4, fig. 9; ICZN Opinion 327 (1955)] [=Lyridon J. de C. SOWERBY, 1823 (obj.); Lyriodon BRONN, 1834 (nom. van.); Lyonodon 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.-V.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. (Kumatrigoria) TAMURA, 1959, p. 213 [*Frenguelliella (Kumatrigoria) 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) KOYAYASHI in KOYAYASHI & TAMURA, 1957; p. 36 [*|Latitrigonia pyramidalis KOYAYASHI & TAMURA, 1957; OD]. Rather small, subquadrat, with wide, mostly smooth area occupying almost half of surface in some species; flank costae widened, 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 antecarinial 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 and area ornament of irregular concentric folds; hinge as in Praegonia. M.Trias. (Ladin., Kaikhuan), 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. N480-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., X1 (Whiteaves, 1876).

Asiatrigotrigonia Cox, 1952, p. 63 [*Trigonia sultanuusi Archangelski, 1916, p. 32; OD]. Obliquely ovate, not tapering or truncated posteriorly, strongly inequilateral; no carinae; area and escutcheon undefined; posterior region ornamented; 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.), Turkistan.—Fig. D66,6. *A. sultanuusi (Archangelski); RV ext., X0.7 (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), X0.7 (Skwarko, 1963).

Buchotrigonia Dietrich, 1938, p. 97 [*Trigonia abrupta von Buch, 1838, p. 65; M]. Trigonal, short; area wide, transversely ridged in early growth stages, later smooth; flank with narrow, nontuberculate costae discretely or obliquely arranged. L.Cret.-U.Cret., S.Am.-Spain-Syria-N.Z.


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., X1 (Noetling, 1886).

Climatritoigonia 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 ruiase; 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., X1 (Cox, n).

Eotrigonia Cossmann, 1912, p. 26 [*Trigonia semiundulata M'Coy, 1866=*T. subundulata Jenkings, 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. semiundulata (Jenkings), Oligo., Australia; RV ext., X2 (161).

Geratrigotrigonia Kobayashi in Kobayashi & Mori, 1954, p. 171 [*Trigonia houourensii Yokoyama, 1904, p. 11; OD]. Trigonal, 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 rather oblique to concentric, 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, bipartite; flank with narrow, subconcentric, nontuberculate costae which are rather irregular, particularly in early growth stages. L.Jur.(L.Lias.), Japan.—Fig. D68,3. *I. masatanii Kobayashi & Tamura; RV ext., X2 (Kobayashi & Tamura, 1957).
Indotrigonia Dietrich, 1933, p. 30 [*Trigonia smeii 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. smeii (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 burckhardtii 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. burckhardtii (Jaworski), L.Jur. (Lias.), Arg.; LV ext., ×0.7 (Jaworski, 1915).

Korobkovitrigonia Saveliev, 1958, p. 99 [*K. korobkowi; OD]. Oval 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. (Barrern.-Turon.), C.Asia-Spain-Port.-Alg.-S. Am.—Fig. D69,2. *K. korobkowi, L.Cret. (Alb.), C.Asia (Mangyshlak); LV ext., ×0.85 (Saveliev, 1958).

Laevitrigonia Lebrüchner, 1932, p. 35 [*Trigonia gibbosa J. Sowerby, 1819, p. 61; OD] [=Laevitrigonia Deecke, 1925 (nom. nud.)]. Ovalate, 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. (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. N483, N485).
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. (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. tarameakensis; 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. tarameakensis; RV and LV ext., ×1 (Freneix, 1958).

Microtrigonia Nakano, 1957, p. 116 [*M. amanoi; OD]. Small, suborbicular; marginal carina in-
Fig. D73. Trigoniidae (p. N485-N487).
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) [==Haidalia CRICKMAY, 1930, p. 51 (type, Trigonia dawsoni WHITHEAVES, 1878, p. 154); Scaphogonia CRICKMAY, 1930, p. 51 (type, S. argo); Scaphitrigon CRICKMAY, 1930, p. 50 (nom. null.)]. Clavitrigonia LEBKUCHNER, 1932, p. 38 (type, Trigonia clavellata J. SOWERBY, 1815, === T. clavellata TOWNSEND, 1813, p. 141); Clavitrigonia LEANZA, 1942, p. 162 (type, T. clavellata J. SOWERBY, 1815; Promyophorella KOBAYASHI & TAMURA, 1955, p. 96 (type, Myophorella (Promyophorella) sigmoidealis)]. 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).


Myophorogonia COX, 1952, p. 52 [*Myophoria puc- ciccotata JAWSORSKI, 1922, p. 126; OD] [=Myo- phorogonia 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 sub-ordinate concentric costae confined in some forms to its anterior part. U.Trias.-M.Jur. (Bajoc.), Peru-Mex.-Bearls.-Eng. === Fig. D71,3. *M. puciccostata (JAWSORSKI), U.Trias., Peru; LV ext., ×2 (446).

Neotrigonia Cossmann, 1912, p. 25 [*Trigonia pec- tinata 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 cari- nae; escutcheon not impressed. Oligo.-Rec., Aus- tralia. === Fig. D71,9. *N. pectinata (LAMARCK), Rec.; RV ext., ×1 (161).

Nipponotrigonia COX, 1952, p. 53 [*Trigonia ki- kuchiana YOKOYAMA, 1891, p. 363; OD]. Trigonal- ly 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 cinucta ETHERIDGE, 1902, p. 28; OD]. Pyriform, elongate, posteriorly subprostrate; escutcheon carina well defined, escutcheon unimpressed; area narrow, radically ribbed; flank with a broad antecarinal de- pression; remainder of its surface with rounded costae. L.Cret., Australia.

N. (Nototrigonia) Antecarinal depression smooth; flank costae moderately oblique, rather sinusus. 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 rib- let; 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 ret- orsra KITCHIN, 1903, p. 57]. Elongate, very inequi- lateral, with narrow, prominent, strongly opisthogyrous umbones and subprostrate posterior extremity; marginal carina well defined, at least near umbo; area narrow, smooth; flank with broad, smooth or transversely ridged antecarinal depres- sion, remainder of its surface with rather irregular, mostly subconcentric costae. U.Jur. (Tithon.), India-E.Afr. === Fig. D70,1. *O. retorsa (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 con- fined 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. combsii; OD]. Ovate, with low prostogyrous 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. combsii; RV ext., ×1 (Fleming, 1962).

Prosogyrotrigonia COX, 1952, p. 57 [*Trigonia seranen- sit KRAMBECK, 1923, p. 211; OD]. Elongate-pyriform, attenuated and subprostrate posteriorly; marginal carina not defined; flank with concentric costae which do not reach smooth pos- terior area. U.Trias., Ceram. === Fig. D71,8. *P. seranensis (KRAMBECK); RV ext., ×1 (486).

Prosogyractrigonia KRAMBECK, 1924, p. 244 [*P. timorenensis; M]. Evenly ovate, strongly inequi- lateral, beaks prostogyrous; marginal carina absent, border of area marked only by change in orna- ment; 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. N487-N488).
Pterotrignia 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.(U.Lias.)-U.Cret., cosmop.

P. (Pterotrignia) Dietrich, 1933, p. 330 [*Trigonia scabra Lamarck, 1819, p. 63; OD]. Posterior end broader than in P. (Pterotrignia) and not rotoste; 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).

Ruitirigonia 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).

Scaphotrignia 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.Cret.(U.Lias.)-Eur.; 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).

Sphenotrignia Rennie, 1936, p. 365 [*Trigonia (Sphenotrigonia) frommursei; OD]. Elongate-cuneiform, with obnute, terminal, prosogyrous umbones; marginal and escutcheon carinae absent except in early growth stages; area smooth; flank with broad, irregular undulations. L.Cret.(Neo-com.), S.Afr.——Fig. D74.5. *S. frommursei; LV ext., ×0.7 (785).

Steinmannella Crickmay, 1930, p. 50 [*Trigonia holubi Kitchin, 1908, p. 103; OD] [=Steinmannella Kobayashi & Amano, 1955 (nom. van.) (non Steinmannella Welter, 1911); Steinmannaea Crickmay, 1962 (pro Steinmannella)]. Oblong to suborbicular; marginal carina rounded off or indistinct; area with median groove and with or without transverse ridges; escutcheon with transverse tuberculate costae; most of flank ornamented with oblique tuberculate costae. L.Cret.-U.Cret., S.Afr.-S.Am.-W.N.Am.-Japan.

S. (Steinmannella) [=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) Savlev, 1958, p. 97 [*Trigonia litschkovii Morbulko, 1953, p. 341; OD]. Like S. (Steinmannella) and 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 (Savlev, 1958).

S. (Setotrigonia) Kobayashi & Amano, 1955, p. 206 [*S. (Setotrigonia) shishoharae; 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.

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S. (Ycharella) 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]. Trigonal, 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. (Orthotrigna) 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 noda 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.) noda (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 umb; 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 Trigonacea, although Kobayashi has suggested that the unionid genus Nippononaia may have been descended from Trigonioides. Cox has advocated reference of the family to the Unionacea and Martinson originally regarded Protunio as a unionid.
FIG. D76. Trigonioididae (p. N489).

**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, *L.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. sculturensis*; SD Martinson, 1961, p. 209]. Sub-trigonal, subtruncate anteriorly, with prominent, anteriorly placed, orthogyrus 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. sculturensis*, 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. Philipp, 1899, p. 74 [*Tri­agonia? 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. Philipp, 1899, p. 94 [*Tri­agonia? 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).