TREATISE ON
INVERTEBRATE PALEONTOLOGY

Prepared under the Guidance of the
Joint Committee on Invertebrate Paleontology

Paleontological Society

Society of Economic Paleontologists and Mineralogists

Palaeontographical Society

Directed and Edited by

RAYMOND C. MOORE

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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 will bear the assigned index letter joined with numbers beginning with 1 and running consecutively to the end of the part. When the parts ultimately are assembled into volumes, no renumbering of pages and figures is required.

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 being undertaken in a separate work, 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 the Joint Committee on Invertebrate Paleontology representing 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.

FORM OF ZOOLOGICAL NAMES

Many questions arise in connection with the form of zoological names. These include such matters as adherence to stipulations concerning Latin or Latinized nature of words accepted as zoological names, gender of generic and subgeneric names, nominative or adjectival form of specific names, required endings for some family-group names, and numerous others. Regulation extends to capitalization, treatment of particles belonging to modern patronymics, use of neo-Latin letters, and approved methods for converting diacritical marks. The magnitude and complexities of nomenclature problems surely are enough to warrant the complaint of those who hold that zoology is the study of animals rather than of names applied to them.

CLASSIFICATION OF ZOOLOGICAL NAMES

In accordance with the "Copenhagen Decisions on Zoological Nomenclature" (London, 135 p., 1953), zoological names may be classified usefully in various ways. The subject is summarized here with introduction of designations for some categories which the *Treatise* proposes to distinguish in systematic parts of the text for the purpose of giving readers comprehension of the nature of various names together with authorship and dates attributed to them.

CO-ORDINATE NAMES OF TAXA GROUPS

Five groups of different-rank taxonomic units (termed *taxa,* sing., *taxon*) are discriminated, within each of which names are treated as co-ordinate, being transferrable from one category to another without change of authorship or date. These are: (1) Species Group (subspecies, species); (2) Genus Group (subgenus, genus); (3) Family Group (tribe, subfamily, family, superfamily); (4) Order/Class Group (suborder, order, subclass, class); and (5) Phylum Group (subphylum, phylum). In the first 3 of these groups, but not others, the author of the first-published valid name for any taxon is held to be the author of all other taxa in the group which are based on the same nominate type and the date of publication for purposes of priority is that of the first-published name. Thus, if author A in 1800 introduces the family name X-idae to include 3 genera, one of which is *X-us;* and if author B in 1850 divides the 20 genera then included in X-idae into subfamilies called X-inae and Y-inae; and if author C in 1950 combines X-idae with other later-formed families to make a superfamily X-acea (or X-oidea, X-icae, etc.); the author of X-inae, X-idae and X-acea is A, 1800, under the Rules. Because taxonomic concepts introduced by authors B and C along with appropriate names surely are not attributable to author A, some means of recording responsibility of B and C are needed. This is discussed later in explaining proposed use of *"nom. transl."*

The co-ordinate status of zoological names belonging to the species group is stipulated in Art. 11 of the present Rules; genus group in Art. 6 of the present Rules; family group in paragraph 46 of the Copenhagen Decisions; order/class group and phylum group in paragraphs 65 and 66 of the Copenhagen Decisions.

ORIGINAL AND SUBSEQUENT FORMS OF NAMES

Zoological names may be classified according to form (spelling) given in original publication and employed by subsequent authors. In one group are names which are entirely identical in original and subsequent usage. Another group comprises names which include with the original subsequently published variants of one sort or another. In this second group, it is important to distinguish names which are inadvertent changes from those constituting intentional emendations, for they have quite different status in nomenclature. Also, among intentional emendations, some are acceptable and some quite unacceptable under the Rules.

VALID AND INVALID NAMES

Valid names. A valid zoological name is one that conforms to all mandatory provisions of the Rules (Copenhagen Decisions, p. 43-57) but names of this group are divisible into subgroups as follows: (1) *"inviolate names,"* which as originally published not only meet all mandatory requirements of the Rules but are not subject to any sort of alteration (most generic and subgeneric names); (2) *"perfect names,"* which as they appear in original publication (with or without precise duplication by subsequent authors) meet all mandatory requirements and need no correction of any kind but which nevertheless are legally alterable under present Rules (as in changing the form of ending of a published class/order-group name); (3) *"imperfect names,"* which as originally published and with or without subsequent duplication meet mandatory requirements but contain defects such as incorrect gender of an adjectival specific name (for example, *Spironema recta* instead of *Spironema rectum*) or incorrect stem or form of ending of a family-group name (for example, Spironemidae instead of Spironematidae); (4) *"transferred names,"* which are derived by valid emendation from either of the 2nd or 3rd subgroups or from a pre-existing transferred name (as illustrated by change of a family-group name from -inae to -idae or making of a superfamily name); (5) *"improved names,"* which include necessary as well as somewhat arbitrarily made emendations allowable under the Rules for taxonomic categories not now covered by regulations as to name form and alterations that are distinct from changes that distinguish the 4th subgroup (including names derived from the 2nd and 3rd subgroups and possibly some alterations of 4th subgroup names). In addition, some zoological names included among those recognized as valid are classifiable in special categories, while at the same time belonging to one or more of the above-listed subgroups. These chiefly include (7) *"substitute names,"* introduced to replace invalid names such as junior homonyms; and (8) *"conserved names,"* which are names that would have to be rejected by application of the Rules except for saving them in their original or an altered spelling by action of the International Commission on Zoological Nomenclature in exercising its plenary powers to this end. Whenever a name requires replacement, any individual may publish a "new name" for it and the first one so introduced has priority over any others; since newness is temporary and relative, the replacement designation is better called substitute name rather than new name. Whenever it is considered desirable to save for usage an otherwise necessarily rejectable name, an individual cannot by himself accomplish the preservation, except by unchallenged action taken in accordance with certain provisions of the Copenhagen Decisions; otherwise he must seek validation through ICZN.

It is useful for convenience and brevity of distinction in recording these subgroups of valid zoological names to introduce Latin designations, following the pattern of *nomen nudum, nomen novum,* etc. Accordingly, the subgroups are (1) *nomina inviolata* (sing., *nomen inviolatum,* abbr., *nom. inviol.*); (2) *nomina perfecta* (sing., *nomen perfectum,* abbr., *nom. perf.*); (3) *nomina imperfecta* (sing., *nomen imperfectum,* abbr., *nom. imperf.*); (4) *nomina translata* (sing., *nomen translatum,* abbr., *nom. transl.*); (5) *nomina correcta* (sing., *nomen correctum,* abbr., *nom. correct.*); (6) *nomina substituta* (sing., *nomen substitutum,* abbr., *nom. subst.*); (7) *nomina conservata* (sing., *nomen conservatum,* abbr., *nom. conserv.*).

Invalid names. Invalid zoological names consisting of originally published names that fail to comply with mandatory provisions of the Rules and consisting of inadvertent changes in spelling of names have no status in nomenclature. They are not available as replacement names and they do not preoccupy for purposes of the Law of Homonomy. In addition to *nomen nudum,* invalid names may be distinguished as follows: (1) *"denied names,"* which consist of originally published names (with or without subsequent duplication) that do not meet mandatory requirements of the Rules; (2) *"null names,"* which comprise unintentional alterations of names; and (3) *"vain or void names,"* which consist of invalid emendations of previously published valid or invalid names. Void names do have status in nomenclature, being classified as junior synonyms of valid names.

Proposed Latin designations for the indicated kinds of invalid names are as follows: (1) *nomina negata* (sing., *nomen negatum,* abbr., *nom. neg.*); (2) *nomina nulla* (sing., *nomen nullum,* abbr., *nom. null.*); (3) *nomina vana* (sing., *nomen vanum,* abbr., *nom. van.*). It is desirable in the *Treatise* to identify invalid names, particularly in view of the fact that many of these names (*nom. neg., nom null.*) have been considered incorrectly to be junior objective synonyms (like *nom. van.*), which have status in nomenclature.

SUMMARY OF NAME CLASSES

Partly because only in such publications as the *Treatise* is special attention to classes 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 classes of names are indicated in boldface type, whereas invalid ones are printed in italics.

Definitions of Name Classes

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

nomen correctum (nom. correct.). Name with intentionally altered spelling of sort required or allowable under the Rules but not dependent on transfer from one taxonomic category to another ("improved name"). (*See* Copenhagen Decisions, paragraphs 50, 71-2-a-i, 74, 75, 79, 80, 87, 101; in addition, change of endings for categories not now fixed by Rules.)

nomen imperfectum (nom. imperf.). Name that as originally published (with or without subsequent identical spelling) meets all mandatory requirements of the Rules but contains defect needing correction ("imperfect name"). (*See* Copenhagen Decisions, paragraphs 50-1-b, 71-1-b-i, 71-1-b-ii, 79, 80, 87, 101.)

nomen inviolatum (nom. inviol.). Name that as originally published meets all mandatory requirements of the Rules and also is uncorrectable or alterable in any way ("inviolate name"). (*See* Copenhagen Decisions, paragraphs 152, 153, 155-157).

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 Rules, is not correctable to establish original authorship and date ("denied name"). (*See* Copenhagen Decisions, paragraph 71-1-b-iii.)

nomen nudum (nom. nud.). Name that as originally published (with or without subsequent identical spelling) fails to meet mandatory requirements of the Rules and having no status in nomenclature, is not correctable to establish original authorship and date ("naked name"). (*See* Copenhagen Decisions, paragraph 122.)

nomen nullum (nom. null.). Name consisting of an unintentional alteration in form (spelling) of a previously published name (either valid name, as *nom. inviol., nom. perf., nom. imperf., nom. transl.;* or invalid name, as *nom. neg., nom. nud., nom. van.,* or another *nom. null.*) ("null name"). (*See* Copenhagen Decisions, paragraphs 71-2-b, 73-4.)

nomen perfectum (nom. perf.). Name that as originally published meets all mandatory requirements of the Rules and needs no correction of any kind but which nevertheless is validly alterable ("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 category 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 emendations having status in nomenclature as junior objective synonyms ("vain or void name"). (*See* Copenhagen Decisions, paragraphs 71-2-a-ii, 73-3.)

Except as specified otherwise, zoological names accepted in the *Treatise* may be understood to be classifiable either as *nomina 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, a few senior synonyms classifiable as *nomina negata* or *nomina nuda,* and numerous junior synonyms which include both objective *(nomina vana)* and subjective (all classes of valid names) types; effort to classify the invalid names as completely as possible is intended.

NAME CHANGES IN RELATION TO GROUP CATEGORIES

SPECIFIC AND SUBSPECIFIC 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 Rules (as in changing originally published *brőggeri* to *broeggeri*) or elimination of a hyphen (as in changing originally published *cornu-oryx* to *cornuoryx* does not require "*nom. correct.*" with it. Revised provisions for emending specific and subspecific names are stated in the report on Copenhagen Decisions (p. 43-46, 51-57).

GENERIC AND SUBGENERIC 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. Revised provisions for emendation of generic and subgeneric names also are given in the report on Copenhagen Decisions (p. 43-47).

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

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

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

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

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

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

Cyrtograptus CARRUTHERS, 1867 [*nom. correct.* LAPWORTH, 1873 (*pro Cyrtograpsus* CARRUTHERS, 1867), *nom. conserv.* proposed BULMAN, 1955 (ICZN pend.)]

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

The Rules now specify the form of endings only for subfamily (-inae) and family (-idae) but decisions of the Copenhagen Congress direct classification of all family-group assemblages (taxa) as co-ordinate, signifying that for purposes of priority a name published for a unit in any category and based on a particular type genus shall date from its original publication for a unit in any category, retaining this priority (and authorship) when the unit 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 emendation 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 emendation. 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 Rules, for the latter is merely the individual who first defined some lower-rank family-group taxon that contains the nominate genus of the superfamily. The publication of the author containing introduction of the superfamily *nomen translatum* is likely to furnish the information on taxonomic considerations that support definition of the unit.

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

Subfamily STYLININAE d'Orbigny, 1851

[*nom. transl.* EDWARDS & HAIME, 1857 (*ex* Stylinidae D'ORBIGNY, 1851]

Superfamily ARCHAEOCTONOIDEA Petrunkevitch, 1949

[*nom. transl.* PETRUNKEVITCH, herein (*ex* Archaeoctonidae PETRUNKEVITCH, 1949)]

Superfamily CRIOCERATITACEAE Hyatt, 1900

[*nom. transl.* WRIGHT, 1952 (*ex* Crioceratitidae HYATT, 1900)]

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

Valid emendations 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 (*ex* Streptelasmidae NICHOLSON, 1889, *nom. imperf.*)]

Family PALAEOSCORPIIDAE Lehmann, 1944

[*nom. correct.* PETRUNKEVITCH, herein (*ex* Palaeoscorpionidae LEHMANN, 1944, *nom. imperf.*)]

Family AGLASPIDIDAE Miller, 1877

[*nom. correct.* STØRMER, herein (*ex* Aglaspidae MILLER, 1877, *nom. imperf.*)]

Superfamily AGARICIICAE Gray, 1847

[*nom. correct.* WELLS, herein (*ex* Agaricioidae VAUGHAN & WELLS, 1943, *nom. transl. ex* Agariciidae GRAY, 1847)]

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

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

Family ARIETITIDAE Hyatt, 1874

[*nom. correct.* HAUG, 1885 (*pro* Arietidae HYATT, 1875), *nom. conserv.* proposed ARKELL, 1955 (ICZN pend.)]

Family STEPHANOCERATIDAE Neumayr, 1875

[*nom. correct.* FISCHER, 1882 (*pro* Stephanoceratinen NEUMAYR, 1875, invalid vernacular name), *nom conserv.* proposed ARKELL, 1955 (ICZN pend.)]

FAMILY-GROUP NAMES; REPLACEMENTS

Family-group names are formed by adding letter combinations (prescribed for family and subfamily but not now for others) to the stem of the name belonging to genus (nominate genus) first chosen as type of the assemblage. The type genus need not be the oldest in terms of receiving its name and definition, but it must be the first-published as name-giver to a family-group taxon among all those included. Once fixed, the family-group name remains tied to the nominate genus even if its name is changed by reason of status as a junior homonym or junior synonym, either objective or subjective. According to the Copenhagen Decisions, the family-group name requires replacement 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.

The aim of family-group nomenclature is greatest possible stability and uniformity, just as in case of other zoological names. Experience indicates the wisdom of sustaining family-group names based on junior subjective synonyms if they have priority of publication, for opinions of different workers as to the synonymy of generic names founded on different type species may not agree and opinions of the same worker may alter from time to time. The retention similarly of first-published family-group names which are found to be based on junior objective synonyms is less clearly desirable, especially if a replacement name derived from the senior objective synonym has been recognized very long and widely. To displace a much-used family-group name based on the senior objective synonym by disinterring a forgotten and virtually unused family-group name based on a junior objective synonym because the latter happens to have priority of publication is unsettling. Conversely, a long-used family-group name founded on a junior objective synonym and having priority of publication is better continued in nomenclature than a replacement name based on the senior objective synonym. The Copenhagen Decisions (paragraph 45) take account of these considerations by providing a relatively simple procedure for fixing the desired choice in stabilizing family-group names. In conformance with this, the *Treatise* assigns to contributing authors responsibility for adopting provisions of the Copenhagen Decisions.

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.

ORDER/CLASS-GROUP NAMES; USE OF *"NOM. CORRECT."*

Because no stipulation concerning the form of order/class-group names is given yet by the Rules, emendation of all such names actually consists of arbitrarily devised changes in the form of endings. Nothing precludes substitution of a new name for an old one, but a change of this sort is not considered to be an emendation. Examples of the use of *"nom. correct."* as applied to order/class-group names are the following.

Order DISPARIDA Moore & Laudon, 1943

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

Suborder FAVIINA Vaughan & Wells, 1943

[*nom. correct.* WELLS, herein (*ex* Faviida VAUGHAN & WELLS, 1943)]

Suborder FUNGIINA Verrill, 1865

[*nom. correct.* WELLS, herein (*ex* Fungiida DUNCAN, 1884, *ex* Fungacea VERRILL, 1865)]

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 of 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 worth while, 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

DEFINITION OF NAMES

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 [*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 DELAUBENFELS, *nom. subst.* [*pro Mystrium* SCHRAMMEN, 1936 (ref. 40, p. 60) (*non* ROGER, 1862)] [**Mystrium porosum* SCHRAMMEN, 1936].

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

Diplophyllum HALL, 1851 [*non* SOSHKINA, 1939] [**D. caespitosum*].

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

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 2 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, but various modes of original designation are not distinguished.

Original designation of type species. The Rules provide that the type species of a genus or subgenus may be recognized as an original designation if only a single species was assigned to the genus at the time of first publication (monotypy), if the author of a generic name employed this same name for one of the included species (tautonymy), if one of the species was named *"typus," "typicus,"* or the like, if the original author explicitly indicated the species chosen as the type, or if some other stipulations were met. According to convention adopted in the *Treatise,* the absence of any indication as to manner of fixing the type species is to be understood as signifying that it is established by original designation, the particular mode of original designation not being specified.

Subsequent designation of type species; use of "SD" and "SM." 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 2 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].

SYNONYMS

Citation of synonyms is given next following record of the type species and if 2 or more synonyms of differing date are recognized, these are arranged in chronological order. Objective synonyms are indicated by accompanying designation "(obj.)," others being understood to constitute subjective synonyms. Examples showing *Treatise* style in listing synonyms follow.

Calapoecia BILLINGS, 1865 [**C. anticostiensis;* SD LINDSTRÖM, 1833] [=*Columnopora* NICHOLSON, 1874; *Houghtonia* ROMINGER, 1876].

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

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

Lyopora NICHOLSON & ETHERIDGE, 1878 [**Palaeopora? favosa* M'COY, 1850] [=*Liopora* LANG, SMITH & THOMAS, 1940 (*non* GIRTY, 1915)].

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

Tetragraptus SALTER, 1863 [*nom. correct.* HALL, 1865 (*pro Tetragrapsus* SALTER, 1863), *nom. conserv.* proposed BULMAN, 1955, ICZN pend.] [**Fucoides serra* BRONGNIART, 1828 (=*Graptolithus bryonoides* HALL, 1858].

ABBREVIATIONS

Some authors' names and most stratigraphic and geographic names are abbreviated in order to save space. General principles for guidance in determining what names should be abbreviated are frequency of repetition, length of name, and avoidance of ambiguity. Abbreviations used in this division of the *Treatise* are explained in the following alphabetically arranged list.

Abbreviations

Abh., Abhandl., Abhandlungen
Abt., Abteilung, -en
Abys., Abyssinia
Acad., Academia, Académie, Academy
Accad., Accademia
Act., Acta, -as, -es, -os
Afghan., Afghanistan
Afr., Africa, -an
Akad., Akademie
Alb., Albian
Alba., Alberta
Alg., Algeria
Am., America, -n
Anis., Anisian
Ann., Analen, Annals, Annual
Apt., Aptian
Arch., Archiv, -es
Arg., Argentina
Ariz., Arizona
Ark., Arkansas
Arth., ARTHABER
AsiaM., Asia Minor
Assoc., Association
Aus., Austria
Austral., Australia
Baj., Bajocian
Baluch., Baluchistan
Barr., BARRANDE
Barrem., Barremian
Bath., Bathonian
Baug.-S., BAUGIER & SAUZÉ
Bayer., Bayerischen
B.C., British Columbia
Behr., BEHRENDSEN
Beil., Beilage
Beitr., Beitrag, Beiträge
Belg., Belgique, Belgium
Ben., BENECKE
Berrias., Berriasian
Beyr., VON BEYRICH
Biol., Biological, Biology
Blainv., DE BLAINVILLE
Blake-H., BLAKE & HUDLESTON
Blanf., BLANFORD
Bol., Boletím, ín
Bol., Bolivia
Bon., BONARELLI
Bor., BORISSJAK
Boule-L.-T., BOULE, LEMOINE & THEVENIN
Braz., Brazil
Breistr., BREISTROFFER
Brit., Britain, British
Brongn., BRONGNIART
Brug., BRUGUIÈRE
Buch, VON BUCH
Buck., BUCKMAN
Bull., Bulletin
Bundesanst., Bundesanstalt
Bur., Bureau
Burck., BURCKHARDT
C., Central
Calif., California
Callov., Callovian
C.Am., Central America
Camp., Campanian
Can., Canada
Carb., Carboniferous
Carn., Carnian
Cauc., Caucasus Mountains
Cenom., Cenomanian
Centralbl., Centralblatt
Cienc., Ciencias
Cl., Classe
Coah., Coahuila
Cock., COCKERELL
Coll., Collection, -s; College
Colo., Colorado
Colom., Colombia
Com., Comité
Comm., Committee
Comp., Comparative
Congr., Congrés, Congreso, Congress
Coni., Coniacian
Connaiss., Connaissance
Contr., Contribution, -s
Coq., COQUAND
cosmop., cosmopolitan
Court., COURTILLER
Cret., Cretaceous
Czech., Czechoslovakia
d., das, der, die
Dec., December
Defr., DEFRANCE
Del., Delaware
Denck., DENCKMANN
Denkschr., Denkschriften
Dept., Department, Departments
Dépt., Département
dét., détaillée
deutsch., deutschen
Dev., Devonian
Dissert., Dissertation
Douv., DOUVILLÉ
Ditt., DITTMAR
Duft., DUFTSCHMID
Dum., DUMORTIER
E., East
Econ., Economiche
Edws., EDWARDS, F. E.
Eichw., EICHWALD
Eng., England
Eth., ETHERIDGE, RORERT, JR.
Eu., Europe
Exped., Expedition
f., för, für
Fac., Facultad, Faculté, Faculty
fasc., fascicle
Festschr., Festschrift
fig., figure, -s
Font., FONTANNES
Forsch., Forschung
Fr., France, Française, -e, French
Freb., FREBOLD
Frech-A., FRECH & ARTHABER
Ga., Georgia
Gemm., GEMMELLARO
Gén., Général
Geog., Geography
Geogn., Geognostische
Geol., Geología, Geological, Geológico, Geologie, Geologisch, Geologiska, Geology
Géol., Géologie, Géologique
Ger., Germany
Gesell., Gesellschaft
Gior., Giornale
Greenl., Greenland
Griep., GRIEPENKERL
Gries., GRIESBACH
Gross., DE GROSSOUVRE
Gümb., GÜMBEL
Gug., GUGENBERGER

Haan, de Haan
Hauteriv., Hauterivian
H.Douv., Douvillé, H.
Helvet., Helvetiae
Hemis., Hemisphere
Herb., Herbich
Hett., Hettangian
Himal., Himalaya Mountains
Hist., Histoire, -ia, Historia, History
Hofmus., Hofmuseums
Hohen., Hohenegger
Holl., Holland
Hond., Honduras
Hung., Hungarica, Hungary
Hyatt-S., Hyatt & Smith
I., Island, -s
ICZN, International Commission on Zoological Nomenclature
Ida., Idaho
Ill., Illinois
illus., illustration, -s
Imp., Imperial
incl., includes
Ind., Indiana
Ind.O., Indian Ocean
Indon., Indonesia
IndoPac., Indo-Pacific
Infravalang., Infravalanginian
Inst., Institut, Institute, Institutet, Institution, Instituto, Instituut
Internat., International, -en
Ire., Ireland
Ital., Italiana
Jaarb., Jaarboek
Jahrb., Jahrbuch
Jahresber., Jahresbericht
Jahresh., Jahreshefte
Jahrg., Jahrgang
Jan., January
J.Buck., Buckman, J.
J.deC.Sow., Sowerby, J. deC.
Johns., Johnston
Jour., Journal
J.Sow., Sowerby, J.
Jur., Jurassic
K., Kaiserlich
K.K., Kaiserlich Königlich
Kak., Kakhadzé
Kans., Kansas
Karp., Karpinsky
Keys., Keyserling
Kimm., Kimmeridgian
Kl., Klasse
Klip., Klipstein
Koenen, von Koenen
Kon., de Koninck
Kongr., Kongress
Krafft-D., Krafft & Diener
Krum., Krumbeck
Kut., Kutassy
Ky., Kentucky
L., Lower; Land
Lab., Laboratoire, Laboratory, Laboratories
Ladin., Ladinian
Lah., Lahusen
Lam., Lamarck
Landesanst., Landesanstalt
Leck., Leckenby
Lias., Liassic
Lief., Lieferung, -en
Linn., Linnean
livr., livraison
Loriol, de Loriol
Low., Lower
M., Middle
Maastr., Maastrichtian
McL., McLearn
Madag., Madagascar
Mag., Magazine
Math., Mathematische
Math., Mathews
Mart., Martelli
Mayer-E., Mayer-Eymar
Meddel., Meddelelser
Medit., Mediterranean
Meek-W., Meek & Worthen
Mem., Memoir, -ia, -s
Mém., Mémoire, -s
Men., Meneghini
Merid., Meridionále
Mex., Mexico
Mich., Michigan
Mijnw., Mijnwezen
Miller-F., Miller & Furnish
Miller-O., Miller & Owen
Min., *see* Mineral
Mineral., Mineralogical, Mineralogie, Mineralogisch, -e
Minéral., Minéralogique
Miss., Mississippi, Mississippian
Mitt., Mitteilungen
Mo., Missouri
Mojs., Mojsisovics
Mon., Monograph
Monatsber., Monatsbericht
Mont., Montana
Moore-S.B., Moore & Sylvester-Bradley
Moroc., Morocco
Münst., Münster
Mus., Musée, Museo, Museum
N., North
N.Am., North America
Nat., Natural; Naturale, -s; Naturali; Naturelle, -s
Natl., National
Nat.-Med., Naturwissenschaftlichen-Medizinischen
Naturf., Naturforschende
Naturh., Naturhistorie, -ischen
Naturk., Naturkunde
Naturwiss., Naturwissenschaftlich
N.Caled., New Caledonia
N.Dak., North Dakota
Nederl., Nederlandsch, -e
Neocom., Neocomian
Neum., Neumayr
Neum.-U., Neumayr & Uhlig
Nev., Nevada
N.Guinea, New Guinea
Nic., Nicolesco
N.J., New Jersey
N.Mex., New Mexico
no., number, -s; numéro, -s; número, -s
Noetl., Noetling
Nomencl., Nomenclature
Nor., Norian
nouv., nouveaux, nouvelle
n.s., new series
N.S.W., New South Wales
N.Y., New York
N.Z., New Zealand
N.Zem., Novaya Zemlya
obj., objective
Oct., October
OD, original designation
Öster., Österreich
Okla., Oklahoma
Orb., d'Orbigny
Ore., Oregon
Oxf., Oxfordian
p., page, -s
Pa., Pennsylvania
Pak., Pakistan
Pak., Pakuckas
Paläont., Paläontologie, Paläontologisch
Palaeont., Palaeontologia
Palaeontogr., Palaeontographia, Palaeontographica, Palaeontographical
Paleont., Paleontologia, Paleontologica, Paleontological, Paleontologiese, Paleontology
Paléont., Paléontologie
Parona-B., Parona & Bonarelli
Patag., Patagonia
pend., pending
Penn., Pennsylvania
Perm., Permian
Perv., Pervinquière
Petitcl., Petitclerc
Petrol., Petrology
Phil., Philippi
Philip., Philippines
Phill., Phillips
Philos., Philosophical
Phys., Physique, Physikalische
Pictet-C., Pictet & Campiche
pl., plates, -s
Pliensb., Pliensbachian
Plummer-S., Plummer & Scott
Pol., Poland
Pomp., Pompeckj
Port., Portugal, Portuguese
Portl., Portlandian
Portl., Portlock
Preuss., Preussische
Prob., Problème, -s; Problem, -s
Proc., Proceedings
Prof., Professional
Protect., Protectorat
pt., part, -s
Pub., Publication
Quart., Quarterly
Queensl., Queensland
Quenst., Quenstedt

R. Douv., DOUVILLE, R.
reconstr., reconstructed, -ion
Redt., REDTENBACHER
Reichsanst., Reichsanstalt
Rein., REINECKE
Renz-R., RENZ & RENZ
Rept., Report, -s
Rev., Review
Rhaet., Rhaetian
Riv., Rivista
Roll., ROLLIER
Roy., Royal, -e
Russ., Russia, Russisch
Ruzh., RUZHENCEV
S., South; Sea
Sal., SALOPEK
SaltR., Salt Range
S.Am., South America
Sandb.-S., SANDBERGER & SANDBERGER
Santon., Santonian
Sard., Sardinia
Sask., Saskatchewan
S.Buck., BUCKMAN, S.
Schind., SCHINDEWOLF
Schloen., SCHLOENBACH
Schloth., SCHLOTHEIM
Schram., SCHRAMMEN
Schweiz., Schweizerische
Sci., Sciences, Scientifique
Scot., Scotland
Scyth., Scythian
SD, subsequent designation
SE., Southeast
sec., section, -s
Sed., Sedimentary
Senckenberg., Senckenbergischen
Senon., Senonian
ser., series, serial
Serv., Serviço, Service
sh., shale
Sib., Siberia
Siem., SIEMIRADZKI
Simion., SIMIONESCU
Simp., SIMPSON
Sinem., Sinemurian
Sitzungsber., Sitzungsbericht
sl., slate
SM, subsequent monotypy
Soc., Sociedad, Società, Société, Society
Somali., Somaliland
Sow., SOWERBY, J. or J.DEC.
Sp., Spain
Spec., Special
Spitz., Spitzbergen
ss., sandstone
Staatsinst., Staatsinstitut
Stchir., STCHIROWSKY
Stef., DI STEFANO
Stol., STOLICZKA
Stoy., STOYANOW
Stratig., Stratigraphy
subgen., subgenera, subgenus
subj., subjective
Suppl., Supplement
SW., Southwest
Swin., SWINNERTON
Switz., Switzerland
Tangan., Tanganyika
Teiss., TEISSEYRE
Terr., Territory
Tex., Texas
Thev., THEVENIN
Thioll., THIOLLIER
Tithon., Tithonian
Toarc., Toarcian
Tornq., TORNQUIST
Tosc., Toscana
Toum., TOUMANSKY
Trans., Transactions
Traut., TRAUTSCHOLD
Trav., Travaux
Trias., Triassic
True.-W., TRUEMAN & WILLIAMS
Turk., Turkey
Turon., Turonian
u., und
U., Upper
Univ., Universidad, Università, Université, Universitets, University
Up., Upper
U.S., United States
USA, United States (America)
USSR, Union of Soviet Socialist Republics
v., volume, -s
Valang., Valanginian
vaterl., vaterländische
Venez., Venezuela
Ver., Verein, -s
Verh., Verhandlung, -en; Verhandelingen
Vern., DE VERNEUIL
Visch., VISCHNIAKOFF
Volg., Volgian
W., West
Waag., WAAGEN
Wdkd., WEDEKIND
Whit., WHITEAVES
Whitf., WHITFIELD
Wiss., Wissenschaften, Wissenschaftliche, -en
Woodw., WOODWARD
Wyo., Wyoming
Yorks., Yorkshire
Yugo., Yugoslavia
Young-B., YOUNG & BIRD
z., zone
Zeitschr., Zeitschrift
Zentralbl., Zentralblatt
Ziet., ZIETEN
Zimm., ZIMMERMANN
Zool., Zoologi, Zoologia, Zoological, Zoologie, Zoologisch, Zoologiska

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 inclosed invariably in parentheses and are distinguishable from dates because the index numbers comprise no more than 3 digits. Ordinarily, index numbers for literature references are given at the end of generic or family diagnoses.

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 to an alphabetically arranged list of authors' names which follows. The names of authors, but generally not individual publications, are cited. Illustrations consisting of exact copies of previously published figures (except for possible change of scale) are distinguished by the use of an asterisk (*) with the index number, and previously unpublished illustrations are marked by the letter "n" (signifying "new") with the index number; all other indications of the sources of illustrations are construed to mean "after" the cited author or authors, that is, embodying some degree of change. Addition of the abbreviation "mod." denotes appreciable alteration of the source figure. RAYMOND C. MOORE

INTRODUCTION TO CEPHALOPODA[1]

By A. K. MILLER and W. M. FURNISH

Class CEPHALOPODA Leach, 1817

[Les Céphalopodes CUVIER, 1797; Mollusca Cephalopoda DUMÉRIL, 1806]

This class comprises both present-day and fossil forms. In the first category belong the relic pearly nautilus, and the relatively widespread and abundant octopuses, cuttlefishes, squids, and argonauts or paper nautiluses. Fossil relatives of many of these are known, some of which have long been extinct, for example, the clymenias, goniatites, ceratites, ammonites, and belemnites. All cephalopods are exclusively marine. They are widely distributed in the present oceans and seas, and it is clear from the fossil record that they had a comparable distribution in the past. They are most abundant in the shallow seas but occur also in the intermediate and even the abyssal depths of oceans. The associations of most, if not all, of the known fossil forms indicate that they were shallow-water dwellers. The class was in existence in the Cambrian and has been well represented ever since. Both embryology and comparative anatomy indicate that it originated from a form close to the primitive gastropods by the forward growth of the so-called molluscan foot, here interpreted very broadly. Accordingly, there are logical objections to the application to these animals of such terms as anterior, posterior, dorsal, and ventral, with what appears to be their customary meaning, but it can be justified on the basis of usage.

Modern cephalopods are, for the most part, agile carnivorous bilaterally symmetrical creatures. They are more highly organized than any of the other mollusks, and among them are the most accomplished swimmers other than the fishes. Some are minute, but they range in size up to such giant squids as several species of *Architeuthis* (largest Recent invertebrates, with a body length up to 6.5 m.)—the largest of the mollusks with external shells comparable to those of some Ordovician nautiloids *(Endoceras)* and immense Cretaceous ammonites *(Pachydiscus),* some 2.5 m. in diameter. Cephalopods have a definite head, the mouth being surrounded by a portion of the primitive molluscan foot modified into processes that commonly are either lobelike and bear tentacles, each with a cirrus, or are armlike and are provided with suckers or hooklets or both. The concrescence of the head and part of the foot to form the so-called head-foot is characteristic of the class, though its name [NL., fr. *cephalo-+-poda*] was given because it was believed that the cephalic appendages are used for crawling, which in some forms is true to a certain extent. The foot also gives rise to a swimming funnel, or hyponome, for the egress of water from the mantle cavity. This structure arises as a pair of flaps, the margins of which overlap ventrally in *Nautilus* but are fused together in the other present-day cephalopods. In many forms there is a small

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[1] *Note.*—Advance publication of introductory statements concerning the nature of Cephalopoda in general is thought to be appropriate here because issuance of Part L of the *Treatise* on Ammonoidea precedes that of Part K on the structurally simpler nautiloid types of cephalopods which undoubtedly included ancestors of the Ammonoidea. This short chapter is planned to belong in initial regularly numbered pages of Part K and therefore here is excluded from the section beginning with page L1; when Parts are assembled for binding together in volumes, prefatory pages which accompany the separately published Parts will be omitted because essential contents of each will be assembled in Part A, Introduction. Much of the material presented in this discussion was contributed by LESLIE BAIRSTOW; for assistance thus furnished the authors express acknowledgment and appreciation.—EDITOR.

supplementary flap in the hyponome which acts as a check valve, permitting water to flow only in an outward direction. A hyponome is peculiar to the class, and the forceful ejection of water through it results in rapid swimming by jet propulsion.

From the head-foot may be distinguished a more or less elongated visceral mass enveloped by the mantle. The mantle, besides commonly secreting a shell, has a forward-projecting fold that forms the outer wall of a ventral mantle cavity, within which the gills are suspended. These consist of paired plumes, of which there are 2 (a pair) in all modern forms except *Nautilus,* which has 4 (2 pairs). Unlike those of other mollusks, they are not ciliated but are immersed in the sea water that is forced in and out of the mantle cavity by muscular action of the walls of that cavity and the hyponome. A median anus and the genital and renal ducts open into the mantle cavity.

Cephalopods also have a buccal mass with a beak (upper and lower jaws or mandibles) like an inverted parrot beak, and usually with a rasping tongue (radula) similar to that characteristic of the Amphineura, Gastropoda, and Scaphopoda. Furthermore, there are salivary glands, esophagus, stomach, caecum, liver, and intestine. The alimentary canal does not extend from pole to pole but forms a loop so that the anus, as well as the mouth, is more or less anterior in position. The circulation of water through the mantle cavity serves to carry away the waste products, as well as for locomotion and respiration. As in gastropods, the perivisceral cavity is partly coelomic and partly haemocoelic. The heart has a median ventricle and as many auricles as there are gills. A separate renal organ is associated with the afferent vein of each gill.

The nervous system is more highly developed than that of other mollusks, and the cerebral, pleural, and pedal ganglia are closely aggregated in the cephalic region. The concentration of these ganglia is unusual in the rest of the mollusks, though it occurs also in certain gastropods. There is a tendency in the cephalopods for the ganglia to be protected to some extent by cartilage-like tissue. Most of the sense organs also exhibit a high state of advancement, and the eyes, for example, though relatively primitive in *Nautilus,* have an elaborate structure in the other living cephalopods.

The sexes are separate, and the animals are oviparous. There is a single gonad which discharges by 1 or 2 genital ducts into the mantle cavity. A long tubular spermatophore is formed around each modicum of sperm during its passage through the male genital duct. The spermatophores are then transferred to the females by special copulatory organs that are quite separate from the genital ducts. The eggs are commonly protected by individual capsules or aggregated in gelatinous tubes. Each egg is large and is so rich in yolk that segmentation is incomplete, and in some forms a yolk sac is present during development. This development, where known, differs from that of other mollusks, for the embryo proceeds directly to the adult form without any intervening trochosphere or veliger larval stage.

All members of this class have hard parts, but only the shells (of those that possessed them) were commonly preserved as fossils. The shell, which is univalved, is external in *Nautilus* and presumably was borne in a similar manner in the many fossil nautiloids and ammonoids. However, it is internal in the other present-day cephalopods, as it was in their fossil kin, including the belemnites. The external shells can be thought of as more or less modified hollow cones which are straight, curved, or coiled (generally in a single plane). These shells are divided by septa into chambers pierced by a tube called the siphuncle. The septa and especially the siphuncle readily differentiate the external shells of cephalopods from those of gastropods and scaphopods; furthermore, in only a few of the gastropods is the coiling planispiral.

Many of the external shells of ancient cephalopods are among the best index fossils because of their rapid and diverse evolution, widespread occurrence, abundance, and ease of identification even when incomplete and when preserved only as internal molds. Because these shells were relatively light in weight and contained camerae that presumably were buoying gas chambers, it was possible for the animals which bore them to range widely in the shallow seas and some of them may well have crossed the oceans; as a result, many genera and possibly some species are common to the eastern and western hemisphere.

There are several fundamental differences between *Nautilus* and other living cephalopods such as *Sepia, Loligo,* and *Octopus.* This fact was recognized by OWEN in 1832, and he divided the class into 2 groups which he named Tetrabranchiata and Dibranchiata in accordance with the number of gills present in living representatives. From the start he grouped in the Tetrabranchiata not only present-day *Nautilus* but also fossil nautiloids as well as the extinct ammonoids. Later he came to recognize that with the exception of *Nautilus* all living cephalopods are 2-gilled, and that the extinct belemnites also should be referred to the Dibranchiata.

The legitimacy of thus applying this classification not only to present-day but also to fossil forms has been seriously questioned, as no fossil cephalopods are known in which the number of gills can be observed and correlation with other characters is partly conjectural. Such uncertainties have been emphasized as regards fossil nautiloids and especially the ammonoids. Some authors (avoiding particularly the name Tetrabranchiata) have preferred as an alternative classification a 3-fold division on a different basis, and they have used at this level such names as Nautiloidea, Ammonoidea, and Coleoidea or Belemnoidea—the last, however, most probably should be employed in a much narrower sense. It has even been claimed that the Ammonoidea and the Coleoidea should be associated as divisions of one broad group opposed to another containing only the nautiloids, but this view has not found much favor. Other students of fossil cephalopods (for example, TEICHERT and MILLER) are inclined to believe that the Paleozoic nautiloids exhibit so much variation, especially in the size and structure of the siphuncle, that they should be divided into several groups co-ordinate in rank with the Ammonoidea and Coleoidea.

Provisionally, at any rate, it seems best to regard cephalopods as falling into 2 categories as follows: (1) a group of relatively primitive forms constituted by the nautiloids and the ammonoids together, and (2) a group of more-advanced forms among which are the belemnites and the 2-gilled cephalopods of the present day—the former (in particular the nautiloids) being generally believed to have given rise to the latter. Not all authors who have favored some such grouping have wished to use the number of gills as the primary taxonomic and nomenclatorial basis. Tentaculifera of D'ORBIGNY, 1852, and Acetabulifera OWEN, 1836 [=Acetabulifères FERUSSAC & D'ORBIGNY, 1835] were based on the nature of the circumoral appendages; Schizosiphona and Holosiphona of LANKESTER, 1883, and Tomochonia (or Funnaperta) and Gamochonia (or Funnoclausa) of HAECKEL, 1896, on the structure of the hyponome. As applied to fossil forms, these characters are not much more serviceable than the number of gills. Ectocochlia and Endocochlia of SCHWARZ, 1894, were based on the external or internal situation of the shell, but use of this criterion is not entirely free from difficulty even as regards present-day forms, since some of the octopods have no shell and since females of the octopod *Argonauta* have a shell that is external but is not homologous with the external shell of other cephalopods. The names Protocephalopoda and Metacephalopoda of GRIMPE, 1922, are free from positive objection. Nevertheless, of all the names available, the only ones that are widely current for the 2 primary divisions of the Cephalopoda are Tetrabranchiata and Dibranchiata, sometimes employed in the shorter forms Tetrabranchia and Dibranchia. All in all, it seems best to retain these familiar names provisionally, with the understanding that, especially as regards Tetrabranchiata, it must not be taken for granted that the name furnishes a literal description applicable throughout the group.

The stratigraphic distribution of Cephalopoda is from Cambrian to Recent.

PART L
MOLLUSCA

CEPHALOPODA
AMMONOIDEA

By W. J. Arkell, W. M. Furnish, Bernhard Kummel, A. K. Miller, R. C. Moore, O. H. Schindewolf, P. C. Sylvester-Bradley, and C. W. Wright

CONTENTS

INTRODUCTION TO AMMONOIDEA

By A. K. Miller and W. M. Furnish

The clymenias, goniatites, ceratites, and ammonites, which together constitute the order Ammonoidea, have long been extinct, but their fossilized shells are common in all continents and many oceanic islands. Numerous specimens are remarkably well preserved, even spectacular, and their exceptional value as a basis for stratigraphic correlations has been recognized for well over a century. Accordingly, they have attracted the attention of both layman and scientist for generations, and the literature in regard to them is voluminous. Almost all our knowledge of these creatures comes from studies of the shells and the enclosing matrices, but a few opercula are also preserved. The shells are comparable to that of modern *Nautilus,* a presumed relative of the group.

The nautiloids and ammonoids, which together constitute the subclass Tetrabranchiata, were widespread and abundant in the past but are now almost extinct, being represented by only a few species of the single genus, *Nautilus.* All members of the entire group are characterized by the possession of an external univalved camerate shell. Typically this shell is bilaterally symmetrical, being straight, curved, or coiled in one plane; but helicoid and irregular forms are not rare. Some authors have expressed the opinion that at least certain of the ammonoid shells were internal. However, the presence of color markings and the absence of surficial deposits indicate that they were external.

Living representatives of *Nautilus* differ from all other present-day cephalopods in that they have 4 gills, rather than a single pair, and the 2 flaps which form the hyponome overlap ventrally, rather than being fused together. Whether or not their fossil relatives possessed these features is a matter of conjecture; the shape of the body chamber and the aperture indicate only the general nature of the soft parts of the animal.

Conventionally, tetrabranchiate cephalopod illustrations are oriented with the peristome above the phragmocone. *Nautilus,* however, is well stabilized in the reverse manner and cannot change its position materially. Most ammonoids had a comparable low center of gravity. Nevertheless, certain forms with body chambers about a volution in length may have been able to invert themselves.

The present-day representatives of the subclass live in the moderately shallow waters of the southwest Pacific Ocean. However, their ancient relatives ranged in the oceans and the seas all over the world, most of the known fossil remains coming from rocks that represent shallow-water marine deposits. The subclass made its debut in the Cambrian. It developed and evolved so rapidly that in the Ordovician it was perhaps the pre-eminent group of animals, some of its members attaining enormous proportions and being the largest creatures of the time. It continued unabated in the Silurian, and very early in the Devonian the ammonoids evolved from the nautiloids. Both these groups flourished until near the close of the Triassic, when they almost became extinct, only to be revitalized in the Jurassic. Throughout the Mesozoic, ammonoids were more numerous than nautiloids. During the Cretaceous, ammonoids were the largest and among the most abundant of the invertebrates, and nautiloids were not rare. However, at the end of that period, the former became extinct, and after the early Tertiary the nautiloids dwindled rapidly. Few if any are known from the Pliocene and none from the pre-Recent Pleistocene, though, of course, the ancestors of modern *Nautilus,* a relic, must have been in existence during those times.

The tetrabranchiate cephalopods are among the very best of our guide or index fossils. The ammonoids in particular are good stratigraphic indices, and the marine strata of the later Paleozoic and the Mesozoic are zoned with reference to them.

Order AMMONOIDEA Zittel, 1884

Tetrabranchiate cephalopods characteristically tightly coiled in a plane and symmetrical, with a bulbous calcareous protoconch, septa that form angular sutural flexures, and a small marginal siphuncle. *L. Dev.-U.Cret.*

MORPHOLOGICAL TERMS APPLIED TO AMMONOIDEA

By W. J. Arkell, Bernhard Kummel, A. K. Miller, and C. W. Wright

The preparation of a glossary of morphological terms applied to Ammonoidea arranged in a single alphabetical list was advocated by the Editor at the outset of work undertaken by authors contributing to this volume. Surely, the availability of a glossary giving concise definitions or explanations of terms should be useful to readers and therefore Arkell, Kummel, Miller, and Wright accepted the task of reviewing terms to be included and of drafting definitions. Soon many difficulties appeared, several of these relating to terms such as camera, chamber, conch, shell, test, siphon, siphuncle, and others that belong also to nautiloid and dibranchiate cephalopods as well as to ammonoids. Authors concerned with these divisions were consulted. For some time a voluminous exchange of letters and memoranda seemed to bring out greater divergence than agreement on choice of terms and how to use them; eventually, however, decisions were made to accept some terms and to reject others, some measure of disagreement remaining also as to wording of definitions. The inclusion of many terms classed as obsolete was deemed inexpedient. As here published, the glossary contains no indication of the relative importance attached to various terms, some being classified as essential, others as important because commonly used, and still others as rather unimportant. By and large, terminology given in the glossary relates more to Mesozoic than Paleozoic ammonoids.—R. C. MOORE.

GLOSSARY OF MORPHOLOGICAL TERMS

accessory (lobe or saddle). Secondary or minor element of sutures.

acute (periphery). With sides of shell meeting at sharp angle without shoulders.

adapertural. *See* adoral.

adapical. Toward apex of shell; backward direction.

adoral. Toward mouth of ammonoid or aperture of shell; forward direction.

adventitious (or **adventive**) **lobe.** Lobe of suture formed secondarily by subdivision of 1st lateral saddle.

ammonitic (suture). With all lobes and saddles of suture denticulate or frilled.

anaptychus. Single plate closing aperture of some ammonoids.

aperture. Open end of body chamber of shell.

approximated (ribs). Crowded toward present or past position of aperture, usually associated with maturity of growth.

approximated (sutures). Crowded toward body chamber, usually indicating maturity of growth.

aptychus. Pair of plates serving for closure of aperture of some ammonoids (strict sense); single plate (anaptychus) or pair of plates (aptychus) (loose sense).

auxiliary (lobe or saddle). Lateral lobe or saddle of suture springing from umbilical lobe or saddle between 2nd lateral and umbilical seam.

bicarinate. With 2 keels on venter.

biconcave (rib). With 2 distinct portions concave toward aperture.

biconvex (rib). With 2 distinct portions convex toward aperture.

bifurcate (rib). Dividing into 2 branches toward venter.

biplicate. *See* bifurcate.

bisulcate. With 2 longitudinal grooves.

body chamber. Large undivided space in shell extending adapically from aperture, inhabited by living animal.

bulla. Tubercle elongated radially; adj. bullate.

bundled (ribs). United in bunches or sheaves at or near umbilical edge, usually at a tubercle (*see* fasciculate).

cadicone. Depressed barrel-shaped shell with more or less evolute coiling, wide venter, and crater-like umbilicus (as in *Cadoceras*).

caecum. Closed pouch or sac at apex of siphuncle; commonly termed siphuncular caecum.

camera. Compartment between 2 adjacent septa comprising one of the spaces into which entire shell between protoconch and body chamber is divided by the septa.

capricorn. Shell encircled by distant blunt ribs and subequal rounded interspaces, resembling a goat's horn (as in *Androgynoceras capricornus*).

carina. *See* keel; adj. carinate, bearing a keel.

ceratitic (suture). With rounded unbroken saddles and denticulate lobes (as in *Ceratites*).

chamber. *See* body chamber, camera.

chevron. V-shaped ridge on shell surface, commonly on venter.

clavus. Tubercle elongated in direction of coiling (longitudinally); adj. clavate.

collared (aperture). Encircled by flared rib and constriction close behind peristome.

compressed (whorl section). Higher than wide.

concave (side or venter). Broadly impressed. Concave rib, bowed away from aperture.

conch. Complete shell of ammonoid less the protoconch.

connecting ring. Porous segment of siphuncle between 2 adjacent septal necks, partly chitinous and partly calcareous spicular.

constricted (aperture). Encircled by constriction close behind peristome. Constricted conch, with several constrictions.

constriction. Depression encircling a whorl.

contracted (peristome). With diameter smaller than that of body chamber.

convergent (whorl sides). Converging toward venter.

convex (rib). Bowed toward aperture.

coronate. With whorl section resembling a crown viewed from side.

costa. *See* rib.

cruciform. Cross-shaped.

cuneiform. Wedge-shaped.

cyrtocone. Shell curved without completing a single whorl.

dense (ribs). Closely spaced.

dependent. *See* retracted.

depressed (whorl section). Wider than high.

distant (ribs). Widely spaced.

divergent (whorl sides). Diverging toward venter.

dorsal lobe. Median primary lobe of suture on dorsum (internal in normally coiled conchs).

dorsolateral area. Side of impressed area on each flank of dorsum in involute shells.

dorsum. Dorsal side of conch (opposite ventral), generally grading into dorsolateral areas; in slightly involute shells equivalent to impressed area but in deeply involute shells refers only to portion of conch adjacent to venter of preceding whorl.

ellipticone. Shell with elliptical coiling of last whorl or half whorl which slightly breaks regularity of spiral form.

endogastric. Shell curved or coiled so that venter is on inner (concave) area of whorls.

evolute. With whorls overlapping little or not at all and therefore having a wide umbilicus. (As commonly used, evolute and involute are relative terms, since a shell form called evolute in one family may be classed as involute in another.)

excentric (umbilicus). Type characterized by abrupt opening up of spiral described by umbilical seam or tendency to closing of this spiral while the peripheral spiral is relatively unchanged.

excentrumbilicate. *See* excentric umbilicus.

exogastric. Shell curved or coiled so that venter is on outer (convex) area of whorls; nearly all ammonoids are exogastric.

external lobe. *See* ventral lobe.

external saddle. *See* lateral saddle (1st) and ventral saddle.

external suture. Part of suture (in coiled forms only) which is exposed on outside of whorls between the umbilical seams.

falcate (rib). Sickle-shaped.

falcoid (rib). Approaching sickle-shaped.

fasciculate (ribbing). With ribs bunched or bundled to form sheaves.

fastigate. With roof-shaped venter, periphery of shell being sharpened but not keeled.

fillet. Longitudinal raised smooth band on venter or whorl side.

flank. *See* whorl side.

flare. Random annulation or very distinct rib that usually marks location of a former peristome and denotes a temporary halt in growth.

flared peristome. With diameter larger than that of body chamber.

flared rib. Swollen so as to stand in higher relief than average ribs.

floored (hollow keel). Divided from chambers by a partition (septum) external to the siphuncle.

foliole. Minor element of saddle of a suture.

goniatitic (suture). With most or all lobes and saddles of suture entire (not denticulate or frilled), the only common exception being the ventral lobe, which is subdivided.

growth lines. Striae encircling whorl, in some shells separating lamellae, marking repeated minor halts in growth.

gyrocone. Loosely coiled shell which completes only a single whorl approximately.

helicoid. Coiled in regular 3-dimensional spiral form with constant spiral angle, as in most gastropods.

heteromorph. Ammonoid shell of any form except plane spiral with whorls in contact.

hyponomic sinus. Ventral notch or re-entrant in peristome through which the hyponome protrudes, useful for orienting shells because it is invariably ventral where present.

impressed area. Concave dorsal part of shell and in some including dorsolateral part of coiled shell; comprises part of whorl between umbilical seams that is in contact with preceding whorl.

intercalatory (rib). Secondary rib not attached to primary rib, at least on one side of whorl.

intercosta. *See* interspace.

internal lobe. *See* dorsal lobe.

internal suture. Part of suture located within impressed area and extending between umbilical seams.

interspace. Area between adjacent ribs.

involute. With whorls overlapping considerably and hence with narrow umbilicus (*see* evolute).

keel. Continuous distinct longitudinal ridge on venter; may be either solid or hollow, those of hollow type being floored (septicarinate) or without floor so as to open inward to chambers.

labial ridge. Linear elevation of shell corresponding to former apertural border (peristome).

lanceolate. Spear-shaped, referring to form of suture lobes or cross section of acute periphery of shell.

lappet. Simple or necked (spatulate) projection of peristome on whorl sides or venter (called ventral lappet when located on venter); also called ear or auricle.

last septum. Septum separating body chamber from adjoining camera at any stage of growth; adoral septum.

lateral lobes. Primary lobes of external suture other than ventral lobe: **1st lateral lobe** next to ventral lobe, usually on whorl side but in depressed whorls commonly on venter; **2nd lateral lobe** next to 1st lateral, commonly on whorl side and morphogenetically part of umbilical lobe.

lateral saddles. Primary saddles of external suture other than ventral saddle: **1st lateral saddle** (external saddle) separating ventral lobe from 1st lateral lobe; **2nd lateral saddle** (often called 1st lateral saddle) separating 1st and 2nd lateral lobes.

lateral sinus. Notch or re-entrant in peristome on whorl sides.

lateral sulcus. Spiral groove on whorl sides.

lipped (peristome). With liplike extension of shell set at an angle to the apertural rim.

lira. Fine raised line on shell surface.

lobe. Element of suture directed backward (adapically).

lobule. Minor element of sutural lobe.

longitudinal. In direction of shell growth, generally equivalent to spiral.

looped (ribs). United on ventrolateral angle, usually at a tubercle.

median saddle. *See* ventral saddle.

mouth. *See* aperture.

node. Large blunt or formless tubercle.

oblique whorl height. *See* whorl height.

occluded (umbilicus). So narrow or closed that inner whorls are not visible.

ornament. Features of shell exterior such as ribs, tubercles, bullae, clavi, spines, and strigations.

oxycone. Discoidal shell with acute periphery and very narrow or occluded umbilicus (as in *Oxynoticeras*).

parabola. Collective term for rib, node, or constriction of parabolic form.

parabolic node. Small node or tubercle near ventrolateral angle of whorl, associated with an earlier growth halt and independent of ordinary tuberculation.

peristome. Edge of aperture of body chamber; mouth border.

phragmocone. Camerated part of shell.

phylloid. Leaf-shaped, commonly referring to saddle endings (folioles) of sutures.

pila. *See* rib.

planulate. Moderately evolute compressed shell with open umbilicus and bluntly rounded venter (as in *Perisphinctes*).

platycone. Shell with flattened form, without implication as to width of umbilicus or shape of venter.

plicate (-d). With vague coarse radial folds, commonly denoting last stage in obsolescence of ribbing.

primary rib. Main stem or simple inward part of a branched rib.

prochoanitic (septal neck). Directed forward (adaperturally).

projected (rib). Swung forward (adaperturally) at or near venter.

prorsiradiate (rib). With general forward (adapertural) inclination from umbilical side toward venter.

prosepta. Initial partitions in apical part of shell.

prosiphon. Small structure extending from adapical part of caecum to wall of protoconch and having form of a partial cone.

prosiphonate. *See* prochoanitic.

prosuture. Line of junction of proseptum with walls of shell.

protoconch. First chamber of shell, closed by proseptum; sometimes called initial chamber or apical chamber.

pseudoceratitic (suture). Approximating ceratitic in form (but not related to ceratites).

radial. Direction outward from center of umbilicus, at right angles to axis of coiling and growth; transverse.

rectiradiate (rib). In straight radial position, bending neither forward nor backward.

retracted (suspensive lobe). Bent backward (adapically) on approaching umbilical edge and in umbilical area.

retrochoanitic (septal neck). Directed backward (adapically).

retrosiphonate. *See* retrochoanitic.

rib. Radially directed ridge on shell; sometimes called costa or pila.

rostrum. Pointed projection of peristome on venter; may continue spiral line of coiling or diverge from it.

runcinate. *See* tabulate.

rursiradiate (rib). Inclined backward (adapically) proceeding from umbilical area toward venter.

saddle. Element of suture directed forward (adaperturally).

secondary rib. Outer part of branched rib.

septal foramen. Opening in septum at siphuncle.

septal lobe. Lobe formed on adoral face of preceding septum.

septal neck. Tubular extension of septum around siphuncle, termed prochoanitic if directed forward (adaperturally) and retrochoanitic if directed backward (adapically).

septal funnel. *See* septal neck.

septate (whorl). Divided into camerae by transverse septa.

septicarinate. Having a hollow floored keel.

septum. Transverse partition dividing shell into camerae, attached to inside of shell wall along suture line.

serpenticone. Very evolute many-whorled shell with whorls hardly overlapping, like coiled snake or rope (as in *Skirroceras*): sometimes called tarphycone.

serrated (keel). Toothed or notched.

shell. Complete hard parts of ammonoid, including protoconch and conch (but excluding aptychus and beaks or jaw structures, which generally are separated from the conch if preserved at all).

shoulder. Ventrolateral blunt angle of whorl.

sigmoid (rib). S-shaped, sinuous, flexuous.

simple (peristome). Devoid of lappets or rostrum.

simple (rib). Unbranched.

simple (suture). Not appreciably subdivided.

sinus. Re-entrant curve or notch in any part of peristome.

sipho, siphon. *See* siphuncle.

siphuncle. Narrow longitudinal tube passing through camerae and septa from protoconch to base of body chamber.

spatulate (lappet). Spoon-shaped, stalked, bud-shaped.

sphaerocone. Involute globular shell with small or occluded umbilicus which commonly opens out suddenly along last whorl (as in *Sphaeroceras*).

stria. Minute groove on shell surface, especially on otherwise smooth shell.

strigate. Shell surface finely ridged or furrowed longitudinally (as in *Strigoceras*).

sulcate. With longitudinal groove on venter.

sulcus. Groove on shell surface, usually referring to longitudinal groove on venter.

suspensive lobe. Visible external part of umbilical lobe of suture on exposed part of whorl, comprising portion from which auxiliaries spring.

sutural elements. Major undulations of suture alternately directed forward (adaperturally) as saddles and backward (adapically) as lobes.

suture. Line of junction of septum with walls of shell, visible only when this wall is removed; sometimes termed septal suture, suture line.

tabulate (venter). Truncate or flattened; sometimes termed runcinate (planed off).

tarphycone. *See* serpenticone.

test. Fossil shell substance; material of the shell as opposed to the fossil as an object.

torticone. Shell coiled in irregular 3-dimensional spiral with progressive twisting of conch.

transverse. *See* radial.

tricarinate. Bearing 3 keels on venter.

trifurcate (rib). Dividing into 3 branches.

triplicate. *See* trifurcate.

tubercle. Projection or pimple on shell surface, or on internal mold (cast) commonly representing base of a spine.

umbilical angle. Generally blunt angle between whorl side and umbilical area.

umbilical area. Inner part of whorl on each side, separating umbilical angle from umbilical seam; called umbilical wall if it rises somewhat vertically from spiral plane and umbilical slope if it rises gently.

umbilical border. *See* umbilical angle.

umbilical callus. Plug of test that more or less fills umbilicus.

umbilical edge. *See* umbilical angle.

umbilical lobe. Large primary lobe of suture centered on or near umbilical seam and forming part of both external and internal sutures.

umbilical perforation. Vacant space around axis of coiling and connecting umbilici.

umbilical seam. Helical line of overlap of successive whorls, comprising "line of involution" analogous to suture of gastropods.

umbilical shoulder. *See* umbilical angle.

umbilical suture. *See* umbilical seam.

umbilical width. Diameter of umbilicus measured either between umbilical angles (outside diameter) or between umbilical seams (inside diameter).

umbilicus. External depression on each side of shell centered on axis of coiling, its rim being the umbilical angle or edge.

unipolar. *See* ceratitic.

venter. Peripheral wall of whorl comprising part of shell radially farthest from protoconch; in heteromorphs, the homologous wall.

ventral area. *See* venter.

ventral lappet. *See* lappet.

ventral lobe. Median primary lobe of suture located on venter, external in normally coiled shells and therefore sometimes called external lobe.

ventral saddle. Median saddle of suture located on venter, external in normally coiled shells and therefore sometimes called external saddle.

ventrolateral angle. Angle between venter and whorl side, called shoulder if blunt.

ventrolateral edge (or margin). *See* ventrolateral angle.

virgatotome. Type of ribbing in which 3 to 6 straight secondaries may branch off in succession from forward (adapertural) side of a primary rib (as in *Virgatites*).

volution. *See* whorl.

whorl. Complete turn of shell through 360 degrees.

whorl flank. *See* whorl side.

whorl height. Height of whorl measured at right angles to maximum width, comprising distance from middle of venter to middle of dorsum plus depth of impressed area; in practice, oblique whorl height commonly is used, consisting of distance from umbilical seam to middle of venter.

whorl section. Transverse section of a whorl.

whorl side. Lateral wall of whorl between umbilical seam and venter.

whorl thickness. *See* whorl width.

whorl width. Maximum horizontal distance between points located between ribs or spines on opposite whorl sides.

SUMMARY OF CLASSIFICATION

By W. J. Arkell, W. M. Furnish, Bernhard Kummel, A. K. Miller, O. H. Schindewolf, and C. W. Wright

An outline of the classification of ammonoids as developed by authors working on this group of fossils for the *Treatise* is introduced here for the purpose of summarizing taxonomic relationships, stratigraphic distribution, and numbers of genera and subgenera which now are known in each family-group and higher-rank taxon. Where a single number is recorded, this refers to genera, and where 2 numbers are given, the first indicates genera and the second indicates subgenera (for example, "4; 6" signifies 4 genera and 6 subgenera). The outline furnishes also a convenient means of explicit statement of the authorship of systematic descriptions given in following parts of the volume, which is made by recording with each division the initial letters of the author's name (as A for Arkell, F for Furnish, K for Kummel, M for Miller, S for Schindewolf, and W for Wright).

This section on summary of Classification has been compiled by R. C. Moore from the typescript submitted by the several authors.

Suprageneric Divisions of Ammonoidea[1]

- Ammonoidea *(order)* (1,554; 384) (incl. genera of aptychi, 1,570; 384). *L.Dev.-U.Cret.* (A-F-K-M-S-W)
  - Anarcestina *(suborder)* (34; 2). *L.Dev.-U.Dev.* (F-M)
    - Anarcestaceae *(superfamily)* (16; 2). *L.Dev.-U. Dev.* (F-M)
      - Mimoceratidae (4). *L.Dev.-M.Dev.* (F-M)
        - Mimoceratinae (1). *L.Dev.-M.Dev.* (F-M)
        - Mimosphinctinae (3). *L.Dev.* (F-M)
      - Agoniatitidae (3). *L.Dev.-M.Dev.* (F-M)
      - Anarcestidae (9; 2). *L.Dev.-U.Dev.* (F-M)
        - Anarcestinae (4; 2) *L.Dev.-U.Dev.* (F-M)
        - Pinacitinae (5). *L.Dev.-M.Dev.* (F-M)
    - Prolobitaceae *(superfamily)* (6). *M.Dev.-U.Dev.* (F-M)
      - Prolobitidae (6). *M.Dev.-U.Dev.* (F-M)
        - Prolobitinae (3). *M.Dev.-U.Dev.* (F-M)
        - Sandbergeroceratinae (3). *U.Dev.* (F-M)
    - Pharciceratacaeae *(superfamily)* (12). *U.Dev.* (F-M)
      - Gephuroceratidae (5). *U.Dev.* (F-M)
      - Pharciceratidae (4). *U.Dev.* (F-M)
      - Beloceratidae (3). *U.Dev.* (F-M)
  - Clymeniina *(suborder)* (30; 5). *U.Dev.* (S)
    - Gonioclymeniaceae *(superfamily)* (16; 2). *U.Dev.* (S)
      - Hexaclymeniidae (3). *U.Dev.* (S)
      - Acanthoclymeniidae (1). *U.Dev.* (S)
      - Gonioclymeniidae (5; 2). *U.Dev.* (S)
      - Wocklumeriidae (5). *U.Dev.* (S)
      - Glatziellidae (2). *U.Dev.* (S)
    - Clymeniaceae *(superfamily)* (11; 3). *U.Dev.* (S)
      - Clymeniidae (6; 3).*U.Dev.* (S)
      - Cyrtoclymeniidae (3). *U.Dev.* (S)
      - Rectoclymeniidae (2). *U.Dev.* (S)
    - Parawocklumeriaceae *(superfamily)* (3). *U.Dev.* (S)
      - Parawocklumeriidae (3). *U.Dev.* (S)
  - Goniatitina *(suborder)* (93; 14). *M.Dev.-U.Perm.* (F-M)
    - Cheilocerataceae *(superfamily)* (17; 7). *M.Dev.-M.Perm.* (F-M)
      - Tornoceratidae (4; 4). *M.Dev.-U.Dev.* (F-M)
      - Cheiloceratidae (13; 3). *M.Dev.-U.Perm.* (F-M)
        - Cheiloceratinae (3; 3). *U.Dev.* (F-M)
        - Raymondiceratinae (1). *U.Dev.* (F-M)
        - Sporadoceratinae (3). *U.Dev.* (F-M)
        - Imitoceratinae (6). *U.Dev.-M.Perm.* (F-M)
    - Agathicerataceae *(superfamily)* (8). *L.Penn.-M. Perm.* (F-M)
      - Agathiceratidae (2). *L.Penn.-M.Perm.* (F-M)
      - Shumarditidae (4). *U.Penn.* (F-M)
      - Perrinitidae (2). *L.Perm.-M.Perm.* (F-M)
    - Cyclolobaceae *(superfamily)* (8). *M.Penn.-U. Perm.* (F-M)
      - Popanoceratidae (5). *M.Penn.-U.Perm.* (F-M)
        - Popanoceratinae (2). *L.Perm.-M.Perm.* (F-M)
        - Marathonitinae (2). *M.Penn.-U.Perm.* (F-M)
        - Hyattoceratinae (1). *M.Perm.* (F-M)
      - Cyclolobidae (3). *M.Perm.-U.Perm.* (F-M)
    - Goniatitaceae *(superfamily)* (44; 7). *L.Miss-U. Perm.* (F-M)
      - Goniatitidae (22; 7). *L.Miss.-L.Perm.* (F-M)
        - Goniatitinae (9). *L.Miss.-M.Penn.* (F-M)
        - Neoglyphioceratinae (2). *U.Miss.* (F-M)
        - Pericyclinae (2; 7). *L.Miss.-U.Miss.* (F-M)
        - Girtyoceratinae (3). *U.Miss.* (F-M)
        - Bisatoceratinae (3). *U.Miss.-U.Penn.* (F-M)
        - Gonioloboceratinae (3). *M.Penn.-L.Perm.* (F-M)
      - Neoicoceratidae (12). *L.Penn.-U.Perm.* (F-M)
      - Metalegoceratidae (4). *L.Perm.-M.Perm.* (F-M)
      - Schistoceratidae (6). *L.Penn.-L.Perm.* (F-M)
        - Schistoceratinae (5). *L.Penn.-L.Perm.* (F-M)
        - Welleritinae (1). *M.Penn.* (F-M)

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[1] The group of bactritids, comprising the suborder Bactritina Miller & Furnish, 1954, and component divisions, is excluded from description and discussion in this volume of the *Treatise*, although it has been accepted generally as belonging to the Ammonoidea. By agreement of authors who are working to prepare the *Treatise* text and illustrations for the nautiloid cephalopods, the Bactritina are to be included in Part K.—Editor.

  - Adrianitaceae *(superfamily)* (8). *M.Penn.-M.Perm.* (F-M)
    - Adrianitidae (8). *M.Penn.-M.Perm.* (F-M)
      - Adrianitinae (5). *L.Perm.-M.Perm.* (F-M)
      - Dunbaritinae (2). *M.Penn.-U.Penn.* (F-M)
      - Clinolobinae (1). *M.Perm.* (F-M)
  - Dimorphocerataceae *(superfamily)* (8). *U.Miss.-M.Perm.* (F-M)
    - Dimorphoceratidae (3). *U.Miss.-U.Penn., ?L.Perm.* (F-M)
    - Thalassoceratidae (5). *U.Miss.-M.Perm.* (F-M)
- Prolecanitina *(suborder)* (27). *U.Dev.-U.Trias.* (F-M)
  - Prolecanitaceae *(superfamily)* (9). *U.Dev.-M.Perm.* (F-M)
    - Prolecanitidae (5). *U.Dev.-U.Miss.* (F-M)
    - Prodromitidae (1). *L.Miss.* (F-M)
    - Daraelitidae (3). *U.Miss.-M.Perm.* (F-M)
  - Medlicottiaceae *(superfamily)* (18). *U.Miss.-U.Trias.* (F-M)
    - Pronoritidae (6). *U.Miss.-M.Perm.* (F-M)
    - Medlicottiidae (8). *L.Penn.-L.Trias.* (F-M)
      - Uddenitinae (3). *L.Penn.-U.Penn.* (F-M)
      - Medlicottiinae (5). *U.Penn.-L.Trias.* (F-M)
    - Sageceratidae (4). *L.Trias.-U.Trias.* (F-M)
- Ceratitina *(suborder)* (390; 36). *M.Perm.-U.Trias.* (K)
  - Otocerataceae *(superfamily)* (17; 9). *M.Perm.-L.Trias.* (K)
    - Xenodiscidae (6). *M.Perm.-U.Perm.* (K)
    - Otoceratidae (5; 2). *U.Perm.-L.Trias.* (K)
    - Ophiceratidae (5; 7). *L.Trias.* (K)
    - Dieneroceratidae (1). *L.Trias.* (K)
  - Noritaceae *(superfamily)* (94). *L.Trias.-M.Trias.* (K)
    - Gyronitidae (8). *L.Trias.* (K)
      - Gyronitinae (6). *L.Trias.* (K)
      - Kymatitinae (2). *L.Trias.* (K)
    - Flemingitidae (6). *L.Trias.* (K)
    - Xenoceltitidae (5). *L.Trias.* (K)
      - Xenoceltitinae (3). *L.Trias.* (K)
      - Inyoitinae (2). *L.Trias.* (K)
    - Paranoritidae (6). *L.Trias.* (K)
    - Proptychitidae (8). *L.Trias.* (K)
      - Proptychitinae (6). *L.Trias.* (K)
      - Owenitinae (2). *L.Trias.* (K)
    - Paranannitidae (15). *L.Trias.* (K)
      - Paranannitinae (7). *L.Trias.* (K)
      - Columbitinae (8). *L.Trias.* (K)
    - Ussuriidae (3). *L.Trias.* (K)
    - Hedenstroemiidae (12). *L.Trias.-M.Trias.* (K)
      - Hedenstroemiinae (7). *L.Trias.* (K)
      - Lanceolitinae (1). *L.Trias.* (K)
      - Aspenitinae (3). *L.Trias.* (K)
      - Beneckeinae (1). *L.Trias.-M.Trias.* (K)
    - Kashmiritidae (4). *L.Trias.* (K)
    - Meekoceratidae (10). *L.Trias.* (K)
      - Meekoceratinae (3). *L.Trias.* (K)
      - Arctoceratinae (5). *L.Trias.* (K)
      - Dagnoceratinae (2). *L.Trias.* (K)
    - Noritidae (5). *L.Trias.-M.Trias.* (K)
    - Prionitidae (4). *L.Trias.* (K)
    - Sibiritidae (8). *L.Trias.* (K)
  - Ceratitaceae *(superfamily)* (67; 5). *L.Trias.-U.Trias.* (K)
    - Stephanitidae (3). *L.Trias.* (K)
    - Tirolitidae (6). *L.Trias.* (K)
    - Dinaritidae (4). *L.Trias.* (K)
    - Hellenitidae (1). *L.Trias.* (K)
    - Acrochordiceratidae (2; 3). *M.Trias.* (K)
    - Beyrichitidae (5; 2). *L.Trias.-M.Trias.* (K)
    - Ceratitidae (16). *M.Trias.* (K)
    - Danubitidae (4). *M.Trias.* (K)
    - Balatonitidae (3). *M.Trias.* (K)
    - Hungaritidae (9). *L.Trias.-U.Trias.* (K)
    - Carnitidae (7). *M.Trias.-U.Trias.* (K)
    - Proteusitidae (1). *M.Trias.* (K)
    - Aplococeratidae (6). *M.Trias.* (K)
  - Clydonitaceae *(superfamily)* (70; 12). *M.Trias.-U.Trias.* (K)
    - Trachyceratidae (8; 6). *M.Trias.-U.Trias.* (K)
    - Clydonitidae (2). *U.Trias.* (K)
    - Clionitidae (8; 4). *U.Trias.* (K)
    - Arpaditidae (14). *M.Trias.-U.Trias.* (K)
    - Heraclitidae (1). *U.Trias.* (K)
    - Lecanitidae (2). *M.Trias.-U.Trias.* (K)
    - Cyrtopleuritidae (4). *U.Trias.* (K)
    - Tibetitidae (10). *M.Trias.-U.Trias.* (K)
    - Buchitidae (7). *U.Trias.* (K)
    - Thisbitidae (5) *U.Trias.* (K)
    - Noridiscitidae (1). *U.Trias.* (K)
    - Distichitidae (3). *U.Trias.* (K)
    - Choristoceratidae (4; 2). *U.Trias.* (K)
    - Cochloceratidae (1). *U.Trias.* (K)
  - Tropitaceae *(superfamily)* (87; 4). *M.Trias.-U.Trias.* (K)
    - Tropitidae (12). *U.Trias.* (K)
    - Tropiceltitidae (6). *U.Trias.* (K)
    - Celtitidae (8). *M.Trias.-U.Trias.* (K)
    - Metasibiritidae (2). *U.Trias.* (K)
    - Haloritidae (29; 2). *U.Trias.* (K)
      - Haloritinae (25). *U.Trias.* (K)
      - Sagenitinae (1; 2). *U.Trias.* (K)
      - Episculitinae (3). *U.Trias.* (K)
    - Didymitidae (30; 2). *U.Trias.* (K)
  - Lobitaceae *(superfamily)* (6). *M.Trias.-U.Trias.* (K)
    - Lobitidae (6). *M.Trias.-U.Trias.* (K)
  - Arcestaceae *(superfamily)* (16; 6). *M.Trias.-U.Trias.* (K)
    - Arcestidae (1; 6). *M.Trias.-U.Trias.* (K)
    - Joannitidae (3). *M.Trias.-U.Trias.* (K)
    - Sphingitidae (1). *U.Trias.* (K)
    - Cladidiscitidae (5). *M.Trias.-U.Trias.* (K)
    - Megaphyllitidae (5). *M.Trias.-U.Trias.* (K)
    - Nathorstitidae (1). *M.Trias.-U.Trias.* (K)
  - Ptychitaceae *(superfamily)* (17). *M.Trias.-U.Trias.* (K)
    - Ptychitidae (12). *M.Trias.-U.Trias.* (K)
    - Isculitidae (4). *M.Trias.* (K)

    - ?Nannitidae (1). *U.Trias.* (K)
  - Pinacocerataceae *(superfamily)* (16). *L.Trias.-U.Trias.* (K)
    - Pinacoceratidae (8). *M.Trias.-U.Trias.* (K)
    - Gymnitidae (8). *L.Trias.-U.Trias.* (K)
- Phylloceratina *(suborder)* (34). *L.Trias.-U.Cret.* (A-K-W)
  - Phyllocerataceae *(superfamily)* (34). *L.Trias.-U.Cret.* (A-K-W)
    - Ussuritidae (7). *L.Trias.-U.Trias.* (K)
    - Discophyllitidae (4). *U.Trias.* (K)
    - Phylloceratidae (15). *L.Jur.-U.Cret.* (A-W)
      - Phylloceratinae (8). *L.Jur.-U.Cret.* (A-W)
      - Calliphylloceratinae (7). *L.Jur.-L.Cret.* (A)
    - Juraphyllitidae (8). *L.Jur.* (A)
- Lytoceratina *(suborder)* (165; 24). *L.Jur.-U.Cret.* (A-W)
  - Lytocerataceae *(superfamily)* (49; 4). *L.Jur.-U.Cret.* (A-W)
    - Pleuroacanthitidae (2). *L.Jur.* (A)
      - Analytoceratinae (1). *L.Jur.* (A)
      - Pleuroacanthitinae (1). *L.Jur.* (A)
    - Ectocentritidae (5). *L.Jur.* (A)
    - Derolytoceratidae (3). *L.Jur.* (A)
    - Lytoceratidae (17; 2). *L.Jur.-U.Cret.* (A-W)
      - Lytoceratinae (9; 2). *L.Jur.-U.Cret.* (A-W)
      - Metalytoceratinae (3). *M.Jur.* (A)
      - Villaniinae (1). *M.Jur.* (A)
      - Alocolytoceratinae (4). *M.Jur.* (A)
    - Nannolytoceratidae (2). *L.Jur.-M.Jur.* (A)
    - Protetragonitidae (3). *U.Jur.-L.Cret.* (W)
    - Tetragonitidae (13; 2). *L.Cret.-U.Cret.* (W)
      - Gaudryceratinae (8). *L.Cret.-U.Cret.* (W)
      - Kossmatellinae (1). *L.Cret.-U.Cret.* (W)
      - Tetragonitinae (4; 2). *L.Cret.-U.Cret.* (W)
    - Macroscaphitidae (3). *L.Cret.* (W)
    - Cicatritidae (1). *L.Cret.* (W)
  - Spirocerataceae *(superfamily)* (4). *L.Jur.-U.Jur.* (A)
    - Arcuceratidae (1). *L.Jur.* (A)
    - Spiroceratidae (3). *M.Jur.-U.Jur.* (A)
  - Ancylocerataceae *(superfamily)* (40; 4). *U.Jur.-L.Cret.* (W)
    - Bochianitidae (7). *U.Jur.-L.Cret.* (W)
      - Protancyloceratinae (3). *U.Jur.-L.Cret.* (W)
      - Bochianitinae (4). *U.Jur.-L.Cret.* (W)
    - Ancyloceratidae (28). *L.Cret.* (W)
      - Crioceratinae (12). *L.Cret.* (W)
      - Ancyloceratinae (16). *L.Cret.* (W)
    - Heteroceratidae (2; 4). *L.Cret.* (W)
    - Hemihoplitidae (3). *L.Cret.* (W)
  - Turrilitaceae *(superfamily)* (55; 14). *L.Cret.-U.Cret.* (W)
    - Ptychoceratidae (5). *L.Cret.* (W)
    - Hamitidae (5; 3). *L.Cret.-U.Cret.* (W)
    - Baculitidae (6). *L.Cret.-U.Cret.* (W)
    - Anisoceratidae (7) *L.Cret.-U.Cret.* (W)
    - Phlycticrioceratidae (2). *U.Cret.* (W)
    - Turrilitidae (10; 7). *L.Cret.-U.Cret.* (W)
    - Nostoceratidae (11; 2). *U.Cret.* (W)
    - Diplomoceratidae (9; 2). *U.Cret.* (W)
  - Scaphitaceae *(superfamily)* (17; 2). *L.Cret.-U.Cret.* (W)
    - Scaphitidae (13). *L.Cret.-U.Cret.* (W)
      - Scaphitinae (11). *L.Cret.-U.Cret* (W)
      - Otoscaphitinae (2). *L.Cret.-U.Cret.* (W)
    - Labeceratidae (4; 2). *L.Cret.* (W)
- Ammonitina *(suborder)* (781; 303). *L.Jur.-U.Cret.* (A-W)
  - Psilocerataceae *(superfamily)* (67; 5). *L.Jur.* (A)
    - Psiloceratidae 16; 3). *L.Jur.* (A)
      - Psiloceratinae (8; 3). *L.Jur.* (A)
      - Alsatitinae (8). *L.Jur.* (A)
    - Schlotheimiidae (9). *L.Jur.* (A)
    - Arietitidae (25; 2). *L.Jur.* (A)
      - Arietitinae (13). *L.Jur.* (A)
      - Arnioceratinae (3). *L.Jur.* (A)
      - Asteroceratinae (8). *L.Jur.* (A)
      - Cymbitinae (1; 2). *L.Jur.* (A)
    - Oxynoticeratidae (10). *L.Jur.* (A)
    - Echioceratidae (7). *L.Jur.* (A)
  - Eoderocerataceae *(superfamily)* (43; 12). *L.Jur.* (A)
    - Eoderoceratidae (16; 2). *L.Jur.* (A)
      - Xipheroceratinae (4). *L.Jur.* (A)
      - Eoderoceratinae (5; 2). *L.Jur.* (A)
      - Phricodoceratinae (2). *L.Jur.* (A)
      - Coeloceratinae (5). *L.Jur.* (A)
    - Polymorphitidae (9; 2). *L.Jur.* (A)
      - Polymorphitinae (7; 2). *L.Jur.* (A)
      - Acanthopleuroceratinae (2). *L.Jur.* (A)
    - Liparoceratidae (6; 4). *L.Jur.* (A)
    - Amaltheidae (3; 2). *L.Jur.* (A)
    - Dactylioceratidae (9; 2). *L.Jur.* (A)
  - Hildocerataceae *(superfamily)* (75: 21). *L.Jur.-M.Jur.* (A)
    - Hildoceratidae (34; 10). *L.Jur.-M.Jur.* (A)
      - Arieticeratinae (5). *L.Jur.* (A)
      - Harpoceratinae (13; 6). *L.Jur.-M.Jur.* (A)
      - Hildoceratinae (4; 2). *L.Jur.* (A)
      - Bouleiceratinae (4). *L.Jur.* (A)
      - Grammoceratinae (7; 2). *L.Jur.-M.Jur.* (A)
      - Tmetoceratinae (1). *M.Jur.* (A)
    - Graphoceratidae (16; 2). *M.Jur.* (A)
      - Leioceratinae (5; 2). *M.Jur.* (A)
      - Graphoceratinae (11). *M.Jur.* (A)
    - Hammatoceratidae (12; 4). *L.Jur.-M.Jur.* (A)
      - Phymatoceratinae (7; 2). *L.Jur.* (A)
      - Hammatoceratinae (5; 2). *L.Jur.-M.Jur.* (A)
    - Sonniniidae (13; 5). *M.Jur.* (A)
  - Haplocerataceae *(superfamily)* (60; 38). *M.Jur.-L.Cret.* (A-W)
    - Strigoceratidae (3). *M.Jur.* (A)
    - Haploceratidae (9; 2). *M.Jur.-L.Cret.* (A)
    - Oppeliidae (48; 36). *M.Jur.-L.Cret.* (A)
      - Oppeliinae (7; 15). *M.Jur.-U.Jur.* (A)
      - Hecticoceratinae (2; 9). *M.Jur.-U.Jur.* (A)
      - Ochetoceratinae (5; 3). *U.Jur.* (A)
      - Distichoceratinae (8). *M.Jur.-U.Jur.* (A)
      - Taramelliceratinae (9; 5). *U.Jur.* (A)

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  -
    - Phlycticeratinae (1). *M.Jur.* (A)
    - Streblitinae (9; 2). *U.Jur.* (A)
    - Mazapilitinae (2). *U.Jur.* (A)
    - Aconeceratinae (5; 2). *L.Cret.* (W)
- Stephanocerataceae *(superfamily)* (69: 67). *M.Jur.-U.Jur.* (A)
  - Otoitidae (6; 4). *M.Jur.* (A)
  - Stephanoceratidae (7; 7). *M.Jur.* (A)
  - Thamboceratidae (3). *M.Jur.* (A)
  - Clydoniceratidae (4; 2). *M.Jur.* (A)
  - Sphaeroceratidae (4). *M.Jur.* (A)
  - Tulitidae (7; 2). *M.Jur.* (A)
  - Macrocephalitidae (12; 7). *M.Jur.* (A)
  - Oecoptychiidae (2). *M.Jur.-U.Jur.* (A)
  - Pachyceratidae (2; 6). *M.Jur.-U.Jur.* (A)
  - Mayaitidae (5; 2). *U.Jur.* (A)
  - Kosmoceratidae (7; 10). *M.Jur.* (A)
  - Cardioceratidae (10; 27). *M.Jur.-U.Jur.* (A)
    - Cadoceratinae (5; 3). *M.Jur.* (A)
    - Cardioceratinae (5; 24). *M.Jur.-U.Jur.* (A)
- Perisphinctaceae *(superfamily)* (210: 81). *M.Jur.-L.Cret.* (A-W)
  - Parkinsoniidae (8; 9). *M.Jur.* (A)
  - Morphoceratidae (4; 2). *M.Jur.* (A)
  - Reineckeiidae (4; 3). *M.Jur.* (A)
  - Perisphinctidae (90; 36). *M.Jur.-U.Jur.* (A)
    - Leptosphinctinae (4; 3). *M.Jur.* (A)
    - Zigzagiceratinae (5; 4). *M.Jur.* (A)
    - Proplanulitinae (6). *M.Jur.* (A)
    - Pseudoperisphinctinae (12: 5). *M.Jur.* (A)
    - Perisphinctinae (5; 12). *U.Jur.* (A)
    - Ataxioceratinae (8). *U.Jur.* (A)
    - Pictoniinae (6; 4). *U.Jur.* (A)
    - Aulacostephaninae (13). *U.Jur.* (A)
    - Virgatosphinctinae (18; 3). *U.Jur.* (A)
    - Dorsoplanitinae (10; 5). *U.Jur.* (A)
    - Virgatitinae (3). *U.Jur.* (A)
  - Aspidoceratidae (28; 11). *M.Jur.-U.Jur.* (A)
    - Peltoceratinae (10; 3). *M.Jur.-U.Jur.* (A)
    - Aspidoceratinae (7; 8). *M.Jur.-U.Jur.* (A)
    - Simoceratinae (11). *U.Jur.* (A)
  - Craspeditidae (10; 6). *U.Jur.-L.Cret.* (A)
    - Craspeditinae (1; 4). *U.Jur.-L.Cret.* (A)
    - Garniericeratinae (6; 2). *U.Jur.-L.Cret.* (A)
    - Tolliinae (3). *L.Cret.* (A)
  - Olcostephanidae (18; 7). *U.Jur.-L.Cret.* (A-W)
    - Spiticeratinae (6; 3). *U.Jur.-L.Cret.* (A-W)
    - Olcostephaninae (4; 2). *L.Cret.* (W)
    - Polyptychitinae (5; 2). *L.Cret.* (W)
    - Simbirskitinae (3). *L.Cret.* (W)
  - Berriasellidae (46; 7). *U.Jur.-L.Cret.* (A-W)
    - Berriasellinae (17; 2). *U.Jur.-L.Cret.* (A)
    - Himalayitinae (8; 2). *U.Jur.* (A)
    - Neocomitinae (21; 3). *L.Cret.* (A-W)
  - Oosterellidae (2). *L.Cret.* (A-W)
- Desmocerataceae *(superfamily)* (61; 23). *L.Cret.-U.Cret.* (W)
  - Desmoceratidae (29; 15). *L.Cret.-U.Cret.* (W)
    - Eodesmoceratinae (3; 4). *L.Cret.* (W)
    - Puzosiinae (13; 8). *L.Cret.-U.Cret.* (W)
    - Beudanticeratinae (6). *L.Cret.* (W)
    - Desmoceratinae (5; 3). *L.Cret.-U.Cret.* (W)
    - Hauericeratinae (2). *U.Cret.* (W)
  - Holcodiscidae (8). *L.Cret.* (W)
  - Silesitidae (2). *L.Cret.* (W)
  - Kossmaticeratidae (4; 6). *L.Cret.-U.Cret.* (W)
  - Pachydiscidae (16; 2). *L.Cret.-U.Cret.* (W)
  - Muniericeratidae (2). *U.Cret.* (W)
- Hoplitaceae *(superfamily)* (84; 10). *L.Cret.-U.Cret.* (W)
  - Pulchelliidae (7). *L.Cret.* (W)
  - Trochleiceratidae (1). *L.Cret.* (W)
  - Douvilleiceratidae (18; 2). *L.Cret.* (W)
    - Cheloniceratinae (7; 2). *L.Cret.* (W)
    - Parahoplitinae (2). *L.Cret.* (W)
    - Acanthohoplitinae (7). *L.Cret.* (W)
    - Douvilleiceratinae (2). *L.Cret.* (W)
  - Deshayesitidae (4). *L.Cret.* (W)
  - Engonoceratidae (7). *L.Cret.-U.Cret.* (W)
  - Placenticeratidae (9). *L.Cret.-U.Cret.* (W)
  - Leymeriellidae (3). *L.Cret.* (W)
  - Hoplitidae (28; 8). *L.Cret.-U.Cret.* (W)
    - Cleoniceratinae (5; 2). *L.Cret.* (W)
    - Hoplitinae (17; 6). *L.Cret.-U.Cret.* (W)
    - Gastroplitinae (6). *L.Cret., ?U.Cret.* (W)
  - Schloenbachiidae (6). *L.Cret.-U.Cret.* (W)
  - Forbesiceratidae (1). *U.Cret.* (W)
- Acanthocerataceae *(superfamily)* (112; 46). *L.Cret.-U.Cret.* (W)
  - Brancoceratidae (19; 18). *L.Cret.-U.Cret.* (W)
    - Brancoceratinae (3; 2). *L.Cret.* (W)
    - Mojsisovicziinae (5; 6). *L.Cret.* (W)
    - Mortoniceratinae (11; 10). *L.Cret.-U.Cret.* (W)
  - Flickiidae (3). *L.Cret.-U.Cret.* (W)
  - Lyelliceratidae (7; 4). *U.Cret.-U.Cret.* (W)
  - Acanthoceratidae (24; 2). *U.Cret.* (W)
    - Mantelliceratinae (8; 2). *U.Cret.* (W)
    - Acanthoceratinae (8). *U.Cret.* (W)
    - Metoicoceratinae (2). *U.Cret.* (W)
    - Mammitinae (6). *U.Cret.* (W)
  - Binneyitidae (2). *U.Cret.* (W)
  - Vascoceratidae (12). *U.Cret.* (W)
  - Tissotiidae (8; 8). *U.Cret.* (W)
    - Pseudotissotiinae (3; 5). *U.Cret.* (W)
    - Tissotiinae (5; 3). *U.Cret.* (W)
  - Coilopoceratidae (3). *U.Cret.* (W)
  - Collignoniceratidae (28; 14). *U.Cret.* (W)
    - Collignoniceratinae (8; 2). *U.Cret.* (W)
    - Peroniceratinae (4). *U.Cret.* (W)
    - Texanitinae (6; 6). *U.Cret.* (W)
    - Barroisiceratinae (5; 6). *U.Cret.* (W)
    - Lenticeratinae (5). *U.Cret.* (W)
  - Sphenodiscidae (6). *U.Cret.* (W)
- Aptychi (16 form-genera). *U.Dev.-U.Cret.* (A)[1]

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[1] Moore & Sylvester-Bradley, in last chapter of Part L, recognize 17 generic units classed as valid.—Editor.

PALEOZOIC AMMONOIDEA

By A. K. Miller, W. M. Furnish, and O. H. Schindewolf

CONTENTS

The systematic descriptions of the Clymeniina and its subdivisions, limited to the Upper Devonian, are by O. H. Schindewolf. Those of the other Paleozoic taxa were prepared by A. K. Miller and W. M. Furnish, who, as a matter of expediency, contributed also the text on Triassic medlicotiids and sageceratids. Bernhard Kummel has included a systematic treatment of the Permian constituents of the Otocerataceae together with the Triassic representatives of that superfamily. Thus, the divisions of Ammonoidea occurring near the Paleozoic-Mesozoic boundary have been allocated to authors on a systematic basis rather than a strictly stratigraphic basis.

MORPHOLOGY

The early ammonoids are intermediate between their ancestral nautiloids and ammonites of the Upper Paleozoic and Mesozoic. The latter, in general, are much more specialized in being diverse in form and having complex sutures. Several phylogenetic groups, with fundamental sutural differences, can be recognized in the Paleozoic, and only one of these continued into the Mesozoic. Therefore, more taxonomic significance is attributed to the sutures in the earlier than in later ammonoids. Otherwise, construction of the shells is relatively uniform throughout the order.

PROTOCONCH

The ammonoid shell consists of a small **protoconch** and a much larger **conch,** both of which were calcified and were therefore commonly preserved as fossils. Typically, the conch consists of a circinate spiral tightly coiled about the protoconch, and it is involute, as the whorls are impressed dorsally by the ventral portion of the preceding volution (Fig. 1). However, in a very few of the early members of the group there is an **umbilical perforation.** In rare specimens the coiling is subtriangular or subquadrangular; modifications at maturity are fairly common. For the most part the shells are of modest proportions, with maximum overall measurements of only a few centimeters; the largest Paleozoic forms attained diameters of only about a tenth that of huge Cretaceous species more than 2.5 m. across.

The protoconch, though spheroidal in some primitive ammonoids, is generally ellipsoidal, with its longer axis normal to the plane of coiling. It is distinctly wider than the extreme adapical part of the conch and is therefore rather conspicuous despite its small size. In its adoral portion are located the structures that are antecedent to the siphuncle (Fig. 4).

CONCH

The conch comprises all of the shell except the protoconch. In typical mature individuals it is several volutions in length. It consists of a camerate **phragmocone** and a **body chamber;** presumably the former served as a float, whereas the latter housed almost all of the soft parts of the living animal. The subdivisions of the phragmocone are sometimes called "air chambers" or "gas chambers," but it seems better to use the noncommittal term **camerae** for them. In general, their length increased progressively during ontogenetic development; but when the animal had attained full maturity it tended to form very short camerae, a fact which makes it possible to distinguish mature individuals. The partitions of the conch, which bound each camera adorally and adapically, are termed **septa.** Typically, at least, their peripheral portions are crenulate, presumably to increase the strength of the conch without adding unduly to its weight. A small conchiolin tube, the **siphuncle,** extends from the protoconch to the body chamber.

The ventral portion of the conch of many ammonoids is modified near the adoral end of the 1st volution. In some shells this modification takes the form of a constriction, whereas in others it is an expansion. This feature may be analogous to the so-called nepionic line of modern *Nautilus,* which has been interpreted as indicating the size of the individual when it hatched from the large egg, some 25 mm. in diameter. The embryogeny of *Nautilus* is still not known. However, the apical portion of the test is small in comparison to size of the egg, and presumably the embryonic development takes place within the attached egg capsule. In *Nautilus* there is no counterpart of the ammonoid protoconch, which may have served as an efficient buoying apparatus for a newly hatched animal.

The material of which the shell is composed, the **test,** is rarely if ever preserved in the original condition, but almost certainly it was largely aragonite, as in modern *Nautilus.* It consists of 3 main layers, a thin **periostracum,** a relatively thick **ostracum,** and a thin **hypostracum.** The growth lines and color markings are limited to the outer layer, the periostracum. Characteristically there are fine ridges or nodes (or both) on the surface of the hypostracum, which is therefore commonly designated the **runzelschicht** or "wrinkle-layer." The shell walls are remarkably thin for the most part, and therefore light in weight, suggesting that these animals were active and the shell buoyant. Color markings are unknown on Paleozoic ammonoids but have been recorded on a few Mesozoic forms; longitudinal, transverse, and zigzag bands have been found on nautiloids of various ages. As would be expected of creatures adapted for swimming, the surface of the shell tends to be rather smooth and the **growth lines** are generally fine and not very prominent.

Nevertheless, many ammonoids bear keels, lirae, ribs, nodes, and spines, and such protuberances are more common in the ammonites and the ceratites than in the nautiloids and the primitive ammonoids. Furthermore, in many cases the conch bears transverse **constrictions** which are more prominent on the internal mold than on the exterior of the test and which tend to be more or less parallel to the growth lines and to strengthen the shell. Characteristically they are limited to the phragmocone at maturity, except for an apertural constriction, which reinforces the peristome. In *Agathiceras* the constrictions of the phragmocone are not discernible on the exterior of the test, and they consist exclusively of internal thickenings of the ostracum.

The **shape of growth lines** in most ammonoids can be expressed briefly by a nomenclature propounded by WEDEKIND in 1918 but not widely used. Growth lines that are straight or nearly so on both the lateral and ventral areas of the conch are said to be **linear;** those that form a single broad rounded salient on each of the lateral areas and a sinus on the venter are said to be

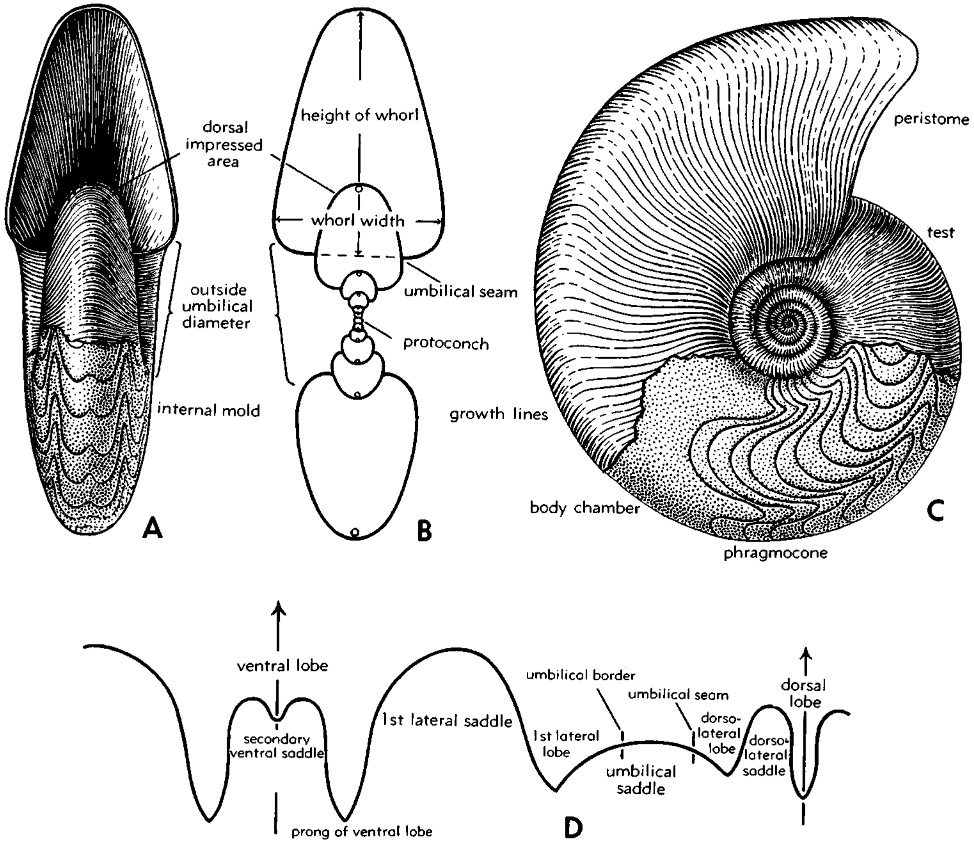


FIG. 1. Diagrammatic ventral *(A)*, cross-sectional *(B)*, and lateral *(C)* views of a typical goniatite, *Manticoceras*, about natural size; and *(D)* enlarged representation of a suture of the same. The upper part of *A* and *C* portrays the exterior of the test and shows the growth lines, whereas the lower part represents the internal mold with the sutures (110).

convex; those that form a single broad sinus on each of the lateral areas and a salient on the venter are said to be **protractive;** and those that form salients on both the umbilical margins and ventrolateral areas of the conch are said to be **biconvex** (Fig. 1*C*). In the last type, the growth lines, of course, form sinuses on the venter and on the median portion of the lateral areas. Biconvex growth lines are comparable to those of *Nautilus* in which the lateral re-entrants of the peristome are designated ocular sinuses as they enable the animal to see when the body is partially retracted.

The **aperture** or **peristome** of the ammonoid conch was not appreciably modified until maturity had been attained, and its shape is indicated by the growth lines. However, during late ontogenetic stages many forms contracted the adoral portion of the conch, and in some cases it was modified greatly by the development of lappets. In many forms the fully mature shell was strengthened by the formation of an adapertural constriction. The development of these modifications at full maturity suggests a change in the living habits of the individual. The presence of constricted apertures or short adoral camerae or both of these features is not indicative of gerontism, as has been believed.

Our knowledge of modifications at maturity in Paleozoic ammonoids is very incomplete. None seem to be present in the Ceratitina or the Prolecanitina. As early as the Devonian, certain of the Anarcestina and Clymeniina showed a tendency toward uncoiling after full maturity was attained. During the late Paleozoic other prominent traits were evolved (Fig. 2). For example, some forms became ellipsoidal (Fig. 2*C,D,E*), and some developed prominent ribs and spines. A few genera (e.g., *Eumorphoceras* and some thalassoceratids) evolved ventrolateral grooves that were associated with apertural lappets. These modifications tended to strengthen the body chamber, protect the soft parts of the animal, lower the center of gravity, and streamline the shell. Many species attained a remarkably uniform size. No differences attributable to sexual dimorphism can be recognized. As in *Nautilus,* neither the rate of growth nor the life span is known, but presumably the individuals attained maturity in a relatively short period of time.

APTYCHI

Aptychi, together with **anaptychi,** are now regarded as ammonoid opercula, though there has been much difference of opinion as to their biologic affinities (Fig. 3). A few of these plates have been found just inside and even closing the aperture of ammonoids, and therefore corresponding to the hood of *Nautilus* and the opercula of certain gastropods. It is readily apparent that they would fit into the apertural portion of the ammonoid shell, for they are more or less cordate in outline. There are 2 general types. Some (anaptychi) are simple arched chitinoid disks. Others (aptychi) consist of a symmetrical pair of calcareous plates, either in juxtaposition or coalesced along a median dorsoventral line. Both anaptychi and aptychi appear in the Devonian but are rare in the Paleozoic and the Triassic. Aptychi are more common in the Jurassic and the Cretaceous; locally they are so abundant that they characterize certain strata. In some of these beds, ammonoid shells are rare, suggesting that, as in the case of certain present-day gastropods, the opercula were more readily preserved. Although some anaptychi and aptychi can be associated with ammonoid genera that are based on conchs, these opercula are generally treated as biologic entities. TRAUTH has published comprehensive studies of them and classified them in form genera, the taxonomic status of which is indefinite. Because of the uncertainties, we are not listing these "genera."

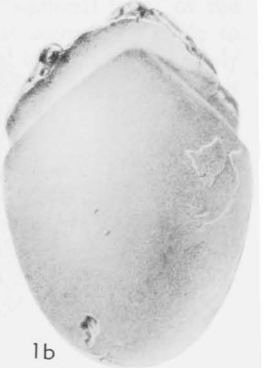
(*see facing page*)

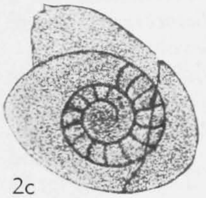
FIG. 2. Middle Permian ammonoids showing various mature modifications.——*1a,b, Waagenoceras guadalupense* GIRTY, Texas; ×1 (110).——*2a-c, Hyattoceras abichi* GEMMELLARO, Sicily; ×1.25 (24).——*3a,b, Adrianites kingi* GEMM., Sicily; ×1.25 (24).——*4, A. ensifer* GEMM., Sicily; ×1.25 (24).——*5a,b, A. distefanoi* GEMM., Sicily; ×1.25 (24).——*6, Doryceras spinosum* (MILLER), Coahuila; ×2 (110).——*7a,b, Hyattoceras geinitzi* GEMM., Sicily; ×1.25 (24).——*8a,b, Popanoceras scrobiculatum* GEMM., Sicily; ×1 (24). Lappets are portrayed in *3a, 4, 5b;* spines in *6;* flattened venters in *5a, 6, 7a;* an accentuated ventral sinus in *8a*.

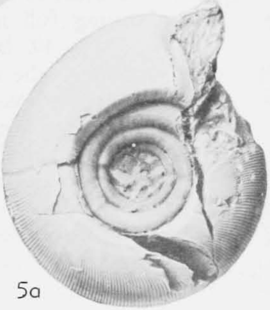

1a
Waagenoceras


2b
Hyattoceras


3b
Adrianites

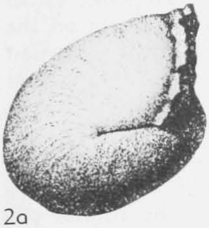

1b
Waagenoceras


2c


5a

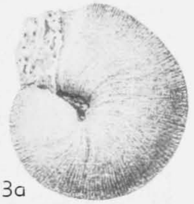

5b
Adrianites


4
Adrianites


2a
Hyattoceras

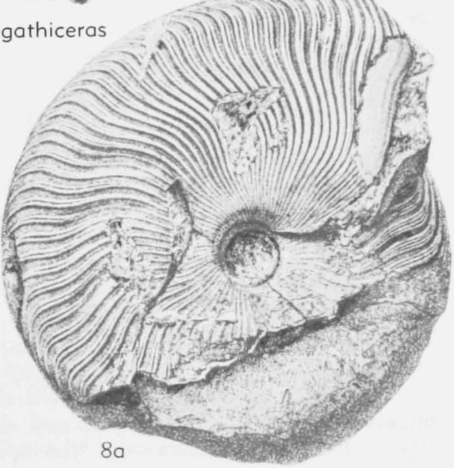

7b


6
Pseudagathiceras


3a
Adrianites


8b


7a


8a

Popanoceras Hyattoceras Popanoceras

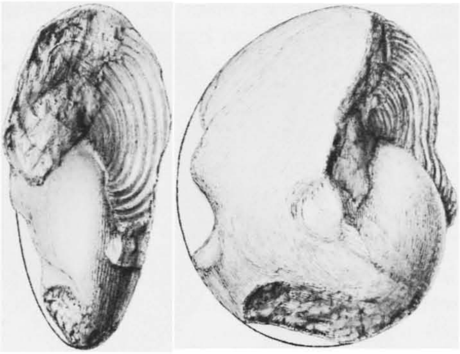


FIG. 3. The aptychus in place in *Manticoceras*, Upper Devonian, Germany, ×1 (21).

BODY CHAMBER

The body chamber is not generally preserved in its entirety, for it bears no such internal supports (septa) as does the phragmocone. Typically its length varies from about half a volution to a little more than a full volution, but in some forms at least the outer one and a half whorls are nonseptate. During ontogenetic development there was a tendency for the relative length of the body chamber to decrease. However, the volume ratio of that chamber to the phragmocone remained fairly constant. Furthermore, forms with a relatively large cross-sectional area had a proportionately short body chamber. It seems clear that the length of this chamber is of only secondary taxonomic value. Traces of the **contact areas** of the shell muscles and possibly aponeurotic bands, comparable to those of modern *Nautilus,* have been observed in some specimens.

SEPTA AND SUTURES

The **septa** were secreted periodically at the adapical end of the body chamber during the development of the individual. Adjacent septa reveal only such differences as were permitted by the growth that took place during the interval between their formation. The septa appear to have been constructed of the same material as the shell walls, to which they were cemented. In at least some forms, 2 **prosepta** (Fig. 4) occur in the extreme adapical portion of the conch. As a general rule these are considerably thicker than the adapical septa, and they appear to be continuous with the spiral shell wall, rather than cemented to it. A small adjacent structure, called a **flange,** is an adapical extension of the shell wall.

The **number of septa** per volution, though variable, tended to increase during ontogenetic development. This tendency was marked in form which, in the 1st volution, had a small number of septa, as few as 4. Tabulation in several late Paleozoic genera has shown that by the 5th to 7th volution the number of septa per volution tended to stabilize at some 15 to 20. However, in many forms, during full maturity, it became as high as 35 to 40, largely because of very close spacing in the adoral quarter-volution of the phragmocone. Nevertheless, in a unique Devonian genus, *Beloceras,* there are as many as 100 septa to a volution.

In the early ammonoids, the septa were convex adapically, much as in the nautiloids. However, in later forms this general shape was obscured by numerous inflections and was even reversed. **Septal diagrams** (Fig. 5) have been employed to show configuration.

The **sutures** (junctions of the septa with the shell wall) are of high taxonomic value. They can be observed readily only on the internal mold. In involute forms, the portion of the suture that extends across the ventral and lateral areas to the umbilical seams is designated the **external suture,** and its continuation across the dorsal impressed area is called the **internal suture** (Fig. 1).

Terminology applied to the **sutural element** varies. However, it is generally agreed that the basis of nomenclature should be ontogenetic development rather than morphologic resemblance. Furthermore, adapical inflections of the sutures are invariably known as **lobes** and adoral inflections as **saddles.**

In many of the earliest ammonoids, the **1st-formed suture** tends to be virtually a simple circle. However, in later representatives, this suture (the so-called **prosuture**) characteristically shows a prominent ventral saddle. The **2nd suture,** which is located close to the 1st, forms a slight ventral lobe (Fig. 6). This lobe is accentuated in the later-formed sutures. The unique shape of the 1st suture does not seem to suggest a phylogenetic relationship to any known form, whereas the remainder of the sutures show a normal progression in complexity.

The closely spaced 1st 2 sutures presumably represent the edges of the prosepta.

During early **ontogenetic development** the sutures characteristically form lobes on the venter, dorsum, and lateral zones, and then in the umbilical regions. All 6 of these lobes appear in certain species as early as the 2nd suture. These 3 pairs are commonly regarded as more or less fundamental, as are also the pair of dorsolateral lobes. The primary lobe on the venter is referred to by some authors as the "siphonal lobe" or the "external lobe," but it seems preferable to designate it the **ventral lobe,** as is commonly done. Similarly, the lobe on the dorsum is best termed the **dorsal lobe,** rather than the "antisiphonal lobe," the "internal lobe," or the "columellar lobe," though all of these are to be found in the literature. In some of the clymenias the ventral lobe is obliterated during early adolescence, and its place is taken by a secondary saddle; but in all other

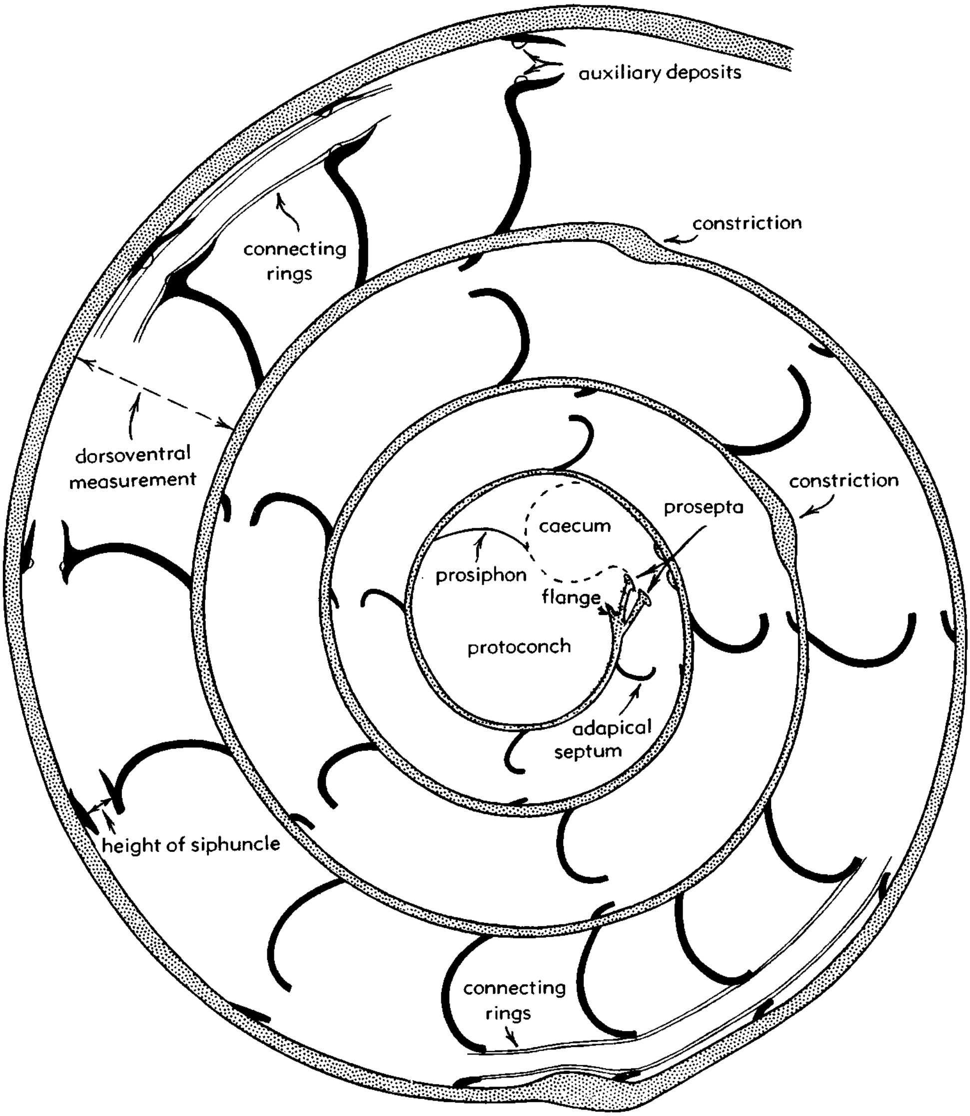


Fig. 4. Enlarged median dorsoventral section of the adapical portion of the shell of a typical ammonoid, showing diagrammatically the various internal structures (54).

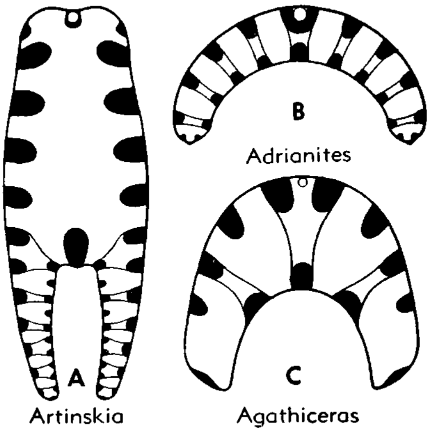


FIG. 5. Septal diagrams of *Artinskia (A), Adrianites (B),* and *Agathiceras (C);* all from Permian of Urals (65,66).

ammonoids it persists and is typically quite conspicuous.

Primary lobes, other than the fundamental ones, were added in the umbilical regions during ontogenetic development, and from there they migrated toward both the venter and dorsum. The saddles adjacent to the ventral lobe, though called "external saddles" by some authors, are better termed the **1st lateral saddles,** and the lobes that follow them the **1st lateral lobes.** The subsequent elements are then the **2nd lateral saddles** and **2nd lateral lobes.** If additional primary inflections are present between the 2nd lateral saddle and the umbilicus, they are termed **auxiliaries.** Prominent inflections that evolved secondarily from ventral and lateral elements of the suture are said to be **adventitious.** Auxiliary and adventitious lobes may be as large as primary lobes (Fig. 11*E*). The elements of the internal suture, other than the dorsal lobe, bear comparable names, but the term **dorsolateral** is employed instead of lateral (Fig. 1).

Ammonoids in which all or most of the lobes of the sutures are undivided are called **goniatites;** those in which the great majority of the lobes (but not the saddles) are serrate are termed **ceratites;** whereas those in which both lobes and saddles are finely subdivided are known as **ammonites.** These terms originated as generic names when classification was primitive. As knowledge advanced, many intermediate forms were found and the latitude allowed genera diminished. Nevertheless, the terms are still useful in a broad way, as well as in a very restricted sense for genera with relatively narrow limits.[1] Goniatites are more or less characteristic of the Paleozoic, ceratites of the Triassic, and ammonites of the later Mesozoic. However, goniatites range well up into the Triassic, typical ceratites (e.g., *Prodromites*) appear as early as the Early Mississippian, and well-developed ammonites (e.g., *Perrinites*) are known from the Middle Permian. Many representatives of all 3 of these categories occur in the Permian (Fig. 7). In the later Mesozoic, most of the ammonites developed extremely complex sutures, but owing to atavism some of them resemble goniatites and ceratites—the last are called **pseudoceratites.**

Commonly ammonoid sutures are portrayed diagrammatically, as shown by Fig. 1*D*. Such drawings are attempts to represent in a single plane a suture pattern that, as a general rule, is developed on a coiled expanding cone which is modified by being impressed dorsally. Accordingly, they are projections, subject to the limitations of the method employed and affected by the preservation of the specimens and the interpretation of the investigator. For these reasons, drawings prepared under different circumstances are not precisely similar, but it is generally possible to compensate for the slight deviations. It should, of course, be kept in mind that a suture is generally portrayed as a line, whereas in reality it is a narrow zone of varying width. Inasmuch as almost all ammonoids are bilaterally symmetrical, the drawings usually depict only a little more than half a suture. However, individuals of certain species may reveal conspicuous asymmetry.

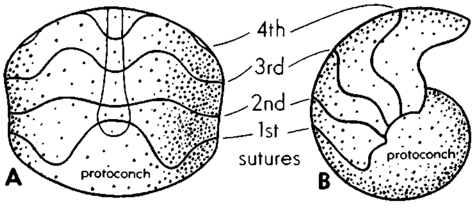


FIG. 6. Ventral *(A)* and side *(B)* views of protoconch and extreme adapical part of ammonoid phragmocone showing early sutures, greatly enlarged (10).

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[1] The generic name *Ammonites,* however, has been suppressed by the International Commission on Zoological Nomenclature (ICZN).—EDITOR.

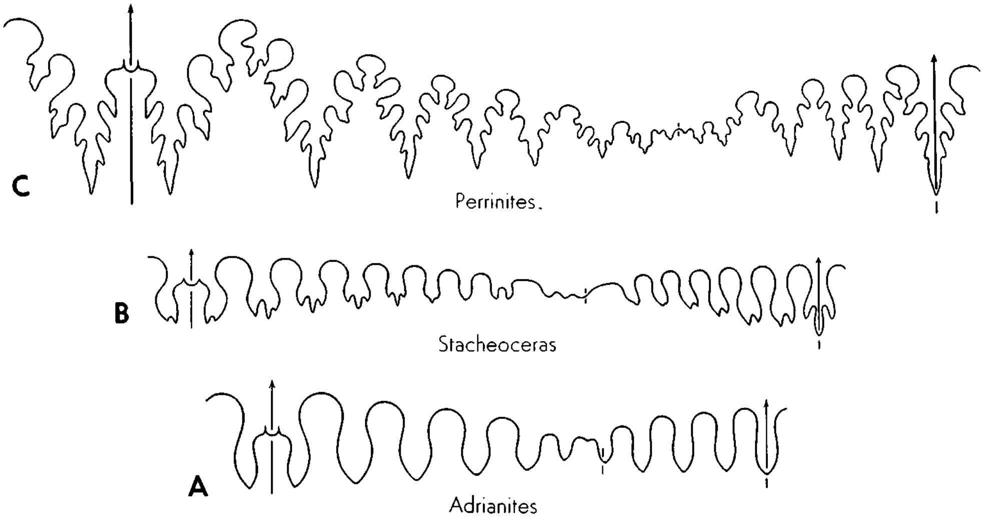

FIG. 7. Diagrams illustrating differences in types of ammonoid sutures, all based on Permian species: *A*, goniatitic, *Adrianites defordi* MILLER & FURNISH, ×1.3; *B*, ceratitic, *Stacheoceras toumanskyae* MILLER-F., ×2; *C*, ammonitic, *Perrinites hilli* (SMITH), ×2.7 (110).

Sutures which consist of many elements developed an **arcuate** shape in some groups of ammonoids. This feature is especially well illustrated by the cyclolobids of the late Paleozoic. In general, the sutures of the cyclolobids became strongly arcuate during late growth stages; peculiarly, however, specimens are known in which the adoral sutures became relatively straight. In some discoidal forms, such as the medlicottiids of the late Paleozoic and early Mesozoic, the amount of curvature of the sutures is greatly accentuated in the extreme adoral portion of the fully mature phragmocone.

Another **modification** of the **sutures** occurred in some forms during late ontogenetic development. When the septa became very closely spaced their edges overlapped at a few points and the details of the adapical portion of the lobes were altered.

In Europe, especially Germany, the configuration of the sutures is frequently expressed by means of **formulas.** In 1905 NOETLING propounded an elaborate system in which each lobe and saddle is designated by a symbol, but his formulas have never been used extensively. WEDEKIND subsequently proposed a simpler system in which a symbol is used for each lobe and the saddles are neglected, it being understood that in every suture lobes are separated by saddles. He used the letter **E** to refer to the ventral (external) lobe, **J** to the dorsal (internal) lobe, **L** to the 1st-formed lateral lobes, **U** to later-formed lateral (umbilical) lobes, and **A** to adventitious lobes. WEDEKIND's system of formulas has been employed rather widely in Germany, and by such authors as SPATH in England, BASSE in France, and RUZHENCEV in Soviet Russia. Unfortunately, most users have injected modifications of their own, so that, except to the specialist, their formulas are scarcely recognizable. For example, the suture formula of the well-known Devonian genus *Tornoceras* (Fig. 47*B*) was written "E. A_I Lu J" by WEDEKIND in 1918, "I L A_I" by SCHINDEWOLF in 1922, and "E A_1 L I" by MATERN in 1931. The use of these formulas obviously makes for brevity, but if they are not readily understandable they do not serve a good purpose.

SIPHUNCLE

The **siphuncle** of the ammonoids is not nearly so variable as is that of the nautiloids, and therefore it is of relatively little taxonomic value. Nevertheless, because at maturity it is marginal in position, it serves to differentiate the ammonoids from the great majority of nautiloids. Furthermore, it has been used to divide the ammonoids into 2 suborders: **Intrasiphonata** (clymenias), with dorsal siphuncles, and **Extrasiphonata,** which includes the host of other ammonoids with ventral siphuncles. In most ammonoids the siphuncle is ventral in position throughout ontogenetic development. However, in a few unrelated forms from various parts of the geologic column, it is subcentral or even subdorsal during early adolescence. The significance of this fact has been variously interpreted, but probably it means only that the position of the siphuncle was unstable during early growth stages.

The **structure of the siphuncle** in earliest ammonoids is reminiscent of that of the orthochoanitic nautiloids, for the **septal necks** or funnels extend adapically from the septa (**retrochoanitic** = "retrosiphonate"), and the connecting rings are small and cylindrical. In the more advanced ammonoids, during early adolescence the septal necks developed adoral projections and eventually became **prochoanitic** ("prosiphonate"), with the septal necks extending adorally. In the late Paleozoic at least, most of the prochoanitic forms developed small **auxiliary deposits** inside of the septal necks (Fig. 4). In a few fossils these deposits seem to consist of simple rings, but in others they are relatively complex. The siphuncle started in the adoral portion of the protoconch as a thin-walled bulbous **caecum.** An associated structure, the **prosiphon,** had the form of a partial cone and served to fasten the caecum to the inside surface of the protoconch. The adapical part of the siphuncle proper is relatively large, whereas in the mature portions of the conch it is invariably small; its cross-sectional area varies from more than a tenth to less than a thousandth that of the conch.

ONTOGENY

The development of the individual can be studied to particular advantage in the ammonoids. The immature portion of the shell was encompassed and therefore protected and preserved.

In general, the inner whorls of ammonoids are relatively broad and smooth. However, in some forms the reverse is the case, and there are inner whorls which are narower and more highly sculptured than the outer. Schindewolf has concluded that the latter types introduced evolutionary changes and are illustrative of **proterogenetic** development. Furthermore, in 1933 Spath stated that he is "now accepting it as a matter of course that in ammonites at least ontogeny is not an epitome of phylogeny and that new characters appear in the young and only afterwards encroach on the later whorls."

Ontogenetic studies of the sutures may be of more value, however, for their shape is of basic taxonomic significance. The complexity of the sutures is known to have increased progressively with geologic time. Also, it can be seen that similar ammonoids added elements to their sutures in an orderly fashion. The changes which were first noted in a chronologic sequence of rocks were found to be more or less duplicated in the ontogenetic development of many ammonoids. This fact was noted as early as 1872 by Hyatt, and soon Branca illustrated it precisely in a variety of materials of various ages. Then Karpinsky used it as a basis for phylogenies and demonstrated clearly that one could correlate the early sutures with mature ones of ancestral genera. He was followed by Hyatt, J. P. Smith, and a host of others, and the work has continued to the present day. Thus, insofar as ontogenetic development of the sutures is an index, phylogenies have been established for all of the major groups of Paleozoic ammonoids and for some of those of the Mesozoic.

The **ontogeny** is, of course, only an approximation of the **phylogeny,** and the abbreviation of ancestral characters varies inversely with chronologic proximity. That is, in some Mesozoic forms even the most adapical sutures show only an obscure resemblance to Paleozoic ancestors, whereas the next sutures reveal a clear indication of the later progenitors.

Ontogenetic studies can be used for several purposes, as is elucidated by Figures 8-11. The first of these shows how a complicated suture evolved, passing through a sequence of stages that are characteristic of older, more primitive types. In it, *A* is reminiscent of *Goniatites* of the Upper Mississippian, *B* of *Proshumardites* of the Lower Pennsylvanian, *C* of *Shumardites* of the Upper Pennsylvanian, *D* of *Peritrochia* of the Upper Pennsylvanian and Lower Permian, *E* of *Properrinites* of the Lower Permian, and *F* is *Perrinites* of the Middle Permian. Figure 9 shows a comparable relationship in a **phylogenetic series** of forms varying in age from Mississippian to Permian.

Figure 10 offers direct comparison of an ontogenetic and phylogenetic sequence that should become classic. In 1897, J. P. SMITH observed that from ontogenetic studies one

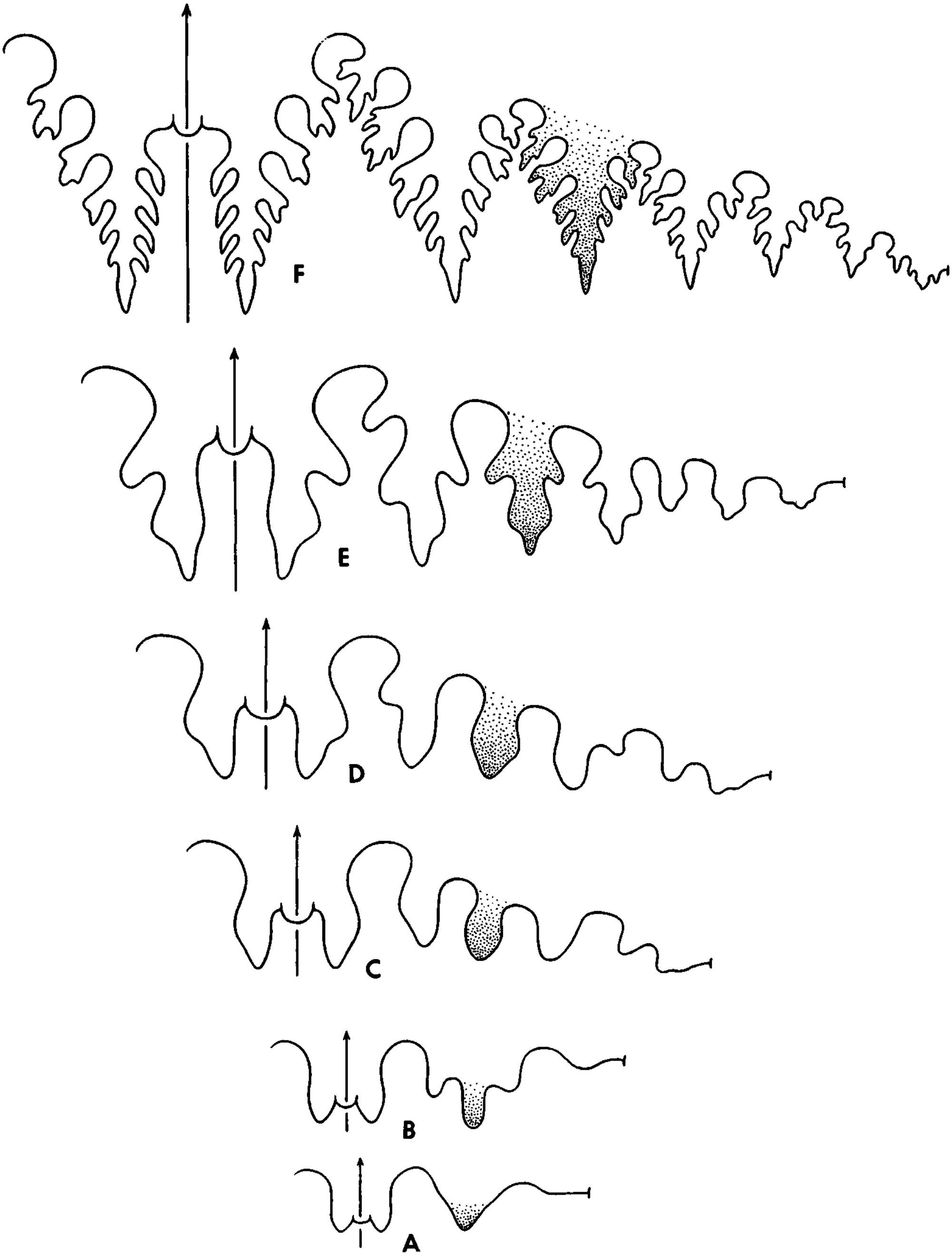

FIG. 8. Ontogenetic development of the external sutures in *Perrinites hilli* (SMITH) from the Permian of Texas.

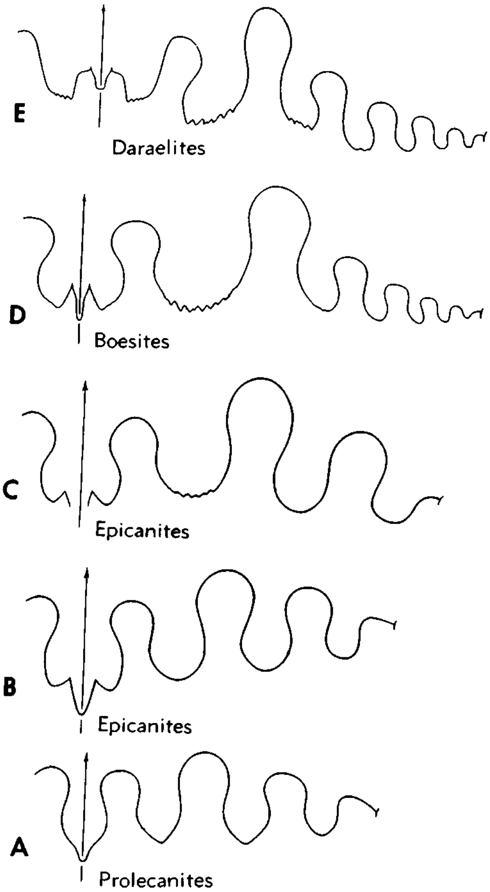

FIG. 9. Phylogenetic series of late Paleozoic ammonoids, showing development of daraelitids from prolecanitids: *A, Prolecanites hesteri* MOORE of the L.Carb., Eng.; *B, Epicanites sandbergeri* (SCHMIDT) of slightly younger Early Carb. age in Algeria; *C, E. culmiensis* (KOBOLD) of German strata of the same general age as *B; D, Boesites texanus* (BÖSE) from the Pennsylvanian of Texas; *E, Daraelites meeki* GEMMELLARO of the Sicilian Permian (110).

"can even prophesy concerning the occurrence of *unknown* genera in certain horizons when he finds their minute counterparts in youthful stages of later forms; in fact he could often furnish just as exact a description of the form as if he had the adult genus before him." In 1929 this same author noted that the medlicottiids, which are almost exclusively Permian, evolved from the Carboniferous *Pronorites,* which, however, he concluded is "separated from its descendants by at least one generic step." He then emphasized that *Uddenoceras* and *Uddenites* of the latest Pennsylvanian are intermediate forms, and by studying their early sutures he clearly demonstrated the nature of the "missing link" between them and *Pronorites.* The very next year that form was found in the Upper Pennsylvanian and was appropriately named *Prouddenites.*

EVOLUTION

Homeomorphy is not particularly rare in Mesozoic ammonoids and is known also in Paleozoic forms (Fig. 11). The range of possible variation in the ammonoid shell was somewhat limited. The causes of such variation were omnipresent and were locally recurrent. Therefore, morphologic types were repeated. Of course no phylogenetic significance is to be attributed to the resemblance of forms that are widely separated stratigraphically or to the similarity of contemporaneous species for which different ancestry can be established by ontogenetic studies.

PALEOECOLOGY

Ammonoids are confined to strata of marine origin. They occur in various lithologic types, but most of those that have been secured are from shales and marls, largely because of a natural concentration and ease of collecting. Locally, however, they are abundant in argillaceous and "detrital" limestones and in sandstones. Clearly a variety of sedimentary environments is represented.

Little or no paleoecologic significance can be attached to the occurrence of isolated specimens; these have been interpreted as individuals that drifted from their normal habitat. Presumably, assemblages containing various growth stages of the same species accumulated *in situ.* Those that consist exclusively of mature individuals probably indicate that the animals had changed their habitat during ontogenetic development. Concentrations of small individuals resulted from mechanical sorting by waves and currents. Concentrations of aptychi are believed to have resulted from the drifting away of the shells after separation from the decaying bodies.

The fact that ammonoid zones can be recognized all over the world indicates that these creatures were typically nektonic and were able to invade a variety of habitats.

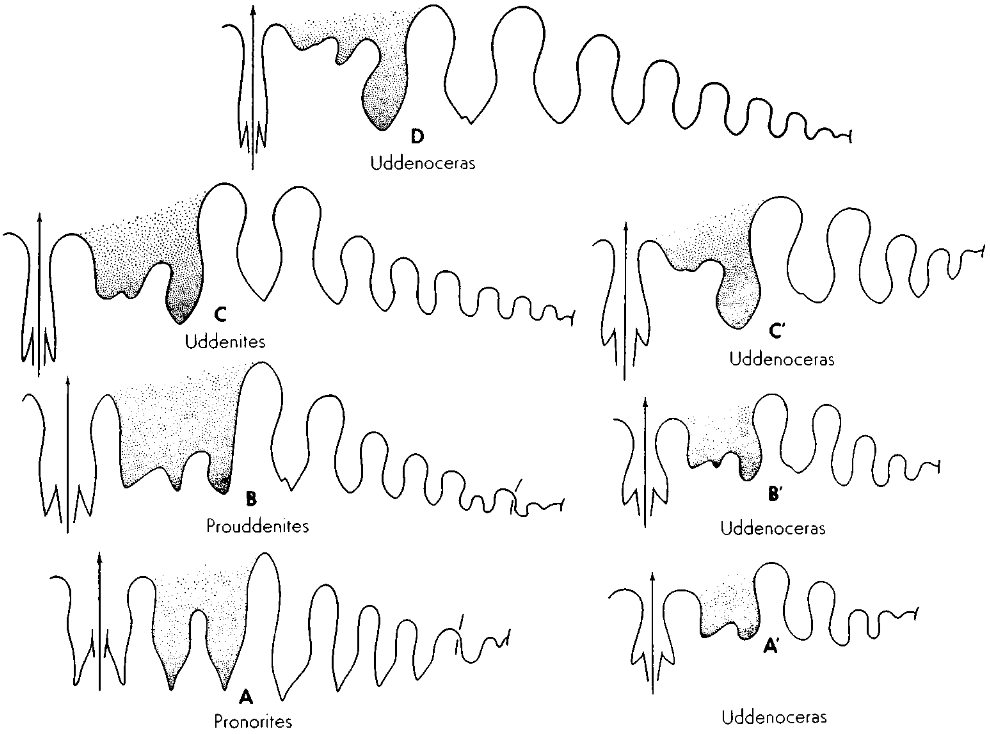

FIG. 10. Phylogenetic and ontogenetic development of *Uddenoceras*. Mature sutures of *Pronorites (A)*, *Prouddenites (B)*, *Uddenites (C)*, and *Uddenoceras (D)*, with comparable ontogenetic stages of *Uddenoceras (A′-C′)*; all Pennsylvanian, southwestern United States (110).

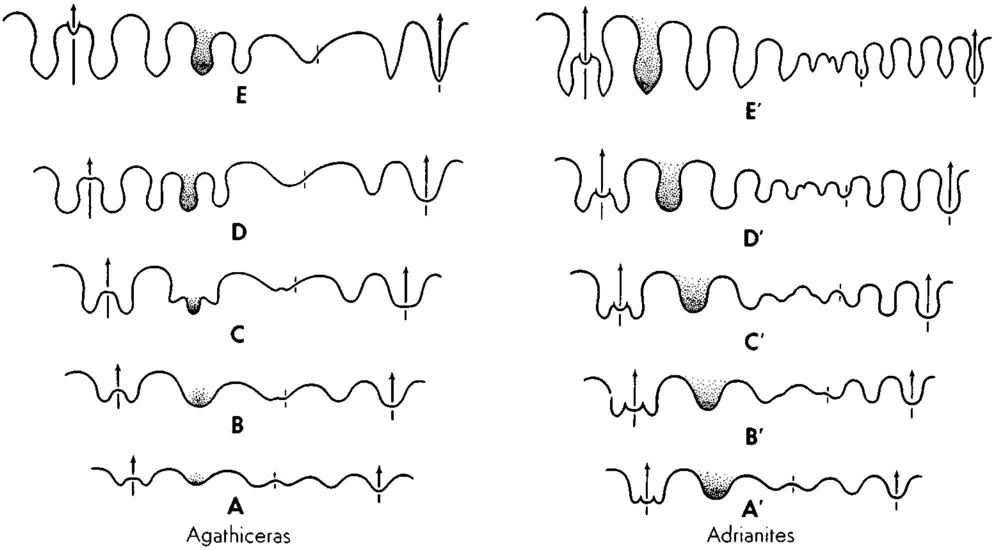

FIG. 11. The ontogenetic development of the sutures in 2 similar but not closely related Permian ammonoids: *A-E*, *Agathiceras uralicum* KARPINSKY, from the Ural region, and *A′-E′*, *Adrianites dunbari* MILLER & FURNISH, from Mexico. The mature external suture of the former contains adventitious lobes; that of the latter, auxiliaries (110).

Certain black shales contain only ammonoids, pelagic foraminifers, and fish remains. The color marks, known on only a very few ammonoids, suggest that they were shallow-water dwellers.

The form and sculpture of the ammonoid shell may be a clue to the living habits. Bilateral symmetry and lenticular shape are presumably to be associated with mobility. Prominent sculpture would tend to retard locomotion, and irregular heteromorphs must have been benthonic.

GEOGRAPHIC AND STRATIGRAPHIC DISTRIBUTION

Many ammonoid genera seem to have been world-wide in distribution, and closely related, if not identical, species are known to occur on different continents. Even the same phylogenetic series can be recognized in widely separated localities. Furthermore, latitude does not seem to have been a controlling factor in geographic distribution. The often-cited geographic limitations of certain aberrant forms (e.g., *Prodromites*), like the scarcity of Paleozoic ammonoids in South America, is probably more apparent than real. However, peculiarities in distribution do exist; for example, the perrinitids, which are characteristic of the lower half of the Permian in the Americas, are not known in the related faunas of the Ural region, where most associates occur. Within recent years our knowledge of the geographic distribution of ammonoids has increased greatly, and comparable advances can be expected in the future. Some of the most significant faunas known represent "chance discoveries."

TABLE 1. *Distribution of Paleozoic Ammonoidea*

SYSTEM	SERIES	ZONE	TYPE AREA	OTHER IMPORTANT OCCURRENCES
PERMIAN	Upper	*Cyclolobus*	SaltR.	Himal.-Armenia-Madag.-Greenl.
	Middle	*Timorites*	Timor	USA(Tex.)-Mex.(Coah.)
		Waagenoceras	Sicily	Tunisia-Pamirs-China-Timor-USA(Tex.)-Mex.(Coah.)
		Perrinites	USA(Tex.)	Mex.-Colom.-USA-Can.-Urals-Crimea-AsiaM.-Timor.
	Lower	*Properrinites*	USA(Tex.)	USA(Kans.)-Timor-Urals-Crimea
PENNSYLVANIAN	Upper	*Uddenites*	SW.USA	Urals
		Prouddenites	SW.USA	USA(Ohio-Pa.)-Urals
	Middle	*Eothalassoceras*	SW.USA	Turkestan
		Wellerites	SW.USA	USA(Ohio)-Urals
		Owenoceras	SW.USA	?Argentina
	Lower	*Paralegoceras*	USA(Iowa)	SW.USA-C.USA-Peru-N.Afr.-S.China
		Gastrioceras	Eng.	
MISSISSIPPIAN	Upper	*Eumorphoceras*	USA(Okla.)	USA-W.Can.-Alaska-Eu.-N.Afr.
		Goniatites	Eng.	USA-W.Can.-Alaska-Eu.-N.Afr.
	Lower	*Beyrichoceras*	Eng.	Eu.-N.Afr.-C.USA
		Protocanites	USA(Ind.)	USA-Eu.-N.Afr.-Austral.(N.S.W.)
DEVONIAN	Upper	*Wocklumeria*	C.Eu.	N.Afr.
		Clymenia	C.Eu.	N.Afr.
		Platyclymenia	C.Eu.	N.Afr.-W.Austral.-USA(Mont.)
		Cheiloceras	C.Eu.	N.Afr.-W.Austral.-USA(Pa.)
		Manticoceras	USA(N.Y.)	USA-W.Can.-China-Austral.-N.Afr.
	Middle	*Maenioceras*	Ger.	USA-E.Can.-N.Afr.-Austral.
		Anarcestes	Ger.	USA-E.Can.-N.Afr.-Austral.
	Lower	*Mimosphinctes*	Ger.	

Ammonoids are commonly used as **index fossils** because of their widespread occurrence, easy recognition, and stable evolution. Many of the **faunal zones** recognized in intercontinental correlation are based on these fossils.

The oldest known ammonoids are from the European Lower Devonian (Fig. 159). During the remainder of that period, there was a progressive increase in numbers and complexity. In central Europe, where Devonian ammonoids are found in sequence, WEDEKIND and SCHINDEWOLF have shown that 2 or 3 zones can be recognized in the Middle and 5 in the Upper Devonian (Table 1). From the work in Europe, it is known that near the close of the Devonian several groups of ammonoids became extinct and the Goniatitina appeared. This suborder underwent a great development during the late Paleozoic, where it existed alongside the Prolecanitina.

Four ammonoid zones occur in the Mississippian. These are best known in Germany and England. The type Mississippian of central United States contains all 4 zones, but in this region the boundary with the Devonian has not been delimited on the basis of ammonoids. Furthermore, these cephalopods indicate that the dividing line between the American Mississippian and Pennsylvanian is stratigraphically higher than that between the European Lower and Upper Carboniferous.

In the well-known Pennsylvanian of the American Mid-Continent region, 7 ammonoid zones are recognized. Counterparts of most of these have been recorded from Europe, especially in the Ural region. The ammonoids of the Pennsylvanian are gradational with those of both the Mississippian and the Permian, though there are minor differences in stage of evolution.

Near the end of his long career, J. P. SMITH stated that the "Permian was the Golden Age for the ammonoids"; and the many forms known from that period are a culmination of the several Paleozoic stocks and therefore reveal a great amount of fundamental diversity. Five zones are differentiated. Peculiarly, the 1st 4 of these are well developed in 2 widely separate localities, Texas-Coahuila and Timor. The 5th, uppermost, is known from Greenland, Madagascar, and 3 areas in southwestern Asia; and in every place it is directly overlain by an early Triassic zone but is not underlain by older Permian ammonoid-bearing strata.

ORIGIN OF AMMONOIDEA

The ammonoids evolved from the nautiloids, but intermediate forms are not known. The only possible exception is the Bactritina, of uncertain affinities. Typically, ammonoids have a tightly coiled thin shell, a bulbous protoconch, and a small marginal siphuncle. *Bactrites* and its affines possess these characters except for their straight conchs. It has long been contended that they gave rise to the ammonoids by becoming coiled. This belief is conjectural. An alternative hypothesis postulates that the ammonoids arose from some Silurian coiled nautiloids of the general type of *Barrandeoceras*.

The oldest undoubted ammonoids, which are from the Lower Devonian, are reminiscent of certain contemporaneous and slightly older nautiloids. Nevertheless, it may be significant that some of the early Devonian goniatites are loosely coiled, and still others have an umbilical perforation. Thus, it appears that there are no preponderant supporting data to establish the identity of the ancestral form.

CLASSIFICATION

In taxonomy, previous authors have emphasized such characters as the shape of the conch, length of the body chamber, position of the siphuncle, and "ornamentation" of the test, as well as configuration of the sutures. All of these features are important, but in the Paleozoic ammonoids the one listed last is the best guide to phylogenetic relationships. The generic affinities of most forms can be determined from the shape of the sutures alone, a character in which homeomorphy is relatively rare and easily recognized.

Paleozoic ammonoid genera tend to be interpreted rather broadly. This attitude is responsible for the fact that many of the names proposed are placed in synonymy subjectively. In certain unstable groups, liberal subdivision would result in the number of genera being increased 10-fold or more. Some 425 generic names have been proposed for Paleozoic ammonoids, but less than half are now regarded as valid.

A tabular summary of suprageneric divisions permitting a survey of the whole Paleozoic assemblage of ammonoids is given on preceding pages. The number of genera and subgenera in each division is indicated by the figures enclosed in parentheses. A phylogenetic chart (Fig. 12) elucidates the major concepts on which the classification is based.

The suborder Anarcestina is the ancestral stock of the ammonoids. Its most primitive representatives are the Anarcestaceae. Forms with only slightly sinuous sutures, noninvolute whorls, and perforate umbilici are placed in the Mimoceratidae. Those with simple but nevertheless rather sinuous sutures, deeply involute conchs, compressed whorls, and imperforate umbilici are assigned to the Agoniatitidae. Similar forms with low whorls and relatively broad conchs constitute the Anarcestidae. The superfamily is known to be widespread geographically, but stratigraphically it is confined to the Devonian. All of the Lower Devonian representatives are from Europe.

The Prolobitaceae, which consist of a single family, are distinguished primarily by the sutures. These are characterized especially by the fact that the primary lateral lobes evolved on the flanks of the conch and remained there throughout ontogenetic development. The lobes of the sutures are few in number and are undivided. Stratigraphically the superfamily is limited to the latter half of the Devonian, and geographically it seems to be limited to the eastern hemisphere.

The Pharcicerataceae are a small compact unit that is characteristic of the lower Upper Devonian all over the world. The large prominently subdivided ventral lobe distinguishes its members from all other Devonian ammonoids but is superficially similar to that of the late Paleozoic goniatitids. The Beloceratidae evolved from the Gephuroceratidae by the addition of secondary elements to the sutures; the Pharciceratidae constitute a parallel development.

The Clymeniina have long been regarded as quite distinct from other ammonoids because of the dorsal position of their siphuncle. The group is quite diverse, limited to the Upper Devonian and world-wide in distribution. The oldest known representative, *Acanthoclymenia,* is from the lower Upper Devonian of New York, but clymenias are far more rare in the western than in the eastern hemisphere. They are generally regarded as excellent index fossils.

The Goniatitina constitute the great bulk of the Paleozoic ammonoids. During the latter part of the era, members underwent marked evolution and became quite varied. Among them are some of our best index fossils. The basic suture of the group consists of 4 pairs of lobes, though certain of the primitive representatives in the Cheilocerataceae did not attain that stage. The suborder is divided into superfamilies primarily defined by major modifications of basic elements of the sutures.

The Cheilocerataceae consist of 2 families, Tornoceratidae and Cheiloceratidae. In both of these the sutures typically consist of 3 pairs of lobes, of which the external lateral pair arises adventitiously. According to WEDEKIND, the chief difference between the 2 families lies in the fact that in the Tornoceratidae growth lines are biconvex, whereas in the Cheiloceratidae they are convex. Members of the former family are widespread and locally abundant in the Middle and Upper Devonian, whereas cheiloceratids appear in the Upper Devonian, are abundant in the Lower Mississippian, and continue in the Middle Permian. This latter family is the stock that gave rise to the rest of the Goniatitina.

The Agathicerataceae contain forms in which the 3 pairs of external lateral lobes originated as subdivisions of a single pair of goniatitid lateral lobes. The superfamily made its debut in the Early Pennsylvanian, became fairly abundant during the latter part of the same period, and climaxed in the Permian. The Agathiceratidae, the most primitive family of the group, are a long-ranging stable unit. The Shumarditidae are quite variable in both form and occurrence. The Perrinitidae, a closely knit group confined to the first half of the Permian, have the same number of major sutural elements, which, however, are strongly digitate. Members of the last family are among the best index fossils.

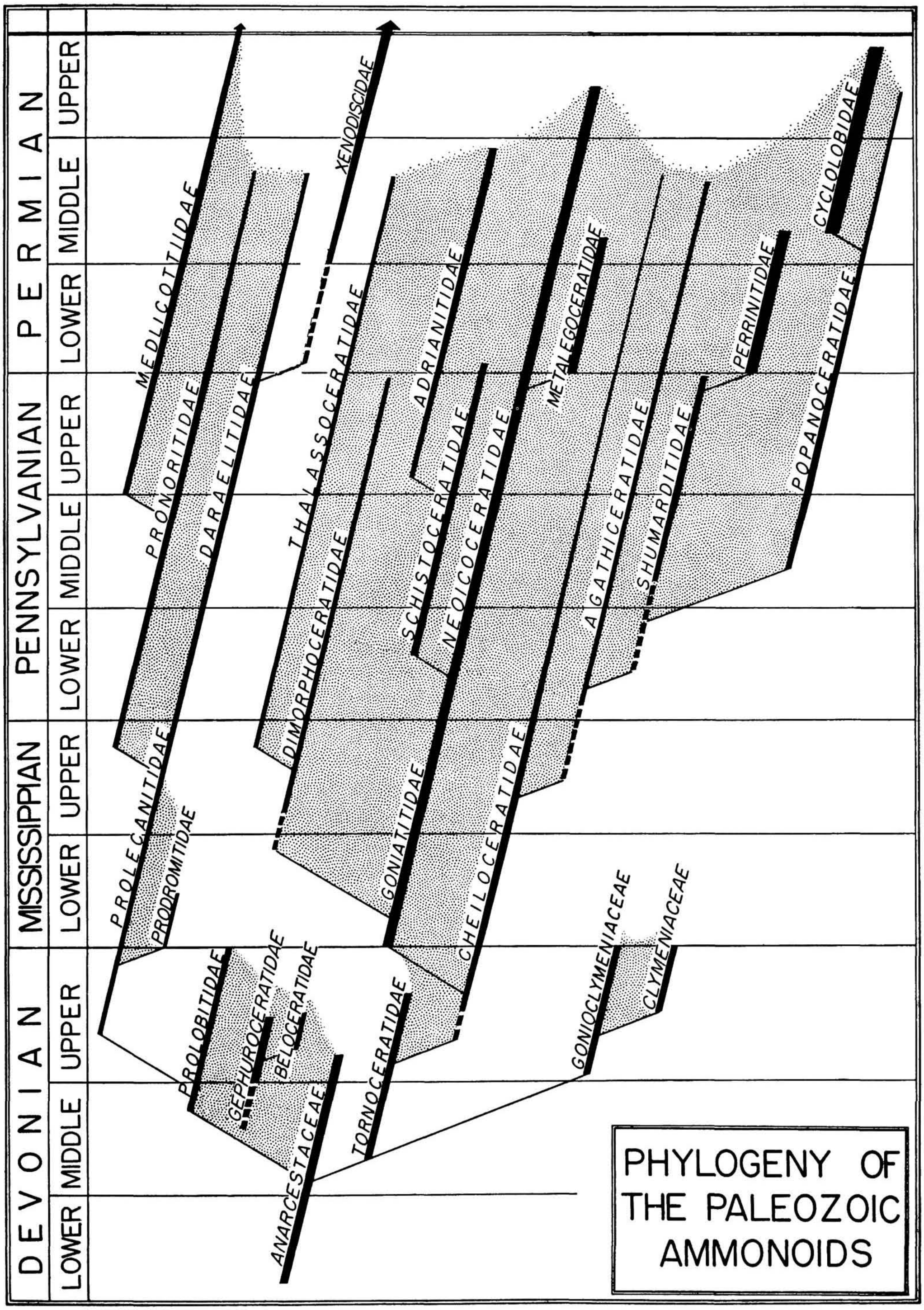
DEVONIAN
LOWER
MIDDLE
MIDDLE
UPPER
MISSISSIPPIAN
LOWER
LOWER
UPPER
UPPER
PENNSYLVANIAN
LOWER
LOWER
MIDDLE
MIDDLE
UPPER
UPPER
PERMIAN
LOWER
LOWER
MIDDLE
MIDDLE
UPPER
ANARCESTACEAE
GEPHUROCERATIDAE
PROLOBITIDAE
BELOCERATIDAE
TORNOCERATIDAE
GONIOCLYMENIACEAE
CLYMENIACEAE
PROLECANITIDAE
PRODROMITIDAE
GONIATITIDAE
CHEILOCERATIDAE
DIMORPHOCERATIDAE
PRONORITIDAE
DARAELITIDAE
THALASSOCERATIDAE
SCHISTOCERATIDAE
NEOICOCERATIDAE
AGATHICERATIDAE
SHUMARDITIDAE
POPANOCERATIDAE
MEDLICOTTIIDAE
ADRIANITIDAE
METALEGOCERATIDAE
PERRINITIDAE
XENODISCIDAE
CYCLOLOBIDAE
PHYLOGENY OF THE PALEOZOIC AMMONOIDS

FIG. 12.

The Cyclolobaceae are characterized especially by the possession of a series of auxiliary lobes in their sutures, which generally are ceratitic. Primitive members of both the Popanoceratidae and the Cyclolobidae did not develop many auxiliaries. However, in the more advanced representatives of these families the number of such lobes increased, culminating in *Cyclolobus* of the very late Permian. The Popanoceratidae appeared during mid-Pennsylvanian time and continued to the close of the Permian, being most abundant during the Late Pennsylvanian and the first half of the Permian. In general, these forms are not as good index fossils as are members of the Cyclolobidae, which represent a single phylogenetic sequence that evolved during the latter half of the Permian.

The Goniatitaceae include *Goniatites s.s.* and its affines, plus the neoicoceratids (=gastrioceratids) and their immediate descendants, the metalegoceratids and the schistoceratids. The Goniatitidae have received careful consideration over a period of many years, and the general evolutionary development is well known. Morphological details which are not believed to be particularly significant in other groups seem to have stratigraphic value in this family. The basic suture was evolved during early ontogenetic development, and then the number of lobes remained constant. Neoicoceratids are very widespread and abundant in the Pennsylvanian and the Permian, but, except in a general way, they are of limited stratigraphic value. The Metalegoceratidae, the last of the superfamily to be recognized, consist of a very few genera, which are limited to the Early Permian but are widespread geographically. The schistoceratids, with one exception, illustrate the development of a single evolutionary trend, viz., progressive increase in complexity of the suture by addition of lobes in the umbilical regions. The exception is *Wellerites,* in which a pair of adventitious lobes is developed as prominent subdivisions of the 1st lateral saddles of the external sutures, a difference of subfamily significance.

The Adrianitaceae, which comprise a single family, resemble superficially certain of the Agathicerataceae. However in the adrianitids the sutures, which are goniatitic, consist of elements that are added in the umbilical region. Stratigraphically the superfamily is limited to the upper Pennsylvanian and Permian, but typical forms are known from only the mid-Permian. Geographically, they are of world-wide distribution.

In the Dimorphocerataceae the sutures are basically the same as those of the Goniatitidae, but they are more or less ceratitic. Typical representatives of the Dimorphoceratidae have sutures in which the prongs of the ventral lobe are bifid. However, in advanced forms the lateral lobes of the external sutures are also bifid, and the prongs of the ventral and lateral lobes become more or less serrate. In the thalassoceratids the prongs of the ventral lobe and lateral and umbilical lobes are serrate; however, in the most advanced representative of this group all of the external suture is digitate and the internal lateral lobes are bifid. Both of the families of the Dimorphocerataceae are known from the Mississippian, and they range well up into the Permian.

The Prolecanitina, a relatively small suborder of discoidal Paleozoic ammonoids, are especially important because they are the stock from which all Mesozoic forms arose. Presumably the group evolved from the prolobitids during late Devonian times. With one minor exception, it continued as 3 stable trends through the late Paleozoic. One of these persisted into the Triassic, and another gave rise to the Ceratitina, of which the chief development was in the Triassic. Members of this suborder are of much more stratigraphic value in the Mississippian than in the later Paleozoic. Characteristically the sutures form a large number of lobes, which were added progressively in the umbilical regions. It may be significant that the siphuncle is simple and retrochoanitic, much as in the Devonian goniatites and in the most primitive members of the Goniatitina.

The Prolecanitaceae include the simplest members of the suborder. In the Prolecanitidae the sutures are goniatitic, whereas in the Prodromitidae and the Daraelitidae the lobes are serrate. The Prodromitidae consist of one unique species which is known from only the Lower Mississippian of central United States and which can be thought of as more or less "precocious" because of its similarity to the Ceratitina. The Daraelitidae are the classic example of a small compact group which exhibits an evolutionary trend that continued throughout the late Paleozoic. Both prolecanitids and daraelitids are world-wide in their distribution.

The Medlicottiaceae are widespread and abundant in the late Paleozoic and not particularly rare in the Triassic. However, only one genus crosses the Permo-Triassic boundary. The suture forms a number of subequal auxiliary lobes. Characteristically the 1st lateral lobes are modified; in the Pronoritidae they are bifid, whereas in the Medlicottiidae the changes are much more extreme. Most genera in this superfamily have a long range in the late Paleozoic. It has been thought that the typical medlicottiids evolved from the pronoritids through *Prouddenites, Uddenites, Propinacoceras,* and *Artinskia*. However, it seems more probable that during the late Pennsylvanian, *Artinskia* arose directly from *Uddenites* and then gave rise to *Propinacoceras* in the Permian.

Although the Ceratitina underwent their great development in the Triassic, they are known from strata as old as the Middle Permian. The shape of their conch, the nature of their sutures, and especially the structure of their siphuncle indicate that they arose from the Daraelitidae. The 1st superfamily of the suborder to appear, the Otocerataceae, includes the closely related Permian Xenodiscidae. However, except on a stratigraphic basis, it is difficult to differentiate many xenodiscids from Triassic ophiceratids, though the latter in general are farther advanced. The other 8 superfamilies of the Ceratitina are exclusively Triassic.

SYSTEMATIC DESCRIPTIONS[1]

Suborder ANARCESTINA Miller & Furnish, 1954

Primitive ammonoids with ventral retrochoanitic siphuncle and goniatitic sutures having a variable number of lobes. Some have only the basic minimum 3 or 4 lobes, whereas others possess auxiliaries or adventitious lobes or both. *L.Dev.-U.Dev.*

Superfamily ANARCESTACEAE Steinmann, 1890

[*nom. transl.* Miller & Furnish, 1954 (*ex* Anarcestinae Steinmann, 1890)]

Open umbilicus and sutures with small V-shaped ventral lobe. Characteristically, sutures form only 3 or 4 lobes, with all but ventral one rounded; but advanced representatives have 6 or even 8 lobes (73). *L. Dev.-U.Dev.*

Family MIMOCERATIDAE Steinmann, 1890

[*ex* Mimoceratinae]

Discoidal conch, whorls not impressed dorsally, with large umbilical perforation. Sutures form 3 lobes, a V-shaped ventral, and shallow laterals (19, 73). *L.Dev.-M.Dev.*

Subfamily MIMOCERATINAE Steinmann, 1890

No prominent sculpture; whorls in contact (19, 73). *L.Dev.-M.Dev.*

Gyroceratites Meyer, 1831 [**G. gracilis* Bronn, 1835] [=*Aphyllites* Mojsisovics, 1882; *Mimoceras* Hyatt, 1884]. *L.Dev.-M.Dev.,* Eu.-Fr.N.Afr.-SE. Austral.——Figs 13*A;* 14. **G. gracilis,* M.Dev., Ger.; enlarged (73).

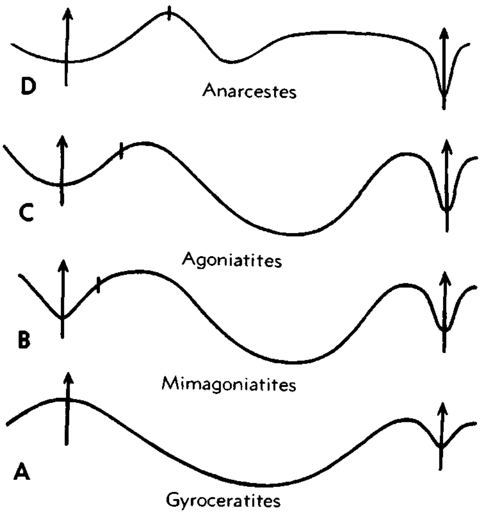

Fig. 13. Sutures of *Gyroceratites (A), Mimagoniatites (B), Agoniatites (C),* and *Anarcestes (D)* (110).

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[1] Miller & Furnish prefer to omit information concerning various sorts of nomenclatural alteration of family-group taxa and statement of synonymies applicable to these taxa because the preparation of such records would require too great labor and consumption of time, particularly in view of the inadequacy of literature readily at hand. Accordingly, only a few nomenclatural annotations are given and generally these do not specify authors and dates of original publication relating to altered family-group names.

Also, type species of genera and subgenera of Paleozoic ammonoids (other than Clymeniina), which are indicated invariably as defined by original designation, may include several established by subsequent designation (SD), for the manner of fixing type species has not been investigated comprehensively.—Editor.

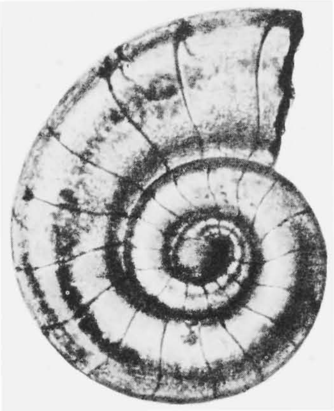


Fig. 14. *Gyroceratites gracilis* Bronn, M.Dev., Ger.; enlarged (73).

Subfamily MIMOSPHINCTINAE Erben, 1953

Characterized by prominent ribs that extend across the venter (19). *L.Dev.*

Mimosphinctes Eichenberg, 1931 [**M. tripartitus*]. Whorls in contact; ribs bifurcate ventrally (19, 73). *L.Dev.*, Ger.——Fig. 15. **M. tripartitus;* ×2 (104).

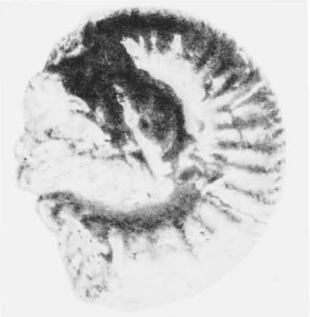


Fig. 15. *Mimosphinctes tripartitus* Eichenberg, L. Dev., Ger.; ×2 (104).

Anetoceras Schindewolf, 1934 [**Cyrtoceratites arduennensis* Steininger, 1853]. Loosely coiled with whorls not in contact, ribs prominent (19, 74). *L.Dev.*, Ger.

Paleogoniatites Hyatt, 1900 [**Gon. lituus* Barrande, 1865]. Whorls subcircular and in contact, ribs moderately prominent. Sutures nearly straight laterally (1, 19,73). *L.Dev.*, Czech.——Fig. 16. **P. lituus* (Barrande); ×2 (1).

Family AGONIATITIDAE Holzapfel, 1899

[= Agoniatitides Haug, 1898 (invalid vernacular name)]

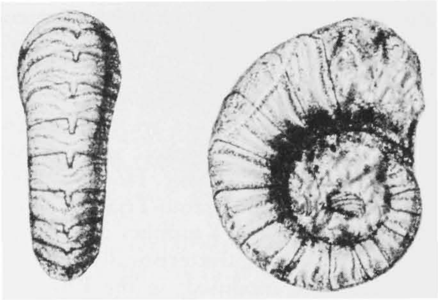


Fig. 16. *Paleogoniatites lituus* (Barrande), L.Dev., Czech.; ×2 (1).

Conch discoidal, with moderate umbilici and biconvex growth lines. Sutures with small ventral and broad lateral and dorsal lobes (46, 73). *L.Dev.-M.Dev.*

Agoniatites Meek, 1877 [**Gon. vanuxemi* Hall, 1879]. Imperforate umbilicus. Sutures form 4 lobes (46, 73). *?L.Dev.-M.Dev.*, widespread in Eurasia-N.Afr.-Austral.-N.Am.——Figs. 17; 18. **A. vanuxemi* (Hall), M.Dev., N.Y.; 17,×0.3; 18, ×0.7 (107).——Fig. 13*C*. *A. costulatus* (D'Archaic & De Verneuil), M.Dev., Ger.; enlarged (73).

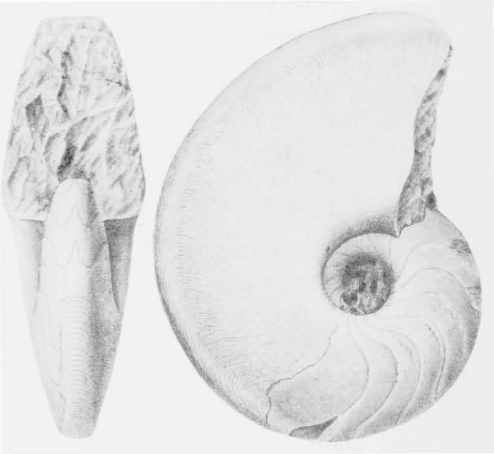


Fig. 17. *Agoniatites vanuxemi* (Hall), M.Dev., N.Y.; ×0.3 (107).

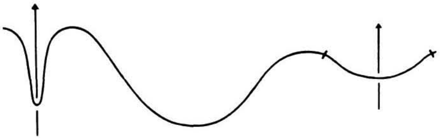


Fig. 18. Suture of *Agoniatites vanuxemi* (Hall), M. Dev., N.Y.; ×0.7 (107).

Mimagoniatites Eichenberg, 1930 [**Gon. zorgensis* Roemer, 1866]. Like *Agoniatites* but umbilicus perforate (19, 73). *L.Dev.-M.Dev.*, Ger.-N.Afr.——Fig. 13*B;* 19. **M. zorgensis* (Roemer), L. Dev., Ger.; 13*B*, enlarged; 19, ×7.5 (73).

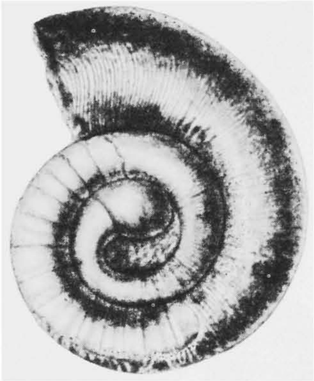


Fig. 19. *Mimagoniatites zorgensis* (Roemer), L. Dev., Ger.; ×7.5 (73).

Paraphyllites Hyatt, 1900 [**Gon. tabuloides* Barrande, 1865]. Like *Agoniatites* but suture with small umbilical lobe (1, 73). *M.Dev.,* Czech.-Turkey-N.Afr.——Fig. 20. **P. tabuloides* (Barrande), Czech.; 20, ×0.7 (1).

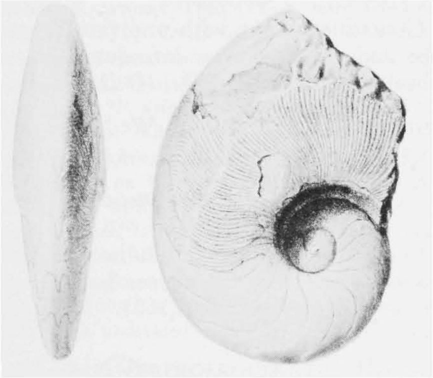


Fig. 20. *Paraphyllites tabuloides* (Barrande), M. Dev., Czech.; ×0.7 (1).

Family ANARCESTIDAE Steinmann, 1890

[*ex* Anarcestinae Steinmann, 1890]

Like Agoniatitidae but characteristically whorls broader and 1st lateral lobes appear in umbilical region rather than in lateral areas (73). *L.Dev.-U.Dev.*

Subfamily ANARCESTINAE Steinmann, 1890

Subglobular to thickly discoidal, widely umbilicate conchs. Sutures form 4 lobes (73). *L.Dev.-U.Dev.*

Anarcestes Mojsisovics, 1882 [**Gon. plebeius* Barrande, 1865] [=*Clarkeoceras* Wedekind, 1918]. Umbilicus perforate. Suture with lateral lobe variable in size and position (73, 100). *L.Dev.-M.Dev.*

A. (Anarcestes). Lateral lobe small and near umbilical shoulder. *L.Dev.-M.Dev.;* widespread Eurasia-N.Afr.——Fig. 21. **A. (A.) plebeius* (Barr.), M.Dev., Czech.; ×1 (117).——Fig. 13*D, A. (A.) lateseptatus* (Beyrich), M.Dev., Ger.; enlarged (73).

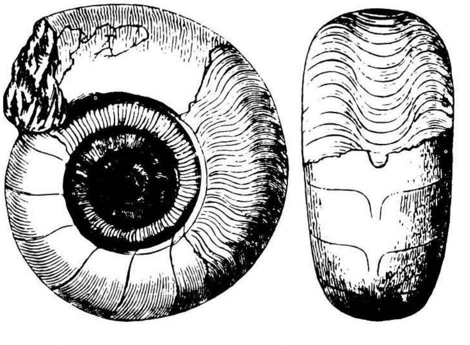


Fig. 21. *Anarcestes (Anarcestes) lateseptatus plebeius* (Barrande), M.Dev., Czech.; ×1 (1).

A. (Latanarcestes) Schindewolf, 1933 [**Am. noeggerati* von Buch, 1832]. Lateral lobe large and on lateral area. *M.Dev.;* Ger.-Czech.

Subanarcestes Schindewolf, 1933 [**S. macrocephalus*]. Conch subglobular, with imperforate umbilicus. Sutures as in typical *Anarcestes* (73). *M.Dev.,* Ger.——Fig. 25*A*. **S. macrocephalus;* enlarged (73).

Werneroceras Wedekind, 1918 [**Gon. ruppachensis* Kayser, 1879]. Like *Subanarcestes* but lateral lobe of suture on lateral area (46, 73, 100). *L.Dev.-U.Dev.,* Eu.-N.Afr.-E.USA.——Fig. 22. *W. ruppachense* (Kayser), M.Dev., Ger.; *A,B,* ×1 (108); *C,* ×1.5 (100).——Fig. 22*D. W. plebeiforme* (Hall), M.Dev., NY.; ×1 (107).

Sellanarcestes Schindewolf, 1933 [**Gon. wenkenbachi* Kayser, 1884]. Like *Werneroceras* but suture with secondary dorsal saddle (19, 73). *L.Dev.-M. Dev.,* Ger.

Subfamily PINACITINAE Schindewolf, 1933

[=Pinnacitidae Hyatt, 1900 (invalid name *ex Pinacites*)]

Subdiscoidal to lenticular conch with narrow imperforate umbilicus. Sutures from 6 to 10 lobes. *L.Dev.-M.Dev.*

Pinacites Mojsisovics, 1882 [**Gon. jugleri* Roemer, 1843]. Lenticular conch with acute venter. Sutures with 6 lobes and narrowly rounded 1st lateral saddle (73, 100). *M.Dev.,* Ger.-Czech.——Fig. 23. **P. jugleri* (Roemer), Ger.; ×0.7 (111).

Parodicerellum Strand, 1929 [**Tornoceras convolutum* Holzapfel, 1895] [=*Parodiceras* Wedekind, 1913 (*non* Hyatt, 1884); *Holzapfeloceras* Miller, 1932]. Like *Pinacites* but with wider conch and rounded venter (73). *M.Dev.,* Ger.

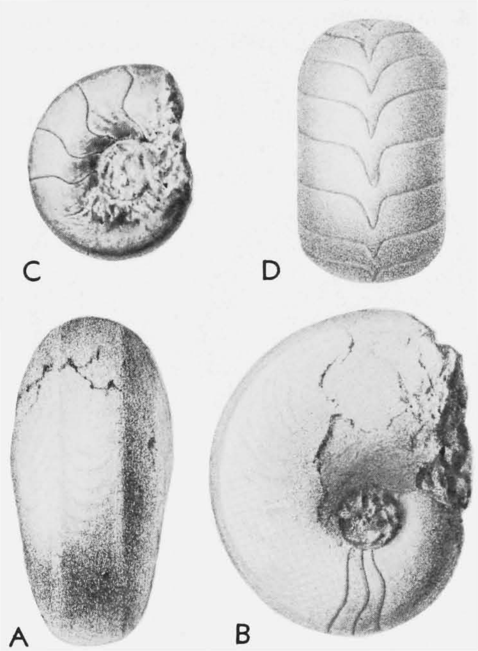


FIG. 22. *Werneroceras. A-C, W. ruppachense* (KAYSER), M.Dev., Ger.; *A,B,* ×1 (108); *C,* ×1.5 (100). *D, W. plebeiforme* (HALL), M.Dev., N.Y.; ×1 (107).

Wedekindella SCHINDEWOLF, 1928 [**Gon. retrorsus brilonensis* KAYSER, 1872]. Like *Parodicerellum* but suture with secondary dorsal saddle (73). *M. Dev.,* Ger.

Foordites WEDEKIND, 1918 [**Aphyllites occultus platypleura* FRECH, 1889]. Like *Parodicerellum* but flattened laterally and ventrally, and with ventrolateral sulci (73, 100). *M.Dev.,* Ger.

Maenioceras SCHINDEWOLF, 1933 [**Gon. terebratus* SANDBERGER & SANDBERGER, 1851] [=*Maeneceras auctt.* (*non* HYATT, 1884)]. Like *Foordites* but suture with 10 lobes (73). *M.Dev.,* Eurasia-N.Afr.-?W.Austral.——FIG. 24. **M. terebratum* (SANDB.-S.), M.Dev., Ger.; ×1.5 (68).

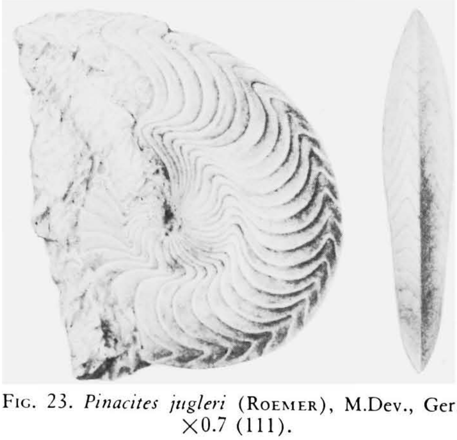


FIG. 23. *Pinacites jugleri* (ROEMER), M.Dev., Ger.; ×0.7 (111).

FIG. 24. *Maenioceras terebratum* (SANDBERGER & SANDBERGER), M.Dev., Ger.; ×1.5 (68).

Superfamily PROLOBITACEAE Wedekind, 1913

[*nom. transl.* MILLER & FURNISH, 1954 (*ex* Prolobitidae WDKD., 1913)]

Goniatitic sutures with undivided ventral lobe and primary lobes introduced in umbilical region (100). *M.Dev.-U.Dev.*

Family PROLOBITIDAE Wedekind, 1913

Characters of superfamily. *M.Dev.-U.Dev.*

Subfamily PROLOBITINAE Wedekind, 1913

[*ex* Prolobitidae WDKD., 1913]

Conch subglobular to subdiscoidal, with moderate to closed umbilicus. Sutures with no auxiliaries (41,68,96,100). *M.Dev.-U. Dev.*

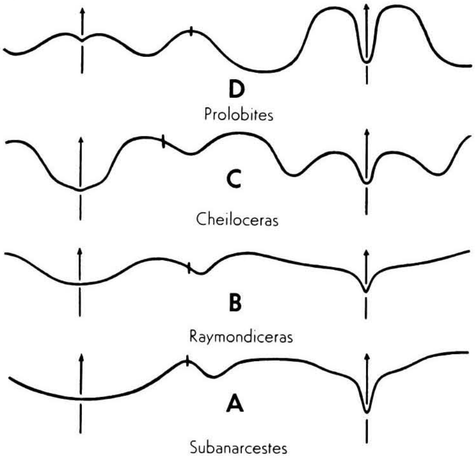


FIG. 25. Sutures of *Subanarcestes (A), Raymondiceras (B), Cheiloceras (C),* and *Prolobites (D)* (110).

FIG. 26. *Sporadoceras* and *Prolobites*. *A, S. biferum* (PHILLIPS), U.Dev., Ger.; ×1 (68). *B,C, P. delphinus* (SANDBERGER & SANDBERGER), Ger.; ×1 (68).

Prolobites KARPINSKY, 1885 [**Gon. bifer delphinus* SANDB.-S., 1851]. Conch subglobular, with closed umbilicus. Suture forms 6 lobes, lateral ones rounded (68,100). *U.Dev.*, Eu.-N.Afr.——FIGS. 25*D;* 26*B,C*. **P. delphinus* (SANDB.-S.), Ger.; 25*D*, enlarged (73); 26*B,C*, ×1 (68).

Sobolewia WEDEKIND, 1913 [**Gon. cancellatus* D'ARCHIAC & DE VERNEUIL, 1842]. Conch thickly subdiscoidal; with small to closed umbilicus. Suture forms 4 lobes, lateral ones shallow and rounded (100). *M.Dev.*, Ger.-N.Afr.

Clymenoceras SCHINDEWOLF, 1937 [**C. insolitum*]. Like *Prolobites* but with moderate umbilicus and suture with undivided dorsal saddle. *U.Dev.*, Ger.

Subfamily SANDBERGEROCERATINAE Miller, 1938

Conch discoidal, with transverse ribs, umbilicus large. Sutures form auxiliaries except in primitive forms (46). *U.Dev.*

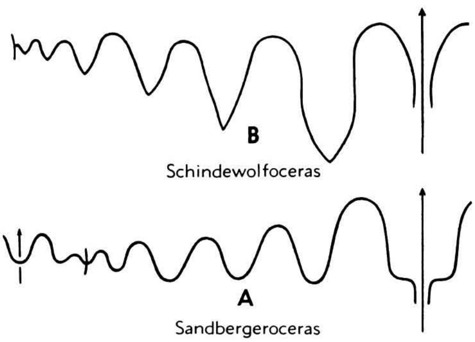


FIG. 27. Sutures of *Sandbergeroceras (A)* and *Schindewolfoceras (B)* (110).

Sandbergeroceras HYATT, 1884 [**Gon. tuberculosocostatus* SANDB.-S., 1850] [=*Triainoceras* HYATT, 1884 *(Triaenoceras auctt.)*]. Sutures form gradational series of rounded lobes and saddles, few auxiliaries (21,46,68). *U.Dev.*, Ger.-N.Y.——FIGS. 27*A;* 28. **S. tuberculosocostatum* (SANDB.-S.), Ger.; 27*A*, enlarged; 28, ×1 (68).

Pseudarietites FRECH, 1902 [**P. silesiacus*] [=*Pseudoarietites auctt.*]. Like *Sandbergeroceras* but sutures without auxiliaries (22). *U.Dev.*, Ger.

Schindewolfoceras MILLER, 1938 [**Gon. chemungensis* VANUXEM, 1842]. Like *Sanderbergoceras* but sutures with smaller ventral lobe and more auxiliaries (46). *U.Dev.*, N.Y.——FIG. 27*B*. **S. chemungensis* (VANUXEM); ×2 (107).

FIG. 28. *Sandbergeroceras tuberculosocostatum* (SANDBERGER & SANDBERGER), U.Dev., Ger.; ×1 (68).

Superfamily PHARCICERATACEAE Hyatt, 1900

[*nom. transl.* MILLER & FURNISH, herein (*ex* Pharciceratidae HYATT, 1900)]

Conch subdiscoidal to lenticular, umbilicus moderate to large, growth lines biconvex, no prominent sculpture. Sutures with large divided ventral lobe (22,46,68,100). *U.Dev.*

Family GEPHUROCERATIDAE Frech, 1901

[*nom. correct.* proposed MILLER & FURNISH, 1955 (*pro* Gephyroceratidae FRECH, 1901) ICZN pend.] [=Manticoceratidae WEDEKIND, 1918]

Sutures with large bifid ventral lobe and characteristically few or no auxiliaries (100). *U.Dev.*

Manticoceras HYATT, 1884 [**Gon. simulator* HALL, 1874] [=*Gephuroceras* HYATT, 1884 (*Gephyroceras* AUCTT.); *Crickites* WEDEKIND, 1913]. Conch subdiscoidal to lenticular, umbilicus moderate to large. Sutures form 6 lobes (46,100). *U. Dev.*, widespread in N.Am.-Eurasia-N.Afr.-W. Austral.——FIGS. 29; 30*C*. *M. sinuosum* (HALL),

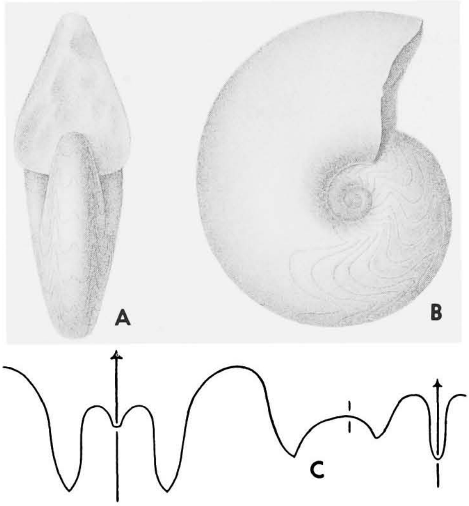


Fig. 29. *Manticoceras sinuosum* (Hall), U.Dev., N.Y.; *A,B,* ×0.5; *C,* enlarged (12).

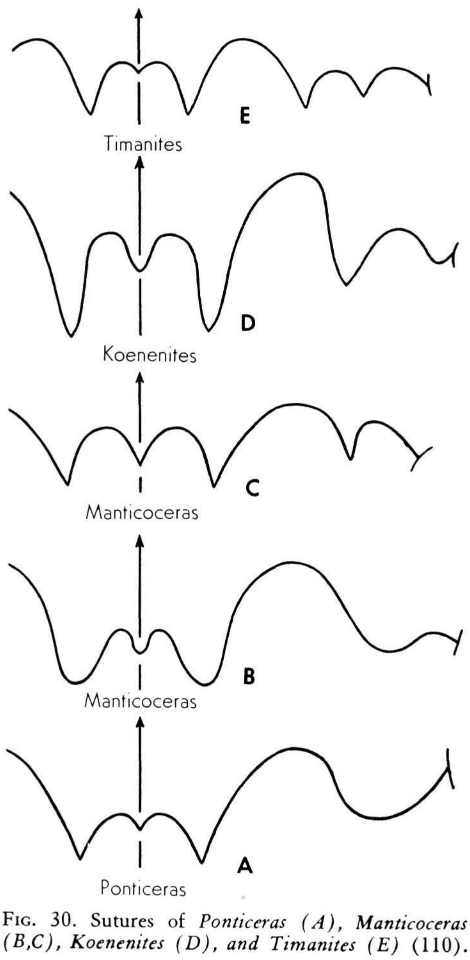


Fig. 30. Sutures of *Ponticeras (A), Manticoceras (B,C), Koenenites (D), and Timanites (E)* (110).

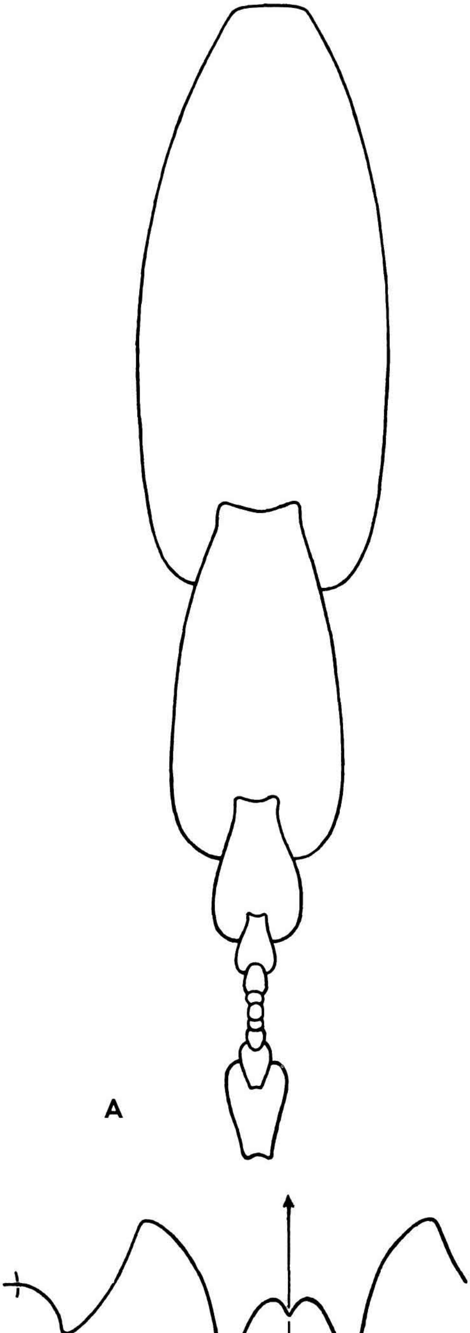


Fig. 31. *Probeloceras lutheri* (Clarke), U.Dev., N.Y.; *A,* enlarged; *B,* ×5 (12).

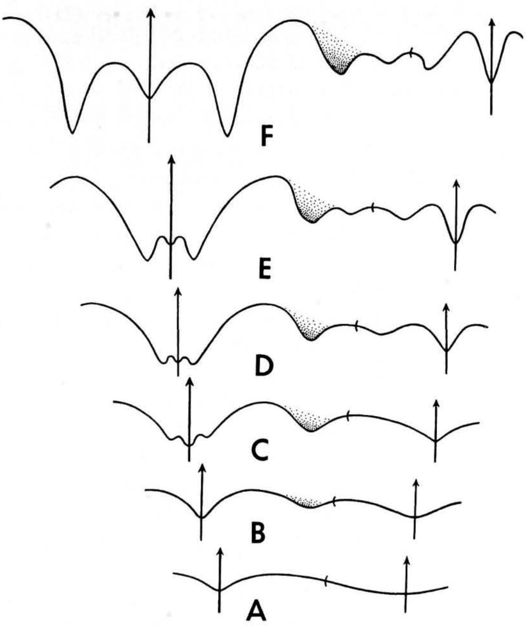


FIG. 32. Ontogeny of sutures in *Koenenites cooperi* MILLER, U.Dev., Mich.; *A-E,* enlarged; *F,* ×2 (46).

N.Y.; 29*A,B,* ×0.5 (12); 29*C,* enlarged (12); 30*C,* ×1 (107).——FIGS. 30*B;* 35*A.* **M. simulator* (HALL), N.Y.; both ×2 (107).

Ponticeras MATERN, 1929 [**Am. aequabilis* BEYRICH, 1837]. Like *Manticoceras* but with wider umbilici and more primitive sutures which form only 4 distinct lobes (46). *U.Dev.,* Eu.-N.Afr.-USA.——FIG. 30*A.* **P aequabilis* (BEYRICH), Ger.; ×2.5 (3).

Probeloceras CLARKE, 1899 [**Gon. lutheri* CLARKE, 1885]. Thinly discoidal conch with flattened venter and wide umbilici. Sutures form 4 lobes and subangular 1st lateral saddle (12,46). *U.Dev.,* E. USA.——FIG. 31. **P. lutheri* (CLARKE), N.Y.; *A,* enlarged; *B,* ×5 (12).

Koenenites WEDEKIND, 1913 [**Gon. lamellosus* SANDB.-S., 1851]. Like *Manticoceras* but sutures with additional lobe (on umbilical wall) (46,100). *U.Dev.,* Ger.-Fr.-N.Afr.-USA.——FIGS. 32; 33. *K. cooperi* MILLER, Mich.; 32*A-E,* enlarged; 32*F,* ×2; 33*A,* ×1.3; 33*B,* ×7 (all 46).——FIG. 30*D.* **K. lamellosus* (SANDB-S.), Ger.; ×2 (68).

Timanites MOJSISOVICS, 1882 [**T. keyserlingi* MILLER, 1937] [=*Hoeninghausia* GÜRICH, 1896]. Conch lenticular with angular venter and small umbilici. Sutures form 10 lobes (46). *U.Dev.,* Eu.-N.Afr.-W.Can.——FIGS. 30*E;* 34. **T. keyserlingi* MILLER, Timans; 30*E,* ×1; 34*A,B,* ×0.7 (all 35).

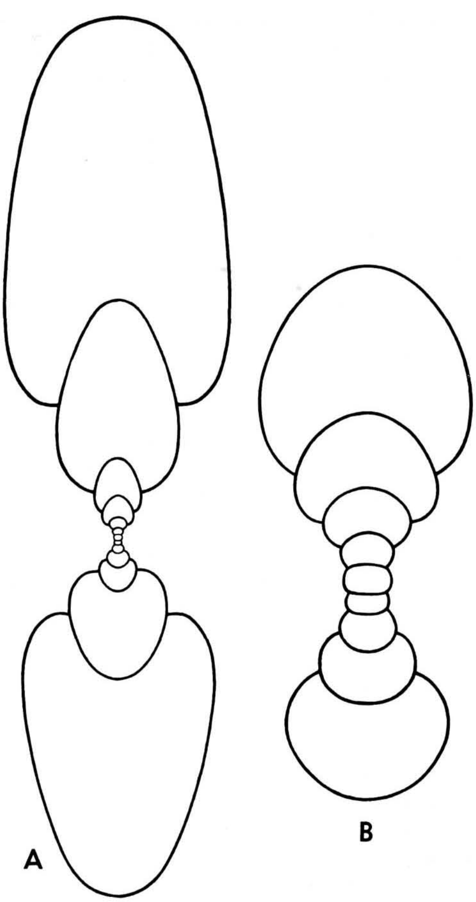


FIG. 33. Cross sections of *Koenenites cooperi* MILLER, U.Dev., Mich.; *A,* ×1.3; *B,* ×7 (46).

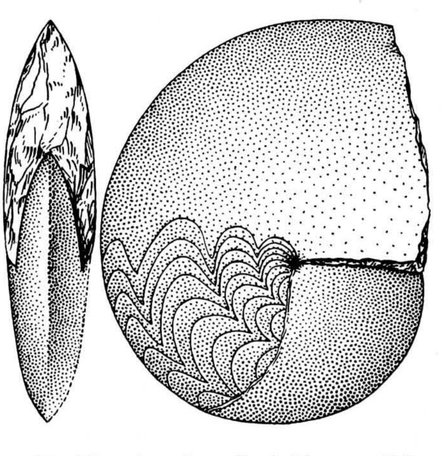


FIG. 34. *Timanites keyserlingi* MILLER, U.Dev., Russ.; ×0.7 (35).

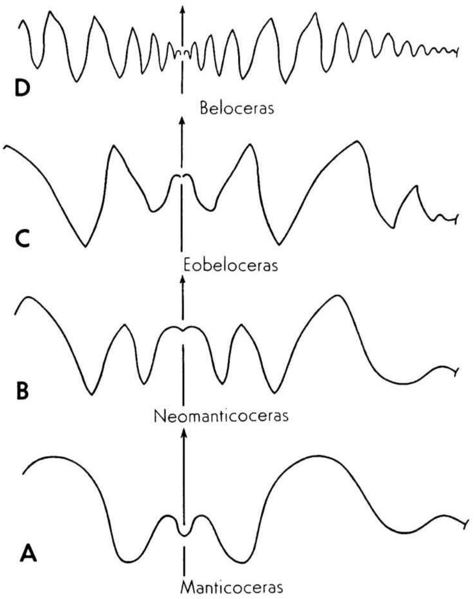


FIG. 35. Sutures of _Manticoceras (A)_, ×2; _Neomanticoceras (B)_, enlarged; _Eobeloceras (C)_, enlarged; and _Beloceras (D)_, ×1 (110).

Family PHARCICERATIDAE, Hyatt, 1900

[=Synpharciceratidae SCHINDEWOLF, 1936]

Conch globular to subdiscoidal; sutures with rounded lobes (100). _U.Dev._

Pharciceras HYATT, 1884 [*_Gon. tridens_ SANDB.-S., 1850]. Conch thickly subdiscoidal; sutures with 3 to 6 pairs of lateral and auxiliary lobes (68,100). _U.Dev._, Eurasia-N.Afr.

Synpharciceras SCHINDEWOLF, 1940 [*_Gon. clavilobus_ SANDB. S., 1850] [=_Neopharciceras_ BOGOSLOVSKY, 1955]. Like _Pharciceras_ but conch discoidal and with more sutural elements (68). _U.Dev._, Eurasia-N.Afr.

Nordiceras BOGOSLOVSKY, 1955 [*_Prolecanites timanicus_ HOLZAPFEL, 1899]. Like _Pharciceras_ but conch thinly discoidal (35). _U.Dev._, Eurasia.

Sphaeropharciceras BOGOLOVSKY, 1955 [*_S. sandbergerorum_]. Like _Pharciceras_ but conch globular and suture simpler (68). _U.Dev._, Eurasia-N.Afr.

Family BELOCERATIDAE Frech, 1902

[_nom. transl._ J.P.SMITH, 1903 (_ex_ Beloceratinae FRECH, 1902)]

Conch subdiscoidal to lenticular, umbilicus small to moderate. Suture forms angular adventitious lobes within ventral lobe (68, 100). _U.Dev._

Beloceras HYATT, 1884 [*_Gon. sagittarius_ SANDB.-S., 1851]. Conch lenticular, umbilicus moderately small. Suture forms series of adventitious lobes within ventral lobe and series of auxiliaries (21, 68,100). _U.Dev._, Eurasia-N.Afr.-N.Y.——FIG. 35_D_. *_B. sagittarium_ (SANDB.-S.), Ger.; ×1 (68).

Neomanticoceras SCHINDEWOLF, 1936 [*_Manticoceras paradoxum_ MATERN, 1931] [=_Anabeloceras_ CLARKE, 1897 _(nom. nud.)_]. Like _Manticoceras_ but suture has pair of adventitious lobes within ventral lobe (46). _U.Dev._, Ger.-N.Y.——FIGS. 35_B_; 36. _N. naplesense_ (CLARKE), N.Y.; 35_B_, enlarged; 36, ×1 (12).

FIG. 36. _Neomanticoceras naplesense_ (CLARKE), U. Dev., N.Y.; ×1 (12).

Eobeloceras SCHINDEWOLF, 1936 [*_Am. multiseptatus_ VON BUCH, 1832]. Like _Neomanticoceras_ but suture has auxiliaries (11,46). _U.Dev._, Ger.-N.Afr.-N.Y.——FIGS. 35_C_; 37. _E. iynx_ (CLARKE), N.Y.; 35_C_, enlarged; 37, ×2 (12).

FIG. 37. _Eobeloceras iynx_ (CLARKE), U.Dev., N.Y.; ×2 (12).

Suborder CLYMENIINA Hyatt, 1884

[*nom. correct.* MILLER & FURNISH, 1954 (*pro* Clymeninae HYATT, 1884)] [=Intrasiphonata ZITTEL, 1895; Clymeniacea WEDEKIND, 1914; Clymenoidea SCHINDEWOLF, 1923]

Primitive Ammonoidea with dorsally situated marginal siphuncle (Fig. 38,*1*). As reported in 2 genera (*Acanthoclymenia, Cymaclymenia*), the siphuncle primarily has a ventral position in the 1st few septa (Fig. 38,*2b*) and then migrates to its definite dorsal location during early adolescence. This seems to indicate derivation of the Clymeniina from goniatites with a ventrally placed siphuncle. Septal necks cylindrical, retrochoanitic, commonly very long, forming a continuous siphuncular tube (Fig. 38,*1*). Shell tightly coiled, without umbilical perforation, typically subdiscoidal and widely umbilicate, but some subglobular and deeply involute, smooth or strongly ribbed and spinose. Growth lines usually denote a lateral and a deep ventral hyponomic sinus. Protoconch (Fig. 38,*2a,b*) spheroidal or ellipsoidal, with latisellate prosuture (Fig. 38,*2c*) (in those few shells where it can be observed); following early adolescent sutures (Fig. 38,*2d*) invariably with ventral lobe, which in Gonioclymeniaceae persists throughout ontogenetic development, whereas in Clymeniaceae it is replaced by a very characteristic ventral saddle fused with the 2 1st lateral saddles (Fig. 38,*3a-c*). The dorsal lobe persists in these 2 groups, but in Parawocklumeriaceae it also, as well as the ventral lobe, is replaced by a secondary saddle during ontogeny (Fig. 38,*4*). Both evolutionary trends are unique among ammonoids. Lobes and saddles rounded or pointed, not denticulate. Septa concave in the median plane. Length of body chamber about one volution and more. Aptychi or anaptychi not observed. *U.Dev.*

The Clymeniina apparently represent a monophyletic group derived from *Archoceras* or some related form of Anarcestidae and confined to the Upper Devonian. The group is distributed mainly in Europe and northern Africa; it is more scarcely represented also in the other continents (with possible exception of Asia).

Superfamily GONIOCLYMENIACEAE Hyatt, 1884

[*nom. transl. et correct.* MILLER & FURNISH, 1954 (*ex* Gonioclymenidae HYATT, 1884)] [=Gonioclymeniacea SCHINDEWOLF, 1923; Gonioclymenida SCHIND., 1937]

Dorsal and ventral lobes retained throughout ontogenetic development, but latter may be secondarily divided by a median saddle. Septal necks usually very long, forming more or less continuous tube for siphuncle. Suture in primitive members consisting of ventral, lateral, and dorsal lobes only, in more advanced forms additionally with umbilical and adventitious lobes. Shell variable, in typical forms narrowly subdiscoidal and widely umbilicate, with compressed whorl section, in some offshoots broadly subdiscoidal or subglobular, with narrow or closed umbilicus and depressed whorl section. *U. Dev. (Manticoceras z.-Wocklumeria z.).*

The Gonioclymeniacea are considered to be the conservative group of Clymeniina and the root stock of Clymeniaceae and Parawocklumeriaceae.

Family HEXACLYMENIIDAE Lange, 1929

Shell small (few cm. in diameter), narrowly subdiscoidal, slightly involute, widely umbilicate, with depressed whorls, increasing slowly in height. Suture with ventral, lateral, and dorsal lobes only; ventral lobe moderately deep, broadly rounded. Septal necks originally short but in later forms long, forming a continuous siphuncular tube. Growth lines with lateral sinus, prominent ventrolateral salient, and deep hyponomic sinus. *U.Dev.(Platyclymenia z.-Wocklumeria z.).*

Hexaclymenia SCHINDEWOLF, 1923 [**Clymenia hexagona* WEDEKIND, 1908]. Whorl section subtriangular, with rounded whorl sides and carinate venter; keel flanked by pair of broad grooves on ventrolateral shoulders. Growth lines with deep lateral sinus and prominent ventrolateral salient, without marked ribs. Septal necks short. *U.Dev. (Platyclymenia z.),* Eu.——FIG. 39,*1*. **H. hexagona* (WDKD.), Ger.; *1a,b,* ×1; *1c,* suture at maturity (enlarged) (99).

Progonioclymenia SCHINDEWOLF, 1937 [**Clymenia acuticostata* BRAUN in MÜNSTER, 1842]. Whorl section rectangular, with flattened whorl sides and sulcate venter. Ribs strong, prorsiradiate, faintly sinuous, partly with ventrolateral spines. Septal necks long, forming continuous tube. *U.Dev. (Clymenia z.),* Eu.——FIG. 39,2. **P. acuticostata*

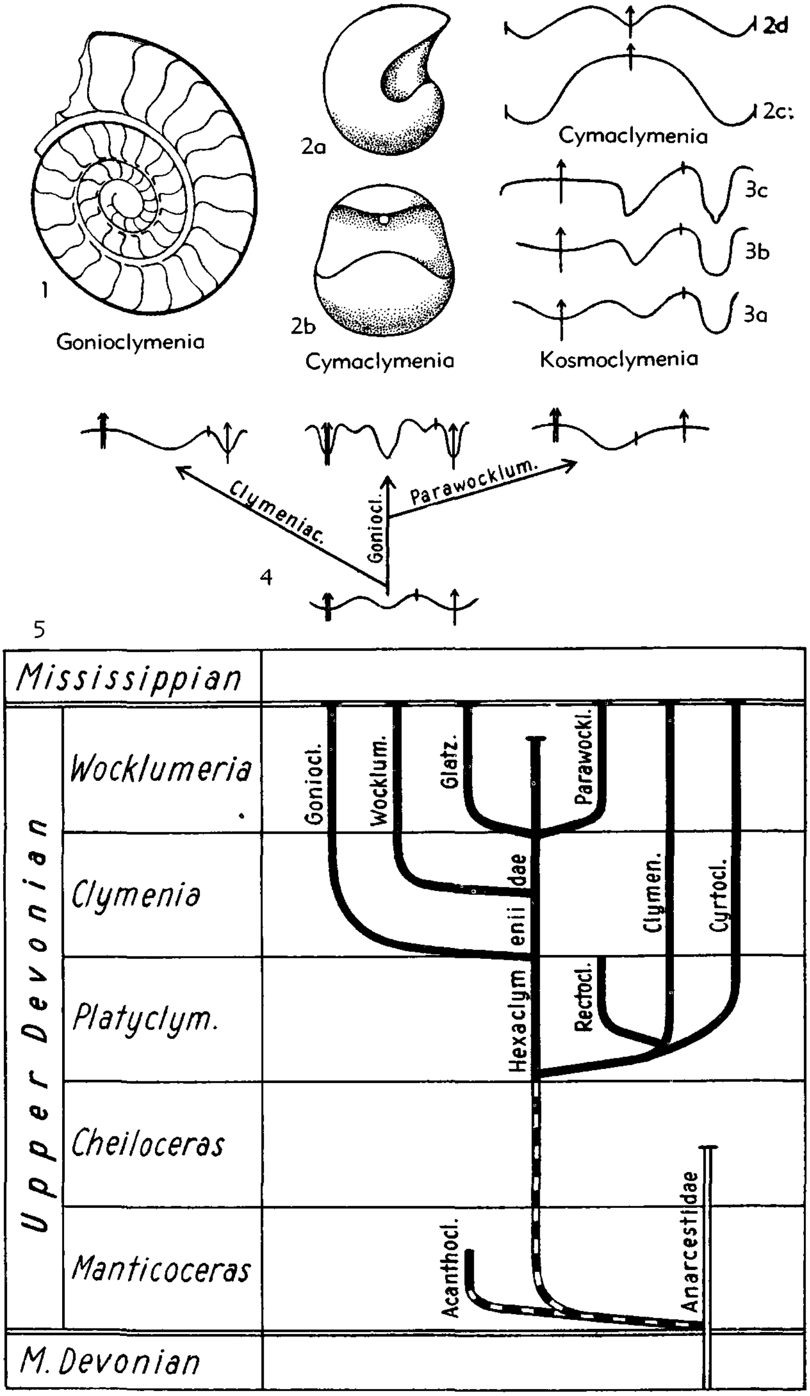


FIG. 38. General features of Clymeniina (113n).——*1, Gonioclymenia subcarinata* (MÜNSTER), U.Dev., *Clymenia* zone, Ger.; *median section* (×2).——*2, Cymaclymenia euryomphala* SCHINDEWOLF, U.Dev., *Wocklumeria* zone, Ger.; *2a,b,* protoconch, side and front view (×40); *2c,* prosuture; *2d,* primary suture.——*3, Kosmoclymenia undulata* (MÜNSTER), U.Dev., *Clymenia* zone, Ger.; *3a-c,* development of suture (enlarged).——*4,* Evolution of sutures in superfamilies of Clymeniina.——*5,* Supposed phylogenetic relationships of the families of Clymeniina.

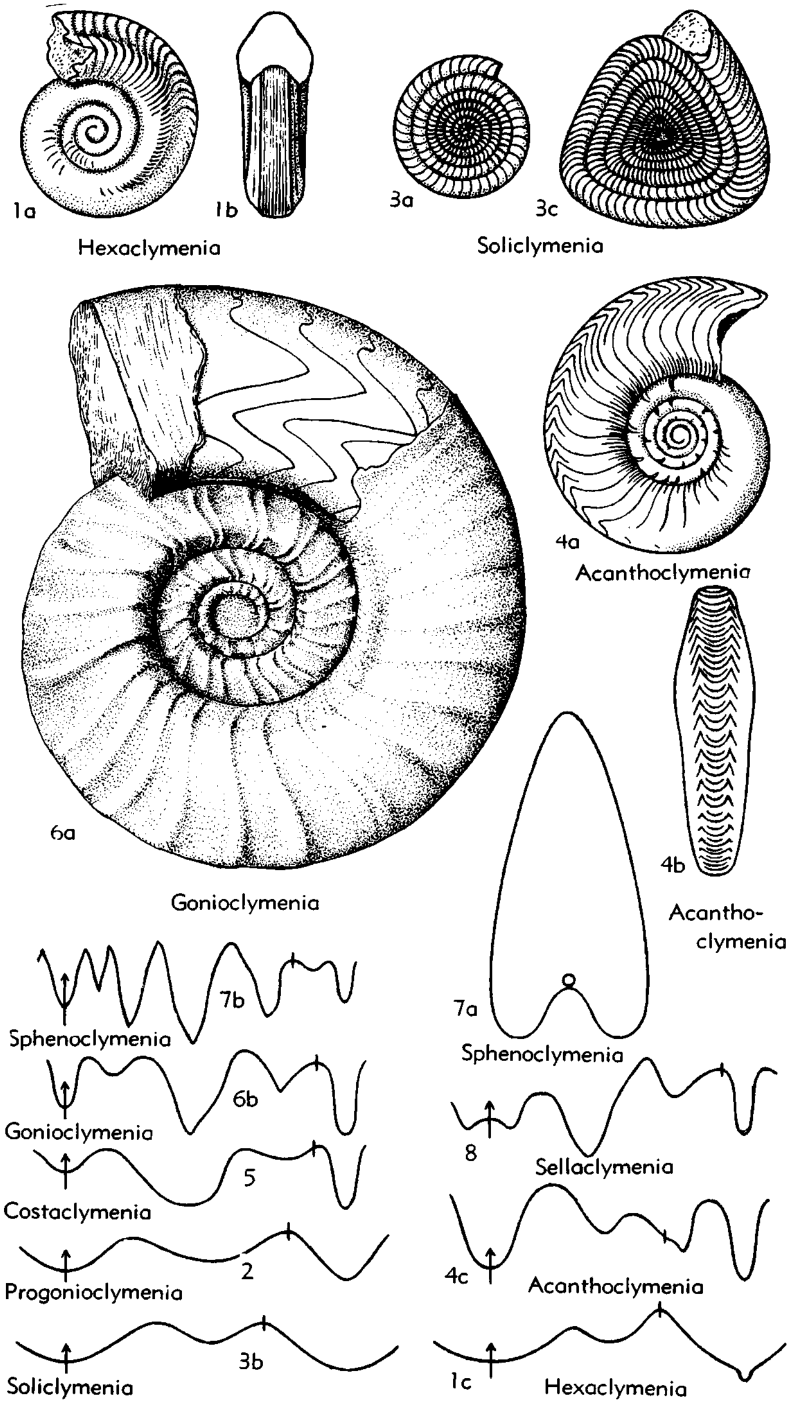


FIG. 39. Hexaclymeniidae, Acanthoclymeniidae, Gonioclymeniidae (p. L37-L40).

(BRAUN), Ger.; suture at maturity (enlarged) (114).

Soliclymenia SCHINDEWOLF, 1937 [**Goniatites solarioides* VON BUCH, 1840]. Whorl section broadly reniform, with rounded sides and venter. Ribs fine, densely crowded, deeply concave on the whorl sides, without spines. Shell in some forms with triangular coiling. *U.Dev.(Wocklumeria z.),* Eu.——FIG. 39,*3a,b*. **S. solarioides* (BUCH), Ger.; *3a*, ×2; *3b*, suture at maturity (enlarged) (114). ——FIG. 39,*3c*. *P. paradoxa* (MÜNSTER), Ger.; ×2 (114).

Family ACANTHOCLYMENIIDAE Schindewolf, 1955

Shell small (few cm. in diameter), subdiscoidal, slightly involute, widely umbilicate, with compressed whorls. Suture with ventral, lateral, and dorsal lobes supplemented by pointed umbilical lobe situated inside the umbilical seam; ventral lobe deeply rounded. Growth lines with lateral sinus, prominent angular ventrolateral salient, and deep hyponomic sinus. *U.Dev. (Manticoceras z.).*

The only genus so far known *(Acanthoclymenia)* was formerly included in the family Gonioclymeniidae, for its characters would not mean more than a generic difference from *Costaclymenia* of this family. But since *Acanthoclymenia* appears to be a very early isolate offshoot of Hexaclymeniidae, not in evolutionary continuity with the coherent group of Gonioclymeniidae, it seems advisable to place it in a family of its own.

Acanthoclymenia HYATT, 1900 [**Clymenia (Cyrtoclymenia) neapolitana* CLARKE, 1892]. Whorl section subtrapezoidal. Suture with lateral lobe shallow, rounded; dorsal lobe angular. *U.Dev. (Manticoceras z.),* N.Am.——FIG. 39,*4*. **A. neapolitana* (CLARKE), N.Y.; *4a,b*, ×3; *4c*, suture at maturity (enlarged) (46).

Family GONIOCLYMENIIDAE Hyatt, 1884

[*nom. correct.* WEDEKIND, 1913 (*pro* Gonioclymenidae HYATT, 1884)]

Shell large (up to 25 cm. in diameter), narrowly subdiscoidal, slightly involute, widely umbilicate, with compressed whorls, increasing rapidly in height. Suture, in addition to ventral, lateral, and dorsal lobes, comprising one or more umbilical and adventitious lobes. Septal necks long, forming continuous siphuncular tube. Growth lines with shallow sinus near umbilical seam, a broad shallow ventrolateral salient, and deeply rounded hyponomic sinus. Usually with prominent ribs and spines. *U.Dev. (Clymenia z.-Wocklumeria z.).*

Costaclymenia SCHINDEWOLF, 1920 [**Goniatites binodosus* MÜNSTER, 1832] [?=*Trochoclymenia* SCHIND., 1926]. Shell narrowly subdiscoidal, very widely umbilicate, with rectangular, compressed whorl section. Ribs faint or strong, nearly rectilinear, radiate, with or without ventrolateral and dorsolateral spines. Suture with shallow, rounded ventral lobe, broadly rounded lateral lobe, shallow, rounded umbilical lobe outside the umbilical seam, and deep, pointed dorsal lobe. *U.Dev.(Clymenia z.),* Eu.——FIG. 39,*5*. **C. binodosa* (MÜNSTER), Ger.; suture at maturity (114).

Gonioclymenia HYATT, 1884 [**Goniatites speciosus* MÜNSTER, 1832] [=*Schizoclymenia* SCHINDEWOLF, 1920 (obj.)]. Shell as in *Costaclymenia* but with somewhat broader, subtrapezoidal whorl section and sulcate venter. Ribs faintly prorsiradiate, with broad shallow ventrolateral salient and ventrolateral spines. Suture with deep angular ventral lobe, pointed lateral and umbilical lobes, and an additional adventitious lobe. *U.Dev.(Clymenia z.),* Eu.-N.Afr.——FIG. 39,*6a,b*. **G. speciosa* (MÜNSTER), Ger.; *6a*, ×1; *6b*, suture at maturity (114n).

Kalloclymenia WEDEKIND, 1914 [**Goniatites subarmatus* MÜNSTER, 1832; SD SCHINDEWOLF, herein]. Suture and sculpture as in *Gonioclymenia* but with lower rectangular whorl section and without ventral sulcus. *U.Dev.(Wocklumeria z.),* Eu.-N. Afr.

K. (Kalloclymenia). Without distinct parabolic ribs and nodes. Occurrence as for genus.

K. (Otoclymenia) SCHINDEWOLF, 1923 [**Gonioclymenia uhligi* FRECH, 1902]. With marked parabolic ribs and nodes. Occurrence as for genus.

Sphenoclymenia SCHINDEWOLF, 1920 [**Goniatites maximus* MÜNSTER, 1832]. Shell narrowly subdiscoidal, with high fastigate or subrectangular whorl section, without marked ribs and spines. Suture highly differentiated with 2 umbilical and 2 adventitious lobes. *U.Dev.(Wocklumeria z.),* Eu.-N.Afr..——FIG. 39,*7*. **S. maxima* (MÜNSTER), Ger.; *7a*, whorl sec., ×0.5; *7b*, suture at maturity, enlarged (28).

Sellaclymenia HYATT, 1884 [**Clymenia angulosa* MÜNSTER, 1843 (=**Goniatites planus* MÜNSTER, 1832)]. Shell narrowly subdiscoidal, with high subrectangular whorl section, smooth or with ventrolateral ribs and spines. Suture with same number of elements as in *Costaclymenia* but ventral lobe divided by a low, broad median saddle. *U.Dev.(Clymenia z.-Wocklumeria z.),* Eu.——FIG. 39,*8*. **S. plana* (MÜNSTER), Ger.; suture at maturity, enlarged (114).

Family WOCKLUMERIIDAE Schindewolf, 1937

[*nom. correct.* SCHIND., 1949 (*ex* Wocklumeridae SCHIND., 1937] [=?Miroclymeniinae SCHIND., 1924; Biloclymeniidae BOGOSLOVSKY, 1955]

Shell of moderate size, broadly subdiscoidal or subglobular, strongly involute, more or less narrowly umbilicate, with triangular coiling in later representatives, without ventral keel. Suture with additional umbilical lobes; deep ventral lobe without median saddle (except in one uncertain genus). Septal necks long cylindrical, in some genera forming a continuous siphuncular tube. Growth lines nearly rectilinear; without prominent ribs. *U.Dev.(Clymenia z.-Wocklumeria z.).*

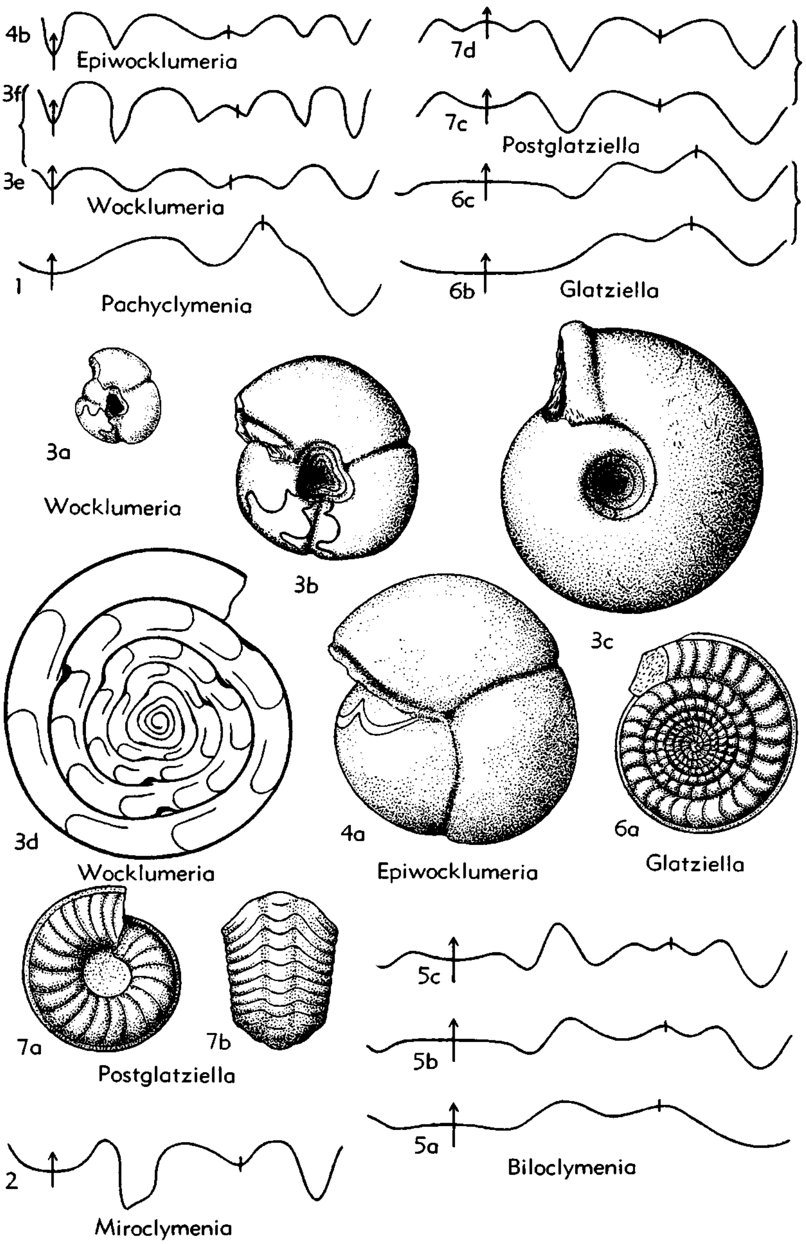


FIG. 40. Wocklumeriidae, Glatziellidae (p. L42).

The subfamily Miroclymeniinae was founded on the doubtful genus *Miroclymenia,* represented by a single specimen, which might be an immature stage of some other clymeniid. The type has been lost and no additional specimens have yet been discovered. It seems inadvisable to maintain this *genus inquirendum* as type genus of a subfamily and possibly of the family here called Wocklumeriidae.

Pachyclymenia SCHINDEWOLF, 1937 [**P. abeli*]. Shell broadly subdiscoidal, with moderately wide umbilicus, without constrictions and triangular coiling. Suture consisting of ventral, lateral, dorsal lobes, and an incipient umbilical lobe inside the umbilical seam; ventral lobe shallow, rounded. Growth lines with broad, shallow ventrolateral salient. *U.Dev.(Clymenia z.),* Eu.——FIG. 40,*1*. **P. abeli,* Ger.; suture at maturity, enlarged (114).

?**Miroclymenia** SCHINDEWOLF, 1923 [**M. interpres*]. Like *Pachyclymenia* but more narrowly umbilicate. Umbilical lobe well developed, divided by the umbilical seam; lateral lobe pointed. Genus very doubtful. *U.Dev.(Clymenia z.),* Eu.——FIG. 40,*2*. **M. interpres,* Ger.; suture at maturity, enlarged (114).

Wocklumeria WEDEKIND, 1918 [**W. denckmanni* (=**Goniatites sphaeroides* RH. RICHTER, 1848)]. Shell broadly subdiscoidal or subglobular, with moderately wide umbilicus and depressed whorl section; in youth with triangular coiling and deep, straight constrictions, at maturity spirally coiled, without constrictions. Suture with 3 umbilical lobes; ventral lobe deep and pointed, others likewise pointed. Growth lines practically rectilinear. *U.Dev.(Wocklumeria z.),* Eu.-N.Afr.——FIG. 40,*3*. **W. sphaeroides* (RICHTER), Ger.; *3a,d,* ×2; *3b,* ×1.5; *3c,* ×1; *3e-f,* development of suture, enlarged (all 114).

Epiwocklumeria SCHINDEWOLF, 1937 [**Wocklumeria paradoxa* var. *applanata* WEDEKIND, 1918]. Like *Wocklumeria* but narrowly subdiscoidal, with closed umbilicus and compressed whorl section. Shell at maturity also with subtriangular periphery and strong, adorally convex constrictions. Umbilical lobes rounded. *U.Dev.(Wocklumeria z.),* Eu.——FIG. 40,*4*. **E. applanata* (WDKD.), Ger.; *4a,* ×1.3; *4b,* suture at maturity, enlarged (114).

Biloclymenia SCHINDEWOLF, 1923 [**Clymenia bilobata* MÜNSTER, 1839] [=Cymaclymeniae GÜMBEL, 1863 (*non Cymaclymenia* HYATT, 1884); *Kiaclymenia* BOGOSLOVSKY, 1955]. Spirally coiled like *Pachyclymenia* but with 2 umbilical lobes and median saddle in broad external lobe. Doubtful taxonomic position. *U.Dev.(Clymenia z.),* Eu.——FIG. 40,*5*. **B. bilobata* (MÜNSTER), Ger.; *5a-c,* development of suture, enlarged (114).

Family GLATZIELLIDAE Schindewolf, 1928

[*nom. transl.* SCHIND., 1939 (*ex* Glatziellinae SCHIND., 1928)]

Shell small, broadly subdiscoidal or subglobular, strongly involute, more or less narrowly umbilicate, without triangular coiling, venter carinate. Suture invariably with median saddle. Septal necks short to long cylindrical but not forming a continuous tube. Growth lines with deep lateral sinus and prominent ventrolateral salient. Mostly ribbed. *U.Dev.(Wocklumeria z.).*

Glatziella RENZ, 1913 [**G. helenae;* SD SCHINDEWOLF, herein]. Shell subdiscoidal, evolute, widely umbilicate or subglobular, involute, narrowly umbilicate. Suture with 3 lobes only; ventral lobe broad, divided by median saddle; lateral lobe shallow, rounded, situated near umbilical seams. *U. Dev.(Wocklumeria z.),* Eu.——FIG. 40,*6*. **G. helenae,* Ger.; *6a,* ×1 (RENZ); *6b,c,* development of suture, enlarged (114).

Postglatziella SCHINDEWOLF, 1937 [**P. carinata*]. Like *Glatziella* but subglobular and narrowly umbilicate. Suture with additional umbilical lobe; lateral lobe deep, pointed, situated on middle of whorl sides. *U.Dev.(Wocklumeria z.),* Eu.——FIG. 40,*7*. **P. carinata,* Ger.; *7a,* ×2; *7c,d,* development of suture, enlarged (all 114).

Superfamily CLYMENIACEAE Edwards, 1849

[*nom. transl. et correct.* MILLER & FURNISH, 1954 (*ex* Clymenidae EDW., 1849)] [=Platyclymeniacea SCHINDEWOLF, 1923; Platyclymenida SCHIND., 1937]

Ventral lobe developed in earliest ontogenetic stages only, later replaced by ventral saddle; dorsal lobe persisting throughout ontogenetic development; suture mostly simple, undifferentiated. Septal necks usually short, not forming continuous tube for siphuncle. Shell variable, narrowly or more broadly subdiscoidal, with wide or narrow umbilicus. Growth lines with lateral and hyponomic sinus and more or less prominent ventrolateral salient. *U.Dev. (Platyclymenia z.-Wocklumeria z.).*

Family CLYMENIIDAE Edwards, 1849

[*nom. correct.* MILLER & FURNISH, 1954 (*pro* Clymenidae EDW., 1849)] [=Platyclymeniidae WEDEKIND, 1914]

Shell narrowly subdiscoidal, widely umbilicate, increasing slowly in height, with low whorl section, and rounded or flattened, rarely fastigate or carinate venter, smooth or ribbed. Growth lines with shallow, narrowly rounded ventrolateral salient. Suture simple, with lateral and dorsal lobes only, which may be supplemented by an adventitious lobe. *U.Dev.(Platyclymenia z.-Wocklumeria z.).*

Platyclymenia Hyatt, 1884 [**Goniatites annulatus* Münster, 1832] [=*Varioclymenia* Wedekind, 1908; *Annulites* Wdkd., 1914 (obj.); *Choneclymenia* Perna, 1914 *(nom. nud.)*; *Stenoclymenia* Lange, 1929]. Shell subdiscoidal, widely umbilicate, either ribbed or smooth. Growth lines and ribs with broad, shallow sinus on the whorl sides, without dorsolateral salient. Lateral lobe broadly rounded, no adventitious lobe. *U.Dev.(Platyclymenia z.),* Eu.-N.Afr.-N.Am.-?W. Austral.

P. (Platyclymenia). Whorl section rectangular,

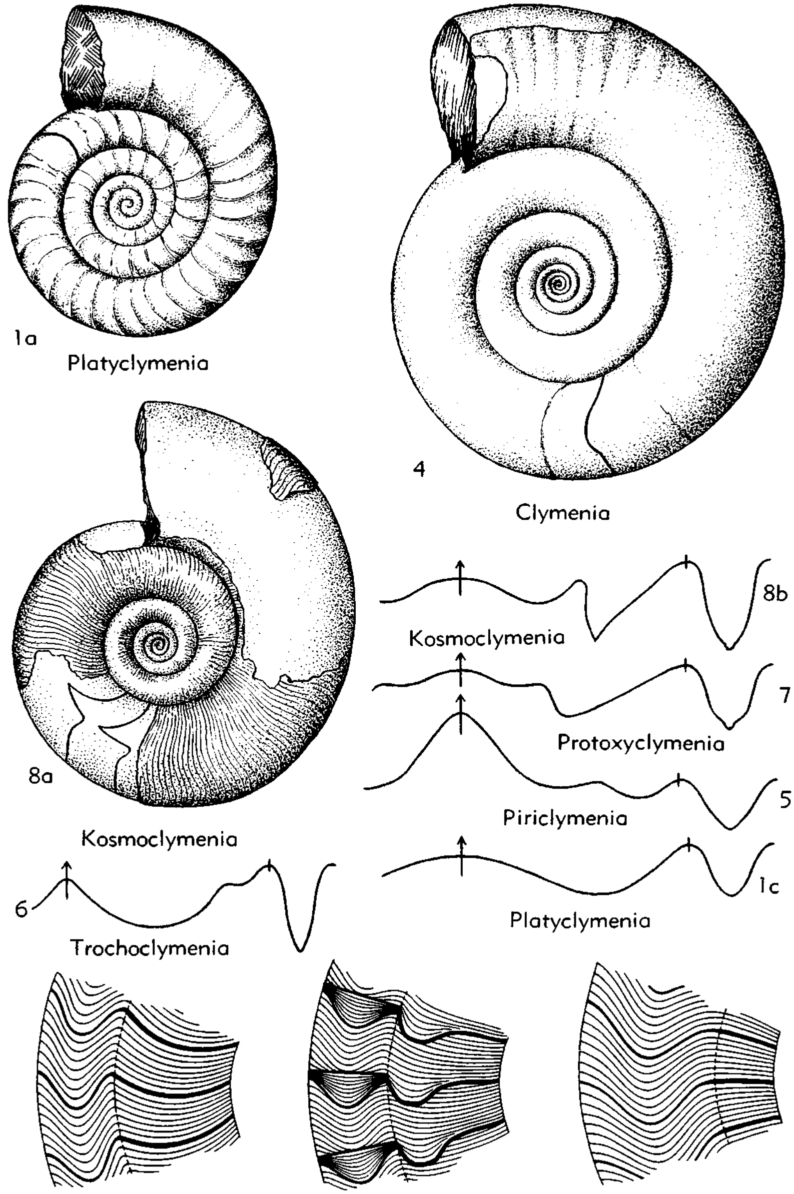


Fig. 41. Clymeniidae (p. L43-L44).

with flattened sides and relatively narrow venter. Ribs, if present, without parabolic ears and subtriangular structures on venter. Occurrence as for genus.——Fig. 41,*1*. **P.* (*P.*) *annulata* (Münster), Ger.; *1a*, ×1.5; *1b*, ×2.5; *1c*, suture at maturity, enlarged (all 113).

P. (Trigonoclymenia) Schindewolf, 1934 [**Clymenia spinosa* Münster, 1842]. Like *P.* (*Platyclymenia*) but with parabolic ears and subtriangular structures on venter. Occurrence as for genus.——Fig. 41,*2*. **P.* (*T.*) *spinosa* (Münster), Ger.; ×2.5 (114).

P. (Pleuroclymenia) Schindewolf, 1934 [**P.* (*Pl.*) *crassissima* Schind., 1955 (*nom. nov. pro Platyclymenia crassa* Schind., 1923, preoccupied)]. Whorl section broadly reniform with rounded sides and broad venter. Ribs without parabolic ears and subtriangular structures on venter. Occurrence as for genus.——Fig. 41,*3*. *P.* (*Pl.*) *americana* (Raymond), Mont.; ×2.5 (112).——Fig. 42. *P.* (*Pl.*) *polypleura* (Raymond), Mont.; *A-C*, ×0.5; *D*, enlarged (46).

Clymenia Münster, 1834 [*pro Planulites* Münster, 1832 (*non* Lamarck, 1801)] [**Planulites laevigatus* Münster, 1832; SD Frech, 1902] [=*Clymenites* Münster, 1835 (*nom. nud.*); *Endosiphonites* Ansted, 1838 (*nom. nud.*); *Oxyclymenia* Hyatt, 1884 (obj.); *Orthoclymenia* Wdkd., 1908 (*nom. nud.*); *Laevigites* Wdkd., 1914 (*nom. nud.*)]. Like *Platyclymenia* but with very faint, approximately rectilinear growth lines, without marked ribs. Venter rounded or fastigate. *U.Dev.*(*Clymenia z.*), Eu.-?W.Austral.——Fig. 41,*4*. **C. laevigata* (Münster), Ger.; ×0.75 (114n).

Piriclymenia Schindewolf, 1937 [**Platyclymenia piriformis* H. Schmidt, 1924]. Shell subdiscoidal, widely umbilicate, with subtriangular whorl section and fastigate venter, strongly ribbed. Suture with highly elevated ventral saddle, rounded lateral lobe situated near umbilical seam, and shallow, rounded adventitious lobe. *U.Dev.*(*Clymenia z.*), Eu.——Fig. 41,*5*. **P. piriformis* (Schmidt), Ger.; suture at maturity, enlarged (114).

?Trochoclymenia Schindewolf, 1926 [**Clymenia wysogorskii* Frech, 1902]. Shell narrowly subdiscoidal, evolute, widely umbilicate. Suture as in *Clymenia* but with an additional small, shallow umbilical lobe. (Genus doubtful; founded on single specimen, which may be an abnormal representative of *Costaclymenia*). *U.Dev.*(*Wocklumeria z.*), Eu.——Fig. 41,*6*. **T. wysogorskii* (Frech), Ger.; suture at maturity enlarged (114).

Protoxyclymenia Schindewolf, 1923 [**Clymenia dunkeri* Münster, 1839]. Like *Platyclymenia* but growth lines with dorsolateral salient, without marked ribs. Suture with shallow, incipient adventitious lobe. *U.Dev.*(*Platyclymenia z.-Clymenia z.*), Eu.——Fig. 41,*7*. **P. dunkeri* (Münster), *Clymenia* z., Ger.; suture at maturity, enlarged (114).

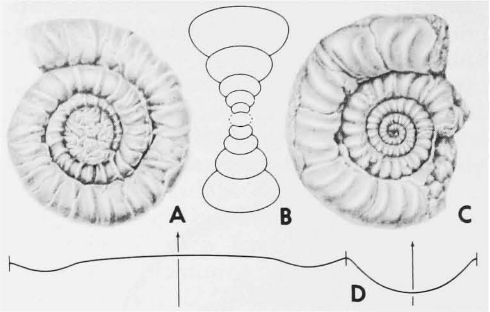


Fig. 42. *Platyclymenia* (*Pleuroclymenia*) *polypleura* (Raymond), Mont.; *A-C*, ×0.5; *D*, enlarged (46).

Kosmoclymenia Schindewolf, 1949 [**Planulites undulatus* Münster, 1832] [=Oxyclymeniae Gümbel, 1863 (*non Oxyclymenia* Hyatt, 1884)]. Like *Protoxyclymenia* but with deep, pointed lateral lobe and with distinct, moderately deep adventitious lobe. Venter rounded, flattened, fastigate or carinate. *U.Dev.*(*Clymenia z.-Wocklumeria z.*), Eu.-N.Afr.——Fig. 41,*8*. **K. undulata* (Münster), *Clymenia z.*, Ger.; *8a*, ×1; *8b*, suture at maturity, enlarged (114n).

Family CYRTOCLYMENIIDAE Hyatt, 1884

[*nom. correct.* Schindewolf, 1949 (*pro* Cyrtoclymenidae Hyatt, 1884)] [=Cymaclymenidae Hyatt, 1884; Striatoclymenidae Miller, 1938]

Shell broadly subdiscoidal, narrowly umbilicate, increasing quickly in height, with low whorl section and rounded, rarely carinate venter. Growth lines with prominent, broad ventrolateral salient. Suture, in addition to lateral and dorsal lobes, may comprise an umbilical and an adventitious lobe. *U.Dev.*(*Platyclymenia z.-Wocklumeria z.*).

Cyrtoclymenia Hyatt, 1884 [**Planulites angustiseptatus* Münster, 1832] [=*Protactoclymenia* Wedekind, 1908; *Lenticlymenia* H. Schmidt, 1924 (*nom. nud.*)]. Shell broadly subdiscoidal or subglobular, smooth or faintly ribbed. Suture with broadly rounded lateral lobe and dorsal lobe only. *U.Dev.*(*Platyclymenia z.-Wocklumeria z.*), Eu.-N.Afr.-W.Austral.——Fig. 43,*1*. *C. frechi* (Tokarenko), *Platyclymenia z.*, Ger.; ×1.3 (113n).——Fig. 43,*2*. **C. angustiseptata* (Münster), *Clymenia* z., Ger.; suture at maturity, enlarged (114).

Genuclymenia Wedekind, 1908 [**G. frechi*; SD Schindewolf, herein]. Shell subdiscoidal with crowded ribs. Suture with rounded lateral lobe, shallow, rounded umbilical lobe, inside umbilical seam, and likewise shallow adventitious lobe. *U. Dev.*(*Platyclymenia z.*), Eu.——Fig. 43,*3*. **G. frechi*, Ger.; *3a*, ×1; *3b*, suture at maturity, enlarged (99).

Cymaclymenia Hyatt, 1884 [*non* Cymaclymeniae

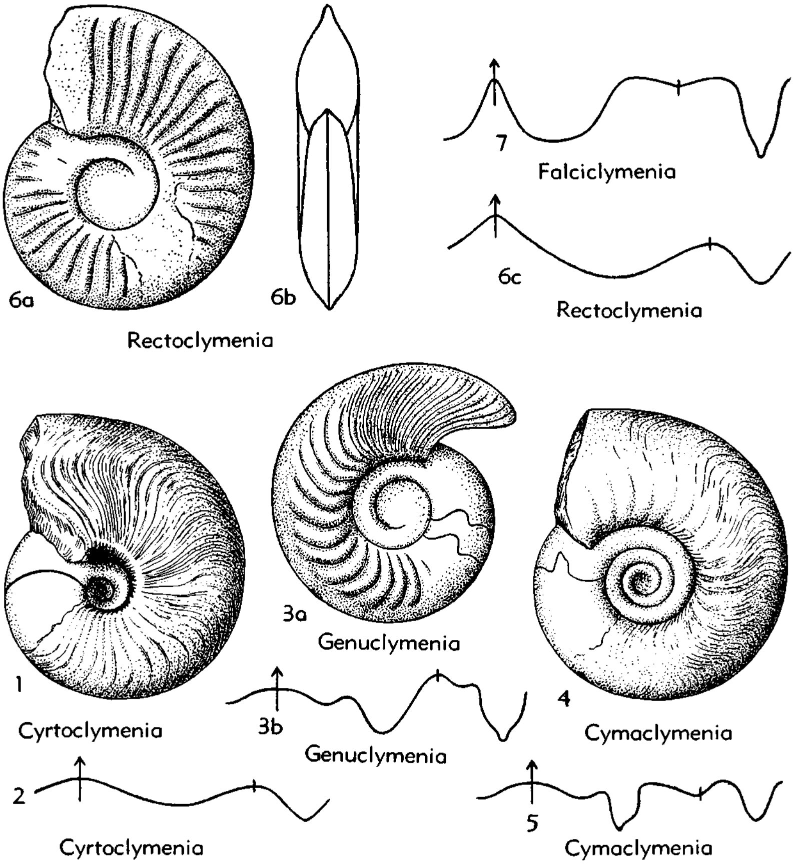


Fig. 43. Cyrtoclymeniidae, Rectoclymeniidae (p. L44-L45).

Gümbel, 1863] [**Planulites striatus* Münster, 1832] [=*Postclymenia* H. Schmidt, 1924; *Striatoclymenia* Matern, 1931 *(nom. nud.)*]. Like *Genuclymenia* but with pointed, asymmetrical lateral lobe and deep, pointed umbilical lobe, divided by umbilical seam. Smooth or ribbed. *U.Dev. (Platyclymenia z.-Wocklumeria z.),* Eu.-N.Afr.——Fig. 43,*4*. *C. camerata* Schindewolf, *Clymenia* z., Ger.; ×1.3 (113).——Fig. 43,*5*. **C. striata* (Münster), *Clymenia* z., Ger.; suture at maturity, enlarged (114).

Family RECTOCLYMENIIDAE Schindewolf, 1923

Shell thinly subdiscoidal, narrowly or rather widely umbilicate, increasing rapidly in height, with high whorl section and more or less fastigate venter. Growth lines with low dorsolateral and ventrolateral salients and shallow lateral sinus, approximately rectilinear. Ribs likewise nearly straight. Suture simple, with lateral and dorsal lobes only, which may be supplemented by an umbilical lobe. *U.Dev.(Platyclymenia z.).*

Rectoclymenia Wedekind, 1908 [**R. roemeri;* SD Wdkd., 1914]. Suture with a shallow, very broad lateral lobe and dorsal lobe only. *U.Dev.(Platyclymenia z.),* Eu.——Fig. 43,*6*. **R. roemeri,* Ger.; *6a,b,* ×1; *6c,* suture at maturity, enlarged (99).

Falciclymenia Schindewolf, 1923 [**Goniatites falcifer* Münster, 1840]. Suture with moderately deep lateral lobe, narrowed by newly added umbilical lobe. *U.Dev.(Platyclymenia z.),* Eu.-N.Am.——Fig. 43,*7*. **F. falcifera* (Münster), Ger.; suture at maturity, enlarged (114).——Fig. 44. *F. bowsheri,* N.Mex.; *A,B,* ×0.6; *C,* ×0.9 (Miller & Collinson).

Superfamily PARAWOCKLUMERIACEAE Schindewolf, 1937

[*nom. transl.* Schind., 1955 (*ex* Parawocklumeridae Schind., 1937)]

Ventral as well as dorsal lobe developed in early ontogenetic stages only, replaced

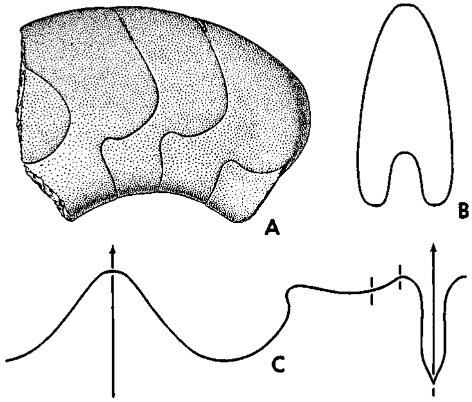


Fig. 44. ***Falciclymenia bowsheri*** Miller & Collinson, U.Dev., USA(N.Mex.); *A,B,* ×1; *C,* enlarged.

by saddles during ontogeny. Septal necks originally long cylindrical, in more advanced forms short, not forming a continuous tube. Small but autonomous group, for the present involving one family only. *U.Dev. (Wocklumeria z.).*

Family PARAWOCKLUMERIIDAE Schindewolf, 1937

[*nom. correct.* Schind., 1949 (*pro* Parawocklumeridae Schind., 1937)]

Shell in earlier forms subdiscoidal, widely umbilicate, later subglobose, narrowly umbilicate with depressed whorls, invariably with triangular coiling. Growth lines originally with lateral and hyponomic sinus, in derived forms nearly rectilinear. Without marked ribs. *U.Dev.(Wocklumeria z.).*

Kamptoclymenia Schindewolf, 1937 [**K. endogona*]. Shell subdiscoidal, widely umbilicate, in youth coiled triangularly or quadrangularly, at maturity with normal spiral or triangular coiling. Ventral and dorsal lobe each divided by a rising saddle, no umbilical lobes. *U.Dev.(Wocklumeria z.),* Eu.——Fig. 45,*1*. **K. endogona,* Ger.; *1a,* reduced; *1b,c,* development of suture, enlarged (113).——Fig. 45,*2*. *K. trigona* Schind., Ger.; reduced (113).——Fig. 45,*3*. *K. trivaricata* Schind., Ger.; *3a,* reduced; *3b,* suture at maturity, enlarged (114).

Triaclymenia Schindewolf, 1937 [**T. triangularis*]. Shell with moderately wide umbilicus, triangularly coiled also in adult. Ventral and dorsal lobe each

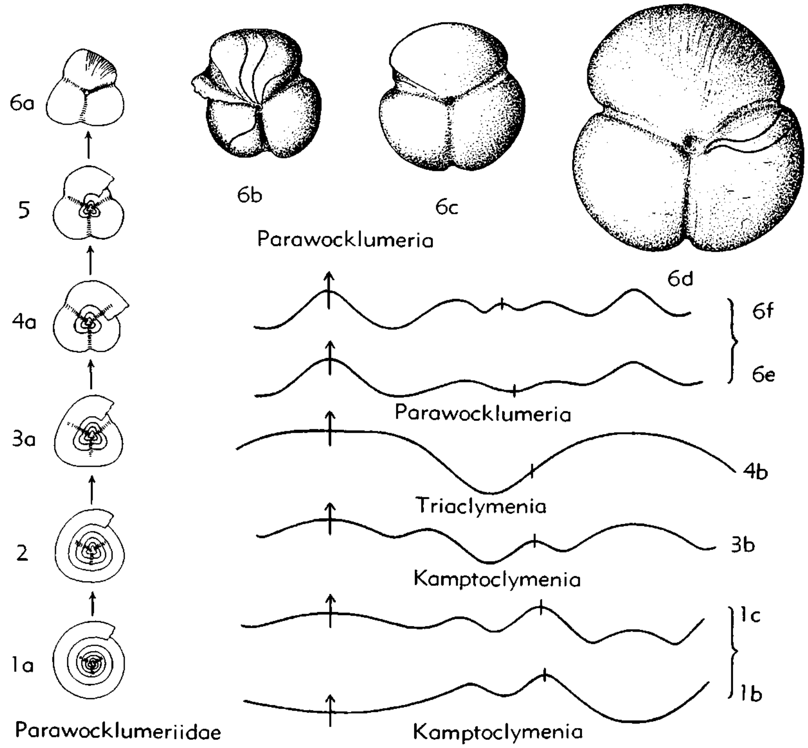


Fig. 45. Parawocklumeriidae (p. L46-L47).

definitely replaced by a broad saddle, no umbilical lobes. *U.Dev.(Wocklumeria z.),* Eu.——Fig. 45,*4.* **T. triangularis,* Ger.; *4a,* reduced; *4b,* suture at maturity, enlarged (114).

Parawocklumeria Schindewolf, 1926 [**Wocklumeria paradoxa* Wedekind, 1918]. Shell with moderately wide or narrow umbilicus, triangularly coiled also in adult and trilobate by deep constrictions. Suture with 3 umbilical lobes. *U.Dev. (Wocklumeria z.),* Eu.——Fig. 45,*5. P. distorta* (Tietze), Ger.; reduced (113).——Fig. 45,*6.* **P. paradoxa* (Wdkd.), Ger.; *6a,* reduced; *6b,c,* ×2; *6d,* ×1.3; *6e,f,* development of suture, enlarged (all 114).

Suborder GONIATITINA Hyatt, 1884

[*nom. correct.* Delepine, 1952 (*pro* Goniatitinae Hyatt, 1884)]

Basic suture of 8 lobes but primitive forms have fewer and advanced forms have ammonitic sutures with auxiliaries; in all but primitive representatives, siphuncle prochoanitic (46,50,52,78,100). *M.Dev.-U.Perm.*

Superfamily CHEILOCERATACEAE Frech, 1897

[*nom. transl.* Miller & Furnish, 1954 (*ex* Cheiloceratidae Frech, 1897)]

Sutures typically with 3 pairs of lobes of which the external lateral pair arises adventitiously (52,100). *M.Dev.-M.Perm.*

Family TORNOCERATIDAE Arthaber, 1911

[*nom. correct.* J.P.Smith, 1913 (*ex* Tornoceratea Arth., 1911)]

Conch subdiscoidal, growth lines biconvex. Sutures form 6 to 10 lobes, the ventral one undivided and those on lateral areas originating as subdivisions of external and internal lateral saddles (46,100). *M.Dev.-U.Dev.*

Tornoceras Hyatt, 1884 [**Gon. uniangularis* Conrad, 1842] [=*Parodiceras* Hyatt, 1884 *(Parodoceras, auctt.); Epitornoceras* Frech, 1902]. Sutures form 6 lobes, lateral ones rounded. Sculpture, umbilicus, and shape of sutures variable (46,100). *M.Dev.-U.Dev.*

T. (Tornoceras). Closed umbilicus and moderate sutural flexures. *M.Dev.-U.Dev.;* widespread N. Am.-Eurasia-N.Afr.-W.Austral.——Fig. 46; 47*B.* **T. (T.) uniangulare,* U.Dev., N.Y.; 46, ×1; 47*B,* ×2.5 (107).——Fig. 47*A. T. (T.) discoideum* (Hall), M.Dev., N.Y.; ×1.3 (12).——Fig. 48. *T. (T.) crebriseptum* Raymond, U.Dev., Mont.; *A-D,* enlarged (110).

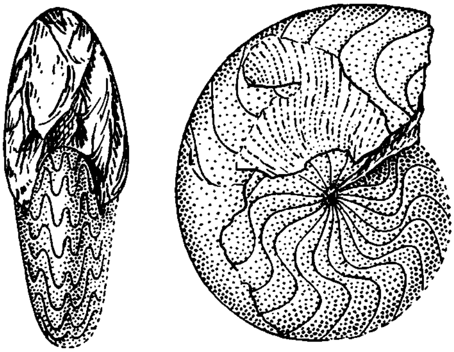


Fig. 46. *Tornoceras uniangulare* (Conrad), U.Dev., N.Y.; ×1 (110).

T. (Aulatornoceras) Schindewolf, 1922 [**Gon. auris* Quenstedt, 1846]. Conch with ventrolateral grooves. *U.Dev.,* N.Am.-Eu.——Fig. 47*C.* **T. (A.) auris* (Quenst.), U.Dev., Ger.; ×5 (110).——Figs. 49; 50. *T. (A.) bicostatum* (Hall), U.Dev., N.Y.; 49, enlarged; 50, ×3 (12).

T. (Protornoceras) Dybczyński, 1913 [**P. polonicum*] [=*Pernoceras* Schindewolf, 1922]. Umbilicus open. Sutures with little relief. *M.Dev.-U.Dev.,* Eu.

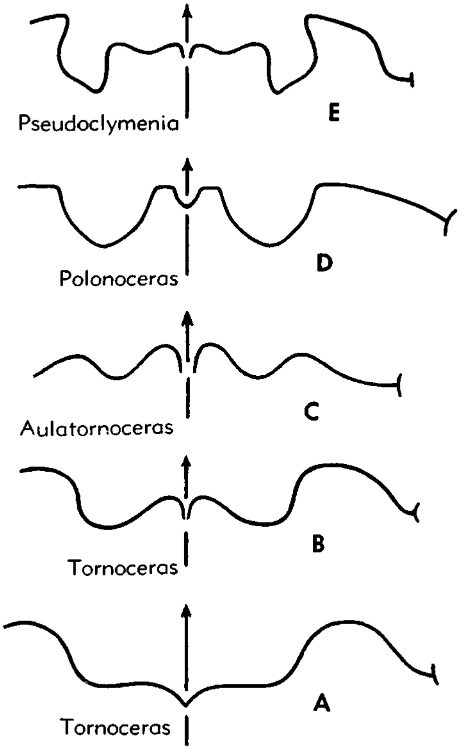


Fig. 47. Sutures of 3 subgenera of *Tornoceras (A-D),* and *Pseudoclymenia (E)* (110).

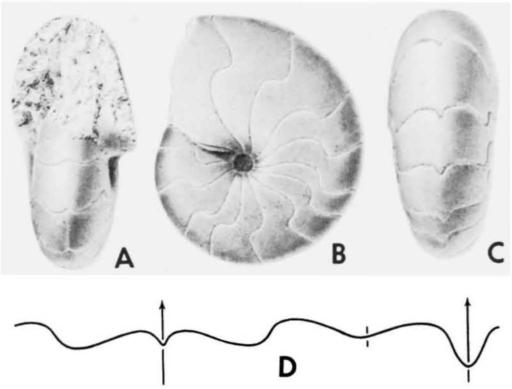
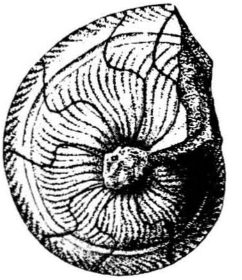


FIG. 48. *Tornoceras (Tornoceras) crebriseptum* RAYMOND, U.Dev., Mont.; *A-D*, enlarged (110).



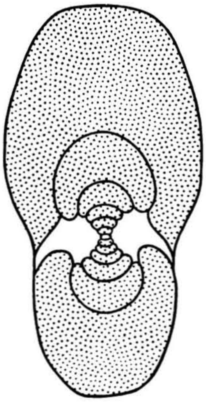


FIG. 49. *Tornoceras (Aulatornoceras) bicostatum* (HALL), U.Dev., N.Y., enlarged (12).

FIG. 50. Cross section of *Tornoceras (Aulatornoceras) bicostatum* (HALL), U.Dev., N.Y.; ×3 (12).

T. (Polonoceras) DYBCZYŃSKI, 1913 [**P. planum*]. Conch angular ventrolaterally. Sutures form prominent ventrolateral saddles. *U.Dev.*, Eu.——FIG. 47*D*. **T. (P.) planum*, U.Dev., Pol.; ×2 (105).

Pseudoclymenia FRECH, 1897 [**Gon. sandbergeri* GÜMBEL, 1862 (*non* FOORD & CRICK, 1897)]. Like *Tornoceras* but characteristically narrower conch and wider umbilicus (100). *U.Dev.*, Eu.-N.Afr.-W. Austral.——FIG. 47*E*. **P. sandbergeri* (GÜMBEL), Ger.; ×1.3.

Lobotornoceras SCHINDEWOLF, 1936 [**Gon. ausavensis* STEININGER, 1855]. Like *Tornoceras* but internal sutures form additional pair of lobes (46). *U.Dev.*, Eu.

Posttornoceras WEDEKIND, 1910 [**P. balvei*]. Like *Sporadoceras* but biconvex growth lines (100). *U.Dev.*, Ger.-?Pol.

Family CHEILOCERATIDAE Frech, 1897

Sutures form 4 to 12 lobes, ventral one undivided and those of lateral areas originating as subdivisions of external and internal lateral saddles (70,100). *U.Dev.-M.Perm.*

Subfamily CHEILOCERATINAE Frech, 1897

[*ex* Cheiloceratidae]

Sutures consist of 6 to 10 lobes, of which 5 (including umbilical) are external. Growth lines convex, forming lateral salients. *U.Dev.*

Cheiloceras FRECH, 1897 [**Gon. subpartitus* MÜNSTER, 1839] [=*Eucheiloceras* SCHMIDT, 1921; *Cheilocerotes* STRAND, 1929]. Conch subglobular to thickly lenticular; umbilicus closed. Lateral and dorsal lobes of sutures variable (45,97,100). *U. Dev.*

C. (Cheiloceras). Suture with shallow lateral and flat undivided dorsal lobes (100). *U.Dev.*, Eurasia-N.Afr.-W.Austral.——FIG. 51. **C. (C.) subpartitum* (MÜNSTER), U.Dev., Ger.; ×1 (100).——FIG. 25*C*. *C. (C.)* sp., U.Dev., Ger.; enlarged (73).

FIG. 51. *Cheiloceras subpartitum* (MÜNSTER), U. Dev., Ger.; ×1 (100).

C. (Torleyoceras) WEDEKIND, 1918 [**Gon. retrorsus curvispina* SANDB.-S., 1851] [=*Centroceras* WDKD., 1908 (*non* HYATT, 1884); *Staffites* WDKD., 1918; *Centroceratos* STRAND, 1929]. Sutures with deep lateral lobes and more or less trifid dorsal lobe (100). *U.Dev.*, Eu.

C. (Dyscheiloceras) SCHMIDT, 1921 [**C. (D.) biesenbergense*]. Conch subdiscoidal; dorsal lobe of sutures bifid (45). *U.Dev.*, Ger.

Dimeroceras HYATT, 1884 [**Gon. mamillifer* SANDB.-S., 1850]. Like *Cheiloceras* but suture has large lateral lobe and umbilical lobe outside umbilicus (100). *U.Dev.*, Eurasia-N.Afr.-W.Austral.

Heminautilinus HYATT, 1884 [**Gon. hybridus* MÜNSTER, 1832]. Poorly known. May be senior synonym of *Cheiloceras* (46,73). *U.Dev.*, Ger.

Subfamily RAYMONDICERATINAE Miller & Furnish, nov.

Sutures have 4 distinct lobes; growth lines convex. *U.Dev.*

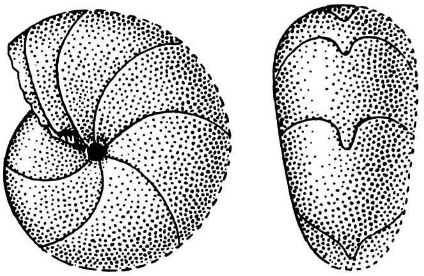


FIG. 52. *Raymondiceras simplex* (RAYMOND), U. Dev., Mont.; ×2 (112).

Raymondiceras SCHINDEWOLF, 1934 [**Prolobites simplex* RAYMOND, 1909]. Conch subglobular with small closed umbilici. Sutures have incipient lobe in broad 1st lateral saddle (46). *U.Dev.,* Mont.——FIG. 25*B;* 52. **R. simplex* (RAYMOND); 25*B,* enlarged; 52, ×2 (112).

Subfamily SPORADOCERATINAE Miller & Furnish, nov.

Sutures with 10 to 12 lobes, of which 3 (excluding umbilical) are internal (70,100). *U.Dev.*

Sporadoceras HYATT, 1884[**Am. muensteri* VON BUCH, 1832] [=*Cryptoclymenia, Maeneceras* HYATT, 1884]. Conch subglobular to discoidal, umbilicus small, closed. Sutures with lobes next to ventral lobe formed adventitiously in 1st lateral saddles (46,70,100). *U.Dev.,* Eurasia-N.Afr.-W. Austral.-E.USA.——FIG. 53. **S. muensteri* (BUCH), Ger.; ×1 (68).——FIG. 26*A. S. biferum* (PHILLIPS), Ger.; ×1 (68).——FIG. 54. *S. milleri* (FLOWER & CASTER), Pa.; ×1.5 (110).

Discoclymenia HYATT, 1884 [**Gon. cucullatus* VON BUCH, 1839] [=*Wedekindoceras* SCHINDEWOLF, 1923]. Like *Sporadoceras* but suture with additional adventitious lobes in 1st lateral saddles (70). *U.Dev.,* Eu.-N.Afr.

Praeglyphioceras WEDEKIND, 1908 [**Sporadoceras pseudosphaericum* FRECH, 1902]. Like *Sporadoceras* but lobes of sutures next to ventral lobe develop by that lobe becoming trifid. Affinities uncertain (22). *U.Dev.,* Ger.

Subfamily IMITOCERATINAE Ruzhencev, 1950

[*nom. transl.* MILLER & FURNISH, herein (*ex* Imitoceratidae RUZHENCEV, 1950)]

Sutures with 8 distinct lobes. *U.Dev.-M. Perm.*

Imitoceras SCHINDEWOLF, 1923 [**Am. rotatorius* DE KONINCK, 1844] [=*Brancoceras* HYATT, 1884 (*non* STEINMANN, 1881); *Balvia* LANGE, 1929; *Neoaganides* PLUMMER & SCOTT, 1937; *Irinoceras* RUZHENCEV, 1947; *non Aganides* DE MONTFORT, 1808]. Conch globular to discoidal, with closed umbilici (48,70). *U.Dev.-M.Perm.;* widespread in Eurasia-N.Afr.-USA.——FIG. 55. **I. rotatorium* (KON.), L.Miss., Ind.; *A-C,* ×0.9; *D,* ×1.75.——FIG. 56. *I. grahamense* (PLUMMER-S.), U.Penn., Kans.; ×2 (110).

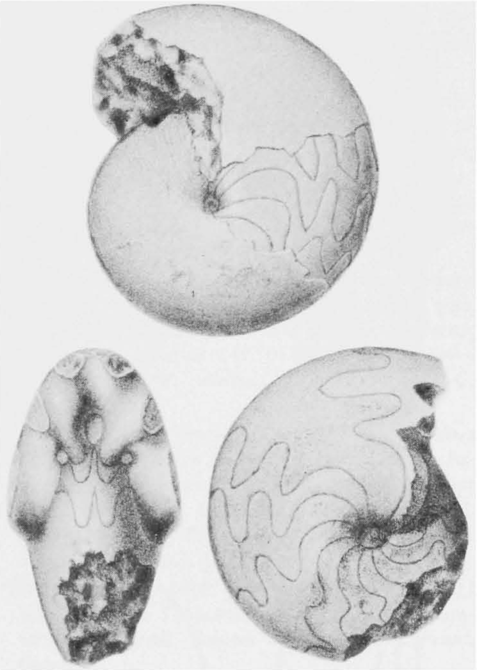


FIG. 53. *Sporadoceras muensteri* (VON BUCH), U. Dev., Ger.; ×1 (68).

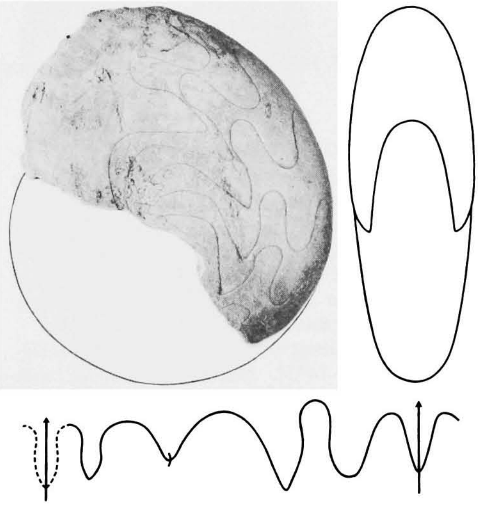


FIG. 54. *Sporadoceras milleri* (FLOWER & CASTER), U.Dev., Pa.; ×1.5 (110).

Prionoceras HYATT, 1884 (*non* BUCKMAN, 1920) [**Gon. divisus* MÜNSTER, 1843] [=?*Postprolobites*

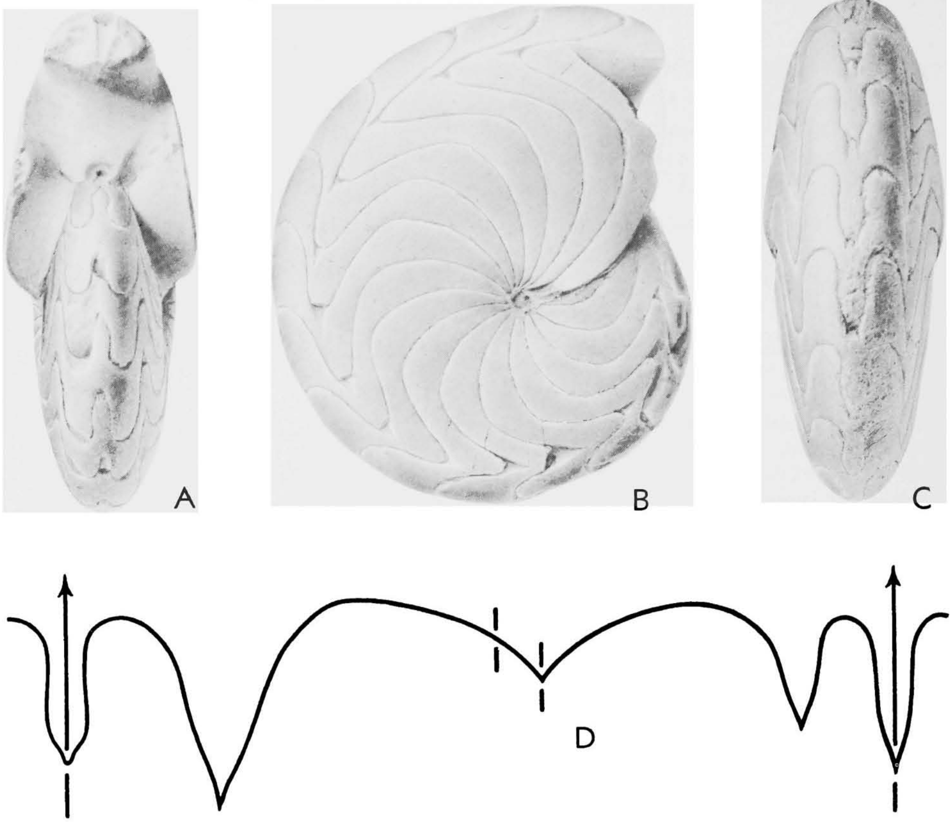


Fig. 55. *Imitoceras rotatorium* (De Koninck), L.Miss., Ind.; *A-C*, ×0.9; *D*, ×1.75 (110).

Wedekind, 1913]. Subglobular conch with constrictions that form lateral salient. Sutures poorly known. May be senior synonym of *Imitoceras* (48, 70). *U.Dev.-L.Carb.*, Ger.

Hunanites Chao, 1940 [**H. hsiehi*]. Globular conch with transverse ribs and closed umbilici. Sutures as in *Imitoceras* but ventral and lateral lobes serrate. *Perm.*, Arabia-China (Hunan).

Gattendorfia Schindewolf, 1920 [**Gon. subinvolutus* Münster, 1843]. Like *Imitoceras* but with open umbilici; umbilical lobe centers outside umbilical seam (44,48,70). *U.Dev.-L.Carb.(Miss.)*, widespread in Eurasia-N.Afr.-USA.

Paralytoceras Frech, 1902 [**Cly. crispa* Tietze, 1870]. Subdiscoidal conch with moderately large umbilicus. Sutures poorly known. May be senior synonym of *Gattendorfia* (22). *U.Dev.*, Ger.

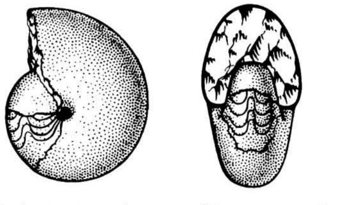


Fig. 56. *Imitoceras grahamense* (Plummer & Scott), U.Penn., Kans.; ×2 (60).

Kazakhstania Librovitch, 1940 [**Gattendorfia (K.) karagandaensis*]. Like *Gattendorfia* but with large umbilici (44,53). *L.Carb.(Miss.)*, Kazakhstan-Mich.

Superfamily AGATHICERATACEAE Arthaber, 1911

[*nom. transl.* Miller & Furnish, 1954 (*ex* Agathiceratidae Arthaber, 1911)]

Subdiscoidal to globular conchs with variable umbilici and sutures that are goniatitic to ammonitic. In primitive representatives sutures have trifid lateral lobe, which gives rise to 3 (or 4) independent lobes in advanced forms. *L.Penn.-M.Perm.*

Family AGATHICERATIDAE Arthaber, 1911

Conch subdiscoidal to globular, umbilicus small, test prominently longitudinally lirate. Sutures goniatitic (30,50). *L.Penn.-M.Perm.*

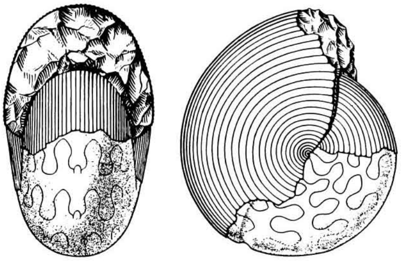


FIG. 57. *Agathiceras suessi* GEMMELLARO, M.Perm., Sicily; ×2 (24).

Agathiceras GEMMELLARO, 1887 [**A. suessi*] [=*Gaetanoceras* RUZHENCEV, 1938; *Paragathiceras* RUZH., 1950]. Suture forms 3 subequal lateral lobes but a single dorsolateral lobe; external lobes spatulate, internal ones V-shaped. Siphuncle retrochoanitic with long septal necks (54,65). *L.Penn.-M.Perm.*, widespread, locally very abundant.——FIG. 57. **A. suessi,* M.Perm., Sicily; ×2 (110).——FIG. 11*A-E*. *A. uralicum* KARPINSKY, M.Perm., Urals; enlarged.——FIG. 58. *A. frechi* BÖSE, U. Penn., Tex.; ×2 (110).

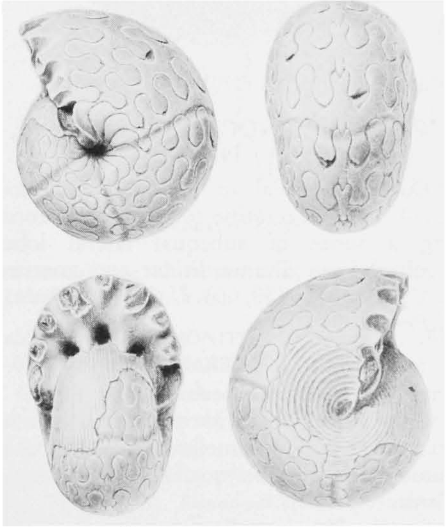


FIG. 58. *Agathiceras frechi* BÖSE, U.Penn., Tex.; ×2 (54).

Proshumardites RAUSER, 1928 [**P. karpinskii*]. Like *Agathiceras* but sutures more primitive (15,65). *U.Carb.,* M.Asia-Urals-Sp.-N.Afr.

Family SHUMARDITIDAE Plummer & Scott, 1937

Conch subglobular to globular, with moderately small to large umbilicus and generally advanced goniatitic sutures in which external and internal lateral lobes and dorsal lobe are trifid. Gradational with and ancestral to Popanoceratidae and Perrinitidae (49,60,65). *U.Penn.(U.Carb.).*

Shumardites SMITH, 1903 [**S. simondsi*]. Umbilicus moderately large. Divisions of external lateral lobe of suture subequal, umbilical lobe relatively simple, dorsolateral lobe asymmetrical (49,65). *U.Carb.(U.Penn.),* Tex.-N.Mex.-Urals.——FIG. 59*F*. **S. simondsi*, U.Penn., Tex.; ×2. [*Shumardites*=*Postaktubites* RUZHENCEV, 1955.]

Vidrioceras BÖSE, 1919 [**V. uddeni*]. Like *Shumardites* but with smaller umbilicus. Sutures with broad trifid umbilical lobe and divisions of dorsolateral lobe subequal (49,50). *U.Penn.,* Tex.——FIG. 59*A-D*. **V. uddeni,* U.Penn., Tex.; *A-C,* ×1.25; *D,* ×2.

Subshumardites SCHINDEWOLF, 1939 [**Shumardites fornicatus* PLUMMER & SCOTT, 1937] [=*Parashumardites* RUZHENCEV, 1939]. Like *Shumardites* but suture with broad trifid umbilical lobe (65). *U. Carb.(U.Penn.),* Tex.-Okla.-USSR.——FIG. 59*E*. *S. eurinus* (RUZH.), U. Carb., Urals; ×2 (65).

Pericleites RENZ, 1910 [**Paralegoceras (Pericleites) atticum*]. Like *Shumardites* but with smaller umbilicus; internal sutures unknown. *?U.Penn.,* Greece.

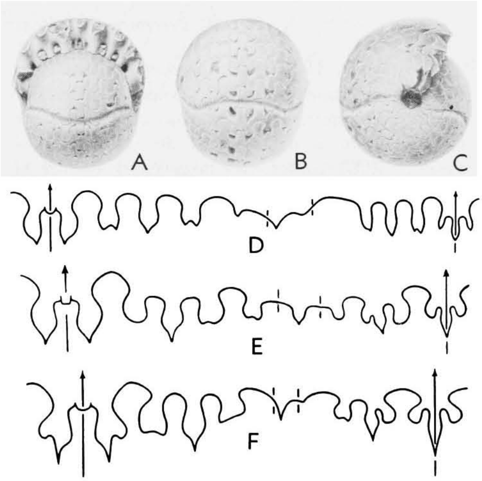


FIG. 59. *Vidrioceras (A-D), Subshumardites (E),* and *Shumardites (F),* U.Penn. (110, 65).

Family PERRINITIDAE Miller & Furnish, 1940

Conch thickly subdiscoidal to subglobular and involute, umbilicus small. Sutures ammonitic with distinctly V-shaped lateral lobes of which there are 5 pairs both externally and internally. Evolved directly from Shumarditidae (50). *L.Perm.-M.Perm.*

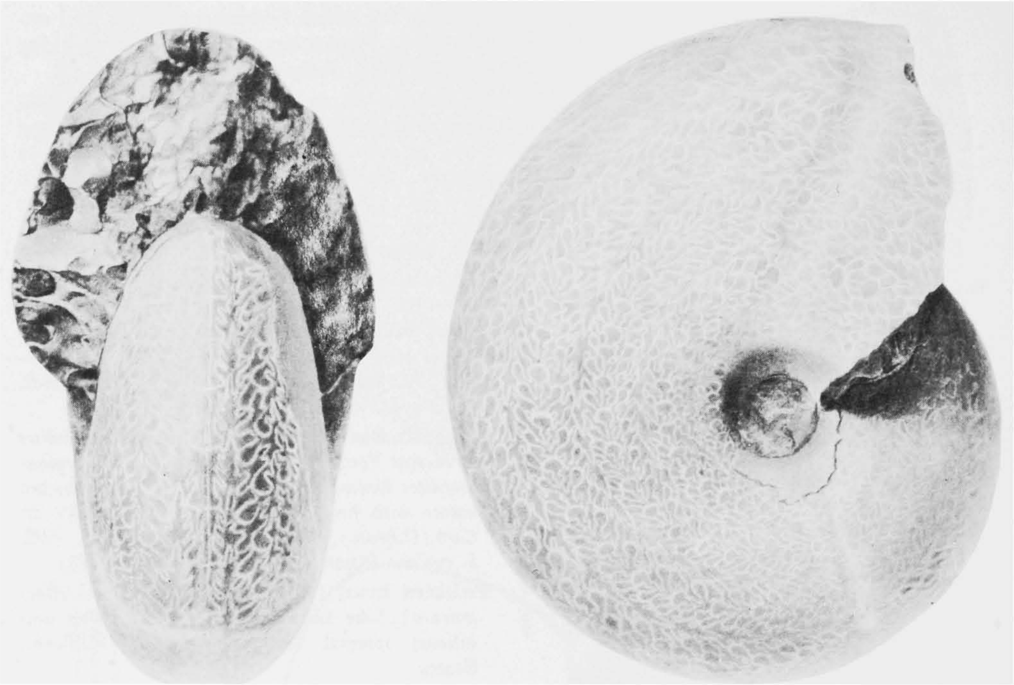


FIG. 60. *Perrinites hilli* (SMITH), M.Perm., Tex.; ×1.8 (110).

Perrinites BÖSE, 1919 [**Waagenoceras hilli* SMITH, 1903] [=*Paraperrinites* TOUMANSKY, 1939]. External and internal sutures prominently digitate. Conch attains a diameter of 30 cm. (50). *M. Perm.,* W.USA.-Mex.-Colombia-Timor-Crimea-M. Asia.——FIGS. *7C; 8A-F;* 60; *61B.* **P. hilli* (SMITH), M.Perm., Tex.; *7C,* ×1.3; *8A-F,* enlarged; 60, ×1.8; *61B,* ×2.

Properrinites ELIAS, 1938 [**Perrinites boesei* PLUMMER & SCOTT, 1937]. Like *Perrinites* but sutures less strongly digitate. Gradational with and intermediate between *Shumardites* and *Perrinites. L. Perm.,* SW.USA.-M.Asia-Timor.——FIG. *61A.* **P. boesei* (PLUMMER-S.), L.Perm., Tex.; ×10. [*Properrinites*=*Metaperrinites* RUZHENCEV, 1955.]

Superfamily CYCLOLOBACEAE Zittel, 1895

[*nom. transl.* MILLER & FURNISH, 1954 (*ex* Cyclolobidae ZITTEL, 1895)]

Thickly discoidal to globular conchs, typically with small umbilici and ceratitic sutures that possess auxiliary lobes. Primitive representatives have few auxiliary lobes, but advanced forms have many and have ammonitic sutures. *U.Carb.(M.Penn.)-U. Perm.*

Family POPANOCERATIDAE Hyatt, 1900

Conch discoidal to globular, umbilicus small. Sutures ceratitic to ammonitic, forming a series of subequal lateral lobes. Evolved from Shumarditidae and ancestral to Cyclolobidae (50, 66). *U.Carb.(M.Penn.)-U.Perm.*

Subfamily POPANOCERATINAE Hyatt, 1900

[*nom. transl.* (*ex* Popanoceratidae HYATT, 1900)]

Conch discoidal, with prominent sinuous transverse growth lamellae. Lateral lobes of sutures tend to be quadrifid. *L.Perm.-M. Perm.*

Popanoceras HYATT, 1884 [**Gon. sobolewskyanus* DE VERNEUIL, 1845] [=*Gemmellaroceras* TOUMANSKY, 1937 (*non* HYATT, 1900); *Tauroceras* TOUM., 1938; *Neopopanoceras* SCHINDEWOLF, 1939]. Lateral areas of conch bear series of depressions during adolescence. Prongs of ventral lobe of sutures large and multidigitate (50). *M.Perm.,* Urals-N. Zem.-Crimea-Alps-Sicily-Tunisia-M. Asia - Timor-Tex.——FIG. 62. *P. bowmani* (BÖSE), Tex.; *A-C,* ×1.5; *D,* ×4.——FIG. *2,8a,b. P. scrobiculatum* GEMMELLARO, Sicily, ×1 (24).

Propopanoceras TOUMANSKY, 1938 [**Popanoceras lahuseni* KARPINSKY, 1889] [=*Protopopanoceras* RUZHENCEV, 1938]. Like *Popanoceras* but prongs

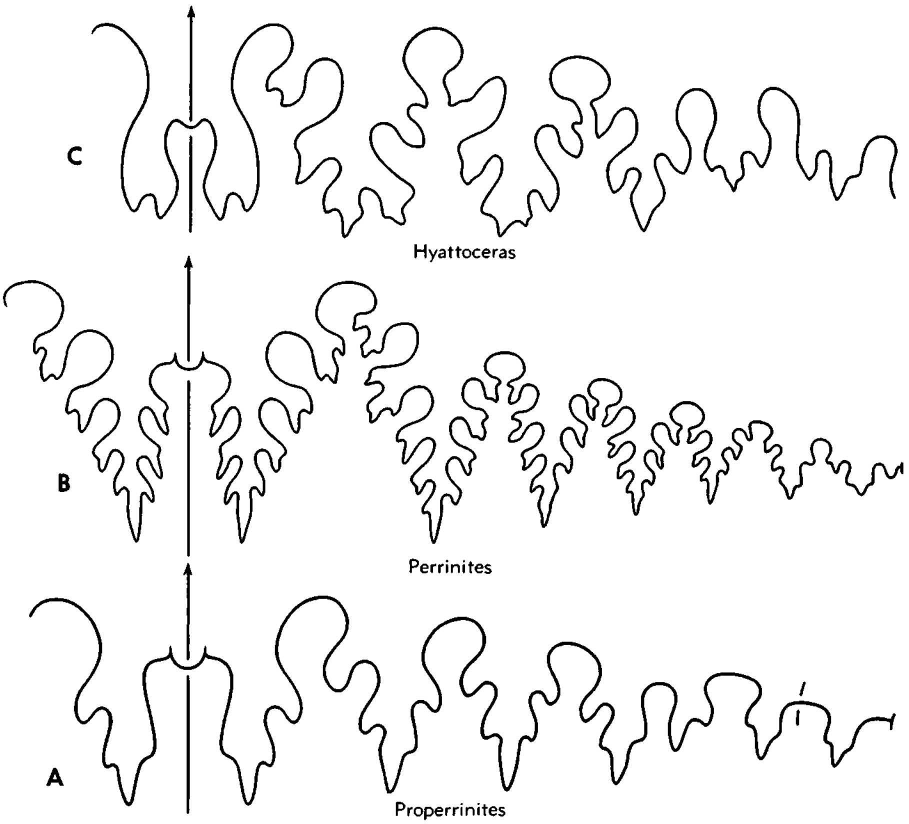


Fig. 61. Sutures of *Properrinites (A), Perrinites (B),* and *Hyattoceras (C),* Perm. (110).

of ventral lobe of sutures small and bifid (66). *L.Perm.-M.Perm.,* Urals.

Subfamily MARATHONITINAE Ruzhencev, 1938

[*ex* Marathonitidae]

Conch subglobular to globular. Lateral lobes of sutures tend to be trifid. *U.Carb. (M.Penn.)-U.Perm.*

Peritrochia Girty, 1908 [**P. erebus*] [=*Marathonites* Böse, 1919; *Pseudovidrioceras* Ruzhencev, 1936; *Prostacheoceras* Ruzh., 1937; *Kargalites* Ruzh., 1938; *Policeras* Toumansky, 1939; *Almites* Toum., 1941; *Martites* Toum., 1949; *Subkargalites, Neomarathonites* Ruzh., 1950; *Tabantalites* Ruzh., 1952]. Both external and internal sutures form 3 to 5 pairs of lateral lobes. Gradational with *Shumardites* and *Stacheoceras* (30,50,65). *U.Carb.-(M.Penn.)-M.Perm.,* W.USA-Chiapas-Sicily-Crimea-Urals-M.Asia-Timor.——Fig. 64. *P. ganti* (Smith), U.Penn., Tex.; ×1.

Stacheoceras Gemmellaro, 1887 [**S. mediterraneum*] [=*Waagenia* Krotow, 1885 (*non* Kriechbaumer, 1874, *et auctt.*); *Waagenina* Krotow, 1888, *Neostacheoceras* Schindewolf, 1931; *Martoceras, Pamirites* Toumansky, 1938]. Like *Peritrochia* but both external and internal sutures form 5 to 10 pairs of lateral lobes (50). *M.Perm.-U. Perm.,* Sicily-Croatia-Tunisia-Crimea-Urals-Pamirs-Armenia-Salt R.-Himal.-Timor - Japan - SW.USA-Coah.——Fig. 7*B;* 64. *S. toumanskyae* Miller & Furnish, M.Perm., Coah.; 7*B,* ×3; 64, ×1.

Subfamily HYATTOCERATINAE Miller & Furnish, nov.

Umbilicus closed; sutures ammonitic. *M. Perm.*

Hyattoceras Gemmellaro, 1887 [**H. geinitzi*] [=*Abichia* Gemm., 1887; *Prohyattoceras* Oyens, 1938 *(nom. nud.)*]. Superficially resembles perrinitids, but subdivisions of ventral lobe of sutures small and bifid (24). *M.Perm.,* Sicily-Timor.——Fig. 2,7*a,b;* 61*C.* **H. geinitzi,* Sicily; 2,7*a,b,* ×1.25; 61*C,* enlarged (24).——Fig. 2,2*a-c. H. abichi* Gemm., Sicily; ×1.25 (24). [*Hyattoceras*= *Demarezites* Ruzhencev, 1955.]

Family CYCLOLOBIDAE Zittel, 1895

Conch thickly subdiscoidal to subglobular,

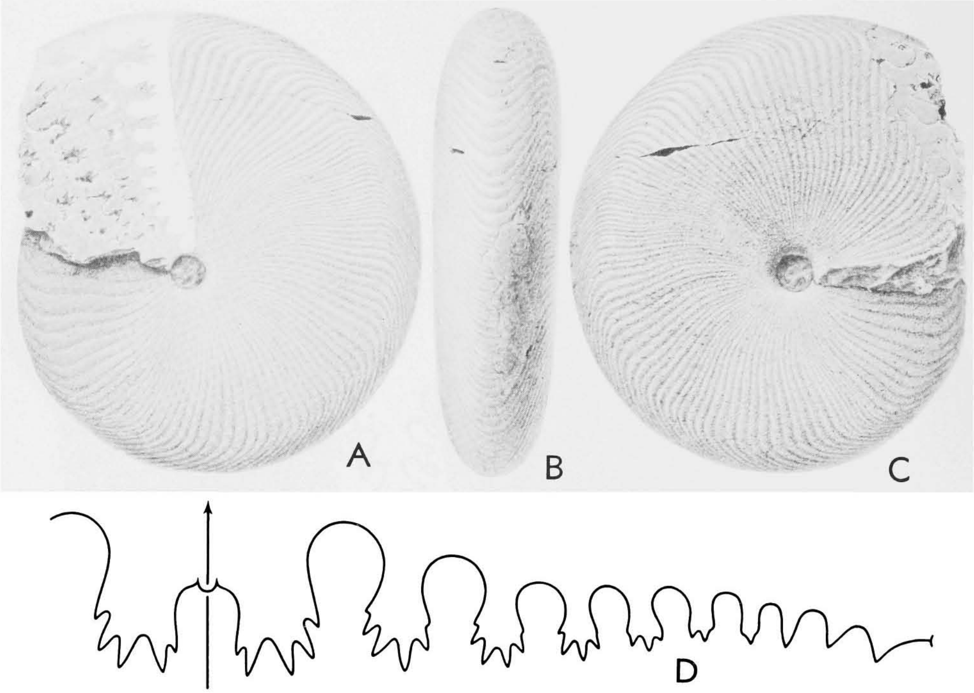


FIG. 62. *Popanoceras bowmani* (BÖSE), M.Perm., Tex.; *A-C*, ×1.5; *D*, ×4 (110).

umbilicus open but small. Sutures ammonitic, with numerous lobes that have subparallel flanks. Evolved from Marathonitinae (50). *M.Perm.-U.Perm.*

Cyclolobus WAAGEN, 1879 [**C. oldhami*] [=*Krafftoceras* DIENER, 1903; *Godthaabites* FREBOLD, 1932]. Conch thickly subdiscoidal. Both external and internal suture arcuate, with 10 to 15 pairs of lateral lobes and 1st lateral saddle divided (93,95). *U.Perm.*, SaltR.-Himal.-S.China-Madag.-Greenl.——FIG. 65. **C. oldhami*, SaltR.; *A,B*, ×0.9; *C*, ×1.7 (95).

Timorites HANIEL, 1915 [**T. curvicostatus*] [=*Hanieloceras* MILLER, 1933; *Wanneroceras* TOUMANSKY, 1937 *(nom. nud.)*]. Like *Cyclolobus* but sutures form only 8 to 10 pairs of lateral lobes and conch bears relatively prominent ribs (47, 50). *M.Perm.*, Timor-Japan-E.Sib.-Tex.-Coah.——FIG. 66. **T. curvicostatus*, Timor; *A,B*, ×0.5; *C*, ×1 (96).

Waagenoceras GEMMELLARO, 1887 [**W. mojsisovicsi*]. Conch subglobular. Both external and internal sutures more or less arcuate and form 4 to 8 pairs of lateral lobes (47,50). *M.Perm.*, Sicily-Tex.-Coah.-Timor.-E.China.——FIGS. 2,*1a,b*; 67*A,B*. *W. guadalupense* GIRTY, Tex.; all ×1.——FIG. 67*C,D*. *W. dieneri* BÖSE, Tex.; ×1.7. [*Waagenoceras*=*Mexicoceras* RUZHENCEV, 1955.]

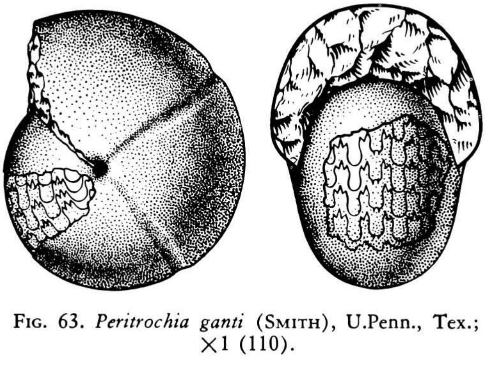


FIG. 63. *Peritrochia ganti* (SMITH), U.Penn., Tex.; ×1 (110).

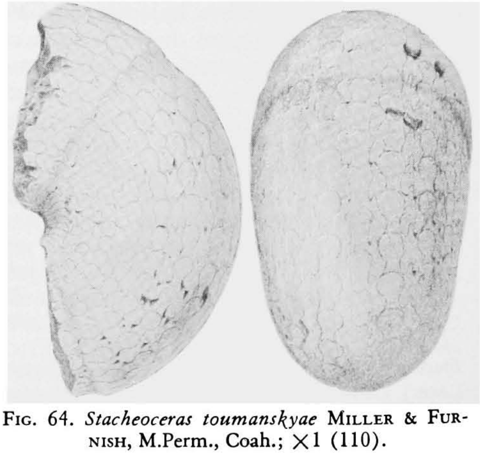


FIG. 64. *Stacheoceras toumanskyae* MILLER & FURNISH, M.Perm., Coah.; ×1 (110).

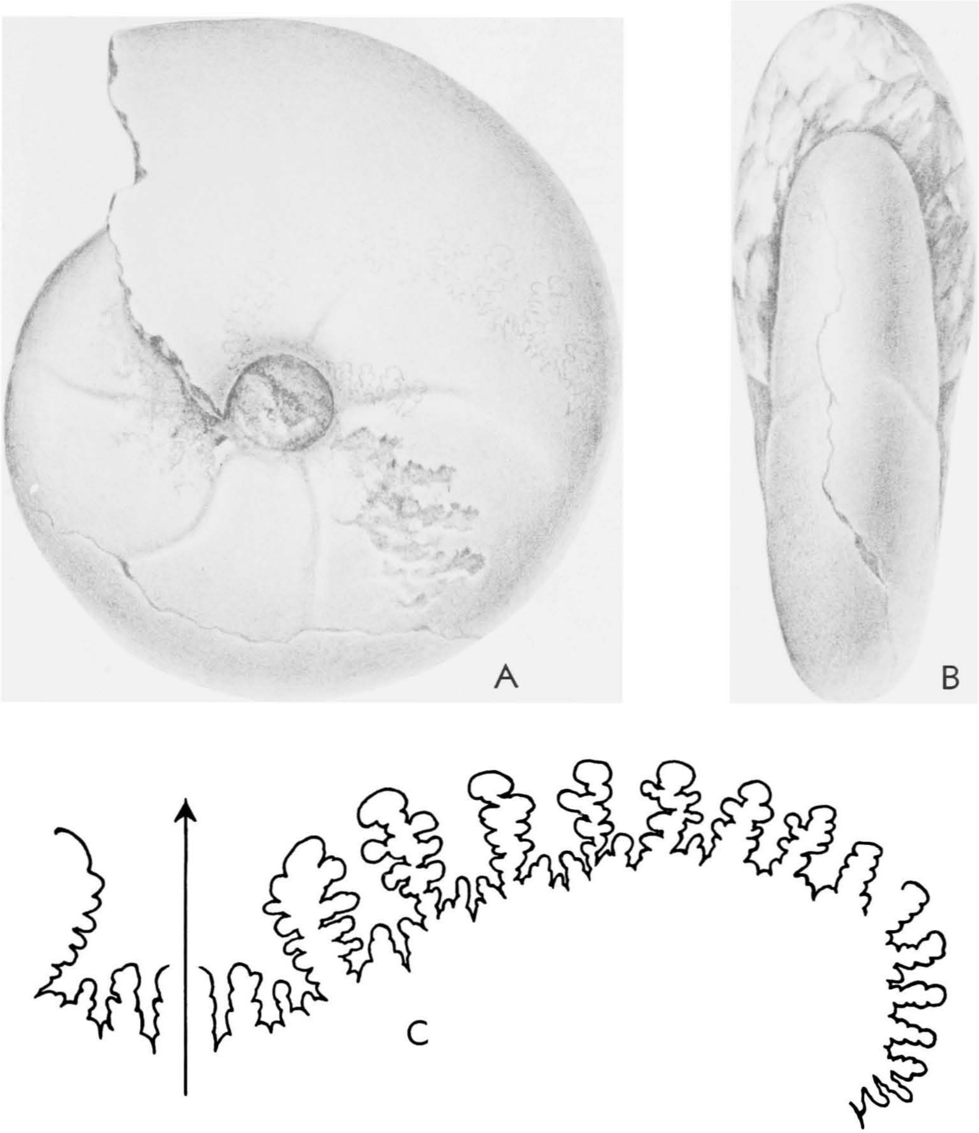


Fig. 65. *Cyclolobus oldhami* Waagen, U.Perm., SaltR.; *A,B*, ×0.9; *C*, ×1.7 (95).

Superfamily GONIATITACEAE de Haan, 1825

[*nom. transl.* Miller & Furnish, 1954 (*ex* Goniatitea de Haan, 1825)]

Thinly discoidal or lenticular to globular conchs with variable umbilici and sculpture. Sutures goniatitic, with ventral lobe prominently bifid and lateral lobe undivided. *L. Carb.(L.Miss.)-U.Perm.*

Family GONIATITIDAE de Haan, 1825

[*pro* Goniatitea]

Characteristically without prominent sculpture. Sutures form 8 lobes (4,22,44,55, 60,78). *L.Carb.(L.Miss.)-L.Perm.*

Subfamily GONIATITINAE de Haan, 1825

[*ex* Goniatitea]

Typical goniatites with small to moderate umbilici. Suture with narrow ventral lobe. *L.Carb.(L.Miss.)-M.Penn.*

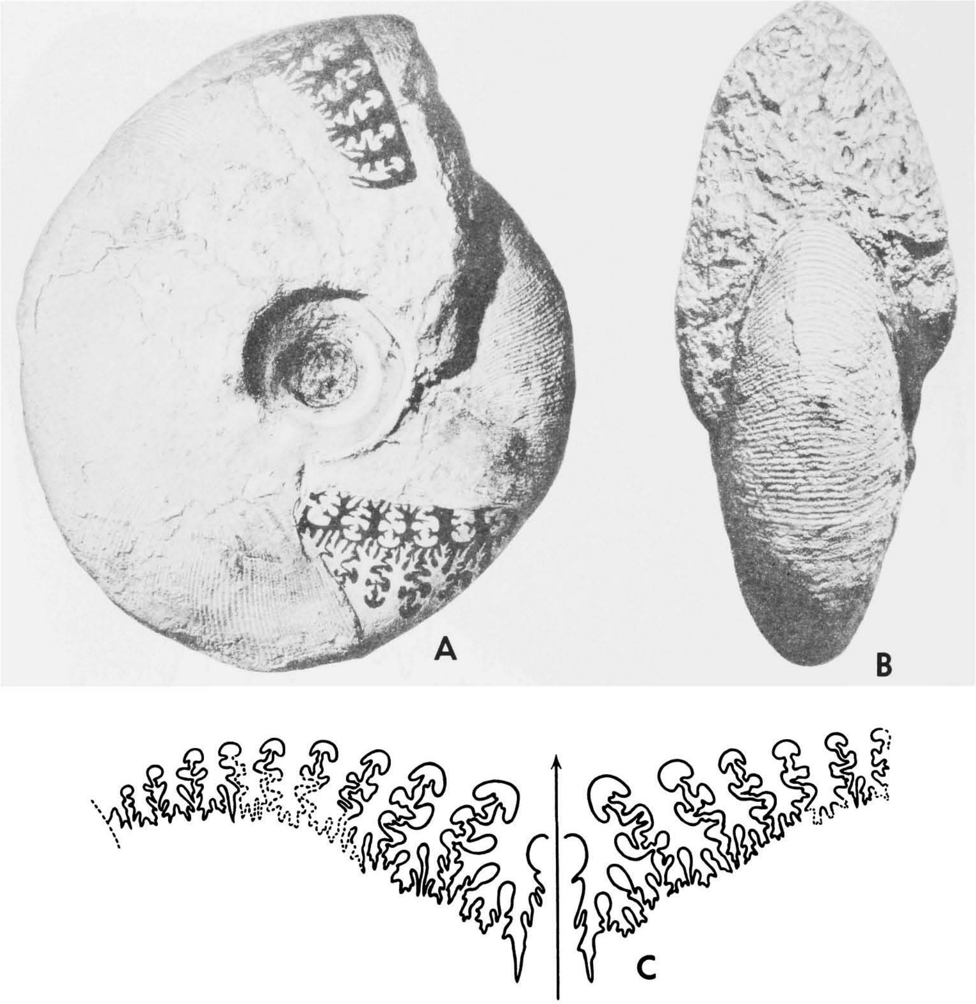


Fig. 66. *Timorites curvicostatus* Haniel, M.Perm., Timor; *A,B,* ×0.5; *C,* ×1 (96).

Goniatites de Haan, 1825 [**Conchyliolithus Nautilites sphaericus* Martin, 1809] [=*Glyphioceras* Hyatt, 1884; *Sphenoceras* Foord, 1903; *Paraglyphioceras* Brüning, 1923]. Conch globular, umbilicus small. First lateral saddle of suture subangular to angular (4,20,21). *L.Carb.(U.Miss.),* widespread in Eurasia-N.Afr.-N.Am.——Fig. 68. *Gon. choctawensis* Shumard, Tex.; *A-C,* ×2; *D,* ×4.

Nautellipsites Parkinson, 1822 [**Ellipsolites ovatus* Sowerby, 1813]. Poorly known. May be senior synonym of *Goniatites* or *Beyrichoceras* (4,16,21). *L.Carb.,* Ire.

Cravenoceras Bisat, 1928 [**Homoceras malhamense* Bisat, 1924]. Like *Goniatites* but 1st lateral saddles of sutures rounded (55,60). *L.Carb.(U.Miss.)-U.Carb.(L.Penn.),* locally abundant in Eurasia-N. Afr.-N.Am.——Fig. 69. *S. hesperium* Miller & Furnish, U.Miss., Nev.; ×2 (102). [*Cravenoceras* =*Richardsonites* Elias, 1956.]

Homoceras Hyatt, 1884 [**Gon. calyx* Phillips]. Poorly known; type immature (4). *L.Carb.,* Eng.

Homoceratoides Bisat, 1924 [**H. prereticulatum*]. Conch discoidal, with small umbilici and biconvex growth lines. Sutures of type species unknown (4). *L.Carb.,* Eurasia.

Reticuloceras Bisat, 1924 [**Gon. reticulatus* Phillips, 1836] [=*Verneuilites* Librovitch, 1939]. Conch subdiscoidal to lenticular with small umbilici and biconvex growth lines. Suture with small ventral lobe (4). *L.Carb.,* Eurasia.

Anthracoceras Frech, 1899 [**Nomismoceras (Anthracoceras) discus*]. Like *Reticuloceras* but suture with wider ventral lobe. Type poorly known. *L.Carb.(U.Miss.)-U.Carb.(M.Penn.),* Eurasia-?N.Afr.-?N.Am.-?S.Am.

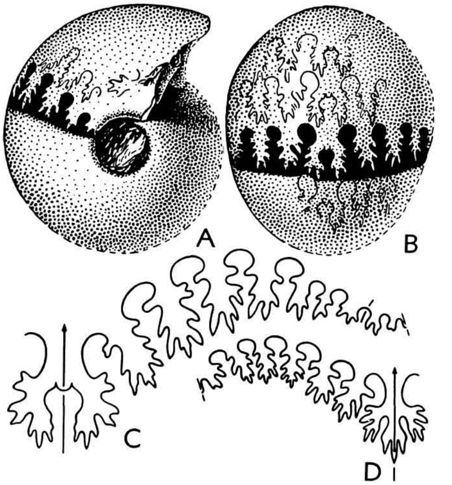


FIG. 67. *Waagenoceras,* M.Perm., Tex.; *A,B, W. guadalupense* GIRTY, ×1; *C,D, W. dieneri* BÖSE, ×1.7 (110).

Beyrichoceras FOORD, 1903 [**Gon. obtusus* PHILLIPS, 1836] [=*Cravenites* BISAT, 1950; *Cowdaleoceras* BISAT, 1952]. Conch thickly subdiscoidal with small umbilici. Ventral lobe of suture constricted distally (4,20,53). *L.Carb.(Miss.),* Eu.-N.Afr.-N.Am.——FIG. 70. *B. hornerae* MILLER, L.Miss., Mo.; *A-C,* ×0.4; *D,* ×1.

Muensteroceras HYATT, 1884 [**Gon. oweni parallela* HALL, 1860] [=*Eoglyphioceras* BRÜNING, 1923; *Beyrichoceratoides* BISAT, 1924; *Karakoramoceras* MILLER, 1931; *Bollandites, Bollandoceras* BISAT, 1952]. Conch discoidal to globular, with small to moderate umbilici. Ventral lobe of suture narrow and with parallel sides (6,15,44,48,53). *L. Carb.(Miss.),* N.Am.-Eurasia-N.Afr.-Austral.——FIG. 71. **M. parallelum* (HALL), L.Miss., Ind.; *A-C,* ×1.8; *D,* ×3.4.

Subfamily NEOGLYPHIOCERATINAE Plummer & Scott, 1937

[*ex* Neoglyphioceratidae]

Conch subdiscoidal, umbilicus small to

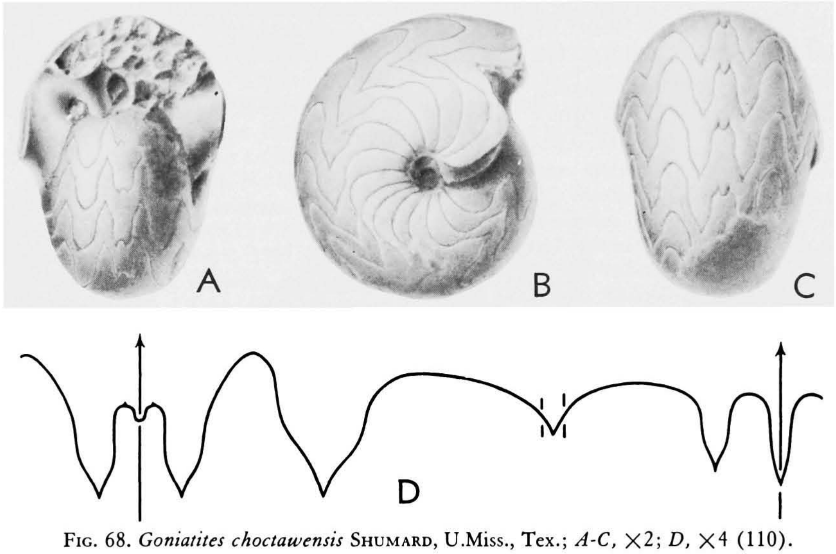


FIG. 68. *Goniatites choctawensis* SHUMARD, U.Miss., Tex.; *A-C,* ×2; *D,* ×4 (110).

FIG. 69. *Cravenoceras hesperium* MILLER & FURNISH, U.Miss., Nev.; ×2 (102).

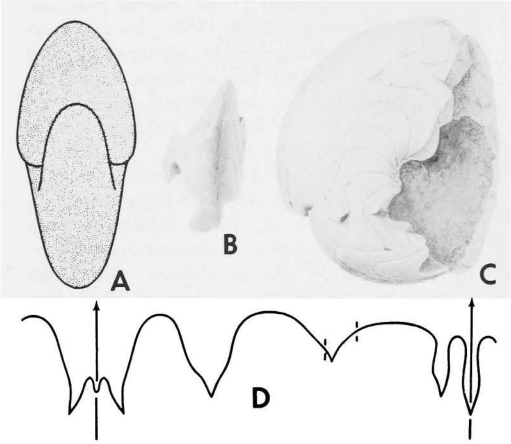


FIG. 70. *Beyrichoceras hornerae* MILLER, L.Miss., Mo.; *A-C*, ×0.4; *D*, ×1 (110).

moderately large, prominent longitudinal sculpture. Ventral lobe of suture broad (51). *L.Carb.(U.Miss.)*.

FIG. 72. *Lyrogoniatites newsomi georgiensis* MILLER & FURNISH, U.Miss., Ga.; ×1 (110).

Lyrogoniatites MILLER & FURNISH, 1940 [**L. newsomi georgiensis*] [=*Entogonoceras* PLUMMER & SCOTT, 1937 *(nom. nud.)*]. Umbilicus moderately large (51,60). *L.Carb.(U.Miss.)*, USA-Eng.-N.Afr.——FIG. 72. **L. newsomi georgiensis*, Ga.; ×1.

Neoglyphioceras BRÜNING, 1923 [**Gon. spiralis* PHILLIPS, 1841] [=*Lusitanoceras* PEREIRA DE SOUSA, 1924; *Paragoniatites* LIBROVITCH, 1938]. Umbilicus small (51). *L.Carb.(U.Miss.)*, N.Am.-Eurasia-N.Afr.——FIG. 73. *N. subcirculare* (MILLER), Ky.; *A,B*, ×2; *C*, enlarged.

Subfamily PERICYCLINAE Miller & Furnish, nov.

Conch subdiscoidal to globular; umbilicus moderate to large; prominent transverse sculpture; narrow ventral lobe (21,76). *L. Carb.(Miss.)*.

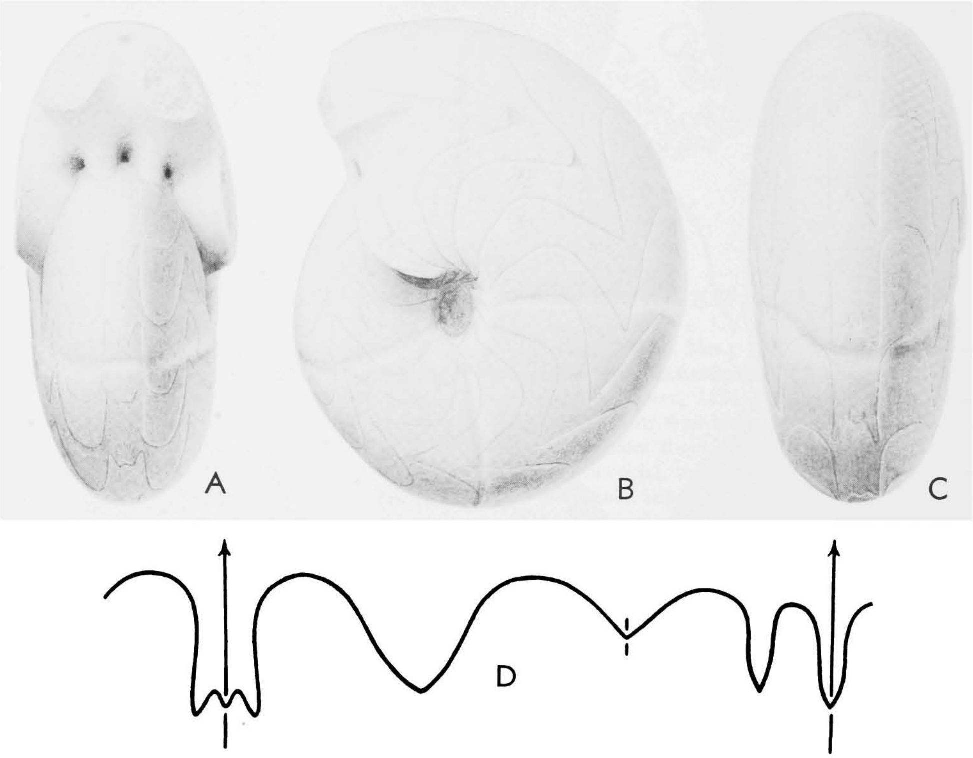


FIG. 71. *Muensteroceras parallelum* (HALL), L.Miss., Ind.; *A-C*, ×1.8; *D*, ×3.4 (110).

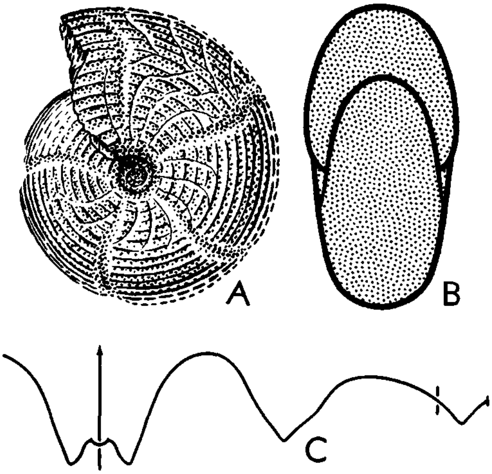


FIG. 73. *Neoglyphioceras subcirculare* (MILLER), U. Miss., Ky.; *A,B,* ×2; *C,* enlarged (110).

Pericyclus MOJSISOVICS, 1882 [**Gon. princeps* DE KONINCK, 1842]. May be junior synonym of *Ammonellipsites* (14,20,42,44,76). *L.Carb.(Miss.).*

P. (Pericyclus). Conch thickly subdiscoidal with wide umbilicus and prominent undivided ribs parallel to constrictions (14). *L.Carb.(L.Miss.),* locally abundant in Eurasia-N.Afr., rare in USA.——FIG. 74. **P. (P.) princeps* (KON.), L. Carb., Belg.; *A,B,* ×1; *C,* ×1.25 (14).

P. (Caenocyclus) SCHINDEWOLF, 1922 [**P. (C.) perisphinctoides*]. Conch discoidal, ribs divided; sutures unknown (76). *L.Carb.,* Ger.

P. (Fascipericyclus) TURNER, 1948 [**Gon. fasciculatus* M'COY, 1844] [=*Schizocyclus* SCHINDEWOLF, 1951]. Sutures with subangular first lateral saddles and low saddle dividing ventral lobe (76). *L.Carb.,* Eurasia.

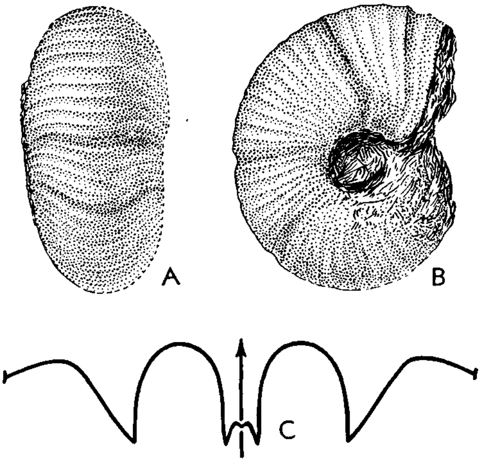


FIG. 74. *Pericyclus princeps* (DE KONINCK), L.Carb., Belg.; *A,B,* ×1; *C,* ×1.25 (14).

P. (Rotopericyclus) TURNER, 1948 [**P. rotuliformis* CRICK, 1899] [=*Hammatocyclus* SCHINDEWOLF, 1951]. Wide umbilicus with nodose margins (76). *L.Carb.,* Eu.

P. (Trapezocyclus) TURNER, 1948 [**P. trapezoidalis* CRICK, 1899]. Conch with fine longitudinal lirae (20). *L.Carb.,* Ire.

P. (Helicocyclus) SCHINDEWOLF, 1951 [**P. (H.) gracillimus*]. Conch discoidal, umbilicus very wide (76). *L.Carb.,* Eurasia.

P. (Stenocyclus) SCHINDEWOLF, 1951 [**P. (P.) carinatus* SCHIND., 1926]. Conch with ventral carina, narrow umbilicus, divided ribs. *L.Carb.,* Ger.

Ammonellipsites PARKINSON, 1822 [**A. funatus*] [=*Discus* KING, 1884 (*non* FITZINGER, 1833); *Trematodiscus* MEEK & WORTHEN, 1861 (*non* HAECKEL, 1860); *Trematoceras* HYATT, 1884 (*non* EICHWALD, 1851); *Coelonautilus* FOORD, 1889; *Streptodiscus* MILLER, 1892; *Kaypericyclus* TURNER, 1948; *Eurycyclus* SCHINDEWOLF, 1951]. Poorly known. May be senior synonym of *Pericyclus* (21, 76). *L.Carb.,* Ire.-?W.Eu.

Subfamily GIRTYOCERATINAE Wedekind, 1918

Conch discoidal to lenticular; umbilicus variable. Ventral lobe of sutures broad (51, 55). *L.Carb.(U.Miss.).*

Eumorphoceras GIRTY, 1909 [**E. bisulcatum*]. Conch thickly discoidal, venter flattened, umbilicus moderate, sculpture prominent, sinuous ribs and ventrolateral sulcus (55). *L.Carb.(U.Miss.),* W.USA-W.Eu.-?Morocco.——FIG. 75. **E. bisulcatum,* Tex.; *A-C,* ×3.5; *D,* ×7. [*Eumorphoceras*=*Edmooroceras* ELIAS, 1956.]

Girtyoceras WEDEKIND, 1918 [**Adelphoceras meslerianum* GIRTY, 1909] [=*Adelphoceras* GIRTY, 1909 (*non* BARRANDE, 1874); *Sagittoceras* HIND, 1918; *Dryochoceras* MORGAN, 1924; ?*Sudeticeras* PATTEISKY, 1929; ?*Karagandoceras* LIBROVITCH, 1940; *Hudsonoceras* MOORE, 1946]. Conch lenticular, venter angular at maturity. Gradational with

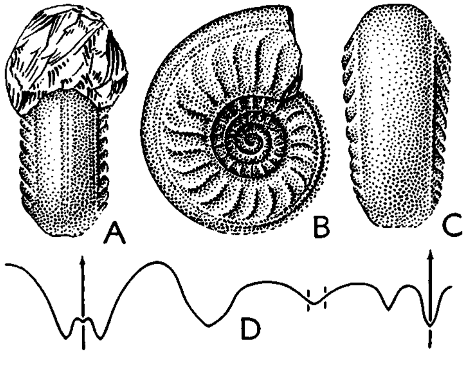


FIG. 75. *Eumorphoceras bisulcatum* GIRTY, U.Miss., Tex.; *A-C,* ×3.5; *D,* ×7 (110).

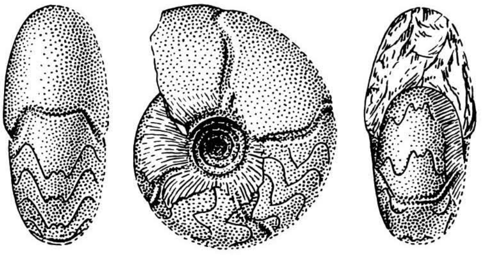


Fig. 76. *Girtyoceras meslerianum* (Girty), U.Miss., Okla.; ×2.5 (110).

Fig. 77. *Girtyoceras meslerianum* (Girty), U.Miss., Tex.; ×0.8 (110).

Eumorphoceras and superficially similar to *Gonioloboceras* (51). *L.Carb.(U.Miss.),* N.Am.-Eurasia-N.Afr.——Fig. 76,77. **G. meslerianum* (Girty); 76, Okla., ×2.5; 77, Tex., ×0.8 (110).

Nomismoceras Hyatt, 1884 [**Gon. spirorbis* Phillips]. Conch discoidal; umbilicus large. Syntypes of type species small and probably immature. *L. Carb.,* Eng.

Entogonites Kittl, 1904 [**Tetragonites grimmeri* Kittl, 1904] [=*Tetragonites* Kittl, 1904 (*non* Kossmat, 1895); *Kittliella* Frech, 1906]. Conch thinly discoidal, with large umbilicus; prominent ribbed sculpture with ventrolateral salient and sulcus; inner whorls coiled quadrangularly. Sutures may have extra pair of lobes (78). *L.Carb.(L. Miss.),* Ger.-Yugo.-Alaska.

Subfamily BISATOCERATINAE Miller & Furnish, nov.

Conch thickly subdiscoidal to globular, umbilicus small and characteristcally closed. Ventral lobe of suture broad and bifid with rounded or linear-lanceolate prongs (4). *L. Carb.(U.Miss.)-U.Carb.(U.Penn.).*

Bisatoceras Miller & Owen, 1937 [**B. primum*] [=*Schartymites* Librovitch, 1939; *Pseudobisatoceras* Maximova, 1940]. Conch thickly subdiscoidal, umbilicus closed. Ventral lobe of sutures with prominent linear-lanceolate prongs. *L.Penn.-M.Penn.;* C.USA-SW.USA.——Fig. 78. **B. primum,* M.Penn., Okla.; ×1.

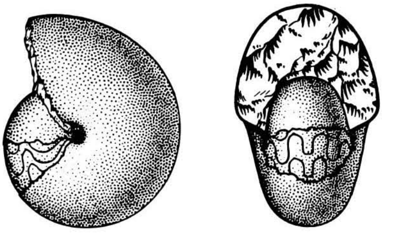


Fig. 78. *Bisatoceras primum* Miller & Owen, M. Penn., Okla.; ×1 (110).

Pennoceras Miller & Unklesbay, 1942 [**P. seamani*]. Conch subglobular, umbilicus closed, prominent transverse sculpture. Ventral lobe of sutures with small rounded prongs. *U.Penn.,* Ohio-Pa.

Nuculoceras Bisat, 1924 [**N. nuculum*]. Conch globular, umbilicus small, transverse sculpture. Ventral lobe of sutures with small rounded prongs (4). *L.Carb.,* Eng.

Subfamily GONIOLOBOCERATINAE Spath, 1934

[*ex* Gonioloboceratidae]

Conch sublenticular, umbilicus small. Sutural inflections prominent and ventral lobe broad (60). *M.Penn.-L.Perm.*

Gonioloboceras Hyatt, 1900 [**Gon. goniolobus* Meek, 1877] [=*Milleroceras* Hyatt, 1900; *Gurleyoceras* Miller, 1932]. Venter narrowly rounded. First lateral saddle of sutures angular (49). *M. Penn.-L.Perm.,* C.USA-SW.USA.——Fig. 79. **G. goniolobum* (Meek), U.Penn., Kans.; ×1.

Gonioglyphioceras Plummer & Scott, 1937 [**Gonioloboceras welleri gracile* Girty, 1911] [=*Eudissoceras* Miller & Owen, 1937]. Like

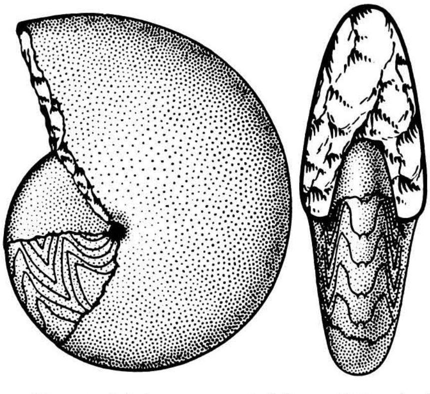


Fig. 79. *Gonioloboceras goniolobum* (Meek), U. Penn., Kans.; ×1 (110).

Gonioloboceras but with retuse venter and sutures with rounded lateral lobe (60). *M.Penn.*, Okla.-Ill.-Ohio.

Wiedeyoceras MILLER, 1932 [**Eumorphoceras sanctijohanis* WIEDEY, 1929]. Like *Gonioloboceras* but 1st lateral saddle of suture rounded. *M.Penn.*, Iowa.

Family NEOICOCERATIDAE Hyatt, 1900

[=Gastrioceratea ARTHABER, 1911]

Conch variable in shape and characteristically with prominent sculpture, umbilicus moderately small to large. Sutures form 8 lobes (24,50,60,65,78). *L.Carb.(L.Penn.)-U.Perm.*

Gastrioceras HYATT, 1884 [**Conchyliolithus Nautilithes Ammonites (Listeri)* MARTIN, 1809] [=*Neoicoceras* HYATT, 1900; *Branneroceras* PLUMMER & SCOTT, 1937]. Conch subdiscoidal to globular, umbilicus moderate to large, with nodose or ribbed margins. Suture with prongs of ventral lobe relatively narrow (4,60,78). *U.Carb.(Penn.)*, widespread.——FIG. 80. **G. listeri* (MARTIN), L. Penn., Eng.; *A,B*, ×1.——FIG. 81*A,B*. *G. reticulatum* YIN, U.Carb., China; ×0.5 (101).——FIG. 81*C*. *G. branneri* SMITH, L.Penn., Ark., ×1.5. [*Gastrioceras*=*Tschungḳuoceras* GERTH, 1950.]

Eoasianites RUZHENCEV, 1933 [**E. subhanieli*] [=*Prometalegoceras, Glaphyrites* RUZH., 1936; *Trochilioceras, Preshumardites* PLUMMER & SCOTT, 1937; *Syngastrioceras* LIBROVITCH, 1938; *Ambiguites* SMITH, 1938; *Neoglaphyrites, Somoholites* RUZH., 1938]. Conch subglobular to globular, umbilicus moderate in size, with margins not prominently nodose or ribbed (50,65,66). *L.Carb.-L.Perm.*, widespread, locally abundant.——FIG. 82. *E. angulatus* (GIRTY), M.Penn., Okla.; ×0.7. [*Eoasianites*=*Pronoceras* PLUMMER-S., 1950 *(nom. nud.)*.]

Neoshumardites RUZHENCEV, 1936 [**N. triceps*]. Like *Eoasianites* but with lateral lobe of suture distinctly trifid (49,65). *M.Penn.-M.Perm.*, Tex.-Okla.-Ohio-Urals.——FIG. 83. *N.* sp., U.Penn., Okla.; ×1.——FIG. 84. *N. cuyleri* (PLUMMER & SCOTT), U.Penn., Tex.; ×1.6. [*Neoshumardites*=*Aḳtubites* RUZHENCEV, 1955.]

Pseudoparalegoceras MILLER, 1934 [**Gastrioceras russiense* TZWETAEV, 1888] [=*Strawnoceras*

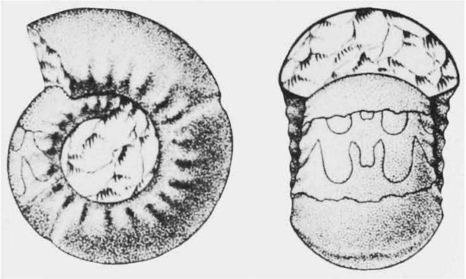


FIG. 80. *Gastrioceras listeri* (MARTIN), U.Carb., Eng.; ×1 (110).

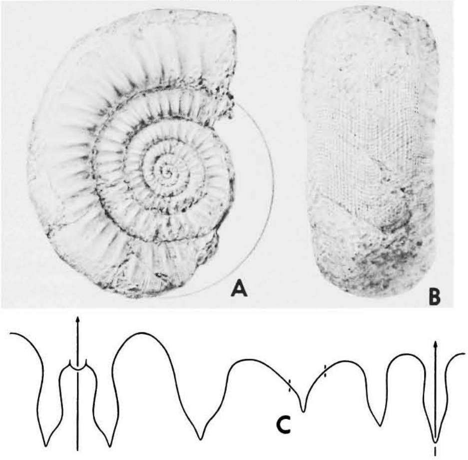


FIG. 81. *Gastrioceras. A,B, G. reticulatum* YIN, L. Penn., China; ×0.5 (101). *C, G. branneri* SMITH, L.Penn., Ark.; ×1.5 (110).

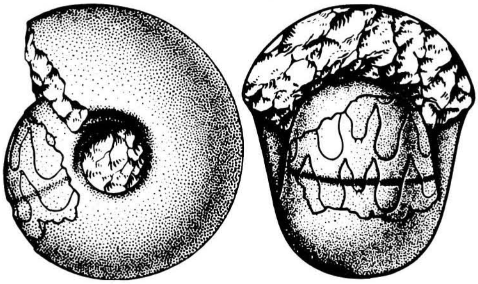


FIG. 82. *Eoasianites angulatus* (GIRTY), M.Penn., Okla.; ×0.7 (110).

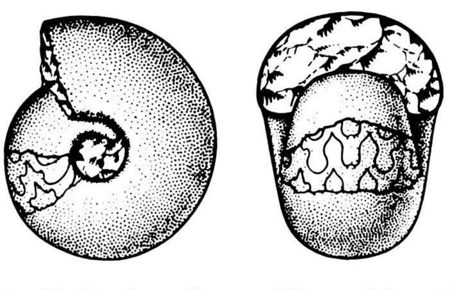


FIG. 83. *Neoshumardites* sp., U.Penn., Okla.; ×1 (110).

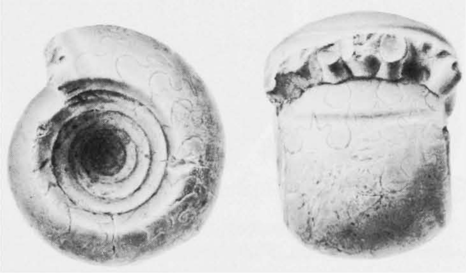


FIG. 84. *Neoshumardites cuyleri* (PLUMMER & SCOTT), U.Penn., Tex.; ×1.6 (110).

FIG. 85. *Pseudoparalegoceras williamsi* MILLER & DOWNS, L.Penn., Ark.; ×0.6 (110).

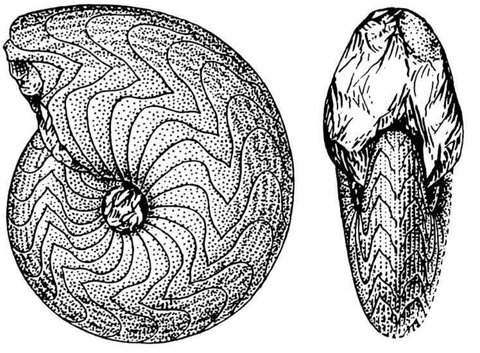


FIG. 88. *Pseudogastrioceras abichianum* (MÖLLER), U.Perm., Armenia; ×0.8 (103).

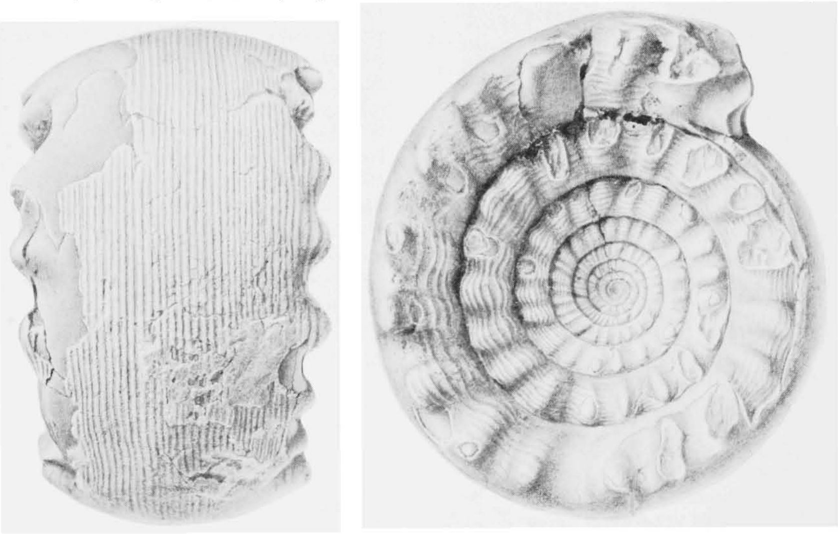


FIG. 86. *Paragastrioceras jossae* (DE VERNEUIL), M.Perm., Urals; ×1.5 (110).

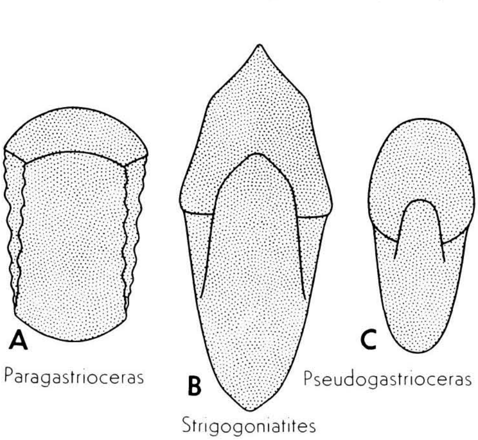


FIG. 87. *Paragastrioceras (A)*, ×1.5; *Strigogoniatites (B)*, ×0.5; *Pseudogastrioceras (C)*, ×0.5 (110).

PLUMMER & SCOTT, 1935 *(nom. nud.)*; *Phaneroceras* PLUMMER-S., 1937; *Eoparalegoceras* DELÉPINE, 1939]. Like *Eoasianites* but conch thickly subdiscoidal and with umbilical lobe of suture on umbilical margin or adventral to it (51). *U.Carb. (Penn.)*, SW.USA - Peru - N.Afr. - Russ.(Moscow). ——FIG. 85. *P. williamsi* MILLER & DOWNS, L. Penn., Ark.; ×0.6——FIG. 94*A*. *P. bellilineatum* MILLER & FURNISH, L.Penn., Tex.; ×1.5.

Owenoceras MILLER & FURNISH, 1940 [**Neoglyphioceras bellilineatum* MILLER & OWEN, 1939]. Like *Eoasianites* but longitudinally lirate (51). *M.Penn.*, Mo.-Okla.

Paragastrioceras TCHERNOW, 1907 [**Gon. jossae* DE VERNEUIL, 1845] [=*Girtyites* WEDEKIND, 1918]. Conch thickly subdiscoidal, with broad low whorls and large umbilicus with prominently nodose margin; test longitudinally lirate (50). *M.Perm.*, Urals. ——FIGS. 86; 87*A*. **P. jossae* (VERNEUIL), M. Perm., Urals; 86, ×1.5 (110); 87*A*, ×1.5 (110).

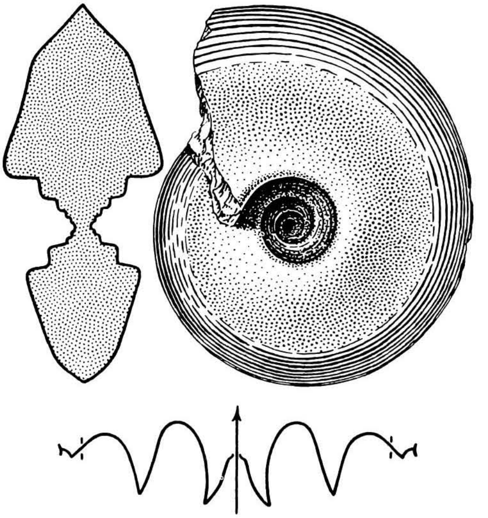


FIG. 89. *Strigogoniatites angulatus* (HANIEL), M.Perm., Timor; ×0.5 (110).

Pseudogastrioceras SPATH, 1930 [**Gon. abichianus* MÖLLER, 1879] [=*Uraloceras* RUZHENCEV, 1936; *Altudoceras* RUZH., 1940]. Like *Paragastrioceras* but with characteristically narrower whorls, smaller umbilicus with marginal ribs rather than nodes, and coarser longitudinal sculpture (50,66). *L. Perm.-U.Perm.,* widespread.——FIGS. 87*C;* 88. **P. abichianum* (MÖLLER), U.Perm., Armenia; 87*C,* ×0.5; 88, ×0.8 (103).

Synuraloceras RUZHENCEV, 1952 [**S. carinatum*]. Like *Eoasianites* but discoidal conch with angular venter (67). *L.Perm.,* Urals.

Strigogoniatites SPATH, 1934 [**Glyphioceras angulatum* HANIEL, 1915]. Like *Pseudogastrioceras* but with angular venter (50). *M.Perm.,* Timor-?China-Sicily-Tex.-Coah.——FIGS. 87*B;* 89. **S. angulatus* (HAN.), Timor; 87*B,* ×0.5; 89, ×0.5 (30). [*Strigogoniatites*=?*Grabauites* SUN, 1939.]

Atsabites HANIEL, 1915 [**A. weberi*]. Like *Pseudogastrioceras* but discoidal, with whorls slightly impressed dorsally (50). *M.Perm.,* Timor-Tex.

FIG. 90. *Metalegoceras schucherti* MILLER & FURNISH, M.Perm., Tex.; ×1.3 (110).

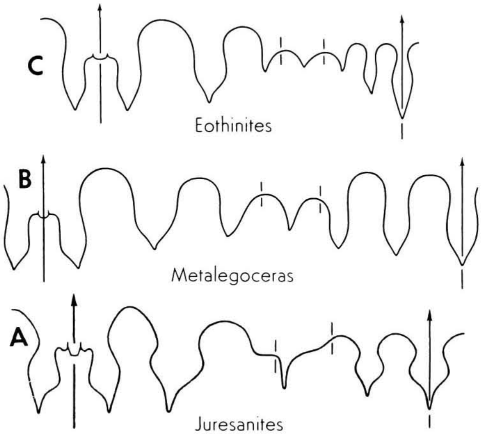


FIG. 91. Sutures of *Juresanites (A),* ×1.7; *Metalegoceras (B),* ×1.3; *Eothinites (C),* enlarged (110).

Eupleuroceras MILLER & CLINE, 1934 [**E. bellulum*]. Like *Atsabites* but keeled ventrally, not longitudinally lirate, and sutures more primitive. Only immature stages known (60). *U.Penn.,* Okla.-Tex.

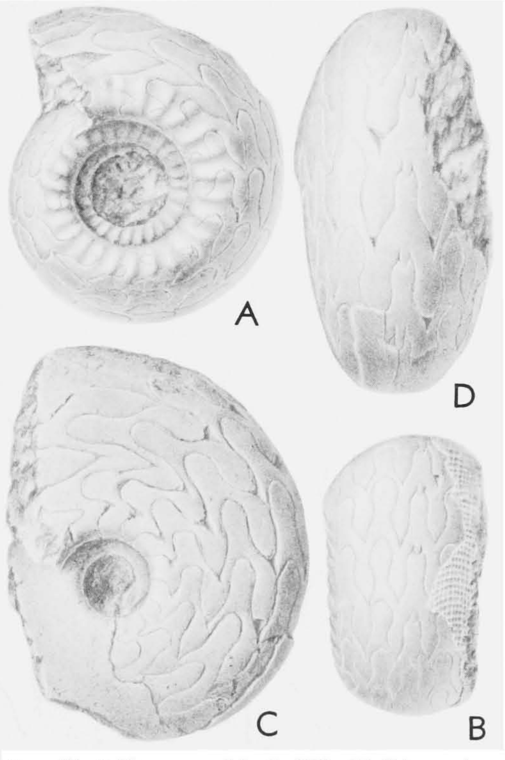


FIG. 92. *Schistoceras. A,B, S. hildrethi* (MORTON), U.Penn., Mo.; ×1.5 (110). *C,D, S. missouriense* (MILLER & FABER), U.Penn., Mo.; ×1.5 (110).

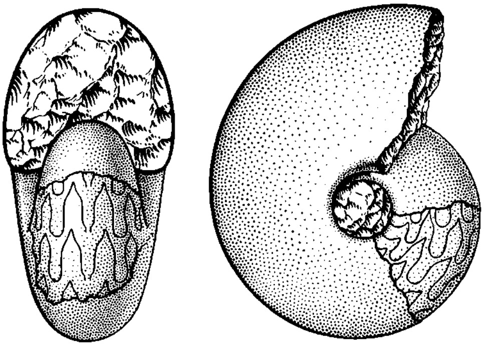


FIG. 93. *Schistoceras missouriense* (MILLER & FABER), U. Penn., Tex.; ×0.9 (110).

Epiglyphioceras SPATH, 1930 [**Glyphioceras meneghinii* GEMMELLARO, 1887]. Thinly discoidal conch with wide umbilicus and slightly involute whorls, prominent sinuous growth lines (24). *M.Perm.;* Sicily.

Family METALEGOCERATIDAE Plummer & Scott, 1937

Conch discoidal to subglobular with moderate to large umbilicus. Sutures goniatitic, forming 12 to 14 lobes (50,66). *L.Perm.-M.Perm.*

Metalegoceras SCHINDEWOLF, 1931 [**Paralegoceras sundaicum evoluta* HANIEL, 1915] [=*Epilegoceras* TCHERNOW, 1907 *(nom. nud.); Asianites* RUZHEN-

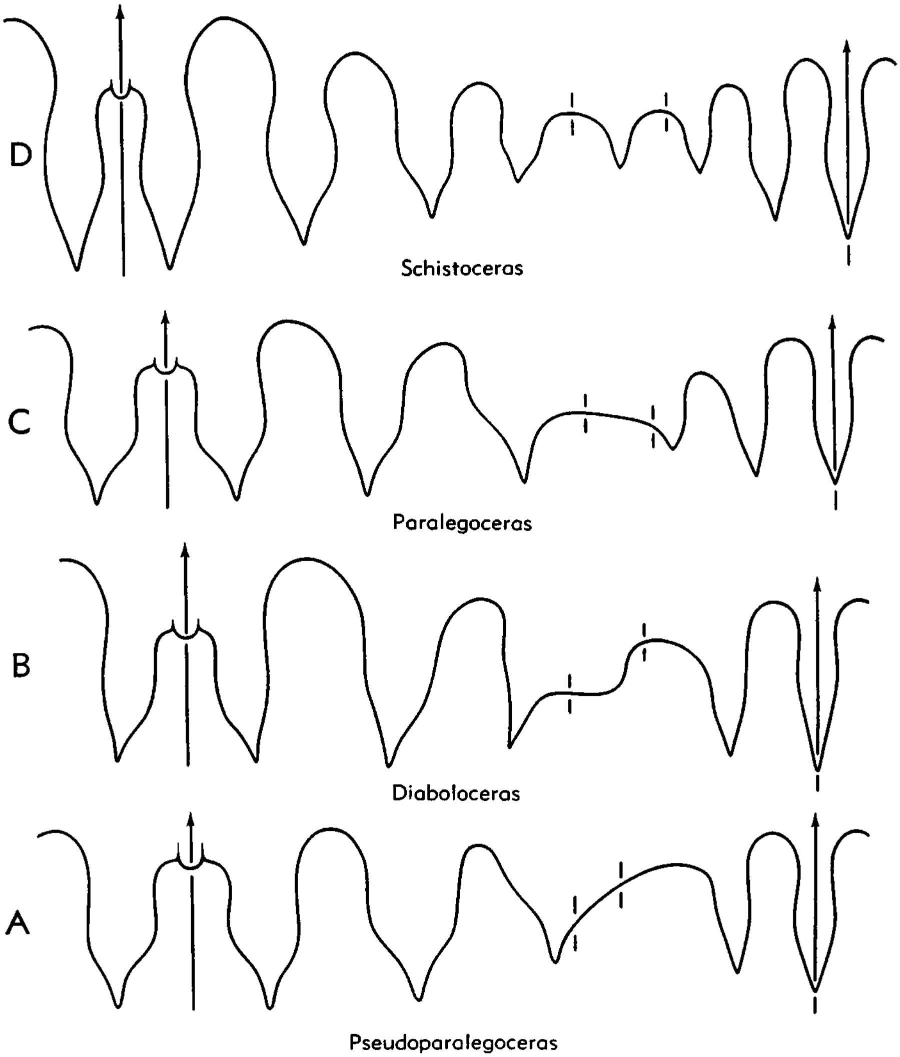


FIG. 94. Sutures of *Pseudoparalegoceras (A)*, ×1.5; *Diaboloceras (B)*, ×2.5; *Paralegoceras (C)*, ×1.5; *Schistoceras (D)*, ×2 (110).

cev, 1933; *Dodecalegoceras* Voinova, 1934; *Bransonoceras* Miller & Parizek, 1948]. Conch thickly subdiscoidal to subglobular. Sutures forming 12 lobes (30, 50, 66, 67). *L.Perm.-M.Perm.*, Tex.-N.Mex.-Urals-Arabia-Timor-W.Austral.——Fig. 90. *M. schucherti* Miller & Furnish, M.Perm., Tex.; ×1.3.——Fig. 91*B*. **M. evolutum* (Han.), M. Perm., Timor; ×1.3 (30).

Eothinites Ruzhencev, 1933 [**E. ḳargalensis*] [=*Uralites* Tchernow, 1907 *(nom. nud.), non* Voinova, 1934 *(nom. nud.); Rhiphaeites* Ruzh., 1933]. Like *Metalegoceras* but with narrower conch (50). *M.Perm.*, Urals-Timor-Tex.——Fig. 91*C*. *E. uralensis* (Ruzh.), Urals; enlarged (113).

Juresanites Maximova, 1940 [**J. primitivus*]. Like *Metalegoceras* but with more primitive sutures (66). *L.Perm.*, Urals.——Fig. 91*A*. **J. primitivus;* ×1.6 (66).

Pseudoschistoceras Teichert, 1944 [**P. simile*]. Like *Metalegoceras* but sutures form an additional lobe in umbilical region. *?L.Perm.*, W.Austral.

Family SCHISTOCERATIDAE Schmidt, 1929

Conch discoidal to subdiscoidal with moderate to large umbilicus, reticulate surface, and goniatitic sutures forming 10 to 16 lanceolate lobes (51,65). *U.Carb.(L.Penn.)-L.Perm.*

Subfamily SCHISTOCERATINAE Schmidt, 1929

[*ex* Schistoceratidae]

Conch thickly subdiscoidal. Sutures forming gradational series of 10 to 14 lobes. *U. Carb.(L.Penn.).*

Schistoceras Hyatt, 1884 [**Gon. missouriensis* Miller & Faber, 1892] [=*Paraschistoceras, Metaschistoceras* Plummer & Scott, 1937]. Moderate to large umbilicus with more or less nodose borders. Sutures form 14 lobes (51,60). *M.Penn.-L.Perm.*, USA-Urals.——Fig. 92*A,B*. *S. hildrethi* (Morton), U.Penn., Mo.; ×1.5.——Figs. 92*C,D;* 93; 94*D*. **S. missouriense* (Miller & Faber), U.Penn., USA; 92*C,D*, ×1.5 (Mo.); 93, ×0.9 (Tex.); 94*D*, ×2 (Tex.).

Pintoceras Plummer & Scott, 1937 [**P. postvenatum*] [=*Eoschistoceras* Ruzhencev, 1952]. Like *Schistoceras* but with depressed conch, large umbilicus, triangularly coiled inner whorls, and more primitive sutures. *U.Carb.(M.Penn.)*, Tex.-Okla.-Turkistan.

Paralegoceras Hyatt, 1884 [**Gon. iowensis* Meek & Worthen, 1860] [=*Bendoceras* Plummer & Scott, 1937]. Like *Pintoceras* but sutures form 10 lobes (51). *L.Penn.*, Iowa-Ark.-Okla.-Tex.——Figs. 94*C;* 95*D;* 96. **P. iowense* (Meek-W.), Iowa-Tex.; 94*C*, ×1.5; 95*D*, ×0.5; 96, ×0.75.——Fig. 95*A-C*. *P. texanum* (Shumard), Okla.; *A,B*, ×1.3; *C*, ×0.7.

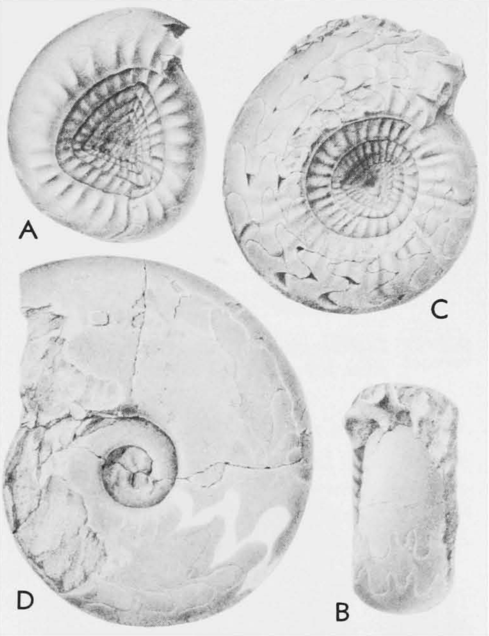


Fig. 95. *Paralegoceras. A-C, P. texanum* (Shumard), L.Penn., Okla.; *A,B*, ×1.3; *C*, ×0.7 (110). *D, P. iowense* (Meek & Worthen), L.Penn., Iowa; ×0.5 (110).

Diaboloceras Miller & Furnish, 1940 [**D. varicostatum*]. Like *Paralegoceras* but with more primitive sutures (51). *L.Penn.*, Tex.-Okla.——Figs. 94*B;* 97. **D. varicostatum*, Tex.; 94*B*, ×2.5; 97, ×1.5.

Winslowoceras Miller & Downs, 1948 [**W. henbesti*]. Like *Paralegoceras* and *Diaboloceras* but with discoidal conch and flattened venter. *L.Penn.*, Ark.-Okla.——Fig. 98. **W. henbesti*, Ark.; *A,B*, ×0.7; *C*, ×1.3.

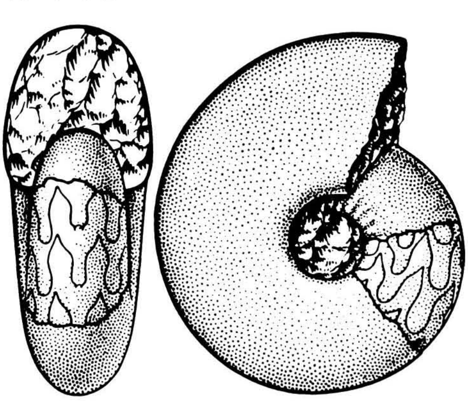


Fig. 96. *Paralegoceras iowense* (Meek & Worthen), L.Penn., Tex.; ×0.75 (110).

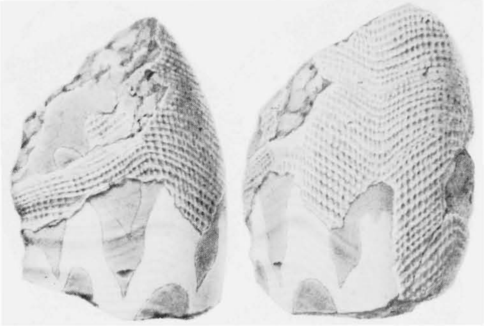


FIG. 97. *Diaboloceras varicostatum* MILLER & FURNISH, L.Penn., Tex.; ×1.5 (110).

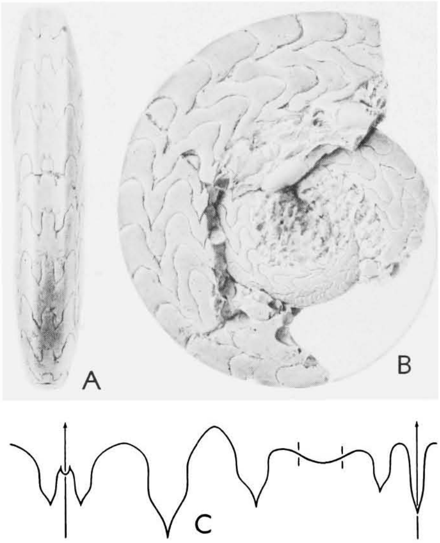


FIG. 98. *Winslowoceras henbesti* MILLER & DOWNS, L.Penn., Ark.; *A,B,* ×0.7; *C,* ×1.3 (110).

Subfamily WELLERITINAE Plummer & Scott, 1937

[*ex* Welleritidae]

Conch discoidal. Sutures forming 16 lobes of which ventrolateral 2 are adventitious. *M.Penn.*

Wellerites PLUMMER & SCOTT, 1937 [**W. mohri*] [=*Walkerites* SMITH, 1938]. Probably evolved from *"Paralegoceras" moorei* (PLUMMER-S.) (60). *U.Carb.(M.Penn.),* Tex.-Okla.-Ohio-Urals.——FIG. 99; 100. **W. mohri,* Tex.; 99, ×0.5; 100, ×4 (60).

Superfamily ADRIANITACEAE Schindewolf, 1931

[*ex* Adrianitidae]

Discoidal to globular conchs with variable umbilici. Goniatitic suture with 10 to 30 lobes which tend to be subequal (24,30,50). *U.Carb.(M.Penn.)-M.Perm.*

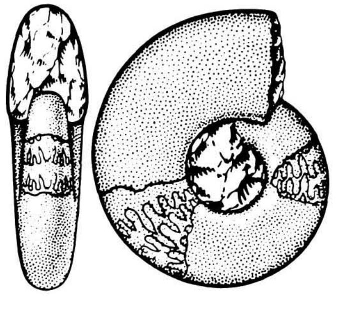


FIG. 99. *Wellerites mohri* PLUMMER & SCOTT, M. Penn., Tex., ×0.5 (110).

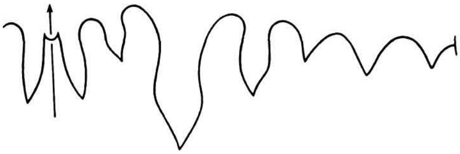


FIG. 100. Suture of *Wellerites mohri* PLUMMER & SCOTT, M.Penn., Tex.; ×4 (110).

Family ADRIANITIDAE Schindewolf, 1931

Characters of superfamily. *U.Carb.(M. Penn.)-M.Perm.*

Subfamily ADRIANITINAE Schindewolf, 1931

[*ex* Adrianitidae]

Typical more advanced adrianitids, with sutures forming 14 to 30 lobes. *L.Perm.-M. Perm.*

Adrianites GEMMELLARO, 1887 [**A. elegans*] [=*Epadrianites* SCHINDEWOLF, 1931; *Palermites* TOUMANSKY, 1937; *Neocrimites* RUZHENCEV, 1940; *Aricoceras, Basleoceras, Metacrimites, Metaricoceras, Neoaricoceras, Sosiocrimites* RUZH., 1950]. Subglobular to globular conchs with small umbilici, generally longitudinally lirate test. Sutures with 20 to 30 lobes (24,30,50,65). *M.Perm.,* widespread. ——FIG. 101. **A. elegans,* Sicily; ×2.——FIG. 7*A*. *A. defordi,* MILLER & FURNISH, Tex.; ×1.3.——FIG. 11*A′-E′*. *A. dunbari* MILLER-F., Coah.; enlarged.——FIG. 2,*3a,b*. *A. kingi* GEMM., M.Perm., Sicily; ×1.25 (24).——FIG. 2,*4*. *A. ensifer* GEMM., M.Perm., Sicily; ×1.25 (24).——FIG. 2,*5a,b*. *A. distefanoi* GEMM., Sicily; ×1.25 (24).

Hoffmannia GEMMELLARO, 1887 [**Adrianites (H.) hoffmanni*]. Like *Adrianites* but discoidal conchs with large umbilici, prominent growth lines, and sutures forming about 20 lobes (24). *M.Perm.,* Sicily-?Tex.

Doryceras GEMMELLARO, 1887 [**D. fimbriatum*]

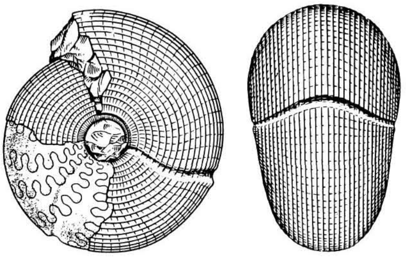


FIG. 101. *Adrianites elegans* GEMMELLARO, M.Perm., Sicily; ×2 (110).

[=?*Pseudagathiceras* SCHINDEWOLF, 1931; *Sizilites* TOUMANSKY, 1937]. Like *Adrianites* but subdiscoidal to subglobular conch with large umbilici and sutures forming 14 to 18 lobes (24,47,65). *M. Perm.*, Sicily-Timor-Coah.——FIG. 2,6. *D. spinosum* (MILLER), M.Perm., Coah.; ×2 (110).

Crimites TOUMANSKY, 1937 [**C. pamiricus*]. Like *Adrianites* but a globular conch with sutures forming about 14 lobes (65). *L.Perm.-M.Perm.*, Pamirs-Urals-Timor.

Texoceras MILLER & FURNISH, 1937 [**Agathoceras texanum* GIRTY, 1908]. Like *Adrianites* but subglobular conch with reticulate surface and sutures forming 14 rounded lobes (50). *M.Perm.*, Tex. ——FIG. 102. **T. texanum* (GIRTY); *A,B,* ×1.3; *C,* ×2; *D,* ×3.

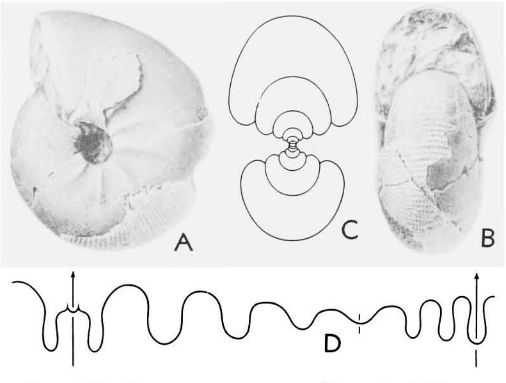


FIG. 102. *Texoceras texanum* (GIRTY), M.Perm., Tex.; *A,B,* ×1.3; *C,* ×2; *D,* ×3 (110).

Subfamily DUNBARITINAE Miller & Furnish, nov.

Primitive adrianitids with sutures forming 10 lobes. *M.Penn.-U.Penn.*

Dunbarites MILLER & FURNISH, 1940 [**Paralegoceras rectilaterale* MILLER, 1930]. Thickly discoidal conch with flattened venter (51). *M.Penn.-U. Penn.*, Tex.-Okla.

Emilites RUZHENCEV, 1938 [**Paralegoceras incertum* BÖSE, 1919] [=*Plummerites* MILLER & FURNISH, 1940]. Like *Dunbarites* but globular conch with sutures denticulate in umbilical regions (50,65). *U.Penn.*, Tex.-Urals.——FIG. 103. **E. incertus* (BÖSE), Tex.; ×3.

FIG. 103. *Emilites incertus* (BÖSE), U.Penn., Tex.; ×3 (110).

Subfamily CLINOLOBINAE Miller & Furnish, nov.

Conch thinly discoidal and keeled ventrally, with large umbilicus, prominent transverse sculpture, and sutures forming ?14 lobes; general course of external sutures V-shaped (24). *M.Perm.*

Clinolobus GEMMELLARO, 1887 [**C. telleri*]. Unique; known from few small specimens. *M. Perm.*, Sicily.—FIG. 104. **C. telleri;* ×4 (24).

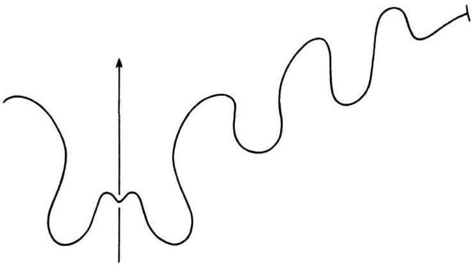


FIG. 104. Suture of *Clinolobus telleri* GEMMELLARO, M.Perm., Sicily; ×4 (24).

Superfamily DIMORPHOCERATACEAE Hyatt, 1884

[*ex* Dimorphocerae]

Subdiscoidal to lenticular conch with inconspicuous closed umbilici. Sutures goniatitic with large prominently bifid ventral lobe and external lobes more or less subdivided. *L.Carb.(U.Miss.)-M.Perm.*

Family DIMORPHOCERATIDAE Hyatt, 1884

[*pro* Dimorphocerae]

External lateral lobes and prongs of ventral lobe of sutures tend to be bifid (49,65). *L.Carb.(U.Miss.)-U.Carb.(U.Penn.), ?L. Perm.*

Dimorphoceras HYATT, 1884 [**Gon. gilbertsoni*

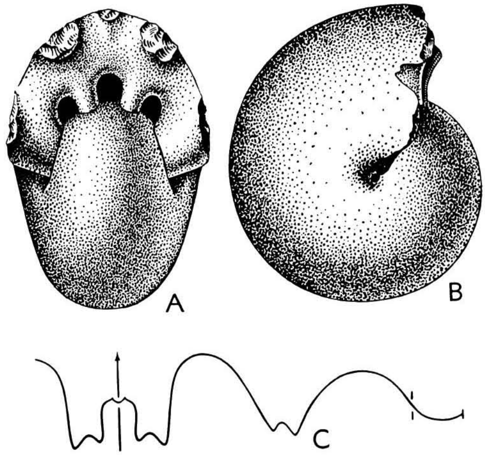


FIG. 105. *Dimorphoceras edwini* MILLER & FURNISH, U.Miss., Ky.; *A,B,* ×5; *C,* ×7 (110).

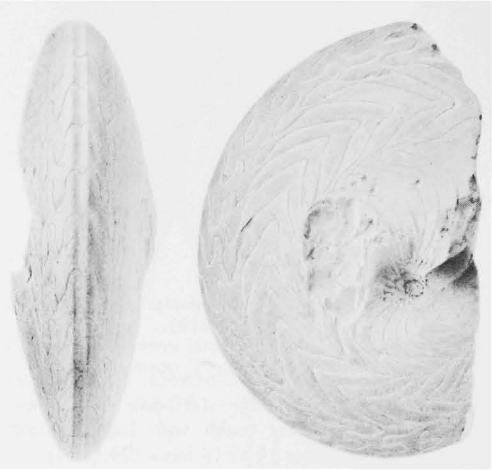


FIG. 106. *Neodimorphoceras texanum* (SMITH), U. Penn., Tex.; ×0.8 (110).

PHILLIPS, 1836] [=*Trizonoceras* GIRTY, 1909; *Politoceras* LIBROVITCH, 1946; *Paradimorphoceras* RUZHENCEV, 1949]. Venter rounded; external lobes of sutures variably serrate (4,15,21,51,65). *L.Carb. (U.Miss.)-U.Carb.(M.Penn.),* Eurasia-N.Afr.-N. Am.——FIG. 105. *D. edwini* MILLER & FURNISH, U.Miss., Ky.; *A,B,* ×5; C, ×7.

Neodimorphoceras SCHMIDT, 1925 [**Dimorphoceras texanum* SMITH, 1903] [=*Texites* SMITH, 1927; *Berkhoceras* LIBROVITCH, 1938; *Kazakhoceras* RUZHENCEV, 1947]. Conch lenticular; venter subacute or retuse. Sutures with prongs of ventral lobe prominently bifid and 1st lateral saddle subangular (49). *L.Carb.(U.Miss.)-U.Carb.(U.Penn.),* Tex. - Okla. - Eng. -Menorca-Urals-N.Zem.——FIGS. 106; 107; 108. **N. texanum* (SMITH), U.Penn., Tex.; 106, ×0.8; 107, ×10; 108*A-C,* ×15; 108*D,* ×4.5.

Shuichengoceras YIN, 1935 [**S. yohi*] [=*Pinoceras* RUZHENCEV, 1941]. Like *Neodimorphoceras* but venter rounded (101). *U.Carb.(U.Penn.), ?L. Perm.,* Kweichow-Urals-SW.USA.

Family THALASSOCERATIDAE Hyatt, 1900

Lobes of external sutures serrate to digitate (50,65). *L.Carb.(U.Miss.)-M.Perm.*

Thalassoceras GEMMELLARO, 1887 [**T. phillipsi*] [=*Prothalassoceras* BÖSE, 1919]. Lobes of external sutures digitate (24,50,65). *L.Perm.-M.Perm.,* widespread in Eurasia-Austral.-N.Am. —— FIG. 109,*B. T. welleri* (BÖSE), L.Perm., Tex.; ×2.5.

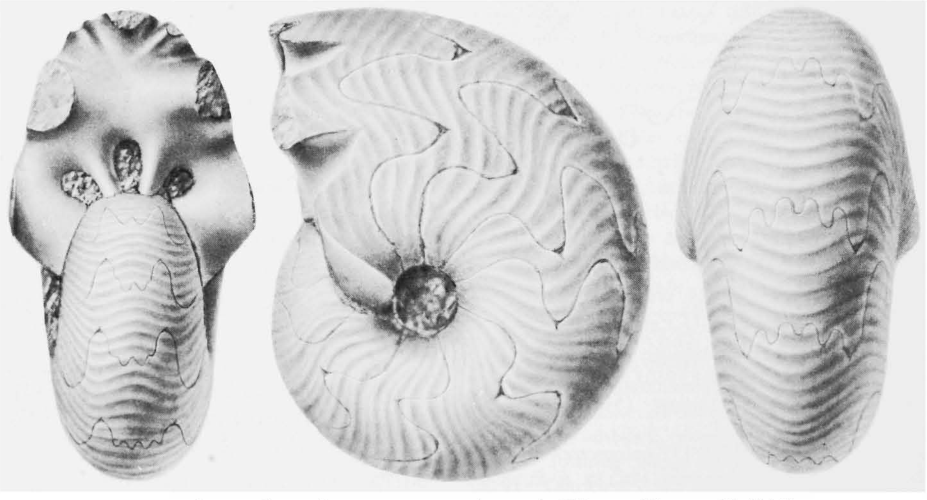


FIG. 107. *Neodimorphoceras texanum* (SMITH), U.Penn., Tex.; ×10 (110).

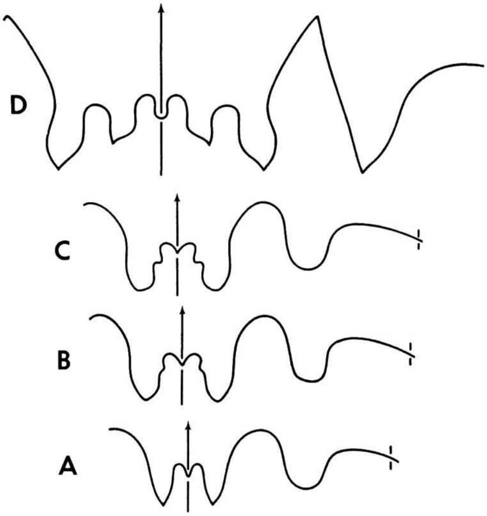


Fig. 108. Ontogeny of sutures in *Neodimorphoceras texanum* (Smith), U.Penn., Tex.; *A-C,* ×15; *D,* ×4.5 (110).

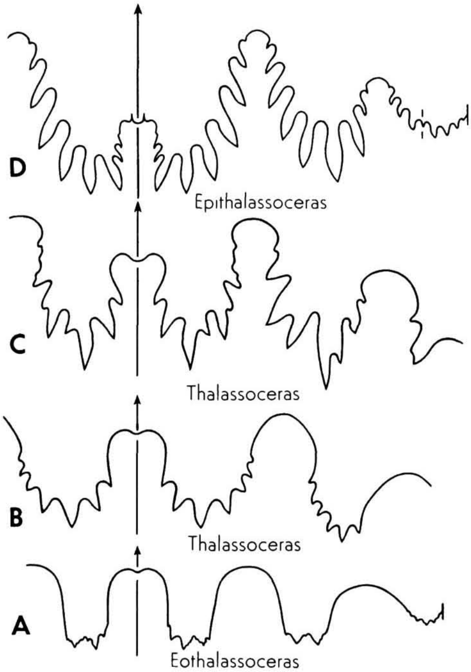


Fig. 109. Sutures of *Eothalassoceras (A),* ×2.5; *Thalassoceras (B,C),* ×2.5, enlarged; *Epithalassoceras (D),* ×3 (110).

——Fig. 109*C.* **T. phillipsi,* M.Perm., Sicily; enlarged (24).

Eothalassoceras Miller & Furnish, 1940 [**Prothalassoceras inexpectans* Miller & Owen, 1937]

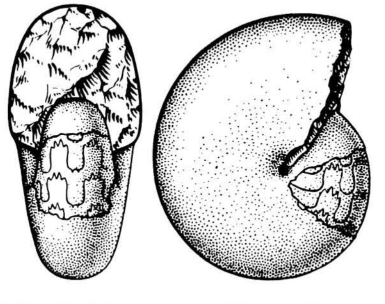


Fig. 110. *Eothalassoceras caddoense* Plummer & Scott, U.Penn., Okla.; ×1 (110).

[=*Uralites* Voinova, 1934 *(nom. nud.), non* Tchernow, 1907 *(nom. nud.); Aristoceras* Ruzhencev, 1940]. Lobes of external sutures irregularly serrate (49,50,65). *U.Carb.(L.Penn.)-L. Perm.,* W.USA-Urals-N.Afr.——Fig. 109*A.* **E. inexpectans* (Miller-O.), M.Penn., Okla.; ×2.5. ——Fig. 110. *E. caddoense* (Plummer & Scott), U.Penn., Okla.; ×1.

Delepinoceras Miller & Furnish, 1954 [**Dimorphoceras thalassoide* Delépine, 1937]. Like *Thalassoceras* but lobes of sutures somewhat trifid (52). *L.Carb.,* Pyrenees-N.Afr.

Gleboceras Ruzhencev, 1950 [**G. mirandum*]. Like *Eothalassoceras* but sutures with prongs of ventral lobe not subdivided (65). *U.Carb.,* Urals.

Epithalassoceras Miller & Furnish, 1940 [**E. ruzencevi*]. Like *Thalassoceras* but sutures more advanced, with internal lateral lobes bifid (47,50). *M.Perm.,* Coah.——Fig. 109*D.* **E. ruzencevi;* ×3.

Suborder PROLECANITINA Miller & Furnish, 1954

Discoidal to thinly lenticular conchs with goniatitic to ceratitic sutures characteristically forming auxiliary lobes; simple retrochoanitic siphuncles (50,52,54). *U.Dev.-U. Trias.*

Superfamily PROLECANITACEAE Hyatt, 1884

[*ex* Prolecanitidae]

Conch characteristically with large umbilici; no prominent sculpture. Sutures goniatitic to ceratitic (50,52). *U.Dev.-M. Perm.*

Family PROLECANITIDAE Hyatt, 1884

Conch discoidal to lenticular with moderate to large umbilicus. Sutures goniatitic, characteristically forming a series of subequal lobes and saddles with undivided ventral lobe (16,53,71,78). *U.Dev.-L.Carb.(U. Miss.).*

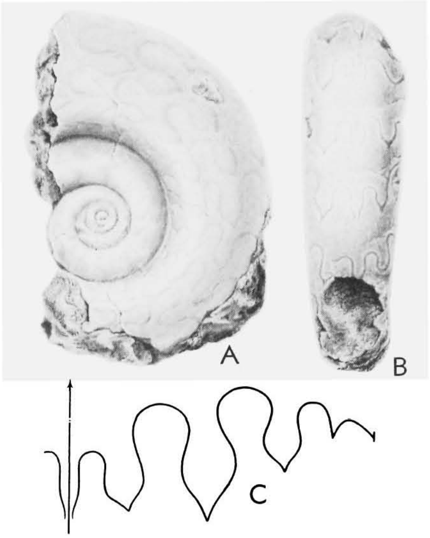


Fig. 111. *Prolecanites americanus* Miller & Garner, U.Miss., Ind.; *A,B,* ×1; *C,* ×2 (110).

Prolecanites Mojsisovics, 1882 [**P. mojsisovicsi* Miller, 1938] [=*Paraprolecanites* Karpinsky, 1889; *Metacanites* Schindewolf, 1922; *Dombarocanites, Rhipaeocanites* Ruzhencev, 1949]. Discoidal conch with large umbilici. Sutures form 12 lobes (68,78). *L.Carb.(U.Miss.),* Ger.-Eng.-Yugo.-?Sp.-Urals-?Kazak-USA (Ind.)-Can. (Alba.).——Fig. 111. *P. americanus* Miller & Garner, Ind.; *A,B,* ×1; *C,* ×2.——Fig. 9*A. P. hesteri* Moore, Eng.; ×7.

Protocanites Schmidt, 1922 [**Gon. lyoni* Meek & Worthen, 1860]. Like *Prolecanites* but sutures form 8 lobes (48). *L.Carb.(L.Miss.),* USA-Eurasia-N.Afr.-SE.Austral.——Fig. 112. **P. lyoni* (Meek-W.), Mo.; *A,B,* ×1; *C,* ×2.

Cycloclymenia Hyatt, 1884 [**Cly. planorbiformis* Münster] [=*Phenacoceras* Frech, 1902; *Balvites* Wedekind, 1914]. Like *Protocanites* but depressed whorls and prominent growth increments (41,70). *U.Dev.,* Ger.

Merocanites Schindewolf, 1922 [**Ellipsolites compressus* Sowerby, 1813]. Like *Prolecanites* but sutures form 10 lobes (53). *L.Carb.(L.Miss.),* Eurasia-C.USA.

Acrocanites Schindewolf, 1922 [**A. multilobatus*]. Like *Prolecanites* but angular venter, moderate umbilici, and suture with numerous auxiliary lobes (14,71). *L.Carb.,* Ger.-Belg.-N.Afr.

Family PRODROMITIDAE Arthaber, 1911

Conch thinly lenticular with keeled venter and small umbilicus. Sutures ceratitic, with broad trifid ventral lobe and numerous auxiliaries (48). *L.Miss.*

Prodromites Smith & Weller, 1901 [**Gon. gorbyi* Miller, 1891]. Known from single species. *L. Miss.,* Mo.-Iowa-Ill.-Ind.——Figs. 113; 114. **P. gorbyi* (Miller), Mo.; 113, ×1; 114*A-F,* enlarged (48).

Family DARAELITIDAE Tchernow, 1907

[*ex* Daraelitinae]

Conch discoidal with no prominent sculpture, umbilicus moderately large. Sutures goniatitic to ceratitic, with trifid ventral lobe and few auxiliary lobes. Evolved from prolecanitids (50,51,65). *L.Carb.(U.Miss.)-M. Perm.*

Daraelites Gemmellaro, 1887 [**D. meeki*] [=*Prodaraelites* Tchernow, 1907]. Ceratitic sutures with broad ventral lobe (24,50). *L.Perm.-M.Perm.,* Sicily-Urals-M.Asia-Timor-Tex.——Fig. 9*E. *D. meeki,* M.Perm., Sicily; ×4 (24).

Boesites Miller & Furnish, 1940 [**Daraelites texanus* Böse] [=*Metadaraelites* Ruzhencev, 1940]. Like *Daraelites* but suture with narrower ventral lobe and broader 1st lateral lobe, serration largely confined to 1st lateral lobe. Ancestral to and gradational with *Daraelites* (51,65). *L.Penn.-L.Perm.,* Tex.-Okla.-Urals.——Figs. 9*D;* 115. **B. texanus* (Böse), U.Penn., Tex.; 9*D,* ×7; 115, ×1.5.

Epicanites Schindewolf, 1926 [**Paraprolecanites sandbergeri* Schmidt, 1925] [=*Praedaraelites* Schind., 1934]. Like *Boesites* but with more primtive sutures (51). *L.Carb.(U.Miss.),* Alg.-Menorca-Pyrenees-Eng.-Ger.-Indochina-Okla. —— Fig. 9*B. *E. sandbergeri* (Schmidt), Alg.; enlarged (106).——Fig. 9*C. E. culmiensis* (Kobold), Ger.; ×4 (109).——Fig. 116. *E. loeblichi* Miller & Furnish, Okla.; *A,B,* ×5; *C,* ×15.

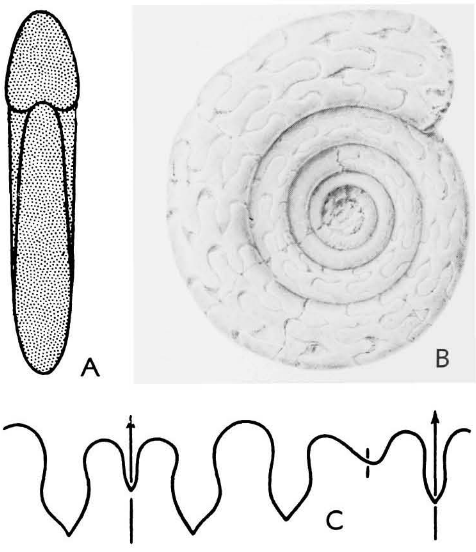


Fig. 112. *Protocanites lyoni* (Meek & Worthen), L.Miss., Mo.; *A,B,* ×1; *C,* ×2 (110).

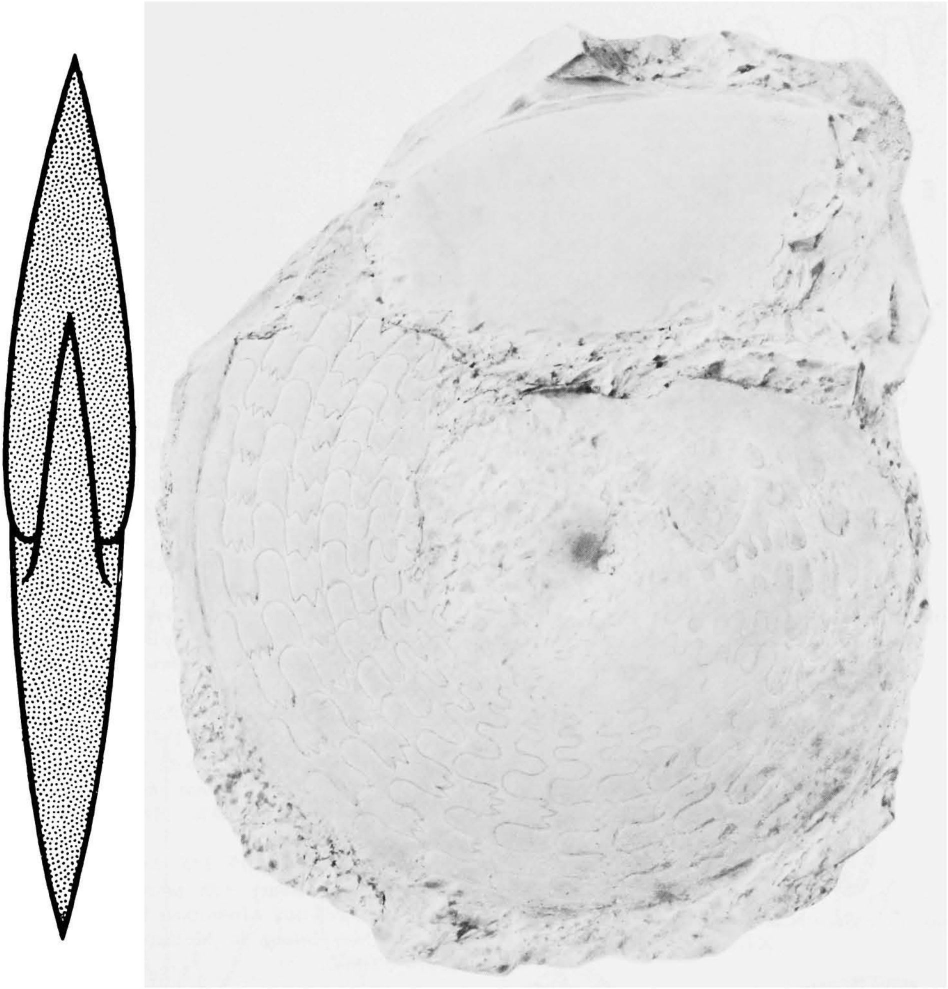


FIG. 113. *Prodromites gorbyi* (MILLER), L.Miss., Mo.; ×1 (110).

Superfamily MEDLICOTTIACEAE Karpinsky, 1889

[*nom. transl. et correct.* MILLER & FURNISH, 1954 (*ex* Medlicottinae KARP., 1889)] [=Pronoritacea HYATT & SMITH, 1905; Pronoritaceae BASSE, 1952]

Discoidal to thinly lenticular conchs with flattened or retuse venter, small umbilici, and commonly ventrolateral nodes or ribs. Sutures have modified 1st lateral lobe or saddle or both and form a series of undivided or bifid auxiliary lobes (50,64,65, 66, 83a). *L.Carb.(U.Miss.)-U.Trias.*

Family PRONORITIDAE Frech, 1901

[*ex* Pronoritinae]

Conch discoidal with no prominent sculpture. Sutures with trifid ventral lobe, large bifid 1st lateral lobe, and characteristically unmodified 1st lateral saddle (50,65). *L. Carb.(U.Miss.)-M.Perm.*

Pronorites MOJSISOVICS, 1882 [**Gon. cyclolobus* PHILLIPS, 1836] [=*Ibergiceras* KARPINSKY, 1889; *Subpronorites* TCHERNOW, 1907; *Megapronorites* RUZHENCEV, 1949]. Sutures with prongs of 1st lateral lobe not subdivided (21,78). *L.Carb.(U. Miss.)-U.Carb.(Penn.),* Eurasia-N.Afr.-N.Am.-S. Am.——FIGS. 10*A;* 117. *P. arkansasensis* SMITH, L.Penn., Okla.; 10*A,* ×1; 117, ×0.9.

Stenopronorites SCHINDEWOLF, 1934 [**Pronorites cyclolobus uralensis* KARPINSKY, 1889]. Like *Pronorites* but has ventral ribs (50). *U.Carb.(U. Penn.),* Urals-Kans.

Tridentites RUZHENCEV, 1936 [**Pronorites tridens* SCHMIDT, 1925]. Like *Pronorites* but suture with dorsal prong of 1st lateral lobe bifid. *L.Carb.,* Belg.

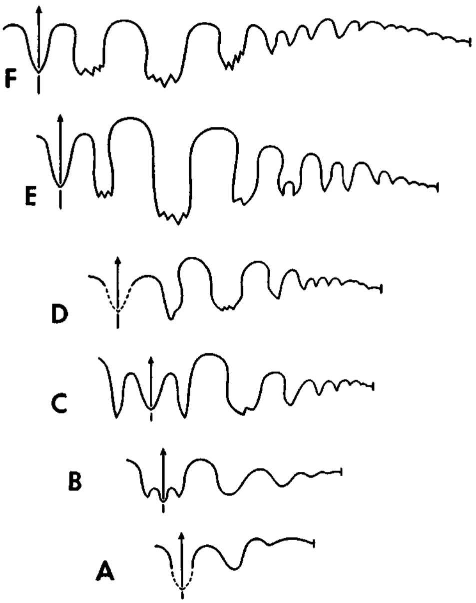


FIG. 114. Ontogeny of sutures in *Prodromites gorbyi* (MILLER), L.Miss., Mo.; enlarged (48).

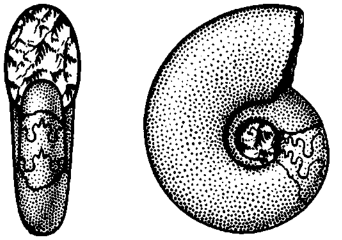


FIG. 115. *Boesites texanus* (BÖSE), U.Penn., Tex.; ×1.5 (110).

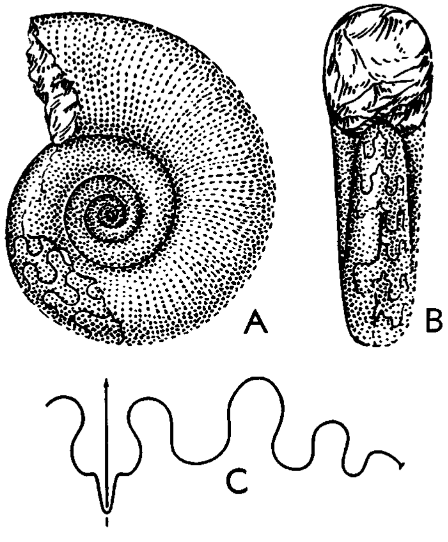


FIG. 116. *Epicanites loeblichi* MILLER & FURNISH, U. Miss., Okla.; *A,B,* ×5; *C,* ×15 (110).

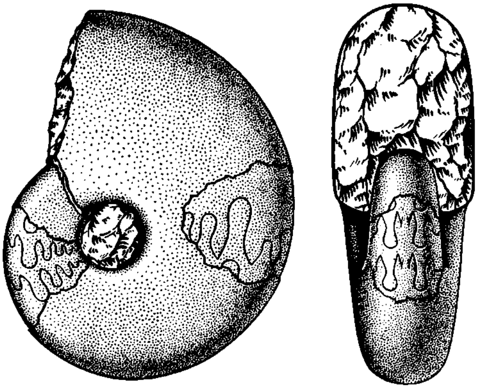


FIG. 117. *Pronorites arkansasensis* SMITH, L.Penn., Okla.; ×0.9 (110).

Neopronorites RUZHENCEV, 1936 [**Parapronorites permicus* TCHERNOW, 1907] [=*Sakmarites* RUZH., 1936; *Epipronorites* MAXIMOVA, 1938; *Shikanites* RUZH., 1938; *Metapronorites* LIBROVITCH, 1938]. Like *Pronorites* but suture with prongs of 1st lateral lobe and adjacent lateral lobes serrate (50,65, 66). *U.Penn.-M.Perm.,* Urals-Bukhara-Timor-W. Tex.——FIG. 118*A*. **N. permicus* (TCHERNOW), M.Perm., Urals; ×10 (85).——FIG. 118*B*. *N. bakeri* MILLER & FURNISH, L.Perm., Tex.; ×8.

Parapronorites GEMMELLARO, 1887 [**P. konincki*]. Like *Pronorites* but suture with prongs of 1st lateral lobe and several adjacent lobes bifid (24). *M. Perm.,* Sicily-Timor.——FIG. 118*C*. **P. konincki,* Sicily; enlarged (24).

Sundaites HANIEL, 1915 [**S. levis*]. Like *Parapronorites* but suture with prongs of 1st lateral lobe undivided and adventitious lobe in 1st lateral saddle. May belong in Medlicottiinae (30). *M. Perm.,* Timor.

Family MEDLICOTTIIDAE Karpinsky, 1889

[*ex* Medlicottinae]

Conch discoidal to thinly lenticular and with flattened or retuse venter. Sutures with narrow ventral lobe and modified 1st lateral saddle (50). *U.Carb.(L.Penn.)-L.Trias.*

Subfamily UDDENITINAE Miller & Furnish, 1940

Discoidal conch. Sutures with auxiliary lobes undivided. Transitional between pronoritids and typical medlicottiids (50,51,65). *U.Carb.(Penn.).*

Uddenites BÖSE, 1919 [**U. schucherti*]. Venter retuse. Sutures with ventral portion of 1st lateral lobe intermediate in depth (50,65). *U.Carb.(U. Penn.),* Tex.-Urals.——FIG. 10*C*. **U. schucherti,* Tex.; ×5.

Prouddenites MILLER, 1930 [**P. primus*] [=*Daix-*

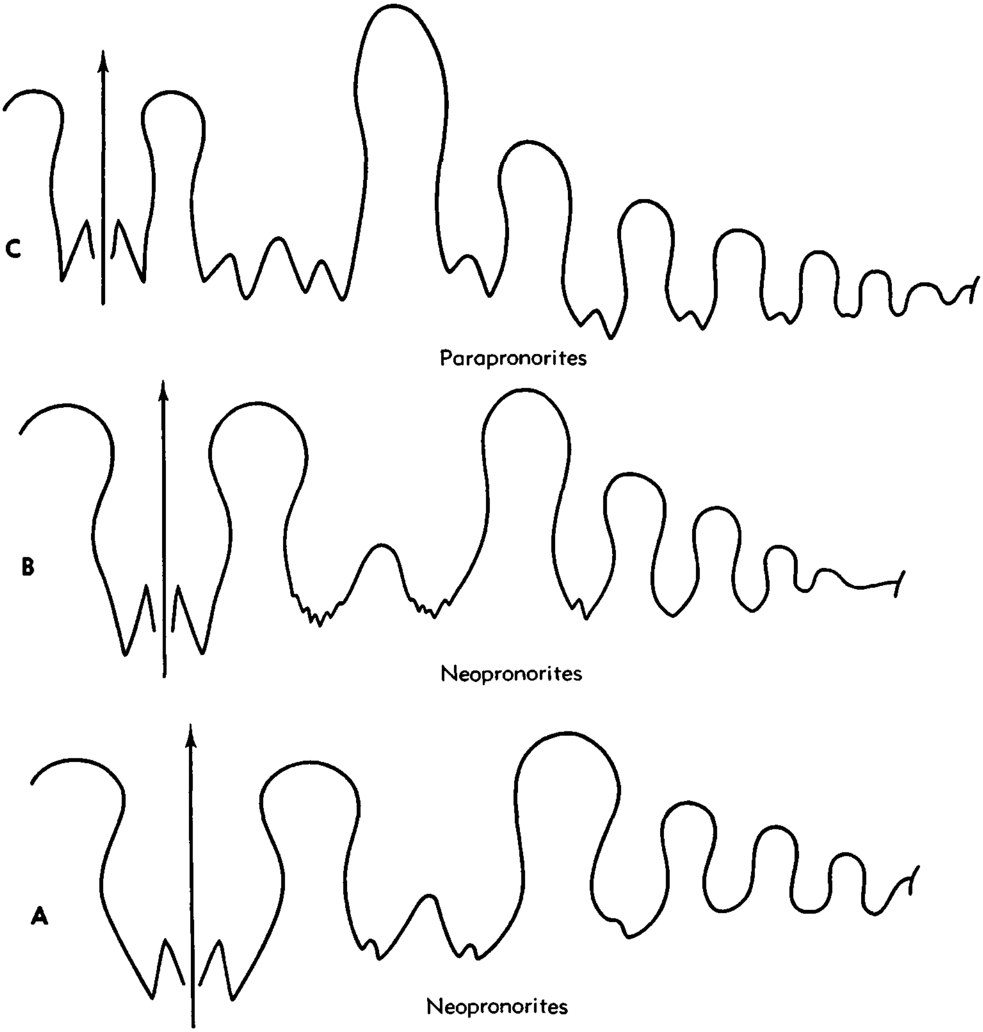


FIG. 118. Sutures of *Neopronorites (A,B)*, ×10, ×8 (85); *Parapronorites (C)*, enlarged (24).

ites RUZHENCEV, 1941; *Uralopronorites* LIBROVITCH, 1947]. Venter flattened. Sutures with 1st lateral lobe unequally trifid. Intermediate between *Pronorites* and *Uddenites* (51,65). *L.Penn.-U.Penn.*, Tex.-Okla.-Kans.-Mo.-Urals.——FIGS. 10*B;* 119. **P. primus*, U.Penn.; 10*B*, ×4 (Tex.); 119, ×1.5 (Okla.).

Uddenoceras MILLER & FURNISH, 1954 [**Uddenites oweni* MILLER-F., 1940]. Like *Uddenites* but ventrolateral portion of suture forms broad saddle (50,65). *U.Penn.*, Tex.-Urals.——FIGS. 10*A'-C',D;* 120. **U. oweni* MILLER-F., Tex.; 10*A'-C'*, ×10; 10*D*, ×5; 120*A,B*, ×2; 120*C*, ×3.

Subfamily MEDLICOTTIINAE Karpinsky, 1889

[*pro* Medlicottinae]

Discoidal to thinly lenticular conch with

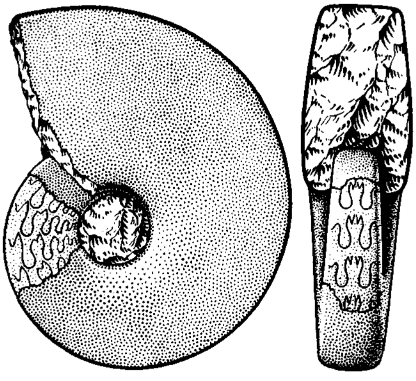


FIG. 119. *Prouddenites primus* MILLER, U.Penn., Okla.; ×1.5 (110).

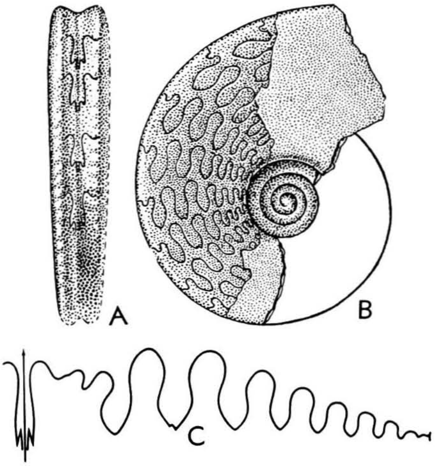


FIG. 120. *Uddenoceras oweni* MILLER & FURNISH, U.Penn., Tex.; *A,B,* ×2; *C,* ×3 (110).

retuse venter. Sutures with bifid auxiliary lobes (24,30,50,64). *U.Carb.(U.Penn.)-L. Trias.*

Medlicottia WAAGEN, 1880 [**Gon. orbignyanus* DE VERNEUIL] [=*Eumedlicottia* SPATH, 1934; *Neogeoceras* RUZHENCEV, 1947]. Thinly lenticular conch, characteristically without prominent ventrolateral sculpture. Sutures with 1st lateral saddle high and digitate (50,64). *L.Perm.-U.Perm.,* widespread.——FIG. 121. *M. whitneyi* BÖSE, M.Perm., Tex.; ×1.3.

Artinskia KARPINSKY, 1926 [**Gon. falx* EICHWALD, 1857] [=*Prosicanites* TCHERNOW, 1907 *(nom. nud.); Prosicanites* TOUMANSKY & BORNEMAN, 1937; *Synartinskia* RUZHENCEV, 1939; *Akmilleria* RUZH., 1940; *Aktubinskia* RUZH., 1947]. Discoidal conch with ventrolateral nodes. Sutures as in *Medlicottia* but more primitive (50,64,66). *U. Penn.-M.Perm.,* widespread in Eurasia-SW.USA. ——FIG. 122. **A. falx* (EICHW.), M.Perm., Urals; *A,B,* ×1; *C,* ×2.

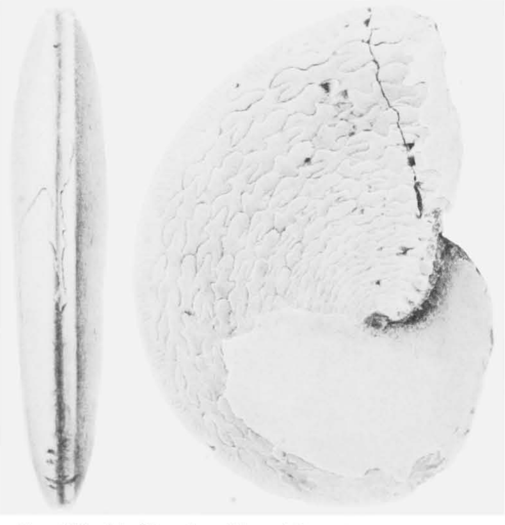


FIG. 121. *Medlicottia whitneyi* BÖSE, M.Perm., Tex.; ×1.3 (110).

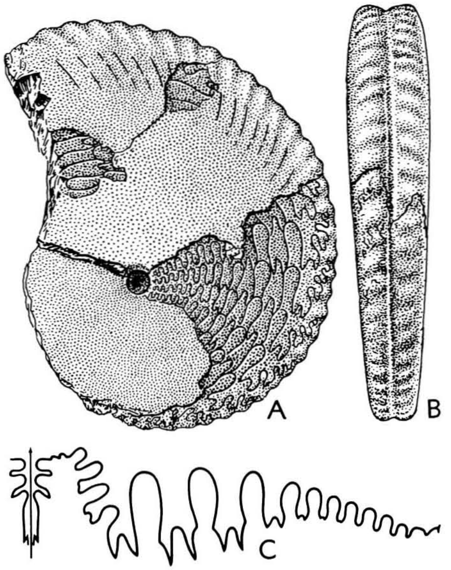


FIG. 122. *Artinskia falx* (EICHWALD), M.Perm., Urals; *A,B,* ×1; *C,* ×2 (110).

Propinacoceras GEMMELLARO, 1887 [**P. beyrichi*] [=*Artioceras* RUZHENCEV, 1947]. Like *Artinskia* but sutures with 1st lateral saddles lower, broader, and lacking subdivisions on ventral flank (24,50). *M.Perm.,* widespread in Eurasia-N.Am.

Episageceras NOETLING, 1904 [**Sageceras (Medlicottia) wynnei* WAAGEN, 1887]. Like *Medlicottia* but broader conch and sutures with smaller 2nd lateral lobe (93; SPATH, 1934). *U.Perm.-L.Trias.,* SaltR.-Himal.-?Japan-Timor-Madag.

Sicanites GEMMELLARO, 1887 [**Medlicottia schopeni* (=*S. mojsisovicsi*) GEMM., 1887]. Like *Medlicottia* but sutures with enlarged adventitious lobe in 1st lateral saddle (24,50). *M.Perm.,* Sicily-?Croatia-Timor.

Family SAGECERATIDAE Hyatt, 1900

Conch thinly lenticular or discoidal. Sutures ceratitic, with series of adventitious lobes in 1st lateral saddle (83a). *L.Trias.-U. Trias.*

Sageceras MOJSISOVICS, 1873 [**Gon. haidingeri* HAUER, 1847]. Lenticular conchs with flattened bicarinate venter and small umbilici. Sutures form numerous subequal auxiliary and adventitious lobes (SPATH, 1934). *M.Trias.-U.Trias.,* S.Eu.-Tur-

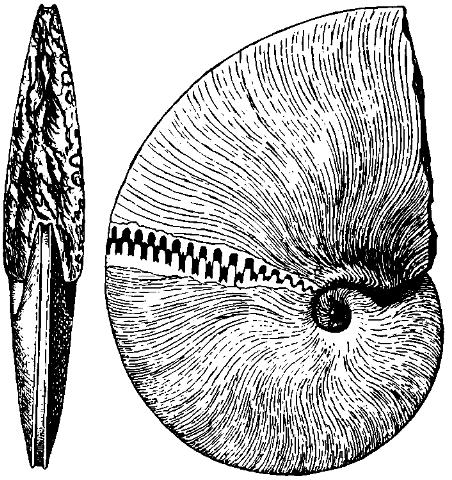


FIG. 123. *Sageceras haidingeri* (HAUER), U.Trias., Aus.; ×1 (115).

key-Timor.-W.USA.——FIG. 123. **S. haidingeri* (HAUER), U.Trias., Aus.; ×1 (115).

Pseudosageceras DIENER, 1895 [**P. multilobatum* NOETLING, 1905] [=*Frechiceras* KRAFFT, 1902; *Metasageceras* RENZ & RENZ, 1948]. Like *Sageceras* but has narrow angular or retuse venter and closed umbilicus (83a). *L.Trias.,* E.Sib.-S.China-Timor-Himal.-SaltR.-Balkans-Spitz.-W.USA.

Cordillerites HYATT & SMITH, 1905 [**C. angulatus*]. Like *Sageceras* but umbilicus closed and sutures with lobes not subequal (HYATT & SMITH, 1905). *L.Trias.,* W.USA-Greece.

Parasageceras WELTER, 1915 [**P. discoidale*]. Like *Sageceras* but discoidal conch with rounded venter and closed umbilicus (WELTER, 1915). *M.Trias.,* Timor.

UNRECOGNIZED GENERIC NAMES APPLIED TO PALEOZOIC AMMONOIDEA

Aganides DE MONTFORT, 1808. Type, which was not named specifically, is of uncertain derivation and affinities. The nautiloid generic name *Aturia* BRONN, 1838, may be a junior synonym.

Prehoffmannia PLUMMER & SCOTT, 1937 [**P. milleri*]. Sutures unknown; type small and probably immature. *U.Penn.,* Tex.

Pseudonomismoceras FRECH, 1899 [**P. silesiacum*]. Type specimen small, evolute. Sutures unknown (78). *L.Carb.,* Ger.

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(109) **Kobold, Albrecht**
(110) **Miller, A. K., & Furnish, W. M.**
(111) **Quenstedt, F. A.**
(112) **Raymond, P. E.**
(113) **Ruzhencev, V. E.**
(114) **Schindewolf, O. H.**
(115) **Zittel, K. A. von**

MESOZOIC AMMONOIDEA

By W. J. Arkell, Bernhard Kummel, and C. W. Wright

CONTENTS

INTRODUCTION TO MESOZOIC AMMONOIDEA

By W. J. ARKELL

Although the Ammonoidea appeared in the Early Devonian and did not become extinct until the end of the Cretaceous, our knowledge of them is confined almost entirely to the hard parts, the shells and (more rarely) opercula. The soft parts are completely unknown, except for such inferences as can be drawn from the living chambers of the shells they inhabited (which very rarely retain vague muscle scars) and from distribution of the shells in time and space and their ecological associations (Fig. 124). Not even any tracks are definitely attributable to the animals. It follows that classification of the ammonoids, and even their position in the Tetrabranchiata, is to a large extent conjectural and tentative. Nevertheless, their extreme abundance, world-wide distribution, multiplicity of forms, and rapidity of evolution, make them almost ideal zonal fossils and justify the great amount of attention they have received.

MORPHOLOGY

GENERAL FEATURES OF SHELL

The shell is univalve, coiled, normally in a plane spiral but also in a variety of other ways or nearly straight, and is generally assumed to have been external, though arguments have been put forward for supposing that certain types were internal. It forms an elongated cone, divisible into 3 main sections: the **protoconch** or initial chamber; a long camerate portion or **phragmocone;** and a single large terminal **body chamber,** which in at least many genera is known to have been closed by a separate, simple or compound operculum, the **aptychus** (Fig. 124). In size the adult shells vary from about a centimeter to extremes of up to nearly 3 meters in diameter. The phragmocone and body chamber together constitute the **conch,** as opposed to the small initial chamber, the protoconch.

The whole of the shell substance, or **test,** with minor exceptions mentioned below, is calcareous. By analogy with *Nautilus* shell, and from the fact that fossil ammonite shells have frequently been removed by solution while incrusting oysters and serpulids, which are known to be of calcite, remain intact, it is inferred that ammonoid shells were of aragonite. Commonly the aragonite has been replaced by secondary calcite, but studies of some shells based on refraction (39a, p. 323) and x-rays (375a) have demonstrated the persistence of primary aragonite. The **siphuncle** tube (see below), however, is phosphatic, and many aptychi are carbonaceous, probably in life being at least partly chitinous ("horny"), though basically composed of calcite. The test is generally made up of 2 shelly layers, of which the outer is lamellar and the inner is prismatic and much thinner (39a). The total thickness of the test varies widely and seems to be of

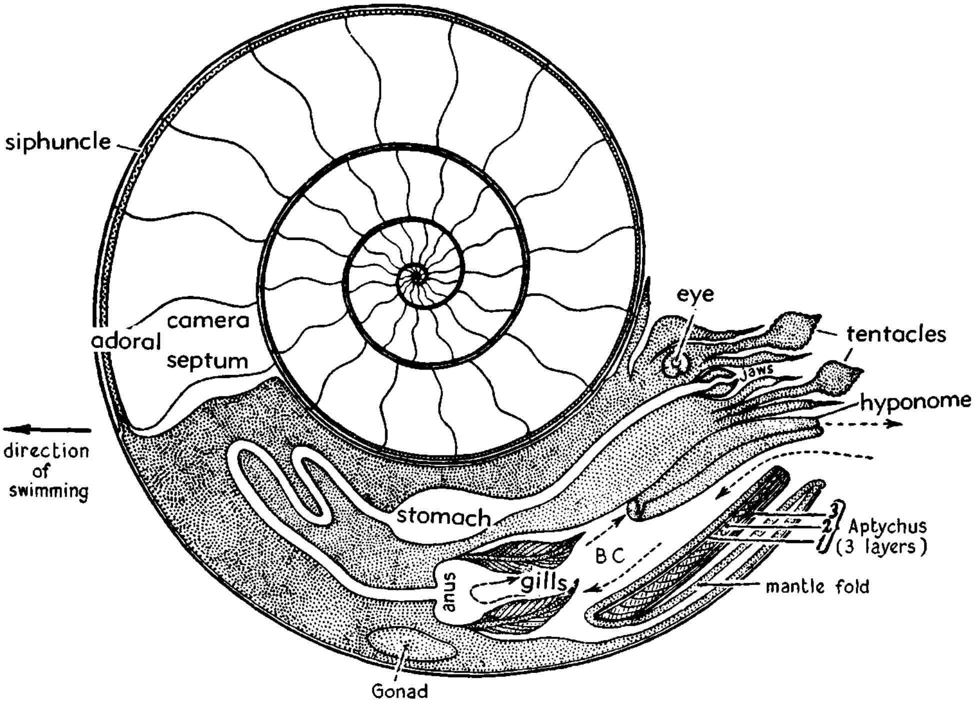

FIG. 124. Median section of ammonite shell in the plane of coiling, showing the septate phragmocone with siphuncle, and the body chamber, the whole in the supposed position in life. In the body chamber is a hypothetical "reconstruction" of the animal, based on analogy with living *Nautilus,* as envisaged by M. SCHMIDT and F. TRAUTH, with a cross section of the aptychus in its inferred retracted position on the ventral side of the body chamber. The arrows show water circulation to the gills and out through the hyponome. *BC,* bronchial chamber of mantle cavity (509).

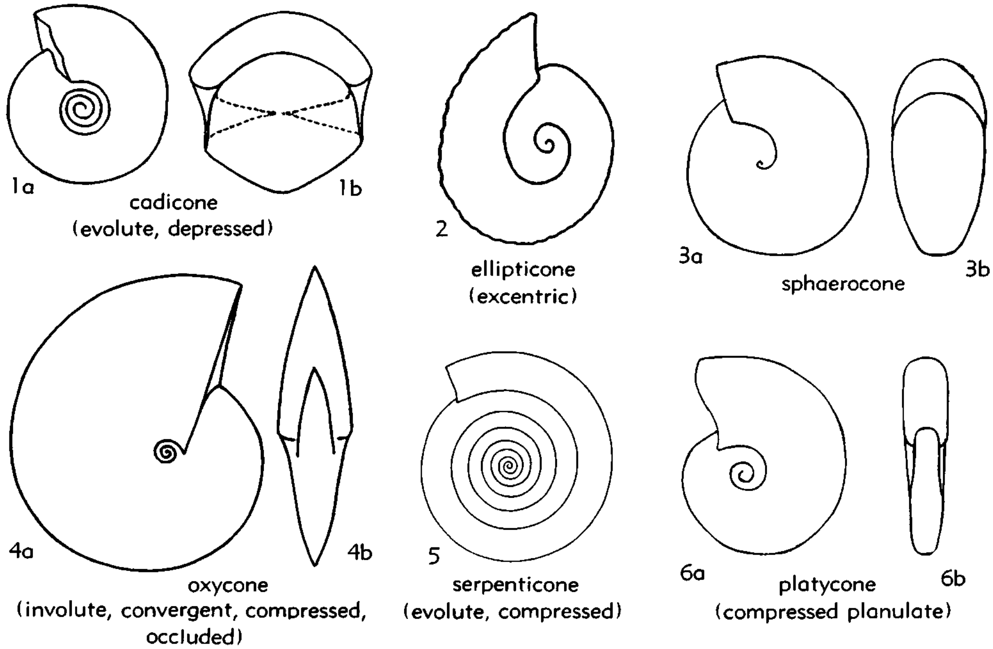

FIG. 125. Types of coiling in ammonoid conchs; planispiral forms (583, 650).

little systematic importance. As a rule, it is very thin in the suborders Phylloceratina and Lytoceratina, but in some species of *Lytoceras* it is as thick as in most other ammonites. In parts of some large forms of Ammonitina the thickness may reach 1 cm. During solution of the test, recrystallization sometimes results in leaving small crystals of calcite or, more rarely, nests or groups of minute calcite pyramids, called **conellae,** attached to the natural internal mold. Conellae occur chiefly under hollow keels and tubercles, where they result from diagenetic chemical change of a late-formed shell layer secreted after withdrawal of the mantle from parts of the primary test (195,196) (Fig. 136).

The typical ammonoid is tightly coiled in a plane spiral about the protoconch. Each coil or volution is called a **whorl.** The concave surface on each side enclosed by the last whorl is called the **umbilicus,** and the coiling is said to be **evolute** or **involute** according to whether the umbilicus is wide or narrow. These terms are vague and relative, varying with the style of coiling normal for different famiiles or genera. Another way of assessing them is by the degree to which the whorls overlap one another. A typically coiled ammonoid shell, neither evolute nor involute, neither compressed nor inflated, is called **planulate.** More inflated forms are **sphaerocones** or **cadicones;** more compressed forms are **platycones** or **oxycones** (see glossary and Fig. 125).

Some forms develop elliptic coiling in the last whorl **(ellipticones).** Some are not tightly coiled at the center, where there is an umbilical perforation; others begin to uncoil with the last whorl. These and other more aberrant forms are known as **heteromorphs** (Fig. 126). Definitions of the principal forms will be found in the glossary under **cyrtocone, gyrocone, helicoid,** and **torticone** (Figs. 125, 126). As in gastropods, the great majority of ammonoids are coiled in the same direction, which is assumed to be dextral, but a few are sinistrally coiled.

In describing features of the conch, those which are nearer to the apex or protoconch are called **adapical,** those which are nearer the aperture are called **adoral.** These terms are also used in a directional sense: for instance, "the whole cone enlarges adorally, from the first or adapical chamber." For the walls of the conch and for directional indi-

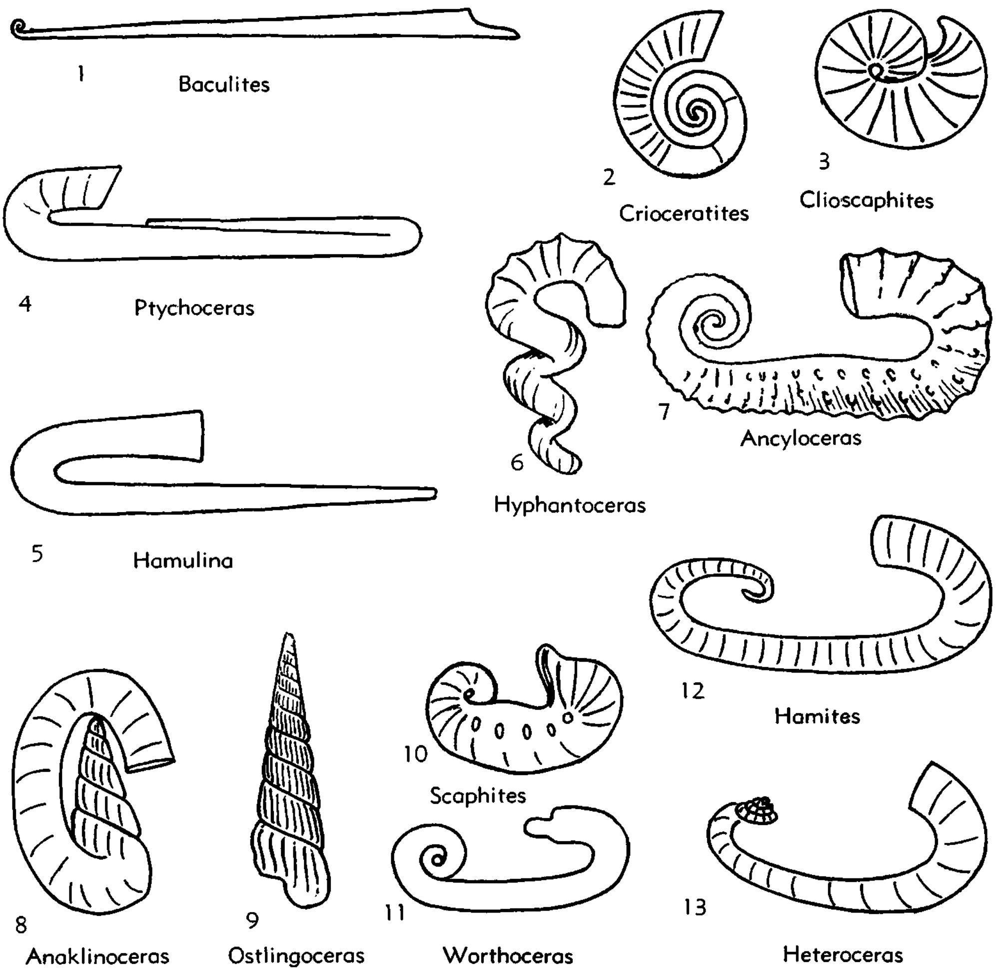

Fig. 126. Types of coiling in ammonoid conchs; heteromorphs (735).

cations at right angles to the long axis, the conventional terms **ventral** and **dorsal** and left and right whorl sides are used, based on the assumption that in normally coiled forms the animal was orientated as in living *Nautilus,* with the dorsum towards the center of the coil and venter outwards (Fig. 124). Thus, the periphery of the ammonite is the **venter** and the opposite side is the **dorsum** (Fig. 127). There is evidence to show that in life, as with living *Nautilus,* the **aperture** must normally have lain at the underside, though facing horizontally or upward (523). The dimensions usually measured are the same for Mesozoic as for Paleozoic ammonoids and have been explained in the first part of this volume (Fig. 124).

PROTOCONCH

All ammonoid shells begin with a globular or barrel-shaped embryonic chamber, the **protoconch,** which forms the apex of the cone and is different in character from all subsequent chambers (Fig. 128). Its longer axis is normal to the plane of coiling, and generally it is wider than the initial (1st postembryonic) chamber of the conch. It is separated adorally from the conch by the **prosiphon** and 2 **prosepta,** which appear to be continuous with the shell wall instead of cemented to it as are the true septa (Fig. 129). The shell wall ends in a blind projection, the **flange** ("internal ridge" of Grandjean, 1910).

PHRAGMOCONE

The **phragmocone** (Figs. 124,130) comprises the bulk of the ammonoid shell and gives it the characteristic chambered appearance. The chambers, or **camerae,** are divided by a series of more or less regularly spaced walls, or **septa.** These were laid down presumably by the mantle of the animal, which moved forward periodically as the shell grew. The septa become gradually more widely spaced (absolutely, not relatively) until maturity, after which they tend to become crowded, or **approximated.** This fact affords a method of recognizing a mature shell.

The septal edges, where they join the inside of the walls of the whorl, are on the whole simple in primitive ammonoids and in the earliest growth stage of all ammonoids, and they become more complex and frilled in the adult of more advanced types. Some late types, however, show reversionary simplification. The pattern formed by the septal edges, or **sutures,** is an important systematic character and has been much studied: the septal sutures, therefore, are dealt with in a separate section.

All the septa of the phragmocone are pierced by a hollow tube, the **siphuncle,** which runs through all the camerae and opens into the body chamber (Figs. 124, 130). It consists of a phosphatic tube or sheath which enclosed a membranous organ not preserved in the fossil state except sometimes as a structureless, carbonaceous mass (?conchiolin). The siphuncle begins with a bulblike sac, the **caecum,** which occupies most of the initial chambers (Fig. 129). In the earliest whorls, the position of the siphuncle is unstable and it may wander from central or dorsal to ventral (Spath, 1933, 1950), but in general it settles down to a dorsal position in the clymenias and to a ventral position in all other ammonoids (Figs. 124, 130). As growth proceeds it enlarges relatively little and soon occupies a very much smaller proportion of the whorl. Mineralization of the sheath appears to have lagged behind general shell growth, for in both young and old ammonoids the phosphatic tube is absent in the last-formed camerae, although the septa are pierced. The number of camerae without the tube increases with age of the individual and may reach from a half to a whole whorl (Trueman, 1920).

At the opening in each septum **(septal foramen)** where the siphuncle passes through, the edges of the foramen are produced in a ringlike extension called the **septal neck** or **septal funnel,** which surrounds and clasps the siphuncle. In primitive ammonoids, as in nautiloids, the septal necks project adapically and are called **retrochoanitic;** in more advanced forms the septal necks begin from early adolescence to be projected adorally **(prochoanitic).**

BODY CHAMBER

The **body chamber,** or living chamber, is distinguished from the rest of the conch by being nonseptate (Fig. 124). It varies greatly

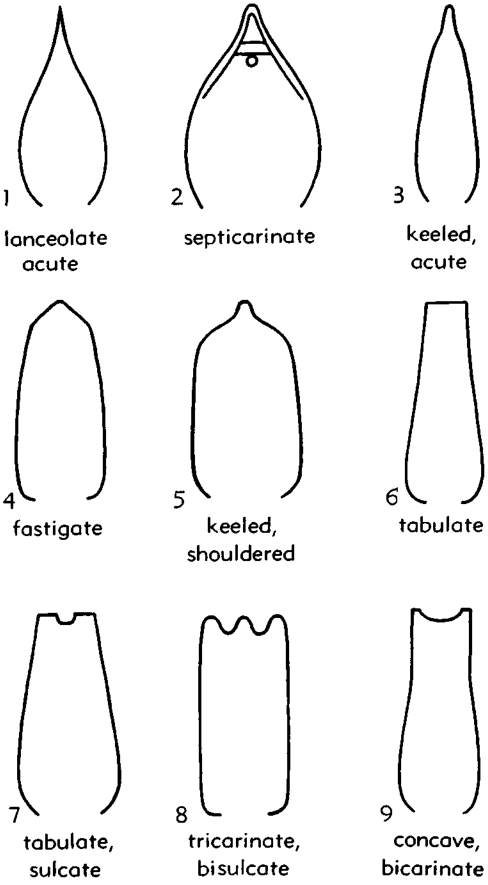

Fig. 127. Types of whorl sections and venters of ammonoid conchs (583,650).

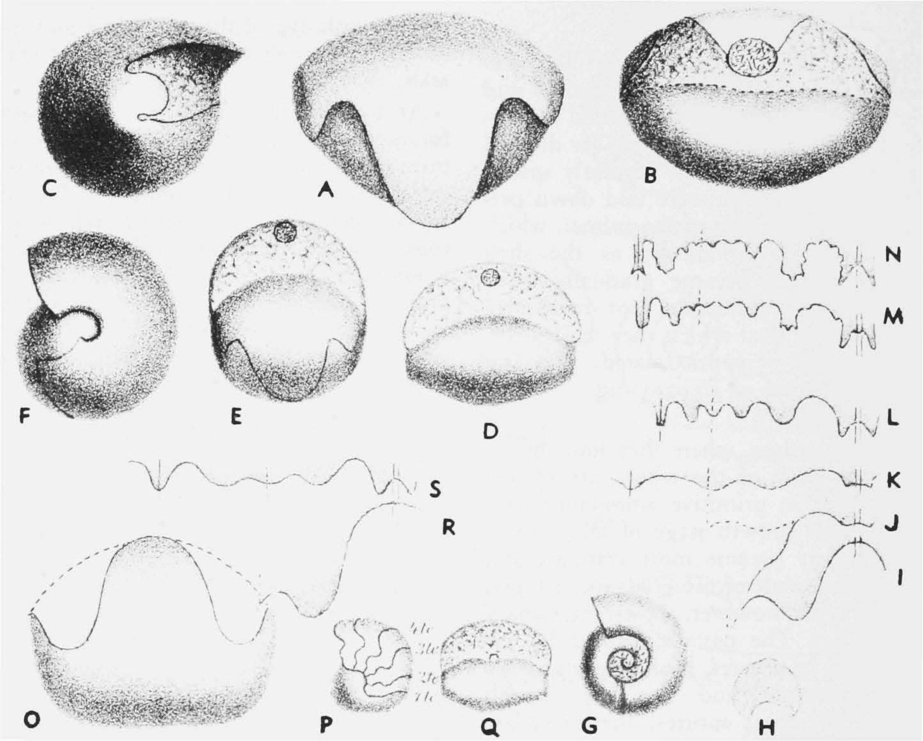

FIG. 128. Protoconchs and early sutures of Jurassic and Cretaceous ammonoids (47).——*A-N, Oxynoticeras,* L.Jur.(Sinem.); *A-C,* protoconch from above, front, and side; *D,* appearance at diameter of 0.6 mm.; *E,F,* at diameter of 0.8 mm.; *G,* conch with 1st constriction; *H,* whorl section at diameter of 4 mm.; *I-K,* 1st 3 sutures; *L-N,* sutures at diameter of 2.5 mm., 5 mm., and 11 mm.——*O-S, Hysteroceras,* L.Cret.(Alb.); *O,* protoconch from above; *P,Q,* appearance at 6th suture; *R,* 1st suture; *S,* 3rd suture. (Much enlarged.)

in length in different groups, from less than half a whorl to more than a whorl and a half, but in most ammonites the length is between half a whorl and one whorl. In some forms it tends to decrease in length with growth, but in others its length relative to whorl length remains constant, as does its volume relative to that of the phragmocone. As a rule there is an inverse relation between length of body chamber and area of whorl section, the longest body chambers being usually found in many-whorled, evolute planulates. Owing to the fact that there were no septa to obstruct the passage of mud into the body chamber after decay of the animal, it often happens that the body chamber alone is preserved in its original form, whereas the phragmocone, with its hollow camerae or partial filling of secondary calcite crystals, was crushed; in other circumstances, however, especially in shales, phragmocones are pyritized and intact but body chambers crushed and destroyed.

Very rarely, natural internal molds of the body chamber show more or less obscure muscle scars (90,227,545).

Commonly, but not invariably, the adult body chamber undergoes modifications of form. The commonest is contraction of the whorl section, which generally begins at the dorsum. Consequently, it is common for the ventral (outer) surface to continue in the normal spiral while the inner edge of the last whorl **(umbilical seam)** departs from the spiral and runs out tangentially, either gradually or abruptly. The venter also may develop a hump or knee bend. Such excentric coiling of the last whorl or last half or quarter whorl may take many forms (Figs. 125, 126). All are evidence of a mature shell. The contraction is often seen to be accompanied by modification or disappearance of ornament.

APERTURE AND PERISTOME

Many ammonites have a simple apertural

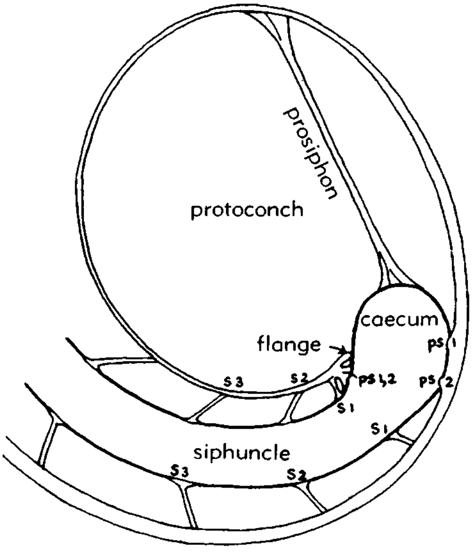

FIG. 129. Median section at apex of *Sphaeroceras,* M. Jur., in plane of coiling, much enlarged (*ps1,* 1st proseptum; *ps2,* 2nd proseptum; *s1, s2, s3,* 1st 3 septa) (178).

margin, or **peristome,** at all growth stages. In these forms the body chamber simply ends like a severed tube, or else the end is marked by a simple contraction, or by a contraction and raised band or collar, and in some shells, with a narrow liplike extension of the ventral area. Many other forms, however, identical with the simple forms in almost every particular, have a greatly modified or elaborated peristome (Fig. 131). The commonest adjunct to the aperture is a pair of **lappets,** one on each side. These are flaplike, or elongate, digitate, or necked (spatulate) extensions of the shell. In some forms they are nearly a quarter whorl in length, and they may be directed outward and dorsally so as to embrace the sides of the preceding whorl, or inward so as to touch at the extremities and divide the aperture into 2 parts. With or without these, a ventral extension of the lip may form a **ventral lappet;** or the ventral extension may be developed as a long, tapering **rostrum,** which can be straight or recurved like a horn, or even recoiled. Such apertures contrast strongly with those of many Paleozoic goniatites and clymenias, which have a hyponomic sinus on the venter, as in nautiloids. In some extreme forms of Jurassic age (*Oecoptychius,* Callov.), long spatulate lappets are accompanied by a modified rostrum which ends in a hooded structure shaped like a tea cozy. In such forms the aperture is divided into 3 parts, and the movement of the animal must have been much restricted. In some others (*Ebrayiceras,* Bath.), 2 digitate ventral lappets join projections of the greatly extended lateral lappets and between them almost completely close the aperture, leaving 5 small holes (130).

DIMORPHISM

It is a remarkable fact that all ammonites with lappets (but not necessarily those with rostra) are smaller than those with simple aperture which most closely resemble them in other respects. In the Mesozoic, especially in the Middle and Upper Jurassic, there is repeated dimorphism in nearly all families: large forms with simple or merely contracted apertures are found side by side with small forms bearing lappets. The size ratio is commonly 1:1.5 or 1:2, but it may be even more. This fact early led to the suggestion (529) that lappets were a feature of

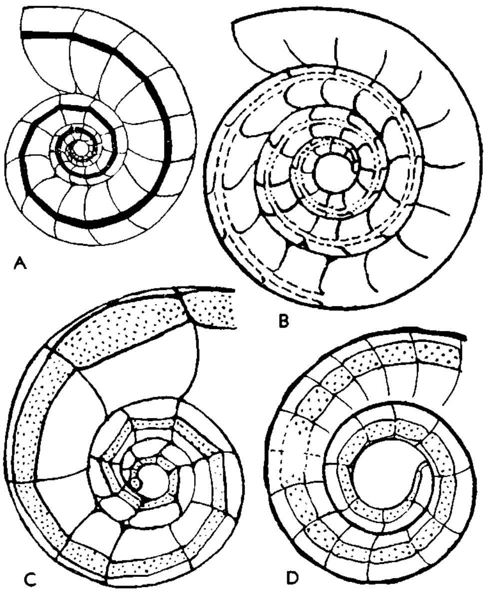

FIG. 130. Median sections through inner whorls of ammonoid conchs which show wandering in position of the siphuncle in early ontogeny (713). *A, Lissoceras,* ×20; *B, Leiophyllites,* ×28; *C, Strigoceras,* ×28; *D, Tropites,* ×40. In *B,* the siphuncle is external in the 1st 3 camerae but in others its initial position is internal, later wandering about until it settles into an external position.

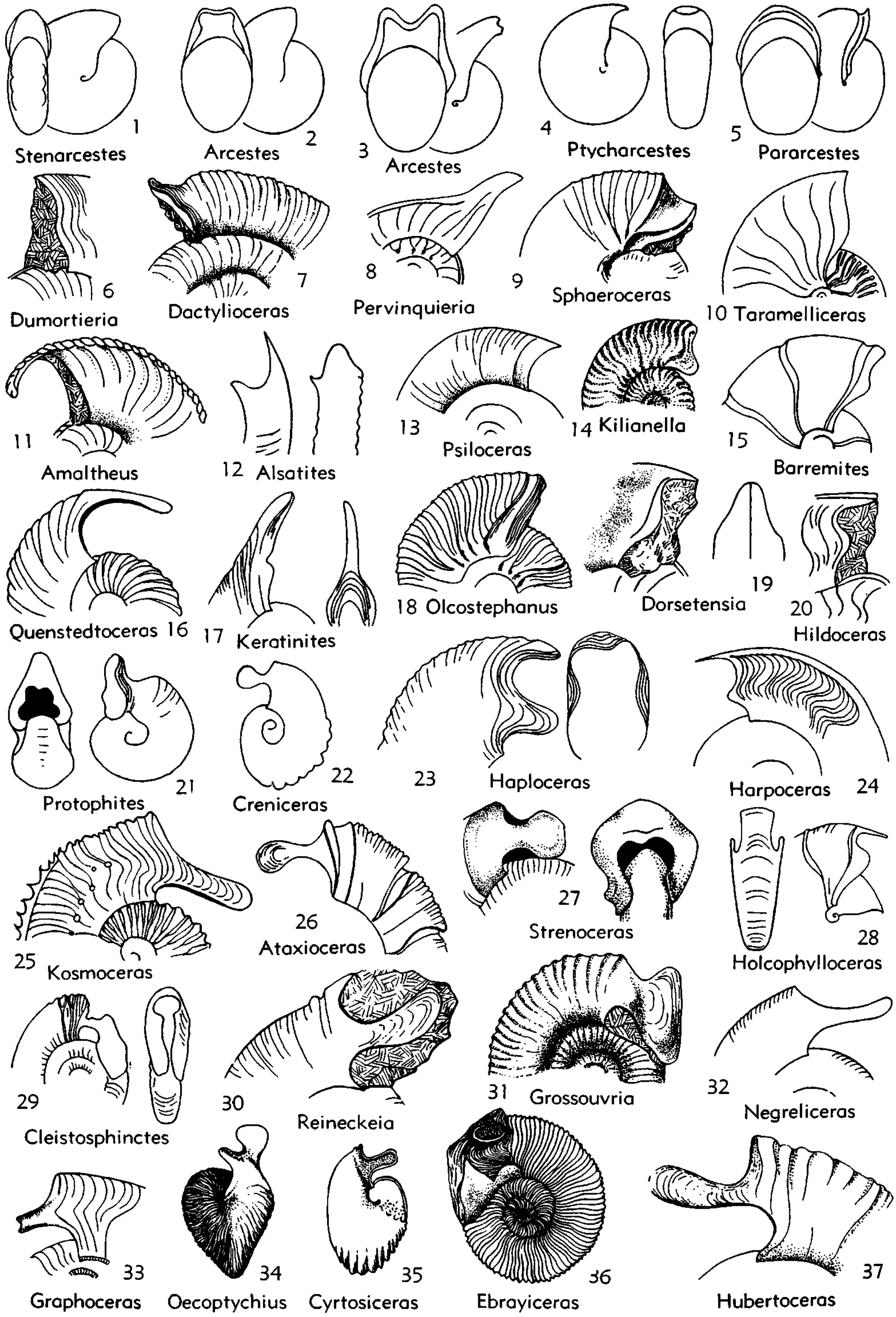

Fig. 131. Types of apertures in ammonoid conchs (650).

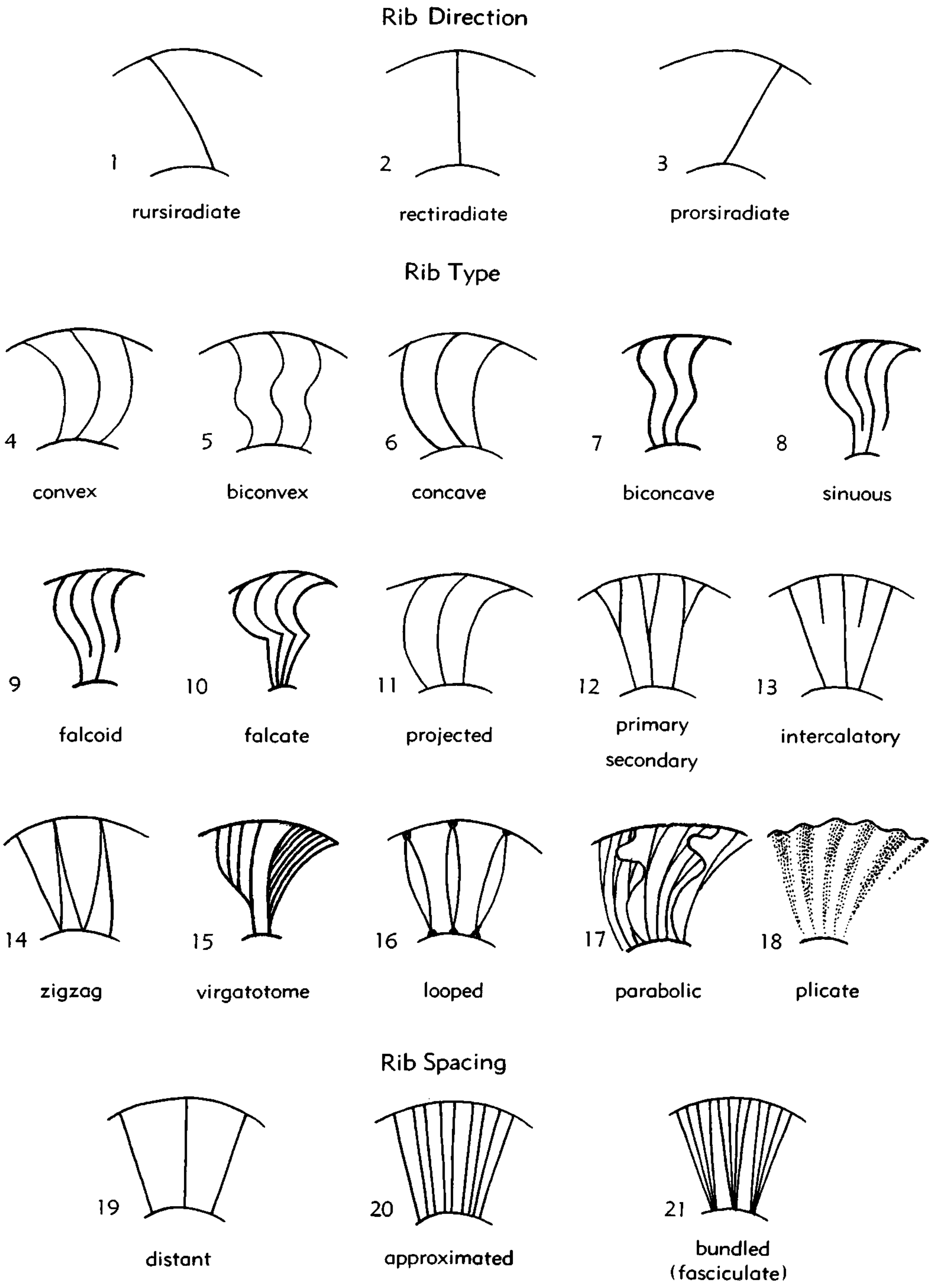

FIG. 132. Types of ribbing on ammonoid conchs (650).

the young. But one of the difficulties of this hypothesis is the necessity of assuming that these large structures were repeatedly cast off or resorbed to allow shell growth to proceed. Moreover, all the other indications generally show that the shells with lappets were adult. An exhaustive treatment of the problem by Pompeckj (347) showed that lappets (and elaborated rostra) are features only of maturity. In many species the growth lines and ornament are clearly seen to bend forward on the whorl sides in gradually increasing degree to conform to the shape of the lappet, providing unmistakable evidence for the gradual growth and differentiation of the lappet in maturity.

In the late 19th and early 20th centuries this dimorphism was generally assumed to be sexual. The theory was propounded by Munier Chalmas (305) and was accepted by most of the principal authorities (e.g., Glangeaud, 176; Haug, Rollier, and others). According to the theory, the small forms with lappets were males and the large forms with simple peristome were females, which required a larger body chamber to accommodate their ova. Buckman & Bather (67), however, were sceptical and preferred to regard the lappets and other elaborations of the peristome as features of either gerontism or phylogerontism. One of the objections mentioned by them has since been confirmed; namely, that in living *Nautilus* the male shell is slightly broader and more commodious than the female. It may be objected further that the resemblance of lappets to male claspers of insects is misleading, since the lappets were of rigid shell and some of them met in the middle of the aperture. Their only conceivable function seems to be protective, and it is more likely to have been the female than the male that had delicate organs or ova or young brood in need of protection. It is attractive to seek an analogy in the shell grown by the female argonaut specially to serve as a brood pouch.

There are some families in strata as high as the Middle and Upper Jurassic in which no lappets have been reported (e.g., Macrocephalitidae), and the theory of sexual dimorphism can only be shelved as unproved, until new evidence is forthcoming. Meanwhile lappets are regarded as of at least subgeneric rank in the present classification; an open verdict must be passed for the time being on their function, if any.

ORNAMENT

RIBBING

The surface of even the smoothest ammonites is covered with **growth lines,** each one of which represents a former peristome.

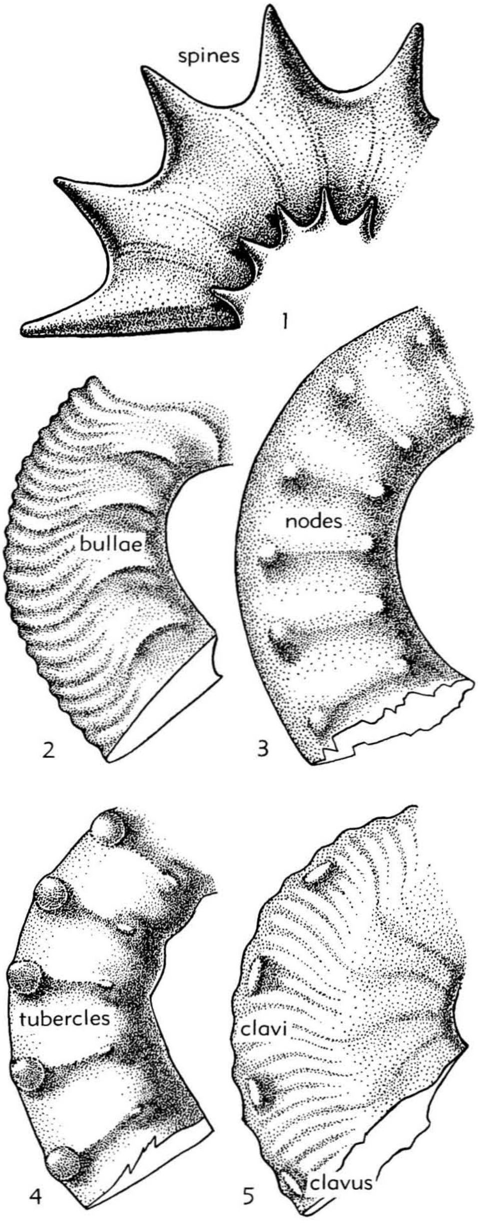

Fig. 133. Types of tubercles on ammonoid conchs (650).

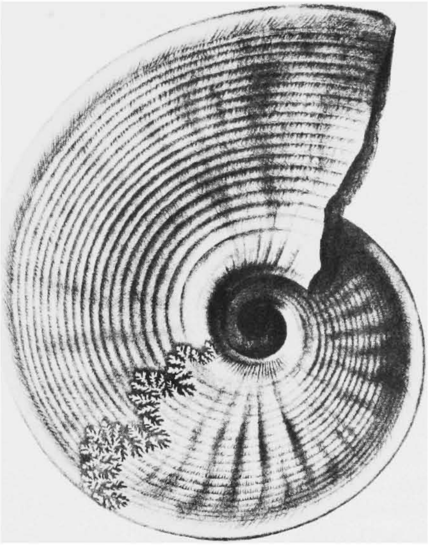

FIG. 134. Strigation as shown on the conch of *Amaltheus pseudamaltheus,* L.Jur.(Pliensb.), Eng. (737).

In many shells the growth lines are accentuated or raised as lamellae, which may be crinkled, or they appear as fine radial lines **(lirae)** or are accompanied by them. Usually the surface is also more or less covered by raised radial **ribs.** Generally these are folds in the test which consequently show almost as strongly on the internal mold, although less sharply. Ribs are not necessarily parallel to the growth lines, and commonly they are quite independent of them. Ribs (Fig. 132) may be simple or branched (**biplicate, triplicate,** etc.), or bundled (**fasciculate**), either close together **(dense)** or far apart **(distant),** straight, curved, flexuous **(sigmoid),** sickle-shaped **(falcate),** or curved forward only at the periphery **(projected);** and their general direction may be radial **(rectiradiate)** or inclined forward **(prorsiradiate)** or backward **(rursiradiate).** The main stem of a branched rib is called the **primary** and the branches the **secondaries.** A loose secondary (usually, however, joined to a primary on the other side) is an **intercalatory.** Some ribs are flared.

Either on the ribs or independent of them almost any number of rows of **tubercles** may occur (Fig. 133). Tubercles on the internal mold commonly represent spines on the test, and large spines may be hollow. Tubercles or nodes elongated radially are termed **bullae,** those elongated in the direction of coiling are **clavi.** Clavi are commonly found on the venter or ventrolateral edge **(shoulder),** and ribs may be looped to them.

In addition, many ammonites bear spiral systems of ornament: i.e., linear ornament running in the direction of coiling. The umbilicus may have a raised rim; the middle of the whorl sides or the venter may bear a groove or a raised flattened band **(fillet);** or the whole or part of the whorls may be covered with longitudinal lines **(lirae)** or corded or knotted ridges **(strigation)** (Fig. 134).

KEELS

The venter may have one or more raised longitudinal ridges **(keels).** The common form of keel is central and single, but it may be bounded by **furrows,** beyond which a pair of **false keels** may occur, one on each

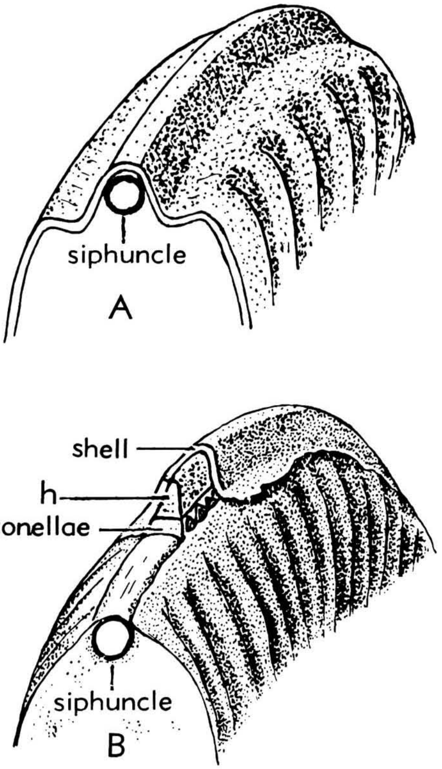

FIG. 135. Cross sections through the keels of ammonoid conchs showing *(A)* open type and *(B)* hollow floored type, in both indicating structure and position of the siphuncle (*h,* hollow keel filled with matrix, conellae appearing in the keel floor) (196).

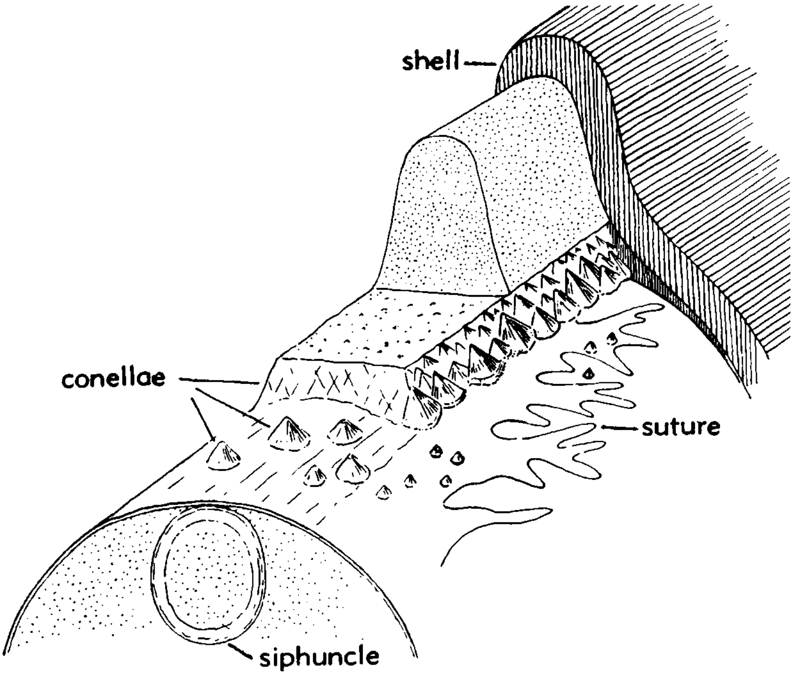

FIG. 136. Diagrammatic dissection of hollow floored keel showing keel floor in various stages of diagenetic dissolution, being converted into conellae, those scattered toward the flank denoting an original lateral extension of the keel floor substance (corresponds to vertically ruled area) (196).

ventrolateral edge. Such a venter is said to be **tricarinate-bisulcate.** The true keel covers the siphuncle and may have protected it. The keel may be solid, or a hollow extension of the shell cavity, or hollow and floored, being separated from the camerae by a shell floor (195, 196) (Figs. 135, 136). The hollow floored keel in some genera is a transient feature in the growth of individuals; it may pass from unfloored to floored and back again before maturity is reached, but in none does the floor continue far over the body chamber. In some forms a keel on early and middle whorls fades and then gives place to a ventral groove on the last whorl (*Semiformiceras,* Tithon.); in others a groove on early whorls gradually fills up and is followed by a tall keel on the last whorl (*Styracoceras,* Callov.). Also, a persistent keel on the test may be represented by a groove on parts of the internal mold (*Schistophylloceras,* Sinem.), such a ventral groove on a mold being deceptively simulated, however, by falling away of the siphuncle. Keels may be **entire** (smooth) or **serrate** or **clavate,** or they may be represented only by a median ventral row of serrations or clavi.

FEATHER STRUCTURE

A rarer kind of ornament that is seldom seen because it is apparently confined to the structure of the inner shell layers occurs on all or the outer half of the whorl sides, chiefly in oxycones; this consists of a band of delicate, forwardly directed chevrons, standing in scarcely perceptible relief and thus generally visible only by low-angle lighting (Fig. 137). It has been figured in some Cretaceous pseudoceratites (*Placenticeras,* HYATT, 1903, p. 222, pl. 47) and in Bathonian and Oxfordian oppeliids (WAAGEN, 1869, pl. 18, fig. 5; PETITCLERC, 1918) and has been observed by ARKELL in a Bajocian *Protoecotraustes* and by WRIGHT an Albian *Beudanticeras* and *Brewericeras.*[1] The explanation is unknown.

COLOR

Traces of color patterns are confined to the outer shell layer and seem to require special preservation—usually in a clay—to

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[1] Since this was written, feather structure has been figured in *Taramelliceras* (Kimm.) (197).

survive (Fig. 138). They take the form of longitudinal brown stripes on a white ground in *Amaltheus, Androgynoceras,* and *Tragophylloceras* (all Pliensb.) (475), and of one or more lateral longitudinal white stripes on brown in *Leioceras* (Baj.) and *Asteroceras* (Sinem.) (GREPPIN, 1898, p. 22). Radial stripes have been noticed in *Pleuroceras* (Pliensb.) (411). Other and bolder patterns occur in Paleozoic straight and curved nautiloids (395).

CONSTRICTIONS AND PARABOLAE

In many ammonites, especially from Jurassic rocks, the phragmocone is periodically constricted. Some shells carry 8 or more **constrictions** on each whorl (Fig. 139). They vary in kind and direction in different families, being definable as **rectiradiate, prorsiradiate, sigmoid,** or **angular**. In phylloceratids they may exhibit a backward knee bend on the whorl sides and a marked sinus, convex forward, on the venter. Some are conspicuous on both test and internal mold; some are prominent on the internal mold but invisible on the test; others correspond to a ridge on the test.

Rather commonly constrictions are accompanied on one or both sides by an oblique simple rib, or a flared or merely oblique simple rib may replace the constriction. Such constrictions or ribs or both commonly cut more or less obliquely across the ordinary ribbing, being more prorsiradiate than the previously formed ribs which they truncate, but parallel to the next-formed ribs. Extreme examples are *Morphoceras* (Baj.-Bath.) and *Spitidiscus* (Neocom.). Such special oblique ribs are distinguished as **parabolic ribs;** with any accompanying irregularities and associated features they are known collectively as **parabolae.**

In many perisphinctids the segment of whorl following a constriction starts larger than the preceding segment **(segmental growth).** From this fact and the new phase of ribbing laid down in a more prorsiradiate direction which starts after each constriction, it is clear that the parabolae represent growth halts. They are not, however, the same as the peristomes of the adult shell, for often no such constrictions or other features may be found at the end of the adult body chamber.

In other perisphinctids (especially *Grossouvria,* Callov.) the parabolae, which are numerous, have no constriction but consist of a parabolic line, barely visible by any difference of relief, but perceptible by the fact that it and succeeding growth lines cut across the previously formed set. Such parabolae swing gently forward on the whorl sides and back on the shoulders and have a more marked and even angular flaplike forward projection or lip on the venter; and between, on the shoulders, a small parabolic node occurs on each side. The nodes are placed on small backward extensions of the new segment. They overrun the growth lines of the previously formed segment and their edge is parallel to the subsequently formed growth lines (Fig. 140). They belong, therefore, to the next-formed segment of whorl, perhaps infillings of notches in the former peristome (290, 499, 502). In some

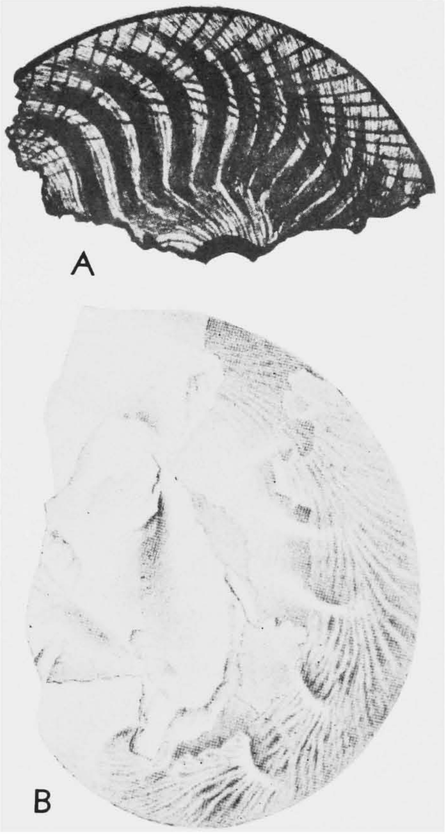

FIG. 137. Feather ornament or structure in the inner or middle layer of the test of an Oxfordian *Oppelia* (*A*) and an Upper Cretaceous *Placenticeras* (*B*) (*A*, 680; *B*, 202).

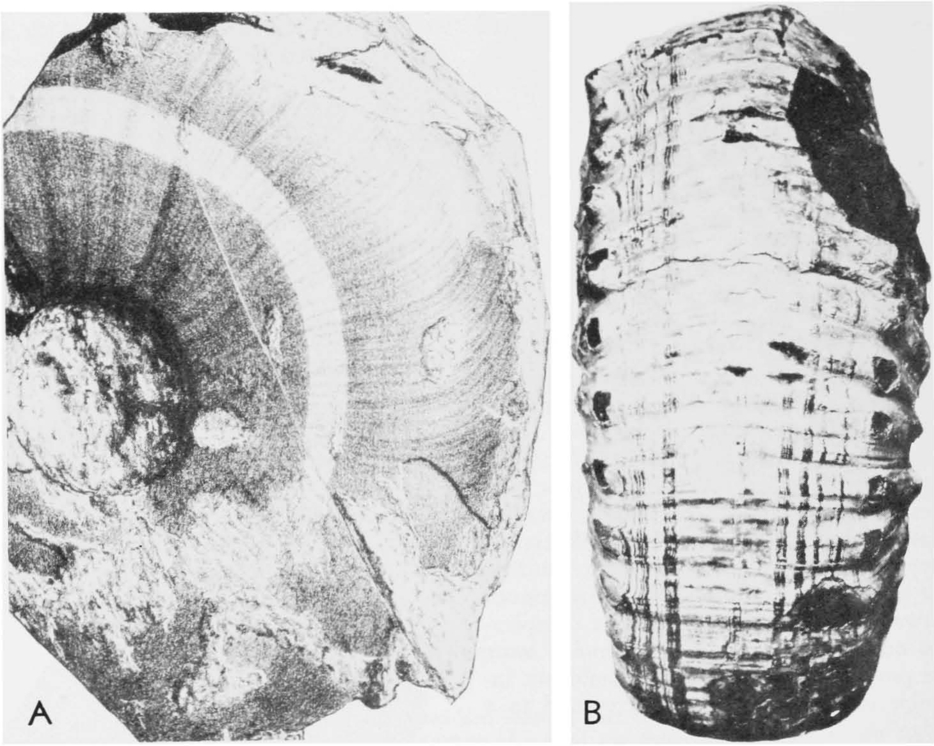

FIG. 138. Color banding on the side of a *Leioceras (A)*, M.Jur.(Baj.), Schleifenberg, near Basel, Switz., and on the venter of an *Androgynoceras (B)* L.Jur.(Pliensb.), Napton, Eng.; both ×1 (*A*, 629a; *B*, 475).

perisphinctids, parabolae are so numerous that they almost completely overwhelm the normal ribbing (see *Paraboliceras,* in systematic section).

SUTURES

Sutures are the lines or patterns traced on the surface of the internal mold of the phragmocone by the septal edges. They represent the junction of septum with shell wall. Each departure from a simple annular line represents a corresponding fold in the septum; and since all such folds die out towards the center of the septum, the more worn an internal mold, the simpler will be the sutures displayed. All sutures rightly should be studied as part of the septa as a whole, but it is only by great labor and destruction of material or chance favorable preservation that complete septa are visible. Outstanding studies of such material, to which the student is referred, are those by BRANCO (47), PFAFF (343), and SWINNERTON & TRUEMAN (501). Moreover, it is normally only the external suture, that is, the part traced upon the externally exposed parts of the whorl (whorl sides and venter), that is visible (Fig. 141). In perfect material of normally involute shells, an operation is necessary to expose the internal suture (part pertaining to the impressed area). Nevertheless, features of the internal suture may have great systematic value and cannot safely be ignored.

All major backward (adapical) inflections of the suture are known as **lobes** and forward (adoral) inflections as **saddles.** In more highly differentiated sutures, which may trace an extremely complex pattern, the minor frills upon the lobes are called **lobules** and those (commonly leaf-shaped) upon the saddles are called **folioles.**

In the earliest ammonites, the 1st-formed suture tends to be a simple annulus or ring, but in later forms it shows a prominent external saddle (Fig. 128). The 2nd suture, which is close to the 1st, always has a ventral lobe, but it is slight in the earliest ammonites and becomes more accentuated in later forms. The subsequent sutures become

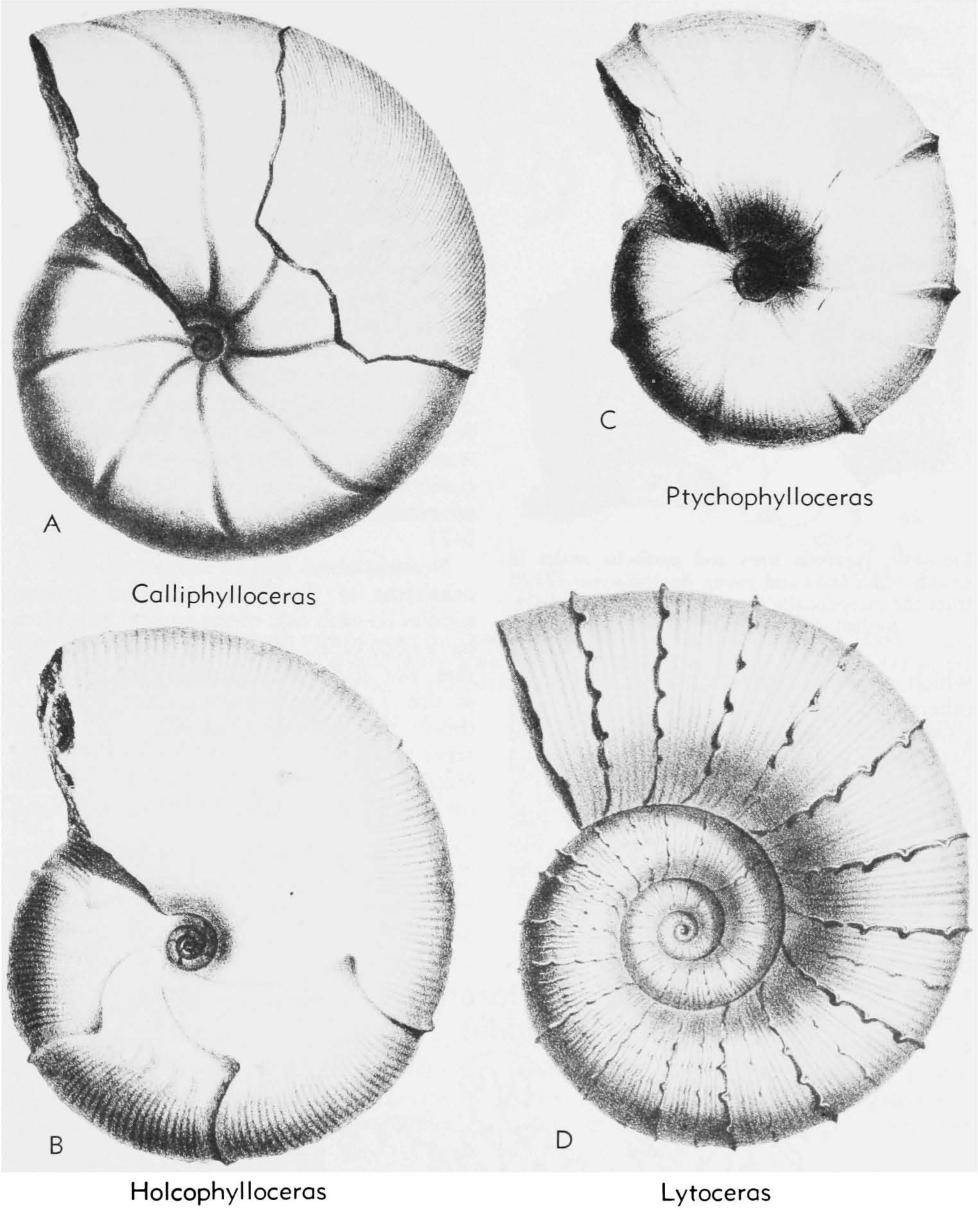

FIG. 139. Constrictions and flares are illustrated by the fundamental stocks Phylloceratina and Lytoceratina (330).——*A, Calliphylloceras,* constrictions on internal cast, not on test.——*B, Holcophylloceras,* constrictions on cast and test, and with median lateral knee bend and ventral labial ridge.——*C, Ptychophylloceras,* riblike flares or labial ridges.——*D, Lytoceras,* crinkled flares on test only.

progressively more differentiated in all ammonites, though the extent to which differentiation is carried differs greatly.

The 1st primary lobes, formed at an early stage of development, are the **ventral lobe** (sometimes called external or siphonal), **dorsal lobe** (sometimes called internal or antisiphonal), **lateral lobe** ("first lateral"), and **umbilical lobe.**[1] The umbilical lobe,

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[1] Various systems of symbols have been devised for representing these lobes and their relative lengths but are not used in this section of the *Treatise*.

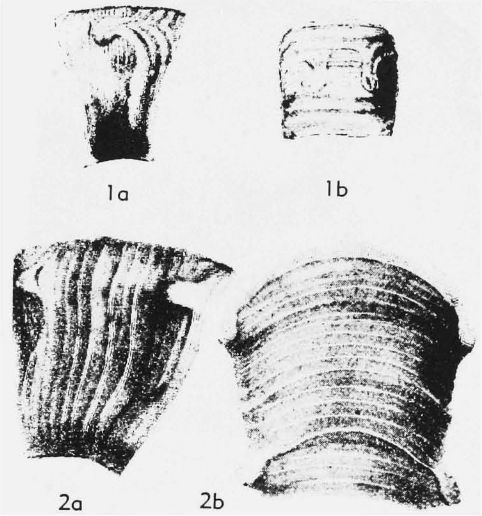

FIG. 140. Parabolic lines and parabolic nodes in *Grossouvria (1a,b)* and young *Euaspidoceras (2a,b)* from the exceptionally preserved Callovian and Oxfordian of Poland and Russia (290).

which appears somewhat later than the others, belongs partly to the external and partly to the internal suture, being centered usually on the umbilical seam. Its external portion (which alone is visible normally) is known as the **suspensive lobe,** and its subdivisions are the **auxiliary lobes.** The suspensive lobe may run straight toward the umbilical seam or be curved steeply backward (adapically) when it is said to be **retracted.** It has been shown that ontogenetically the so-called 2nd lateral lobe of many ammonites is really a development from the primary umbilical lobe; in other words, the 2nd lateral of some forms is homologous with the 1st auxiliary of others.

As differentiation proceeds, in the later ammonites, minor accessory lobes are formed between the primaries. Such lobes may acquire special importance between the ventral and lateral lobes, originating either from near the base of these primary lobes or from the intervening saddle, and they may become as large as the primary lobes and impossible to distinguish from them except by tracing them back to early whorls and discovering their ontogeny. Such are called **adventitious lobes** (or adventive lobes) (Fig. 142).

Nomenclature of the saddles is very inconsistent in the literature. The primary saddles on each side of the ventral lobe often have been called the ventral or external saddles, but it has been decided to call them in this *Treatise* (following some other authors) the 1st lateral saddles, and to reserve the term ventral saddle for the single median secondary saddle formed by subdivision of the ventral lobe.[2] The 2nd lateral

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[2] The initial "ventral saddle" of the first suture, from which both the ventral lobe and resulting first lateral saddles are formed, may be distinguished as the initial external saddle.

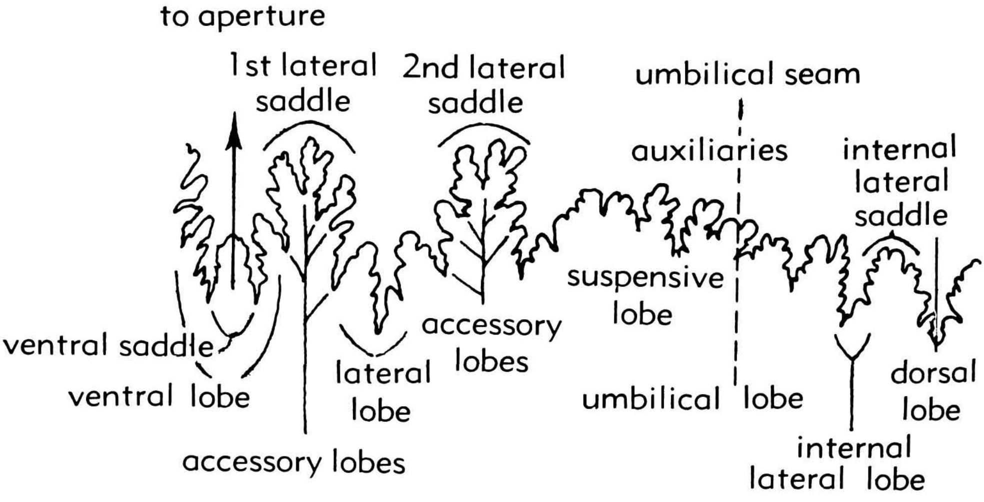

FIG. 141. Terminology of suture line. The arrowed black line on left represents the median line of the venter, the parallel unbroken line on right the median line of the dorsum. The broken parallel line (umbilical seam) separates the external and internal parts of the suture (583).

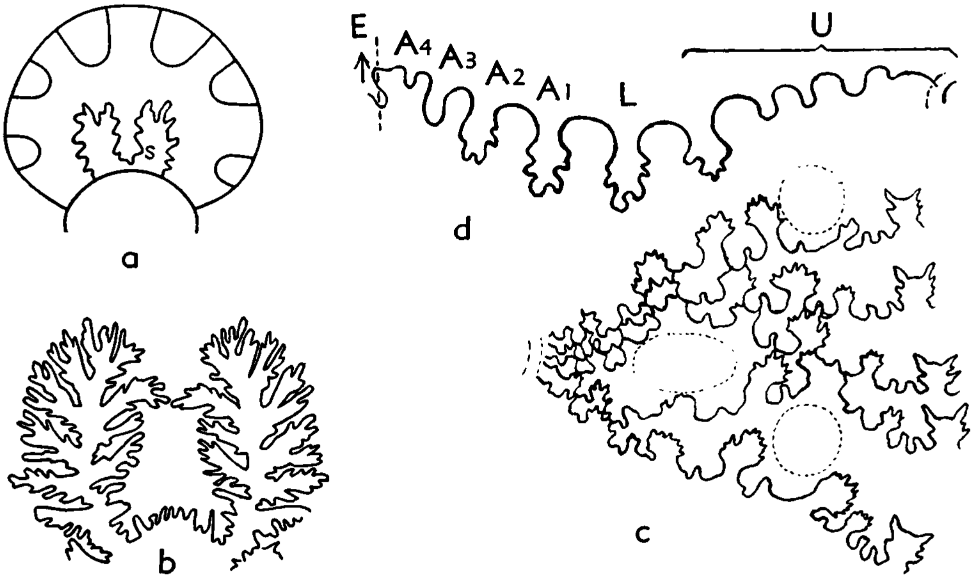

FIG. 142. Special types of septal sutures from the Cretaceous; *a,b*, septal lobe in a lytoceratid (585); *c*, unstable sutures in *Knemiceras* sp., a pseudoceratite from Persia (713); *d*, adventitious lobes *(A1-A4)* in the suture of *Engonoceras* sp., from Texas.——*E*, external lobe, *L*, lateral lobe, *U*, umbilical lobe (713).

saddle is thus the saddle between the lateral and the umbilical lobes. On the internal suture the term dorsolateral is used for the corresponding lateral lobes and saddles (Fig. 141).

On the basis of their general plan, ammonoid sutures are classed in 3 main categories: goniatitic, ceratitic, and ammonitic. **Goniatitic sutures** have all or most of the lobes and saddles plain, without frilling (entire, not denticulate), though the ventral lobe alone may be denticulate; **ceratitic sutures** have the saddles entire but the lobes denticulate; **ammonitic sutures** have all the elements denticulate. (Abundant figures of all 3 types will be found in the systematic parts of this volume.) In a general way these categories represent phylogenetic grades; the names, indeed, are taken from the 3 ancient "genera," *Goniatites* (characteristic of the Paleozoic), *Ceratites* (characteristic of the Triassic), and *Ammonites* (characteristic of the whole Mesozoic). But highly complex, typically ammonitic sutures are found in some families of the Early Permian; ceratitic sutures appear in some families of the Early Mississippian; goniatitic sutures occur in some Triassic and Cretaceous ammonites unrelated to the true goniatites; and more or less ceratitic sutures reappear in both the Jurassic and Cretaceous in numerous families totally unrelated to the Triassic ceratites. The Jurassic and Cretaceous forms are known as pseudoceratites, and they are explained as reversionary, or atavistic, modifications of normal ammonites (Figs. 142-144).

The general direction and course of the suture line is to a large extent linked to whorl shape. Thus, a highly compressed whorl shape is commonly associated with a straight or arcuate suture line with numerous relatively short elements, whereas a round or depressed whorl section is generally linked with few and elongated elements and, commonly, a highly retracted suspensive lobe.

The width of the spaces between the sutures (and septa) may vary greatly on a single ammonite and still more between similar individuals. Apart from this, like the ribs, they tend to become approximated toward the adult body chamber, and thus afford another means of recognizing a mature ammonite. In approximated sutures the lobes and saddles become shorter. Where highly differentiated sutures are close together it may often be observed that the extremities of some lobes impinge against the saddle of the preceding suture and a con-

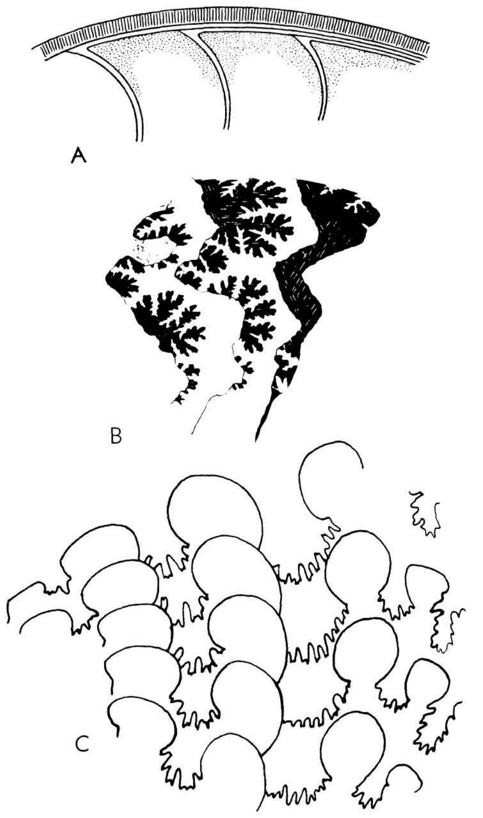

FIG. 143. Overlapping septal sutures.——*A,* diagrammatic longitudinal section (196).——*B,* Overlapping septal layers in a *Sonninia* from Goslar, Ger., with some lobules showing through (196).——*C,* Truncated lobe-endings in *Tissotia* sp., a pseudoceratite from the Peruvian Andes (233).

siderable part of such lobes may appear to be missing. In reality, however, they are continued underneath the preceding septal edge and concealed by matrix filling the preceding camera (Fig. 143). This results from the fact that toward the end of ontogeny the mantle begins to form a new septum without moving forward a full camera length in the whorl, so that the frills of the new septum are built on the inside of the old, instead of against the shell wall (195). In some Lytoceratina a form of this process is normal and becomes a character of systematic value. In these ammonites a bifid extension of the internal lobe climbs halfway up the face of the preceding septum, forming a **septal lobe** (Fig. 142).

A great deal of variation in sutural details must be allowed for within species—much more than has been admitted by some systematic workers who limited their field of study. The degree of variation and its nature differs from family to family, however, and must be assessed with discrimination. Variation is greatest among regressive types in which the suture is undergoing secondary simplification; it reaches extremes in some Jurassic and Cretaceous pseudoceratites (Figs. 142, 144). It should be borne in mind, moreover, that figures of sutures in the literature, even if they show the internal as well as external suture (which is rare), commonly are more or less distorted from the

FIG. 144. Unstable or otherwise unusual sutures of ammonites from the Jurassic of Jebel Tuwaiq, Central Saudi Arabia (15).——*1a-c. Nejdia bramkampi,* L.Jur.(Toarc.); *1a,* normal; *1b,c,* progressively abnormal lobes, the auxiliary lobes and saddles in *1c* becoming pseudoceratitic and subequal.——*2. Nejdia furnishi,* L.Jur.(Toarc.), with adventitious lobe *(A).*——*3. Bouleiceras* sp., L.Jur.(Toarc), pseudoceratitic suture.——*4. Bramkampia steinekei* M.Jur. (Bath.) with degenerated digitate suture reminiscent of Cretaceous patterns.

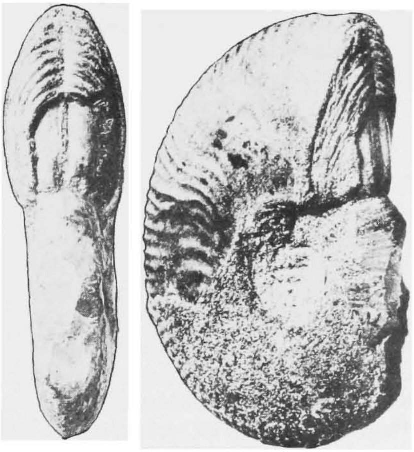

FIG. 145. Aptychus (Lamellaptychus) in position, closing aperture of an *Oppelia,* M.Jur.(Baj.), Dundry, Eng.; the inner or dorsal part of both valves is broken away, showing natural internal mold. (509).

necessity of delineating a cone on a plane surface, and in any case portray only one-half of a complete suture, whereas it is well known that the same suture may show considerable differences on opposite sides of the whorl. In some heteromorphs such bilateral asymmetry reaches extreme lengths and becomes standardized.

Sometimes an ammonite is found with the last septum incomplete, death having cut short its growth. In such specimens it is invariably the umbilical part of the suture that is present, showing that this was the first part to be formed (501, p. 35).

APTYCHI

The calcareous or horny plates called **aptychi** are generally agreed to have been ammonoid opercula. For the most part they are found separately, but enough have been discovered in place, either closing the aperture of ammonites or in various positions (usually ventral) within the body chamber, to leave no doubt of their nature.

The commonest forms, the true aptychi *sensu stricto,* consist of a pair of subtriangular calcareous plates joined along a hinge-like straight edge and gently convex, with a superficial resemblance to an open pair of pelecypod valves. When found united in an ammonite, the combined outline of the plates almost exactly fits the aperture. The concave smooth surface faces inward; the convex ornamented surface faces outward (Fig. 145). Another type, the **anaptychus,** consists of a single plate and is chitinous, or "horny," instead of calcareous and may only partly close the aperture with considerable misfit (Fig. 146). Anaptychi occur from the Lower Devonian to the Cretaceous, but bivalved aptychi (which are much commoner) so far as known are confined to the Mesozoic. In the Upper Cretaceous a 3rd type appears, the **synaptychus,** a calcareous operculum formed by fusion of bivalved aptychus plates.

Many finds of all sorts of aptychi suggest that when not serving as an operculum the aptychus was withdrawn into the ventral

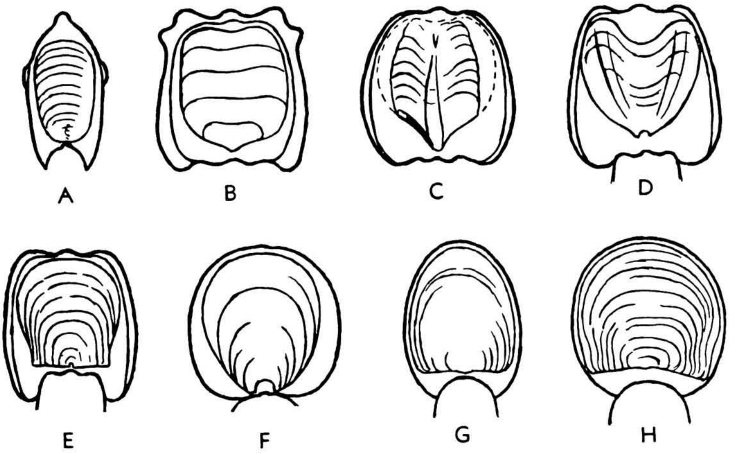

FIG. 146. Anaptychi of the Lias, drawn in closed position in the aperture of ammonite genera with which they have been found associated (425). *A, Amaltheus; B, Pleuroceras; C, Metophioceras; D, Arietites; E, Euasteroceras; F, Alsatites; G, Psiloceras; H, Lytoceras* (425).

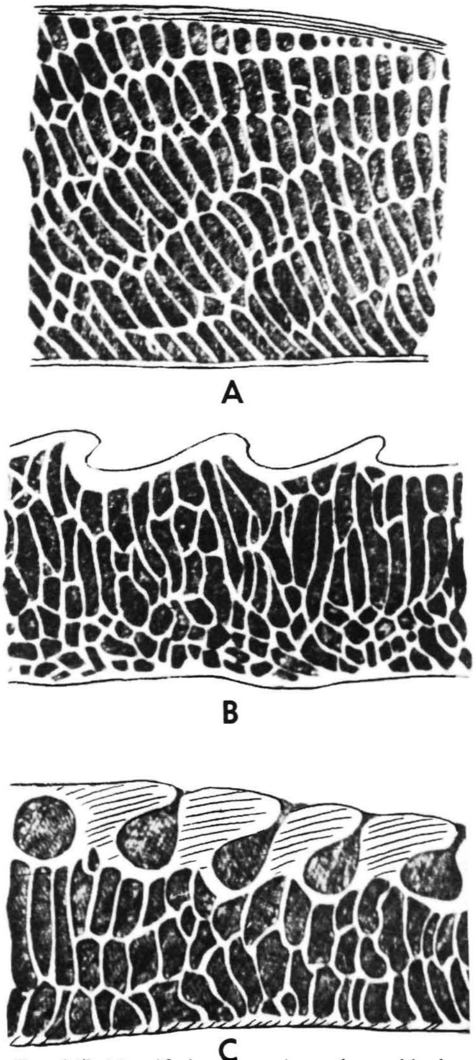

Fig. 147. Magnified cross sections of aptychi, showing internal structure of the shell (661). *A*, Laevaptychus; *B*, Lamellaptychus; *C*, Punctaptychus.

side of the body chamber with the dorsal end directed adorally (Fig. 124).

Aptychi consist of 3 layers: 2 thin lamellar layers enclosing a thicker middle layer with a cellular or tubular structure (Fig. 147). The surface of the outer layer is commonly punctate, granulated, or ribbed and furrowed, while the inner layer, adjacent to the mantle of the animal, is smooth but for growth lines. Current classification is mainly based on the ornamentation of the outer, convex surface, and to a smaller extent on shape and thickness. The technical descriptive terms used for bivalved aptychi, and a list of the "form genera," will be found at the end of the systematic part of this volume (Figs. 556-558). In the body of the systematic part, brief descriptions of aptychi are inserted whenever these have been found inside body chambers of species of the ammonoid families or subfamilies treated. There are many genera and families, however, and even suborders, containing no species with which aptychi have ever been found intimately associated, while in other groups, no more abundant in species or individuals, such an association is not uncommon (e.g., Aspidoceratidae, Oppeliidae). The taxa with which no aptychi have been found associated are so numerous (for instance, the whole of the Clymeniina and Phylloceratina) that there is a strong presumption that they never possessed aptychi capable of preservation.

Aptychi are especially common in bituminous shales of the Toarcian and Lower Kimmeridgian and in Tithonian limestones in many parts of the world. They may form so-called aptychus beds, where they abound to the exclusion of ammonites. Various explanations of this have been put forward and more than one may be correct in different circumstances. In limestone formations, abundance of aptychi most likely may be due to vagaries of current-sorting; on decay of the animal the aptychi might have fallen to the bottom while the chambered shells were carried elsewhere by currents. In bituminous shales, however, it is possible that differences of chemical composition played a leading part; the aptychi, being calcitic or chitinous, may have resisted chemical and physical changes which destroyed the aragonite shells of the ammonites.

ONTOGENY

It is generally assumed that the larva of the ammonoid, inhabiting the protoconch, was free-swimming or drifting (meroplanktonic). This hypothesis explains well the world-wide distribution of so many ammonite genera and even of species, and their sudden (cryptogenic) appearance in regions where no likely ancestors can be found, but the assumption is only a hypothesis. In any case, the protoconch represents a separate episode in the life history of the animal, totally different from all that followed.

The development of the conch, by contrast, was a reasonably continuous process, in which the shell enlarged as an expanding cone, typically coiling in a logarithmic spiral.[1] When examined in detail, the process of enlargement is found to be not so continuous as it appears superficially, but to have proceeded in stages of 2 orders. In the first place, the body of the animal did not move forward continuously in the shell but periodically rested while a septum was secreted. At every forward move the previously formed camera (but not the siphuncle) was vacated entirely by the animal—a process which has been likened to the molting (ecdysis) of arthropods and arthropod larvae, except that the abandoned parts were not discarded (as in some orthocone nautiloids) but were retained as a hydrostatic apparatus (28).

Superimposed on this periodicity there was a longer-term periodicity in the growth of the shell as a whole. In all Jurassic genera dissected by Currie (94), a change of growth ratios at the 2nd-3rd half whorl was observed and this was interpreted to define the end of the 1st postlarval growth stage (?nepionic stage of Hyatt, 1889, p. 18).[2] Similar changes take place at varying intervals throughout the phragmocone. In many shells they are marked by parabolae, as previously described. In some families a sudden increase in size and change in direction of ribbing follows each constriction. This has been described as "segmental growth" and attributed to periodical slowing down of activity to allow enlargement of the soft parts (315, p. 94; 445).

Other changes, progressive or sudden, are illustrated by many of the morphological shell features described above; for instance, the conversion of a ventral groove into a keel or vice versa, the development or disappearance of tubercles and spines, the change of narrow dense ribs into enormous swollen wedges (this last being a major change in the accommodation of the animal, since the ribs are folds in the shell, not superficial features). The greatest changes of all took place in many individuals at the beginning of the adult stage, involving more or less profound alterations of volume and shape of the body chamber and specialization of the aperture.

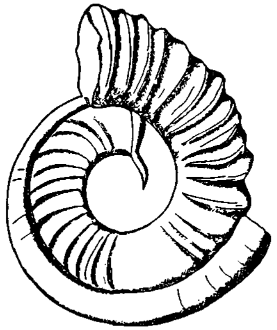

Fig. 148. *Serpula* growing on the venter of an ammonite *(Schlotheimia)* and partly covered by growth of the ammonite whorl (415).

All these ontogenetic changes have to be borne in mind and are serious obstacles to the application of statistical and graphical methods for identification and classification of ammonites. No set of measurements can be plotted directly against another for the comparison of 2 individual shells, for the various changes took place at different diameters according to the ultimate size of the individual, or to whether its growth was precocious or retarded at any stage (549). The philosophical soundness of elaborate use of statistical methods for selected features of complex organisms (such as those attempted for ammonites, for instance, by Brinkmann, 1929, and Fradin, 1950) is questionable in any case (58).

In the final (?gerontic) growth stage, secretion of carbonate of lime seems to have gone on at undiminished rate after enlargement of the soft parts slackened off. This is the only possible interpretation of the crowding of septa and ribs toward the end of the mature conch; or the enlargement of ribs where there was no crowding. The same surplus of capacity for secretion of shell substance may also have played a part in the production of lappets, rostra, and other features of so many adult peristomes.

It is impossible to put any absolute value on the rate of growth of the ammonite shell,

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[1] The mathematics of the spiral has been studied by Rollier (1924), Currie (1942, 1943, 1944), D'Arcy Thompson (1942, p. 748-822), Vecchia (1945), and others.

[2] Currie's description of this as the "post-embryonic" stage seems open to objection.

but an estimate has been made by SCHINDEWOLF (415). He found that certain Lower Lias ammonites are completely encircled by a single large *Serpula* tube, which must have grown in some sort of symbiotic association with the ammonites (Fig. 148). From a number of the most closely related living serpulids he estimated that the rate of growth of the ammonites was of the order of one whorl in 4 months to 3 years. On the assumption that growth stages were seasonal, CURRIE (94, p. 198) estimated for certain genera development of about 6 whorls in 4 years.

PHYLOGENY, CLASSIFICATION, EVOLUTION

To the idealistically minded taxonomist it is a maxim that classification must be based on phylogeny. To some of his more practically minded colleagues it is a truism that phylogeny can only be deduced from an accurate morphological classification. It is certain that attempts to pursue either classification or phylogeny separately lead to progression in circles. Both depend entirely on accurate knowledge of the morphology of all the forms that lived (and this includes their ontogeny), and on their stratigraphical order. The principal aim of this *Treatise* is to present a synoptic picture of the facts so far known, not to give directives or guidance on the evaluation and interpretation of the facts. The present subsection therefore attempts only a brief explanation and justification of the arrangement that has been adopted in the systematic sections.

ORIGIN OF MESOZOIC AMMONOIDEA

The oldest undoubted ammonoids are the Anarcestaceae, which occur in the Lower Devonian. From them the Palaeozoic ammonoids diverged in 3 main streams. One was the Clymeniina, with dorsal siphuncle, which became extinct at the end of the Devonian. The 2nd was the Goniatitina, which comprised the great majority of Upper Paleozoic ammonoids and became extinct in the Permian. The 3rd (which appeared already in the Late Devonian) was the Prolecanitina, which carried on over the Paleozoic-Mesozoic boundary and gave rise to all Mesozoic ammonoids.

The primary distinction between the Prolecanitina and the Goniatitina rests, according to SCHINDEWOLF (419), on the ontogeny of the suture line. In the Prolecanitina, the lateral lobe arises near the umbilical seam and in the course of development shifts ventrally until it occupies a normal position, midway between the umbilical seam and the mid-line of the venter, while at the same time a new umbilical lobe arises in the vicinity of the umbilical seam. This is the normal course of development for all Mesozoic ammonoids and indicates their ancestry in the Prolecanitina. In the Goniatitina, on the other hand, the lateral lobe remains small and close to the umbilical seam throughout development, while a false lateral lobe gradually forms in the middle of the lateral saddle. Thus, the lateral lobe of adult goniatites is not homologous with that of later ammonites but is really an adventitious lobe.

COURSE OF EVOLUTION OF MESOZOIC AMMONOIDEA

In the Early Triassic a great burst of evolutionary radiation sprang from the xenodiscids, a stock derived from the Prolecanitina. Most of these are grouped by KUMMEL (1952) in 8 superfamilies, together comprising the suborder Ceratitina (Fig. 149). All of them became extinct before the end of the Triassic. But one entirely new stock, which arose already in the Early Triassic, survived the general extinction in the Rhaetian and carried on into the Jurassic. This was the Phylloceratina, which must have been the rootstock of all the Jurassic and Cretaceous ammonoids (Figs. 150, 151).

With the beginning of the Jurassic a new phenomenon appears. This is the side-by-side existence of a persistent stock (the same superfamily Phyllocerataceae which began in the Early Triassic and continued with little change to the end of the Cretaceous) and a number of new radiations from it consisting of superfamilies and families, each of which itself radiated repeatedly so as to form a complicated tangle of lineages. At the beginning of the Jurassic, one of these branches, the Lytoceratina, which presumably arose from the Phylloceratina some-where during the passage from Trias to Lias but soon became completely differentiated, itself became a persistent stock and gave off more radiations than arose directly from the parent Phylloceratina (Figs. 150, 151).

PRACTICAL DIFFICULTIES OF CLASSIFICATION

The key to unravelling the resulting tangle of Jurassic and Cretaceous ammonites on sound phylogenetic lines has long been sought but not yet found. A phylogenetic classification here breaks down. There are so many ammonites (at least in the Jurassic) which cannot reliably be traced back to their parent stock that it is still a practical necessity to retain a polyphyletic suborder Ammonitina for all those ammonites (the vast majority) that do not bear a definitely recognizable affinity to either the stable Phylloceratina or the stable Lytoceratina. It is probable that the rootstock of most of those that appeared after the Sinemurian and before the Valanginian was the Lytoceratina, but accessions from the Phylloceratina also may have recurred, especially to the superfamily Haplocerataceae (Fig. 150).

Attempts in the past to construct phylogenetic trees as a basis for a classification have relied upon a variety of characters and have been influenced by principles or "laws" fashionable in different periods and countries, which may without cynicism be described as the current prejudices with which successive workers have evaluated morphological characters and chosen those on which they laid emphasis.

The 19th century pioneers, from von Buch and Quenstedt onwards, based their classification upon shell form: all oxycones were grouped together, regardless of age, and so on for all the main form types. This "forthright morphological" school has had its adherents down to recent times; for instance, Rollier (384) and Steinmann (494, 496) did not flinch at including in the same genus similar forms from any part of the Triassic, Jurassic, or Cretaceous. Theirs was "vertical" classification *par excellence.* This simple principle was attacked by many workers, such as Pompeckj (352), Hyatt, Buckman, and others, and substitutes were sought.

ITERATIVE EVOLUTION

This hypothesis was first propounded by Salfeld (396, 400-402) and elaborated by Frebold (150), Spath, and others. It postulates that the conservative Phylloceratina and Lytoceratina repeatedly gave off waves of fresh derivatives which at different times and places rang fresh changes on all the well-tried shell forms. Salfeld announced in 1922: "So it is certain that of all the families erected for the Jurassic and Cretaceous ammonites nothing remains." All new studies of faunas have added to the crowd of known examples of heterochronous homeomorphy. As a specially interesting example one may cite *Cymbites,* a series of small, globular, rather featureless ammonites found at successive horizons in the lower Lias. Buckman (62) regarded these as the "radical of all the ammonites" which was derived from a similar Triassic form, perhaps *Nannites.* Spath considered them degenerate "end forms" and distributed them among 3 separate Liassic families according to their stratigraphical horizon, and they are so retained here. *Lissoceras* and *Haploceras,* however, other small smooth ammonite genera of the Middle and Upper Jurassic, which Buckman regarded as degenerate end forms, were believed by Spath to be iterative passage forms from Phylloceratina to Oppeliidae. The present writer believes Buckman more likely to have been right (Fig. 150). These examples serve to illustrate what has happened throughout the classification.

The possibilities of variation in all characters of the ammonite shell are limited, and so are the possible combinations of environmental factors to which the ammonites had to adapt themselves. Accordingly, similar adaptations must have recurred repeatedly throughout Mesozoic time. The logical conclusion to which acceptance of this hypothesis leads is an increasingly "horizontal" classification that depends absolutely on accurate stratigraphical information. The complexity of the modern classification, seen in the systematic parts of this *Treatise,* results mainly from acceptance in large measure of the theory of iterative evolution, although there are comparatively few proved examples of its occurrence. We often feel sure that it has occurred and that we should be deceived if we accepted similarities at their face value

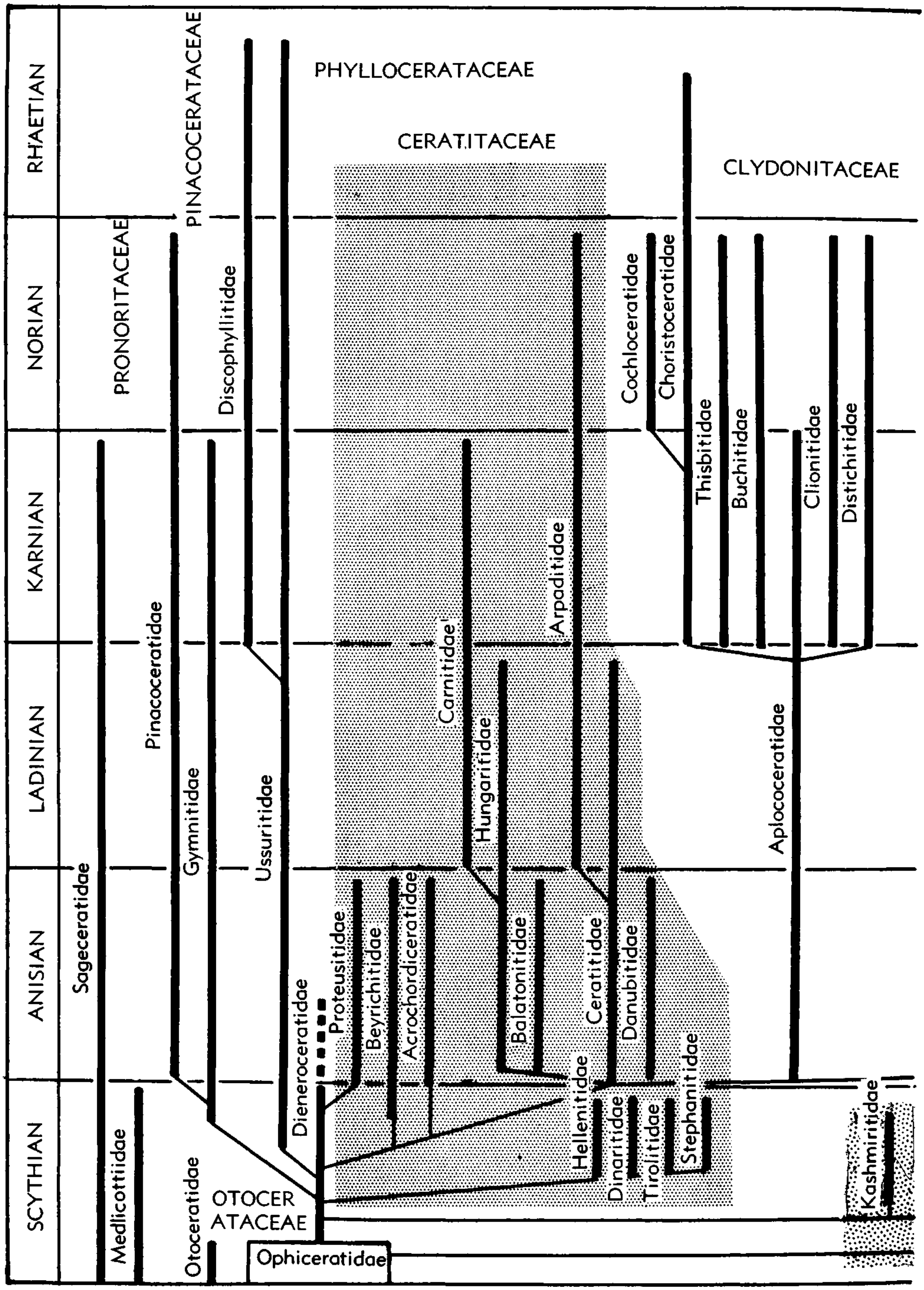

Fig. 149. Chart showing diagrammatically the phylogeny and range of the Triassic ammonoid families and superfamilies (650).

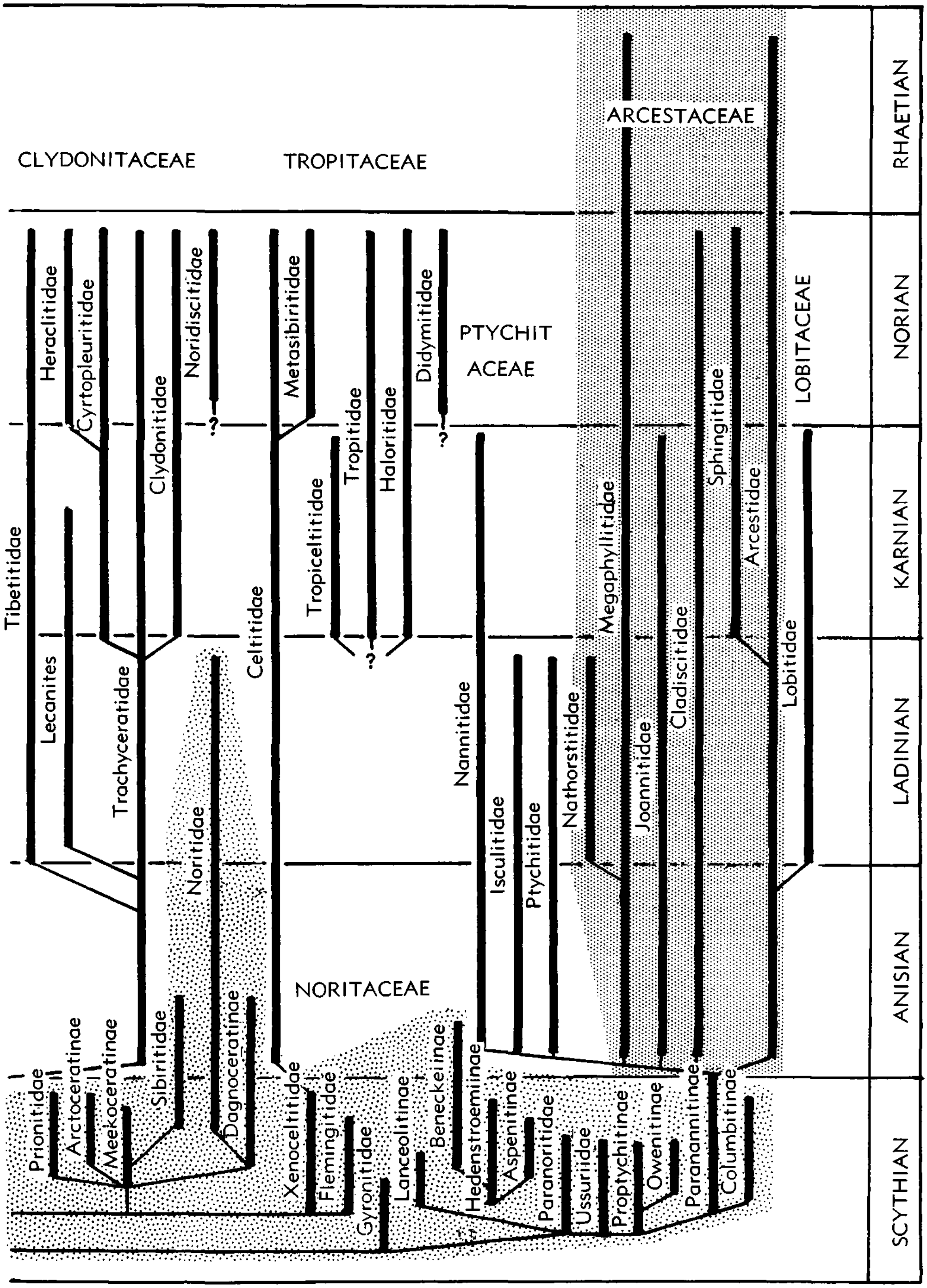

Fig. 149. *(continued from facing page).*

(Haas, 1942, has brought together a few outstanding examples), but we can seldom demonstrate just what the "iterative" relationships are. The most baffling families are still those with relatively little ornament; they may always be just those critical transitions from the smooth "liostraca" (Phylloceratina) to ornamented "trachyostraca," or they may be secondarily simplified "regressions." The long-ranged, smooth Haploceratidae and Desmoceratidae have long been debated and are still a bone of contention. H. Douvillé as long ago as 1916 held that the Desmoceratidae descended directly from

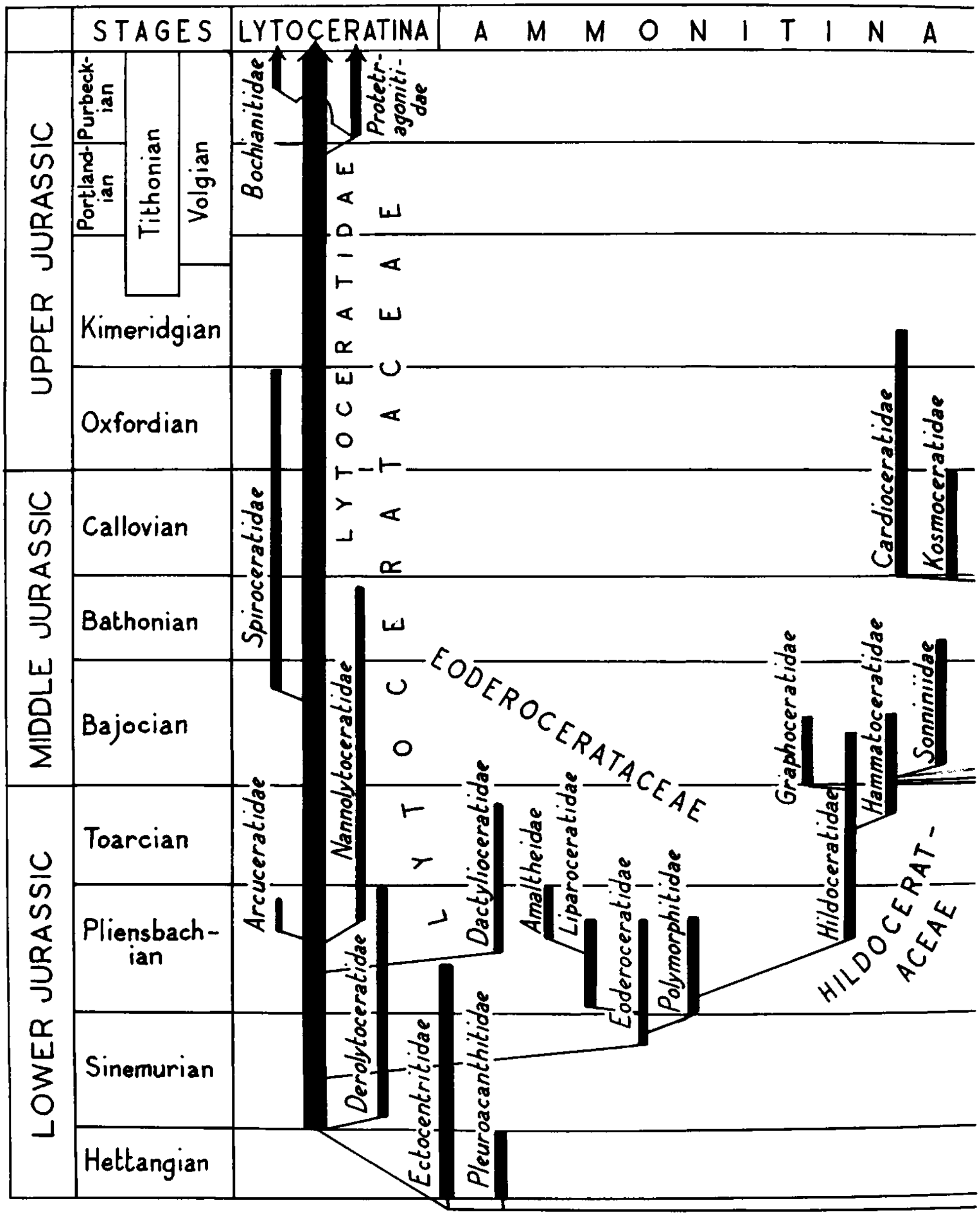

Fig. 150. Chart showing diagrammatically the phylogeny and range of the Jurassic ammonoids down to the family level (583).

the Phylloceratidae *(Sowerbyceras)* and this view is accepted here.

RECAPITULATION

For about half a century (roughly 1880-1930) these difficulties daunted few. In those happy years specialists thought they had the key in the theory of recapitulation ("palingenesis," "morphogenesis"). According to this theory, the ontogeny of the individual is a recapitulation of the phylogeny of the race, so that it was only necessary to study the ontogeny of an ammonite to discover the nature of its ancestors and therefore its posi-

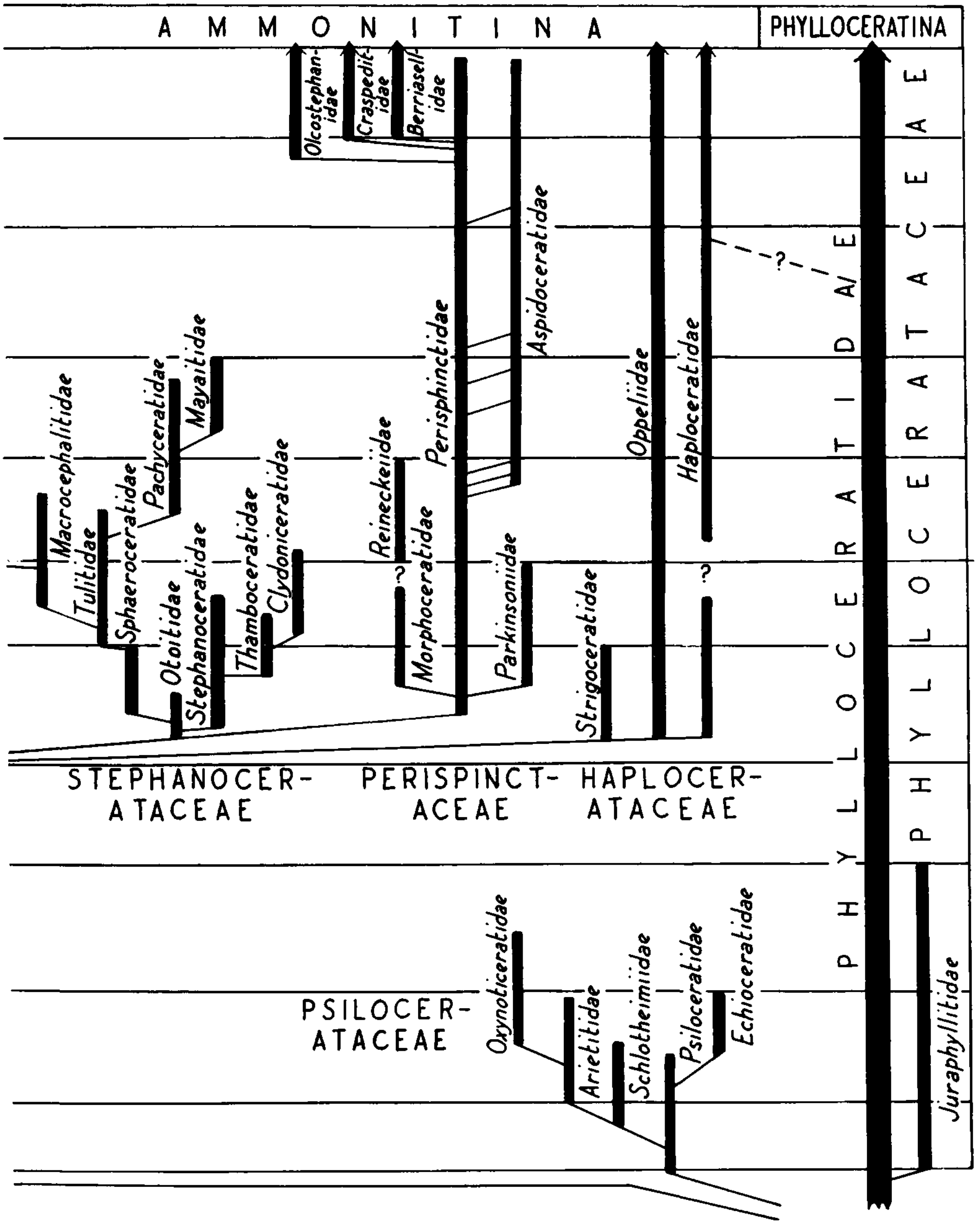

FIG. 150 *(continued from facing page).*

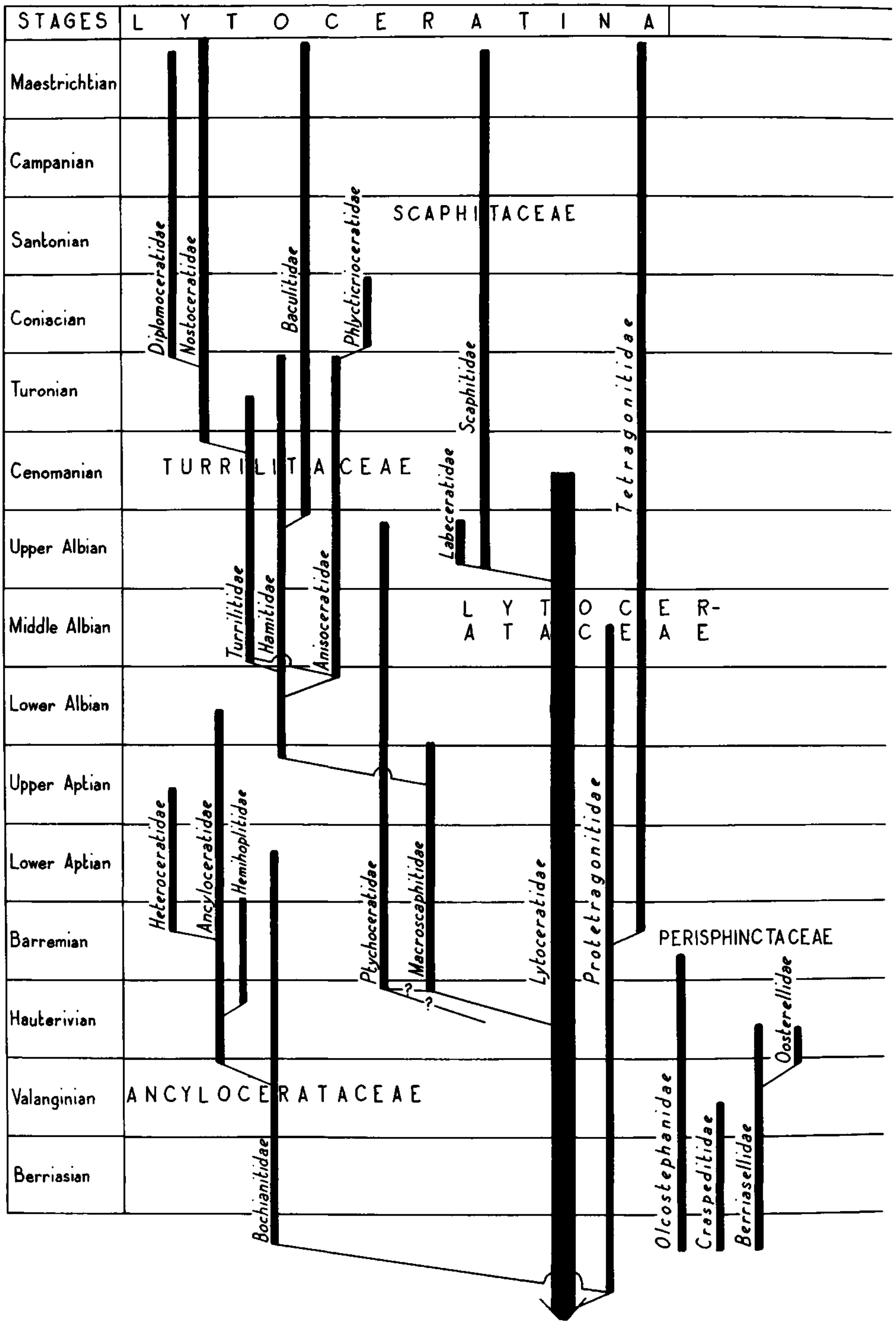

FIG. 151. Chart showing diagrammatically the phylogeny and range of the Cretaceous ammonoids down to family level (735).

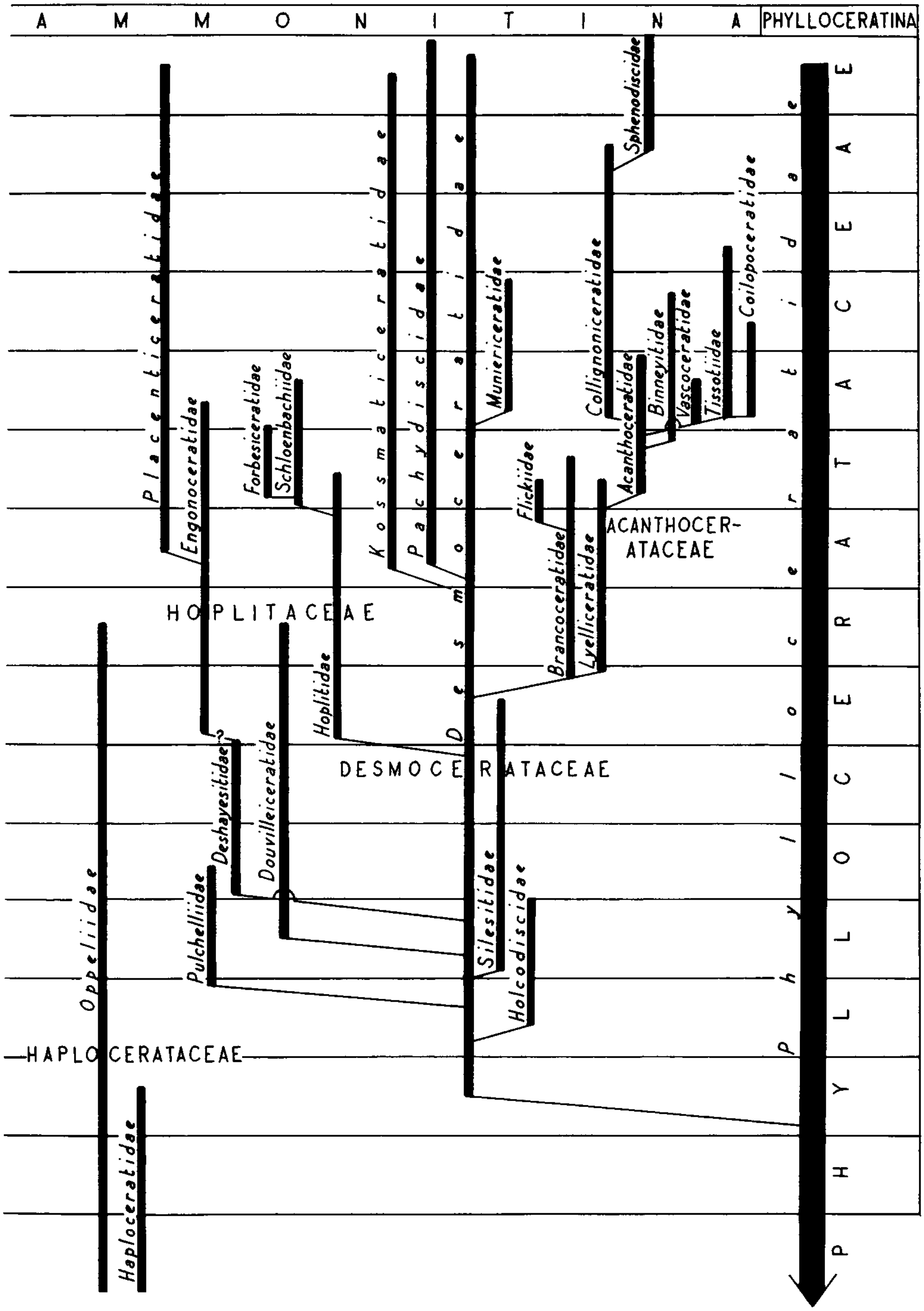

Fig. 151 *(continued from facing page).*

tion on the family tree. The imposing works of HYATT (especially 1889) were the principal source of this doctrine, which was accepted wholesale by BUCKMAN and most other workers. The papers of the 2nd and 3rd decades of the 20th century, written in the recapitulationist faith, make strange reading now. If, as was often found, all the expected stages were not present in ontogeny, they must have been skipped; then the "fact" that a stage had been skipped became itself of great significance, and forms were classed together because of characters which none of them possessed! All this was, of course, wrapped up in a scientific jargon: "tachygenesis," "bradygenesis," "palingenesis," "lipopalingenesis," and other terms. BUCKMAN was enabled to pronounce with comfortable certainty and *ex cathedra* authority on the phylogeny and relationships of all the ammonites with which he dealt.

Whenever early stages of ammonites (nuclei) are well preserved in large numbers, however, they are found to show a greater range of variation in form and ornament than the adults. The young, in fact, are more "plastic." A classification based on them generally would be very different from that based on the middle and outer whorls. Large ammonites from the same horizon, otherwise identical, may possess surprisingly different nuclei. Thus, the painstaking quest after the early stages, the unraveling and destruction of many ammonites by time-consuming techniques, would lead to the conclusion that all groups are polyphyletic, if the recapitulation theory were invariably correct.

Nevertheless, studies of ontogeny undertaken in this period, especially those on the development of sutures, were a substantial contribution to knowledge (456, 519-521) which brought to light still more cases of homeomorphy. For instance, GEORGE (1930) showed that the Sinemurian oxycones united under the genus *Oxynoticeras* had various distinct types of sutural development and probably therefore sprang from different genera or subfamilies of the Arietitidae, although he could not indicate the likely ancestors of each. Like conclusions have been reached on the basis of ornament and shell form for the similar, much later oxycones classed as Cardioceratidae, with their component genera, and many other Jurassic and Cretaceous families.

CENOGENESIS AND PROTEROGENESIS

The recapitulation theory was fatally shaken in 1901, when PAVLOW published the observation that in a number of Jurassic genera it is the young ammonites, in the neanic stage of HYATT's scheme, that first show new characters of ribbing and whorl shape, which only at higher stratigraphical horizons spread on to the adults. He called this process "phylogenic acceleration" or "precession of characters," and because the inner whorls foretell the characters of their racial descendants he called them also the "prophetic phase." PAVLOW pointed to similar phenomena among the belemnites, gastropods, and vertebrates, concluding: "It is to be hoped that, under the influence of the facts, the limitations of the recapitulation hypothesis will soon be realized and that outside those limits the field will be left free for other interpretations." But it was not until more than 20 years later that PAVLOW's observations were independently repeated in the west, by LEWINSKI (1923), SPATH (1924), and SCHINDEWOLF (1925, 1929, 1936) and gradually came to be taken into account in teaching. The early appearance of a new character is known to biologists as **cenogenesis;** and this term seems suitable for the process described by PAVLOW, except that in the paleontological concept the subsequent incorporation of the character in descendent adults, as a firm character of the stock, is the most important element. SCHINDEWOLF coined for the process the term **proterogenesis.**

DOLLO'S LAW

Another "law" much relied on in early decades of the 20th century as the basis for phylogenetic pronouncements concerning ammonites was DOLLO's (1922) "law of irreversibility of evolution." According to this "law," all evolutionary departures from the normal ammonite (usually conceived as a regularly coiled planulate) were dead ends. Thus, not only could heteromorphs not produce normally coiled descendants, but also oxycones and sphaerocones invariably must be at the end of their line of evolution, doomed productions destined for extinction.

Like most such hypotheses, this contains much truth and applies in numerous cases, but it led to error when accepted as a law. Most heteromorphs, oxycones, and sphaerocones do seem to have been dead ends, "specialized end forms." But the ammonites, as usual, produced exceptions which served to test the rule. For instance, while pronouncing on numerous cases in which DOLLO's "law" seems to apply, authors persistently disregarded the oxycone genus *Amaltheus* which gave rise to the planulate genus *Pleuroceras,* and the oxycone *Cardioceras* which evolved into the planulate *Amoeboceras* and its subgenera. In both these examples, it is typical, normal planulates which are the end forms of lineages and indeed, of whole families. Moreover, the Cretaceous heteromorphs are by no means all "end forms" headed for early extinction. On the contrary, many of them persisted almost as long as the unmodified parent stock of the lytoceratids from which they arose.

EVALUATION OF CHARACTERS

Nearly all parts of the shell have been used at some time by some author as the basis for classification: protoconch and proseptum; body chamber (whether large or small); shape of the aperture (simple, constricted, or with lappets); presence or absence of a keel, nature of the keel (whether solid, hollow and open, or hollow and floored); ribbing and other ornament, its nature and direction (the "radial line"); and sutures. All have proved unreliable and no more worthy of singling out as of special importance than any other characters. Keels of all sorts, and grooves and other ventral features, come and go in any stock and may appear suddenly in the most unexpected context in an otherwise unkeeled or ungrooved family; SALFELD (1921) rightly declared that "ventral keels and furrows are secondary characters of subordinate systematic value." Body chambers of all types (113) and apertures of any kind appear in almost all stocks which otherwise agree in a great majority of characters, as already shown above. Ribbing and tubercles of 3 or 4 different types may follow each other in the life cycle of a single individual, and this may happen in almost any order (see examples cited by DEECKE, 1913, p. 250 ff.). Too close attention to the radial line led BUCKMAN into such elaborate subdivision of the Graphoceratidae that his monograph is practically unusable; this feature can hardly have even varietal significance in many groups where he assigned it generic rank. Sutures may be widely different on opposite sides of the same specimen and so different on otherwise identical shells that on the basis of sutures alone any number of genera might be made out of one species (for example, Fig. 144). Nor is there any reason to ascribe greater infallibility to details of the internal suture (402) than to those of the external suture. It is unsound to judge that the more difficult any character is to observe the greater is its importance.

It is against this background of scepticism learned by hard experience in the 1st half of the 20th century that one must evaluate attempts to find the thread that will enable phylogeny to be recognized and classification reorganized on a sound basis. A praiseworthy attempt has been made, using details of the early ontogeny of sutures, in a series of interesting papers by SCHINDEWOLF (410, 413, 417, 418). In a sample of genera examined, he finds that in the early suture lines certain details of the umbilical lobe develop in a different order in different genera (Fig. 152). In one group ("heterochrons," typically represented by the Stephanoceratidae) the 1st branch of the umbilical lobe is delayed in appearance for 2 or more sutures after the appearance of the 2nd and 3rd branches, while in the other group ("orthochrons," represented by the Perisphinctidae) the 1st branch appears from the start. On this basis SCHINDEWOLF would reclassify the Stephanocerataceae and Perisphinctaceae of the Middle and Upper Jurassic, involving many drastic rearrangements and separating some genera from all apparently related, contemporaneous forms which agree with them in most other characters. He considers that although this sutural peculiarity may appear trivial because it occurs only in the earliest stages of ontogeny, for that reason it is all the more significant, because independent of changing shell form and mode of life. However, it seems to the present writer unacceptable to separate, for instance, *Bigotites* and *Parkinsonia* from the other perisphinctids, and

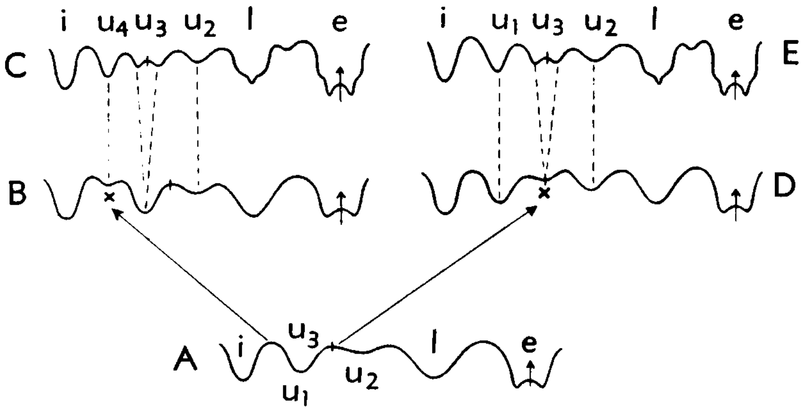

FIG. 152. Early ontogenetic development of the umbilical lobe in Stephanoceratidae *(B,C)* and "orthochrons" *(D,E)*; for further explanation see text (internal lobe, *i;* umbilical lobes u^1, u^2, u^3, u^4; lateral lobe, *l;* external lobe, *e*) (418).

Pseudoperisphinctes from the almost identical *Grossouvria,* on the grounds that they are "heterochrons," when among SCHINDEWOLF's list of "orthochrons" are found such completely unrelated Cretaceous genera as *Desmoceras, Puzosia, Leopoldia, Parahoplites, Schloenbachia,* and *Metaplacenticeras* (418, p. 127). On the inadvisability of reorganizing the entire classification on such a basis in the *Treatise,* all 3 authors of the Mesozoic ammonoid sections are agreed. We regard these differences in details of the earliest sutures as one more example of the vagaries of the "plastic young."

MACROEVOLUTION, MICROEVOLUTION, AND TRENDS

The most striking feature that emerges from study of the Mesozoic ammonites from the evolutionary point of view is the frequency with which history repeats itself during the approximately 125 million years of the era. The repetitions are of course never exact, but sufficiently close to be striking and to impose a rough pattern on the whole course of evolution of the order. It seems desirable to present a brief statement here, in order that the contribution which ammonites can make to the theory of evolution may be better known; for when they are mentioned in treatises on evolution their contribution is still commonly represented by out-of-date quotations from recapitulationist days.

Evolution is above all very uneven. Certain periods were outstandingly productive of new and virile forms, which often seem to have sprung into existence from nowhere (the so-called "cryptogenic" types of NEUMAYR, 1878) and to have become dominant almost simultaneously over a large part of the world. These are the periods of **paedomorphosis, macroevolution, saltative evolution, explosive radiation,** or evolutionary deployment, according to the terminology of various biologists and geneticists. How such sudden multiple creations were brought about is a task for the future to determine; but whether the process was one of adaptation to subtle nongeographical niches, or due to genetic drift and preadaptation, or to some mysterious manifestation of an *élan vital,* it must in any case go on record that they occurred. It would occupy too much space to give adequate examples; one of the earliest known (in the clymeniids) has been well illustrated by SCHINDEWOLF (416, p. 42, fig. 25).

Two other features of the phenomenon are common: the major innovations occurred cenogenetically (the new forms are different from the start of their postlarval ontogeny, and either incorporated the new features immediately in the whole of the ontogeny or progressively in succeeding generations, proterogenetically); and the new forms then proceeded to evolve more gradually on divergent or more or less parallel lines, going through one or more of a series of standard changes, which were repeated after each explosive phase.

This 2nd phase of slower, less spectacular, stereotyped evolution is, in biological terms, the phase of microevolution or gerontomorphosis. In it the new genera became specialized in a number of well-tried directions, such as running to sphaerocones or oxycones, or giant size, developing a keel (if the initial forms had none) or a groove or smooth band on the venter, and simplifying (smoothing out) the ribbing and sutures. This is the phenomenon of trends, which so strongly suggests an orthogenetic cause but must not necessarily be explained by orthogenesis. Moreover, some outstanding exceptions, such as the explosive evolution of the oxycone amaltheids from a planulate *Oistoceras* and their gradual evolution into planulate *Pleuroceras,* weigh heavily against a blind orthogenetic explanation of trends. It was parallel evolution of lineages on similar trends that repeatedly produced homeomorphs by leveling down and elimination of distinctive features or by repetition of stock characters; and they can be either isochronous or heterochronous. Extreme cases may appear to be atavistic because the simplification inevitably produces more primitive-looking types.

EXAMPLES OF AMMONOID EVOLUTION

Waagen (1869) in a pioneer work attempted to demonstrate **lineages,** or lines of descent, in the Oppeliidae from the Middle Bajocian to the Upper Callovian. His work contains an excellent discussion of the principles and difficulties, which should be read by all students of ammonites. The chief obstacle to such studies is that a lineage is an oversimplified concept; it is impossible to pick out a stratified succession of individuals which can with certainty be said to be genetically connected in the strict ancestor-descendant relationship. While we aim at deciphering such a lineage (*Formenreihe* of Waagen; *série genétique* of Pavlow), what we actually deal with is a series of populations which may be made up of indefinite numbers of lineages, either evolving parallel in one stream (a **plexus**), or radiating in a variety of directions (*rameau genétique* of Pavlow, 1901, p. 59) which may not be apparent because often not fulfilled, owing to premature extinction or merely preservation failure or collection failure. From these populations we have presented to us through the vagaries of (1) random preservation and (2) chance rock exposures, minute samples, from which in turn we pick individuals which we deem to be typical. Even then, in default of statistical analysis of the whole available population for a large number of characters, it is difficult to be sure that our choice of individuals is not guided by preconceptions of what we are looking for. These warnings must always be borne in mind, for disregard of them has led to erection of hypothetical family trees which further stratigraphical collecting showed to be impossible, as were *a fortiori* the phylogenetic "laws" deduced from them.

Nevertheless, detailed collecting in a circumscribed area, especially from cliff exposures, from geological sequences of reasonable lithological continuity, has produced examples of evolutionary lineages and radiations which may be accepted with some confidence. It is noteworthy that these examples invariably disprove one or more of the previously accepted "laws" discussed above (morphogenesis, irreversibility, etc.).

LIPAROCERATIDAE AND AMALTHEIDAE

The best and most detailed example that can be quoted probably is the phylogeny of the families Liparoceratidae and Amaltheidae, spanning the whole Pliensbachian stage. The Liparoceratidae of the lower Pliensbachian have been collected in great detail from the cliffs of the Dorset coast by W. D. Lang and monographed by L. F. Spath (1938), and the Amaltheidae of the upper Pliensbachian (Domerian) have been similarly collected from all the British exposures by M. K. Howarth, who is preparing a monograph and has kindly contributed his results and Fig. 153.

The ancestral liparoceratid is an evolute, finely ribbed, bituberculate form which still shows much resemblance to the evolute Eoderoceratidae from which the stock sprang. At the same horizon (lower *jamesoni* zone) there are similarly ribbed and bituberculate forms which differ by being more involute (Fig. 153,*1a,b*) and therefore more like later typical *Liparoceras.* These latter gave rise at a slightly higher horizon in the *jamesoni* zone to still more involute sphaerocones, with coarsened and lengthened primary ribs and recessive inner and accentuated outer tubercles (Fig. 153,*2a,b*). From this in turn diverged 2 streams, one *(Liparoceras, Becheiceras)* becoming extreme sphaerocone and mainly fine-ribbed, the other *(Androgynoceras)* producing coarse and simple ribs in the inner whorls (Fig. 153,*3a,b, 4*). In this remarkable lineage the inner whorls are capricorn, and when separated would hardly be supposed to be congeneric with the sphaerocone ancestors and collaterals, or even with the hemisphaerocone and finely ribbed outer whorls of the same individuals. In successive species, however, the capricorn stage gradually spread (by proterogenesis) on to the middle and eventually the outer whorls, producing finally in the middle *davoei* zone complete capricorns (Fig. 153,*5a,b*).

At and near the top of the *davoei* zone the capricorn *Androgynoceras* is replaced by the capricorn *Oistoceras,* which is indistinguishable in side view but differs by significant developments of the venter. Instead of passing straight over the venter and remaining simple, the ribbing of *Oistoceras* (Fig. 153, *6a,b*) is projected forward, forming ventral chevrons; and in some morphologically advanced species the chevron ribs tend to bifurcate and the venter rises to an embryonic keel. These are the earliest manifestations of the essential characters of the succeeding family Amaltheidae. Exposures of the passage beds from lower to upper Pliensbachian, in which these changes occur, are adequate, and intensive collecting by HOWARTH and his predecessors has failed to reveal any other ammonites from which the amaltheids could have sprung.

The earliest forms in which a proto-keel has been found are nuclei from the topmost subzone of the *davoei* zone (SPATH, 1938, pl. 26, fig. 16). In the lowest subzone of the next-higher *margaritatus* zone there are passage forms (Fig. 153,*7*) from *Oistoceras* to fully differentiated *Amaltheus* (Fig. 153, *8a,b*). The transformation was rapid, and it is not at present possible to affirm that it was either proterogenetic or palingenetic. Although the first modifications of the venter took place apparently on the inner whorls, the further rise and crenulation of the keel and compression of the whorls to form the first oxycones *(Amaltheus stokesi)* occurred on the middle or outer whorls, while the nuclei remained stout and *Oistoceras*-like.

Amaltheus stokesi formed the rootstock for all the amaltheids, which are celebrated for their polymorphism. Attainment of the oxycone shape, far from being lethal, coincided with the beginning of repeated radiations. *Amaltheus margaritatus,* the zonal index fossil which typifies the genus for most of us, was not on the direct line of descent but on a divergent branch in which oxycone shape was pressed back to earlier whorls than in the direct line, and it ended in the extreme oxycone *Pseudoamaltheus.* Another side line ended in the completely smooth dwarf *Amauroceras.*

Meanwhile the main stream retained its stout inner whorls (in some species tuberculate and coronate) and relatively evolute coiling and gave rise, by way of passage forms (such as Fig. 153,*9a,b, 10a,b*) to the evolute, planulate, tuberculate genus *Pleuroceras* of the *spinatum* zone at the top of the Pliensbachian. *Pleuroceras* also seems to have arisen from a single ancestral stock and radiated into a number of species characterized by different styles of ribbing and tuberculation. The family then became extinct, leaving no successors in the Toarcian faunas.

This history illustrates the evolution of planulates into sphaerocones, dimorphs, and capricorns; of capricorns into keeled and

FIG. 153. Evolution of the Liparoceratidae (713) and Amaltheidae (637a).——*1a,b. Tetraspidoceras reynesi* SPATH, ancestral form, basal *jamesoni* zone.——*2a,b. Liparoceras (Parinodiceras) parinodus* (QUENST.), early sphaerocone, *jamesoni* zone.——*3a,b. Androgynoceras sparsicosta* (TRUEMAN), dimorph sphaerocone, with capricorn ribbing on the inner whorls, *centaurus* subzone.——*4. Androgynoceras henleyi* (J.SOWERBY), more evolute dimorph, with prolonged capricorn stage, *lataecosta* subzone.——*5a,b. Androgynoceras lataecosta* (J.DEC.SOWERBY), capricorn with normal venter, *lataecosta* subzone.——*6a,b. Oistoceras figulinum* (SIMPSON), capricorn with chevron ribs on venter, *figuli* subzone.——*7*. an early *Amaltheus* sp., oxycone, basal *stokesi* subzone.——*8a,b. Amaltheus stokesi* (J.SOWERBY), *stokesi* subzone.——*9a,b. Amaltheus subnodosus* (YOUNG & BIRD), *subnodosus* subzone.——*10a,b.* an early *Pleuroceras* sp., transitional from *Amaltheus,* basal *apyrenum* subzone.——*11a,b. Pleuroceras spinatum* (BRUGUIÈRE), a tuberculate planulate, *hawskerense* subzone. Figs. 1-11 are in stratigraphical order and show evolution of the stock through the whole Pliensbachian stage (198a).

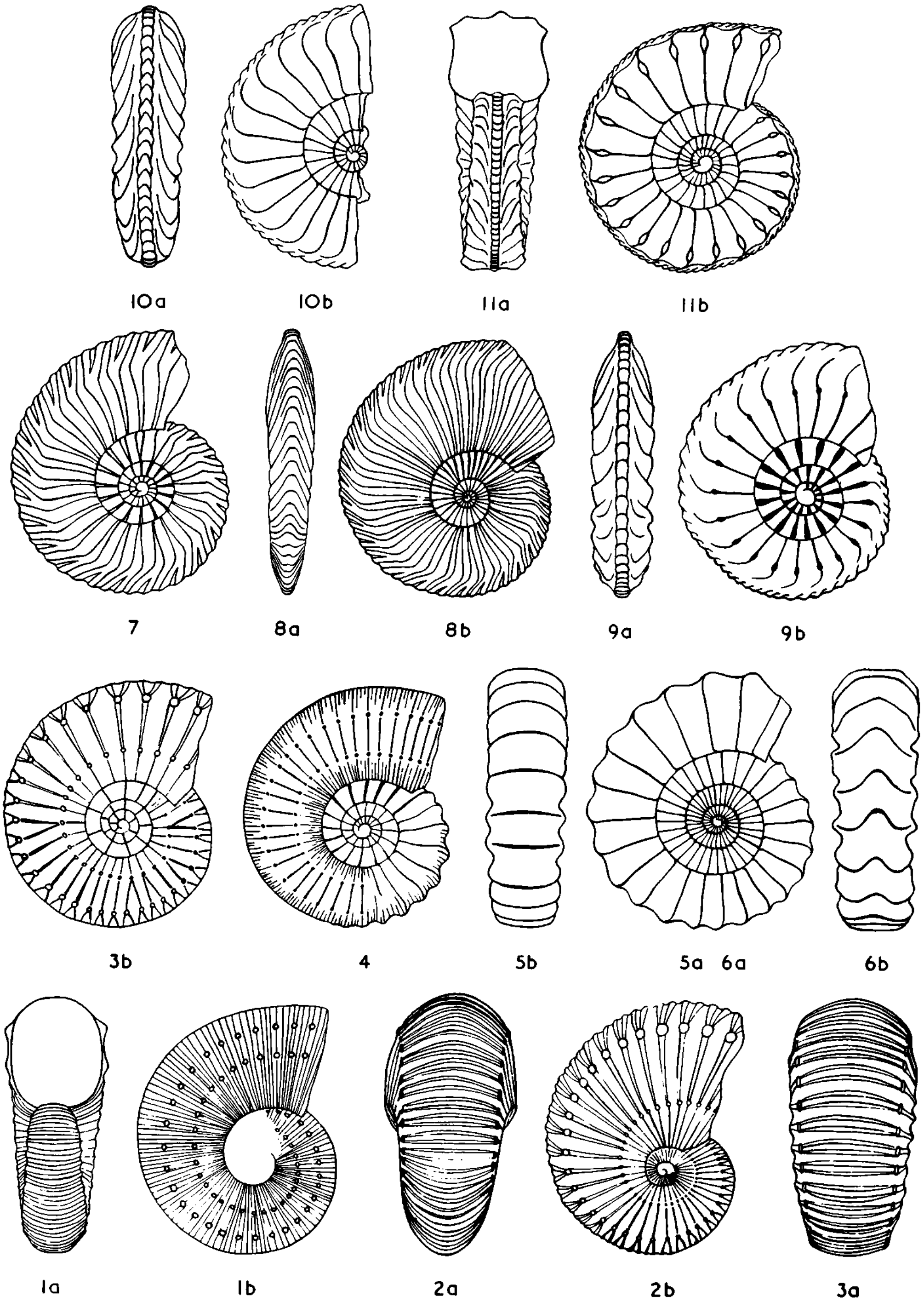

FIG. 153. *(Explanation on facing page).*

ribbed oxycones; and of these in turn back to planulates.

MACROCEPHALITIDAE AND CARDIOCERATIDAE

The whole story was repeated by the Macrocephalitidae and Cardioceratidae of the Middle and Upper Jurassic. There the sphaerocones *Macrocephalites* and *Tulites,* derived from the essentially planulate *Stephanoceras* stock of the Bajocian-Bathonian, are usually supposed to have produced the cadicone *Cadoceras* and oxycone *Quenstedtoceras* and *Cardioceras,* which reverted to planulate *Amoeboceras* and, before extinction in the Lower Kimmeridgian, finally produced various aberrant end forms, including smooth almost keel-less dwarfs *(Nannocardoceras)* analogous with *Amauroceras.*[1] There is an extraordinary resemblance between various successive stages in the 2 lineages and some of their offshoots (Arkell, 1950, p. 356), for example, (1) *Oistoceras* —>*Amaltheus*—>*Pleuroceras* and (2) *Quenstedtoceras (s.s.)*—>*Cardioceras (s.s.)* —>*Amoeboceras(s.s.)* and *Amoebites.*

The course of evolution of the Amaltheidae, as described above from M. K. Howarth's data, differs in an important respect from that inferred for the Cardioceratidae (Arkell, 1948, pp. 380-382, and in Arkell & Moy-Thomas, 1940). In the Cardioceratidae it seems that a number of different lineages evolved more or less parallel, each passing through comparable grades in respect of the main characters, whorl shape, ribbing style, keel development, etc., and also developing repeated lateral offshoots; and the morphologically defined genera *Cadoceras, Quenstedtoceras, Cardioceras,* and *Amoeboceras* are therefore polyphyletic grades—namely, cross sections of a plexus and its side branches. Taxa are of more stratigraphic value and less hypothetical if so defined than if the names were applied to lineages and defined vertically. Where possible, subgeneric names are used for the lineages and the old generic names are retained for the horizontal groupings of parallel grades.

DISCOHOPLITES AND HYPHOPLITES

It is highly probably that analysis of many supposed lineages would reveal a similar complexity and at least micropolyphyletic (if not macropolyphyletic) constitution of generic, subgeneric, and even family taxa. Some instances at family level are apparent in the phylogenetic charts (Figs. 149-151). A good example at generic or subgeneric level has been demonstrated for *Discohoplites* and *Hyphoplites* of the upper Albian and lower Cenomanian (Wright & Wright, 1949). Two species of *Discohoplites* are believed to have given rise by parallel evolution to 2 groups of *Hyphoplites.* The characters which arose in both lineages and transformed them from *Discohoplites* into *Hyphoplites* were regular peripheral tuberculation, at least on the early part of the adult body chamber, with consequent angular whorl section, and increased definition of the primary part of the falcate ribs. The 2 genera are thus polyphyletic grades in related parallel lineages.

CADOCERAS, MACROCEPHALITES, KOSMOCERAS, AND ASSOCIATED FORMS

The transformation of *Cadoceras* into *Quenstedtoceras* and the presumed origin of *Cadoceras* in a macrocephalitid illustrates proterogenetic acquisition of the oxycone form (Fig. 154). Another branch from *Macrocephalites* is supposed to have produced *Kepplerites* and *Kosmoceras* by proterogenetic acquisition of a tabulate venter. This last was one of the first instances of proterogenesis ever pointed out (Pavlow, 1901, p. 62) (see footnote, p. L116) (Fig. 154).

The genus *Kosmoceras* has been subjected to detailed and elaborate statistical analysis by Brinkmann (1929) on the basis of crushed shells collected at centimeter levels in the Oxford Clay brickpits at Peterborough, England.[2] On the strength of this analysis he distinguished 5 subgenera: *Kosmoceras s.s., Gulielmiceras, Gulielmites, Zugokosmokeras,* and *Spinikosmokeras,* which evolved side by side and are characterized by differences in whorl shape, habits of ribbing and tuberculation, and

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[1] *Macrocephalites,* however, is of Tethyan origin, while *Cadoceras* and the Cardioceratidae probably originated in the Boreal Sea from some contemporary collateral such as *Arctocephalites.*

[2] For *Zugokosmoceras* Brinkmann *(partim)* read *Gulielmites* Buckman, and for *Anakosmoceras* Brinkmann read *Gulielmiceras* Buckman; Brinkmann's usage does not accord with the Rules of Nomenclature.

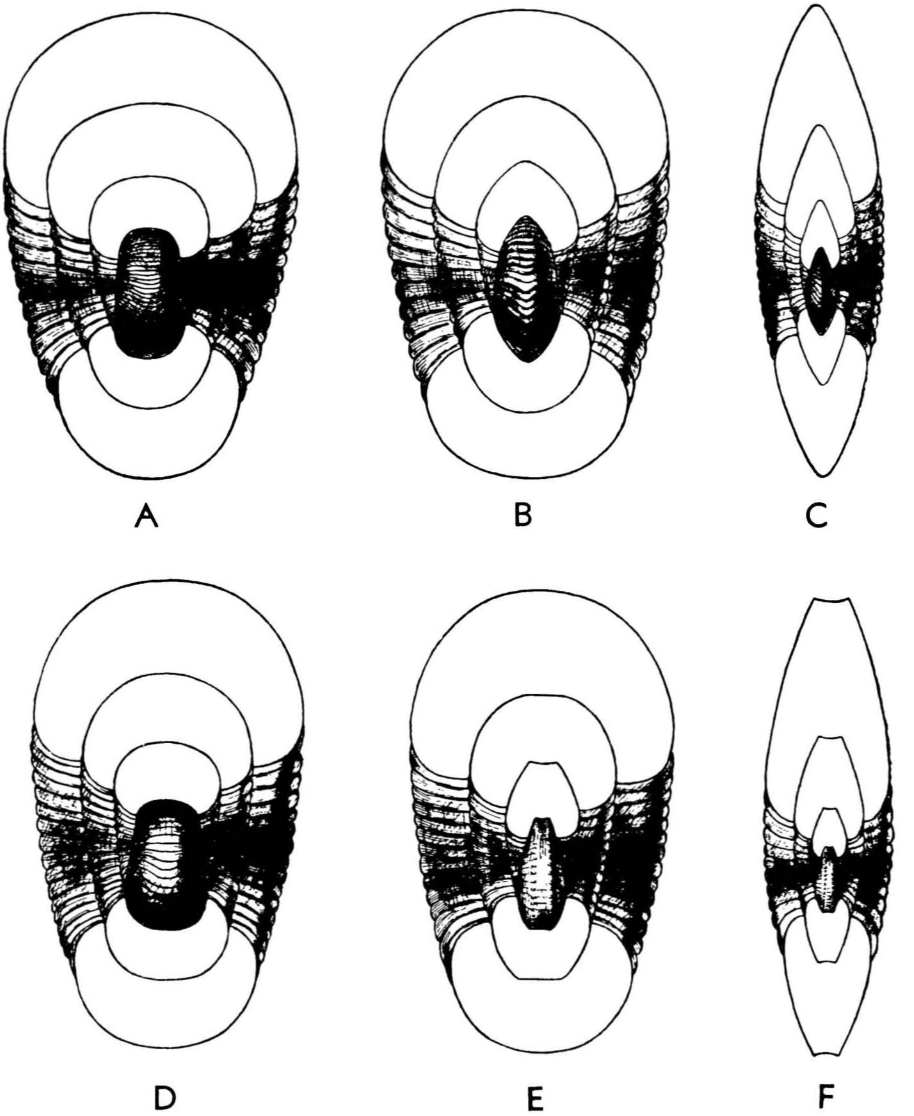

FIG. 154. Two examples of proterogenesis from the Callovian (416). *A,D,* the ancestral *Macrocephalites,* with rounded venter throughout. *B, Cadoceras. C, Quenstedtoceras,* showing sharpening of the venter beginning on early whorls. *E, Kepplerites, F, Kosmoceras,* showing tabulate venter beginning on early whorls.

structure of aperture (presence or absence of lappets) (Fig. 155).

CALLIZONICERAS AND LEYMERIELLIDAE

Another interesting phylogenetic series was made out by BRINKMANN in 50 m. of lower Albian clays exposed in a canal between Hanover and Peine, Germany, and neighboring brick pits. This series shows the evolution of *Callizoniceras (Wollemanniceras)*[1] *keilhacki* into Leymeriellidae (Fig. 156). At the start of the series the whorls have many plain constrictions with flat interspaces, on which at higher horizons simple ribs develop. Then a median ventral groove sets in and is further developed with differing depth and width in 2 parallel branches of the stock.

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[1] Called *Desmoceras* in BRINKMANN (57).

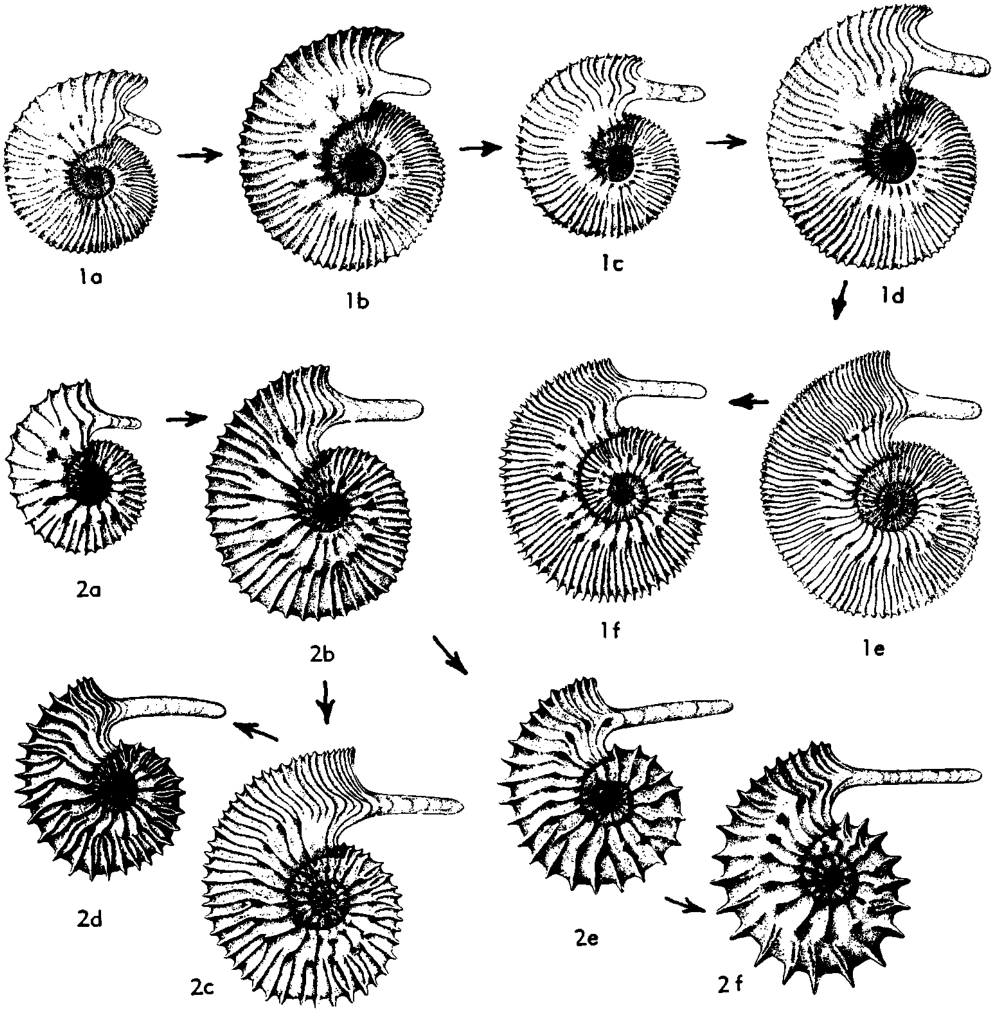

FIG. 155. Evolution of ornament and lappets in two lineages (subgenera) of *Kosmoceras*, M.Jur.(M. Callov.), Peterborough, Eng. (55).——*1a-f. Gulielmiceras.*——*2a-f. Spinikosmokeras.*

Decipherment of these sequences is favored by unusual continuity of lithology and therefore probably near-continuity of evolving faunas, prerequisites for any safe deductions as to descent. Where the stratigraphy is unfavorable, marked by wide changes in lithology, frequent absence of ammonites due to unfavorable environments, condensed faunas, etc., the decipherable history may be so fragmentary that classification is perforce horizontal and the taxa are bound to be more or less polyphyletic.

PALEOECOLOGY

So great is their variety in size, shape, style of coiling, thickness of test, external ornament, and internal complexity of sutures, that the Ammonoidea seem to comprise adaptations to a wide range of marine niches. There is a noticeable absence of ammonites (or they occur as rarities, usually worn or broken) from coral reef rocks and from rapidly deposited false-bedded sands and oölites (ARKELL, 1933, pp. 562-567, gives analysis of the distribution of ammonites in relation to these rocks in the British

Jurassic). In such environments the ammonites found may have been floated in, either unwillingly in life or posthumously. Practically all other types of sediment may be expected to yield ammonites in abundance, though commonly they are unaccountably barren.

RELATION OF SHELL FORM TO SEDIMENTARY ENVIRONMENT

Various attempts have been made, on lines also suggested by Vaughan (1940), to relate different types of shell to particular lithologies (for instance, Miller & Furnish, 1937; Scott, 1940). Scott's attempt contains many interesting and stimulating observations and suggestions, but most of his conclusions apply only to the area and formations studied and one is immediately confronted by contradictions on trying to apply his methods to other areas and other formations.

One repeatedly made observation is that the sharp-edged discoidal shell form with smooth surface appears to be ideally adapted to rapid swimming, and attention has been drawn to a number of occurrences where such forms are associated with clays and marls, whereas more or less contemporary tumid and highly ornamented forms are associated with a shallower, calcareous and detrital shelly facies. Examples of this in the Bajocian have been cited by Westermann (1954, pp. 35-37). Others readily come to mind: for instance, dominance of the discoidal genus *Amaltheus* throughout Europe in the dominantly clayey lower Domerian and its replacement by the planulate, spinous *Pleuroceras* in the upper Domerian, this change coinciding in most areas with a change of lithology to limestones and ironstones; or the dominance of the discoidal *Oxycerites* in the Bathonian clays (Fuller's Earth facies); or the abundance of flat *Kosmoceras* and *Hecticoceras* in the Oxford Clay; and so on. But there are many obstacles to the acceptance of any generalization. For instance, the abundance of *Oxynoticeras* in lower Lias clays ("Oxynoticeratan") was a temporary phenomenon, for the similar, much thicker clays (also lower Lias) formed earlier and later contain all manner of other ammonites but no oxycones. Again, oxycone *Oxycerites* is most abundant of all in the limestone-ironstone facies of the Bathonian in Germany, although rare in that facies in England; the oxycone *Clydoniceras* is abundant in Bathonian shelly limestones wherever it occurs; and in the middle of the Oxford Clay over large tracts of the world is a zone characterized by and named after one of the stoutest of the stephanoceratacean types of shell, *Erymnoceras coronatum* and its allies, and by the stout and spinous *Reineckeia anceps* and its allies. Moreover, it is just the oxycones which most

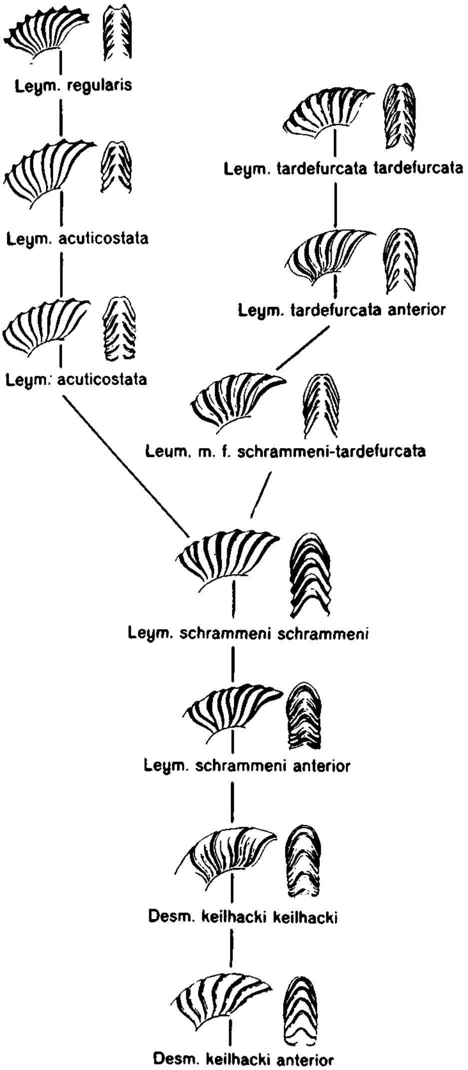

Fig. 156. Diagram illustrating the evolution of *Callizoniceras keilhacki* ("*Desmoceras*") into 2 lineages of *Leymeriella,* L.Cret.(L.Alb.), Ger. (57).

commonly display simplified, regressive, even pseudoceratitic types of suture, which have been explained as a sign of sluggishness and bottom-dwelling (454, 455).

RELATION OF SIZE TO ENVIRONMENT

Attempts have also been made to relate size of shell to sedimentary facies (Reuter, 1908), the conclusion being advanced that dwarf assemblages probably indicate some kind of unfavorable environment, deficient in aeration or salinity or warmth (246). On the other hand, large size (gigantism) has been claimed as an evolutionary trend independent of environment (314), for certainly it seems to occur in any stock at any time and irrespective of lithology, although perhaps the majority of giant ammonites are found in limestones. To ascribe size differences in ammonites to any particular environment is impossible, since small and large forms too often thrived together. (The total range of size in adult ammonites is from about 1 cm. to 3 m., or a ratio of 1:300, but the vast majority are intermediate about 10 to 30 cm.)

MODE OF LIFE

The mode of life of ammonites has been endlessly debated. The reader is referred especially to papers by Walther (1897), Solger (1901, 1902), Jaekel (1902), Benecke (1905, p. 544), John (1909), Rothpletz (1909), Diener (1912), Dollo (1912), Scupin (1912), Frech (1915), Prell (1921), Stieler (1923), H. Schmidt (1925, 1930), Berry (1928), Beurlen (1928), Trueman (1941), and Arkell (1949). At least 90 per cent of these fascinating discussions amount to conjecture. The total absence of tracks attributable to ammonites, with one possible exception (525) suggests that the majority of them were not habitually crawlers. Many could, however, have lived in mud on kinds of bottom in which no tracks would be preserved—for instance, among seaweed or sea grass. Stieler (1922) believes that the possession of a recurved rostrum can only be explained as an adaptation to such a bottom life, its advantage being that it would raise the aperture above the mud. Berry (1928) attributed the coiling of the shell itself to the same cause, the straight ancestor having abandoned a nektonic for a benthonic mode of life. Asymmetry of sutures or siphuncle in some genera also suggests a life on the bottom, on one side, but other explanations are possible.

A number of the deductions made in these and other discussions by different authors are startlingly contradictory. For instance, Beurlen (1928) asserted that the ammonite shell was not protective as in gastropods but served essentially as a hydrostatic apparatus, whereas Berry (1928) asserted that the shell was essentially protective and the idea of a hydrostatic apparatus a myth. The weight of evidence seems to be on the side of Beurlen and the similar views of Diener (1912, 1922), who wrote with great experience and much persuasion. It is difficult to imagine that such a structure as the ammonite phragmocone evolved as a by-product, for only the body chamber at each stage of growth could have played any part in protecting the animal (Fig. 124). If the phragmocone functioned as a hydrostatic apparatus, it must have been possible for gas of some sort to pass through the siphuncle to and from the camerae; and this could only have occurred if in at least the larger, later formed camerae, the siphuncle tube did not become solid during life. Possibly the lag in phosphatization, previously mentioned, has a bearing on this problem. In any case, it appears that the camerae in living *Nautilus* and *Spirula* do contain gas (mainly nitrogen). If the purpose of this gas is merely "to render the shell buoyant once for all," as has been suggested, ammonites cannot have lived at great depths or their shells would have been crushed. The pressure exerted by sea water amounts to about a ton to the square inch at 1,000 fathoms. Therefore, if ammonites descended to more than about half this depth their shells (judging by some experiments with the much smaller and therefore much stronger *Spirula*) would be crushed unless the internal gas pressure could be raised to equalize the external water pressure. Provided that gas could pass through non-hardened parts of the siphuncle, this could be brought about simply by passive generation of gas, which would be sucked into the camerae by the partial vacuum. The shell would also be strengthened by its ribbing.

On moving suddenly upward, toward the surface, the shell would have a tendency to burst. The most efficient means imaginable to counteract this bursting tendency would be a series of septa, each having the maximum possible attachment to the inside of the shell and tied into the fabric of the shell walls just as the septal edges are found to be (ARKELL, 1949, p. 409). If these deductions are sound, elaboration of sutures would denote adaptation to active swimming habits in deep water, and simplification of sutures would imply change of habitat to shallower waters, or sluggishness.

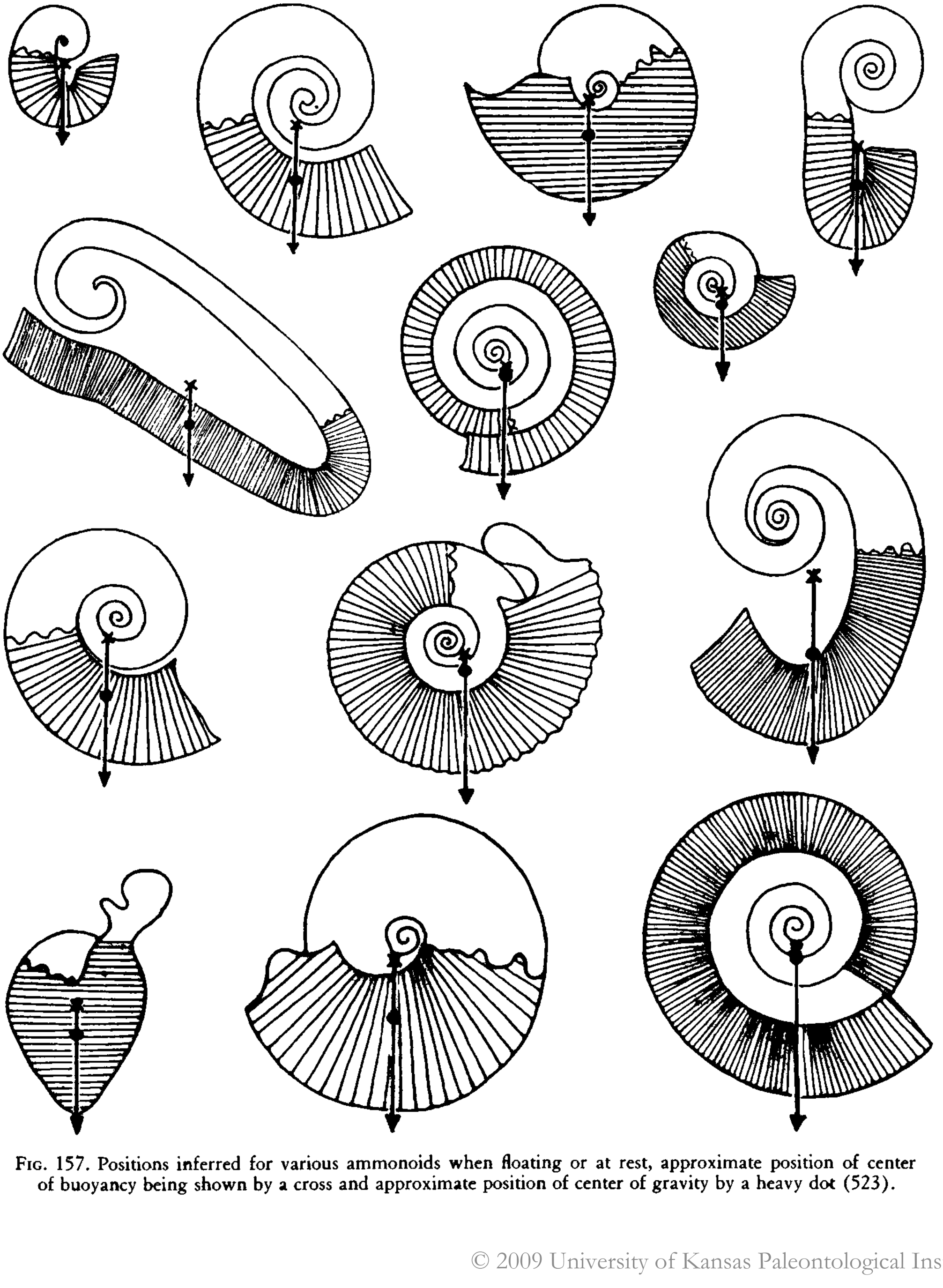

FIG. 157. Positions inferred for various ammonoids when floating or at rest, approximate position of center of buoyancy being shown by a cross and approximate position of center of gravity by a heavy dot (523).

This agrees with the fact that some of the most elaborate sutures are those of all the phylloceratids and lytoceratids, for which a free-swimming life in the open seas has always been postulated on general grounds.

New light on the normal attitude of the shells during life was thrown by TRUEMAN (1941), who calculated the positions of the center of gravity and center of buoyancy in a number of genera. He found that in evolute many-whorled shells the centers of gravity and buoyancy are so close together that the animal could easily have changed its position considerably, though the normal position of rest would be with the aperture facing half upward (Figs. 157, 158). The involute forms, however, must have been much more stable, and in them the aperture faced almost completely upward, as it does in the living *Nautilus*. The conclusion is that most ammonites probably did not habitually crawl, that some could do so fairly easily, and that others could crawl only by holding on to the bottom. In the uncoiled forms, such as scaphitids, the buoyant effect of the camerae would have made crawling almost impossible. If such heteromorphs lived on the bottom, theirs could only have been a stationary existence amongst mud and weeds. Most probably the majority of ammonites hovered and soared through the water not far above the bottom, resting near it without touching it, as does *Nautilus*. Spines could have served as balancers or stabilizers, or as protection against enemies.

TRUEMAN's calculations are confirmed by impressions of perisphinctids on the Solnhofen Slates. ROTHPLETZ (1909) showed that some of the perisphinctids which lie on the bedding planes at Solnhofen have beside them an impression of part of the venter (Fig. 158). He pointed out that the only possible interpretation of these is that the ammonite floated in shallow water, presumably on a receding tide, with its spiral plane vertical, that it first touched the bottom with its venter, and as the water continued to shallow the shell fell over on its side and was eventually left high and dry. In every specimen, the impression of part of the venter is just where it should be according to TRUEMAN's figures. The impression on the mud is so clear that if any of the animal had protruded from the shell it too must have left impressions. The inference is that the animals were completely retracted within their shells, perhaps dead.

FIG. 158. A perisphinctid with impression of its venter beside it, marking where it first "touched down" on the mud; U.Jur.(Kimm.), Solnhofen, Eu.; ×1 (110).

BREEDING HABITS

Light was also thrown by TRUEMAN (1941) on the breeding habits of ammonites. On measuring large numbers of shells massed together in the Marston Marble of the English lower Lias, he found that the material fell into 5 size groups. He interpreted these as showing that all the ammonites were killed at once and that 5 successive broods are represented. Whether the broods were seasonal or more frequent is unknown. Here successive broods of larvae grew into ammonites on the spot, but it is likely that the world-wide distribution of so many forms of ammonites is due chiefly to the larvae being carried away by ocean currents; this cause is likely to have been far more potent than *post mortem* drifting of shells.

FOOD

Direct evidence of the food eaten by ammonites is very meager. A mass of broken miniature aptychi and segments of siphuncles found in the body chamber of an *Oppelia steraspsis* from Solnhofen was originally thought to be remains of an unborn brood, but has been reinterpreted as the masticated remains of young oppeliids eaten cannibalistically (GÜRICH, 1924; SCHWARZBACH, 1936).

ENEMIES, INJURIES

Indications of the enemies that preyed on ammonites are little less rare. *Amaltheus* and belemnites have been found in the stomach of a saurian (FRENTZEN, 1936), and many belemnites have been discovered in the stomach of a fish, *Hybodus*. In the Upper Jurassic of southern Germany, many haploceratids and oppeliids have tongue-shaped pieces taken out of them, generally in the hinder part of the body chamber, as if they had been bitten. Decapod crustaceans are thought to have been the most likely causes of these mortalities (ROLL, 1935).

Injuries to the body chamber during life were numerous and often produced monstrosities. When they were inflicted before maturity, subsequent parts of the shell may bear to the end various kinds of distortion in shape, ornament, and suture, commonly with displacement of siphuncle and keel and marked asymmetry. These distortions take various well-known forms and can usually be recognized with experience. A number have been figured and discussed in papers by FRAAS (1863), BOONE (1926), DESTOMBES (1938), SPATH (1945), MAUBEUGE (1949), DROUTCHTCHINE (1954), and POPOV (1954). The abnormalities may continue to the end of the mature shell or, in less severe ones, disappear suddenly, with complete return to normal. When injured early, the whole shell may have quite different characters on opposite sides, producing divergences which, if found separated, would be taken for 2 different species or even genera. Perhaps the most remarkable example on record is that of a *Hysteroceras* in which the last 5 suture lines are completely reversed, the lobes pointing forward and the saddles backward, without any appreciable disfigurement of their elements or details (HAAS, 1941). All such injuries were clearly inflicted on parts of the shell that were body chamber at the time. Contrary to some statements, no valid evidence is known indicating that injuries to camerae could be repaired.

GEOGRAPHIC DISTRIBUTION

The earliest ammonoids, found in Lower Devonian rocks, are known so far only in central Europe, but knowledge is still too incomplete to allow one safely to regard this as the cradle of all ammonoids. Most of the Paleozoic and Mesozoic forms are largely cosmopolitan. Their distribution seems to have been little influenced by latitude and therefore by any climatic zones. Nevertheless, some assemblages are much more widespread than others, and in all faunas there are genera, subfamilies, or even families, which are restricted in their distribution to certain parts of the world.

For the Jurassic, knowledge has now advanced to the point where maps can be drawn with some confidence showing distribution of faunas (ARKELL, 1956). It emerges that in the Early Jurassic the ammonite faunas were world-wide at generic and often specific level. In the Bajocian they retreated from the Arctic Ocean border seas. In the Bathonian this retreat reached a climax and ammonites became greatly restricted. With the Callovian a general readvance began, but successive advances from the south and north can be traced over Europe. In the late Late Jurassic 2 distinct realms – Boreal and Tethyan-Pacific – became differentiated and correlation between them is extremely difficult. For some periods a subdivision of the latter into Tethyan and Pacific realms is possible, and at times various provinces developed marked characteristics. For instance, in the Toarcian, Callovian, and Oxfordian, certain special families mark out an Indian-Ethiopian province of the Tethyan realm, although stragglers from the province have lately been found in the western Tethys.

In the 19th century literature the "liostracous" suborders Phylloceratina and Lytoceratina were always portrayed as characteristic of the Tethys and of peculiar, deeper-water deposits, and the beds that produce them were put in opposition to the shallow-water deposits in which the trachyostracous families lived. It is true that the 2 liostracous suborders are usually far more abundant in the Tethys than farther north, but in southern Europe, including the middle of the Mediterranean and North Africa, and in the Caucasus and East Africa, there is a complete mixture at various horizons; Phylloceratina and Lytoceratina are as common as anywhere and the same shallow-water trachyostraca abound as well. Isolated occurrences of Phylloceratina and Lytoceratina, moreover, are now known in both Jurassic and Cretaceous deposits inside the Arctic Circle, in northern Siberia and Greenland.

The Mesozoic ammonoid faunas of the Arctic regions, and the rich Upper Cretaceous fauna of the Antarctic continent, prove that there can have been no ice caps in Mesozoic times—at least none anywhere near their present positions. The only positions in which cold poles could have been situated without affecting the evidence are in the North Pacific and a corresponding position in the South Atlantic (Arkell, 1956. This agrees with the long-known occurrence of very similar Jurassic temperate floras in Graham Land and east Greenland. The evidence is so unequivocal that it should be more widely realized and reckoned with by paleometeorologists and astronomers.

STRATIGRAPHIC DISTRIBUTION

The pre-eminence of ammonites as zonal marker fossils for local and world-wide correlations is undisputed. No other organisms enable the Upper Paleozoic and Mesozoic systems to be classified and correlated in anything like such detail. This usefulness is due to their rapidity of evolution, with wealth of forms changing rapidly up the stratal column, their wide distribution and comparative indifference to facies, and usually their ease of recognition, even in the field, without use of the microscope or laborious techniques.

Next after these qualities, the most remarkable fact about the stratigraphic distribution of the order is their 3 lean periods, at end of the Permian, end of the Triassic, and end of the Cretaceous (Figs. 159, 160). The first 2 crises were survived in each case by a single family, which then blossomed anew by explosive radiation to repopulate all the seas of the world, but the 3rd brought sudden extinction to the whole order. The last ammonites of the Late Cretaceous, in the Maastrichtian, show no special signs of degeneration. Their sutures are elaborately frilled and they differ in no perceptible way from the generations that preceded them and perpetuated their kind. Nor do the solitary families that managed to survive the 2 previous crises reveal in what characters they were superior to all the other families that went under at those times. It is, however, probably no coincidence that it was the Phylloceratina that came through from the Triassic to the Jurassic, for this was the most

Table 1. *Standard Stages and Ammonite Zones of the Triassic* (Bernhard Kummel)

Stages	Zones
Rhaetian	*Choristoceras marshi*
Norian	*Sirenites argonauta*
	Pinacoceras metternichi
	Cyrtopleurites bicrenatus
	Cladiscites ruber
	Sagenites giebeli
	Discophyllites patens
Carnian	*Tropites subbullatus*
	Carnites floridus
	Trachyceras aonoides
	Trachyceras aon
Ladinian	*Protrachyceras archelaus*
	Protrachyceras reitzi
Anisian	*Paraceratites trinodosus*
	Paraceratites binodosus
	Nicomedites osmani
	Neopopanoceras haugi
Scythian	*Prohungarites similis*
	Columbites parisianus
	Tirolites cassianus
	Anasibirites multiformis
	Meekoceras gracilitatis
	Flemingites flemingianus
	Koninckites volutus
	Xenodiscoides fallax
	Prionolobus rotundatus
	Proptychites rosenkrantzi
	Vishnuites decipiens
	Ophiceras commune
	Otoceras woodwardi

TABLE 2. *Standard Stages and Ammonite Zones of the Jurassic of Northwest Europe* (W. J. ARKELL)

	Stages	Zones
UPPER JURASSIC	Purbeckian	[No ammonites]
	Portlandian	*Titanites giganteus*
		Glaucolithites gorei
		Zaraiskites albani
	Kimmeridgian	*Pavlovia pallasioides*
		Pavlovia rotunda
		Pectinatites pectinatus
		Subplanites wheatleyensis
		Subplanites spp.
		Gravesia gigas
		Gravesia gravesiana
		Aulacostephanus pseudomutabilis
		Rasenia mutabilis
		Rasenia cymodoce
		Pictonia baylei
	Oxfordian	*Ringsteadia pseudocordata*
		Decipia decipiens
		Perisphinctes cautisnigrae
		Perisphinctes plicatilis
		Cardioceras cordatum
		Quenstedtoceras mariae
MIDDLE JURASSIC	Callovian	*Quenstedtoceras lamberti*
		Peltoceras athleta
		Erymnoceras coronatum
		Kosmoceras jason
		Sigaloceras calloviense
		Proplanulites koenigi
		Macrocephalites macrocephalus
	Bathonian	*Clydoniceras discus*
		Oppelia aspidoides
		Tulites subcontractus
		Gracilisphinctes progracilis
		Zigzagiceras zigzag
	Bajocian	*Parkinsonia parkinsoni*
		Garantiana garantiana
		Strenoceras subfurcatum
		Stephanoceras humphriesianum
		Otoites sauzei
		Sonninia sowerbyi
		Ludwigia murchisonae
		Tmetoceras scissum
		Leioceras opalinum
LOWER JURASSIC	Toarcian	*Lytoceras jurense*
		Hildoceras bifrons
		Harpoceras falcifer
		Dactylioceras tenuicostatum
	Pliensbachian	*Pleuroceras spinatum*
		Amaltheus margaritatus
		Prodactylioceras davoei
		Tragophylloceras ibex
		Uptonia jamesoni
	Sinemurian	*Echioceras raricostatum*
		Oxynoticeras oxynotum
		Asteroceras obtusum
		Euasteroceras turneri
		Arnioceras semicostatum
		Arietites bucklandi
	Hettangian	*Schlotheimia angulata*
		Psiloceras planorbis

TABLE 3. *Upper Jurassic Ammonite Zones of the Western Tethys (Central and Southern Europe)* (W. J. ARKELL)

Stages	Zones
Tithonian (upper)	*Virgatosphinctes transitorius (Berriasella chaperi, B. delphinensis)*
(middle)	*Semiformiceras semiforme*
(lower)	*Berriasella ciliata, Anavirgatites palmatus*
	Subplanites vimineus
	Taramelliceras lithographicum, Hybonoticeras hybonotum
Kimmeridgian (middle and lower)	*Hybonoticeras beckeri*
	Aulacostephanus pseudomutabilis
	Streblites tenuilobatus
Oxfordian	*Epipeltoceras bimammatum*
	Gregoryceras transversarium
	Cardioceras cordatum
	Quenstedtoceras mariae

persistent and unchanging stock, with the longest range of all ammonoids; they survived from the Early Triassic until the Late Cretaceous, with only minor changes in their form, mode of coiling, ornament, and highly peculiar sutures.

What were the causes of the final extinction at the end of the Cretaceous can only be conjectured, and speculations in this field would hardly be appropriate in this *Treatise*. It must be said, however, that a hypothesis

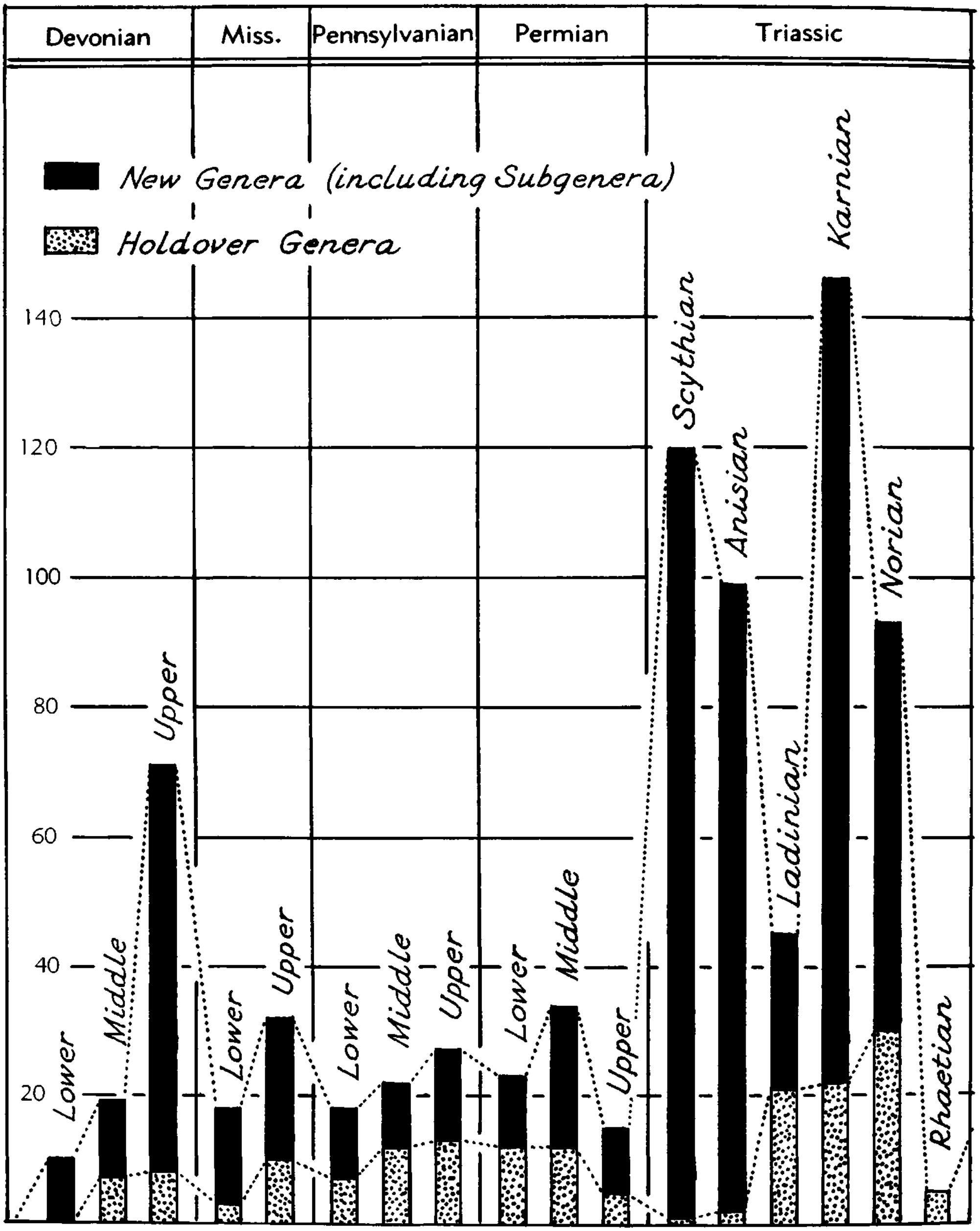

Fig. 159. Number of Ammonoid genera recorded in *Treatise* in main divisions of Paleozoic and Triassic rocks containing them, showing new genera introduced in each and holdover genera (Moore).

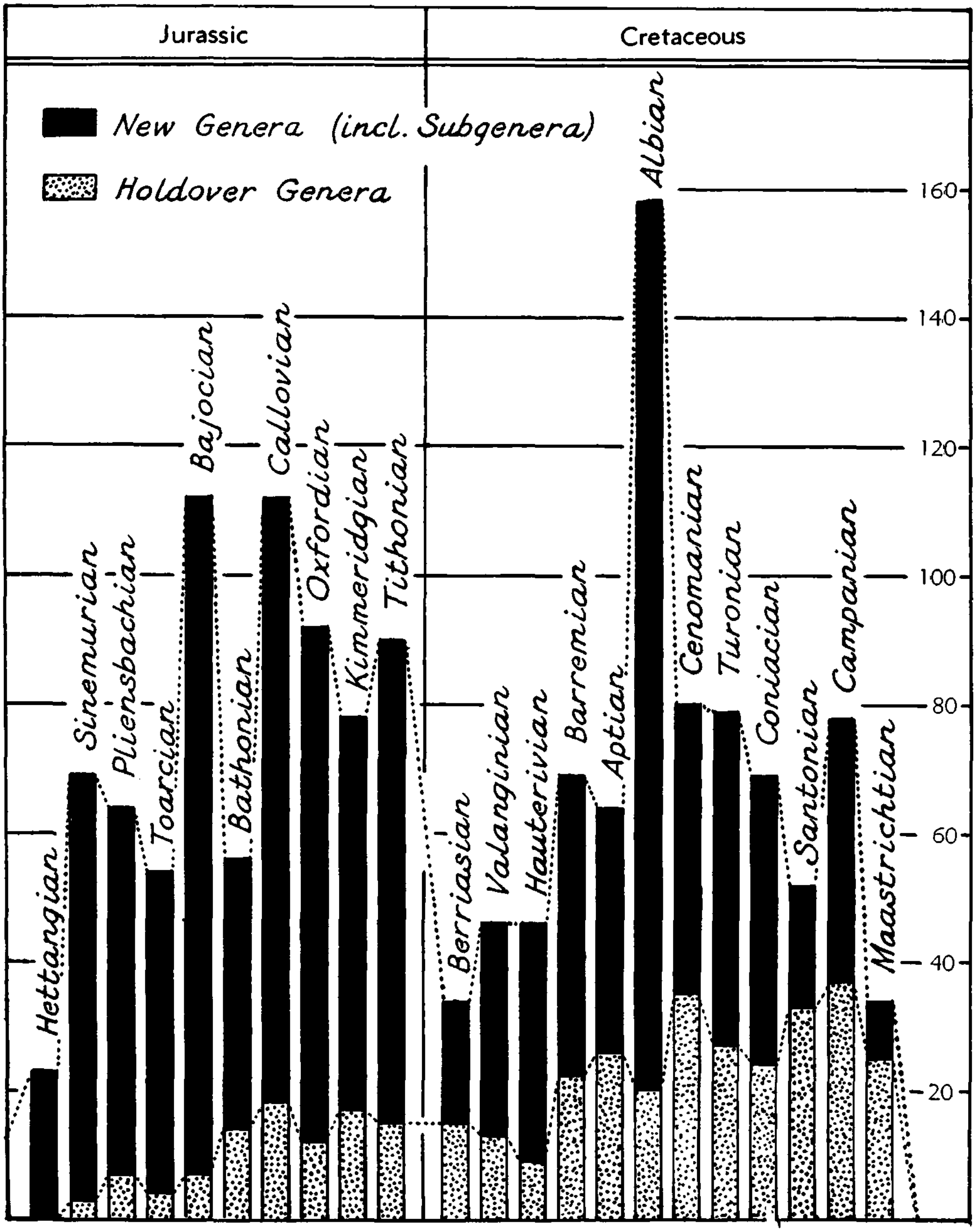

FIG. 160. Number of ammonoid genera recorded in *Treatise* in main divisions of Jurassic and Cretaceous rocks, showing new genera introduced in each and holdover genera (MOORE).

TABLE 4. *Standard Stages and Ammonite Zones of the Cretaceous of Classic Areas of Western Europe*[1] (C. W. WRIGHT)

	Stages	Zones
UPPER CRETACEOUS	Maastrichtian	*Sphenodiscus* sp.
		Pachydiscus neubergicus
	Campanian	*Hoplitoplacenticeras vari*
		Menabites delawarensis
		Diplacmoceras bidorsatum
	Santonian	*Placenticeras syrtale*
		Texanites texanus
	Coniacian	*Paratexanites emscheris*
		Barroisiceras haberfellneri
	Turonian	*Subprionocyclus neptuni*
		Collignoniceras woollgari
		Mammites nodosoides
		Metoicoceras whitei
	Cenomanian	*Utaturiceras vicinale*
		Acanthoceras rhotomagense
		Mantelliceras mantelli
		Mantelliceras martimpreyi
LOWER CRETACEOUS	Albian (upper)	*Stoliczkaia dispar*
		Mortoniceras inflatum
	(middle)	*Euhoplites lautus*
		Hoplites dentatus
	(lower)	*Douvilleiceras mammillatum*
		Leymeriella tardefurcata
	Aptian (upper)	*Diadochoceras nodosocostatum*[2]
		Parahoplites nutfieldensis
		Cheloniceras martini
	(lower)	*Deshayesites deshayesi*
	Barremian	*Costidiscus recticostatus*
		Heteroceras astierianum
		Crioceratites emericianus
	Hauterivian	*Pseudothurmannia angulicosta*[3]
		Subsaynella sayni
		Crioceratites duvali
		Acanthodiscus radiatus
	Valanginian	*Kilianella roubaudiana*
		________[4]
	Berriasian	*Thurmanniceras boissieri*

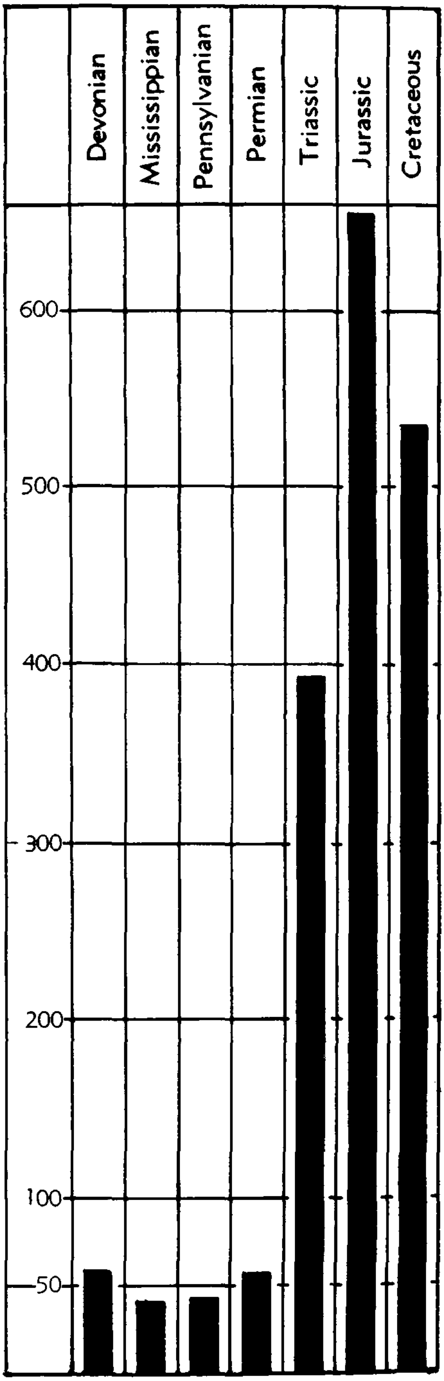

FIG. 161. Bar graph showing number of ammonoid genera (including subgenera) as recognized in the *Treatise*, occurring in each geologic period (MOORE).

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[1] Since the characteristic exposure of the stages or the best-described ones are in different areas, the zones given in the table do not apply over the whole of western Europe.

[2] This zone is often placed in the lower Albian.

[3] This zone is sometimes placed in the Barremian.

[4] There seems to be an unnamed gap here in the classic zones of southern France.

TABLE 5. *Ammonite Zones of the Volgian* (W. J. ARKELL)

Stages	Zones
Volgian (upper)	*Riasanites rjasunensis* *Craspedites nodiger* *Craspedites subditus* *Craspedites fulgens*
(lower)	*Lomonossovella blakei,* *Epivirgatites nikitini* *Virgatites virgatus* *Zaraiskites scythicus* *Dorsoplanites dorsoplanus*

postulating that the ammonites suddenly cast away their shells and that their descendants are to be found at the present day as the Octopoda or other Dibranchiata, has no evidence to support it.

Nor is this the place for a discussion of the nature and scope of ammonoid zones or ages; that is a stratigraphical matter. The principal zones, and the stages in which they are grouped for purposes of the *Treatise,* will be found in Tables 1-5. It should be noted in connection with the tables that the zones of the Paleozoic are not comparable with Mesozoic zones but are more in the nature of the "ages" sometimes distinguished in the Mesozoic, namely, periods dominated by certain genera or families. The distribution of genera in time is shown in Fig. 161.

SYSTEMATIC DESCRIPTIONS

By W. J. ARKELL, BERNHARD KUMMEL, and C. W. WRIGHT

INTRODUCTION

AUTHORSHIP

The systematic descriptions of all Triassic taxa in following pages have been prepared by BERNHARD KUMMEL. In general, W. J. ARKELL is the author of all Jurassic ammonoid taxa and C. W. WRIGHT of all Cretaceous units, but because some families contain both Jurassic and Cretaceous genera, contributions to the text by ARKELL and WRIGHT are intermixed in some places. In the section mainly devoted to description of Jurassic forms, WRIGHT is author of the text on Protetragonitidae (p. L199), Macroscaphitidae (p. L204), Cicatritidae (p. L205), Aconeceratinae (p. L285), as well as diagnoses of Cretaceous genera assigned to otherwise Jurassic families of Phylloceratina and Lytoceratina. Descriptions of the Neocomitinae (p. L356), Oosterellidae (p. L362), and Spiticeratinae (p. L345) are the product of collaboration by ARKELL and WRIGHT.

Because of placement in the predominantly Paleozoic suborder Prolecanitina, the Triassic family Sageceratidae has been described by MILLER & FURNISH in the preceding section of this volume on Paleozoic Ammonoidea, and conversely, Permian genera of the Xenodiscidae and Otoceratidae, included in the predominantly Triassic Ceratitina, have been described by KUMMEL.

ACKNOWLEDGMENTS

Special appreciation is expressed here for help furnished by L. F. SPATH in connection with KUMMEL's work on Triassic ammonoid taxa, both during studies at the British Museum in 1951-1952 and through subsequent correspondence.

Valuable help with Liassic families and genera was received at all stages of preparation from Dr. D. T. DONOVAN, University of Bristol. Assistance in connection with Cretaceous units by providing important specimens for study, by furnishing advance copies of manuscripts, or by advancing publication of their own work on various ammonoids was given by Vicomtesse ELIANE BASSE DE MÉNORVAL (Paris), G. BOTERO-ARANGO (Colombia), RAYMOND CASEY (London), W. A. COBBAN (Colorado), J. P. CONLIN (Texas), TATSURO MATSUMOTO (Japan), R. A. REYMENT (Nigeria), and Comtesse DE VILLOUTREYS (Monaco). All illustrations that accompany systematic descriptions of Mesozoic ammonoids have been prepared by RAYMOND C. MOORE. Appreciation of the aid furnished by these individuals and various others who are unnamed is expressed here.

SPECIAL FEATURES OF STYLE

For the most part, systematic descriptions of Mesozoic Ammonoidea conform precisely in style to those given in other sections of the *Treatise,* but some deviations which have been allowed call for explanation.

ABBREVIATION OF GENERIC NAME AMMONITES

Very many Mesozoic genera of Ammonoidea are based on type species that originally were assigned to the very widely inclusive genus named *Ammonites.* This generic name is indicated by the abbreviation "*Am.*"

DESIGNATION OF SUBGENERA

In parts of the text devoted to Jurassic ammonoids (but not in parts describing Triassic and Cretaceous ammonoids), genus-group taxa (genera, subgenera) are treated as co-ordinate units, except that those considered to be of subgeneric rank are indicated by the abbreviation "Subgen." and those postulated to have such rank by "?Subgen." Genus-group taxa so marked are construed to belong with the next preceding taxon which is not indicated as having subgeneric status; a consequent of this arrangement is omission of all nominate *(sensu stricto)* subgenera. The chief reason for this mode of treatment is the very great difficulty in deciding on the appropriate taxonomic rank of a large number of generic names, especially of many introduced by S. S. BUCKMAN. Hundreds of these names have been reduced to the rank of subjective synonyms, although some are likely to be promoted from this status when the families to which they belong come to be monographed. In the light of present knowledge it is not possible to evaluate all available generic names satisfactorily. Accordingly, the author (ARKELL) of text describing Jurassic ammonoids declines to formalize subgenera, because to do so would, in his opinion, give a spurious appearance of finality in classification and certainly would beg many questions. Much unevenness in the relative size of families is due to nothing more than the publication by BUCKMAN or some other author of numerous available generic names in some family groups and lack of such publication in others.

DESIGNATION OF SYNONYMS

The names of genus-group taxa which are classed as synonyms are cited in manner conforming to *Treatise* plan as explained in the Editorial Preface, except that the equals sign (=) is reserved for subjective synonyms of a certain kind, namely, junior synonyms based on a type species that is closely allied to or perhaps conspecific with the type species of the senior synonym but not nominally identical (in which case the names would be objective synonyms). The distinction here explained is employed in Jurassic and Cretaceous parts of systematic descriptions but not in the Triassic part of the text.

Suborder CERATITINA Hyatt, 1884

[*nom. correct.* KUMMEL, 1952 (*pro* suborder Ceratitinae HYATT, 1884; *non* subfamily Ceratitinae MOJSISOVICS, 1879)}

Derivatives of Daraelitidae which underwent extensive evolutionary radiation in development of numerous new adaptive types. Characterized by greater elaboration of suture and acquisition of ornamentation in many groups. Adaptive range of this suborder, which includes most Triassic ammonoids, is very much larger than that shown by Paleozoic groups. *Perm.-Trias.*

Superfamily OTOCERATACEAE Hyatt, 1900

[*nom. transl.* MILLER & FURNISH, 1954 (*ex* Otoceratidae HYATT, 1900)] [=Xenodisciaceae FRECH, 1902 (*nom. transl.* KUMMEL, 1952, *ex* Xenodiscidae FRECH, 1902)]

Evolute to involute descendants of Daraelitidae with suture increasingly more ceratitic (488). *Perm.-Trias.*

Family XENODISCIDAE Frech, 1902

[=Paraceltitidae, Paralecanitidae SPATH, 1930; Cibolitidae PLUMMER & SCOTT, 1937]

Conch compressed, discoidal, evolute; venter rounded to acute; lateral ribs commonly present. Suture goniatitic or weakly ceratitic, with 2 lateral lobes. Group derived from Daraelitidae and is itself the ancestral stock of the Lower Triassic Ophiceratidae. *M. Perm.-U.Perm.*

Xenodiscus WAAGEN, 1879 [**X. plicatus;* SD WAAGEN, 1895] [=*Proceratites* KITTL, 1903 (obj.) (type *X. plicatus* WAAGEN; SD KUMMEL, herein)]. Venter low, arched, shoulders abruptly rounded, sides flattened and with radial ribs. Suture ceratitic (547). *U.Perm.,* SaltR.-Timor.——FIG. 162,*1.* **X. plicatus,* U.Perm., SaltR.; *1a,b,* ×0.7; *1c,* ×1.5 (547*).

Xenodiscites Miller & Furnish, 1940 [**X. waageni*]. Like *Xenodiscus* but periphery acute, suture more primitive, lobes only slightly denticulate (291). *U.Perm.*, Mex.-Tex.——Figs. 162,*4;* 163*D*. **X. waageni;* suture, ×2 (291).

Xenaspis Waagen, 1895 [**Ceratites carbonarius* Waagen, 1873]. Like *Xenodiscus* but no lateral ribs on phragmocone; weak folds or ribs may be present on living chamber (547). *U.Perm.*, SaltR.-Himalaya-Madag.-Timor-Tex.——Fig. 162,*2*. **X. carbonarius* (Waagen), SaltR.; *2a,b,* ×0.7; *2c,* ×1.5 (291*, 547).

Paraceltites Gemmellaro [**P. hoeferi*] [=*Paralecanites* Diener, 1897]. Whorls compressed, venter

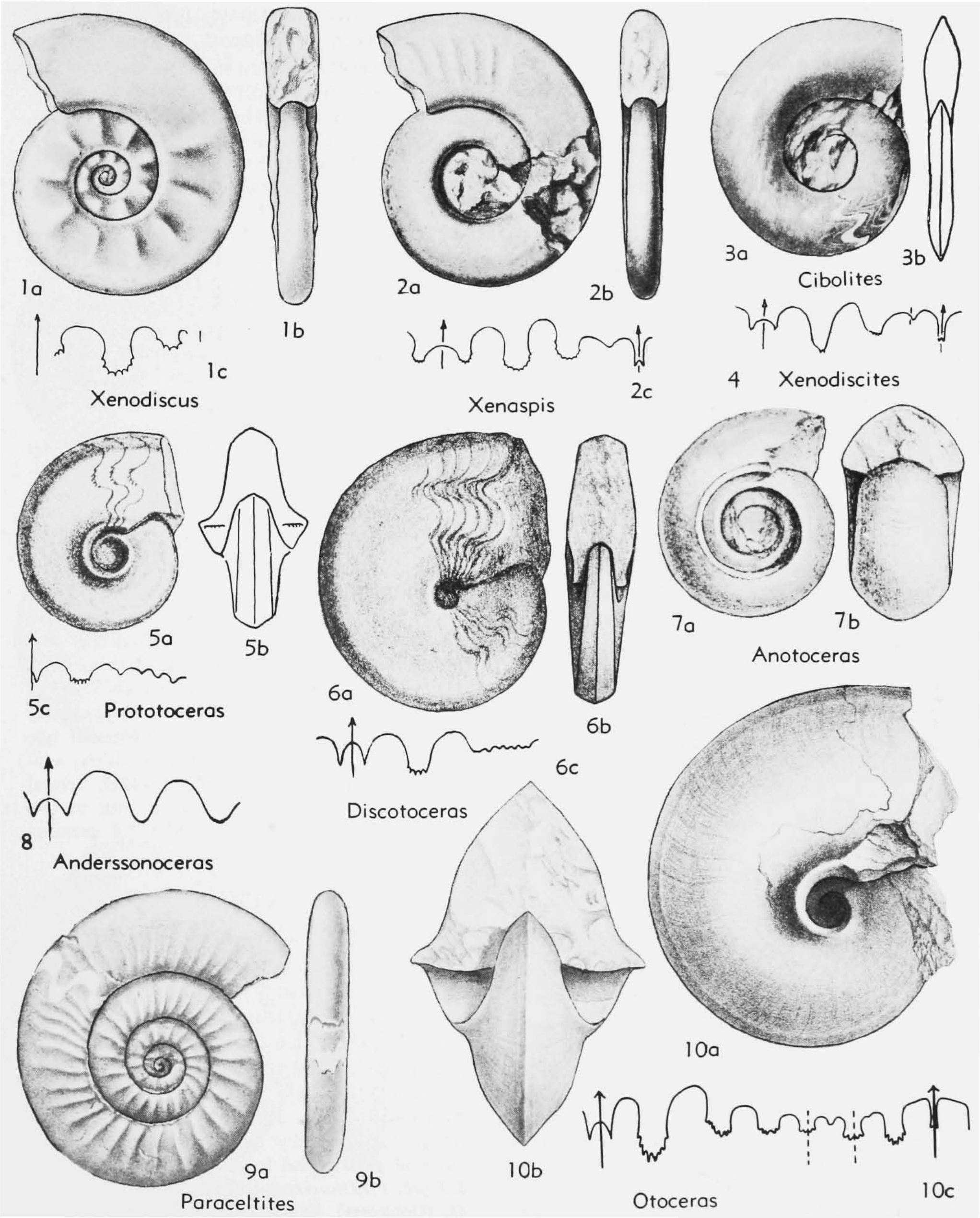


Fig. 162. Xenodiscidae, Otoceratidae (p. L130-L132).

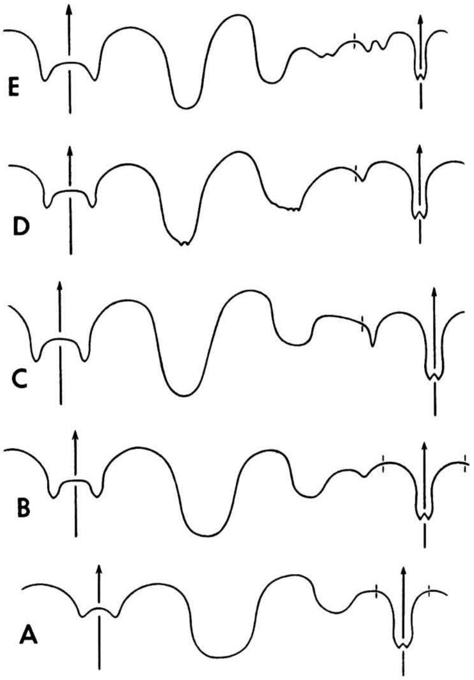


Fig. 163. Sutures of *Paraceltites (A)*, *Cibolites (B,C)*, *Xenodiscites (D)*, and *Kingoceras (E)* (110).

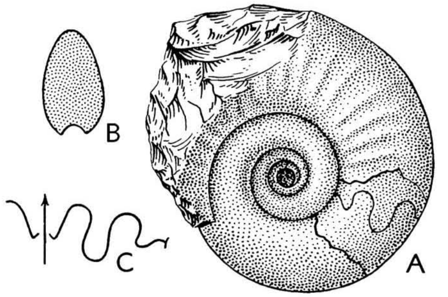


Fig. 164. *Paralecanites sextensis* Diener, U.Perm., Eu.; ×1 (110).

arched; lateral area with prorsiradiate ribs, venter smooth. Suture goniatitic (291). *M.Perm.-U.Perm.*, Sicily - Alps - Crimea - Tex. - Mex.——Figs. 162,*9;* 163*A*. *P. elegans* Girty, M.Perm., Tex.; 162,*9a,b*, conch, ×0.7 (291*); 163*A*, suture, enlarged.——Fig. 164. *P. sextensis* (Diener), U.Perm., Eu.; ×1 (291).

Cibolites Plummer & Scott, 1937 [**C. uddeni*]. Like *Xenodiscites* but suture goniatitic, conch smooth (291). *U.Perm.*, Tex.-Mex.——Figs. 162,*3;* 163*B,C*. **C. uddeni*, Tex.; 162,*3a,b*, conch, ×0.7 (291*); 163*B,C*, suture (291).

Palaeolecanites Reed, 1944 [**P. chapriensis*]. Whorls higher than in *Paraceltites*, venter narrow, tabulate; umbilical shoulder subrectangular. Suture goniatitic with 3 low lateral lobes. Genus based on single badly weathered specimen, form of suture and whorl section doubtful. *U.Perm.*, SaltR.

Family OTOCERATIDAE Hyatt, 1900

Involute forms with subtrigonal whorl section; venter tricarinate, umbilical shoulders generally prominent, umbilicus deep. Suture ceratitic (472). *U.Perm.-L.Trias.*

Otoceras Griesbach, 1880 [**O. woodwardi*] (472). *L.Trias.* (*L. Scyth.*), Himalaya-E.Greenl.-Alaska.

O. (Otoceras). Umbilical rim acutely flared (472). *L.Scyth.*, Himalaya - E.Greenl. - Alaska. —— Fig. 162,*10*. **O. (O.) woodwardi*, Himalaya; *10a,b*, ×0.5; *10c*, ×1 (102*).

O. (Metotoceras) Spath, 1930 [**O. (M.) dieneri* (=*Hungarites* sp. Diener, 1897)]. With no umbilical rim (472). *Scyth.*, Himalaya.

Anotoceras Hyatt, 1900 [**Prosphingites nala* Diener, 1897 (holotype, Diener's pl. 1, fig. 4; SD Spath, 1930)]. Evolute, reduced otoceratids with rounded or bluntly fastigate venter (472). *L.Trias. (Scyth.)*, Himalaya.——Fig. 162,*7*. **A. nala* (Diener); *7a,b*, ×1 (102*).

Prototoceras Spath, 1930 [**Ceratites trochoides* Abich, 1878]. Like *Otoceras* but small, with fastigate venter and flared umbilical rim. Suture ceratitic and simpler (468). *U.Perm.*, Armenia.——Fig. 162,*5*. **P. trochoides* (Abich); *5a-c*, ×1 (622*).

Discotoceras Spath, 1930 [**Hungarites raddei* Arthaber, 1900]. Involute smooth; platycones, venter fastigate; umbilical shoulder sharply rounded. Suture ceratitic with broad low saddles and narrow lobes (468). *U.Perm.*, Armenia.——Fig. 162,*6*. **D. raddei* (Arth.); *6a-c*, ×1 (622*).

Anderssonoceras Grabau, 1924 [**Glyphioceras (Anderssonoceras) anfuense*]. Small smooth like *Prototoceras*, with flared umbilical shoulders; venter low, arched, with low median keel, ventral shoulders angular. Suture goniatitic with narrow lobes. *U.Perm.*, China.——Fig. 162,*8*. **A. anfuense* (629*).

Family OPHICERATIDAE Arthaber, 1911

Serpenticones with compressed elliptical whorl sections; venter generally rounded; ornamentation usually weakly developed. Suture simple, ceratitic. Descendants of U. Perm. Xenodiscidae (488). *L.Trias.*

Ophiceras Griesbach, 1880 [*non* Suess, 1865 (ICZN Opinions 130, 194)] [**O. tibeticum*] [=*Griesbachoceras* Miller, 1932]. Venter rounded, umbilical wall generally high; conch smooth, with striae of growth and in places a few ribs (472). *L.Scyth. (U.Otoceratan-L.Gyronitan)*, N.Am.-Asia.

O. (Ophiceras). Evolute, with high umbilical wall and no tendency toward tuberculation (472).

L.Scyth., N.Am.-Asia.——Fig. 165,*5*. **O. (O.) tibeticum*, Himalaya; *5a,b*, ×0.7; *5c*, ×1 (102*).

O. (Lytophiceras) Spath, 1930 [**O. chamunda* Diener, 1897]. Like *O. (Ophiceras)* but more discoidal and involute; without high umbilical rim (472). *L.Scyth.*, N.Am.-Greenl.-Asia.——Fig. 165,*6*. **O. (L.) chamunda*, Himalaya; ×0.7 (102*).

O. (Acanthophiceras) Diener, 1916 [**Trachyceras (?) gibbosum* Griesbach, 1880]. Like *O. (Ophiceras)* but with tendency toward blunt, lateral tuberculation (472). *L.Scyth.*, Greenl.-Asia.——Fig. 165,*3*. **O. (A.) gibbosum* (Gries.), Himalaya; *3a,b*, ×0.66 (102*).

O. (Discophiceras) Spath, 1935 [**O. (Lytophiceras) subkyoticum* Spath, 1930]. *Ophiceras* with tendency to flat, discoidal conch and narrowing of venter; umbilicus small, often eccentric (473). *L.Scyth.*, N.Am.-Asia.

O. (Metophiceras) Spath, 1935 [**O. (M.) subdemissum*]. Evolute with compressed whorl section. First lateral lobe near middle of whorl side and second lateral saddle on umbilical slope (473). *L.Scyth.*, N.Am.-Asia.

Glyptophiceras Spath, 1930 [**Xenodiscus aequicostatus* Diener, 1913]. Like *Ophiceras* but with coarse, sigmoidal ribs which tend to degenerate adorally (472). *L.Scyth.*, N.Am.-Asia.——Fig. 165,*1*. **G. aequicostatum* (Diener), Himalaya; *1a,b*, ×0.7 (110*).

Vishnuites Diener, 1897 [**V. pralambha*]. Evolute

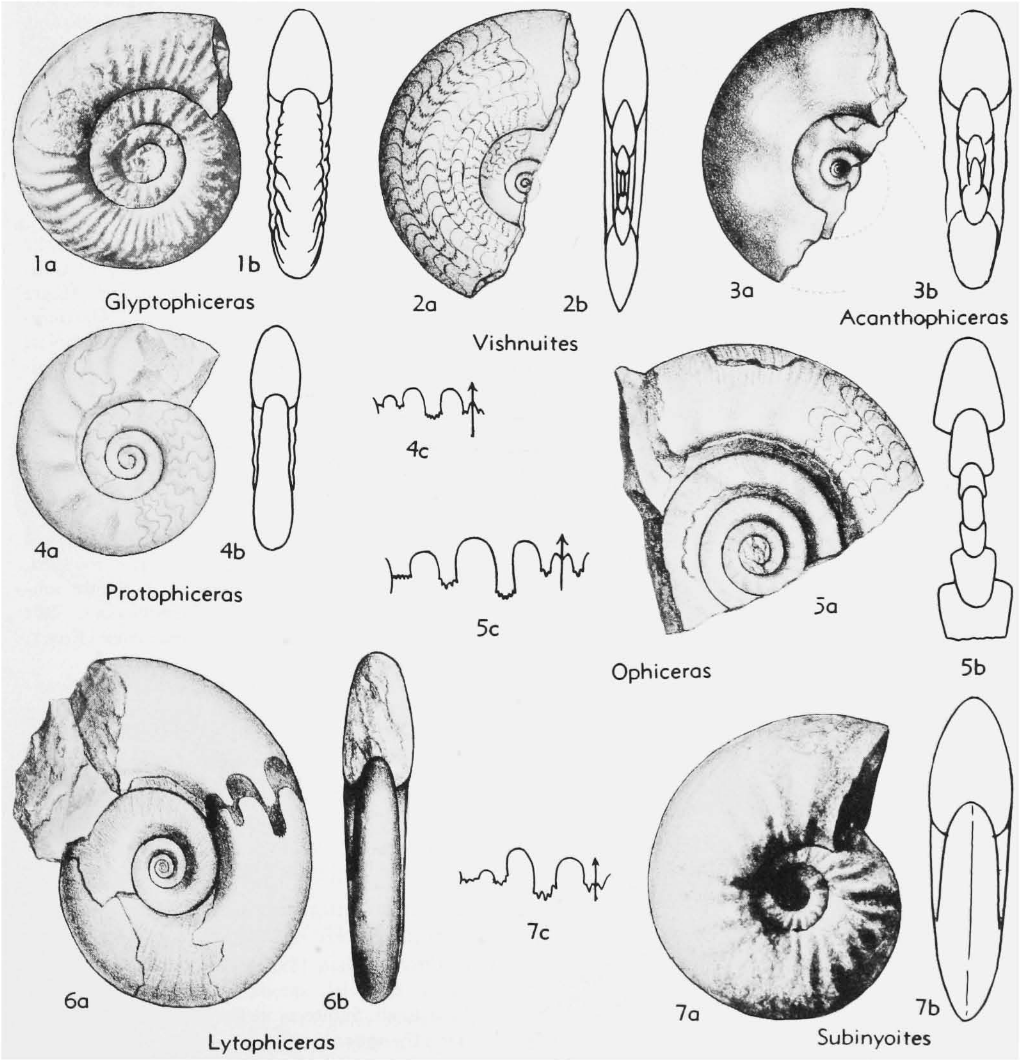


Fig. 165. Ophiceratidae (p. L133-L134).

compressed Ophiceratidae with acute venter (472). *L.Scyth.,* E.Greenl.-Himalaya.

V. (Vishnuites). Conch generally smooth (472). *Scyth.,* E.Greenl.-Himalaya.——FIG. 165,*2*. **V. (V.) pralambha,* Himalaya; *2a,b,* ×0.7 (102*).

V. (Paravishnuites) SPATH, 1935 [**V. (P.) oxynotus*]. Like *V. (Vishnuites)* but more involute and with faint, almost radial lineations (473). *Scyth.,* E.Greenl.

Subinyoites SPATH, 1930 [**Inyoites kashmiricus* DIENER, 1913]. Compressed, involute Ophiceratidae with blunt radial folds and acute venter. Second lateral saddle high (472). *L.Scyth.,* Kashmir. ——FIG. 165,*7*. **S. kashmiricus* (DIENER); *7a,b,* ×0.7; *7c,* ×1 (110*).

?**Protophiceras** HYATT, 1900 [**Danubites nicolai* DIENER, 1895]. Evolute, whorl section compressed, sides flattened, venter arched; faint ribbing on inner whorls and distant blunt costae on inner lateral area of outer whorls, projecting adorally and weakening peripherally (472). *L.Scyth.,* E.Sib.——FIG. 165,*4*. **P. nicolai* (DIENER); *4a,b,* ×0.7; *4c,* ×1 (101*).

Family DIENEROCERATIDAE Kummel, 1952

Evolute, slightly compressed, whorl section rounded, venter arched. Suture ceratitic or goniatitic, generally with only 2 lateral lobes. Considered to be persisting stock from ophiceratids and probably root of some later ornamented stocks (472). *L.Trias.*

Dieneroceras SPATH, 1934 [**Ophiceras dieneri* HYATT & SMITH, 1905]. *Scyth.,* Calif.-Nev.-Ida. ——FIG. 166,*1*. **D. dieneri* (HYATT-S.); *1a,b,* ×1; *1c,* ×2 (203*).

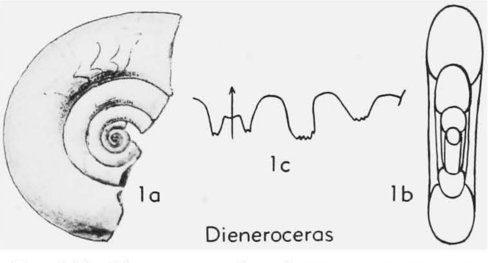


FIG. 166. *Dieneroceras dieneri* (HYATT & SMITH), L.Trias.(Scyth.), Calif.; *1a,b,* ×1; *1c,* ×2 (638).

Superfamily NORITACEAE Karpinsky, 1889

[*nom. transl.* MILLER & FURNISH, 1954 (*ex* Noritinae KARPINSKY, 1889)] [=Meekocerataceae WAAGEN, 1895 (*nom. transl.* KUMMEL, 1952, *ex* Meekoceratidae WAAGEN, 1895)]

Typically smooth, more or less discoidal shells with rounded or truncate peripheries and ceratitic sutures, but producing globose, carinate, or ribbed offshoots that may have complicated or simplified sutures. These families are direct or indirect derivatives of the lower Scythian ophiceratids (472). *L. Trias.-M.Trias.*

Family GYRONITIDAE Waagen, 1895

Evolute to involute, discoidal ammonites with flattened sides and rounded or truncate periphery. Suture ceratitic to subgoniatitic (472). *L.Trias.*

Subfamily GYRONITINAE Waagen, 1895

Evolute, with ceratitic suture. *L.Trias.*

Gyronites WAAGEN, 1895 [**G. frequens;* SD SMITH, 1904]. Venter tabulate, sides flattened, umbilical shoulder rounded, some with strigation near periphery and on it. Suture generally with distinct auxiliary series. *L.Scyth.(Gyronitan),* SaltR.——FIG. 167,*6*. **G. frequens; 6a,b,* ×1 (548*).

Gyrolecanites SPATH, 1934 [**Lecanites impressus* WAAGEN, 1895]. Venter tabulate, sides convex, umbilical walls rounded but abrupt. Suture goniatitic with 2nd lateral saddle close to umbilical wall. *L.Scyth.(Gyronitan),* SaltR.——FIG. 167,*1*. **G. impressus* (WAAGEN); *1a,b,* ×0.7 (548*).

Prionolobus WAAGEN, 1895 [**P. atavus;* SD HYATT & SMITH, 1905]. Discoidal, with rounded or tabulate venter and tendency toward involution. Suture as in *Gyronites. Scyth.(U.Gyronitan-L.Flemingitan),* SaltR. - Himalaya-Timor-Madag.-Mont.-Nev. ——FIG. 167,*3*. *P. impressus* (WAAGEN), Gyronitan, SaltR.; *3a,b,* ×0.7 (548*).

Ambites WAAGEN, 1895 [**A. discus;* SD SPATH, 1934]. More involute, compressed discoidal, with moderately small umbilicus; venter tabulate. Suture subgoniatitic. *Scyth.(Flemingitan),* SaltR.——FIG. 167,*2*. **A. discus; 2a,b,* ×0.5 (548*).

?**Gyrophiceras** SPATH, 1934 [**Lecanites gangeticus* (DEKONINCK) WAAGEN, 1895]. Venter rounded, sides convex, umbilical wall rounded. Suture subgoniatitic. *L.Scyth.(Gyronitan-Flemingitan),* Salt R.-Timor.——FIG. 167,*5*. **G. gangeticum* (KON.), SaltR.; *5a,b,* ×1; *5c,* ×2 (548*).

?**Catalecanites** SPATH, 1934 [**C. planus* (=*Lecanites* sp. DIENER, 1897)]. Like *Gyronites* but more compressed, with distinct umbilical shoulder; conch smooth. Suture goniatitic. *Scyth.(Flemingitan),* Himalaya.——FIG. 167,*7*. **C. planus; 7a,b,* ×1; *7c,* ×1 (102*).

Subfamily KYMATITINAE Waagen, 1895

With increasing involution and subgoniatitic suture, being discoidal developments of Gyronitinae (472). *L.Trias.*

Kymatites WAAGEN, 1895 [**K. typus*]. Conch compressed, discoidal, smooth; venter tabulate, umbilicus small. Suture as in Gyronitinae but simpler. *Scyth.(Gyronitan),* SaltR.——FIG. 167,*4*. **K. typus; 4a,b,* ×0.7; *4c,* ×1 (548*).

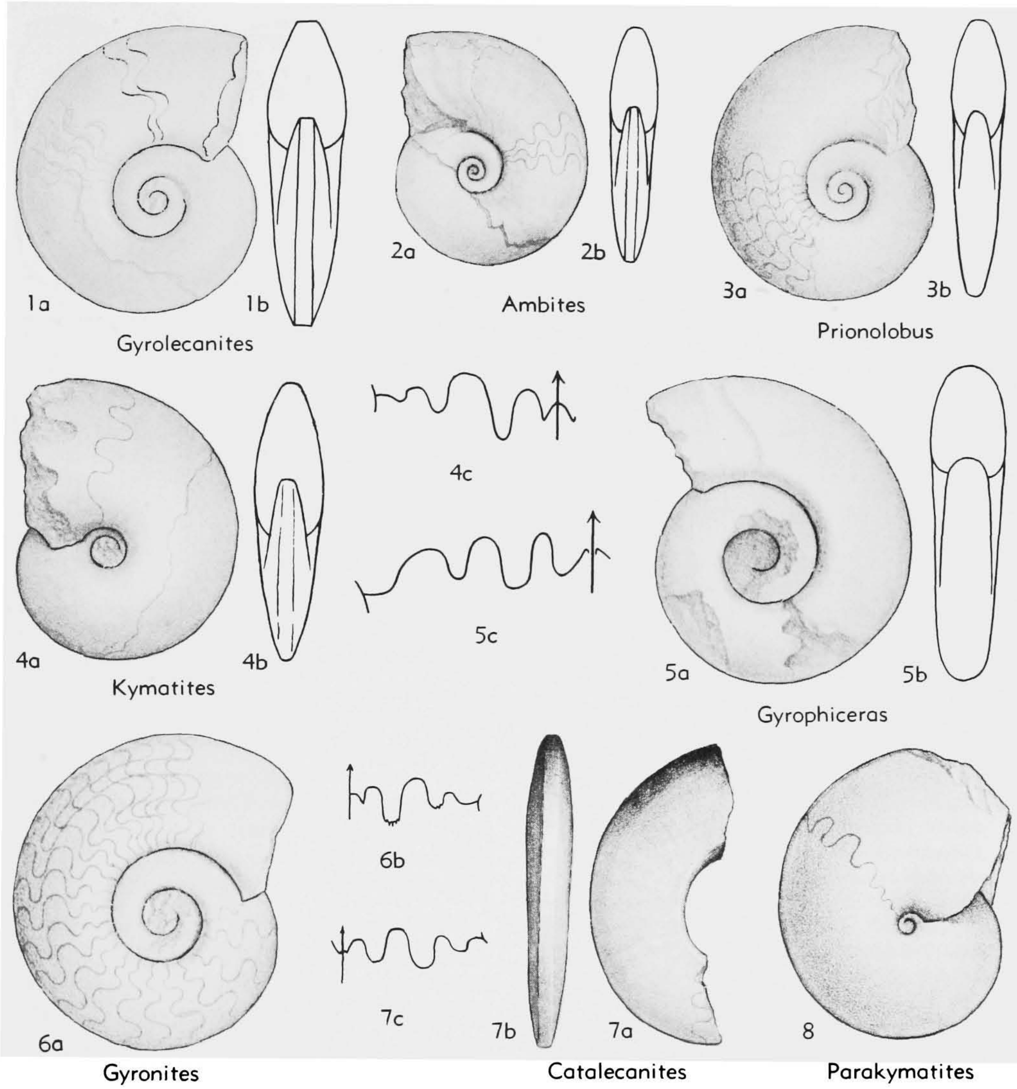


Fig. 167. Gyronitidae (p. L134-L135).

Parakymatites Waagen, 1895 [**P. discoides*]. Like *Kymatites* but more involute and discoidal. Suture with wide ventral lobe and 3 auxiliary saddles (548). *Scyth.(Flemingitan),* SaltR.——Fig. 167,*8*. **P. discoides;* ×0.75 (548*).

Family FLEMINGITIDAE Hyatt, 1900

Evolute, discoidal, generally with robust ornamentation. Suture tending to greater elaboration than in ancestral Ophiceratidae (472). *L.Trias.*

Flemingites Waagen, 1892 [**Ceratites flemingianus* DeKoninck, 1863]. Ribbing prominent and generally also strigation; venter rounded to subtruncate. Suture ceratitic but more advanced than in Gyronitidae. *Scyth.(Flemingitan-Owenitan),* Salt R.-Madag.-Timor.-Ida.-Mont.——Fig. 168,*4*. *F. radiatus* Waagen, Flemingitan, SaltR.; *4a,b,* ×0.5 (548*).

Euflemingites Spath, 1934 [**Flemingites guyerdetiformis* Welter, 1922]. More or less involute serpenticones with slightly compressed whorls, arched venter, and rounded umbilical wall, with distinct strigation but no radial ornamentation. *Scyth.,* Timor-Himalaya-Spitz.-Ida.——Fig. 168,*3*. **E. guyerdetiformis* (Welter), Timor; *3a,b,* ×0.7; *3c,* ×1 (560*).

Pseudoflemingites Spath, 1930 [**P. timorensis*]. Serpenticones with ribbing as in *Xenodiscoides* or

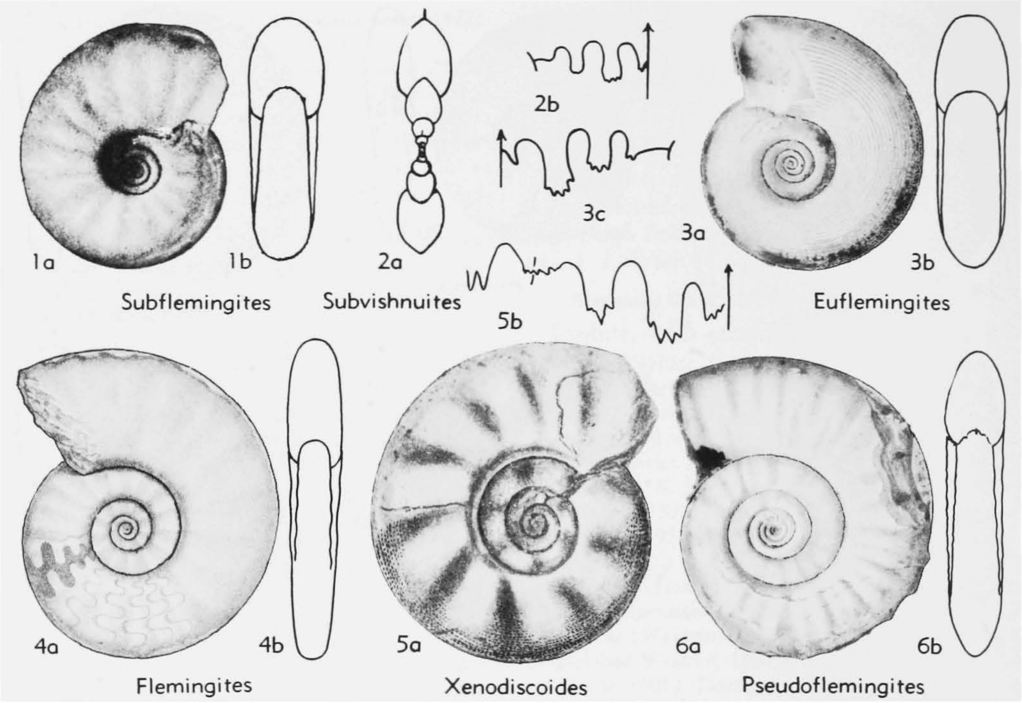


Fig. 168. Flemingitidae (p. L135-L136).

strigation as in *Flemingites*, but with very evolute smooth inner whorls and simpler suture. *Scyth.(Owenitan)*, Timor.——Fig. 168,6. **P. timorensis; 6a,b*, ×0.5 (560*).

Subvishnuites Spath, 1930 [**S. welteri*]. Evolute, smooth, with inner whorls as in *Pseudoflemingites* and similar suture; with tendency for periphery to become fastigate. *Scyth.(Owenitan)*, Timor.——Fig. 168,2. **S. welteri; 2a*, ×0.7; *2b*, ×1 (560*).

Subflemingites Spath, 1934 [**S. involutus* (=*Aspidites meridianus involutus* Welter, 1922)]. Involute, subdiscoidal, with smooth serpenticone inner whorls; umbilical wall rounded, venter arched. Suture with irregular auxiliaries as in *Clypeoceras*. *Scyth.*, Timor.——Fig. 168,*1*. **S. involutus* (Welter); *1a,b*, ×1 (560*).

Xenodiscoides Spath, 1930 [**Xenodiscus perplicatus* Frech, 1905]. Strongly ribbed shells resembling the inner whorls of *Flemingites*, but without strigation; venter rounded or subtabulate. Suture slightly simpler than in *Flemingites* (468). *Scyth.(Flemingitan)*, Salt.R.——Fig. 168,*5*. **X. perplicatus* (Frech); *5a*, ×0.8; *5b*, ×2 (156*).

Family XENOCELTITIDAE Spath, 1930

Conch evolute, discoidal, generally ribbed, especially on inner whorls, or constricted, with ribs often projected forwards across a smooth, arched or keeled venter. Suture ceratitic or goniatitic. Derived from primitive "ophiceratid" stock that modified its primitive (*Glyptophiceras*) characters only in ventral area (472). *Up.L.Trias.*

Subfamily XENOCELTITINAE Spath, 1930

Smooth, venter arched or slightly sharpened; may be crenulate when traversed by faint prolongations of lateral ribs. *L.Trias.*

Xenoceltites Spath, 1930 [**X. subevolutus* (=*Xenodiscus* cf. *comptoni* Frebold, 1930; *non* Diener)]. Compressed serpenticone with faint distant bulges on inner whorls and irregular costation, on outer whorl generally causing constrictions. Suture with 2 weakly toothed lateral lobes (468). *U.Scyth.*, Spitz.-Sib.-SaltR.-Utah.——Fig. 169,*1*. *X. russkiensis* Spath, Sib.; *1a,b*, ×1; *1c*, ×2 (101*).

Preflorianites Spath, 1930 [**Danubites strongi* Hyatt & Smith, 1905]. Venter tending to become acute, with radial ribbing most prominent on inner whorls, not reaching periphery (468). *U.Scyth.*, Calif.-Ida.-Timor-Albania. —— Fig. 169,*2*. **P. strongi* (Hyatt-S.), Owenitan, Calif.; *2a,b*, ×0.7; *2c*, ×2 (203*).

?**Hemilecanites** Spath, 1934 [**Lecanites discus* Arthaber, 1908]. Smooth, evolute, with tendency to oxynote venter, mouth border constricted with ventral lappet. Suture reduced. *U.Scyth.*, Calif.-

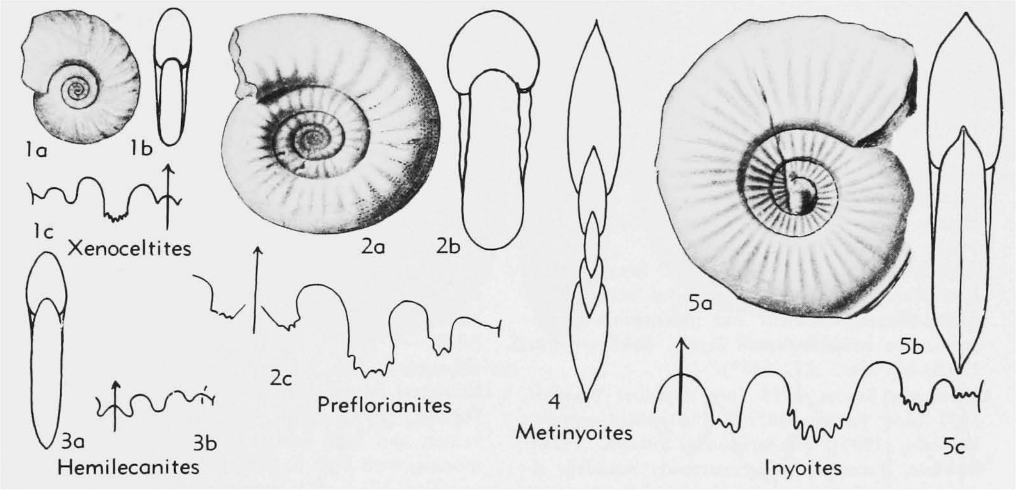


Fig. 169. Xenoceltitidae (p. L136-L137).

Albania.——Fig. 169,*3*. **H. discus* (Arth.), Albania; *3a,b*, ×2 (472*).

Subfamily INYOITINAE Spath, 1934

Compressed, keeled offshoots of same stock that produced *Preflorianites*, with similar costation degenerating into striation and comparable ceratitic suture (472). *L.Trias.*

Inyoites Hyatt & Smith, 1905 [**I. oweni*]. Platycones with high hollow keel and distinct umbilical shoulder; radial ribs that diminish toward compressed venter (203). *Scyth.(Owenitan)*, Calif.-?Indochina.——Fig. 169,*5*. **I. oweni*, Calif.; *5a,b*, ×0.7; *5c*, ×2 (203*).

Metinyoites Spath, 1930 [**Vishnuites discoidalis* Welter, 1922]. More compressed and highly keeled than *Inyoites* and suture more specialized (468). *Scyth.(Owenitan)*, Timor.——Fig. 169,*4*. **M. discoidalis* (Welter); ×0.7 (560*).

Family PARANORITIDAE Spath, 1930

Discoidal, more or less involute, with flattened sides and rounded or truncate venter which tends to sharpen. Suture ceratitic, with auxiliaries becoming fairly well individualized (472). *L.Trias.*

Paranorites Waagen, 1895 [**P. ambiensis*]. Conch more or less involute, periphery narrowly rounded, sides slightly convex, umbilical wall high but rounded. Suture ceratitic, with ventral saddles and lobes more differentiated than in ***Ophiceras*** or *Prionolobus*. *Scyth.(U.Gyronitan-Flemingitan)*,

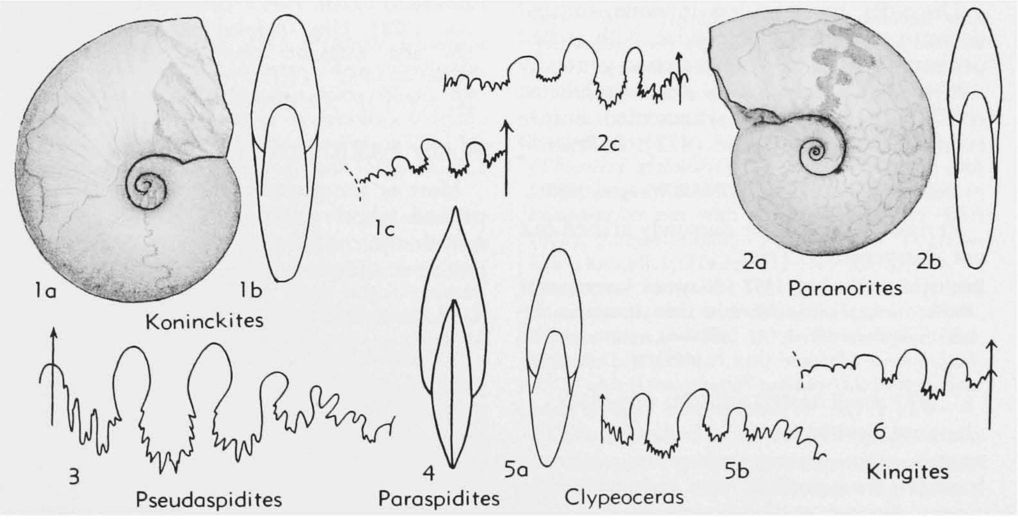


Fig. 170. Paranoritidae (p. L137-L138).

SaltR.——FIG. 170,*2*. **P. ambiensis; 2a,b,* ×0.3; *2c,* ×0.7 (548*).

Koninckites WAAGEN, 1895 [**K. vetustus;* SD SMITH, 1904]. Involute, compressed, with flattened sides and narrowly rounded to subtabulate venter; umbilical wall gently rounded. Suture with greater individualization of elements in auxiliary series. *Scyth.(Gyronitan-Flemingitan),* SaltR.-Himalaya-Mont.——FIG. 170,*1*. **K. vetustus,* SaltR.; *1a,b,* ×0.7; *1c,* ×1 (548*).

Kingites WAAGEN, 1895 [**K. lens;* SD SPATH, 1934]. Like *Koninckites* but with rounded venter, deep funnel-shaped umbilicus and indentations of suture more individualized. *Scyth.,* SaltR.——FIG. 170,*6*. **K. lens;* ×1 (548*).

Clypeoceras SMITH, 1913 [*pro Aspidites* WAAGEN, 1895 (*non* PETERS, 1877)] [**Aspidites superbus* WAAGEN, 1895] [=*Aspiditella* STRAND, 1929]. Involute, discoidal; venter narrowly rounded, almost acute. Suture advanced, especially auxiliary series. *Scyth.(Gyronitan-Flemingitan),* SaltR.-Himalaya-Timor.——FIG. 170,*5*. **C. superbum* (WAAGEN), SaltR., *5a,* ×0.1; *5b,* ×0.3 (548*).

Paraspidites SPATH, 1934 [**P. praecursor* (FRECH) (=*Aspidites superbus* WAAGEN, mut. *praecursor* FRECH, 1905)]. Involute oxycones with deep umbilicus. Auxiliaries less developed than in *Clypeoceras. Scyth.(Flemingitan),* SaltR.——FIG. 170,*4*. **P. praecursor;* ×0.7 (156*).

Pseudaspidites SPATH, 1934 [**Aspidites muthianus* KRAFFT in KRAFFT & DIENER, 1909]. Involute, with rounded or subtruncate venter. Suture subammonitic with submonophyllic saddles. *Scyth. (Owenitan),* Himalaya-Ida.——FIG. 170,*3*. **P. muthianus* (KRAFFT), Himalaya; ×1 (240*).

Family PROPTYCHITIDAE Waagen, 1895

Discoidal, more or less involute, inflated derivatives of the Ophiceratidae, with arched or sharpened venter; whorl section generally subtrigonal, producing a deep umbilicus; conch smooth or feebly ornamented. Suture ceratitic to subammonitic (472). *L.Trias.*

Subfamily PROPTYCHITINAE Waagen, 1895

Periphery broadly or narrowly arched but not sharpened. *L.Trias.*

Proptychites WAAGEN, 1892 [**Ceratites lawrencianus* DEKONINCK, 1863]. More or less involute, discoidal, with tendency to inflation; venter arched. Suture more advanced than in ancestral Ophiceratidae. *Scyth.(U.Gyronitan-Flemingitan),* Asia-N.Am.——FIG. 171,*3*. **P. lawrencianus* (KON.), SaltR. *3a,b,* ×0.3 (548*).

Pachyproptychites DIENER, 1916 [**Proptychites otoceratoides* DIENER, 1895]. With narrowly rounded venter, flattened or slightly concave sides, high umbilical rim and funnel-shaped umbilicus. *Scyth.,* Sib.——FIG. 171,*7*. **P. otoceratoides* (DIENER); *7a,b,* ×0.5 (101*).

Proptychitoides SPATH, 1930 [**P. decipiens* (=*Proptychites latifimbriatus* ARTHABER, 1911 (*non* DEKONINCK))]. Like *Proptychites,* with narrowly rounded venter and deep umbilicus but suture subammonitic, with monophyllic saddles. *U.Scyth.,* Albania-Chios.——FIG. 171,*6*. **P. decipiens,* Albania; ×0.66 (472*).

Eoptychites SPATH, 1930 [**Proptychites obliqueplicatus* WAAGEN, 1895]. With rursiradiate, bifurcating, blunt ribs and arched venter. *Scyth.(Flemingitan),* SaltR.——FIG. 171,*2*. **E. obliqueplicatus* (WAAGEN); *2a,b,* ×0.7 (548*).

Ussuriceras SPATH, 1930 [**Proptychites acutisellatus* DIENER, 1895]. With weak radial ribs, arched venter, and high umbilical wall. Suture subammonitic, with high linguiform saddles. *Scyth.,* Sib.——FIG. 171,*5*. **U. acutisellatus* (DIENER); ×1 (101*).

?**Procarnites** ARTHABER, 1911 [**Parapopanoceras kokeni* ARTH., 1908]. Discoidal, involute, ?with increased number of sutural elements. *U.Scyth.,* Albania-Chios.——FIG. 171,*4*. **P. kokeni* (ARTH.); ×2 (22*).

Subfamily OWENITINAE Spath, 1934

Lenticular to oxynote developments of Proptychitidae, parallel with paranannitids and with similar globose, constricted young, but distinguished by suture (472). *L.Trias.*

Owenites HYATT & SMITH, 1905 [**O. koeneni*]. Involute, smooth, lenticular tending to become oxycones. Suture ceratitic with numerous lobes and saddles (203). *Scyth.(Owenitan),* Calif.-Nev.-Ida.-Mont.-Timor.——FIG. 171,*8*. **O. koeneni,* Calif.; *8a,b,* ×1; *8c,* ×2 (203*).

Parowenites SPATH, 1934 [**Owenites simplex* WELTER, 1922]. Like *Owenites* but with sigmoidal ribs and goniatitic suture. *Scyth.(Owenitan),* Timor.——FIG. 171,*1*. **P. simplex* (WELTER); *1a,* ×0.7; *1b,* ×2 (560*).

Family PARANANNITIDAE Spath, 1930

More or less globular ammonites with depressed whorl sections, at least in young; commonly constricted. Suture ceratitic or goniatitic, simple (472). *L.Trias.*

Subfamily PARANANNITINAE Spath, 1930

Venters broadly arched with no tendency towards carination. Suture generally with more than one lateral lobe. *L.Trias.*

Paranannites HYATT & SMITH, 1905 [**P. aspenensis*]. Conch involute, subglobose, compressed; early-formed part smooth, later with radial folds or constrictions. Suture ceratitic (203). *Scyth.(Owenitan),*

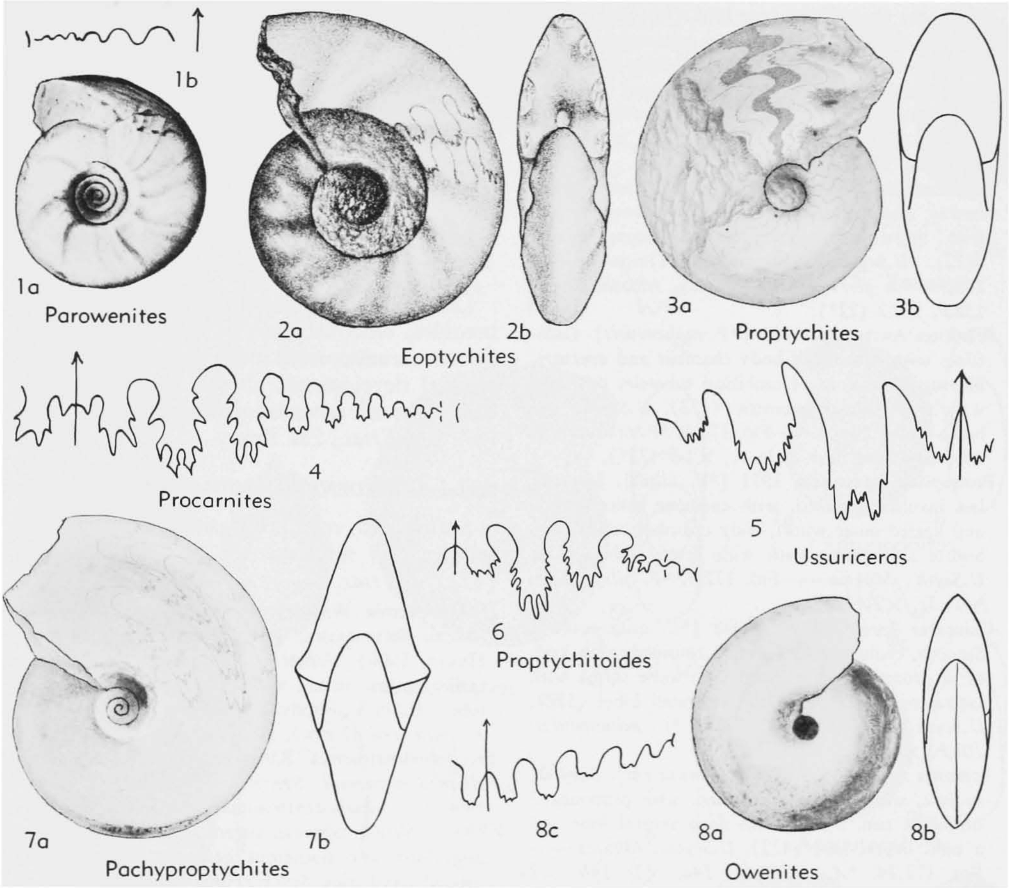


FIG. 171. Proptychitidae (p. L138).

Ida.——FIG. 172,*7*. **P. aspenensis; 7a,b,* ×1; *7c,* ×3 (203*).

Arnautoceltites DIENER, 1916 [**Celtites arnauticus* ARTHABER, 1911] [=*Juvenites, Thermalites* SMITH, 1927]. Like *Paranannites* but with oblique constrictions. Suture goniatitic or ceratitic. *U.Scyth.*, Albania-Chios-Calif.-Nev.-Ida.——FIG. 172,*9*. **A. arnauticus* (ARTH.), Albania, *9a,b,* ×1; *9c,* ×2 (22*).

Prosphingites MOJSISOVICS, 1886 [**P. czekanowski*]. With globose inner whorls and almost keeled, galeate or compressed outer whorls in some; surface smooth or with faint striae, ridges, constrictions. Suture ceratitic. *U.Scyth.*, Calif.-Nev.-Albania-Spitz.-Sib.——FIG. 172,*6*. **P. czekanowski*, Sib.; *6a,b,* ×0.7; *6c,* ×1 (294*).

Zenoites RENZ & RENZ, 1948 [**Prosphingites (Zenoites) helenae*]. Like *Prosphingites*, with arched venter, but with prominent irregular, nearly radial constrictions that encircle whorl section (372). *U.Scyth.*, Chios.——FIG. 172,*4*. **Z. helenae* (RENZ-R.); *4a,b,* ×1; *4c,* ×2 (372*).

Isculitoides SPATH, 1930 [**Isculites originis* ARTHABER, 1911]. Involute, subglobose, smooth, with contracting body chamber and eccentric umbilicus. Suture ceratitic with two lateral lobes. *U.Scyth.*, Albania-Chios-Timor.——FIG. 172,*13*. **I. originis* (ARTH.), Albania; *13a,b,* ×1; *13c,* ×3 (22*, 372).

Chiotites RENZ & RENZ, 1948 [**Prosphingites (Chiotites) globularis*]. Like *Isculitoides* but with longitudinal striae on body chamber. Suture as in *Prosphingites* but with 2 ceratitic auxiliary lobes (372). *U.Scyth.*, Chios.——FIG. 172,*11*. **C. globularis* (RENZ-R.); *11a,b,* ×1; *11c,* ×3 (372*).

?Paragoceras ARTHABER, 1911 [**P. dukagini*]. Like *Arnautoceltites* but with distinctive suture. *U.Scyth.*, Albania-Chios.——FIG. 172,*3*. **P. dukagini; 3a,b,* ×1; *3c,* ×3 (22*).

Subfamily COLUMBITINAE Spath, 1930

Venters arched to keeled, conch generally evolute, with early coronate stage. Suture typically with one differentiating lateral lobe. *L.Trias.*

Columbites Hyatt & Smith, 1905 [**C. parisianus*]. Evolute, feebly ornamented with ribs, constrictions, and spiral striae; venter arched tending to become acute. Suture ceratitic with large lateral lobe and small 2nd lateral (203). *U.Scyth.*, Ida.-Wyo.-Utah. ——Fig. 172,*2*. **C. parisianus; 2a,* ×0.7; *2b,* ×2 (203*).

Subcolumbites Spath, 1930 [**Columbites perrinismithi* Arthaber, 1908]. Like *Columbites* but with more pronounced tendency to carination (472). *U.Scyth.*, Albania-Chios-?Timor.——Fig. 172,*15*. **S. perrinismithi* (Arth.), Albania-Chios; *15a,b,* ×0.7 (22*).

Prenkites Arthaber, 1911 [**P. malsorensis*]. Cadicones with constricted body chamber and aperture, bearing indications of umbilical tubercles on inner whorls, umbilicus excentric (472). *U.Scyth.*, Albania-Chios-Timor.——Fig. 172,*8*. **P. malsorensis,* Albania-Chios; *8a,b,* ×1; *8c,* ×1.5 (22*).

Protropites Arthaber, 1911 [**P. hilmi*]. More or less involute, inflated, with cadicone inner whorls and keeled outer whorl, body chamber constricted. Suture subceratitic with wide lateral lobe (472). *U.Scyth.*, Albania.——Fig. 172,*5*. **P. hilmi; 5a,b,* ×1; *5c,* ×2 (22*).

Chioceras Renz & Renz, 1948 [**C. mitzopouloi*]. Smooth, evolute, whorl section rounded, with keel, as in *Protropites,* developed late; some forms with lateral nodes. Suture with 3 serrated lobes (372). *U.Scyth.*, Chios.——Fig. 172,*10*. **C. mitzopouloi; 10a,b,* ×1; *10c,* ×2 (372*).

Arianites Arthaber, 1911 [**A. musacchi*]. Smooth, evolute, whorl section depressed, with pronounced umbilical rim. Suture with deep ventral lobe and a bifid lateral lobe (472). *U.Scyth.*, Albania.——Fig. 172,*14*. **A. musacchi; 14a,* ×1; *14b,* ×2 (22*).

Meropella Renz & Renz, 1948 [**Arianites (Meropella) plejanae*]. Like *Arianites* but whorl section not depressed, inner whorls with faint ribs, and suture with 2 bifid lateral lobes (372). *U.Scyth.*, Chios.——Fig. 172,*12*. **M. plejanae* (Renz-R.); ×4 (372*).

Epiceltites Arthaber, 1911 [**E. genti*]. Evolute, compressed, with fine lineation and periodic flares or constrictions. Suture with single, ceratitic lateral lobe (472). *U.Scyth.*, Albania-Chios.——Fig. 172,*1*. **E. genti; 1a,b,* ×0.7; *1c,* ×2 (22*).

Family USSURIIDAE Spath, 1930

[*nom. correct.* Kummel, herein (*pro* Ussuridae Spath, 1930)]

Involute, smooth, discoidal ammonites with arched to narrowly rounded venters and flat whorl sides. Suture ammonitic (472). *L.Trias.*

Ussuria Diener, 1895 [**U. schamarae;* SD Diener, 1895]. Suture submonophyllic with lateral saddles notched on dorsal side. *Scyth.*, Sib.——Fig. 173, *13*. **U. schamarae; 13a,b,* ×0.7 (101*).

Parussuria Spath, 1934 [**Ussuria compressa* Hyatt & Smith, 1905]. All saddles of suture deeply divided. *Scyth.*, Calif.——Fig. 173,*7*. **P. compressa* Hyatt-S.; ×0.7 (203*).

Metussuria Spath, 1934 [**Ussuria waageni* Hyatt & Smith, 1905]. Suture with adventitious lobe and saddle. *Scyth.*, Ida.——Fig. 173,*11*. **M. waageni* (Hyatt-S.); ×0.5 (203*).

Family HEDENSTROEMIIDAE Waagen, 1895

Discoidal, compressed, generally smooth, involute, with tabulate to oxynote venters. Suture ceratitic, with more elements than in parallel development shown by Paranoritidae, and with adventitious saddles and lobes (472). *L.Trias., ?M.Trias.*

Subfamily HEDENSTROEMIINAE Waagen, 1895

Suture with regular ceratitic lobes, smooth saddles and no tendency to simplification (472). *L.Trias.*

Hedenstroemia Waagen, 1895 [**Ceratites hedenstroemi* Keyserling, 1845] [=*Anahedenstroemia* Hyatt, 1900]. Venter acute in adult, tabulate in earlier stages. Suture with prominent adventitious lobe. *U.Scyth.*, Spitz.-Sib.——Fig. 173,*5*. **H. hedenstroemi* (Keys.), Sib.; *5a,b,* ×0.5 (472*).

Pseudohedenstroemia Kummel, *nom. nov.* [*pro Anahedenstroemia* Spath, 1934 (*non* Hyatt, 1900)] [**Anahedenstroemia himalayica* Spath, 1934]. Venter tabulate, suture with outer saddles linguiform and numerous generally well-individualized auxiliaries. *Scyth.*, Himalaya-SaltR.-Timor-Calif.——Fig. 173,*6*. **P. himalayica,* Himalaya; *6a,b,* ×0.7 (102*).

Clypites Waagen, 1895 [**C. typicus*]. Like *Pseudohedenstroemia* but with closed umbilicus and adventitious elements of suture less individualized. *Scyth.*, SaltR.-Himalaya.——Fig. 173,*15*. **C. typicus,* SaltR.; *15a,b,* ×1 (548*).

Parahedenstroemia Spath, 1934 [**Hedenstroemia acuta* Krafft in Krafft & Diener, 1909]. Like *Pseudohedenstroemia* but with oxynote periphery. *Scyth.*, Himalaya.——Fig. 173,*3*. **P. acuta* (Krafft); *3a,b,* ×1 (240*).

Epihedenstroemia Spath, 1934 [**Hedenstroemia skipetarensis* Arthaber, 1911]. Venter tabulate, comparatively broad. Suture with primitive lobes and saddles, and high curvature. *U.Scyth.*, Albania.——Fig. 173,*12*. **E. skipetarensis* (Arth.); ×2 (22*).

Metahedenstroemia Spath, 1934 [**Hedenstroemia kastriotae* Arthaber, 1911]. Highly compressed conch, with narrowly tabulate venter. Suture with bluntly serrated lobes and well individualized auxiliary saddles. *U.Scyth.*, Albania.——Fig. 173,*10*. **M. kastriotae* (Arth.); ×1.5 (22*).

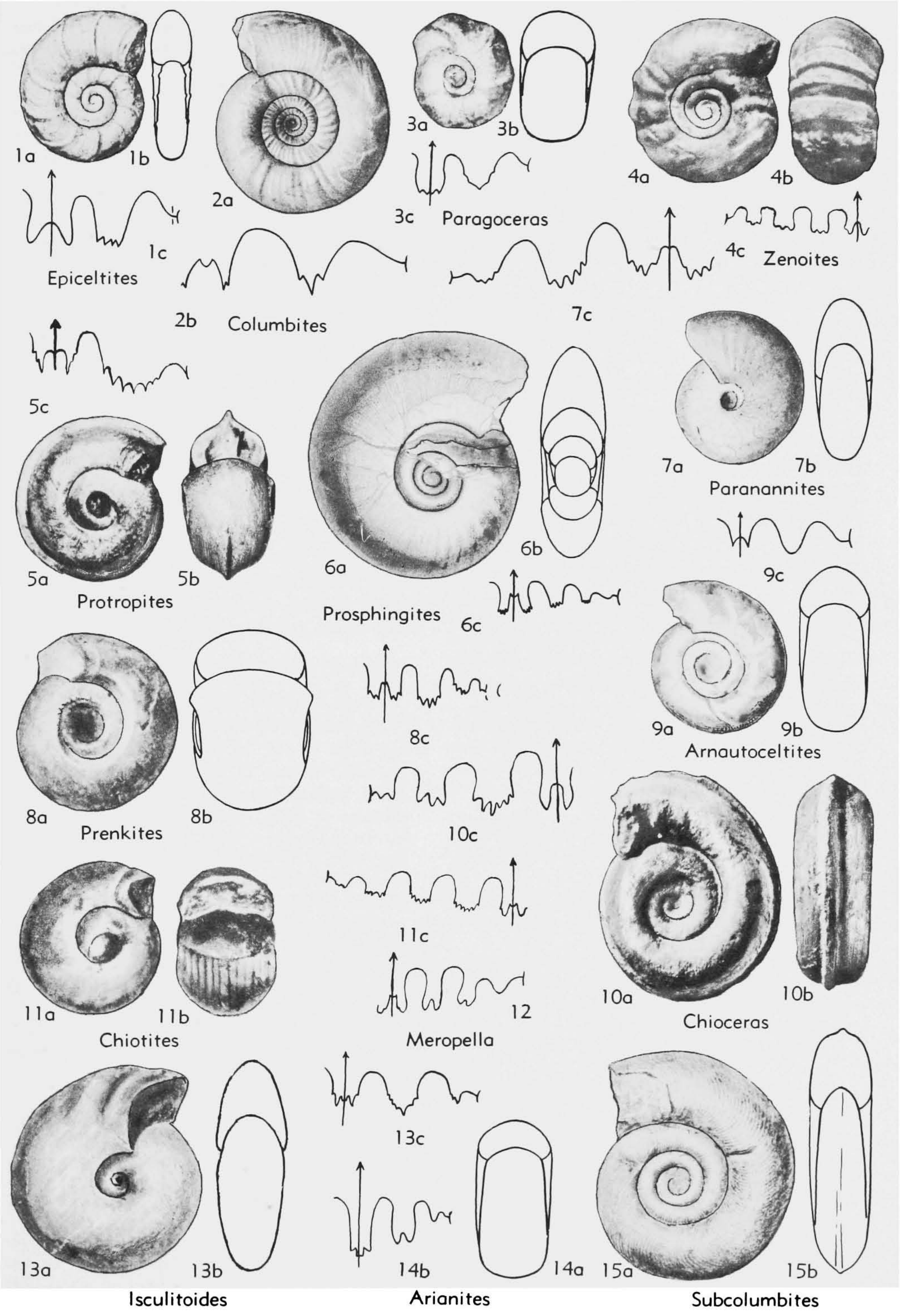


FIG. 172. Paranannitidae (p. L138-L140).

Tellerites Mojsisovics, 1902 [**Ceratites furcatus* Öberg, 1877]. Discoidal, involute, with sulcate venter bordered by 2 keels and faint sigmoidal ribs on sides. Suture with small adventitious saddles. *U.Scyth.*, Spitz.——Fig. 173,*2*. **T. furcatus* (Öberg); *2a,b*, ×1; *2c*, ×2 (294*).

Subfamily LANCEOLITINAE Spath, 1934

Venter tabulate, whorl sides flat. Suture ammonitic with wide, high ventral lobe, indistinct adventitious elements (472). *L. Trias.*

Lanceolites Hyatt & Smith, 1905 [**L. compactus*] (203). *Scyth.(Owenitan)*, Ida.-Calif.——Fig. 173, *8*. **L. compactus; 8a*, ×0.5; *8b*, ×1 (203*).

Subfamily ASPENITINAE Spath, 1934

Venter acute or oxynote, suture almost goniatitic with numerous elements and adventitious lobes (472). *L.Trias.*

Aspenites Hyatt & Smith, 1905 [**A. acutus*]. Venter oxynote, conch smooth or with fine, strong radial folds. Suture ceratitic, with small adventitious lobes and goniatitic auxiliaries (203). *Scyth. (Owenitan)*, Ida.-Timor.——Fig. 173,*1*. **A. acutus*, Ida.; *1a,b*, ×0.66; *1c*, ×3 (203*).

Pseudaspenites Spath, 1934 [**Aspenites layeriformis* Welter, 1922]. Like *Aspenites* but more evolute and with curvature of suture and more numerous auxiliaries. *Scyth.(Owenitan)*, Timor.——Fig. 173, *9*. **P. layeriformis* (Welter); ×1 (560*).

?**Beatites** Arthaber, 1911 [**B. berthae*]. Somewhat strongly evolute, with oxynote venter, greatly compressed. Suture goniatitic. *U.Scyth.*, Albania.——Fig. 173,*4*. **B. berthae;* ×1 (22*).

?Subfamily BENECKEIINAE Waagen, 1895

[*nom. correct.* Kummel, herein (*pro* Beneckeinae Waagen, 1895)]

Compressed, smooth oxycones with entire multilobate suture, with small adventitious lobes (472). *L.Trias.-M.Trias.*

Beneckeia Mojs., 1882 [*non Beneckeia* Uhlig, 1882 (=*Silesites* Uhlig, 1882)] [**Am. buchi* Alberti, 1834] (472). *L.Trias.(U.Scyth.)-M.Trias.(Anis.)*, Ger.-Transjordan.——Fig. 173,*14*. *B. wogauana* (Meyer), Anis., Ger.; *14a,b*, ×1 (702*).

Family KASHMIRITIDAE Spath, 1930

Costate developments of a stock similar to primitive flemingitids or xenoceltitids tending to peripheral ribbing, as in *Anasibirites*, or to carination (472). *L.Trias.*

Kashmirites Diener, 1913 [**Celtites armatus* Waagen; SD Diener, 1915]. More or less evolute, whorls quadrate, with strong, commonly tuberculate ribbing on inner whorls, degenerating into striation on outer whorls; venter wide; subtabulate, costae commonly continuous across venter. Suture ceratitic, generally with only 2 lateral lobes. *Scyth.*, SaltR.-Himalaya-Timor.——Fig. 174,*4*. **K. armatus* (Waagen), Himalaya; *4a,b*, ×1 (110*).

Anakashmirites Spath, 1930 [**Danubites nivalis* Diener, 1897]. Evolute, serpenticones with ribs tending to thicken toward ventrolateral borders and widely arched peripheries. Suture ceratitic. *Scyth.*, Himalaya-Timor.——Fig. 174,*1*. **A. nivalis* (Diener), Himalaya; *1a,b*, ×1 (102*).

Pseudoceltites Hyatt, 1900 [**Celtites multiplicatus* Waagen, 1895]. Like *Kashmirites* but venter more arched and smoother; ribs tending to be prominent at ventral shoulders. Suture ceratitic. *U.Scyth.*, SaltR.-Ida.——Fig. 174,*3*. **P. multiplicatus* (Waagen), SaltR.; *3a-c*, ×1 (548*).

?**Hanielites** Welter, 1922 [**H. elegans*]. More or less strongly ornamented and keeled offshoots of kashmiritids, with coronate inner whorls and ceratitic suture. *Scyth.(Owenitan)*, Timor.——Fig. 174,*2*. **H. elegans; 2a,b*, ×1; *2c*, ×2 (560*).

Family MEEKOCERATIDAE Waagen, 1895

More or less involute, compressed, discoidal forms, smooth or weakly ornamented; venter arched or tabulate. Suture ceratitic with broad saddles (472). *L.Trias.-M.Trias.*

Subfamily MEEKOCERATINAE Waagen, 1895

Venter tabulate but may be rounded on living chamber of some adults. *L.Trias.*

Meekoceras Hyatt, in C. A. White, 1879 [**M. gracilitatis* White, 1879]. Involute to evolute, discoidal, generally smooth. Suture with few denticulations in lobes. *Scyth.(Owenitan)*, Calif.-Nev.-Ida.-Utah-Timor.——Fig. 175,*8*. **M. gracilitatis*, Ida.; *8a,b*, ×0.7; *8c*, ×1 (203*).

Wyomingites Hyatt, 1900 [**Meekoceras aplanatum* White, 1879]. Evolute, compressed, with tabulate venter that tends to widen and become subsulcate; sides smooth or with radial folds. Suture ceratitic, may be goniatitic, with only 2 lateral lobes. *Scyth. (Owenitan)*, Ida.——Fig. 175,*7*. **W. aplanatus* (White); *7a,b*, ×1; *7c*, ×3 (451*).

Svalbardiceras Frebold, 1930 [**S. spitzbergense*]. Flat, discoidal, venter tabulate, tending to round off in adult; faint distant folds on inner whorls. Suture simple, ?goniatitic. *U.Scyth.*, Spitz.

Subfamily ARCTOCERATINAE Arthaber, 1911

With arched venters, slightly sigmoidal striae and folds on outer whorl (472). *L. Trias.*

Submeekoceras Spath, 1934 [**Meekoceras mushbachanum* White, 1880]. Robust, more or less evolute, with striae and blunt folds on whorl sides in some. Suture ceratitic with saddles more slender

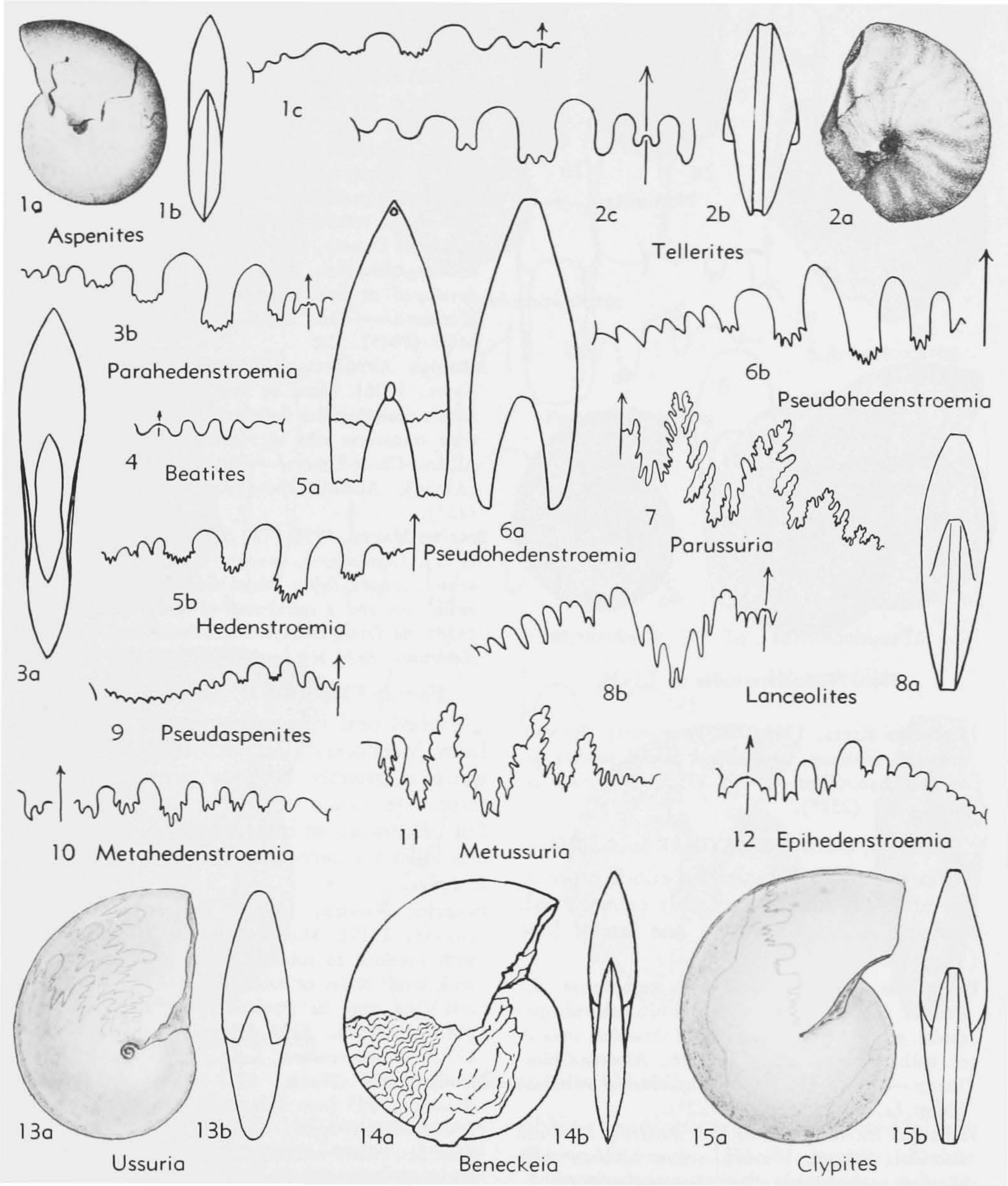


FIG. 173. Ussuriidae (p. L140-L142).

than in *Arctoceras*. *Scyth.(Owenitan)*, N.Am.-Timor.——FIG. 175,*3*. **S. mushbachanum* (WHITE), Ida.; *3a*, ×0.25; *3b*, ×0.7 (203*).

Arctoceras HYATT, 1900 [**Ceratites polaris* MOJSISOVICS, 1886] [=*Arctoceroides* STRAND, 1929]. Generally involute, discoidal, venter narrowly arched; smooth or striate; flattened sides. Suture ceratitic with wide, low saddles. *U.Scyth.*, Spitz.——FIG. 175,*4*. **A. polaris* (MOJS.); *4a,b*, ×0.7 (294*).

Czekanowskites DIENER, 1915 [**Ceratites decipiens* MOJSISOVICS, 1886]. Like *Arctoceras* but inflated, with globose inner whorls. Suture with higher saddles and more digitations of lobes. *U.Scyth.*, Sib.-?Spitz.——FIG. 175,*2*. **C. decipiens* (MOJS.), Sib.; *2a,b*, ×0.7; *2c*, ×2 (294*).

?Pseudokymatites SPATH, 1934 [**Kymatites svilajanus* KITTL, 1903]. Like *Submeekoceras* but smooth and suture with 2 goniatitic lateral lobes. *U.Scyth.*, Yugo.——FIG. 175,*6*. **P. svilajanus* (KITTL); ×1 (232*).

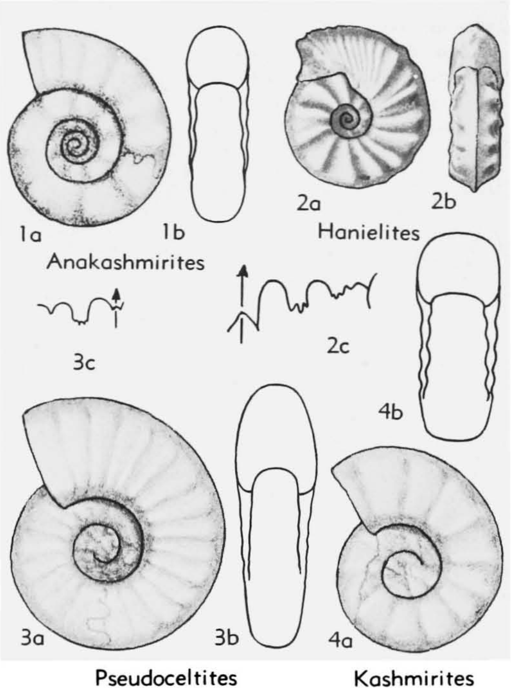


Fig. 174. Kashmiritidae (p. L142).

?**Stacheites** Kittl, 1903 [**S. prionoides*]. Smooth, discoidal, involute, with only 2 lateral saddles. *U. Scyth.*, Yugo.-Chios.——Fig. 175,*5*. **S. prionoides*, Yugo.; ×1 (232*).

Subfamily DAGNOCERATINAE Spath, 1934

Venters arched or tabulate, conch more or less involute, smooth or feebly ornamented. Suture ceratitic with only one lateral lobe (472). *L.Trias.-M.Trias.*

Dagnoceras Arthaber, 1911 [**D. nopcsanum;* SD Diener, 1915]. Venter arched, conch inflated, discoidal, greatest width at umbilical shoulder; smooth or with indistinct folds. *U.Scyth.*, Albania-Chios-Timor.——Fig. 175,*1*. **D. nopcsanum*, Albania-Chios; *1a,b*, ×1; *1c*, ×1.5 (22*).

?**Proavites** Arthaber, 1896 [**P. hueffeli*]. Involute, discoidal, inflated, smooth, venter tabulate with angular ventrolateral edges. Suture goniatitic. *L. Trias.(U.Scyth.)-M.Trias.(Anis.)*, Yugo.——Fig. 175,*9*. *P. avitus* Arth., Anis., *9a-c*, ×1 (584*).

Family NORITIDAE Karpinsky, 1889

Smooth, flat, discoidal; venter tabulate, bordered by pronounced ventral shoulders. Suture ceratitic with club-shaped saddles, 1st lateral lobe divided by median indentation (472). *L.Trias.-M.Trias.*

Norites Mojsisovics, 1878 [**Am. gondola* Mojs., 1869]. Venter with marginal keels, umbilical shoulder sharp, conch involute. *M.Trias.(Anis.-Ladin.)*, Alps-Balkan-Timor.——Fig. 176,*1*. **N. gondola* (Mojs.), Anis., Alps-Balkan-Greece; *1a,b*, ×0.7; *1c*, ×1 (293*).

Arthaberites Diener, 1900 [**A. alexandrae*]. Involute, discoidal, compressed. Suture resembling that of *Pseudosageceras* or *Cordillerites*. *M.Trias. (Anis.)*, Alps-Balkan.——Fig. 176,*3*. **A. alexandrae; 3a*, ×0.66; *3b*, ×1 (22*).

Ananorites Diener, 1907 [**A. monticola*]. Evolute, smooth, discoidal, with sharp ventral shoulders developed at late stage (104). *M.Trias.(Anis.)*, Himalaya.——Fig. 176,*5*. **A. monticola; 5a,b*, ×0.7 (104*).

Albanites Arthaber, 1909 [**Pronorites triadicus* Arth., 1908]. More or less involute, smooth or faintly ribbed, sides flattened; venter tabulate and with transverse ribs in some. *L.Trias.(U.Scyth.)*, Albania-Chios-Timor.——Fig. 176,*2*. **A. triadicus* (Arth.), Albania-Chios; *2a,b*, ×1; *2c*, ×1.5 (22*).

Bosnites Hauer, 1896 [**B. clathratus;* SD Diener, 1915]. Compressed, involute platycone with flat venter, convex sides; whorl sides with low, weak radial ribs and a spiral row of nodes at midpoint (488). *M.Trias.(Anis.)*, Yugo.——Fig. 176,*4*. **B. clathratus; 4a,b*, ×0.5; *4c*, ×0.7 (633*).

Family PRIONITIDAE Hyatt, 1900

Ribbed and tuberculate forms developed from Meekoceratidae with tendency to acquire a broadly tabulate venter, without transverse costae or notches of Sibiritidae. Suture ceratitic as in *Meekoceras*, with 2 lateral lobes and serrated auxiliary series (472). *L.Trias.*

Prionites Waagen, 1895 [**P. tuberculatus;* SD Diener, 1915]. More or less evolute, discoidal, with rounded to subtabulate venters; whorl sides with blunt nodes or tuberculated ribs. Second lateral lobe may be goniatitic, auxiliaries serrated (548). *U.Scyth.*, SaltR.-Himalaya-Timor.——Fig. 177,*2*. **P. tuberculatus*, SaltR.; *2a,b*, ×0.5 (548*).

Hemiprionites Spath, 1929 [*pro Goniodiscus* Waagen, 1895 (*non* Müller & Troschel, 1842)] [**Goniodiscus typus* Waagen, 1895]. Involute, with flat, nearly smooth sides and tabulate venter; indistinct serration of ventrolateral edge and transverse ribs on periphery, as in *Anasibirites*. *U.Scyth. (Owenitan)*, SaltR.-Timor-Utah-Ida.-Spitz.——Fig. 177,*3*. **H. typus* (Waagen), SaltR.; *3a,b*, ×1; *3c*, ×0.7 (548*).

Gurleyites Mathews, 1929 [**G. smithi*]. Like *Hemiprionites* but with excentric umbilicus, rounded body chamber, tending to inflation; with radial ribs and umbilical nodes. Suture ceratitic as in *Hemiprionites*. *U.Scyth.(Owenitan)*, Utah-Ida.-Spitz.——Fig. 177,*4*. **G. smithi*, Utah; ×0.5 (658*).

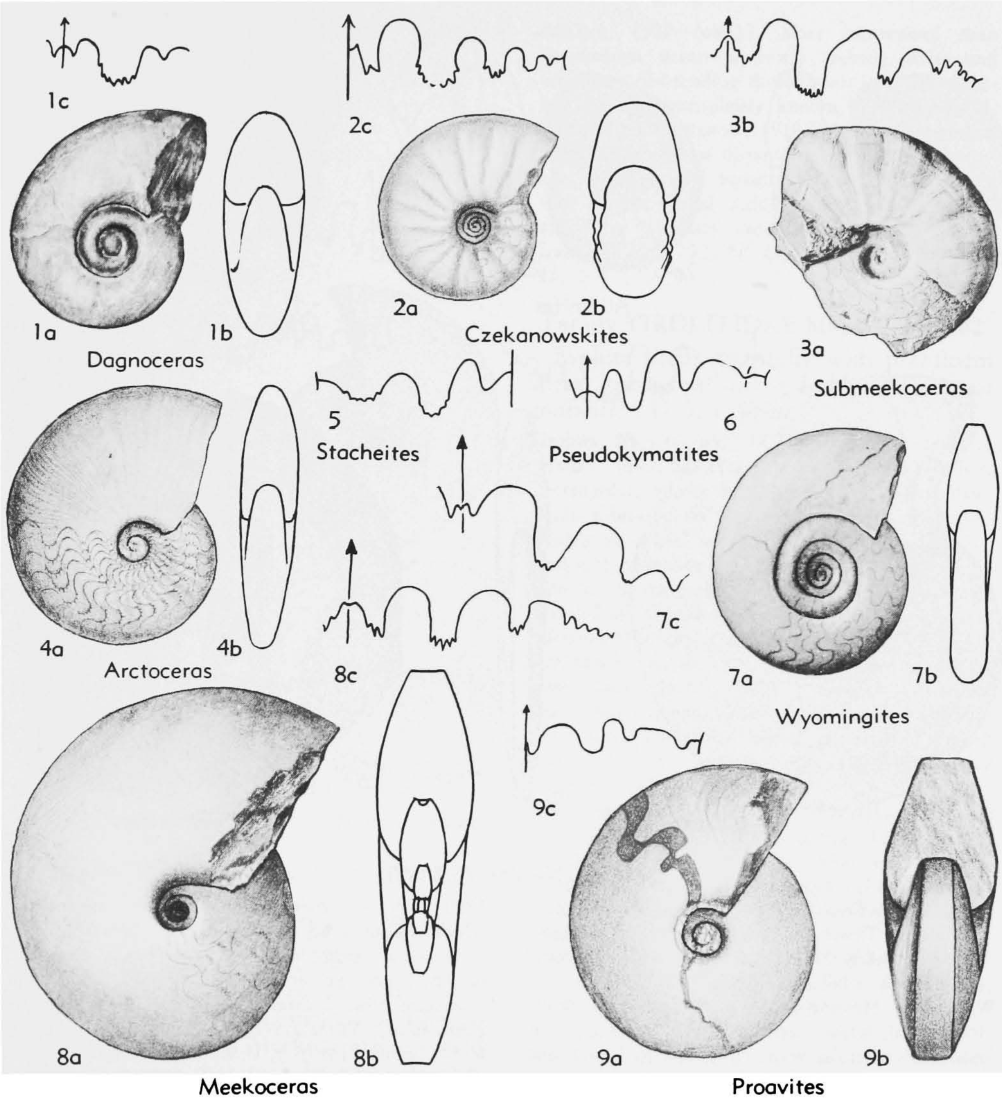


Fig. 175. Meekoceratidae (p. L142-L144).

Arctoprionites Spath, 1930 [**Goniodiscus nodosus* Frebold, 1930]. More or less involute, discoidal ammonites with tabulate venters, tending to develop crenulation of the ventral shoulder and ribbing or tuberculation on the whorl sides. Suture as in *Hemiprionites* but with large 1st lateral saddle and simple ventral lobe. *U.Scyth.*, Spitz.——Fig. 177,*1*. **A. nodosus* (Frebold); *1a,b*, ×0.7 (472*).

Family SIBIRITIDAE Mojsisovics, 1896

Ribbed or tuberculate derivatives of Meekoceratidae with modification of venter ranging from mere widening and transverse ribbing to sulcation (472). *L.Trias-M.Trias.*

Sibirites Mojsisovics, 1886 [**S. pretiosus*]. Evolute, with subtabulate venter; whorl sides with sigmoidal ribs that thicken at ventral shoulders; ribs form adorally projected chevrons on venter, incompletely fused along mid-line. Suture ceratitic, with 2 lateral lobes. *L.Trias.(U.Scyth.)*, Sib.——Fig. 178,*3*. **S. pretiosus; 3a,b*, ×1 (294*).

Anasibirites Mojsisovics, 1896 [*Sibirites kingianus* Waagen, 1895; SD Diener, 1915] [=*Pseudosibirites* Arthaber, 1911]. More or less involute discoidal, with arched or subtabulate venters; with sigmoidal ribs continuous across and commonly thickened on venter and generally absent on body

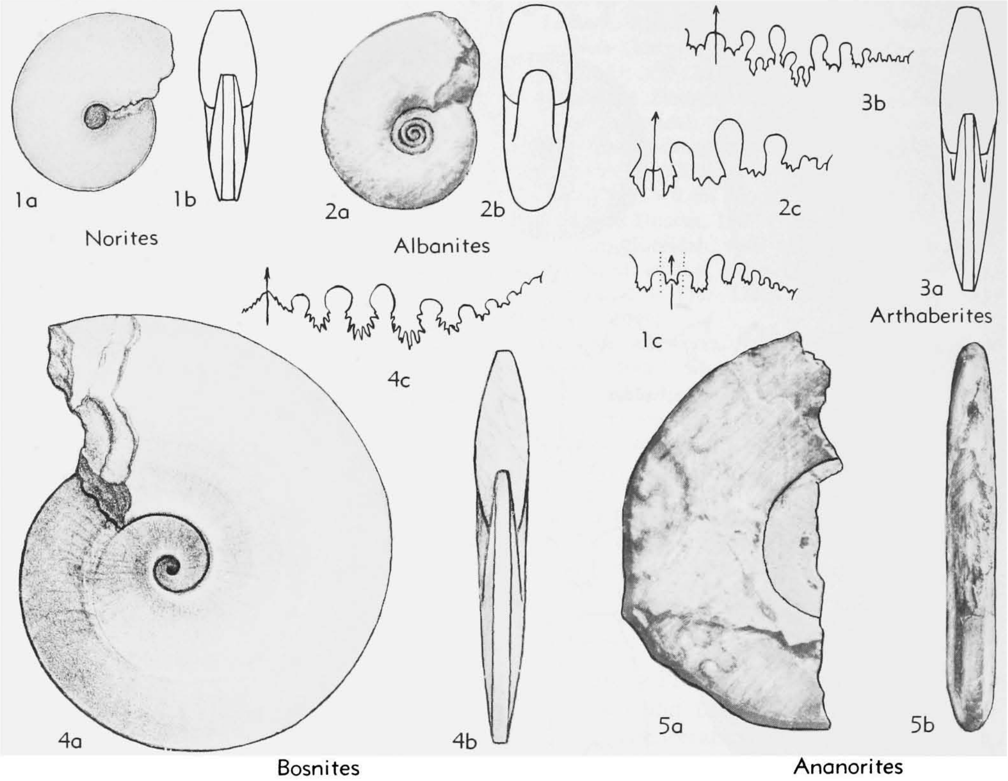


Fig. 176. Noritidae (p. L144).

chamber. *L.Trias.(U.Scyth., Owenitan),* SaltR.-Himalaya - Timor-Japan-Calif.-Utah-Ida.-?Albania-?Chios.——Fig. 178,*4*. **A. kingianus* (Waagen), SaltR.; *4a,b,* ×0.7 (548*).

Wasatchites Mathews, 1929 [**W. perrini*]. With trapezoidal whorl section, tabulate venter, and umbilical tubercles which give rise to lateral ribs that also cross venter. *L.Trias.(U.Scyth.),* Utah-Ida.-B.C.-Timor.-Spitz.——Fig. 178,*2*. *W. tridentinus* Spath, Spitz.; *2a,b,* ×0.7 (472*).

Anawasatchites McLearn, 1945 [**A. tardus*]. Like *Wasatchites* but with slightly excentric umbilicus, nearly smooth inner whorls. *L.Trias.(U.Scyth.),* B.C.

Keyserlingites Hyatt, 1900 [**Ceratites subrobustus* Mojsisovics, 1886] [=*Robustites* Philippi, 1901]. Inflated, with subtabulate to arched venter, with umbilical nodes; with lateral ribs that may cross venter or a row of nodes along ventral shoulder. Suture ceratitic with large 1st lateral saddle. *L.Trias.(U.Scyth.),* Spitz.-Sib.-Ida.——Fig. 178,*7*. **K. subrobustus* (Mojs.), Sib.; *7a,b,* ×0.7 (294*).

Durgaites Diener, 1905 [**Keyserlingites dieneri* Mojsisovics, 1902 (=*Ceratites subrobustus* Diener; *non* Mojs., 1895)] [=*Anastephanites* Spath, 1930]. Like *Keyserlingites* but with coronate inner whorls and tendency to develop ventrolateral nodes after lateral nodes have shifted to below middle of whorl side; venter arched to subtabulate, with transverse ribs. *L.Trias.(U.Scyth.)-M.Trias.(Anis., Beyrichitan),* Himalaya-Timor-Calif.——Fig. 178, *6*. **D. dieneri* (Mojs.), U.Scyth., Himalaya; *6a,b,* ×0.2 (102*).

Pearylandites Kummel, 1953 [**P. troelseni*]. Evolute, with wide deep umbilicus; outer whorls subtrigonal, with prominent umbilical tubercles from which ribs extend ventrally; venter fastigate; inner whorls more depressed, at first rounded, then trapezoidal, with prominent ventrolateral tubercles from which ribs extend dorsally. Suture ceratitic with large 1st lateral lobe. *M.Trias.(Anis.),* Pearyland.——Fig. 178,*1*. **P. troelseni; 1a,b,* ×0.7; *1c,* ×3 (650*).

?Olenikites Hyatt, 1900 [**Dinarites spiniplicatus* Mojsisovics, 1886]. Involute micromorphs with umbilical nodes on phragmocone that tend to disappear on body chamber or earlier. Suture generally goniatitic with 2 lateral lobes. *L.Trias.(U.Scyth.),* Sib.——Fig. 178,*5*. **O. spiniplicatus* (Mojs.), *5a,b,* ×1; *5c,* ×2 (294*).

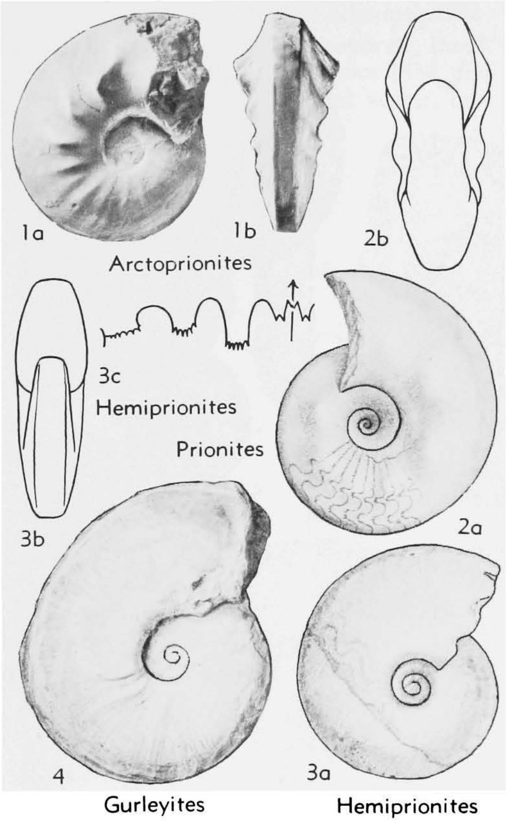


Fig. 177. Prionitidae (p. L144-L145).

Superfamily CERATITACEAE Mojsisovics, 1879

[*nom. transl.* Mojs., 1896 (*ex* Ceratitidae Mojs., 1879)]

Typically highly ornamented or tuberculate descendants of Meekocerataceae, with ceratitic suture that may become goniatitic or ammonitic in some offshoots (472). *L. Trias.-U.Trias.*

Family STEPHANITIDAE Arthaber, 1896

More or less evolute, coronate shells with broadly arched venters, lateral tubercles, and simple ceratitic suture, generally with large 1st lateral saddle (472). *L.Trias.*

Stephanites Waagen, 1895 [**S. superbus;* SD Diener, 1915]. Inflated conch with depressed coronate inner whorls and more rounded body chamber. Suture with 2 lateral lobes (548). *U. Scyth.,* SaltR.——Fig. 179,*2*. **S. superbus; 2a,b,* ×0.25; *2c,* ×0.5 (548*).

Parastephanites Hyatt, 1900 [*Acrochordiceras atavum* Waagen, 1895] [=*Acrochordiceroides* Strand, 1929 (obj.)]. More compressed than *Stephanites,* venter narrowly arched; nodes and secondary ribs tending to disappear on body chamber. Suture incompletely known. *U.Scyth.,* SaltR.

?**Paratirolites** Stoyanow, 1910 [**P. kittli;* SD Spath, 1934]. With coarse distant ribs, prominent ventrolateral nodes, and broadly arched venter. Suture with large ventral saddle, small lateral saddle, and large auxiliary saddles. *U.Scyth.,* Armenia-Iran.——Fig. 179,*1*. **P. kittli,* Armenia; *1a,* ×0.7; *1b,* ×1 (719*).

Family TIROLITIDAE Mojsisovics, 1882

Evolute shells, generally with prominent lateral tubercles; suture feebly ceratitic or goniatitic (472). *L.Trias.*

Tirolites Mojsisovics, 1879 [**Ceratites idrianus* Hauer, 1865; SD Hyatt & Smith, 1905]. Whorl rectangular, venter broadly rounded or tabulate; with tubercles on ventral shoulders, ribs commonly on whorl sides. Suture with large 1st lateral lobe, goniatitic or ceratitic, and small goniatitic 2nd lateral on umbilical wall. *U.Scyth.,* Alps-Balkan-S.Russ.-Himalaya-Ida.——Fig. 180,*4*. **T. idrianus* (Hauer), Yugo.; *4a,b,* ×0.7 (293*).

Tirolitoides Spath, 1934 [*pro Paraceratites* Kittl, 1903 (*non* Hyatt, 1900] [**Ceratites (Paraceratites) prior* Kittl, 1903]. Like *Tirolites* but also with umbilical nodes and 2 denticulated lateral lobes. *U.Scyth.,* Yugo.——Fig. 180,*5*. **T. prior* (Kittl); ×1 (232*).

?**Diaplococeras** Hyatt, 1900 [**Dinarites liccanus* Hauer, 1865] [=*Liccaites* Kittl, 1903 (obj.)]. Compressed, with umbilical nodes and clavi on ventral shoulders. Suture ceratitic. *U.Scyth.,* Alps-Yugo.——Fig. 180,*6*. **D. liccanum* (Hauer), Yugo.; *6a,b,* ×0.3 (293*).

Svilajites Kittl, 1903 [**Tirolites (Svilajites) cingulatus*]. With transverse ribs across arched venter. *U.Scyth.,* Yugo.——Fig. 180,*1*. **S. cingulatus; 1a,b,* ×1 (232*).

Bittnerites Kittl, 1903 [**Tirolites (Bittnerites) bittneri*]. With spinose stage reduced or absent; outer whorl with indistinct, projected ribs that cross venter. *U.Scyth.,* Yugo.——Fig. 180,*3*. *B. malici* Kittl; *3a,b,* ×0.5 (232*).

?**Dorikranites** Hyatt, 1889 [**Am. bogdoanus* von Buch, 1831] [=*Bogdoites* Kittl, 1903 (obj.)]. Ribs or tuberculation as in tirolitids but with acute venters. Suture simple, lobes entire or slightly toothed at siphonal or umbilical ends. *U.Scyth.,* S.Russ.——Fig. 180,*2*. **D. bogdoanus* (Buch); *2a,b,* ×0.3; *2c,* ×0.7 (293*).

Family DINARITIDAE Mojsisovics, 1882

Discoidal, smooth, feebly or strongly ornamented, with simple goniatitic or feebly ceratitic suture and typically only one lateral lobe (472). *L.Trias.*

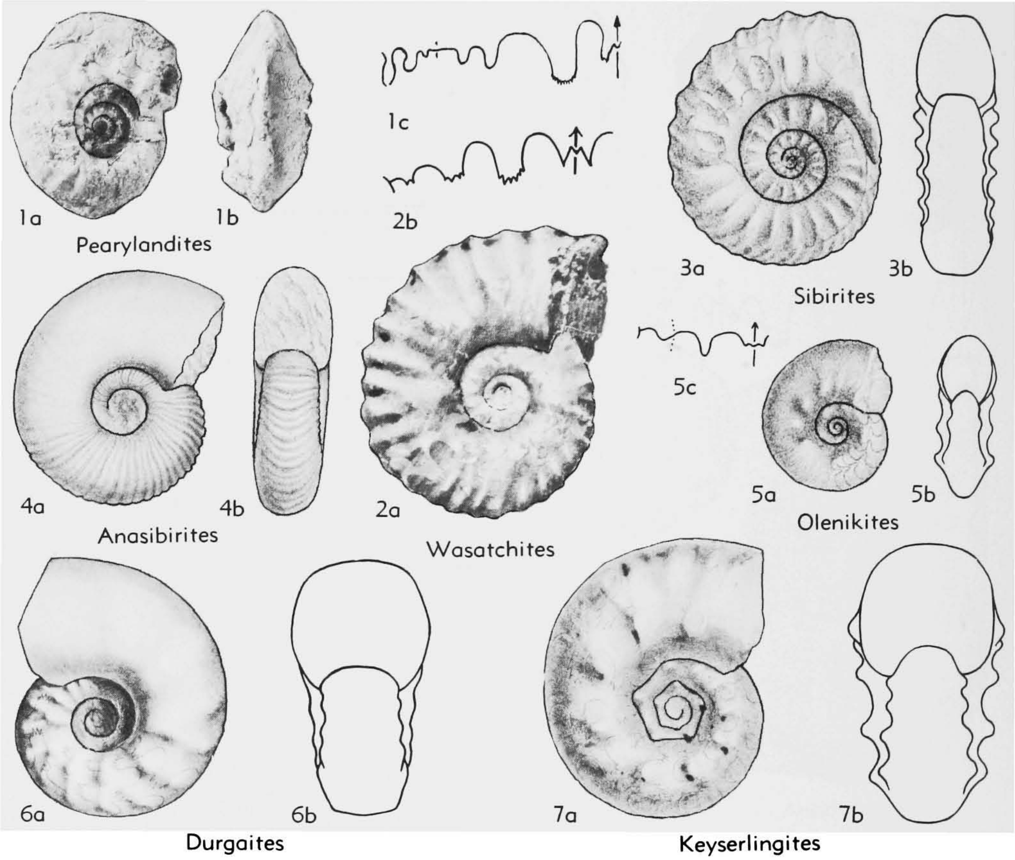


FIG. 178. Sibiritidae (p. L145-L146).

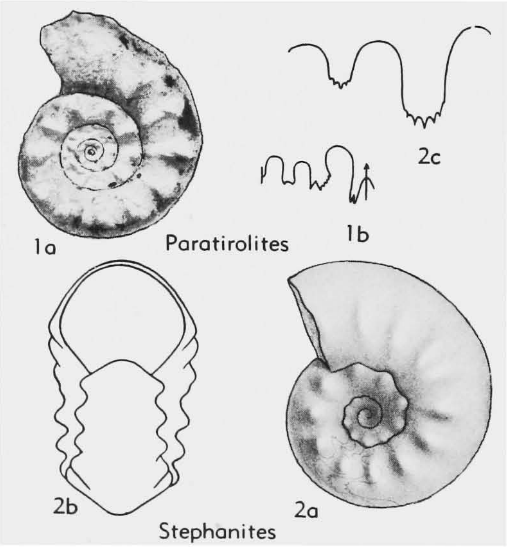


FIG. 179. Stephanitidae (p. L147).

Dinarites MOJSISOVICS, 1882 [**Ceratites dalmatinus* HAUER, 1865; SD HYATT & SMITH, 1905] [=*Plococeras* HYATT, 1900 (obj.)]. More or less involute, with rounded or (rarely) flattened venters; conch smooth or with radial folds. Suture goniatitic. *U.Scyth.*, Alps-Balkan.——FIG. 181,*1*. *D. muchianus* (HAUER), Yugo.; ×0.7 (232*).

Pseudodinarites HYATT, 1900 [**Dinarites mohamedanus* MOJSISOVICS, 1882] [=*Hercegovites* KITTL, 1903 (obj.)]. Evolute, smooth, with ceratitic lobes. *U.Scyth.*, Balkan.

Hololobus KITTL, 1903 [**Tirolites (Hololobus) monoptychus*]. Intermediate between *Dinarites* and *Carniolites*, with entire, undivided ventral lobe. *U.Scyth.*, Yugo.——FIG. 181,*5*. **H. monoptychus*; ×1 (232*).

Carniolites ARTHABER, 1911 [**Tirolites carniolicus* MOJSISOVICS, 1882]. Phragmocone as in *Dinarites* but with a few spines on body chamber. *U.Scyth.*, Yugo.——FIG. 181,*3*. **C. carniolicus* (MOJS.); *3a,b*, ×0.5 (232*).

Family HELLENITIDAE Kummel, 1952

Serpenticones, whorls subquadrate, shoulders well rounded, conspicuous ribs and well-developed keel on arched venter, bordered by narrow furrows. Suture ceratitic, with large 1st lateral lobe, small smooth 2nd lateral lobe. *L.Trias.*

Hellenites Renz & Renz, 1948 [**Tropiceltites prae-*

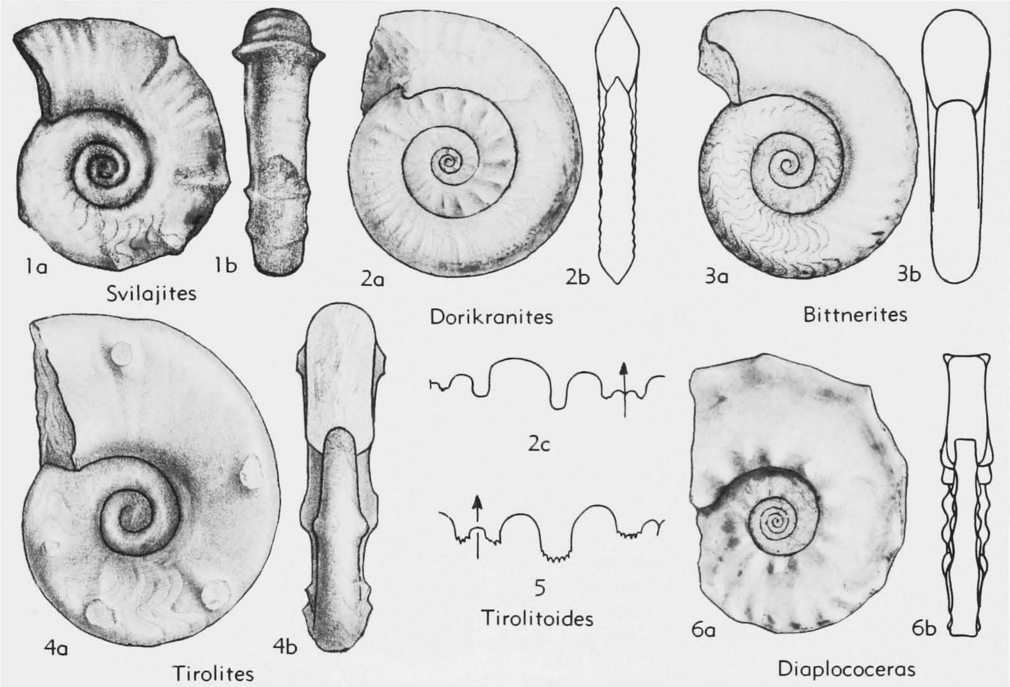


Fig. 180. Tirolitidae (p. L147).

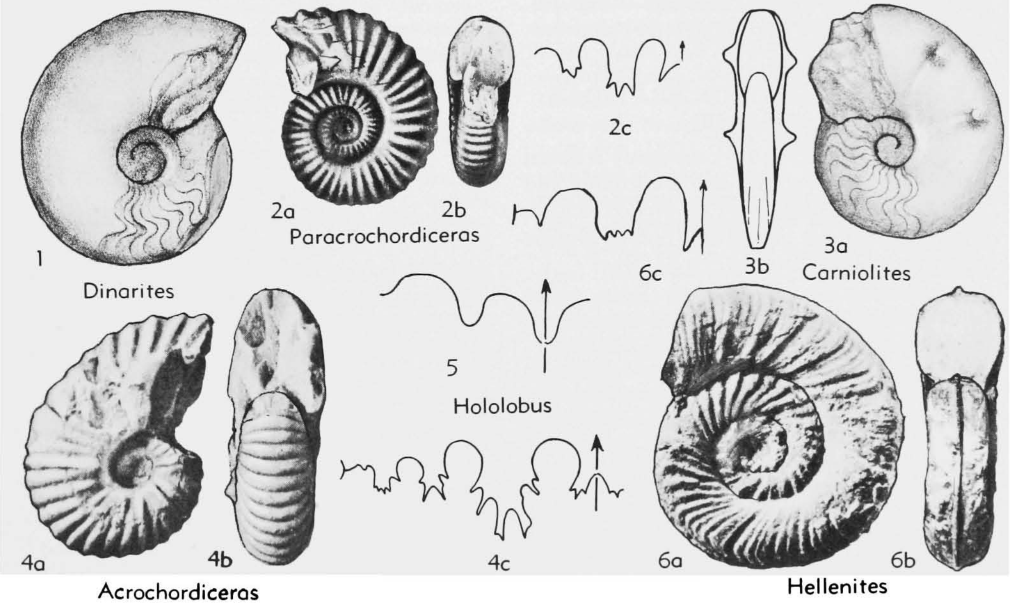


Fig. 181. Dinaritidae, Hellenitidae, Acrochordiceratidae (p. L148-L150).

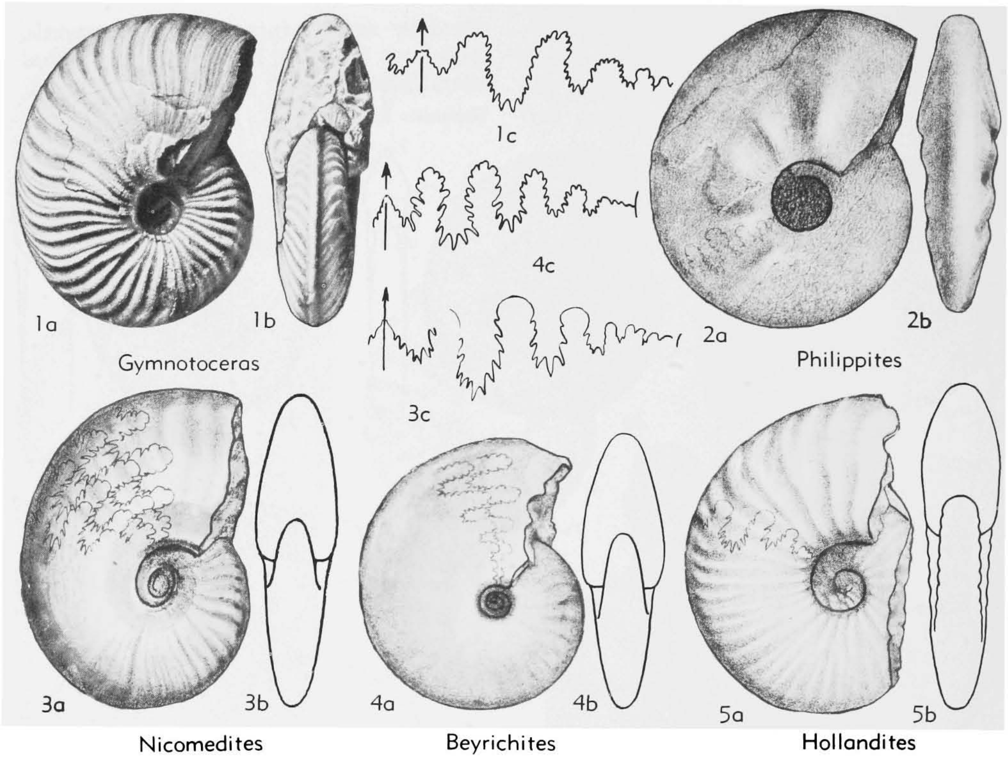


FIG. 182. Beyrichitidae (p. L150-L151).

maturus ARTHABER, 1911] [=*Hellenites (Pallasites)* RENZ-R., 1948; *Pseudarniotites* SPATH, 1951]. *U.Scyth.*, Albania-Chios-Ida.——FIG. 181, 6. **H. praematurus* (ARTH.), Albania-Chios; *6a,b*, ×1; *6c*, ×1.5 (372*).

Family ACROCHORDICERATIDAE Arthaber, 1911

More or less involute, commonly inflated with strong ribs which are continuous and generally most prominent on arched venter; with or without umbilical nodes. Suture ceratitic or ammonitic (472). *M.Trias.*

Acrochordiceras HYATT, 1877 [**A. hyatti* MEEK, 1877]. Suture simpler than in *Silesiacrochordiceras*. *Anis.*, Eurasia-Timor-Calif.-Nev.

A. (Acrochordiceras). With umbilical tubercles on earlier whorls (203). *Anis.*, Eurasia-Calif.-Nev. ——FIG. 181,*4*. **A. (A.) hyatti*, Nev.; *4a,b*, ×0.7; *4c*, ×1 (203).

A. (Paracrochordiceras) SPATH, 1934 [**A. anodosum* WELTER, 1915]. With no tuberculation, suture simple (472). *Anis.*, Timor-B.C.——FIG. 181, *2*, **A. (P.) anodosum* (WELTER), Timor; *2a,b*, ×0.7; *2c*, ×1 (559*).

A. (Epacrochordiceras) SPATH, 1934 [**A. portisi* MARTELLI, 1906]. Nontuberculate as in *A. (Paracrochordiceras)* but more compressed and involute, ribbing lost or weakened at some stage, generally on body chamber. *Anis.*, Alps-Balkan-AsiaM.

Silesiacrochordiceras DIENER, 1916 [**Acrochordiceras damesi* NOETLING, 1880]. Like *A. (Acrochordiceras)* but with different, more subdivided suture. *Anis.*, Silesia.

Family BEYRICHITIDAE Spath, 1934

Involute, discoidal, with falcoid, single or bifurcating ribs. Suture ceratitic with tendency to become subammonitic and complex (472). *L.Trias.-M.Trias.*

Beyrichites WAAGEN, 1895 [**Am. reuttensis* BEYRICH, 1867; SD SMITH, 1904]. Venter narrowly arched; sigmoidal ribbing tends to disappear or become modified on outer whorl. Suture subammonitic. *L.Trias.(U.Scyth.)-M.Trias.(Anis.)*, Alps-Balkan-Chios-Himalaya-Japan-B.C.-Nev.

B. (Beyrichites). Nontuberculate. *L.Trias.(U.Scyth.)-M.Trias.(Anis.)*, Alps-Balkan-Chios-Himalaya-Japan-B.C.-Nev.——FIG. 182,*4*. *B. ḳesava* (DIENER), Anis., Himalaya; *4a,b*, ×0.7; *4c*, ×1 (100*).

B. (Gangadharites) DIENER, 1916 [**Meeḳoceras gangadhara* DIENER, 1895]. Tubercles at middle

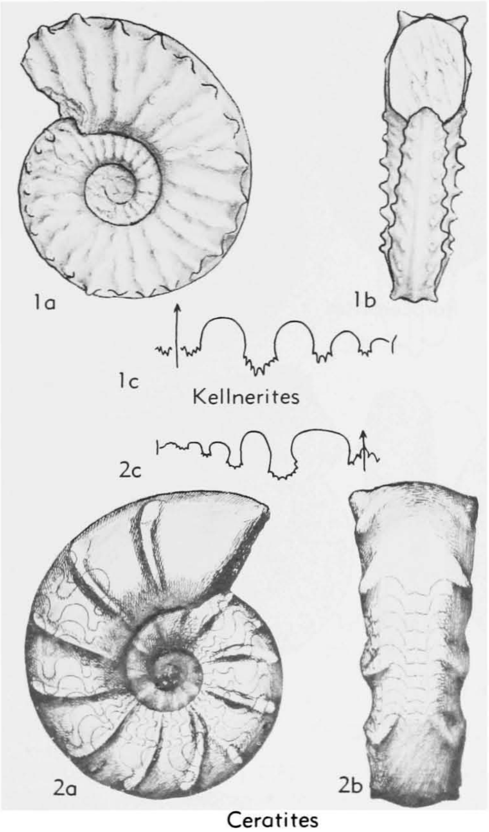


FIG. 183. Ceratitidae (p. L151-L152).

of whorl side and in some also at outer ends of some or all last few ribs on body chamber. *M. Trias.(Anis.)*, Himalaya.

Nicomedites Toula, 1896 [**Ceratites (Nicomedites) osmani;* SD Spath, 1934] [=*Osmanites, Solimanites, Mohamedites* Toula, 1896]. Differs from *Beyrichites* in more compressed form, irregular subfalcate ribbing and subceratitic suture. *M.Trias. (L.Anis.)*, AsiaM.——Fig. 182,*3*. **N. osmani*, *3a-c*, ×0.7 (725*).

Hollandites Diener, 1905 [**Am. voiti* Oppel, 1863]. Evolute, venter arched or subtabulate, ribs subfalcoid, commonly bifurcating, with or without umbilical bullae and only traces of lateral or ventral tubercles; costation tending to be reduced on body chamber to single coarse folds. Suture ceratitic. *M.Trias.(Anis.)*, Alps-Asia-?Sib.-Japan-?B.C.-?Nev.——Fig. 182,*5*. **H. voiti* (Oppel), Himalaya; *5a,b*, ×0.5 (100*).

Philippites Diener, 1905 [**Ceratites erasmi* Mojsisovics, 1882]. Like *Beyrichites* but with blunt ribs, prominent only near umbilical shoulder. *M.Trias. (Anis.)*, Alps-Balkan-Himalaya--?Nev. —— Fig. 182,*2*. **P. erasmi* (Mojs.), Alps; *2a,b*, ×0.7 (293*).

Gymnotoceras Hyatt, 1877 [**Am. blakei* Gabb, 1864]. Venter subtabulate to subcarinate, whorl sides with strong sigmoidal ribs, single or bifurcating. Suture subceratitic (449). *M.Trias.(Anis.)*, Spitz.-Japan- ?Himalaya-B.C.-Nev.——Fig. 182,*1*. **G. blakei*, Nev.; *1a,b*, ×0.7; *1c*, ×1.5 (449*).

Family CERATITIDAE Mojsisovics, 1879

Involute to evolute, generally highly ornamented with ribs and tubercles; venter tabulate to subcarinate. Suture ceratitic (472). *M.Trias.*

Ceratites de Haan, 1825 [**Am. nodosa* Bruguière, 1792; SD Smith, 1904] [=*Haaniceras* Bayle, 1878 (obj.); *Acanthoceratites, Cycloceratites, Doloceratites, Echinoceratites, Gymnoceratites, Hadroceratites, Hoploceratites, Nannoceratites, Opheoceratites, Patagioceratites, Phalacroceratites, Symboloceratites* (obj.) Schrammen, 1928; *Archioceratites, Balioceratites, Pachyceratites* Schram., 1933]. More or less evolute, robust, with coarse ornamentation usually persisting on body chamber. *Ladin.*, Ger.-Fr.-Sp.-Sard.-Rumania.——Fig. 183,*2*. **C. nodosus* (Brug.), Ger.-Fr.; *2a-c*, ×0.7 (743*).

Progonoceratites Schrammen, 1928 [**Ceratites atavus* Philippi, 1901; SD Spath, 1934] [=*Actinoceratites, Caloceratites, Campyloceratites, Leioceratites* Schram., 1928]. Like *Ceratites*, with ornamented inner whorls but more compressed and body chamber more or less smooth. *Ladin.*, Ger.-Fr.——Fig. 184,*6*. **P. atavus* (Phil.), Ger.; *6a,b*, ×0.7 (681*).

Discoceratites Schrammen, 1928 [**Ceratites intermedius* Philippi, 1901; SD Spath, 1934] [=*Cosmoceratites* Schram., 1928]. More or less smooth, involute, discoidal, with narrow to almost oxynote venter. *Ladin.*, Ger.-Fr.——Fig. 185,*4*. **D. intermedius* (Phil.), Ger.; *4a,b*, ×0.3; *4c*, ×0.7 (681*).

Alloceratites Spath, 1934 [**Ceratites schmidi* Zimmermann, 1883]. Like *Discoceratites* in young; later with prominent lateral tubercles and ventrolateral clavi bordering subsulcate venter; indistinct ribbing between tubercles on whorl sides and ribs with strong forward sinus connecting ventrolateral clavi. *Ladin.*, Ger.——Fig. 184,*4*. **A. schmidi* (Zim.); *4a,b*, ×0.7; *4c*, ×1 (681*).

Paraceratites Hyatt, 1900 [*non* Kittl, 1903] [**Ceratites elegans* Mojsisovics, 1882]. Rather involute, commonly compressed, discoidal, with subcarinate venter; typically trituberculate and with ribs that may become feeble. Saddles of suture less entire than in *Ceratites*. *Anis.*, Eurasia-N.Am.——Fig. 184,*2*. **P. elegans* (Mojs.), Alps-Yugo.; *2a*, ×0.7; *2b*, ×0.3; *2c*, ×1 (293*).

Frechites Smith, 1932 [**Ceratites humboldtensis* Hyatt & Smith, 1905]. Like *Gymnotoceras* but with tuberculation on ventral shoulders and at point of bifurcation of ribs; keel faint or absent (451). *Anis.*, Nev.-B.C.——Fig. 185,*2*. **F. hum-*

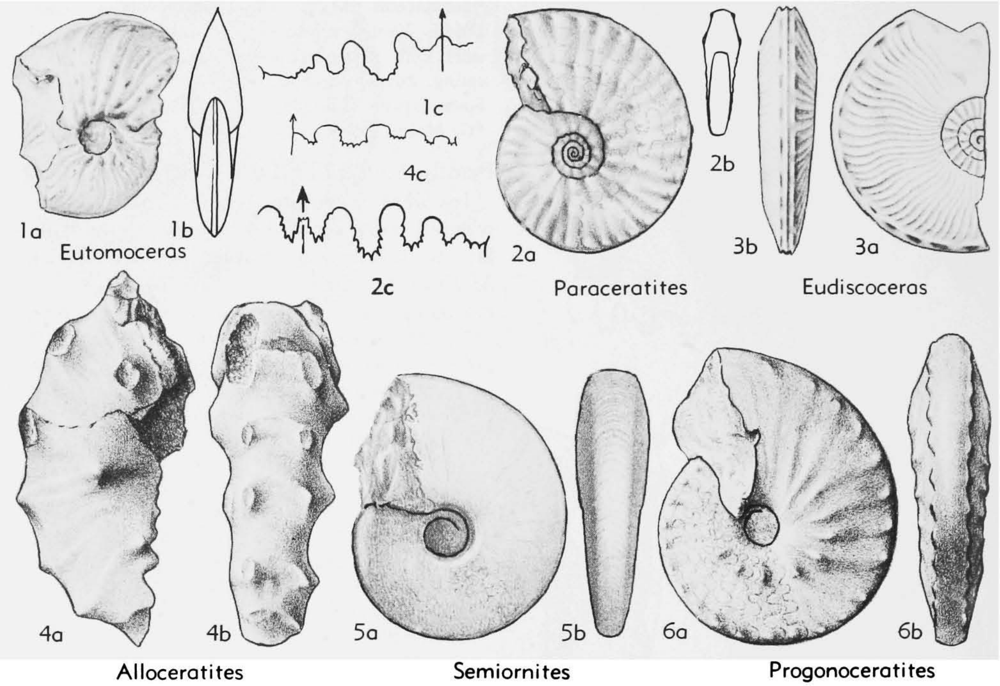


Fig. 184. Ceratitidae (P. L151-L152).

boldtensis (Hyatt-S.), Nev.; *2a,b,* ×0.66; *2c,* ×1.5 (449*).

Semiornites Arthaber, 1912 [**Ceratites cordevolicus* Mojsisovics, 1882; SD Diener, 1915]. Involute, compressed platycone, with either no distinct ribbing or single row of tubercles, or with ribs bifurcating at umbilical edge. *Anis.,* Alps-Balkan-Himalaya.——Fig. 184,*5.* **S. cordevolicus* (Mojs.), Alps; *5a,b,* ×0.7 (293*).

Kellnerites Arthaber, 1912 [**Ceratites bosnensis* Hauer, 1888] [=*Bosnites* Frech, 1908 (*non* Hauer, 1896]; *Popinites* Salopek, 1915 (obj.)]. Highly sculptured, with radial ribs and several rows of tubercles, outer ones most prominent; venter subcarinate. *Anis.,* Alps-Balkan-Greece.——Fig. 183,*1.* **K. bosnensis* (Hauer), Alps-Balkan; *1a,b,* ×0.5; *1c,* ×1 (633*).

Bulogites Arthaber, 1912 [**Ceratites multinodosus* Hauer, 1892]. Whorl section rectangular; venter broad and flattened; ribbing on whorl sides closely spaced, with 3 or 4 rows of more or less equal-sized tubercles. *Anis.,* Alps-Balkan.——Fig. 185,*5.* **B. multinodosus* (Hauer), Alps-Yugo.; *5a,b,* ×0.5; *5c,* ×1 (633*).

Halilucites Diener, 1905 [**Ceratites rusticus* Hauer, 1896]. Like *Kellnerites* but with distinct keel, tubercles not nearly so prominent; tendency toward decrease of ornamentation (488). *Anis.,* Alps-Balkan-Greece.——Fig. 185,*1.* **H. rusticus* (Hauer), Yugo.; *1a,b,* ×0.7; *1c,* ×1 (633*).

Eudiscoceras Hyatt, 1877 [**E. gabbi* Meek, 1877]. Like *Halilucites* but more compressed, discoidal, involute; ribbing closer spaced and finer; venter with keel bordered by clavi (203). *Anis.,* Nev.——Fig. 184,*3.* **E. gabbi; 3a,b,* ×0.7 (203*).

Eutomoceras Hyatt, 1877 [*non* Mojsisovics, 1879 (see Mojs., 1883)] [**E. laubei* Meek, 1877]. Compressed, discoidal, involute, keeled platycone with ribbed early volutions but tending to degeneration of typically multipapillate ribs to final smoothness (203). *Anis.,* Nev.——Fig. 184,*1.* **E. laubei; 1a,b,* ×0.7; *1c,* ×1 (203*).

Koptoceras Spath, 1951 [**K. falconi*]. Like *Eutomoceras* but with falcate ribs, most marked near umbilicus, declining toward venter; rapid degeneration of ornamentation, adult whorls nearly smooth (488). *Anis.,* Spitz.

Salterites Diener, 1907 [**Ceratites (Salterites) oberhummeri*]. Like *Hollandites* but with strong umbilical tubercles which in later stage move outward, still serving as point of bifurcation of ribs which terminate at ventrolateral edge in small tubercles. Suture ceratitic, as in *Hollandites. Anis.,* Himalaya.

Haydenites Diener, 1907 [**Ceratites (Haydenites) hatscheki*]. Evolute, whorl section subrectangular, with broad slightly arched venter; inner whorls with simple radial ribs, outer whorls with nodes at junction of bifurcating ribs, also ribs crossing venter, with small nodes on ventral shoulder. Su-

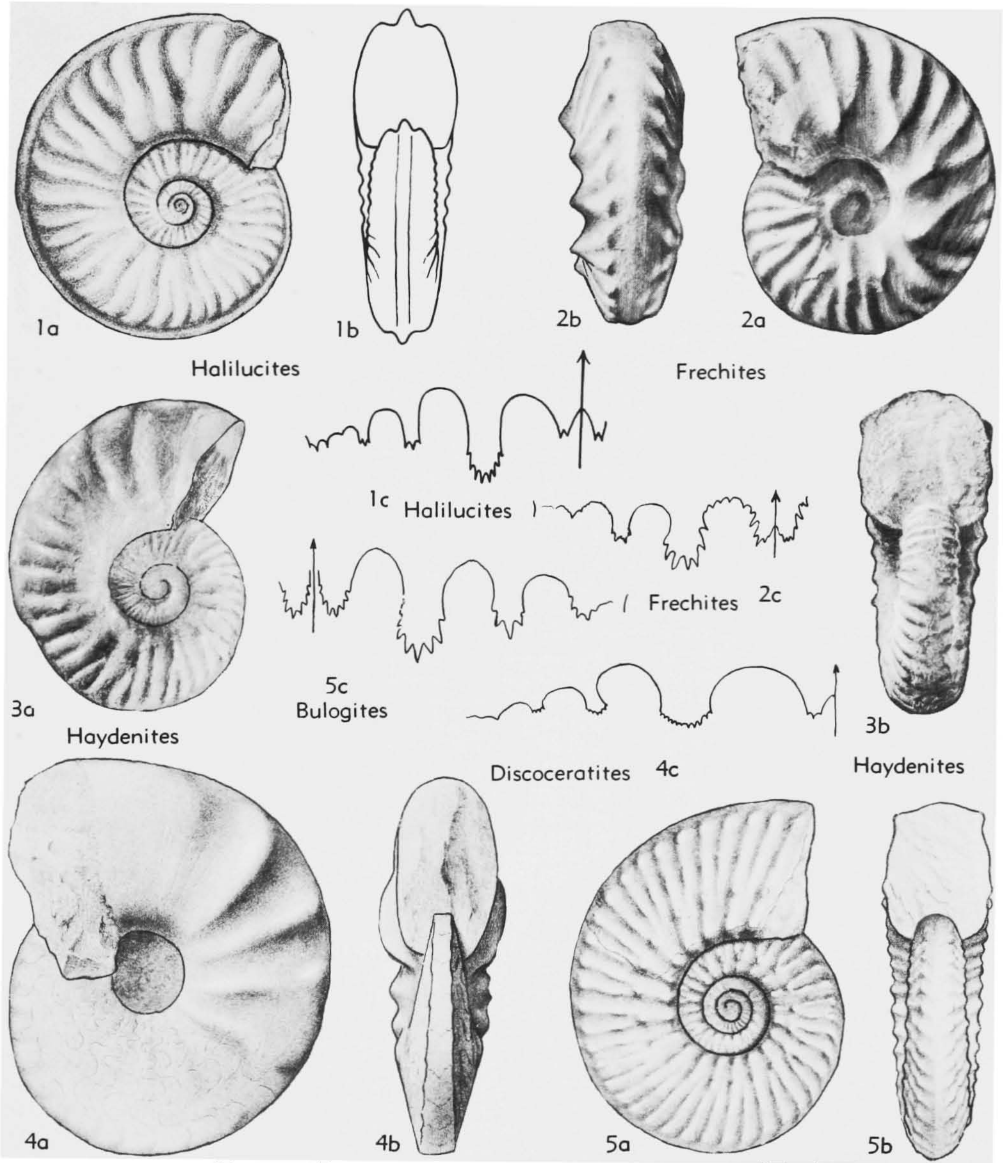


Fig. 185. Ceratitidae (p. L151-L152).

ture ceratitic (104). *Anis.,* Balkan-Himalaya-Nev.——Fig. 185,*3.* **H. hatscheki* (Diener), Himalaya; *3a,b,* ×0.25 (104*).

?**Peripleurocyclus** Diener, 1907 [**Ceratites (Peripleurocyclus) smithianus*]. Compressed, evolute, with rounded venter and strong ribs continuous across venter. Suture ceratitic, with slender saddles (104). *Anis.,* Himalaya.

Family DANUBITIDAE Spath, 1951

Very evolute, with ribbed whorl sides which may be tuberculate or not; venter rounded to subcarinate. Suture ceratitic (488). *M.Trias.*

Danubites Mojsisovics, 1893 [**Celtites floriani* Mojs., 1882] [=*Florianites* Hyatt, 1900 (obj.)].

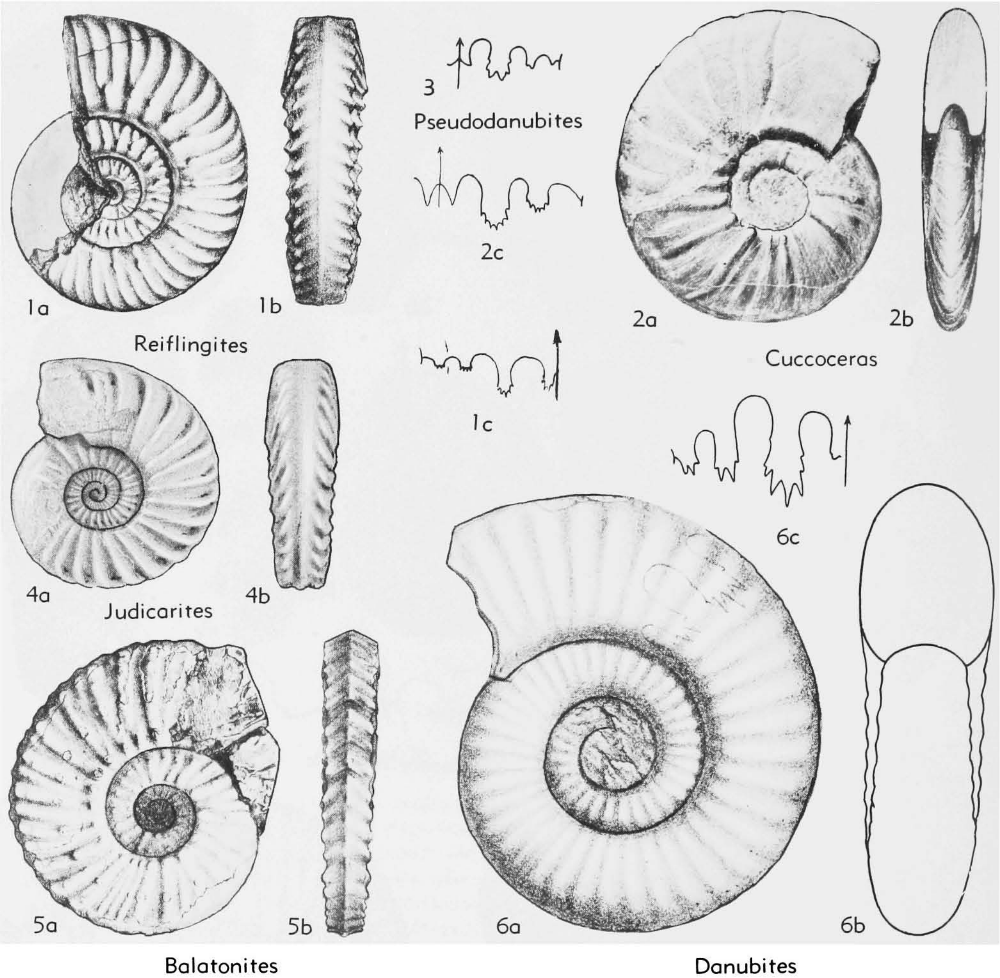


FIG. 186. Danubitidae, Balatonitidae (p. L153-L155).

Whorl section subquadrate, with smooth to feebly carinate venter; whorl sides flattened, with prominent radial ribs that may bend adorally near the ventral shoulder (292). *Anis.*, Alps-Balkan-Himalaya-Timor-Japan.——FIG. 186,*6*. *D. ḳansa* DIENER, Himalaya; *6a-c*, ×0.7 (100*).

Pseudodanubites HYATT, 1900 [**Danubites dritarashtra* DIENER, 1895]. Like *Danubites* but venter obtuse and suture more advanced (100). *Anis.*, Himalaya.——FIG. 186,*3*. **P. dritarashtra* (DIENER); ×1 (100*).

Reiflingites ARTHABER, 1896 [**R. eugeniae*]. Like *Danubites* but whorl section trapezoidal, venter tabulate or subcarinate; whorl sides with lateral projected ribs with 1 to 3 generally faint inner ventrolateral nodes (472). *Anis.*, Alps.——FIG. 186,*1*. **R. eugeniae*; *1a,b*, ×0.7; *1c*, ×1 (584*).

?Rikuzenites YABE, 1949 [**R. nobilis*]. Evolute, whorls slowly expanding; whorl sides with radial ribs; last half volution separated from phragmocone as in *Scaphites*. Suture ceratitic. Type and only specimen may be deformed, genus doubtful. *Anis.*, Japan.

Family BALATONITIDAE Spath, 1951

Widely umbilicate, more or less serpenticone in form, with strong ornamentation; smooth, rounded, fastigate, or keeled venter; constrictions or more rarely tubercles. Simple ceratitic suture (488). *M.Trias.*

Balatonites MOJSISOVICS, 1879 [**Trachyceras balatonicum* MOJS., 1873]. Compressed, highly ornamented, with more or less fastigate venter; radial ribs with variable tuberculation, generally in umbilical, median, and ventrolateral rows, and in

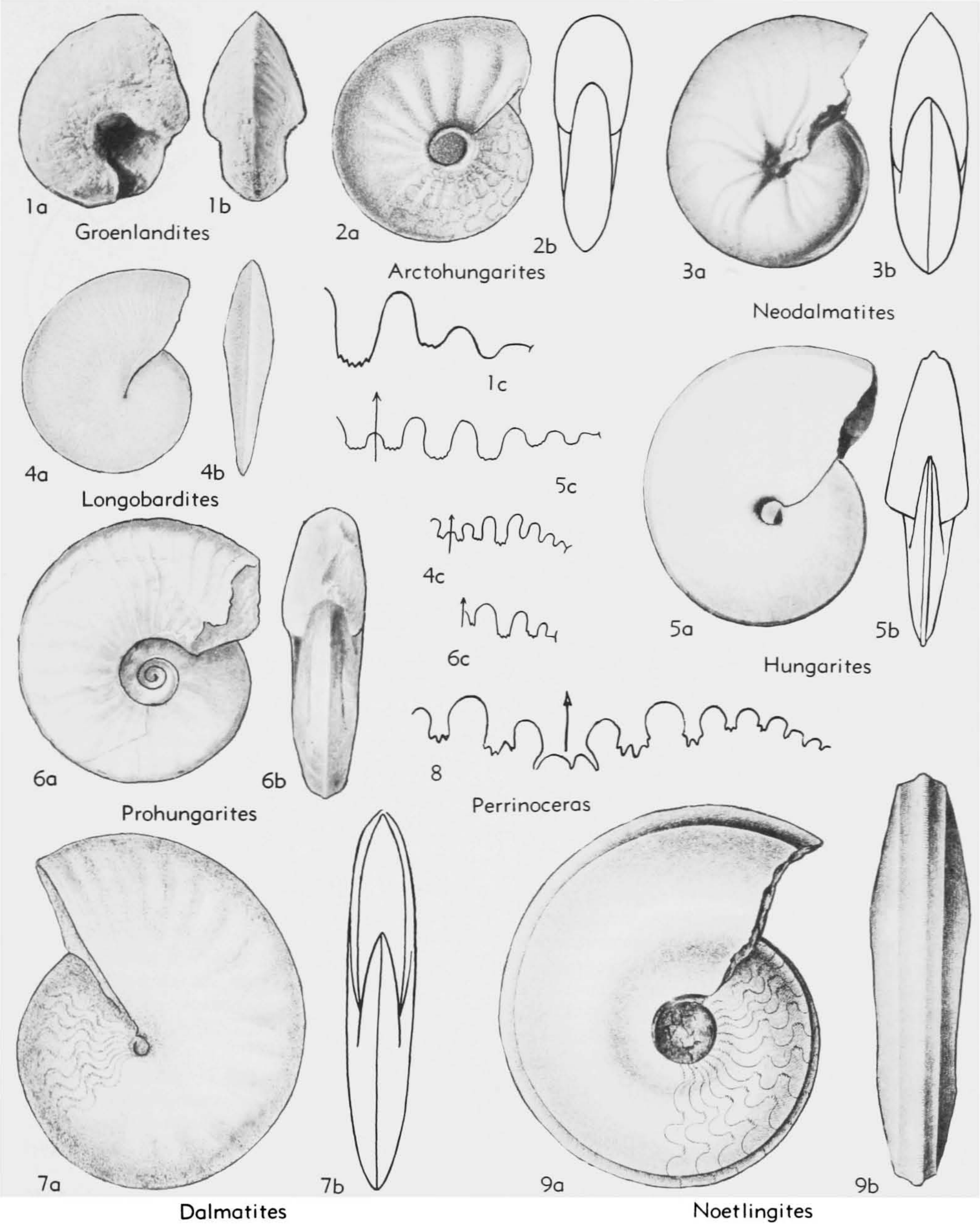


FIG. 187. **Hungaritidae** (p. L156).

some on center of venter (292). *Anis.*, Alps-Balkan-Ger.-Japan-Nev.——FIG. 186,*5*. **B. balatonicus* (MOJS.), Alps; *5a,b*, ×0.7 (293*).

Judicarites MOJSISOVICS, 1896 [**Balatonites arietiformis* MOJS., 1882]. Venter with prominent keel, whorl sides with radial ribs that are inflated and projected adorally on ventral shoulder (295). *Anis.*, Alps-Ger.-Balkan.——FIG. 186,*4*. *J. prezzanus* (MOJS.), Alps-Yugo.; *4a,b*, ×0.7 (293*).

Cuccoceras DIENER, 1905 [**Trachyceras cuccense* MOJSISOVICS, 1873]. Compressed, whorl sides flattened, venter narrowly rounded; with ribs and constrictions that are continuous over venter, some forms also with tubercles on whorl sides (488).

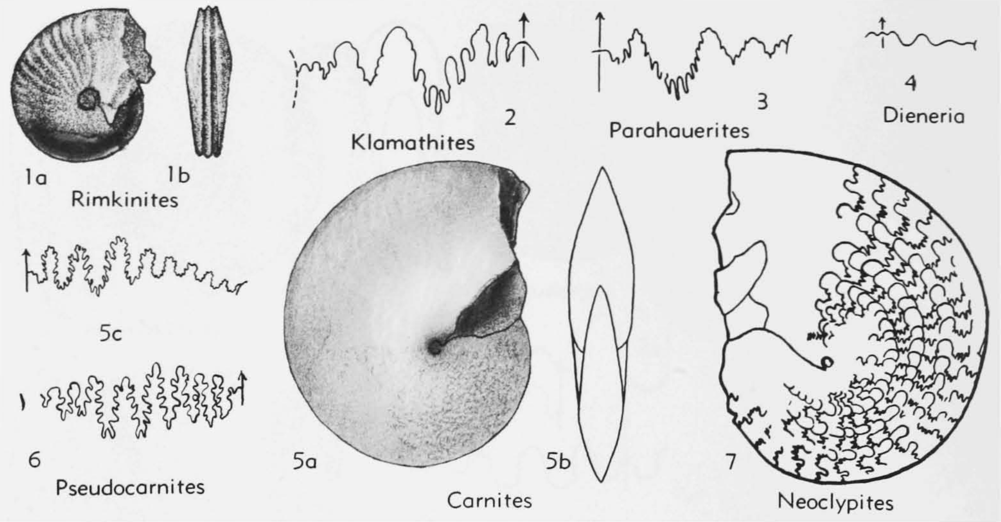


Fig. 188. Carnitidae (p. L157).

Anis., Alps-Yugo.-Himalaya-?Japan-Nev.——Fig. 186,*2*. **C. cuccense* (Mojs.), Alps; *2a-c,* ×1 (584*).

Family HUNGARITIDAE Waagen, 1895

Involute, compressed, discoidal, with keeled or sharpened venter; smooth or weakly costate. Suture ceratitic, usually with numerous elements, may have adventitious lobes (488). *L.Trias.-U.Trias.*

Hungarites Mojsisovics, 1879 [**Ceratites mojsisovicsi* Roth, 1871 (=*Ceratites zalaensis* Boeckh, 1873)] [=*Iberites* Hyatt, 1900]. Involute platycone, with high median keel on subtabulate venter; ventral shoulders usually well marked; smooth or with sigmoidal ribs. Suture ceratitic to subammonitic (203). *M.Trias.(Anis.-Ladin.),* Alps-Sp.-Balkan-Asia M.-Himalaya-N. Sib.-B. C.-Calif.-Nev.——Fig. 187,*5*. *H. yatesi* Hyatt & Smith, Calif.; *5a,b,* ×1; *5c,* ×2 (203*).

Noetlingites Hyatt, 1900 [**Ceratites strombecki* Griepenkerl, 1860]. Like *Hungarites* but venter fastigate throughout. Suture without median saddle in ventral lobe, 3 lateral lobes, broadly rounded saddles (488). *M.Trias.(Anis.),* Ger.——Fig. 187, *9*. **N. strombecki* (Griep.); *9a,b,* ×0.7 (630*).

Longobardites Mojsisovics, 1882 [**L. breguzzanus;* SD Hyatt & Smith, 1905]. Involute oxycones without distinct ventral shoulders; with sigmoidal striations. Suture ceratitic, with adventitious lobes (203). *M.Trias.(Anis.-Ladin.),* Alps-B.C.-Nev.——Fig. 187,*4*. **L. breguzzanus,* Alps; *4a,b,* ×0.7; *4c,* ×1 (293*).

Neodalmatites Spath, 1951 [**Dalmatites parvus* Smith, 1914]. Like *Longobardites* but slightly inflated and with weak lateral folds. Suture simpler (449). *M.Trias.(Anis.),* Nev.——Fig. 187,*3*. **N. parvus* (Smith); *3a,b,* ×1.5 (449*).

Groenlandites Kummel, 1953 [**G. nielseni*]. Like *Neodalmatites* but whorl section subtrigonal, umbilical wall nearly vertical. Suture less advanced. *M.Trias.(Anis.),* Pearyland.——Fig. 187,*1*. **G. nielseni; 1a,b,* ×0.7; *1c,* ×4 (650*).

Perrinoceras Johnston, 1941 [**P. novaditus*]. Conch as in *Longobardites,* with sharp venter. Suture ceratitic but simpler, ventral lobe very simple (488). *U.Trias.(Carn.),* Nev.——Fig. 187,*8*. **P. novaditus;* ×1 (643*).

Arctohungarites Diener, 1916 [**Hungarites triformis* Mojsisovics, 1886]. Involute platycones with weak sigmoidal folds on body chamber; distinct keel only on adoral part of phragmocone, tending to again disappear. Suture ceratitic (294). *M.Trias.(Anis.),* N.Sib.——Fig. 187,*2*. **A. triformis* (Mojs.); *2a,b,* ×1 (294*).

Dalmatites Kittl, 1903 [**D. morlaccus*]. Discoidal, involute, nearly smooth oxycones. Suture ceratitic, simple, with 3 feebly toothed lobes (232). *L.Trias.(U.Scyth.),* Yugo.——Fig. 187,*7*. **D. morlaccus; 7a,b,* ×1 (232*).

Prohungarites Spath, 1934 [**P. similis*]. More or less evolute, discoidal; irregular ribbing continuous across tricarinate or feebly keeled venter. Suture ceratitic, with only 2 lobes (560). *L.Trias.(U.Scyth.),* Timor-Sib.-Ida.——Fig. 187,*6*. **P. similis,* Timor; *6a,b,* ×0.7; *6c,* ×1 (560*).

Family CARNITIDAE Arthaber, 1911

Discoidal, compressed, very involute, venter narrow and bicarinate, tricarinate, sharpened or truncated; weak ribs and tubercles

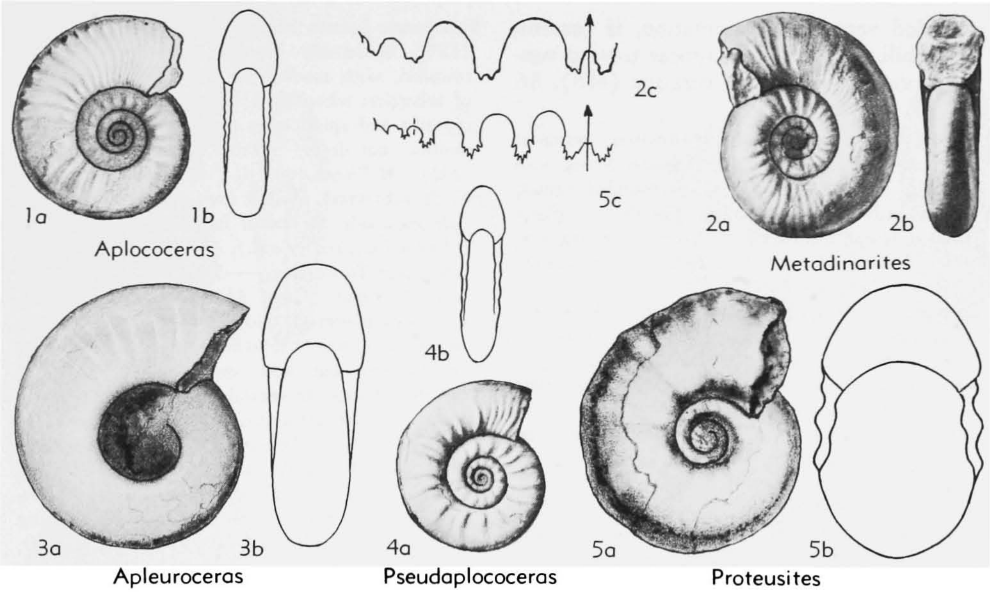


FIG. 189. Proteusitidae, Aplococeratidae (p. L157-L158).

may be present. Suture generally ammonitic, with adventitious and auxiliary elements (488). *M.Trias.-U.Trias.*

Carnites MOJSISOVICS, 1879 [**Nautilus floridus* WULFEN, 1793; SD MOJS., 1882]. Venter tricarinate in young, bicarinate to sharpened in later volutions; sides with low flexuous ribs and in places tubercles along mid-line of sides and near venter. Suture ammonitic (293). *U.Trias.(Carn.),* Alps-Himalaya.——FIG. 188,*5*. **C. floridus* (WULFEN); *5a,b,* ×0.5; *5c,* ×0.7 (293*).

Rimkinites MOJSISOVICS, 1902 [**Hungarites nitiensis* MOJS., 1896]. Tricarinate venter persisting; sides with weak sigmoidal ribs, some forms with clavi at ventrolateral edge. Suture subammonitic with no adventitious elements but with auxiliary elements (295). *M.Trias.(Ladin.)-U.Trias.(Carn.),* Himalaya.——FIG. 188,*1*. **R. nitiensis* (MOJS.), Ladin., Himalaya; *1a,b,* ×1.5 (295*).

Pseudocarnites SIMIONESCU, 1913 [**Carnites (Pseudocarnites) arthaberi*]. Venter truncate, conch smooth. Suture with monophyllic saddle endings (488). *U.Trias.(Carn.),* Rumania.——FIG. 188,*6*. **P. arthaberi;* ×1 (709*).

Klamathites SMITH, 1927 [**K. schucherti*]. Venter grooved or slightly rounded; conch nearly smooth or with weak lateral folds. Suture subammonitic (450). *U.Trias.(Carn.),* Calif.——FIG. 188,*2*. **K. schucherti;* ×1 (450*).

Parahauerites DIENER, 1916 [**Hauerites ashleyi* HYATT & SMITH, 1905] [=*Fremontites* SMITH, 1927 (obj.)]. Like *Klamathites* but with simpler suture (450). *U.Trias.(Carn.),* Calif.——FIG. 188, *3*. **P. ashleyi* (HYATT-S.); ×1 (450*).

Dieneria HYATT & SMITH, 1905 [**D. arthaberi*]. Compressed platycone, venter truncate, conch smooth. Suture simple, with only 1st lateral lobe slightly serrated, others entire (203). *U.Trias.(Carn.),* Calif.——FIG. 188,*4*. **D. arthaberi;* ×2 (450*).

Neoclypites SPATH, 1951 [**Metahedenstroemia? desertorum* JOHNSTON, 1941]. Venter truncate or grooved; sides with falciform radial growth lines that may be bundled at intervals. Suture ceratitic, multilobate, with adventitious and auxiliary lobes (488). *U.Trias.(Carn.),* Nev.——FIG. 188,*7*. **N. desertorum* (JOHNSTON); ×0.7 (643*).

Family PROTEUSITIDAE Spath, 1951

Generally involute, with arched venter; tendency for outer volution to be excentric; conch extremely variable in degree of involution and relative dimensions; broad fold like ribs, strigation, and umbilical tubercles may all be present or only some of these. Suture ceratitic to slightly ammonitic (488). *M. Trias.*

Proteusites HAUER, 1887 [**P. kellneri*] (488). *Anis.,* Balkan-Himalaya-Alaska.——FIG. 189,*5*. **P. kellneri,* Balkan; *5a,b,* ×0.7; *5c,* ×1 (633*).

Family APLOCOCERATIDAE Spath, 1951

Ceratitids with very simplified suture and tendency to lose their ornamentation; generally evolute, more or less compressed, with rounded venter; ornamentation, if present, of umbilical ribs that disappear toward venter. Suture goniatitic or ceratitic (488). *M. Trias.*

Aplococeras Hyatt, 1900 [**Dinarites avisianus* Mojsisovics, 1882]. Evolute discoidal forms with convex, converging whorl sides, rounded venter, and slightly flexuous umbilical ribs that disappear toward venter. Suture with 2 lateral lobes (?goniatitic). *Ladin.*, Alps.——Fig. 189,*1*. **A. avisianum* (Mojs.); *1a,b,* ×0.7 (293*).

Velebites Salopek, 1918 [**Dinarites (Velebites) dinaricus*]. Like *Aplococeras* but ribs more recurved and suture ceratitic. *Ladin.*, Yugo.

Apleuroceras Hyatt, 1900 [**Ceratites sturi* Mojsisovics, 1882]. Evolute, essentially smooth conch, with subquadrate whorl section, broadly rounded venter. Suture ceratitic with 2 lateral lobes (293). *Ladin.*, Alps.——Fig. 189,*3*. **A. sturi* (Mojs.); *3a,b,* ×0.5 (293*).

Pseudaplococeras Spath, 1951 [**Lecanites vogdesi* Hyatt & Smith, 1905]. Compressed, evolute, discoidal conch with flexuous umbilical ribs; venter narrowing adorally. Suture goniatitic. *Anis.*, Nev.-N.Alaska.——Fig. 189,*4*. **P. vogdesi* (Hyatt-S.), Nev.; *4a,b,* ×0.7 (449*).

Metadinarites Spath, 1951 [**Dinarites desertorum* Smith, 1914]. Like *Pseudaplococeras* but whorls more robust. Suture with 2 ceratitic lobes. *Anis.*, Nev.——Fig. 189,*2*. **M. desertorum* (Smith); *2a,b,* ×0.7; *2c,* ×3 (449*).

?Dobrogeites Kittl, 1908 [**D. tirolitiformis*]. Evolute, compressed platycone, with rounded venter, whorl sides divergent; inner whorls with *Tirolites*-like ornamentation, outer whorls smooth, Suture multilobate and smooth. *Anis.*, Rumania.

Superfamily CLYDONITACEAE Mojsisovics, 1879

[*nom. transl.* Miller & Furnish, 1954 (*ex* Clydonitidae Mojs., 1879)] [=Trachyceratacea Haug, 1894 (*nom. transl.* Kummel, 1952, *ex* Trachyceratidae Haug, 1894)]

Generally costate, tuberculate ammonoids with smooth, grooved, or keeled venters. Suture ceratitic or ammonitic, goniatitic in a few offshoots. Includes some genera with heteromorph coiling of shell. Whole group descended from Ceratitaceae. *L.Trias.-U. Trias.*

Family TRACHYCERATIDAE Haug, 1894

More or less involute, highly ornamented derivatives of Ceratitidae; venter generally with median furrow bordered by rows of tubercles or continuous keel; whorl sides with flexuous ribs usually tuberculate, arranged in spiral pattern. Suture ceratitic to ammonitic (488). *M.Trias.-U.Trias.*

Trachyceras Laube, 1869 [**Ceratites aon* Münster, 1834]. Moderately involute, compressed; venter rounded, with median furrow bordered by rows of tubercles; whorl sides with single and bifurcating ribs and spiral rows of tubercles. Suture ammonitic, not deeply serrated, with 2 lateral lobes (292). *M.Trias.(Anis.)-U.Trias.(Carn.),* cosmop.

T. (Trachyceras). With 2 rows of tubercles bordering each side of ventral furrow (292). *M.Trias. (Ladin.)-U.Trias.(Carn.),* Alps-Balkan-AsiaM.-Himalaya-Timor-Nev.——Fig. 190,*5*. **T. (T.) aon* (Münster), Carn., Alps; *5a-c,* ×1 (293*).

T. (Protrachyceras) Mojs., 1893 [**Trachyceras archelaus* Laube, 1869; SD Diener, 1915]. Like *Trachyceras* but with only a single row of tubercles bordering ventral furrow (292). *M.Trias. (Anis.)-U.Trias.(Carn.),* Alps-Sp.-Sard.-Balkan-AsiaM.-Himalaya-Timor-Indochina-Calif.-Nev.

T. (Paratrachyceras) Arthaber, 1914 [**T. hofmanni* Boeckh, 1873] [=*Meginoceras* McLearn, 1930]. With little or no tuberculation, ribbing dense (23). *M.Trias.(Ladin.)-U.Trias.(Carn.),* Alps-Sp.-Balkan-Japan-Indochina-B. C. - Nev.——Fig. 190,*8*. **T. (P.) hofmanni* (Boeckh), Carn., Balkan; *8a,b,* ×1 (293*).

Nevadites Smith, 1914 [**N. merriami*]. Evolute, with subrectangular whorl section increasing slowly in height; whorl sides and venter flattened; no ventral furrow; with strong lateral ribs and tubercles, prominent tubercle at end of rib on ventrolateral shoulder. Suture ceratitic (449). *M. Trias.(Anis.),* Nev.-Balkan-?Japan.——Fig. 190, *10*. **N. merriami,* Nev.; *10a,b,* ×0.7 (449*).

Anolcites Mojsisovics, 1893 [**Trachyceras doleriticum* Mojs., 1869]. Trachyceratids with no distinct ventral furrow and ribs that cross venter (292). *M.Trias.(Anis.-Ladin.),* Alps-Balkan-?Himalaya-Nev.——Fig. 190,*7*. **A. doleriticum* (Mojs.), Ladin., Alps; *7a,b,* ×1 (293*).

Sirenites Mojsisovics, 1893 [**Am. senticosus* Dittmar, 1866; SD Hyatt & Smith, 1905]. Compressed, with distinct furrow on venter; whorl sides flattened-convex with sigmoidal ribs that bifurcate near ventrolateral edge on a tubercle and project sharply adorally, 2 rows of tubercles on whorl side, one on umbilical shoulder. Tubercles arranged in spiral lines. Suture ammonitic (292). *U.Trias.(Carn. - Nor.),* Alps-Sicily-Balkan-Himalaya-Timor-Alaska-B.C.-Calif.-?Mex.

S. (Sirenites). With a single row of tubercles bordering ventral furrow (292). *U.Trias.(Carn.-Nor.),* Alps - Balkan - Himalaya - Timor - Alaska-Calif.-?Mex.——Fig. 190,*9*. **S. (S.) senticosus* (Dittmar) Carn., Alps; *9a,b,* ×1 (292*).

S. (Diplosirenites) Mojsisovics, 1893 [**S. (D.) raineri;* SD Diener, 1915]. Ventral termination of ribs with double tubercles (292). *U.Trias. (Carn.),* Alps.

S. (Anasirenites) Mojsisovics, 1893 [**S. (A.) ekkehardi* Mojs.; SD Diener, 1915]. Ventral fur-

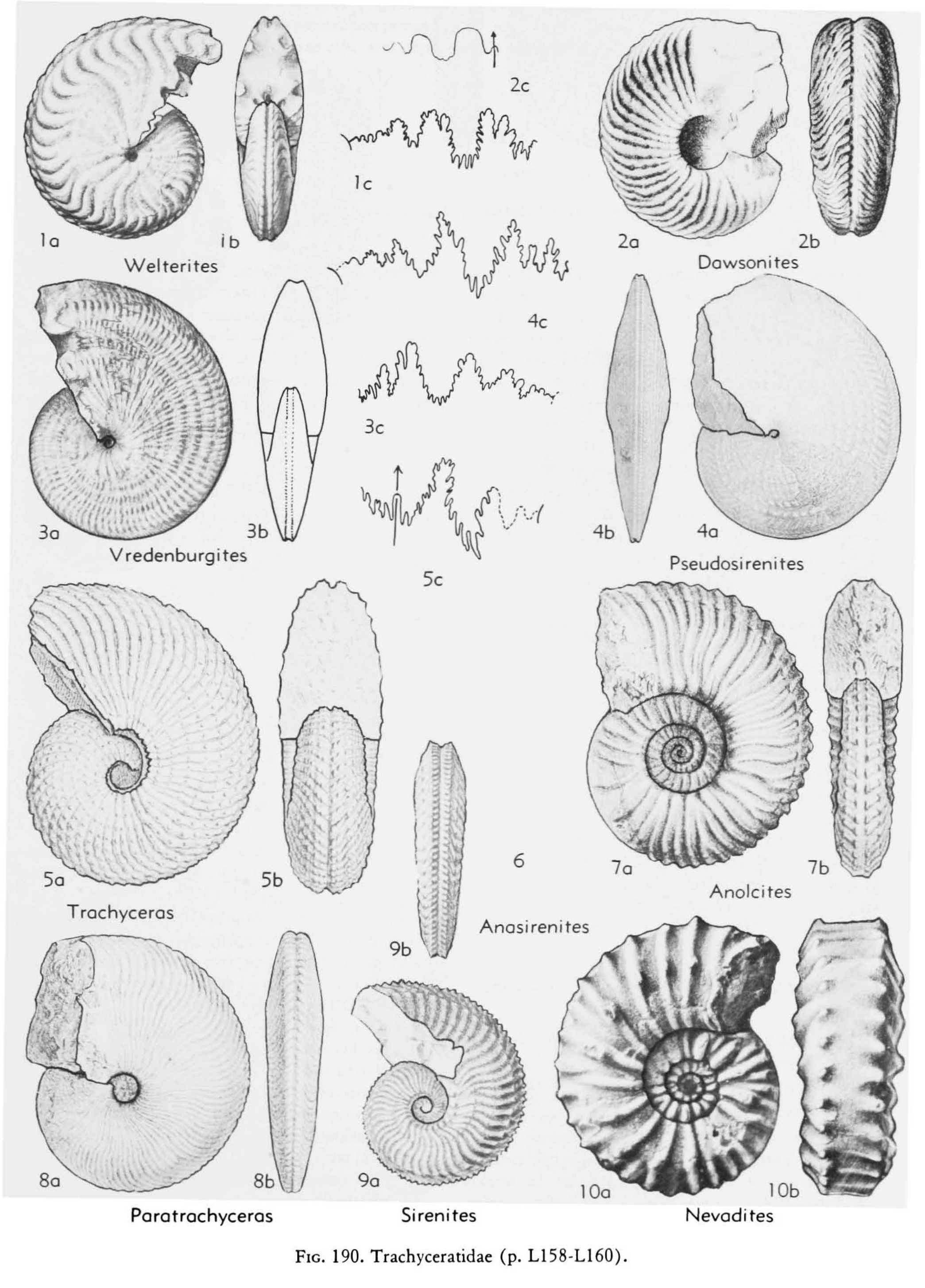


FIG. 190. Trachyceratidae (p. L158-L160).

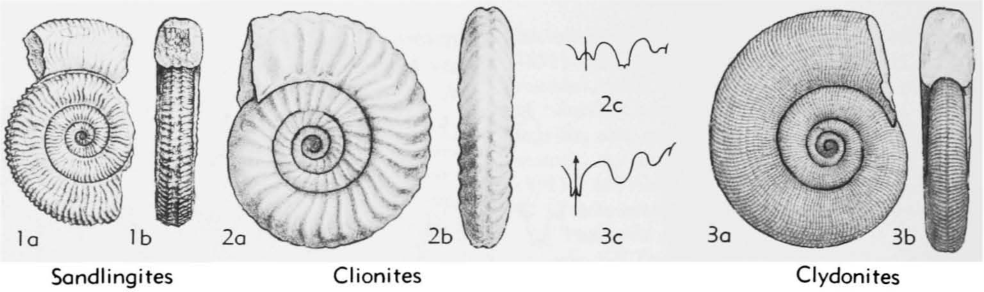


FIG. 191. Clydonitidae, Clionitidae (p. L160).

row bordered by continuous keel (292). *U.Trias. (Carn.-Nor.),* Alps-Sicily-Himalaya.——FIG. 190, 6. **S. (A.) ekkehardi,* Carn., Alps; ×1 (292*).

Pseudosirenites ARTHABER, 1911 [**Sirenites stachei* MOJSISOVICS, 1893; SD SPATH, 1951]. Like *Sirenites,* with narrow venter bordered by nodose keel. Suture with 2 adventitious elements (292). *U. Trias.(Nor.),* Alps.——FIG. 190,*4*. **P. stachei* (MOJS.); *4a,b,* ×0.5; *4c,* ×1 (292*).

Welterites DIENER, 1923 [**W. egregius*]. Involute, compressed, discoidal; median furrow bordered by nodose keels; whorl sides with flexuous ribs that project sharply forward on ventrolateral area. Suture ammonitic (115). *U.Trias.(Nor.),* Timor.——FIG. 190,*1*. **W. egregius; 1a,b,* ×0.5; *1c,* ×0.7 (115*).

Vredenburgites DIENER, 1916 [**Sirenites vredenburgi* DIENER, 1906]. Surface with thin flexuous ribs and numerous spiral rows of bullae. Suture with adventitious elements in 1st lateral saddle (115). *U.Trias.(?Carn.-Nor.),* Himalaya-Timor. ——FIG. 190,*3*. *V. vredenburgiformis* DIENER, Nor., Timor; *3a,b,* ×0.5; *3c,* ×0.7 (115*).

Dawsonites BÖHM, 1903 [**Trachyceras canadense* WHITEAVES, 1889]. Moderately evolute, venter broadly rounded, with deep furrow; whorl sides with radial ribs that bifurcate on whorl side and then project sharply adorally; ribs with spiral rows of tubercles. Suture ceratitic, with rounded saddles (450). *U.Trias.(Carn.),* B.C.-Alaska-BearI.——FIG. 190,*2*. **D. canadense* (WHITEAVES); *2a,b,* ×0.7; *2c,* ×1 (732*).

Family CLYDONITIDAE Mojsisovics, 1879

Generally evolute, compressed, with fine, dense, irregularly granular ribs; median groove on venter. Suture goniatitic or weakly ceratitic (488). *U.Trias.*

Clydonites HAUER, 1860 [**Gon. decoratus* HAUER, 1846]. Venter arched, granular ribs not crossing median groove. Suture goniatitic, may be weakly ceratitic (292). *Carn.-Nor.,* Alps-Sicily.——FIG. 191,*3*. **C. decoratus* (HAUER), Nor., Alps; *3a,b,* ×0.7; *3c,* ×1 (292*).

Sandlingites MOJSISOVICS, 1893 [**Am. oribasus* DITTMAR, 1866; SD HYATT & SMITH, 1905]. Venter broad, flattened, granular ribs crossing median groove; with umbilical tubercles. Suture goniatitic or ceratitic (292). *Carn.-Nor.,* Alps-Balkan-Himalaya-Timor-Calif.——FIG. 191,*1*. *S. archibaldi* MOJS., Nor., Himalaya-Timor; *1a,b,* ×0.7 (295*).

Family CLIONITIDAE Arabu, 1932

Generally evolute, with median ventral furrow usually bordered by rows of tubercles; whorl sides with sigmoidal ribs which may bear spiral rows of tubercles. Suture ceratitic (488). *U.Trias.*

Clionites MOJSISOVICS, 1893 [**C. angulosus;* SD HYATT & SMITH, 1905]. Evolute, whorl section subquadrate; with sigmoidal ribs, generally bifurcating, projected on ventrolateral area; little or no tuberculation on ribs. Suture ceratitic with 2 lateral lobes (292). *Carn.-Nor.,* Alps-Balkan-Asia M. - Himalaya - Timor-?Indochina-BearI.-Nev.——FIG. 191,*2*. **C. angulosus,* Carn., Alps; *2a,b,* ×0.7; *2c,* ×1 (292*).

Alloclionites SPATH, 1951 [**A. timorensis (=Clionites ares timorensis* WELTER, 1914)]. With many tubercles which tend to diminish on body chamber (558). *Carn.-Nor.,* Alps-Balkan-Himalaya-Timor-B.C.——FIG. 192,*9*. **A. timorensis* (WELTER), Timor; *9a,b,* ×0.5 (558*).

Californites HYATT & SMITH, 1905 [**C. merriami*]. Evolute, whorl section trapezoidal, sides flattened, with radial tuberculate ribs which end in strong ventrolateral spines; venter low-arched, nearly smooth (203). *Carn.,* Calif.——FIG. 192,*3*. **C. merriami; 3a,b,* ×1; *3c,* ×2 (203*).

Traskites HYATT & SMITH, 1905 [**Clionites (Traskites) robustus*]. Evolute, whorl section quadrate, with tuberculate radial ribs which extend on venter to median groove (203). *Carn.,* Calif.

T. (Traskites). Ribs coarse, tuberculate. Suture ceratitic with 2 lateral lobes (203).——FIG. 192,*1*. *T. (T.) robustus; 1a,b,* ×0.7; *1c,* ×1 (203*).

T. (Shastites) HYATT & SMITH, 1905 [**Clionites (Shastites) compressus*]. More compressed, involute, ribs and tubercles finer, more dense (203).

——FIG. 192,*6*. **T. (S.) compressus* (HYATT-S.); *6a,b,* ×0.7 (450*).

T. (Stantonites) HYATT & SMITH, 1905 [**Clionites (Stantonites) rugosus*]. More evolute, compressed, with coarse sigmoidal tuberculate ribs and most prominent rows of tubercles on ventrolateral edge, ventral groove aligned by tubercles (203).——FIG. 192,*8*. **T. (S.) rugosus* (HYATT-S.); *8a,b,* ×0.7 (450*).

T. (Neanites) HYATT & SMITH, 1905 [**Clionites*

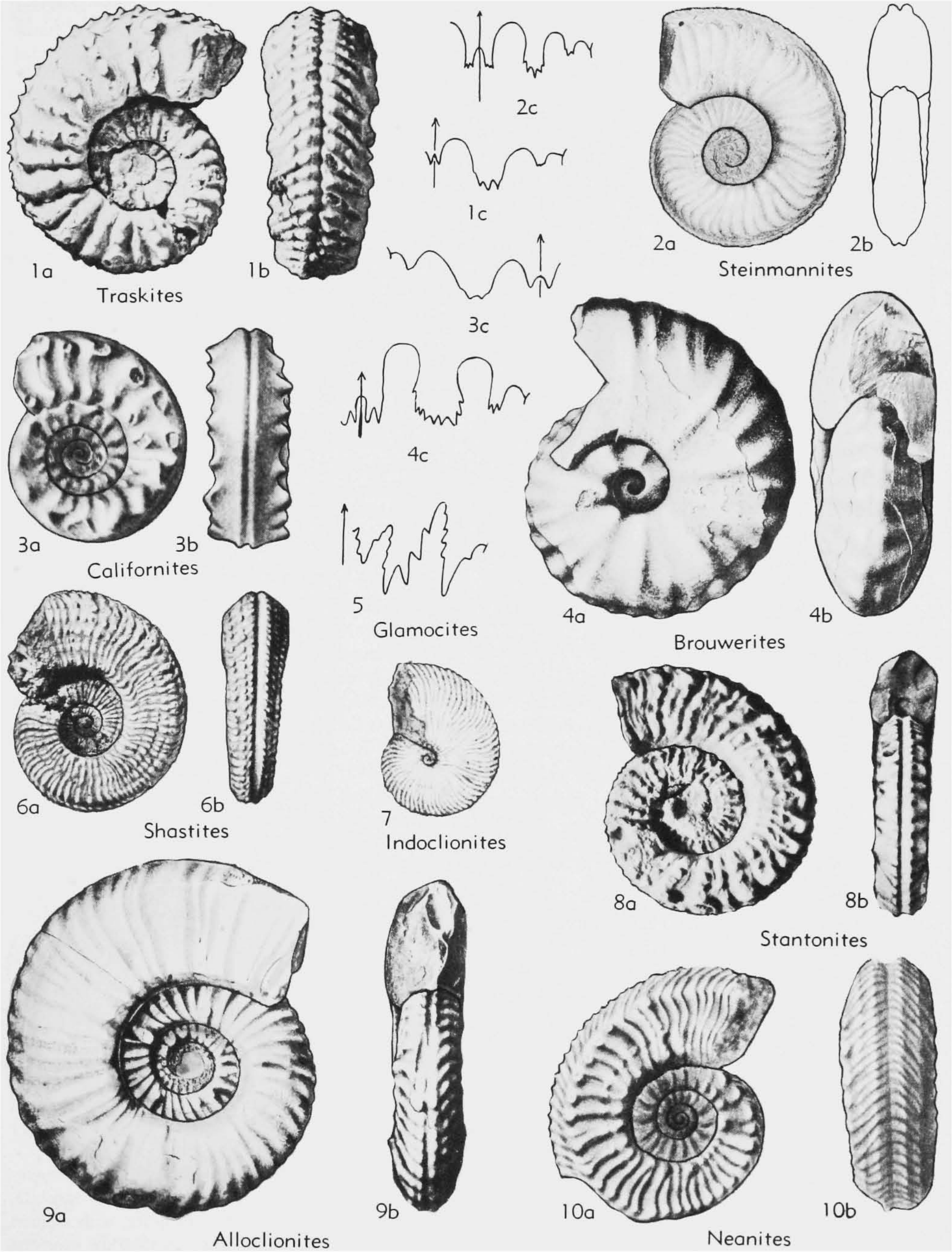


FIG. 192. Clionitidae (p. L160-L162).

(Neanites) californicus]. Evolute, whorl sections subquadrate, sigmoidal tuberculate ribs continuous to shallow median groove, ventrolateral tubercles most prominent (203).——Fig. 192,*10*. **T. (N.) californicus* (Hyatt-S.); *10a,b*, ×1 (450*).

Indoclionites Diener, 1916 [**Clionites gracilis* Diener, 1906]. Involute, compressed conch, whorl sides with fine sigmoidal ribs, bundled at umbilical margin, secondary ribs intercalated at middle of whorl side; tubercles on umbilical margin and ventrolateral area (103). *U.Trias.*, Himalaya.——Fig. 192,*7*. **I. gracilis* (Diener); ×1 (103*).

Steinmannites Mojsisovics, 1893 [**Am. hoernesi* Hauer, 1849; SD Diener, 1915]. Evolute, whorl section subrectangular, nodes on flexuous ribs at umbilical margin and distinct swelling of ribs at ventrolateral margin; median groove on venter with raised crenulate edge (292). *Carn.-Nor.*, Alps-Himalaya-Timor.——Fig. 192,*2*. **S. hoernesi* (Hauer), Nor., Alps; *2a,b*, ×0.3; *2c*, ×0.7 (292*).

Brouwerites Diener, 1923 [**Clionites involutus* Welter, 1914]. Involute, inflated, venter rounded; whorl sides with flexuous ribs ending at prominent node next to median groove; prominent fine strigation (115). *Carn.*, Timor.——Fig. 192,*4*. **B. involutus* (Welter); *4a,b*, ×0.5; *4c*, ×1 (558*).

?Glamocites Diener, 1917 [**G. katzeri*]. Evolute, whorl section subrectangular, venter arched; radial ribs that pass over venter projecting strongly; tubercles on umbilical and ventrolateral edge. Suture with high 2nd lateral saddle (488). *Carn.*, Yugo.——Fig. 192,*5*. **G. katzeri;* ×1 (606*).

Family ARPADITIDAE Hyatt, 1900

Generally evolute, compressed, with median furrow bordered by continuous, smooth or crenulated keels, or edges of siphonal groove simulating keel, or by clavi; sigmoidal ribs and tubercles present. Suture ceratitic to ammonitic (488). *M.Trias. U. Trias.*

Arpadites Mojsisovics, 1879 [**Am. arpadis* Mojs., 1870; SD Hyatt & Smith, 1905]. Compressed, discoidal, evolute; with radial or faintly sigmoidal ribs; ventral keels continuous, smooth; generally umbilical tubercles but lateral and ventrolateral tubercles may occur also. Suture ceratitic with 2 lateral lobes (293). *M.Trias.(Ladin.)-U.Trias.(Carn.)*, Alps-Italy-Balkan-Himalaya-Japan.——Fig. 193,*12*. **A. arpadis* (Mojs.), Ladin., Alps; *12a,b*, ×0.7 (293*).

Hyparpadites Spath, 1951 [**Arpadites liepoldti* Mojsisovics, 1882]. Median groove narrow, adjacent area on venter arched to form simulated keels; prominent umbilical and ventrolateral tubercles; weak radial ribs. Suture ceratitic, with 3 lateral lobes (293). *M.Trias.(Ladin.)*, Alps.——Fig. 193,*6*. **H. liepoldti* (Mojs.); *6a,b*, ×0.5 (293*).

Edmundites Diener, 1916 [**Arpadites rimkinensis* Mojsisovics, 1896]. With sigmoidal, distant primary ribs, weaker secondaries; keels prominent, smooth. Suture ammonitic (295). *M.Trias.(Ladin.)-U.Trias.(Carn.)*, Himalaya.——Fig. 193,*10*. **E. rimkinensis* (Mojs.); *10a,b*, ×1 (295*).

Klipsteinia Mojsisovics, 1882 [**Am. achelous* Münster, 1834; SD Diener, 1915]. With crenulated keels delayed in appearance; lateral tuberculation present or absent (293). *U.Trias.(Carn.)*, Alps.——Fig. 193,*13*. **K. achelous* (Münster); *13a,b*, ×0.7 (293*).

Trachystenoceras Johnston, 1941 [**Arpadites gabbi* Hyatt & Smith, 1905]. Involute, discoidal; median groove bordered by slightly beaded marginal ridges; sides with low folds made up of sigmoidal striae. Suture ceratitic (203). *U.Trias.(Carn.)*, Calif.-Nev.——Fig. 193,*7*. **T. gabbi* (Hyatt-S.); ×1 (203*).

Silenticeras McLearn, 1930 [**Daphnites (Silenticeras) hatae*]. Involute, discoidal, compressed, venter with prominent median groove but no distinct keels; strong growth lines projected (488). *U.Trias. (Carn.)*, B.C.

Dittmarites Mojsisovics, 1893 [**Am. rimosus* Münster, 1841; SD Diener, 1915]. Median groove bordered by prominent continuous keels; sides with falcate ribs projected on ventrolateral area. Suture ammonitic (292). *U.Trias.(Carn.-Nor.)*, Alps-Greece-Himalaya.——Fig. 193,*2*. *D. rimosus* (Münster), Carn., Alps; *2a,b*, ×1 (293*).

Trachypleuraspidites Diener, 1906 [**Arpadites (Trachypleuraspidites) griffithi*]. Like *Dittmarites* but falcate bifurcating ribs multituberculate (103). *U.Trias.(Carn.-Nor.)*, Himalaya-Timor.——Fig. 193,*9*. *T. griffithi* (Diener), Himalaya; *9a,b*, ×0.5 (103*).

Asklepioceras Renz, 1910 [**Arpadites (Dittmarites) segmentatus* Mojsisovics, 1893]. Evolute to involute, discoidal to subglobose; median furrow not bordered by keels; prominent, distant projected constrictions that pass over venter. Suture ceratitic, simple (365). *M.Trias.(Ladin.)-U.Trias.(Carn.)*, Alps-Balkan-AsiaM.-B.C.——Fig. 193,*8*. **A. segmentatum* (Mojs.), Carn., Alps; *8a,b*, ×0.7 (292*).

Muensterites Mojsisovics, 1893 [**Arpadites (Münsterites) ectodus*]. Involute, slightly inflated, venter rounded; median furrow bordered by row of nodes, no continuous keel; also row of nodes on ventrolateral area; nodes decline adorally; ribs broad, low closely spaced, projected (292). *U.Trias.(Carn.)*, Alps.——Fig. 193,*11*. **M. ectodus; 11a,b*, ×1 (292*).

Drepanites Mojsisovics, 1893 [**Arpadites (Drepanites) hyatti;* SD Diener, 1915]. Very involute, compressed, discoidal, venter truncate, with median furrow; sides with sigmoidal ribs that are strongest near periphery, ventrolateral angle serrated. Suture ammonitic (292). *U.Trias.(Nor.)*, Alps-Sicily-Timor.——Fig. 193,*1*. **D. hyatti; 1a,b*, ×0.7; *1c*, ×1 (292*).

Daphnites Mojsisovics, 1893 [**Arpadites (Daphnites) berchtae;* SD Diener, 1915]. Compressed, involute, venter rounded, median furrow with keel-like edge; whorl sides with fine, sinuous, bifurcating, prorsiradiate, projected ribs, usually bundled at umbilical edge. Suture ceratitic (292). *U.Trias.(Nor.)*, Alps-Sicily-Himalaya.——Fig. 193, *3*. *D. ungeri* Mojs., Alps; *3a,b*, ×1; *3c*, ×2 (292*).

Dionites Mojsisovics, 1893 [*Arpadites (Dionites) caesar;* SD Diener, 1915]. Compressed, involute, venter arched, distinct median furrow bordered by clavi; sides with dense, sigmoidal, broad ribs, spiral lines, spiral rows of tubercles; sculpture decreases adorally. Suture ammonitic (292). *U.Trias. (Nor.)*, Alps-Himalaya-Timor.——Fig. 193,*5*. **D. caesar*, Alps; *5a,b*, ×0.25; *5c*, ×0.3 (292*).

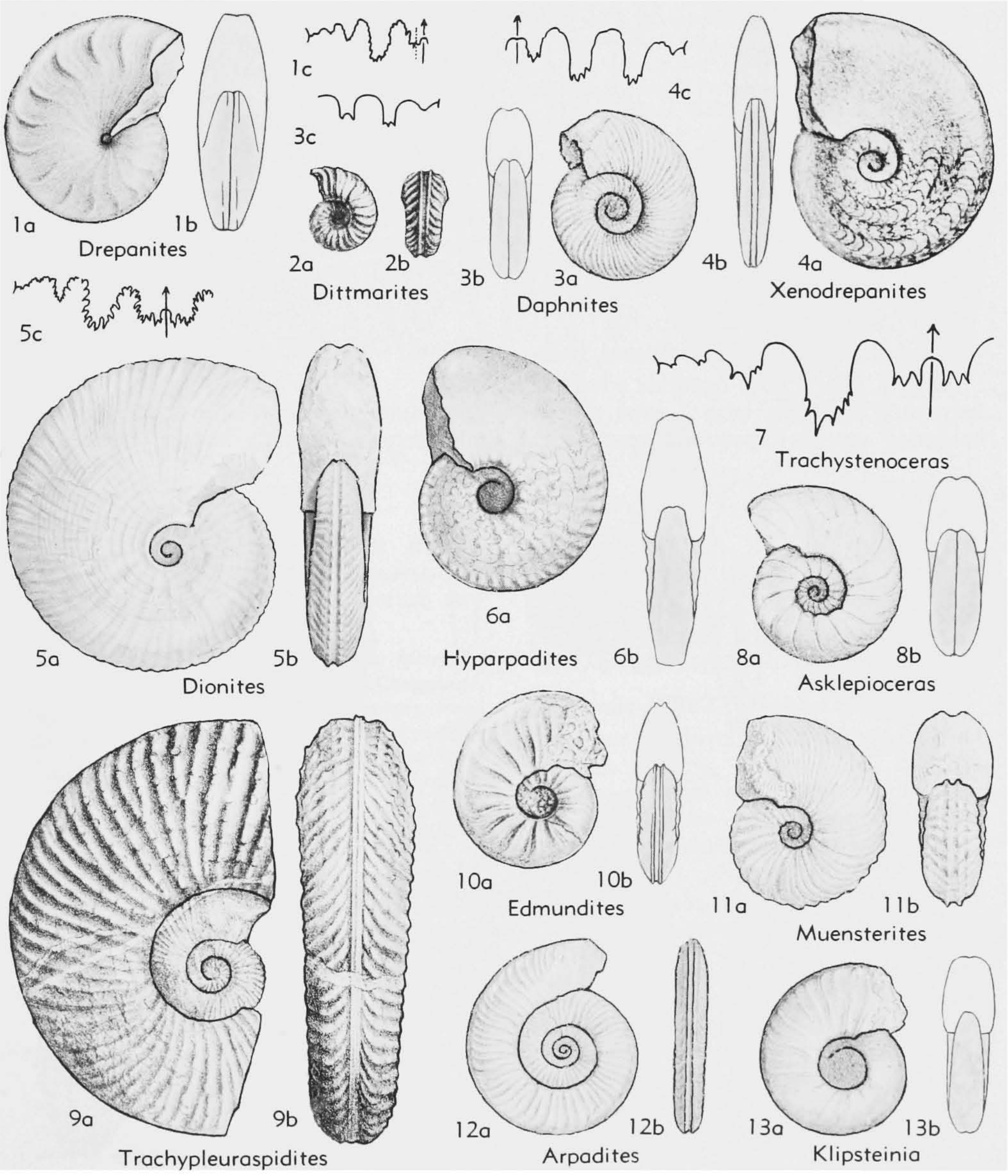


Fig. 193. Arpaditidae (p. L162-L164).

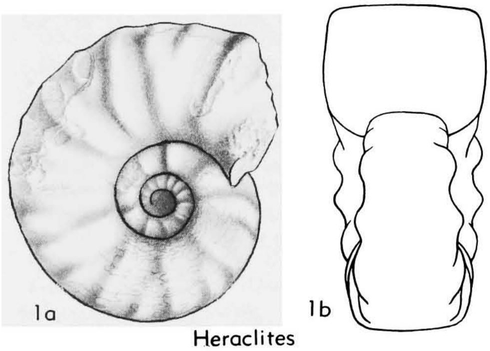


Fig. 194. *Heraclites robustus* (Hauer), U.Trias. (Nor.), Alps; *1a,b*, ×0.25 (p. L164).

Xenodrepanites Diener, 1916 [**Drepanites schucherti* Diener, 1906]. Very compressed, discoidal, more evolute than *Drepanites;* ventral furrow bordered by crenulated keels; sides with low sigmoidal ribs. Suture subammonitic (103). *U.Trias.*, Himalaya.——Fig. 193,*4*. **X. schucherti* (Diener); *4a,b*, ×0.7; *4c*, ×1 (103*).

Family HERACLITIDAE Diener, 1920

Evolute, robust, with quadrate whorl section; early volutions with 2 rows of clavi bordering ventral furrow and ventrolateral row; venter of outer volution smooth, flattened; sides with distant prorsiradiate ribs. Suture subammonitic (488). *U.Trias.*

Heraclites Mojsisovics, 1879 [**Am. robustus* Hauer, 1855; SD Diener, 1915] (292). *Nor.*, Alps-Timor. ——Fig. 194,*1*. **H. robustus* (Hauer); *1a,b*, ×0.25 (292*).

Family LECANITIDAE Hyatt, 1900

Very primitive ammonites, evolute, discoidal, compressed, with goniatitic suture (488). *M.Trias.-U.Trias.*

Lecanites Mojsisovics, 1882 [**Am. glaucus* Münster, 1834]. Essentially smooth, some forms with weak sigmoidal ribs (293). *M.Trias.(Ladin.)-U. Trias.(Carn.)*, Alps-Nev.——Fig. 195,*2*. **L. glaucus* (Münster); *2a,b*, Alps; ×1 (293*).

Badiotites Mojsisovics, 1882 [**Am. eryx* Münster, 1834]. With sigmoidal ribs and smooth siphonal band; venter acutely rounded (293). *M.Trias. (Ladin.)-U.Trias.(Carn.)*, Alps-Greece-Hung.——Fig. 195,*4*. **B. eryx* (Münster); ×1 (293*).

Family CYRTOPLEURITIDAE Diener, 1925

Involute, generally compressed, with narrow furrowed venter which is bordered by

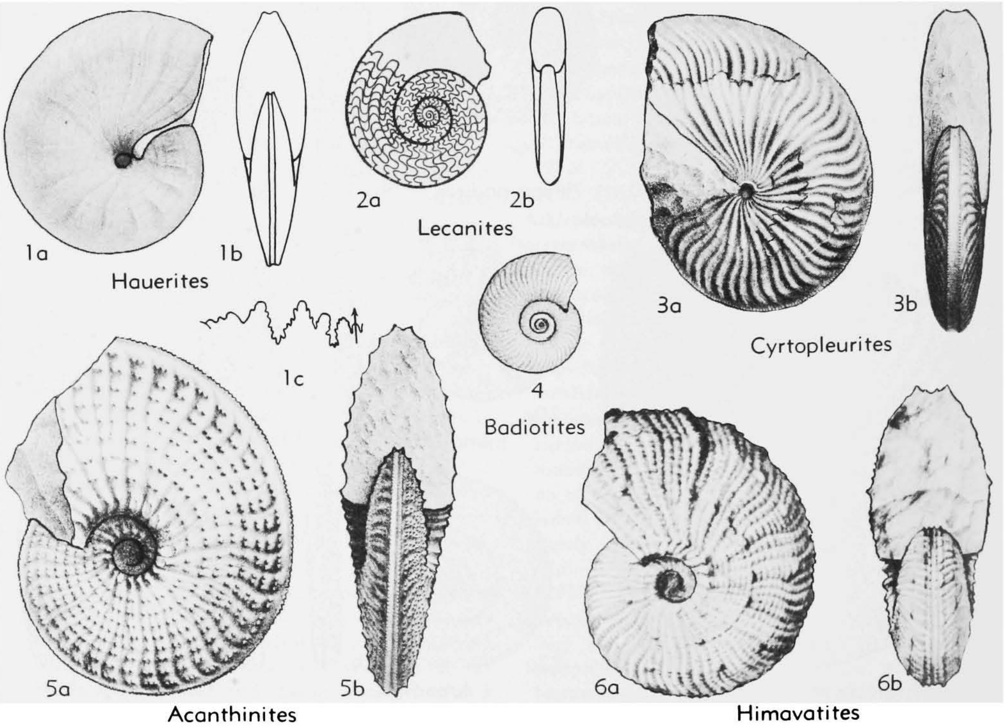


Fig. 195. Lecanitidae, Cyrtopleuritidae (p. L164-L165).

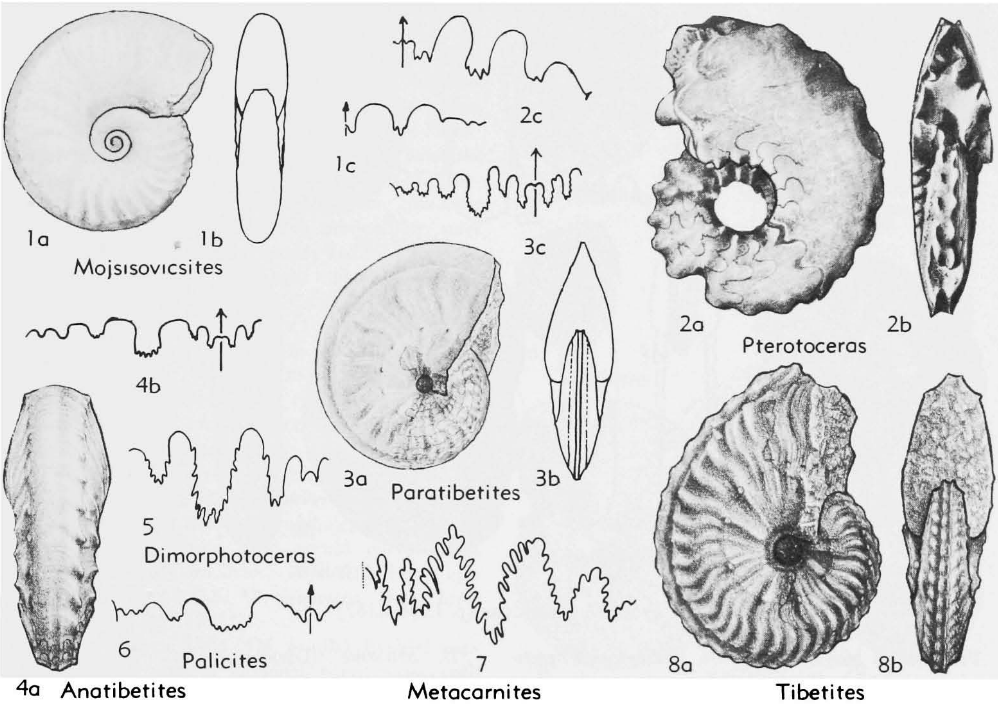


Fig. 196. Tibetitidae (p. L165-L166).

crenulated tubercles or keels or smooth keels; lateral area usually with flexuous ribs and spiral rows of tubercles. Suture ammonitic (488). *U.Trias.*

Cyrtopleurites Mojsisovics, 1893 [**Am. bicrenatus* Hauer, 1846; SD Diener, 1915]. Compressed, involute, umbilicus small, venter narrow; whorl sides with sigmoidal ribs that end in crenulated tubercles at edge of and align ventral furrow; inner whorls with few spiral rows of tubercles which decrease adorally (292). *Carn.-Nor.,* Alps-Sicily-Himalaya-Timor-B.C.——Fig. 195,*3*. **C. bicrenatus* (Hauer), Nor., Alps; *3a,b,* ×0.5 (292*).

Acanthinites Mojsisovics, 1893 [**Cyrtopleurites (Acanthinites) excelsus;* SD Diener, 1915]. Like *Cyrtopleurites* but with numerous lateral, spiral rows of tubercles and continuous serrated keels aligning ventral furrow (292). *U.Trias.(Nor.),* Alps-Himalaya-Timor.——Fig. 195,*5*. **A. excelsus* (Mojs.), Alps; *5a,b,* ×0.5 (292*).

Himavatites Diener, 1906 [**Acanthinites (Himavatites) watsoni*]. Whorl sides with flexuous primary and secondary bifurcating ribs, large nodes on primary ribs in spiral pattern, numerous spiral rows of spines on all ribs; ventral furrow shallow, bordered by spirally elongated tubercles (103). *Nor.,* Himalaya-Timor-B.C.——Fig. 195,*6*. **H. watsoni,* Himalaya-Timor; *6a,b,* ×0.5 (115*).

Hauerites Mojsisovics, 1893 [**Am. rarestriatus* Hauer, 1849; SD Hyatt & Smith, 1905]. With continuous keels bordering ventral furrow; lateral ribs weak, no tubercles (292). *Carn.-Nor.,* Alps-Timor.——Fig. 195,*1*. **H. rarestriatus* (Hauer), Nor., Alps; *1a,b,* ×0.5; *1c,* ×1 (292*).

Family TIBETITIDAE Hyatt, 1900

More or less involute, compressed, venter generally narrow, bordered by clavi or tubercles at some stage; whorl sides with ribs and tubercles. Suture ceratitic to ammonitic with incipient or actual adventitious elements (488). *M.Trias.-U.Trias.*

Tibetites Mojsisovics, 1896 [**T. raylli;* SD Diener, 1915]. Involute, compressed, with narrow venter bordered by 2 rows of clavi; with flexuous lateral ribs and spiral row of nodes at mid-section. Suture ceratitic with incipient adventitious lobule in 1st lateral saddle (295). *U.Trias.(Carn.-Nor.),* Himalaya-Timor.——Fig. 196,*8*. *T. perrinsmithi* Mojs., Nor., Himalaya; *8a,b,* ×1 (295*).

Anatibetites Mojsisovics, 1896 [**Tibetites (Anatibetites) kelvini*]. Like *Tibetites* but venter of body chamber flattened and without clavi (295). *U. Trias.(Carn.-Nor.),* Himalaya-Timor.——Fig. 196, *4*. **A. kelvini,* Nor., Himalaya; *4a,* ×0.7; *4b,* ×1 (295*).

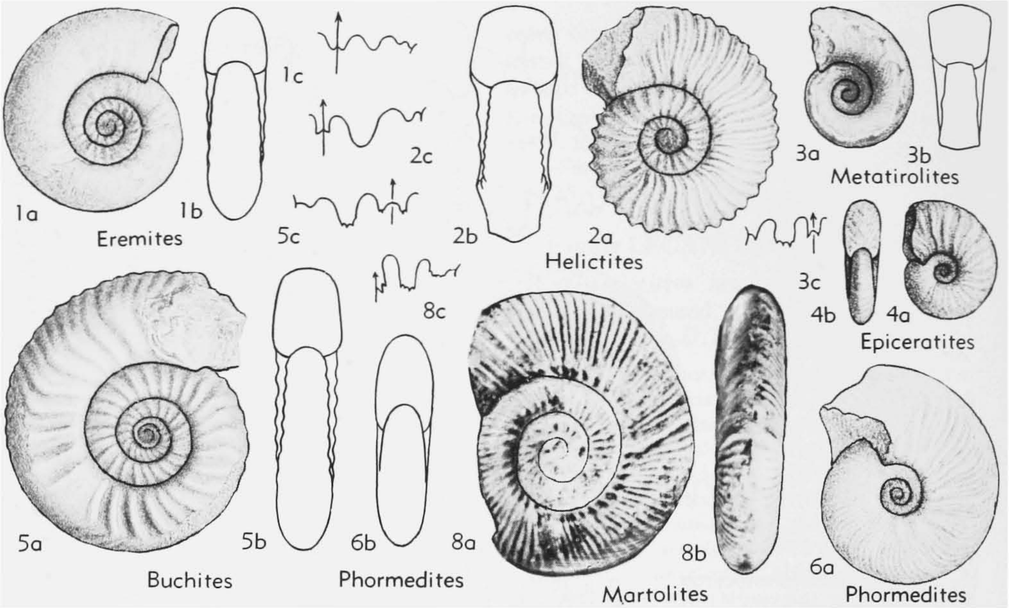


FIG. 197. Buchitidae (p. L166-L167).

Paratibetites MOJSISOVICS, 1896 [**Tibetites (Paratibetites) bertrandi*]. Like *Tibetites* in young; then ventral furrow appears bordered by distinct continuous keels, this followed by stage where ventral groove disappears and venter becomes obtusely rounded; ribbing and tuberculation decrease adorally. Suture ceratitic to ammonitic, more complex than in *Tibetites* (295). *U.Trias.(Carn.-Nor.)*, Himalaya-Timor.——FIG. 196,*3*. *P. adolphi* MOJS., Nor., Himalaya; *3a,b*, ×0.5; *3c*, ×1 (295*).

Neotibetites KRUMBECK, 1913 [**N. weteringi*]. Like *Tibetites* in young with bicarinate venter, changing to carinate venter and then smooth continuous keel-like venter; ribbing and tuberculation decreases adorally. Suture ceratitic, simple (488). *U.Trias. (Carn.-Nor.)*, E.Indies.

Metacarnites DIENER, 1908 [**Carnites (Metacarnites) footei;* SD DIENER, 1915]. Like *Paratibetites* but with a more complex ammonitic suture (105). *U. Trias.(Nor.)*, Himalaya-Timor-B.C.——FIG. 196, *7*. **M. footei*, Himalaya; ×0.5 (606*).

Pterotoceras WELTER, 1915 [**P. arthaberi*]. More or less evolute, compressed, discoidal, with ventral furrow bordered by clavi; with umbilical, lateral, and ventrolateral tubercles which decrease adorally. Suture ceratitic (559). *M.Trias.(Ladin.)-U.Trias. (Carn.)*, Timor-B.C.-Alps.——FIG. 196,*2*. **P. arthaberi*, Ladin., Timor; *2a,b*, ×0.7; *2c*, ×1 (559*).

Dimorphotoceras SPATH, 1951 [**Pterotoceras abnorme* DIENER, 1923]. Like *Pterotoceras* but tuberculation remaining strong to end. Suture ammonitic, with adventitious saddle in ventral lobe (488). *U.Trias.(Carn.-Nor.)*, Alps-Timor.——FIG. 196,*5*. **D. abnorme* (DIENER), Nor., Timor; ×0.5 (115*)

Palicites GEMMELLARO, 1904 [**P. mojsisovicsi*]. Like *Anatibetites*, ventral tubercles disappearing but lateral tubercles persisting to end. Suture ceratitic, simple, with incipient adventitious lobule in 1st lateral saddle (168). *U.Trias.(Carn.)*, Sicily. ——FIG. 196,*6*. **P. mojsisovicsi;* ×0.7 (168*).

Mojsisovicsites GEMMELLARO, 1904 [**M. crassecostatus;* SD DIENER, 1915]. Inner whorls with 2 ventral and 2 ventrolateral rows of nodes, disappearing adorally, outer whorl smooth; venter arched, sides with low folds. Suture ceratitic, simple (168). *U.Trias.(Carn.)*, Sicily.——FIG. 196,*1*. *M. orethensis* GEMM.; *1a-c*, ×0.7 (168*).

Stikinoceras MCLEARN, 1930 [**S. kerri*]. Compressed, evolute, sides flattened and with flexuous ribs; primary ribs slightly enlarged at umbilical edge; node on ventrolateral area, and on ventral shoulder adjoining a smooth venter bearing a thin, low keel. Suture ceratitic (488). *U.Trias.*, B.C.

Family BUCHITIDAE Hyatt, 1900

Generally evolute, with subquadrate to suboval whorls; flattened to rounded venter; sides with radial ribs that may cross venter. Suture ceratitic (488). *U.Trias.*

Buchites MOJSISOVICS, 1893 [**B. aldrovandii*]. Whorls increasing slowly, venter rounded; sides with flexuous projected ribs that end at smooth siphonal band or cross venter. Suture ceratitic (292). *Carn.-Nor.*, Alps-Sicily-Greece-Himalaya.

——Fig. 197,*5*. **B. aldrovandii*, Carn., Alps-Greece; *5a,b*, ×0.7; *5c*, ×1 (292*).

Helictites Mojsisovics, 1879 [**Am. geniculatus* Hauer, 1855; SD Diener, 1915]. Like *Buchites* but flexuous, with bifurcating ribs that cross straight over venter (292). *Carn.-Nor.*, Alps-Himalaya-Timor-Peru.——Fig. 197,*2*. **H. geniculatus* (Hauer), Nor., Alps; *2a,b*, ×1; *2c*, ×2 (292*).

Metatirolites Mojsisovics, 1893 [**Am. foliaceus* Dittmar, 1866]. Whorl section subquadrate, sides slightly divergent, venter broad, flattened; ventrolateral angle with prominent tubercles. Suture ceratitic (450). *Carn.*, Alps-Calif.——Fig. 197,*3*. **M. foliaceus* (Ditt.); *3a,b*, ×1; *3c*, ×1.5 (292*).

Epiceratites Diener, 1915 [**Am. elevatus* Dittmar, 1866]. Involute, venter rounded, smooth; sides with weak radial projected ribs. Suture ceratitic (292). *Carn.-Nor.*, Alps-Greece.——Fig. 197,*4*. **E. elevatus* (Ditt.), Carn., Alps; *4a,b*, ×1.5 (292*).

Phormedites Mojsisovics, 1893 [**P. juvavicus;* SD Diener, 1915]. Like *Epiceratites* but with dense prorsiradiate ribs, bundled at umbilical edge, strongly projected forming deep adoral curve across venter (292). *Carn.-Nor.*, Alps-Sicily-Himalaya-Timor.——Fig. 197,*6*. **P. juvavicus*, Nor., Alps-Timor; *6a,b*, ×1 (292*).

Martolites Diener, 1906 [**M. kraffti*]. Evolute, venter rounded, smooth siphonal band; sides with bifurcating ribs; a few oblique constrictions that cross venter; umbilical tubercles on outer volution. Suture ceratitic (488). *Nor.*, Himalaya.——Fig. 197,*8*. **M. kraffti*; *8a,b*, ×1; *8c*, ×2 (606*).

Eremites Mojsisovics, 1893 [**Trachyceras orientale* Mojs., 1882]. Evolute, smooth, whorls subquadrate, venter rounded; early volutions with 2 rows of ventral tubercles and rursiradiate ribs. Suture ceratitic (292). *Carn.*, Alps.——Fig. 197,*1*. *E. crassitesta* Mojs.; *1a,b*, ×1; *1c*, ×1.5 (292*).

Family THISBITIDAE Spath, 1951

Evolute to involute, compressed, with median continuous keel; whorl sides with falcoid ribs, some constrictions on conch. Suture ceratitic, simple (488). *U.Trias.*

Thisbites Mojsisovics, 1893 [**T. agricolae;* SD Diener, 1915]. Evolute to involute, whorl sides with single and bifurcating falcate ribs which terminate at ventrolateral nodes; venter with smooth keel. Suture simple, goniatitic to ceratitic (292). *Carn.-Nor.*, Alps-Sicily-Himalaya-Timor.——Fig. 198,*3*. **T. agricolae*, Carn., Alps; *3a,b*, ×1 (292*).

Parathisbites Mojsisovics, 1893 [**Am. scaphitiformis* Hauer, 1855; SD Diener, 1915]. Like *Thisbites* but generally more involute, keel more prominent, ribs may cross venter. Suture ceratitic (488). *Nor.*, Alps-Himalaya-Timor-B.C.——Fig. 198,*4*. **P. scaphitiformis* (Hauer), Alps; *4a,b*, ×0.7; *4c*, ×1 (292*).

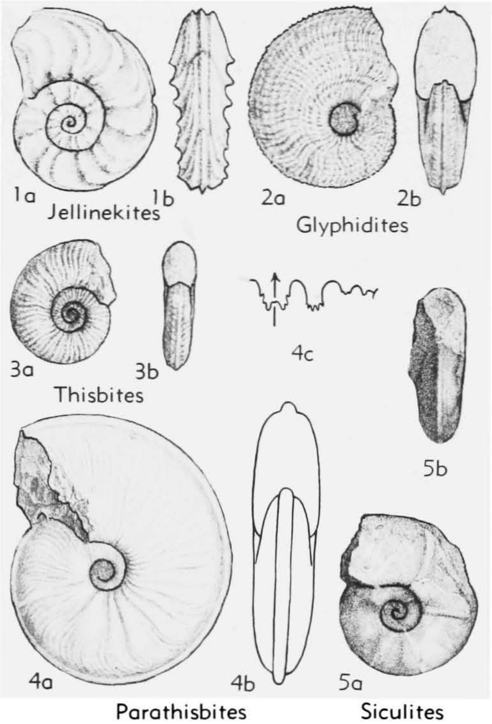


Fig. 198. Thisbitidae (p. L167).

Glyphidites Mojsisovics, 1893 [**G. docens*]. With serrated keel and granular ribs as in *Clydonites* (292). *Nor.*, Alps-Sicily.——Fig. 198,*2*. **G. docens*, Alps; *2a,b*, ×1.5 (292*).

Jellinekites Diener, 1906 [**J. barnardi;* SD Diener, 1915]. Venter tricarinate, marginal keels formed by junction of projected ends of lateral ribs; venter locally interrupted by constrictions; whorl sides with strong single or bifurcating ribs. Suture ceratitic (103). *Carn.-Nor.*, Himalaya-Timor.——Fig. 198,*1*. **J. barnardi*, Himalaya; *1a,b*, ×0.7 (103*).

?**Siculites** Gemmellaro, 1904 [**S. dolomiticus;* SD Diener, 1915]. More or less involute, compressed, venter arched with slight keel; with constrictions and in some species spiral striations. Suture ceratitic (488). *Carn.*, Sicily.——Fig. 198,*5*. **S. dolomiticus*; *5a,b*, ×1 (168*).

Family NORIDISCITIDAE Spath, 1951

Evolute, compressed, discoidal, with truncated venter and sharp ventrolateral shoulders. Suture ceratitic (488). *U.Trias.*

Noridiscites Spath, 1951 [**Ceratites viator* Mojsisovics, 1893]. *Nor.*, Alps.——Fig. 199,*1*. **N. viator* (Mojs.); *1a,b*, ×0.7; *1c*, ×1.5 (292*).

Family DISTICHITIDAE Diener, 1920

Evolute, compressed, generally robust;

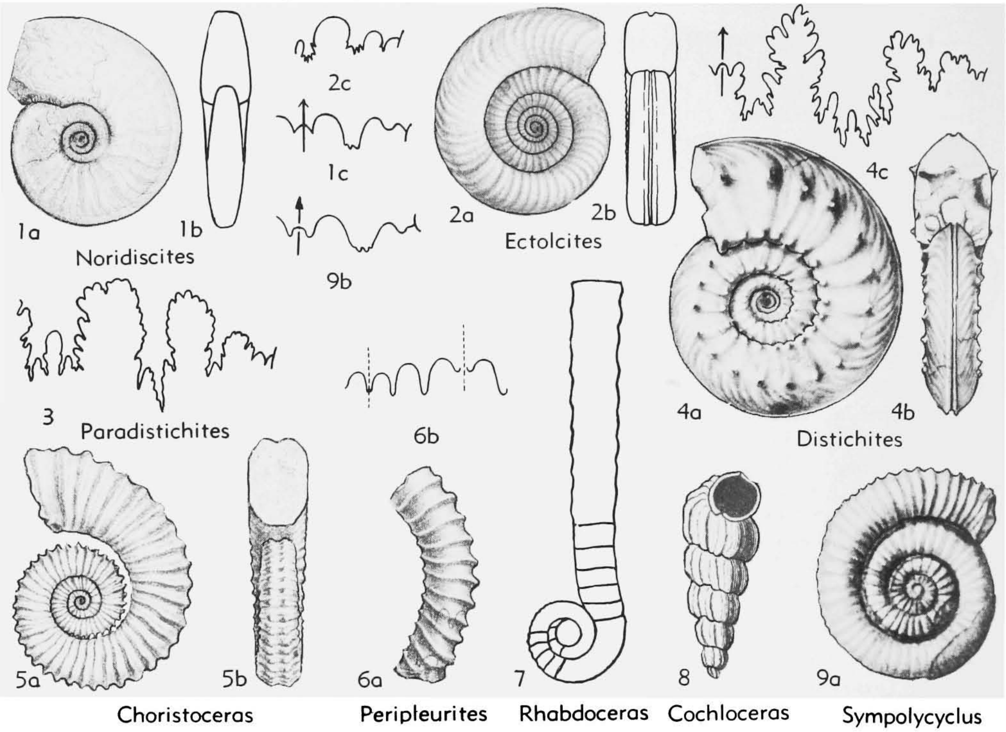


FIG. 199. Noridiscitidae, Distichitidae, Choristoceratidae, Cochloceratidae (p. L167-L169).

venter with median furrow bordered by smooth, low, continuous keel; whorl sides with ribs that bend sharply forward on ventrolateral area, ribs may be tuberculate. Suture ceratitic to ammonitic (488). *U. Trias.*

Distichites MOJSISOVICS, 1893 [**D. megacanthus;* SD DIENER, 1915]. Generally with row of nodes on umbilical and ventrolateral areas. Suture ammonitic (292). *Carn.-Nor.,* Alps-Himalaya-Timor-B.C.——FIG. 199,*4*. **D. megacanthus,* Nor., Alps-Timor; *4a,b,* ×0.25; *4c,* ×0.7 (115*).

Paradistichites DIENER, 1916 [**Distichites ectolcitiformis* DIENER, 1906]. Like *Distichites* but more involute, sculpture more delicate; saddles of suture less serrated (103). *U.Trias.,* Himalaya-Timor.——FIG. 199,*3*. **P. ectolcitiformis* (DIENER); ×1 (103*).

Ectolcites MOJSISOVICS, 1893 [**Am. pseudoaries* HAUER, 1849; SD DIENER, 1915]. Widely umbilicate, with subquadrate whorl section, rounded shoulders. Suture ceratitic to subammonitic (292). *Carn.-Nor.,* Alps-Himalaya-Timor.——FIG. 199,*2*. **E. pseudoaries* (HAUER), Nor., Alps; *2a,b,* ×0.5; *2c,* ×1 (292*).

Family CHORISTOCERATIDAE Hyatt, 1900

Evolute ammonites that may become uncoiled or straight in outer volutions; whorl sides with radial ribs that pass over venter; ventral furrow present in some forms. Suture simple, ceratitic or goniatitic (488). *U. Trias.*

Choristoceras HAUER, 1865 [**C. marshi*]. Very evolute, outer whorl tending to uncoil, whorl section subquadrate, sides with strong radial ribs that may cross shallow ventral furrow; generally tubercles on ribs at ventrolateral area. Suture goniatitic to simple ceratitic (292). *Carn.-Rhaet.,* Alps-Timor-B.C.-Calif.-Nev.——FIG. 199,*5*. **C. marshi,* Rhaet., Alps; *5a,b,* ×1 (292*).

Hannaoceras TOMLIN, 1931 [*pro Polycyclus* MOJSISOVICS, 1893 (*non* LAMARCK, 1815; =*Smithoceras* HANNA, 1924, *non* DIENER, 1907)] [**Am. nasturtium,* DITTMAR, 1866] [=*Polysphinctoceras* SPATH, 1934 (obj.)]. Widely umbilicate, compressed, with radial ribs passing over venter, intercostal area narrow. Suture goniatitic or ceratitic. *Carn.-Nor.,* Alps-Sicily-Balkan-Cyprus-Timor-Calif.-Nev.

H. (Hannaoceras). Ribs become more widely spaced and thick on outer volution, no ventral furrow (292).

H. (Sympolycyclus) Spath, 1951 [**Polycyclus nodifer* Hyatt & Smith, 1905]. More compressed and with shallow ventral groove at some stage (203). *Carn.,* Calif.——Fig. 199,*9*. **H. (S.) nodifer* (Hyatt-S.); *9a,* ×1; *9b,* ×2 (203*).

Peripleurites Mojsisovics, 1893 [**Choristoceras (Peripleurites) roemeri;* SD Diener, 1915]. Ventral groove only on inner whorls, ribs continuous across venter; conch not coiled in one plane, strongly uncoiled. Suture goniatitic (292). *Nor.,* Alps-Hung.——Fig. 199,*6*. **P. roemeri,* Alps; *6a,* ×1; *6b,* ×2 (292*).

Rhabdoceras Hauer, 1860 [**R. suessi*]. Straight or curved, only larval portion coiled; coarse ribs encircle conch. Suture goniatitic (292). *Nor.,* Alps-Sicily-Hung.-Indon.-Calif.-Peru.——Fig. 199,*7*. **R. suessi,* Alps-Sicily-Indon.-Peru; ×10 (641*).

Family COCHLOCERATIDAE Hyatt, 1900

Turriliticones with radial ribs. Suture goniatitic (488). *U.Trias.*

Cochloceras Hauer, 1860 [**C. fischeri*] (292). *Nor.,* Alps-Timor.——Fig. 199,*8*. **C. fischeri,* Alps; ×1 (743*).

Paracochloceras Mojsisovics, 1893 [**Cochloceras canaliculatum* Hauer, 1860; SD Diener, 1915]. Suture of coiling with smooth band, umbilical area generally smooth (292). *Nor.,* Alps.

Superfamily TROPITACEAE Mojsisovics, 1875

[*nom. transl.* Mojs., 1896 (*ex* Tropitidae Mojs., 1875)]

Involute to evolute generally ornamented ammonoids with ribs and/or nodes. Venter may bear keel, be smooth, or crossed by ribs. Suture generally ammonitic but ceratitic or goniatitic in some offshoots. Body chamber long. *M.Trias.-U.Trias.*

Family TROPITIDAE Mojsisovics, 1875

Conch involute to evolute, subspherical to discoidal, body chamber long; ventral keel and bordering furrows present, in some forms with keel appearing late; surface with ribs, nodes, spines or smooth. Suture generally ammonitic but may be ceratitic or goniatitic (488). *U.Trias.*

Tropites Mojsisovics, 1875 [**Am. subbullatus* Hauer, 1849; SD Smith, 1904]. Whorl shape cadicone, venter broad, arched, with keel and bordering furrows; umbilical shoulder sharply rounded; umbilicus deep and wide; whorl sides with prorsiradiate ribs and umbilical nodes; final whorl contracting; spiral lines on shell. Suture ammonitic (450). *Carn.-Nor.,* Alps-Himalaya-Timor-Alaska-B.C.-Calif.-Nev.——Fig. 200,*6*. **T. subbullatus* (Hauer), Carn., Alps-Himalaya-Timor-Calif., *6a,b,* ×0.7; *6c,* ×1 (292*).

Discotropites Hyatt & Smith, 1905 [**Am. sandlingensis* Hauer, 1850] [=*Eutomoceras* Mojsisovics, 1879 (*non* Hyatt, 1877)]. Involute compressed, discoidal, with acutely rounded venter and high hollow keel without bordering furrows; whorl sides with sigmoidal ribs, small umbilical tubercles and spiral lines. Suture ammonitic (203). *Carn.,* Alps-Sicily-Himalaya-Hung. - ?Indochina - Alaska-Calif.——Fig. 200,*3*. **D. sandlingensis* (Hauer), Alps-Sicily-Calif.; *3a-c,* ×0.5 (292*).

Anatropites Mojsisovics, 1893 [**Tropites (Anatropites) spinosus;* SD Diener, 1915]. With spines instead of nodes on umbilical shoulder, at least on early whorls; conch more compressed and less extreme in cross section (292). *Carn.,* Alps-Sicily-Himalaya-Timor-Calif.——Fig. 200,*10*. **A. spinosus,* Alps; *10a,b,* ×1 (292*).

Paratropites Mojsisovics, 1893 [**Am. saturnus* Dittmar, 1866; SD Diener, 1915]. Involute, laterally compressed; mature and early stages similar (203). *Carn.,* Alps-Sicily-Italy-Yugo.-Hung.-Himalaya-Indochina-Timor-Calif.——Fig. 200,*9*. **P. saturnus* (Dittmar), Alps; *9a,b,* ×1 (292*).

Gymnotropites Hyatt & Smith, 1905 [**Paratropites (Gymnotropites) americanus*]. Like *Paratropites* but with smooth shell (203). *Carn.,* Calif.

Paulotropites Mojsisovics, 1893 [**Am. janus* Dittmar, 1866; SD Diener, 1915]. No umbilical tubercles and with paulostome constriction on body chamber (292). *Carn.,* Alps-Sicily-Calif.——Fig. 200,*5*. **P. janus* (Dittmar), Alps; *5a,b,* ×1 (292*).

Microtropites Mojsisovics, 1893 [**Am. galeolus* Hauer, 1860; SD Diener, 1915]. Dwarfed, involute forms; sculpture tending to become obsolete; body chamber leaving regular spiral, becoming contracted (292). *Carn.,* Alps-Sicily-Calif.——Fig. 200,*4*. **M. galeolus* (Hauer), Alps; *4a,b,* ×1 (292*).

Hoplotropites Spath, 1929 [*pro Margarites* Mojsisovics, 1889 (*non* Gray, 1847)] [**Am. jokelyi* Hauer, 1855; SD Diener, 1915]. Evolute, whorl section subrectangular, venter broad, rounded, with keel; whorl sides with spines on ribs at umbilical or ventral shoulder or both. Suture ammonitic (292). *Carn.,* Alps-Sicily-Himalaya-?Indochina-Timor-Alaska-Calif.——Fig. 200,*8*. **H. jokelyi* (Hauer), Alps-Sicily-Alaska-Calif.; *8a,b,* ×0.7; *8c,* ×0.3 (633*).

Margaritropites Diener, 1916 [**Anatropites margaritiformis* Diener, 1906]. Like *Hoplotropites* but with large true umbilical tubercles and furrows bordering keel very low (103). *Carn.,* Himalaya.——Fig. 200,*7*. **M. margaritiformis* (Diener) *7a,b,* ×0.7 (103*).

Timorotropites Diener, 1916 [**Tropites dubiosus* Welter, 1914]. Involute, globose, venter arched; keel appearing late in ontogeny; whorl sides with

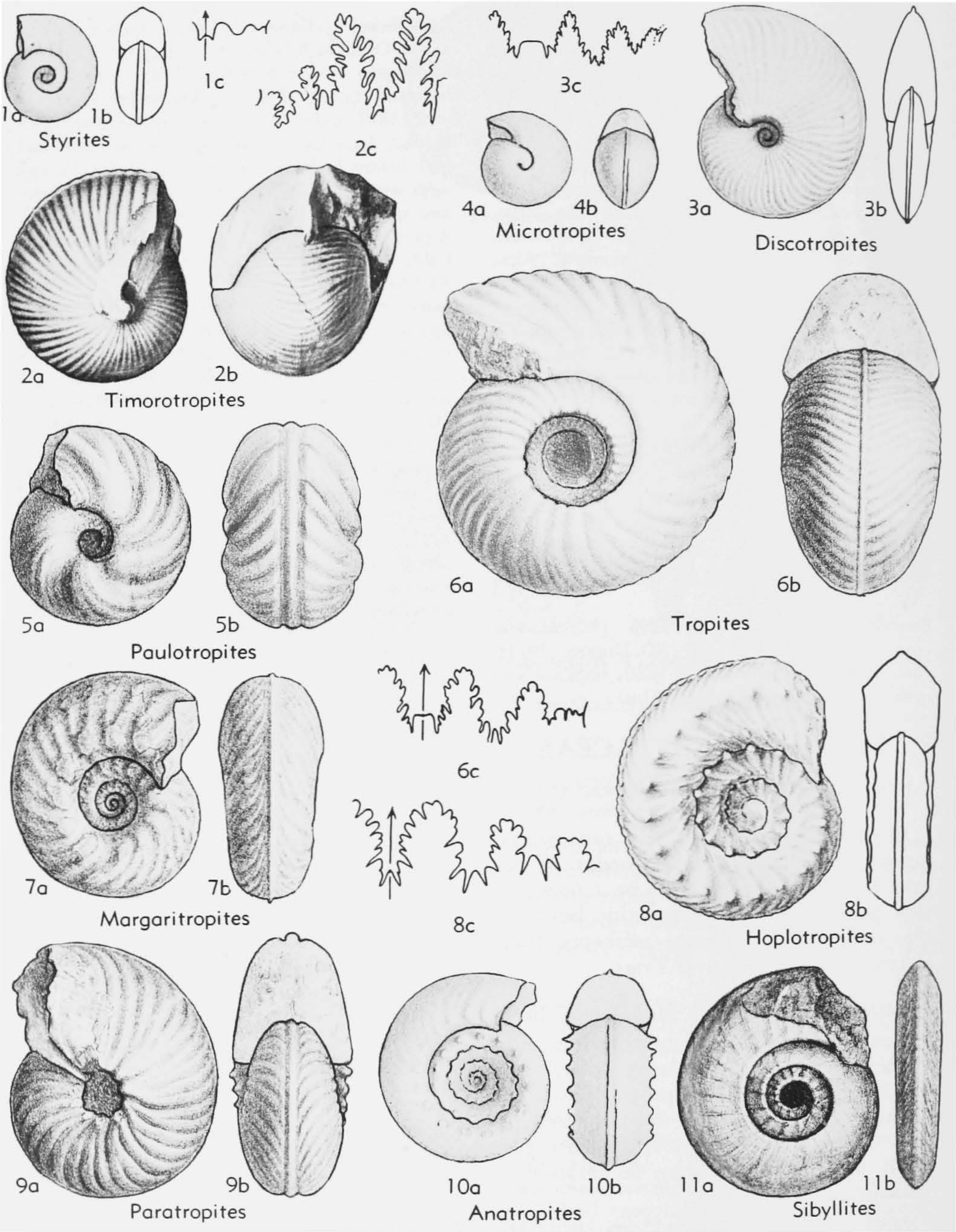


FIG. 200. Tropitidae (p. L169-L171).

radial single and bifurcating ribs and spiral lines. Suture ammonitic but more digitate than in typical tropitids (558). *U.Trias.*, Timor.——FIG. 200,*2*. **T. dubiosus* (WELTER); *2a,b*, ×0.7; *2c*, ×1 (558*).

Styrites MOJSISOVICS, 1893 [**S. tropitiformis*; SD DIENER, 1915]. Smooth, small, evolute, compressed, discoidal; venter acute with prominent keel; body chamber contracting. Suture goniatitic (292). *Carn.*, Alps-Hung.-Sicily-Timor.——FIG. 200,*1*. **S. tropitiformis*, Alps; *1a,b*, ×1; *1c*, ×2 (292*).

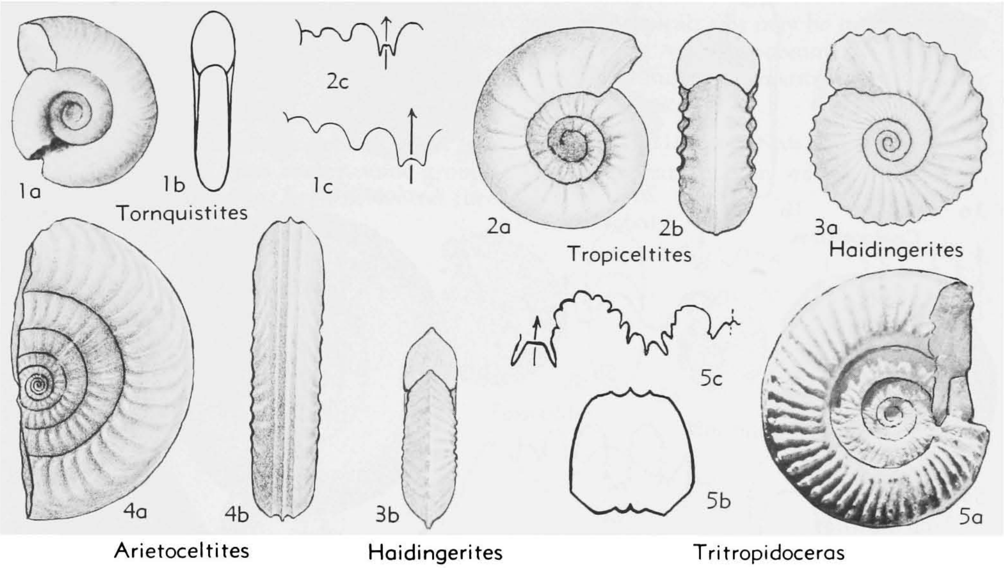


FIG. 201. Tropiceltitidae (p. L171).

Sibyllites MOJSISOVICS, 1893 [**S. tenuispinatus;* SD HYATT & SMITH, 1905]. Evolute, compressed, inner whorls with nodes and ribs on whorl sides, venter rounded; venter on outer whorl becoming acute with a blunt keel, commonly combined with decline in ornamentation. Suture ammonitic (292). *Carn.,* Alps.——FIG. 200,*11*. **S. tenuispinatus* (MOJS.); *11a,b,* ×1 (292*).

Family TROPICELTITIDAE Spath, 1951

Widely umbilicate, allied to Tropitidae, with ventral keel generally on smooth venter; whorl sides with ribs and some nodes; body chamber long. Suture usually simple (488). *U.Trias.*

Tropiceltites MOJSISOVICS, 1893 [**T. rotundus;* SD HYATT & SMITH, 1905]. Whorl section subquadrate, venter broadly rounded, smooth, with median keel but no aligning furrows; whorl sides with radial ribs that bend adorally on ventral shoulder. Suture goniatitic (292). *Carn.,* Alps-Calif.——FIG. 201,*2*. **T. rotundus,* Alps; *2a,b,* ×1; *2c,* ×1.5 (292*).

Arnioceltites MOJSISOVICS, 1893 [**Am. caducus* DITTMAR, 1866; SD DIENER, 1915]. Like *Tropiceltites* but lateral ornamentation becoming obsolescent on outer whorl (292). *Carn.-Nor.,* Alps-Sicily-?Calif.

Arietoceltites DIENER, 1916 [**Tropiceltites arietitoides* DIENER, 1906]. Very evolute forms with lateral sculpture strong and deep furrows bordering ventral keel. Suture simple, ceratitic (103). *Carn.,* Himalaya-Alps.——FIG. 201,*4*. **A. arietitoides* (DIENER), Himalaya; *4a,b,* ×0.5 (103*).

Tritropidoceras SCHENK, 1935 [**T. packardi*]. Whorl section subquadrate, with tuberculate prorsiradiate ribs that curve sharply adorally on ventral shoulder; venter with prominent keel bordered by furrows. Suture weakly ammonitic (488). *Carn.,* Ore.——FIG. 201,*5*. **T. packardi; 5a,* ×0.7; *5b,* ×1; *5c,* ×1.5 (699*).

Haidingerites MOJSISOVICS, 1893 [**Am. acutinodis* HAUER, 1860]. Evolute, discoidal, with convergent whorl sides; venter acute and with spirally elongated nodes; whorl sides with radial ribs that terminate at ventral nodes (292). *Carn.,* Alps.——FIG. 201,*3*. **H. acutinodis* (HAUER); *3a,b,* ×1 (292*).

Tornquistites HYATT & SMITH, 1905 [**T. evolutus*]. Evolute, compressed, whorl sides flattened, venter narrowly rounded; with distinct keel on inner whorls but only faint thin elevation on outer whorl; ornamented with fine sigmoidal ribs that cross venter. Suture goniatitic to weakly ceratitic (203). *Carn.,* Calif.——FIG. 201,*1*. **T. evolutus; 1a,b,* ×1; *1c,* ×3 (203*).

Family CELTITIDAE Mojsisovics, 1893

Widely umbilicate with radial or prorsiradiate ribs that may or may not pass over the venter; body chamber very long. Suture generally simple (488). *M.Trias.-U.Trias.*

Celtites MOJSISOVICS, 1882 [**Trachyceras epolensis* MOJS., 1878; SD HYATT & SMITH, 1905]. Whorl section subquadrate, venter arched, smooth; sides with numerous fine prorsiradiate ribs. *M.Trias. (Ladin.),* Alps.——FIG. 202,*4*. **C. epolensis* (MOJS.); ×1 (293*).

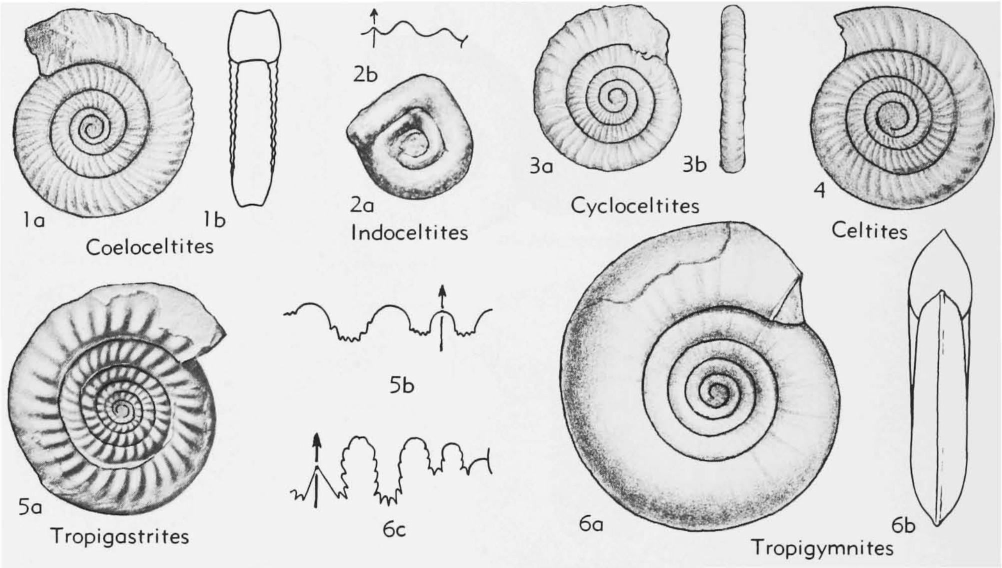


Fig. 202. Celtitidae (p. L171-L172).

Orthoceltites Spath, 1951 [***Goniatites buchii* Klipstein, 1843 (*non* de Verneuil; =*Aganides klipsteini* d'Orbigny, 1850)]. Like *Celtites* but with radial ribs and more rapid coiling of conch (488). *U.Trias.(Carn.)*, Alps.

Cycloceltites Mojsisovics, 1893 [***Celtites (Cycloceltites) arduini*; SD Diener, 1915]. With fine and close ribs continuous across venter except in young; also with regular flared ribs. *U.Trias. (Carn.-Nor.)*, Alps.——Fig. 202,*3*. **C. arduini*, Nor., Alps; *3a,b*, ×0.7 (292*).

Otoceltites Diener, 1916 [***Celtites perauritus* Diener, 1908]. With ribs interrupted along venter by narrow, smooth zone and with distinct flared ribs that pass over venter uninterrupted. Suture goniatitic. *M.Trias.(Ladin.)*, Himalaya.

Indoceltites Diener, 1919 [***Celtites trigonalis* Diener, 1908]. With trigonal coiling, faint ornamentation confined to apertural end of outer whorl. Suture goniatitic. *M.Trias.(Ladin.)*, Himalaya.——Fig. 202,*2*. **I. trigonalis* (Diener); *2a*, ×1; *2b*, ×1.5 (105*).

Coeloceltites Spath, 1951 [***Am. rectangularis* Hauer, 1860]. Venter and sides flattened; venter with longitudinal striations, tending to become concave and bordered by distinct subtuberculate ventrolateral edges. *U.Trias.(Carn.)*, Balkan.——Fig. 202,*1*. **C. rectangularis* (Hauer); *1a,b*, ×1 (292*).

Tropigastrites Smith, 1914 [***T. trojanus*]. Widely umbilicate, whorl section depressed to compressed, whorl sides convergent, venter tending to become acute; with umbilical prorsiradiate ribs. Suture ceratitic or weakly ammonitic (449). *M.Trias. (Anis.)*, Nev.-Alps-Balkan.——Fig. 202,*5*. **T. trojanus*, Nev.; *5a*, ×0.7; *5b*, ×2 449*).

Tropigymnites Spath, 1951 [***Sibyllites planorbis* Hauer, 1896]. More compressed than *Tropigastrites*, venter carinate, whorl sides with weak radial ribs. *M.Trias.(Anis.)*, Alps-Balkan-Himalaya-Nev.——Fig. 202,6. **T. planorbis* (Hauer), Yugo.; *6a,b*, ×0.7; *6c*, ×1 (633*).

Family METASIBIRITIDAE Spath, 1951

Small, evolute ammonites derived from Celtitidae, with bifurcating ribs that cross venter, generally tuberculate. Suture simple, ceratitic to goniatitic (488). *U.Trias.*

Metasibirites Mojsisovics, 1896 [***Am. spinescens* Hauer, 1855]. Whorl section rounded, generally depressed, venter arched; with bifurcating ribs and usually umbilical nodes (292). *Nor.*, Alps-Peru.——Fig. 203,*2*. **M. spinescens* (Hauer), Alps; *2a,b*, ×1; *2c*, ×2 (292*).

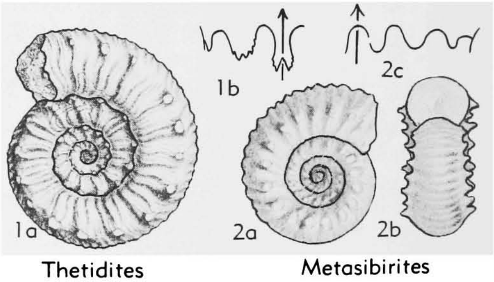


Fig. 203. Metasibiritidae (p. L172).

Thetidites Mojsisovics, 1896 [***T. huxleyi*; SD Diener, 1915]. Differs from *Metasibirites* in that ribs bifurcate at ventrolateral nodes rather than lower on whorl side. Suture simple, ceratitic (295). *Nor.*, Himalaya-Timor.——FIG. 203,1. *T. huxleyi, Himalaya; 1a, ×0.7; 1b, ×1 (295*).

Family HALORITIDAE Mojsisovics, 1893

Subglobose, involute, commonly with lateral ribs that may cross venter, some groups also with nodes on ribs; keels or ventral furrows not typical; ribs may be interrupted on venter; last volution commonly excentric. Suture ammonitic, ceratitic, or goniatitic (488). *U.Trias.*

Subfamily HALORITINAE Mojsisovics, 1893

Spiral ornamentation weak or absent. *U. Trias.*

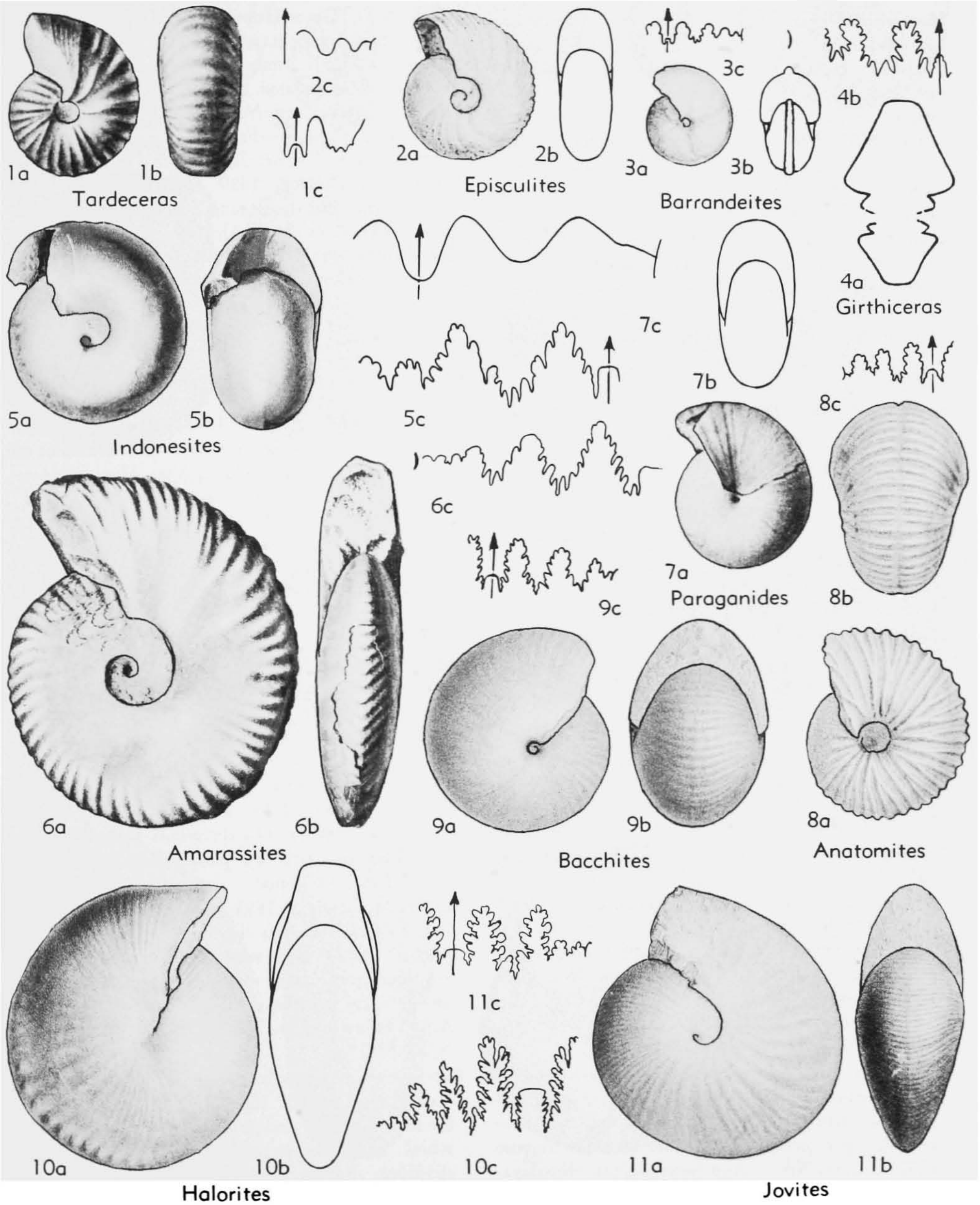


FIG. 204. Haloritidae (p. L174-L176).

Halorites Mojsisovics, 1879 [**Am. ramsaueri* Hauer, 1846; SD Hyatt & Smith, 1905]. Involute, compressed, subglobose, venter rounded, sides convex; with radial ribs or rows of tubercles diagonal across shell; body chamber long, contracted, excentric. Suture ammonitic (292). *Nor.*, Alps-Sicily-Himalaya-Timor-Calif.——Fig. 204,*10*. **H. ramsaueri* (Hauer), Alps; *10a,b*, ×0.3; *10c*, ×0.7 (292*).

Homerites Mojsisovics, 1893 [**Am. semiglobosus* Hauer, 1855; SD Hyatt & Smith, 1905]. Small, involute, globose, with excentric outer volution; phragmocone like *Halorites*, body chamber with slight ventral keel and radial dichotomous ribs that usually terminate at spines on ventral shoulder. Suture subammonitic (292). *Carn.*, Alps-Calif.——Fig. 205,*2*. **H. semiglobosus* (Hauer); *2a,b*, ×0.7 (633*).

Jovites Mojsisovics, 1893 [**Tropites dacus* Mojs., 1875; SD Diener, 1915]. Like *Halorites* but with faint keel-like ridge on venter and fewer elements in suture (292). *Carn.-Nor.*, Alps-Sicily-Balkan-Himalaya-Timor-Calif.——Fig. 204,*11*. **J. dacus* (Mojs.), Carn., Alps; *11a,b*, ×0.5; *11c*, ×1.5 (292*).

Bacchites Smith, 1927 [**Juvavites bacchus* Mojsisovics, 1893]. Subspherical, with closed umbilicus, surface almost smooth but with faint transverse ribs, vestigial constrictions, and faint threadlike keel ridge. Suture ammonitic (450). *Carn.*, Alps-Timor-Calif.——Fig. 204,*9*. **B. bacchus* (Mojs.); *9a,b*, ×0.7; *9c*, ×1 (292*).

Amarassites Welter, 1914 [**A. egrediens;* SD Diener, 1915]. Like *Halorites* but more compressed, umbilicus more open, excentric; venter fastigate, sigmoidal ribs that cross venter (558). *Nor.*, Timor-Alps.——Fig. 204,*6*. **A. egrediens*, Timor; *6a,b*, ×0.7; *6c*, ×1 (558*).

Indonesites Welter, 1914 [**I. dieneri*]. Very involute, inflated, with broad rounded venter and faint keel; with faint ribs, outer volution excentric. Suture degenerate (558). *U.Trias.*, Timor.——Fig. 204,*5*. **I. dieneri; 5a,b*, ×0.5; *5c*, ×1 (558*).

Juvavites Mojsisovics, 1879 [**Am. ehrlichi* Hauer, 1855; SD Hyatt & Smith, 1905]. Involute, subglobose, some flattened to subdiscoidal, venter rounded; whorl sides with dichotomous ribs that pass over venter but may be interrupted along venter. Suture ammonitic (292). *Carn.-Nor.*, Alps-Sicily-Himalaya-Timor-Indochina - Alaska - B. C. - Calif.——Fig. 205,*5*. **J. ehrlichi* (Hauer), Nor., Alps; *5a,b*, ×0.7 (633*).

Anatomites Mojsisovics, 1893 [**Juvavites (Anatomites) rotundus;* SD Diener, 1915]. Like *Juvavites* but with periodic constrictions that pass over venter; ribs interrupted on venter by slight furrow (292). *Carn.-Nor.*, Alps-Sicily-Balkan-Himalaya-Timor-Kotelny-Alaska-Calif.-Mex.——Fig. 204,*8*. **A. rotundus*, Carn., Alps; *8a-c*, ×1 (292*).

Griesbachites Mojsisovics, 1896 [**Am. medleyanus* Stoliczka, 1865]. Like *Juvavites* but with clavi or nodes on ventrolateral area of the phragmocone; no constrictions (295). *Carn.-Nor.*, Alps-Himalaya-Timor-B.C.——Fig. 205,*12*. **G. medleyanus*, Carn., Himalaya; *12a,b*, ×0.5 (295*).

Molengraaffites Welter, 1914 [**Juvavites (Griesbachites) hanni* Mojs., 1896; SD Diener, 1915]. Like *Griesbachites* but with constrictions (558). *Carn.-Nor.*, Timor-Himalaya.

Gonionotites Gemmellaro, 1905 [**G. italicus;* SD Diener, 1915]. Inner volutions like *Juvavites*, body chamber inflated, smooth, with only traces of ribs (168). *Carn.-Nor.*, Sicily-Alps-Himalaya-Timor-B.C.-Calif.——Fig. 205,*3*. *G. megasthenis* Diener, Nor., Timor; *3a,b*, ×0.5 (115*).

Heinrichites Diener, 1920 [**H. paulckei*]. Like *Gonionotites* but developing fine spiral ornamentation (488). *Carn.-Nor.*, Alps.

Guembelites Mojsisovics, 1896 [**Heraclites (Gümbelites) jandianus*]. With smooth flattened venter; whorl sides with sigmoidal ribs that end at clavi on ventral shoulder; body chamber short. Suture ammonitic (295). *Nor.*, Himalaya-Timor.——Fig. 205,*11*. **G. jandianus*, Himalaya; *11a,b*, ×1 (295*).

Parajuvavites Mojsisovics, 1896 [**P. blanfordi;* SD Diener, 1915]. Like *Juvavites* but umbilicus of last volution excentric (295). *Nor.*, Himalaya.——Fig. 205,*4*. **P. blanfordi;* ×0.5 (295*).

Malayites Welter, 1914 [**M. informis;* SD Diener, 1915]. Like *Juvavites* but with spiral lineation (558). *Carn.-Nor.*, Timor-Alps-Sicily.

Dimorphites Mojsisovics, 1893 [**Juvavites (Dimorphites) selectus;* SD Diener, 1915]. Compressed, involute, discoidal, with narrow flattened venter, distinct angular ventral shoulders; whorl sides with sigmoidal ribs that may or may not cross venter; constrictions only on inner whorls (292). *Carn.*, Alps-Sicily-Greece-Timor.——Fig. 205,*7*. **D. selectus*, Alps; *7a,b*, ×0.7 (292*).

Indojuvavites Diener, 1916 [**Juvavites angulatus* Diener, 1908]. Like *Dimorphites* but venter rounded; sigmoidal ribs on whorl sides that meet on venter in sharp V's pointing adorally (105). *Nor.*, Himalaya-Timor.

Miltites Mojsisovics, 1893 [**M. rastli;* SD Diener, 1915]. More or less involute, discoidal, venter rounded, whorl sides with weak flexuous ribs that are interrupted along mid-part of venter; tubercles on umbilical edge in early volutions (292). *Carn.*, Alps-Timor.——Fig. 205,*9*. **M. rastli*, Alps; *9a,b*, ×0.7 (292*).

Barrandeites Mojsisovics, 1893 [**Am. tubina* Dittmar, 1866]. Small forms, very involute, venter broadly rounded and with keel on outer whorl; whorl sides smooth except for prominent constrictions. Suture ceratitic (292). *Carn.*, Alps-Sicily.——Fig. 204,*3*. **B. tubina* (Dittmar), Alps; *3a,b*, ×1; *3c*, ×1.5 (292*).

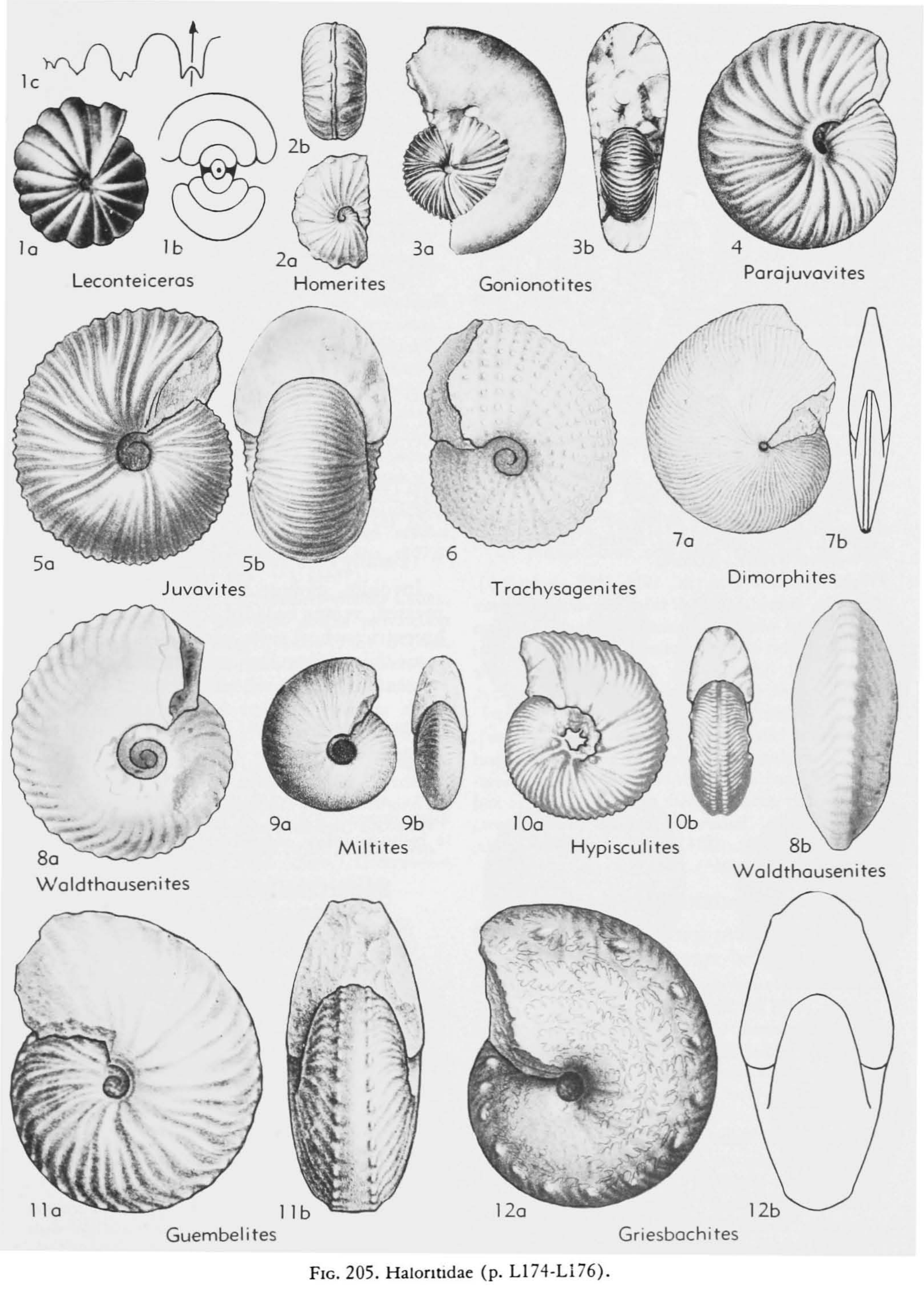


FIG. 205. Haloritidae (p. L174-L176).

Paraganides Hyatt & Smith, 1905 [**P. californicus*]. Small involute, compressed, with flattened whorl sides, weak radial ribs that pass straight over rounded venter. Suture goniatitic (203). *Carn.*, Calif.——Fig. 204,*7*. **P. californicus; 7a,b,* ×2; *7c,* ×5 (203*).

Tardeceras Hyatt & Smith, 1905 [**T. parvum*]. Like *Paraganides* but venter flatter, whorl sides with umbilical nodes giving rise to ribs that weakly cross venter. Suture ceratitic, simple (203). *Carn.*, Calif.——Fig. 204,*1*. **T. parvum; 1a,b,* ×2; *1c,* ×4 (203*).

?**Leconteiceras** Smith, 1914 [*pro Leconteia* Hyatt & Smith, 1905 (*non* Champion, 1893)] [**Leconteia californica* Hyatt-S., 1905]. Small, involute, globose ammonites, venter arched; whorl sides with broad low radial ribs that pass over venter, intercostal area narrow; inner whorls with low median furrow aligned with small nodes. Suture ceratitic (203). *Carn.*, Calif.——Fig. 205,*1*. **L. californicum* (Hyatt-S.); *1a,b,* ×1; *1c,* ×2 (203*).

?**Pseudohalorites** Yabe, 1920 [**P. subglobosus*]. Subglobose, involute, lateral areas convex, venter broadly rounded; surface with radial bifurcating ribs that cross venter. Suture ceratitic with undivided ventral lobe and 2 serrated lateral lobes. *?Perm.* or *?Trias.*, S.China.

?**Waldthausenites** Welter, 1914 [**W. malayicus*]. Involute discoidal, whorl sides convergent, venter narrow and with keel formed by angular junction of lateral ribs; umbilical tubercles on early whorls; with spiral lines. Suture ammonitic but simple (558). *Carn.-Nor.*, Timor-Alps.——Fig. 205,*8*. **W. malayicus*, Nor., Timor; *8a,b,* ×1 (558*).

?**Girthiceras** Diener, 1909 [**G. pernodosum*]. Small, involute, with flattened convergent whorl sides, flattened venter; umbilical and ventral shoulders sharply rounded; with umbilical tubercles and radiating ribs. Suture ammonitic (488). *Carn.*, Himalaya.——Fig. 204,*4*. **G. pernodosum; 4a,* ×1; *4b,* ×1.5 (606*).

Subfamily SAGENITINAE Spath, 1951

With prominent spiral ornamentation and more subdivided suture. *U.Trias.*

Sagenites Mojsisovics, 1879 [**Am. reticulatus* Hauer, 1849; SD Smith, 1904]. Subglobose, somewhat compressed, involute, venter arched; whorl sides with radial folds or ribs that pass over venter; also spiral ornamentation. Suture ammonitic (203). *Carn.-Nor.*, Alps-Sicily-Timor-Himalaya-Calif.-Peru.

S. (Sagenites). Spiral ornamentation consisting of lines or ridges only (203). *Carn.-Nor.*, Alps-Sicily-Timor-Himalaya-Calif.-Peru.

S. (Trachysagenites) Mojsisovics, 1893 [**Am. erinaceus* Dittmar, 1866; SD Hyatt & Smith, 1905]. Spiral ornamentation consisting of short spines in regular rows on ribs (203). *Carn.*, Alps-Sicily-Balkan-Himalaya-Timor-Calif.——Fig. 205, *6*. **S. (T.) erinaceus* (Dittmar), Alps; ×0.7 (292*).

Subfamily EPISCULITINAE Spath, 1951

With simplified suture and uncoiling of body chamber. *U.Trias.*

Episculites Spath, 1951 [**Am. decrescens* Hauer, 1855] [=*Isculites* Diener, 1916 (*non* Mojs., 1886)]. Small, involute, compressed, with arched venter; whorl sides with projected ribs that pass over venter and constrictions. Suture goniatitic (488). *Nor.*, Alps-?Timor-B.C.——Fig. 204,*2*. **E. decrescens* (Hauer), Alps; *2a,b,* ×1; *2c,* ×1.5 (292*).

Euisculites Spath, 1951 [**Isculites bittneri* Gemmellaro, 1904]. Like *Episculites* but with ammonitic suture (488). *Carn.-Nor.*, Sicily-Alps-Himalaya-?Timor.

Hypisculites Spath, 1951 [**Isculites dieneri* Pakuckas, 1928]. Like *Episculites* but with umbilical nodes and lateral ribs that end at nodes on ventrolateral area aligning smooth median band on venter. Suture goniatitic (488). *Carn.*, Timor-B.C.——Fig. 205,*10*. **H. dieneri* (Pak.); *10a,b,* ×1 (674*).

Family DIDYMITIDAE Haug, 1894

Involute, globose conch, somewhat compressed, venter broadly arched, last volution excentric; whorl sides with growth lines and some faint ribs; low median keel may be present on outer whorl. Suture ammonitic with saddles divided by prominent lobule (488). *U.Trias.*

Didymites Mojsisovics, 1875 [**Am. globus* Quenstedt, 1849; SD Diener, 1915] [=*Paradidymites, Timorodidymites* Diener, 1916]. *Nor.*, Alps-Sicily-Himalaya-Afghan.-Timor.——Fig. 206,*1*. *D. quenstedti* Mojs., Alps; *1a,b,* ×0.7; *1c,* ×1 (292*).

Superfamily LOBITACEAE Mojsisovics, 1882

[*nom. transl.* Hyatt, 1900 (*ex* Lobitinae Mojs., 1882)]

Involute, generally subglobose, with excentric last volution, contracted body chamber. Suture with 2 bifid lateral lobes in which median division becomes very large. An isolated group, probably descended from Arcestidae (488). *M.Trias.-U.Trias.*

Family LOBITIDAE Mojsisovics, 1882

Characters of superfamily. *M.Trias.-U. Trias.*

Lobites Mojsisovics, 1875 [**Clydonites ellipticus* Hauer, 1860; SD Mojs., 1902]. Whorl sides with low radial ribs that cross venter. Suture goniatitic (292). *M.Trias.(Ladin.)-U.Trias.(Carn.)*, Alps-

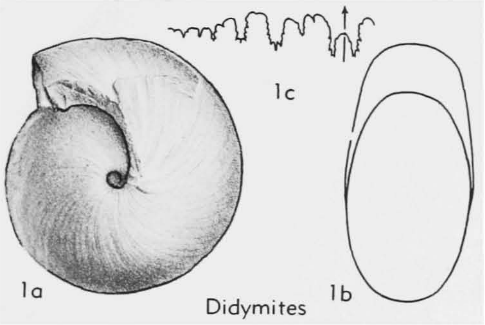


FIG. 206. *Didymites quenstedti* MOJSISOVICS, U.Trias. (Nor.), Alps; *1a,b,* ×0.7; *1c,* ×1 (p. L176).

Balkan-AsiaM.-Himalaya-B.C.-Nev.——FIG. 207, *2.* **L. ellipticus* (HAUER), Carn., Alps; *2a,b,* ×1; *2c,* ×1.5 (292*).

Paralobites MOJSISOVICS, 1902 [**Gon. pisum* MÜNSTER, 1841]. Like *Lobites* but conch smooth and inner whorls with constrictions (292). *U.Trias. (Carn.),* Alps-Himalaya.

Psilobites RENZ, 1911 [**Lobites (Psilolobites) argolicus*]. Like *Paralobites* but with no constrictions and simple pointed lobes and rounded saddles (365). *U.Trias.(Carn.),* Balkan.——FIG. 207,*4.* **P. argolicus,* Greece; *4a,b,* ×1 (365*).

Coroceras HYATT, 1877 [**Clydonites monilis* LAUBE, 1869]. Like *Lobites* but with double constriction on body chamber forming 2 hoods (292). *U.Trias. (Carn.),* Alps-Balkan-Himalaya-Timor-Nev.——FIG. 207,*1.* **C. monilis* (LAUBE), Alps; *1a,b,* ×1 (292*).

Indolobites RENZ, 1911 [**Clydonites oldhamianus* STOLICZKA, 1865]. With incipient subdivisions of lobes (365). *?M.Trias.,* Himalaya.——FIG. 207,*3.* **I. oldhamianus* (STOL.); *3a,b,* ×1 (101*).

Orestites RENZ, 1911 [**O. frechi*]. Smooth, with suture lobes trifid to irregular, weakly toothed at base and sides (365). *U.Trias.(Carn.),* Greece.——FIG. 207,*5. O. pelopsi* RENZ; ×1.5 (687*).

Superfamily ARCESTACEAE Mojsisovics, 1875

[*nom. transl.* MOJS., 1896 (*ex* Arcestidae MOJS., 1875)]

Typically involute, smooth, subglobular shells with complex ammonitic sutures, saddles phylloid in some groups; body chamber typically long, commonly with modified apertures. Principal families very abundant, long-ranging; group probably derived from Parannitidae along with the Ptychitidae. *M. Trias.-U.Trias.*

Family ARCESTIDAE Mojsisovics, 1875

Smooth many-whorled ammonites with long body chambers and modified peristomes; constrictions and flared ribs may be present. Suture ammonitic, lobes and saddles triangular, septa closely spaced (488). *M.Trias.-U.Trias.*

Arcestes SUESS, 1865 [**Am. galeiformis* HAUER; 1850 (*pro Am. galeatus* HAUER, 1846; *non* VON BUCH); SD MOJS., 1893]. Characters of family. *M.Trias.(Anis.)-U.Trias.(Rhaet.),* cosmop.

A. (Arcestes) [=*Gonarcestes* DIENER, 1919; *Rhaetites* HYATT, 1900]. Periodic constrictions confined to phragmocone (292). *U.Trias.(Carn.-Rhaet.),* cosmop.——FIG. 208,*1d,e. A. (A.) intuslabiatus* MOJS., Nor., Alps; *1d,* ×0.7; *1e,* ×1 (743*).——FIG. 208,*1c. A. (A.) gigantogaleatus* MOJS., Nor., Alps; ×0.25 (584*).——FIG. 208,*1a. A. (A.) pinacostomus* DIENER, Carn., Alps; ×0.5 (584*).——FIG. 208,*1b. A. (A.) colonus* MOJS., Carn., Alps; ×0.5 (584*).

A. (Anisarcestes) KITTL, 1908 [**Anisarcestes subdimidatus*]. Smooth, globose inner whorls, with radial ridges on body chamber, strongest on venter; umbilicus open (488). *U.Trias.(Carn.),* Alps-Balkan-?Nev.

A. (Pararcestes) MOJSISOVICS, 1893 [**Arcestes sublabiatus* MOJS., 1875; SD DIENER, 1915] [=*Galeites* ROLLIER, 1909]. Constrictions and flared ribs on phragmocone and body chamber, the latter

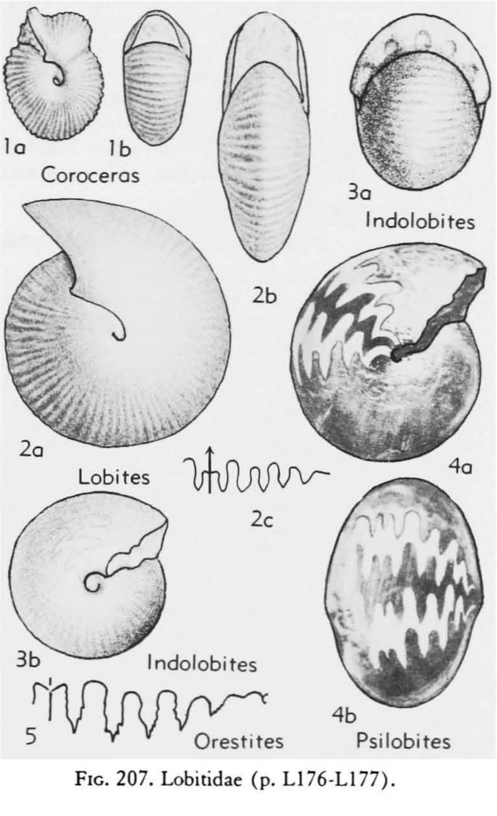


FIG. 207. Lobitidae (p. L176-L177).

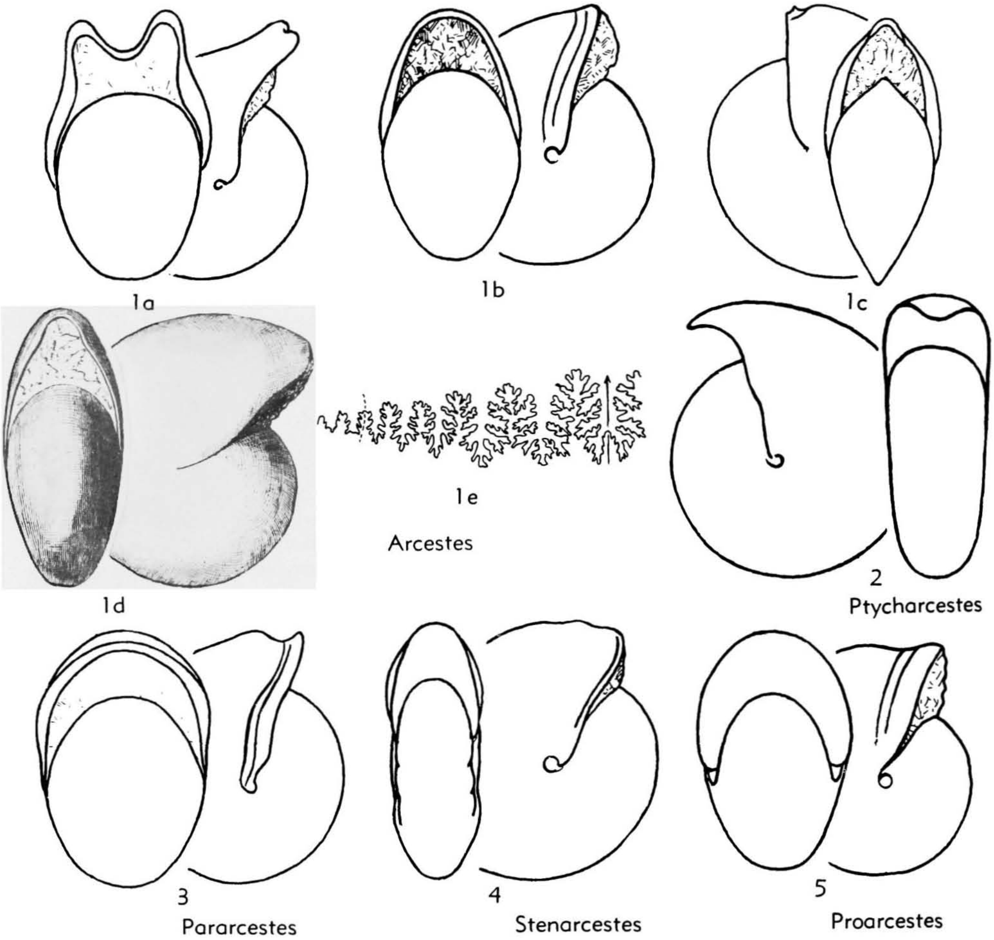


Fig. 208. Arcestidae (p. L177-L178).

also modified; umbilicus closed by callus (292). *M.Trias.(Anis.)-U.Trias.(Carn.),* Alps - Balkan - Himalaya-Timor.——Fig. 208,*3. A. (P.) kerneri* Diener, Carn., Alps; ×0.5 (584*).

A. (Proarcestes) Mojsisovics, 1893 [**Arcestes bramantei* Mojs., 1869; SD Hyatt & Smith, 1905]. Constrictions and flared ribs on phragmocone and body chamber similar (292). *M.Trias.(Anis.)-U.Trias.(Carn.),* Alps - Balkan - Sicily - Himalaya-Timor-Kotelny-Alaska-Calif.-Nev. —— Fig. 208,*5. A. (P.) gibbus* Hauer, Anis., Yugo.; ×0.5 (584*).

A. (Ptycharcestes) Mojsisovics, 1893 [**A. (P.) rugosus*]. With radial ribbing on body chamber (292). *U.Trias.(Carn.-Nor.),* Alps.——Fig. 208, *2. A. (P.) heinrichi* Diener; ×1 (709).

A. (Stenarcestes) Mojsisovics, 1895 [**Am. subumbilicatus* Hauer, 1846]. Discoidal, resembling *Joannites* in shape but with deepened umbilicus surrounded by spiral depression or mere dimples (488). *U.Trias.(Carn.-Nor.),* Alps-Sicily-Himalaya-Timor-N.Caled.——Fig. 208,*4. A. (S.) rotulaeformis* Gemmellaro, Sicily; ×0.5 (584*).

Family JOANNITIDAE Mojsisovics, 1882

Suture ammonitic, generally curved anteriorly and with bifid saddles. Body chamber long, conch compressed, discoidal, with constrictions or strigations common (488). *M.Trias.-U.Trias.*

Joannites Mojsisovics, 1879 [**Nautilus cymbiformis* Wulfen, 1793]. Very involute, surface smooth, conch with periodic constrictions. Suture ammonitic, multilobate, curved (293). *M.Trias.(Anis.)-U.Trias.(Carn.),* Alps - Balkan - Turk. - Himalaya-Timor-Nev.——Fig. 209,*1. J. johannisaustriae* (Klipstein), Carn., Alps-Greece-Rumania; *1a,b,* ×0.25; *1c,* ×0.5 (292*).

Istreites Simionescu, 1913 [**Joannites (Istreites)*

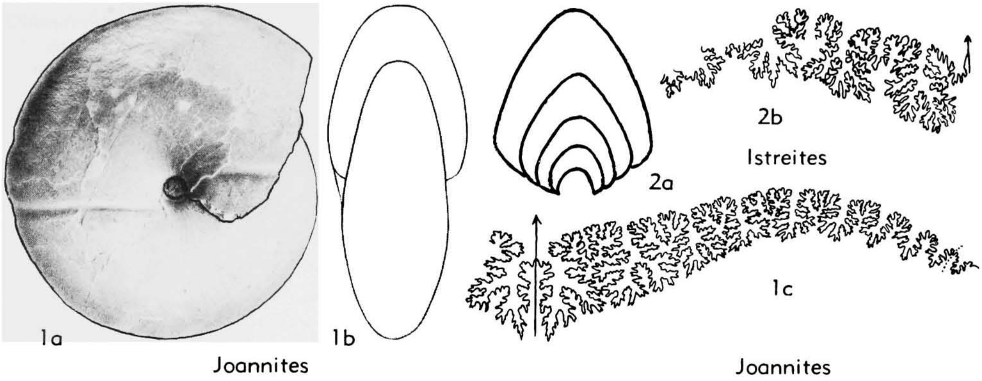


FIG. 209. Joannitidae (p. L178).

ptychitiformis]. Like *Ptychites;* differs from *Joannites* in having no constrictions and suture with small but high ventral lobe and no conspicuous curvature (488). *U.Trias.(Carn.),* Balkan-Timor.——FIG. 209,*2*. **I. ptychitiformis* (SIMION.), Balkan; *2a,b,* ×0.5.

Romanites KITTL, 1908 [**R. simionescui*]. Like *Joannites* but strigate and with no constrictions (488). *U.Trias.(Carn.),* Rumania-Greece-Timor.

Family SPHINGITIDAE Arthaber, 1911

Numerous, generally depressed whorls, umbilicus wide; body chamber long, with oblique constrictions or flared ribs. Suture as in *Arcestes* (488). *U.Trias.*

Sphingites MOJSISOVICS, 1879 [**Am. coangustatus* HAUER, 1860; SD DIENER, 1915]. *Carn.-Nor.,* Alps-Sicily-Balkan-?AsiaM.——FIG. 210,*1*. **S. coangustatus* (HAUER), Carn., Alps; *1a,b,* ×0.7; *1c,* ×2 (292*).

Family CLADISCITIDAE Zittel, 1884

Involute, robust, generally with flattened whorl sides and venter; body chamber long. Suture with retracted suspensive lobe; phylloid saddles in M.Trias. and ammonitic in U.Trias. No constrictions or radial ribs. Family rather homogeneous (488). *M. Trias.-U.Trias.*

Cladiscites MOJSISOVICS, 1879 [**Am. tornatus* BRONN, 1832; SD DIENER, 1915]. Strigate, whorl section subrectangular. Suture ammonitic with bifid saddles (292). *U.Trias.(Carn.-Rhaet.),* Alps-Sicily-Balkan-Himalaya-Timor-Alaska-Kotelny. —— FIG. 210,*2*. **C. tornatus* (BRONN), Nor., Alps-Timor; *2a,b,* ×0.7; *2c,* ×1.5 (292*).

Hypocladiscites MOJSISOVICS, 1896 [**Arcestes subtornatus* MOJS., 1873; SD DIENER, 1915]. Differs from *Cladiscites* in depth of principal lateral lobe (295). *U.Trias.(Carn.-Nor.),* Alps-Balkan-Sicily-Himalaya-Timor.——FIG. 210,*7*. **H. subtornatus* (MOJS.), Carn., Alps-Balkan-Timor; ×0.5 (293*).

Paracladiscites MOJSISOVICS, 1896 [**Am. multilobatus* BRONN, 1832; SD DIENER, 1915]. Differs from *Cladiscites* in having smooth conch and no strigations (295). *U.Trias.(Carn.-Nor.),* Alps-Himalaya-Timor-Spitz.-Nev.

Procladiscites MOJSISOVICS, 1882 [**P. brancoi;* SD DIENER, 1915] [=*Phyllocladiscites* MOJS., 1902]. Like *Cladiscites* but suture with phylloid saddle endings (293). *M.Trias.(Anis.-Ladin.),* Alps-Balkan-Himalaya-Timor-Nev.——FIG. 210,*8*. **P. brancoi,* Alps-Balkan; ×1 (293*).

Psilocladiscites MOJSISOVICS, 1896 [**Procladiscites molaris* HAUER, 1887]. Like *Cladiscites* but with smooth conch and suture with phylloid saddle endings (295). *M.Trias.(Anis.),* Balkan.

Family MEGAPHYLLITIDAE Mojsisovics, 1896

Generally small, very involute, compressed to subglobose; usually smooth. Suture ceratitic with phylloid saddles (488). *M.Trias.-U.Trias.*

Megaphyllites MOJSISOVICS, 1879 [**Am. jarbas* MÜNSTER, 1841]. Compressed, involute, low arched venter; smooth but with periodic constrictions, mainly on body chamber. Suture with large number of elements (292). *M.Trias.(Anis.)-U.Trias.(Rhaet.),* Alps - Balkan - Sicily - AsiaM.-Himalaya-Indochina-Timor.——FIG. 210,*4*. **M. jarbas* (MÜNSTER), Ladin.-Carn., Alps-Balkan-Himalaya-Timor; *4a-c,* ×1 (293*).

Parapopanoceras HAUG, 1894 [**Popanoceras verneuili* MOJSISOVICS, 1886] [=*Dienerites* MOJS., 1902 (obj.); *Beaumontites* BROWNE, 1952]. Like *Megaphyllites* but more discoidal, body chamber modified (294). *M.Trias.(Anis.),* Spitz.-N.Sib.-N. Greenl.-N.Z.-B.C.——FIG. 210,*3* **P. verneuili* (MOJS.), Spitz.; *3a,b,* ×0.7 (294*).

Ptychopopanoceras SPATH, 1951 [**Popanoceras*

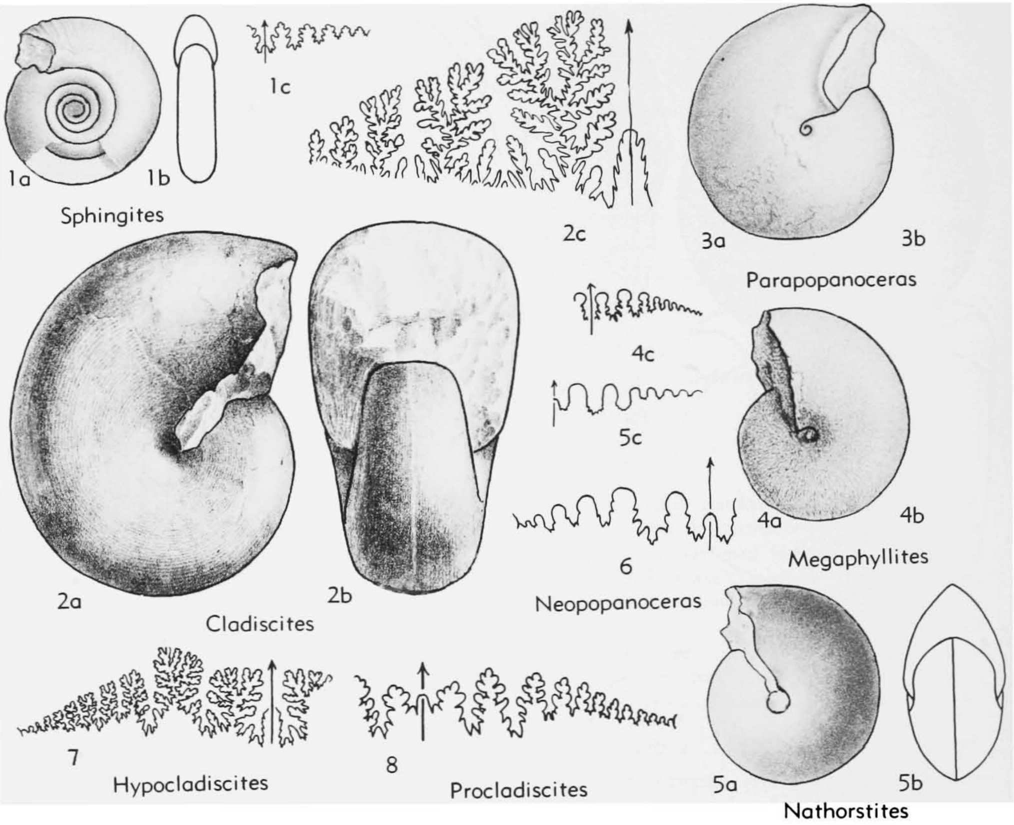


FIG. 210. Sphingitidae, Cladiscitidae, Megaphyllitidae, Nathorstitidae (p. L179-L180).

hyatti MOJSISOVICS, 1886]. Like *Parapopanoceras* but with radial folds (294). *M.Trias.(Anis.),* Spitz.

Neopopanoceras SPATH, 1951 [**Popanoceras (Parapopanoceras) haugi* HYATT & SMITH, 1905]. Subglobose, moderately evolute, whorls depressed, venter broadly rounded. Saddles of suture not so phylloid as in *Parapopanoceras* (203). *M.Trias. (Anis.),* Calif.——FIG. 210,*6*. **N. haugi* (HYATT-S.); ×1.5 (203*).

?**Nitanoceras** MCLEARN, 1937 [**Arcestes? selwyni* MCLEARN, 1930]. Like *Parapopanoceras* but more evolute and with simpler suture (488). *U.Trias. (?Carn.),* B.C.

Family NATHORSTITIDAE Spath, 1951

Involute, discoidal, compressed, smooth; venter sharp; inner volutions globular. Suture ceratitic, multisellate, with phylloid saddles (488). *M.Trias.-U.Trias.*

Nathorstites BÖHM, 1903 [**Popanoceras mcconnelli* WHITEAVES, 1889]. *M.Trias.(Ladin.)-U.Trias. (Carn.),* Spitz.-BearI.-Kotelny-Alaska-B.C.——FIG. 210,*5*. **N. mcconnelli* (WHITEAVES), Carn., B.C.; *5a,b*, ×0.5; *5c*, ×1 (732*).

Superfamily PTYCHITACEAE Mojsisovics, 1882

[*nom. transl.* SPATH, 1951 (*ex* Ptychitidae MOJS., 1882)]

Typically involute, subglobular to discoidal descendants of L. Triassic paranannitids, with globose inner whorls. Suture ammonitic but including some forms with ceratitic or goniatitic sutures. Conch smooth with lateral folds or strigations (488). *M. Trias.-U.Trias.*

Family PTYCHITIDAE Mojsisovics, 1882

Involute, subglobular, discoidal to highly compressed; smooth or with lateral ribs or strigations; inner whorls globose. Suture ammonitic (488). *M.Trias.-U.Trias.*

Ptychites MOJSISOVICS, 1875 [**Am. rugifer* OPPEL, 1865; SD SPATH, 1951]. Subovoid, compressed, discoidal, umbilicus small, umbilical walls steep; sides with distant radial folds (293). *M.Trias. (Anis.-Ladin.),* Alps-Ger.-Balkan-Himalaya-Timor-Japan-N.Sib.-Spitz.——FIG. 211,*1*. **P. rugifer* (OPPEL), Anis., Himalaya; *1a,b*, ×0.3; *1c*, ×0.7 (100*).

Discoptychites Diener, 1916 [**Am. megalodiscus* Beyrich, 1867]. More discoidal than in *Ptychites,* with narrowly rounded to acute venter; raised umbilical edge developed already in early volutions (293). *M.Trias.(Anis.),* Alps-Balkan-AsiaM.-Himalaya.——Fig. 211,*10.* **D. megalodiscus* (Beyrich), Alps-Balkan-AsiaM.; *10a,* ×0.5; *10b,* ×1 (293*).

Flexoptychites Spath, 1951 [**Ptychites flexuosus* Mojsisovics, 1882]. Like *Ptychites* but more compressed and with flexuous folds or ribs (293). *M. Trias.(Anis.-Ladin.),* Alps-Balkan-Himalaya.——Fig. 211,*6.* **F. flexuosus* (Mojs.), Anis., Alps-Balkan; *6a,b,* ×0.5; *6c,* ×0.5 (293*).

Aristoptychites Diener, 1916 [**Am. gerardi* Blanford, 1863]. With triangular whorl section, venter acutely rounded, umbilical walls steep; radial folds weak. Suture curved (100). *M.Trias.(Anis.),*

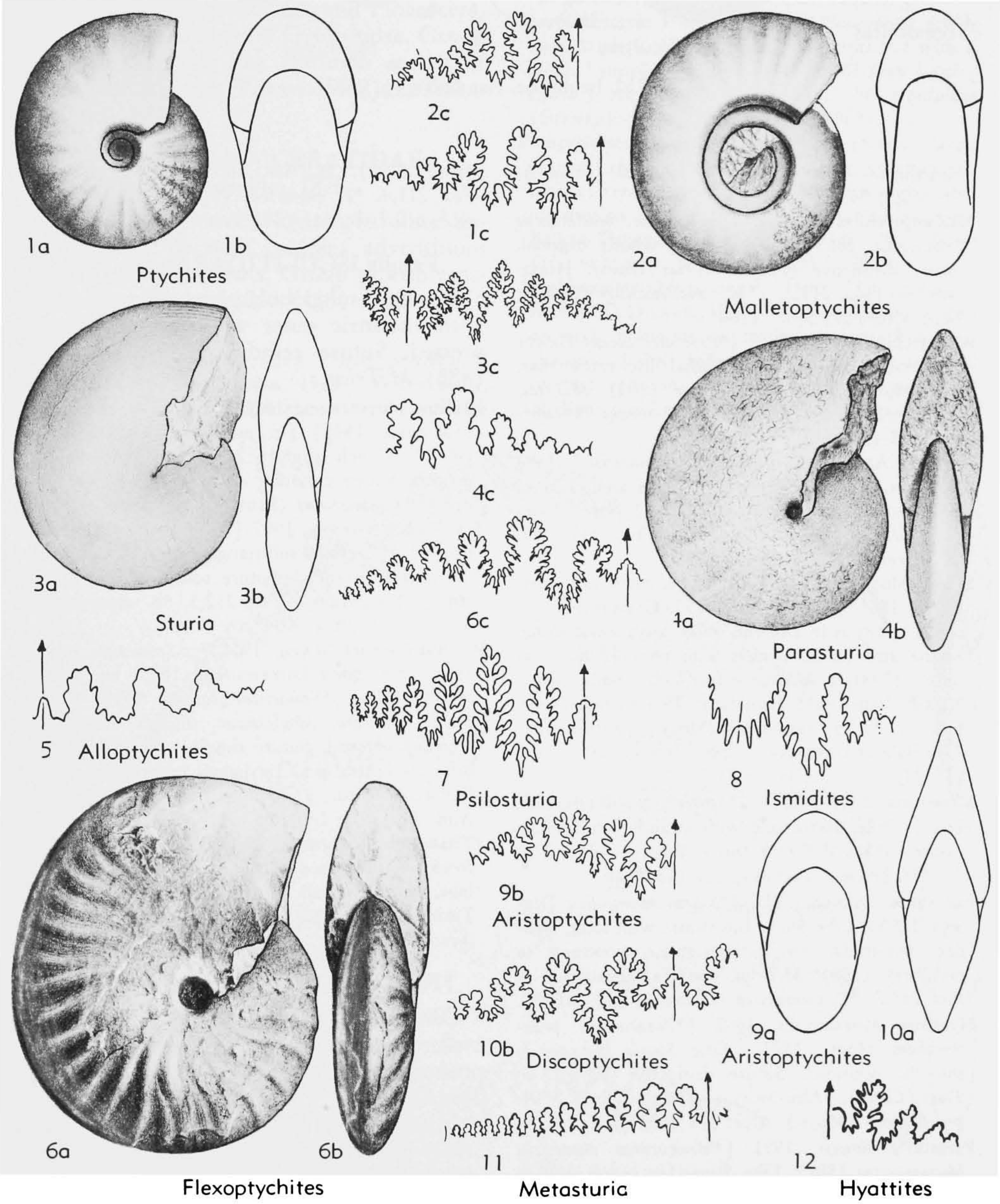


Fig. 211. Ptychitidae (p. L180-L182).

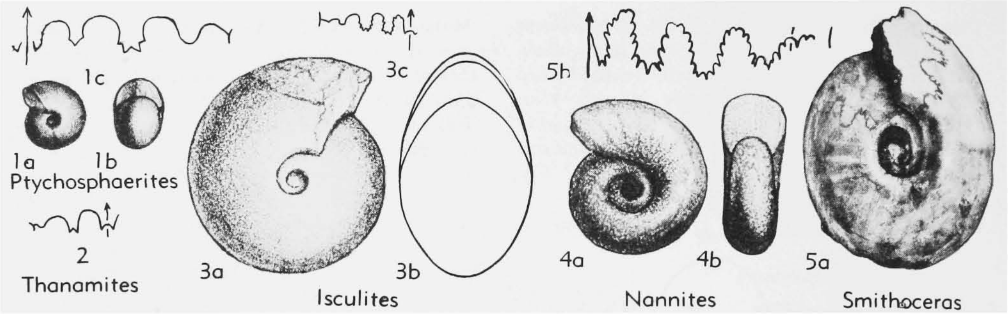


Fig. 212. Isculitidae, Nannitidae (p. L182).

Himalaya.——Fig. 211,*9*. **A. gerardi* (Blanf.); *9a*, ×0.5; *9b*, ×1 (100*).

Malletoptychites Diener, 1916 [**Am. malletianus* Stoliczka, 1865]. Very evolute, whorls trigonal, suture distinctive (100). *M.Trias.(Anis.)*, Himalaya.——Fig. 211,*2*. **M. malletianus* (Stol.); *2a,b*, ×0.3; *2c*, ×0.7 (100*).

Alloptychites Spath, 1951 [**Ptychites meeki* Hyatt & Smith, 1905]. With fine radial lines rather than folds and much simpler suture (203). *M.Trias. (Anis.)*, Nev.——Fig. 211,*5*. **A. meeki* (Hyatt-S.); ×2 (203*).

Ismidites Arthaber, 1914 [**I. marmarensis*]. Like *Ptychites*, with acute umbilical edge and flexuous ribs; short ammonitic suture, only 2 lateral lobes (23). *M.Trias.(?Anis.)*, AsiaM.——Fig. 211,*8*. **I. marmarensis*; ×1 (23*).

Sturia Mojsisovics, 1882 [**Amaltheus sansovinii* Mojs., 1869; SD Diener, 1915]. Compressed discoidal conch as in *Discoptychites*, with spiral striae. Suture ammonitic, saddles with phylloid terminations (293). *M.Trias.(Anis.) - U.Trias.(Carn.)*, Alps-Balkan-AsiaM.-Himalaya - Timor - Japan.——Fig. 211,*3*. **S. sansovinii* (Mojs.), *Anis.-Ladin.*, Alps-Balkan-Himalaya; *3a,b*, ×0.3; *3c*, ×0.5 (293*).

Metasturia Spath, 1951 [**Sturia? gracilis* Hauer, 1892]. Like *Sturia* but with straight multisellate suture (488). *M.Trias.(Anis.)*, Yugo.——Fig. 211, *11*. **M. gracilis* (Hauer); ×1 (633*).

Psilosturia Diener, 1916 [**Sturia mongolica* Diener, 1895]. Like *Sturia* but suture with long, slender, pyramidal saddles; strigation confined to periphery (100). *M.Trias.(Anis.)*, Himalaya.——Fig. 211,*7*. **P. mongolica* (Diener); ×1 (100*).

Hyattites Mojsisovics, 1902 [**Pinacoceras praefloridum* Mojs., 1873]. Like *Sturia* but conch smooth, occluded. Suture distinctive (292). *U. Trias.(Carn.)*, Alps-Sicily.——Fig. 211,*12*. **H. praefloridus* (Mojs.), Alps; ×1 (292*).

Parasturia Spath, 1951 [**Meekoceras emmrichi* Mojsisovics, 1882]. Like *Sturia* but conch smooth with weak, distant falcoid ribs, saddles of suture not pyramidal, phylloid saddle endings finely divided (293). *M.Trias.(Anis.-Ladin.)*, Alps.——Fig. 211,*4*. **P. emmrichi* (Mojs.), Ladin., Alps; *4a,b*, ×0.7; *4c*, ×1 (293*).

Family ISCULITIDAE Spath, 1951

Involute, subglobular, smooth ammonites with excentric outer volution; whorls depressed. Suture ceratitic to subammonitic (488). *M.Trias.*

Isculites Mojsisovics, 1886 [**Clydonites hauerinus* Stoliczka, 1865] [=*Spitisculites* Diener, 1916 (obj.)]. Conch slightly compressed, whorls depressed. Suture ceratitic. *Anis.*, Himalaya.——Fig. 212,*3*. **I. hauerinus* (Stol.); *3a-c*, ×1 (100*).

Smithoceras Diener, 1907 [**S. drummondi*]. Evolute, whorl sections subtriangular, umbilical shoulder sharply rounded. Suture subammonitic (104). *Anis.*, Himalaya.——Fig. 212,*5*. **S. drummondi*; *5a*, ×0.5; *5b*, ×1 (104*).

Ptychosphaerites Spath, 1951 [=*Sphaerites* Arthaber, 1896 (*non* Duftschmid, 1805; *nec* Quenstedt, 1852)] [**Sphaerites globulus* Arth., 1896]. Small, involute, subglobular, smooth, resembling a young arcestid. Suture simple, adventitious lobe between ventral and 1st lateral lobe (488). *Anis.*, Balkan.——Fig. 212,*1*. **P. globulus* (Arth.), Alps; *1a,b*, ×2; *1c*, ×6 (584*).

?**Thanamites** Diener, 1908 [**T. bicuspidatus*]. Like *Isculites* but suture very simple, bifid 1st lateral lobe, rounded small 2nd (105). *Ladin.*, Himalaya-Timor-B.C.——Fig. 212,*2*. **T. bicuspidatus*, Himalaya; ×1 (105*).

?Family NANNITIDAE Diener, 1897

Conch very small, subglobose, generally evolute, smooth; venter rounded, whorls depressed. Suture goniatitic, simple (488). *M. Trias.-U.Trias.*

Nannites Mojs., 1881 [**Gon. spurius* Münster, 1843; SD Hyatt & Smith, 1905]. *M.Trias. (Ladin.)-U.Trias.(Carn.)*, Alps.——Fig. 212,*4*. **N. spurius* (Münster), Carn., Alps; *4a,b*, ×3 (293*).

Superfamily PINACOCERATACEAE Mojsisovics, 1879

[*nom. transl.* Mojs., 1896 (*ex* Pinacoceratidae Mojs., 1879)]

Evolute to involute, generally smooth, compressed ammonoids. Suture ammonitic, with adventitious and auxiliary elements, reaching acme of ammonite sutural specialization in some genera. Gymnitidae seem to stem from Dieneroceratidae and Pinacoceratidae to be derived from Gymnitidae. Group represents one of the common stocks of Middle and Upper Triassic (488). *L.Trias.-U.Trias.*

Family PINACOCERATIDAE Mojsisovics, 1879

Highly compressed, oxynote, involute. Suture ammonitic with complex adventitious and auxiliary elements. Group probably derived from Gymnitidae (488). *M.Trias.-U.Trias.*

Pinacoceras Mojsisovics, 1873 [**Am. metternichi* Hauer, 1846; SD Diener, 1915]. Venter acute, conch smooth. Suture represents acme of ammonite specialization (292). *U.Trias.(Carn.-Nor.),* Alps-Sicily-Balkan-Himalaya-Timor - Kotelny. —— Fig. 213,*1*. **P. metternichi* (Hauer), Nor., Alps-Himalaya-Timor; *1a,* ×0.25; *1b,* ×0.5 (607*).

Eupinacoceras Spath, 1951 [*pro Parapinococeras* Arthaber, 1928 (*non* Diener. 1916)] [**Pinacoceras subimperator* Mojsisovics, 1873]. Like *Pinacoceras* but more evolute and with simpler suture (24). *U.Trias.(Nor.),* Alps-Timor.——Fig. 213,*3*. **E. subimperator* (Mojs.); ×0.7 (292*).

Parapinacoceras Diener, 1916 [**Pinacoceras aspidoides* Diener, 1900]. Like *Pinacoceras* but with a much simpler suture (488). *M.Trias.(Anis.-Ladin.),* Alps-Yugo.——Fig. 213,*5*. **P. aspidoides* (Diener); *5a,* ×0.5; *5b,* ×0.7 (606*).

Pompeckjites Mojsisovics, 1902 [**Am. layeri* Hauer, 1847]. Umbilicus of outer volution excentric; ventral portion of whorl sides with radial or sinuous folds (292). *U.Trias.(Carn.),* Alps-Balkan-Timor-Calif.——Fig. 213,*6*. **P. layeri* (Hauer); *6a,b,* ×0.25; *6c,* ×0.7 (292*).

Bambanagites Mojsisovics, 1896 [**B. schlagintweiti;* SD Diener, 1915]. With sculpture, at least on early volutions, as in *Pompeckjites* but body chamber slightly inflated, venter broadly rounded on last volution. Suture simpler and with subphylloid saddle endings (295). *U.Trias.(Nor.),*

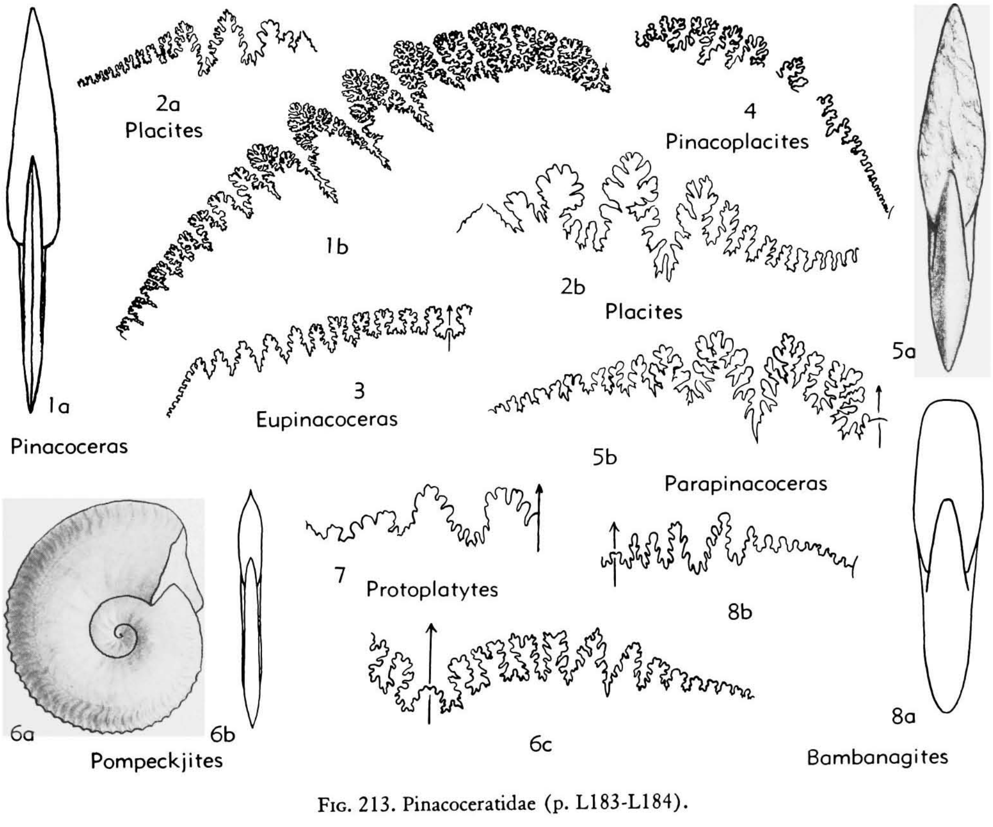


Fig. 213. Pinacoceratidae (p. L183-L184).

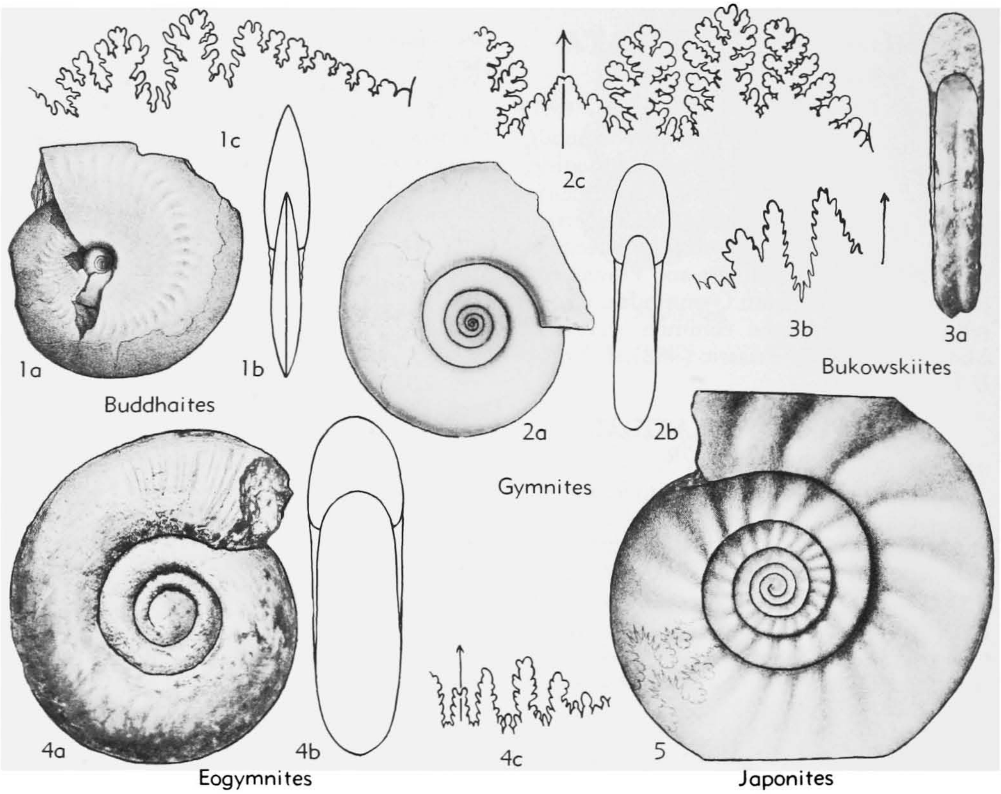


FIG. 214. Gymnitidae (p. L184-L185).

Himalaya.——FIG. 213,*8*. **B. schlagintweiti; 8a,* ×0.5; *8b,* ×1.5 (295*).

Protoplatytes COCKERELL, 1905 [*pro Platytes* MOJSISOVICS, 1902 (*non* GUENÉE, 1845)] [**Pinacoceras neglectus* MOJS., 1873]. More or less evolute, smooth pinacoceratid with a simple gymnitid suture (292). *U.Trias.(Nor.),* Alps.——FIG. 213,*7*. **P. neglectus* (MOJS.); ×1.5 (292*).

Placites MOJSISOVICS, 1896 [**Pinacoceras platyphyllum* MOJSISOVICS, 1873] [=*Paragymnites* HYATT, 1900; *Paraplacites* KUTASSY, 1928 *(nom. nud.)*]. Involute, smooth, compressed, with closed umbilicus, flattened whorl sides, rounded venter. Suture not as complex as in *Pinacoceras* (295). *U.Trias.(Carn.-Nor.),* Alps-Sicily-Balkan-Himalaya-Timor-Sib.-Calif.-Nev.-Peru.——FIG. 213,*2b*. *P. oxyphyllus* (MOJS.), Nor., Alps-Sicily; ×1 (292*).——FIG. 213,*2a*, *P. postsymmetricum* (MOJS.), Nor., Alps, ×0.7 (292*).

Pinacoplacites DIENER, 1916 [**Placites meridianus* WELTER, 1914]. Like *Placites* but with an opening umbilicus. Suture with development of adventitious elements similar to those in *Pinacoceras* (558). *U. Trias.,* Timor.——FIG. 213,*4*. **P. meridianus* (WELTER); ×1 (558*).

Family GYMNITIDAE Waagen, 1895

Evolute to involute, compressed; venters rounded to sharpened, conch generally smooth. Suture ammonitic. Group closely related to Pinacoceratidae (488). *L.Trias.-U. Trias.*

Gymnites MOJSISOVICS, 1882 [**Am. incultus* BEYRICH, 1867; SD DIENER, 1915]. Evolute, whorl section oval, venter arched; shell smooth, outer volutions may have costation or rows of nodes or both. Suture ammonitic with 2 lateral lobes and retracted auxiliaries (293). *M.Trias.(Anis.-Ladin.),* Alps-Balkan-Himalaya-Timor-B.C.-Nev. —— FIG. 214,*2*. **G. incultus* (BEYRICH), Anis., Alps-Balkan-Himalaya; *2a,b,* ×0.25; *2c,* ×1 (293*).

Anagymnites HYATT, 1900 [**Am. lamarcki* OPPEL, 1863]. Like *Gymnites* but periphery sharpened or bluntly keeled (100). *M.Trias.(Anis.),* Alps-Balkan-B.C.-Nev.

Epigymnites DIENER, 1916 [**Gymnites ecki* MOJSISOVICS, 1882]. Like *Gymnites* but more involute and commonly with row of lateral tubercles on outer volution (293). *M.Trias.(Ladin.)-U.Trias. (Carn.),* Alps-Balkan.

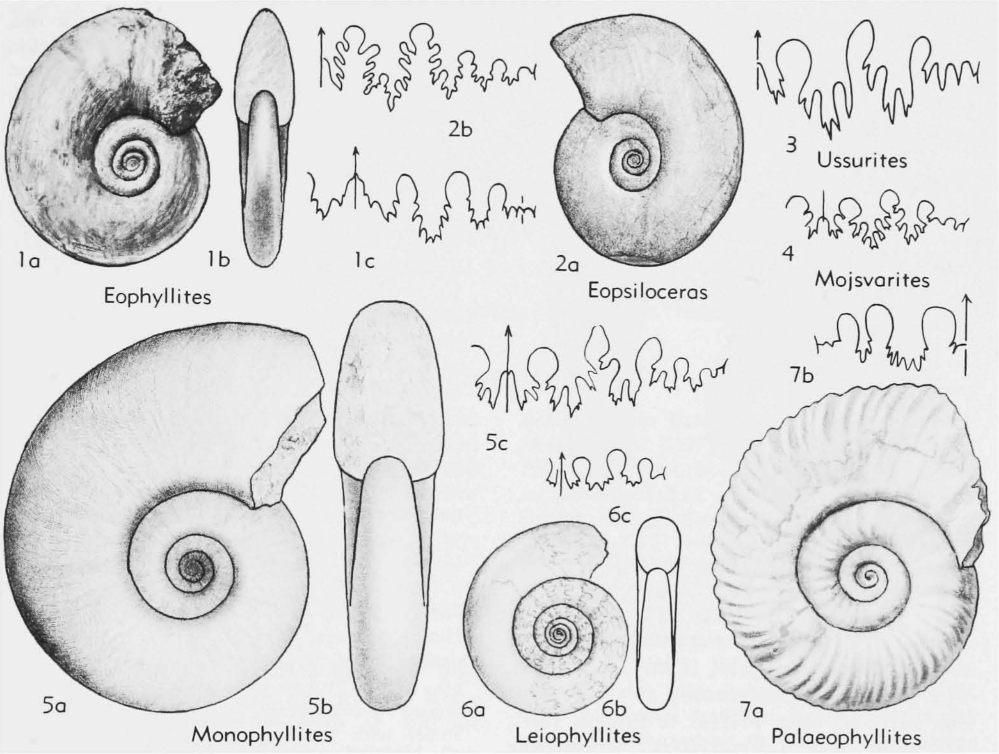


FIG. 215. Ussuritidae (p. L186).

Xiphogymnites SPATH, 1951 [**Gymnites spiniger* DIENER, 1917]. Like *Gymnites* but with row of tubercles on venter followed by constrictions (488). *M.Trias.(Anis.)*, Yugo.

Buddhaites DIENER, 1895 [**Gymnites (Buddhaites) rama*]. Involute oxycone with flexuous ribs, strongest along mid-portion of whorl side. Suture with long series of auxiliaries (100). *M.Trias.(Anis.)*, Himalaya.——FIG. 214,*1*. **B. rama; 1a,b,* ×0.3; *1c,* ×1 (100*).

Eogymnites SPATH, 1951 [**Japonites arthaberi* DIENER, 1915 (=*Japonites sugriva* DIENER var. ARTHABER, 1911; *E. decipiens* SPATH, 1951)]. Like *Gymnites* but whorl section more robust, suture simpler (22). *L.Trias.(U.Scyth.)*, Albania.——FIG. 214,*4*. **E. arthaberi* (DIENER); *4a,b,* ×0.5; *4c,* ×0.7 (22*).

Japonites MOJSISOVICS, 1893 [**Ceratites planiplicatus* MOJS., 1888]. Evolute compressed; whorl sides convergent, venter acute or narrowly rounded; with lateral recurved ribs and umbilical bulges. Suture distinctive (488). *M.Trias.(Anis.)*, Japan-Himalayas-Timor-Alps.——FIG. 214,*5*. **J. planiplicatus* (MOJS.), Japan; ×0.3 (664*).

?**Bukowskiites** DIENER, 1907 [**B. colvini*]. Widely umbilicate, with elliptical whorl section, venter rounded and with distinct, narrow siphonal groove. Suture ammonitic, similar to that of *Japonites* (104). *M.Trias.(Anis.)*, Himalaya.——FIG. 214,*3*. **B. colvini; 3a,* ×0.7; *3b,* ×1 (104*).

Suborder PHYLLOCERATINA Arkell, 1950

Smooth or feebly ornamented derivatives of Meekocerataceae, characteristically with phylloid saddle endings. An exceptionally persistent, conservative stock, which gave rise to all post-Triassic ammonoids as offshoots, but itself remained relatively very little changed (12). *Trias.-Cret.*

Superfamily PHYLLOCERATACEAE Zittel, 1884

[*nom. transl.* HYATT, 1900 (as Phylloceratida) (*ex* Phylloceratidae ZITTEL, 1884); *nom. correct.* ARKELL, 1952]

The typical, least divergent Phylloceratina. Test thin. Ornament typically confined to fine lineation or liration and some foldlike ribs, with or without constrictions. Suture typically has several auxiliary elements, with

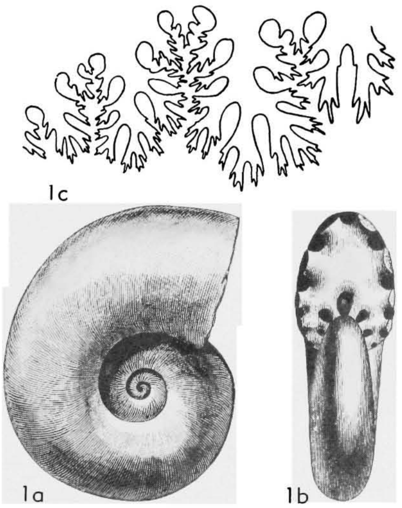


FIG. 216. *Rhacophyllites neojurensis* (QUENSTEDT), U.Trias.(Nor.), Alps (743*) (p. L186).

lobes trifid and saddles normally diphyllic or tetraphyllic. Aptychi, if any, unknown. This is the only superfamily of ammonoids that survived from Triassic to Jurassic (201, 357, 536, 577) *L.Trias.-Cret.,* world-wide but scarce in the Boreal realm.

Family USSURITIDAE Hyatt, 1900

[=Monophyllitidae J. P. SMITH, 1913]

Discoidal, evolute; venters rounded; little or no ornamentation. Suture with primitive monophyllic saddles, dorsal lobe lituid (472). *L.Trias.-U.Trias.*

Monophyllites MOJSISOVICS, 1879 [**Am. sphaerophyllus* HAUER, 1850; SD MOJS., 1902]. Whorl section rounded, venter arched, conch with sigmoidal growth lines. Suture with irregularly trifid 1st lateral lobe, 4 or more monophyllic saddles (472). *M.Trias.(Anis.)-U.Trias.(Carn.),* cosmop.——FIG. 215,*5*. **M. sphaerophyllus* (HAUER), Eu.-Asia-Timor; *5a,b,* ×0.4; *5c,* ×0.7 (293*).

Eophyllites SPATH, 1930 [**Monophyllites dieneri* ARTHABER, 1908] [=*Monophyllites (Schizophyllites)* RENZ & RENZ, 1948]. Evolute, compressed, discoidal, with subtrigonal whorl section, arched venter, flattened sides; with nearly radial growth lines and indistinct folds. Suture with shallow wide ventral lobe, which tends to be divided by short rounded saddle, long 1st lateral lobe, saddle monophyllic (472). *L.Trias.(U.Scyth.),* Albania-Chios-Timor.——FIG. 215,*1*. **E. dieneri* (ARTH.), Albania; *1a-c,* ×0.7 (22*).

Palaeophyllites WELTER, 1922 [**P. steinmanni*]. Like *Monophyllites* but with smooth inner whorls with some flares, outer whorl with irregular ribs, slightly projected peripherally. Suture monophyllic, simple (472). *L.Trias.(U.Scyth.),* Chios-Timor.——FIG. 215,*7*. **P. steinmanni,* Timor; *7a,* ×0.75; *7b,* ×1 (560*).

Ussurites HYATT, 1900 [**Monophyllites sichoticus* DIENER, 1895]. Like *Monophyllites* but with simpler suture. First lateral saddle typically indented only on ventral side, 2nd lateral on dorsal side (472). *M.Trias.(Anis.),* Sib.-Spitz.-Himalaya-Timor-Japan-B.C.-Calif.-?Albania.——FIG. 215,*3*. **U. sichoticus* (DIENER), Sib.; ×0.5 (101*).

Leiophyllites DIENER, 1915 [**Monophyllites suessi* MOJSISOVICS, 1882]. Serpenticone, generally smooth with simple monophyllic suture (472). *L.Trias.(U.Scyth.)-M.Trias.(Anis.),* Eu.-Asia.——FIG. 215,*6*. **L. suessi* (MOJS.), Anis., Eu.-Asia; *6a,b,* ×0.7; *6c,* ×1 (293*).

Mojsvarites POMPECKJ, 1895 [**Am. (Ceratites) agenor* MÜNSTER, 1834; SD DIENER, 1915]. Evolute, smooth, with rounded slightly compressed whorl section and arched venter. Suture as in *Monophyllites* but saddles more indented (472). *U.Trias.(Carn.-Nor.),* Alps-Hung.-Himalaya.——FIG. 215,*4*. **M. agenor* (MÜNSTER), Carn., Alps-Hung.-Himalaya; ×1 (293*).

Eopsiloceras SPATH, 1930 [**Am. planorboides* GÜMBEL, 1861]. Evolute, smooth, discoidal, with compressed whorl section, narrowly rounded venter. Suture with terminal monophyllic saddle leaflet and with phylloid lateral leaflets (472). *U.Trias.(Nor.-Rhaet.),* Alps.——FIG. 215,*2*. **E. planorboides* (GÜMBEL), Rhaet., Alps; *2a,* ×0.7; *2b,* ×1 (348*).

Family DISCOPHYLLITIDAE Spath, 1927

Like Monophyllitidae but principal saddles have di- or triphyllic terminations (488). *U.Trias.*

Discophyllites HYATT, 1900 [**Lytoceras patens* MOJSISOVICS, 1873]. First lateral saddle unsymmetrically monophyllic (472). *Carn.-Nor.,* Alps-Sicily-Himalaya-Timor-Calif.-Alaska.——FIG. 217,*2*. **D. patens* (MOJS.), Nor., Alps-Alaska; ×1 (292*).

Rhacophyllites ZITTEL, 1884 [**Am. neojurensis* QUENSTEDT, 1845; SD SMITH, 1927] [=*Diphyllites, Triphyllites* JULLIEN, 1911]. First lateral saddle diphyllic, adjacent lateral saddles diphyllic or triphyllic (472). *Carn.-Nor.,* Alps-Hung.-Sicily-Himalaya-Timor.——FIG. 216,*1*. **R. neojurensis* (QUENST.), Nor., Alps-Timor; *1a,b,* ×0.5; *1c,* ×1 (743*).

Tragorhacoceras SPATH, 1927 [**Phylloceras occultum* MOJSISOVICS, 1873]. With peripheral ribs on outer whorl, and suture with large leaflets in diphyllic saddle (472). *Nor.,* Alps-Sicily.——FIG. 217,*3*. **T. occultum* (MOJS.), Alps; *3a,b,* ×0.7 (621*).

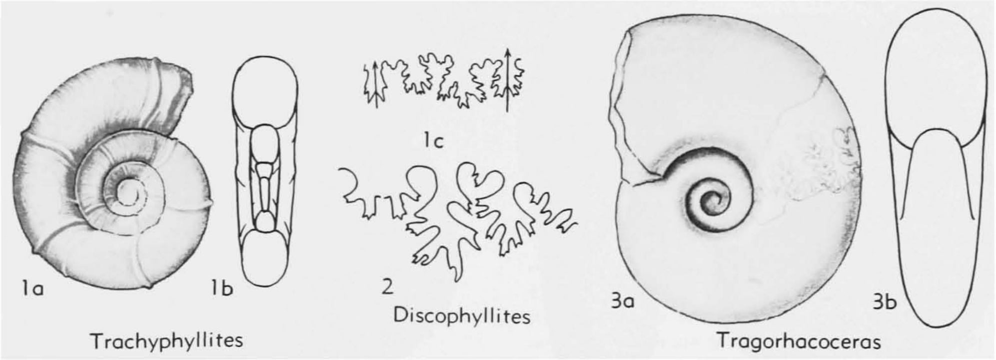


FIG. 217. Discophyllitidae (p. L186).

Trachyphyllites Arthaber, 1927 [**Monophyllites (Trachyphyllites) costatus*]. Evolute, with rounded whorl section; sides with sigmoidal growth lines and about 6 ribs or flares per whorl. Suture less phylloid than other genera of family (472). *Nor.*, Timor.——Fig. 217,*1*. **T. costatus; 1a,b,* ×0.7; *1c,* ×1 (24*).

Family PHYLLOCERATIDAE Zittel, 1884

Involute, smooth shells with very thin test, many covered with fine growth lines, usually without ribbing, with or without sigmoid constrictions. Sutures complex, major and minor branches of saddles with phylloid or spatulate endings of double (diphyllic), triple (triphyllic), or quadruple (tetraphyllic) type. Probably derived from Triassic Discophyllitidae (239, 466, 577). *U.Jur.-U.Cret.,* world-wide (except Boreal unless stated), especially abundant in Tethyan and Pacific realms.

Subfamily PHYLLOCERATINAE Zittel, 1884

[Includes Hypophylloceratinae Spath, 1927, and Phyllopachyceratinae Collignon, 1937]

Without flares and usually without constrictions. *L.Jur.(L.Lias.)-U.Cret.(Maastr.),* world-wide.

Phylloceras Suess, 1865 [**Am. heterophyllus* J. Sowerby, 1820] [=*Rhacoceras* Hyatt, 1867 (obj.); *Xeinophylloceras* Buckman, 1921; *Heterophylloceras* Kovacs, 1939 (obj.)]. Involute, compressed forms with gentle umbilical slope, dense, fine radial lirae on test but not on internal mold, and some more or less vague radial folds on whorl sides. Sutures with triphyllic saddles. *L.Jur. (Sinem.)-L.Cret.(Valang.),* world-wide.——Fig. 218,*5*. **P. heterophyllum* (Sow.), L.Jur.(Toarc.), Eng.; *5a,b,* ×0.2 (583n).

Partschiceras Fucini, 1923 [**Am. partschi* Stur, 1851 (*non* Klipstein, 1843), =*P. monestieri* Breistroffer, 1947; SD Spath, 1927] [=*Partschiphylloceras* Roman, 1938 (obj.); *Macrophylloceras* Spath, 1927]. In addition to lirae as in *Phylloceras,* blunt ribbing gradually sets in on venter and outer half of whorl sides. Sutures with very slender, diphyllic saddles. *L.Jur.(Sinem.)-L.Cret. (Valang.), ?L. Cret.(Barrem.),* world-wide.——Fig. 218,*3a,b*. **P. monestieri* Breistroffer, L.Jur. (U.Pliensb.), Italy; ×0.75 (628*).——Fig. 218, *3c,d*. *P.* sp.; ×0.5 (743*).

Phyllopachyceras Spath, 1925 [**Am. infundibulum* d'Orbigny, 1841]. Moderately to very involute, inflated, widest point usually at mid-side with flat slope to a minute umbilicus. Smooth to a varying diameter (?throughout in some) with strong rounded ribs on outer part of whorl. Sutures with 1st and 2nd lateral saddles tetraphyllic. *L.Cret. (Barrem.)-U.Cret.(Maastr.),* Eu.-N.Afr.-S.India-W.Austral.-N.Z.-Japan-Greenl.——Fig. 218,*2a,b*. **P. infundibulum* (Orb.), Barrem, Fr.; ×0.75 (329*).——Fig. 218,*2c*. *P. rouyanum* (Orb.), L. Cret.(Apt.), Fr.; ×1 (329*).

Procliviceras Fucini, 1920 [**Phylloceras proclive* Rosenberg, 1909] [=*Procliviceras* Roman, 1938 (obj.)]. Very involute; whorl section oval; adult ribbed on venter and outer part of whorl sides; inner whorls feebly constricted in some. Sutures moderately complex, saddles diphyllic. *L.Jur.(Pliensb.),* Eu.——Fig. 218,*4*. **P. proclive* (Rosenberg), Aus.; *4a,b,* ×1 (694*).

Zetoceras Kovacs, 1939 [**Am. zetes* d'Orbigny, 1850]. Compressed, involute. Sutures with saddle endings commonly tetraphyllic. *L.Jur.(Sinem.)-M. Jur.(Baj.),* probably also *U.Jur.,* Eu.——Fig. 218,*7*. **Z. zetes* (Orb.), L.Jur.((Lias.), Ger.; *7a,b,* type, ×0.3 (358*).

Hantkeniceras Kovacs, 1939 [**Phylloceras hantkeni* Schloenbach, 1867 (fig'd. Prinz, 1904)]. Large, smooth, evolute, whorls somewhat quadrate, flat-sided. Sutures rather simple, with 1st lateral lobe shorter than 2nd lateral. *L.Jur.(U.Pliensb.),* Hung.-Ger.——Fig. 218,*1*. **H. hantkeni* (Schloen.), Hung.; *1a-c,* ×0.25 (357*).

Geyeroceras Hyatt, 1900 [**Am. cylindricus* J. de C. Sowerby, 1831] [incl. *Lavizzaroceras* Kovacs,

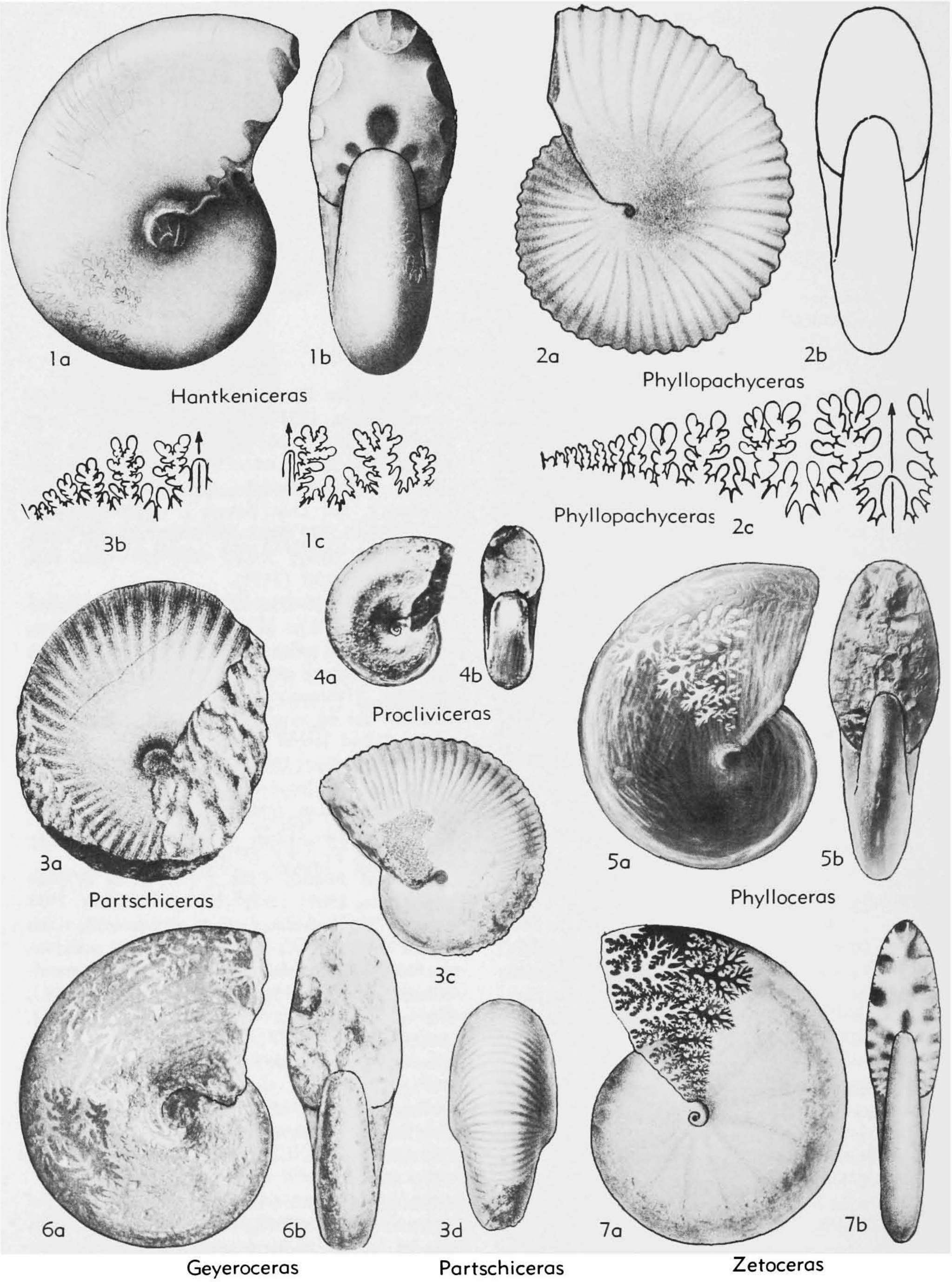
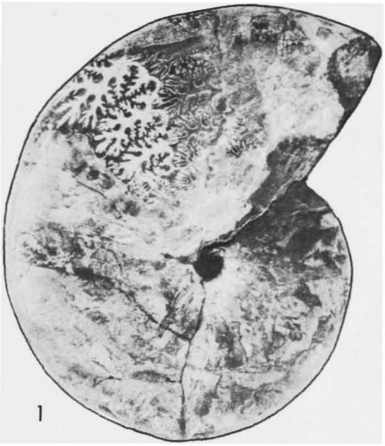


FIG. 218. Phylloceratidae (Phylloceratinae) (p. L187).

1939]. Involute, smooth, compressed, sides and venter flattened. First lateral lobe long; lateral saddles diphyllic to tetraphyllic; internal suture with 3 monophyllic saddles. *L.Jur.(Pliensb.)*, Eu.——FIG. 218,*6*. **G. cylindricum* (Sow.), Italy; *6a,b*, ×0.7 (307*).



Hypophylloceras

FIG. 219. *Hypophylloceras ononense* (STANTON), L. Cret.(Apt.), Calif.; ×0.5 (2*) (p. L189).

Hypophylloceras SALFELD, 1924 [**Phylloceras onoense* STANTON, 1895] [incl. *Neophylloceras* SHIMIZU, 1934; =*Paraphylloceras* SHIMIZU, 1935 *(nom. nud.)* (*non* SALFELD, 1919); *Hyporbulites* BREISTROFFER, 1947; *Goretophylloceras* COLLIGNON, 1949; *Aphroditiceras* MAHMOUD in BREISTR., 1952 *(n.n.)*]. Compressed, finely ribbed, some with periodic stronger ribs or folds. Sutures complex, lobes large and finely divided, asymmetric, 1st lateral much larger than external and 2nd lateral, saddle endings commonly not phylloid. *L.Cret.(Hauteriv.)-U.Cret.(Maastr.)*, world-wide except Boreal.——FIG. 219,*1*. **H. onoense* (STANTON), L.Cret.(Apt.), Calif.; ×0.5 (2*).

Subfamily CALLIPHYLLOCERATINAE Spath, 1927

Regularly with constrictions or flares or both (466). *L.Jur.(Hett.)-L.Cret.(Alb.)*.

Calliphylloceras SPATH, 1927 [**Phylloceras disputabile* ZITTEL, 1869 (?=*Am. demidoffi* ROUSSEAU, 1841)] [*Neocalliphylloceras* BESAIRIE, 1936; *Capitanioceras* KOVACS, 1939; *Euphylloceras* DROUCHTCHITZ, 1953]. Smooth, involute, compressed, with rounded venter and periodic sigmoid constrictions on internal mold, with or without corresponding flares on ventral half of test; surface also with lirae, as in *Phylloceras*. First and 2nd lateral saddles usually triphyllic, others diphyllic. *L.Jur.(Hett.)-L.Cret.(M.Alb.)*, world-wide.——FIG. 220, *3*. **C. disputabile* (ZITTEL), M.Jur.(Bath. or Callov.), Hung.; *3a,b*, holotype, ×0.5 (649*).

Holcophylloceras SPATH, 1927 [**Phylloceras mediterraneum* NEUMAYR, 1871 (=*Am. zignodianum* ORB., 1848)] [*Salfeldiella* SPATH, 1927; *Telegdiceras* KOVACS, 1939]. Resembles *Calliphylloceras* but constrictions affect test as well as internal mold and are more acutely sigmoid, linguate, or angular, and outer half of whorl is ribbed. Saddles of sutures diphyllic except 1st lateral saddle, which becomes triphyllic in later forms. *M.Jur.(Baj.)-L.Cret.(Apt.)*, world-wide.——FIG. 220,*5*. **H. mediterraneum* (NEUM.); *5a-c*, ×0.5 (667*).——FIG. 220,*4*. *H. guettardi* (RASPAIL), L.Cret.(Apt.), Fr.; type species of *Salfeldiella*, *4a,b*, ×1; *4c*, enlarged (329*).

Ptychophylloceras SPATH, 1927 [**Phylloceras feddeni* WAAGEN, 1875] [*Tatroceras* KOVACS, 1939; =*Neumayriceras* SORRENTINO, 1942 (*non* ROLLIER, 1909)]. Smooth, involute shells with broadly rounded venter crossed by periodic labial ridges, or flares, which are present even on internal mold; umbilical slope gentle. Suture saddles diphyllic and triphyllic. *M.Jur.(Baj.)-U.Jur.(Tithon.)*, probably world-wide.——FIG. 220,*6*. **P. feddeni* (WAAGEN), M.Jur.(Callov.), Cutch; *6a-c*, ×0.3 (546*).

Haplophylloceras SPATH, 1925 [**Phylloceras strigile* BLANFORD in UHLIG, 1903]. Inner whorls smooth, venter rounded; outer whorl developing flattened venter and large foldlike ribs which strengthen and sharpen in approaching venter, projected as they cross it; umbilical slope gentle. Sutures with saddle endings tending to lose phylloid form and become multifid. *Jur.* or *Cret.*, Spiti sh., India-Indon.-N. Guinea.——FIG. 220,*7*. **H. strigile* (BLANFORD), Spiti sh.; *7a,b*, ×1 (533*).

Sowerbyceras PARONA & BONARELLI, 1895 [**Am. tortisulcatus* D'ORBIGNY, 1849] [=*Martelliceras* SORRENTINO, 1942 (obj.) (*non* SCHINDEWOLF, 1925)]. Evolute, compressed, with flattened sides and venter and abrupt or stepped umbilical edge; smooth except for distant, acutely sigmoid constrictions on test and internal mold (but in some unconstricted). Sutures with short lobes. *U.Jur.* (chiefly *Oxf.-Kimm.*), Eu.-N.Afr.-Anatolia-Cauc.-Persia-India.——FIG. 220,*1*. **S. tortisulcatum* (ORB.), U.Jur.(U.Oxf.), Fr.; *1a-c*, ×0.5 (330*).

Calaiceras KOVACS, 1939 [**Am. calais* MENEGHINI, 1881]. Evolute, with rounded whorls of medium height, sides somewhat divergent; internal mold with 4 or 5 forwardly curved constrictions per whorl, increasing with growth. Sutures complex, 1st lateral saddle high and diphyllic. *L.Jur.(U. Pliensb.)*, S.Eu.——FIG. 220,*2*. **C. calais* (MEN.), Italy; *2a,b*, ×1 (660*).

?Holcolissoceras SPATH, 1928 [**Lissoceras pintacudae* DI STEFANO, 1884]. Evolute, with deep gently falcoid constrictions. Sutures unknown. *U. Jur.(Kimm.)*, Eu.——FIG. 220,*8*. **H. pintacudae* (STEF.), Sicily; *8a,b*, ×0.75 (716*).

Family JURAPHYLLITIDAE Arkell, 1950

[=Rhacophyllitinae SPATH, 1927 (name based on *Rhacophyllites* AUCTT., *non* ZITTEL, 1884)]

Compressed, evolute, with modified body chamber which usually carries coarse ventral ribbing. A few genera are more involute but all are compressed, and a few lack ribbing. First lateral saddles diphyllic, others

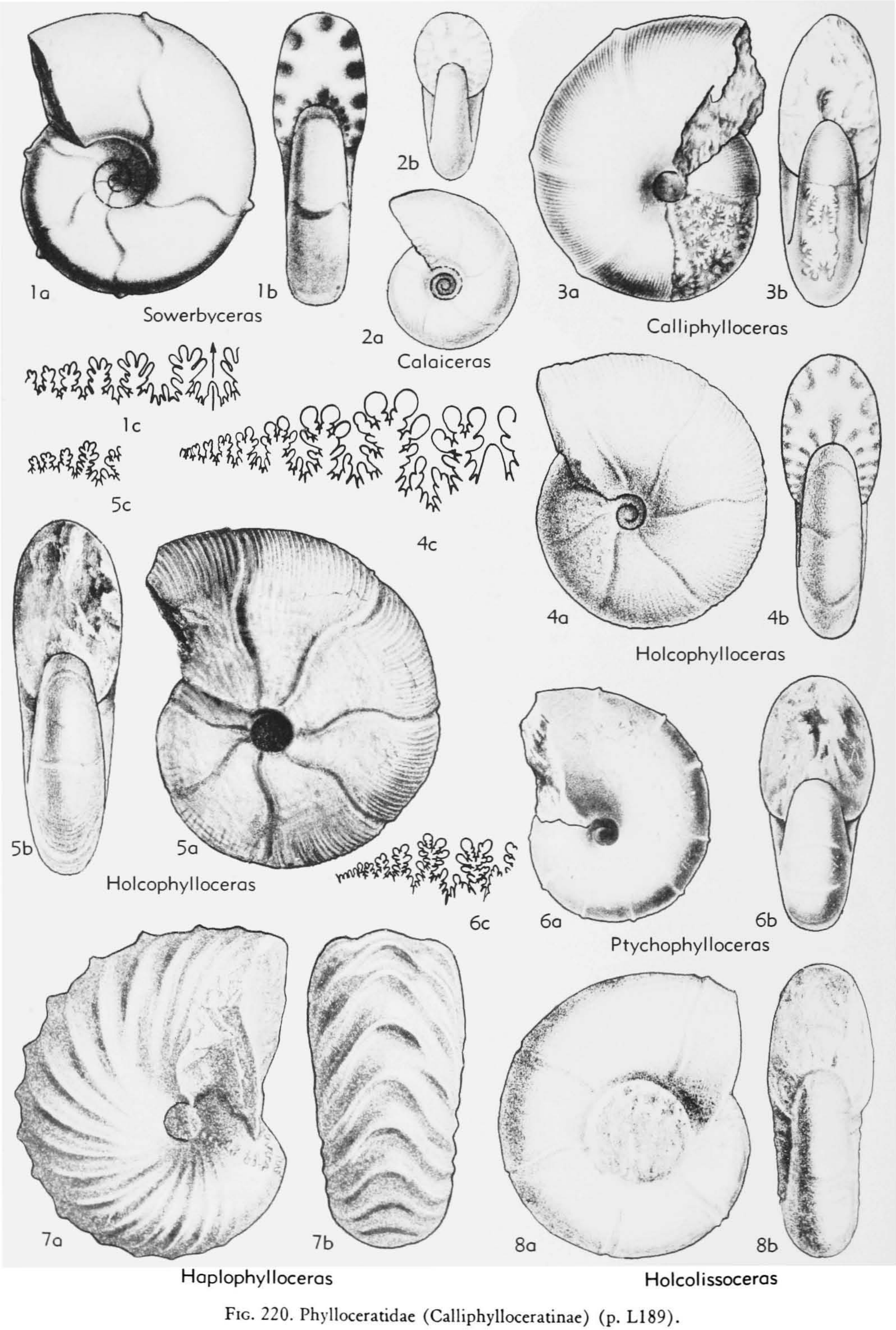


FIG. 220. Phylloceratidae (Calliphylloceratinae) (p. L189).

diphyllic or triphyllic; internal saddles monophyllic. Probably independent descendants of Triassic Discophyllitidae (12, 260, 466, 536). *L.Jur.(L.Lias.-M.Lias.),* S. Eu.-N.Afr.-Tibet-Indon.-Japan-N.Z.-Arg.

Juraphyllites Müller, 1939 [**Phylloceras diopsis* Gemmellaro, 1884] [=*Rhacophyllites* auctt. (*non* Zittel, 1884)]. Evolute, with sharp umbilical edge; smooth except for prorsiradiate ribs or folds on body chamber. *Sinem.-Pliensb.*——Fig. 221,*8*. **J. diopsis* (Gemm.), L.Jur.(Pliensb.), Italy; *8a-c,* ×0.5 (627*).

Tragophylloceras Hyatt, 1900 [**Am. heterophyllus numismalis* Quenstedt, 1845; SD Buckman, 1912] [*Phyllolobites* Vadasz, 1907]. Evolute, umbilical

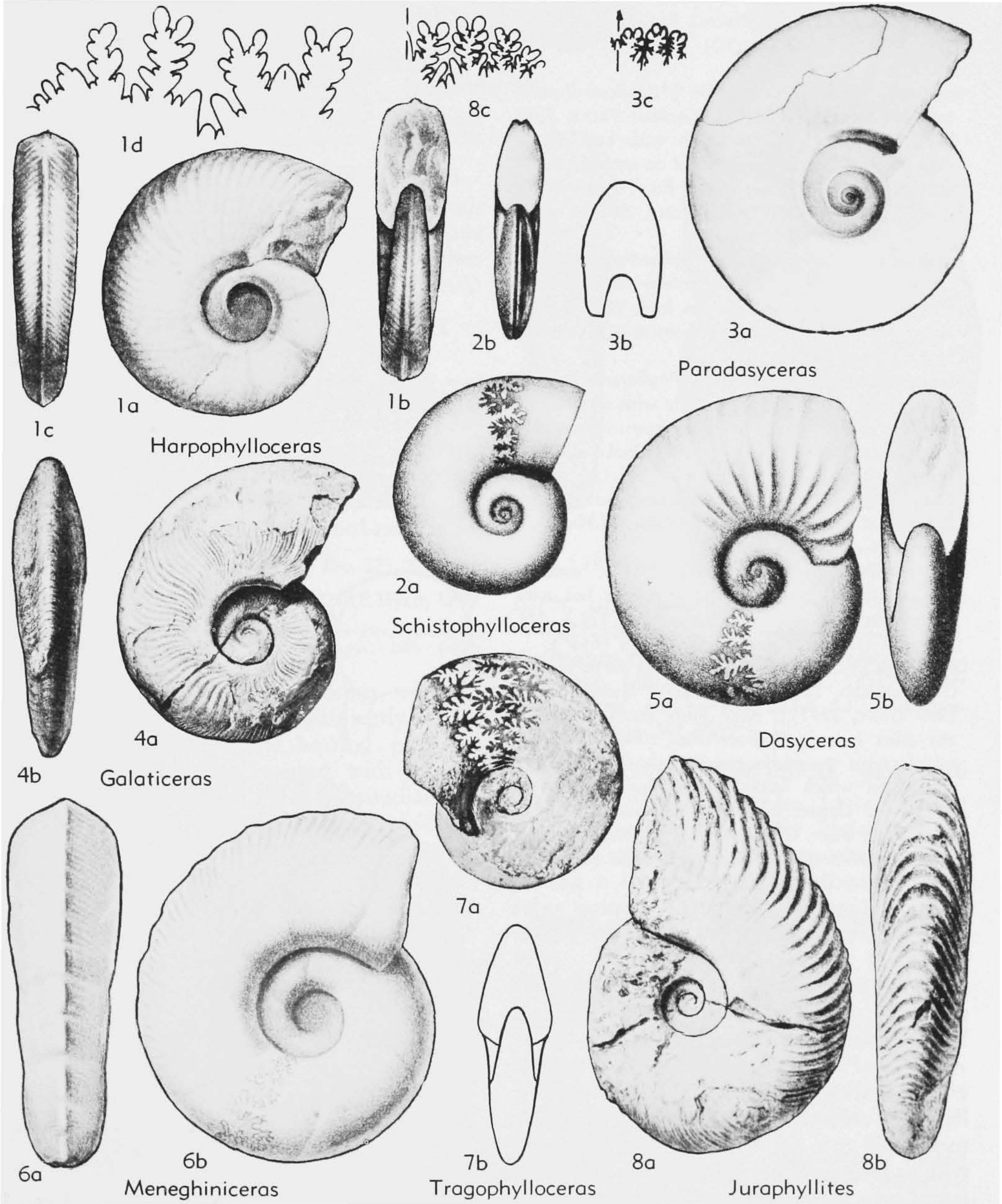


Fig. 221. Juraphyllitidae (p. L191-L192).

angle blunt; ventral half of outer whorl with falcoid foldlike ribs which become plications as they cross venter. *Pliensb.*——Fig. 221,*7*. **T. numismalis* (Quenst.); *7a,b,* ×0.3 (65*).

Dasyceras Hyatt, 1900 [**Phylloceras rakosense* Herbich, 1878] [=*Paradadyceras* Cossmann, 1901 (obj.)]. Evolute; inner whorls smooth, outer whorl gradually developing coarse falcoid ribs which originate close to umbilical margin and do not pass on to venter. *Sinem.*, Eu.——Fig. 221,*5*. **D. rakosense* (Herbich), SE.Eu.; *5a,b,* ×1 (635*).

Schistophylloceras Hyatt, 1900 [**Phylloceras aulonotum* Herbich, 1878] [=*Kochites* Prinz, 1905 (obj.)]. Evolute, smooth shells with keel, which may correspond to ventral sulcus on internal mold; umbilical slope blunt. *Hett.*, Eu.-Tibet.——Fig. 221,*2*. **S. aulonotum* (Herbich), SE.Eu.; *2a,b,* ×0.7 (635*).

Paradasyceras Spath, 1923 [**Phylloceras ürmösense* Herbich, 1878]. Smooth, compressed, evolute, with sharp umbilical angle, no keel. *Hett.* Eu.-N. Caled.——Fig. 221,*3*. **P. uermoesense* (Herbich), SE.Eu.; *3a-c,* ×0.25 (550*).

Meneghiniceras Hyatt, 1900 [**Phylloceras lariense* Meneghini, 1867]. Evolute shells with simple, forward-curved or gently sigmoid constrictions (on type species 8 per whorl); and on body chamber ventral ribbing and median row of clavi which form a serrated keel. *Sinem.-Pliensb.*, Eu.——Fig. 221,*6*. **M. lariense* (Men.), L.Jur.(U.Pliensb.), Italy; *6a,b,* ×0.75 (660*).

Harpophylloceras Spath, 1927 [**Am. eximius* Hauer, 1854]. Similar to *Juraphyllites* but with continuous keel. *Pliensb.*, Eu.——Fig. 221,*1*. **H. eximium* (Hauer), Aus.; *1a-d,* ×0.75 (633*).

Galaticeras Spath, 1938 [**Amphiceras harpoceroides* Gemmellaro, 1884] [*Amphiceras* Gemm., 1884 (*non* Gray, 1847)]. Shell more evolute than in any other Jurassic Phylloceratina, compressed, discoidal, with rounded-quadrate, slowly enlarging whorls on which feeble juraphyllitid ribbing remains, but sutures have lost their phylloid character as in some Cretaceous forms. *Pliensb.*, Eu.-?Cauc.——Fig. 221,*4*. **G. harpoceroides* (Gemm.), Italy; *4a,b,* ×0.5 (627*).

Suborder LYTOCERATINA Hyatt, 1889

[*nom. correct.* Arkell, 1950 (*pro* suborder Lytoceratinae Hyatt, 1889)] [=Lytocerataceae Buckman, 1894 (ranked as suborder)] [Both Hyatt and Buckman included Triassic genera in this division of the ammonoids, although no pre-Jurassic forms now are placed here.]

Evolute, loosely coiled, usually round-whorled shells, ornamented with growth lines and commonly flares, rarely ribbed. Sutures with few but very complex elements, with mosslike endings, usually not phylloid; septal lobe present in some. Aptychi single-valved, with shiny surface, striated concentrically (Anaptychus) (found *in situ* in *Lytoceras cornucopia* Young & Bird L. Toarc. and various Cret. forms). Descended from Triassic Ussuritidae or Discophyllitidae or both, but not known from the Rhaetian (62, 63, 200). *Jur.-Cret.*, world-wide, but especially abundant in Tethyan and Pacific realms, though occurring at certain horizons as far north as Greenl.

Superfamily LYTOCERATACEAE Neumayr, 1875

[*nom. transl.* Arkell, 1950 (*ex* Lytoceratidae Neumayr, 1875)] [*non* Lytocerataceae Buckman, 1894 (ranked as suborder)]

Coiled Lytoceratina which persisted throughout Jurassic and most of Cretaceous and periodically gave off more or less uncoiled families, especially in Cret. (12). *Jur.-Cret.*

Family PLEUROACANTHITIDAE Hyatt, 1900

[*nom. correct.* Arkell, 1950 (*pro* Pleuracanthitidae Hyatt, 1900; validation proposed Arkell, 1955, ICZN pend.)]

Lytocerataceae which combine some characters of Lytoceratina, Phylloceratina, and earliest Ammonitina, and show as well special characters of their own. *L.Jur.(Hett.),* S.Eu-Tibet-Indon.

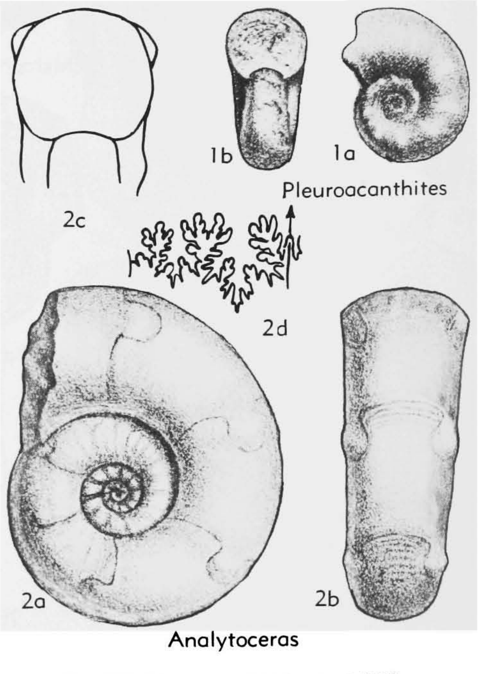


Fig. 222. Pleuroacanthitidae (p. L193).

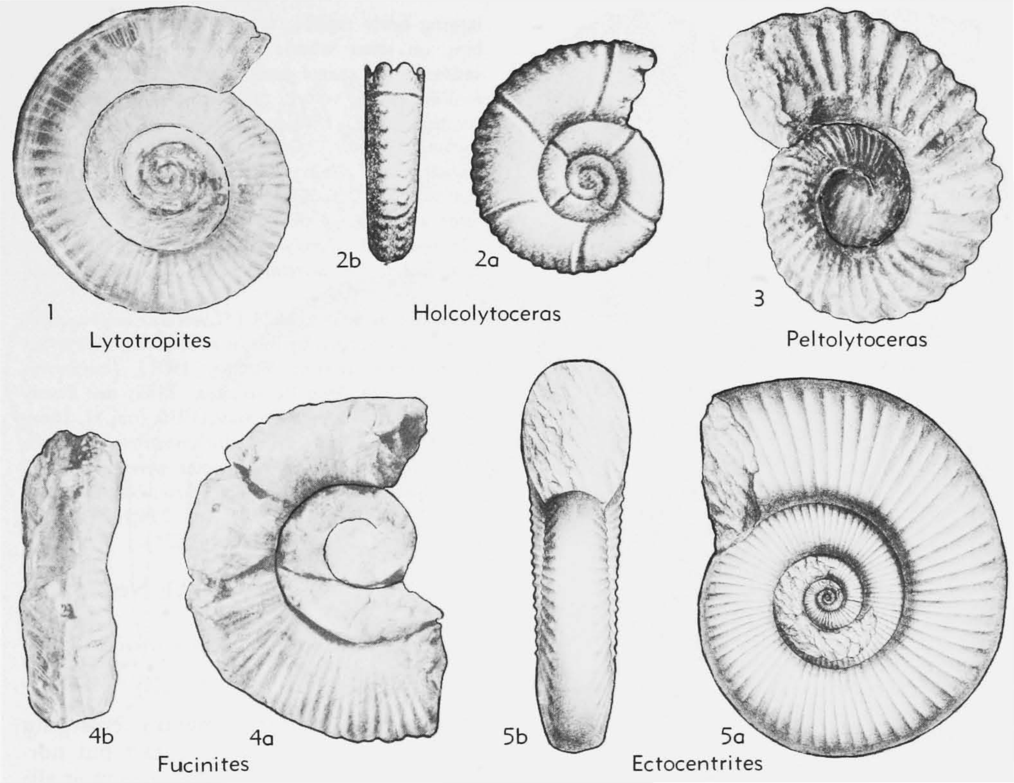


FIG. 223. Ectocentritidae (p. L193-L194).

Subfamily PLEUROACANTHITINAE Hyatt, 1900

[*nom. transl. et correct.* ARKELL, 1950 (*ex* Pleuracanthitidae HYATT, 1900), validation proposed ARKELL, 1955 (ICZN pend.)]

Very evolute, whorls numerous, subcircular in section, becoming incipiently keeled in adult; early whorls bearing parabolic nodes, later whorls covered with oblique parabolic lines which are rursiradiate on sides, prorsiradiate on shoulders, and form a long ventral sinus. Sutures with general plan and lobes of Lytoceratina but saddle endings more or less phylloid (12, 201, 550). *L.Jur.(Hett.).*

Pleuroacanthites CANAVARI, 1883 [**Am. biformis* J.DEC.SOWERBY, 1831 (fig'd CANAVARI, 1882); SD HAUG, 1889] [=*Pleuracanthites* ZITTEL, 1884 (obj.)]. Only genus. *Hett.,* Italy.——FIG. 222,*1*. **P. biformis* (Sow.); *1a,b,* ×1 (597*).

Subfamily ANALYTOCERATINAE Spath, 1927

[*nom. transl.* ARKELL, 1950 (*ex* Analytoceratidae SPATH, 1927)]

Inner whorls constricted; middle whorls with parabolic lines and conspicuous parabolic nodes; outer whorls with sigmoid flares; adult body chamber with ventrolateral spines (466, 550). *L.Jur.(Hett.).*

Analytoceras HYATT, 1900 [**Am. articulatus* J. DE C. SOWERBY, 1831 (fig'd WAEHNER, 1894)]. Only genus. *Hett.,* Aus.——FIG. 222,*2*. **A. articulatum* (Sow.); *2a-d,* ×1 (550*).

Family ECTOCENTRITIDAE Spath, 1926

Straight-ribbed planulate Lytoceratacea with smooth or incipiently keeled venter; sutures complex, of lytoceratacean type but having a longer ventral lobe, with lateral lobes more symmetrical and produced and saddle endings tending to be phylloid (466, 550). *L.Jur.(Hett.-Sinem.),* one genus *L. Pliensb.,* S.Eu.-N.Afr.-Tibet-Indon.-N.Z.

Ectocentrites CANAVARI, 1888 [**Am. petersi* HAUER, 1856; SD BONARELLI, 1900] [incl. *Cosmolytoceras* SPATH, 1924]. Ribs fine to medium; venter broad, smooth, flattened; whorls quadrate or rounded; no constrictions. *Hett.* Aus.——FIG. 223,*5*. **E. petersi* (HAUER); *5a,b,* ×0.3 (550*).

Lytotropites SPATH, 1924 [**Ectocentrites fucinii* BONARELLI, 1900]. Very evolute, constricted; whorl depressed, rounded, with straight, large but weak radial ribs; venter with incipient keel. (?Sub-

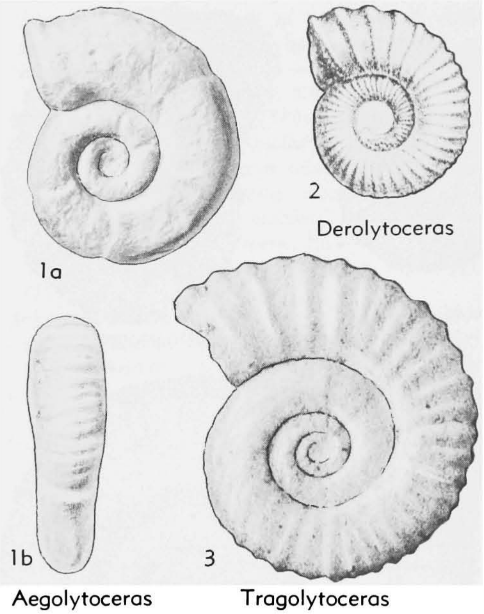


FIG. 224. Derolytoceratidae (p. L194).

gen. of *Ectocentrites.*) *Sinem.*, Italy.——FIG. 223, *1*. **L. fucinii* (BON.); ×0.3 (42*).

Fucinites GUGENBERGER, 1936 [**F. sicilianus;* SD ARKELL, herein]. Resembles *Lytotropites* but whorl shape has divergent sides and ribbing is finer. (?Subgen. of *Ectocentrites.*) *Hett.*, Sicily.——FIG. 223,*4*. **F. sicilianus* GUG.; *4a,b,* ×0.5 (181*).

Holcolytoceras SPATH, 1924 [**Am. nodostrictus* QUENSTEDT, 1885]. Compressed, planulate, very evolute, whorl shape quadrate-elliptical; inner whorls smooth; internal mold of outer whorls develops comma-shaped ventrolateral bullae which probably represent ribs on test; about 4 to 6 deep constrictions per whorl. Sutures as in *Ectocentrites. L.Pliensb.(ibex z.)*, Ger.——FIG. 223,*2*. **H. nodostrictus* (QUENST.); *2a,b,* ×2 (682*).

Peltolytoceras SPATH, 1924 [**Ectocentrites giordanii* BONARELLI, 1900]. Massively ribbed *Schlotheimia*- or *Peltoceras*-like forms; whorls enlarging rapidly, subquadrate to somewhat compressed, covered with large, strong, simple ribs, which project beyond ventrolateral angle, but leave middle of venter smooth. *Sinem.*, Italy.——FIG. 223,*3*. **P. giordanii* (BON.); ×0.3 (42*).

Family DEROLYTOCERATIDAE Spath, 1927

Lytocerataceae developing capricorn ornament. *L.Jur.(Sinem.-Pliensb.)*.

Derolytoceras ROSENBERG, 1909 [**Am. lineatus tortus* QUENSTEDT, 1885; SD ROMAN, 1938] [=*Dolytoceras* ROMAN, 1938 (obj.), ?misprint]. Small forms, evolute, whorls only just in contact but enlarging fairly rapidly, subquadrate in section; ribbing on inner whorls fine and dense, changing suddenly to coarse and prorsiradiate, becoming foldlike across venter. Sutures as in young Lytoceratidae (466). *U.Pliensb.*, Eu.——FIG. 224,*2*. **D. tortum* (QUENST.), Ger.; ×2 (682*).

Tragolytoceras SPATH, 1924 [**Am. altecinctus* HAUER, 1866]. Similar to *Derolytoceras* but larger and with coarse ribs starting more gradually. (?Subgen. of *Derolytoceras.*) *Sinem.*, S.Eu.——FIG. 224,*3*. **T. altecinctum* (HAUER), Italy; ×1 (42*).

Aegolytoceras SPATH, 1924 [**Lytoceras serorugatum* GEYER, 1886, cited by SPATH as *Lytoceras (Geyeria) serorugatum* (STUR) FUCINI, 1901] [=*Geyeria* FUCINI, 1901 (*non* BUCHECKER, 1880; *nec* BUCKMAN, 1899); *Fucinia* TOMLIN, 1930 (obj.)]. Inner whorls round, smooth but for constrictions which are gently convex forward; outer whorl becoming compressed and developing coarse, blunt, curved ventral ribs. *Pliensb.*, Eu.——FIG. 224,*1*. **A. rugatum* (STUR), Italy; *1a,b,* ×1 (162*).

Family LYTOCERATIDAE Neumayr, 1875

[*sic;* NEUMAYR used correct form of designation for this assemblage but inconsistently used vernacular names only for some other families] [=Thysanoidae HYATT, 1867; incl. Hemilytoceratinae SPATH, 1927]

Shells very evolute, generally enlarging rapidly, having whorls in contact but normally overlapping only slightly or not at all; surface ornamented with various combinations of straight or crinkled growth lines, flares, constrictions and, more rarely, plications. Sutures highly complex, with mosslike detail but few major elements; lateral lobes widely splayed and blunt or obliquely deflected at ends; external lobe short. Aptychus single-valved (Anaptychus) (466). *Jur.-Cret.*, world-wide.

Subfamily LYTOCERATINAE Neumayr, 1875

Whorls bearing growth lines or lamellar flares or both, corresponding commonly to constrictions on internal mold. External suture with 2 lateral lobes, of which 1st is much the larger, internal suture with cruciform dorsal lobe (466). *L.Jur.(Pliensb.)-U. Cret.(Cenom.)*.

Lytoceras SUESS, 1865 [**Am. fimbriatus* J.SOWERBY, 1817; ICZN Opinion 130] [=*Ophiceras* SUESS, 1865 (obj.) (*non* GRIESBACH, 1880, ICZN-validated L.Trias. genus; *Fimbrilytoceras* BUCKMAN, 1918 (obj.); *Thysanoceras* HYATT, 1867; *Thysanolytoceras* BUCK., 1905; *Kallilytoceras* BUCK., 1921; *Crenilytoceras* BUCK., 1926]. Whorls round or quadrate, covered with crinkled growth lines or riblets; some species with lamellar flares, under

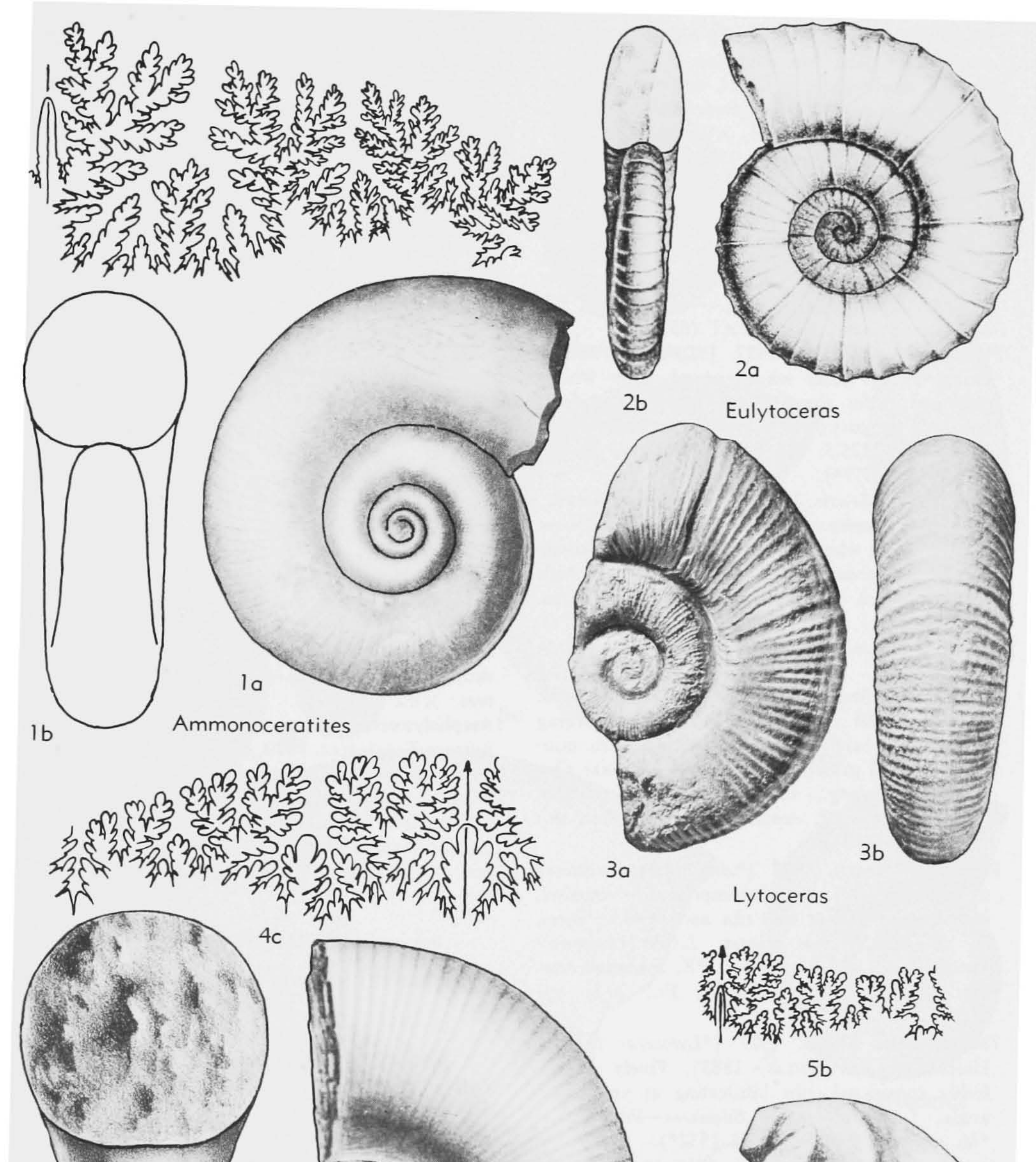


FIG. 225. Lytoceratidae (p. L194-L196).

which slight constriction usually occurs on internal mold; some with fine strigation. *L.Jur.(Sinem.)-U.Cret.*, world-wide, as far N. as Greenl. and N. Alaska.——FIG. 225,*3*. **L. fimbriatum* (SOW.), L. Jur.(L.Pliensb.), Eng.; *3a,b*, ×0.5 (65*).

Trachylytoceras BUCKMAN, 1913 [**Am. nitidus* YOUNG & BIRD, 1828] [*?Orcholytoceras* BUCK., 1926]. Smooth but for rursiradiate plain growth lines which stand out as irregularly spaced rings of variable size. If *Orcholytoceras* is congeneric, the larger species have later growth lines minutely crinkled. *L.Jur.(Toarc.)*, Eng.——FIG. 226,*3*. **T. nitidum* (YOUNG-B.); *3a,b*, ×1 (65*).

Ptycholytoceras SPATH, 1927 [**Lytoceras humile* PRINZ, 1904]. Inner whorls round, outer whorls depressed; sides thrown into prorsiradiate folds which do not pass on to venter. *L.Jur.(Toarc.)*, SE. Eu.——FIG. 225,*5*. **P. humile* (PRINZ), Hung.; *5a,b*, ×0.7 (357*).

Hemilytoceras SPATH, 1927 [**Am. immanis* OPPEL, 1865] [*?Saturnoceras* ANDERSON, 1938 *(nom. nud.)*]. Inner whorls round, smooth, outer whorls becoming depressed and in some developing high lamellae which bend forward over venter. *U.Jur.(Oxf.-Tithon.)*, S.Eu.-C.Eu.-N.Afr.-Cutch.——FIG. 226,*2*. **H. immane* (OPPEL), U.Jur.(Tithon.), Eu.; ×0.7 (389*).

Pterolytoceras SPATH, 1927 [**Am. exoticus* OPPEL, 1863]. Whorls subcircular in section, enlarging very slowly, barely in contact; surface with minutely crinkled growth lines and fine irregular ribs. *?Tithon., Valang.*, Himalaya(Spiti sh.)-Punjab.——FIG. 226,*1*. **P. exoticum* (OPPEL), Spiti sh.; *1a-c*, ×0.5 (533*).

Eulytoceras SPATH, 1927 [**Am. inaequalicostatus* D'ORBIGNY, 1840]. Whorls compressed or rounded, with regular distant fine ribs and periodic flares, all of which cross venter. *L.Cret.(Hauteriv.-Barrem.)*, Eu.——FIG. 225,*2*. **E. inaequalicostatum* (ORB.), L.Cret.(Barrem.), Fr.; *2a,b*, ×1 (329*).

?**Metalytoceras** SPATH, 1927 [**Lytoceras triboleti* HOHENEGGER in UHLIG, 1883]. Finely ribbed, feebly constricted, ribs bifurcating at very acute angle. *L.Cret.(Valang.)*, Silesia.——FIG. 227,*4*. **M. triboleti* (HOHEN.); ×1 (532*).

Ammonoceratites RAFINESQUE, 1815 [**A. lamarcki* BOWDITCH, 1822] [*Ammonoceras* LAMARCK, 1822]. Large, evolute; whorls almost circular, only just in contact; with dense, strongly crinkled fine ribs or growth lines. *L.Cret.(U.Apt.)-U.Cret.(Cenom.)*, Eu.-Sinai-India-Greenl.——FIG. 225,*1*. *A. (A.) mahadeva* (STOLICZKA), U.Alb., S.India; *1a,b*, ×0.25; *1c*, ×0.5 (718*).

Argonauticeras ANDERSON, 1938 [**Lytoceras argonautarum* ANDERSON, 1902]. Whorl section trapezoidal, whorls increasing rapidly in height; ribs weakly crinkled. (Subgen. of *Ammonoceratites*.) *L.Cret.(U.Apt.)*, Fr.-Cauc.-Calif., *?L.Cret.(?M.Alb.)*, Madag.——FIG 226,*7* **A. (A.) argonautarum* (ANDERSON), L.Cret.(U.Apt.), Calif.; *7a,b*, ×0.5 (580*).

Pictetia UHLIG, 1883 [**Crioceras astierianum* D'ORBIGNY, 1842]. Loosely coiled with whorls not touching, section circular to depressed; body chamber may straighten; surface with feeble, irregular, weakly crinkled ribs. *L.Cret.(L.Alb.-M.Alb.)*, W. Eu.-Madag.-India.——FIG. 225,*4*. **P. astieriana* (ORB.), L.Cret.(M.Alb.), Fr.; *4a-c*, ×0.75 (329*).

Subfamily MEGALYTOCERATINAE Spath, 1927

Planulate forms which tend to lose lytoceratid characters of whorls and sutures and to resemble perisphinctids (466). *L.Jur.(Toarc.)-M.Jur.(Baj.)*, mainly *Baj.*

Megalytoceras BUCKMAN, 1905 [**Lytoceras confusum* BUCK., 1881]. Early whorls elliptical in section, bearing periodic flares; later whorls becoming smooth and planulate, with convergent sides, rather wide umbilical area and abrupt umbilical edge. *M.Baj.*, Eng.——FIG. 226,*5*. **M. confusum* (BUCK.); *5a,b*, ×0.3 (595*).

Metrolytoceras BUCKMAN, 1923 [**M. metretum*]. Early whorls unknown; middle and outer whorls smooth, planulate, with flat sides. Sutures much simplified. *M.Baj.*, Eng.——FIG. 226,*6*. **M. metretum;* ×0.2 (65*).

?**Asapholytoceras** SPATH, 1927 [**Lytoceras forojuliense* TARAMELLI, 1880, cited by SPATH as *Lytoceras forojuliense* MENEGHINI in PRINZ, 1904]. Whorls high, compressed, with fine riblets or growth lines which do not show on internal mold; umbilical angle sharp. Exernal suture with 4 lateral lobes; dorsal lobe not cruciform. *Toarc.*, SE. Eu.

Subfamily VILLANIINAE Arkell, nov.

Planulates retaining typical lytoceratid external sutures but lacking cruciform character of dorsal lobe and with somewhat peltoceratid type of ribbing (505). *M.Jur.(Callov.)*.

Villania TILL, 1911 [**V. densilobata*]. Inner whorls compressed, ribbed on sides; outer whorls smooth, rounded. [LOCZY'S (1915, p. 422, pl. 8, 10, 13) identification of several ordinary perisphinctids with *V. densilobata* cannot be accepted.] *M.Jur.(Callov.)*, Hung.-Ger.——FIG. 227,*3*. **V. densilobata*, Hung.; *3a,b*, ×0.7 (505*).

Subfamily ALOCOLYTOCERATINAE Spath, 1927

Forms with many deep constrictions, which produce some resemblance to capricorns in middle whorls but pass to a smooth and more involute stage. Saddle endings of sutures tend to be phylloid (466). *L.Jur.(Toarc.)-M.Jur.(Baj.)*.

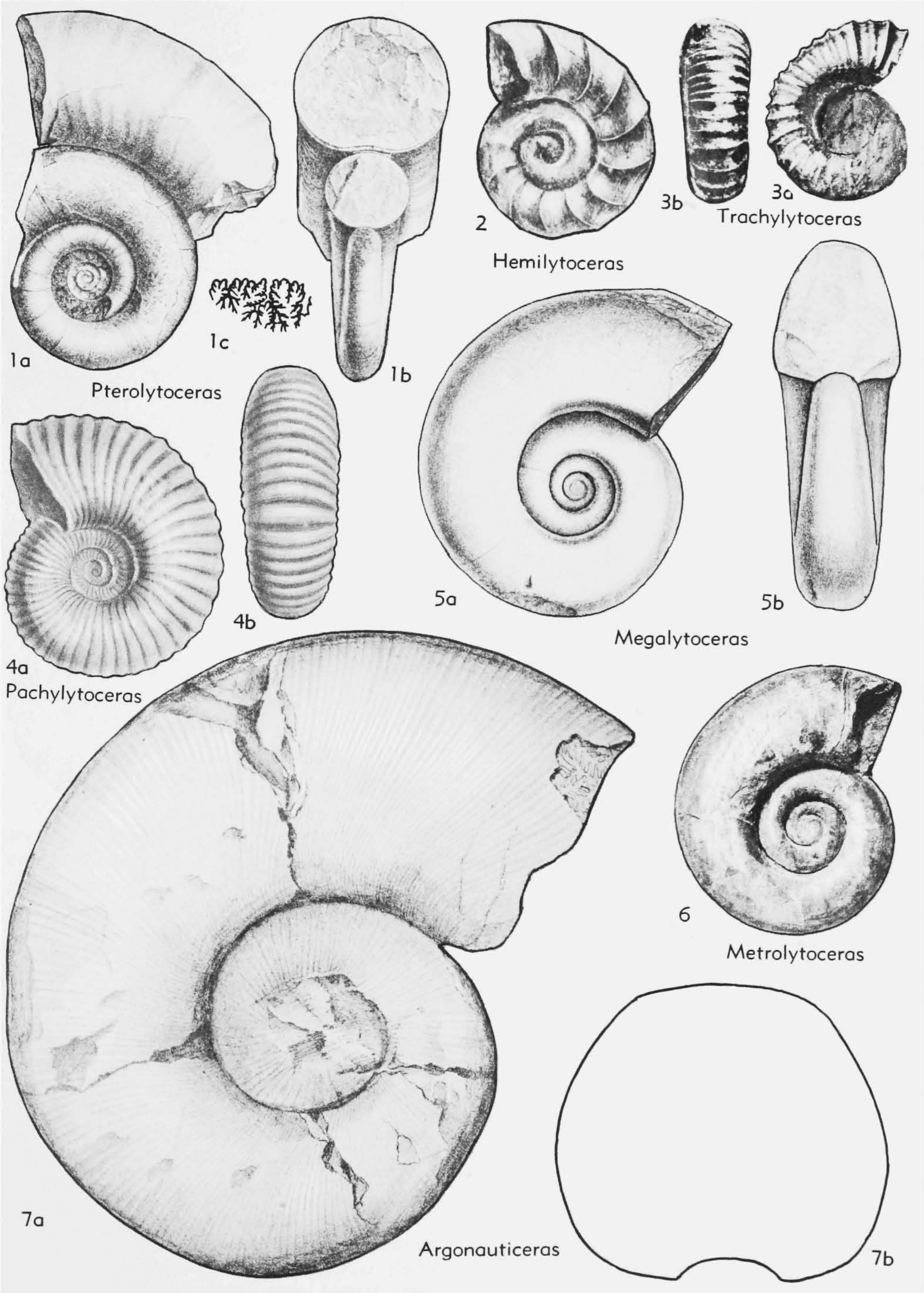


Fig. 226. Lytoceratidae (p. L194-L198).

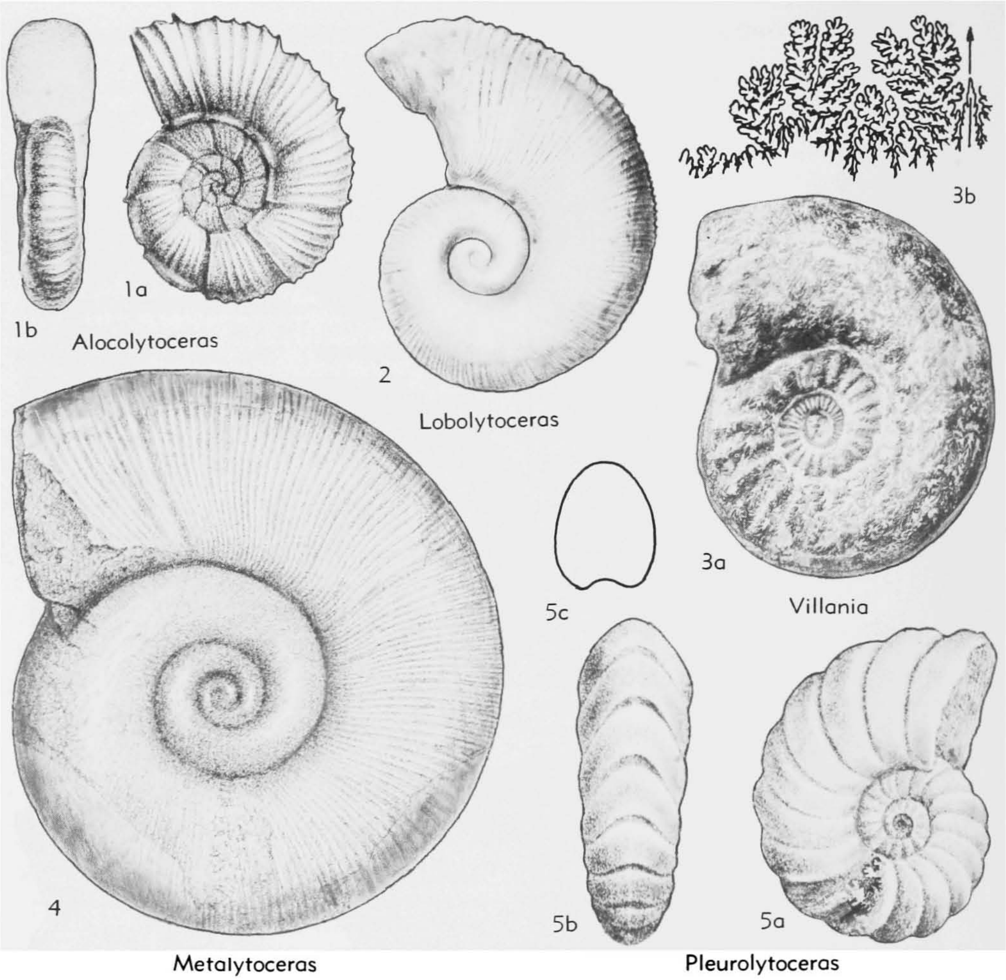


FIG. 227. Lytoceratidae (p. L196-L198).

Alocolytoceras Hyatt, 1900 [*_Am. germaini_ d'Orbigny, 1845]. Whorls passing from round to oval, rounded-quadrate, or compressed; with about 10 deep constrictions per whorl and 4 to 20 sharp ribs between constrictions. _Toarc.,_ Eu.-Himalaya. ——Fig. 227,_1_. *_A. germaini_ (Orb.), Fr.; _1a,b,_ ×1 (330*).

Pleurolytoceras Hyatt, 1900 [*_Am. hircinus_ Schlotheim, 1820 (fig'd Quenst., 1849)]. Whorl section triangular-elliptical, with narrower venter, constrictions more numerous (17 per whorl in type) and interspaces smooth. _Toarc.,_ Eu.——Fig. 227,_5_. *_P. hircinus_ (Schloth.), Ger.; _5a-c,_ ×1 (358*).

Pachylytoceras Buckman, 1905 [*_Am. torulosus_ Zieten, 1831]. Early whorls round, generally with numerous constrictions, which break up surface into a series of swollen ribs; later whorls becoming elliptical. In the _jurense_ group constrictions fail on middle and outer whorls, or in some species entirely, leaving whole shell smooth. _Toarc.-L.Baj.,_ Eu.-Crimea-E.Asia-Indon.——Fig. 226,_4_. *_P. torulosum_ (Zieten), Toarc., Ger.; _4a,b,_ ×0.5 (742*).

Lobolytoceras Buckman, 1923 [*_Am. siemensi_ Denckmann, 1887]. Innermost whorls only have large swollen ribs; later whorls become compressed-elliptical with crinkled growth lines or riblets, which coarsen somewhat near aperture and develop strigation. _Toarc.,_ Eu.——Fig. 227,_2_. *_L. siemensi_ (Denck.), U.Toarc., Ger.; ×0.25 (605*).

Family NANNOLYTOCERATIDAE
Spath, 1927

Dwarf, evolute, compressed, unribbed forms, with deep constrictions. Sutures relatively simple, with long ventral lobe and 2 main lateral lobes (466). _L.Jur.(U.Pliensb.)-M.Jur.(Bath.)._

Nannolytoceras Buckman, 1905 [**Am. pygmaeus* d'Orbigny, 1846] [*Polystomiceras* Spath, 1924; *Polystomites* Spath, 1931]. Smooth, many-whorled, with varying number of deep constrictions, which are oblique to acutely sigmoid, running forward on whorl sides, backward on venter; whorl section quadrate. *Baj.-Bath.*, Eu.-N.Afr.——Fig. 228,*2*. **N. pygmaeum* (Orb.), Baj., Fr.; *2a-c*, ×1 (330*).

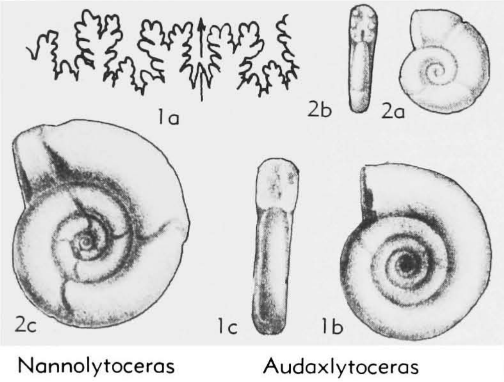


Fig. 228. Nannolytoceratidae (p. L199).

?**Audaxlytoceras** Fucini, 1923 [**Lytoceras audax* Meneghini, 1881; SD Arkell, herein]. Small, evolute, smooth, compressed, with a few narrow constrictions, which are gently convex forward on whorl sides and straight over venter. *U.Pliensb.*, Italy.——Fig. 228,*1*. **A. audax* (Men.); *1a-c*, ×1 (660*).

Family PROTETRAGONITIDAE Spath, 1927

Very evolute, with circular to oval whorl section and regular radial straight or slightly curved constrictions; test smooth or with fine gowth lines only. Suture with a tendency to develop one or more auxiliaries. Probably derived from *Lytoceras (s.s.)*, young whorls of which commonly have a few strong constrictions, as in *Protetragonites* (466). *U.Jur.(U.Tithon.)-L.Cret. (M.Alb.)*.

Protetragonites Hyatt, 1900 [**Am. quadrisulcatus* d'Orbigny, 1840]. Whorl section circular; constrictions few, straight to slightly curved. *U.Jur. (U.Tithon.)-L.Cret.(Valang.)*, Eu.——Fig. 229,*1*. **P. quadrisulcatus* (Orb.), Valang., Fr.; *1a,b*, ×1 (329*).

Leptotetragonites Spath, 1927 [**Am. honnoratianus* d'Orbigny, 1840]. Section compressed oval; 10 or more constrictions to whorl, with strong, rounded rib in front. *L.Cret.(Berrias.-Valang.)*, Fr.——Fig. 229,*2*. **L. honnoratianus* (Orb.), Valang., Fr.; ×0.75 (329*).

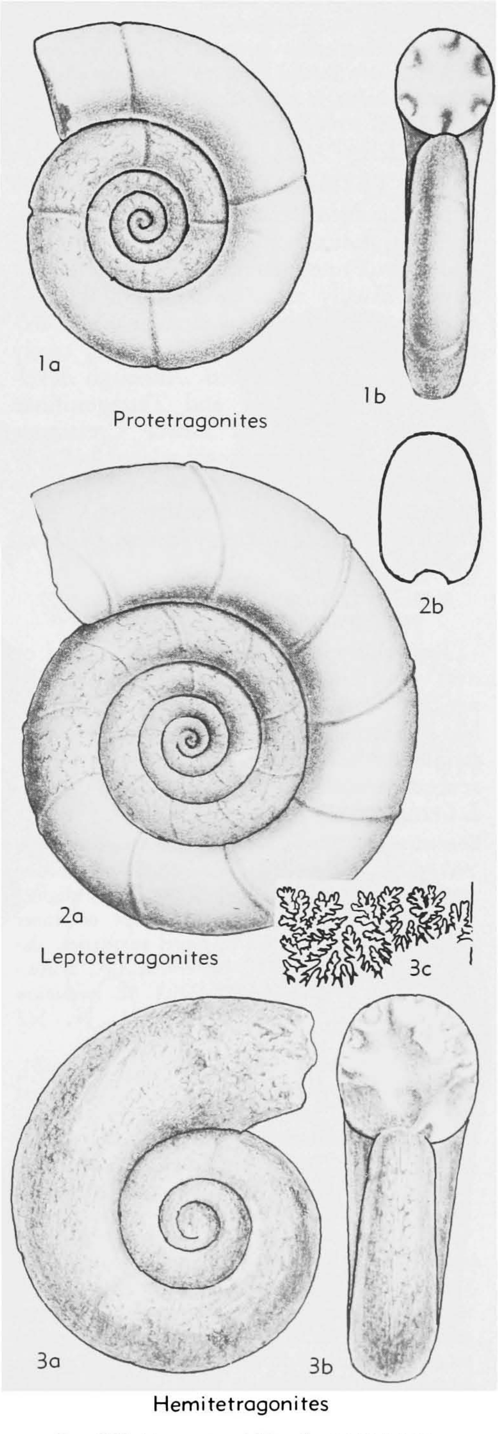


Fig. 229. Protetragonitidae (p. L199-L200).

Hemitetragonites SPATH, 1927 [**Am. crebrisulcatus* UHLIG, 1883]. Whorl section more or less round but tending to be slightly flattened on sides and venter; constrictions straight or slightly curved. Suture more incised than in *Protetragonites*. *L. Cret.(Hauteriv.-M.Alb.)*, Fr.-C.Eu.-Madag.——FIG. 229,*3*. **H. crebrisulcatus* (UHLIG), Barrem., Aus.; *3a-c*, ×1 (530*).

Family TETRAGONITIDAE Hyatt, 1900

Distinguished from Lytoceratidae by having several auxiliary elements in the suture and from Protetragonitidae, its ancestor, in having usually more auxiliaries and being more involute, with less circular whorl section. Shell lirate, striate or smooth, rarely folded or strongly ribbed. Although developed Gaudryceratinae and Tetragonitinae are very distinct, the Lower Cretaceous members are all very closely related and subfamilial separation, as recommended by BREISTROFFER, seems adequate (53, 214, 230, 238, 571). *L.Cret.(Barrem.)-U.Cret.(Maastr.)*.

Subfamily GAUDRYCERATINAE Spath, 1927

[Includes Hypogaudryceratinae SHIMIZU, 1934]

Typically with rounded and depressed or oval whorl section, becoming higher with age, very fine to coarse lirae. With more or less symmetrically bifid saddles and a single saddle in the internal suture, but there are several exceptions (53, 214, 230, 238, 571). *L.Cret.(Barrem.)-U.Cret.(Maastr.)*.

Eogaudryceras SPATH, 1927 [**Am. numidus* COQUAND in SAYN, 1890]. Evolute, whorl section round to rounded-trapezoidal; fine, dense slightly sinuous lirae; no constrictions except on inner whorls. Suture with 2 or more auxiliaries, descending in straight line. *Barrem.-M.Alb.*, W.Eu.-C.Eu.-N.Afr.-Madag.——FIG. 230,*1*. **E. numidum* (COQUAND), U.Apt., Fr.; *1a,b*, ×1; *1c*, ×2 (214*).

Eotetragonites BREISTROFFER, 1947 [**E. raspaili*]. Differs from *Eogaudryceras* only in its slightly less regularly bifid saddles of suture, its emphatic oblique dense constrictions and (in some species only) its more angular whorl section. Internal suture still has only one saddle. *?Barrem., U.Apt.-L.Alb.*, S.Eu.-C.Eu.-?Madag.-N.Afr.——FIG. 230,*3*. **E. raspaili*, U.Apt., Fr.; *3a,b*, ×1 (229*).

Anagaudryceras SHIMIZU, 1934 [**Am. sacya* FORBES, 1846] [=*Paragaudryceras* SHIMIZU, 1934]. Inner whorls with circular to rather depressed but not angular whorl section, becoming higher than wide on outer whorls; shell with very fine more or less straight but prorsiradiate lirae, rarely smooth; some bearing periodic weak constrictions with strong collar; body chamber usually with more or less strong foldlike ribs. *U.Alb.-Maastr.*, S.Eu.-C.Eu.-N.Afr.-Madag.-S.India-Japan.——FIG. 230,*4*. **A. sacya* (FORBES), Cenom., S.India; ×1 (620*).

Mesogaudryceras SPATH, 1927 [**Am. leptonema* SHARPE, 1855]. Early whorls compressed, later whorls less so, sides convex, venter narrowly rounded. Sinuous lirae and absence of constrictions distinguish it from *Anagaudryceras* and *Zelandites* and nature of early whorl section from *Gaudryceras*. Suture with shallow external lobe. *Cenom.*, Eng.-Greenl.——FIG. 232,*1*. **M. leptonema* (SHARPE), Eng.; *1a,b*, ×1 (440*).

Zelandites MARSHALL, 1926 [**Z. kaiparaensis*] [=*Varunaites* SHIMIZU, 1926; *Hypogaudryceras* SHIMIZU, 1934; *Anazelandites* MATSUMOTO, 1938]. Small; initially with round whorl section but rapidly becoming more high-whorled and involute; compressed, nearly smooth and with weak to strong, straight or sinuous, radial or prorsiradiate constrictions in some shells marked on outside by a threadlike rib. Suture with very asymmetrical 1st lateral lobe in adult. May include a series of compressed offshoots of other genera but no real distinction is seen between species groups of different dates. *U.Alb.-Maastr.*, N.Afr.-SE.Afr.-S.India-Japan-N.Z.-Chile.——FIG 230,*5a,b*. **Z. kaiparaensis* Camp., N.Z.; *5a*, ×1.5; *5b*, ×7 (274*).——FIG. 230,*5c*. *Z. varuna japonica* MATSUMOTO, Camp., Japan; ×1 (659*).

Parajaubertella MATSUMOTO, 1943 [**P. kawakitana*]. Like *Anagaudryceras* at first but whorls rapidly become very depressed, with broad rounded ribs on last whorl. *?Cenom.*, Japan.——FIG. 231,*5*. **P. kawakitana*; *5a,b*, ×4 (659*).

Gaudryceras GROSSOUVRE, 1894 [**Am. mitis* HAUER, 1866; SD BOULE, LEMOINE & THEVENIN, 1906] [*Epigaudryceras*, *Pseudogaudryceras* SHIMIZU, 1934; *Neogaudryceras* SHIMIZU, 1935]. Lirae coarser than in *Anagaudryceras*, close or distant, simple or branching, moderately to very sinuous; last whorl may bear variable close or distant strong foldlike ribs. Suture with retracted auxiliaries. May be divisible into subgenera but nominal groups cited in synonymy are not well differentiated. *Turon.-Maastr.*, world-wide except N.Eu.-N.Am.——FIG. 230,*6*. *G. varagurense* KOSSMAT, Santon., S.India; *6a-c*, ×1 (238*).

Vertebrites MARSHALL, 1926 [**V. murdochi*]. With many more whorls, depressed to a later stage than in rest of family; shoulders tending to be nearly angular; lirae very fine, branching regularly at shoulder into still finer ones. Internal suture (at least in type species) with several saddles, decreasing in size to umbilical suture. *Santon.-Maastr.*, N.Afr.-Madag.-S.India-N.Z.-Japan-Calif.-Mex.-Chile.——FIG. 230,*2*. **V. murdochi*, Camp., N.Z.; *2a*, ×1; *2b*, ×2; *2c*, ×4.5; *2d*, ×3 (274*).

Subfamily KOSSMATELLINAE Breistroffer, 1953

Depressed or oval whorl section with

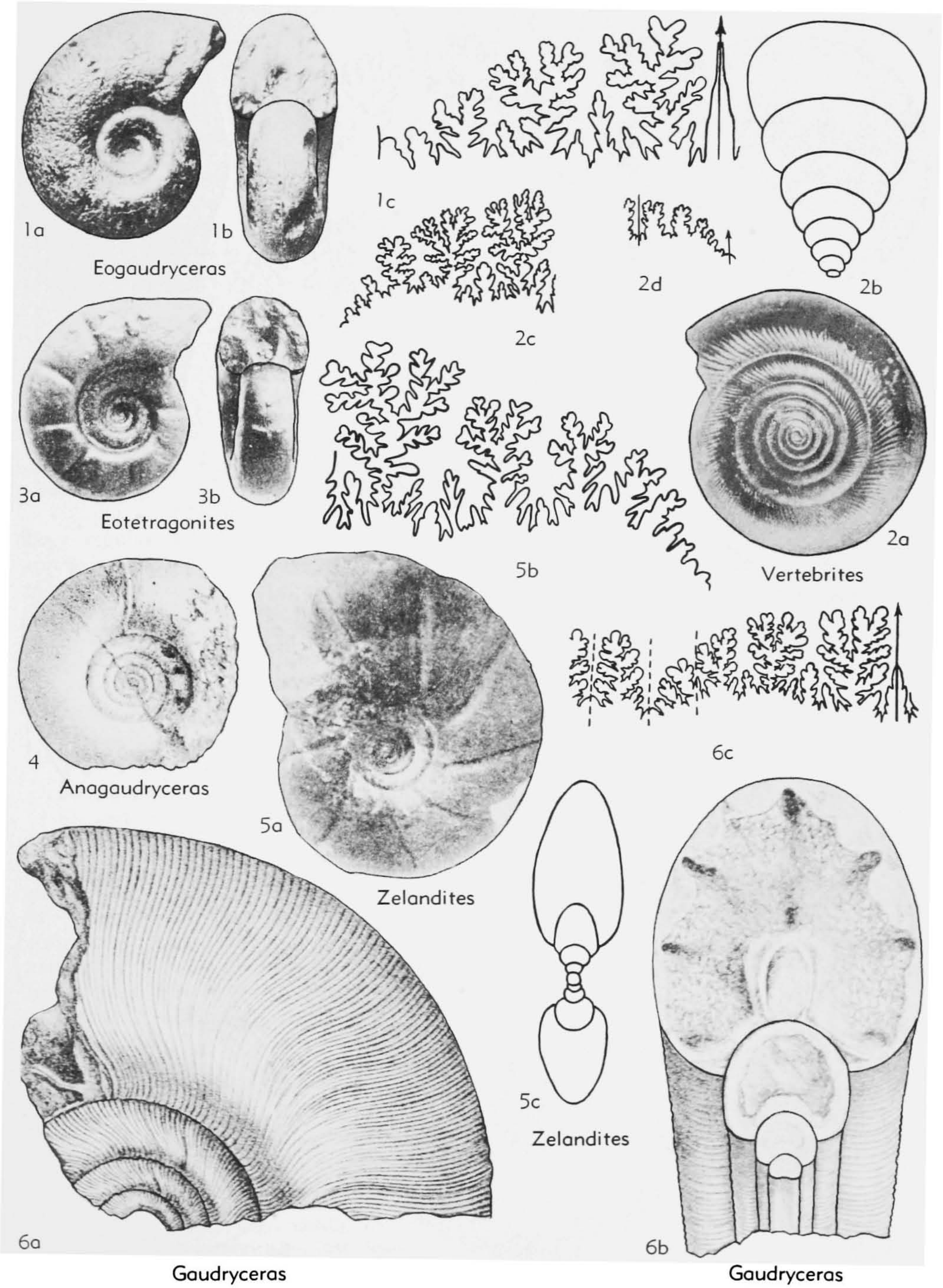


Fig. 230. Tetragonitidae (p. L200).

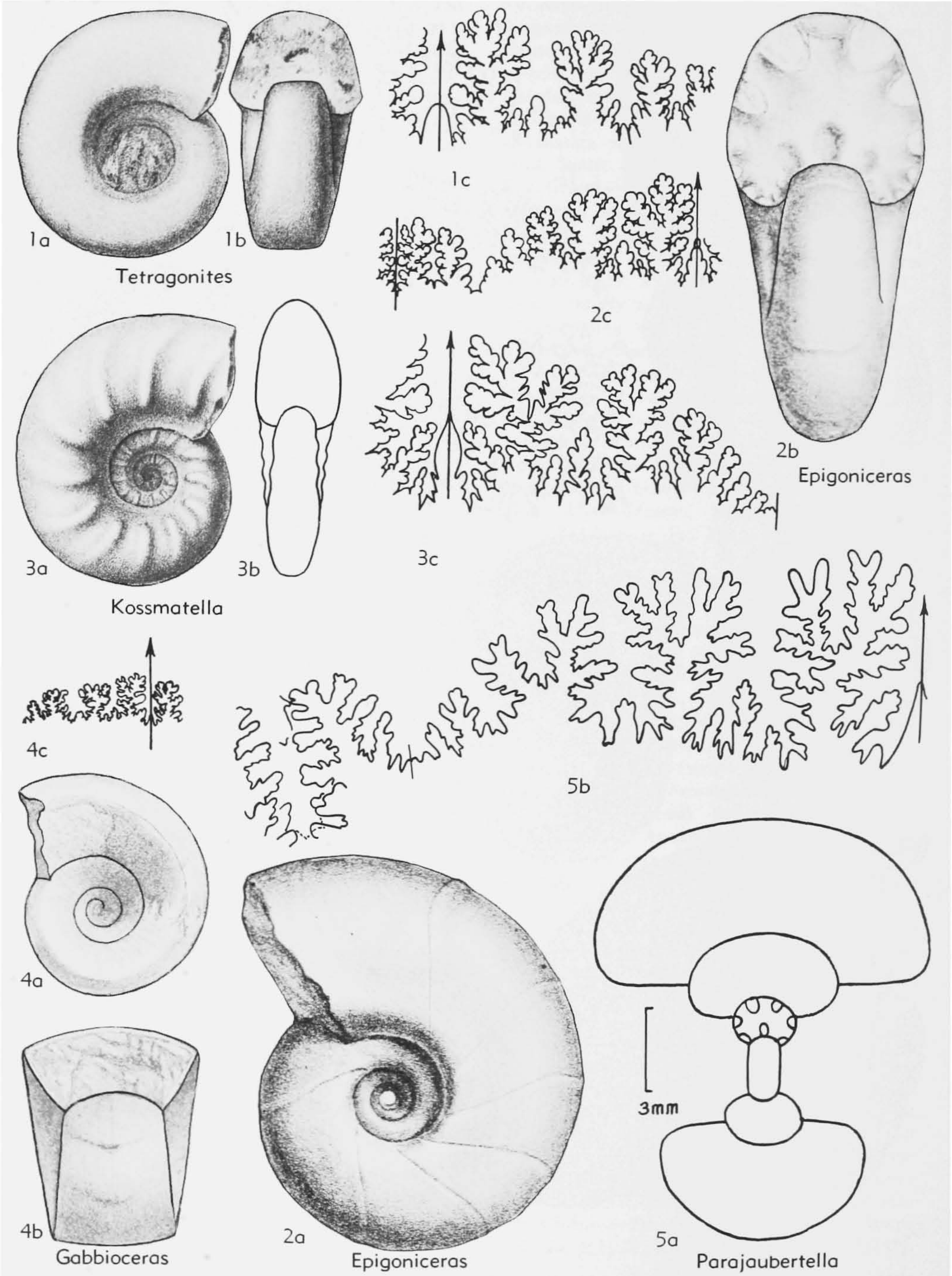


FIG. 231. Tetragonitidae (p. L200-L203).

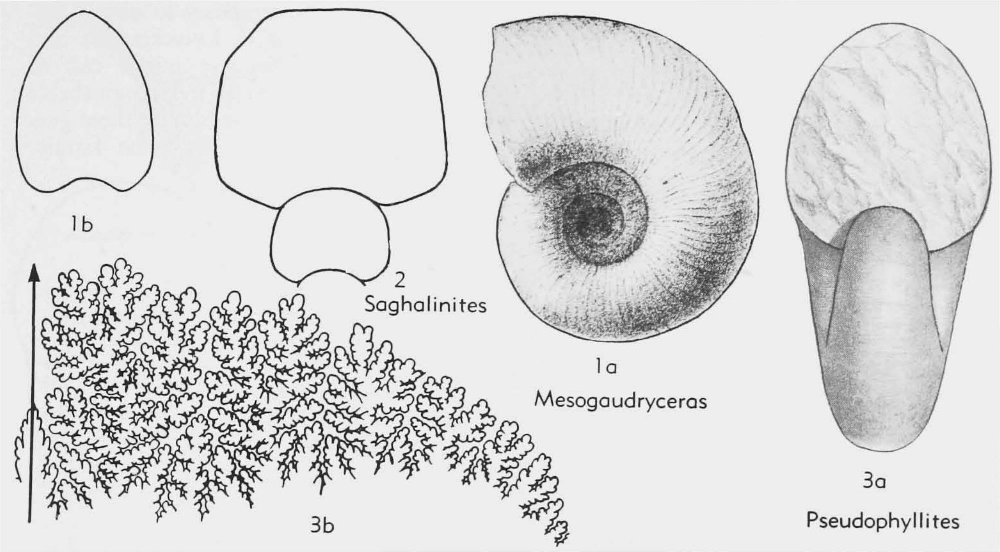


FIG. 232. Tetragonitidae (p. L200-L203).

large regular lateral bulges, derived from approximation of the constrictions of *Eotetragonites;* lirate test and suture as in Gaudryceratinae (53, 214, 230). *L.Cret.(L.Alb.)-U.Cret.(L.Cenom.).*

Kossmatella JACOB, 1907 [**Am. agassizianus* PICTET, 1847]. *L.Alb.-L.Cenom.,* Fr.-C.Eu.-Sinai-S.India-Calif.-Tex.-Mex.——FIG. 231,*3*. **K. agassiziana* (PICTET), M.Alb., Fr.; *3a,b,* ×1; *3c,* enlarged (346*).

Subfamily TETRAGONITINAE Hyatt, 1900

[Incl. Gabbioceratinae BREISTROFFER, 1953]

Typically with square or trapezoidal whorl section, at least during some growth stage; shell usually smooth but some lirate or striate; constrictions usually present, strongly projected on sides and recurved on venter but forming no feature on outside of test. Suture with varying number of auxiliary saddles, internal suture with 2 or more; typically major saddles are irregularly trifid. Derived from *Eotetragonites* (50, 214, 238, 571). *L.Cret.(Apt.)-U.Cret.(Maastr.).*

Gabbioceras HYATT, 1900 [**Am. batesi* GABB, 1869 (*non* TRASK, 1855), =**Gabbioceras angulatum* ANDERSON, 1903, ICZN pend.] [=*Jauberticeras* JACOB, 1907; *Jaubertella* JACOB, 1908]. Whorl section round to depressed with a lateral angle distinct at some growth stage, usually very sharp; with or without constrictions, test lirate (?or smooth). *U.Apt.-L.Cenom.,* Fr.-Pol.-Cauc.-Madag.-Calif.——FIG. 231,*4*. *G. latecarinatum* (ANTHULA), U.Apt., Cauc.; *4a-c,* ×1 (581*).

Tetragonites KOSSMAT, 1895 [**Am. timotheanus* PICTET, 1847]. Moderately evolute; whorl section usually squarish but may be round; oblique constrictions usually present. Suture with auxiliaries in straight line and 4 saddles in internal suture. *M.Alb.-U.Cenom.,* Eu. - Sinai - Zululand - S.India-Japan-Tex.-Mex.——FIG. 231,*1*. **T. timotheanus* (PICTET), U.Alb., Fr.; *1a,b,* ×1; *1c,* enlarged (346*).

Epigoniceras SPATH, 1925 [**Tetragonites epigonus* KOSSMAT, 1895]. Differs from *Tetragonites* primarily in suture having a retracted suspensive lobe and, usually, more auxiliaries. *L.Turon.-Maastr.,* N.Afr.-W.Afr.-Madag.-S.India-Japan-W.Austral.-N.Z.-Peru.

E. (Epigoniceras) [=*Eoepigoniceras, Neoepigoniceras* SHIMIZU, 1935 *(nom. nud.)*]. Moderately involute, whorl section square or trapezoidal. *L.Turon.-Camp.,* distr. as for genus.——FIG. 231, *2*. **E. (E.) epigonum* (KOSSMAT), Camp., S.India; *2a-c,* ×1 (238*).

E. (Saghalinites) WRIGHT & MATSUMOTO, 1954 (*ex* SHIMIZU, 1935, *nom. nud.*) [**Am. cala* FORBES, 1845]. Very evolute, whorls increasing very slowly in height; section round to octagonal; regular weak or strong sinuous constrictions. *?U.Santon., Camp.,* Tunis.-Madag.-S.India-Sakhalin.——FIG. 232,*2*. **E. (S.) cala* (FORBES), Camp., S. India; ×1 (238*).

Pseudophyllites KOSSMAT, 1895 [**Am. indra* FORBES, 1845]. Early whorls as in *E. (Epigoniceras)* but later more involute, without constrictions and with much higher and more rounded whorl section; test finely striate. Suture very finely divided. *Camp., ?Maastr.,* S.Afr.-S.India-W.Austral.-N.Z.-Japan-B.

C.——Fig. 232,*3*. **P. indra* (Forbes), ?Maastr., S.India; *3a*, ×0.5; *3b*, ×1 (238*).

Family MACROSCAPHITIDAE Hyatt, 1900

Distinctly ribbed or spinose derivatives of Lytoceratidae, with tendency to uncoil. Suture more or less as in Lytoceratidae and invariably ornate. Because initial coil of hooked *Macroscaphites* is indistinguishable from normally coiled *Costidiscus*, these genera must be placed in the same family;

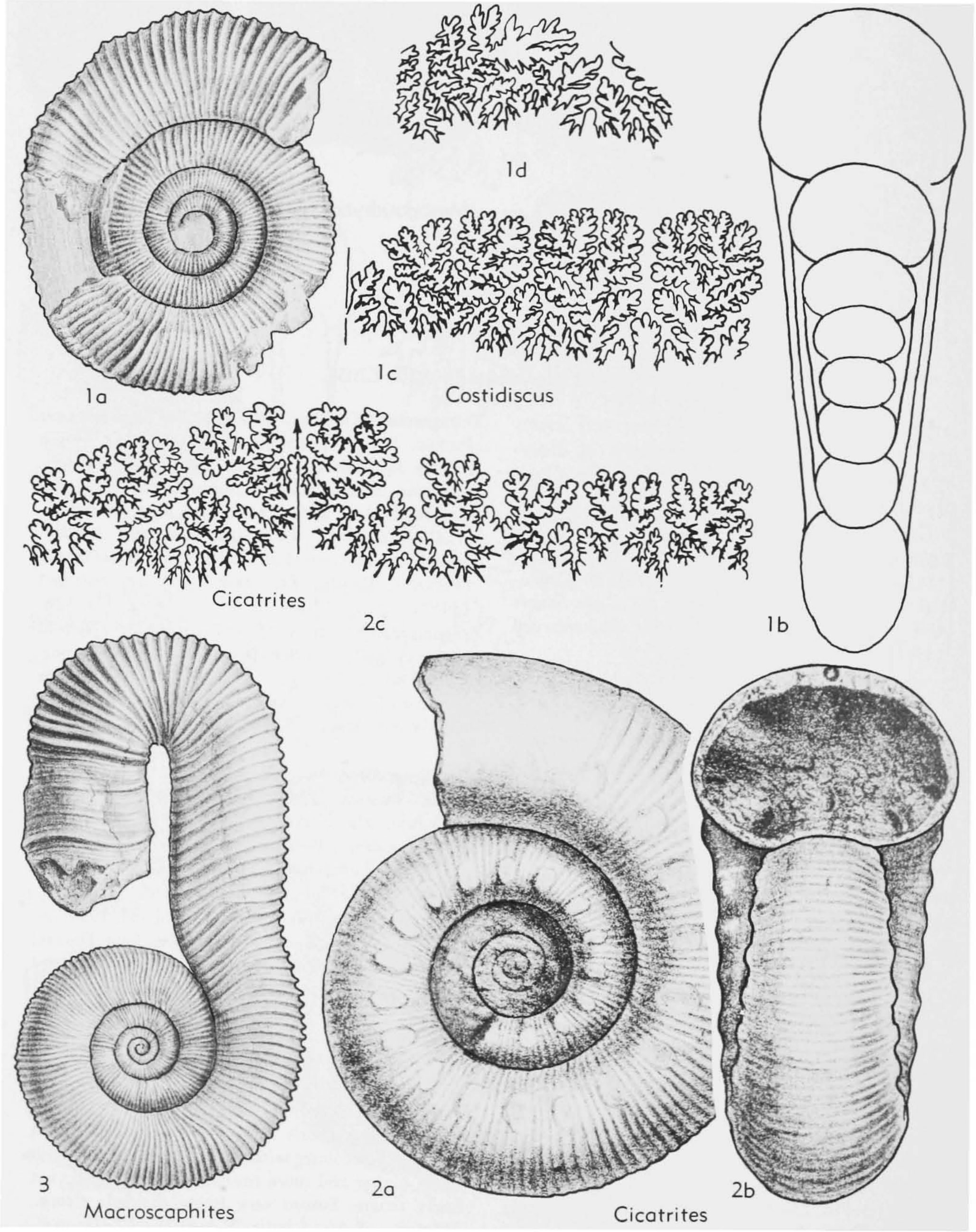


Fig. 233. Macroscaphitidae, Cicatritidae (p. L205).

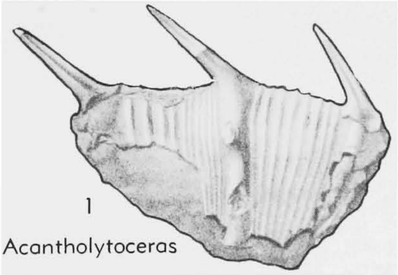


FIG. 234. *Acantholytoceras longispinus* (UHLIG), L. Cret. (Barrem.), Silesia; ×0.5 (530*) (p. L205).

Macroscaphites apparently gave rise to various heteromorph offshoots by reduction and disappearance of normally coiled part of shell (229, 530). *L.Cret.(Barrem.-U. Apt.).*

Costidiscus UHLIG, 1882 [**Am. recticostatus* D'ORBIGNY, 1841]. Normally coiled, rather evolute, with dense strong straight radial ribs, which in some species are thickened on umbilical edge or even tuberculate; some forms also with distinct small ventrolateral tubercles; constrictions with enlarged ribs in front and behind usually present. Suture with sharp ends to all lobules; internal lobe with single point. *Barrem.-L.Apt.,* S.Eu.-C.Eu.-Sinai-Mex.——FIG. 233,*1*. **C. recticostatus* (ORB.), Barrem., Silesia; *1a,b,* ×0.75; *1c,d,* ×1 (530*).

Macroscaphites MEEK, 1876 [**Scaphites yvani* PUZOS, 1831]. Septate whorls exactly as in untuberculate or tuberculate species of *Costidiscus* (but usually smaller) followed by uncoiled body chamber with straight or even recurved shaft and final hook. *Barrem.-Apt.,* S.Eu.-C.Eu.-N.Afr.——FIG. 233,*3*. **M. yvani* (PUZOS), Barrem., Silesia; ×0.75 (530*).

Acantholytoceras SPATH, 1923 [**Hamites (Pictetia) longispinus* UHLIG, 1883]. Whorls not in contact, whorl section oval; periodic enlarged ribs with long hollow umbilical, lower and upper lateral and ventrolateral spines. *Barrem.,* C.Eu.-E.Eu.——FIG. 234,*1*. **A. longispinum* (UHLIG), Barrem., Silesia; ×0.5 (530*).

Family CICATRITIDAE Spath, 1927

Known only in a few examples of a single species which seems to be derived from *Costidiscus* but differs primarily in its asymmetric suture (3). *L.Cret.(Apt.).*

Cicatrites ANTHULA, 1899 [**C. abichi*]. Very evolute with depressed whorl section; regular flattened umbilical bullae each cover 3 of the dense straight ribs and presumably formed bases of long hollow spines. Suture with bifid elements but irregular and with asymmetric 1st lateral lobe. *L.Apt.-U. Apt.,* Fr.-Cauc.——FIG. 233,*2*. **C. abichi,* U.Apt., Cauc.; *2a-c,* ×1 (581*).

Superfamily SPIROCERATACEAE Hyatt, 1900

[*nom. transl.* ARKELL, 1950 (*ex* Spiroceratidae HYATT, 1900)]

Uncoiled ammonoids of Jurassic. Possibly offshoots derived from Lytoceratina and hence classifiable with this suborder (12, 201, 355). *L.Jur.(Pliensb.)-U.Jur.(Oxf.).*

Family ARCUCERATIDAE Arkell, 1950

Shell in form of open bow, enlarging very slowly; no ventral sulcus; ribs never oblique. Sutures unknown (12, 355). *L.Jur. (Pliensb.).*

Arcuceras POTONIÉ, 1929 [**A. marthae*]. Only genus. *Pliensb.,* Eu.——FIG. 235,*4*. **A. marthae* POTONIÉ, Ger.; × (360*).

Family SPIROCERATIDAE Hyatt, 1900

[=Parapatoceratidae BUCKMAN, 1926]

Suture lines simple, consisting of 3 lobes

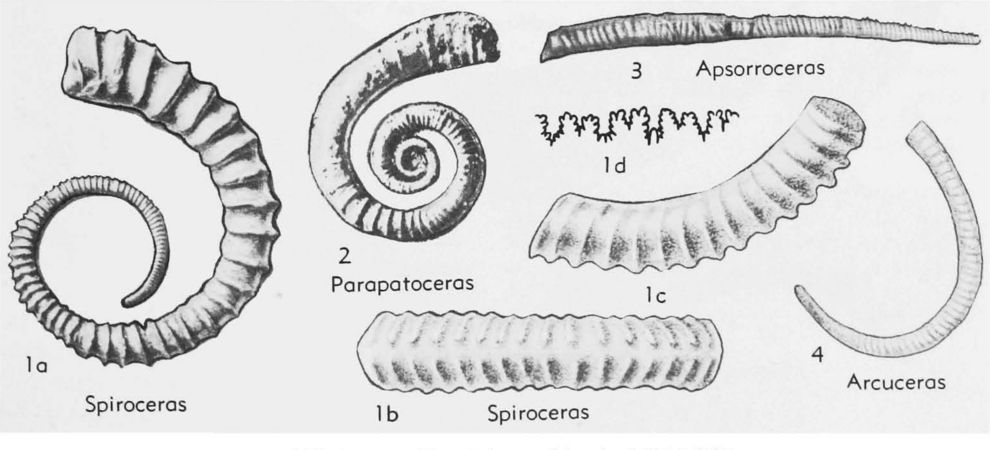


FIG. 235. Arcuceratidae, Spiroceratidae (p. L205-L207).

(external, lateral, internal), but according to SCHINDEWOLF (1951) lateral lobe not homologous with that in coiled ammonoids but ontogenetically comprising "2nd lateral" (2nd umbilical lobe), true 1st lateral having been suppressed to status of a small accessory. The presence of *Arcuceras* in the Lias makes it unlikely that Spiroceratidae are derived from Parkinsoniidae, despite strong resemblance to *Strenoceras*. The hypothesis adopted here is that Spirocerataceae are derivatives of Lytoceratina, perhaps of Ectocentritidae, analogous with the many Cretaceous uncoiled forms generally agreed (since HYATT, 1900) to have arisen from Lytoceratina. POTONIÉ (1929) proved a lineage from *Baj.* to *M.Callov.* The latest known form is *"Ancyloceras" ischeri* FAVRE, *Oxf.(bimammatum z.),* Switz. (201, 355). *M.Jur.(U.Baj.)-U.Jur.(U.Oxf.).*

Apsorroceras HYATT, 1900 [**Hamites baculatus* QUENSTEDT, 1858]. Shell long, mostly straight; distinction from *Spiroceras* difficult and in many doubtful. *U.Baj.(subfurcatum z.),* Eu.——FIG. 235,3. **A. baculatum* (QUENST.), Ger.; ×0.2 (355*).

Spiroceras QUENSTEDT, 1858 [**Hamites bifurcati* QUENST., 1846; SD MASCKE, 1907; lectotype (QUENST., 1846, pl. 11, fig. 14) SD herein (designations by BUCKMAN, 1924, and POTONIÉ, 1929, invalid because not based on syntypes)] [=*Patoceras* MEEK, 1876; *Rhabdodites* BUCK., 1923; *Plagiamites* BUCK., 1925]. Shell usually in form of open spiral (cyrtocone) but genus includes twisted and loose helicoid forms; ribs simple, usually with 2 rows of tubercles or spines (lateral and ventrolateral) and broken by a ventral smooth band; on

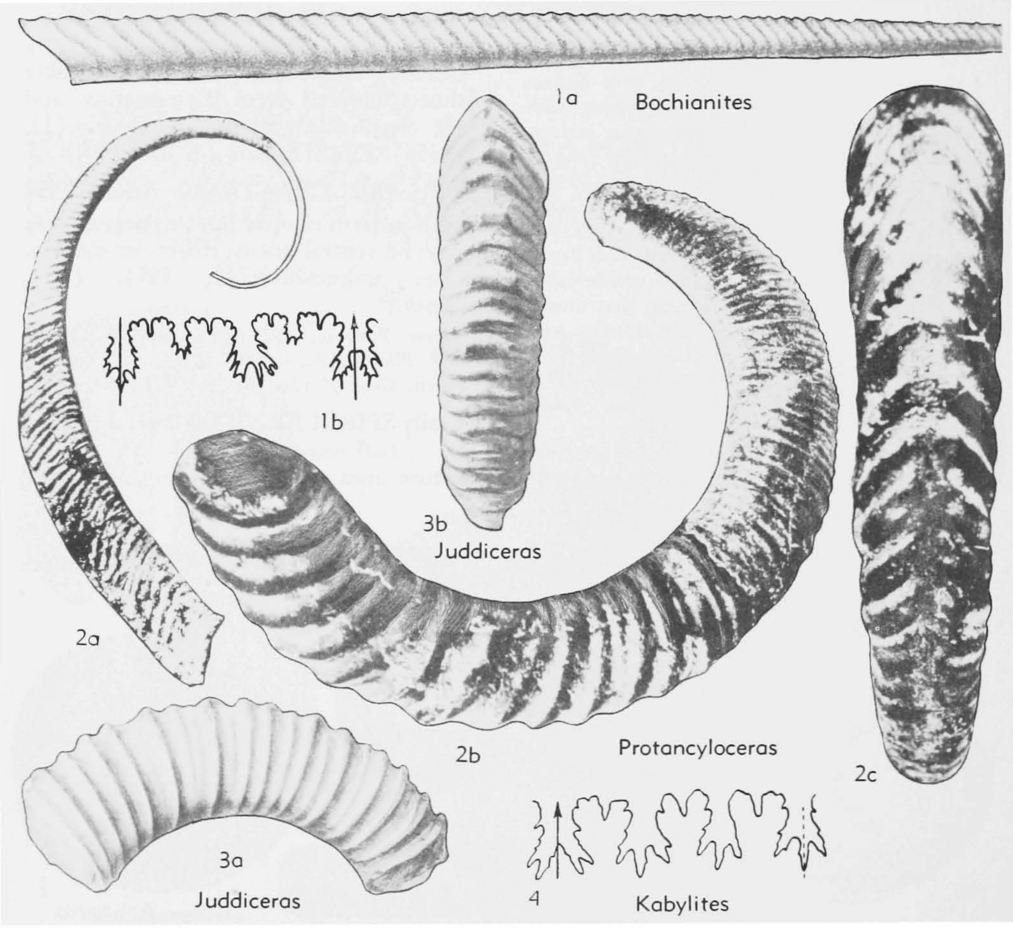


FIG. 236. Bochianitidae (p. L207).

dorsal area ribs invariably swing forward and weaken or die out. *U.Baj.-U.Bath.*, Eu.-Donetz-N. Afr.-Sinai-Kenya.——Fig. 235,*1*. **S. bifurcati* (Quenst.), U.Baj., Ger.; *1a*, ×0.7 (355*); *1b-d*, ×1 (358*).

Parapatoceras Spath, 1924 [**Ancyloceras calloviense* Morris, 1845 (=**A. distans* Baugier & Sauzé, 1843)] [=*Crioconites* Buckman, 1925]. Shell at first more closely coiled than in *Spiroceras*, later becoming straighter; ribs usually more distant than in *Spiroceras*, passing strongly over dorsum without fading or projecting. *U.Bath.-U.Oxf.*, Eu.-Persia-Cutch-Madag.——Fig. 235,*2*. **P. distans* (Baug.-S.), Callov.; ×1 (65*).

Superfamily ANCYLOCERATACEAE Meek, 1876

[*nom. transl.* Wright, herein (*ex* Ancyloceratidae Meek, 1876)] [=Crioceratitaceae Wright, 1952 (*nom. transl. ex* Crioceratitidae Wright, 1952, erroneously attributed to Hyatt, 1900)]

Majority of members uncoiled but form of coiling may vary much within genera. Stratigraphical association and intrinsic evidence suggests derivation from Lytocerataceae, but the succession and relation of many forms are obscure. The probable main course of phylogeny is that late Jurassic Protetragonitidae produced an uncoiled offshoot with strong ribs (*Protancyloceras*), which in turn gave rise both to straight forms (*Bochianites*) and by late Valanginian or early Hauterivian to more closely coiled but still open-whorled genera (Crioceratitinae). During the Hauterivian one stock became more closely coiled and apparently led to Hemihoplitidae, while another developed hooked body chambers (Ancyloceratinae). The Heteroceratidae, with initially helical coiling, probably were derived from Ancyloceratinae. While earliest forms may retain a lytoceratid suture, the lobes soon become trifid. *U.Jur.(Tithon.)-L.Cret.(L.Alb.).*

Family BOCHIANITIDAE Spath, 1922

[*nom. transl.* Breistroffer, 1947 (*ex* Bochianitinae Spath, 1922)]

Loosely coiled to straight, normally with oblique ribs, rarely smooth. Tubercles occur very rarely. The suture has the same number of elements as in Lytoceratidae, but the lobes, except for the external one, are in most cases trifid (50, 486). *U.Jur.(Tithon.)-L.Cret.(L.Apt.).*

Subfamily PROTANCYLOCERATINAE Breistroffer, 1947

[*nom. transl.* Wright, 1952 (*ex* Protancyloceratidae Breist., 1947)]

Loosely coiled, rarely helical, strongly ribbed; a few tuberculate forms. *U.Jur.(Tithon.)-L.Cret.(Valang.).*

Protancyloceras Spath, 1924 [**Ancyloceras gümbeli* Oppel in Zittel, 1868]. Coiled in very open spiral; whorls slender, with round, oval, or subquadrate section; ribs fine on early whorls, typically coarser on later, prorsiradiate to radial, forming chevrons or interrupted on venter; ventrolateral tubercles may occur and pairs of ribs may join at these points. Suture with irregularly bifid saddles and trifid lateral lobes. *U.Jur.(Tithon.)-L.Cret.(Berrias.)*, Fr.-C.Eu.-Crimea-N.Afr.-Kurdistan-Mex.-Peru-Cuba.——Fig. 236,*2*. *P. kurdistanense* (Spath), Tithon., Kurdistan; *2a-c*, ×1 (713*).

Cochlocrioceras Spath, 1950 [**C. turriculatum*]. Differs from *Protancyloceras* in its helically coiled inner whorls, with ribs interrupted on venter. *U. Jur.(Tithon.)*, Kurdistan.

Juddiceras Spath, 1924 [**Crioceras curvicosta* Koenen, 1902]. Rather large, known only in slightly curved fragments but probably not completing 360°. Prominent, rather distant, slightly concave ribs, irregularly stronger and weaker, former with pair of ventral tubercles. *L.Cret.(U. Valang.)*, Ger.——Fig. 236,*3*. **J. curvicostum* (Koenen); *3a,b*, ×0.5 (237*).

Subfamily BOCHIANITINAE Spath, 1922

Straight forms with oblique annular ribs or smooth. *U.Jur.(Tithon.)-L.Cret.(L.Apt.).*

Bochianites Lory, 1898 [**Baculites neocomensis* d'Orbigny, 1842]. Smooth or with weak to strong oblique annular ribs. Sutures have short elements; umbilical lobe much reduced in size, no larger than lobule that divides 1st lateral saddle. *U.Jur.(Tithon.)-L.Cret.(Hauteriv.)*, Eu.-?CapeVerdeI.-N. Afr.-Natal-Himalaya-Indon.-Calif.-Mex. —— Fig. 236,*1*. **B. neocomensis* (Orb.), U.Valang., Fr.; *1a*, ×1; *1b*, enlarged (329*).

Janenschites Durand Delga, 1954 [**Bochianites janenschi* Zwierzycki, 1914]. Doubtfully distinct from *Bochianites*. Suture with long and narrow elements, more denticulate than in *Bochianites*. *L. Cret.(Barrem.)*, Tanganyika.

Kabylites Durand Delga, 1954 [**Bochianites superstes* Pervinquière, 1910]. Differs from *Bochianites* in having umbilical lobe of suture more or less same in size as 1st lateral. *L.Cret.(Barrem.-L.Apt.)*, Fr.-Ger.-N.Afr.——Fig. 236,*4*. **K. superstes* (Pervinquière), Barrem., Algeria; ×1 (616*).

?**Baculina** d'Orbigny, 1847 [**B. rouyana* (*nom. dub.*)]. Holotype of *B. rouyana* may be a worn *Bochianites*. *L.Cret.(Valang.)*, Fr.

Family ANCYLOCERATIDAE Meek, 1876

[=Crioceratidae, Pedioceratidae HYATT, 1900; Crioceratitidae WRIGHT, 1952 (erroneously attributed to HYATT, 1900)]

Typically regularly coiled with the whorls not in contact but some forms have early or all whorls in contact, whereas others have straight or hooked body chambers; whorl section ranging from circular to square; ribs weak or strong, showing tendency to have stronger periodic ribs with umbilical, lateral and ventrolateral spines; ornament rarely constant through growth. Sutures ornate, of lytoceratid plan, without auxiliaries, but with trifid lobes (2, 394, 405, 460, 566). *?L. Cret. (Valang.), L. Cret. (L. Hauteriv. - U. Apt.), ?L.Cret.(L.Alb.).*

Although the outer whorls of some early species resemble the outer whorls of evolute Berriasellidae *(Distoloceras)*, the sutures are different and resemblance is restricted to certain growth stages. Monophyletic origin in *Juddiceras* or some as yet unknown Upper Valanginian member of the Protancylocera-tinae seems probable.

Subfamily CRIOCERATITINAE Wright, 1952

[*nom. transl.* WRIGHT, herein (*ex* Crioceratitidae WRIGHT, 1952, erroneously attributed to HYATT, 1900; *nom. conserv.* proposed WRIGHT, 1955, ICZN pend.)]

Normally coiled in a regular plane open spiral; if body chamber is hooked, it is only so irregularly and does not have a distinct straight shaft. *L.Cret.(L.Hauteriv.-U.Apt.).*

Aegocrioceras SPATH, 1924 [**Crioceras capricornu* ROEMER, 1841]. Differs from *Juddiceras* in having all ribs equal, strong, rather distant and with ventrolateral spines on inner whorls, and in being more closely and regularly coiled. *Hauteriv.*, N.Eu. ——FIG. 237,*3*. **A. capricornu* (ROEMER), L. Hauteriv., Eng.; *3a,b*, ×1 (679*).

Crioceratites LEVEILLÉ, 1837 [**C. duvali*] [*Crioceras, Toxoceras* D'ORBIGNY, 1842; *?Emericiceras* SARKAR, 1954]. Typically coiled in open, equiangular spiral but spiral angle may increase with age; whorl section may be oval or subquadrate, with more or less distinctly trapezoidal top; ribs generally dense, rounded, straight or slightly curved and untuberculate, with periodic stronger ribs strengthened on shoulders or carrying ventrolateral or umbilical, lateral and ventrolateral spines. *Hauteriv.-Barrem.*, Eu. - Turkey - Madag. - Japan - Calif.-Mex.——FIG. 237,*6*. *C. nolani* (KILIAN), U. Hauteriv., Fr.; *6a,b*, ×0.25; *6c*, ×0.5 (329*).

Balearites SARKAR, 1954 [**Crioceras balearense* NOLAN, 1894]. Compressed, with rounded venter. For most of growth fine, flexuous, equal ribs branch 2, 3 or 4 from weak umbilical tubercles, but there are a few periodic stronger ribs and rather feeble ventrolateral tubercles may occur. *U.Hauteriv.*, Fr.-Balearics.——FIG. 238,*1*. **B. balearensis* (NOLAN), Balearics; *1a,b*, ×1 (671*).

[**Neohoplites** GERTH, 1921 *(nom. nud.)*].

[**Jaubertites** SARKAR, 1954 *(nom. nud.)*].

[**Sapthicrioceras** *(errore pro Spathicrioceras)* SARKAR, 1954 *(nom. nud.)*].

Paracrioceras SPATH, 1924 [**Crioceras occultum* SEELEY, 1865] [*?Peltocrioceras, ?Hemicrioceras* SPATH, 1924]. Early whorls bearing fine equal more or less straight nontuberculate ribs. Differs from *Crioceratites* mainly in having more frequent and stronger periodic ribs with larger spines between which there may be no intermediate ribs on outer whorls; some forms have close coiling and reduced ornament from an early stage. *U.Hauteriv.-Barrem.*, Eu.-Patag.——FIG. 238,*3*. *P. elegans* (KOENEN), Barrem., Ger.; ×0.7 (237*).

Menuthiocrioceras COLLIGNON, 1949 [**Crioceras (M.) lenoblei*]. Whorls touching each other, whorl sections becoming more inflated with growth and with flat venter to a late stage; ribs nearly straight and radial at first, then sinuous and finally biconcave, fairly fine and dense, up to 8 plain ribs occurring between enlarged trituberculate ribs. *U. Hauteriv.*, Madag.——FIG. 238,*2*. *M. hourcqui* COLLIGNON; inner whorls, *2a,b*, ×1 (601*).

Hoplocrioceras SPATH, 1924 [**Hamites phillipsi* BEAN in PHILLIPS, 1828]. Early whorls with subquadrate section, ribs springing in bundles from subdued umbilical tubercles, with or without ventrolateral spines, on later whorls with ribs single and more distant; body chamber may straighten and ornament disappear. *U.Hauteriv.-Barrem.*, W. Eu.-Calif.——FIG. 237,*7*. *H. fissicostatum* (ROEMER), L.Barrem., Ger.; ×0.25 (237*).

Shasticrioceras ANDERSON, 1938 [**S. poniente;* SD WRIGHT, herein]. Early whorls compressed, with dense single rarely branching sinuous ribs, which may be flat, bearing slightly clavate tubercles on sharp shoulders; later the section becomes quadrate and ribs coarse and distant, wtih blunt ventrolateral tubercles. *Barrem.*, Japan-Calif.——FIG. 237, *2*. **S. poniente*, Calif.; ×1 (2*).

Pedioceras GERHARDT, 1897 [**P. cundinamarcae*] [*Pseudocrioceras* SPATH, 1924]. Early whorls much as in *Menuthiocrioceras*, subquadrate, with equal, straight or sinuous, mainly single ribs angulate or with upper and lower tubercles on shoulders, ribs then differentiated into plain and tuberculate ones; later coiling loosens and ornament becomes coarser and weaker. *Barrem.-Apt.*, Cauc.-Calif.-Mex.-Colombia.——FIG. 237,*5*. **P. cundinamarcae*, Barrem., Colombia; inner whorls, *5a-c*, ×1 (173*).

Parancyloceras SPATH, 1924 [**Crioceras bidentatum* KOENEN, 1902]. Coiled either in plane spiral with whorls just touching or not in contact or straight-

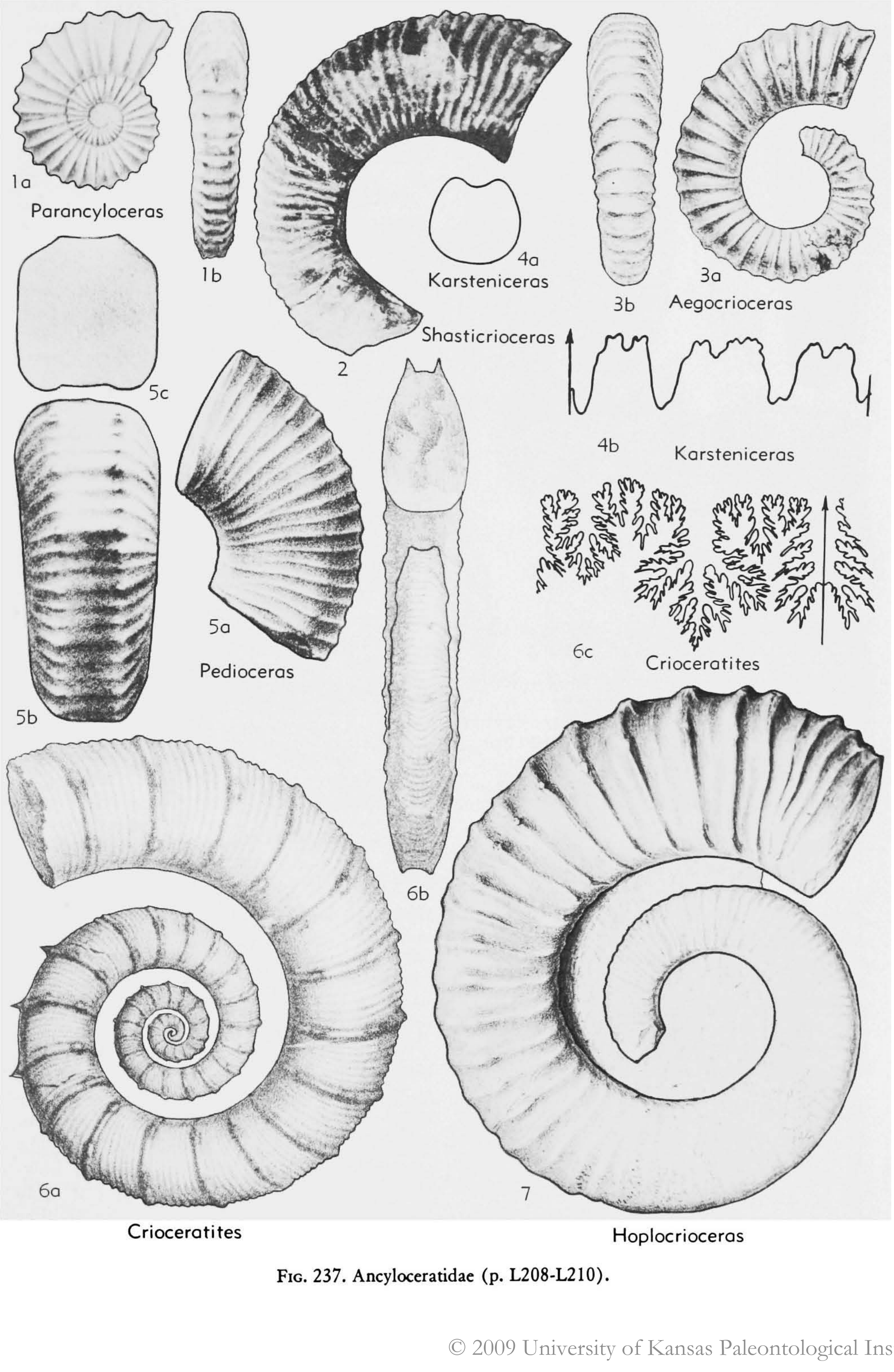


FIG. 237. Ancyloceratidae (p. L208-L210).

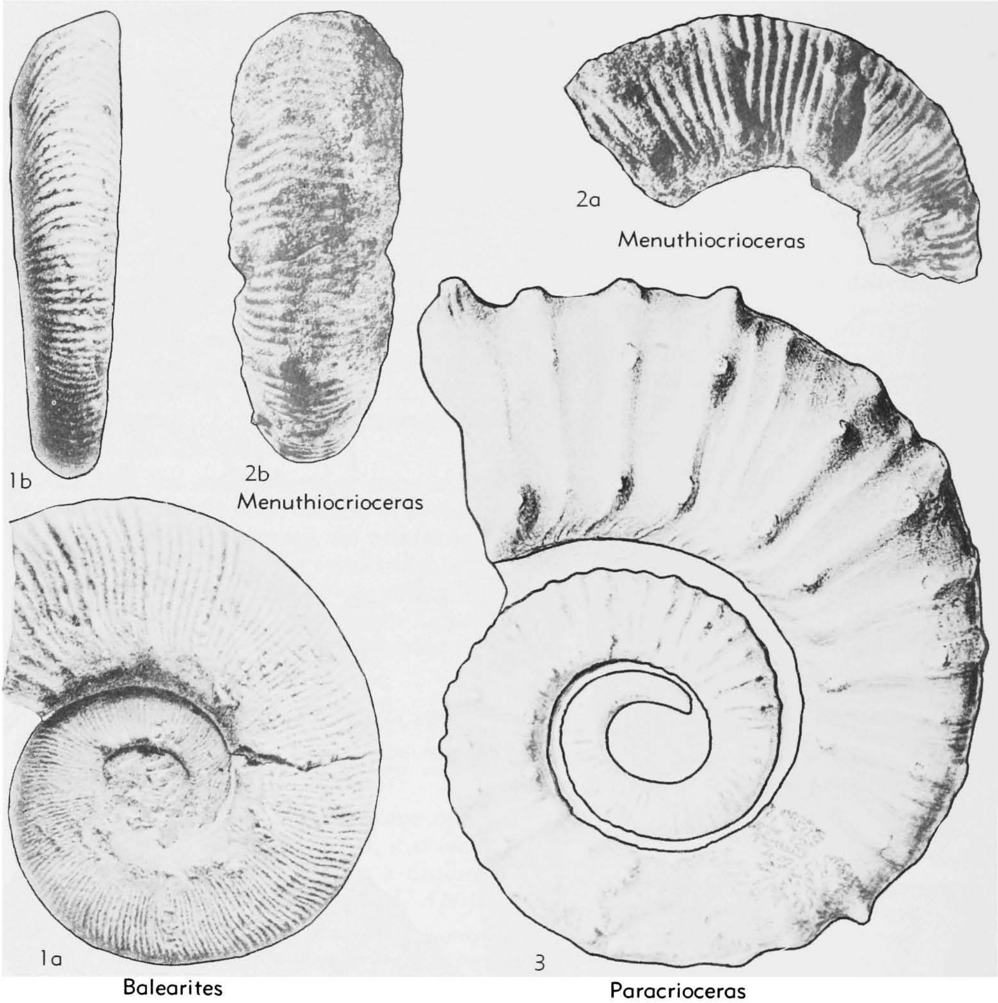


FIG. 238. Ancyloceratidae (p. L208).

ening (?and then hooked) after a few coiled whorls; ribs distant, sharp, equal, steep, radial or oblique, with more or less distinct upper and (in some species) also lower ventrolateral tubercles; ribs may be doubled between outer tubercles. *U. Barrem.*, Eng.-Ger.——FIG. 237,*1*. **P. bidentatum* (KOENEN), U.Barrem., Ger.; *1a,b*, ×1 (237*).

?Karsteniceras ROYO Y GOMEZ, 1945 [**Ancyloceras beyrichi* KARSTEN, 1858]. Coiling more or less as in *Crioceratites;* ribs sharp and irregularly strong and weak. Suture with finger-like lobes and equal, square, feebly bifid saddles. *Barrem.*, Colombia. ——FIG. 237,*4*. **K. beyrichi* (KARSTEN); *4a*, ×1; *4b*, ×4 (394*).

?Veleziceras WRIGHT [*nom. nov.* herein, *pro Orbignyiceras* ROYO Y GOMEZ, 1945 (*non* GÉRARD & CONTAUT, 1936)] [**Orbignyiceras veleziense* ROYO Y GOMEZ, 1945]. Only straight or slightly curved shafts are known. Ribs fairly prominent and oblique, without tubercles. Suture much as in *Karsteniceras*. *Barrem.*, Colombia.

Subfamily ANCYLOCERATINAE Meek, 1876

[*nom. transl.* WRIGHT, herein (*ex* Ancyloceratidae MEEK, 1876)] [=Helicancylidae HYATT, 1894]

Typically with early whorls forming a more or less regular open spire, commonly with periodic trituberculate ribs and fine intermediaries, followed by curved or straight shaft and terminal hook. Many genera, however, show fine subdued equal ribs at some stage and coarse tuberculate ones at another (2, 51, 329, 566). *L.Cret.-(U.Hauteriv.-U. Apt.), ?L.Cret.(L.Alb.).*

Acrioceras Hyatt, 1900 [**Ancyloceras tabarelli* Astier, 1851] [?Includes as subgenera *Mesocrioceras* Breistroffer, 1952 *(nom. nud.)*; *Dissimilites* Sarkar, 1954]. Small; spire composed of 1 or 2 loosely coiled whorls bearing fine ribs with periodic enlarged ones carrying 1 to 3 tubercles, periodic ribs weakening or disappearing on shaft; rather strong ribs that branch irregularly from weak umbilical tubercles occur on hook. *U.Hauteriv.-L. Apt.*, W.Eu.-C.Eu.-Calif.——Fig. 239,*1*. **A. tabarelli* (Astier), ?L.Barrem., Fr.; ×1 (405*).

Aspinoceras Anderson, 1938 [**A. hamlini*]. Small, with few regularly coiled whorls followed by short shaft and rounded hook; ribs very close, regular, alternately simple and branched, nontuberculate, obliquely disposed on shaft; constrictions may occur. *U.Hauteriv.-L.Barrem.* (reference of type species to Valang. very doubtful), W.Eu.-C.Eu.-Calif.——Fig. 240,*5*. *A. dilatatum* (Orb.), L. Barrem., Fr.; ×0.75 (329*).

Uhligia Koenen, 1904 [**Hamites minutus* Neumayr & Uhlig, 1881]. Early part more or less straight, then sharply bent, with following straight shaft and final hook; ribs nontuberculate, fine, weak and irregular, prorsiradiate on early part, radial on later. *L.Barrem.*, Ger.——Fig. 240,*2*. **U. minutus* (Neumayr & Uhlig); *2a-c*, ×1 (237*).

Lytocrioceras Spath, 1924 [**Ancyloceras jauberti* Astier, 1851] [*?Paraspinoceras* Breistroffer, 1952 *(nom. nud.)*]. Very loosely coiled, with long shaft and irregular hook; periodic tuberculate ribs on spire but otherwise all are equal, dense, fine, straight, and prorsiradiate. *Barrem.*, Fr.-Switz.——Fig. 239,*2*. **L. jauberti* (Astier), Barrem., Fr.; diagram (726*).

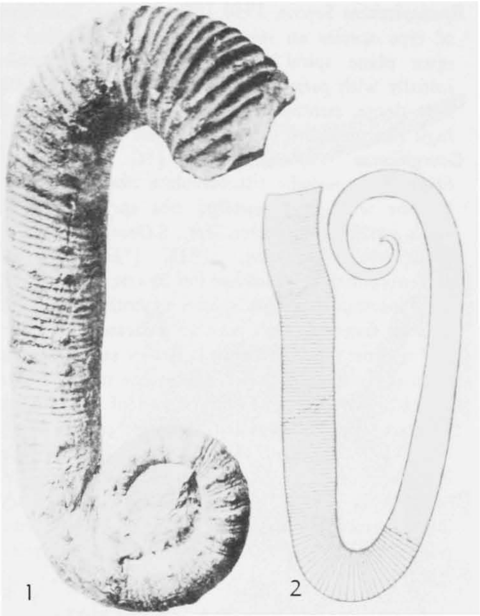
Leptoceras Uhlig, 1883 [**L. pumilum*]. Small; slight spire followed by relatively long shaft and massive hook; ribs equal and nontuberculate on spire, a few periodic ribs with 1 or 2 tubercles on shaft, ribs on hook branch in pairs from weak tubercles or none. *Barrem.*, Fr.-C.Eu.

Ancyloceras d'Orbigny, 1842 [**A. matheronianum* Orb., 1842; SD Haug, 1889]. Plane open spiral followed by fairly long shaft and final hook; ribs fine, straight, radial or prorsiradiate, with periodic trituberculate ones at least on early whorls and hook; tubercles all spinose. *U.Barrem.-L.Apt.*, Eu.-Japan-Calif.-Colombia.——Fig. 240,*1*. **A. matheronianum* (Orb.), Barrem., Fr.; ×0.125 (329*).

Tonoceras Hyatt, 1900 [**Ancyloceras duvalianum* d'Orbigny, 1842]. Differs from *Ancyloceras* in having short, curved shaft and prominent lateral and ventrolateral clavate (not spinate) tubercles. *U.Barrem.*, Fr.

Dirrymoceras Hyatt, 1900 [**Ancyloceras simplex* d'Orbigny, 1842]. Large, with coiling of *Ancyloceras* but ornament of *Aspinoceras*. *U.Barrem.-L. Apt.*, Fr.-Calif.

Shastoceras Anderson, 1938 [**S. californicum*]. Very large; ribs as in *Dirrymoceras* but most of hook swollen and smooth. *L.Apt.*, Calif.



Acrioceras Lytocrioceras

Fig. 239. Ancyloceratidae (p. L211).

Australiceras Whitehouse, 1926 [**Crioceras jacki* Etheridge, Jr., 1880] [*?Colombiaticeras* Royo y Gomez, 1949]. Coiled in a more or less regular spiral with no final hook; alternate ribs with stout blunt or conical umbilical, ventrolateral and normally mediolateral tubercles persist to a late stage but sooner or later ribs lose their tubercles. *L.Apt.-U.Apt.*, *?L.Alb.*, Pak.-Austral.-Calif.-?Colombia. ——Fig. 240,*6*. **A. jacki* (Eth.), L.Apt., Queensl.; ×0.75 (566*).

Ammonitoceras Dumas, 1876 [**A. ucetiae*]. Initial whorls irregular, then whorls just in contact to body chamber which uncoils slightly; periodic ribs with umbilical and mediolateral tubercles and 1 to 3 intermediate ribs persisting to fairly late stage; tubercles gradually weaken, then disappear, leaving rather close rounded ribs; on body chamber ribs are simple, distant and high. *?U.Barrem.*, *L.Apt.-U.Apt.*, Eu.-Transcaspia.

Tropaeum J.deC.Sowerby, 1837 [**Crioceratites bowerbanki* J.deC.Sow., 1837]. Large; like *Ammonitoceras* but mainly without tubercles; earliest part with some trituberculate ribs, then all ribs equal, fine and dense to last whorl, on which they become coarse and distant. *U.Apt.*, W.Eu.-Spitz.-S.Russ.-Alaska-Calif.-Patag.-Greenl.——Fig. 240,*4*. **T. bowerbanki* (J.deC.Sow.), U.Apt., Ger.; ×0.25 (237*).

Epancyloceras Spath, 1930 [**E. hythense* (holotype of type species an injured specimen)]. Coiled in open plane spiral followed by terminal hook; initially with periodic trituberculate ribs, then with fine, dense, nontuberculate ones, finally with very high ribs produced into thin bullae. *U.Apt.,* W.Eu.

Georgioceras Wilckens, 1947 [**G. kohllarseni*]. Stage with periodic trituberculate ribs is followed by one with fine, bundled ribs springing from weak umbilical tubercles. *Apt.,* S.Georgia.

Hamiticeras Anderson, 1938 [**H. pilsbryi*] [*?Toxoceratoides, Tonohamites* Spath, 1924 *(nom. dub.* inasmuch as type species of both are known only in fragments too poor to indicate their form and ornament at all stages)]. Rather small; coiling as in *Ancyloceras;* ribs oblique, some trituberculate on early part, then on some or all of shaft; hook without tubercles, rounded and close or sharp and distant. *U.Barrem.-U.Apt.,* W.Eu.-Calif.——Fig. 240,*3*. **H. pilsbryi,* U.Apt., Calif.; ×0.5 (2*).

Helicancylus Gabb, 1869 [**H. aequicostatum*]. Only initial helix known; it has oblique subdued ribs, periodically with 3 rather prominent tubercles. *Apt.,* Calif.

Family HETEROCERATIDAE Hyatt, 1900

Helically coiled initial whorls are followed by a more or less plane spiral of loosely or tightly coiled whorls, in some shells comprising only a straightened shaft and final hook; usually with dense, fairly fine ribs throughout; tubercles rarely present and if so not very prominent. Suture with bifid saddles and asymmetrically trifid lobes. Origin uncertain but presumed to lie in some Barremian members of Ancyloceratinae (229, 393). *L.Cret.(Barrem.-Apt.).*

Heteroceras d'Orbigny, 1849 [**H. emericianum;* SD Meek, 1876] [*Lindigia* Karsten, 1858]. More or less tightly coiled helix followed by long slightly curved shaft; ribs concave and oblique on helix but straight and radial later. *Barrem-Apt.,* Fr.-C.Eu.-Cauc.-Peru.

H. (Heteroceras). Aperture level with base of helix; no tubercles. Occurrence as for genus.——Fig. 241,*4*. *H. (H.) tardieui* Kilian, Barrem., Fr.; ×0.38 (229*).

H. (Argvethites) Rouchadzé, 1933 [**H. (A.) lashense*]. Aperture level with top of helix; venter of shaft and hook flat, in some bearing paired ventral tubercles; on shaft ribs may join these tubercles in pairs; some branching ribs on hook. *L.Apt.,* Cauc.

Hemibaculites Hyatt, 1900 [**Toxoceras obliquatum* d'Orbigny, 1942] [*?Moutoniceras* Sarkar, 1954]. With small spire followed by straight or slightly curved shaft with open hook; no tubercles present; ribs strong or weak, rounded, prorsiradiate and may form a chevron on venter at point of which they are weak or interrupted. *U.Barrem., ?Apt.,* Fr.-Calif.

Colchidites Djanelidzé, 1924 [**C. colchicus*] [*Santandericeras* Royo y Gomez, 1945]. Initial tightly coiled helix surrounded by plane spiral of more or less tightly coiled whorls with axis of coiling at right angles to that of the helix. *Barrem.-Apt.,* Fr.-Cauc.-Transcaspia-Colombia.

C. (Colchidites). No tubercles. *Barrem.-Apt.,* Fr.-Cauc.——Fig. 241,*3*. *C. (C.) sarasini* Rouchadzé, L.Apt., Cauc.; ×0.75 (393*).

C. (Imerites) Rouchadzé, 1933 [**Heteroceras giraudi* Kilian, 1888 (=**Crioceras cristatum* d'Orbigny, 1842)] [*Atopoceras* Jaubert in Kilian, 1888 *(nom. nud.); Escragnolleites* Sarkar, 1954]. With pair of ventral tubercles or both ventral and ventrolateral tubercles generally only on early whorls of helix. *Barrem.,* Fr.-Cauc.-Transcaspia.

Family HEMIHOPLITIDAE Spath, 1924

Compressed, moderately evolute to uncoiled forms, with flat venter and simple straight or branched flexuous ribs; umbilical and single or double ventrolateral tubercles may occur. Suture apparently without auxiliary elements and resembling that of many Crioceratitidae. Since transitional forms between typical *Crioceratites* and *Pseudothurmannia* are known, the family is more probably related to Crioceratitidae than to early hoplitacean families derived from Desmoceratidae, with which it has many points of resemblance (459, 460). *L.Cret.(Hauteriv.-U.Barrem.).*

Pseudothurmannia Spath, 1923 [**Am. angulicostatus* d'Orbigny, 1841]. Uncoiled or evolute; whorl section with sloping or parallel sides, venter arched to flat; umbilical tubercles and weak lower and stronger upper ventrolateral tubercles may be present. *?L.Hauteriv., U.Hauteriv.-Barrem.,* Fr.-Balearics-Turkey-Georgia.——Fig. 241,*1*. **P. angulicostata* (Orb.), U.Hauteriv., Fr.; *1a,b,* ×1 (329*).

Hemihoplites Spath, 1924 [**Am. feraudianus* d'Orbigny, 1841] [*Matheronites* Renngarten, 1926]. Rather evolute, compressed, with rectangular whorl section; ribs simple or branching, long and short, well spaced, straight or slightly flexuous, crossing flat venter transversely, typically with fairly distinct umbilical and ventrolateral tubercles. *U.Hauteriv.-Barrem.,* Fr.-Balearics-Georgia.——Fig. 241,*2;* 554,*6*. *H. soulieri* (Matheron), Barrem., Fr.; 241,*2a,b,* ×1 (Matheron, 1878); 554,*6,* enlarged (143*).

Pascoeites Spath, 1933 [**P. budavadensis*]. Ill known. *?Barrem.,* W.India.

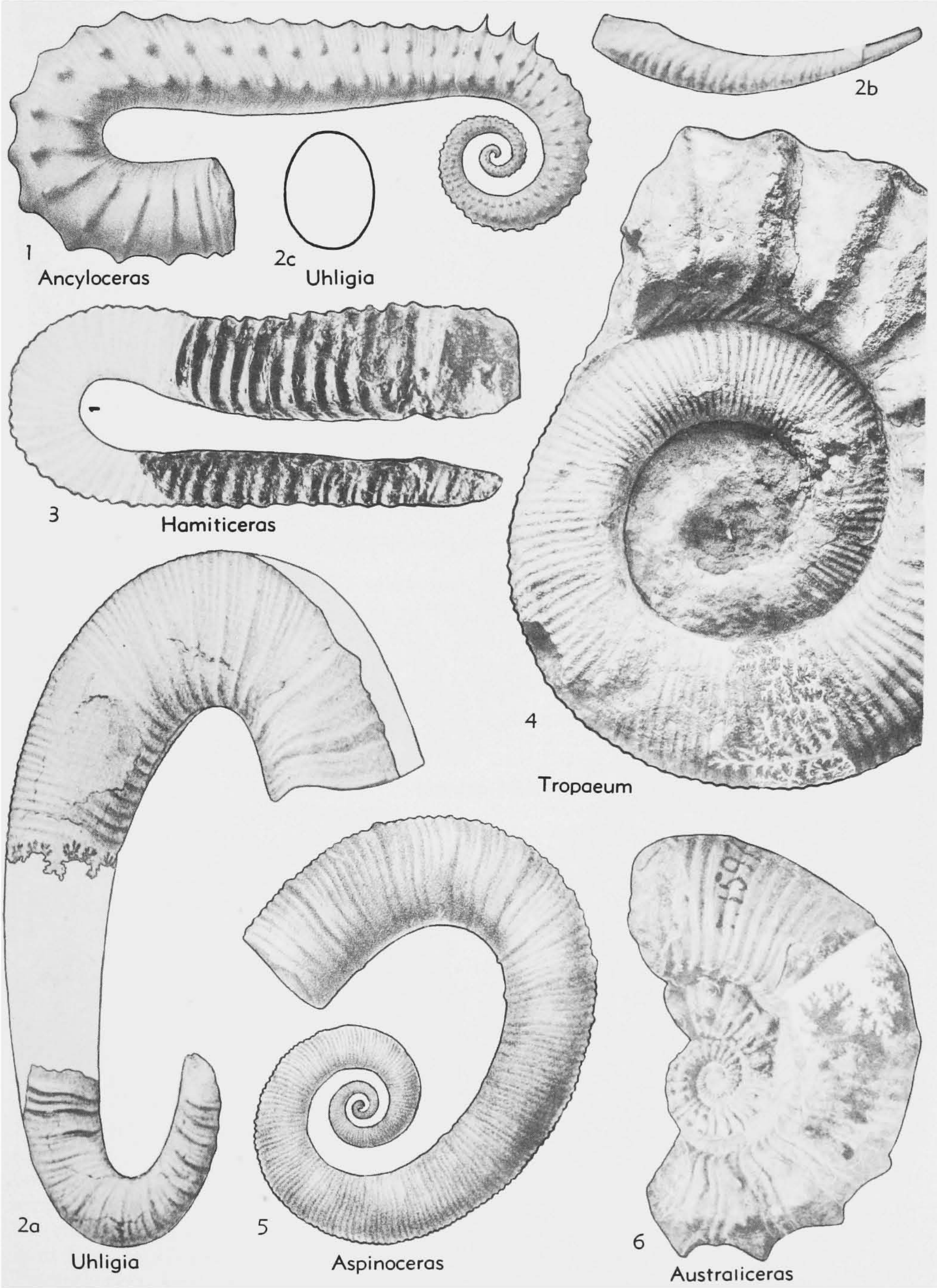


FIG. 240. Ancyloceratidae (p. L211-L212).

Superfamily TURRILITACEAE Meek, 1876

[*nom. transl.* WRIGHT, herein (*ex* Turrilitidae MEEK, 1876)] [=Hamitaceae HYATT, 1900 (*nom. transl.* WRIGHT & WRIGHT, 1951, *ex* Hamitidae HYATT, 1900)]

Comprises a series of families presumed to be derived by way of Hamitidae from Macroscaphitidae. They exhibit almost every known form of heteromorph coiling and include smooth, ribbed and tuberculate genera. The suture generally has no auxiliary elements but does not in all forms retain the ancestral bifidity of the lobes. With these families are associated Ptychoceratidae

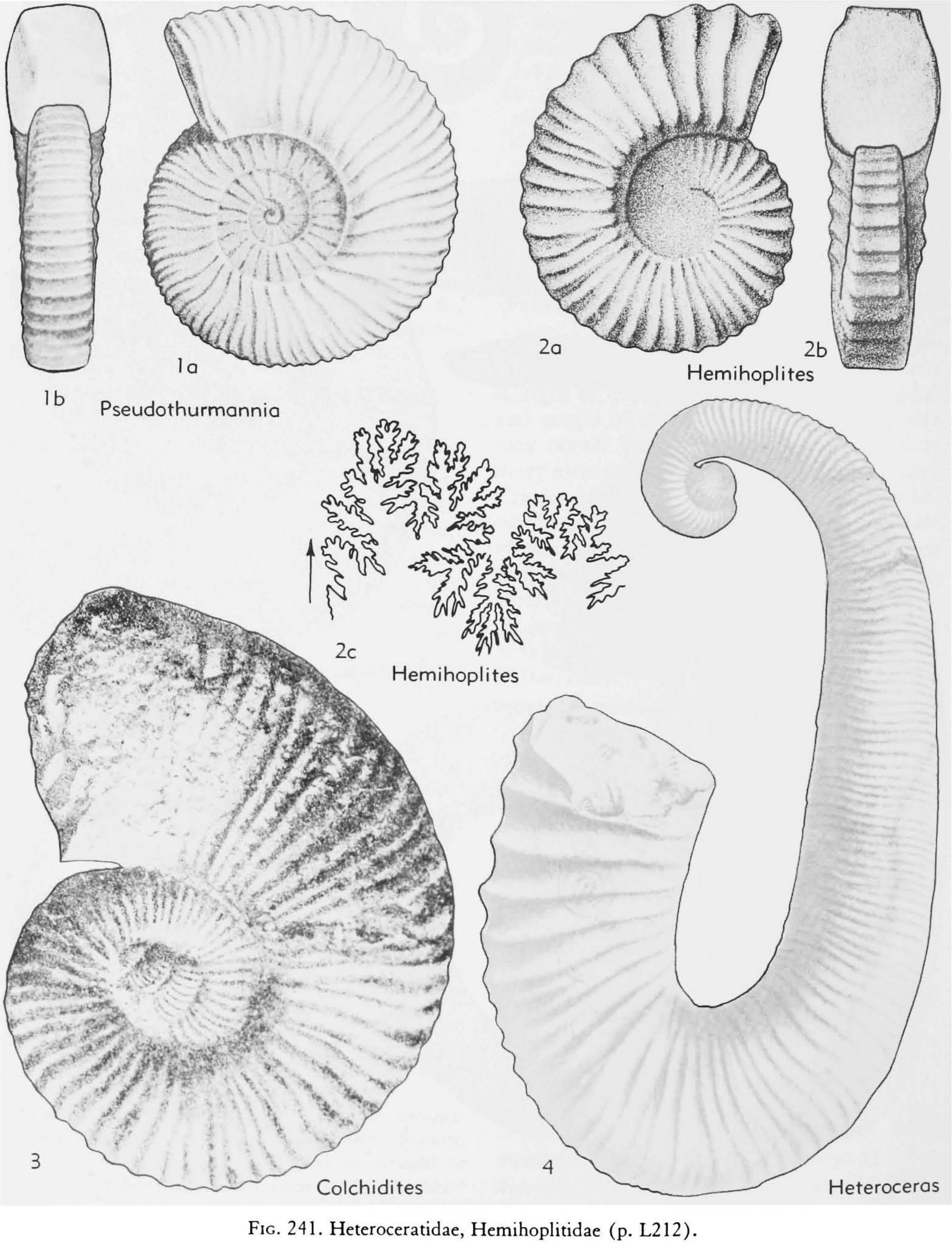


FIG. 241. Heteroceratidae, Hemihoplitidae (p. L212).

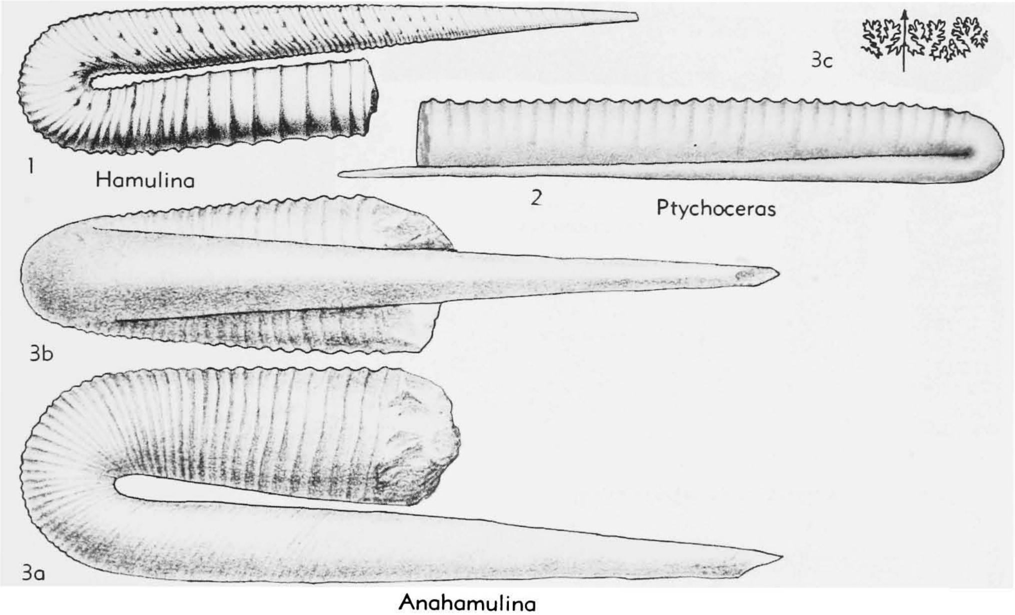


FIG. 242. Ptychoceratidae (p. L215-L216).

which may be descended from Macroscaphitidae or may have had an independent origin in some other member of the Lytocerataceae at about the same date. So far as form of shell goes, the Ptychoceratidae might be related to certain Crioceratitidae, but since there are Ptychoceratidae with bifid lobes, it is reasonable to assume a direct connection with the Lytocerataceae (568). *L.Cret.(Barrem.)-U.Cret.(Maastr.).*

Family PTYCHOCERATIDAE Meek, 1876

[Incl. Anahamulinidae BREISTROFFER, 1951]

With 2 or 3 nearly straight parallel shafts, smooth or with fine or coarse straight, radial or oblique ribs, which may be trituberculate. Suture primitively lytoceratoid, with bifid lobes, but in some genera with trifid lobes (51, 530). *L.Cret.(U.Hauteriv.-U.Alb.).*

Too little is known of the order of appearance of the heteromorphs from Upper Hauterivian deposits of southeastern France to be sure of the phylogeny of this family, but on assumption of their origin in Lytocerataceae, *Anahamulina* is interpretable as the most primitive form, continuing with bifid lobes to *Hamulina* and giving rise to *Euptychoceras* and its successors by closer contact of the shafts of the shell and by increasing trifidity of the lobes. *Anahamulina* probably originated in a form with macroscaphitid coiling derived by acceleration in appearance of the uncoiled hook and consequent dropping of the normally coiled spire.

Anahamulina HYATT, 1900 [**Hamulina subcylindrica* D'ORBIGNY, 1849]. Of moderate size, with long slowly increasing straight shaft that bends sharply (commonly with constriction at the bend) to a much shorter 2nd shaft, which is not in contact with the 1st; fine dense annular ribs, oblique on 1st shaft, radial and stronger on 2nd. Suture with lobes symmetrically bifid or asymmetric and tending to trifidity. *U.Hauteriv.-Barrem.,* S.Eu.-C.Eu.-Calif.——FIG. 242,*3*. **A. subcylindrica* (ORB.), Barrem., Silesia; *3a-c,* ×1 (530*).

Hamulina D'ORBIGNY, 1843 [**H. astieriana* ORB., 1843; SD ROMAN, 1938]. Much as *Anahamulina* but larger, with bifid lobes and periodic trituberculate ribs on part of shell. *Barrem.,* S.Eu.-C.Eu.-Calif.——FIG. 242,*1*. **H. astieriana* ORB., Barrem., Fr.; ×0.2 (673*).

Hamulinites PAQUIER, 1900 [**Hamulina munieri* NICKLÈS, 1894]. Differs from *Anahamulina* in its small size, strong ribs and simple sutures with distinctly trifid lobes. *Barrem.,* Sp.-?Fr.

Euptychoceras BREISTROFFER, 1952 [**Ptychoceras meyrati* OOSTER, 1860]. With long straight slowly increasing initial shaft followed by rather longer 2nd shaft parallel to it and barely or not touching it, and finally by 3rd shaft which may slightly overlap 1st; smooth or with rather weak ribbing ex-

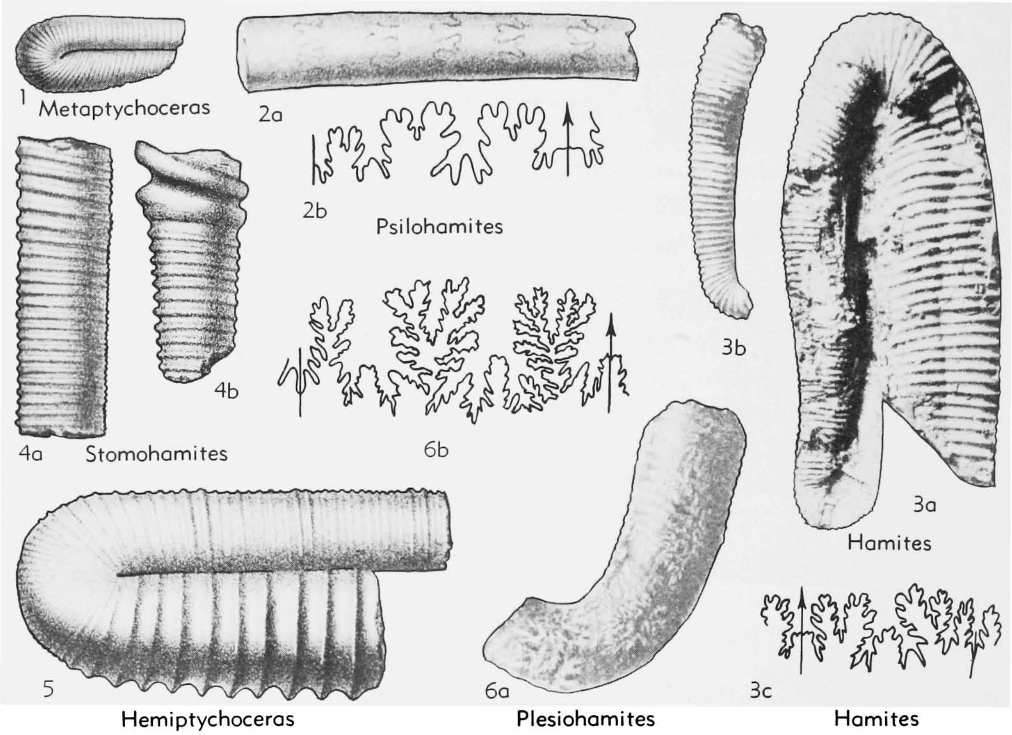


Fig. 243. Hamitidae (p. L216-L217).

cept that prominent broad scalelike ribs may occur on last shaft. Suture with trifid lobes. *Barrem.*, S. Eu.-C.Eu.-Calif. (*E. teschenense* Hohenegger in Uhlig, 1901, is said to be Upper Valanginian, but this is doubtful.)

Ptychoceras d'Orbigny, 1842 [**P. emericianum* Orb., 1842; SD Diener, 1925] [*Diptychoceras* Gabb, 1869; *Mastigoceras* Boehm, 1925 (*non* Handschin, 1924; *?Tricoloceras* Whitehouse, 1928; *Mastigohamites* Breistroffer, 1947]. Differs from *Euptychoceras* only in being smaller, having initial shaft closely pressed into dorsum of 2nd and in having weaker ornament except on venter where strong rounded ribs may be present. *U.Apt.-U.Alb.*, Fr.-Cauc.-Madag.-S.India-?B.C.-Calif.-Mex. ——Fig. 242,*2*. **P. emericianum* Orb., U.Apt., Fr.; side of 1st shaft and part of 2nd, ×1 (329*).

Family HAMITIDAE Hyatt, 1900

Coiling rather irregular but typically an open plane spiral tending to end in 2 or 3 more or less parallel shafts; early whorls may be helical; section circular to compressed; dense, normally straight radial or oblique ribs, continuous over venter, in some shells interrupted on dorsum; no tubercles. Suture lytoceratoid. The earliest *Hamites* are probably U.Apt. and derived from *Macroscaphites* by loosening of the coiling (50, 459). *L. Cret.(U.Apt.)-U.Cret.(Turon.).*

Hamites Parkinson, 1811 [**H. attenuatus* J.Sowerby, 1814; SD Diener, 1925] [=*Torneutoceras* Hyatt, 1900]. Typically with 3 well-separated subparallel shafts but early helical coiling often persists; section circular, depressed or compressed; ribs typically strong, fine and dense to coarse and distant. Suture with small, not bifid 3rd lateral saddle. *U.Apt.-U.Alb.*, Eu.-Afr.-India-USA.

H. (Hamites). Coiling after early whorls in one plane; ribs invariably present. Occurrence as for genus.——Fig. 243,*3*. **H. (H.) attenuatus* J.Sow., M.Alb., Eng.; ×1 (713*).

H. (Hamitella) Breistroffer, 1947 [**Helicoceras annulatum* d'Orbigny, 1842] [=*Helicoceras* Orb., 1842 (*non* Koenig, 1825)]. Coiled asymmetrically throughout, forming loose helix (doubtfully distinct). *M.Alb.*, Fr.-Zululand.

H. (Psilohamites) Spath, 1941 [**Hamites bouchardianus* d'Orbigny, 1842]. Almost smooth; only straight shafts are known. *U.Alb.*, W.Eu. ——Fig. 243,*2*. **H. (P.) bouchardianus* Orb., U.Alb., Fr.; *2a*, ×1; *2b*, enlarged (329*).

Hemiptychoceras Spath, 1925 [**Ptychoceras gaultinum* Pictet, 1847]. With 3 shafts of typical

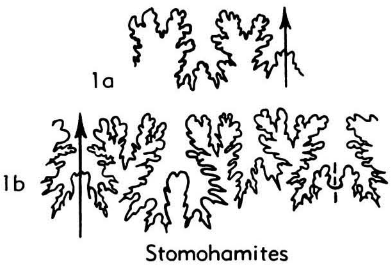


FIG. 244. *Stomohamites duplicatus* (PICTET & CAMPICHE), L.Cret.(U.Alb.), Fr.; *1a,b,* ×3 (713*) (p. L217).

Hamites closely pressed together; ribs as in *Hamites* except on 2nd bend where they tend to be scale-like, as in some *Euptychoceras. U.Alb.,* W.Eu.——FIG. 243,*5.* **H. gaultinum* (PICTET), U.Alb., Fr.; ×1 (346*).

Stomohamites BREISTROFFER, 1940 [**Hamites virgulatus* BRONGNIART, 1822]. Typically with denser ribs than *Hamites* and at least some species have strongly collared and constricted aperture; venter tends to be flat. Suture with 3rd lateral saddle nearly as big as others and symmetrically bifid. U.Alb.-L.Turon., Eu.-USA-Mex.——FIG. 243,*4;* 244,*1. S. duplicatus* (PICTET & CAMPICHE), U.Alb., Fr.; 243,*4a,b,* ×1 (346*); 244,*1a,b,* ×3 (713*).

Metaptychoceras SPATH, 1926 [**Ptychoceras smithi* WOODS, 1896]. Small; much like *Hemiptychoceras* but has fine ribbing of *Stomohamites. U.Turon.,* Eng.——FIG. 243,*1.* **M. smithi* (WOODS); ×2 (734*).

Plesiohamites BREISTROFFER, 1947 [**Hamites multicostatus* BROWN, 1837]. Rather large, with straight shafts and fine straight oblique ribs. Suture florid. Generally resembles in fragments some *Hamulina* or *Diplomoceras. U.Alb.,* W.Eu.——FIG. 243,6. **P. multicostatus* (BROWN), U.Alb., Eng.; *6a,* ×1; *6b,* ×2 (713*).

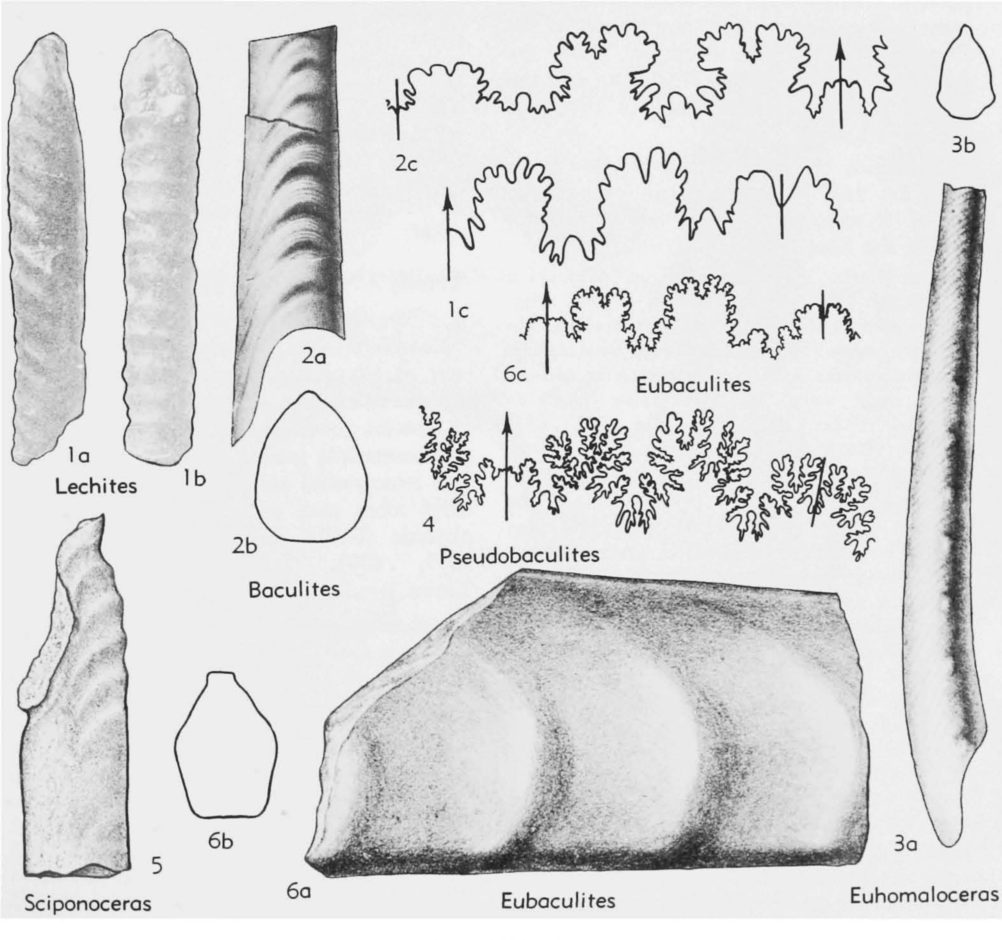


FIG. 245. Baculitidae (p. L218).

Family BACULITIDAE Meek, 1876

Minute initial coil of 1 or 2 whorls followed by straight or very slightly curved single shaft; section circular, oval, pear-shaped, or acute; constrictions may be present; surface smooth or with flexuous striae or ribs, which may be enlarged into tubercles on sides or venter; aperture oblique, with or without collar, or simple and directed forward. Suture with all elements more or less bifid except for internal and (rarely) external lobes, varying in floridity and detail. Rugaptychi are present in *Baculites* at least (323, 459, 465). *L.Cret.(U.Alb.)-U.Cret. (Maastr.).*

Rather small forms appear in the Upper Albian, representing hamitids that have straightened, lost their ribs and are developing oblique apertures. There is little important change until the Santonian, when some species several feet long occur. In the Campanian and Maastrichtian there are forms as much as 6 feet (2m.) long and the family reaches its maximum of diversity, though a limited one.

Baculitids are often found in very large numbers and representing all ontogenetic stages. It seems that they lived in colonies on the sea floor.

Lechites NOWAK, 1908 [**Baculites gaudini* PICTET & CAMPICHE, 1861]. Section circular or oval, without constrictions; regular low prorsiradiate ribs may be grouped in 2's or 3's or even amalgamated to form scalelike swellings; aperture facing dorsum, with slight collar and constriction. *U.Alb.-L. Cenom.,* W.Eu.-C.Eu.-Mex.——FIG. 245,*1*. **L. gaudini* (PICTET-C.), U.Alb., Eng.; *1a,b,* ×1; *1c,* ×2 (713*).

Sciponoceras HYATT, 1894 [**Hamites baculoides* MANTELL, 1822] [=*Cyrtochilus* MEEK, 1876 (*non* JAKOWLEW, 1875); *Cyrtochilella* STRAND, 1929]. With strong prorsiradiate constrictions; aperture differs from that of *Lechites* in having few strong, broad folds and high collar and in some forms lateral lappets. Suture more finely divided than in *Lechites*. In latest species ribs on body chamber are rursiradiate on inner 3rd and then prorsiradiate, with faint tubercle at the bend, thus foreshadowing *Baculites*. *U.Alb.-U.Turon.,* Eu.-N.Afr.-Madag.-S. India-USA.——FIG. 245,*5*. **S. baculoides* (MANTELL), Cenom., Eng.; lateral view of body chamber, venter to right, ×1 (602*).

Baculites LAMARCK, 1799 [**Baculites vertebralis* DEFRANCE, 1830; SD MEEK, 1876] [=*Homaloceras* HUBSCH, 1786 (*non. binom.*)]. Straight shell, some large, surface smooth or with sinuous striae, rursiradiate on inner and prorsiradiate on outer part, in some with large curved bulla at the bend; venter narrowly rounded to acute; aperture typically directed forward, with long dorsal rostrum but a gradual transition occurs during Turonian and Coniacian from *Sciponoceras*-type of aperture. Suture more florid than in earlier genera. *U.Turon.-Maastr.,* world-wide.——FIG. 245,*2*. *B. anceps* (LAM.), Camp., Fr.; *2a,* side of body chamber, venter to left, ×0.5; *2b,* ×1; *2c,* enlarged (329*).

Pseudobaculites COBBAN, 1952 [**P. nodosus*]. Differs from *Baculites* in its more rapidly expanding section and broad, much divided, asymmetric saddles. *Coni.,* Wyo.-Utah.——FIG. 245,*4*. **P. nodosus;* ×2 (599a).

Euhomaloceras SPATH, 1926 [**Baculites incurvatus* DUJARDIN, 1837]. Body chamber gently curved with distinct rounded siphonal and laterodorsal tubercles. *?Coni., Santon.-Camp.,* Fr.——FIG. 245, *3*. **E. incurvatus* (DUJARDIN); *3a,b,* ×0.75 (329*).

Eubaculites SPATH, 1926 [**Baculites otacodensis* STOLICZKA, 1866]. Section pear-shaped, with flat venter; ribs normally faint toward venter but on inner part form prominent long curved bullae; row of lower lateral tubercles may be present. Suture with plump, minutely frilled elements. *Maastr.,* Madag.-S.India-W.Austral.-Japan-Chile. —— FIG. 245,*6a,b*. **E. otacodensis* (STOLICZKA), L.Maastr., S.India; *6a,* ×1; *6b,* ×0.5 (238*).——FIG. 245, *6c*. *E. vagina* (FORBES), L.Maastr., S.India; ×1 (238*).

Family ANISOCERATIDAE Hyatt, 1900

[Includes Algeritidae SPATH, 1925]

Loosely coiled, irregularly helical at first, later part typically in one plane, some with straight final shaft. There is normally a pair of ventral tubercles on some ribs at least and commonly lateral tubercles as well. Suture lytoceratoid except that in some genera trifid lobes may occur. Probably a monophyletic family derived from Hamitidae (345, 459). *L.Cret.(L.Alb.)-U.Cret.(U. Turon.).*

Prohelicoceras SPATH, 1925 [**Hamites thurmanni* PICTET & CAMPICHE, 1861]. Coiling twisted at all stages; sharp annular ribs, normally some with pair of ventral tubercles. *L.Alb.-M.Alb.,* W.Eu.-Madag.——FIG. 246,*4*. **P. thurmanni* (PICTET-C.), M.Alb., Switz.; *4a,b,* ×1 (345*).

Protanisoceras SPATH, 1923 [**Hamites raulinianus* D'ORBIGNY, 1842]. More or less regular loose slightly helical spire that normally ends in 1 or 2 straight shafts; prominent sharp or blunt ribs with sharp lateral and a pair of ventral tubercles joined over venter by double rib. Suture simpler than in *Anisoceras*. *L.Alb.-M.Alb.,* W.Eu.-Madag.-India-

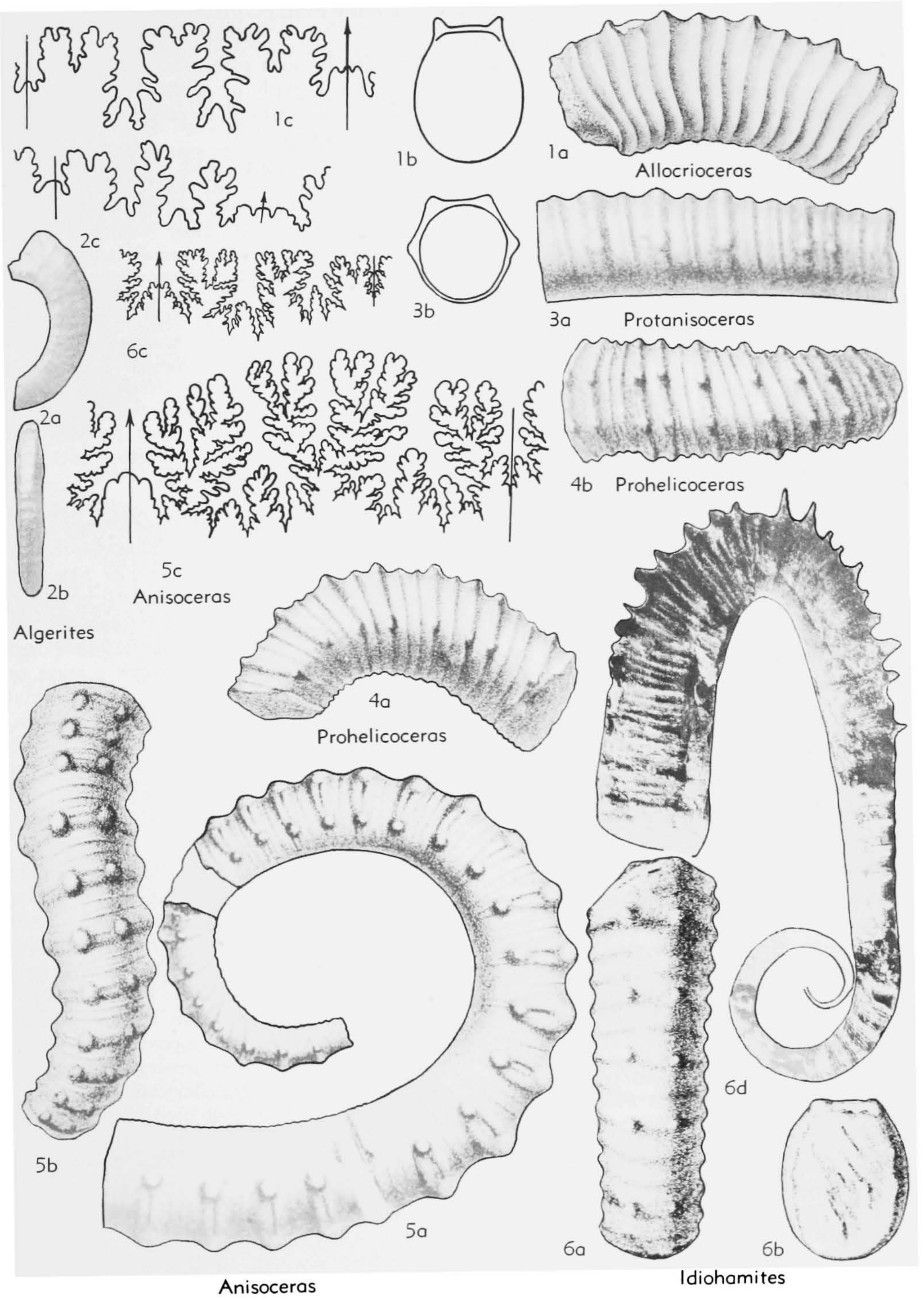


FIG. 246. Anisoceratidae (p. L218-L220).

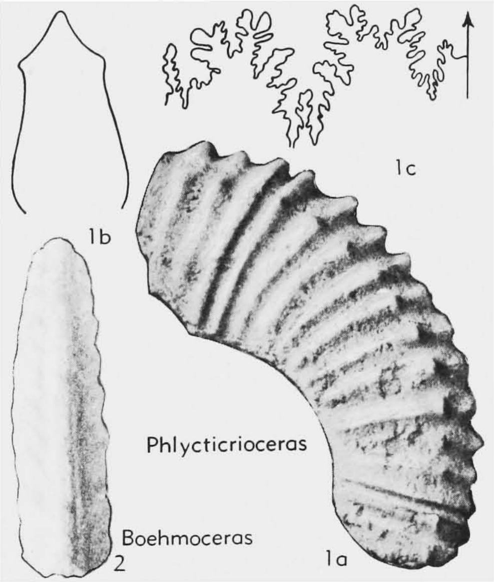


FIG. 247. Phlycticrioceratidae (p. L220).

Peru.——FIG. 246,*3*. **P. raulinianum*, L.Alb., Fr.; *3a,b*, ×1 (329*).

Anisoceras Pictet, 1854 [**Hamites saussureanus* Pictet, 1847]. Differs little from *Protanisoceras* but ornament is generally coarser and suture more complicated. *U.Alb.-U.Turon.*, Eu.-N.Afr.-E.Afr.-Madag.-Pak.-India-Tex.-Mex.——FIG. 246,*5*. **A. saussureanum* (Pictet), U.Alb., Fr.; *5a,b*, ×1; *5c*, enlarged (346*).

Metahamites Spath, 1930 [**Hamites sablieri* d'Orbigny, 1842]. Differs from *Protanisoceras* in that coiling is in one plane, with final hook on which ornament may change. *M.Alb.*, Fr.-Madag.-India.

Idiohamites Spath, 1925 [**Hamites tuberculatus* J. Sowerby, 1818]. Coiling rather irregular, in one plane; ribs straight or oblique, with pair of ventral tubercles, joined only by single rib on venter; lateral tubercles rarely present. *U.Alb.-Cenom.*, W. Eu.-N.Afr.-Madag.-Tex.——FIG. 246,*6a-c*. *I. dorsetensis* Spath, U.Alb., Eng.; *6a,b*, ×1; *6c*, enlarged (345*).——FIG. 246,*6d*. *I. spiniger* (J. Sow.), U.Alb., Fr.; ×0.4 (713*).

Algerites Pervinquière, 1910 [**A. sayni*]. Regularly and (after initial open whorls) closely coiled, with whorls in contact; pair of sharp ventral tubercles on every rib. Derived from closely coiled *Idiohamites*. *Cenom.*, N.Afr.——FIG. 246,*2*. **A. sayni; 2a,b*, ×1; *2c*, ×4 (340*).

Allocrioceras Spath, 1926 [**A. woodsi*]. Similar to the more finely ribbed and sharply tuberculate species of *Idiohamites* but early whorls at least are distinctly helical and twisted. *Turon.*, Eng.-Ger.-USA.——FIG. 246,*1*. **A. woodsi;* U.Turon., Eng.; *1a,b*, ×0.75; *1c*, enlarged (734*).

Family PHLYCTICRIOCERATIDAE Spath, 1926

Coiled in open plane spiral; section oval; ribs strong, with or without ventrolateral tubercles; keel strong, serrate or entire (465). *U.Cret.(Coni.)*.

Phlycticrioceras Spath, 1926 [**Ancyloceras* (?) *douvilléi* de Grossouvre, 1894]. Sharp, straight, radial or rursiradiate ribs, with strong ventrolateral and siphonal tubercles, latter forming a serrate keel; collared constrictions normally present. Probably derived from *Allocrioceras*. *Coni.*, Fr.-Ger.-Wyo.-Mex.——FIG. 247,*1*. **P. douvillei* (Gross.), Fr.; *1a,b*, ×1; *1c*, ×2 (179*).

?**Boehmoceras** Riedel, 1931 [**Ancyloceras krekeleri* Wegner, 1905; SD Wright, herein]. Whorl height increases rapidly; with strongly curved primary ribs, which may form large distant bulges, split into several secondaries on outer part of sides; keel entire and rounded. *Coni.*, Ger.——FIG. 247, *2*. **B. krekeleri* (Wegner); ×1 (690*).

Family TURRILITIDAE Meek, 1876

Helical forms, dextral or sinistral, loosely or tightly coiled, typically regular but early and late whorls somewhat unstable; apical angle more or less acute, less than 90°; in early species, siphon is in middle of exposed side but later migrates to upper margin or even to upper internal angle of whorl; ornamented with strong ribs or tubercles or both, rarely smooth. Suture asymmetrical because of the helical coiling; primitively, lobes are bifid but they are variable and tend to trifidity (52, 459). *L.Cret.(M.Alb.)-U.Cret.(Turon.)*.

Two genera appear in the early Middle Albian, *Proturrilitoides* without tubercles and *Pseudhelicoceras* with them. The former seems to be derived from a helical hamitid, the latter from *Protanisoceras*. Any subfamily division should reflect distinction of the stocks descended from these 2 genera, but because of doubt concerning the stock to which certain later genera belong subfamilies (e.g., Pseudhelicoceratinae Breistroffer, 1953) are not used here.

The last typical Turrilitidae appear in the Lower Turonian. The occasional tightly coiled Senonian forms belong to Nostoceratidae.

Proturrilitoides Breistroffer, 1947 [**Turrilites astierianus* d'Orbigny, 1842]. Whorl section more or less circular, with siphuncle at middle of exposed part; apical angle variable; umbilicus wide; aperture slightly constricted and collared; ribs more or less dense, radial or prorsiradiate, strong and simple, without tubercles. *M.Alb.*, Fr.-Pol.——FIG. 248,*1*. **P. astierianus* (ORB.), M.Alb., Fr.; ×1 (329*).

Turrilitoides SPATH, 1923 [**Turrilites hugardianus* D'ORBIGNY, 1842]. Apical angle more acute than in *Proturrilitoides*, more tightly coiled, with oval or angular whorl section and flatter sides; siphuncle at upper margin of side; aperture with strong constriction, collared on both sides. *U.Alb.*, Eu.-Pak.——FIG. 248,*3*. *T. densicostatus* PASSENDORFER, U.Alb., Eng.; *3a*, ×1; *3b*, ×2 (713*).

Ostlingoceras HYATT, 1900 [**Turrilites puzosianus* D'ORBIGNY, 1842]. Very closely coiled, with acute apical angle; whorl section more angular and flat-sided than in *Turrilitoides*, although it becomes more inflated in latest species; dense straight or slightly flexuous ribs, with up to 3 tubercles at lower end. Derived from *Proturrilitoides* in parallel with *Turrilitoides*. *M.Alb.-L.Cenom.*, Eu.-N. Afr.-Madag.

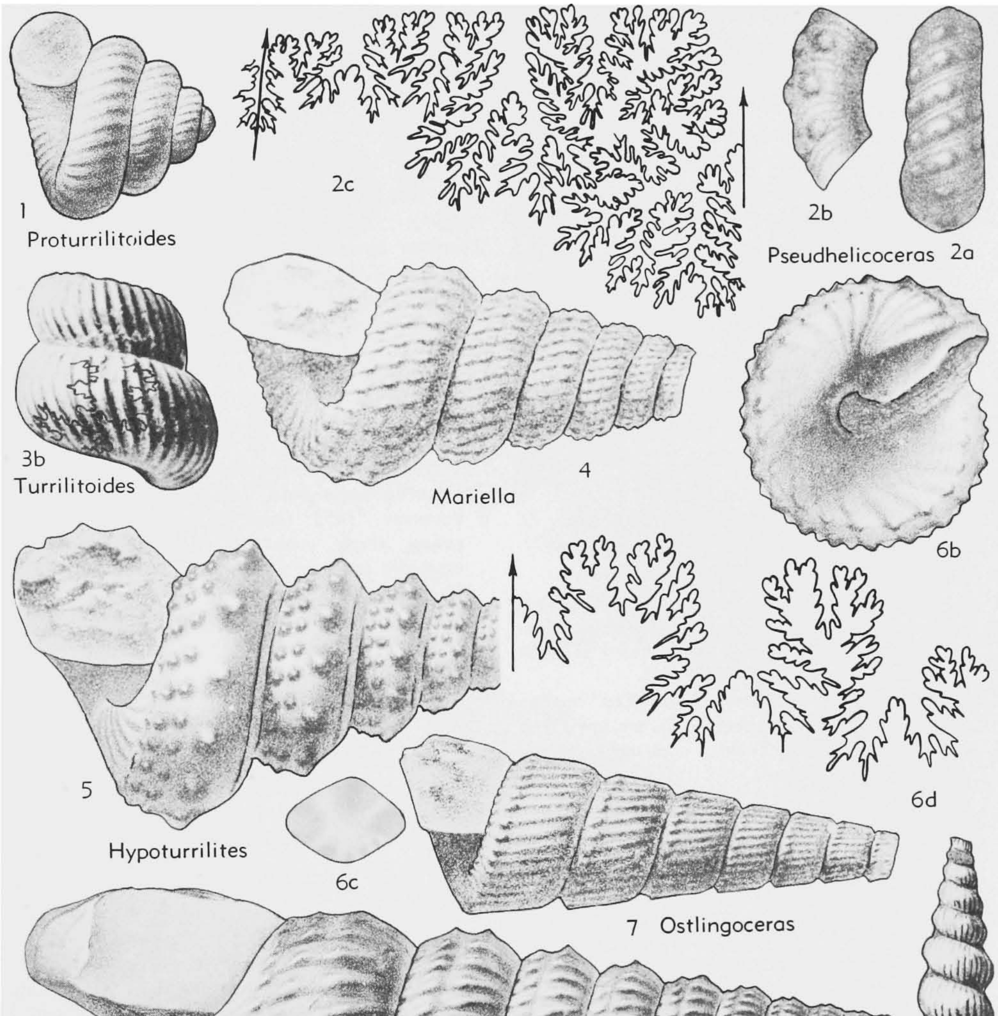


FIG. 248. Turrilitidae (p. L220-L222).

Fig. 249. *Plesioturrilites brazoensis* (Roemer), U. Cret.(L.Cenom.), Tex.; *1*, ×0.75 (653*) (p. L222).

O. (Parostlingoceras) Breistroffer, 1953 [**Turrilites moutonianus* d'Orbigny, 1842]. Ribs rather irregular, angulate or weakly tuberculate at lower angle of side. *M.Alb.*, Fr.-Pol.

O. (Ostlingoceras) Hyatt, 1900. Ribs regular, with 2 or 3 distinct tubercles at the lower end of each. *U.Alb.-L.Cenom.*, occurrence as for genus.——Fig. 248,7. **O. (O.) puzosianum* (Orb.), U.Alb., Fr.; ×1 (329*).

Pseudhelicoceras Spath, 1921 [**Turrilites robertianus* d'Orbigny, 1842] [=*Subhelicoceras, Parahelicoceras* Breistroffer, 1953]. Apical angle moderately to very acute; coiling loose or tight; as here interpreted, ribbing variable, branching or simple, radial or prorsiradiate, with 2 to 4 tubercles, which may cover several ribs, normally with intermediate nontuberculate ribs; siphuncle at or near middle of exposed side. *M.Alb.-U.Alb.*, W.Eu.-C.Eu.-Madag.——Fig. 248,*2*. **P. robertianum* (Orb.), U.Alb., Fr.; *2a,b*, ×1; *2c*, enlarged (329*).

Mariella Nowak, 1916 [not invalidated by *Mariaella* Gray, 1855] [**Turrilites bergeri* Brongniart, 1822] [*Paraturrilites* Breistroffer, 1947; *?Hemiturrilites* Breistr., 1953] Apical angle variable; closely coiled; ribs slightly oblique, rather feeble, each with 4 more or less equal tubercles. *U.Alb.-Cenom.*, Eu.-N.Afr.-Madag.-Iran-S.India-Tex.

M. (Mariella). Tubercles more or less equidistant, intercostal section rounded. Occurrence as for genus.——Fig. 248,*4*. **M. (M.) bergeri* (Brongn.), U.Alb., Fr.; ×1 (329*).

M. (Plesioturrilites) Breistroffer, 1953 [**Turrilites brazoensis* Roemer, 1852]. Upper and lower pairs of tubercles separated by marked spiral furrow; body chamber uncoils. *L.Cenom.*, Tex.——Fig. 249,*1*. **P. brazoensis* (Roemer); ×0.75 (653*).

Hypoturrilites Dubourdieu, 1953 [Shimizu, 1935 *(nom. nud.)*] [**Turrilites gravesianus* d'Orbigny, 1842]. Differs from *Mariella* in that ribs are almost absent and middle row of tubercles contain fewer and much larger tubercles than remainder. May be large. *Cenom.*, Eu.-Afr.-India-Japan-Tex.——Fig. 248,*5*. **H. gravesianus* (Orb.), Fr.; ×1 (329*).

Turrilites Lamarck, 1801 [**T. costatus*]. Apical angle acute, shell tightly coiled; ribs weak to strong, with or without 3 or 4 rows of equal numbers of tubercles. Probably derived from *Mariella. Cenom.*, *?L.Turon.*, Eu.-Afr.-India-USA-Mex.

T. (Turrilites). Ribs weak, tubercles strong, bullate or spinate. Occurrence as for genus.——Fig. 248, *6*. **T. (T.) costatus*, L.Cenom., Fr.; *6a,b*, ×0.75; *6c*, ×0.5; *6d*, enlarged (329*).

T. (Euturrilites) Breistroffer, 1953 [**Turrillites scheuchzerianus* Bosc, 1801] [=*Turbinites* Dubourdieu, 1953 (*non* Martin, 1809)]. Ribs strong, simple, commonly depressed in middle, especially on early whorls; no tubercles. *Cenom.*, Eu.-W.Afr.-Madag.-Japan.

T. (Mesoturrilites) Breistroffer, 1953 [**Turrilites aumalensis* Coquand, 1862]. Ribs almost absent; tubercles clavate, tending to form spiral ridges. *L.Cenom.*, W.Eu.-N.Afr.-Madag.

Wintonia Adkins, 1928 [**W. graysonensis*]. Like small *Turrilites* but with initial part consisting of 2 subparallel nearly straight shafts. *L.Cenom.*, Tex.

Raynaudia Dubourdieu, 1953 [**Carthaginites raynaudiensis* Collignon, 1932]. Smooth, suture with reduced elements; siphuncle at external upper angle of whorl. *U.Alb.*, Madag.

Carthaginites Pervinquière, 1907 [**Turrilites (Carthaginites) kerimensis*]. Only minute fragments known. Differs from *Raynaudia* in having spiral groove long middle of side, with or without a single row of small tubercles, and siphuncle at inner upper angle of whorl. *L.Cenom.*, N.Afr.-Tex.

Family NOSTOCERATIDAE Hyatt, 1894

[Includes Jouaniceratidae Wright, 1952; Hyphantoceratinae, Bostrychoceratinae, Emperoceratinae, and Neocrioceratinae Spath, 1953]

Helicoid forms in which coiling is normally irregular in early or late stages or both or throughout life. Several stocks tend to revert to bilateral symmetry. Tubercles commonly occur but are typically subordinate to dense ribs. Constrictions are general. Suture normally of lytoceratid type and florid. Although form of the genera is very variable, they are closely connected and separation into subfamilies is probably unnecessary. The family is almost certainly monophyletic, being derived (presumably in the Cenomanian) from a descendant of the Albian *Turrilitoides* (489, 497, 572). *U.Cret.* *(Cenom.-Maastr.).*

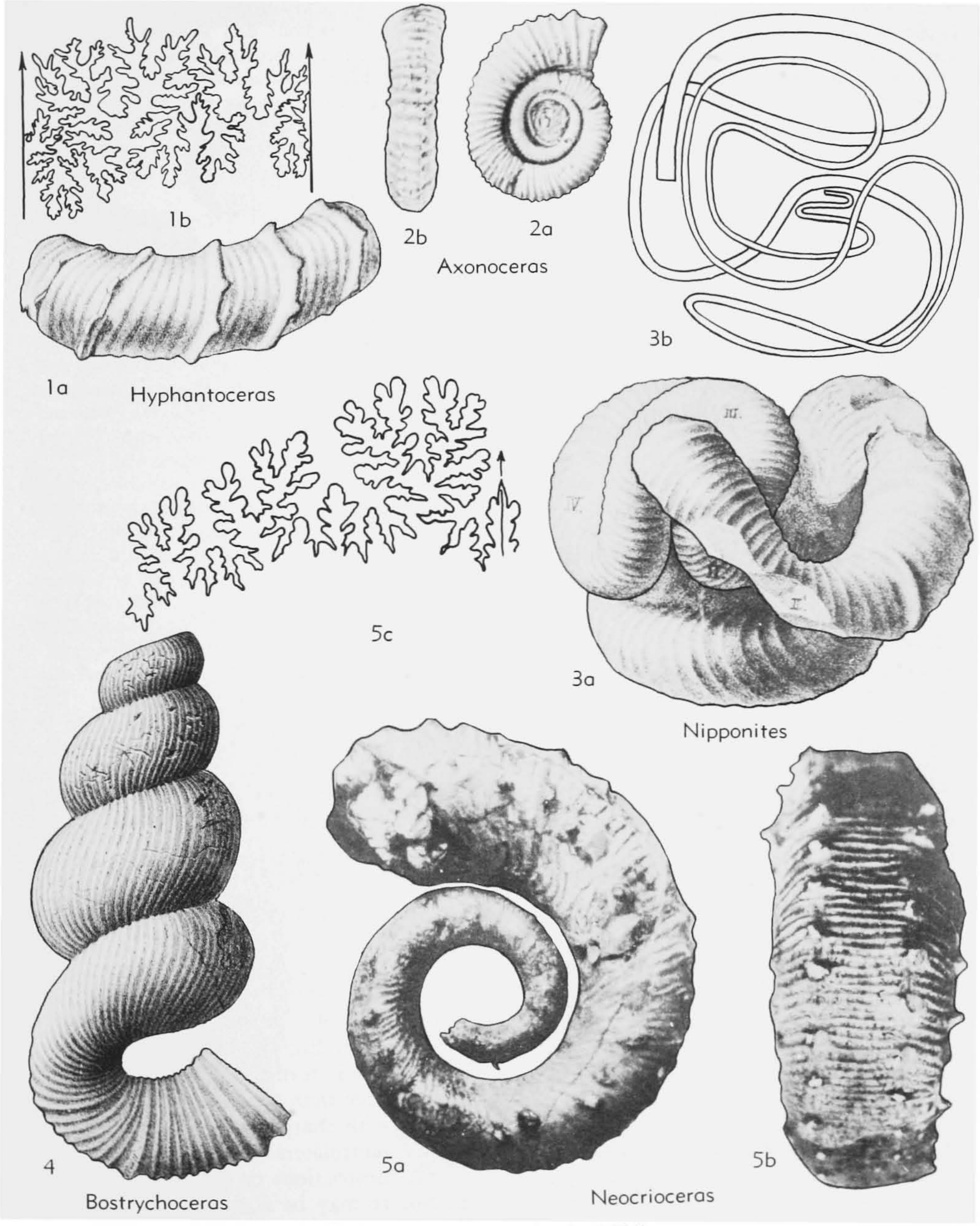


FIG. 250. Nostoceratidae (p. L224).

Bostrychoceras Hyatt, 1900 [**Turrilites polyplocus* Roemer, 1841]. More or less acute-angled, tightly coiled spire with loose, U-shaped body chamber; dense, rather strong ribs, normally slightly sinuous and oblique; with or without strong constrictions, but with no flared ribs. *Cenom.-L.Maastr.*, Eu.-N. Afr. - Madag. - S. India-Japan-W. Austral.-Tex.-Mex.——Fig. 250,*4*. **B. polyplocum* (Roemer), Camp., N.Ger.; ×0.5 (422*).

Nipponites Yabe, 1904 [**N. mirabilis*]. Coiled in a succession of U's in 3 dimensions, forming a tangle; single regular ribs and constrictions as in *Bostrychoceras*. *?U.Turon., L.Santon.*, ?Eng.-Madag.-Japan.——Fig. 250,*3*. **N. mirabilis*, Coni., Japan; *3a*, ×0.75; *3b*, diagram of coiling ×0.5 (739*).

Jouaniceras Basse, 1939 [**Heteroceras sicardi* de Grossouvre, 1894]. First 2 or 3 whorls as in *Bostrychoceras*, then suddenly becoming coiled in plane spiral with axis at right angles to that of initial spire; on plane part there are distant, thin, high ribs that become sharper with age, some on outer whorl being flared. *Santon.*, Fr.——Fig. 251, *4*. **J. sicardi* (Gross.); *4a,c*, ×2; *4b*, ×1 (585*).

Hyphantoceras Hyatt, 1900 [**Hamites reussianus* d'Orbigny, 1850 (=**Heteroceras reussianum* Schlüter, 1872)] [=*Euhyphantoceras, Orientoceras* Shimizu, 1935]. Loosely and commonly irregularly coiled spire ending in U-shaped or irregular body chamber; whorl section circular or oval; dense slightly oblique weak nontuberculate ribs, with periodic very thin flared ones, normally with 2 or 4 tubercles; no constrictions. *Turon.-Santon.*, N.Eu.-N.Afr.-S.India-N.Z.-Japan.——Fig. 250,*1*. **H. reussianum* (Schlüter), U.Turon., Eng.; *1a*, ×1; *1b*, ×2 (734).

Nostoceras Hyatt, 1894 [**N. stantoni*]. Differs from *Bostrychoceras* mainly in having on most of shell 2 rows of more or less prominent tubercles on all or some ribs; collared constrictions may or may not be present. *Camp.*, Angola-Eng.-Madag.-USA.

- **N. (Nostoceras)**. Final U-shaped part hanging below spire. Occurrence as for genus.——Fig. 251,*6*. **N. (N.) stantoni*, Camp., Tex.; ×1 (497*).
- **N. (Anaklinoceras)** Stephenson, 1941 [**A. reflexum*]. Final part bent up one side of spire and down other. *Camp.*, Tex.——Fig. 251,*2*. **N. (A.) reflexum;* ×1 (497*).

Axonoceras Stephenson, 1941 [**A. compressum*]. Small; coiled almost symmetrically in one plane, initial hoop being followed by whorls irregularly in contact or not; fine, dense simple ribs; bituberculate periphery. Derived from *Nostoceras* with wide apical angle. *Camp.*, Angola-Tex.——Fig. 250,*2*. **A. compressum*, Camp., Tex.; *2a,b*, ×1.5 (497*).

Exiteloceras Hyatt, 1894 [**Ancyloceras jenneyi* Whitfield, 1880; SD Diener, 1925]. Coiling elliptical, almost symmetrically in one plane, at least until beginning of body chamber; whorl section oval; ribs simple at first, later some branching, looped and intercalated, all with ventrolateral spines. *Camp.*, N.Dak.——Fig. 251,*7*. **E. jenneyi* (Whitf.); *7a,b*, ×1; *7c*, ×2 (733*).

Solenoceras Conrad, 1860 [**Hamites annulifer* Morton, 1842] [*Oxybeloceras* Hyatt, 1900]. Two straight or slightly curved parallel or diverging shafts, in some shells closely in contact, with circular to oval section; first shaft normally constricted, aperture constricted and collared; ribs straight, radial or rursiradiate, bearing small sharp ventrolateral spines, but ribs may be weakened or interrupted on venter. *Camp.-Maastr.*, N.Eu.-Angola-Madag.-USA-GrahamLand.——Fig. 251,*1*. *S. multicostatum* (Stephenson), Camp., Tex.; *7a,b*, ×2 (497*).

Neocrioceras Spath, 1921 [**Crioceras spinigerum* Jimbo, 1894]. Initially irregular, loose, shallow helix but later in one plane with J-shaped body chamber on which ribs coarsen; section circular to depressed; periodic strong ribs have lateral and ventrolateral tubercles, ribs commonly being looped between them, as in *Anisoceras;* up to 3 fine nontuberculate intermediate ribs, in some angulate on shoulders. *Camp.*, Eng.-Ger.-Rumania-Pondoland-Japan.——Fig. 250,*5*. **N. spinigerum* (Jimbo), Camp., Japan; *5a,b*, ×1; *5c*, enlarged (708*).

Cirroceras Conrad, 1868 [**Ammonceratites conradi* Morton, 1841] [*Didymoceras* Hyatt, 1894]. Similar to *Nostoceras* but larger and with whorls of spire not touching; as in *Nostoceras*, 2 rows of tubercles may be present throughout or only on body chamber. *Camp.-Maastr.*, W.Eu.-Nigeria-Angola-B.C.-USA.——Fig. 251,*3*. *C. nebraskense* (Hyatt), Camp., N.Dak.; ×0.3 (638*).

Emperoceras Hyatt, 1894 [**E. beecheri* (=*Helicoceras simplicicostatum* Whitfield, 1880)]. Like *Cirroceras* except body chamber may not be U-shaped and early part consists of 2 elliptical whorls, nearly in one plane, with 2 ribs joining at most of ventrolateral tubercles. *Camp.*, N.Dak.——Fig. 251, *5*. **E. simplicicostatum* (Whitf.); *5a,b*, ×0.3 (638*).

[**Neoturrilites** Shimizu, 1935 *(nom. nud.)*].

Family DIPLOMOCERATIDAE Spath, 1926

[Includes Polyptychoceratidae Matsumoto, 1938; Proavitoceratinae Spath, 1953]

Offshoots of Nostoceratidae, loosely coiled and tending to bilateral symmetry; ptychoceratoid forms develop which are more extreme than those in Nostoceratidae; typically with sharp annular nontuberculate ribs but ventrolateral spines occur in a few genera; constrictions or flares may be present. Suture may be florid, as in Nostoceratidae, or may simplify in extreme genera.

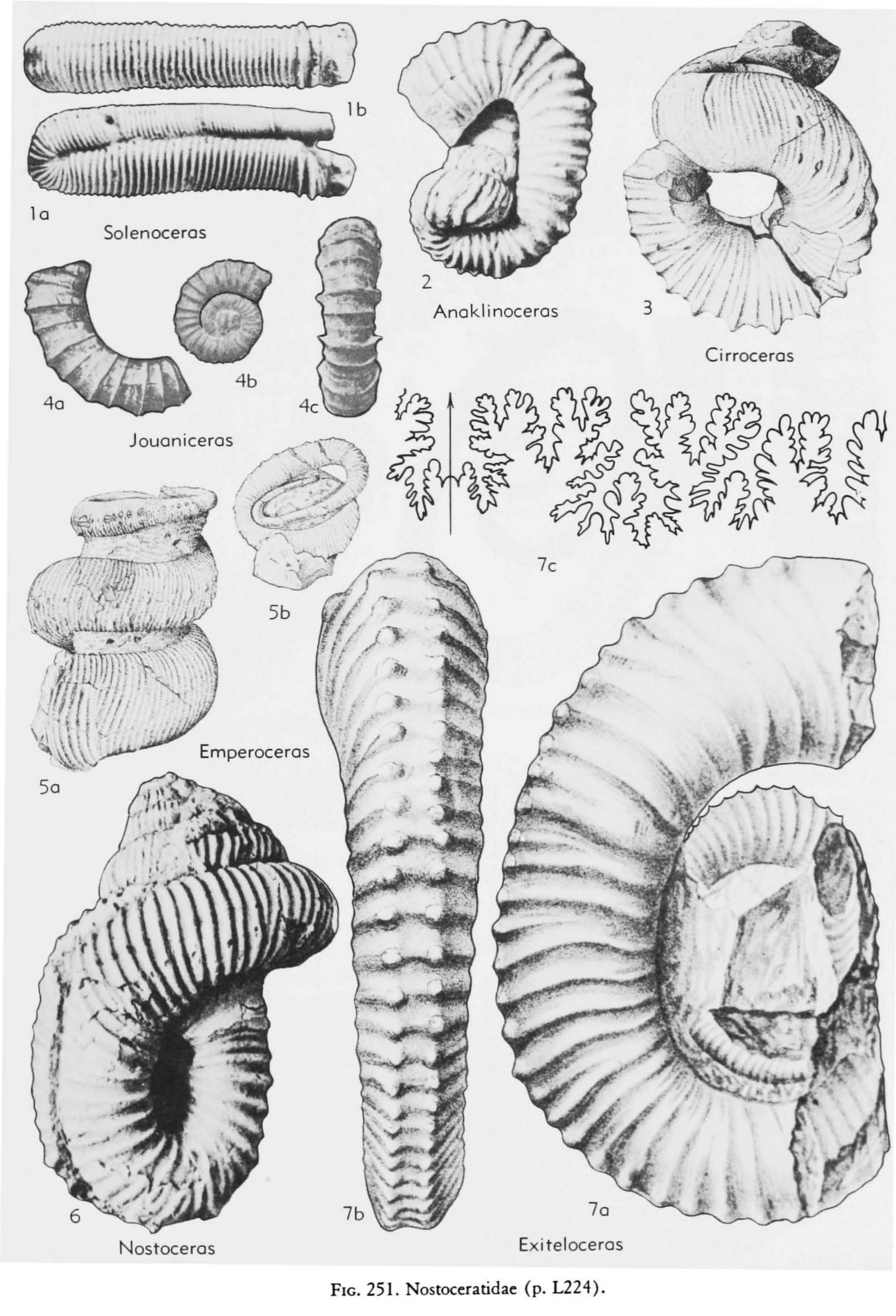


FIG. 251. Nostoceratidae (p. L224).

The family probably has single origin in *Hyphantoceras* of the Nostoceratidae but may include parallel offshoots of other members of that family (465, 489, 571). *U.Cret. (Turon.-Maastr.)*.

Scalarites Wright & Matsumoto, 1954 [*Helioceras scalare Yabe, 1904]. Very shallow open helicoid spire followed by loose elliptical coiling nearly in one plane; section more or less circular; ribs simple and annular, with sparse flared ribs or

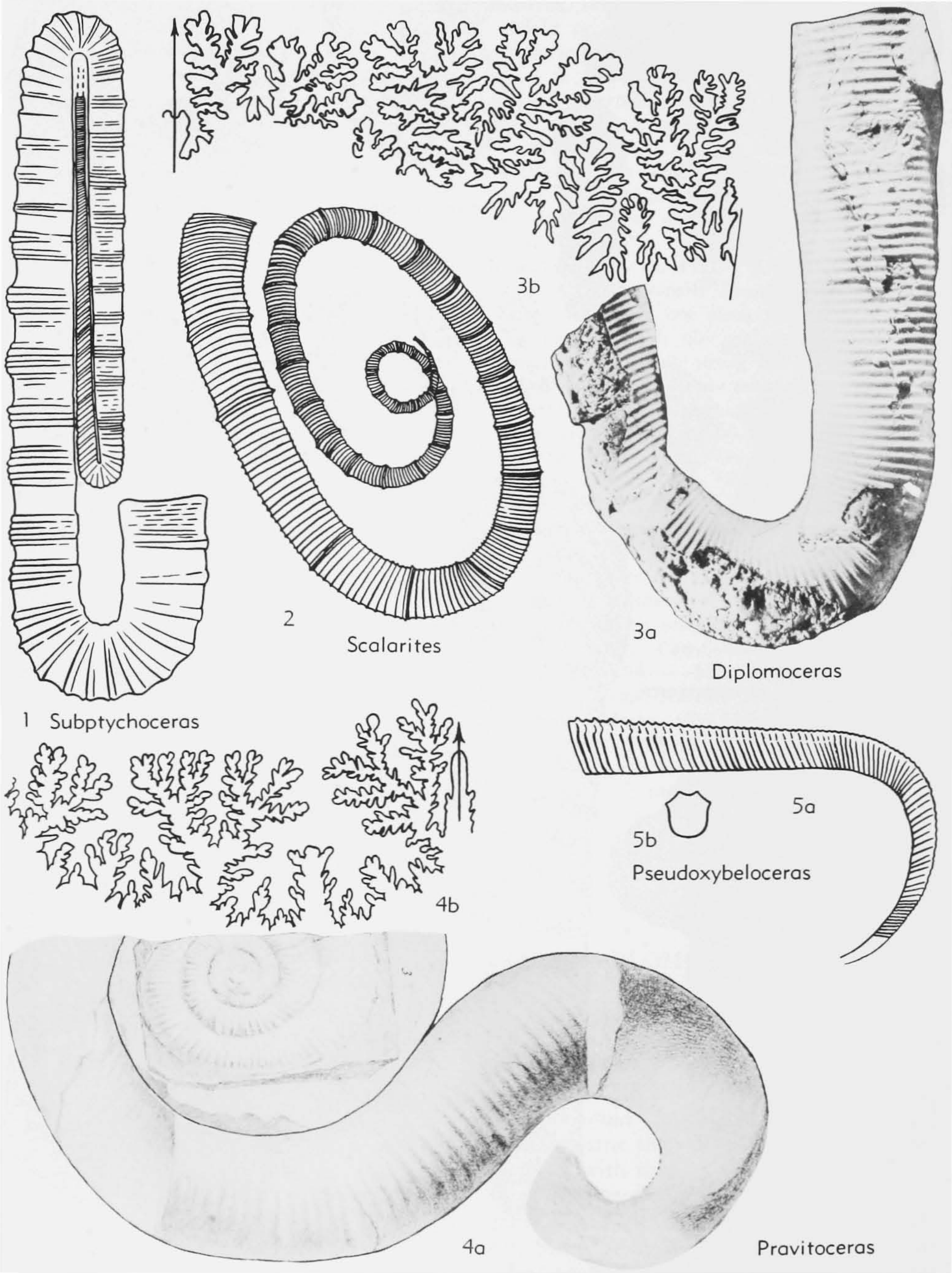


Fig. 252. Diplomoceratidae (p. L226-L228).

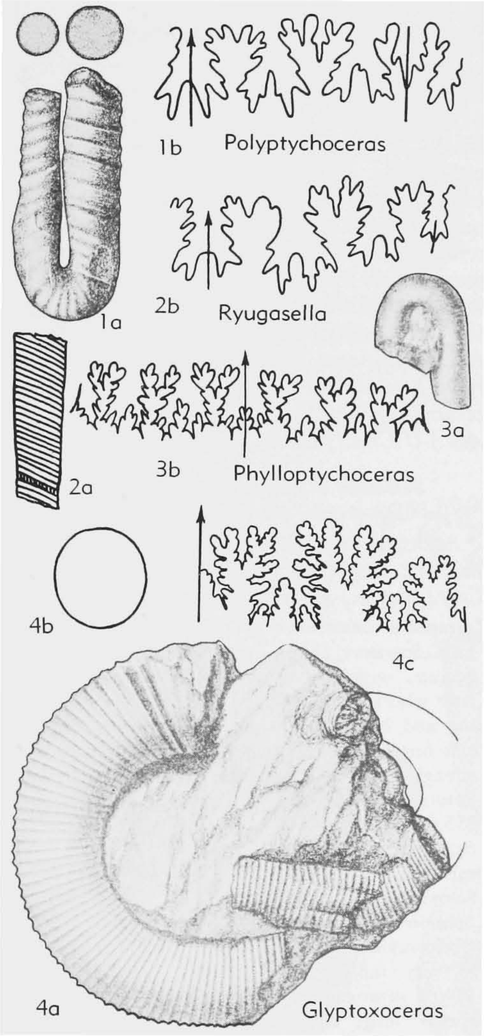


FIG. 253. Diplomoceratidae (p. L227-L228).

constrictions or both. *Turon.-Coni.,* ?Eng.-Japan. ——FIG. 252,*2*. **S. scalaris* (YABE), Turon., Japan; diagrammatic, ×0.5 (571*).

Glyptoxoceras SPATH, 1925 [**Hamites rugatus* FORBES, 1845]. Initial shallow helix followed by loose, regular or elliptical coiling; section circular to oval; ribs sharp, straight, close or distant, annular; a few collared constrictions. *Santon.-Maastr.,* N.Eu.-S.India-Japan-USA-Brazil.——FIG. 253,*4*. *G. indicum* (FORBES), Camp., S.India; *4a-c,* ×1 (238*).

Neancyloceras SPATH, 1926 [**Hamites bipunctatus* SCHLÜTER, 1872]. Differs from open-whorled species of *Glyptoxoceras* in less regular coiling and bituberculate periphery. *Camp.,* Eu.-Angola.

Diplomoceras HYATT, 1900 [**Hamites cylindraceus* DEFRANCE, 1822]. Loose helicoid spire followed by 2 or 3 subparallel straight or curved shafts; section circular to oval; fine, dense, rather subdued ribbing, weaker on inside than on outside of shell; collared constriction at aperture. Suture very florid. *Camp.-Maastr.,* Eu.-S.India-Japan-N.Z.-B.C.-GrahamLand. ——FIG. 252,*3*. *D. notabile* WHITEAVES, Camp., B.C.; *3a,* ×0.5; *3b,* ×1 (535*).

Pravitoceras YABE, 1902 [**P. sigmoidale*]. Camerate whorls are coiled regularly in one plane and just touching; body chamber uncoiled and irregularly S-shaped; section more or less circular; nearly straight radial ribs, a few with rather sharp ventrolateral bulla. Suture as in *Diplomoceras. Maastr.,* Japan.——FIG. 252,*4*. **P. sigmoidale; 4a,b,* ×0.4; *4c,* ×1 (739*).

Polyptychoceras YABE, 1902 [**Ptychoceras pseudogaultinum* YOKOYAMA, 1890]. Three parallel shafts which may or may not touch, followed by more or less open hook; oblique nontuberculate ribs on 1st shaft, later tending to become radial; constrictions on 1st and in some shells on later shafts. *Coni.-Camp.,* Sinai-S.India-Japan-B.C.

P. (Polyptychoceras). Ribs remain simple and sharp throughout. Occurrence as for genus.——FIG. 253,*1*. **P. (P.) pseudogaultinum* (YOKOYAMA), Santon., Japan; *1a,* ×1; *1b,* enlarged (741*).——FIG. 254,*1*. *P. obstrictum,* Santon., Japan; ×0.5 (571*).

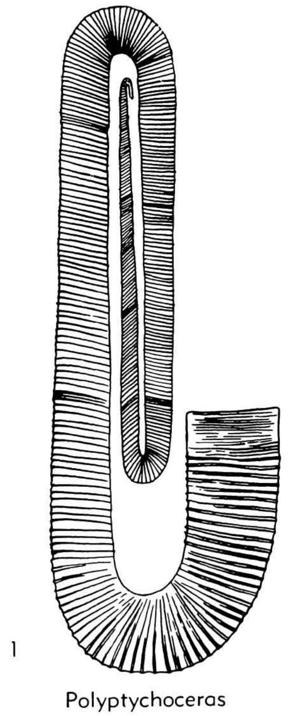


FIG. 254. *Polyptychoceras (Polyptychoceras) obstrictum* (JIMBO), U.Cret.(Santon.), Japan; ×0.5 (571*) (p. L227).

P. (Subptychoceras) SHIMIZU, 1935 [**Hamites (Polyptychoceras) yubarensis* YABE, 1927]. On last 2 shafts and hook ribs are in groups on broad low bulges. *Camp.*, Japan-B.C.——FIG. 252,*1*. **P. (S.) yubarense* (YABE), Camp., Japan; diagrammatic, ×0.4 (571*).

Phylloptychoceras SPATH, 1953 [**Ptychoceras sipho* FORBES, 1845]. Two shafts closely in contact followed by final hook; smooth at first, then with irregular ribs, then blunt folds on last shaft, finally closer ribs grading to striae on hook; aperture flared. Suture very simple. *Camp.*, S.India-N.Z.-Chile.——FIG. 253,*3*. **P. sipho* (FORBES), Camp., S.India; *3a*, ×1; *3b*, enlarged (718*).

Ryugasella WRIGHT & MATSUMOTO, 1954 [**R. ryugasensis*]. Broadly curved at first, then straight, with dense annular, prorsiradiate, nontuberculate ribs and few oblique constrictions. *?U.Santon., Camp.*, Japan-Sakhalin-GrahamLand.——FIG. 253,*2*. **R. ryugasensis*, Camp., Sakhalin; *2a*, ×0.75; *2b*, enlarged (571*).

Pseudoxybeloceras WRIGHT & MATSUMOTO, 1954 [**Hamites quadrinodosus* JIMBO, 1894]. Early part of shell slightly helical, coiling flattened elliptical in plan; with fine simple prorsiradiate ribs, each bearing lower and upper ventrolateral spines. *U. Santon.-Camp.*, Pondoland - Japan - Sakhalin - N.Z. ——FIG. 252,*5*. **P. quadrinodosum* (JIMBO), Camp., Japan; *5a,b*, diagrammatic, ×0.5 (571*).

Superfamily SCAPHITACEAE Meek, 1876

[*nom. transl.* WRIGHT & WRIGHT, 1951 (*ex* Scaphitidae MEEK, 1876)]

Coiled in loose or tight plane spiral, followed usually by terminal hook on short or long shaft. The 2 included families probably originated independently but at about the same date in Lytocerataceae. One family (Labeceratidae) remains loosely coiled, whereas the other (Scaphitidae) has a spire that tends to become tightly coiled and eventually the shaft shortens so that the hook comes into contact with the spire. Each family includes members with lappeted and nonlappeted apertures and varying much in ornament. The suture is of lytoceratid type in some early forms but soon varies considerably. *L. Cret.(U. Alb.) - U. Cret. (Maastr.)*.

While Labeceratidae are mainly restricted to the Albian of the Southern Hemisphere, Scaphitidae belong mainly, though not entirely, to the Northern Hemisphere and commonly are dominant ammonites in the Campanian and Maastrichtian.

Family SCAPHITIDAE Meek, 1876

Except in the earliest genus, more or less involute camerate whorls are followed by a long or short shaft with terminal hook, which in some genera is closely wrapped round the camerate whorls; constrictions may occur in the inner whorls. The aperture may be simple, collared, and constricted or with dorsal, ventral, or lateral lappets. Ornament varies from fine lirae to strong branching ribs, with or without tubercles. Synaptychi have been found in several members of the Scaphitinae. The family is probably derived direct from some member of the Lytoceratidae (79, 324, 362, 459). *L.Cret.(U. Alb.)-U.Cret.(Maastr.)*.

Subfamily SCAPHITINAE Meek, 1876

[*nom. transl.* WRIGHT, 1953 (*ex* Scaphitidae MEEK, 1876)]

Aperture simple or collared and constricted; lappets, if present, dorsal only. *L. Cret.(U.Alb.)-U.Cret.(Maastr.)*.

Eoscaphites BREISTROFFER, 1947 [**Am.? circularis* J.DEC.SOWERBY, 1836]. Initial whorls more or less evolute, with or without umbilical perforation; later whorls more involute but followed by uncoiling and hooked body chamber; aperture simple; ribs fine and dense, single or branching, reclined, strengthening on body chamber; no tubercles. Suture lytoceratid. *U.Alb.*, Eng.-Fr.-Alg.——FIG. 255,*6*. **E. circularis* (J.DEC.SOW.); *6a,b*, ×1; *6c*, enlarged (713*).

Scaphites PARKINSON, 1811 [**Scaphites equalis* J. SOWERBY, 1813; SD MEEK, 1876] [*Anascaphites, Jahnnites* HYATT, 1900; *Yezoites* YABE, 1910; *Holcoscaphites* NOWAK, 1911 (obj.)]. Compressed to very inflated, more or less involute, early whorls invariably in contact, shaft short or moderately long, hook not curved over camerate whorls; aperture constricted and commonly collared, in some shells with long dorsal lappet; ribs normally branching or intercalated on coiled part, commonly single or joining at ventrolateral tubercles on shaft; umbilical and normally ventrolateral tubercles present on shaft or hook. Suture soon ceases to be regularly lytoceratid. *U.Alb.-Camp.*, N.Hemis.-Madag.-Queensl.——FIG. 256,*3*. **S. equalis* (J.SOW.), Cenom., Fr.; *3a,b*, ×1; *3c*, enlarged (329*).

Clioscaphites COBBAN, 1952 [**C. montanensis*]. Very involute and inflated, with hook closely pressed to initial spire; inner whorls very inflated, bearing strong rounded ribs. First lateral lobe trifid or more asymmetrically bifid than in *Scaphites*. Includes close homeomorphs of M.Jur. Sphaeroceratidae. *Santon.-Camp.*, USA.——FIG. 255,*7*. *C. vermiformis* (MEEK & HAYDEN), Santon., Mont.; *7a,b*, ×1 (79*).

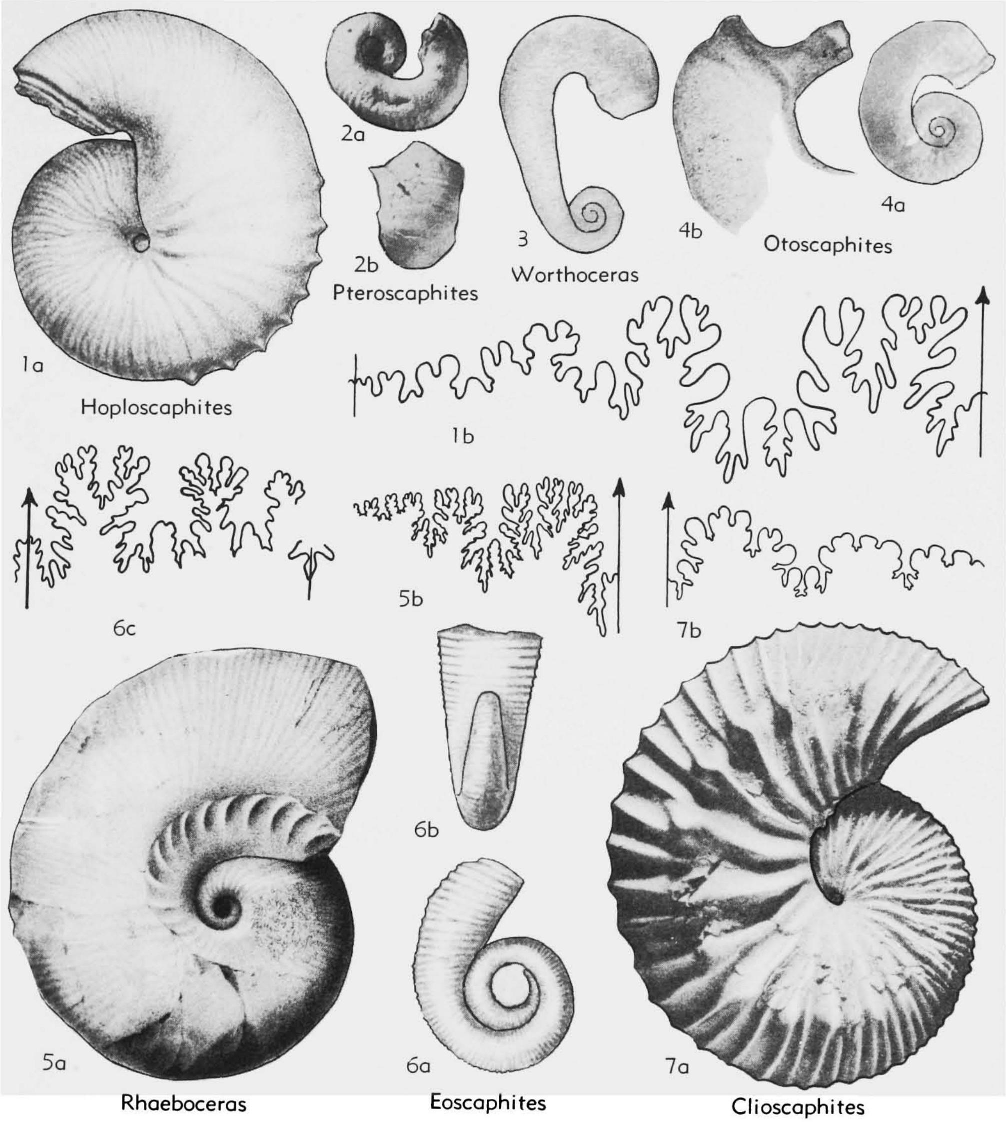


FIG. 255. Scaphitidae (p. L228-L231).

Desmoscaphites REESIDE, 1927 [**D. bassleri*]. Differs from *Clioscaphites* principally in having constrictions on inner whorls. *U.Santon.-Camp.*, USA.

Rhaeboceras MEEK, 1876 [**Phylloceras? halli* MEEK, 1876] [*Ponteixites* WARREN, 1934]. Differs from *Clioscaphites* in its less involute and more compressed inner whorls with strong, slightly sinuous, rounded ribs, resembling *Parahoplites;* outer whorls with dense fine ribs. *Camp.*, Alba.-USA.——FIG. 255,*5*. **R. halli* (MEEK), USA; *5a*, ×0.5; *5b*, ×0.75 (285*).

Hoploscaphites NOWAK, 1911 [**Scaphites constrictus* J.SOWERBY, 1817]. Compressed and flat-sided to inflated with convex sides; venter flat or rounded, bordered with strong ventrolateral clavi, at least on shaft and hook; shaft normally short. *Camp.-Maastr.*, Eu.-S.Afr.-Can.-USA-Chile-GrahamLand. ——FIG. 255,*1*. **H. constrictus* (J.Sow.), Maastr., Fr.; *1a*, ×1; *1b*, enlarged (329*).

Indoscaphites SPATH, 1953 [**Am. cunliffei* FORBES, 1845]. Compressed, with flat venter and very short shaft; ornament of single ribs joining distinct umbilical and ventrolateral tubercles starts at a much earlier stage than in other genera. *Maastr.*, S.India.

Discoscaphites MEEK, 1870 [**Scaphites conradi* MORTON, 1834]. Compressed and normally flat-sided with hook coiled in over spire; ribs moderately strong, with 3 or more rows of small, more or less equal tubercles. *Camp.-Maastr.*, N.Afr.-Can.-USA.——Fig. 256,*2*. **D. conradi* (Morton), Maastr., N.Dak.; *2a,b*, ×0.5; *2c*, ×1.5 (285*).

Acanthoscaphites Nowak, 1911 [**Scaphites tridens* Kner, 1850]. Large and inflated, with fine ribs and only umbilical tubercles until body chamber, which has also ventrolateral and typically siphonal rows of large blunt tubercles connected by irregu-

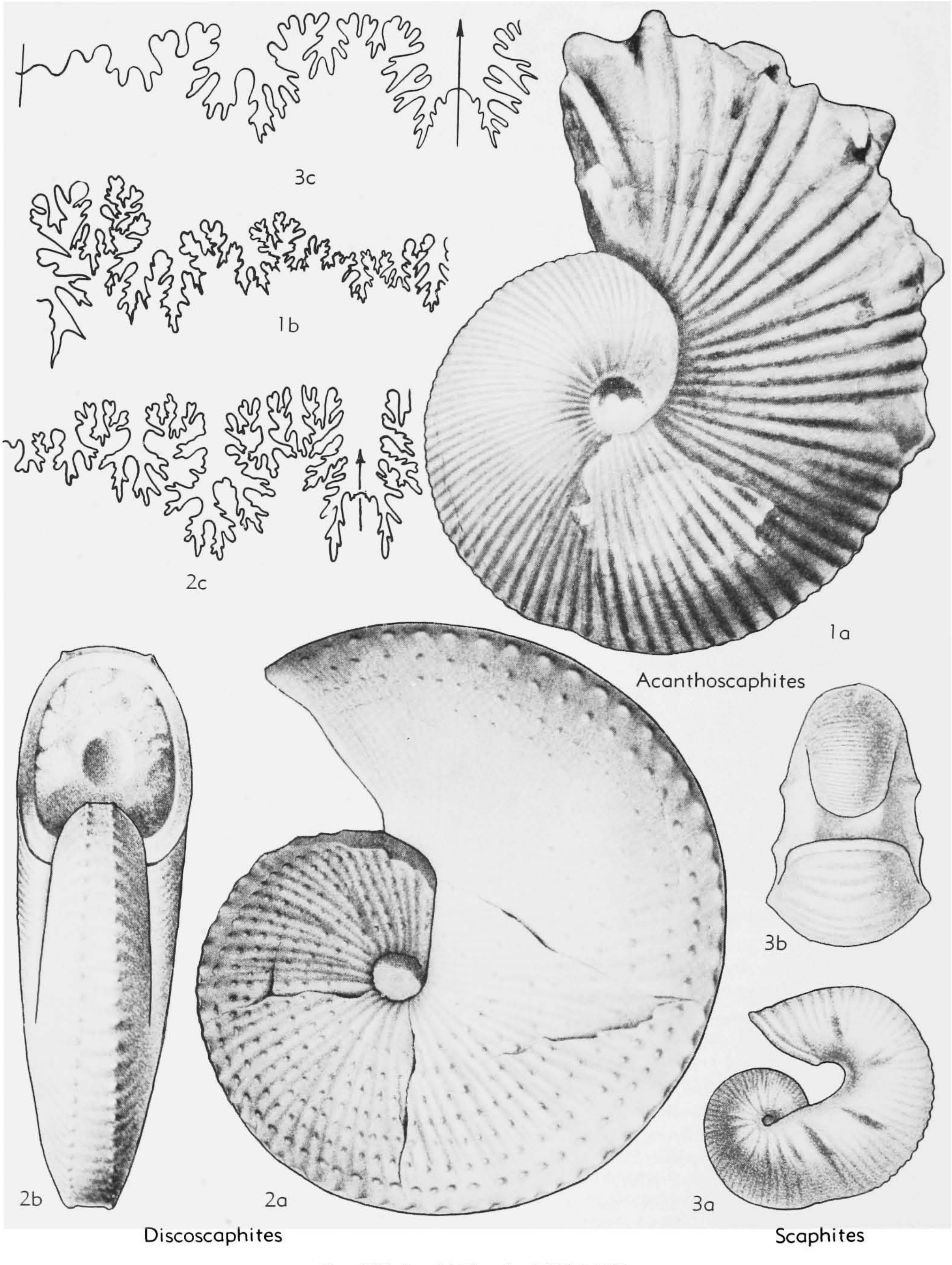


Fig. 256. Scaphitidae (p. L228-L230).

lar ribs. *Camp.*, C.Eu.-E.Eu.——Fig. 256,*1*. *A. tridens trispinosus* (Geinitz), Pol.; *1a*, ×0.5; *1b*, ×1 (324*).

Pteroscaphites Wright, 1953 [**Scaphites auriculatus* Cobban, 1952]. Small, with weak ornament or none; aperture with sides and ventral edge pinched to form projecting points. Probably a local offshoot of *S. larvaeformis*. *Coni.*, Mont.-N.Dak.——Fig. 255,*2*. **P. auriculatus* (Cobban), Mont.; *2a,b*, ×2 (79*).

?Zuluscaphites van Hoepen, 1955 [**Z. orycteropusi*]. Whorl section inflated, increasing rapidly, then decreasing before last suture; with long and short ribs, with siphonal tubercles on at least part of shell. First lateral lobe trifid. Doubtfully a scaphitid. *M.Alb.* (or *U.Alb.*), Zululand.

Subfamily OTOSCAPHITINAE Wright, 1953

Aperture with large lateral lappets. Ornament weaker than in contemporary Scaphitinae but tending to strengthen. Probably an early offshoot of *Eoscaphites* developing in parallel with Scaphitinae (569). *L.Cret.(U. Alb.)-U.Cret.(Coni.)*.

Worthoceras Adkins, 1928 [**Macroscaphites platydorsus* Scott, 1924]. Small, with evolute spire followed by long straight shaft and final hook; aperture with long straight lappets; smooth or with fine striae. Suture with bifid saddles and lobes of very simple outline. *U.Alb.-L.Turon.*, Fr.-C.Eu.-Tex.——Fig. 255,*3*; 554,*1*. **W. platydorsus* (Scott), U.Alb., Tex.; 255,*3*, ×4 (705*); 554,*1*, ×10 (579*).

Otoscaphites Wright, 1953 [**Am. bladenensis* Schlüter, 1871]. With rather evolute spire followed by curved shaft and hook, more open than in Scaphitinae; whorl section compressed to coronate; strong, long and short or branching ribs on spire at least, shaft and hook smooth or with weak to rather strong ribs; in later species with umbilical or ventrolateral tubercles. Suture has an irregularly bifid 1st lateral lobe but elements are more frilled than in *Worthoceras*. The genus includes all species referred to *Yezoites* Yabe except the type, which is a *Scaphites*. *L.Turon.-Coni.*, Eu.-Japan-Tex.-Mex.——Fig. 255,*4*. **O. bladenensis* (Schlüter), U.Turon., Eng.; *4a*, ×1; *4b*, ×2 (736*).

Family LABECERATIDAE Spath, 1925

[Includes Aleteceratidae Whitehouse, 1926; Myloceratidae Spath, 1939]

At first coiled in open spiral but later whorls may be in contact, shell ending in hook; aperture with weak to moderate rounded lateral lappets; whorl section moderately to very compressed; all genera have fine branching ribs that pass over venter, some having also umbilical or ventrolateral tubercles or both. Suture with bifid saddles and generally small trifid lobes. The family is probably derived, like Scaphitidae, from the Lytoceratidae (459, 566). *?L.Cret.(M. Alb.), L.Cret.(U.Alb.)*.

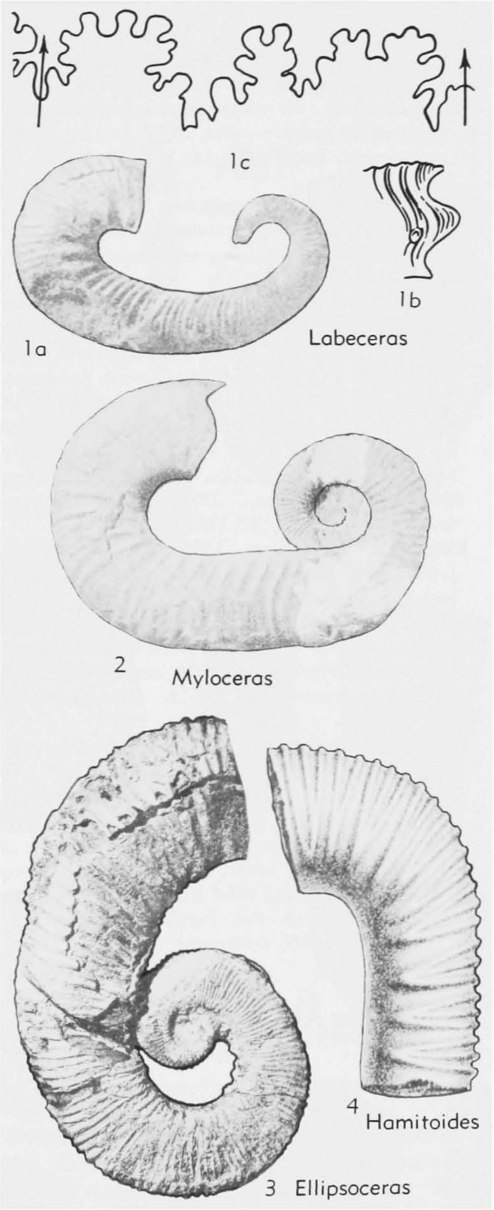


Fig. 257. Labeceratidae (p. L231-L232).

Labeceras Spath, 1925 [**L. bryani* Whitehouse, 1926 (ICZN pend.)]. Small, with open spire of few whorls followed by curved shaft and final hook, aperture facing inward; ribs fine, concave and prorsiradiate; umbilical tubercles may occur on shaft and hook, with ventrolateral tubercles also in some. *U.Alb.*, SE.Afr.-Madag.-Queensl.

L. (Labeceras). No ventrolateral tubercles. Occurrence as for genus.——FIG. 257,*1*. *L. (L.) plasticum* SPATH, Port.E.Afr.; *1a*, ×1; *1b*, ×1.5; *1c*, ×4 (713*).

L. (Appurdiceras) WHITEHOUSE, 1926 [**Ancyloceras corcycepoides* ETHERIDGE, JR., 1905]. Whorl section subquadrate; strong ventrolateral tubercles. *U.Alb.*, Queensl.

Myloceras SPATH, 1925 [**Crioceras ammonoides* ETHERIDGE, JR., 1909] [*Aleteceras, Flindersites* WHITEHOUSE, 1926]. Larger than *Labeceras*, with spire more closely coiled after initial few open whorls and aperture not facing inward to same extent; whorl section generally compressed, with flat venter; strong, distant ventrolateral spines may be present. *Low.U.Alb.*, Port.E.Afr.-Madag.-Queensl.-?N.Z.——FIG. 257,*2*. *M. serotinum* SPATH, Port.E.Afr.; ×0.5 (713*).

Ellipsoceras COLLIGNON, 1950 [**E. expansum*] [*Abadieceras* COLLIGNON, 1950]. Coiling of later part less regular than in *Myloceras*, whorl section more compressed and much higher; fine, well-spaced, slightly sinuous ribs are sharpened on ventrolateral edges but tubercles are lacking. *Low. U.Alb.*, Madag.——FIG. 257,*3*. **E. expansum*; ×0.5 (601*).

?**Hamitoides** SPATH, 1925 [**Hamites studerianus* PICTET, 1847]. Nature of coiling uncertain, since only fragments are known; whorl section circular to oval; ribs branch irregularly at umbilical edge or on sides, in many shells forming tubercle at point of branching. Suture not adequately known, with bifid saddles and trifid lobes. *Up.M.Alb.-Low. U.Alb.*, Fr.-Switz.-Pol.-Port.E.Afr.-Madag.-Pak.——FIG. 257,*4*. **H. studerianus* (PICTET), U.Alb., Fr.; ×1 (346*).

Suborder AMMONITINA Hyatt, 1889

[*nom. correct.* ARKELL, 1950 (*ex* "suborder Ammonitinae of the Trias, Jura, and Cretaceous")]

Normally coiled derivatives of Phylloceratina and Lytoceratina, in which thick test and strong ornament are characteristic, though by no means universal. Sutures only very rarely with bifid lobes or phylloid saddle endings (200). *L.Jur.-U.Cret.*, world-wide.

In this suborder are grouped all post-Triassic Ammonoidea except the 2 fundamental stocks, Phylloceratina and Lytoceratina, and their immediate and uncoiled descendants or offshoots. It is not yet possible to determine for some families whether they originated from Phylloceratina or Lytoceratina and it is therefore best, at the present stage of knowledge, to keep them all in one polyphyletic suborder. This arrangement also best brings out the fundamental distinction between the 2 persistent stocks and all other Jurassic and Cretaceous ammonites.

Superfamily PSILOCERATACEAE Hyatt, 1867

[*nom. transl.* WEDEKIND, 1917 (as Psiloceratoidea, *ex* Psiloceratidae HYATT, 1867, *nom. correct.* ARKELL, herein (as Psilocerataceae)] [=Ammonitacea BUCKMAN, 1905; Psiloceratacea BUCK., 1919; Arietitaceae ARKELL, 1950]

Derivatives of Phylloceratina. The earliest Jurassic Ammonitina (Psiloceratidae) are probably direct descendants of *Eopsiloceras* (Rhaet.) and so of *Mojsvarites* (Carn.-Nor.) of the Ussuritidae (=Monophyllitidae). *L. Jur.*(mainly *Hett., Sinem.*, 2 genera only lingering into *L.Pliensb.*), world-wide.

Family PSILOCERATIDAE Hyatt, 1867

[=Caloceratidae BUCKMAN, 1906]

Evolute, smooth or with blunt primary ribbing, venter rounded and smooth to nearly smooth or feebly keeled in some. Sutures simple, with retracted suspensive lobe, saddle endings phylloid in some. Aptychus single-valved, with concentrically striated shiny surface (Anaptychus) (found *in situ* in *Psiloceras*) (65, 123, 250, 251, 253, 464, 550). *L.Jur.(Hett.-Sinem.*, mainly *Hett.)*, world-wide.

Subfamily PSILOCERATINAE Hyatt, 1867

[*nom. transl.* LANGE, 1941 (*ex* Psiloceratidae HYATT, 1867)]

Venter unkeeled. *L.Jur.(Hett.)*.

Psiloceras HYATT, 1867 [**Am. planorbis* SOWERBY, 1824; SD SPATH, 1924 (ICZN Opinion 324)] [=*Psilonoticeras* QUENSTEDT, 1883 (obj.)]. Small, compressed planulates, smooth, unribbed or with sporadic blunt rib. Eu.-Indon.-N.Z.-Can.-Nev.-Peru.——FIG. 258,*10*. **P. (P.) planorbis* (SOW.), Eng.; *10a*, holotype, ×0.7 (18*); *10b,c*, drawings, ×1 (737*).

Caloceras HYATT, 1870 [**Am. torus* D'ORBIGNY, 1844; SD BUCKMAN, 1912]. Blunt primary ribbing on all whorls; many-whorled. Subgen. of *Psiloceras*. Eu.-Peru.——FIG. 258,*1*. **P. (C.) torus* (ORB.), Fr.; *1a-c*, ×0.5 (330*).

Franziceras BUCKMAN, 1923 [**F. ruidum*]. Differs from *Caloceras* in having normal planulate coiling and sutures with longer lobes. Subgen. of *Psiloceras*. Eng.——FIG. 258,*7*. **P. (F.) ruidum* (BUCK.); *7a,b*, ×0.5 (65*).

Discamphiceras SPATH, 1923 [**Aegoceras kammerkahrense* GÜMBEL, 1861 (fig'd. WAEHNER, 1884)].