

# TREATISE ON INVERTEBRATE PALEONTOLOGY

*Prepared under Sponsorship of  
The Geological Society of America*

*The Paleontological Society    The Society of Economic Paleontologists and Mineralogists  
The Palaeontographical Society    The Palaeontological Association*

Directed and Edited by  
RAYMOND C. MOORE

## Part K MOLLUSCA 3

CEPHALOPODA—GENERAL FEATURES  
ENDOCERATOIDEA—ACTINOCERATOIDEA—NAUTILOIDEA  
BACTRITOIDEA

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and D. E. NODINE ZELLER

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# TREATISE ON INVERTEBRATE PALEONTOLOGY

Directed and Edited by

RAYMOND C. MOORE

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## PARTS

Parts of the *Treatise* are distinguished by assigned letters with a view to indicating their systematic sequence while allowing publication of units in whatever order each may be made ready for the press. The volumes are cloth-bound with title in gold on the cover. Copies are available on orders sent to the Publication Department of The Geological Society of America at 231 East 46th Street, New York 17, N.Y. The prices quoted very incompletely cover costs of producing and distributing the several volumes, but on receipt of payment the Society will ship copies without additional charge to any address in the world. Special discounts are available to members of sponsoring societies under arrangements made by appropriate officers of these societies, to whom inquiries should be addressed.

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- Part K. MOLLUSCA 3 (Cephalopoda General Features, Endoceratoidea, Actinoceratoidea, Nautiloidea, Bactritoidea), xxviii+519 p., 2382 fig., 1964.

## VOLUMES IN PREPARATION (1964)

- Part A. INTRODUCTION.  
 Part B. PROTISTA 1 (Chrysomonadida, Coccolithophorida, Charophyta, Diatomacea, etc.).  
 Part H. BRACHIOPODA.  
 Part J. MOLLUSCA 2 (Caenogastropoda, Opisthobranchia).  
 Part M. MOLLUSCA 5 (Endocochlia).  
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 Part R. ARTHROPODA 4 (Crustacea, Branchiopoda, Cirripedia, Malacostraca; Myriapoda; Hexapoda).  
 Part S. ECHINODERMATA 1 (Echinodermata General Features, Cystoidea, Cyclocystoidea, Paracrinoidea, Edrioblastoidea, Blastoidea, Edrioasteroidea, Eocrinoidea, Carpoidea).  
 Part T. ECHINODERMATA 2 (Crinoidea).  
 Part U. ECHINODERMATA 3 (Echinozoa, Asterozoa).  
 Part X. ADDENDA, INDEX.

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### Alphabetical List

(Numbers refer to preceding list arranged by countries and institutions.)

- |                           |                               |                                    |
|---------------------------|-------------------------------|------------------------------------|
| Ager, D. V. (59)          | Frizzell, D. L. (121)         | Lowenstam, H. A. (77)              |
| Amsden, T. W. (126)       | Furnish, W. M. (105)          | Ludbrook, N. H. (4)                |
| Arkell, W. J. (166)       | Gardner, Julia (169)          | McAlester, A. L. (164)             |
| Bairstow, Leslie (44)     | Gibson, T. G. (134)           | Manning, R. B. (157a)              |
| Barker, R. W. (138)       | Glaessner, M. F. (1)          | Manton, S. M. (147)                |
| Bassler, R. S. (167)      | Glenister, B. F. (106)        | Marwick, J. (31)                   |
| Batten, R. L. (68)        | Gordon, Isabella (46)         | Melville, R. V. (13)               |
| Bayer, F. M. (153)        | Gordon, Mackenzie, Jr. (147)  | Miller, A. K. (173)                |
| Beaver, H. H. (98)        | Grant, R. E. (156)            | Montanaro Gallitelli, Eugenia (23) |
| Benson, R. H. (109)       | Haas, Fritz (85)              | Moore, R. C. (111)                 |
| Berdan, J. M. (145)       | Hanai, Tetsuro (25)           | Morrison, J. P. E. (158)           |
| Biernat, Gertruda (37)    | Hanna, G. D. (72)             | Muir-Wood, H. M. (48)              |
| Boardman, R. S. (154)     | Häntzschel, Walter (17)       | Müller, K. J. (15)                 |
| Bold, W. A. van den (115) | Harrington, H. J. (143)       | Newell, N. D. (71)                 |
| Boschma, H. (26)          | Hass, W. H. (170)             | Newman, W. A. (94)                 |
| Boucot, A. J. (75)        | Hatai, Kotori (24)            | Okulitch, V. J. (7)                |
| Bowsher, A. L. (141)      | Hawkins, H. L. (63)           | Olsson, A. A. (131)                |
| Bramlette, M. N. (84)     | Hedgpeth, Joel (129)          | Palmer, A. R. (149)                |
| Branson, C. C. (128)      | Henningsmoen, Gunnar (34)     | Palmer, K. V. W. (130)             |
| Brooks, H. K. (91)        | Hertlein, L. G. (73)          | Pawson, David (33)                 |
| Brown, D. A. (2)          | Hessland, Ivar (39)           | Peck, R. E. (120)                  |
| Bulman, O. M. B. (50)     | Hessler, R. R. (163)          | Petrunkevitch, Alexander (165)     |
| Campbell, A. S. (137)     | Hill, Dorothy (3)             | Pitrat, C. W. (112)                |
| Carpenter, F. M. (92)     | Hoffman, R. L. (136)          | Popenoe, W. D. (82)                |
| Casey, Raymond (55)       | Holthuis, L. B. (27)          | Poulsen, Chr. (10)                 |
| Caster, K. E. (87)        | Howe, H. V. (116)             | Powell, A. W. B. (28)              |
| Chavan, André (12)        | Howell, B. F. (135)           | Puri, H. S. (90)                   |
| Cole, W. S. (88)          | Hyman, L. H. (70)             | Rasetti, Franco (108)              |
| Cooper, G. A. (155)       | Jaanusson, Valdar (41)        | Rasmussen, H. W. (11)              |
| Cox, L. R. (45)           | Jeffords, R. M. (99)          | Regnéll, Gerhard (38)              |
| Curry, Dennis (65)        | Jeletzky, J. A. (8)           | Rehder, H. A. (159)                |
| Davies, L. M. (168)       | Johnson, J. G. (76)           | Reichel, Manfred (42)              |
| Dechaseaux, Colette (14)  | Keen, A. Myra (142)           | Reymont, R. A. (40)                |
| Dell, W. K. (29)          | Kesling, R. V. (117)          | Rhodes, F. H. T. (64)              |
| Douglass, R. C. (146)     | Kier, P. M. (157)             | Richter, Emma (174)                |
| Durham, J. W. (79)        | Knight, J. B. (171)           | Richter, Rudolf (175)              |
| Eames, F. E. (49)         | Kummel, Bernhard (93)         | Robertson, Robert (132)            |
| Elliott, G. F. (57)       | La Rocque, Aurèle (124)       | Rolfe, W. D. I. (52)               |
| Emerson, W. K. (69)       | Laubenfels, M. W. de (172)    | Rosewater, Joseph (160)            |
| Erben, H. K. (16)         | Lecompte, Marius (6)          | Rowell, A. J. (60)                 |
| Exline, Harriet (121)     | Leonard, A. B. (110)          | Rudwick, M. J. S. (51)             |
| Fay, R. O. (127)          | Levinson, S. A. (100)         | Schindewolf, O. H. (20)            |
| Fell, H. B. (32)          | Lochman-Balk, Christina (122) | Schmidt, Herta (18)                |
| Fischer, A. G. (133)      | Loeblich, A. R., Jr. (78)     | Scott, H. W. (103)                 |
| Fisher, D. W. (123)       | Loeblich, A. R., III (80)     | Sdzuy, Klaus (21)                  |
| Fleming, C. A. (30)       | Lohman, K. E. (148)           |                                    |

Shaver, R. H. (104)  
 Sieverts-Doreck, Hertha (22)  
 Sinclair, G. W. (9)  
 Smith, A. G. (74)  
 Sohn, I. G. (150)  
 Soot-Ryen, T. (35)  
 Spencer, W. K. (176)  
 Stainbrook, M. A. (177)  
 Staton, R. D. (95)  
 Stehli, F. G. (161)  
 Stenzel, H. B. (139)  
 Stephenson, L. W. (178)  
 Størmer, Leif (36)  
 Stough, Joan (101)  
 Struve, Wolfgang (19)  
 Stubblefield, C. J. (56)

Stumm, E. C. (118)  
 Swain, F. M. (119)  
 Sweet, W. C. (125)  
 Sylvester-Bradley, P. C. (58)  
 Tappan, Helen (83)  
 Tasch, Paul (162)  
 Teichert, Curt (151)  
 Thompson, M. L. (102)  
 Thompson, R. H. (113)  
 Tiegs, O. W. (179)  
 Tripp, R. P. (66)  
 Turner, Ruth (96)  
 Ubaghs, Georges (5)  
 Van Sant, J. F. (107)  
 Vokes, H. E. (144)  
 Wagner, C. D. (81)

Wainwright, John (140)  
 Wanner, Johannes (180)  
 Weir, John (53)  
 Weller, J. M. (86)  
 Wells, J. M. (89)  
 Whittington, H. B. (97)  
 Williams, Alwyn (61)  
 Wills, L. J. (43)  
 Withers, T. H. (181)  
 Wright, A. D. (62)  
 Wright, C. W. (67)  
 Wrigley, Arthur (182)  
 Yochelson, E. L. (152)  
 Yonge, C. M. (54)  
 Zeller, D. E. Nodine (114)  
 Zullo, V. A. (163a)

## 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 given in the *Treatise on Marine Ecology and Paleoecology* (H. S. LADD, Editor, Geological Society of America, Memoir 67, 1957), prepared under auspices of a committee of the United States National Research Council. A selected list of references is furnished in each part of the *Treatise*.

Features of style in the taxonomic portions of this work have been fixed by the Editor with aid furnished by advice from 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.

In December, 1959, the National Science Foundation of the United States, through its Division of Biological and Medical Sciences and the Program Director for Systematic Biology, made a grant in the amount of \$210,000 for the purpose of aiding the completion of yet-unpublished volumes of the *Treatise*. Payment of this sum was provided to be made in installments distributed over a five-year period, with administration of disbursements handled by the University of Kansas. Expenditures planned are primarily for needed assistance to authors and may be arranged through approved institutions located anywhere. Important help for the Director-Editor of the *Treatise* has been made available from the grant, but no part of his stipend comes from it. Grateful acknowledgment to the Foundation is expressed on behalf of the societies sponsoring the *Treatise*, the University of Kansas, and innumerable individuals benefited by the *Treatise* project.

#### 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 proper names, use of neo-Latin letters, and approved methods for converting diacritical marks. The magnitude and complexities of nomenclatural 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 transferable 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) suprafamilial group (suborder, order, subclass, class, subphylum, phylum). In groups (1), (2), and (3), 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 introduced the family name X-idae to include 3 genera, one of which is X-us; and if author B in 1850 divided the 20 genera then included in X-idae into subfamilies called X-inae and Y-inae; and if author C in 1950 combined 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 use of "*nom. transl.*" Taxa of group (4) are not regulated by the zoological Code (1961); they are discussed later under the heading "Suprafamilial Taxa."

The co-ordinate status of zoological names belonging to the species group is stipulated in Art. 46 of the present Rules; genus group in Art. 43 of the present Rules; family group in Art. 36 of the present Rules.

#### 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. Such names are divisible into groups as follows: (1) "*inviolable 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 super- or suprafamilial 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 groups 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 group (including names derived from the 2nd and 3rd groups and possibly some alterations of 4th group 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 groups. 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.

It is useful for convenience and brevity of distinction in recording these groups of valid zoological names to introduce Latin designations, following the pattern of *nomen nudum*, *nomen novum*, etc. Accordingly, the groups 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 Homonymy. 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 the 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 GROUPS

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

#### Definitions of Name Groups

**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 zoological Code (1961) 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 Code, Arts. 26-b, 27, 29, 30-a-3, 31, 32-c-i, 33-a; 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 Code, Arts. 26-b, 27, 29.)

**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 ("inviolable name").

*nomen negatum* (*nom. neg.*). Name that as originally published (with or without subsequent identical spelling) constitutes invalid original

spelling and although possibly meeting all other mandatory requirements of the Rules, is not correctable to establish original authorship and date ("denied name").

*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").

*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").

**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").

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 under-

stood 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 *bröggeri* to *broeggeri*) or elimination of a hyphen (as in changing originally published *cornuoryx* to *cornuoryx*) does not require "*nom. correct.*" with it.

#### 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.

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** THOMPSON, 1875 [*\*K. concentricum*; SD GREGORY, 1917] [= *Kumatiophyllum* THOMPSON, 1876 (*nom. null.*); *Cymatophyllum* THOMPSON, 1901 (*nom. van.*); *Cymatiophyllum* LANG, SMITH & THOMAS, 1940 (*nom. van.*)].
- Stichophyma** POMEL, 1872 [*\*Manon turbinatum* RÖMER, 1841; SD RAUFF, 1893] [= *Styphophyma* 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 Cyrtograptus* 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 the Code defines 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, 1955 (*ex Archaeoctonidae* PETRUNKEVITCH, 1949)]

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

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

Valid emendations classed as *nomina correctae* 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, 1955 (*ex* Palaeoscorpionidae LEHMANN, 1944, *nom. imperf.*)]

**Family AGLASPIDIDAE Miller, 1877**  
[*nom. correct.* STØRMER, 1959 (*ex* Aglaspidae MILLER, 1877, *nom. imperf.*)]

**Superfamily AGARICIICAE Gray, 1847**  
[*nom. correct.* WELLS, 1956 (*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 zoological Code, 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.

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 as to whether the author of the family or some subsequent author introduced subdivisions.

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

SUPRAFAMILIAL TAXA

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

The Colloquium on zoological nomen-

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

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

(1) The name of any suprafamilial taxon must be a Latin or latinized uninflected noun of plural form, or treated as such, (a) with a capital initial letter, (b) without diacritical mark, apostrophe, diaeresis, or hyphen, and (c) if component consisting of a

numeral, numerical adjective, or adverb is used, this must be written in full (e.g., Stethostomata, Trionychi, Septemchitonina, Scorpiones, Subselliflorae). No uniformity in choice of ending for taxa of a given rank is demanded (e.g., orders named Gorgonacea, Milleporina, Rugosa, Scleractinia, Stromatoporoidea, Phalangida).

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

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

(4) Authors who accept priority as a determinant in nomenclature of a suprafamilial taxon may change its assigned rank at will, with or without modifying the terminal letters of the name, but such change(s) cannot rationally be judged to alter the authorship and date of the taxon

as published originally. (a) A name revised from its previously published rank is a "transferred name" (*nom. transl.*), as illustrated in the following.

**Order CORYNEXOCHIDA Kobayashi, 1935**

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

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

**Order DISPARIDA Moore & Laudon, 1943**

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

**Suborder AGNOSTINA Salter, 1864**

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

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

**Order ORTHIDA Schuchert & Cooper, 1931**

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

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

**Order ENDOCERIDA Teichert, 1933**

[*nom. correct.* TEICHERT, 1963 (pro order Endoceroidea TEICHERT, 1933)]

**Suborder ENDOCERINA Teichert, 1933**

[*nom. correct.* TEICHERT, 1963 (pro suborder Endoceroidea SCHINDEWOLF, 1935, *nom. transl.* ex order Endoceroidea TEICHERT, 1933)]

**Subclass ENDOCERATOIDEA Teichert, 1933**

[*nom. transl.* TEICHERT, 1963 (ex superorder Endoceroidea SHIMANSKIY & ZHURAVLEVA, 1961, *nom. transl.* ex order Endoceroidea TEICHERT, 1933)]

(6) A suprafamilial taxon may or may not contain a family-group taxon or taxa having the same type-genus, and if it does, the respective suprafamilial and family-group taxa may or may not be nominate (having names with the same stem). The zoological Code (Art. 61) affirms that

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

**Class ARACHNIDA Lamarck, 1801**

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

**Subclass CAULOGASTRA Pocock, 1893**

[type, *Araneus* CLERCK, 1757]

**Superorder LABELLATA Petrunkevitch, 1949**

[type, *Araneus* CLERCK, 1757]

**Order ARANEIDA Clerck, 1757**

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

**Suborder DIPNEUMONINA Latreille, 1817**

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

**Division TRIONYCHI Petrunkevitch, 1933**

[type, *Araneus* CLERCK, 1757]

**Superfamily ARANEOIDEA Leach, 1815**

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

**Family ARANEIDAE Leach, 1815**

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

**Subfamily ARANEINAE Leach, 1815**

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

**TAXONOMIC EMENDATION**

Emendation has two measurably distinct aspects as regards zoological nomenclature. These embrace (1) alteration of a name itself in various ways for various reasons, as has been reviewed, and (2) alteration 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 gener-

ally has been paid to this distinction in spite of its significance.

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

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

## STYLE IN GENERIC DESCRIPTIONS

### CITATION OF TYPE-SPECIES

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

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

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

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

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

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

*Fixation of type-species originally.* The type-species of a genus or subgenus, according to provisions of the Rules, may be fixed in various ways originally (that is, in the publication containing first proposal of the generic name) or it may be fixed in specified ways subsequent to the original publication. Fixation of a type-species originally may be classified as automatic if the new genus was introduced for a single species (monotypy), or if the names of species referred to the genus are objectively synonymous. In addition, fixation of a type-species originally may be established in several ways by original designation, as by explicit statement given by an author, by use of *typus* or *typicus* as a new specific name, and by absolute tautonymy (e.g., *Mesolobus mesolo-*

*bus*). According to convention adopted in the *Treatise*, the absence of indication as to the manner of fixing the type-species is to be understood as signifying fixation of the type-species in one way or another originally. Where an author wishes to specify the mode of original fixation, however, this may be done by such abbreviations as "M" (monotypy), "OS" (objective synonymy), and "OD" (original designation), the first- and last-mentioned being most common and the other very rare.

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

Another mode of fixing the type-species of a genus that may be construed as a special sort of subsequent designation is action of



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

## HOMONYMS

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

**Hallopora** BASSLER, 1911, *nom. subst.* [*pro Callopora* HALL, 1851 (*non* GRAY, 1848)].

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

**Mysterium** DE LAUBENFELS, *nom. subst.* [*pro Mysterium* SCHRAMMEN, 1936 (ref. 40, p. 60) (*non* ROGER, 1862)] [*\*Mysterium porosum* SCHRAMMEN, 1936].

For some replaced homonyms, a footnote reference to the literature is necessary. A

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

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

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

*Homonyms by misidentification.* When an author uses a generic name for species not congeneric with the type-species, it is needful to record the misuse of the generic name, even though this is only determinable subjectively. In the *Treatise* homonyms by misidentification are cited in synonymies as illustrated in the following example.

**Asmussia** PACTH, 1849 [*\*A. membranacea*] [= *Posidonomya* PACTH, 1852 (*non* BRONN, 1834); *Esteria* JONES, 1856 (*non* ROBINEAU-DESVOIDY, 1830; *nec* RUEPPELL, 1837)].

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

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

distinguished in the *Treatise* as in dealing with generic names.

#### SYNONYMS

Citation of synonyms is given next following record of the type-species and if 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, 1883] [= *Columnopora* NICHOLSON, 1874; *Houghtonia* ROMINGER, 1876].

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

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

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

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

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

#### ABBREVIATIONS

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

#### *Abbreviations*

adj., adjective  
aff., *affinis* (related to)  
Afr., Africa, -an  
Ala., Alabama  
Alb., Albanian  
Alba., Alberta  
Am., America, -n  
Anis., Anisian  
ant., anterior  
apert., apertural  
approx., approximately  
Apt., Aptian  
Arch., Archipelago  
Arct., Arctic  
Arenig., Arenigian  
Arg., Argentina  
Ariz., Arizona  
Ark., Arkansas  
art., article  
Artinsk., Artinskian  
Ashgill., Ashgillian  
auctt., *auctorum* (of others)  
Aus., Austria

Balt., Baltic  
B.C., British Columbia  
Belg., Belgium, Belgique  
Blackriver., Blackriverian  
Boh., Bohemia  
Bol., Bolivia  
Brit., Britain, British  
Bull., Bulletin

C., Central  
ca., circa  
Calif., California  
Callov., Callovian  
Cam., Cambrian  
Can., Canada  
Canad., Canadian  
Caradoc., Caradocian  
Carb., Carboniferous  
Carn., Carnian  
Cenoman., Cenomanian  
cf., *confer* (compare)  
Chazy., Chazyan  
cm., centimeter  
Coblentz., Coblentzian  
Colo., Colorado  
Colom., Colombia  
cosmop., cosmopolitan  
Cret., Cretaceous  
Czech., Czechoslovakia

Dev., Devonian  
diagram., diagrammatic  
Dol., Dolomite  
dors., dorsal  
dorsovent., dorsoventral

E., East  
ed., edition, editor  
e.g., *exempli gratia* (for example)  
Eifel., Eifelian  
emend., *emendatus* (-a)

Ems., Emsian  
endosiph., endosiphuncular  
Eng., England  
Eoc., Eocene  
equiv., equivalent, -s  
err., *errore* (by error)  
Est., Estonia  
et al., *et alii* (and others, persons)  
etc., *et cetera* (and others, objects)  
Eu., Europe  
ext., exterior

F., Formation  
fam., family  
fig., figure, -s  
Fr., France, French, Français, -e

G.Brit., Great Britain  
Geol., Geology, Geological, Geologische, etc.  
Ger., Germany, German  
Givet., Givetian  
Gr., Group  
Greenl., Greenland

Hauteriv., Hauterivian  
H'st., History  
Holl., Holland

hom., homonym  
Hung., Hungary, Hungarica

ICZN, International Commission  
on Zoological Nomenclature  
i.e., *id est* (that is)  
Ill., Illinois  
illus., illustration, -s  
In., Inner  
incl., including  
indet., indetermined  
Ind., Indiana  
Ire., Ireland  
Is., Island, -s

jr., junior  
Jur., Jurassic

Kans., Kansas  
Kazakh., Kazakhstan  
Kimmeridg., Kimmeridgian  
Kinderhook., Kinderhookian  
Ky., Kentucky

L., Low., Lower  
Ladin., Ladinian  
lat., lateral  
Leonard., Leonardian  
Lias., Liassic  
Lith., Lithuania  
Llandeil., Llandeilian  
Llanvirn., Llanvirnian  
long., longitudinal  
Ls., Limestone  
Ludlov., Ludlovian

m., meter  
M., Mid., Middle  
M, monotypy  
Maastricht., Maastrichtian  
Madag., Madagascar  
mag., magnification  
Man., Manitoba  
max., maximum  
Md., Maryland  
Me., Maine  
med., median  
Mem., Memoir, -s  
Mém., Mémoire  
Meramec., Meramecian  
Mex., Mexico  
Mich., Michigan  
Minn., Minnesota  
Mio., Miocene  
M.ss., Mississippi, Mississippian  
mm., millimeter, -s  
Mo., Missouri  
Mus., Museum

n., new  
N., North  
N.Am., North America, -n  
Namur., Namurian  
Nat., Natural  
Natl., National  
NE., Northeast  
Neb., Nebraska  
Neocom., Neocomian  
Neth., Netherlands  
Nev., Nevada

Newf., Newfoundland  
Niag., Niagara  
N.J., New Jersey  
N.Mex., New Mexico  
no., number  
nom. conserv., *nomen conservatum* (conserved name)  
nom. correct., *nomen correctum* (corrected or intentionally altered name)  
nom. imperf., *nomen imperfectum* (imperfect name)  
nom. neg., *nomen negatum* (rejected name)  
nom. nov., *nomen novum* (new name)  
nom. nud., *nomen nudum* (naked name)  
nom. null., *nomen nullum* (null, void name)  
nom. subst., *nomen substitutum* (substitute name)  
nom. transl., *nomen translatum* (transferred name)  
nom. van., *nomen vanum* (vain, void name)  
Nor., Norian  
NW., Northwest  
N.Y., New York

O., Ocean  
obj., objective  
OD, original designation  
Okla., Oklahoma  
Oligo., Oligocene  
Ont., Ontario  
Opin., Opinion  
Ord., Ordovician  
orig., original

p., page, -s  
Pa., Pennsylvania  
Pac., Pacific  
Pak., Pakistan  
Paleoc., Paleocene  
Paleog., Paleogene  
Paleoz., Paleozoic  
pend., pending  
Penin., Peninsula  
Penn., Pennsylvanian  
Perm., Permian  
pl., plate, -s, plural  
Pleist., Pleistocene  
Pol., Poland  
Port., Portugal  
post., posterior  
Prov., Province  
pt., part, -s  
publ., published

Que., Quebec  
Queensl., Queensland

Rec., Recent  
reconstr., reconstructed, -ion  
reg., region  
Rept., Report  
Richmond., Richmondian

S., South, Sea

Scot., Scotland  
Scyth., Scythian  
SD, subsequent designation  
S.Dak., South Dakota  
SE., Southeast  
sec., section, -s  
Senon., Senonian  
ser., series, serial, etc.  
Sh., Shale  
Shrops., Shropshire  
Sib., Siberia  
Siegen., Siegenian  
Sil., Silurian  
siph., siphuncle  
s.l., s.lat., *sensu lato* (in the wide sense, broadly defined)  
SM, subsequent monotypy  
Somali., Somaliland  
sp., species  
Sp., Spain  
Spitz., Spitzbergen  
sr., senior  
ss., s.str., *sensu stricto* (in the strict sense, narrowly defined)

St., Saint  
subfam., subfamily  
subj., subjective  
superfam., superfamily  
suppl., supplement  
surf., surface  
SW., Southwest  
Swed., Sweden  
syn., synonym

Tasm., Tasmania  
Tenn., Tennessee  
Terr., Territory, -ies  
Tert., Tertiary  
Tex., Texas  
Tithon., Tithonian  
Tournais., Tournaisian  
transl., translated, translation  
transv., transverse  
Trenton., Trentonian  
Trias., Triassic

U., Up., Upper  
Univ., Universidad, Università,  
Universität, Université, Uni-  
versitets, University  
U.S., United States  
USA, United States (America)  
USSR, Union of Soviet Socialist  
Republics

v., volume, -s  
Va., Virginia  
var., variety  
Venez., Venezuela  
vent., ventral  
ventrolat., ventrolateral  
Visé., Viséan  
Vt., Vermont

Wash., Washington  
Wenlock., Wenlockian  
Westphal., Westphalian  
Wis., Wisconsin  
Wyo., Wyoming

Yugo., Yugoslavia

## REFERENCES TO LITERATURE

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

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

### *List of Serial Publications*

- Académie des Sciences, Comptes Rendus. Paris.
- Académie des Sciences URSS, Comptes Rendus [Akademiya Nauk SSSR, Leningrad].
- Académie Impériale des Sciences de St. Pétersbourg, Mémoires [Akademiya Nauk SSSR, Leningrad].
- Académie Royale des Sciences, des Lettres et des Beaux-Arts de Belgique, Bulletins. Bruxelles.
- Académie Tchèque des Sciences, Bulletin International, Classe des Sciences Mathématiques, Naturelles et de la Médecine [Česká Akademie věd a umění v Praze].
- Academy of Natural Sciences of Philadelphia, Proceedings.
- Accademia Pontaniana, Atti. Naples.
- [R.<sup>1</sup>] Accademia della Scienze di Torino, Memories. Acta Palaeontologica Polonica [Polska Akademia Nauk, Komitet Geologiczny]. Warszawa.
- Acta Palaeontologica Sinica. Peking.
- Acta Universitatis Lundensis; Arsskrift. Lund.
- [K.<sup>1</sup>] Akademie der Wissenschaften, St. Petersburg [Akademiya Nauk SSSR, Leningrad].
- Akademie der Wissenschaften und der Literatur, Mainz, mathematisch-naturwissenschaftliche Klasse, Abhandlungen.
- Akademie der Wissenschaftlichen zu München, mathematische-physikalische Klasse, Sitzungsberichten.
- Akademie der Wissenschaftlichen zu Wien, mathematisch-naturwissenschaftliche Klasse, Sitzungsberichten, Denkschriften.
- Akademiya Nauk SSSR, Doklady, new series; Geologicheskikh Institut; Institut Paleontologicheskikh, Materialy Osnovam Paleontologii; Seriya Biologicheskaya, Izvestiya; Trudy; Paleontologicheskii Zhurnal. Moskva, Leningrad.
- American Association for the Advancement of Science, Proceedings; Publications. Washington, D.C.
- American Association of Petroleum Geologists, Bulletins. Tulsa, Okla.
- American Geologist. Minneapolis, Minn.
- American Journal of Conchology. Philadelphia, Pa.
- American Journal of Science. New Haven, Conn.
- American Midland Naturalist. Notre Dame, Ind.
- American Museum of Natural History, Novitates; Memoires. New York.
- American Naturalist. Lancaster, Pa.
- American Philosophical Society, Proceedings. Philadelphia, Pa.
- Amsterdam, Universiteit van, Geologisch Instituut, Medeling.
- Annals and Magazine of Natural History. London.
- Annales de Paléontologie. Paris.
- Annales d'Histoire Naturelle. Paris.
- Annales des Sciences Naturelles, Zoologie. Paris.
- Archiv für Anatomie, Physiologie und Wissenschaftliche Medizin, Jahrgang. Leipzig.
- Archiv für Molluskenkunde. Frankfurt am Main.
- Archiv für Naturgeschichte. Leipzig.
- Archiv für Zoologie und Zootomie. Berlin.
- Archives de Musée Teyler. Haarlem.
- Arkiv för Mineralogi och Geologi utgivet av K. Svenska Vetenskapsakademien. Stockholm.

<sup>1</sup> R. or K. preceding a serial title stands for all forms meaning royal, imperial, e.g., Royale, Reale, Königliche, Kaiserliche, Kongelig, etc.

- Arquivos do Museu Paraense. Curitiba, Brazil.
- Beiträge zur naturkundlichen Forschung in Südwestdeutschland. Karlsruhe.
- Beiträge Petrefactenkunde. Bayreuth.
- Beiträge zur Paläontologie und Geologie Österreich-Ungarns und des Orients. Wien.
- [K.] Böhemische Gesellschaft der Wissenschaften, Sitzungsberichten; Abhandlungen. [České Společnosti Náuk, Prague.]
- Boston Society of Natural History, Proceedings, Memoirs.
- Breviora (Museum of Comparative Zoölogy). Cambridge, Mass.
- Buffalo Society of Natural Science, Bulletins. Buffalo, N.Y.
- Bulletin of American Paleontology. Ithaca, N.Y.
- Bulletin of Zoological Nomenclature. London.
- Cambridge Philosophical Society, Biological Reviews. Cambridge, Eng.
- Canada, Geological Survey of, Department of Mines & Resources, Mines & Geology Branch, Bulletins. Ottawa.
- Canadian Alpine Journal. Winnipeg, Canada.
- Canadian Naturalist. Montreal, Canada.
- Carnegie Museum, Annals. Pittsburgh, Pa.
- Challenger. Report on the Scientific Results of the Exploring Voyage of HMS Challenger. Zoology. Edinburgh.
- [K.] Česká Společnost Náuk, Prague, Třída Matematicko-Přírodovědecká, Věstník.
- China, Geological Survey of, Palaeontologia Sinica. Peking.
- Cincinnati Society of Natural History, Journals.
- Comité Geologique, Mémoires. St. Petersburg. (see Geologicheskago Komiteta, Trudy. Leningrad.)
- Connecticut Geological and Natural History Survey, Bulletins. Hartford.
- Czechoslovakia, Geological Survey of, Sbornik. Paleontology. Praha.
- Dansk Geologisk Forening, Meddelelser. København.
- [K.] Danske Videnskabernes Selskabs, Matematisk-Fysiske, Skrifter. København. [Académie royale des Sciences et Lettres de Denmark].
- Decheniana. Verhandlungen des Naturhistorischen Vereins der Rheinlande und Westfalens. Bonn.
- Denison University Bulletin, Journal of the Scientific Laboratories. Granville, Ohio.
- Deutsche geologische Gesellschaft, Zeitschrift; Sonder-Abdruck. Berlin.
- Edinburgh Geological Society, Transactions.
- Ergebnisse und Fortschritte der Zoologie. Jena.
- Evolution. Lancaster, Pa.
- Experientia. Basel.
- Ezhegodnik Vsesoyuznogo Paleontologicheskogo Obshchestva. Moskva.
- Fieldiana, Geology. Chicago.
- Field Museum of Natural History, Publications, Geological Series. Chicago.
- Földtani Közlöny [Magyaroni Földtani Társulat, Folyóirat]. Budapest.
- Fortschritte der Geologie. Köln & Leipzig.
- Fortschritte der Paläontologie. Berlin.
- Freiberger Forschungshefte. Berlin.
- [K.] Fysiografiska Sällskapet i Lund, Handlingar. (Lund Universitet.)
- Geological Magazine. London & Hertford.
- Geological Society of America, Bulletins; Special Papers; Memoirs. New York.
- Geological Society of China, Bulletins. Peking.
- Geological Society of Japan, Journals. Tokyo.
- Geological Society of London, Memoirs; Proceedings; Quarterly Journal; Transactions.
- Geological Survey of [see under name of country, state, or province].
- Geologie. Berlin.
- Geologische Blätter für Nordost-Bayern und angrenzende Gebiete Erlangen.
- Geologicheskago Komiteta, Trudy. Leningrad. (see Comité Geologique, Mémoires. St. Petersburg.)
- [K.K.] Geologische Reichsanstalt Wien, Abhandlungen; Jahrbuch; Verhandlungen. [Geologische Bundesanstalt.]
- Geologische Rundschau (Geologische Vereinigung). Stuttgart, Leipzig & Berlin.
- Geologiska Föreningen i Stockholm, Förhandlingar.
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## SOURCES OF ILLUSTRATIONS

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

## STRATIGRAPHIC DIVISIONS

Classification of rocks forming the geologic column as commonly cited in the *Treatise* in terms of units defined by concepts of time is reasonably uniform and firm throughout most of the world as regards major divisions (e.g., series, systems, and rocks representing eras) but it is variable and unfirm as regards smaller divisions (e.g., substages, stages, and subseries),

which are provincial in application. Users of the *Treatise* have suggested the desirability of publishing reference lists showing the stratigraphic arrangement of at least the most commonly cited divisions. Accordingly, a tabulation of European and North American units, which broadly is applicable also to other continents, is given here.

### *Generally Recognized Divisions of Geologic Column*

#### EUROPE ROCKS OF CENOZOIC ERA NEOGENE SYSTEM<sup>1</sup>

Pleistocene Series (including Recent)  
Pliocene Series  
Miocene Series

#### PALEOGENE SYSTEM

Oligocene Series  
Eocene Series  
Paleocene Series

#### ROCKS OF MESOZOIC ERA

##### CRETACEOUS SYSTEM

###### Upper Cretaceous Series

Maastrichtian Stage<sup>2</sup>  
Campanian Stage<sup>3</sup>  
Santonian Stage<sup>3</sup>  
Coniacian Stage<sup>2</sup>  
Turonian Stage  
Cenomanian Stage

###### Lower Cretaceous Series

Albian Stage

Aptian Stage

Barremian Stage<sup>3</sup>  
Hauterivian Stage<sup>3</sup>  
Valanginian Stage<sup>3</sup>  
Berriasian Stage<sup>3</sup>

##### JURASSIC SYSTEM

###### Upper Jurassic Series

Portlandian Stage<sup>4</sup>  
Kimmeridgian Stage  
Oxfordian Stage

###### Middle Jurassic Series

Callovian Stage (or Upper Jurassic)  
Bathonian Stage  
Bajocian Stage

#### NORTH AMERICA ROCKS OF CENOZOIC ERA NEOGENE SYSTEM<sup>1</sup>

Pleistocene Series (including Recent)  
Pliocene Series  
Miocene Series

#### PALEOGENE SYSTEM

Oligocene Series  
Eocene Series  
Paleocene Series

#### ROCKS OF MESOZOIC ERA

##### CRETACEOUS SYSTEM

###### Gulfian Series (Upper Cretaceous)

Navarroan Stage  
Tayloran Stage  
Austinian Stage

Woodbinian (Tuscaloosan) Stage

###### Comanchean Series (Lower Cretaceous)

Washitan Stage

Fredericksburgian Stage  
Trinitian Stage

###### Coahuilan Series (Lower Cretaceous)

Nuevoleonian Stage

Durangoan Stage

##### JURASSIC SYSTEM

###### Upper Jurassic Series

Portlandian Stage  
Kimmeridgian Stage  
Oxfordian Stage

###### Middle Jurassic Series

Callovian Stage (or Upper Jurassic)  
Bathonian Stage  
Bajocian Stage



**Lower Jurassic Series (Liassic)**

Toarcian Stage  
Pliensbachian Stage  
Sinemurian Stage  
Hettangian Stage

**TRIASSIC SYSTEM**

**Upper Triassic Series**

Rhaetian Stage<sup>5</sup>  
Norian Stage  
Carnian Stage

**Middle Triassic Series**

Ladinian Stage  
Anisian Stage (Virgilorian)

**Lower Triassic Series**

Scythian Series (Werfenian)

**ROCKS OF PALEOZOIC ERA**

**PERMIAN SYSTEM**

**Upper Permian Series**

Tartarian Stage<sup>6</sup>  
Kazanian Stage<sup>7</sup>  
Kungurian Stage

**Lower Permian Series**

Artinskian Stage<sup>8</sup>  
Sakmarian Stage

**CARBONIFEROUS SYSTEM**

**Upper Carboniferous Series**

Stephanian Stage

Westphalian Stage

Namurian Stage

**Lower Carboniferous Series**

Viséan Stage

Tournaisian Stage  
Strunian Stage

**DEVONIAN SYSTEM**

**Upper Devonian Series**

Famennian Stage

Frasnian Stage

**Lower Jurassic Series (Liassic)**

Toarcian Stage  
Pliensbachian Stage  
Sinemurian Stage  
Hettangian Stage

**TRIASSIC SYSTEM**

**Upper Triassic Series**

(Not recognized)  
Norian Stage  
Carnian Stage

**Middle Triassic Series**

Ladinian Stage  
Anisian Stage

**Lower Triassic Series**

Scythian Stage

**ROCKS OF PALEOZOIC ERA**

**PERMIAN SYSTEM**

**Upper Permian Series**

Ochoan Stage  
Guadalupian Stage

**Lower Permian Series**

Leonardian Stage  
Wolfcampian Stage

**PENNSYLVANIAN SYSTEM**

**Kawvian Series (Upper Pennsylvanian)**

Virgilian Stage  
Missourian Stage

**Oklahoma Series (Middle Pennsylvanian)**

Desmoinesian Stage  
Bendian Stage

**Ardian Series (Lower Pennsylvanian)**

Morrowan Stage

**MISSISSIPPIAN SYSTEM**

**Tennessee Series (Upper Mississippian)**

Chesterian Stage

Meramecian Stage

**Waverly Series (Lower Mississippian)**

Osagian Stage  
Kinderhookian Stage

**DEVONIAN SYSTEM**

**Chautauquan Series (Upper Devonian)**

Conewango Stage  
Cassadagan Stage

**Seneca Series (Upper Devonian)**

Chemungian Stage  
Fingerlakesian Stage

**Middle Devonian Series**

Givetian Stage

Couvinian Stage

**Lower Devonian Series**

Coblenzian Stage

Gedinnian Stage

**SILURIAN SYSTEM**

Ludlow Series

Wenlock Series

Llandovery Series

**ORDOVICIAN SYSTEM**

Ashgill Series

Caradoc Series

Llandeilo Series  
Llanvirn Series

Arenig Series  
Tremadoc Series

**CAMBRIAN SYSTEM**

Upper Cambrian Series

Middle Cambrian Series  
Lower Cambrian Series

**EOCAMBRIAN SYSTEM  
ROCKS OF PRECAMBRIAN AGE**

**Erian Series (Middle Devonian)**

Taghanican Stage  
Tioughniogan Stage  
Cazenovian Stage

**Ulsterian Series (Lower Devonian)**

Onesquethawan Stage  
Deerparkian Stage  
Helderbergian Stage

**SILURIAN SYSTEM**

**Cayugan Series**

Includes age equivalents of middle and upper Ludlow (in New York)

**Niagaran Series**

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

**Medinan Series**

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

**ORDOVICIAN SYSTEM**

**Cincinnatian Series (Upper Ordovician)**

Richmondian Stage  
Maysvillian Stage  
Edenian Stage

**Champlainian Series (Middle Ordovician)**

Mohawkian Stage  
Trentonian Substage  
Blackriveran Substage  
Chazyan Stage

**Canadian Series (Lower Ordovician)**

**CAMBRIAN SYSTEM**

**Croixian Series (Upper Cambrian)**

Trempealeauan Stage  
Franconian Stage  
Dresbachian Stage

**Albertan Series (Middle Cambrian)  
Waucoban Series (Lower Cambrian)**

**EOCAMBRIAN SYSTEM  
ROCKS OF PRECAMBRIAN AGE**

RAYMOND C. MOORE

<sup>1</sup> Considered by some to exclude post-Pliocene deposits.

<sup>2</sup> Classed as division of Senonian Subseries.

<sup>3</sup> Classed as division of Neocomian Subseries.

<sup>4</sup> Includes Purbeckian deposits.

<sup>5</sup> Interpreted as lowermost Jurassic in some areas.

<sup>6</sup> Includes some Lower Triassic and equivalent to upper Thuringian (Zechstein) deposits.

<sup>7</sup> Equivalent to lower Thuringian (Zechstein) deposits.

<sup>8</sup> Equivalent to upper Autunian and part of Rotliegend deposits.

<sup>9</sup> Classed as uppermost Cambrian by some geologists.

# PART K

# MOLLUSCA 3

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## CEPHALOPODA—GENERAL FEATURES

## ENDOCERATOIDEA—ACTINOCERATOIDEA

## NAUTILOIDEA—BACTRITOIDEA

BY CURT TEICHERT, BERNHARD KUMMEL, W. C. SWEET, H. B. STENZEL,  
W. M. FURNISH, BRIAN F. GLENISTER, H. K. ERBEN, R. C. MOORE, AND  
D. E. NODINE ZELLER

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### CONTENTS

	PAGE
INTRODUCTION (Curt Teichert and R. C. Moore) .....	K2
CEPHALOPODA—GENERAL FEATURES (W. C. Sweet) .....	K4
ENDOCERATOIDEA—ACTINOCERATOIDEA—NAUTILOIDEA (Curt Teichert <i>et al.</i> ) .....	K13
Morphology of Hard Parts (Curt Teichert) .....	K13
Glossary of Morphological Terms (Curt Teichert) .....	K54
Living Nautilus (H. B. Stenzel) .....	K59
Classification and Stratigraphic Distribution (Curt Teichert and R. C. Moore) .....	K94
Phylogeny and Evolution (W. C. Sweet, Curt Teichert, and Bernhard Kummel).....	K106
Paleoecology (W. M. Furnish and Brian F. Glenister) .....	K114
Biostratonomy (Curt Teichert) .....	K124
DESCRIPTIONS OF SUBCLASSES AND ORDERS (Curt Teichert <i>et al.</i> ) .....	K127
Introductory Discussion (Curt Teichert and R. C. Moore) .....	K127
Nautiloidea—Ellesmerocerida (W. M. Furnish and Brian F. Glenister) .....	K129
Endoceratoidea (Curt Teichert) .....	K160
Actinoceratoidea (Curt Teichert) .....	K190
Nautiloidea—Orthocerida (W. C. Sweet) .....	K216

Nautiloidea—Ascocerida (W. M. Furnish and Brian F. Glenister) .....	K261
Nautiloidea—Oncocerida (W. C. Sweet) .....	K277
Nautiloidea—Discosorida (Curt Teichert) .....	K320
Nautiloidea—Tarphycerida (W. M. Furnish and Brian F. Glenister) .....	K343
Nautiloidea—Barrandeocerida (W. C. Sweet) .....	K368
Nautiloidea—Nautilida (Bernhard Kummel, with addition by W. M. Furnish and Brian F. Glenister) .....	K383
References (Endoceratoidea, Actinoceratoidea, Nautiloidea) .....	K457
Rhyncholites (Curt Teichert, R. C. Moore, and D. E. Nodine Zeller) .....	K467
Doubtful Taxa (Curt Teichert) .....	K484
Bactritoidea (H. K. Erben) .....	K491
INDEX .....	K506

## INTRODUCTION

By CURT TEICHERT and R. C. MOORE

[United States Geological Survey; The University of Kansas]

The cephalopods described in this volume are divided into the orders Ellesmerocerida, Endocerida, Intejocerida, Actinocerida, Orthocerida, Ascocerida, Discosorida, Oncocerida, Tarphycerida, Barrandeocerida, and Nautilida. Descriptions of them are followed by that of the Bactritida, the taxonomic status and affinities of which are unsettled. The named orders include all the cephalopods which from the middle of the 19th century until comparatively recently were assigned to a single taxon "Nautiloidea," first recognized and named by DE BLAINVILLE in 1825 and generally regarded as a suprafamilial category, being classified by different authors as suborder, order, superorder, or subclass. This taxon was long contrasted with the Ammonoidea (*Treatise*, Part L), and considered to be equal in rank with this assemblage.

In general, and as compared with other molluscan groups, including ammonoids, "nautiloid" cephalopods are rare fossils. Most fossiliferous formations contain no, or only a few, nautiloid conchs. Mass occurrences

such as are abundantly known among ammonoids, gastropods, and pelecypods, are very rare. Among the few recorded mass occurrences of fossil "nautiloids" the following deserve mention: the widespread mass accumulations of large endocerids in the Middle Ordovician (Vaginatum Limestone and equivalents) of Norway, Sweden, and Estonia (2), the so-called Maquoketa coquina of Late Ordovician age in Iowa, consisting of large concentrations of conchs of *Dolorthoceras sociale* (3), mass occurrences of *Pseudorthoceras* in the Lower Permian of north-central Texas (CLIFTON, 1944).

MILLER & YOUNGQUIST (3), FLOWER (1), and REYMENT (4) have cited and discussed a few additional examples, but such occurrences are uncommon. A considerable number of nautiloid genera recognized and described in the present volume are known from only a few specimens, and some from only one specimen. STENZEL (6) reports that in rocks of Tertiary age the proportion of nautilids to other mollusk specimens may be of the order of 1:1,000 to as much as 1:10,000. The fossil record suggests that,

in spite of their considerable morphological diversification and their long geological record, nautiloid cephalopods were at all times and in most places subordinate constituents of contemporaneous faunas.

Systematic and structural studies during the last three decades have shown that the "Nautiloidea" include several specialized taxa that, although doubtless stemming from the common ancestral stock of the Ellesmerocerida, had diverged strongly in morphological and structural characters. In fact, some of the taxa are less similar to each other than some of them are to the ammonoids. Although it is difficult to distinguish various early ammonoids from their "nautiloid" ancestors, no difficulties exist, as a rule, in distinguishing between representatives of different taxa within the so-called "Nautiloidea." Thus, no longer does any sound biologic foundation seem to exist for uniting the many diverse "nautiloid" taxa into one taxonomic unit.

Subsequent to a decision by TEICHERT and others concerned with preparation of *Treatise* Part K that the recognized main assemblages of nautiloid cephalopods should be described independently under the informal heading of "Nautiloid Orders," SHIMANSKIY & ZHURAVLEVA in 1961 (5) published a penetrating discussion of these groups: this was intended to provide a classification suitable for adoption in the Soviet paleontological treatise (*Osnovy Paleontologii*). Following SCHWARZ (1894) they divided the class Cephalopoda into two subclasses, the first (named Ectocochlia) containing all forms characterized by the presence of an external shell and the second (named Endocochlia) consisting of the internal-shell and shell-less forms. The Ectocochlia were defined to include five main groups designated as superorders, namely, Nautiloidea, Actinoceratoidea, Endoceratoidea, Bactritoidea, and Ammonoidea. This arrangement seems superior to classification of external-shell cephalopods in a dozen or more orders, all of equal rank, one of which embraces the host of highly varied ammonoids. Accordingly, the systematic framework proposed by SHIMANSKIY & ZHURAVLEVA is accepted by us, except for classifying their so-called superorders as subclasses and adopting the name Coleoidea in place of Endocochlia. The Ammonoidea

(already published in *Treatise* Part L) are then to be defined as a subclass in a projected future revision, and the suborders given in Part L will be raised to the rank of orders. *Treatise* Part M will describe and illustrate representatives of the subclass Coleoidea.

The originally determined sequence of "nautiloid orders" in Part K is retained, in spite of the seemingly anomalous separation of Ellesmerocerida from the remaining orders of the subclass Nautiloidea. Reasons for such retention are (1) the avoidance of otherwise necessary extensive resetting of type, accompanied by rearrangement of figures with already assigned numbers, and (2) the maintained judgment that ellesmerocerids comprise the rootstalk from which other main groups of nautiloids were evolved.

Because of the generally clear morphological differentiation of nautiloid orders, individual authors' assignments were well defined as a rule and authorship of individual contributions is indicated in the table of contents.

The preparation of this volume of the *Treatise* has encountered sundry difficulties and special problems. The chief of these have arisen from the need to revise authorship assignments drastically and from what now is seen as a premature start on publication. Firmly assured completion dates given by some authors could not be met, and since the sequence of the several nautiloid orders in the section on systematic descriptions had been agreed upon previously, various unfinished units had to be skipped if typesetting work on others was to go forward. Therefore, this volume has been built like a wall with gaping holes into which properly shaped stones later had to be fitted with minimum visible signs of patchwork. TEICHERT was charged with assembling and co-ordinating the individual typescripts, and he reviewed the contributions of all other authors up to the time of his departure for an extended stay in Pakistan; this was in October, 1961. Subsequently, a half-dozen chapters and co-ordination of the whole volume have been handled editorially by MOORE. The chapter describing general features of cephalopods was prepared last of all by SWEET, substituting on short notice for originally designated authors who failed to write it.

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CEPHALOPODA—GENERAL FEATURES<sup>1</sup>

By WALTER C. SWEET

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## CEPHALOPODA Cuvier, 1797

[*nom. correct.* DUMÉRIL, 1806 (*pro* Les Céphalopodes CUVIER, 1797)] [NAEF (1923) attributed authorship of the name Cephalopoda to SCHNEIDER, 1784, who actually only grouped all living cephalopods into two "classes" of a category he termed "Octopodia." Thus we cannot ascribe the name to SCHNEIDER, since he seems not to have used it.]

## BIOLOGY OF CEPHALOPODA

Mollusks of the class Cephalopoda are agile, bilaterally symmetrical, predacious carnivores that have achieved a structural complexity and metabolic efficiency without peer among unsegmented invertebrates. The class is represented in the modern marine fauna by some 650 species of octopuses, squids, cuttlefishes, argonauts (Lane, 1957, *Kingdom of the Octopus*), and *Nautilus*, the only living form with an external shell. The class also includes more than 10,000 fossil species informally termed nautiloids and bactritids (the subjects of this volume), ammonoids (described in *Treatise* Part L, 1957), and coleoids (to be discussed in *Treatise* Part M).

The oldest undisputed cephalopods are from strata of Late Cambrian age, and a

very considerable fossil record indicates that they were most abundant in the Paleozoic and Mesozoic. Except for such now-flourishing coleoid orders as Teuthidida, Sepiida, and Octopodida, the class has declined in both numbers and diversity since the Triassic and especially since the Cretaceous. Invertebrates associated with fossil cephalopods indicate that the class has always been exclusively marine in habitat, as is true of all living representatives. Although some of the latter are adapted to intermediate and abyssal depths of the oceans, the majority are most abundant in shallow seas. The ecology of fossil species is more difficult to reconstruct, for, after the animal's death, the gas-filled shells of *Nautilus*, drift widely in modern oceans and those of many fossil species are assumed to have done so in the past. However, both the rocks and the remains of other invertebrate groups commonly associated with fossil cephalopods suggest that the group has always been most abundant in shallow seas on continental shelves.

Both embryology and comparative anatomy indicate that cephalopods arose from an "ancestral mollusk" similar in form to certain primitive gastropods. The steps by which this may have taken place are ably outlined by YONGE (6) and need only be summarized here. The initial stage probably involved isolation of segments in the

<sup>1</sup> A short chapter by A. K. MILLER & W. M. FURNISH, entitled "Introduction to Cephalopoda," was included in the Editorial Preface to *Treatise* Part L, published in 1957. Revision of the introductory chapter was undertaken at a very late date by the present author, who has retained large parts of the original and has expanded or partially rewritten others. He acknowledges his debt to MILLER & FURNISH, but assumes full responsibility for the present summary, which also incorporates suggestions by CURT TEICHERT, J. A. JELETZKY, and R. C. MOORE.

apex of the domelike shell of the ancestral mollusk by a succession of transverse partitions (septa) traversed by a fleshy tube, the siphuncle. Associated with this was undoubtedly a pronounced ventral flexure of the animal such that the head and the opening to the pallial cavity, separated only by a much modified foot, came to face ventrally. The primitive molluscan foot developed into the muscular hyponome, or swimming funnel of the cephalopods, and the chambered, gas-filled shell came gradually to serve as a functional hydrostatic device.

Because of the developmental pattern suggested by YONGE, logical objections have been voiced to the application to cephalopods of such terms as anterior, posterior, dorsal, and ventral, with what appears to be their customary meaning. That is, if shells of fossil cephalopods, or the bodies of living forms, are oriented for descriptive purposes in a manner anatomically comparable with that employed in describing pelecypods and gastropods, the adapical portion of the body is dorsal, the head and arms ventral, the hyponomic side posterior, and the opposed side anterior. However, it is doubtful if more than a few groups of early cephalopods (and some specialized later derivatives) lived in any such position. Consequently, the more familiar terminology is applied to animals oriented in a living position (insofar as this can be determined) and the few anatomical terms commonly used by paleontologists are employed in a functional sense. The head, bearing eyes, tentacles or arms, and the mouth, is anterior; the opposite end of the visceral complex is posterior; the hyponomic side of the body is ventral; and the opposed side dorsal. After more than a century of error, it is doubtful that the revised orientation urged by MUTVEI (1957) will come to be widely adopted (see p. K15).

Cephalopods are the most highly organized mollusks and among them are the most accomplished swimmers other than the fishes. Some are minute, but the class also includes the giant squid, *Architeuthis*, which, with a body (including tentacles) as much as 16 m. (52 feet) long, is not only the largest living mollusk, but also the largest living invertebrate. The shells of some Ordovician nautiloids (e.g., *Cameroceras*)

attained a length of nearly 10 m., and those of immense Cretaceous ammonoids (e.g., *Pachydiscus*) have a diameter of some 2.5 m.

The principal anatomic features of two living cephalopods are shown in Figure A. It can be seen that the body is elongate, with a distinct anterior head that bears large eyes and a mouth that is surrounded by a crown of mobile, prehensile arms or tentacles. Behind the head is the saclike visceral mass, and ventrally is the hyponome and a capacious branchial cavity. The latter is completely enveloped by the mantle, which is undivided and also encloses the remainder of the body. In ten-armed coleoids lateral fins are developed from the mantle, and in *Nautilus*, the mantle is prolonged posteriorly as the siphuncular cord.

The head is built around an internal cartilaginous skeleton that supports or encloses the central nervous system and balance organs, and provides attachment for the hyponome and many of the principal muscles. At its anterior end is the mouth, surrounded by one or several series of arms or tentacles and equipped with a buccal mass that includes a parrot-like beak with upper and lower jaws or mandibles (see p. K62, K470).

The cephalic processes that surround the mouth vary considerably in number, structure, and size in living cephalopods. Most authors hold that they are elaborations of the anterior part of the primitive molluscan foot, but that interpretation is rejected by others. In *Nautilus*, 94 sheathed cirrate tentacles are arranged on ocular, labial, and digital lobes (Fig. A,1); in other living cephalopods the number of arms is less. Many living ten-armed coleoids (e.g., squids) have the arms arranged in five pairs (Fig. A,2). Four pairs are short, stout, and bear suckers on their inner sides, whereas tentacles of the fifth pair are long, retractile, and have suckers only at their somewhat expanded distal ends. Suckers of many ten-armed coleoids have horny or toothed rims; denticles of some of these develop into large formidable hooks. Octopods, as the name suggests, have eight circumoral arms provided with suckers; in some (*Vitreledonellidae*) the arms are joined by a web and are used for swimming.

Eyes, which are particularly well developed in various coleoids but are primitive "pin-hole" structures in *Nautilus*, are borne laterally on the head. In *Nautilus*, they are open water-filled pits at the ends of short stalks, and have a retina but lack iris, cornea, lens, or eyelid. In other cephalopods, however, they are complex organs of ectodermal origin capable of forming an image and similar in both structure and development to those of vertebrates.

The dorsal surface of the head is protected by a thick, commonly warty, hood in *Nautilus* (Fig. A,1), which serves to close the aperture of the external shell when the animal is retracted into it. No comparable feature is found in other living cephalopods, which lack an external shell.

The foot of the ancestral mollusk is represented in cephalopods by the muscular hyponome, through which water is ejected from the mantle cavity. The tip of this structure is highly mobile; it arises as a pair of flaps, the margins of which overlap in *Nautilus*, but are fused together in other living cephalopods. In many forms a small supplementary flap in the hyponome acts as a check valve, permitting water to flow only in an outward direction. A hyponome is peculiar to the class, and rapid swimming results when water is forcefully ejected from it either by pulsations of the muscular hyponome (in *Nautilus*) or by powerful contraction of the muscular mantle (in all other living cephalopods).

The more or less elongate visceral mass is enveloped by the mantle, which is only weakly muscular in *Nautilus*, but contains thick layers of both circular and longitudinal muscle in other living forms. Besides commonly secreting a shell, the mantle has a forward-projecting undivided fold that forms the outer wall of a ventral pallial or branchial cavity, within the posterior portion of which the gills are suspended. Except in the Vitreledonellidae in which they are vestigial, the gills are paired plumelike structures, of which two (a pair) occur in all living forms but *Nautilus*, which has four (two pairs). In *Nautilus*, gills are attached only at the base, but in other living forms they are attached also along the afferent sides of the axis. Ctenidial filaments are alternately arranged on either

side of a central axis, and their respiratory surface is greatly increased by lateral and secondary folding. Some living ten-armed coleoids have 40 filaments on either side of the axis; in octopods, however, the number is smaller and in some abyssal forms gill filaments are further reduced in number and length. Supporting rods occur on the afferent sides of gill filaments; these arise in a membrane that extends from the afferent surface of the filaments to the afferent membrane. These apparently serve as ties between the margins of filaments and the afferent membrane (5). Unlike those of other mollusks, the ctenidia of cephalopods are not ciliated, probably because they are constantly bathed and cleansed by sea water forced into and out of the mantle cavity either by pulsations of the hyponome or by muscular contractions of its walls.

Contraction of the longitudinal mantle muscles causes the mantle cavity of coleoids to be enlarged and sea water is drawn into it laterally and ventrally between the anterior margin of the mantle and the head. Subsequent contraction of the powerful circular muscles (and relaxation of the longitudinal ones) reduces the capacity of the cavity and locks the mantle firmly around the head so that water is forced out of the hyponome under great pressure. Consequently, the inhalant current is ventral to the exhalant one. The mantle of *Nautilus* is only slightly muscular; hence, water both enters and leaves the pallial cavity by way of the hyponome and inhalant and exhalant currents are correspondingly weaker than in coleoids. In *Nautilus* the mantle cavity also contains an **osphradium**, situated below the gills and directly in the path of the respiratory current. Such organs have commonly been interpreted as chemoreceptors concerned with testing the water that enters the mantle cavity or with detecting food. YONGE (5), however, has interpreted the osphradium as a tactile organ, the principal function of which is estimation of the amount of sediment entering the pallial cavity. This interpretation would explain the presence of an osphradium in *Nautilus* and its absence in coleoids, for sediment would be more likely to accumulate in the mantle cavity of bottom-living *Nautilus* (which has a relatively feeble respiratory



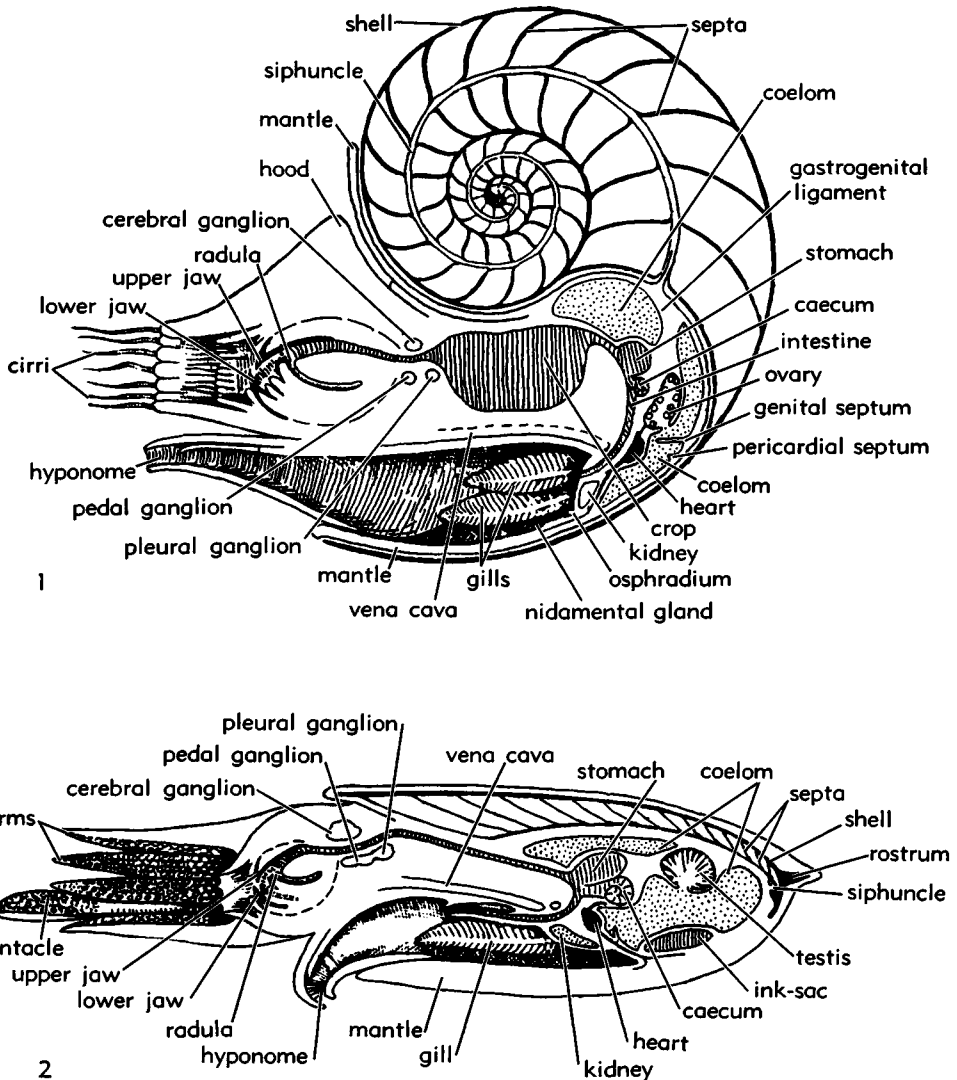


FIG. A.—Median longitudinal sections of (1) *Nautilus* and (2) *Sepia*, showing anatomy of typical representatives of the two major groups of living cephalopods (from NAEF, 1928, p. 83).

current) than in that of the living ten-armed coleoids and octopods, from which water is violently expelled.

The mantle of coleoids (but not of *Nautilus*, in which it is largely covered by shell) is liberally supplied with chromatophores that, in various species, contain black, pink, brown, blue, or purple pigment. Contraction of muscle fibers attached to these structures flattens or draws them out and cephalopods so equipped can simulate the color of their surroundings with astonishing

rapidity. The change is so obvious in *Octopus* that the animal literally blushes when frightened. In some living ten-armed coleoids and in one octopod species, which live at great depths, special phosphorescent organs are developed in various parts of the mantle, arms, and head.

The alimentary canal does not extend from pole to pole but forms a loop so that the mouth as well as the anus is more or less anterior in position. The buccal cavity, which contains a toothed radula or its de-

generate equivalent, and into which two pairs of salivary glands discharge, gives way posteriorly to a muscular esophagus, which expands to form a crop in *Nautilus* and *Octopus*, but not in other cephalopods. Peristaltic contraction of the esophagus passes food back to the muscular stomach, to which is attached a large caecum that is straight in squids, but spirally constructed in *Sepia*, *Octopus*, and *Nautilus*.

A process of **digestion**, entirely extracellular, is accomplished by enzymes discharged into the caecum by the small "pancreas" and the large "liver." When food reaches the stomach, digestive enzymes stored in the caecum pour into it and digestion begins. The process is completed in the caecum itself and absorption takes place largely through its walls. Indigestible refuse is returned to the second portion of the stomach, from which it passes to the straight or coiled intestine and is ultimately discharged through the anus, which opens into the pallial cavity near the posterior end of the hyponome.

Squids and *Octopus* have two compact, saclike **nephridia** which enclose the renopericardial canal, but the four nephridia of *Nautilus* have no connection with the pericardial cavity. Waste is excreted through renal pores which open into the mantle cavity near the anus.

An **ink sac**, containing ink gland and reservoir, opens into the rectum of all cephalopods but *Nautilus* through a duct situated just behind the anus. The black or brown alkaloid ink is rich in melaniniferous pigment, which, when discharged, forms a murky cloud that apparently anesthetizes the chemoreceptors of some predators and provides a screen behind which the cephalopod can escape.

The **circulatory system** of cephalopods is fundamentally molluscan, but is modified in several noteworthy respects. The heart, enclosed in a pericardium, has a median ventricle and as many auricles as there are gills. Ventricles pump blood to the body through anterior and posterior aortas which branch to form several arterial systems. In *Nautilus*, returning blood trickles back to the haemocoel through interconnected sinuses, then passes by way of the vena cava to the gills. In coleoids, however, the system is entirely closed and veins replace the

sinuses of *Nautilus*. In these forms, blood returns from the head via the vena cava, which divides into right and left branches. The right branch receives blood from veins that drain the ink sac and gonad, and each branch passes through a nephridial sac and a muscular branchial heart before entering the ctenidia. Anterior and posterior vein pairs return blood from the mantle and visceral mass. Supplementary branchial hearts provide coleoid cephalopods with the additional pressure necessary to impel blood through the gill capillaries, from which it is sucked into the auricles of the heart and eventually passed to the median ventricle.

The **nervous system** of cephalopods is complex in that the typical molluscan ganglia blend to form a massive circum-esophageal "brain." Above the esophagus of living coleoids are the large cerebral ganglia, which give rise not only to large optic nerves but also to a pair of buccal nerves extending anteriorly to an upper pair of buccal ganglia and then, by way of a commissure around the esophagus, to a lower pair of buccal ganglia. The pedal ganglia supply nerves to the hyponome and forward divisions send nerves to each arm, which suggests to some that both hyponome and arms were derived from the primitive molluscan foot. Visceral ganglia give rise to three pairs of posteriorly directed nerves: one pair innervates various internal organs and the gills; another pair joins in a gastric ganglion between stomach and caecum, which it innervates; and the third pair, which contains giant motor neurons, innervates the mantle and its respiratory muscles. The nervous system of *Nautilus* is described in detail by STENZEL in another part of this volume. It is sufficient to point out here that it is similar to that of living coleoids, but the brain is much less concentrated and forms a heavy collar around the esophagus. For these and other reasons it is regarded as the more primitive structure.

The **sexes** are separate, the animals are oviparous, and in some (e.g., the octopod *Argonauta*) sexual dimorphism is conspicuous. A single saclike gonad in the large genital coelom discharges by one or two genital ducts into the mantle cavity. A capped, club-shaped spermatophore, which contains a springlike ejaculatory organ and

masses of sperm and cement, is formed in the male seminal vesicle. Spermatophores are transferred to the mantle cavity or to suboral seminal receptacles of females by special copulatory structures quite separate from the genital ducts. In adult males of *Nautilus*, four modified arms form a permanent erectile intromittent organ (the spadix), but in other living cephalopods the male copulatory structure is a seasonally modified arm, the hectocotylus. Eggs are commonly protected by individual capsules secreted by the oviductal glands and may be aggregated in masses that are embedded in a gelatinous material secreted by the nidamental glands.

Cephalopod eggs are large and contain greater quantities of yolk than do those of other mollusks. Nothing is known about the early stages of development in *Nautilus*, but in other living forms cleavage is meroblastic and results in formation of a germinal cap of cells at the animal pole. The margins of this grow downward and envelop the yolk to form a yolk sac, which is gradually absorbed during later development. Development is direct and differs from that of other mollusks in that the embryo proceeds to the adult form without any intervening trochophore or veliger larval stage.

All cephalopods have **hard parts**; in many, however, they are inconspicuous and only the shells are commonly preserved as fossils. The univalved shell is external in *Nautilus* and presumably was borne in a similar manner in the many fossil nautiloids, bactritids, and ammonoids. In the modern coleoids and their fossil kin, the shell is overgrown by the muscular mantle and is at least largely internal. The well-developed shell of the extinct belemnoids and phragmoteuthids is typical of the subclass; its chambered part, the phragmocone, does not differ materially from that of ammonoids and nautiloids, including the apparently ancestral bactritids. It is enveloped, however, in the more or less massive, calcitic sheath, the guard, which does not seem to have any equivalents in ammonoids and nautiloids. Furthermore, the shelly wall of the ammonoid and nautiloid body chamber is reduced in belemnoids and phragmoteuthids to a dorsal, blade- or fan-shaped rudiment, the proostracum, which is perhaps the most diagnostic feature of coleoid shells.

This typical coleoid shell is considerably reduced or modified in teuthidoids and sepioids. Only the proostracum is well developed in teuthidoids, the majority of which lack any trace of the phragmocone and guard of their presumably *Phragmoteuthis*-like ancestors. In most sepiids, just the greatly modified, dorsal part of the phragmocone remains; its ventral and lateral parts, as well as the siphuncle, are represented by small, nearly unrecognizable vestiges. The shell of the sepiid *Spirula*, a bathypelagic drifter, is a coiled normally chambered phragmocone that includes a siphuncle. In octopods the shell is reduced to paired or unpaired cartilaginous stylets.

Most living cephalopods are denser than the sea water in which they live and support themselves by active swimming. *Sepia*, *Spirula*, and *Nautilus*, however, have a density near that of sea water because of the presence of gas in the chambers of their rigid shells. *Sepia* can adjust its buoyancy in submarine-like fashion by pumping liquid into and out of shell chambers (1). This liquid has a salt content lower than the body fluid; hence osmotic pressure aids in counteracting hydrostatic pressure, at least at moderate depth. BIDDER (in 1) has noted the presence of liquid in the chambers of *Nautilus*, which is also known to accommodate itself effectively to greatly different depths during its lifetime. Presumably gas pressure can also be increased to prevent liquid from flowing into chambers and to prevent implosion of the shell. However, BIDDER has also noted that gas in the chambers of a *Nautilus* hauled up from 200 m. was not under noticeable pressure.

External shells, which form the bulk of the fossil record of cephalopods, can be visualized as more or less modified hollow cones that are straight, curved, or coiled (generally in a single plane). These are divided by septa into camerae pierced by the siphuncle. The septa and siphuncle readily distinguish the external shells of cephalopods from those of gastropods and scaphopods; furthermore, in only a few gastropods is coiling of the shell planispiral.

Both the external and internal shells of ancient cephalopods are among the best of stratigraphic indexes, for the animals evolved rapidly and along many different lines and this development is traceable in

their hard parts. Furthermore, fossil cephalopods are abundant in rocks of many ages and they are easily identified even though incomplete and when preserved only as internal molds. Because many cephalopod shells were gas-filled and relatively light in weight, it was possible for the animals that bore them to range widely in shallow seas and some of them may have had the cosmopolitan distribution of many modern species. Many genera and possibly some extinct species are common to the eastern and western hemispheres.

## MAJOR DIVISIONS OF CEPHALOPODA

The problem of defining main divisions of cephalopods, with designation of their names and authorship, offers sundry difficulties. First to be determined are the most acceptable criteria for classification, taking account of both living and fossil forms. Then, arrangement of assemblages of widely different comprehensiveness and magnitude in appropriate categories of taxonomic rank must be undertaken. Finally, questions of nomenclature must be settled and decisions reached about authorship of names and their dates.

It is clear from our summary discussion of their anatomy that living cephalopods can be divided readily into two major groups. The first, represented only by *Nautilus*, has an external shell, a bilobed hyponome, 94 tentacles, a mantle that is weakly muscular, two pairs of gills, and a primitive circulatory system. The second includes all other living cephalopods, which have 8 to 10 arms, a highly muscular mantle, a fused hyponome, a circulatory system that includes well-developed capillaries and supplementary branchial hearts, a single pair of ctenidia, and a shell that is internal or so reduced as to be vestigial.

Several (but not all) of these facts were noted by OWEN (4) in 1832, and he divided the Cephalopoda into two divisions, which he named Tetrabranchiata and Dibranchiata in accordance with the number of gills present in living representatives. Other authors have recognized the same two divisions, but have named them from other anatomic or developmental features. For

example, Tentaculifera of D'ORBIGNY, 1852, and Acetabulifera of OWEN, 1836 [=Acetabulifères FÉRUSSAC & D'ORBIGNY, 1835] refer to the nature of the circumoral appendages; and Schizosiphona and Holo-siphona of LANKESTER, 1883, as well as Tomochonia (or Funnaptera) and Gamochonia (or Funnoclausia) of HAECKEL, 1896, recognize differences in the structure of the hyponome. Ectocochlia and Endocochlia of SCHWARZ, 1894, give major prominence to the external or internal situation of the shell. Protocephalopoda and Meta-cephalopoda were proposed without explanation by GRIMPE (1922) as replacements for Tetrabranchiata and Dibranchiata, respectively, apparently to underscore the prevalent view (emphasized repeatedly by NAEF) that the characters of *Nautilus*, and thus supposedly of all fossil nautiloids and ammonoids, are primitive and represent those of the ancient stock from which all other cephalopods were derived.

Of all the many names available for major cephalopod divisions, only Tetrabranchiata and Dibranchiata (sometimes used in the shortened forms Tetrabranchia and Dibranchia) have been generally adopted. Even though this classification is eminently sound for living forms and has become firmly entrenched in most leading texts on invertebrate zoology, the legitimacy of applying it to other than living forms can be seriously questioned. That is, no fossil cephalopods are known in which the number of gills or arms (or the nature of the hyponome) can be observed and correlation of gill or arm number (or hyponome structure) with other anatomical features must always be at least partly conjectural. Furthermore, it is probable that the structures that distinguish the two modern groups of cephalopods are somewhat different answers to a common problem in cephalopod development, that of increasing respiratory and metabolic efficiency in connection with increased size and mobility (5). If this is so, both living groups are derived; neither is ancestral to, or more "primitive" than, the other.

From the start, however, OWEN (4) grouped in the Tetrabranchiata not only present-day *Nautilus* but also fossil nautiloids and extinct ammonites, as these groups were then understood. Later he in-

cluded the extinct belemnites in the Dibranchiata. Although OWEN's classification has been followed by nearly all subsequent students of cephalopods, it is here rejected in large part, as are the denominations Tetrabranchiata and Dibranchiata (and their many equivalents).

Reasons are certainly in order for what may appear to be such summary rejection of a venerable and widely accepted scheme of cephalopod classification. Although not supported by concrete evidence, there are sound reasons for assuming that the earliest cephalopods had a single pair of gills (6, p. 32). This is a logical attribute of the "ancestral mollusk" and is the pattern displayed by primitive gastropods that have diverged from the ancient pattern far less than living cephalopods. Furthermore, a limited number of observations (summarized on page K111) supports the view that some Ordovician and Silurian nautiloids (Orthocerida and possibly Actinocerida, and thus supposedly tetrabranchiate) had some coleoid characters; that is, they possessed an ink sac and had few arms. Orthocerids were derived from the even more primitive ellesmerocerids (which include the oldest known cephalopods) (Fig. 70), and they undoubtedly gave rise to the bactritids, from which the belemnoids and most modern coleoids probably are descended. Although such speculation is probably idle, it is nevertheless tempting to attribute some dibranchiate characters not only to orthocerids and bactritids but to ellesmerocerids, as well. Beyond this, however, there is no information whatsoever as to the number of arms or gills in such important groups of nautiloids as the Endocerida, Actinocerida, Discosorida, Barandeocerida, or Tarphycerida.

It is probably sound to assume that the entire order Nautilida, like its sole survivor *Nautilus*, was tetrabranchiate. This might also have been the condition of the Oncocerida (the supposed progenitors of the nautilids). However, it is the possibly dibranchiate Orthocerida, not the nautilids, that are usually singled out as ancestors of the bactritids, from which the Ammonoidea are thought to have evolved (Fig. 70). Al-

though it is probable that ammonoids had essentially the same mode of life as nautilids and thus may have solved the problem of increasing respiratory needs by adopting the tetrabranchiate option, they must have done so independently of the stock that ultimately gave rise to *Nautilus*. Thus, the Tetrabranchiata, in which OWEN and others have consistently included both Nautiloidea and Ammonoidea, is polyphyletic in this inclusive sense and should either be abandoned or revised to include only the Nautilida (and possibly the Oncocerida). This possibility is rejected because it requires drastic revision in content of a well-known taxon and is based on assumptions too tenuous to be acceptable.

Finally, it is by no means certain that all living Dibranchiata have common ancestors in the Belemnoidea. Even if they do, however, they are clearly separated from the possibly dibranchiate ellesmerocerids, orthocerids, and bactritids by the profound structural and anatomical differences already noted. A major cephalopod division conceived to embrace them all would merely be meaningless; in any event, it would not serve the more pragmatic ends of paleontological taxonomy. The possibility of revising the Dibranchiata to include orthocerids, ellesmerocerids, and possibly actinocerids is rejected on that basis.

As an alternative, several authors prefer a threefold division of the Cephalopoda on a different basis. Major divisions, variously termed classes, subclasses, superorders, or orders, are recognized in these schemes as Nautiloidea, Ammonoidea, and Coleoidea; or as Nautiloidea, Ammonoidea, and Dibranchiata (e.g., BASSE, 1952). Rankings in all these schemes suggest that nautiloids, ammonoids, and dibranchiates (or coleoids) are of equivalent taxonomic rank, although it has been clear for more than a century that fossil representatives of the Nautiloidea (*sensu lato*) are characterized by a diversity of fundamental structural plans quite without parallel in either the ammonoids or dibranchiates. RUZHENTSEV's scheme of 1960, in which cephalopods are divided into subclasses Ectocochlia and Endocochlia (with the former subdivided into superorders Nautiloidea, Ammonoidea, and Bactrit-

oidea) fails, also, to recognize this diversity among nautiloids and tends to perpetuate the unrealistic dichotomy suggested by study of living forms alone.

The arrangement of nautiloid orders in groups of higher taxonomic rank as proposed by SHIMANSKIY & ZHURAVLEVA (1961) is judged by contributors to the present volume to be the most suitable yet formulated in that (1) it provides indication that some orders are more closely related among themselves than to others and in that (2) it supplies an improved expression of classificatory rank correlated with the main non-nautiloid divisions of the Cephalopoda (e.g., Ammonoidea and Coleoidea). However, instead of the category superorder, used by SHIMANSKIY & ZHURAVLEVA, it is preferred to adopt subclass for rank designation of main divisions of the class Cephalopoda; furthermore, the name Coleoidea is preferred to Endocochlia. Elevation of cephalopods to the rank of a subphylum, as suggested by FLOWER & KUMMEL (1950), lacks merit in the view of the *Treatise* editor and authors working on the present volume.

An outline of the general classification adopted for organization of the present *Treatise* volume is given at the end of this chapter. Because this classification proposes revisions in rank of major taxa previously published in *Treatise* Part L on Ammonoidea, and includes names, authors, and dates that may appear novel, a statement of the principles followed in compiling it seems in order.

Guidance in naming species, genera, and family-group taxa is furnished by the Zoological Code (1961), but suprafamilial groups are expressly omitted from mention in it. Consequently, students of cephalopods, like workers on any large division of the animal kingdom, are faced with the task of rejecting various published suprafamilial names, accepting others, and possibly of coining entirely new names. Seemingly, choice must depend entirely on judgment, influenced but not controlled by usage. These matters are discussed in the Editorial Preface, accompanied by statement of a few informal rules that pertain especially to the *Treatise*.

### Major Classification

- Class Cephalopoda Cuvier, 1797
  - Subclass Nautiloidea Agassiz, 1847
    - Order Ellesmerocerida Flower in Flower & Kummel, 1950
    - Order Orthocerida Kuhn, 1940
    - Order Ascocerida Kuhn, 1949
    - Order Oncocerida Flower in Flower & Kummel, 1950
    - Order Discosorida Flower in Flower & Kummel, 1950
    - Order Tarphycerida Flower in Flower & Kummel, 1950
    - Order Barrandeocerida Flower in Flower & Kummel, 1950
    - Order Nautilida Agassiz, 1847
  - Subclass Endoceratoidea Teichert, 1933
    - Order Endocerida Teichert, 1933
    - Order Intejocerida Balashov, 1960
  - Subclass Actinoceratoidea Teichert, 1933
    - Order Actinocerida Teichert, 1933
  - Subclass Bactritoidea Shimanskiy, 1951
    - Order Bactritida Shimanskiy, 1951
  - Subclass Ammonoidea Zittel, 1884
    - Order Anarcestida Miller & Furnish, 1954
    - Order Clymeniida Hyatt, 1884
    - Order Goniatitida Hyatt, 1884
    - Order Prolecanitida Miller & Furnish, 1954
    - Order Cerititida Hyatt, 1884
    - Order Phylloceratida Arkell, 1950
    - Order Lytoceratida Hyatt, 1889
    - Order Ammonitida Zittel, 1884 [*non* Hyatt, 1889]
  - Subclass Coleoidea Bather, 1888 [includes Decapoda Leach, 1818 (*non* Latreille, 1802, Crustacea)]
    - Order Belemnitida Naef, 1912
    - Order Phragmoteuthidida Jeletzky, new
    - Order Teuthidida Naef, 1916
    - Order Sepiida Naef, 1916
    - Order Octopodida Leach, 1818

### REFERENCES

Accounts of the anatomy and biology of cephalopods are to be found in nearly every good text on invertebrate zoology. No list of these is attempted here. The following contain supplementary information especially pertinent to matters discussed in this chapter.

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part of v. 1 (p. 1-148, pl. 1-19) appeared in 1921 and the second part (p. 149-863) in 1923; v. 2 (364 p., 37 pl.), dealing with embryology, was published in 1928.]

- (3) 1922, *Die fossilen Tintenfische*: p. 1-322, text-figs. 1-101, Gustav Fischer (Jena).

#### Owen, Richard

- (4) 1832, *Memoir on the pearly Nautilus* (*Nautilus pompilius*, Linn.) with illustrations of its external form and internal structure: p.

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#### Yonge, C. M.

- (5) 1947, *The pallial organs in the aspidobranch Gastropoda and their evolution throughout the Mollusca*: Phil. Trans. Roy. Soc. London, ser. B, v. 232, p. 443-518, pl. 18.  
(6) 1960, *General characters of Mollusca*: in Mollusca 1, Treatise on Invertebrate Paleontology, MOORE, R. C., ed., Pt. I, p. 3-36.

## ENDOCERATOIDEA—ACTINOCERATOIDEA— NAUTILOIDEA

By CURT TEICHERT AND OTHERS

### MORPHOLOGY OF HARD PARTS

By CURT TEICHERT

[United States Geological Survey]

In this chapter only those morphological features will be discussed that are common to two or more orders of the subclasses Nautiloidea<sup>1</sup>, Endoceratoidea<sup>1</sup>, Actinoceratoidea<sup>1</sup>, and Bactritoidea. These cephalopod groups are highly diversified in regard to external shape and internal structure, and discussion of specialized structures within particular orders, and their terminology, is relegated to the introductory chapters under the orders concerned.

#### GENERAL FEATURES

All hard parts secreted by the animal, with exception of the jaws (*see* Rhyncholites), constitute the **conch** or shell, also (more rarely) called **conothea** (Fig. 1). The conch consists of a posterior part, customarily called the **phragmocone** (although only partly homologous to the phragmocone of the Belemnoida), which is divided into **chambers** (or **camerae**) by **septa**, and of an anterior, undivided and open part, the **body chamber**, which contains most of the soft tissues of the live animal. The septa are perforated by **septal foramina** through which passes the siphuncular cord, a fleshy extension from the body of the animal, called the **sipho**. The siphuncular cord is enclosed by **septal necks**, which are backward inflections of the septa extending from

the periphery of the septal foramina, and by a series of distinct walls or sheaths, extending between successive septal necks, called **connecting rings**. Septal necks and connecting rings are jointly known as **ectosiphuncle**; the ectosiphuncle and the siphuncular cord compose the **siphuncle**.

#### CONCH

The conch can be visualized as a primarily conical wall of conchiolin and calcium carbonate (probably aragonite commonly), in the apical part of which septa are inserted with their concave faces directed toward the broad end of the cone. The outer wall of the conch is known as the **shell wall** or **wall of the conch**, sometimes erroneously referred to as the **test**. Little is known about the structure of the shell wall in fossil nautiloids.

The two principal layers that give rigidity to the shell of modern *Nautilus* and that are supposedly preserved in fossils are the porcelainous ostracum and the inner, nacreous layer (*see* chapter on "Living *Nautilus*"). The ostracum consists of microscopic aragonite grains cemented by conchiolin, the nacreous layer of interlayered very thin lamellae of aragonite and conchiolin (Fig. 2,6). Shell walls of *Cimomia* and *Aturia* and of *Eutrephoceras* have been shown to consist wholly or in part of aragonite and thus may be supposed to have

<sup>1</sup> Referred to in this chapter, prepared before final classification was adopted, as "nautiloids" or "nautiloid orders."

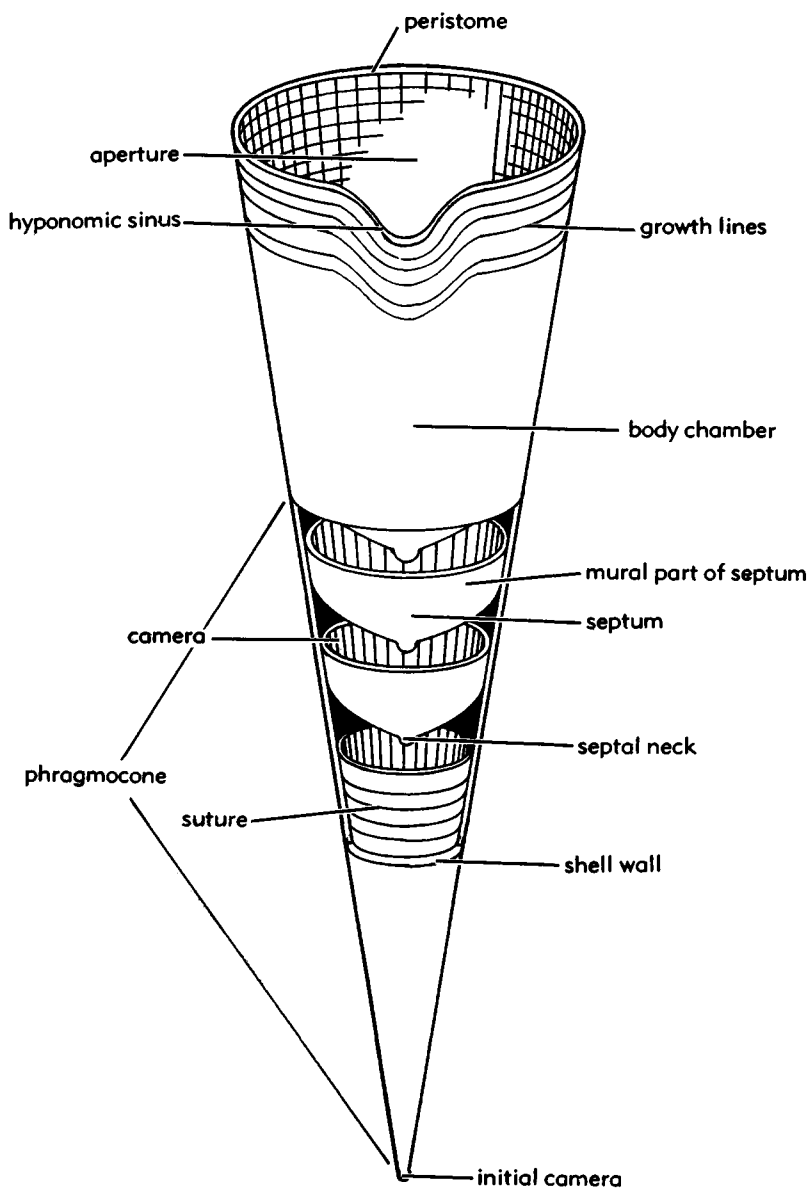


FIG. 1. Diagrammatic sketch of orthoconic conch. In the anterior part of the phragmocone septa are shown widely spaced to demonstrate their true shape (Teichert, n).

had a structure similar to that of *Nautilus* (3,36a). In Paleozoic *Dawsonoceras*, *Discoceras*, and ?*Ptenoceras*, however, BøGCILD found an outer layer of regularly prismatic calcite and an inner layer of irregularly granular calcite. The outer layer is probably primary calcite while the inner layer is recrystallized, possibly from a primary aragonitic nacreous layer. An outer

calcite and an inner aragonite layer is also present in many living bivalves and gastropods.

Excellent preserved shells of Pennsylvanian *Pseudorthoceras*, embedded in asphaltic substance, consist of aragonite (31).

In shells of Cretaceous nautilids, chiefly *Eutrephoceras*, TUREKIAN & ARMSTRONG (36a) found a relatively high concentration



of some trace elements: Mg 375-1,615 ppm, Sr 1,650-10,000 ppm, Ba 95-1,000 ppm. These amounts are much higher than those in the shell of Recent *Nautilus* and are probably due to secondary enrichment during diagenesis.

When studied with the electron microscope, the conchiolin of the nacreous layer of fossil nautiloids (e.g., *Dolorthoceras*, *Pseudorthoceras*, *Eutrophoceras*, *Aturia*) exhibits the same characteristic reticulate texture as that of modern *Nautilus* (13, 14) (compare Fig. 2,1-4 and Fig. 61).

Artificially or naturally etched surfaces of the nacreous layer, possibly also those of individual laminae within this layer, are characteristically sculptured by very fine, winding and contorted, or more rarely straight, raised lines. These are the "wrinkled layers," well seen on internal molds or where shell layers are exfoliated (=épidermides of BARRANDE, *Runzelschicht* of German authors) (Fig. 3).

In most fossil nautiloids the original material of the shell wall has been converted to granular calcite, as demonstrated by BØGGILD (3) and by REYMENT & EKSTRAND (23).

Diagenetic recrystallization of shell layers of the type that results in formation of minute calcite pyramids, called *conellae*, well known from Mesozoic ammonoids (*Treatise*, p. L83) appears to occur extremely rarely in nautiloid shells. The only record of *conellae* in nautiloids is in a specimen of *Permonautilus* from the Permian of Kazan (USSR) (14a).

Formation of pearls in or upon the nacreous layer is rare in living *Nautilus*. One case of fossil-pearl formation has been reported in Triassic *Pleuromutilus* (18).

### ORIENTATION OF CONCHS

As long as chambered cephalopods have been studied, at least since the early 19th century, orientation of the conch has been expressed in the following terms (Fig. 4): **anterior**, area of the aperture; **posterior**, apex of conch; **ventral**, side on which the hyponome and hyponomic sinus are situated; **dorsal**, side opposite the ventral side as defined above; **lateral**, areas between ventral and dorsal sides.

This terminology is based on comparison

with the living *Nautilus*, in which the head-foot is anterior and the hyponome is the ventral part of the head-foot (compare chapter on "Living *Nautilus*").

As pointed out by FLOWER (8) and others, this conventional orientation of cephalopod shells perhaps is not in harmony with the biologic orientation as referred to the so-called hypothetical "primitive cephalopod." If, as is assumed by some authors, the *Nautilus* hyponome is a modified molluscan foot, its position is ventral, not anteroventral as in the conventional orientation. The "hypothetical" and "conventional" orientations are compared in Figure 4.

In view of the fact that the conventional orientation of cephalopods has been employed for more than a century and a half, being used in thousands of papers, and has been applied to descriptions of tens of thousands of specimens belonging both to nautiloid and ammonoid orders, any attempt to replace the conventional terminology with one based on hypothetical considerations would result in much confusion and would render difficult the use of all previously published literature dealing with chambered cephalopods. In this volume, as in the ammonoid volume of the *Treatise*, the conventional orientation is accepted, therefore.

For purposes of illustration the generally adopted orientation of figures on a page differs from both the conventional and the hypothetical orientation. Customarily, illustrations of orthoconic and cyrtconic conchs are arranged with the apical end pointing to the lower edge of the page. Gyroconic and more tightly coiled conchs are shown with the aperture or, in case of fragmentary preservation, with the open end of the last preserved whorl pointing either to the upper left or to the upper right. This orientation of illustrations can be traced back to early monographs by SANDBERGER, QUENSTEDT, EICHWALD and others, and was more firmly established through publication by BARRANDE of the many volumes of plates illustrating Bohemian Paleozoic cephalopods. Over the years there have been comparatively few deviations from this pattern.

The following features of shell morphology may be used as evidence for the (conventional) orientation of fossil conchs.

## Criteria Used for Orientation of Cephalopod Conchs

Morphological Feature	Special Characteristics	Position
Hyponomic sinus	Position ascertained from growth lines if aperture not preserved	Ventral
Conchal furrow	Continuous along inside of test (ridge on steinkern)	Ventral
Dorsal furrow	Discontinuous along mural part of septa (discontinuous ridges on steinkern)	Dorsal
Color markings	Rare and not unfailing	Dorsal and lateral
Marginal siphuncle position	Valid for euryisiphonate forms only	Ventral
Endosiphuncular canal closer to one side of siphuncle than to other	Valid for endocerids, actinocerids, some discosorids	Dorsal
Cameral deposits more strongly developed in one half of camerae than in other		Ventral

## CONCH SHAPE

The shape of conchs of fossil nautiloid cephalopods ranges from conical, with straight central axis, through all degrees of curvature and coiling to tightly involute forms such as modern *Nautilus* (Fig. 5). Straight conchs are called **orthocones**;

conchs curved in varying degrees, though completing less than one full circle, are called **cyrtoco**nes. Both may be either **longi**-conic (long, slender, tapering gradually), or **brevi**conic (short, stout, tapering rapidly). Conchs curved through 360 degrees have completed one **whorl** or **volution**. Each ad-

## EXPLANATION OF FIGURE 2, 1-4

The micrographs show lacelike reticulated sheets of conchiolin from nacreous fragments of shell walls or of septa of various fossil nautiloids. The organic remnants, obtained by decalcification, were thinned by shaking or ultrasonic treatment into sheets permeable to electrons. Drops of aqueous suspensions of this material were deposited on screens previously coated with support films of formvar or carbon. Figures 1-4 illustrate exceptionally well-preserved organic residues from Pennsylvanian nautiloids collected in the Buckhorn asphaltic formations at Sulphur, Oklahoma. The chief features of the nautiloid "pattern"—sturdy trabeculae, sprinkled with hemispheric tuberosities, elongated or rounded openings (see chapter on "Modern *Nautilus*")—are recognizable. (Grégoire, 1958, Arch. internat. Physiol. Biochem., v. 66, p. 674; 1959, Bull. Inst. royal Science Nat. Belg., v. 35, p. 1; 1959, Nature, v. 184, p. 1157; and 1962, Bull. Inst. royal Sci. Nat., Belgique, v. 38, no. 49.)

1.—Unidentified orthoconic nautiloid, supplied by C. C. BRANSON. Iridescent blue-violet loose flakes of the shell wall. Decalcification left substantial, biuret-positive, brown organic particles.

In this fragment of sheet, preserved small tuberosities scattered on the trabeculae, are still visible ( $\times 42,000$ ).

- 2.—*Pseudorthoceras knoxense* MCCHESENEY, supplied by G. A. COOPER and U.S. National Museum. Biuret-positive residues. Flattening of trabeculae and disappearance of tuberosities are shown ( $\times 42,000$ ).
- 3.—Splinter of fracture of curved, dark brown, iridescent flake from shell wall of an unidentified specimen, supplied by W. M. FURNISH. This splinter was part of a fragment of a coiled shell, either an unidentified nautiloid, or possibly an ammonoid, identified by FURNISH as *Eoasianites?* sp. The brown organic residues of the splinter were biuret-positive. The edges of three crystals belonging to the lamella, originally resting on this reticulated sheet and dissolved by the decalcifier, appear as white ridges rising slightly above the sheet ( $\times 42,000$ ).
- 4.—Dark brown, curved, loose flake from an unidentified specimen supplied by N. D. NEWELL. Substantial biuret-positive organic residues. In other fragments of this sample, reticulated sheets closely resembled those represented in Fig. 1-3 ( $\times 42,000$ ).

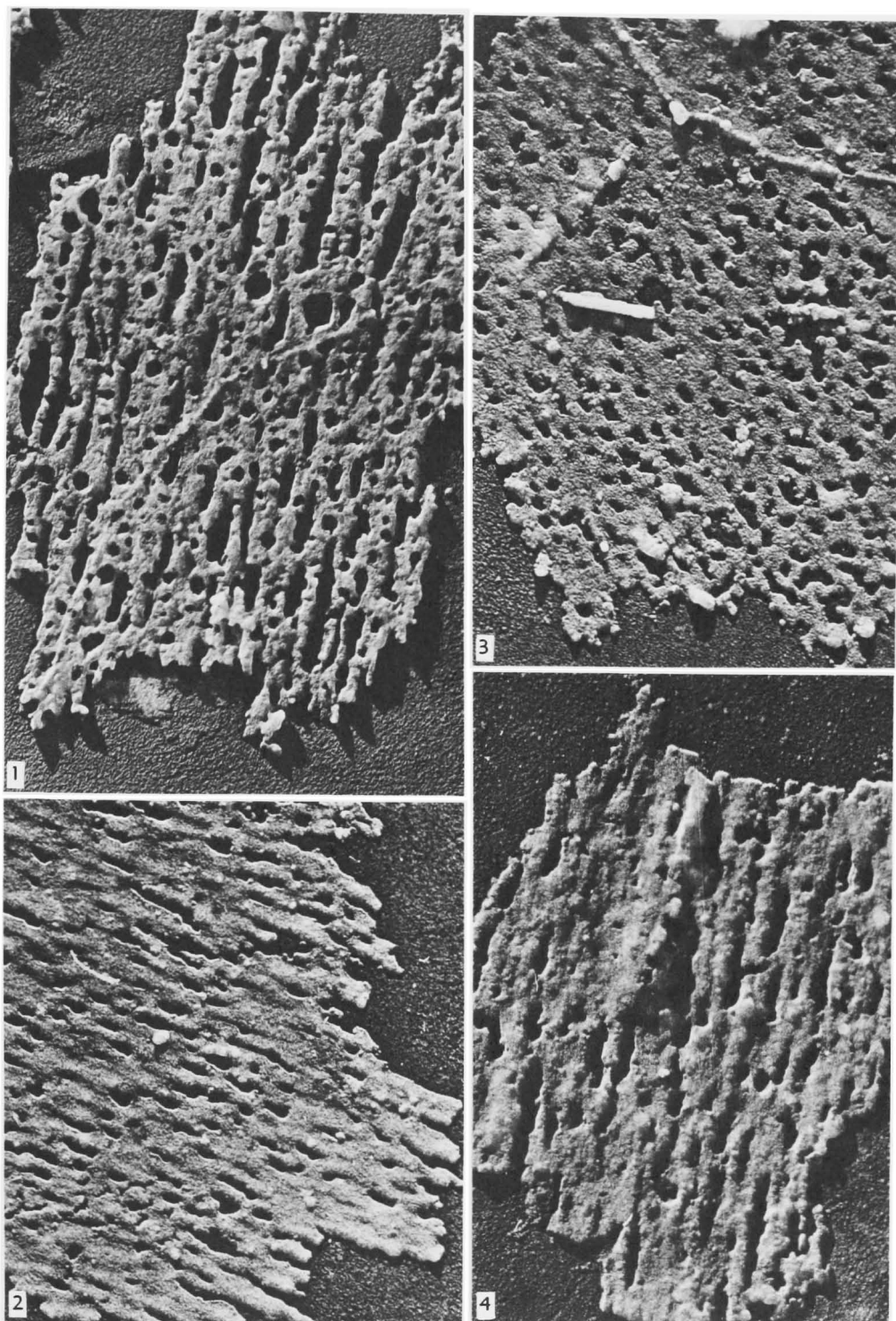


FIG. 2,1-4. Electron micrographs of mother-of-pearl from fossil nautiloids (explanation on facing page) (compare Fig. 61, 62) (courtesy of Charles Grégoire).

ditional coiling through 360 degrees constitutes another whorl. Openly coiled conchs in which successive whorls are not in contact with each other are called **gyrocones**. In closely coiled conchs, successive whorls are in contact with each other, and a number of terms are commonly applied to them to express degree of coiling and general shape: **serpenticone**, **tarphycone**, **ellipticone**, **sphaerocone**, **nautilicone**, **oxycone**, **platycone** (see glossary). Conchs that are closely coiled in early ontogeny but straight at maturity are known as **lituicones**. Conchs that are not coiled in a plane spiral, but in a three-dimensional spiral, like most gastropods, are **torticones** (often called **trocho- ceroid**, especially in older literature).

Coiled and curved conchs that have the venter on the outer, or convex, side are called **exogastric**; those that have it on the inner, or concave, side are **endogastric** (Fig. 6). In many forms in which the ventral side cannot be determined through observation of the hyponomic sinus, the position of the siphuncle is conventionally taken to be near the ventral side and endogastric or exogastric nature of the curvature is determined by siphuncle position.

Cross sections of orthocones or cyrtocones are generally circular, elliptical, or ovoid in shape. If the dorsoventral diameter

exceeds the lateral one, the cross section is called **compressed**; if the lateral diameter is greater, the cross section is said to be **depressed** (Fig. 7). In coiled conchs, **whorl sections** may be modified in many ways.

A coiled conch in which all successive whorls are exposed in lateral view is called **evolute**; when successive whorls partly overlap and envelop preceding ones the conch is **convolute**; and if the last whorl envelops and covers all preceding ones the conch is **involute**, as in *Nautilus pompilius*.

In convolute and involute conchs, the concave, dorsal part of a whorl in contact with the convex, ventral part of the preceding whorl is called the **impressed zone** or **impressed area** (Fig. 8). The sides of the whorls are generally called **flanks** but are also known as **whorl sides** or **lateral areas**. As in straight or cyrtoconic forms, the cross section, or whorl section, of coiled conchs may be compressed or depressed, or more rarely, circular, or its shape may be modified in various ways, being subquadratic (with angular shoulders), **oxyconic** (with sharp external keel), or having other shapes.

The center of a coiled shell is the **umbilicus**, which may be **closed**, or **open** (**perforated**), according to whether the first whorl is tightly coiled around itself or not. The line of contact between the flanks of

#### EXPLANATION OF FIGURE 2,5-8

The preparation of specimens is the same as stated for Figures 1-4. The nacreous patterns of conchiolin are less well preserved in Figures 5, 7, and 8.

- 5.—Debris of a reticulated sheet from "*Nautilus*" sp., Eocene (Bartonian, Sables de Wemmél) from Brabant, Belgium, supplied by M. GLIBERT and Institut Royal des Sciences Naturelles de Belgique. The nautiloid pattern is still recognizable ( $\times 36,000$ ). (Grégoire, 1959, Bull. Inst. royal Science Nat. Belg., v. 35, fig. 13, with permission of the Editor.)
- 6.—Positive carbon replica, shadow-cast with palladium, of a polished and heavily etched shell wall of *Nautilus* sp., Eocene (Bartonian), from the Wemmél, Brabant, Belgium. Plane of polishing transverse to the surface of mother-of-pearl and sectioning about 14 consecutive nacreous lamellae. A substantial system of interlamellar and intercrystalline organic reticulated sheets was freed by the decalcification process ( $\times 23,000$ ). (Grégoire, 1959, Bull. Inst.

royal Science Nat. Belg., v. 35, fig. 12, with permission of the Editor.)

- 7.—Iridescent silvery material from nacreous layers of shell wall or septum of *Aturia* sp., Oligocene (U. Rupellian), from Boom, Belgium, supplied by M. GLIBERT and Institut Royal des Sciences Naturelles de Belgique. Pebble-like alterations of the trabeculae are shown. All transition stages were found between a relatively well-preserved nautiloid pattern (see Grégoire, 1959, Bull. Inst. royal Science Nat. Belg., v. 35, fig. 14) and this structure ( $\times 42,000$ ) (Grégoire, n).
- 8.—Remnants of brownish-gray fragments of shell wall of *Domatoceras* or *Stenoceras*, from Permian (San Andres Ls.), New Mexico, supplied by R. H. FLOWER. Pebble-like alteration and shrinkage in decalcified, organic, slightly biuret-positive material ( $\times 42,000$ ) (Grégoire, n). [Some inorganic salts resistant to decalcifiers may assume, when agglutinated, shapes resembling those here shown. It is then necessary to use special procedures allowing these salts to dissolve while the organic matter remains unaffected.]

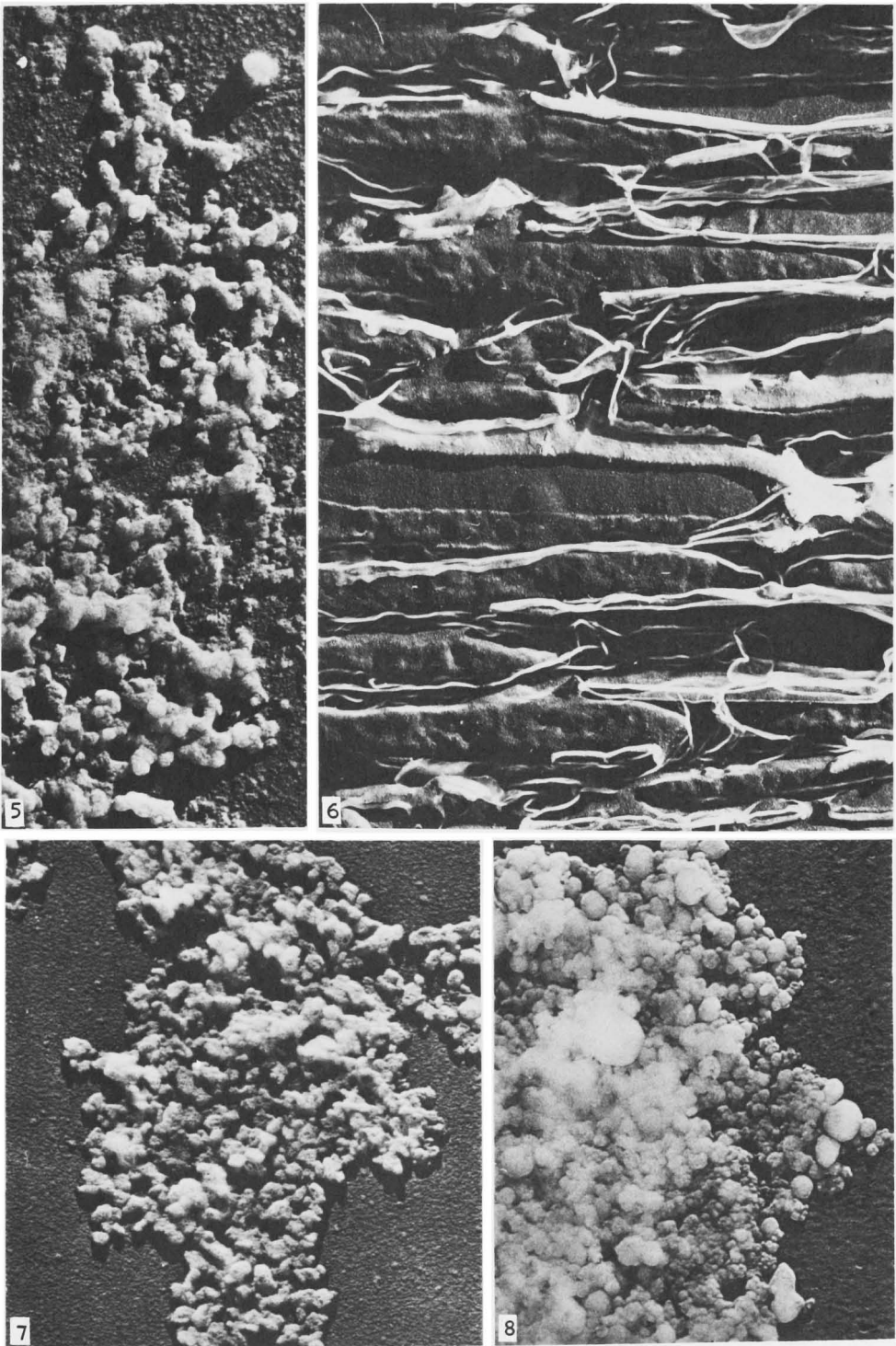


FIG. 2,5-8. Electron micrographs of conchiolin and mother-of-pearl from fossil nautiloids (explanation on facing page) (compare Fig. 61, 62) (courtesy of Charles Grégoire).

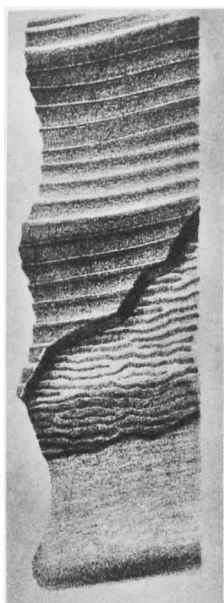


FIG. 3. Wrinkled layer in *Leurocyloceras subannulare* (MÜNSTER), Sil., Czech.,  $\times 8$  (2).

successive whorls is called the **umbilical seam** (or **suture**). The flanks may at some point be bent strongly toward the umbilical seam and this portion is called the **umbilical angle** (or **umbilical shoulder**). The inner area of the whorl side tilted toward the umbilicus is called **umbilical slope**, or if sloping very steeply, **umbilical wall**.

### SURFACE OF CONCH

The most delicate type of external ornamentation is represented by **growth lines**, which are lines on the surface of the conch marking its gradual increase in size. Their course is roughly transverse to the longitudinal axis of the conch, but generally they are sinuous. Most marked is the **ventral sinus**, a backward-bent indentation of the growth lines. Since every growth line marks a former aperture, the position of the ventral sinus indicates position of the hypnomic sinus of the body chamber and thus serves to orient conch fragments with imperfectly preserved or missing body chambers. Conchs in which growth lines form the only kind of external sculpturing present are generally called smooth.

The conch wall of many nautiloids is more or less elaborately sculptured. Simple parallel, small to minute grooves are called **striae**, and corresponding small ridges or raised lines, **lirae**. Both striae and lirae may run parallel or transverse to the longitudinal axis of the conch. **Costae** or ridges are larger elevations that in straight or cyrtconic nautiloids generally run subparallel (longitudinally) to the long axis of the conch. In coiled conchs costae may be arranged parallel to the umbilical seam (revolving costae, striae, lirae) or they may be a feature of the flanks, arranged more or less radially with respect to the umbilicus.

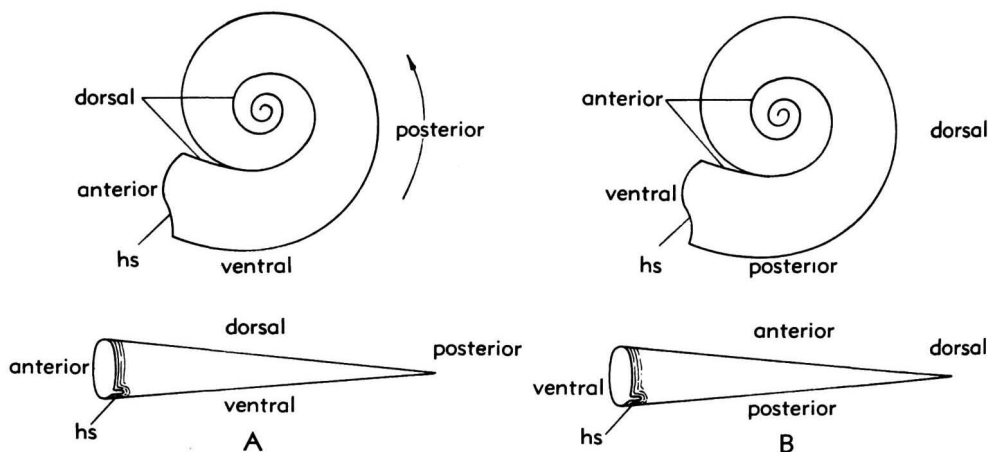


FIG. 4. Comparison of (A) "conventional" and (B) "hypothetical" orientation of coiled and straight cephalopod shells (*hs*, hypnomic sinus) (Teichert, n).

Transverse elevations that surround the entire conch in orthocones and cyrtocones are called **annulations**; shells with annulations are **annulate (annulated)**. Annulations may be thickenings of the walls of the

conch, in which case the internal mold of the conch is smooth. More commonly annulations are due to undulations of the conch wall and then the internal mold is annulate as well.

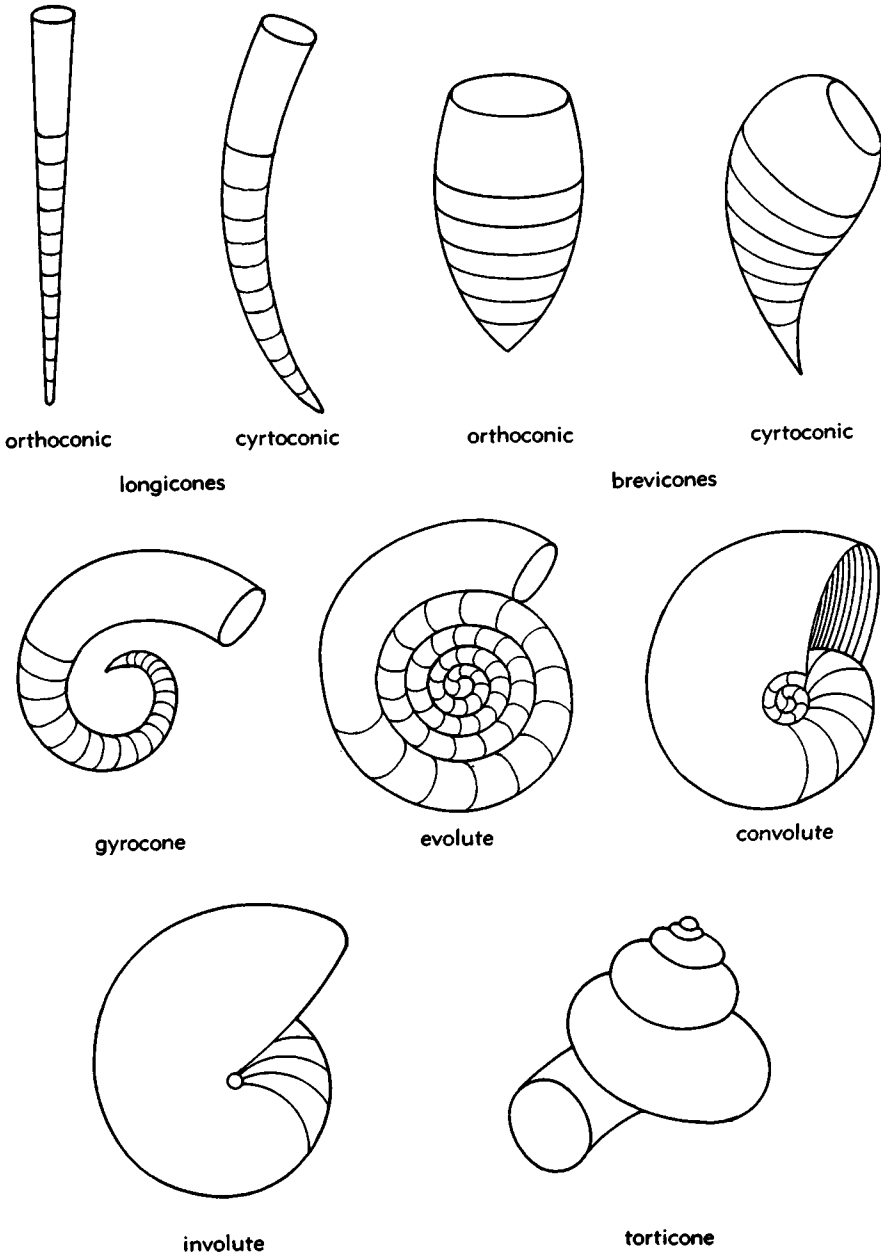


FIG. 5. Some common types of nautiloid conchs (Teichert, n).

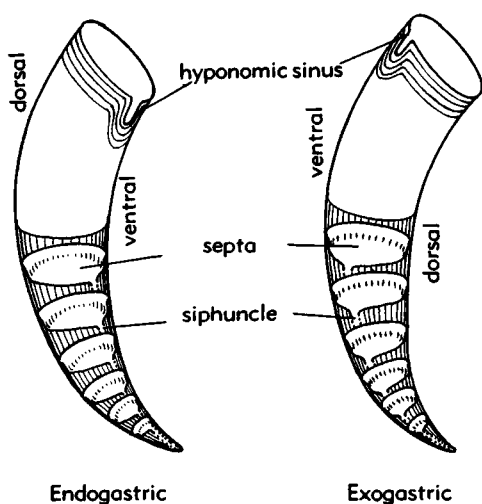


FIG. 6. Diagram explaining difference between endogastric and exogastric conchs. Body chamber shown in external view, phragmocone cut in half (Teichert, n).

In different genera many combinations of transverse and longitudinal striae, lirae, and costae occur, with or without presence of annulations, especially among the Orthocerida.

The surface of many nautiloids, especially curved and coiled ones, is ornamented with nodes, more rarely with spines or ribs. A special type of ornamentation consists of **apertural flanges**, more or less regularly

spaced, giving some shells a frilled exterior (*Zittelloceras*, some *Rutoceratidae*). Apertural flanges are known in nautiloids of all ages excepting the Cenozoic ones, beginning in those of the Lower Ordovician (*Diastoloceras*, *Aethoceras*).

To describe the ornamental features of coiled conchs, essentially the same terminology applies as that used for ammonoids, although in a somewhat simplified form, because nautiloid conchs, in general, never attain the elaborate surface sculpturing that is characteristic of many ammonoids, es-

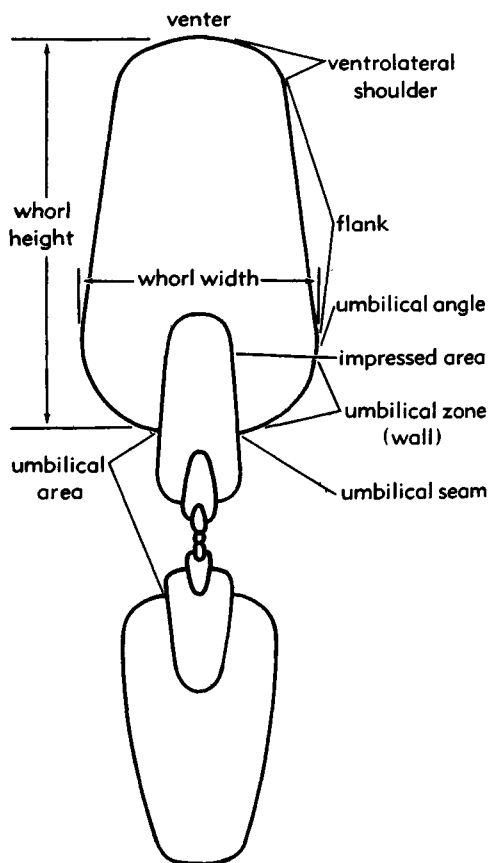


FIG. 8. Diagrammatic cross section of coiled conch (Teichert, n).

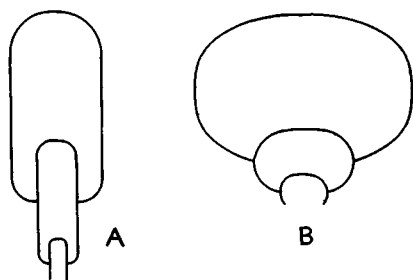
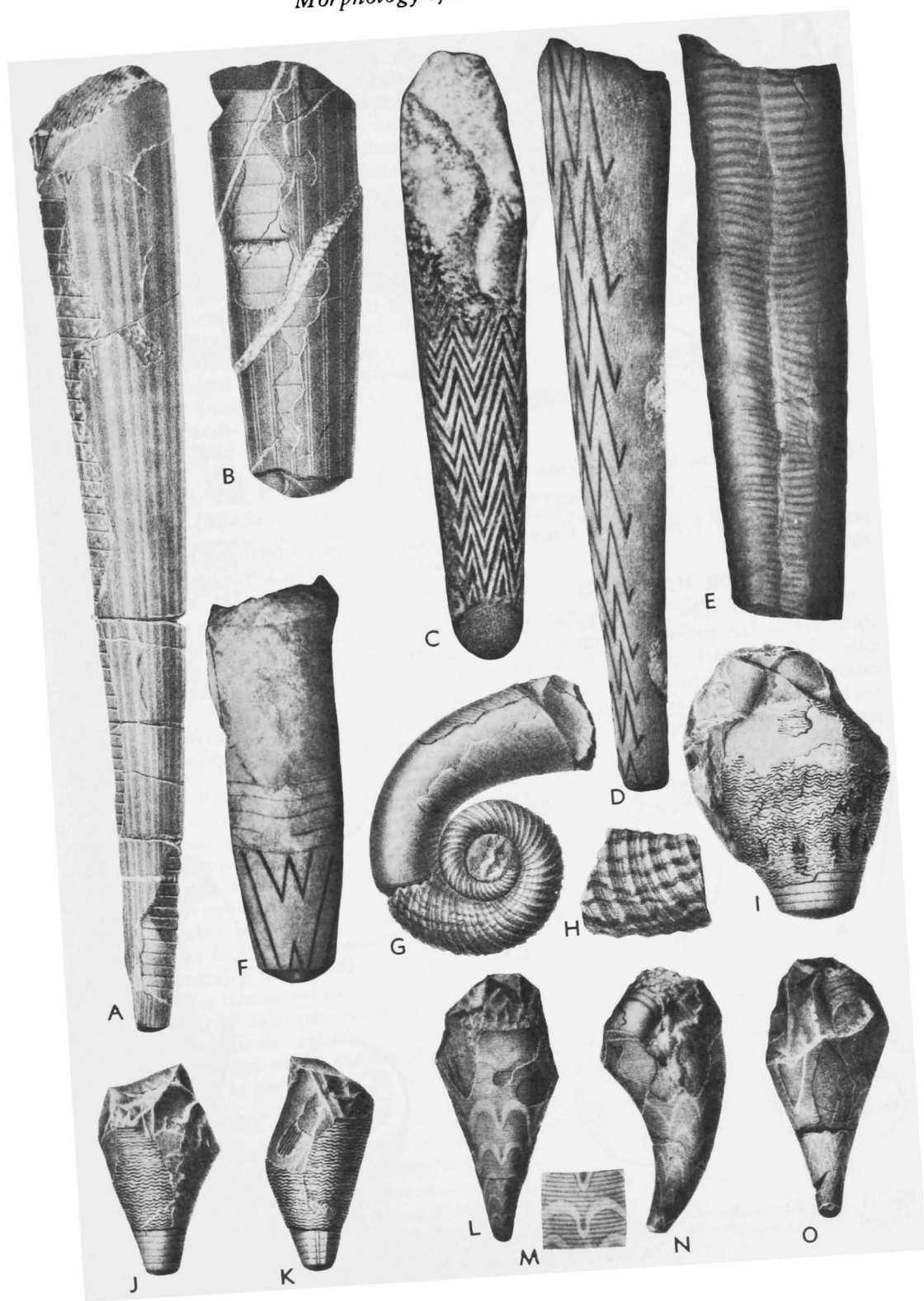


FIG. 7. Compressed (A) and depressed (B) whorl section in coiled conchs (Teichert, n).

FIG. 9. (Facing page.) Principal pigmentation patterns of nautiloid conchs.—A.B. *Ormoceras? pellucidum* (BARRANDE), Sil., Czech.,  $\times 0.7$ .—C. *Michelinoceras? anguliferum alpenense* FOERSTE, Dev., USA (Mich.),  $\times 1.1$ .—D. *M.? anguliferum* (D'ARCHAIC & DE VERNEUIL), Dev., Ger.,  $\times 1.3$ .—E. *M.? dunbari* FOERSTE, Penn., USA (Okla.),  $\times 1$ .—F. *Hedstroemoceras haelluddenense* FOERSTE, Ord., Sweden,  $\times 1$ .—G. *H. Trochoceras pulchrum* BARRANDE, Sil., Czech.,  $\times 0.7$ ,  $\times 1$ .—I. *Rizosceras? zebra* (BARRANDE), Sil., Czech.,  $\times 0.7$ .—J.K. *R.? cyathus* (BARRANDE), Sil., Czech.,  $\times 0.7$ .—L.O. *R.? parvulum* (BARRANDE), Sil., Czech.,  $\times 0.7$  (2; 12).





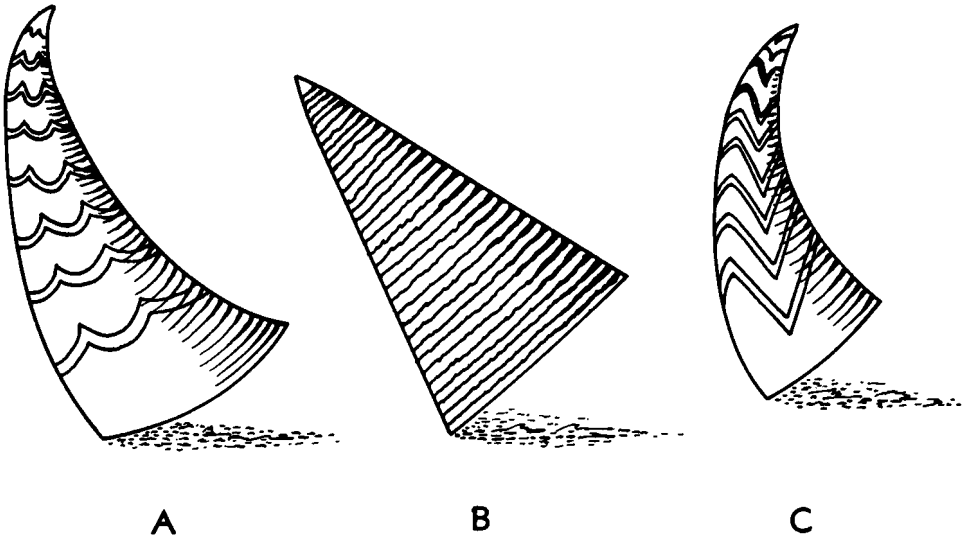


FIG. 10. Color patterns in some cyrtconic brevicones, shown in shell position which probably occurred during life (25).

pecially those of Jurassic and Cretaceous age.

#### COLOR MARKINGS

The so-called color markings of fossil shells are in fact patterns of pigmentation, either light or dark gray, or black, indicating presence of former color patterns. No unchanged, original colors are ever preserved in fossil cephalopods.

Some 40 species retaining color markings have been described, ranging from Ordovician to Tertiary in age and including representatives of the Orthocerida, Actinocerida, Discosorida, Barrandeocerida, Oncocerida, and Nautilida. Most of the relevant observations have been collected and summarized by FOERSTE (12).

In straight and weakly curved longicones and brevicones a considerable variety of

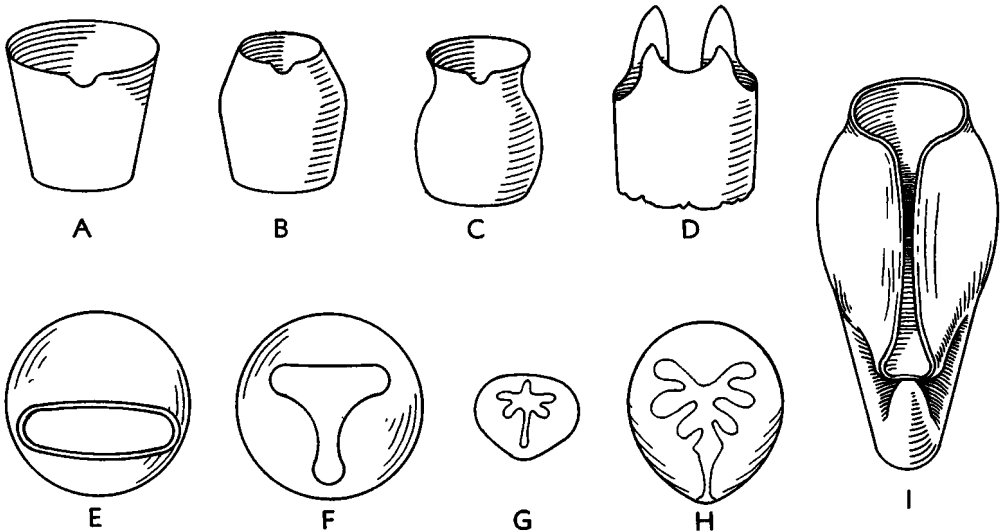


FIG. 11. Different shapes of body chambers in nautiloids: A, open; B, contracted; C, constricted; D, pronged; E-H, various types of contracted apertures (*Mesoceras*, *Mandaloceras*, *Pentameroceras*, *Octamerella*); I, visored (*Phragmoceras*) (Teichert, n).

patterns of color banding has been observed: (1) transverse, wavy, narrow bands (Silurian *Rizosceras?* from Bohemia) (Figs. 9,J,K; 10,B); (2) transverse, broad bands (Silurian *Rizosceras?* from Bohemia, Carboniferous orthocerids from Oklahoma and Belgium) (Fig. 9,E); (3) longitudinal bands and lines (orthocerids from Silurian of Bohemia, Ordovician and Silurian of North America) (Fig. 9,A,B); (4) combination of longitudinal and transverse lines (Silurian *Hexameroceras*); (5) longitudinal series of short transversely oriented lines (Silurian *Rizosceras?* from Bohemia); (6) irregularly arranged black blotches (Silurian *Rizosceras?* from Bohemia) (Fig. 9,I); (7) oblique bands with zigzag pattern across venter (Ordovician *Hedstroemoceras* from Sweden) (Fig. 9,F); (8) bands in chevron pattern with 6 to 8 chevrons per circumference (Silurian *Rizosceras?* from Bohemia, orthocerids from Devonian of Germany and Michigan, and Lower Carboniferous of Belgium) (Fig. 9,C,D, L-O; 10,A,C).

In coiled forms color markings have been described from Devonian *Trochoceras*, where they appear as longitudinal, revolving bands (Fig. 9,G,H). A *Vestinautilus* from the Carboniferous of Ireland is colored by irregular spots and bands. A *Stenopoceras* from the Permian of Texas has been described as having a colored growth-line pattern and a Tertiary *Aturia* was found to have semicircular, transverse zones or bands.

No fossil coiled conch has been found with a color pattern closely similar to that of modern *Nautilus*.

In a number of orthoconic forms, color markings are found on only one side of the conch. Generally, this is demonstrably the dorsal side, or is assumed to be so.

In general, the color patterns of the shells of fossil nautiloids exhibit considerable diversity and even within individual orders no uniformity in patterns can be discerned.

### BODY CHAMBER

In stenosphonate conchs, just as in living *Nautilus*, the body chamber contained the animal's entire visceral mass, but in eury-siphonate form, part of the visceral mass was probably lodged in the anterior division of the siphuncle.

The body chambers of some nautiloid

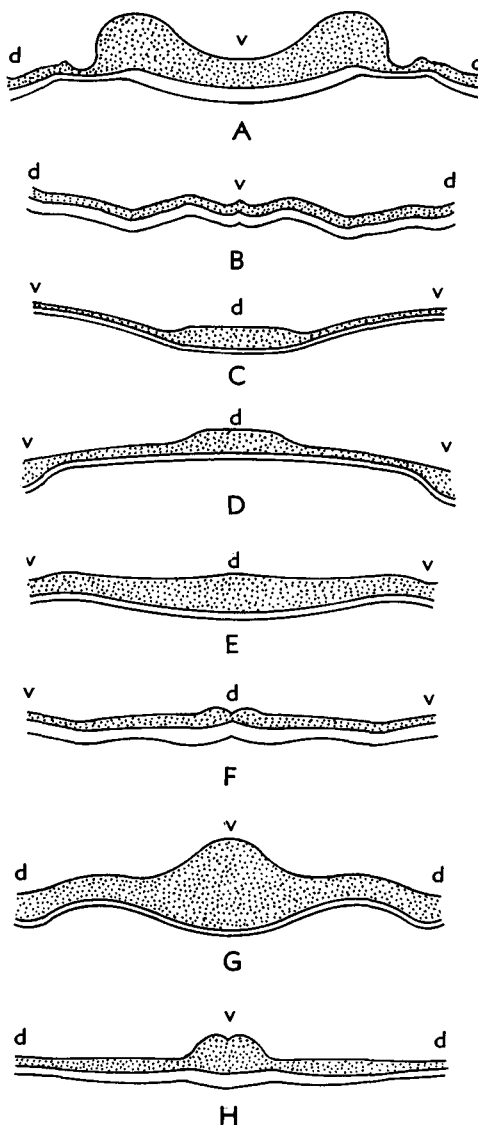


FIG. 12. The periphraet (stippled) in some nautiloid orders (v, ventral and d, dorsal side of body chamber).—A. Nautilida (*Eutrophoceras*) (21).—B. Orthocerida (*Clinoceras*) (Mascke, 1876).—C. Ellesmerocerida (*Cochlioceras*) (21).—D. Orthocerida (*Lycoceras*) (21).—E. Endocerida (*Cameroceras?*) (Schröder, 1882).—F. Tarphycerida (*Lituites*) (22).—G. Tarphycerida (*Estonioceras*) (21).—H. Barrandeocerida (*'Uranoceras?'*) (21).

orders exhibit an extraordinary variety of form (Fig. 11). The body chamber is open at the anterior end, where head and tentacles of the animal protrude. This is the **aperture**; the edge of the conch surround-

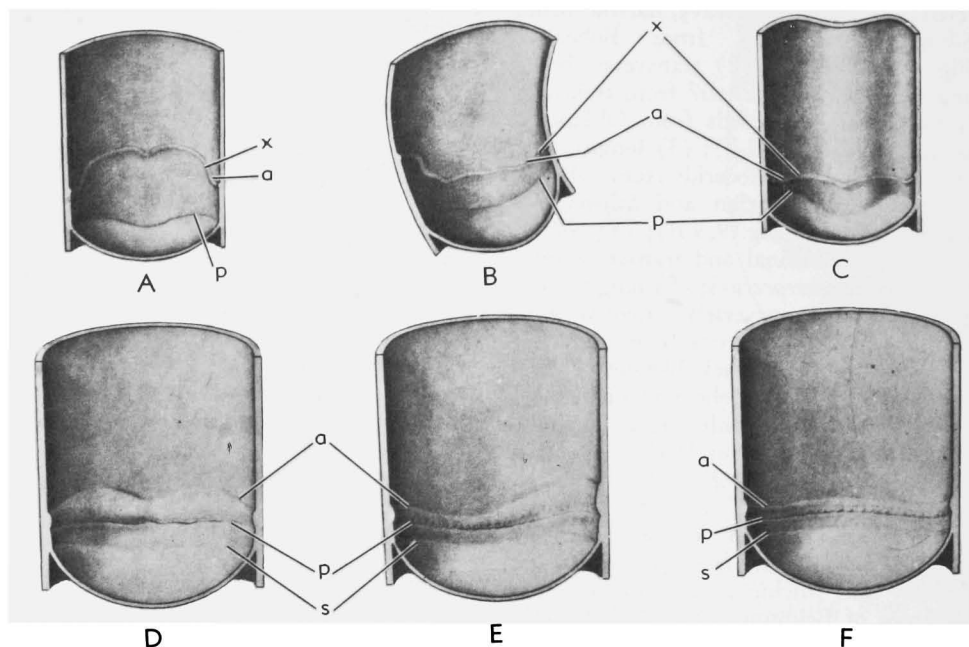


FIG. 13. Reconstructions of body chambers showing periphractions (*a*, anterior and *p*, posterior margins of annular elevation, *x*, anterior annular ridge; *s*, edge of free part of septum).—A-C. *Discoceras* sp., Ord., Est.; vent., lat., dors. interiors (ventromyarian),  $\times 1.25$  (21).—D-F. *Lycoceras?* sp., Sil., Swed.; dors., lat., vent. interiors (dorsomyarian),  $\times 2$  (21).

ing the aperture is called the **peristome**. The peristome has a ventral indentation, termed the **hyponomic sinus**. Apart from this, the peristome may be smooth, or it may have additional indentations. Rarely, the peristome may be produced into pointed salients and broadly rounded recesses, as in *Lituities*.

The simplest form of body chamber expands from the base to the aperture at the same rate as the anterior portion of the phragmocone and has an unmodified, **open** and **entire aperture** with outline larger than, but congruent to any chosen cross section of the conch. Such simple geometrical relationships are present in the Ellesmerocerida, Orthocerida, Endocerida, and in most coiled forms.

In the orders Ascocerida, Actinocerida, Discosorida, and Oncocerida, many modifications in the shape of the body chamber, and especially of its aperture, occur. A body chamber may first expand from its base, then gradually diminish toward the aperture. Such apertures are said to be **contracted**. Body chambers with their smallest

diameters a short distance behind the aperture are called **contracted**, and the constricted part is sometimes called the **neck**. In front of the neck, the body chamber of such forms expands into a **flared aperture**.

In some body chambers an internal thickening occurs behind the aperture. In such chambers only the interior (and the internal mold) may appear to be constricted.

Contracted apertures may be either simple and congruent to the general cross section of the conch, or they may be greatly modified by being compressed or incised in various manners (Fig. 11, E-H). The most elaborately shaped apertures are found among the Oncocerida.

In a few Orthocerida the body chamber has two or more external grooves or furrows (*Orthoceras*, *Bifoveoceras*, *Ctenoceras*).

A **conchal furrow** may also be present on the inside of the body chamber, though generally only along the posterior part of its ventral side (see under phragmocone).

The problem of attachment of the body to the body chamber is of a different magni-

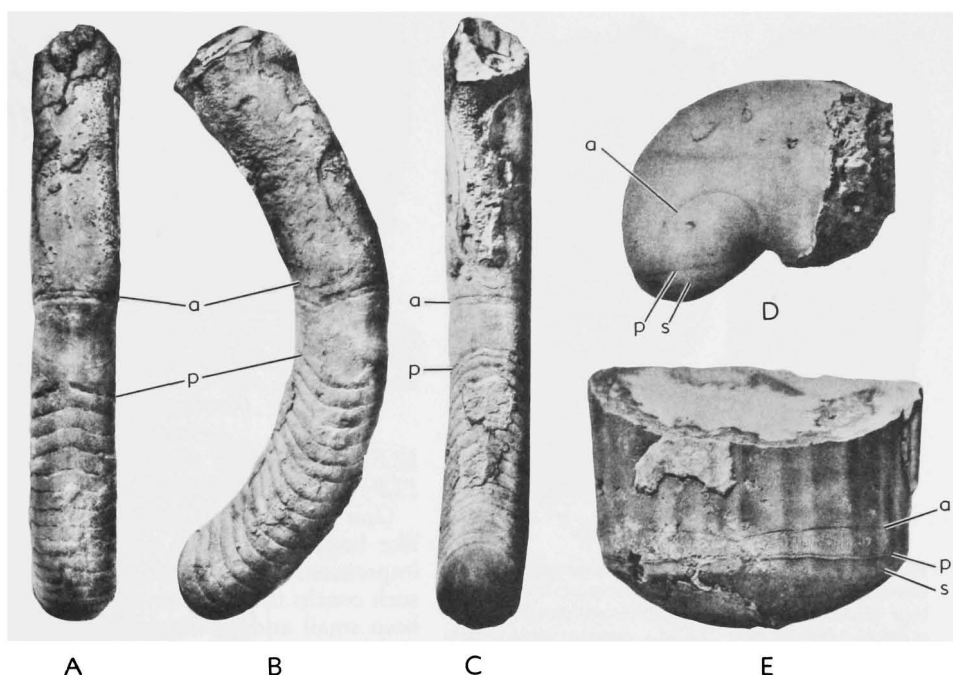


FIG. 14. Types of periphractions shown as impressions on internal molds (*a*, anterior and *p*, posterior edges of periphractions; *s*, edge of free part of septum).—*A-C*. *Tragoceras falcatum* (VON SCHLOTHEIM), Ord., Est.; vent., lat., dors. (ventromyarian),  $\times 0.7$ .—*D*. *Eutrophoceras bellerophon* (LUNDGREN), Swed.; lat. (pleuromyarian),  $\times 0.7$ .—*E*. *Kionoceras angulatum* (WAHLENBERG), Sil., Swed.; dors. (dorsomyarian),  $\times 0.7$  (21).

tude in conchs with contracted and with open apertures.

In body chambers with open apertures the body must be firmly anchored to the wall as in *Nautilus* (see below), where the attachment areas of the retractor muscles and sheetlike tendons (aponeuroses) form a continuous ring, the periphractic imprint. This condition is found in all groups that have body chambers with open apertures, but several modifications from the nautilid pattern are observed (Fig. 12). The anterior and posterior borders of the periphractions may be slightly raised and are then called the **anterior** and **posterior annular ridges** (Fig. 13, *D-F*).

In living *Nautilus* it is possible, within the ring of attachments, which are flush with the shell wall, to discern the attachment areas of various muscles and ligaments. In fossil nautiloids these areas cannot be discerned, but the place or places where the ring of attachments is wide indicates the area, or areas, of attachment of the powerful retractor muscles. In addition, the at-

tachment areas are often buttressed or elevated (annular elevation of MURVEI) in these fossils. In *Nautilus* (see chapter on "Living Nautilus") the retractor muscles are attached to the opposite flanks of the body chamber, a condition known as **pleuromyarian**. This disposition of the retractor muscles is typical, as far as is known, for all members of the order Nautilida (Figs. 12, *A*, 14, *D*), and has been traced back to Early Carboniferous forms.

Present investigations suggest that the pleuromyarian disposition of the retractor muscles is a comparatively late feature in evolution of the nautiloids and that the retractor muscles of earlier nautiloids were closely paired either on the ventral or dorsal side of the body chamber. The former condition is called **ventromyarian**, the latter **dorsomyarian**. In view of the extreme scantiness of information on the periphractions and its retractor muscle impressions in fossil nautiloids, it is difficult to give generally valid characterizations of the various orders in regard to these features, but some interesting facts have emerged.

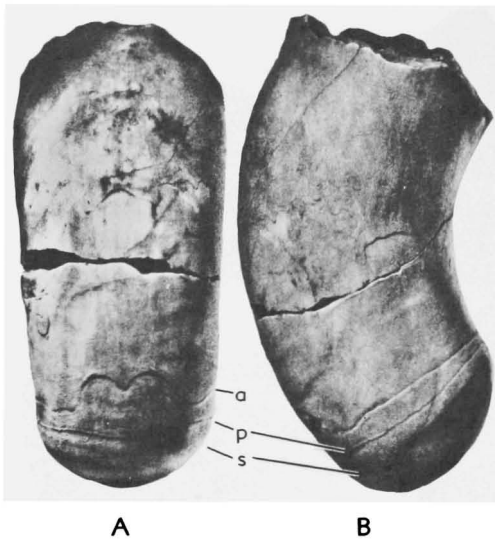


FIG. 15. Types of periphractions shown as impressions on internal molds (explanation of letter symbols as for Fig. 14).—A,B. *Uranoceras? longitudinale* (ANGELIN), U.Ord., Swed.; vent., lat. (ventromyarian),  $\times 0.5$  (21).

The dorsomyarian condition is possibly the most primitive one. It appears in *Cochlioceras* (Fig. 12,C), the only ellesmerocerid in which presence of this feature has as yet been demonstrated. It has been found in various orthocerids (*Orthoceras*, *Geisonoceras*, *Kionoceras*, *Lyecoceras*) (Figs. 12,D; 13,D-F, 14,E), in the Endocerida (Fig.

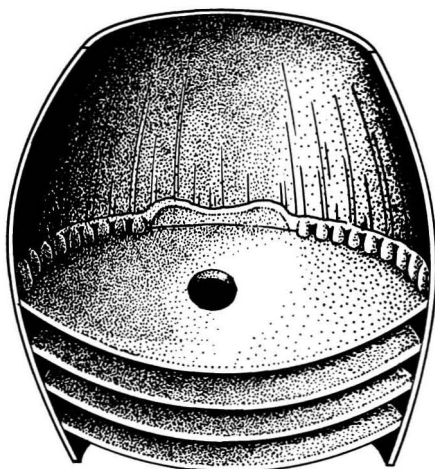


FIG. 16. Body chamber of typical oncocerid, showing periphractions with buttresses of the "basal zone" and ventromyarian muscle impressions (Teichert, n).

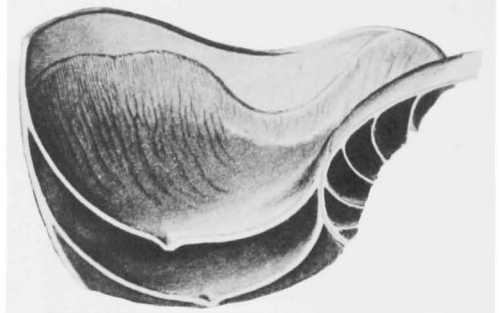


FIG. 16A. Sectioned specimen of *Nautilus pompilius* showing impressions of vascular system on adoral side of septum that adjoins body chamber,  $\times 1$  (Deecke, 1913).

12,E), and in the family Lituitidae (Fig. 12,F) of the Tarphycerida.

One orthocerid (*Clinoceras*) has a ring-like imprint in which no retractor muscle impressions are discernible (Fig. 12,B). In such conchs the retractor muscles must have been small and weak, perhaps indicating a sluggish, inactive mode of life of the animal concerned.

The ventromyarian condition is known to occur in openly or closely coiled Tarphycerida (Figs. 12,G; 13,A-C; 14,A-C) and in the Ascocerida and Barrandeocerida (Figs. 12,H; 15,A,B). It is illustrative of the unsatisfactory state of our knowledge that for the two last-mentioned orders only one specimen of Ascocerida and very few of the Barrandeocerida are known that show the imprints. In slender, open chambers, such as that of *Tragoceras* (Fig. 14,A-C), the annular elevation may be exceptionally wide, providing a greater muscle attachment area.

The Oncocerida and Discosorida are also ventromyarian, but the tendon and muscle imprints are modified by the appearance of short longitudinal ridges or buttresses (Fig. 16). This ridged area was formerly described as the "basal zone," a designation that is now obsolete. The purpose of the ridges is not immediately evident. They enlarge the surface of the muscle attachments, but most forms that have them also have contracted apertures and were, therefore, not in great need of an increased muscle-attachment area.

No actinocerid in which impressions of the muscles are preserved has as yet been described.

Very rarely, impressions of a vascular system have been observed on the concave side of the last septum in modern *Nautilus* (37; DEECKE, 1913, fig. 5). DEECKE observed its presence also in fossil conchs identified as *Eutrephoceras*. I have been able to confirm these observations by examination of DEECKE's specimens (Fig. 16A).

### PHRAGMOCONE

The phragmocone is the chambered part of the conch. It extends from the apex to the last septum which forms the base of

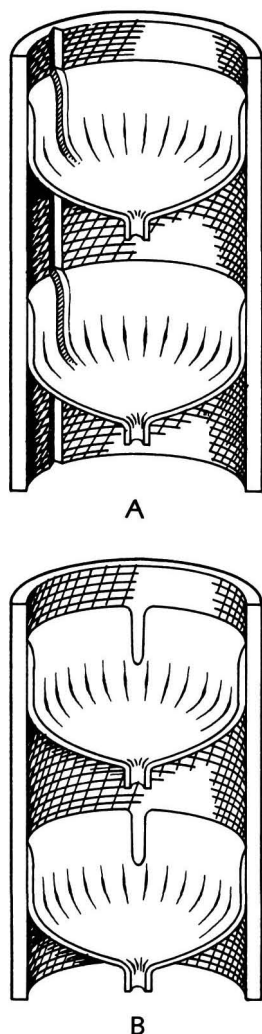


FIG. 17. Diagram to explain difference between conchal furrow (A) and dorsal furrow (B) (Teichert, n).

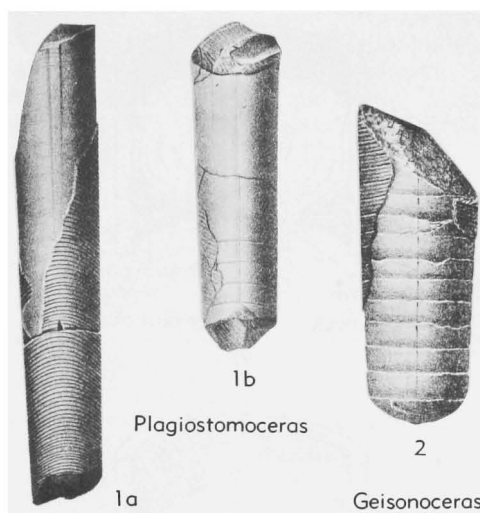


FIG. 18. Appearance of conchal and dorsal furrows on internal molds.—1a,b. Body chambers of *Plagiostomoceras* with double and single conchal furrows; Sil., Czech.,  $\times 0.7$  (Barrande, pl. 297, 1870).—2. Steinkern of phragmocone of *Geisonoceras bipellis* (BARRANDE), showing impression of dorsal furrow; Sil., Czech.,  $\times 0.7$  (Barrande, pl. 308, 1870).

the body chamber. The following description is concerned with features of the mature phragmocone. Special conditions in the extreme apical part will be described in the chapter on early ontogeny.

The inside of the wall of the phragmocone is generally smooth, except for a sharply incised mid-ventral furrow that is present in many nautiloids and which is called the **conchal furrow** (Fig. 17,18). On internal molds it appears as a fine mid-ventral line or ridge. It occurs frequently in the Orthocerida, the Nautilida, and also in the Bactritida. In some genera (e.g., *Plagiostomoceras*) there may be two parallel conchal furrows; in others (e.g., *Striacoceras*) the main conchal furrow is paralleled by weaker furrows, the **ventrolateral furrows**, one on each side.

The septa that subdivide the phragmocone into camerae are saucer- or cup-shaped partitions that fit tightly into the inside of the conch wall (Fig. 19). Degree of concavity of the septa and their spacing in relation to the conch diameter are important criteria for differentiation of species. Occasionally, odd septa may be found missing



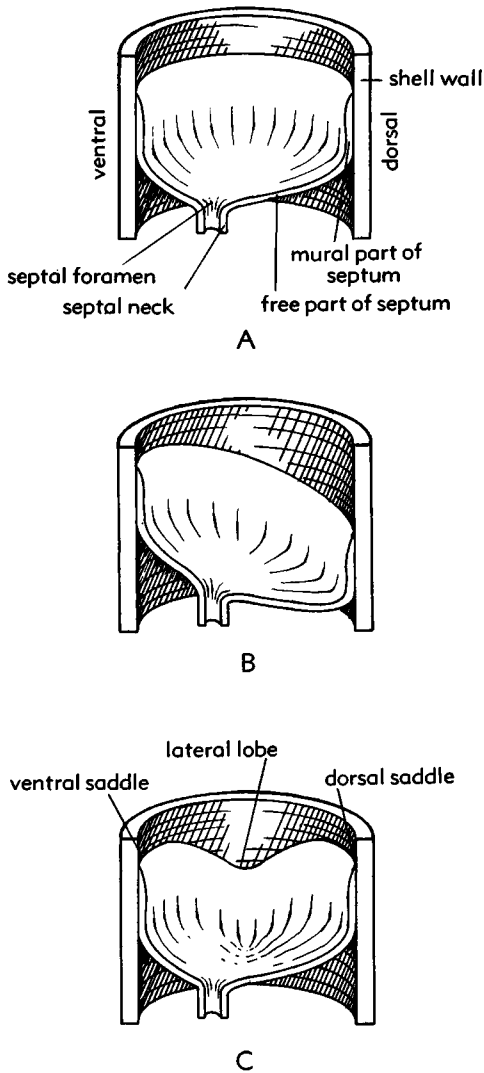


FIG. 19. Relationship of septum to shell: *A*, septum with straight, transverse suture; *B*, with straight, oblique suture; *C*, with suture having dorsal and ventral saddles and lateral lobes (Teichert, n).

or only incompletely developed, but such cases are rare (17) (Fig. 20).

Normally the septa are equidistantly spaced except for the last two or three septa which at maturity are more closely spaced than the others. Spacing of the septa just behind the body chamber is thus a diagnostic feature for separation of mature conchs from those that have not yet reached maturity.

Abnormal crowding of septa in other parts of the phragmocone indicates almost certainly a pathologic condition (Fig. 21).

Each septum consists of an anterior, cylindrical part firmly attached to the inside of the shell wall and called the **mural part** of the septum, and of an evenly concave part which crosses the conch transversely and is called the **free part** of the septum (Fig. 19). The free part is perforated by a circular to oval opening, the **septal foramen**, around which the septum extends backward to form the **septal neck** either resembling an open cylinder or various modifications of a cylindrical form. The septal necks are generally regarded as part of the siphuncular structure of the conch, and they will be discussed in more detail in the subsequent description of the siphuncle.

The length of the mural part of the septum differs greatly in different groups. In the Actinocerida it extends the full length of one camera—that is, the inside of the shell wall is entirely lined by the mural parts of all septa. In *Nautilus* the mural parts of the septa are very short. In other groups they are of intermediate length.

In many genera, erratically distributed in various orders (Orthocerida, Actinocerida, Nautilida), the mural parts of septa are not developed along a narrow mid-dorsal line. This is the **septal furrow**, also called **dorsal furrow**, because it is present only on the dorsal side of the conch (see Fig. 64). It is the "*ligne normale*" of BARRANDE, and the "*Normallinie*" of earlier German authors (DEWITZ, SCHRÖDER, and others). Where present, it is generally discontinuous, because in many nautiloids the mural part of the septum extends only part of the way between one septum and the next (Figs. 17, 18).

The free part of a septum in its simplest form is concave forward, the concavity varying greatly in different forms. This simple condition is found in the majority of nautiloids, straight, curved, or coiled. In some advanced Nautilida, however, the free part of the septum may be undulating.

On an internal mold (steinkern) of a conch, the outer edge of the free part of the septum is visible as a transverse line, which is called the **suture**. In its simplest form the suture is circular or elliptical, and



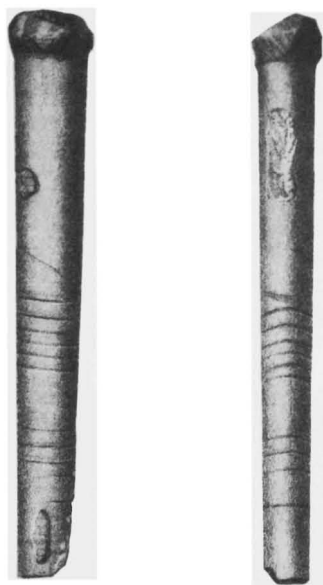


FIG. 20. Portions of phragmocones of *Plagiostomoceras panderi* (BARRANDE) with missing septa. Sil., Czech.,  $\times 1$  (Barrande, pl. 225, 1866).

transverse, with the diameters of the circle or ellipse oriented perpendicularly to the long axis of the conch. Such a suture is called straight, because sutures are best illustrated as if they were unrolled on a flat plane.

If the peripheral area of the free part of the septum is wavy, the suture is sinuous. The major parts of a suture directed alternately forward and backward are called **sutural elements**. The forward bulging parts of a suture are called **saddles**, and the backward bulging parts **lobes**. The simplest and most common type of sinuous suture has one saddle on the ventral side, and another on the dorsal side, and one lobe on each of the flanks of the conch (Fig. 19,C).

In coiled conchs the part of a suture exposed on the outside of a whorl, between the umbilical seams, is called the **external suture**, and the part situated on the dorsum, hidden from view in an undamaged shell, is the **internal suture**. Many coiled conchs possess a small, acute dorsal lobe occupying the center of the main internal lobe. This is called the **annular lobe** (see Fig. 58).

Only among the Nautilida do somewhat more elaborate sutures develop, especially in certain Triassic and early Tertiary groups (Syringonaulitidae, Siberionautilidae, Her-

coglossidae, Aturiidae, and some others). The most complex suture yet found among nautiloids is that of *Siberionautilus*, in which the suture across the ventral region is subdivided into numerous small saddles and lobes.

### CAMERAL DEPOSITS

In many nautiloids the camerae are wholly or partly filled by linings of calcium carbonate deposits, which, as suggested by various lines of evidence, were secreted by the animal while it was alive. These are called **cameral deposits**.

Most cephalopod shells when entombed in sediment have empty camerae except for water that may enter them. Later, during diagenesis, calcite from circulating solutions gradually is deposited in the camerae.

Distinction between deposits due to diagenetic infiltration ("secondary deposits") and deposits made by the living animal ("primary deposits") is generally easy to establish. Secondary (diagenetic) deposits surround more or less uniformly all walls of camerae (including septa), inside the



FIG. 21. Conch of "*Cyrtoceras*" *repletulum* BARRANDE with retarded growth stages of camerae and siphuncle, probably due to disease. Sil., Czech.,  $\times 0.7$  (Barrande, pl. 499, 1877).

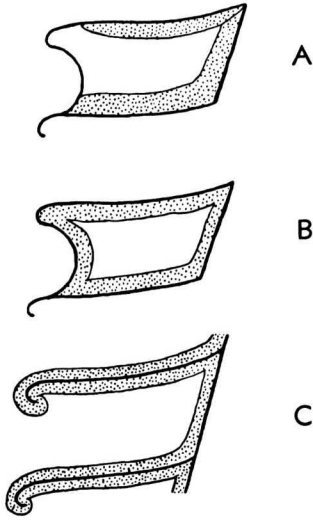


FIG. 22. Primary and secondary deposits in camerae: A, primary (no deposits along connecting ring); B, secondary (connecting ring preserved); C, secondary (connecting ring destroyed) (35).

shell wall, and ectosiphuncle (Fig. 22). Primary (organically precipitated) deposits cover only the anterior and posterior parts of the septa and their mural parts (Fig. 23). Furthermore, primary deposits decrease in bulk from the apical toward the oral end of the phragmocone, in some genera with great regularity (Fig. 24). They may be absent in the anterior portion of the phragmocone and they are never present at the bottom of the body chamber.

Cameral deposits are of the following basic types (Fig. 25): (1) **episeptal**, deposited on the anterior, or concave, surface of a septum; (2) **hyposeptal**, deposited on the posterior, or convex, surface of a septum. Episeptal deposits covering the mural parts of septa are often referred to as **mural deposits**.

Episeptal (and mural) deposits may be present either alone or in combination with hyposeptal deposits. The latter rarely occur alone, except in adoral portions of phragmocones, where their formation may precede that of episeptal deposits.

As episeptal and hyposeptal deposits grow, they may meet somewhere approximately at mid-height of the camerae. In transverse section their contact plane appears as a thin line running from the anterior outer corner

of a camera down the middle of the camera to the vicinity of the siphuncle, generally ending in a small, open space of subtriangular cross section not occupied by deposits.

This contact plane has been called the "pseudoseptum" by several earlier students of cephalopods (HOLM, SCHRÖDER, and others), because a brown amorphous substance is often seen between the epi- and hyposeptal deposits. Most probably this substance stems from an organic membrane that originally covered the deposits and was functionally connected with their formation.

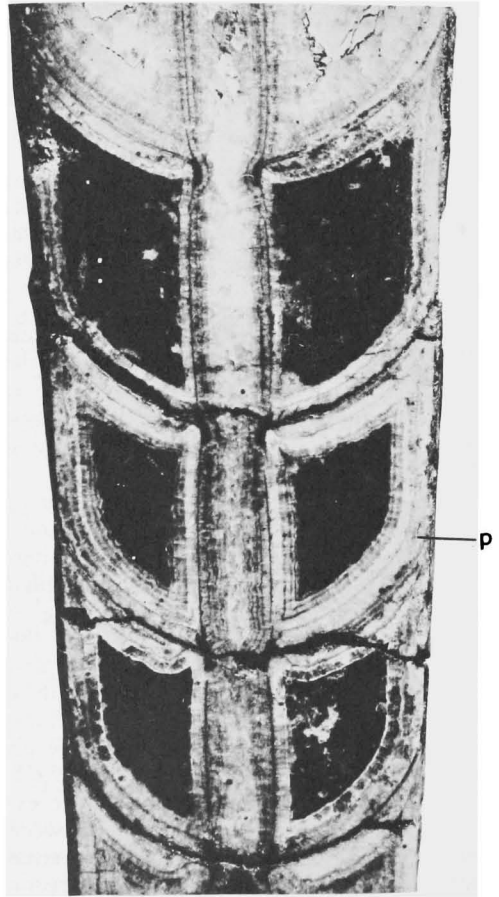


FIG. 23. Portion of phragmocone of *Geisonoceras teichertii* FLOWER, camerae lined with primary and secondary deposits. Outermost layer (*p*) extends along anterior, posterior, and mural parts of septa, but not along outside of connecting ring. This is a primary cameral deposit; all other layers in the camerae and in the siphuncle are inorganically deposited during diagenesis. M.Dev., USA(N.Y.) (35).

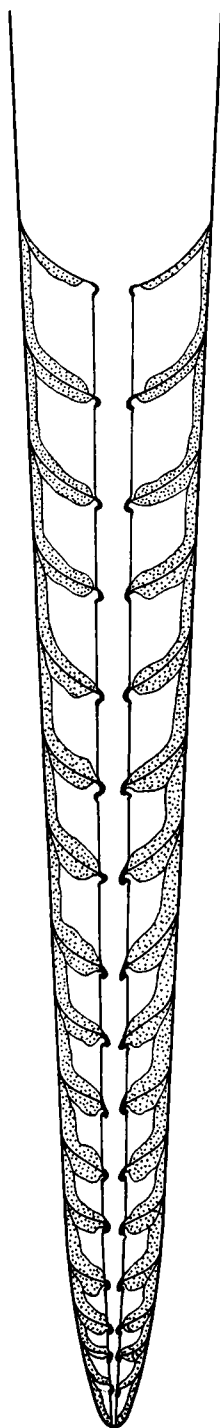


FIG. 24. Reconstructed longitudinal section of *Geisonoceras teichertii* FLOWER, showing regular disposition of cameral deposits in phragmocone (35).

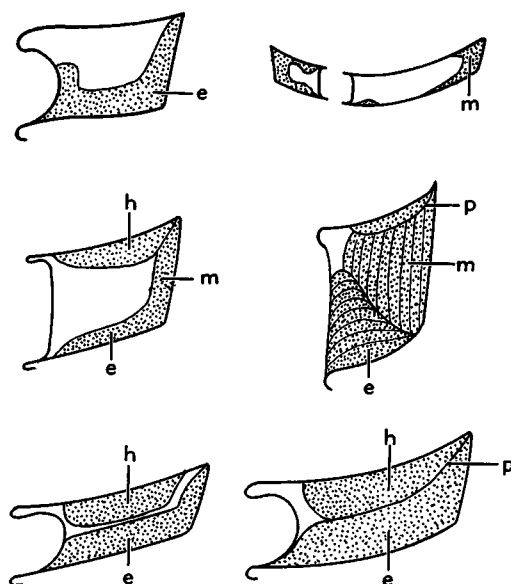


FIG. 25. Various types of cameral deposits: *e*, epi-septal; *h*, hyoseptal; *m*, mural; *p*, "pseudoseptum" (35, and Teichert, n).

This suggestion is supported by the observation of vascular tubes on the surface of cameral deposits. These were seen, described, and correctly interpreted in Ordovician and Silurian orthocerids and lituitids by such early observers as DEWITZ, NOETLING, SCHRÖDER, HOLM, and REMELÉ (Fig. 26, *A*). They were largely ignored by later workers. More recently FLOWER (1941) has called attention to the presence of "circumferential tubes" on the surface of cameral deposits in *Leurocycloceras* and other forms (Fig. 26, *B*).

It seems that the inner surface of cameral deposits which can sometimes be studied on internal molds may be mammillate or pitted (Fig. 26, *C-G*).

While in most conchs cameral deposits form laterally continuous layers covering the septa, modifications may occur such as in the Lamellorthoceratidae (order Orthocerida), where cameral deposits are secreted as longitudinal radial lamellae (TEICHERT, 1961).

The disposition of the deposits within individual camerae is, as a rule, asymmetrical, the deposits being more strongly developed in the ventral than dorsal half of the camerae (Fig. 27). This demonstrates that it was the function of the cameral deposits to

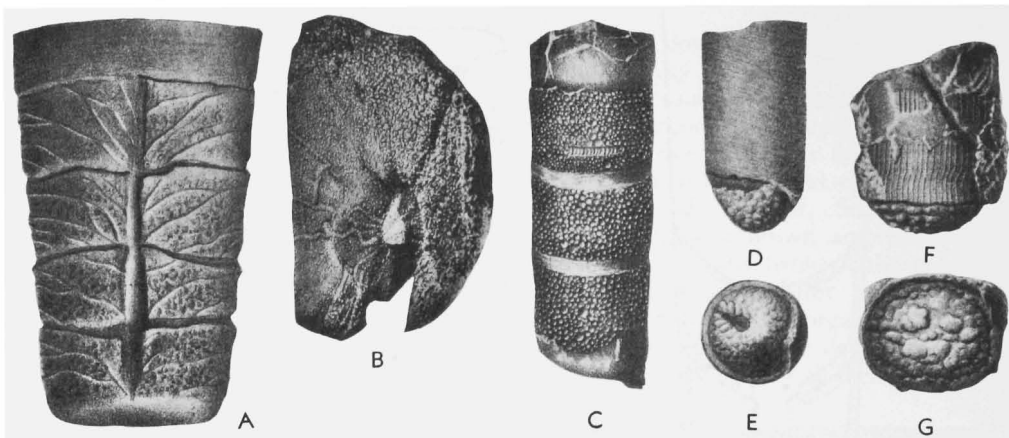


FIG. 26. Features of the inner surface of cameral deposits.—A. Steinkern of orthocerid with impressions suggesting vascular tissues on the surface of the mural deposits or of the mural part of the septa; Sil. (Pleist. drift), Ger.,  $\times 1.3$  (29).—B. Dolomitized camera filling of *Leurocycloceras* sp., cf. *L. niagarensis*, preserving replica of surface of cameral deposits with vascular tubes, Sil., USA (Wis.),  $\times 1.3$  (Flower, 1941).—C. Steinkern of orthocerid phragmocone showing replica of mammillate surface of mural cameral deposits, Sil., Czech.,  $\times 0.7$  (Barrande, pl. 227, 1868).—D-G. Replicas of cameral deposit surfaces in orthocerids, showing especially regular pattern in F; D,E, Dev., F,G, Sil., Czech.,  $\times 0.7$  (Barrande, pl. 228, 1868).

help stabilize the conch in a position with the ventral side downward during the life of the animal.

Some forms, especially *Pseudorthocera*-ceae, have a furrow in the cameral deposits along the ventral side. Heavy accumulations on both sides of this ventral furrow have been called **ventrolateral masses**.

In view of their stabilizing role, it is obvious that cameral deposits are most important in straight or nearly straight forms. They reach their greatest development in the Orthocerida and Actinocerida, but thin and slender shells may be without them. Cameral deposits are erratically developed in the Discosorida, and in the Oncocerida they are, when present, very thin. In the Ellesmerocerida they are found only in the advanced families Baltoceratidae and Protocycloceratidae. Cameral deposits do not occur in the Endocerida, where the stabilizing function is exercised by heavy endosiphuncular deposits. True cameral deposits are also unknown in the Barrandeocerida and reports of their presence in Nautilida are few (Fig. 28). Among Tarphycerida cameral deposits occur only in the family Lituitidae which has conchs that are straight at maturity. Coiled shells generally had no need for stabilizers of this type.

The mode of origin of cameral deposits and the time of their formation have been

much discussed. Some authors have rejected even the postulate of their organic origin. Criteria which may be applied to differentiate between organic (primary) and inorganic (secondary) deposits of calcium carbonate in the camerae have already been discussed. As may be expected, cameral deposits in fossil conchs generally consist of calcite. However, FISCHER, LOWENSTAM, & TEICHERT observed that cameral deposits occurring in exceptionally well-preserved specimens of *Pseudorthoceras* found in asphalt consist of aragonite. These deposits consist of thin lamellae composed of fine aragonite needles separated by thin, dark membranes. According to GRÉGOIRE (written communication and Fig. 29) these membranes consist of minute mineral prisms in parallel orientation, separated by shreds of organic matter. Presence of aragonite and of organic substance in the cameral deposits of *Pseudorthoceras* is incontrovertible proof of the organic origin of these deposits. As may be expected, preservation of these delicate cameral structures is extremely rare, but all primary cameral deposits are sufficiently similar in gross features of morphology to allow of only one unified interpretation.

Two hypotheses have been offered to explain the formation of organic cameral deposits: (1) They were formed simultaneous-

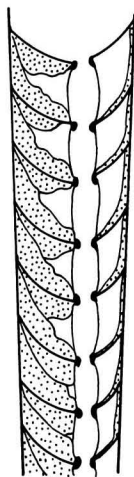


FIG. 27. Strongly asymmetrical distribution of cameral deposits in an orthocerid; Sil., Czech.,  $\times 0.7$  (Barrande, pl. 285, 1868).

ly with the septa with which they belong and are thus excretions of the mantle; (2) They were formed later than the septa and after the camerae had been closed by the siphuncle.

The principal proponent of the first hypothesis was BARRANDE. Others were DEWITZ, HOLM, and GRABAU, to mention only a few. Considerable difference in interpretation of structural details and of the exact sequence of events leading to the formation of the deposits is indicated, however. Some authors regarded the "pseudosepta" as purely mechanical contact planes of epi- and hyposeptal deposits. Others believed that they represent organic membranes secreted by the mantle in intermediate positions between the septa and indicating positions of rest in the process of almost continuous secretion of calcium carbonate either as septa or as cameral deposits.

The postulate in either form is here regarded as unlikely, first, because the anterior portion of the phragmocone, and especially the last few septa, are generally entirely free from cameral deposits; second, because in almost all cases cameral deposits increase gradually and regularly in bulk and thickness from chamber to chamber in an apical direction. This condition is suggestive of progressive growth of the deposits during life of the animal, because it is quite unlikely that young shells should have been

almost or entirely filled with calcareous deposits.

The hypothesis of continuing formation of cameral deposits within the camerae during life of the animal and after the camerae had been completed was first proposed by TEICHERT (35), who envisaged the possibility that the camerae might have contained some kind of organic tissue that formed the cameral deposits. This concept was explored by FLOWER (8), who succeeded in putting it on a biologically sound basis. FLOWER suggested that the camerae were lined with tissue which he proposed to call **cameral mantle**. This was presumed to develop from the mantle enveloping the posterior part of the visceral mass, when the animal was moving into position to build the next following septum. According to reasonable interpretation, part of the old mantle remained adherent to the old septum, and the new septum was secreted by a newly formed posterior mantle. The mantle remaining in the camera continued to be supplied with blood through the newly formed connecting ring. It continued to grow over the posterior side of the newly formed septum, and in due course excess supply of mineral matter to the cameral mantle led to secretion and continued growth of cameral deposits.

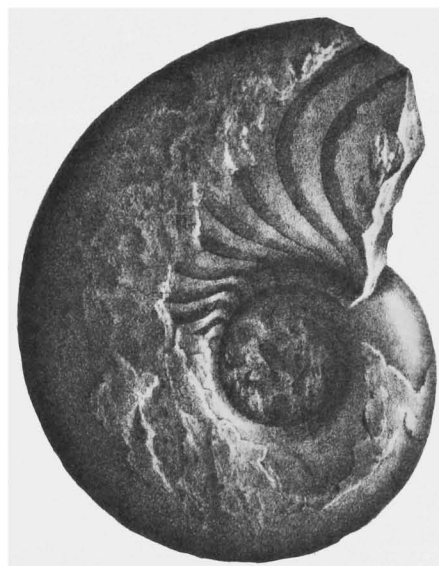


FIG. 28. Cameral deposits in a nautilid, *Grypoceras obtusum* (MOJSISOVICS); Trias., Alps,  $\times 0.7$  (Mojsisovics, 1873).

Contrary to FLOWER's opinion, the cameral mantle probably did not envelop the connecting ring, because no cameral deposits are ever found on its outer surface.

The "pseudoseptum" was the plane along which the hyposeptal and the episeptal portions of the cameral mantle were brought into contact through growth of the deposits secreted by them. Earlier authors, especially HOLM, APPELLÖF, NOETLING, and SCHRÖDER, have described the "pseudoseptum" as a distinct membrane on which, in rare cases, impression of vascular systems have been observed. HOLM (15) believed that the "pseudoseptum" represents a membranous soft "double sack" which surrounded the posterior end of the mantle and became detached from it as the animal moved on in the conch to build a new septum.

The cameral mantle, as here described, is a hypothetical organ which was developed in some extinct nautiloids and which was lost in evolution of the nautiloid lineage.

It should be remembered, however, that small secretions of aragonite are also known in the camerae of living *Nautilus*. APPELLÖF has shown that the anterior corner of the camerae of *Nautilus pompilius* contains a filling of conchiolin in which small bodies of aragonite are embedded. The formation of this filling ("*Ausfüllungsmasse*" of APPELLÖF) must have followed that of the septum behind which it occurs. GRÉGOIRE

(1962) found that this filling consists of several substances of aragonitic and organic composition. The electron microscopic structure of some of the substances is strikingly similar to that of cameral deposits of *Pseudorthoceras*.

Some specialized features of cameral deposits of Actinocerida and Orthocerida are discussed in descriptions of these orders.

### SIPHUNCLE

In fossil cephalopods the term *siphuncle* is applied to all fossilizable structures connected with the siphuncle of the living animal. Conchs with relatively wide siphuncles are called *euryisiphonate* and those with narrow siphuncles *stenosiphonate*. Use of these terms is generally restricted to very large (e.g., Endocerida) and very narrow (e.g., Orthocerida) siphuncles, respectively. No special terms for intermediate siphuncle sizes exist.

In euryisiphonate cephalopods, such as the Endocerida and Actinocerida, but also in some Discosorida, Ellesmerocerida, and even in some Oncocerida, part of the endosiphuncle not occupied by deposits is so large in relation to volume of the body chamber that it must have contained important organs of the body. Whereas in forms like modern *Nautilus*, the siphuncle no longer contains more than an extension of the mantle, the siphuncle of euryisiphonate forms must have included

#### EXPLANATION OF FIGURE 29, 1-3

Representative aspects of the structure of cameral deposits, with increasing amounts of organic substance from 1 to 3, are shown by positive carbon replicas (shadow-cast with palladium) of polished surfaces of shell sections.

- 1.—Sagittal section of region having marble-like hardness, parallel crystals without visible interposition of organic substance, probably revealing local recrystallization of calcium carbonate (reversed print),  $\times 9,000$ .
- 2.—Transverse section of shell showing partially calcified portion of cameral deposits. The basic mineral unit consists of elongated, sharp-edged tablets, blades, or bars, appearing as needles or spindles viewed on edge, the parallel spindle-shaped crystals being grouped in variously oriented bundles with components disposed at different angles to crystals of neighboring bundles. Shreds of organic substance are visible (white) and incidental twinnings appear in

right-hand part of figure (reversed print),  $\times 22,000$ .

- 3.—Polished sagittal section of thinly stratified dark brown area of cameral deposits, etched by chelation (Titrplex III for 2 minutes). Parallel elongated mineral elements seen on edge are arranged in palisade alternating with shreds of organic substance (white ribbons), decalcification of this area having left substantial organic residues (reversed print),  $\times 22,000$ .

[Other regions of poorly calcified cameral deposits (not illustrated) mostly in central parts of camerae near the siphonal complex, consist of soft, dark brown, crumbly organic material, in part birefringent. Polished surfaces could not be prepared from these regions. Thoroughly decalcified and thinned mechanically for examination with phase-contrast and electron microscopes, the soft material appears as fragments of sheets in which traces of structural organization are visible but not so far identifiable.]



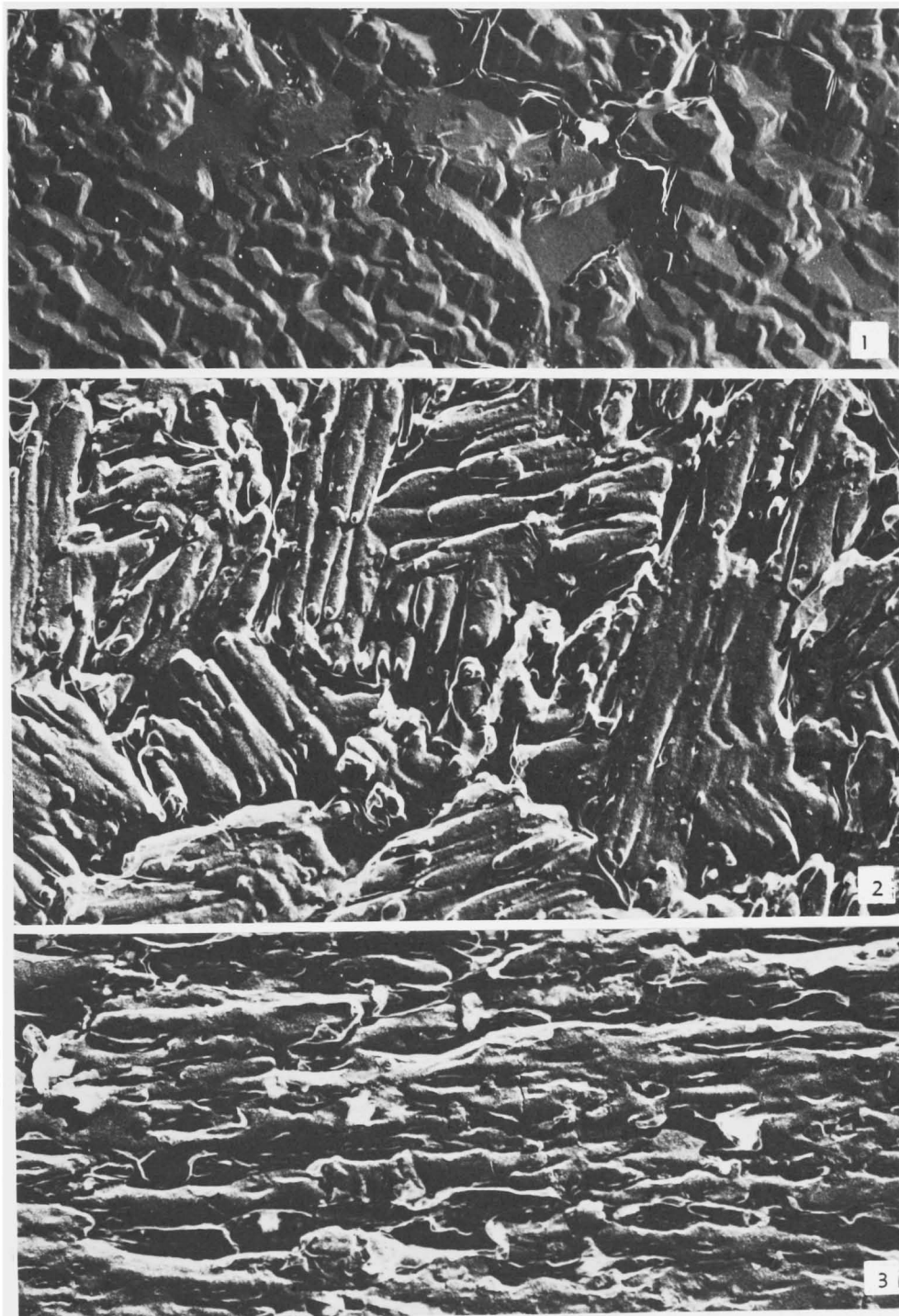


FIG. 29,1-3. Electron micrographs of cameral deposits of *Pseudorthoceras knoxense* (McCHESNEY) from lower Middle Pennsylvanian deposits (Buckhorn asphalt) near Sulphur, Oklahoma (Grégoire, n; specimens supplied by A. G. Fischer) (explanation on facing page).

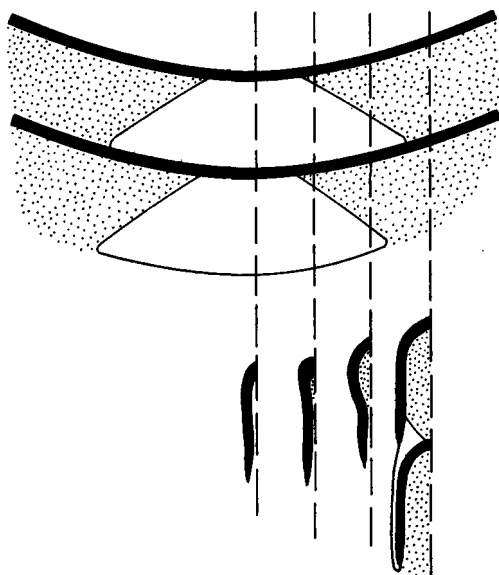


FIG. 30. Ectosiphuncular suture diagrammatically showing ventral surface of two camerae (shell removed) and four longitudinal sections of the ectosiphuncle (septa represented by thick black lines and unshaded areas adjacent to septa indicating regions where septal necks are flattened against the inner shell wall). An ectosiphuncular suture occurs on either side of the mid-ventral line in each camera. They are lines along which the gap between the septal necks and the inner shell wall becomes sufficiently wide for introduction of matrix (dotted) between these two components of the conch (Teichert & Glenister, n).

some of the visceral mass. It has been suggested that it might have housed the liver and the gonads—in analogy to the gastropods, where these organs are found in the dorsal (or posterior) part of the body.

The outer sheath, inside which the fleshy siphon or siphuncular cord was situated, is the **ectosiphuncle**, also called the siphonal tube. The space inside it is the **endosiphuncle** and fossilized structures of any kind in this space are known as **endosiphuncular structures**.

This terminology, though convenient for purposes of morphological description, is somewhat artificial, because all structures concerned were probably secreted by the same mantle surface.

The early ontogeny of the siphuncle will be treated in the general chapter on early ontogeny of the nautiloid conch.

The position of the siphuncle within the phragmocone may be anywhere from mar-

ginal to central. Most euryisiphonate forms have marginal to submarginal siphuncles, whereas these positions are rare in stenosisiphonate conchs. Wide, marginal siphuncles may be in broad contact with walls of the conch (*Cameroceras*, *Kocho-ceras*). In groups with broadly expanded siphuncle segments (actinocerids, onco-cerids, some discosorids), the contact area between segments and conch wall is well seen on the surface of internal molds, where it is set off from the camerae by the **ectosiphuncular suture** (Fig. 30).

#### ECTOSIPHUNCLE

The ectosiphuncle consists basically of septal necks and connecting rings.

The septal necks may not be developed or they may be rudimentary, indicated by a

achoanitic



loxochoanitic



orthochoanitic



suborthochoanitic



cyrtchoanitic



hemichoanitic



subholochoanitic



holochoanitic



macrochoanitic



FIG. 31. Diagram explaining septal neck terminology (Teichert & Glenister, 1954).



slight inflection of septa around the septal foramen. This condition is known as **achoanitic** (Fig. 31). Septal necks of nautiloid cephalopods are invariably **retrochoanitic**, that is, pointed backward toward the apex of the conch. The principal terms for different types of septal necks which have long been recognized are **orthochoanitic**, for short cylindrical necks; **cyrtchoanitic**, for necks that are bent outwardly in cross section; and **holochoanitic**, for long, cylindrical necks reaching from one septum to the preceding one. More recently, it has become necessary to establish a more elaborate terminology for intermediate or deviating types of necks (Fig. 31, and glossary).

The distribution of these various types of septal necks among the different orders is approximately as follows: (1) **Achoanitic necks** are rare; restricted to the Ellesmerocerida. (2) **Orthochoanitic necks** are found in many Ellesmerocerida, in the superfamily Orthocerataceae of the order Orthocerida, and in most coiled forms (Tarphycerida, Barrandocerida, Nautilida). (3) **Hemichoanitic necks** are most common in the Proterocameroceratidae (order Endocerida), occurring also, though rarely, in the Orthocerida. (4) **Loxochaoanitic** and **subholochoanitic necks** are almost restricted to Ellesmerocerida and early Endocerida, and are found in a few Orthocerida. (5) **Cyrtchoanitic necks** characterize the Actinocerida, Oncocerida, and Discosorida, and the superfamily Pseudorthocerataceae of the Orthocerida. (6) **Holochoanitic necks** are most typical of the Endocerida, but occur in some genera (e.g., *Aturia*) of the Nautilida. (7) **Macrochoanitic necks** are found only in the Endocerida.

Orthochoanitic and cyrtchoanitic necks were formerly collectively called **ellipchoanitic** and contrasted with the long, holochoanitic necks. This term, though still useful on occasion, is no longer part of formal terminology, because of the discovery that many septal necks are intermediate between the ellipchoanitic and holochoanitic conditions.

The connecting ring is a cylindrical or ring-shaped sheath, which extends between two succeeding septa or septal necks. The connecting ring of living *Nautilus* is very thin; it consists of an inner layer of conchio-

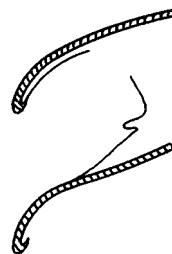


FIG. 32. Torn and folded connecting ring in a specimen of *Actinoceras* (35).

lin and an outer layer of aragonite spicules and granules, cemented by conchiolin. This outer layer is porous. All members of the order Nautilida have similarly thin connecting rings and it is reasonable to suppose that all had a similar composition. The same may be true for the thin connecting rings of extinct orders such as the Barrandocerida, Oncocerida, Actinocerida, and Orthocerida. They are known to have consisted of a rigid, yet flexible material (Fig. 32).

In the Ellesmerocerida, Endocerida, Discosorida, and Tarphycerida, the connecting rings are thick and commonly of complex structure and elaborate shape. In many genera the connecting ring is clearly composed of two or even three layers of different structure, color, and transparency, but little is known about the nature of the original material of which these complex connections consisted. The connecting ring of *Cochlioceras* is said to consist of calcium carbonate with an admixture of phosphorite (27).

Thin connecting rings are as a rule attached anteriorly to the thin edge or to the area just outside the edge of the proximal septal neck, posteriorly to the inside of the distal septal neck in which they form a continuous lining (Fig. 33,A,B). Thick rings are attached to the entire outside of the septal necks and to the posterior and anterior surfaces of the septa in a narrow area surrounding septal neck and septal foramen (Fig. 33,C-E).

The simplest form of connecting ring is cylindrical, as usual in orthochoanitic siphuncles. In conchs with suborthochoanitic to cyrtchoanitic septal necks, the connecting ring bulges outward and may be barrel-

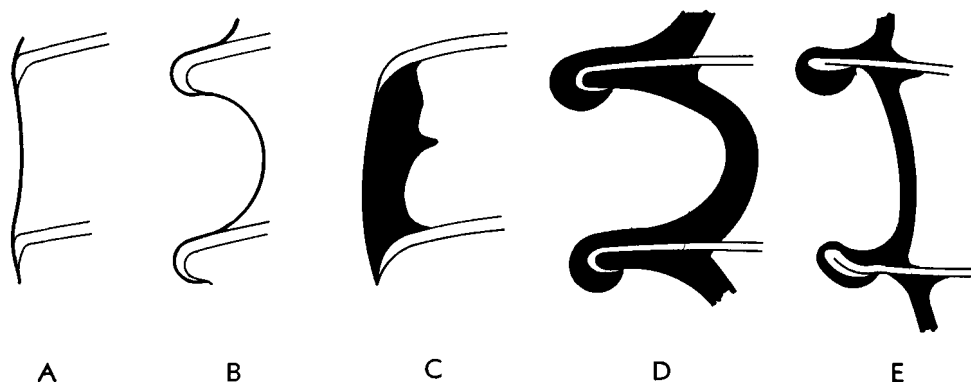


FIG. 33. Various kinds of thin (A,B) and thick (C-E) connecting rings and their mode of attachment to septa and septal necks (Teichert, n).

shaped, globular, or even very broadly expanded. Siphuncles with globular to broadly expanded segments are often called **nummuloidal**. The area of attachment of expanded segments to the anterior, more rarely the posterior surface of septa, is called **adnation area**.

The comparatively rare condition in which the connecting rings are convex inward is called **concavosiphonate**. It is almost entirely restricted to the *Oncocerida*.

Further specializations of shape and structure of the connecting rings occur in the *Ellesmerocerida*, *Endocerida*, and *Discosorida*, and will be described in the introductions to the systematic treatment of these orders.

#### ENDOSIPHUNCLE

For descriptive purposes, the endosiphuncle includes the space inside the ectosiphuncle and all contained fossilizable structures built by organic activity during the life of the animal. Like cameral deposits, many of these are difficult to interpret, because they lack analogies in modern cephalopods. All calcareous, primary structures in the endosiphuncle are collectively referred to as **endosiphuncular deposits**.

Noncalcareous inward expansions or outgrowths of the connecting rings, as seen in some *Ellesmerocerida* (*Eothinoceras*, *Cyrtoceras*, *Bathmoceras*), are analogous, not homologous to endosiphuncular deposits and are not grouped with them. They have been little studied as yet.

Endosiphuncular deposits exhibit considerable variety in regard to morphology

and structure. Some features are characteristic of certain orders; others occur in different combinations in different orders.

Endosiphuncular deposits are known to occur in the following orders: *Ellesmerocerida* (diaphragms only), *Endocerida*, *Actinocerida*, *Discosorida*, *Orthocerida*, and *Oncocerida*. They are virtually absent in the *Ascocerida* and such stenosphonate groups as the *Tarphycerida*, *Barrandocerida*, and *Nautilida*.

In most orders in which endosiphuncular structures occur, the latter may attain a considerable degree of complexity and many specialized features have developed, which will be discussed separately for each order. This introductory chapter can serve only as a review of and an introduction to the general field of endosiphuncular structures.

Endosiphuncular deposits are of the following six basic types (Fig. 34): (1) Transverse diaphragms. (2) Longitudinal lamellae in radial orientation, converging from the ectosiphuncle toward a longitudinal axis in the siphuncle; this structure is called **actinosiphonate**. (3) Superimposed cone-shaped layers, with the axes of the cones in, or parallel to, the central axis of the siphuncle and with their apices pointing backward toward the apex of the conch. (4) Cylindrical tubes running along or close to the longitudinal axis of the siphuncle. (5) Internal linings of the ectosiphuncle. (6) Deposits first developing on the inside of the septal necks, then growing and expanding inward to fill almost the entire endosiphuncle, but not coming into contact with the connecting rings; these are the

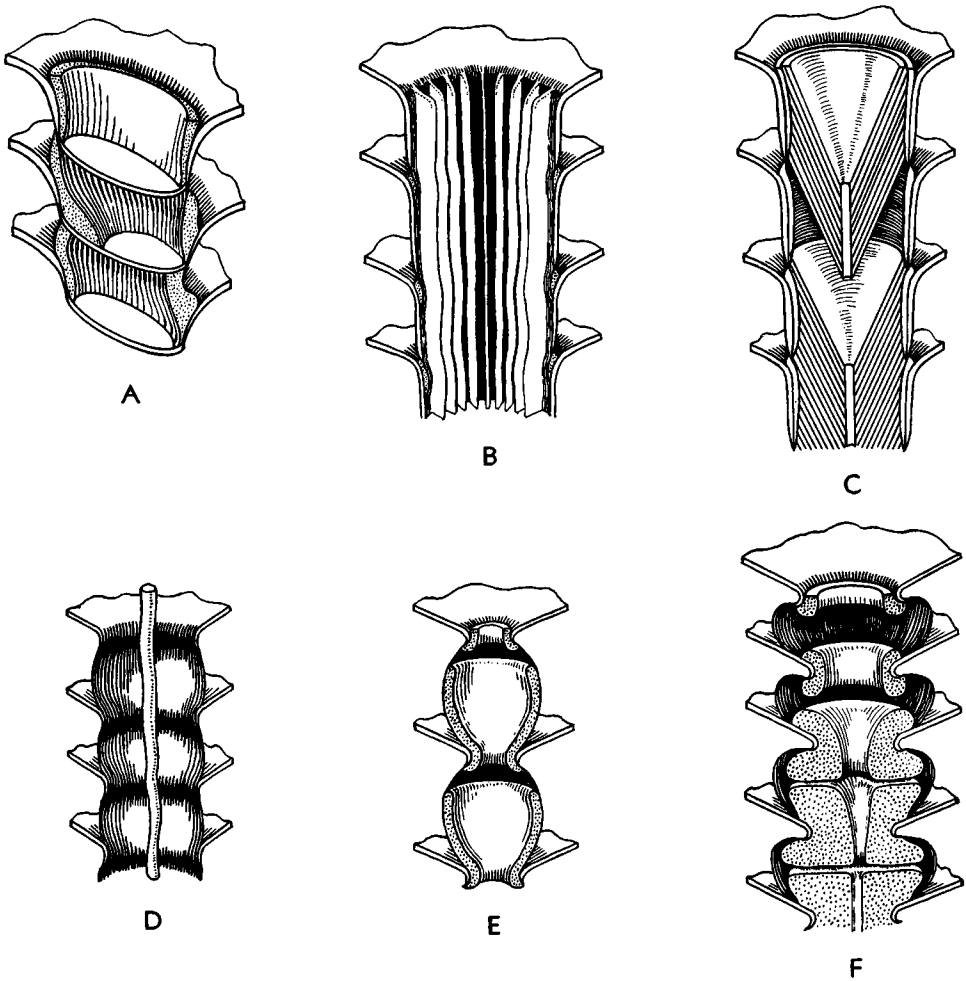


FIG. 34. Types of endosiphuncular structures; *A*, diaphragms; *B*, longitudinal lamellae; *C*, endocones; *D*, central cylindrical tube; *E*, parietal deposits; *F*, "annulosiphonate" deposits (not to scale). In *A* and *B* connecting rings are stippled; in *E* and *D* endosiphuncular deposits are stippled (Teichert, n).

**annulosiphonate deposits** of HYATT and other authors, but the term is now rarely used, because in the mature stage these deposits fill the entire siphuncle with the exception of a usually complex system of **endosiphuncular canals**.

These six basic types will now be briefly discussed, leaving specializations to later treatment. They may occur alone or in combination. Thus, diaphragms are found in some *Ellesmerocerida*. Radial, longitudinal lamellae occur in the *Intejocerida* and *Oncocerida*. Cone-shaped deposits are common in the *Endocerida*, but are also found in many *Discosorida*, and very rarely in the

*Orthocerida*. Cylindrical tubes are known rarely from *Orthocerida*, *Discosorida*, and *Oncocerida*. Interior linings of the ectosiphuncle are characteristic of the *Discosorida* and of a large group of *Orthocerida*, the *Pseudorthocerataceae*. Deposits growing out from the inside of the septal neck are the most characteristic feature of the *Actinocerida*, but are also very typical of some *Oncocerida* and *Orthocerida*.

**Type 1.** Transverse diaphragms are of rare occurrence. They are known in some genera of the *Ellesmerocerida*, where, with few exceptions, they have not been studied in great detail. Some diaphragms have been

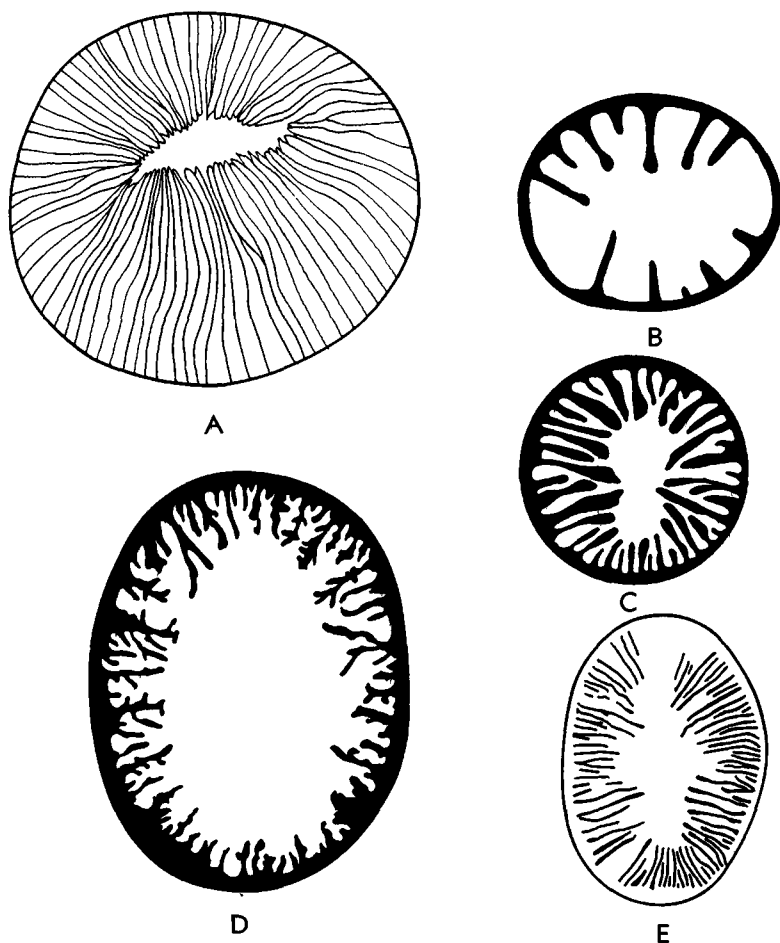


FIG. 35. Several types of actinosiphonate structures.—A, Endocerida (*Padunoceras*,  $\times 2$ ).—B-E, Onco- cerida (B, *Conostichoceras*,  $\times 4$ ; C, *Jovellania*,  $\times 5.5$ ; D, *Pectinoceras*,  $\times 7$ ; E, *Polyelasmoceras*,  $\times 2.7$ ) (Adapted from Balashov, 1960; Teichert, 1939; Lemaitre, 1940; Teichert, 1940; Teichert & Glenister, 1952).

described to have a structure similar to that of the connecting rings, from which, however, they are always distinct. Endosiphuncular diaphragms are homologous to the transverse partitions found in the endosiphuncular central canals of certain endocerids (Fig. 34,A).

**Type 2.** Structures of this type are in need of much more detailed study. They probably fall into several different groups some of which may be characterized as follows: (a) Closely spaced lamellae converging from the ectosiphuncle on the center or an off-center axis of the siphuncle; known in the orders Intejocerida and Endocerida,

and almost certainly of calcium carbonate (Fig. 35,A). (b) Closely or widely spaced, short to medium long lamellae which are of the same material as the connecting ring and may be club-shaped in cross section; they are inward folds or extensions of the connecting ring (e.g., *Conostichoceras*, *Jovellania*, *Archiacoceras*) (Fig. 35,B,C). (c) Closely spaced, thin lamellae, irregularly alternating long and short, slightly irregular or wavy in cross section, rarely dichotomous (e.g., *Polyelasmoceras*) (Fig. 35,E). (d) Closely spaced lamellae, irregularly alternating long and short, all (except shortest) developing lateral projec-

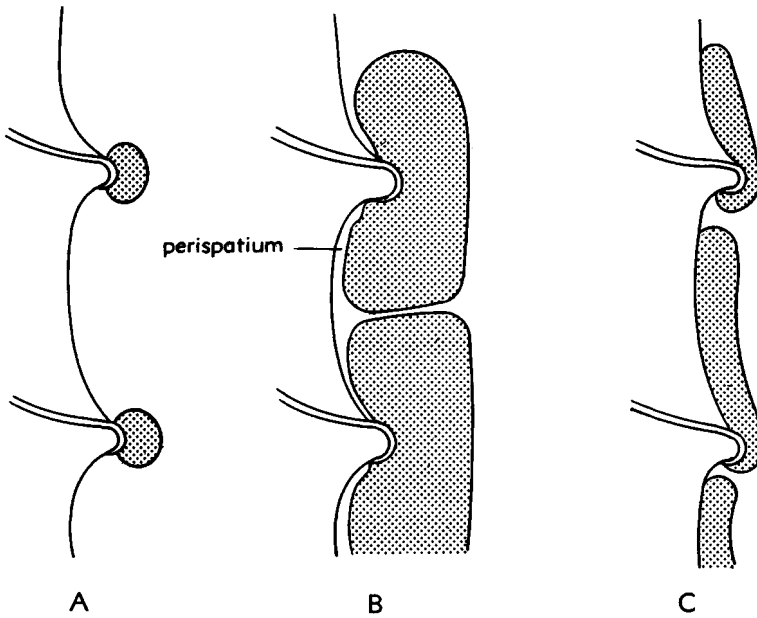


FIG. 36. Parietal and annulosiphonate deposits: *A*, incipient rings; *B*, annulosiphonate deposits, fully developed, with perispantium; *C*, parietal deposits, not yet quite fused to form continuous lining (adapted from 9).

tions, longer lamellae being bipectinate in cross section; primarily probably excrescences of the connecting ring, but secondarily covered with film of calcium carbonate (e.g., *Pectinoceras*, *Actinomorpha*) (Fig. 35,D).

Structures of groups (b) to (d) are known from various families of the Oncocerida and probably persist in their derivatives, the earliest Rutoceratidae. The lamellae may be continuous throughout a considerable part of the siphuncle or through several segments only, or they may occur in discontinuous clusters around successive septal necks. Some evidence suggests that lamellae generally may first form inside the septal necks and that they may coalesce into longitudinally continuous structures through gradual growth.

**Type 3.** The basic type consists of conical layers, called **endocones**, consisting of calcium carbonate, not more than a few millimeters thick, with a perforated, backward-directed apex. The apical foramina line up into a straight (or in cyrtconic forms, curved) cylindrical tube, the **endsiphuncular canal**. In some forms this canal is tra-

versed by transverse diaphragms. Many modifications of this simple pattern are observed. The endocones may be greatly modified in cross section, being elliptical, subtriangular, or crescent-shaped (e.g., *Meniscoceras*, *Tasmanoceras*). Two or more systems of endocones may be present (Chihlioceratidae, Allotrioceratidae). The endsiphuncular canal may be flattened or crescent-shaped (e.g., *Emmonsoceras*), and if a multiple endocone system is present, there is one canal for each set of endocones. Additional specialized features associated with this type of endsiphuncular structure are restricted to the Endocerida and will be discussed under that order (Fig. 34,C).

**Type 4.** Cylindrical tubes have been observed in many unrelated genera. They are either straight or slightly wavy, probably generally circular in cross section and situated close to the longitudinal axis of the siphuncle. Apparently, these tubes were embedded unsupported in the siphuncular tissues. When they are found in contact with the septal neck, it may be assumed that they came to rest on them, when the tissue decayed after death of the animal. They have

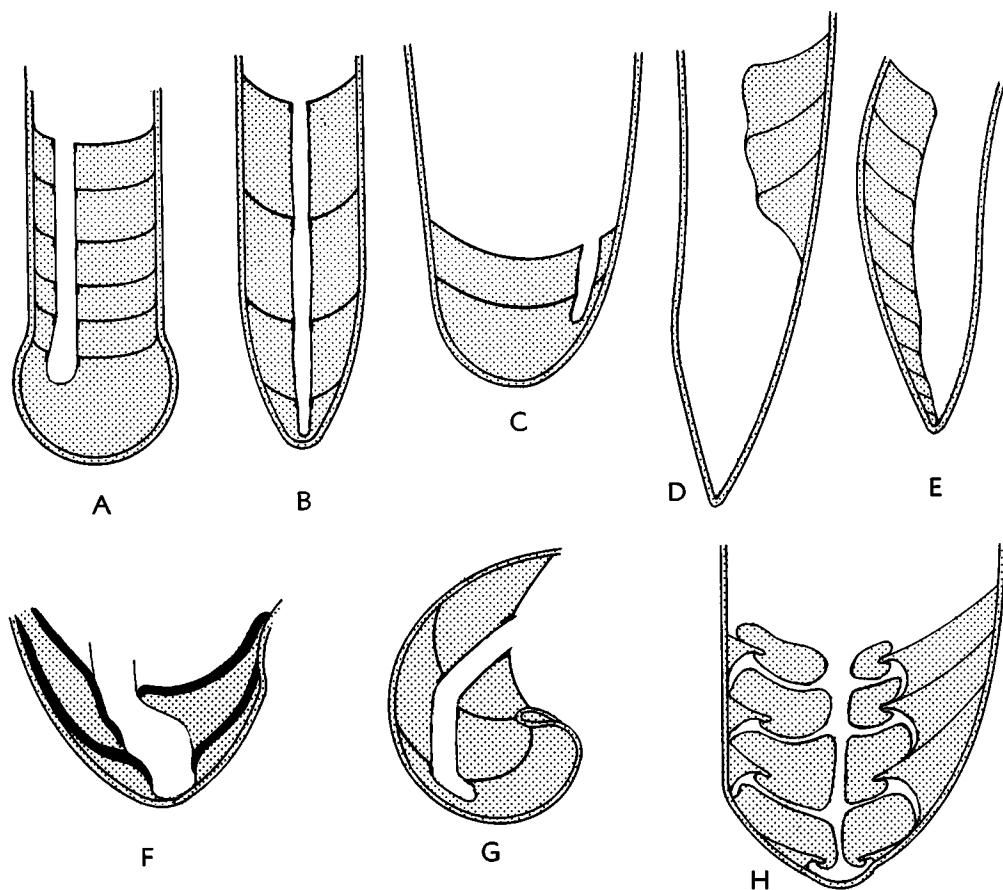


FIG. 37. Initial parts of conchs of several nautiloid orders (camerae stippled) (not to scale).—A, Orthocerida (*Orthoceras*?), Ord.—B, Orthocerida (*Trematoceras*), Trias.—C, Oncocerida (genus?), Sil.—D, Endocerida (*Suecoceras*), Ord.—E, Endocerida (*Nanno*), Ord.—F, Nautilida (*Nautilus*), Rec.—G, Tarphycerida (*Curtoceras*), Ord.—H, Actinocerida (*Armenoceras*), Ord. (adapted from Balashov, 1959; 19; 27; 38; Holm, 1884).

so far been found only in siphuncles of orthoconic or near-orthoconic forms (e.g., *Harrisoceras*, *Madiganella*, *Diestoceras*) (Fig. 34,D).

**Type 5.** Internal linings of the ectosiphuncle originate in the form of thin deposits along insides of septal necks (Fig. 34,E; 36,A) which, when small and of semi-circular cross section, comprise a structure often called **annulus**.<sup>1</sup> They develop rapidly into ringlike structures of kidney-shaped cross section, called **bullettes**. These deposits extend generally predominantly in an anterior direction along the connecting

rings. Less rapidly they also develop posteriorly into the preceding siphuncular segment (Fig. 36,C). They may then fuse and begin to form a continuous internal lining of the ectosiphuncle.

Considerable variation occurs in the morphology of these structures. The lining may be strongly developed along the ventral side of the siphuncle, being rudimentary or absent on the dorsal side. In other genera (e.g., *Buchanoceras*, *Bergoceras*) the bullettes grow strongly toward the center of the siphuncle, obstructing the septal foramen greatly. They then grow anteriorly and posteriorly until deposits issuing from successive septal neck regions approach each other very closely. In a dorsoventral section

<sup>1</sup>It has not been possible in this volume to eliminate completely the inconvenience arising from use of the word *annulus* for a feature of the body chamber and also for an endosiphuncular structure. For recommended usage consult the glossary of morphological terms.

of the siphuncle this condition resembles closely that of certain actinocerids, but in siphuncles with parietal deposits, these deposits are in contact with the connecting rings, whereas Actinocerida invariably have a well-developed perispatium.

Quite commonly, especially in the Pseudorthocerataceae, parietal deposits occur in combination with cameral deposits. The physiologic conditions under which both types of deposits could be formed at the same time are not yet understood.

Parietal deposits may be accompanied by more complex endosiphuncular structures, including tubes in the Pseudorthocerataceae, and endocones in the Discosoridae.

**Type 6.** This type of endosiphuncular structure is found only in the Actinocerida and will be discussed in greater detail in the description of that order. It suffices to state here that, like parietal deposits, annulosiphonate deposits begin to form in the general area of the septal neck. Contrary to the parietal deposits, however, they do not grow along the inner side of the connecting ring (Fig. 36,B). Instead, they spread rapidly inward in the endosiphuncle, avoiding contact with the connecting ring. The space between them and the ring is called **perispatium**. When they have reached their maximum development, the endosiphuncular space not occupied by them forms an elaborate system of one or more central, longitudinal canals, connected with the perispatia by radiating lateral canals. (See Figs. 34,F; 36,B.)

## EARLY ONTOGENY

Knowledge of the early ontogeny of fossil chambered cephalopods is based entirely on study of the most apical portions of the conch and of the siphuncle. These parts are well preserved in coiled conchs, though mostly difficult to expose or to extract from a fossil specimen. In orthocones and cyrtococones apical conch parts are rarely well preserved and knowledge of early ontogenetic stages of most such forms is very scanty.

An added handicap lies in the fact that many studies of early ontogenetic stages of orthoconic and cyrtococonic conchs are based on tiny, immature specimens, identification of which with species, or even genera, based on mature forms, is often in doubt.

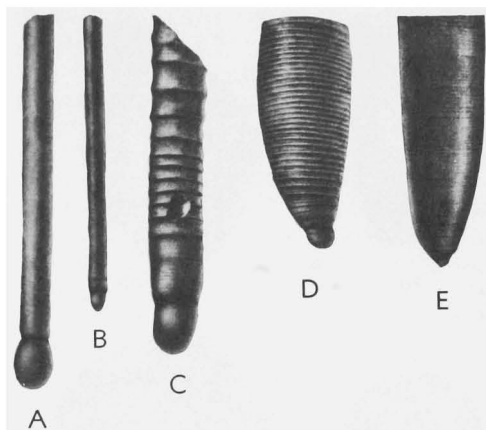


FIG. 38. Initial portions of nautiloid conchs: A, orthocerid, M.Dev., Ger.; B, orthocerid, U.Dev., Ger.; C, *Leurocyloceras?* sp., M.Dev., Ger.; D, *Geisonoceras?* *clavatum* (CORRENS), M.Dev., Ger.; E, *Trematoceras* sp., cf. *T. elegans* (MÜNSTER), U. Trias., Aus.,  $\times 6.6$  (27).

The most apical part of the phragmocone is the space enclosed between the actual apex of the conch and the first septum. This is the **first** or **initial** or **apical camera**. Since it is the first shelly structure built by the animal it may also be called the **protoconch**, but this term has been controversial in nautiloid morphology and is now little used.

The initial camerae of nautiloid cephalopods have many different shapes (Fig. 37). They are better known from orthocerids, endocerids, and the orders that include coiled conchs (Tarphycerida, Barrandeocerida, Nautilida) than from actinocerids, ascocerids, and oncocerids.

In orthocerids the initial camera may be bulbous or bluntly cone-shaped. Bulbous initial camerae may have a larger or slightly smaller diameter than the next following camera (Fig. 38). Bluntly cone-shaped camerae may be slightly impressed near the apex (Fig. 37,B). Initial camerae of cyrtococonic conchs may themselves show a faint indication of curvature (Fig. 39,2,3).

In breviconic conchs the initial chambers are probably deeply cup-shaped (Fig. 37,C), but little is known about the early growth stages among the Oncocerida and the Discosorida, the two orders containing the bulk of breviconic shells.

In coiled conchs the initial camera is short and shallow. This is probably true for all

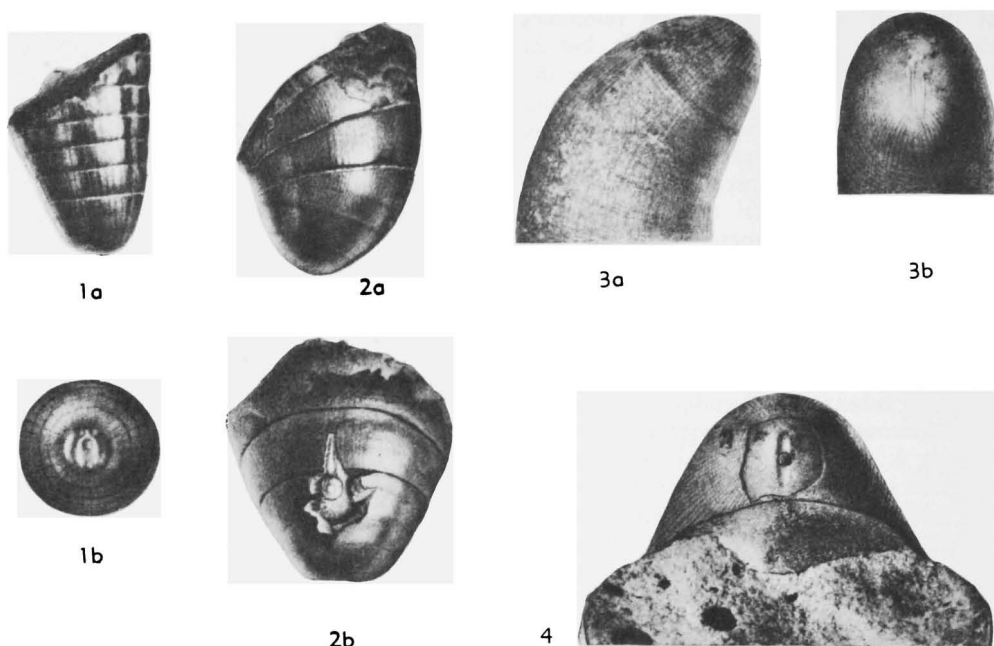


FIG. 39. Initial portions of nautiloid conchs with "cicatrix."—1a,b, *Kionoceras hyatti* (BARRANDE), U. Dev., Ger.—2a,b, *Oncoceras*, U.Dev., Ger.—3a,b, *Trochoceras* sp., Sil., Czech.—4. ?*Cymatoceras lineatum* (SOWERBY), M.Jur., Fr.;  $\times 4$  (27).

coiled nautiloids accommodated in the orders Tarphycerida, Barrandeocerida, and Nautilida (Fig. 37,F,G).

The only orthoconic group with short and shallow initial camerae is the Actinocerida, whose early ontogeny is very poorly known (Fig. 37,H), but a few genera (e.g., *Kochoceras*, *Selkirkoceras*, *Carbactinoceras*) seem to possess initial camerae that are broadly conical.

A somewhat different situation exists in the Endocerida (Fig. 37,D,E), but in order to understand the peculiar situation of this order it is necessary to discuss the early ontogeny of the siphuncle in the orders discussed above.

The initial segment of the siphuncle is called the **caecum**. It protrudes into the initial camera through the septal foramen of the first septum and is generally more or less bulbous. In some forms its diameter is slightly greater than that of the immediately following stages of the siphuncle. In living *Nautilus*, in many extinct nautilids, and probably in other coiled conchs, the caecum is attached to the bottom of the initial camera. In orthoconic forms, includ-

ing breviconic oncocerids and in some early coiled shells of the Tarphycerida and Barrandeocerida, the caecum ends freely in the initial chamber (Fig. 37,A-C,G), as in most ammonoids, where it is attached to the apex by means of the prosiphon. Such a structure, however, has not yet been found in nautiloids.

Present evidence suggests that direct attachment of the caecum to the apical part of the initial chamber is a comparatively late development which occurred toward the end of Paleozoic times.

The early ontogeny of the Endocerida presents somewhat different problems. In this order the initial part of the conch is broadly conical. In many endocerids the initial camera is short (Fig. 37,E), but at variance with all forms discussed above, a considerable part—as much as half of it—is occupied by the initial siphuncle segment, which is in broad contact with one side of the initial camera.

In another group of endocerids, formation of the first septum is long delayed and the apical portion of the conch is, for a distance of up to 2 or 3 cm., solely occupied by



the caecum, which takes up almost all the space of the initial camera (Fig. 37,D). Thus, the initial camerae of endocerids differ considerably from those of all other nautiloid orders, suggesting significant differences in organization of the animals during early ontogenetic stages.

On the exterior tip of the conch of living *Nautilus* there is a sharp, though shallow, slitlike furrow (Fig. 63, in chapter on "Living Nautilus"), generally called the *cicatrix*. Similar, or equivalent, features have been described from many fossil conchs (Fig. 39). The *cicatrix* is not always slitlike, as in *Nautilus*, but may be circular, ellipsoidal, cross-shaped, or quite irregular.

The *cicatrix* was regarded as a scar by HYATT and others—the place to which a nonpreservable "protoconch" had been attached, an original opening, later closed by a secondary deposit of calcium carbonate. However, nautiloids are known in which the apex is entirely smooth and it has been shown in *Nautilus* that the test is continuous across the *cicatrix*, with no indication of a secondary deposit. According to SCHINDEWOLF, the *cicatrix* was somehow connected with the caecum of the siphuncle. It is possible that traction exercised by the siphuncle on the inside of the test resulted in formation of a depression outside.

It is probable that at least in some nautiloids the initial camera, and two or three of the succeeding camerae developed inside the egg capsule. In living *Nautilus* the egg is known to be up to 45 mm. in diameter, thus comparable in size to the first whorl of the conch. It is, therefore, supposed that the conch is developed inside the egg at this stage (see chapter on "Living Nautilus"). Most probably, the early ontogeny of extinct members of the Nautilida followed a similar pattern.

In some orthocerids SHIMANSKIY (30) found that the first four or five camerae increase relatively rapidly in length and that a decrease in length occurs in the next following one or two chambers. SHIMANSKIY concluded that the change in camera length coincided with the moment of hatching. The same stage in bactritids is marked by a conspicuous constriction of the conch.

SHIMANSKIY (30) found that the number of septa in the first whorl of the conch is not constant within an investigated species

in each of several members of Nautilida. At the same time SHIMANSKIY observed that the septal angle was greater in the first whorl than in the following volutions. In general, it seems to be difficult to determine at what stage any fossil nautiloid conchs may have hatched from the egg.

The early ontogeny of the soft parts of the Endocerida and Actinocerida cannot be reconstructed with any degree of confidence because of the profound differences of the morphology of their initial camerae and caecum.

## SHELL TRUNCATION

In some orthoconic and cyrtconic forms apical parts of phragmocones were severed during the lifetime of the animals from the rest of the conchs. This process is known as *truncation* or *decollation*. Truncation in such shells occurred once or several times. The truncated part of the phragmocone is called the *deciduous portion*, the body chamber and attached anterior part of phragmocone the *mature portion* of the conch.

Truncation and its effects were first described by BARRANDE (1855, 1877) on the basis of study of over 500 well-preserved specimens of *Orthoceras truncatum*, type-species of the genus *Sphooceras* FLOWER (1962). BARRANDE observed that the number of camerae in specimens of *O. truncatum* varied from four to eight. He calculated that the total length of an average shell without truncation would have been about 50 cm. and that a complete phragmocone would have had some 100 camerae. He, therefore, concluded that truncation had taken place about 24 times in these shells. However, since not all shells can be supposed to have grown to the same size, BARRANDE's figure for number of truncations is probably a maximum rather than an average.

The basal septum of the mature portion of the conch is called *septum of truncation*. At the transition from the deciduous to mature portion of the conch, a slight shift in position of the siphuncle is accomplished by the *siphuncular displacement canal* (see chapter on Ascocerida).

Only the mature portion of the conch of *Sphooceras truncatum* is known with certainty, but FURNISH, GLENISTER & HANS-

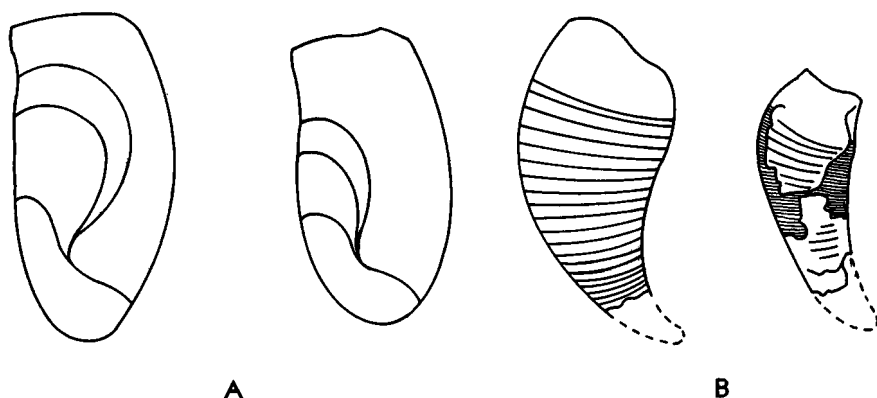


FIG. 40. Possible cases of sexual dimorphism in nautiloid orders (not to scale); A, Ascocerida (*Schuchertoceras*), Ord., USA,  $\times 0.7$ ; B, Oncocerida (*Oncoceras*), Ord., USA,  $\times 0.7$  (adapted from 9a,25).

MAN (1962) have listed several species of "*Orthoceras*" described by BARRANDE which could possibly represent deciduous portions of conchs of the same species. The same authors also called attention to the fact that *Plagiostomoceras pleurotomum* BARRANDE (family Orthoceratidae, subfamily Michelinoceratinae, p. K226) apparently shows a septum of truncation. This species occurs associated with *Sphooceras*, and both are of Silurian age.

Cases of truncation in another family of orthocerids, the Brachycycloceratidae of Carboniferous age, have only recently been demonstrated (12a). The genus *Brachycycloceras* (p. K232) was found to have been based on deciduous portions of conchs whose mature portions had been assigned to the genus *Poterioceras*. Furthermore, FURNISH, GLENISTER & HANSMAN have suggested that representatives of the family Neptunoceratidae (Carboniferous of the Ural Mountains) could well be truncated shells and even be congeneric with *Brachycycloceras*.

While it is thus obvious that the habit of shell truncation developed independently and at different times in at least two, possibly more, families of the Orthocerida, the same feature is characteristic of all representatives of the order Ascocerida, of Late Ordovician to Silurian age. This order is abundantly represented only in the Silurian rocks of the Island of Gotland, and it is from this locality that individuals of several species have been found consisting of de-

ciduous and mature portions before truncation occurred (19a). The morphology and ontogeny of the Ascocerida are discussed in detail in the systematic part of this volume (p. K263).

The biological processes that led to truncation are little understood. BARRANDE suggested that truncation was preceded by formation of a calcareous plug in the siphuncle at the septum of truncation. The posterior portion of the phragmocone was thus cut off from all metabolic processes, resulting in progressive solution and final destruction of the deciduous portion. On the other hand, TASNÁDI-KUBACSKA (34a) believes that truncation may have been due to resorptive processes, activated by the siphuncle and the intracamerar tissues (i.e., cameral mantle) and isolating the deciduous portion which finally broke off.

### SEXUAL DIMORPHISM

The conchs of the two sexes in living *Nautilus* differ only slightly in size and contradictory statements have been made as to the interpretation of these small differences. DEAN (1901) considered that the female conch was wider at the sides and the aperture more oval than that of the male conch, whereas WILLEY (1902) regarded the broader and more evenly rounded conch as that of a male and the narrower shape as a female conch. The latter view seems now, however, to have been confirmed (compare "Living Nautilus," p. K74).

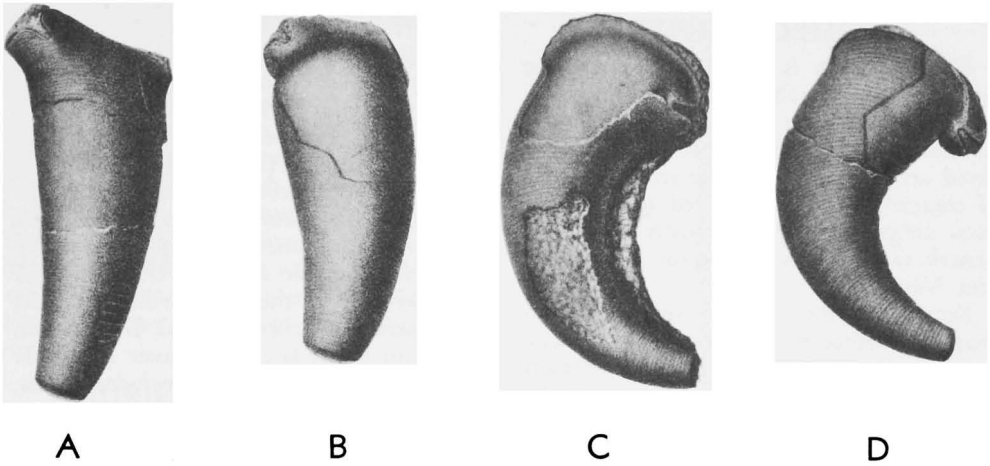


FIG. 41. Possible sexual dimorphism in Oncocerida (*Inversoceras*), M.Sil., Czech. The paired "species," A, *I. perversum* (BARRANDE) and B, *I. constrictum* FOERSTE, possibly are only sexual variants; the same may be true of C, *I. percurvatum* FOERSTE, and D, *I. barrandei* FOERSTE,  $\times 1$  (Barrande, pl. 53, 1865).

The possibility of recognizing sexual dimorphism in fossil nautiloids was first discussed by RUEDEMANN (24, 25) for Ordovician oncocerids. An assemblage of *Oncoceras* specimens studied by him fell into three morphological groups, two of which resembled each other in all respects except size and which RUEDEMANN considered to represent the two sexes of one and the same species. Following DEAN, he suspected that the larger variety might be the female (Fig. 40,B).

Similarly, TEICHERT (36) interpreted size difference of closely associated specimens of *Wadeoceras* as possible manifestation of sexual dimorphism in this genus.

FLOWER (7) also called attention to possible cases of sexual dimorphism among the breviceratid genera *Ovoceras*, *Brevicoceras*, and *Verticoceras*.

FOERSTE (11) suggested that presence or absence of a marked constriction at the base of the dorsal collar in Silurian *Inversoceras* might indicate sexual differences, but this possibility cannot be evaluated until it is more definitely known whether these varieties occur in assorted pairs (Fig. 41).

While all the above-mentioned examples concern members of the order Oncocerida, FLOWER (1946) also has cited cases of pairs of "species" or "varieties" of ascocerids occurring in the same bed, and resembling each other closely except for differences in size. Examples are taken from the genera

*Probillingsites* and *Schuchertoceras* (Fig. 40,A). FLOWER regarded the explanation of sexual dimorphism at least as an "interesting possibility."

In Actinocerida KOBAYASHI (19) called attention to the peculiar fact that in some species of *Armenoceras* and *Cyrtonybyoceras* the first, or first two, segments of the siphuncle are comparatively narrow and that a sudden increase in width takes place in the next following segment. He suggested that this sudden size increase of the siphuncle might indicate the onset of sexual maturity and might be especially characteristic of females. Doubt is thrown on this interpretation by the observation that in some genera (e.g., *Kochoceras*, *Selkirkeroceras*) the first siphuncle segment is invariably larger than any of the following segments.

Few observations on possible sexual dimorphism have been recorded for fossil Nautilida. STENZEL (1940) observed that in *Aturia*, if present at all, such differences were extremely slight.

In summary, no conclusive evidence has as yet been offered to demonstrate beyond doubt the presence of sexual dimorphism in extinct nautiloids. Observations that point in this direction have been cited mostly from the Oncocerida, but also from Ascocerida and Nautilida, and still more vaguely, from the Discosorida and Actinocerida.

## HOMEOMORPHY

Homeomorphy is widespread among the nautiloid orders, which is one reason why recognition of their relationships and their natural classification has been so long delayed and why, until rather recently, hosts of somewhat distantly related species have been assigned to a few, mostly ill-defined generic taxa such as *Orthoceras*, *Cyrtoceras*, and *Nautilus*.

Because of the basically simple conical shape of orthoconic or weakly cyrtoconic conchs, external homeomorphy is common among orders in which such types of conchs predominate. The conchs of many ellesmerocerids are indistinguishable externally from endocerids, on the one hand, and from some orthocerids, on the other. Among the oncocerids and the discosorids are a considerable number of externally homeomorphic, breviconic and short cyrtoconic forms. Considerable confusion prevailed in the classification of these two orders, until their siphuncle structures became better known.

Among coiled groups considerable external homeomorphy exists between the Tarphycerida and the Barrandeocerida, and also within the order Nautilida, examples of which are given in the introduction to that order.

Torticonic shells developed independently in the Tarphycerida (*Aethoceras*), the Barrandeocerida (*Mitroceras* and others), and even in the Oncocerida (*Nothoceras*) and in the Nautilida (*Trochoceras*).

A remarkable case of homeomorphy is the development of constricted ("visored") apertures of the *Phragmoceras*-type several times independently in entirely different lines of descent (FLOWER & TEICHERT, 1957): (1) In the Early Ordovician ellesmerocerid *Burenoceras*, (2) in Ordovician *Antiphragmoceras* (Discosorida), (3) in Middle Silurian *Phragmoceras* (Discosorida), and (4) in the Devonian oncocerid *Bolloceras*. In the Middle Silurian independent of the Phragmoceratidae, additional groups with visored apertures developed. These were the Hemiphragmoceratidae and the Mandaloceratidae.

Homeomorphic development of internal structures is likewise common. Thus, closely similar, evenly curved, cyrtocanitic septal necks appear independently in the Actinocerida, Orthocerida (superfamily

Pseudorthocerataceae and Paraphragmitidae of superfamily Orthocerataceae), Barrandeocerida (Nephriticeratidae), and in some Nautilida (Tainocerataceae). Abruptly recumbent, cyrtocanitic necks develop in the Oncocerida, the Discosorida, as well as in some Actinocerida (Armenoceratidae).

Along with cyrtocanitic septal necks goes the development of expanded, nummuloidal siphuncle segments which appear independently in the Pseudorthocerataceae, Actinocerida, Oncocerida, and Discosorida, and again much later in Triassic Nautilida (e.g., *Germanonautilus*, *Proclydonautilus*, *Pleuronautilus*).

The cameral deposits of many Orthocerataceae are quite similar to those of many Actinocerida, especially, where simple layers of episeptal and hyposeptal deposits are present.

Similar endosiphuncular structures develop homeomorphically in unrelated genera of diverse orders. For example, endosiphuncular central or subcentral tubes occur in the Orthocerida (*Harrisoceras*) Discosorida (*Madiganella*), Oncocerida (*Diestoceras*) and possibly in others. Actinosiphonate deposits are found in the Endoceratoidea (order Intejocerida) and in the Oncocerida, although the similarity of these structures in the two orders is probably more apparent than real. Endocones of very similar structure and appearance occur in the Endoceratoidea (order Endocerida), Discosorida (family Discosoridae and others), and Orthocerida (family Troedssonellidae).

Parietal deposits of closely similar shape and structure are characteristic of the Pseudorthocerataceae (order Orthocerida) and most members of the Discosorida. In certain late Paleozoic Pseudorthocerataceae (Pseudactinoceratinae) the parietal deposits develop to such an extent, filling almost the entire endosiphuncle, as to resemble closely the siphuncles of contemporaneous actinocerids (Carbactinoceratidae). Affinities of some genera are solely established on the basis of presence or absence of a peripatium.

*Brachycycloceras* represents a remarkable case of iterative evolution, resulting in homeomorphy of correlated morphological features with a genetically unrelated group of cephalopods of much earlier geologic age.

The shells of this genus consist of a deciduous, annulate, longiconic stage, and a rather plump, breviconic mature stage and body chamber, mimicking the Ordovician and Silurian *Ascocerida* with which the Pennsylvanian *Brachycycloceras* is not related through descent, although both stem from the *Orthocerida*. The genus shares with the *Ascocerida* such a specialized feature as the siphuncular displacement canal, which is a ventrally deflected portion of the siphuncle along the anterior face of the septum of truncation.

### INJURIES AND DISEASE

Many conchs of living *Nautilus* show evidence of more or less severe damage to the apertural region of the body chamber at various growth stages, but the mantle possesses considerable healing power and the broken edges are soon repaired. WILLEY (1902) described a shell of *Nautilus pompilius* with a deep, almost mid-dorsally situated revolving furrow which must have been due to permanent injury suffered at an early age by the animal, or perhaps by its mantle alone. LOESCH (20) has described a Jurassic nautilid shell with somewhat similar features in which, however, healing of the damaged or diseased mantle took place at full maturity.

BARRANDE (2) described a longiconic conch of *Plagiostomoceras* which is bent at an intermediate growth stage, but which straightened out again in later stages (Fig. 42). Since the test shows no sign of breakage the abnormal growth must have been caused by sickness or by internal injury.

In an assemblage of Cretaceous nautilids from Africa SORNAY (30a) found several specimens which possessed a hollow hump on the ventral sides of their conchs, at growth stages well before maturity was reached. The origin of this feature is obscure, but may be supposed to be connected with some malfunctioning of the mantle tissue. Deformed nautilid shells have also been described from the Cretaceous of France and from the Eocene of North America (Maryland).

It has already been mentioned in the chapter on the phragmocone that abnormal spacing of septa, except of the last few, is a



FIG. 42. Pathological growth disturbance in a conch of *Plagiostomoceras*, Sil., Czech.,  $\times 0.7$  (Barrande, pl. 299, 1868).

pathologic condition due to injury or disease (Fig. 21).

More recently, STUMBUR (33) has described a case of rather severe injury to a *Trocholites* conch at an intermediate growth stage. This injury seems to have affected the ventral sides of two chambers of the phragmocone, but the breakage was

healed when the animal had completed an entire whorl and a new, distorted shell layer was formed over the injured part.

In rare cases, as has already been mentioned in the description of the phragmocone, septa were only incompletely developed or the body advanced in the body chamber for a distance equal to that be-

tween several septa before the animal constructed a new septum. Such conditions have been described by BARRANDE, KESSLER, and HÖLDER in straight and coiled Paleozoic and Mesozoic conchs. The origin of these malformations is not known. Presumably they were caused by malfunctioning of the mantle surface that secreted the septa (14b).

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## GLOSSARY OF MORPHOLOGICAL TERMS USED FOR NAUTILOIDS

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**ACHOANITIC.** Descriptive of condition in which septal necks are vestigial or absent (*syn.*, aneuchoanitic).

**ACTINOSIPHONATE.** Descriptive of endosiphuncular deposits consisting of radially arranged longitudinal lamellae.

**ADNATION AREA.** Area along which connecting ring is in contact with adapertural surface of free part of septum.

**air chamber.** *See* camera.

**AMORPHOUS BAND.** Narrow bands surrounding conchiolinous zone in thick connecting rings of some specialized discosorids.

**aneuchoanitic.** *See* achoanitic.

**annular elevation(\*).** Area on inside of posterior part of body chamber between anterior margin of anterior aponeurotic band and posterior margin of posterior aponeurotic band, and including retractor muscle attachment areas.

**ANNULAR LOBE.** Small, secondary dorsal lobe in center of main internal (dorsal) lobe of suture of some coiled forms.

**ANNULATE.** Marked by or bearing annulations.

**ANNULATION.** Ringlike expansion of conch, either transverse or slightly oblique to longitudinal axis of conch.

**annulosiphonate.** Descriptive of endosiphuncular deposits having shape of rings formed at septal foramen and attached to inside of septal neck.

**ANNULUS.** Thin, ring-shaped endosiphuncular deposit, semicircular in cross section, on inner side of septal neck.

**annulus.** *See* periphraet.

**apertural ridge (\*).** Ridgelike thickening inside apertural margin of body chamber.

**APERTURE.** Opening of shell through which head-foot protrudes.

**APICAL CAMERA or CHAMBER.** First camera of phragmocone. (*syn.*, initial camera or chamber).

**APONEUROTIC BANDS.** Areas of attachment of palliovisceral ligaments on inside of body chamber; anterior and posterior aponeurotic bands are recognized.

**ASCOCEROID CONCH.** Specialized brevicone, bounded at base by septum of truncation; consisting of inflated posterior portion with dorsal phragmocone, and anterior cylindrical neck.

**ASCOCEROID SEPTUM.** Specialized partition between chambers (septum) in late growth stages of Ascocerida, sigmoidal in section, and strongly bent forward on dorsum, with complex (sigmoid) suture.

**BASAL SEPTUM.** Wall (septum) with normal suture between septum of truncation and first ascocerooid septum (Ascocerida only).

**basal zone.** Adapical interior zone of body chamber in which shell wall is thickened, commonly with pitted or banded surface.

**blade.** *See* endosiphuncular blade.

**BODY CHAMBER.** Large undivided, anterior space in conch open at aperture, occupied by animal's body (*syn.*, living chamber).

**BREVICONE.** Short and rapidly expanding conch.

**BRIM.** Flared or recurved portion of cyrtchoanitic septal neck.

**BULLETTE.** Annulosiphonate deposits similar to annulus, but flatter and more elongated in cross section; name derived from knob- or bosslike appearance of deposit in cross section.

**BUNDLED.** Descriptive of ribs in coiled conchs, united in sheaves or bundles at or near umbilical shoulder.

**CADICONE.** Coiled conchs which are strongly depressed, and more or less evolute, with wide venter and deep umbilicus.

**CAECUM.** Sac-shaped apical end of siphuncle; also, cavity associated with digestive system (living *Nautilus*).

**CAMERA.** Space enclosed between two adjacent septa but not including siphuncle (adj., cameral) (*syn.*, chamber, gas chamber, air chamber).

**CAMERAL DEPOSITS.** Calcareous deposits secreted against original walls of camerae during life of animal (*syn.*, intracameral deposits).

**CENTRAL CANAL.** Longitudinal cavity (canal) in or near center of siphuncle of Actinocerida.

**centrifugal deposits.** *See* parietal deposits.

**chamber.** *See* camera.

**chitinous zone.** Referred to by authors who are unaware that mollusks do not secrete chitin; *see* conchiolinous zone.

**CICATRIX.** Small groove or scar on apex of some conchs.

**CIRCULUS.** Cameral deposit on concave surface of cyrtchoanitic septal neck (*syn.*, *Stützring*, supporting ring).



- CIRCUMSIPHUNCULAR RIDGE.** Ridgelike thickening of episeptal deposits in immediate neighborhood of connecting ring.
- collum.** *See* septal neck.
- COMPRESSED.** Descriptive of conch and dorsoventral diameter greater than lateral.
- CONCAVOSIPHONATE.** Descriptive of siphuncles concave in section between septa.
- CONCH.** All hard calcareous parts secreted by nautiloid animal including external shell, septa and siphuncle, but not cameral deposits and any structures within siphuncle (*syn.*, shell, test).
- CONCHAL FURROW.** Shallow groove on inside of conch wall, located mid-ventrally.
- [conchial (*recte*, conchal) zone I(\*).** Anterior aponeurotic band.]
- [conchial (*recte*, conchal) zone II(\*).** Posterior aponeurotic band.]
- conchiolinous zone.** Posterior half of free part of thick connecting ring in some discosorids.
- CONNECTING RING.** Partly calcareous, partly conchiolinous, tubular membrane, that connects septal neck of ellipchoanitic conchs with septum immediately behind it; vestiges of it are also found in holochoanitic forms.
- conotheca.** Part of conch comprising external shell (*syn.*, shell wall).
- CONSTRICTED.** Descriptive of body chamber having smallest diameter close behind aperture.
- CONSTRICITION.** Narrow transverse depression of conch.
- CONTACT LAYER.** Deposit formed between connecting ring and septum on area of adnation in some conchs (Actinocerida only).
- CONTRACTED.** Descriptive of aperture having diameter smaller than maximum diameter of body chamber.
- CORONATE.** Descriptive of whorl section (of coiled conchs) which is depressed and has divergent flanks.
- costae.** *See* ribs.
- CYRTOCHOANITIC.** Descriptive of comparatively short, retrochoanitic septal necks which are curved so as to be concave outward.
- CYRTOCONE.** Curved conch that completes less than one whorl.
- DECIDUOUS CONCH.** Apical juvenile phragmone truncated during ontogeny (e.g., Ascocerida, some Orthocerida, and possibly other groups).
- decollation.** *See* truncation.
- DEPRESSED.** Descriptive of conch with lateral diameter greater than dorsoventral.
- DIAPHRAGM.** Imperforate partition crossing siphuncle.
- distal deposits.** *See* hyposeptal deposits.
- distal division of siphonal funnel(\*).** Connecting ring.
- domiciliary cavity(\*).** Body chamber.
- domiciliary division(\*).** Body chamber.
- DORSAL AREA.** Part of whorl of coiled conch which is in contact with preceding whorl.
- dorsal furrow.** *See* septal furrow.
- DORSAL HIATUS.** Small area without deposits in mid-dorsal region of camerae which have cameral deposits.
- DORSAL LOBE.** Median primary lobe of suture on dorsum; in coiled forms, also called internal lobe.
- DORSOLATERAL BANDS.** Thin layers of cameral deposits on dorsolateral side of camerae.
- DORSOMYARIAN.** Descriptive term applied to nautiloid cephalopods in which retractor muscles of head-foot are attached to shell along interior areas of body chamber adjacent to, or coincident with, its dorsal mid-line.
- DORSOVENTRAL SECTION.** Longitudinal section through straight or symmetrically curved and coiled conchs, intersecting shell wall along mid-dorsal and mid-ventral lines, bisecting conch into two symmetrical parts.
- DORSUM.** Side of animal or conch opposite venter; in live *Nautilus* region occupied by shell coil above body chamber. [Among fossil nautiloids, if the position of the hyponomic sinus (and therefore venter) cannot be established, the term is somewhat loosely applied (1) in coiled forms to the concave side of a whorl, (2) in straight or curved conchs with eccentric siphuncle to the side farthest removed from the siphuncle.]
- ectosiphon.** *See* ectosiphuncle.
- ECTOSIPHUNCLE.** Wall of siphuncle consisting generally of septal necks and connecting rings (*syn.*, ectosiphon).
- ECTOSIPHUNCULAR SUTURE.** Line on inside of shell or on internal mold bounding area of contact of siphuncle and shell wall. [Ectosiphuncular sutures occur in each camera of nautiloids with marginal siphuncles, especially endocerids and actinocerids.]
- ELLIPOCHOANITIC.** Descriptive of relatively short retrochoanitic septal necks which do not reach as far as preceding septum (refers to all types of septal necks except holo-, subholo-, and macrochoanitic).
- ELLIPTICONE.** Coiled conch having elliptical coiling of last whorl or half-whorl, which breaks away from spiral.
- ENDOCON.** One of series of calcareous cones formed in posterior or adapical portion of siphuncle mainly of endocerid and discosorid conchs.
- ENDOGASTRIC.** Descriptive of conchs curved or coiled in manner placing venter on or near inner or concave side.
- endosphoblade.** *See* endosiphuncular blade.
- ENDOSIPHOCOLEON.** Flattened, ?conchiolinous tube or blade surrounding endosiphuncular tube in some endocerids.
- ENDOSIPHOCONE.** Conical space inside last-formed endocone in Endocerida and some Discosorida.
- endospholinizing.** *See* endosiphuncular lining.
- endosphon.** *See* endosiphuncle.
- endosphotube.** *See* endosiphuncular tube.
- endosphowedge.** *See* endosiphuncular wedge.

- ENDOSIPHUNCLE.** Space within ectosiphuncle including all organic tissues and calcareous structures.
- ENDOSIPHUNCULAR BLADE.** Longitudinal membranes or partitions traversing endocones in siphuncle of Endocerida.
- ENDOSIPHUNCULAR LINING.** Dark lining seen inside septal necks of some endocerids, probably formed by continuous connecting rings.
- ENDOSIPHUNCULAR TUBE.** (1) Circular tube formed by adapical thickening of lateral walls of endosiphuncle in some Endocerida; (2) simple tubes connecting apices of endocones where no differentiation of coleon and tube is possible.
- ENDOSIPHUNCULAR WEDGE.** Wedge-shaped deposit in apical part of siphuncles of certain pilocerids.
- EPISEPTAL DEPOSITS.** Cameral deposits on concave (or adapertural) side of septum (*syn.*, proximal deposits).
- episeptal tubercle(\*)**. Dorsal or annular lobe as expressed on posterior side of septum.
- EURYSPHONATE.** General term for forms with relatively large siphuncles.
- EVOLUTE.** Descriptive of coiled conchs in which whorls do not overlap considerably, hence having wide umbilicus.
- EXOGASTRIC.** Descriptive of conchs curved or coiled so that venter is on or near outer or convex side.
- EXTERNAL LOBE.** Often used for ventral lobe of suture in coiled conchs (*syn.*, ventral lobe; in ammonoids, siphonal lobe).
- EXTERNAL SUTURE.** Part of suture of coiled conchs exposed on outside of whorls between the umbilical seams.
- EYELET.** Specialized region in tip of connecting ring in many stenosphonate cephalopods, characterized by dense fine-grained or amorphous material.
- FALCATE.** Sickie-shaped (ribs).
- FALCOID.** Somewhat sickie-shaped (ribs).
- FALSE CONTACT.** Condition in which connecting ring and septum are separated by contact layer (Actinocerida only).
- FASCICULATE.** Descriptive of ribbing in coiled conchs having bunched or bundled ribs at umbilical tubercles or near umbilical margin.
- FIRST LATERAL LOBE.** First primary adapical inflection of suture next to ventral (or external) lobe, usually situated on flank of coiled conchs.
- FLANKS.** Sides of conch between venter and dorsum (*syn.*, whorl sides, lateral areas).
- FLARED.** Descriptive of aperture of constricted body chamber having apertural diameter greater than diameter of inflated portion of body chamber.
- foramen** (pl., **foramina**). *See* septal foramen.
- FREE PART OF CONNECTING RING.** Part of connecting ring not in contact with septa.
- FREE PART OF SEPTUM.** Part of septum which separates camerae.
- funnel.** *See* septal funnel.
- funnel emargination(\*)**. Hyponomic sinus.
- gas chamber.** *See* camera.
- GRANULAR ZONE.** Anterior half of thick, specialized connecting rings in some discosorids.
- GROWTH LINES.** Markings on surface of conch that denote periodic increases in size and hence former positions of aperture.
- GYROCONE.** Loosely coiled conch in which successive whorls are not in contact with each other.
- HEMICHCHOANITIC.** Descriptive of retrochoanitic septal necks that extend one-half to three-fourths of distance to preceding septum.
- HOLOCHCHOANITIC.** Descriptive of retrochoanitic septal necks that extend backward through length of one camera.
- HYPONOMIC SINUS.** Large concave sinus in middle of aperture, marking location of hyponome, invariably ventral.
- HYPOSEPTAL DEPOSITS.** Cameral deposits on convex (adapical) side of septum (*syn.*, distal deposits).
- hyPOSEPTAL fossa(\*)**. Dorsal or annular lobe expressed on anterior side of septum.
- IMPRESSED AREA.** Concave dorsum in coiled conchs, in contact with venter of preceding whorl and tending to overlap it (*syn.*, impressed zone).
- impressed zone.** *See* impressed area.
- INITIAL CHAMBER or CAMERA.** First camera of phragmocone (*syn.*, apical camera or chamber).
- intercostae.** *See* interspaces.
- intermediate area(\*)**. Part of "annular elevation" which does not serve as muscle attachment area.
- INTERNAL LOBE.** Identical with dorsal lobe in coiled forms.
- INTERNAL SUTURE.** Part of suture in coiled conchs situated on dorsum and hidden from view unless conch is broken.
- INTERSEPTAL LINING.** Lining between mural parts of two successive septa, formed after earlier but before later septum.
- INTERSPACES.** Spaces between ribs in coiled conchs.
- intracameral deposits.** *See* cameral deposits.
- INVOLUTE.** Descriptive of coiled conchs with considerably overlapping whorls, hence with narrow umbilicus.
- KEEL.** Continuous sharp ridge along venter of conch, especially in coiled forms.
- LACUNA** (pl., **LACUNAE**). Axial septal discontinuity, within ascoceroid septum, bounded by line of contact with preceding septum.

**LANCEOLATE.** Descriptive of spear-shaped whorl sections with acute periphery.

**LATERAL ANGLE.** Angular bend in lateral part of ascocerid suture.

**lateral areas.** *See* flanks.

**LATERAL LOBE.** Any adapical inflection of suture between ventral and dorsal lobes. [In coiled conchs lateral lobes may be external or internal according to whether they are on flanks or dorsal area.]

**LATERAL SADDLE.** Any adapertural inflection of suture separating lateral lobes from each other or from external or internal lobes; distinction of external and internal lateral saddles same as for lateral lobes.

**LATERAL SINUS.** Re-entrant in lateral portion of apertural margin.

**LINEATION.** Pattern of fine linear markings, whether raised or incised, on surface of conch.

**LIRAE.** Parallel fine ridges or raised lines on surface of conch, transverse or longitudinal, separated by striae. [Restricted to features not easily discernible with the naked eye.]

**LIRATE.** Surface bearing lirae.

**LITUICONE.** Conch which completes few whorls in early stages and then becomes straight (*syn.*, luititicone).

**luititicone.** *See* luititicone.

**living chamber.** *See* body chamber.

**LOBE.** Adapically (or backward) convex undulation of suture (reverse of saddle).

**lower annular ridge(\*).** Ridgeline thickening of anterior edge of "annular elevation."

**LOXOCHOANITIC.** Descriptive of retrochoanitic septal necks that are short, straight, pointing obliquely toward interior of siphuncle.

**lunette.** Sometimes used for annulosiphonate deposits which are large and massive, as in many Actinocerida.

**MACROCHOANITIC.** Descriptive of retrochoanitic septal necks that reach backward beyond preceding septum and are invaginated into preceding septal neck.

**MARGINAL ATTACHMENT BAND.** Attachment area of anterior mantle edge to inside of test along aperture.

**MATURE PART OF CONCH.** Body chamber and anterior portion of phragmocone after loss of deciduous portion of conch by truncation.

**MURAL DEPOSITS.** Cameral deposits along mural parts of septa.

**MURAL PART OF SEPTUM.** Part of the septum attached to wall of conch.

**mural ridge(\*).** Ridgeline thickening of anterior margin of mural part of septum.

**NAUTILICONE.** Strongly involute coiled conch.

**NECK.** Constricted anterior part of body chamber in specialized brevicones between aperture and inflated portion (not to be confused with septal neck).

**nepionic bulb.** Term sometimes used for swollen apical part of siphon in some Endocerida.

**nepionic flange.** Short adapical extension of wall of first camera.

**NEPIONIC LINE.** Very distinct transverse line on test, slightly in front of first whorl of coiled conchs.

**nummuli.** Sometimes used for siphuncular segments that are strongly inflated between septa, mostly in Actinocerida.

**ocular emargination(\*).** Ocular sinus (in *Nautilus*).

**OCULAR SINUS.** One of pair of small and shallow sinuses at sides of aperture in position of eyes in *Nautilus*.

**ORTHOCHOANITIC.** Descriptive of retrochoanitic septal necks which are straight, cylindrical, and extend only a short way to preceding septum.

**ORTHOCONE.** Straight conch.

**OXYCONE.** Laterally compressed coiled conch with acute periphery and usually narrow or occluded umbilicus.

**PIRIETAL DEPOSITS.** Annulosiphonate deposits that grow close against connecting ring and do not normally project markedly into siphuncular cavity (*syn.*, centrifugal deposits).

**PENDENT DEPOSITS.** Annulosiphonate deposits in contact with wall of siphuncle only at their point of origin.

**PERIPHRACT.** Continuous band of muscles and aponeuroses that encircles body, consisting of dorsal aponeurosis, retractor muscles, and anteroventral aponeurosis (*syn.*, annulus). Term derived from Greek (*peri*, around; *phractus*, enclosed); *adj.*, periphractic, multiply connected.

**PERISPATIAL DEPOSITS.** Primary lamellar deposits developed in perispantium of Actinocerida.

**PERISPATIUM.** Space between annulosiphonate deposits and free part of connecting ring in Actinocerida.

**PERISTOME.** Edge of aperture.

**PHRAGMOCONE.** Chambered portion of conch.

**PLANULATE.** Descriptive of coiled conchs which are moderately compressed and moderately evolute, with open umbilicus and bluntly rounded venter.

**PLATYCONE.** Coiled conch with flattened venter, without implications as to width of umbilicus or form of venter.

**PLEUROMYARIAN.** Descriptive term applied to nautiloid cephalopods in which shell or retractor muscles of head-foot are attached along lateral areas of interior of body chamber.

**PLICATE.** Surface covered with vague foldlike ribs.

**PRE-BASAL SEGMENT.** Segment of siphuncle lying between septum of truncation and basal septum (in Ascocerida).

**PROTOCONCH.** First portion of embryonic shell, its preservation in fossil and in living forms uncertain. [Some authors regard the first camera as the protoconch.]

**proximal deposits.** *See* episeptal deposits.

**proximal division of siphonal funnel(\*).** Septal neck.

**pseudoseptum.** Plane of junction between hyposeptal deposits of one septum and episeptal deposits on preceding septum.

**RADIAL CANALS.** Tubes connecting central canal with perispatium in Actinocerida.

**RECUMBENT BRIM.** Brim of cyrtchoanitic septal necks, recurved so sharply that it lies in contact with adapical surface of free part of septum.

**RETROCHOANITIC.** Descriptive of septal necks which are directed backward (*syn.*, retrosiphonate).

**retrosiphonate.** *See* retrochoanitic.

**RIBS.** Raised radial ridges on coiled conch.

**SADDLE.** Adaperturally (or forward) convex undulation of suture (reverse of lobe).

**SEGMENT OF SIPHUNCLE.** Any part of siphuncle between two successive septal foramina.

**septal elements.** *See* sutural elements.

**SEPTAL ANGLE.** Angle between tangents drawn from apex of planispiral shell to two successive septa and measured on a section made along plane of symmetry.<sup>1</sup>

**SEPTAL FORAMEN.** Opening in septum allowing passage of siphuncular cord (*syn.*, siphuncular foramen).

**septal funnel.** Septal neck which extends at least as far as preceding septum and is more or less invaginated into next septal funnel.

**SEPTAL FURROW.** Narrow mid-dorsal region in which mural part of septum is lacking.

**SEPTAL NECK.** Portion of septum which is bent adapically (or backward) around septal foramen (*syn.*, collum).

**septate division**(\*). Phragmocone.

**SEPTUM.** Partitions dividing phragmocone into camerae and attached to inside of wall of conch.

**SEPTUM OF TRUNCATION.** Transverse partition of conch comprising specialized thick septum which forms base of mature shell in groups which decollated juvenile phragmocone (e.g., Asco- cerida, some Orthocerida).

**septum proper**(\*). Free part of septum.

**SERPENTICON.** Coiled many-whorled conch, very evolute, with whorls hardly overlapping.

**shell.** *See* conch.

**SHELL WALL.** Part of conch comprising external shell.

**SIGMOID SUTURE.** Prominent dorsal lobes, and more or less S-shaped suture in lateral aspect, as developed in late growth stages of Asco- cerida.

**SINUS.** Any part of transverse feature (apertural margin, ribs, growth-lines) concave toward aperture.

**siphon.** *See* siphuncular cord (adj., siphonal).

**siphonal caecum.** *See* caecum.

**siphonal funnel**(\*). Ectosiphuncle.

**siphonal lobe.** *See* external lobe.

**siphonal tube**(\*). Ectosiphuncle.

**SIPHUNCLE.** Long slender or thick tube extending through all camerae to apex and consisting of soft and shelly parts, including septal necks, connecting rings, calcareous deposits, and siphuncular cord (adj., siphuncular).

**SIPHUNCULAR CORD.** Fleishy interior tissues of siphuncle.

**SIPHUNCULAR DISPLACEMENT CANAL.** Tube through which the siphuncle was deflected ventrally across anterior face of septum of truncation (e.g., some Asco- cerida and Orthocerida).

**SIPHUNCULAR SEGMENT.** Portion of siphuncle between any two successive septal foramina.

**SPHAEROCON.** Coiled conch, depressed, involute, globular, with round venter and umbilicus quite or nearly occluded.

**STENOSIPHONATE.** General term for forms with relatively narrow siphuncle.

**STRIAE.** Parallel, small to minute grooves or channels on surface of conch, either transverse or longitudinal, separated by lirae. [Restricted to features not easily discernible with the naked eye.]

*Stüttring.* *See* circulus.

**SUBHOLOCHOANITIC.** Descriptive of retrochoanitic septal necks approximately equal in length to distance between two septa, but deflected inward at their tips, leaving appreciable gap between two successive septal necks.

**SUBORTHOCHOANITIC.** Descriptive of retrochoanitic septal necks that are short and straight, with slightly outwardly inclined tips but with no measurable brim.

**supporting ring.** *See* circulus.

**SUTURAL ELEMENTS.** Major parts of suture directed alternately forward (saddles) and backward (lobes) (*syn.*, septal elements).

**SUTURE.** Line of junction of free part of septum and inner side of phragmocone wall (*syn.*, systegnosis).

**systegnosis**(\*). Suture.

**tabulate.** *See* platycone.

**tarphophioceracone.** Specialized litiucone.

**tarphyceracone.** *See* serpenticon.

**test.** *See* conch.

**TORTICON.** Conch coiled in helicoidal spire, as in gastropods (*syn.*, trochoceroid).

**trochoceroid.** *See* torticon.

**TRUNCATION.** Natural loss, in life, of apical portion of shell (*syn.*, decollation).

**UMBILICAL ANGLE.** Same as umbilical shoulder, but angular.

**UMBILICAL AREAS.** Surface of inner whorl of coiled conchs exposed between umbilical seams.

**UMBILICAL PERFORATION.** Vacant space around axis of coiling and connecting umbilicus on opposite sides of shell.

**UMBILICAL SEAM.** Helical line of junction of adjacent whorls of coiled conchs (*syn.*, umbilical suture).

<sup>1</sup> The whole complex of septal angles in an individual is a specific character according to SHIMANSKIY, V. N., 1948 (30) (p. K386).

**UMBILICAL SHOULDER.** Strongly bent portion of whorl between flank and umbilical slope or wall.

**UMBILICAL SLOPE.** Inner part of umbilical area, tilted more or less toward umbilicus and separating umbilical seam from umbilical shoulder.

**umbilical suture.** *See* umbilical seam.

**UMBILICAL WALL.** Inner part of umbilical area sloping toward umbilical seam from umbilical shoulder.

**UMBILICUS.** External depression around axis of coiling near center of whorls of coiled conchs.

**upper annular ridge(\*).** Ridgelike thickening of posterior edge of "annular elevation" (fossil nautiloids only).

**vacuosiphonate.** Sometimes used to describe empty siphuncles, without deposits.

**VENTER.** Underside of organism and of conch, distinguished generally by hyponomic sinus and often by conchal furrow.

**VENTRAL LOBE.** Main adapical inflection of suture on venter, in coiled conchs also called external lobe.

**ventral sinus.** Furrow in the cameral deposits along ventral side.

**VENTROLATERAL ANGLE.** Angle between venter and flank of coiled conch.

**ventrolateral masses.** Cameral deposits on both sides of ventral sinus.

**VENTROLATERAL SHOULDER.** Same as ventrolateral angle but blunt.

**VENTROMYARIAN.** Descriptive term applied to nautiloid cephalopods in which shell or retractor muscles of head-foot are attached along areas of interior of body chamber adjacent to, or coincident with, its ventral mid-line.

**VINCULUM.** Calcitic portion of thick discosorid connecting rings attached to posterior side of septum.

**volution.** *See* whorl.

**WHORL.** Complete turn of coiled conch (*syn.*, volution).

**WHORL SECTION.** Transverse section of whorl.

**whorlsides.** *See* flanks.

## LIVING NAUTILUS

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### ACKNOWLEDGMENTS

The chapter on "Living Nautilus" was the first part of the *Treatise* to be published. A preprint edition appeared 15 April, 1952. The presentation given here is the same in its major features.

Special thanks are expressed to Dr. ANNA BIDDER for information and critical reading of the manuscript, Dr. DON F. McMICHAEL for the photographing of the young shell shown in Figs. 64, 65, Dr. R. TUCKER ABBOTT for help and permission to use the collections at the Academy of Natural Sciences of Philadelphia.

### INTRODUCTION

The fleshy parts of Tetrabranchiata are known only from the sole surviving genus *Nautilus* and traces or imprints of soft parts found in a few Ammonoidea and some of the extinct nautiloid orders. The anatomy of *Nautilus* is described by GRIFFIN (11), MUGGLIN (17), and WILLEY (28). Observations on the general biology of living animals were made by Dean (8) and Willey

(28). In 1960-61 *Nautilus* was studied at New Caledonia, the Loyalty Islands, and New Guinea by Dr. Anna Bidder (2a,2b), who reviewed this chapter.

The fleshy parts of *Nautilus* occupy the interior of the planispirally coiled shell, and the body occupies and conforms exactly to the shape of the body chamber, which is the last or outermost of the chambers and is open at the shell aperture (Figs. 43, 68). In natural position, the plane of bilateral symmetry stands vertical and the shell coil is above or dorsal to the body chamber. The body is nearly horizontal. The head, surrounded by tentacles (together constituting the head-foot), protrudes at the shell aperture, pointing forward.

Morphological orientation of the animal is complicated by planispiral coiling. Hence, to some extent its terminology is arbitrary: the head-foot is anterior, the longitudinal horizontal direction toward the shell away

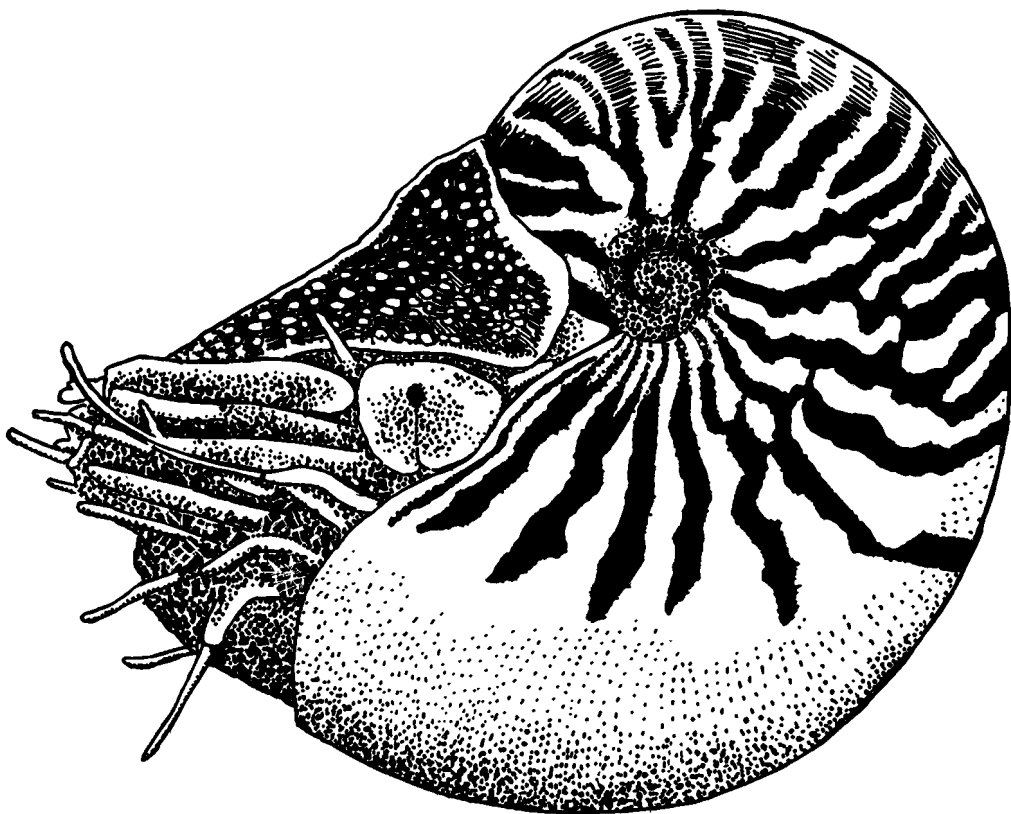


FIG. 43. *Nautilus macromphalus* G. B. SOWERBY (1849), drawn by H. B. STENZEL from photograph of live individual in the aquarium of Dr. RENÉ CATALA in Nouméa, New Caledonia,  $\times 0.7$  (from a photograph in *The Lower Animals* by Ralph Buchsbaum & L. J. Milne).

from the head-foot is called posterior, the shell coil is dorsal, and the convex outside curve of the body is called ventral. However, if only a piece of the shell coil is described, very arbitrarily its convex outside is called ventral and its concave side is called dorsal, irrespective of the particular position this piece may have occupied on the living animal.

### ANATOMY OF SOFT PARTS OF NAUTILUS

The soft parts of the animal consist of the following regions: (1) **head-foot** or cepitopodal region [*cephalopodium*, *Kopffuss*], including mouth, buccal mass, eyes, hood, tentacles, and locomotor organ (hyponome); (2) **body**, from the posterior edge of the head-foot to the septum that closes off the rear end of the body chamber, including

the visceral sac, which contains the viscera, and the mantle with mantle cavity, which encloses the hyponome with its crura and the four gills and into which empty the reproductive, excretory, and digestive systems; and (3) **siphuncular cord**, the fleshy portion of the siphuncle, which is a long, slender, fleshy tube [*siphon* of some authors], extending through all air chambers to the apex of the shell and coiled like the shell.

The head-foot is not as well separated from the body as in the Coleoidea. Body and head-foot together are 15 to 18 cm. long in adult *Nautilus pompilius* LINNÉ.

### HEAD-FOOT

#### CEPHALIC CARTILAGE AND BUCCAL MASS

The head is built on a large strong H-shaped cephalic cartilage, which is 4.75 cm.

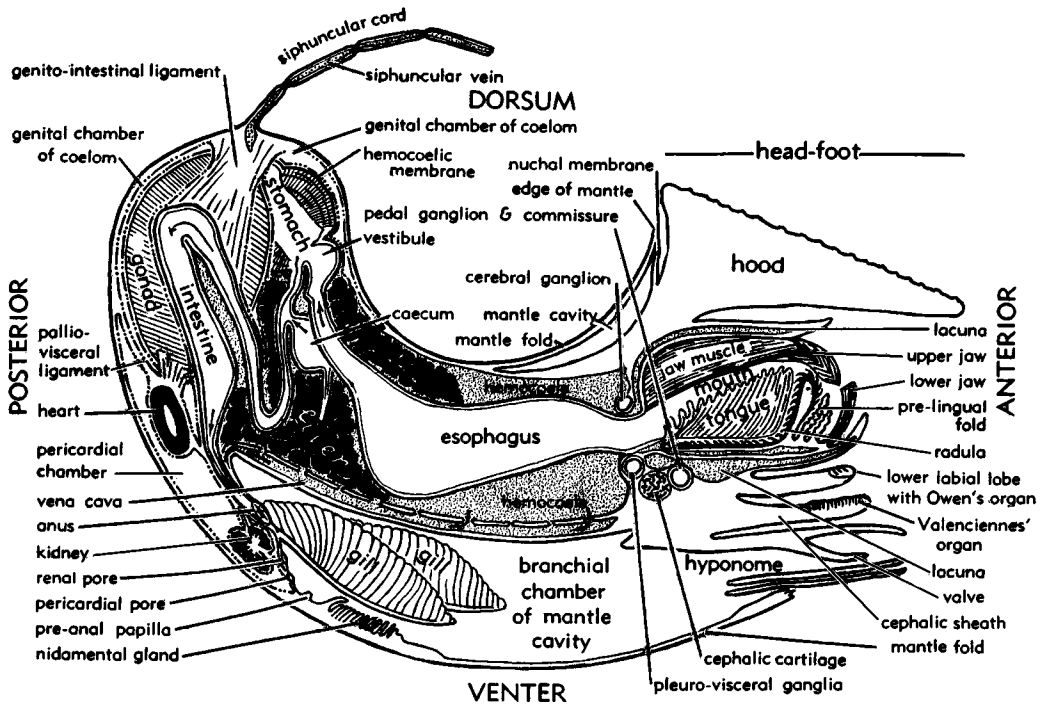


FIG. 44. Diagrammatic median section through the fleshy parts of *Nautilus*; venous blood indicated by stippling and outline of the coelom shown by dash-dot line,  $\times 0.6$  (modified from 11, 12, 30).

long and 3 cm. wide in an average adult (Fig. 44). The cartilage anchors the hyponome and major muscles, supports the nerve centers and balance organs (statocysts) and protects but does not enclose them as in the Dibranchiata.

Adjacent to and connected with the cartilage by muscles is the large and bluntly conical buccal mass, surrounding the mouth; it is built around a large, horny two-jawed beak, like that of a parrot, which is activated by strong muscles anchored on the cartilage. The upper jaw fits snugly into the projecting lower jaw; both are massive and made of conchiolin reinforced by hard calcareous material. The lower jaw is 30 mm. long and 28 mm. wide; the upper is 32 mm. long and 17 mm. wide (Fig. 44A). Both jaws are hooked, the upper less so than the lower one. The upper jaw is more pointed, with calcification concentrated in front to form a strong, sharp beak. The calcified portion has the shape of a low pyramid which is roughly four-sided and bilaterally symmetrical, with two rounded and two sharp edges converging into a tip; the tip curves downward to form the point of the beak and the

sharp edges form its sides to left and right. Its black, tough, conchiolinous portion extends backward into the buccal mass and forms two flanges; the upper flange is much shorter than the lower one, which occupies the roof and sides of the mouth. Calcification of the lower jaw, distributed on both sides of the black conchiolin layer, is less concentrated. The conchiolinous portion of the lower jaw extends backward to form two flanges, the inner much shorter than the outer one, which covers much of the outside of the buccal mass. The upper jaw is rigid, whereas the lower jaw is somewhat flexible because calcification of the beak is less strong and less concentrated. The lower jaw can yield slightly when the jaws bite through bones or the hard coverings of prey, thereby protecting the beaks from accidental fracture. Because of their calcification, the beaks in the jaws may be fossilized; such fossils (rhyncholites) are known, although they are much less common than shells or internal molds of shells.

On the floor of the mouth is the large tongue (subradular organ), which bears a long-toothed radula reaching into

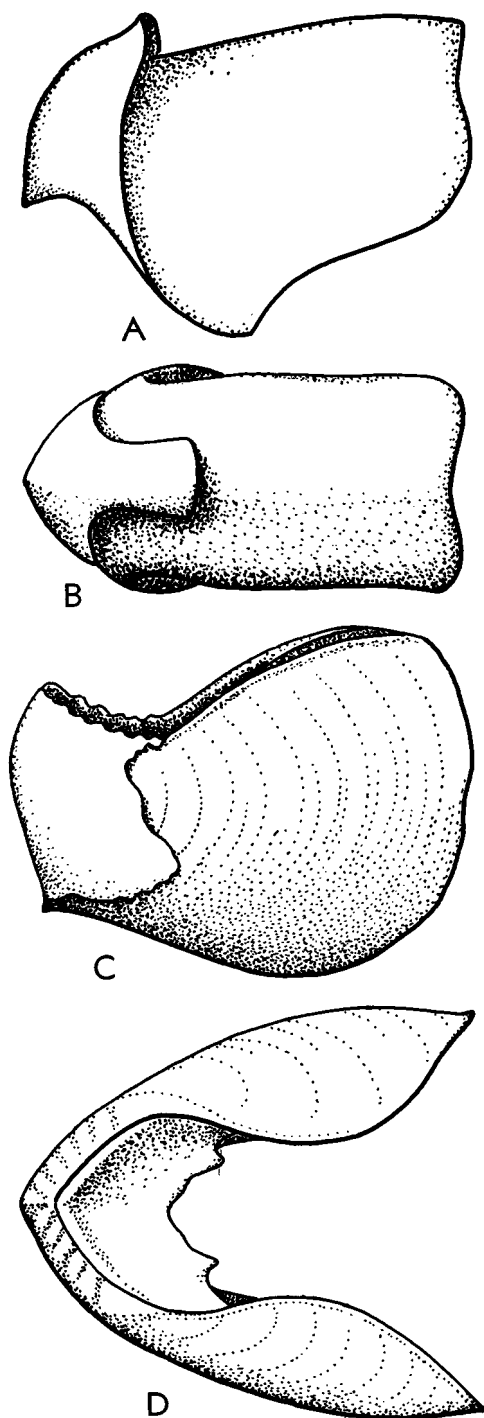


FIG. 44A. Beaks of *Nautilus pompilius* LINNÉ,  $\times 2.4$ . A, upper beak, side view; B, upper beak, occludent view; C, lower beak, side view; D, lower beak, occludent view (Stenzel, n).

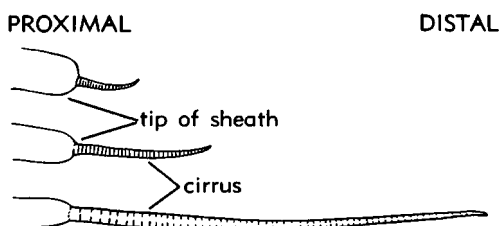


FIG. 45. Digital tentacle of *Nautilus* in 3 stages of protrusion of cirrus from its sheath,  $\times 0.6$  (from 8).

the cavity between the beaks of the jaws. Two prelingual folds rise in front of the radula, near a pair of salivary glands, one at each side of the tongue.

#### TENTACLES AND HOOD

The tentacles are arranged in three separate groups, called ocular, digital, and labial. Ideally, each tentacle, whether ocular, digital, or labial, has a proximal sheath and a distal finger-like cirrus, which can retract into its sheath; but only the ocular and digital cirri can do this completely (Fig. 45). However, there are several modifications of the basic pattern.

The two short ocular tentacles spring from near the base of each eyestalk, one in front and the other behind the eye. They are highly sensitive to touch and smell.

Surrounding the buccal mass are two more or less complete rings of tentacles: an inner ring of labial tentacles and an outer one of digital tentacles. The outer ring and the cephalic sheath, formed by the partial fusion of the individual sheaths of the digital tentacles, are alike in both sexes, but the labial tentacles differ greatly. Those of the female are less specialized than those of the male (Figs. 46, 47).

The digital tentacles and cephalic sheath enclose the labial tentacles and buccal mass. Although the number of digital tentacles is 38, they are strikingly constant in number and position in both sexes and in three of the five living species so far studied. However, different groups among them are highly specialized as to function. Some are primarily olfactory, others respond mainly to touch, but most are prehensile.

At its ventral mid-line, the cephalic sheath has a longitudinal groove ending in a notch, into which the free front of the hyponome fits snugly from below. On the opposite side,



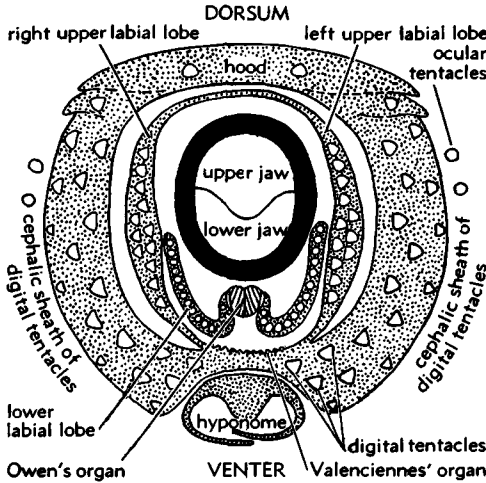


FIG. 46. Arrangement of tentacles in a female *Nautilus*, seen from the front; cirri of tentacles indicated by round or triangular white areas (modified from 11, 30).

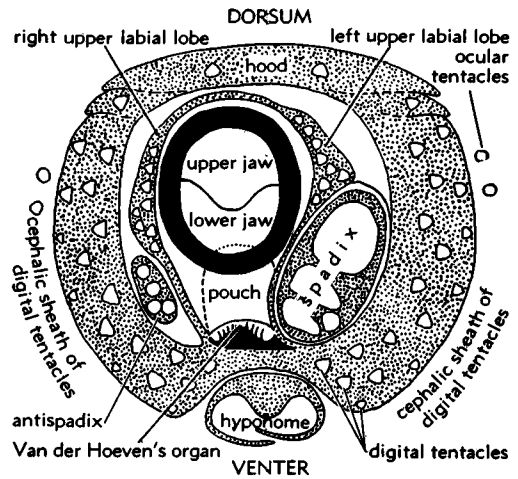


FIG. 47. Arrangement of tentacles in a male *Nautilus*, seen from the front; cirri of tentacles indicated by round or triangular white areas (modified from 11, 30).

at the dorsum, the sheaths of two digital tentacles are much enlarged and fused to form the hood.

The hood (*capuchon céphalique*, *Kopfkappe*) conforms closely in size and outline to the shell aperture (Fig. 48). The outer surface of the hood in *Nautilus pompilius* carries two ridges and has an irregular, somewhat warty brown surface, which has white spots. The warty prominences on the hood of *N. scrobiculatus* SOLANDER are larger and form flat-topped areas having angular outlines, separated by deep grooves. The hood is thickest in the middle-posterior part and slopes from there to a thin outer edge, the front part of which is straight. The rear presses closely against the surface of the dorsal shell coil, and following the shape of the coil, is deeply concave. Laterally and posteriorly, the hood extends on each side into an auricle, which fits into the shell aperture at the umbilicus, but leaves a small gap there that serves as the inhalant passage for the water stream which enters the mantle cavity.

At the tip of the hood, two small orifices lead into deep cavities, in each of which sits a cirrus, similar to that of other tentacles. Some individuals have a cleft of varying penetration in the middle of the tip of the hood. This cleft is caused by incomplete fusion of the two greatly enlarged tentacular sheaths from which the hood originated.

The digital tentacle that lies next to the hood on each side has a broad flattened sheath, which is fused along nearly its entire length to the ventral side of the hood, is overlapped greatly by the margin of the hood, and in turn overlaps the next lower tentacle sheath. Its upper surface resembles that of the hood.

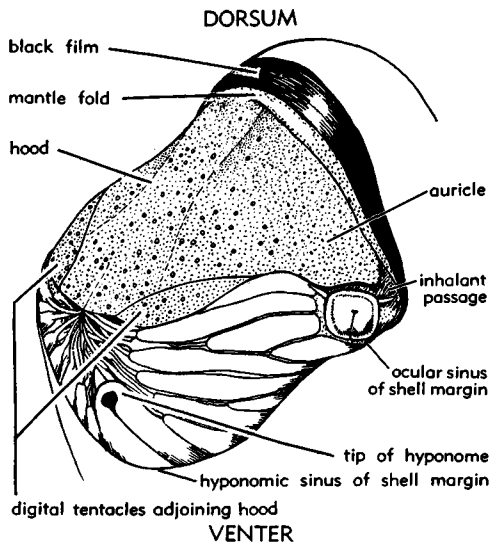


FIG. 48. Oblique frontal view of *Nautilus* in resting position, partially retracted into its shell,  $\times 0.45$  (from 8).

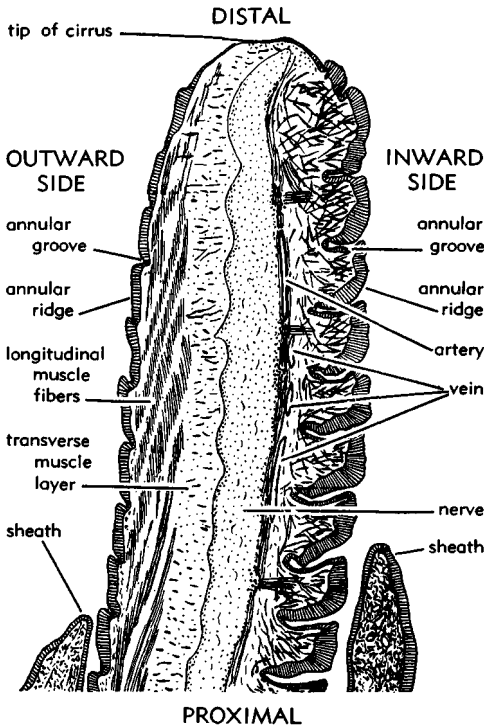


FIG. 49. Longitudinal section through the tip of a digital tentacle of *Nautilus*,  $\times 17$  (from 11). The same annular ridge and groove is labeled on both sides.

The hood and one adjoining tentacular sheath on each side compose the cover that closes over the head-foot, shutting the shell aperture like a countersunk lid and protecting the soft parts when the animal withdraws into its shell. Thick elastic tissue beneath the surface skin makes the hood very tough and difficult to penetrate, but leaves it flexible to some extent.

Next follow 17 digital tentacles upon each side. The sheaths of these tentacles are fused to each other to about 1 or 2 cm. from the distal end of the sheaths. The fusion forms the cephalic sheath, which is ridged on the outside but perfectly smooth on the inside, except that in the female one of the lamellated accessory sexual organs (Valenciennes' organ) is on the inside of the cephalic sheath just behind the ventral notch. This organ receives the spermatophore from the male. Four of the digital tentacles, located on the outside of the cephalic sheath on each side, are so much smaller that they do not reach the distal end of the

sheath; the others are arranged roughly in two rows.

The cirri of the larger digital tentacles are 10 cm. long and 0.4 cm. in diameter. They are muscular, supple, and slender, tapering slightly to a bluntly rounded point. They are three-sided, the broadest with flattest side facing inward toward the mouth. Each cirrus is both adhesive and prehensile and carries many annular grooves and ridges (Fig. 49). The latter are more prominent on the inward face, and this projecting part of each ridge serves as an adhesive organ that functions like a sucking cup. True suckers, like those of the dibranchiate cephalopods, are not present, however. Although the sheaths of the tentacles are shorter than the extended cirri, their cavities are long enough to accommodate the retracted cirri. The sheaths are tough, slightly muscular, and have but little movement of their own.

In the female, the inner ring of labial tentacles is divided into three lobes, the unpaired lower lobe and the right and left upper lobes (Fig. 46). The ventral or lower labial lobe, below the buccal cone, is 2.5 cm. long and 0.8 cm. thick; distally the lobe splits, and each half widens like a fan and bears a single row of 14 labial tentacles at its edge. At the junction of the two fans is a lamellated accessory sexual organ (Owen's organ), probably olfactory in function. The right and left upper labial lobes of the female are each about 3 cm. broad and 2 cm. high; a low ridge unites them dorsally, but ventrally the two lobes end above the hyponome. Each lobe carries 12 tentacles disposed in two unequal rows.

In the male, the lower labial lobe and its tentacles are highly modified as an accessory sexual organ (Van der Hoeven's organ), 2.5 cm. long, which lies in a pouch below the buccal mass (Fig. 47). It is secretory and sensory, but its exact functions are unknown. The right and left upper labial lobes of the male are similar to those of the female but each lobe has only eight tentacles instead of 12. The other four tentacles of each upper labial lobe are permanently and highly modified as copulatory organs, the larger spadix and the smaller antispadix. These two homologous organs are symmetrically placed between the labial lobes and the cephalic sheath. The spadix is on the left and the antispadix is on the

right side in three out of four males; in others, positions are reversed. The spadix transfers the spermatophore from the male to the Valenciennes' organ of the female. Spadix and antispadix are identical and quite small in less than half-grown males; modification into the two and rapid growth come late in the life of *Nautilus*. At maturity, the spadix forms a large, very solid, protrusible organ, 5 to 7 cm. long, 2 to 3 cm. high, and 0.5 cm. thick. Because of its large size, it distorts the arrangement of the surrounding parts of the head-foot and influences even the configuration of the shell cross section (Fig. 50).

All tentacles of *Nautilus*, ocular, digital, and labial ones, are innervated from the pedal ganglia. Hence, they probably evolved from the foot of the molluscan ancestor, and the head-foot arose through fusion of head with foot. Which portion of the foot of the ancestor developed into the tentacles of *Nautilus* has been discussed at length (30, p. 800-804; 16; 23). However, reported homologies are open to question.

Even the derivation of the tentacles of the Cephalopoda from a part of the foot of the molluscan ancestor, at one time widely accepted, is now vigorously denied by KERR (16). The tentacles are said to have developed independently from parts of the head. The fact that in the embryo of dibranchiate cephalopods the tentacles develop from the same region as the hyponome, a region that in other mollusks gives rise to the foot of the adult, is explained by KERR as caused by distortion of the embryonic blastoderm through the large yolk, which is characteristic of the cephalopod egg.

The outer ring of 38 digital tentacles of *Nautilus*, taken as a whole, is homologous to the ring of arms (ten or eight) of the dibranchiate cephalopods, but individual tentacles cannot be homologized. The inner ring of labial tentacles of *Nautilus* may be homologous to the buccal membrane of the dibranchiates—a conical membrane surrounding the mouth present only in the decapodous Coleoidea—which in some species of squid even bears seven to ten rudimentary tentacles carrying suckers.

#### HYPONOME

The long funnel of the hyponome (*si-phonopodium* of WILLEY, or funnel, *enton-noir*, *Trichterrohr*) is part of the head-foot

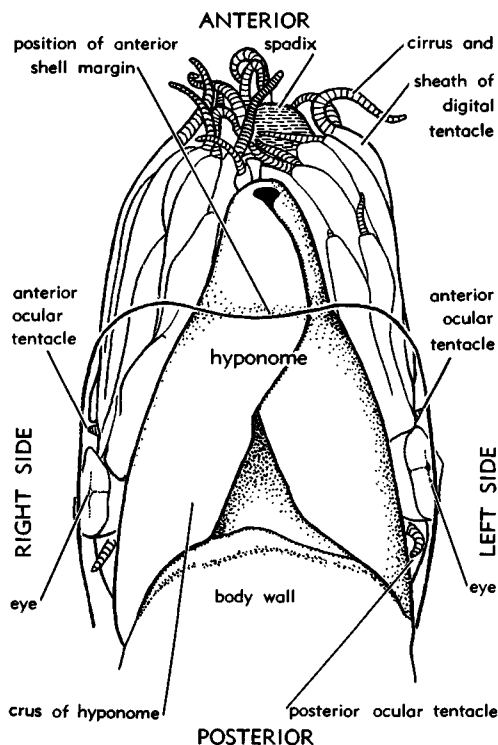


FIG. 50. Male *Nautilus pompilius* LINNÉ, seen from below,  $\times 0.6$  (drawn by Stenzel, based on 11). Shell and mantle fold are represented as transparent, allowing the organs within to be seen in their natural positions.

(Fig. 50). It is about 8 cm. long and 4 cm. wide, presses against the ventral side of the head, and is anchored onto the cartilage of the head. Two ridges outlining the prongs of the cartilage are visible under the roof of the hyponome in live individuals of *Nautilus*. Its wider posterior part extends well into the mantle cavity, its narrower anterior part rests in the ventral groove of the cephalic sheath, and its blunt tip reaches a little beyond the ventral notch of that sheath. Beneath the roof of the hyponome, near its tip, is a thin, tongue-shaped valve capable of blocking water from entering the hyponome from the outside. The ventral edges of the hyponome are not fused, as in the Dibranchiata, but merely overlap one another tightly; hence, they possibly represent a more primitive stage in specialization of the hyponome and recall its primitive condition as a flat surface. At the rear of the hyponome, its edges diverge and pass upward over the sides of the body forming

the crura (plural; crus, singular; alae of WILLEY). The tips of the crura merge into the nuchal membrane, a crescentic skin fold at the dorsum behind the hood. Only the strongly muscular and contractile posterior three-eighths of the hyponome is attached to the head; the free and less muscular anterior portion is able to move and bend in any direction. The crura of the hyponome produce by their rhythmic movements a current of water that enters the inhalant passages behind the auricles of the hood so as to bring oxygen to the gills in the mantle cavity; the hyponome functions secondarily as a powerful locomotor organ.

The hyponome is innervated from the pedal ganglia and is generally considered to have evolved from a portion of the foot of the molluscan ancestor.

#### SENSE ORGANS

The eyes are in the corner between the hood, the roots of the cephalic sheath, and the hyponome with its crura. The eye is large, 2.2 cm. long and 1.5 cm. high, short-stalked, and rounded-triangular in outline. A retina lines the cup of the eye, and a stout cover with a small pupil closes it. It lacks a lens and lets sea water in. A groove leads down from the pupil to the ventral edge. The lack of movement and accommodation of the eye indicates its great limitation as a visual organ.

The two ocular tentacles are tactile and olfactory. The tips of some of the digital tentacles also have tactile functions.

Between the eye and the posterior projecting edge of the cephalic sheath and largely hidden by the eye is the rhinophore, a sense organ of unknown function, possibly olfactory. The rhinophore is a small pyramid only 8 to 10 mm. high. A pair of statocysts lie upon the anterior side of the cephalic cartilage immediately behind the pedal ganglia. They are thin-walled sacs, 3.5 mm. long, filled with a highly fluid milky substance laden with many tiny crystals of calcite (otocones); they are stability sense organs.

The abundant supply of olfactory tentacles in *Nautilus* confirms the observations of WILLEY (30, p. 774) that *Nautilus* finds its food chiefly by smell and that its eye is ill fitted to discern objects.

#### NERVOUS SYSTEM

The central nervous system is concentrated in the head in three half-circle bands around the esophagus. One band passes dorsally over the esophagus and contains the cerebral ganglia; the anteroventral band is composed of the two pedal ganglia and their commissure; the pleurovisceral ganglia and their commissure are posteroventral. The three bands are joined to either side of the esophagus. The cerebral band sends off a thick nerve to each eye, indicating great importance of the eye to the animal in spite of the primitive equipment of the eye; other nerves are sent off to the buccal mass and statocysts. The pedal ganglia innervate the hyponome and all the tentacles with their accessory sexual organs. The pleurovisceral ganglia send nerves to the gills, excretory renal organs, reproductive system, shell muscles, body wall, digestive system, and mantle. The posterior part of the hood receives nerves from the pleurovisceral ganglia as well as from the cerebral and pedal ganglia, but the anterior part is served from the pedal ganglia alone. In comparison with the Coleoidea, the central nervous system of *Nautilus* is much less concentrated, and hence more primitive.

#### BODY

##### MANTLE

The body is fully enclosed by the mantle (pallium), which therefore lines the inside of the body chamber. In the posterior or visceral region, the mantle forms merely the surface membrane of the visceral sac and is so thin that the viscera can be seen through it easily, but in the anterior or pallial region, the mantle forms a fold (pallial fold or duplicature). Between body and mantle fold is the mantle cavity (pallial cavity), which encircles the body. In the dorsum, the cavity is 4 cm. deep; where the umbilical shoulder of the shell is located, it is only 1 cm. deep; but at the venter, it is 10 cm. deep and capacious, containing the hyponome, gills (branchiae), and orifices of the digestive, excretory, and reproductive systems. This ventral portion of the mantle cavity is known as the branchial chamber. The mantle fold lines the inside of the body chamber and is very thin and only slightly

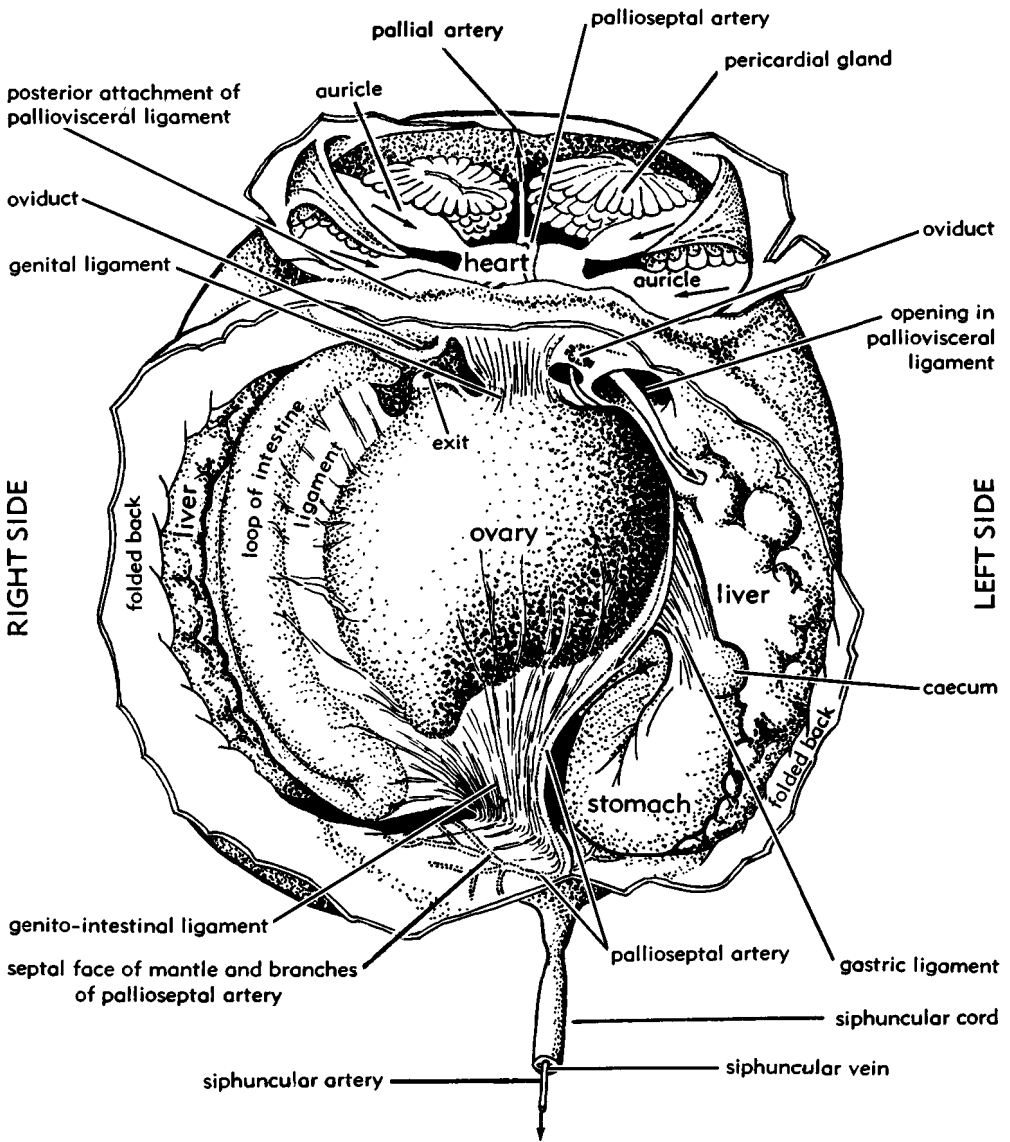


FIG. 51. The visceral sac of an immature female *Nautilus* seen obliquely from the posteroventral side; the genital and pericardial chambers of the coelom are cut open to show the organs contained in them,  $\times 1$  (modified after 12).

muscular for the most part. At the ventral and lateral margins of the shell aperture, it is firmly attached to the body chamber along a band 1 to 1.5 cm. wide. This band of the mantle fold is slightly thicker and its anterior edge has two parallel grooves, separated by a sharp ridge (Fig. 44).

#### GILLS AND EXCRETORY SYSTEM

The four gills are about 5 cm. long, 1.5 to 1.8 cm. wide, and 1 cm. thick. Only their bases are attached to the mantle near the rear of the pallial cavity. Two gills lie on each side, one slightly in front of the other. The gills are not ciliated.

Near the base of each of the four gills is a renal pore, the exit of a kidney. The principal excretion of the kidneys is said to be calcium phosphate (in the form of small, solid, oölitic concretions) and guanine ( $C_5H_5ON_5$ ).

#### DIGESTIVE SYSTEM

The esophagus opens immediately behind the tongue. It is long and distensible, and when full, it forms a capacious crop. The esophagus passes straight through the body into the vestibule of the muscular stomach. The intestine passes from the right side of the stomach, makes two sharp turns, and runs into the posterior part of the pallial cavity. At one point it connects with the caecum, into which the duct of the large-lobed liver empties. The last loop of the intestine is used for storage of feces. The shortness of the digestive system is consistent with the animal's carnivorous nature.

#### REPRODUCTIVE SYSTEM

Although sexes are separate in *Nautilus*, as in all Cephalopoda, the gonad—testis of the male or ovary of the female—occupies the same position in the body, that is, the posterior extremity, directly ventral from the root of the siphuncle, cradled on the last shell septum so that the smooth posterior face of the gonad fits the concavity of the septum, lying between the septal foramen and the ventral part of the septal suture (Fig. 51). The gonad is enveloped and suspended in the body cavity by ligaments, two of which are attached to the rear wall of the stomach (gastric ligament) and second loop of the intestine and one of which is attached to the rear wall of the visceral sac (genito-intestinal ligament). The posterior insertion of the genito-intestinal ligament is 2 cm. long and runs in a dorsoventral direction. Near the middle of this insertion is the root of the siphuncle.

The testis is slightly larger than the ovary, and the male system ends in a penis, which lies in the branchial chamber of the pallial cavity in the mid-line of the ventral body surface. The female system empties through two pores (pore of oviduct) into the branchial chamber near the base of the posterior gills; only the right pore is functional, since the left one is atrophied.

#### CIRCULATORY SYSTEM

The heart is ventral in the body cavity, between the gonad and the rear end of the pallial cavity (Figs. 44, 51). It is transversely oblong, and each of its four auricles receives a branchial vein, bringing oxygenated blood from a gill to the heart. Five aortas and arteries lead the oxygenated blood from the heart to various organs and muscles. Notable is the lesser aorta, because one of its two branches is the pallioseptal artery. The two distal branches of the latter supply the part of the mantle which rests on the last septum of the shell. The siphuncular artery, a branch of one of the two branches of the pallioseptal artery, enters the siphuncle, runs nearly to its posterior tip, and ends there openly. The branchial hearts, so well developed in the Coleoidea are not found in *Nautilus*.

Returning venous blood does not run in closed vessels, as does the arterial blood, but collects in many irregular, intercommunicating blood-filled spaces (lacunae or sinuses) located in and between the organs and muscles. Blood from these lacunae collects in the anterior part of the body in the blood-filled hemocoel, the main portion of which forms a space around esophagus and liver. From the hemocoel, venous blood enters the vena cava through 20 to 75 holes in its dorsal wall. This vein begins near the cephalic cartilage, runs along the ventral body wall, and splits at its posterior into four branches. Each branch takes venous blood to a gill, where it is oxygenated and returned to the heart. Venous blood is blue and of syrupy consistency; it contains dissolved hemocyanin, which becomes colorless on oxygenation.

#### COELOM

The anterior, blood-filled hemocoel and the posteroventral coelom, filled with a watery liquid, are the two distinctly separate portions of the extensive body cavity of *Nautilus*, which is the cavity between the viscera and the body wall. A thin membrane (hemocoelic membrane) separates hemocoel from coelom, and envelops the posterior parts of the liver, stomach, and second loop of the intestine. Pouches of the membrane containing these three organs

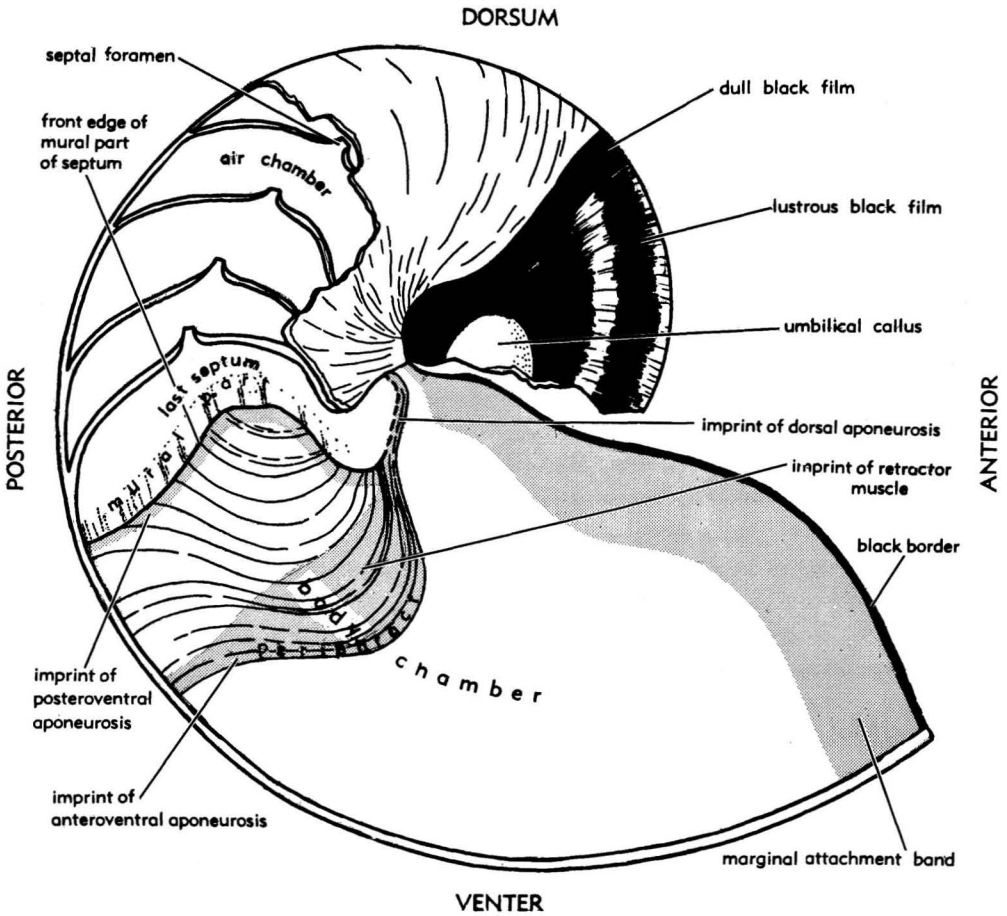


FIG. 52. Shell of mature *Nautilus pompilius* LINNÉ, partly cut open along plane of bilateral symmetry, seen from the right side,  $\times 0.7$  (Stenzel, n).

project backward into the coelom. This thin hemocoelic membrane is attached to the body wall dorsally by a tendon in the form of a fibrous sheet (dorsal aponeurosis); at the sides of the body it is fastened to the inner surfaces of the retractor muscles, passing downward and slightly backward. The ventral margin of the hemocoelic membrane joins the ventral body wall where the body wall and the inner wall of the mantle fold are joined. Placement of these attachments where firm suspension can be provided offers considerable mechanical advantage. The membrane supports the organs which it envelops against hydrostatic pressure of the sea water (Fig. 44).

In the coelom are the gonad, heart, and renal organs. The palliovisceral ligament crosses the coelom from back to front and

divides it into two communicating chambers. On the dorsal side is the large genital chamber (gonocoele), which encloses the gonad and into which the stomach and second loop of the intestine project; on the ventral side is the small pericardial chamber, which encloses the renal organs and into which the heart projects from the ligament that suspends it. The palliovisceral ligament is attached by its posterior end to the body wall about halfway between the two ventral aponeuroses. From there it extends forward in a nearly horizontal plane; its anterior attachment is on the mantle fold.

#### MUSCLES AND SHELL ATTACHMENTS

Two powerful retractor muscles, about 5 cm. long, connect with the cartilage in the

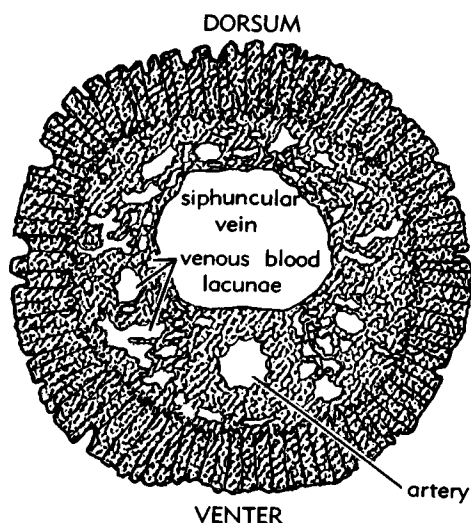


FIG. 53. Cross section of the siphuncular cord showing its blood supply,  $\times 30$  (from data given by 12, 30).

head, where each muscle is inserted on a short prong of the cartilage. From the cartilage, they diverge backward in the shape of a V, forming the sides and part of the ventral wall of the body within the mantle cavity. Each muscle is firmly attached at its origin to the inside of the shell in front of the edge of the last septum. Each area of attachment is 2 by 4 cm. in size and rounded-triangular, because each muscle is convex toward the outside and concave toward the inside of the body and the cross section of each muscle is about the same as the outline of its attachment. A thin, transparent, conchiolin film, secreted by epithelium at the origin of the muscle, covers the attachment area and separates the muscle from the calcareous shell wall. Hence, the imprint made by the muscle on the shell wall is shallow, and the muscle can be pulled off without tearing. When the retractor muscles contract, they withdraw the head-foot of the animal into the shell and the hood closes the shell aperture automatically.

Shell and fleshy parts are firmly joined together in several places (Fig. 52). (1) The anterior edge of the mantle fold is attached to the inside of the shell along the lateral and ventral parts of the aperture. The width of this attachment band is 1 to 1.5 cm. At the shell aperture of adults, this band leaves

a black border, in most individuals 1 to 4 mm. wide but in a few up to 23 mm. wide. The border is continuous with the black film of the dorsal shell coil. (2) The mantle cover of the visceral sac is attached by the periphraet, which leaves a continuous imprint band 3 mm. wide, consisting of the imprints of the dorsal aponeurosis, retractor muscles and anteroventral aponeurosis.<sup>1</sup> As at the retractor muscle attachments a conchiolin film separates shell wall from body wall along the rest of the periphraet imprint. (3) The mantle cover of the visceral sac is attached along the septal contour, which is a continuous, slightly thickened, whitish band of the mantle, about 1 mm. wide, developed along the posterior margins of the dorsal and posteroventral aponeuroses. The narrow band of the septal contour lies at the anterior edge of the mural part of the last septum. Hence, the curves of the septal contour follow closely the curves of the edge of the septum and vice versa. The anteroventral aponeurosis imprint connects the two retractor muscle imprints and is anterior to the edge of the mural part of the septum.

### SIPHUNCULAR CORD

The siphuncle consists of fleshy, conchiolinous, and shelly parts. The conchiolinous and shelly portion (ectosiphuncle) encloses the fleshy portion, the siphuncular cord (siphon of some authors).

The long, slender, fleshy cord passes through every septum to the shell apex. Arterial blood is supplied to it by the siphuncular artery, which branches off from one of the two distal branches of the pallio-septal artery, enters the root of the cord, lies in its ventral wall, and extends through the cord nearly to its beginning at the shell apex (Figs. 51, 53). The venous blood is collected in countless peripheral interconnecting blood lacunae, from which it enters the central cavity of the cord. This large central tubulous cavity is, in effect, a vein that leads the blood back through the whole length of the cord to its root. At the root, the siphuncular vein enters the genito-intestinal ligament, crosses the coelom by way of this ligament, and empties into the hemo-

<sup>1</sup> An aponeurosis differs from a tendon in that the former is a band or sheet and its attachment is linear, whereas the latter is stringlike and its attachment is a small round area; both are fibrous tissues providing means of attachment to muscles or other organs.



coele. Although the siphuncle is narrowed where it passes through a septum, its blood vessels are not blocked off at these places.

None of the blood vessels extend from the siphuncle into the air chambers. This fact confirms the observation that no live epithelium or other live tissue lines the air chambers. If such tissues were present, they would have to have a blood supply.

Contrary to statements made by OWEN (22) and GRIFFIN (11), the coelom has no access to the siphuncular cord, as has been demonstrated by WILLEY (30). Hence, the cord is not a part of the visceral sac, but only an extension of the mantle covering the visceral sac.

The cord is encased in a tube of conchiolin, secreted by the epithelium of the cord. Since the cord is an attenuated extension of the mantle, the deposits secreted by both, that is, ectosiphuncle and septum, are continuous and to some extent similar. At its apical end, the siphuncle is closed, forming the siphuncular caecum, which rests against the concavity of the shell apex. In the first and second air chambers, the siphuncle has a somewhat greater diameter but narrows in the third chamber.

## SHELL

The planispiral, bilaterally symmetrical, external shell (or conch) of *Nautilus* is divided into chambers (*loculi* or *camerae*, *loges*, *Kammern*) by cross walls or septa (*cloisons*, *Scheidewände*), which are concave toward the aperture (procoelous) (Figs. 54, 55). If the shell were unrolled, it would be a long, tapering, chambered cone consisting of shell wall and numerous septa. Each complete 360°-turn of the shell spiral is a whorl or volution (*tour*, *Windung*). Adult *Nautilus* has about three whorls. Because the venter of the animal is at the convex exterior of the body chamber, the shell is called exogastric.

## CHEMICAL COMPOSITION

The shell contains about 2.03 percent of organic matter; of the remaining percentage, comprising the inorganic constituents, 99.50 percent is  $\text{CaCO}_3$ , 0.16 percent  $\text{MgCO}_3$ , 0.15 percent  $(\text{Al, Fe})_2\text{O}_3$ , 0.19 percent

$\text{SiO}_2$ . A trace of calcium phosphate is found, and  $\text{Sr}(\text{atoms})/\text{Ca}(\text{atoms})$  are 3.8–4.8/1000.

The calcium carbonate is aragonite (orthorhombic). Organic matter is chiefly conchiolin—a horny-appearing substance characteristic of the Mollusca, which composes the ligament of Bivalvia, the periostracum of Bivalvia and Gastropoda, and the bonding matrix of the calcium-carbonate crystals in all Mollusca. Conchiolin is a complicated organic substance composed of polysaccharides, polypeptides, and scleroprotein fractions. The amino acids of conchiolin in the nacreous layer of *Nautilus macromphalus* are mainly glycine, alanine, and arginine.

## COLORATION

The shell is brilliantly clean in life, and its ground color is white. A black film covers the shell coil at the dorsal side of the aperture in all species and also the two umbilici in *Nautilus pompilius*. In normal life attitude, the black film is covered by the dorsal fold of the mantle and the rear of the hood, but becomes exposed when the animal withdraws into its shell.

All other color markings are brown, and although they differ in shade and extent from species to species, the living species of *Nautilus* have much in common (Fig. 56). The value and chroma of the brown change rapidly after death of the animal. A variable patch of brown covers the umbilicus and umbilical slopes. Irregular, confluent, transverse bands cover the dorsal shell coil of the adult animal but fade out toward the venter. In some species, the bands run into the umbilical patch, in others they leave a white circumumbilical area. This white area is largest in *N. repertus* IREDALE.

Colorations of shell and exposed fleshy parts harmonize, and in adults at least, the top is brown or striped with brown and the bottom is white. This type of coloration is protective. The brown bands disrupt the contour of the animal, like the bands on zebras and warships; *Nautilus* is extremely difficult to see even in clear shallow water, because the color markings resemble shadows cast by sea fans and seaweeds and simulate the effect of the play of sunlight on surface ripples of the sea.

### BLACK LAYERS

The animal deposits a lusterless, black, organic film at the shell aperture over dorsal shell coil and umbilicus. In adults the

black film continues as a border at the inside of the shell margin all around the aperture but the border is only 1 to 4 mm. wide.<sup>1</sup>

Glands in the dorsal portion of the man-

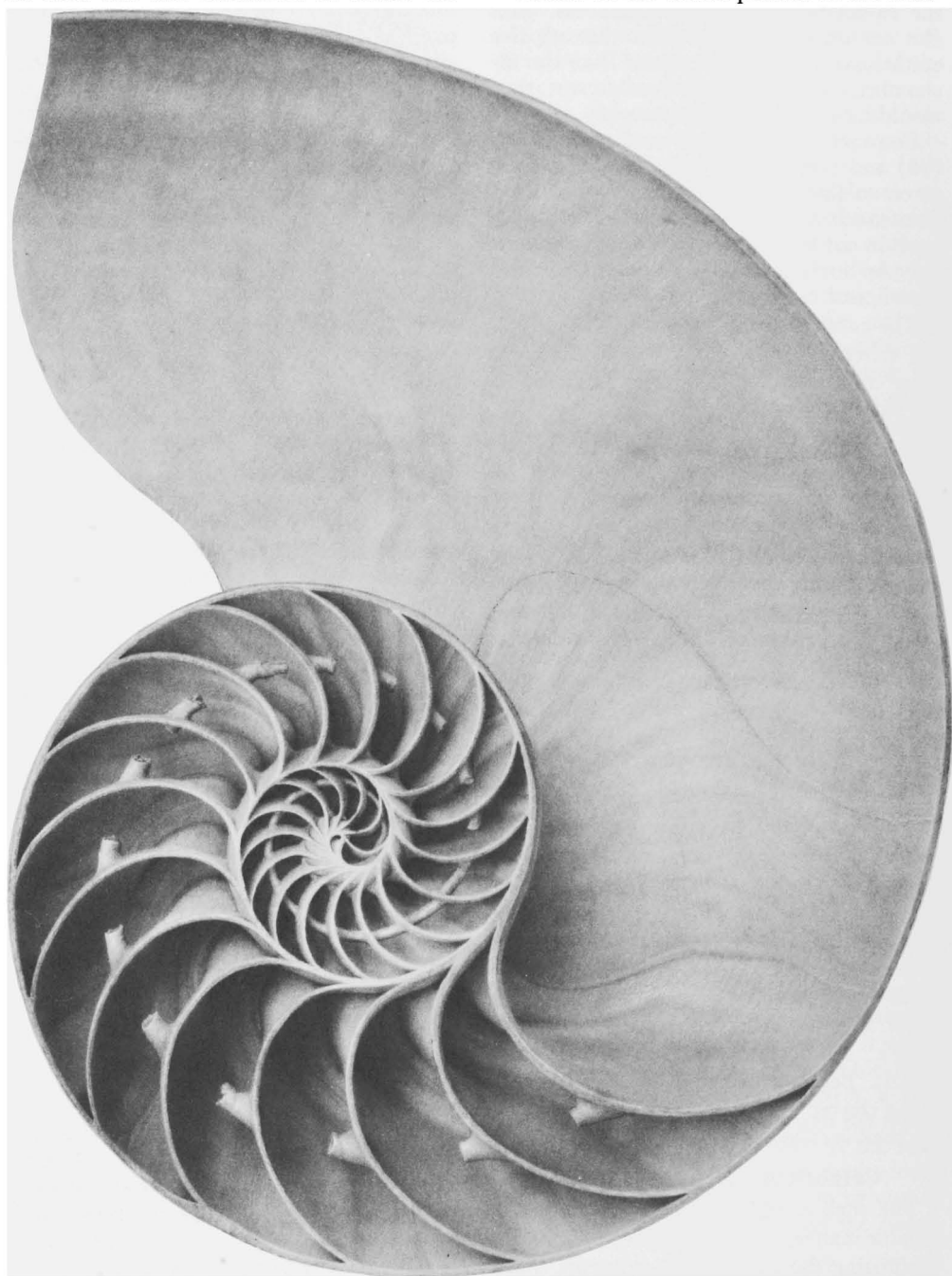


FIG. 54. Shell of *Nautilus pompilius* LINNÉ cut longitudinally slightly to right of the median plane,  $\times 1$  (from 124).

tle fold deposit the film (15). However, GRIFFIN (11, p. 138) suggested that the pos-

<sup>1</sup> Correct observations of border and black film can be made only on shells that have neither been ground off at the apertural margins nor cleaned with acid. Most commercially sold shells have been disfigured in this manner.

terior concave surface of the hood deposits the film. There, the epithelium of the hood is glandular and pigmented. In view of the fact that at least in adults the black deposits extend all around the shell aperture, it seems

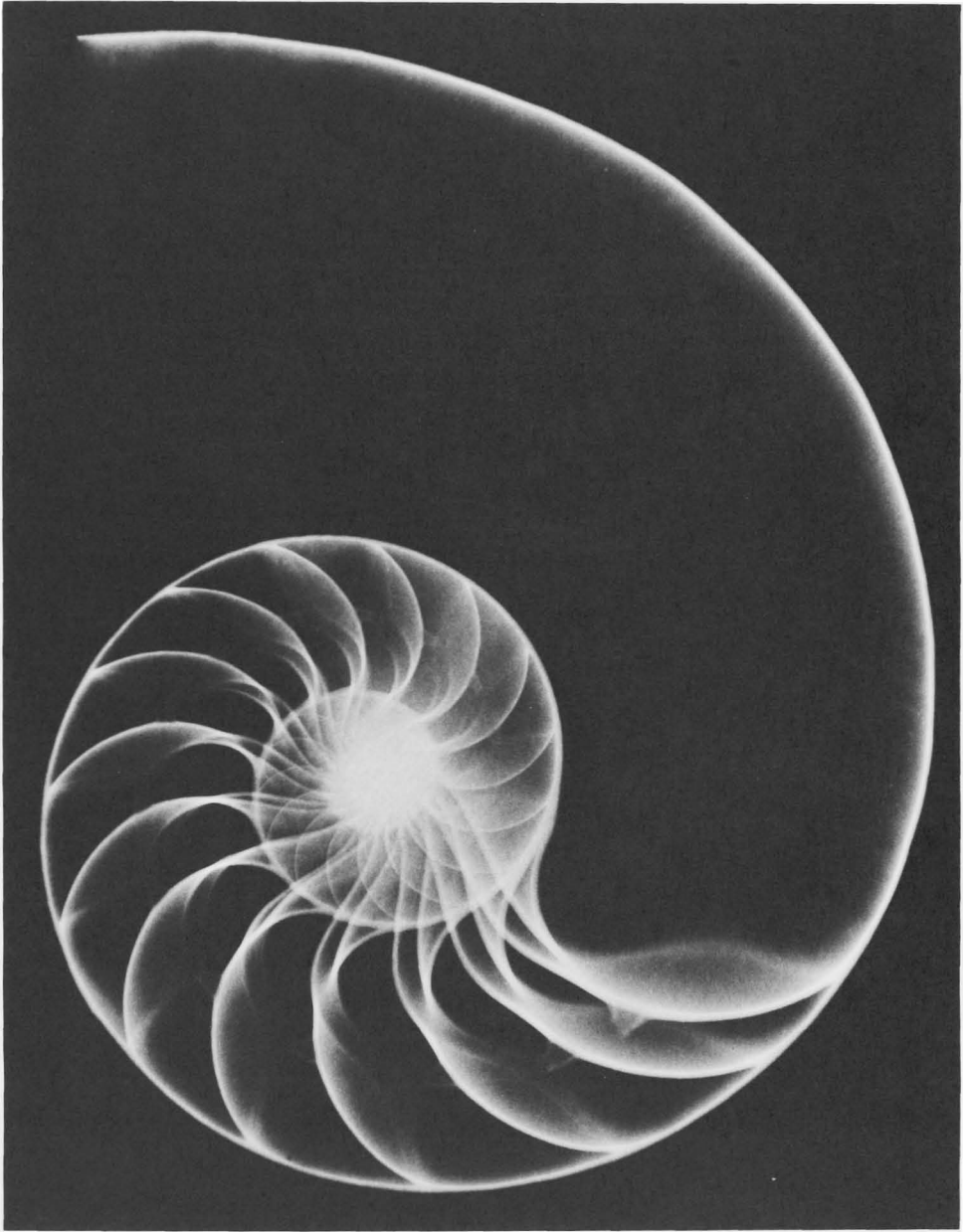


FIG. 55. X-ray photograph of longitudinally sectioned shell of *Nautilus pompilius* showing form of septa both in the axial part of the conch and their lateral extensions toward the umbilicus,  $\times 0.8$  (from *Medical Radiography and Photography*, courtesy Charles F. Bridgman).

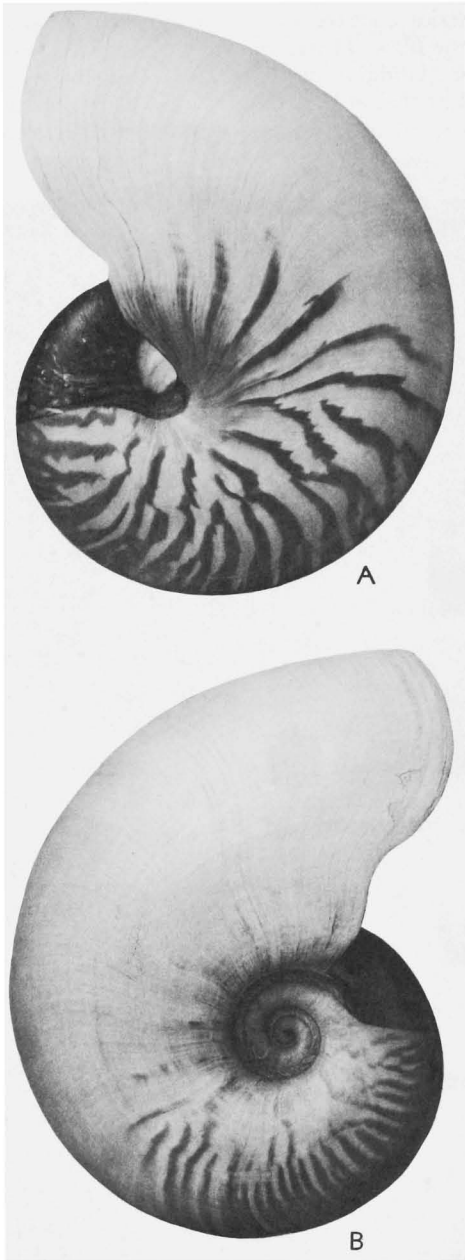


FIG. 56. Exterior of shells of *Nautilus pompilius* LINNÉ (A) and *N. scrobiculatus* (SOLANDER) (B),  $\times 0.5$  (from 124).

more likely that the mantle fold is responsible (24).

The black film is soon covered by an exceedingly thin nacreous shell layer which is translucent and colorless. The layer makes

the originally dull black film lustrous, so that only the outermost, not yet covered, part remains devoid of luster. At the dorsal mid-line of the aperture, the lusterless part sometimes is only 8 mm. in extent; at other times the deposition of the thin shell layer lags behind, so that the lusterless part extends for as much as 60 mm. at the expense of the lustrous part (Fig. 52).

Farther back in the interior of the living chamber, and also at the umbilicus of those species which have an umbilical callus, nacreous shell films gradually pile up over the black film, finally covering it completely. The black film can be seen as a thin black line separating the volutions when the shell is cut in two (see FIG. 66, on right).

The organic material composing the black deposits is regarded by PRUVOT-FOL (24) essentially as an excretion of metabolic waste analogous to the black excretion in the ink sac of the Coleoidea. The cephalopod ink and probably the black deposits of *Nautilus* contain melanins, a group of black, brown, or reddish organic compounds derived from tyrosine (6).

### SEXUAL DIMORPHISM

Males are larger than females and their shells are accordingly different in size. Antispadix and spadix, the bulky secondary sexual organs of the mature male, are situated beside the mouth and hence increase the size of the entire crown of tentacles. As the tentacles have to be protected and concealed under the hood when the animal retracts, the hood of the male must be broader than that of the female. Shape and size of the hood, in turn, determine those of the aperture. Therefore, shells of mature males have a broader and more evenly rounded aperture than those of mature females, but the differences are rarely sufficient to distinguish sexes by shell shape alone (Fig. 57).

### GROWTH LINES

The shell grows in size along the apertural margin by deposition of shell matter from the slightly thickened and attached mantle edge (Fig. 52). As the rate of deposition is not uniform, slight wrinkles parallel to the apertural margin result. These growth lines outline former positions of the shell margin. Irregularities indicate injuries of shell or mantle margin.

The apertural margins and also the growth lines have three sinuses concave toward the aperture, a large one in mid-venter, marking location of the hyponome, called the hyponomic sinus, and a pair of small and shallow ones on the sides, in the position of the eyes, the ocular sinuses. The hyponomic sinus permits free motion of the hyponome and is indicative of the animal's swimming habit. The ocular sinuses allow the eyes to peer out between the hood and shell margin, when the animal is partially withdrawn into its shell (see Fig. 68B).

### CHAMBERS AND SEPTA

The body occupies and conforms exactly to the shape of the body chamber (*chambre d'habitation*, *Wohnkammer*), which is the last or outermost of the chambers and is open at the shell aperture. The body chamber occupies 14/36 to 15/36 of the last volution. All other chambers are air-filled in life; they are air chambers (*Luftkammern*).

The number of septa in mature adults is variable within limits; *Nautilus pompilius* has 33 to 38; *N. macromphalus*, 27 to 28; and *N. scrobiculatus*, 32.

Each septum has a septal foramen near its center; this is a slightly oval to circular hole for the siphuncle, around which the septum is turned toward the shell apex, forming a septal neck (*goulot siphonal*, *Siphonaldüte*). The hole is 4 by 3 mm. in size, and its neck is 4 mm. long in the last septum of mature shells.

The concave face of the septum has shallow, branching grooves symmetrically arranged. These are imprints of the two branches of the pallioseptal artery that supply blood to the septal face of the mantle.

The septum joins the shell at a very acute angle and there the margin, or mural part, of the septum is attached to the wall. Hence, the joint is really a band made by the mural part of the septum, but it is commonly represented in illustrations as a line, the suture or suture line (*suture* or *ligne sutural*, *Sutur* or *Suturlinie*), which is the line of juncture between shell wall and the free unattached part of the septum. The suture has several

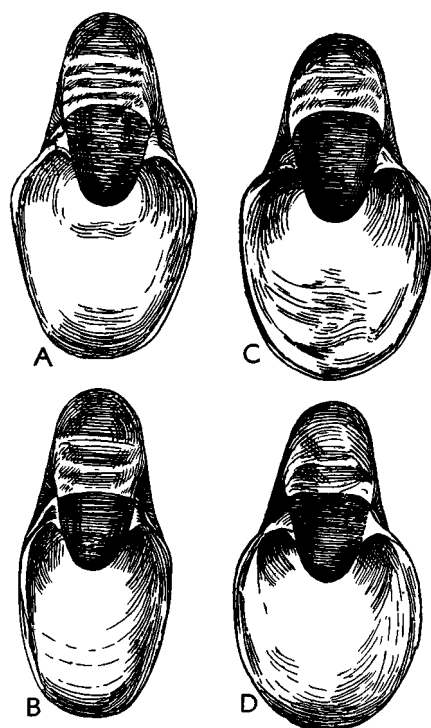


FIG. 57. Sexual dimorphism of the shell in *Nautilus pompilius* LINNÉ, (A,B) females, (C,D) males,  $\times 0.25$  (after 30). Minimum difference is shown in the upper figures (A,C) and maximum in the lower ones (B,D).

bends; those convex to the shell apex are called lobes (*lobes*, *Loben*) and those concave are termed saddles (*selles*, *Sättel*). At the dorsum of the third to 25th septum, approximately, there is a median dorsal lobe (annular lobe), which gradually disappears in later septa and is best developed at the 20th septum approximately (Fig. 58). The edge of the mural part of the septum, in front of the annular lobe, has a V-shaped notch, pointing to the apex and in some shells extending into a furrow, which persists to the last septum made. A similar median dorsal septal furrow (*Normallinie*), V-shaped, linear, or tear-shaped, in which the mural part of the septum is thin or lacking, is present in other nautiloids.

### ECTOSIPHUNCLE

The conchiolinous and aragonitic cover (siphuncle of some authors) of the siphun-

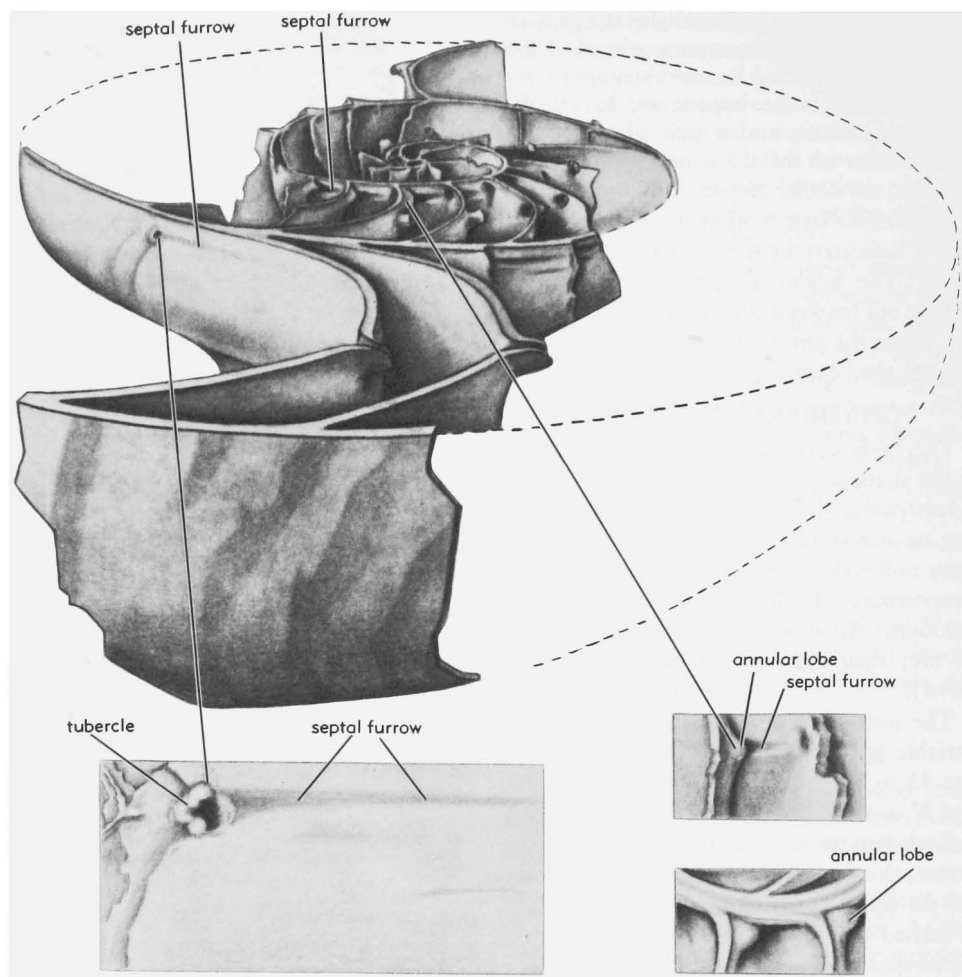


FIG. 58. Shell of *Nautilus pompilius* LINNÉ, cut open parallel to and slightly to the left of the plane of bilateral symmetry to show the annular lobe and septal furrow, enlarged (19).

cular cord consists of a series of tubes, each extending from septum to septum, increasing in diameter with the growth of the shell (Fig. 59). A tube (connecting ring) traversing an air chamber has two layers: (1) an outer layer of tiny calcareous spicules, irregularly arranged and held in place by a porous conchiolin matrix, and (2) an inner thin lining of conchiolin. The spicule-bearing layer continues directly into the conchiolin base layer of that septum of which the tube is the apical extension; it embraces the neck of this septum and extends apically to the septal foramen of the preceding septum, where it is inserted. At the place of

insertion the apical end of the spicule-bearing layer becomes quite dense through abundance and coalescence of spicules. The inner conchiolin lining arises from the apical edge of the nacreous shell layer of the septal neck and extends apically to the next preceding neck, where it is inserted.

Sections of a septal neck (Fig. 59) reveal five layers: (1) an outer spicule-bearing layer formed by the apertural embracing part of the spicule-bearing outer tube (connecting ring), (2) a dark, dense layer restricted to the neck, (3) the nacreous layer of the septal neck, which is a continuation of the nacreous layer of the septum, (4) the apical

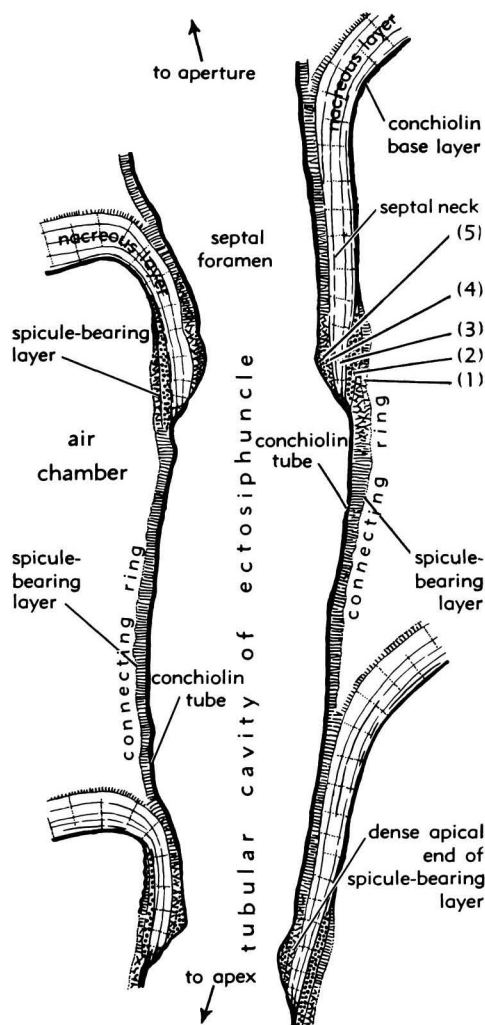


FIG. 59. Longitudinal and vertical section through the ectosiphuncle in *Nautilus*,  $\times 12$  (modified from 2, 5). Conchiolin is shown in solid black, aragonite spicules by crowded cross lines, coalescent spicules by short branching cross lines, dense aragonitic portions by heavy black dots, and naere by widely spaced parallel lines crossed with dotted orthogonal lines. Numbers in parentheses at upper right refer to the 5 layers described in the text.

and dense end of the succeeding siphuncular cover (connecting ring), and (5) a short, dense layer (auxiliary deposit) in the form of a ring, constricting the foramen. The last two layers are not present in the neck of the body-chamber septum; hence they were the last deposits to form in the preceding septal necks (2, 5).

## SHELL STRUCTURE

As the animal grows, it builds onto the shell margin at the aperture and thereby lengthens and enlarges its body chamber. The newly deposited marginal shell material is a continuation of the thin outer shell layer, the porcelaneous ostracum, and is deposited by the apertural edge of the mantle fold alone.

The porcelaneous ostracum (Fig. 60) is composed of microscopic aragonite grains held together by a dark conchiolin matrix; toward the inside of the porcelaneous layer the grains are replaced by microscopic closely packed vertical prisms of aragonite (*Verkalkungstreifen* of APPELLÖF).

The porcelaneous ostracum is later strengthened by the nacreous layer of the ostracum formed from films deposited one over the other inside the body chamber by the whole surface of the mantle. Each film is composed of closely packed, flat-lying, tabular, hexagonal crystals of aragonite (tabular parallel to their crystallographic bases), united into thin lamellae (0.2 microns) and held together by conchiolin. Within a lamella and in successive lamellae the aragonite crystals lie one upon the other like stacks of coins, with the stacks closely crowded. Hence the conchiolin matrix binding the stacks together shows under the microscope as thin vertical slightly irregular dark lines. Some of the lamellae have more

## OUTSIDE

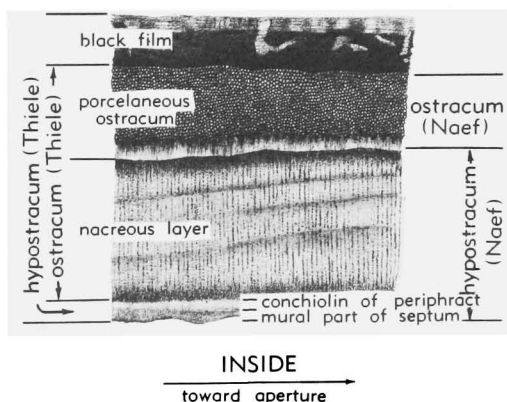


FIG. 60. Section through the shell wall of *Nautilus*,  $\times 30$  (after 2).



conchiolin matrix than others; these show as darker parallel bands slightly inclined to the base of the nacreous layer and converging with the base toward the shell aperture. Over the nacreous layer a conchiolin film is deposited by the periphraet, that is, the retractor muscles and dorsal and antero-ventral aponeuroses.

The conchiolin matrix of the nacreous layer forms extremely thin parallel films, which alternate with the aragonite layers. The films are connected by transverse conchiolin bridges between the individual tabular crystals of the aragonite layers. The whole arrangement resembles mortar in a brick wall.

THIELE (27) regarded the ostracum as composed of two layers, the porcelaneous layer and an adjoining nacreous layer; the conchiolin film deposited by the periphraet and the mainly nacreous septa, deposited upon this film, he called the hypostracum. NAEF (20) restricted the ostracum to the porcelaneous outer layer and united as the hypostracum the two nacreous deposits with the conchiolin film between them. The extent of the hypostracum and ostracum involve exact comparison with these layers as developed in the other mollusks. Such exact homologies have not yet been demonstrated. Provisionally, the following terminology is recommended: **outer ostracum**, composed of the porcelaneous and nacreous layers, **hypostracum**, composed of the conchiolin of the periphraet and the thin layer of columnar crystals lying between the conchiolin film and the nacreous wall layer, and **inner ostracum**, composed of the septa including their mural parts.

The septum is secreted by the septal face of the mantle; therefore, its shape exactly conforms to this face. Not only is it concave toward the aperture, but on its concave face it has faint branching imprints of the ramifying pallioseptal arteries, which supply that part of the mantle, and it even has slightly wrinkled folds spreading from the

anterior edge of the mural part of the septum, marking places where the visceral sac had been suspended from the shell wall by attachment along the septal contour.

The septum has a conchiolin base layer, on which is deposited the nacreous layer of the septum. A layer of aragonite spicules is on top of the nacreous layer (Fig. 59).

### SUBMICROSCOPIC SHELL STRUCTURE

The shell structure under the electron microscope (9, 10, 10a) confirms and extends observations on features seen under ordinary and polarizing microscopes (1, 2, 3).

The main part of the porcelaneous layer has irregularly disposed crystal aggregates, about 6 microns in size. The aggregates are radially divergent or parallel imbricate. In any case, the various aggregates differ greatly in the arrangements of their crystals so that the whole appears disordered (Fig. 60A,1).

Along the boundary with the nacreous layer, the porcelaneous layer develops aggregates of long, parallel sharp-edged bars, rods, or blades of aragonite arranged at right angles to the boundary plane, forming the *Verkalkungstreifen* of APPELLÖF. This special part of the porcelaneous layer has wedge-shaped protuberances that penetrate short distances into the adjoining nacreous layer in a few places, but the boundary is smooth for much of its course (Fig. 60B,1).

Cross sections through the nacreous layer of the outer ostracum show thicker (0.9 to 1.4 microns) and thinner (0.4 to 0.6 microns) tabular aragonite crystals. A single layer of the former alternates with a group of 6 to 7 layers of the latter, exhibiting vertical stacking (Fig. 60B,2). Along the boundary with the porcelaneous layer, stacking does not show and the arrangement is irregular, because the crystals are lenticular rather than tabular (Fig. 60B,1). Here the thinner layers are 0.01 to 0.023 microns and

#### EXPLANATION OF FIGURE 60A,1,2

1. View of polished and etched transverse section through porcelaneous layer of outer ostracum; crystal units are arranged in many different directions and compose aggregates of radially divergent or parallel imbricating bundles;  $\times 19,000$ .—2. View

of slightly etched surface at concave, adapertural side of penultimate septum; thin hexagonal tabular crystals of aragonite, stacked one over the other, leave wide interspaces unfilled between them,  $\times 4,000$  (10a).



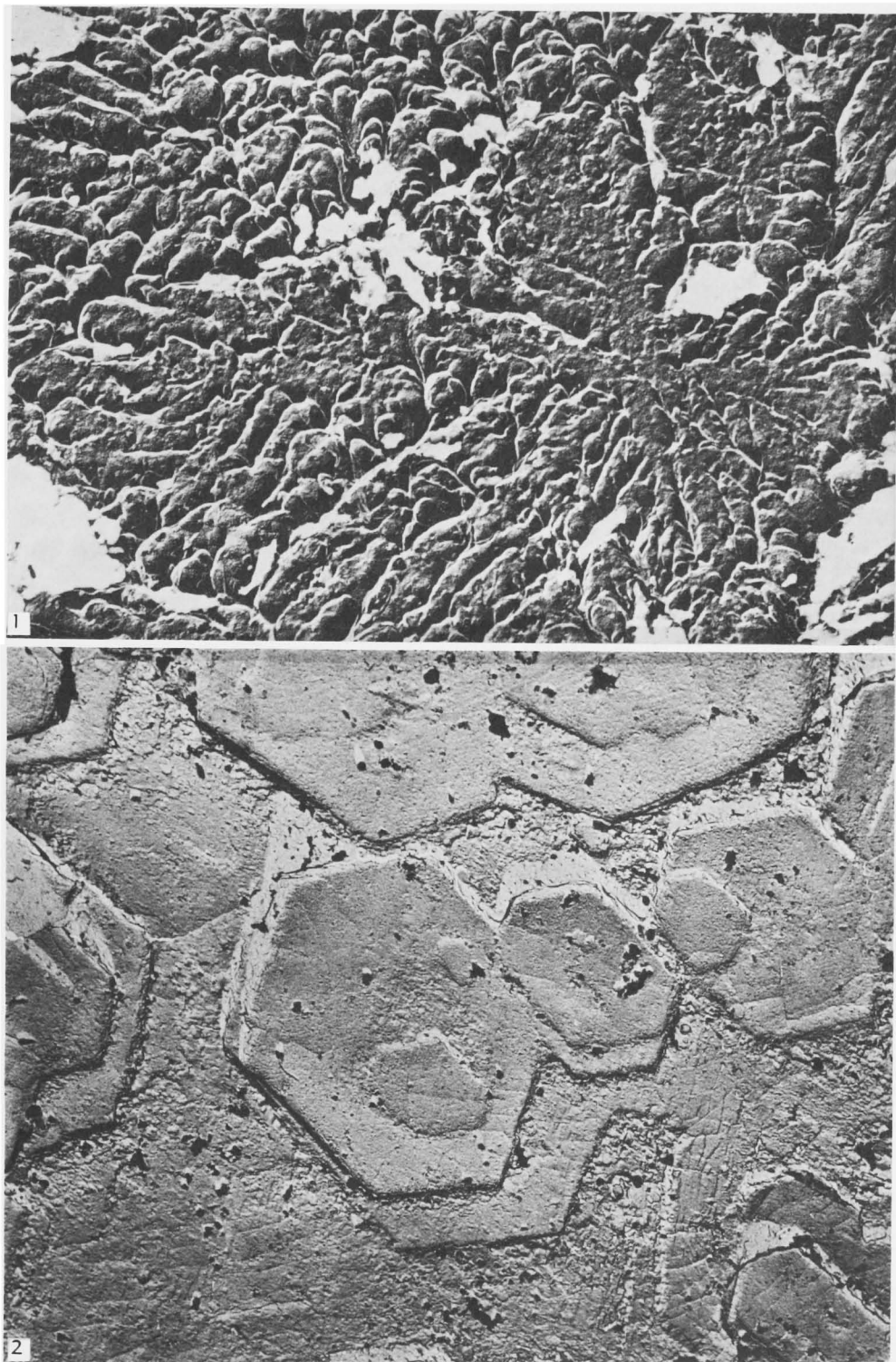


FIG. 60A. 1,2. Electron micrographs showing submicroscopic shell structures of *Nautilus pompilius* LINNÉ, Rec. (explanation on facing page).

the thicker layers are 0.45 to 1.1 microns thick.

Similar features are visible on the surface of the nacreous layer on the concave adapertural face of some septa and on that of the nacreous layer lining the body chamber between aperture and retractor muscle, that is, the growing inner surface of the outer ostracum. These surfaces are partly covered with a pavement of countless flat tabular hexagonal crystals of aragonite, which are very thin and have parallel outlines, although they are separated by wide interspaces as yet unfilled. The crystals are stacked, and as many as 5 superposed crystals can be discerned in some of the stacks. These observations indicate that the last 5 crystals of the stacks were still growing at their peripheries to fill up the empty interspaces until only a narrow crack, filled with conchiolin, separates adjoining stacks (Fig. 60A,2).

The inner surface of the hypostracum, directly beneath the transparent conchiolin film that separates shell from muscle, shows sturdy bundles of columnar girder-like blunt-pointed aragonite crystals forming short, warty protuberances pointing in various directions (Fig. 60B,3). The arrangement of the bundles helps to produce a firm bond between shell and muscle and is probably caused by the tension exerted by the muscle during the growth of the crystals.

The corner spaces between the septa and the outer ostracum and the joint between the outer ostracum and the mural parts of the septa are filled with several layers which are partly conchiolinic and partly aragonitic. Their structure is variable and complicated (2). This complicated and somewhat obscure submicroscopic structure has been described from 17 regions of the shell (10a).

The conchiolin base layer of some of the septa consists of a felting of microfibrils,

which are 4 to 8 millimicrons thick and solitary or associated in bundles, but appear to have no definite orientation. This microfibrillar structure of the base layer presumably results in high tensile strength of this layer. The nacreous layer of the septa has a structure very similar to that of the nacreous layer of the outer ostracum. The thin conchiolin layers between the individual crystals of a stack in these nacreous layers are very characteristic lacelike reticulate films.

The submicroscopic structure, as examined under the electron microscope (Figs. 61, 62), shows pattern differences on the species level and on higher taxonomic levels. For instance, the conchiolin films are 4 to 12 millimicrons thick in *Nautilus*, 8 to 12 in gastropods, and 2 to 9 in bivalves (9, 10).

## ONTOGENY

The ontogeny of *Nautilus* is nearly unknown. The only observations available are those made by WILLEY (29, 30).

## EGGS

Eggs of *Nautilus macromphalus* are laid singly and attached by a spongelike base. The egg is 45 mm. in diameter. As in all cephalopod eggs, there is much yolk.

## EMBRYO

Nothing is known of the embryonic development, but the large yolk makes it certain that when the young emerges from the egg, it already possesses the main features of the adult, bearing a sizable shell, probably provided with several septa, but possibly with yolk sac still attached. Like the embryo of other cephalopods and, unlike that of other mollusks, it probably does not go through such stages as the planktonic veliger larva, either within the eggs or after hatching.

### EXPLANATION OF FIGURE 60B,1-3

1. View of polished and etched transverse section through shell wall of body chamber, showing *Verkalkungstreifen* of the porcelaneous layer (band 20μ wide, at the top) and the nacreous layer. The latter has a thick aragonite crystal (at bottom) and several thinner crystals, all somewhat lenticular. The boundary between the two layers is uneven and has protuberances, ×22,000.—2. View of polished and etched transverse section through shell wall of body chamber, showing the nacreous layer.

A few thicker and many thinner tabular aragonite crystals form a structure like a brick wall and show good vertical stacking. Many conchiolin films between the crystal layers are torn and flapped aside, resting on the crystals and showing their lacelike construction, ×14,400.—3. View of inner surface of hypostracum beneath the conchiolin pad that separates the shell wall from the muscle in the body chamber, ×9,000 (1,3, from *N. pompilius* LINNÉ, 2, from *N. macromphalus* G. B. SOWERBY) (10a).

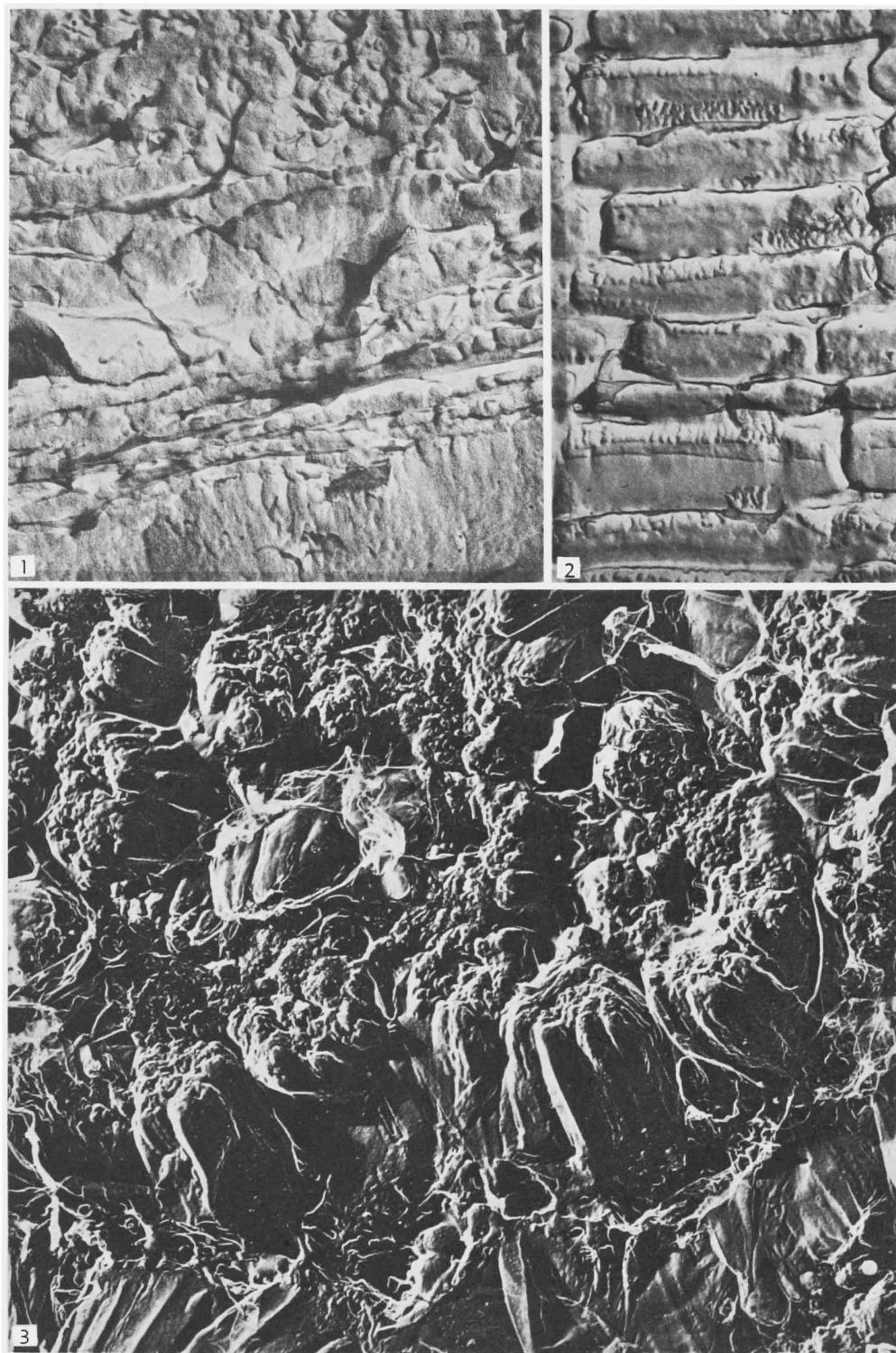


FIG. 60B. 1-3. Electron micrographs showing submicroscopic shell structure of modern *Nautilus* (explanation on facing page).

## PROTOCONCH AND EARLY SHELL

By chipping away the rest of the shell, one can free the first chamber of *Nautilus* (Fig. 63). It is slightly curved and thimble-shaped. Its apex has a slightly raised, elongate boss with a shallow, linear central depression. This feature was discovered and interpreted as a scar (cicatrix) by HYATT (13). According to HYATT, the first embryonic shell, the protoconch, of *Nautilus* is composed of conchiolin only, and does not calcify; therefore, it is destroyed or becomes detached at a later stage, and the cicatrix is either the original attachment area of the conchiolin protoconch or a connecting passage that was closed after the protoconch was shed. If this interpretation is correct, the first calcareous chamber of *Nautilus* is really its second chamber. However, SPATH (25, p. 421) pointed out that HYATT's interpretation of the so-called cicatrix is merely an assumption. SPATH has maintained that *Nautilus* has a calcareous protoconch, which is preserved in the apical portion of the shell. Similarly, NAEF (20) believed that the cicatrix marks the beginning of the shell and that the first air chamber is a modified protoconch. This interpretation is followed here because it is highly unlikely that a conchiolin protoconch can be reabsorbed or detached within the egg. Whether one or the other interpretation is correct can be decided only when the embryology and ontogeny of living *Nautilus* become known. A discussion of this same problem in fossil nautiloids is given in a preceding section on "Morphology."

The shape and size of the embryonic shell, as it was when the young animal emerged from its egg, can be seen on nepionic shells

(Figs. 64, 65). These have a line of discontinuous growth, marked by a shallow and narrow groove, particularly well displayed on the flanks and at the umbilical shoulders. This constriction, signifying the end of the embryonic stage, is at a constant position in all individuals seen, about 1.25 volutions from the apex, and at that stage of growth the shell is 25 to 27 mm. in diameter and 16 mm. wide in *Nautilus pompilius*. From the apex to this terminal embryonic constriction, the shell of this species has (1) glossy luster, (2) light brown color, (3) cancellate sculpture, consisting of very fine, smooth lirae, among which the radial ones are broader than the spiral lirae, (4) no ocular sinuses on the growth lines, (5) a shallow hyponomic sinus on the growth lines, (6) a deep and narrow umbilicus without a callus, and (7) smooth, continuous growth lines without a trace of traumatic breakage of the shell. Beyond this constriction, the nepionic shell of *N. pompilius* has (1) much less glossy luster, (2) darker color of somewhat reddish-brown interrupted by sharply defined white gaps, which become broader as growth continues, (3) either no or only obsolescent cancellate sculpture gradually fading away during growth of the shell, (4) shallow ocular sinuses, which become deeper only as maturity is reached, (5) a deeper hyponomic sinus on the growth lines following the constriction, (6) a wider umbilicus that becomes filled by callus at a late stage of growth, and (7) many broken growth lines and injured former apertural margins. The last of the seven enumerated symptoms is particularly significant, because it proves that the embryonic stage ended at the time the con-

## EXPLANATION OF FIGURE 61

Conchiolin from decalcified mother-of-pearl (inner layer of the shell wall, body chamber). The soft iridescent membranes, freed by decalcification of mother-of-pearl, were cleaved and broken into thin fragments by ultrasonic waves. Drops of aqueous suspensions of the disintegrated materials were deposited on screens coated with supporting films, to which they collapsed by desiccation. The preparation here shown was first coated with a film of carbon (10), then shadow-cast with palladium. The membranes appear in the electron microscope as fragments of lacelike reticulated sheets, with sturdy trabeculae separating rounded

or elongated openings of irregular outlines. The trabeculae are sprinkled with hemispheric tuberosities of various sizes. This type of texture is one of the three "patterns" of conchiolin provisionally described at the electron microscope level in the nacreous shells of mollusks (Grégoire, Duchâteau & Florkin, 1950, 1955; Grégoire, 9, 10). In *Nautilus pompilius* (Grégoire, unpublished), the structure of the reticulated sheets closely resembles that previously observed in *Nautilus macromphalus*, with possible differences in size and arrangement of the tuberosities on the trabeculae ( $\times 42,000$ ). (Micrograph, Grégoire, n).

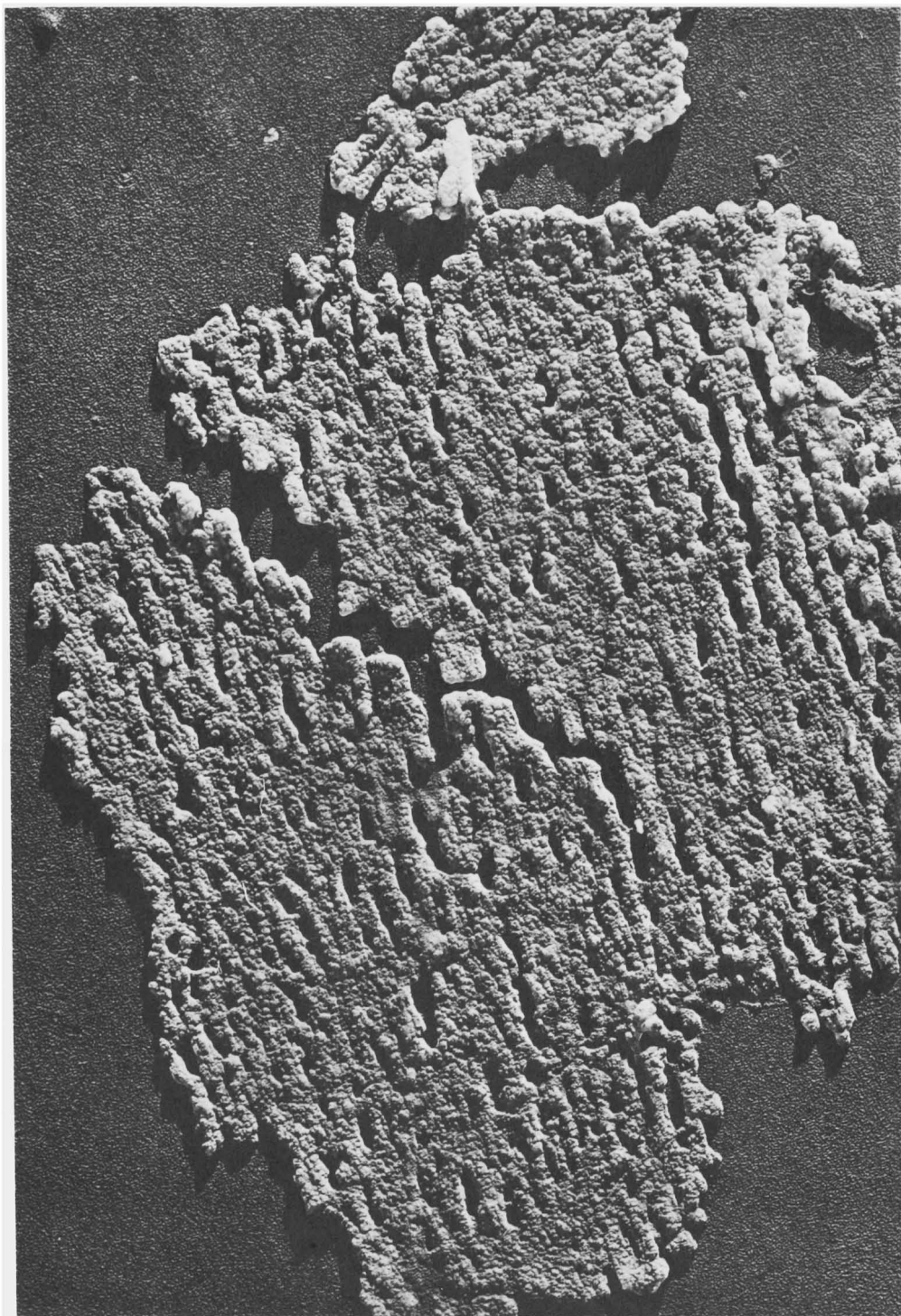


FIG. 61. Electron micrograph of mother-of-pearl from *Nautilus pompilius* (explanation on facing page) (compare Fig. 2).



striction originated, since from the apex to the constriction, shell growth was continuous and no traumatically broken growth lines or repaired former apertural margins are found, whereas immediately beyond the constriction many such breaks are visible and they are more numerous than at later stages of growth. These hitherto unnoticed facts show that growth from the apex to the constriction of the shell was protected from breakage, that is, within the egg.

The white gaps in the color pattern begin to show up first on the flanks and later on the venter. Both kinds appear on the embryonic shell, the first approximately 130 degrees of a volution adapically from the constriction and the second kind approximately 60 degrees of a volution adapically from the constriction. On the embryonic shell, the white gaps are narrow and their margins ill defined, so that the pattern appears out of focus, so to say. The ocular sinuses begin to show as very shallow features shortly before the constriction is developed. The umbilical callus begins to be deposited when the postembryonic shells

reach a diameter of about 5 cm. or a little more; one shell observed by me lacked a completely covered umbilicus at a diameter of 7.7 cm. The umbilicus changes rapidly during the earliest postembryonic stage in that the umbilical seam rapidly changes from one spiral ratio to another and in doing so widens the umbilicus (Fig. 64).

WILLEY (28, p. 225) appears to have been the first to notice the terminal embryonic constriction or line of discontinuous growth and to interpret it as the end of the embryonic stage. According to BÖHMERS (4), it is the position of the aperture when the first septum is built; this interpretation is unlikely, as shown by the observations made by NAEF (20).

On comparing *Nautilus* with *Sepia*, the common cuttlefish, NAEF (20) conjectured that *Nautilus* emerges from the egg having a shell with seven air chambers already formed, because septa 3 to 7 are the most widely spaced and septum 8 is fairly close to its predecessor. However, there is some individual variation in these spacings. One shell seen by me shows the first four septa

#### EXPLANATION OF FIGURE 62, 1-4

1. Positive carbon replica, shadow-cast with palladium, of a fracture surface in the nacreous layer of an adoral septum of *Nautilus pompilius*, showing 18 superimposed broken lamellae in transverse section. Interlamellar reticulated sheets of conchiolin (horizontal white strings in picture) alternate with the aragonite lamellae. The white rectangular structures (on right side of figure) are fragments of aragonite crystals removed with the negative replica and transferred to the positive replica. On the tenth lamella down from the top, a conchiolin bridge (separating two crystals of aragonite in this lamella) forms a right angle with the adjacent interlamellar sheets above and below. The lace-like texture of the interlamellar reticulated sheets of conchiolin are visible as lattice-works protruding from the background and projecting shadows over the second, third, and ninth aragonite lamellae, respectively ( $\times 19,000$ ) (micrograph, Grégoire, n).
2. Positive carbon replica, shadow-cast with palladium, of a nacreous surface (shell wall) of *Nautilus macromphalus* polished obliquely to the plane of the stratified aragonite lamellae. Etching freed seven imbricated interlamellar reticulated sheets of conchiolin. The structural features of the nautiloid pattern (sturdy trabeculae, sprinkled with tuberosities, elongated or rounded, irregular openings) are visible. Except for
- scattered areas with a finely granular surface, the aragonite lamellae alternating with these sheets are either hidden by the superimposed organic structures or were partly dissolved by the corrosion process, leaving the organic sheets piled upon each other ( $\times 27,000$ ). (Grégoire, 1957, *Biophysical and Biochemical Cytology*, fig. 5, with permission of the Editors.)
- 3,4. Membrane coating the adapical convex side of the septum (Edwards, 1849; Barrande, 1857, 1877; Appellöf, 1893) from a living specimen of *Nautilus pompilius* immersed in alcohol immediately after capture and preserved in the U.S. National Museum; material supplied by CURT TEICHERT. The membrane was gently thinned by teasing (3) or treated by ultrasonic waves (4). The chief components of this septal membrane appear to be fibrils and nodules. In the original state of the membrane, the fibrils, either isolated or arranged in bundles, formed a dense felting. The nodules, faintly visible in 3, are thick, irregularly rounded bodies scattered between the fibrils and adhering to them. The fibrils are frequently anchored on the nodules in a beamlike fashion. In 4, the relation between fibrils and nodules is shown after loosening and moderate disintegration of the felting by ultrasonic waves ( $\times 42,000$ ). (Grégoire, n, unpublished observation, 1961.)

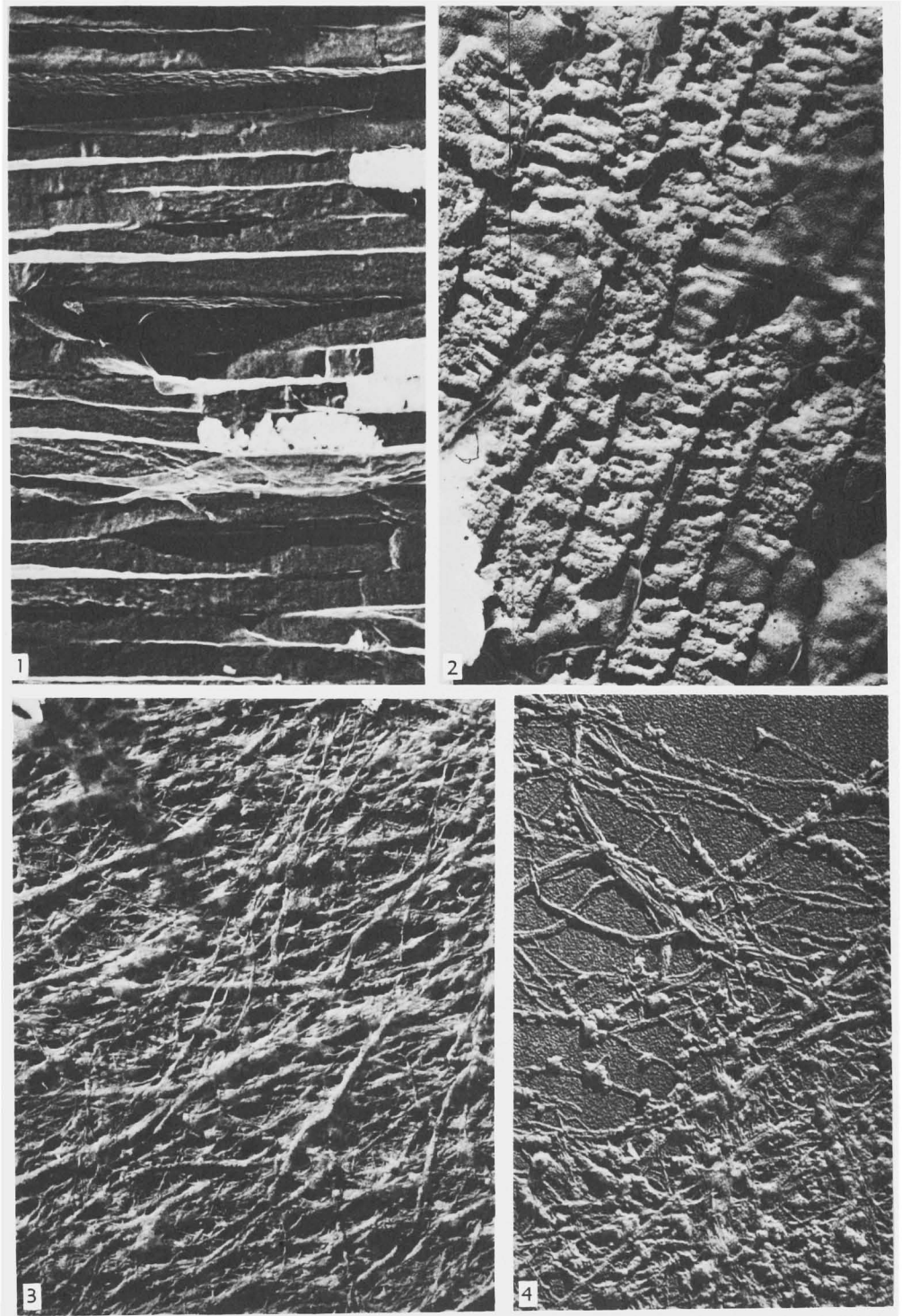


FIG. 62. Electron micrographs of mother-of-pearl from modern *Nautilus* (explanation on facing page) (compare Fig. 2).

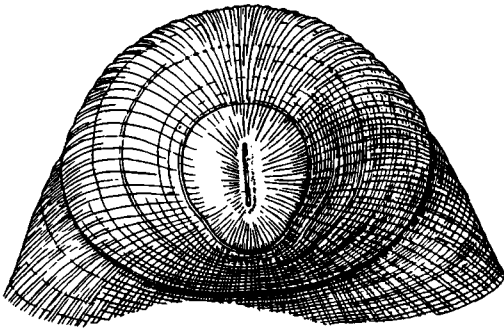


FIG. 63. Apex of the shell of *Nautilus pompilius* LINNÉ, showing the cicatrix of HYATT,  $\times 10$  (from 13).

widely spaced, septa 4 and 5 close together, and septa 5 and 6 spaced wider apart, although not as much as the first three or four septa. Therefore, it is possible that this individual had only four septa at the time when it emerged from the egg.

The apical portion of the shell has reticulate sculpture of fine, raised, intersecting longitudinal and transverse lines (Fig. 63). These become obsolete in later growth stages of all living species except one, *Nautilus scrobiculatus*.

The curvature of the shell is only slight in the first three chambers, but at the third septum it increases abruptly and from then on it continues in a regular spiral (Fig. 66). These changes in curvature produce a small umbilical perforation between the dorsum of the first three chambers and that of the succeeding chambers in the first volution in *Nautilus pompilius*, but in *N. macromphalus* there is no perforation, only a pit on each side.

The beginning of the siphuncle is a closed and sacklike structure, the siphuncular caecum, which rests against the inner surface of the shell apex in a shallow depression located over the cicatrix, or a little to one side or the other of it. In the first and second chambers, the siphuncle has a somewhat greater diameter than in the third and succeeding chambers.

#### GROWTH OF SEPTA

The shell muscles grow with the animal and gradually move forward, together with the whole periphraet, leaving a series of faint concentric growth lines impressed on

the conchiolin film, which they have deposited. Thereby the body gradually slips forward in its chamber; the siphuncular cord grows correspondingly in length. In this way, a space is vacated between the last septum and visceral sac, which with its gradual growth simultaneously fills with air, probably liberated from the pallioseptal arteries that ramify in the mantle covering the rear of the visceral sac. The air space increases until a certain volume is attained. Then the mantle, which covers the visceral sac and as an attenuated extension forms the siphuncular cord, secretes a very thin, somewhat flexible, easily torn membrane of conchiolin. The membrane conforms to the shape of the cord and to that of the rear end of the visceral sac and is firmly attached to the shell wall at the septal contour—the whitish, slightly thickened line in the mantle that encircles the rear end of the visceral sac. Upon this conchiolin membrane successive films of nacre are secreted by the septal face of the mantle, commencing from the suture and gradually spreading to the septal neck, so that a septum, at first thin and fragile, is built up through successive films. The whole process must be rapid, because very few individuals have been caught while growing a septum.

During the making of a new air chamber, particularly during the time the air space between last septum and visceral sac is gradually enlarged, the cord of the siphuncle is kept in position by its insertion in the last septal foramen on one end and on the other end by the genito-intestinal ligament, which rises from the root of the tube and connects with stomach, intestine, and gonad.

The septa are regularly spaced, but distances between them change in an orderly fashion during growth; the first three are close together, septa 3 to 7 are the most widely spaced, from septum 7 on they are fairly close together again. At the end of growth of the individual, the interval between the septa decreases, so that the last two or three septa are more crowded together than their predecessors. It is then that the animal reaches sexual maturity and propagation takes place (Fig. 54, 55).

Each septum is larger and thicker than its predecessor. The increase is gradual and regular, except for the last septum of the



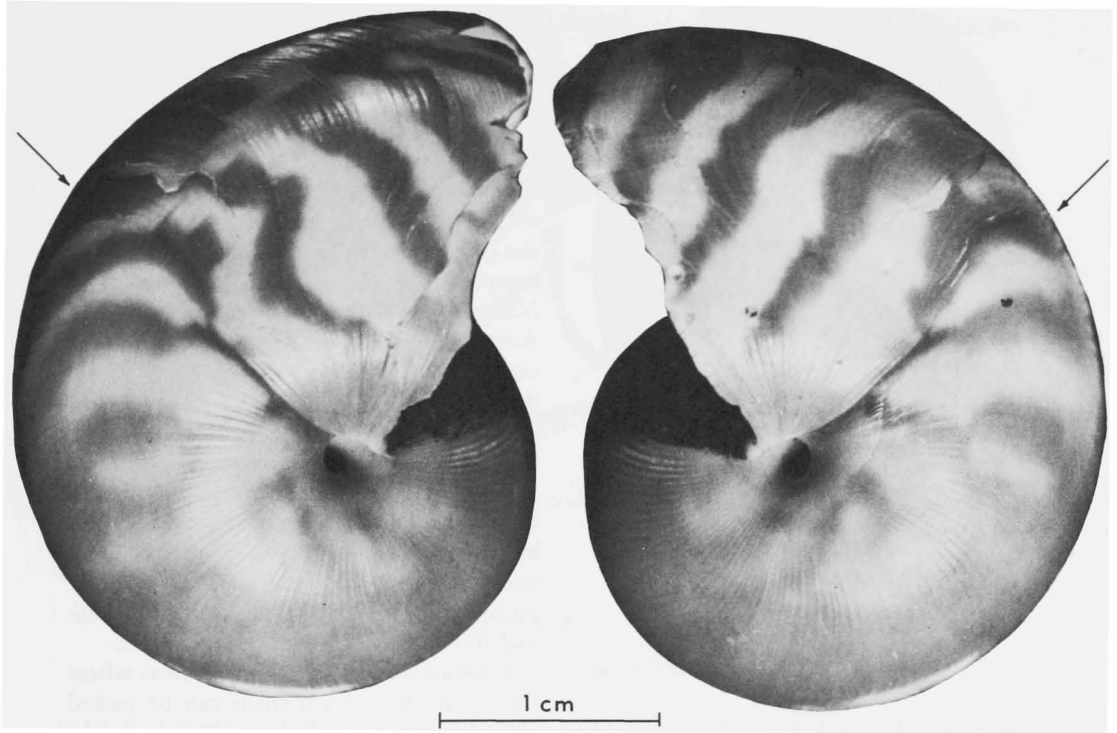


FIG. 64. Side views of a juvenile *Nautilus pompilius* from Cuyo Island, Palawan Province, Philippine Islands (Acad. Nat. Sci. Philadelphia, No. 223519, collected in 1958), showing (arrows) part of terminal embryonic constriction that is particularly well displayed on flanks and umbilical shoulders (Stenzel, n).

mature animal. This septum is not only closer to its predecessor but also noticeably thicker, up to 1.5 mm. in thickness.

#### MATURITY

Propagation takes place only after the final septum has been formed (30, p. 746). Maturity is indicated in the shell by (1) thickening of the apertural shell margin, which is thin and fragile as long as the animal is immature, (2) decrease in the volume of the last air chambers formed, as shown by a crowding together of the last two or three septa, and (3) greater thickness of the last septum, which is noticeably thicker than its predecessor, and (4) widening of the black border on the inside of the shell aperture. The ocular sinuses become more prominent at maturity as age of the animal advances.

Formation of septa and their regular spacing in the shell have nothing to do with reproductive cycles of the animal.

## GENERAL BIOLOGY

### SPECIES

Five species and an unknown number of geographic subspecies of *Nautilus* are living representatives of the genus. The species differ in smoothness or reticulate (scrobiculate) sculpture of the shell, presence or absence of an umbilical callus and perforation, degree of involution, surface features of hood, adult size, number of septa, and coloration of the shell. Coloration, particularly its value and chroma, is variable and cannot be used to the extent that IREDALE thought possible, although subspecies might be defined by it in the future. One of the species, *N. scrobiculatus*, differs in so many features from the others that it is logical to place it in a separate subgenus.

The following species of *Nautilus* are recognized: (1) *N. pompilius* LINNÉ, 1758, type-species of the genus (Figs. 54,55,56,A); (2) *N. repertus* IREDALE, 1944 (14) [=N.

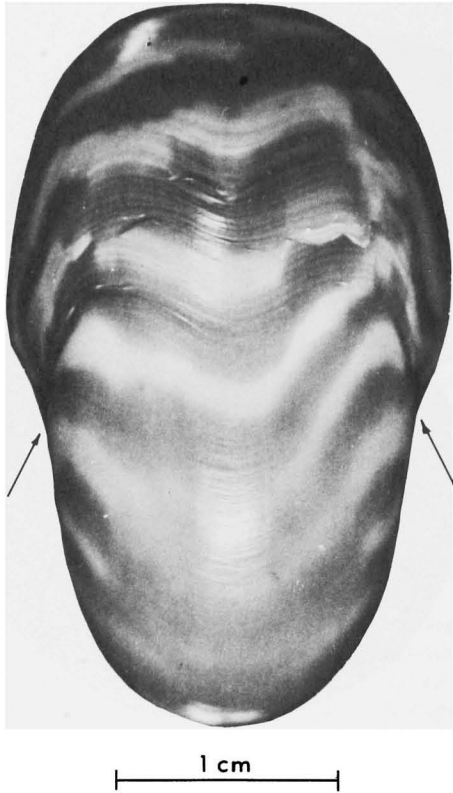


FIG. 65. Ventral side of specimen illustrated in Figure 64 (Stenzel, n).

*ambiguus* G. B. SOWERBY, 1849 (non FICHTEL & MOLL, 1798)]; (3) *N. stenomphalus* G. B. SOWERBY, 1849; (4) *N. macromphalus* G. B. SOWERBY, 1849, and (5) *N. scrobiculatus* SOLANDER, 1786 (Fig. 56,B) [= *N. umbilicatus* LAMARCK, 1822 (non LINNÉ, 1758, which is a foraminifer)].

The first two species listed have an umbilical callus, the next two do not; the last is the only one that has scrobiculate sculpture in the adult. *Nautilus alumnus* IREDALE, 1944 (14), is a *nomen nudum*, since neither a description nor a figure nor adequate literature reference was given to validate the name.

### DISTRIBUTION

The genus *Nautilus* is restricted to the southwestern Pacific Ocean, where it ranges from northwestern Australia and tropical Queensland to the south coast of Luzon Island in the Philippines and from Macassar

Strait to the Fiji Islands (26). Hence the geographic range is very large, embracing 60° of longitude and 35° of latitude (Fig. 67). Nevertheless, it is a relict in the sense that its present range is only a small fraction of the combined geographic ranges of various Tertiary Nautilida.

Some of the species live side by side without interbreeding. The geographic area of the genus apparently is continuous, with the exception of the isolated populations of *Nautilus repertus* off the coast of southern Australia, one of which is now authenticated by the finding of two stranded individuals (7).

Except for these isolated populations, *Nautilus* is restricted to warm tropical marine waters. It is recorded from 315 fathoms, but most catches are made in shallow water by native fishermen. Evidently, it has great tolerance for depth changes. The siphuncle probably plays a role in adapting the animal to changes of hydrostatic pressure.

Dead shells float far from the areas where the species live. Such shells can be picked up on the beach not far from Tokyo, Japan, at least 1,800 miles from the habitat of living species. Other drifted shells have been recorded from the Ryukyu Islands, Taipei, Nicobar Islands, Cocos Keeling Islands, New South Wales, New Zealand, Sunday Island of the Kermadec Islands (26), the east coast of Madagascar,<sup>1</sup> and other places.

### FOOD

The tentacles of *Nautilus* are highly specialized as to functions, and in seizing prey the various groups of tentacles act in a regular sequence. When resting or quietly swimming, all the cirri remain withdrawn in their sheaths, but sometimes their tips are visible. When alerted, the animal extends the ocular tentacles and the four small outer-most digital tentacles on each side. When it notices food, the animal brings out the outer row and part of the median row of digital tentacles and spreads them to form a cone of search. This cone is kept al-

<sup>1</sup> Reported by DAVYDOV, K. N., 1906, Poostrovam Indo-Avstraliyskago Arkhipelaga. Vpechatleniya i nablyudeniya naturalista. Pt. 3. Na ostrovakh Aru: Acad. Impér. Sci. St. Pétersbourg, Bull., ser. 5, v. 25, no. 5, p. 245-351.

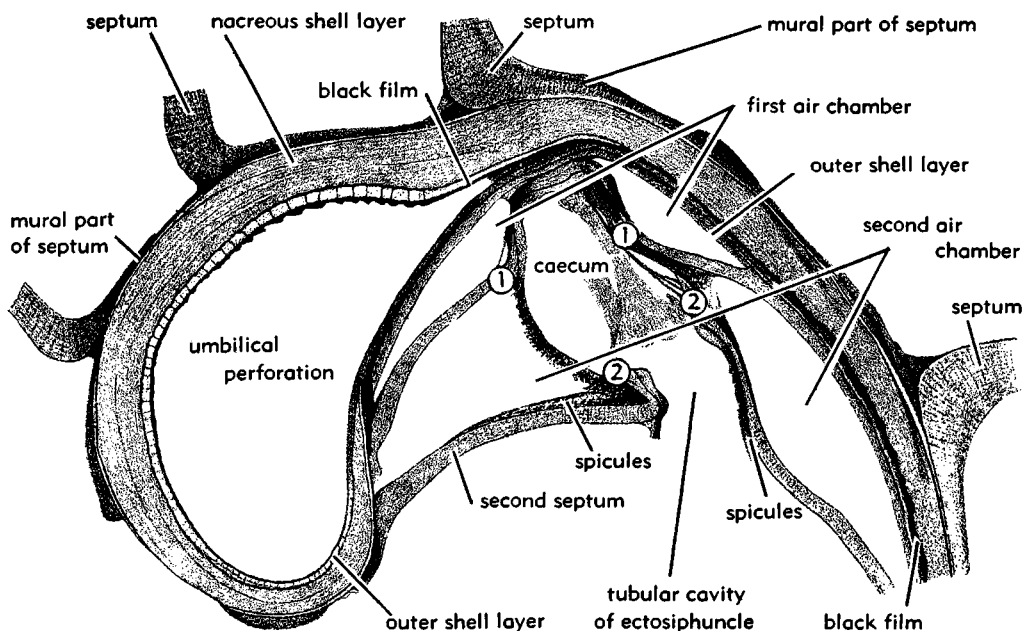


FIG. 66. Vertical section through the apex of the shell of *Nautilus*,  $\times 15$  (after 2).

ways at a constant angle of spread, while the animal backs up or moves forward or circles around, until the food is found. The cone of search is thrust out also when the animal is hungry or explores new territory or swims in search of food. As soon as it touches the food, the animal thrusts out the inner ring of digital tentacles to grasp the food and to draw it under the hood, while the cone-of-search tentacles let go (2b).

Because the suction exerted by the annular ridges of the tentacles is very strong, their hold is tenacious. Laboratory observations show that a tentacle attached to an object can be torn in two by a sudden jerk (30).

The sharp jaws are powerful nippers, capable of shearing through chicken bones. Much of the food, cut into pieces, is first lodged in the extensible esophagus, which serves as a crop; then the muscular stomach takes over the diminution of food. Chief food consists of fish, crabs, and lobsters. The animal is a carnivore and scavenger, probably feeding on or near the sea bottom.

### LOCOMOTION

The tentacles serve to anchor the animal temporarily by adhesion to some suitable

surface, but they are not used for crawling, and the animal does not crawl about on the bottom. Older accounts of crawling *Nautilus* have been disproved definitely and repeatedly.

Swimming is the sole means of moving. *Nautilus* is a rapid swimmer and moves by jet propulsion. Water is ejected forcibly through the hyponome and directed by it, and the tip of the hyponome is very active and flexible. The jet propels the animal backward, as well as in many other directions, depending on the attitude of the hyponome.

The water of the jet comes from the branchial chamber of the pallial cavity. It is forced out rhythmically by the crura and the posterior three-eighths of the hyponome. These strongly muscular and contractile parts lie inside the branchial cavity. The mantle itself does not take part in these contractions, being only slightly muscular and attached to the shell at the apertural margin. Herein the Tetrabranchiata differ from the Coleoidea, which are more powerful and faster swimmers, because their mantle is very muscular and produces the jet. In a swimming animal, the crura of the hyponome have been seen to rise and

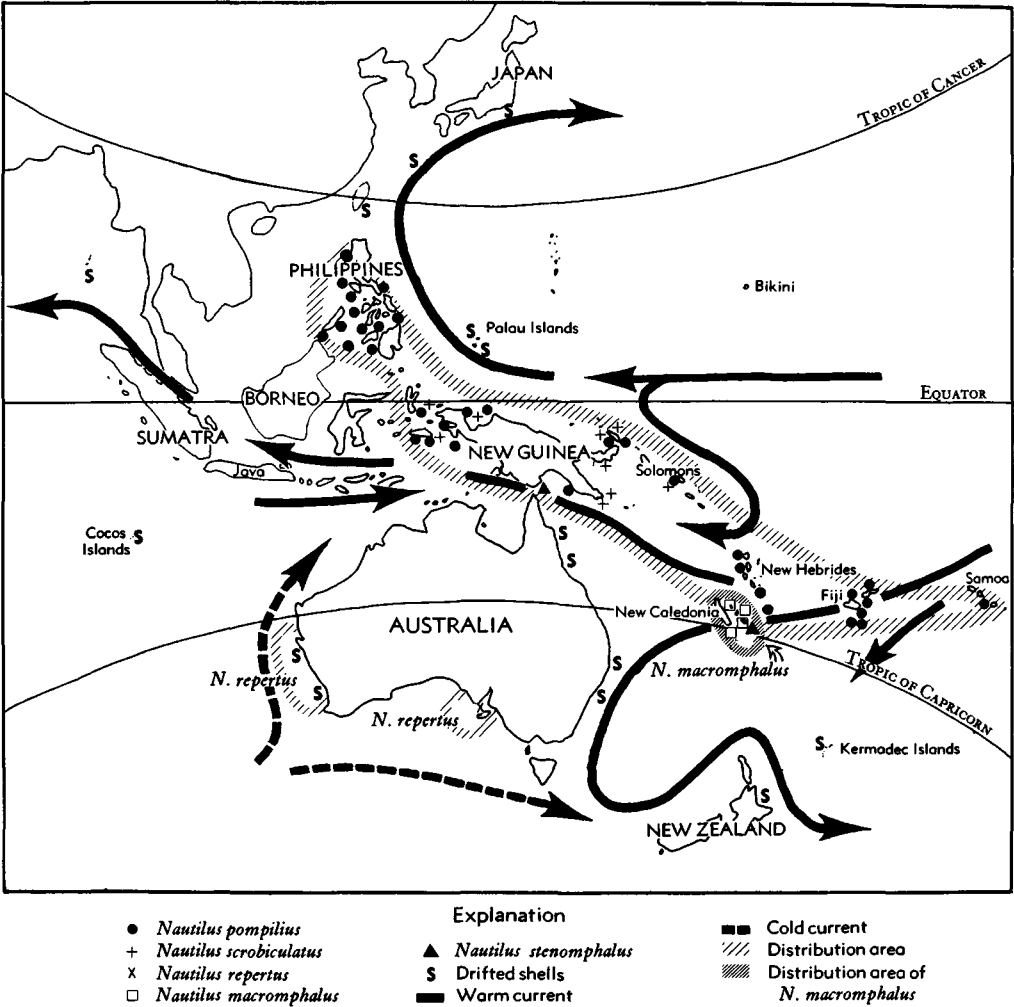


FIG. 67. Geographic distribution of living *Nautilus* (Stenzel, n).

fall with a regular pulsating motion, which also renews rhythmically the water in the branchial chamber, where the four gills lie, allowing the animal to breathe. The inhalant current enters at the inhalant passage, and the exhalant current escapes through the hyponome.

The whole animal, shell and all, is excellently streamlined in the form of a laterally compressed ellipsoid. No ribs or spines break the streamlining of the smooth, clean shell in *Nautilus pompilius*. Some other species of *Nautilus* have low, smooth, falcate ribs that are undulations of the shell wall, parallel to the growth lines on the

flanks between the ocular and hyponomic sinuses. However, these ribs are so low that they offer no serious hindrance to swimming.

FUNCTION OF SHELL

Primary function of the shell is to protect the soft parts of the animal, particularly the visceral sac, in which are organs (such as heart and gonad) indispensable to survival of the individual and the species. Herein its function is the same as that of a gastropod shell.

In addition, it functions as a hydrostatic apparatus. The air in the air chambers coun-

teracts the weight of the animal's shell and fleshy parts so that the whole animal's buoyancy is in balance. To preserve this balance, new air chambers have to be built as long as the animal grows and adds weight to the whole. Hence, the shell aids the animal in swimming, and muscular energies are expended for locomotion only, but need not be used to keep it from sinking.

The air in chambers is approximately at a pressure of 1 atmosphere, both in an animal which had been in an aquarium for some time and in an animal brought up from 100 fathoms (180 meters) 6 to 8 minutes before testing. Two samples of the gas scanned by mass-spectrograph showed that the proportion of argon to nitrogen was three times that of atmospheric air scanned simultaneously. The proportion of oxygen to carbon dioxide was variable (2b).

In addition to air, several of the chambers contain fluid while the animal is alive. The fluid contains organic materials and dissolved salts. The small quantity of fluid found in the older chambers is viscous. The various chambers contain different amounts of fluid.

The fluids in the various air chambers are distributed in such a way as to keep the animal well balanced and in stable equilibrium in the sea water. When tilted or rotated from its normal vertical position, the animal, including its shell, returns automatically to normal. Much greater volumes of fluid are in the last-formed chambers than in the older ones, and counterbalancing the former are the chambers overhanging the back of the hood, which also carry small amounts of fluid. However, the chambers that are in the uppermost dorsal position in life contain little or no fluid, as has been demonstrated by X-ray shadow graphs (2b).

Because the siphuncle fills the hole completely, air chambers are fully sealed from each other, and such gas exchange as may take place between them must go by way of diffusion through the siphuncle and its blood vessels.

The siphuncle is certainly a functional organ and is by no means vestigial, for it is well supplied with arterial blood and is little variable in size, shape, or position in differ-

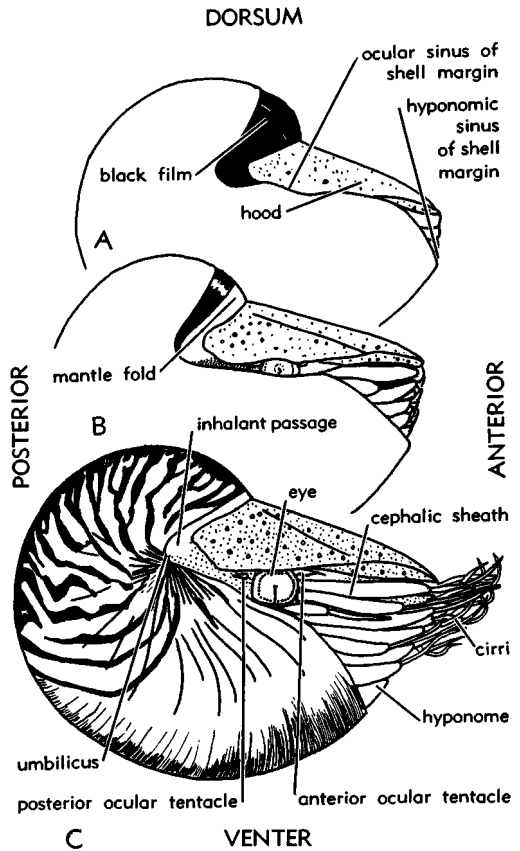


FIG. 68. Living *Nautilus pompilius* LINNÉ, seen from right side in position of rest. (A) Animal completely withdrawn into shell; (B) partially withdrawn; (C) normal attitude of rest;  $\times 0.25$  (modified from 8).

ent individuals. Vestigial organs that have lost their function commonly are highly variable and ill supplied with arterial blood. The exact function of the siphuncle, however, is not known and has been the subject of conjecture. WILLEY's crude experiments showed that it can be cut without seeming to affect the ability of the animal to swim, at least until loss of blood has made itself felt. Because the air chambers are cut off completely by the septa, the siphuncle is the only avenue by which air can be exchanged and gas pressure equalized between the chambers. Possibly the blood in the siphuncle gradually equalizes and adjusts the gas pressure in the air chambers to conform with the hydrostatic pressure of the

water surrounding the animal. When interior and exterior pressures are equal, no undue stress is exerted on the shell; hence, the shell cannot be crushed by the hydrostatic pressure of the surrounding water.

To aid in swimming—or rather, not to be a hindrance—the shell must be symmetrical and as compact as possible. Planispiral coiling and effective streamlining of the shell take care of this need, combining economy of space with added strength of construction.

Strength of construction permits the hydrostatic apparatus to be built with least weight and adds to the primary function as protective cover. Strength of construction is such that the shell can withstand hydrostatic pressure changes very well. Use of enclosed air as hydrostatic apparatus is not unique; a well-known example is the air bladder of fish. For reasons of stability, the air chambers have to be above the dead weight, which comprises the fleshy parts in the body chamber. This is the reason for the exogastric coiling. Only such coiling can bring the air chambers above the dead weight of the animal. *Nautilus* can no more turn over in water than a balloon can float with the gondola on top.

The shell is usually free of encrusting organisms as long as the *Nautilus* lives, because the animal is active and a rapid swimmer. However, a few live individuals of species lacking an umbilical callus bear groups of small tubicolous annelids or small

stalked cirripeds attached at each umbilicus. These are too small to add much weight to the shell.

### ACTIVITY AND REST

During the day the animal rests with the shell touching or nearly touching the sea bottom and the hood almost shut, so that the eyes are hardly showing. About a half hour before sunset the animal becomes active.

When the animal swims and breathes, the hood is raised above the shell aperture so as to expose eyes, tentacles, and the hyponome tip, and to allow free communication between the mantle cavity and surrounding water. In this position, the lower edge of the hood is horizontal, its concave posterior edge concealing the black film entirely, and the tip of the hyponome projects beyond the shell margin at the hyponomic sinus (Fig. 43). The eye, in the corner between hood and shell margin, can protrude slightly beyond the plane of the shell surface.

When disturbed, the animal at first withdraws only partially into its protective shell (Fig. 68). Then the hood exposes part of the black film, and the eye is still able to peer out because of its position at the ocular sinus of the shell margin. The tentacles are largely retracted and arranged in a close fit. If necessary, the animal can retract quickly and completely, shutting the shell aperture with its hood.

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## CLASSIFICATION AND STRATIGRAPHIC DISTRIBUTION

By CURT TEICHERT<sup>1</sup> and R. C. MOORE<sup>2</sup>[<sup>1</sup>United States Geological Survey; <sup>2</sup>University of Kansas]DEVELOPMENT OF  
CLASSIFICATION

The earliest attempts to classify the bewildering variety of shell forms represented by the nautiloid and related orders were handicapped by lack of understanding of their morphology and habitat. Also, recognition of many elementary taxonomic relationships was retarded until well into the 20th century, because of failure to investigate the internal structures of many shells.

*Nautilus* was known to ARISTOTLE and probably named by him. It became available as a generic name in systematic zoology through being listed in the 10th edition (1758) of LINNÉ's "*Systema Naturae*." It is of historical interest that of 17 species originally included in *Nautilus* by LINNÉ, 14 were Foraminifera. The three remaining species, *N. pompilius*, *N. spirula*, and *N. orthocera*, were an odd assortment of not very closely related living and fossil cephalopods.

Until about the year 1800, few authors distinguished between chambered cephalopods and Foraminifera, and many of the latter were described under names such as *Nautilus*, *Orthocera*, and *Orthoceratites*.

Early in the 19th century the distinctiveness of Foraminifera and cephalopods was recognized and the latter were described and grouped according to their external shell form.

The generic name *Nautilus* was formally restricted to cephalopods in 1808 by DE MONTFORT (7), who listed *Nautilus pompilius* as the only formally named (Linnean) species in a long list of synonyms of the "espèce servant de type au genre."

F. A. QUENSTEDT's (8) doctor's dissertation "*De notis Nautiliarum primariis*" (1836) was a milestone in nautiloid classification. Like the pre-Linnean author BREYNIUS (1732) before him, QUENSTEDT grouped all fossil "nautiloids" into three "genera": *Orthoceras*, consisting of straight shells, *Nautilus* of coiled shells, and *Lituites*

comprising all curved, and loosely or imperfectly coiled shells. Within each "genus" he established informal groups of shells sharing certain external, or even internal, characteristics. Thus, within *Orthoceras* he distinguished assemblages termed "Vaginati" (=order Endocerida), "Cochleati" (=families Actinoceratidae + Armenoceratidae), "Gigantei" (=genus *Huronia*), "Regulares" (essentially=order Orthocerida), and others. The other two genera included similarly heterogeneous mixtures of what we now know are unrelated groups.

Monographic work by many paleontologists during the second and third quarter of the 19th century brought to light the existence, especially in early Paleozoic rocks, of very unorthodox types of chambered cephalopods that differed greatly from any of the three simple prototypes separated by BREYNIUS and QUENSTEDT. Consequently, by the middle of the 19th century a sizable number of new genera had been described by STOKES, HALL, SOWERBY, BRONN, M'COY, and other noted paleontologists. Of these early genera some (e.g., *Actinoceras*, *Ormoceras*, *Huronia*, *Gonioceras*, *Endoceras*, *Phragmoceras*) are still in good standing, whereas others (e.g., *Gomphoceras*, *Cyrtoceras*) are no longer recognized as valid genera.

Far ahead of other workers on nautiloids, SAEMANN (10), in 1852, emphasized the importance of endosiphuncular structures and proposed to divide the "Nautilidae" into two major groups, namely, Actinosiphitae, with expanded siphuncle segments and an internal radial apparatus, and Coelosiphitae, with empty siphuncle. SAEMANN's Actinosiphitae included what are now the Actinoceratoidea, as well as some Onco-cerida with actinosiphonate structure. SAEMANN's ideas had little influence on contemporary trends in nautiloid classification.

BARRANDE's description of the cephalopods in his classic "*Système silurien du centre de la Bohême*" (1865-77 marks the culmination and end of the period of nautiloid classification based on external shell



morphology. BARRANDE accommodated almost 1,000 species of European (mostly Bohemian) and North American cephalopods in the two "genera" *Orthoceras* and *Cyrtoceras*. Next in order of number of species were the "genera" *Gomphoceras*, with about 80 species, and *Phragmoceras* and *Trochoceras*, with about 50 species each. But BARRANDE was increasingly troubled by the necessity to erect genera for one or only a few species that differed so distinctively from all other chambered cephalopods that it was impossible to place them in any of the catch-all genera. Among these oddities were such genera as *Bathmoceras*, *Nothoceras*, *Adelphoceras*, *Herco-ceras*, *Mesoceras*, *Ascoceras*, and *Glossoceras*, all of which are recognized today, though their true affinities and relationships are now generally better understood than in BARRANDE's time.

Study of nautiloids during the last quarter of the 19th century was dominated by HYATT, who advanced nautiloid classification by discarding shell shape as the basic criterion. HYATT (2) based his new (1883) classification of the order "Nautiloidea," which he adapted from Agassiz (1847), on the structure of the septal neck and proposed to distinguish two "genetic groups": (1) the Holochoanoida, with septal necks extending from one septum to the next, either forward (Prochoanites, including *Bathmoceras* and *Nothoceras*) or backward (Metachoanites=Endoceratidae), (2) the Ellipochoanoida, "with short funnels and the siphon completed by an intervening connective wall of distinct structure from the septal funnels." Within the Ellipochoanoida, HYATT distinguished the Bac-tritidae as "Macrochoanites," separating them from the "Microchoanites," which included the majority of all nautiloids.

A further refinement of this classification was offered by HYATT (3) in 1898, when he divided the "Nautiloidea" into the following suborders: (1) Holochoanites, with septal necks reaching backward from one septum to the preceding one; (2) Mixochoanites (equivalent to Ascocerida of present usage); (3) Schiztochoanites (*sic*) [*recte* Schistochoanites], with "funnels imperfect, or split on the outer side" (including *Bathmoceras*, but ill-defined by present

standards); (4) Orthochoanites, with straight and short septal necks; (5) Cyrtocchoanites, with septal necks short and bent outward, divided into "subgroups" termed Annulosiphonata (equivalent to present order Actinocerida) and Actinosiphonata (now known to be an artificial grouping of genera within the order Oncocerida).

With minor modifications the same classification was used by HYATT in Part II of the English edition of ZITTEL's *Text-book of Palaeontology*, vol. 1 (1900) (14).

Although HYATT's classification constituted a considerable advance towards disentanglement of the bewildering variety of nautiloid forms which became ever more apparent as new genera continued to be described, it was slow to gain ground outside of North America. In his revision of the last German edition of ZITTEL's *Grundzüge der Paläontologie*, BROILI (1924) retained the Nautiloidea as a suborder, dividing it into five families.

No significant contributions to nautiloid classification were made during the first third of the 20th century, although NAEF (1922) pointed out that such diverse morphological types of *Endoceras*, *Actinoceras*, *Orthoceras*, *Phragmoceras*, *Nautilus*, and the ammonoids could not possibly be regarded as very closely related to each other. In 1933, TEICHERT (13) emphasized the importance of endosiphuncular structures. He proposed subdivision of the Cephalopoda into the following orders: (1) Nautiloidea, with empty, narrow, cylindrical siphuncles; (2) Endoceroidea, with endocones; (3) Actinoceroidea, with an endosiphuncular vascular system; (4) Cyrtoceroidea, with actinosiphonate siphuncular structures; and (5) Gomphoceroidea, with relatively large empty siphuncles, not regarded as a natural unit at the time. These five orders were considered to be equivalent in taxonomic rank to the Ammonoidea and Belemnoida. Although this proposed scheme suffered from many defects, it was adopted by SCHINDEWOLF (11), who, however, preferred to reduce the rank of all above-mentioned groups to suborders.

Essentially the same classification was presented by KUHN (5), who separated the straight, orthochoanitic nautiloids as a new "suborder" termed Orthoceracea. In 1949, the same author adopted the taxonomic pro-

cedure suggested by TEICHERT, elevating all groups to the rank of orders within the superorder Nautiloidea. At the same time KÜHN (6) established a new order termed Ascoceracea for a group of specialized forms previously included in the "Orthoceracea."

Further refinement was offered in 1950 by FLOWER & KUMMEL (1) by combining the criteria of shell form, structure of septal necks and connecting rings, and endosiphuncular structures into an integrated system of classification of the so-called class Nautiloidea. This afforded basis for distinction of 14 orders, named Ellesmeroceratida, Endoceratida, Actinoceratida, Michelinoceratida, Ascoceratida, Bassleroceratida, Oncoceratida, Discosoroidea, Tarphyceratida, Barrandeoceratida, Rutoceratida, Centroceratida, Solenochilida, and Nautilida.

In its major outlines, this classification has stood the test of subsequent investigations, although the number of orders has now been slightly reduced. The very small order, Bassleroceratida, has been divided between the Oncoceratida (Oncocerida) and the Tarphyceratida (Tarphycerida); and the Rutoceratida, Centroceratida, and Solenochilida (=Aipocerataceae of this volume) have been merged as superfamilies within the order Nautilida.

Attempts have been made to arrange these orders (or suborders, according to some authors) into larger taxonomic units, but no entirely natural grouping has as yet been proposed. TEICHERT (13) proposed the Stenosiphonata and the Euryisiphonata, both of unspecified rank, the former to include all conch-bearing cephalopods with narrow siphuncles (including the Ammonoidea), the latter to receive all other nautiloid orders (most of which were as yet ill-defined at the time). This scheme won temporary support from FLOWER and is still being used by DAVITASHVILI. However, since it now appears that the stenosphonate Nautilida developed from euryisiphonate oncocerids, whereas other stenosphonate stocks developed directly from the ellesmerocerids, grouping of the nautiloid orders according to size of siphuncle would be highly artificial.

KOBAYASHI (4) suggested two major divisions of nautiloids according to the primary

position of the siphuncle: Ventrosiphonata for forms with a primarily ventral siphuncle (ellesmerocerids, endocerids), and Centrosiphonata for forms with a primarily central or subcentral siphuncle. As examples of the latter he cited the orthocerids and the actinocerids. Some endocerids have a subcentral siphuncle, however, and many actinocerids show the siphuncle in a ventral position. We may agree with SCHINDEWOLF (1943) that positions of the siphuncle in nautiloids are too variable to serve as reliable guides to classification.

A comprehensive review of the history of classification of the Cephalopoda, with special emphasis on treatment of the nautiloid orders since the time of HYATT, has been given by SHIMANSKIY & ZHURAVLEVA (12).

## CLASSIFICATION ADOPTED IN TREATISE

We accept, with minor changes, grouping of nautiloid orders by SHIMANSKIY & ZHURAVLEVA which leads to a threefold arrangement: (1) subclass Endoceratoidea, comprising the orders Endocerida and Intejocerida; (2) subclass Actinoceratoidea, containing the single order Actinocerida; and (3) subclass Nautiloidea, composed of the remaining orders, Ellesmerocerida, Orthocerida, Ascocerida, Oncocerida, Discosorida, Tarphycerida, Barrandeocerida, and Nautilida. These divisions may be characterized briefly as follows, with accompanying graphic representation of their stratigraphic distribution and approximate abundance of contained genera in successive geologic series and systems (Fig. 69).

An additional subclass, Bactritoidea, is recognized and this assemblage is treated in a chapter at the end of the present volume.

## ENDOCERATOIDEA

This group consists mostly of medium-sized but also some very large forms, mostly with orthoconic, more rarely with cyrtconic conchs. The siphuncles are large, generally marginal; septal necks short in early forms, long in later (Middle Ordovician) representatives. The endoceratoids invariably have deposits within the siphuncle, generally in the form of conical sheaths. They are most abundant in Lower and

Middle Ordovician deposits but range well into the Silurian. The subclass is judged to have been derived from the order Ellesmerocerida of the subclass Nautiloidea. It is divided into two orders named Endocerida and Intejocerida.

#### ENDOCERIDA

The endocerids are distinguished primarily by the nature of their endosiphuncular deposits, which consist of calcareous, conical sheaths. They are found chiefly in Ordovician formations, one genus being recorded doubtfully from the Middle Silurian.

#### INTEJOCERIDA

The intejocerids have generally straight conchs with short chambers, straight sutures, and unusually large siphuncles, which are filled by radially disposed, rather tightly packed, longitudinal lamellae. Four described genera occur in Lower and Middle Ordovician rocks of Siberia.

#### ACTINOCERATOIDEA

The assemblage of actinoceratoids have generally orthoconic conchs with short, bent septal necks and generally broad siphuncle segments which contain many peculiar and specialized structures, such as radial canals and perispatia. Cameral deposits are a characteristic feature of this group that ranges from the Middle Ordovician into the Upper Carboniferous. The subclass contains a single order, named Actinocerida. Genera are most numerous in the Middle and Upper Ordovician.

#### NAUTILOIDEA

All cephalopod groups which formerly were assigned to the order (or suborder) Nautiloidea, excepting the endoceratoids and actinoceratoids, now are included in the subclass Nautiloidea. Even after removal of the two mentioned groups as independent subclasses, the diversity of the Nautiloidea in a restricted sense is so great that no simple diagnosis is possible. Every variety of shell form, from straight to tightly coiled, is represented. The siphuncle is variable in position within the conch, slender to moderately large in diameter (none very large), with septal necks orthochoanitic or cyrtochoanitic (never holo- or macrochoanitic), and connecting rings

which are thick in some earlier forms but invariably thin in later and more advanced genera. Endosiphuncular and cameral deposits may be present or absent. Representatives of the subclass, which are divided among the following eight orders, range from Upper Cambrian to Recent.

#### ELLESMEROCERIDA

This group, because of its antiquity and various primitive morphological characters, probably comprises the rootstock from which the endoceratoids, actinoceratoids, and all nautiloid groups were derived, directly or indirectly (Fig. 69, 70). Most genera have straight to weakly cyrtoconic shells with marginal, empty siphuncles of small to medium size. Earliest representatives of the order are very small forms found in Upper Cambrian; these were followed by genera with larger conchs, yet still moderate in size (perhaps 1 foot in length) in the Lower Ordovician. Three Upper Cambrian genera are known, whereas 60 are recorded from the Lower Ordovician; five genera occur in the Middle Ordovician and only two in the Upper Ordovician. A single genus is doubtfully reported from Silurian rocks.

#### ORTHOCERIDA

The orthocerids are characterized by orthoconic or weakly cyrtoconic, generally slender, shells, formerly collectively referred to the genus *Orthoceras*. They have narrow siphuncles, with cylindrical, or only weakly inflated siphuncle segments, and both endosiphuncular and cameral deposits. They are divided into the essentially orthochoanitic Orthocerataceae and the cyrtochoanitic Pseudorthocerataceae. In the former, endosiphuncular deposits are usually restricted to ring-shaped structures constricting the septal foramina; the latter have more strongly developed and elaborately fashioned parietal deposits. Cameral deposits are present in both superfamilies. In the Pseudorthocerataceae they are commonly characterized by lamellar structure and by heavy emphasis on mural deposits. The Orthocerida range from the Lower Ordovician into the Triassic. Genera are most numerous in Middle and Upper Ordovician and Silurian formations (Fig. 69).

**ASCOCERIDA**

Genera of the ascocerid group possess conchs consisting of two rather distinct growth forms. An early stage is slender cyrtconic, with orthochoanitic septal necks and narrow siphuncle. This is suddenly followed by a bulbous, breviconic stage with large siphuncle and cyrtchoanitic septal necks. The early, slender part of the conch is either thrown off in the adult stage, or it breaks off after death of the animal. The ascocerids are relatively rare fossils, classified in a small number of genera (total, 13). They range from the Middle Ordovician through the Silurian.

**ONCOCERIDA**

This assemblage includes forms with conchs consisting predominantly of brevicones, either straight or curved, but also more slender cyrtcones and even orthocones (Jovellaniidae) and coiled forms (Nothoceratidae). The conchs are characterized by thin septa, recumbent septal necks, thin connecting rings, and usually broadly expanded siphuncle segments. Endosiphuncular structures occur either in the form of bullettes, or as actinosiphonate deposits, or both. Cameral deposits, if present at all, are thin. The order ranges from Middle Ordovician through Lower Carboniferous (Mississippian). Largest numbers of genera are found in the Middle and Upper Ordovician, Silurian, and Middle Devonian (Fig. 69).

**DISCOSORIDA**

The discosorids have mostly breviconic and stoutly cyrtconic conchs, generally with thick, complex connecting rings and differentiated endosiphuncular deposits that consist of parietal deposits, with or without accompanying endocones. Cameral deposits are relatively rare. Advanced forms exhibit a tendency toward contracted and elaborately modified apertures, such as occur in the Phragmoceratidae. The order ranges from the Middle Ordovician well into the Devonian, with chief development in the Ordovician and Silurian (Fig. 69).

**TARPHYCERIDA**

This group of early Paleozoic nautiloids is characterized by genera with mostly

coiled conchs in which the siphuncles bear thick connecting rings. Widely umbilicate shells with slowly expanding whorl diameters prevail, but they include some gyrocones and torticones, as well as conchs which are straight at maturity (Lituitidae). The range of the Tarphycerida is Lower Ordovician to Upper Silurian.

**BARRANDEOCERIDA**

In general morphological character, the barrandeocerids resemble the tarphycerids but are distinguished by their thin connecting rings. The stratigraphic range of the group is relatively large (Middle or possibly Lower Ordovician to Middle Devonian), but the number of known genera in any series or system in which they occur is small (Fig. 69).

**NAUTILIDA**

Cephalopods of the order Nautilida include a rich variety of closely coiled, widely umbilicate to convolute and involute conchs, ranging from Lower Devonian to Recent (Fig. 69). In nautilids, with rare exception, the siphuncle is narrow and cylindrical; it has thin connecting rings and is subcentral in position. In a few specialized groups, however, the siphuncle position is at the margin, either ventral or dorsal. The nautilids include forms with the most elaborate suture patterns known among the nautiloid orders. The sutures of some specialized forms, such as the Triassic *Siberionautilus* or the Paleogene *Aturia*, are considerably more complex than those of primitive ammonoids.

Most Nautilida were of moderate size, the great majority being smaller than the contemporary *Nautilus pompilius*. The order, however, includes the largest known coiled nautiloids, represented by *Titanoceras* (more than 3 feet in diameter) from the Upper Pennsylvanian (Chaffin Ls., Cisco Gr.) of Texas.

## DISTRIBUTION OF SUPRAGENERIC NAUTILOID TAXA

The following tabulations record numbers of genera in suprageneric divisions of the Endoceratoidea, Actinoceratoidea, and Nautiloidea recognized in the *Treatise*, ac-

accompanied by statements of stratigraphic ranges. Family-group taxa or other assemblages which contain subgenera are accompanied by two figures, the number of included genera being indicated by the first

and subgenera additional to nominotypical subgenera by the second. For example, the figures 16;1 indicate 16 genera and 1 subgenus in addition to the nominotypical one, which is not counted.

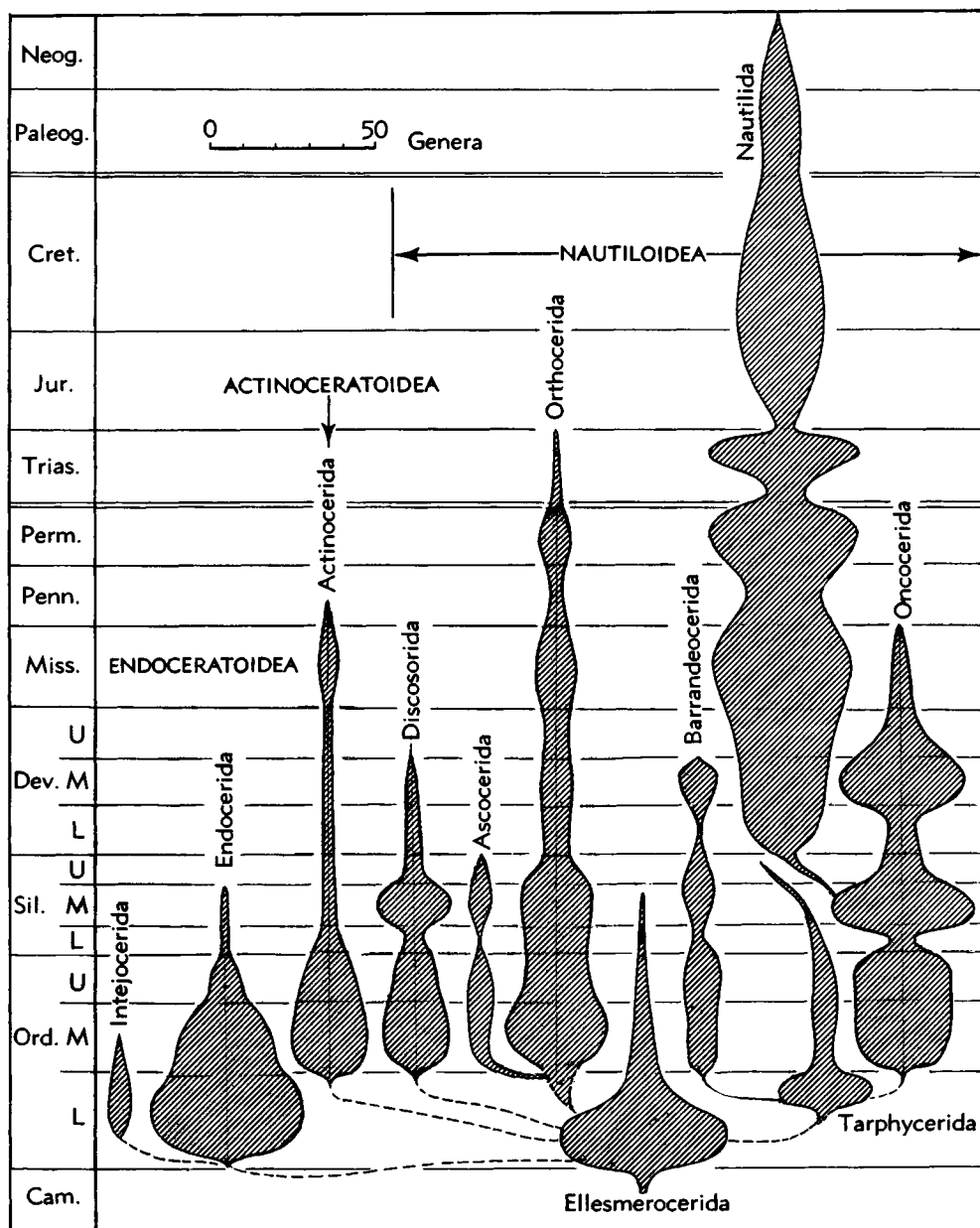


FIG. 69. Stratigraphic distribution, relative numbers of genera, and inferred origins of nautiloid orders (Teichert & Moore, n).

# K100 Cephalopoda—Endoceratoidea—Actinoceratoidea—Nautiloidea

## Main Divisions of Nautiloid Subclasses and Orders

Endoceratoidea (*subclass*) (63). *Ord.*, ?*M.Sil.*

Endocerida (*order*) (59). *Ord.*, ?*M.Sil.*

Thylacoceratidae (2). *L.Ord.*

Proterocameroceratidae (22). *L.Ord.-M.Ord.*

Piloceratidae (5). *L.Ord.*

Endoceratidae (17). *L.Ord.-U.Ord.*, ?*M.Sil.*

Chihlioceratidae (1). *L.Ord.*

Manchuroceratidae (2). *L.Ord.*

Cyrtendoceratidae (4). *L.Ord.-M.Ord.*, ?*U.Ord.*

Emmonsoceratidae (2). *Low.M.Ord.*

Nartheoceratidae (1). *M.Ord.*, ?*U.Ord.*

Allotrioceratidae (2). *M.Ord.*

?Humeoceratidae (1). *M.Sil.*

Intejocerida (*order*) (4). *L.Ord.-M.Ord.*

Intejoceratidae (2). *L.Ord.*, ?*M.Ord.*

Padunoceratidae (1). *M.Ord.*

?Bajkaloceratidae (1). *L.Ord.*

[Excludes 17 endoceratoids of unknown affinities and unrecognizable genera]

Actinoceratoidea (*subclass*) (35). *M.Ord.-U.Carb.*

Actinocerida (*order*) (35). *M.Ord.-U.Carb.*

Polydesmiidae (2). *L.Ord.-M.Ord.*

Actinoceratidae (8). *M.Ord.-L.Sil.*

Armenoceratidae (8). *M.Ord.-Sil.*

Gonioceratidae (2). *M.Ord.-U.Ord.*

Huroniidae (3). *M.Ord.-Sil.*

Ormoceratidae (8). *M.Ord.-Dev.*, ?*M.Dev.*,  
*L.Carb.*

Carbactinoceratidae (3). *L.Carb.-U.Carb.*

Family Uncertain (1)

[Excludes 2 unrecognizable genera]

Nautiloidea (*subclass*) (646;6). *U.Cam.-Rec.*

Ellesmerocerida (*order*) (64). *U.Cam.-U.Ord.*,  
?*M.Sil.*

Ellesmeroceratidae (30). *L.Ord.*, ?*M.Ord.*

Plectronoceratidae (6). *U.Cam.-L.Ord.*

Bassleroceratidae (8). *L.Ord.*

Protocycloceratidae (11). *L.Ord.*

Baltoceratidae (5). *L.Ord.-M.Ord.*

Bathmoceratidae (2). *L.Ord.-M.Ord.*, ?*M.Sil.*

Cyrtocerinidae (1). *M.Ord.-U.Ord.*

Shideleroceratidae (1). *U.Ord.*

Orthocerida (*order*) (125). *L.Ord.-U.Trias.*

Orthocerataceae (*superfamily*) (57). *L.Ord.-U.Trias.*

Orthoceratidae (22). *L.Ord.-U.Trias.*

Orthoceratinae (3). *M.Ord.*

Michelinoceratinae (10). *L.Ord.-U.Trias.*

Kionoceratinae (5). *M.Ord.-L.Perm.*

Leurocycloceratinae (4). *M.Ord.-Sil.*

Sphooceratidae (1). *M.Sil.*

Brachycycloceratidae (1). *U.Miss.-U.Penn.*,  
?*L.Perm.*

Sactorthoceratidae (3). *M.Ord.*

Lamellorthoceratidae (3). *L.Dev.-M.Dev.*,  
?*L.Carb.*

Troedssonellidae (5). *L.Ord.-M.Ord.*

Geisonoceratidae (11). *M.Ord.-M.Dev.*

Dawsonoceratidae (2). ?*U.Ord.*, *L.Sil.-U.Sil.*,  
?*M.Dev.*

Clinoceratidae (3). *M.Ord.-U.Ord.*

Paraphragmitidae (5). *M.Sil.*

Offleyoceratidae (1). *M.Sil.*, ?*L.Dev.*, ?*M.Dev.*

Pseudorthocerataceae (*superfamily*) (54).  
*M.Ord.-Perm.*

Pseudorthoceratidae (43). *L.Sil.-L.Perm.*

Pseudorthoceratinae (7). *M.Dev.-L.Perm.*

Spyroceratinae (23). ?*L.Sil.*, *M.Sil.-Perm.*

Cayutoceratinae (7). *L.Sil.-Dev.*

Pseudactinoceratinae (6). *U.Dev.-L.Carb.*

Mysterioceratidae (1). *M.Ord.*, ?*U.Ord.*

Stereoplasmoceratidae (1). *M.Ord.*

Proteoceratidae (9). *M.Ord.-M.Sil.*

Superfamily and family uncertain (14).

Ascocerida (*order*) (13). *M.Ord.-U.Sil.*

Ascoceratidae (9). *M.Ord.-U.Sil.*

Ascoceratinae (7). *M.Ord.-U.Sil.*

Probillingsitinae (2). *M.Ord.-U.Ord.*

Choanoceratidae (1). *M.Sil.*

Hebetoceratidae (3). *M.Ord.-?U.Ord.*

Oncocerida (*order*) (143). *M.Ord.-L.Carb.*

Graciloceratidae (4). *M.Ord.-U.Ord.*

Oncoceratidae (24). *M.Ord.-U.Sil.*

Tripterooceratidae (5). *M.Ord.-U.Ord.*

Valcouroceratidae (8). *M.Ord.-U.Ord.*

Diestoceratidae (5). *M.Ord.-U.Ord.*

Hemiphragmoceratidae (5). *M.Sil.-U.Sil.*,  
?*M.Dev.*

Trimeroceratidae (6). *M.Sil.*

Brevioceratidae (17). *M.Sil.-U.Dev.*

Jovellaniidae (5). ?*U.Ord.*, *M.Sil.-L.Dev.*

Tripleuroceratidae (2). ?*L.Dev.*, *M.Dev.-L.Carb.*

Nothoceratidae (10). *Sil.-U.Dev.*

Acleistoceratidae (22). *M.Sil.-M.Dev.*

Archiacoceratidae (3). *Dev.*

Karoceratidae (3). *L.Sil.-M.Sil.*, ?*L.Dev.*

Poterioceratidae (7). *L.Dev.-L.Carb.*

Polyelasmoceratidae (13). *M.Sil.-U.Dev.*

Family Uncertain (4).

[Excludes 8 genera dubia]

Discosorida (*order*) (46). *M.Ord.-M.Dev.*,  
?*U.Dev.*

Ruedemannoceratidae (3). *M.Ord.*

Cyrtogomphoceratidae (7). *M.Ord.-L.Sil.*

Westonoceratidae (13). *M.Ord.-L.Sil.*

Lowoceratidae (2). *M.Sil.*

Discosoridae (5). *M.Sil.-M.Dev.*, ?*U.Dev.*

Phragmoceratidae (7). *M.Sil.-L.Dev.*

Mandaloceratidae (7). *M.Sil.*, ?*U.Sil.*

?Mesoceratidae (1). *M.Sil.*

?Greenlandoceratidae (1). *M.Ord.*, ?*U.Ord.-?Sil.*

Tarphycerida (*order*) (38). *L.Ord.-U.Sil.*

Tarphyceratidae (9). *L.Ord.*

Estonioceratidae (9). *L.Ord.*

Trocholitidae (11). *L.Ord.-M.Sil.*

Lituitidae (8). *L.Ord.-U.Ord.*

Ophidioceratidae (1). *U.Sil.*

Barrandeocerida (*order*) (37). *M.Ord.-M.Dev.*

Barrandeoceratidae (10). *M.Ord.-M.Dev.*

Plectoceratidae (1). *M.Ord.-U.Ord.*  
 Uranoceratidae (4). *?U.Ord., M.Sil.*  
 Lechitrochoceratidae (6). *M.Sil.-U.Sil.*  
 Nephriticeratidae (9). *L.Dev.-M.Dev.*  
 ApSIDoceratidae (7). *M.Ord.-U.Ord.*

Nautilida (order) (165). *L.Dev.-Rec.*  
 Tainocerataceae (superfamily) (64). *L.Dev.-Trias.*  
 Tainoceratidae (23). *L.Carb.(Miss.)-Trias.*  
 Rutoceratidae (23). *Dev.-L.Carb.*

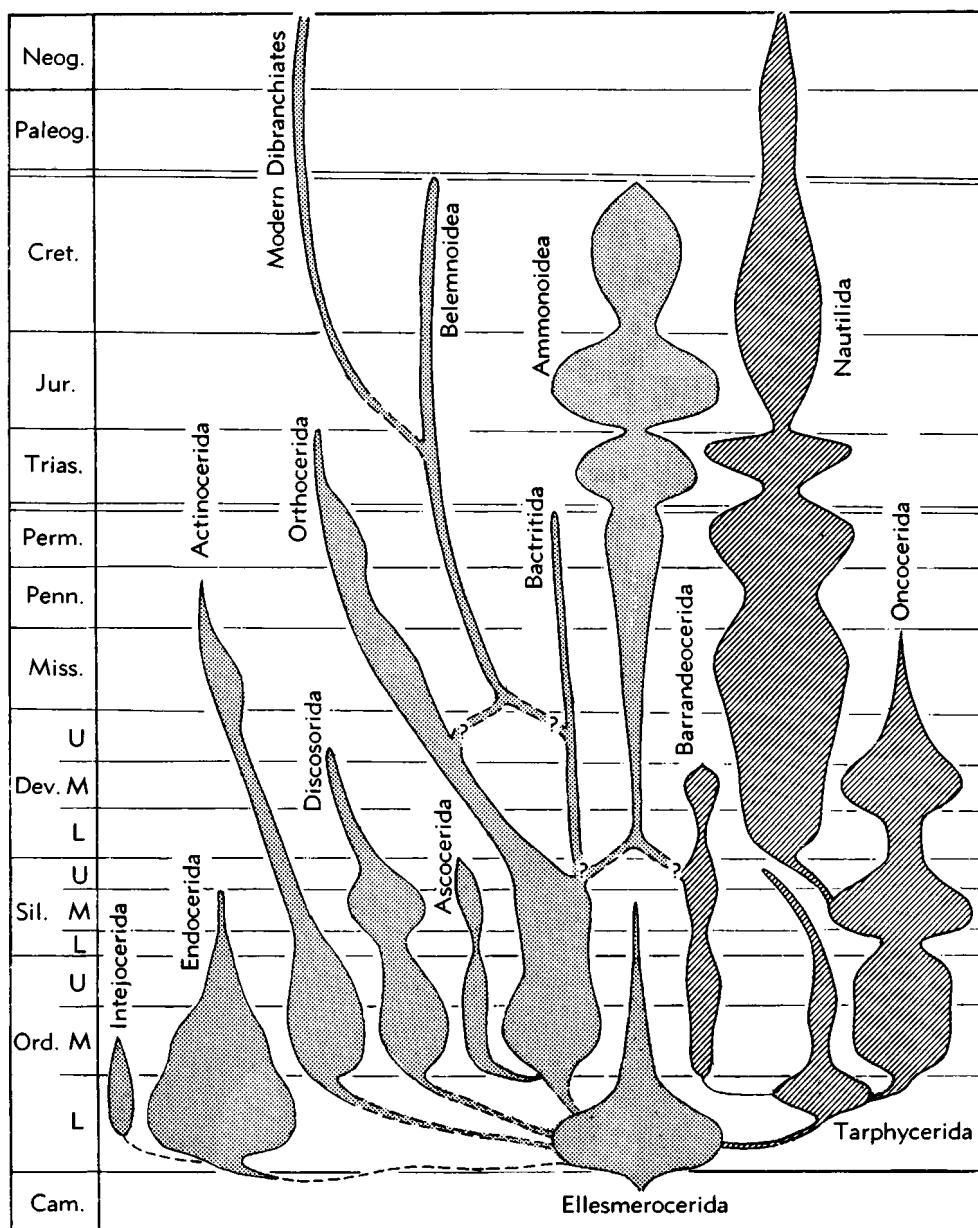


FIG. 70. Inferred phylogeny of nautiloid orders and suggested relationships to other cephalopod groups (Tarphycerida and derivative orders oblique-ruled). Approximate abundance in various periods is indicated by width of pattern, except that divisions other than the nautiloid orders are not drawn at the same scale (Sweet & Moore, n).

- Tetragonoceratidae (3). *M.Dev.*  
 Rhiphaeoceratidae (4). *L.Perm.*  
 Koninckioceratidae (11). *L.Carb.(Miss.)-Perm.*  
 Trigonocerataceae (superfamily) (42). *Dev.-Trias.*  
 Trigonoceratidae (17). *L.Carb.(Miss.)-L.Perm.*  
 Centroceratidae (6). *M.Dev.-L.Perm.*  
 Grypoceratidae (13). *L.Carb.-Trias.*  
 Permoceratidae (1). *L.Perm.*  
 Syringonaulitidae (5). *M.Trias.-U.Trias.*  
 Aipocerataceae (superfamily) (9). *L.Carb.(Miss.)-L.Perm.*  
 Aipoceratidae (3). *L.Carb.(Miss.)-U.Carb.*  
 Solenochilidae (2). *L.Carb.(U.Miss.)-L.Perm.*  
 Scyphoceratidae (4). *L.Perm.*  
 Clydonautillaceae (superfamily) (21). *?U.Dev., L.Carb.-Trias.*  
 Clydonautillidae (5). *M.Trias.-U.Trias.*  
 Liroceratidae (12). *?U.Dev., L.Carb.(Miss.)-Trias.*  
 Ephippioceratidae (2). *L.Carb.(Miss.)-L.Perm.*  
 Gonionautillidae (1). *U.Trias.*  
 Siberionautillidae (1). *U.Trias.*  
 Nautilaceae (superfamily) (29). *U.Trias.-Rec.*  
 Nautilidae (7). *U.Trias.-Rec.*  
 Pseudonautillidae (3). *Jur.-L.Cret.*  
 Paracenoceratidae (4). *M.Jur.-L.Cret.*  
 Cymatoceratidae (10). *M.Jur.-Oligo.*  
 Hercoglossidae (4). *U.Jur.-Oligo.*  
 Aturiidae (1). *Paleoc.-Mio.*  
 Order Uncertain  
 Neptunoceratidae (2). *U.Carb.*  
 Order and Family Uncertain (13;6).  
 Conchs (2).  
 Rhyncholites (11;6).  
 Bactritoidea (subclass) (16;1). *Ord.-Perm.*  
 Bactritida (order) (16;1). *Ord.-Perm.*  
 Bactritidae (8;1). *Ord.-Perm.*  
 Parabactritidae (5). *?Carb., Perm.*  
 Doubtful genera (3). *M.Dev.*  
 Total genera, 760, and 7 subgenera in addition to nominotypical subgenera.
- ### COMPARISON OF TREATISE AND OSNOVY CLASSIFICATION
- The systematic treatment of the “nautiloids” in the Russian treatise *Osnovy* (RUZHENTSEV *et al.*, 1962) (9) follows essentially that proposed by SHIMANSKIY and ZHURAVLEVA (1961) (12). The taxonomic units recognized in the *Osnovy* down to subfamily level are the following (numbers of genera indicated in parentheses):
- Classification of Nautiloid Cephalopods in Osnovy Paleontologii* (1962)  
 Endoceratoidea (superorder) (76). *L.Ord.-U.Ord.*  
 Endoceratida (order) (73). *L.Ord.-U.Ord.*  
 Proterocameroceratina (suborder) (37). *Ord.*  
 Proterocameroceratidae (25). *L.Ord.-M.Ord.*  
 Manchuroceratidae (6). *L.Ord.-M.Ord.*  
 Chihlioceratidae (1). *L.Ord.*  
 Allotrioceratidae (2). *M.Ord.*  
 Cyrtovaginoceratidae (2). *M.Ord.*  
 Narthecoceratidae (1). *M.Ord.-U.Ord.*  
 Endoceratina (suborder) (36). *Ord.*  
 Piloceratidae (4). *L.Ord.*  
 Cyrtendoceratidae (2). *L.Ord.-M.Ord.*  
 Emmonsoceratidae (2). *L.Ord.-M.Ord.*  
 Endoceratidae (28). *Ord.*  
 Intejoceratida (order) (3). *L.Ord.-M.Ord.*  
 Intejoceratidae (2). *L.Ord.*  
 Padunoceratidae (1). *L.Ord.-M.Ord.*  
 Actinoceratoidea (superorder) (52). *L.Ord.-Carb.*  
 Actinoceratida (order) (57). *Ord.-Carb.*  
 Actinocerataceae (superfamily) (51). *Ord.-Carb.*  
 Polydesmiidae (2). *L.Ord.*  
 Deiroceratidae (3). *Ord., ?Dev.*  
 Ormoceratidae (2). *Ord.-Dev.*  
 Actinoceratidae (11). *Ord.-L.Carb.*  
 Armenoceratidae (9). *Ord.-Sil.*  
 Gonioceratidae (4). *M.Ord.-U.Ord.*  
 Huroniidae (3). *Ord.-Sil.*  
 Pseudactinoceratidae (5). *Ord.-Carb.*  
 Sactoceratidae (9). *Ord.-Dev.*  
 Loxoceratidae (3). *L.Carb.*  
 Ellinocerataceae (superfam.) (1). *M.Ord.*  
 Ellinoceratidae (1). *M.Ord.*  
 Nautiloidea (superorder) (672).  
 Ellesmeroceratida (order) (84). *U.Cam.-U.Ord.*  
 Bathmocerataceae (superfam.) (67). *U.Cam.-M.Ord.*  
 Plectronoceratidae (5). *U.Cam.-L.Ord.*  
 Ellesmeroceratidae (28). *Cam.-Ord.*  
 Cyclostomiceratidae (3). *L.Ord.*  
 Protocycloceratidae (10). *L.Ord.*  
 Baltoceratidae (9). *Ord.*  
 Butsoceratidae (1). *L.Ord.*  
 Eothinoceratidae (3). *Ord.*  
 Bathmoceratidae (1). *L.Ord.*  
 Apocrinoceratidae (3). *L.Ord.*  
 Thylacoceratidae (4). *L.Ord.-M.Ord.*  
 Basslerocerataceae (superfam.) (17). *L.Ord.-U.Ord.*  
 Bassleroceratidae (11). *L.Ord.-M.Ord.*  
 Graciloceratidae (5). *Ord.*  
 Shideleroceratidae (1). *U.Ord.*  
 Orthoceratida (order) (103). *Ord.-Trias.*  
 Orthoceratidae (31). *Ord.-Trias.*  
 Orthoceratinae (13). *Ord.-Trias.*  
 Kionoceratinae (6). *Ord.-Perm.*  
 Cycloceratinae (12). *Ord.-Perm.*  
 Sactorthoceratidae (3). *Ord.*  
 Geisonoceratidae (6). *Ord.-Dev.*  
 Pseudorthoceratidae (48). *Ord.-Perm.*  
 Lamellorthoceratidae (4). *Dev.*  
 Eskimoceratidae (2). *Ord.*  
 Clinoceratidae (3). *Ord.*  
 Paraphragmitidae (4). *Sil.*



- Greenlandoceratidae (2). *M.Ord.* or *U.Ord.*  
 Ascoceratida (order) (15). *Ord.-Sil.*  
 Hebetoceratidae (6). *Ord.*  
 Choanoceratidae (1). *Sil.*  
 Ascoceratidae (8). *Ord.-Sil.*  
 Oncoceratida (order) (153). *Ord.-L.Carb., ?Perm.*  
 Cyrtocerataceae (superfam.) (141). *Ord.-L.Carb., ?Perm.*  
 Maelonoceratidae (45). *Ord.-Dev.*  
 Ooceratidae (2). *Ord.-Sil.*  
 Allumettoceratidae (6). *Ord.*  
 Gomphoceratidae (1). *Sil.-Dev.*  
 Hemiphragmoceratidae (5). *Sil.-Dev.*  
 Bolloceratidae (3). *Dev.*  
 Trimeroceratidae (9). *?Ord., Sil.*  
 Oocerinidae (13). *Ord.-Dev.*  
 Diestoceratidae (3). *Ord.*  
 Brevioceratidae (17). *Dev.*  
 Archiacoceratidae (6). *?Sil., Dev.*  
 Polyelasmoceratidae (11). *Sil.-Dev.*  
 Cyrtoceratidae (5). *Sil.-Dev.*  
 Karoceratidae (1). *U.Sil.* or *L.Dev.*  
 Jovellaniidae (5). *Sil.-Dev.*  
 Tripleuroceratidae (2). *Dev.-L.Carb.*  
 Antonoceratidae (2). *L.Carb., ?Perm.*  
 Poterioceratidae (5). *L.Carb.*  
 Ptenocerataceae (superfam.) (12). *Sil.-Dev.*  
 Nothoceratidae (2). *?Sil., Dev.*  
 Naedyceratidae (7). *Sil.-Dev.*  
 Naedyceratinae (5). *Sil.-Dev.*  
 Mitroceratinae (2). *Dev.*  
 Ptenoceratidae (3). *Dev.*  
 Discosorida (order) (45). *Ord.-Dev.*  
 Ruedemannoceratidae (3). *Ord.*  
 Cyrtogomphoceratidae (12). *Ord.-Sil.*  
 Westonoceratidae (8). *Ord.-Dev.*  
 Lowoceratidae (2). *Sil.*  
 Discosoridae (5). *Sil.-Dev.*  
 Phragmoceratidae (7). *Sil.*  
 Mandaloceratidae (7). *Sil.*  
 Mesoceratidae (1). *U.Sil.*  
 Tarphyceratida (order) (88). *Ord.-Dev.*  
 Tarphyceratina (suborder) (37). *Ord.-Sil.*  
 Tarphyceratidae (25). *L.Ord.-M.Ord.*  
 Trocholitidae (11). *Ord.-Sil.*  
 Beekmanoceratidae (1). *L.Ord.*  
 Barrandeoceratina (suborder) (51). *Ord.-Dev.*  
 Barrandeoceratidae (6). *Ord.-Sil.*  
 Bickmoritidae (8). *U.Ord.-Sil.*  
 Uranoceratidae (2). *Sil.*  
 Plectoceratidae (2). *M.Ord.-U.Ord.*  
 Lechritrochoceratidae (6). *Sil.*  
 Apsidoceratidae (6). *Ord.*  
 Lituitidae (11). *Ord.*  
 Rhadinoceratidae (10). *Dev.*  
 Nautilida (order) (184). *?U.Sil., Dev.-Rec.*  
 Rutoceratina (suborder) (32). *?U.Sil., Dev.-Carb.*  
 Rutocerataceae (superfam.) (19). *?U.Sil., Dev.-Carb.*  
 Rutoceratidae (16). *?U.Sil., Dev.-Carb.*  
 Neptunoceratidae (3). *Carb.*  
 Aipocerataceae (superfam.) (13). *Dev.-Carb.*  
 Litogyroceratidae (4). *Dev.-Carb.*  
 Scyphoceratidae (3). *Carb.-Perm.*  
 Dentoceratidae (1). *L.Perm.*  
 Aipoceratidae (5). *Carb.-Perm.*  
 Tainoceratina (suborder) (47). *Dev.-Trias.*  
 Tainocerataceae (superfam.) (30). *Dev.-Trias.*  
 Tetragonoceratidae (4). *Dev.*  
 Tainoceratidae (23). *Carb.-Trias.*  
 Tainoceratinae (14). *Carb.-Perm., ?Trias.*  
 Pleuronautilinae (9). *Perm.-Trias.*  
 Mosquoceratidae (3). *Carb.-Perm.*  
 Encoilocerataceae (superfam.) (1). *U.Trias.*  
 Encoiloceratidae (1). *U.Trias.*  
 Temnocheilaceae (superfam.) (9). *?Dev., Carb.-Perm.*  
 Temnocheilidae (3). *?Dev., Carb.-Perm.*  
 Gzheloceratidae (6). *Carb.-Perm.*  
 Rhiphaeocerataceae (superfam.). *Perm.*  
 Rhiphaeoceratidae (5). *Perm.*  
 Actubonautilidae (2). *Perm.*  
 Centroceratina (suborder) (44). *Dev.-Trias.*  
 Trigonocerataceae (superfam.) (19). *Carb.-Perm.*  
 Trigonoceratidae (16). *Carb.-Perm.*  
 Trigonoceratinae (8). *Carb.-Perm.*  
 Aphelaeceratinae (2). *L.Carb.*  
 Thrinoceratinae (4). *Carb.*  
 Knightoceratidae (2). *Carb.-Perm.*  
 Subclymeniidae (1). *L.Carb.*  
 Phacoceratidae (2). *L.Carb.*  
 Centrocerataceae (superfam.) (25). *Dev.-Trias.*  
 Centroceratidae (4). *Dev.*  
 Grypoceratidae (19). *Carb.-Trias.*  
 Domatoceratinae (12). *Carb.-L.Trias.*  
 Grypoceratinae (2). *Trias.*  
 Syringonautilinae (4). *Trias.*  
 Clymenonautilinae (1). *U.Trias.*  
 Neothrinoceratidae (1). *L.Perm.*  
 Permoceratidae (1). *L.Perm.*  
 Liroceratina (suborder) (28). *?U.Dev., Carb.-L.Cret.*  
 Lirocerataceae (superfam.) (18). *?Dev., Carb.-Perm.*  
 Liroceratidae (9). *?Dev., Carb.-Perm.*  
 Ephippioceratidae (2). *Carb.-Perm.*  
 Koninckioceratidae (3). *Carb.-Perm.*  
 Paranautilidae (4). *?U.Perm., Trias.*  
 Clydonautilaceae (superfam.) (10). *Trias.-L.Cret.*  
 Clydonautilidae (5). *Trias.*  
 Gonionautilidae (1). *U.Trias.*  
 Siberionautilidae (1). *U.Trias.*  
 Pseudonautilidae (3). *U.Jur.-L.Cret.*  
 Nautilina (suborder) (32). *U.Trias.-Rec.*  
 Nautilaceae (superfam.) (31). *U.Trias.-Rec.*  
 Nautilidae (15). *U.Trias.-Rec.*

Nautilinae (12). *U.Trias.-Rec.*  
 Pseudaganidinae (2). *Jur.*  
 Cymatoceratidae (11). *Jur.-Paleog.*  
 Cymatoceratinae (9). *Jur.-Paleog.*  
 Heminautilinae (2). *Cret.*  
 Hercoglossidae (5). *U.Jur.-Paleog.*  
 Aturiaceae (*superfam.*) (2). ?*U.Cret., Paleoc.-Mio.*  
 Aturiidae (2). ?*U.Cret., Paleoc.-Mio.*

In the present volume (Part K) of the *Treatise* a total of 744 valid genera (exclusive of Bactritoidea) are recognized, whereas in the *Osnovy* the total of genera described or listed as valid is 799. The number of family taxa used is 108 in the *Treatise* and 122 in the *Osnovy*. A breakdown of these numbers according to subclasses and orders gives some insight into the main areas of discrepancy.

*Numbers of Genera and Families Recognized in the Treatise and Osnovy*

	No. of genera		No. of families	
	<i>Treatise</i>	<i>Osnovy</i>	<i>Treatise</i>	<i>Osnovy</i>
Endoceratoidea	63	76	13	12
Actinoceratoidea	35	51	7	11
Nautiloidea	646	672		
Ellesmerocerida	64	84	9	13
Orthocerida	125	103	11	9
Ascocerida	13	15	3	3
Oncocerida	143	153	16	21
Discosorida	46	45	9	8
Tarphycerida	38	37	3	3
Barrandeocerida	37	51	6	8
Nautilida	165	184	24	34
Order Uncertain	15			
Totals	744	799	101	122

In addition, the names of 33 invalid genera are listed in the *Osnovy*, whereas the present volume contains bibliographic information on 101 taxa of generic rank which are classified as unrecognizable, invalid, or rejected.

It will be seen that the number of genera by which the *Osnovy* exceeds those of the *Treatise* is almost entirely concentrated in the subclasses Endoceratoidea and Actinoceratoidea and in the order Nautilida. The reasons for this are of two kinds. For the subclass Endoceratoidea the *Treatise* lists 17 genera of unknown affinities, raising the total for the subclass to 80. Of these 17 genera, one is described and 10 are listed in the *Osnovy* as valid, and the names of six

have been omitted. These data suggest a certain divergence of opinion regarding the recognizability of many of the proposed generic taxa. Apart from that, treatment of the subclass is reasonably uniform in both volumes.

The case of the Actinoceratoidea and Nautilida is different, because *Treatise* authors of these two taxa have been unable to recognize a number of more recently established genera, placing them in synonymy of earlier names. In the *Treatise* chapter on Actinoceratoidea 31 generic names are listed as junior synonyms, in the chapter on Nautilida 80. Both figures, however, include a number of *nomina nulla*, a name category which is ignored in the *Osnovy*. In the corresponding *Osnovy* chapters 5 synonyms are cited for the Actinoceratoidea and 32 for the Nautilida. These discrepancies reflect difficulties inherent in the study and systematic treatment of these two groups. In the Actinoceratoidea they lie in insufficient knowledge of many endosiphuncular structures or their inadequate preservation. In the Nautilida, as in the ammonoids, it is difficult to establish, and to agree on, standardized procedures in the taxonomic evaluation of minor variations in shell form and ornamentation.

Similarly, in the *Osnovy* 84 valid genera of Ellesmerocerida are recognized, whereas the *Treatise* recognizes only 64. In addition, however, the *Treatise* lists 23 generic names in synonymies, as against 2 in the *Osnovy*. Total number of ellesmerocerid generic names listed in the *Treatise* is thus 87 (including some *nomina nulla*), in the *Osnovy* 86 (without *nomina nulla*). The *Treatise* authors' reluctance to recognize numerous established genera of Ellesmerocerida was due to the conviction that morphological features of many genera are inadequately known and that in many cases safe criteria for the separation of generic categories are lacking. In many cases this uncertainty is due to the poor state of preservation of the type-specimens.

Difficulties attending the systematic treatment of the Orthocerida and the Oncocerida are of a somewhat different nature. The numbers of genera recognized in these two orders in the two volumes are satis-

factorily close to each other, but considerable discrepancies are apparent on the suprageneric level. Only seven out of 13 families of Orthocerida, used in the present volume, are also found in the *Osnovy*, and the two works have only 11 families of Oncocerida in common (out of 16 in the *Treatise*, and 21 in the *Osnovy*). Obviously, in these two orders the difficulties do not lie so much in differentiation at the generic level, but in arriving at a satisfactory recognition of relationships at the suprageneric level.

The equality of treatment of the Tarphycerida is more apparent than real, because in the *Osnovy* 11 genera of Lituitidae are included in the Barrandeoceratida, whereas in the *Treatise*, based on SWEET's researches, they are treated with the Tarphycerida. With the removal of the Lituitidae from Barrandeocerida the systematic treatment of this order in the two volumes shows good agreement.

The general agreement in treatment of the Discosorida and Ascocerida in the two volumes is explained by the fact that systematic arrangements of these groups in both works are based on standard monographs by North American and European paleontologists, and that no significant recent, "post-monographic" additions to the knowledge of these groups have been made elsewhere.

In the *Osnovy* the rhyncholites are treated somewhat summarily on slightly less than two pages. A total of nine genera and nine subgenera are recognized and seven genera are diagnosed and illustrated. The oldest rhyncholite genus is listed as "*Rhyncholites* Faure-Biguet, 1819," with *Rhombocheilus* SHIMANSKIY, 1947, in synonymy. *Hadrocheilus* TILL, 1907, is listed as a synonym of *Rhynchoteuthis* D'ORBIGNY, 1847. By comparison the *Treatise* describes 11 genera and 6 subgenera and cites 11 generic names in synonymies.

All in all, *Osnovy* authors have shown greater inclination to split genera and families than *Treatise* authors. As compared with the *Treatise*, the *Osnovy* recognizes as valid 10 per cent more genera and 20 per cent more families.

A tabulation of total number of generic names listed in both volumes (exclusive of

Bactritoidea) brings to light some additional interesting differences.

#### Summary of Generic Taxa in *Treatise* and *Osnovy*

	<i>Treatise</i>	<i>Osnovy</i>
Valid genera	744	800
Doubtful, invalid, and rejected generic taxa	67	32
Synonyms	286	62
Total number of names listed	1097	894

A more detailed analysis of the differences in taxonomic treatment of individual orders in the two volumes would, no doubt, lead to a clearer understanding of the causes of these differences and might well suggest future avenues of fruitful research to achieve a better understanding of all these groups and their interrelationships.

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## PHYLOGENY AND EVOLUTION

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### INTRODUCTION

As with nearly every other group of organisms, there is no objective record of the earliest stages in the history of cephalopods. Presumably, however, cephalopods developed from the primitive mollusk in the fashion outlined by YONGE (7) in an earlier volume (Part I) of this *Treatise*. That is, accelerated secretion of shell material by peripheral zones of the mantle altered the primitively domelike shell to a progressively more highly conical one that grew more rapidly than the enclosed visceral mass. In association with this, the body migrated toward the shell opening, and apical parts of the conical shell were isolated by first one, then by a succession of transverse septa, so as to form a series of chambers, progressively evacuated by the animal, but connected with it by the fleshy siphuncle. At the same time, a pronounced ventral flexure of the body developed so that the head and the opening to the mantle cavity, separated only by a much reduced foot, came to be directed ventrally. Ultimately, the foot developed into the hyponome, or swimming funnel.

For several reasons, more fully explored in later parts of this chapter, we agree with

YONGE that the earliest cephalopods probably retained the single pair of ctenidia thought to have characterized the ancestral mollusk, and that the two pairs of gills found in modern *Nautilus* appeared later in the history of cephalopods in association with increased activity and necessarily heightened metabolism. Thus, it seems to us that the dibranchiate plan, perfected in modern Coleoidea, is more fundamental among cephalopods than the tetrabranchiate plan exhibited by *Nautilus*, which probably developed progressively and was finally perfected in the tarphycerid-oncocerid-nautilid line. For several of the same reasons, it is also more attractive to assume that early cephalopods had the small number of arms (8 to 10) characteristic of modern coleoids and their Mesozoic forebears, rather than the large number (40) of modern *Nautilus*, and probably characteristic of the stock of which it is the sole survivor.

### OLDEST CEPHALOPODS

The oldest certain cephalopods are the ellesmerocerids *Palaeoceras*, *Plectronoceras*, *Ruthenoceras*, and *Shantungendoceras*, from Upper Cambrian rocks in the United States, China, Manchuria, and the USSR. The

shell morphology of these genera, together with the developmental trends indicated by the several post-Cambrian nautiloid orders traced back to them, indicates that the earliest shelled cephalopods were less than an inch long and secreted compressed, straight to endogastrically curved, closely septate shells with large subventral siphuncles composed of relatively short septal necks and, if present at all, generally thick, complex connecting rings. The closely spaced septa of the earliest cephalopods known suggest that, even if gas were present in their camerae, phragmocones were probably not very buoyant and were borne horizontally in life.

It should be noted here that tiny, conical, septate shells, referred to *Volborthella*, *Vologdinella*, and *Salterella*, have been reported from both Lower and Middle Cambrian strata, and many have regarded them as remains of the most primitive cephalopods. They are described and discussed by TEICHERT in a later section on "Doubtful Taxa." Although the question of their zoologic affinities has not been settled, these shells are not now generally regarded as belonging to the cephalopods. Shells of these genera are circular to somewhat elliptical in section and the axial tube, regarded by some as a siphuncle, is small and central in position (rather than large and marginal). Furthermore, the shell of *Volborthella* may have been arenaceous (rather than calcareous), and that of *Salterella*, although originally calcareous, seems to have been composed of thick adapically invaginated laminae, which are not separated by spaces that could be considered camerae. None of these characters is consistent with the model of early cephalopods deduced from studies of the morphology and development of Upper Cambrian and later forms (2). If these Lower and Middle Cambrian shells are those of primitive cephalopods, which seems unlikely, they must represent a group that became extinct in the Cambrian and that was not in the main line of cephalopod evolution.

In connection with our discussion of the nature and development of the earliest cephalopods, it should also be mentioned that HUTCHINSON (5) has recently suggested

that preservable shells appeared in several animal groups in connection with the rise of predation in the Lower Cambrian. However, since no indication of powerful predators among known Lower Cambrian fossils is found, he assumes that the predators did not secrete fossilizable skeletons. This chain of reasoning leads him to suppose the existence of Early Cambrian "protonautiloids" with thin, conchiolinous shells, but with powerful horny jaws ". . . cruising about just over the bottom." If we grant the plausibility of HUTCHINSON's hypothesis, it seems necessary to assume that the unfossilized predatory "protonautiloids" of the Early Cambrian were much larger than the tiny Late Cambrian forms that provide our oldest objective record of cephalopods. Possibly, then, there were several stocks of primitive cephalopods in Early and Middle Cambrian seas, of which only the progenitors of the tiny Late Cambrian ellesmerocerids survived. Without doubt the Ordovician and later cephalopods developed from these Upper Cambrian ellesmerocerids.

## EARLY CANADIAN ELLESROCERID RADIATION

Cephalopods developed explosively and radiated widely in early Canadian time (earliest Early Ordovician). Late Cambrian cephalopods are represented by mostly tiny shells, referred to eight species of four ellesmerocerid genera, whereas early Canadian forms are larger, include at least 165 species distributed among more than 20 genera, and represent three ellesmerocerid families (Ellesmeroceratidae, Plectronoceratidae, and Protocycloceratidae). For the most part, early Canadian ellesmerocerids are larger than their Late Cambrian predecessors, and average between one and two inches in over-all length. However, Late Cambrian *Palaeoceras* is estimated by FLOWER (2) to have been about three inches long, and some early Canadian forms (e.g., *Pachendoceras*) were veritable "giants," attaining an over-all length of seven to nine inches. Nearly all early Canadian ellesmerocerids are similar, however, in being laterally compressed, faintly or considerably curved endogastrically, and in having short chambers,

long body chambers, and relatively large ventral or subventral siphuncles. In most early Canadian ellesmerocerids, the latter structures are empty, but diaphragms or dissepiments transverse to the siphuncular axis have been reported in some species (Fig. 70).

## MIDDLE AND LATE CANADIAN DEVELOPMENT

As indicated by Figure 70, the explosive early Canadian development and radiation of primitive ellesmerocerids was followed in the middle and late Canadian (later Early Ordovician) by considerable and fairly rapid morphological diversification among the Ellesmerocerida and by the introduction and principal development of both the Endocerida and Tarphycerida. Each of these groups merits separate discussion.

### ELLESMEROCERIDA

By middle Canadian time, all of the archaic Plectronoceratidae and most of the primitive Ellesmeroceratidae had disappeared. Middle and late Canadian representatives of the latter family retain the primitive features of, but are generally larger and less compressed than, their early Canadian forebears; some retained strong endogastric curvature, but others developed long orthoconic conchs. By the end of the Early Ordovician, the Ellesmeroceratidae were gone entirely.

The Protocycloceratidae, similar in general to their ellesmeroceratid ancestors, developed long, straight (or only faintly curved), annulated shells in the middle and late Canadian, whereas the Baltoceratidae secreted long, straight, smooth conchs with broad, empty siphuncles. Other variations among middle and late Canadian Ellesmerocerida gave rise to the Cyclostomiceratidae (with thick-walled marginal siphuncles and uncompressed, straight to faintly curved or breviconic shells), and to the early Paleozoic Bathmoceratidae, endogastrically curved and straight shells characterized by greatly thickened connecting rings. The latter families, as well as the Baltoceratidae, survived into the Middle and Late Ordovician (Fig. 70).

The Bassleroceratidae are like other ellesmerocerids in being closely septate, laterally compressed, and in retaining a marginal siphuncle with thick, complex connecting rings. They differ in being a first group of cephalopods to develop an exogastrically curved shell, which may be considered to be another answer to the common problem of efficient mobility associated with increased shell buoyancy. In these forms the shell lost its primitively horizontal position and its apex came to point upward and the aperture to face obliquely downward and forward.

### ENDOCERATOIDEA

The Endoceratoidea, which first appeared in the middle Canadian, stem from early Canadian Ellesmeroceratidae, from which they are distinguished primarily by the presence of endocones in the siphuncle. Some endocerids retained the short, primitive septal necks of the Ellesmerocerida; others, however, developed progressively longer, hemichoanitic to subholochoanitic necks, but, for the most part, retained the complex connecting rings of the ellesmerocerids. In the Endoceratidae and Piloceratidae, as well as in some Manchuroceratidae, septal necks became holochoanitic, even macrochoanitic, and virtually all of the Endocerida exhibited a tendency toward great size and considerable elaboration of structures within the endocones.

Although the Endoceratoidea were most numerous and varied in the Early Ordovician, the Endoceratidae underwent a great expansion in the Middle Ordovician, during which time they produced shells as much as 30 feet long—the largest invertebrate fossils of the Paleozoic. Other short-lived, minor families of endocerids also appeared in the Middle Ordovician, but did not survive into the Late Ordovician. The Endoceratidae are represented in the Late Ordovician and may have survived in limited numbers into the Silurian; however, endoceratoids are not well represented in Silurian strata and the order as a whole was clearly extinct well before the end of that period.

The Endoceratoidea appear to represent one of several answers among early Paleozoic cephalopods to the problem of increased

shell buoyancy that came with longer chambers and phragmocones of greater size. It seems fairly clear that the elaborate endocones of the Endocerida were secreted as counterweights and thus served a hydrostatic function in maintaining a near-horizontal position of the shell. The tightly packed longitudinal radial lamellae in the siphuncle of Intejocerida served the same purpose. A similar problem was answered by exogastric coiling in other nautiloids, or through formation of cameral deposits or various other types of siphuncular deposits in additional groups.

No evidence indicates that endoceratoids were ancestral to any other group of cephalopods. They seem to have disappeared without issue in the Silurian (Fig. 70).

### TARPHYCERIDA

The middle and late Canadian also include the early history of the Tarphycerida, a relatively small nautiloid order (five families, 38 genera, about 170 species).

From the Bassleroceratidae developed the loosely to more tightly coiled Tarphyceratidae and Trocholitidae, and, from one of the latter families, developed the partially to completely uncoiled Lituitidae. Both the Trocholitidae and Lituitidae continued into the Late Ordovician; the Ophidioceratidae are Middle and Upper Silurian. Even though coiled (or secondarily uncoiled), typical tarphycerids retain evidence of their ellesmerocerid ancestry in the thick connecting rings of the siphuncle.

Although the exogastrically curved (and ultimately coiled) Tarphycerida solved the problem of increased shell buoyancy by bringing the gas-filled phragmocone to a position above the body mass, it is interesting and perhaps significant to note that some species of the Lituitidae, which became secondarily uncoiled—even orthoconic—secreted heavy organic deposits in chambers of the phragmocone to counterweight the visceral mass and keep the longiconic shell in a nearly horizontal position. Retention by tarphycerids of the capacity to do this suggests, of course, the existence of a fundamentally similar plan of organization in the adapical parts of the mantle and siphuncular tissues in all groups of early cephalopods.

## MIDDLE ORDOVICIAN AND LATER RADIATIONS

The interval between the beginning of the Middle Ordovician and the end of the Middle Silurian may be regarded as the “heyday” of the nautiloid cephalopods, for at no other time in their history had they been either as numerous or as diversely and highly specialized as then. Furthermore, it was during this interval in their history that the lineages of the two major modern groups of cephalopods (dibranchiates and tetrabranchiates) first became clearly distinguished.

Six new “nautiloid” orders (Actinocerida, Discosorida, Orthocerida, Ascocerida, Barrandeocerida, and Oncocerida) appeared in the early Middle Ordovician. As shown in Figure 70, four of these (Actinocerida, Discosorida, Ascocerida, and Barrandeocerida) were successful, varied, and widespread in their distribution in the remaining early Paleozoic, but declined to extinction well before the end of that era. With exception of the Barrandeocerida, which may be ancestral to the Ammonoidea, representatives of these four nautiloid orders seem to have been specialized groups, off the “main line” of cephalopod evolution; there is no evidence that they gave rise to any more advanced group of cephalopods. The remaining two nautiloid orders that appeared for the first time in the earliest Middle Ordovician—Orthocerida and Oncocerida—are of paramount importance in the later history of the Cephalopoda, for not only were they numerous, varied, and important contributors to the Paleozoic fossil record, but they are ancestral to the two surviving groups of modern cephalopods, and one of them (Orthocerida) is ancestral to the Dibranchiata and may well have given rise to the Ammonoidea (Fig. 70).

### ACTINOCERATOIDEA

For the most part, actinocerids are represented in the fossil record by long, straight conchs with heavy cameral deposits and a large siphuncle of broadly expanded segments that contains complex annulosiphonate deposits that are separated from the connecting rings by a perispatium and traversed by a network of complex radial canals. The origin of the subclass is un-

known, for no transitional forms are known that link it with contemporaneous or earlier ellesmerocerids. It has been suggested several times by FLOWER that the late Canadian and early Middle Ordovician *Bathmoceras* is ancestral to the Actinocerida, but that hypothesis is here rejected. That is, the elaborately produced endosiphuncular structures of *Bathmoceras* are clearly outgrowths of greatly thickened connecting rings, whereas endosiphuncular deposits in the actinocerids are separated from connecting rings by a clearly defined perispatium.

Between their introduction in earliest Middle Ordovician time and their eventual extinction in the Pennsylvanian, the Actinoceratoidea exhibited three distinct evolutionary tendencies. As in the evolutionary history of many other groups of animals, actinocerids show the over-all tendency toward a considerable increase in size; conchs as much as 20 feet long were formed by some Carboniferous species. In addition, the actinoceratoids exhibit the tendencies toward progressive decrease in width of siphuncular segments and concomitant simplification of the siphuncular canal systems. The earliest actinoceratoids have siphuncular segments six times as wide as long, whereas in no post-Silurian form is this ratio any greater than two to one. Radial canals in the earliest actinoceratoids are surprisingly complex and form a system of simply curved main canals and a network of dendritic or anastomosing fine canals. Later development resulted in a much simpler pattern. Apparently, these several evolutionary tendencies characterized several co-existing families and were not confined to any single lineage.

### DISCOSORIDA

The Discosorida are dominantly cyrtocones and brevicones. Their origin in the Ellesmerocerida is clearly indicated by the fact that primitive discosorids are endogastric, closely camerated cyrtocones with relatively large siphuncles and thick, complex connecting rings. Siphuncular segments, however, are broadly expanded in all of the earliest Discosorida, suggesting an origin in

the most primitive ellesmerocerids (Plectroceratidae) rather than in one of the more evolved, orthochoanitic families of that order. Discosorids are distinguished from ellesmerocerids by thicker, inflated connecting rings that are clearly differentiated in early forms, at least, into distinct regions and layers. Later developments included the introduction of exogastric curvature in one branch of the order, and in both branches, the addition and elaboration of bullettes, parietal deposits, and endocones within the siphuncle, accompanied by progressive simplification in structure of the initially complex connecting rings.

### BARRANDEOCERIDA

The earliest Barrandeocerida are closely similar in both shell form and external ornamentation to late Early and early Middle Ordovician Tarphycerida, from which they differ primarily in having thin, rather than thickened, connecting rings. Thus, one can hardly doubt that the Tarphycerida are ancestral to the Barrandeocerida. As in the Tarphycerida, tendencies in the later evolutionary history of the Barrandeocerida include a marked tendency to uncoil or even to form torticonic and breviconic conchs, probably in association with the development of a much elongated visceral mass and a very long body chamber. In some families the primitively conspicuous shell ornament was progressively reduced, whereas in others it was accentuated; furthermore, in at least one family a cyrtchoanitic siphuncle and somewhat expanded siphuncular segments developed. The group became extinct before the close of the Devonian and is generally believed to have given rise to no younger forms. SPATH (6) and others, however, have suggested that some species of the Barrandeocerida may have been ancestral to the Ammonoidea. SPATH's suggestion has never gained wide support, but it cannot be said to have been disproved.

### ORTHO CERIDA AND ASCOCERIDA

One of the two most significant events in the early Middle Ordovician history of cephalopods was the development of the



Orthocerida. Orthocerids, which are largely slender, long-chambered orthocones, developed from orthochoanitic Ellesmerocerida (Baltoceratidae) through shrinkage in siphuncle size and reduction in thickness and complexity of connecting rings. Although the order exhibited its greatest diversity and evolutionary advancement in the interval from the Middle Ordovician through the Middle Silurian, orthocerids are common throughout the Paleozoic and did not become extinct until late in the Triassic.

Soon after their differentiation from ancestral ellesmerocerids, two distinct lineages appeared in the Orthocerida. In the most conservative line (Orthocerataceae), the primitive orthochoanitic to suborthochoanitic siphuncle was retained and evolutionary development was confined largely to ornamentation and to formation of a variety of complex cameral deposits and simple endosiphuncular annuli. Early and late Paleozoic branches from this line (Sphooceratidae, Brachycycloceratidae) developed the capacity to shed the early straight to slightly curved phragmocone and, later in its life history, to secrete a gibbous, breviconic conch with a suborthochoanitic to strongly cyrtochoanitic siphuncle and broadly expanded segments. In these capacities, this late Paleozoic derivative of the Orthocerataceae in a sense mimics the Ascocerida, a group derived from orthocerids early in their history, but extinct by the end of the Silurian.

In a more specialized orthocerid lineage (Pseudorthocerataceae), siphuncular segments became slightly to broadly expanded and cyrtochoanitic and, in addition to complex deposits in the camerae, thick annulo-siphonate and parietal deposits developed in the siphuncle.

EHRENBERG (1) has made a convincing case for the presence of an ink-sac in a Middle Silurian *Michelinoceras*, a typical long-ranging genus of the conservative Orthocerataceae. In addition, FLOWER (3, 4) has suggested, from a reasonable interpretation of the trails and tentacular impressions of Late Ordovician orthoconic nautiloids (probably pseudorthoceraceans

or actinocerids) that these forms had relatively few arms, as in the squids, rather than many short arms as in *Nautilus*. Furthermore, comparative morphology indicates fairly certainly that orthocerids were ancestral, in the Devonian or earlier, to the Bactritida, and, in the Mississippian or earlier to the Belemnoida (either directly or via the Bactritida). Belemnoids are almost surely in the direct ancestry of modern dibranchiate cephalopods, which have both the ink-sac and small number of arms apparently possessed by at least some orthocerids.

The several features and presumed relationships just mentioned, together with the fact that only minor internal features separate the oldest orthocerids from the primitive ellesmerocerids, suggest that the dibranchiate (or coleoid) pattern (a single pair of ctenidia, ink-sac, few arms) is probably closer to the primitive cephalopod form than is that of *Nautilus* (two pairs of gills, no ink-sac, 40 arms), which is the only survivor of quite a different lineage, but which has traditionally been considered the most primitive living cephalopod.

Like orthocerids, ammonoids possibly had only a few arms, perhaps no more than eight, as suggested by KOLB (5a) from a study of drag marks made by the arms of a drifting, dead or dying ammonite found in the Solnhofen Limestone.

As MILLER & FURNISH have pointed out in their discussion of Paleozoic Ammonoidea (Treatise, p. L25), ammonoids evolved from nautiloids, but there are as yet no "preponderant supporting data to establish the identity of the ancestral form." Most recent students of cephalopods, however, follow SCHINDEWOLF (5b) in the belief that ammonoids evolved from straight orthocerid nautiloids, either directly, or more probably, by way of the Bactritida, a group that has been included at one time or another both in the Ammonoidea and among the nautiloid orders. Bactritids have many features in common with orthocerids, as do some of the earliest ammonoids, which differ primarily in being loosely to tightly coiled. Thus, it may well be that the Orthocerida are of further significance in cephalopod phylogeny in being directly or indirect-

ly (via the Bactritida) ancestral to the Ammonoidea.

The Ascocerida are specialized offshoots of early Middle Ordovician Orthocerida, which, like the Sphooceratidae and Brachycycloceratidae (Orthocerataceae), developed the capacity to discard an early-formed orthoconic or cyrtoconic conch and retain a later-formed, generally inflated breviconic portion in adulthood. Presumably, as in the Brachycycloceratidae, natural truncation of the shell and late assumption of a much different conch form are to be associated with a change of living habits by the animal during its ontogeny. Primitive ascocerids are sparingly represented in Middle and Late Ordovician rocks; more specialized forms appear in the Silurian, at the end of which period the entire order abruptly became extinct (Fig. 70).

#### ONCOCERIDA AND NAUTILIDA

The Oncocerida, a large group of immensely variable Middle-Ordovician-through-Mississippian cephalopods, bear essentially the same relation to Early Ordovician Bassleroceratidae that the Orthocerida bear to Early Ordovician Baltoceratidae (both Ellesmerocerida). That is, like the Orthocerida, oncocerids developed from their Early Ordovician predecessors primarily through simplification in structure of the connecting rings. Very early in their history, however, oncocerids replaced the primitive orthochoanitic siphuncle by one composed of faintly to broadly expanded segments and cyrtochoanitic septal necks.

Although the earliest oncocerid conchs are elongate, compressed cyrtocones, essentially similar to those of their Early Ordovician ancestors, wide adaptive radiation in the Middle and Late Ordovician produced oncocerids with virtually straight or breviconic shells, some of them faintly curved endogastrically. A second adaptive surge from the primitive oncocerid stock, beginning in the Middle and Late Silurian, produced not only additional series of straight and breviconic species, but gyroconic, torticonic, serpenticonic, and nautiliconic forms, as well. Although the siphuncle of the more or less generalized stem group of the Oncocerida (Oncoceratidae) remained

largely (but not entirely) free of organic deposits throughout its history, the siphuncles of most later, more specialized groups show a rather consistent pattern of variably developed actinosiphonate deposits.

The Nautilida, including the great bulk of the late Paleozoic, and all of the Mesozoic and Cenozoic coiled nautiloids, stem from cyrtoconic and breviconic nautiloids developed in the great oncocerid expansion of the Middle and Late Silurian. Although authors of earlier phylogenetic schemes (e.g., FLOWER & KUMMEL, 1950) reasonably concluded that the dominantly coiled Nautilida developed from coiled Barrandocerida, later evidence has shown the siphuncle in some of the earliest Nautilida (Rutoceratidae) to be cyrtochoanitic and actinosiphonate. Consequently, it now seems clear that the highly ornamented and typically cyrtoconic and gyroconic Rutoceratidae, most of which have empty orthochoanitic siphuncles, but a few of which are cyrtochoanitic and actinosiphonate like ancestral oncocerids, are the most primitive Nautilida.

The later history of the Nautilida includes differentiation of four principal stocks in the Middle and Late Devonian and Early Mississippian. From the Rutoceratidae were developed the Tainocerataceae (characterized by straight to loosely coiled conchs, for the most part ornamented by wings, spines, nodes, ribs, or frills), the Trigonocerataceae (with mostly unornamented evolute to involute conchs), the Clydonautilaceae (which are smooth, involute to occluded shells with straight to highly sinuous sutures), and, in the Mississippian, the Aipocerataceae (coiled conchs with marginal, ventral siphuncles). These four stocks proliferated greatly and became widespread geographically during the late Paleozoic, and all but the Aipocerataceae extended into and through the Triassic. Near the end of the Triassic, the remaining three groups (Tainocerataceae, Trigonocerataceae, Clydonautilaceae) vanished abruptly, leaving behind only a single genus representing the first of the smooth, involute Nautilaceae. From the sole survivor of the Late Triassic nautilid reduction, a second nautilid radiation developed in the Jurassic and Cretaceous, confined to representatives

of the Nautilaceae and never achieving the evolutionary tempo of the pre-Jurassic radiation (Fig. 292, 293).

Most Devonian nautilids belong to the Rutoceratidae, but four genera of the Centroceratidae and three of the Tetragonoceratidae also were present. None of these Devonian genera persisted into the Mississippian, but during that period, there appeared several distinct, long-ranging evolutionary lines derived from the Rutoceratidae and Centroceratidae. The Koninckioceratidae and Tainoceratidae, as well as the Liroceratidae and Aipocerataceae, stemmed from the Rutoceratidae, whereas the Grypoceratidae and Trigonoceratidae descended from the Centroceratidae.

Of the 35 nautilid genera known from the Mississippian, nearly half belong to the Trigonoceratidae, which is almost completely confined to the Mississippian (one genus ranges into the Permian and another is restricted to Lower Permian rocks of Russia). The only other nautilid family that shows a high rate of differentiation in the Mississippian is the Koninckioceratidae, in which 9 of the 11 genera known were introduced in the Mississippian. Remaining Mississippian genera belong to families that have long histories and low rates of evolution (e.g., Ehippioceratidae), or to long-ranging families such as the Tainoceratidae and Grypoceratidae.

We do not regard the reduction in number of nautilid genera in the Pennsylvanian as an indication of a significant decline in the over-all evolutionary development of the order, for if one discounts the Trigonoceratidae, the total number of Mississippian and Pennsylvanian genera is about the same and nearly a half of the remaining Mississippian genera continued into the Pennsylvanian (Fig. 292, 293).

Families that account for peak development of the Nautilida in the late Paleozoic and Triassic are the Tainoceratidae, Grypoceratidae, and Liroceratidae. Except for a liroceratid doubtfully recorded from the Devonian, all these families began in the Mississippian. Whereas the number of

genera gradually increased with time in each of these evolutionary lines, rates of evolution were not such as to produce many new families. Thus, it seems that as early as the Mississippian the principal evolutionary lines of nautilids had become firmly established and these maintained their identity and character until the close of the Triassic. Only a few, minor radiations (families) appeared in this interval. This pattern is also reflected in the number of genera carried over from one period to the next. Eleven genera persisted from Mississippian to Pennsylvanian, and 20 from Pennsylvanian to Permian. Only four Triassic genera are also known from the Permian, but this number is deceptive, for in each of the three evolutionary lineages that extend from the Permian into the Triassic, the core Permian genus evolved directly into the core Triassic genus—*Metaceras* (Penn.-Perm.) to *Mojsvaroceras* (Trias.), *Domatoceras* (Penn.-Perm.) to *Grypoceras* (Trias.), and *Liroceras* (Miss.-Perm.) to *Paranautilus* (M.Trias.-U.Trias.). Consequently, the large number of Triassic genera is the result of a broad evolutionary radiation in each of the principal evolutionary lineages during the Late Triassic. Triassic nautilid evolution, then, represents just the culmination of patterns and trends begun in the Mississippian.

Nautilids nearly became extinct after their peak development in the Late Triassic; only *Cenoceras* survived from the Triassic into the Early Jurassic. At this time, a new radiation began, resulting in a modest proliferation of new genera in the Late Jurassic. In the Cretaceous, the total number of genera was maintained, but the number of new genera began to decline. Decrease in the Cenozoic was very marked and the majority of Cenozoic nautilids are holdovers from the Cretaceous and Jurassic. Although *Nautilus* (Oligo.-Rec.) and the monotypic *Obinautilus* (Oligo.) appeared during this interval, the only successful, widespread new genus that evolved during the Cenozoic was *Aturia* (Oligo.-Mio.) (Fig. 70, 292, 293).

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## PALEOECOLOGY

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## INTRODUCTION

An almost unique series of difficulties is encountered in any attempt to interpret the mode of life and the habitat of fossil cephalopods. *Nautilus*, the single living externally shelled descendant of the abundant and varied nautiloid stocks of the Paleozoic, is restricted geographically and apparently should be regarded as a stenotopic form. However, published information on the ecology of *Nautilus* is far from complete, and danger of misinterpretation must inevitably accompany any attempt to draw general paleoecological inferences from a single extant representative. In fact, great diversity in the morphology of fossil nautiloids<sup>1</sup> suggests strongly that corresponding differences existed in their mode of life and ecology. Likewise important is the presumed susceptibility of most nautiloids to long-range post-mortem transportation after buoyancy was increased by decay of tissues

and possible fragmentation of the body chamber.

Published discussions of nautiloid paleoecology are of necessity highly speculative, even though some are based on careful evaluation of such relevant factors as the ecology of living *Nautilus*, hydrostatic equilibrium of fossil forms, color markings, configuration of the aperture, localization of abrasion, hydrodynamic form, post-mortem distribution, and facies relationships. Summary accounts of previous contributions to understanding of the paleoecology of Paleozoic nautiloids have been given by MILLER & FURNISH (9) and FLOWER (3). Annotated bibliographies are available for Cenozoic nautiloids (15) and modern *Nautilus* (14), but no adequate general treatment of the paleoecology of Mesozoic nautiloids exists.

## ECOLOGY OF MODERN NAUTILUS

Because of morphological resemblances to many fossil cephalopods, *Nautilus* is of

<sup>1</sup> The term "nautiloids" here is used broadly to include the subclasses Endoceratoidea and Actinoceratoidea, as well as the Nautiloidea.—EDITOR.

unique significance. However, extreme caution needs to be exercised in applying generalizations derived from study of this living form to the ancestral nautiloids of the Mesozoic and Paleozoic.

Modern *Nautilus* is confined almost entirely to the southwestern Pacific Ocean. The genus is fairly abundant only in a relatively small area extending northwestward from New Caledonia and the Loyalty Islands to New Guinea and the Bismarck Archipelago. Authenticated extreme ranges for distribution of live specimens are bounded by the Fiji Islands to the east, the Philippines to the north, Makassar Strait and northwestern Australia to the west, and South Australia to the south. All of these localities lie within the tropics, except for South Australia, which has yielded only a single live specimen. Information is insufficient to allow generalizations as to the salinity and temperature of the biotope of *Nautilus*. Dead shells occur in moderate abundance in some areas well beyond the recorded limits of live specimens. Small numbers of shells have been collected from as far south as extreme southwestern Australia and the North Island of New Zealand, as far north as Japan, and from Madagascar to the west. In most instances it is doubtful to what extent these latter occurrences are a function of post-mortem distribution.

Live representatives of *Nautilus* have been secured in moderate abundance from traps set at depths even greater than 300 fathoms. However, they apparently migrate nocturnally, in shoals, to shallow water close to shore. Specimens may be taken in fish traps set as shallow as three fathoms, but all representatives found floating at the surface are in moribund condition. Some degree of success has been achieved in maintaining live *Nautilus* under shallow-water aquarium conditions.

Small decapod crustaceans are a main source of food for modern *Nautilus*. However, the animals are both carnivores and scavengers. They are attracted to traps baited with a great variety of fresh or decomposing marine invertebrates and vertebrates or the remains of domestic animals.

The numerous tentacles of *Nautilus* may be used to anchor the animal to the sub-

stratum for short periods. Reports that the organism crawls by manipulation of the tentacles are incorrect. *Nautilus* is a facile swimmer, and this is virtually the sole means of locomotion. It is an active member of the nekto-benthos. Movement is by jet propulsion and results from rhythmic, forcible ejection of water from the branchial chamber of the pallial cavity. The water leaves the pallial cavity through the infundibular hyponome; movement is backward, and direction is controlled by the attitude of the muscular hyponome. The weight of the animal is delicately balanced by gas in the camerae, so that the mean density of the entire animal is the same as that of sea water. A high degree of stability is achieved by location of the buoyant phragmocone above the heavy body chamber.

A common general pattern of protective coloration characterizes both the soft part and the shell of all postembryonic ontogenetic stages of living *Nautilus*, although interspecific differences are apparent. The effectiveness of the protective pattern is such that *Nautilus* is extremely difficult to distinguish, even in clear shallow water. Upper portions of the shell are characterized by irregular brown transverse bands, whereas the mature lower shell surface is white.

## INFERENCES FROM CONCH MORPHOLOGY

Consideration of the details of conch morphology is generally regarded as the most fruitful approach to interpretation of the life habits of fossil nautiloids. Many uncertainties are involved, but several independent lines of reasoning result in fairly compatible conclusions.

### SHELL EQUILIBRIUM

In order to facilitate level backward propulsion, all active nektonic nautiloids must have maintained the terminal portion of the body chamber and the hyponome in approximately horizontal alignment. Any major variation from this horizontal orientation would have restricted the animal to either a sluggish benthonic mode of life or hyponomic propulsion in a more nearly vertical direction. Whereas the former alter-

native is a distinct possibility, the latter seems highly improbable from both biologic and hydrostatic considerations. Several lines of evidence, particularly the development of primary cameral deposits, indicate that the great majority of fossil nautiloids resembled living *Nautilus* in the presence of gas in the camerae. However, it is possible that septation in the ancestral nautiloid shell developed for mechanical and physiologic functions (12), so that some ancestral ellesmerocerids and perhaps a few of their breviconic descendants may have lacked cameral gas. Even if gas were present in the camerae of all nautiloids, the extremely close spacing of the septa in some ellesmerocerids and a few other brevicones would have precluded the presence of a sufficient volume of gas to balance the weight of the animal. Consequently, it appears that crawling by use of the tentacles may have been the main means of locomotion for at least some nautiloids, and that these forms should be considered as motile members of the epifauna.

With the exception of some ancestral ellesmerocerids and a few breviconic descendants, all nautiloids probably shared the common equilibrium problem of counterbalance of gas in the camerae. The basic requirement for mobile stability in these forms was that the center of buoyancy should lie proximal to the center of gravity. It seems a plausible assumption that almost all nautiloids achieved this condition with the terminal part of the body chamber in approximately horizontal position and that, therefore, most fossil nautiloids resembled living *Nautilus* in swimming prowess. Four fundamentally different solutions to the general problem of shell equilibrium were achieved: coiling of the entire conch or a major part of it, secretion of heavy mineralized cameral and siphuncular deposits, ontogenetic shell truncation, and formation of a breviconic conch.

The recent discovery of aqueous fluid in some of the camerae of living *Nautilus* (BIDDER, 1962) indicates an additional means of maintaining shell equilibrium, although the importance of this mechanism for fossil cephalopods cannot be evaluated in particular cases. Examination of the liquid was inconclusive, although it contains

organic material and dissolved salts and is viscous in the apical chambers. BIDDER indicated that the largest volumes of liquid occur in the camerae adjacent to the body chamber; little or no fluid is present in chambers situated uppermost when the animal is in living position, whereas liquid is present in apical camerae. Variation of the quantity of fluid present in the various ontogenetic stages suggests that fluids within the camerae can be controlled through the siphuncle. Change from positive to negative buoyancy, or vice versa, may occur within a few hours under aquarium conditions.

Cameral liquids may have been of primary importance in maintaining equilibrium in some orthoconic forms, such as the Bac-tritida. Representatives of that order commonly retain all ontogenetic stages and are devoid of siphuncular and cameral deposits.

Coiling alone was sufficient to locate the center of buoyancy close to the center of gravity with the hyponome in horizontal position (Fig. 43, 44, 52; see also *Treatise* Part L, Fig. 124, 157). This solution to the problem of equilibrium was adopted by the Nautilida, Tarphycerida, and Bar-randeocerida. It is significant that primary cameral and siphuncular deposits are practically unknown in these three orders. No such deposits were needed for mobile stability. The only group of coiled nautiloids in which voluminous cameral deposits occur is the tarphycerid family Lituitidae. This group is characterized by association of an adoral orthocone with the adapical spiral (Fig. 268, *1a,b*), so that general coiling of the shell is quite different from that of other members of the three orders.

The center of gravity would have been located adorally from the center of buoyancy in orthoconic longicones if all camerae were retained during ontogeny and the chambers themselves were devoid of mineralized deposits or liquid. Stability was achieved under these conditions only if the shell were held in a vertical position, and effective horizontal hyponomic propulsion would have been precluded by this orientation. It is not surprising, therefore, to find that most longiconic orthocones either developed mineralized primary deposits in the phragmocone or, probably less commonly, underwent periodic truncation of the apical

camerae. The result of either procedure was to move the center of buoyancy forward, coincident with anterior migration of the center of gravity as growth proceeded. Superposition of the centers of buoyancy and gravity with the shell in horizontal position thus allowed effective backward movement by use of the hyponome.

Most representatives of the orders Endocerida, Actinocerida, and Orthocerida are longiconic orthocones in which primary mineralized cameral deposits, siphuncular deposits, or both are found. Secretion of these deposits invariably was progressive, beginning near the apical end of the phragmocone and extending farther adorally at successively later ontogenetic stages (Fig. 23, 24, 33-37). Concentration of deposits adapically served the dual purpose of weighting the apical end and reducing its buoyancy by displacement of gas. In addition, these mineralized deposits undoubtedly strengthened the apical part of the phragmocone, which otherwise would have been vulnerable to damage during backward hyponomic propulsion. Presumably, a delicate balance was achieved at all growth stages so as to allow superposition of the centers of buoyancy and gravity when the conch was in horizontal position and thus permit effective horizontal propulsion by the hyponome. Also, it is reasonable to assume that all active nektonic nautiloids maintained hydrostatic equilibrium, the weight of the organism being balanced by the buoying effect of cameral gas. A noteworthy feature is that both cameral and siphuncular deposits commonly are concentrated in the ventral part of the phragmocone. This had the effect of producing a more stable form by lowering the center of gravity.

A second alternative for reducing the apical buoyancy of horizontally oriented orthoconic longicones was periodic decollation of the apical camerae, or ontogenetic shell truncation (Fig. 190). This means of maintaining mobile stability during horizontal propulsion was utilized by all Ascocerida and at least some Orthocerida (7). Most taxa of orthocones are known only from fragmentary specimens, so that the numerical importance of ontogenetic shell truncation is unknown. Ac-

companying the achievement of periodic decollation in almost all Ascocerida and at least some Orthocerida was an evolutionary trend towards concentration of the camerae dorsally, above the body chamber. Again, the effect of this trend was to decrease the vertical separation of the centers of gravity and buoyancy and thus to improve stability during horizontal movement of the animal. The ascocerid phragmocone was devoid of deposits, but cameral deposits are known in *Sphooceras truncatum*, a species for which periodic decollation has been documented thoroughly (1).

Whereas the mode of life of the coiled nautiloids and orthoconic longicones can be inferred with reasonable confidence, greater difficulties are encountered in paleoecological interpretations for the host of brevicones and cyrtcones included in the Oncocerida and Discosorida. Most straight brevicones, and in fact virtually all oncocerids lack cameral deposits. However, many of the cyrtconic discosorids are characterized by voluminous cameral and siphuncular deposits. The relative volume of the phragmocone and the body chamber varies greatly in orthoconic brevicones. In many forms, the phragmocone was of such relatively small dimensions that buoyancy could not have compensated fully for the weight of the animal. A vagrant benthonic mode of life probably should be attributed to these forms. Other brevicones with proportionally larger phragmocones could have been fully buoyant, and can be considered as swimmers. However, equilibrium would have been achieved only if the axis of the conch were near-vertical in position, and rapid horizontal movement appears to be precluded by this orientation. By contrast, even moderate conch curvature, as in the cyrtcones, would have produced stable orientation of the shell with the hyponome in approximately horizontal position. A nektonic or nektobenthonic mode of life can thus be attributed to buoyant cyrtcones.

### COLOR MARKINGS

Nautiloids which preserve color patterns occur sporadically throughout the geological column and are known from strata as old as the Ordovician (3, 6). They provide a basis for paleoecological interpretation, as the

distinctness of color markings of modern marine shells bears a direct relationship to light intensity. Thus, shells possess more varied colors and more distinct designs in shallow than in deep water, and only some 5 per cent of organisms inhabiting water deeper than 100 fathoms possess conspicuous color markings. In addition most marine organisms resemble living *Nautilus* in lacking color patterns entirely, or having them less conspicuously developed, on the lower surface of the shell.

Color markings in fossil nautiloids are known in a variety of patterns. Commonly they consist of fairly straight longitudinal bands or of chevron-like or sinuous transverse belts (Fig. 9, 10). Evidence is far from conclusive for longiconic orthocones but suggests that color bands were generally absent from one side of the conch, presumably the lower surface. This distribution lends support to the conclusion that the axis of most longicones was oriented horizontally. Color-banded orthoconic and cyrtconic brevicones are more numerous than colored longicones, but are still rare. The majority of these brevicones exhibit equal development of banding on all sides, thus supporting the conclusion from studies of equilibrium that the axis of the conch was oriented at a high angle to the horizontal.

### CONFIGURATION OF APERTURE

The nature of the aperture, particularly the form of the peristome adjacent to the hyponome, provides a basis for paleoecologic inference (Fig. 11). A basic assumption in evaluating this type of evidence is that the presence of a hyponomic sinus, or re-entrant in the peristome adjacent to the hyponome, permitted greater flexibility of that propulsive organ, and that nektonic prowess was thus proportional to the area of the sinus. This assumption may not be justified when applied to the group as a whole, as practically all orthoconic longicones lack a conspicuous hyponomic sinus, whereas most brevicones, cyrtcones, and coiled forms exhibit some modification of the peristome. Other possible features of the peristome, such as a dorsal salient and paired ocular sinuses (Fig. 196,2a-e), are considered to be of secondary importance in paleoecologic interpretations.

Several nautiloid groups exhibit striking ontogenetic changes in form of the aperture. For example, the whorls of the juvenile spire in the tarphycerid *Angelinoceras* (Fig. 267,3) possess a deep hyponomic sinus, whereas this feature is lost almost completely on the adoral parts of the associated orthocone. More commonly, the indentations of the peristome became more pronounced in later ontogenetic stages. Of great interest are the numerous Ascocerida (Fig. 196,2a-e), Oncocerida (Fig. 210, 211), Discosorida (Fig. 247), Tarphycerida (Fig. 268, 269), and Nautilida (Fig. 319) which developed spectacular modifications of the aperture only near full maturity. The implications of these modifications are not fully understood. It is tempting to postulate that drastic modification of the aperture was accompanied by a correspondingly pronounced alteration in habitat and mode of life. This is probably valid in most genera, but in at least some groups the juvenile conchs are associated directly with mature forms. For example, evidence from known occurrences suggests that the juvenile and mature ascocerids occupied the same habitat, as is the case with modern *Nautilus*.

Apertural modifications were apparently relatively rare in longiconic orthocones in comparison with the more nearly equidimensional brevicones. However, the paucity of evidence for such modifications is to some extent a function of the greater susceptibility of longicones to post-mortem fragmentation.

### LOCALIZATION OF ABRASION

A few nautiloids are known to exhibit local abrasion of portions of the shell. These worn areas are interpreted as having resulted from repeated contact with the sea floor. The best-documented examples are referred to the nautilid genus *Cooperoceras* (10). Representatives of this genus show conspicuous beveling of the ventrolateral spines in the ultimate one-third of the fully mature whorl.

Abrasion of the lower shell surface of an active nektobenthonic nautiloid appears plausible when it is realized that nautiloids generally were incapable of adding to the outer shell after attainment of full maturity and coincident development of mature



modifications. Whereas presently known examples of this type of abrasion are few, there is a good possibility that many other instances will be recognized once the paleoecologic significance of the phenomenon is generally understood. FLOWER (2) recorded numerous grouped trails and impressions which he attributed to the tentacles and shell of nautiloids (see "Nautiloid Trace Fossils," p. K487). These trails, if rightly interpreted, indicate repeated contact of nautiloids with the sea floor and imply the possibility of abrasion of the lower surface of the shell.

### STREAMLINED FORM

The hydrodynamic form of the nautiloid provides an additional basis for paleoecologic inference. Quantitative data on relative streamlining of coiled cephalopod shells were presented by KUMMEL & LLOYD (8). They confirmed the previously held notions that involute and compressed shells are better streamlined than evolute and depressed whorls. No such quantitative data are available for most nautiloid groups, but it is certain that the orthocones presented less hydrodynamic resistance than cyrtocones and coiled forms. Spines and ribs would also have increased resistance drastically and thus have reduced the efficiency of jet propulsion.

### POST-MORTEM DISTRIBUTION

Evidence already presented suggests that most, but not all, fossil nautiloids resembled living *Nautilus* in achieving a delicate balance between the total weight of the live animal and the buoyancy of gas in the phragmocone. The mean density of these live animals presumably was the same as that for the sea water in which they lived. As in the case of modern *Nautilus*, the mean density probably could have been changed slightly by physiological processes, thus enabling the animal to sink or rise.

The shell of those nautiloids which achieved equilibrium would have floated to the surface after death of the animal and consequent decay and loss of the content of the body chamber. Such floating shells were certainly susceptible to extensive post-mortem distribution by tides and ocean currents.

Many aspects of the phenomenon of post-mortem distribution of cephalopods were considered in detail by REYMENT (13). Experiments by that author confirmed that the orientation of a floating dead shell and the eventual mode of settling of a stranding conch are determined largely by the weight of the walls of the body chamber in relation to the buoyancy of the gas-filled phragmocone. Many coiled cephalopods with strongly depressed or highly compressed whorls were determined by REYMENT to be posthumous sinkers, whereas a great variety of other conch forms represented potential posthumous floaters, many of which would have been deposited near the strand line irrespective of original habitat. REYMENT also drew attention to the probability that damaged shells, unable to float at the surface, achieved additional dispersal at depth owing to presence there of denser bodies of more highly saline or colder water. (See chapter on Biostratonomy, p. K124.)

Distribution of rhyncholites commonly is different from that of the associated conch. This may be explained readily by assuming that the rhyncholites dropped from the rotting nautiloid bodies close to the habitat of the organisms, whereas the empty shells achieved more extensive post-mortem distribution.

### INFERENCES FROM FACIES RELATIONSHIPS

Lithofacies and biofacies associations of fossil nautiloids are generally considered unreliable as a guide to habitat, and many apparently contradictory ecologic conclusions are based upon such associations. Errors in interpretation of habitat stem largely from extensive post-mortem distribution of most morphological types. However, practically all living cephalopods undergo seasonal and monthly migration, and it is reasonable to assume that similar changes of habitat were common in extinct groups. Because of these two factors, many of the sites of preservation of fossil faunas are undoubtedly far removed from areas in which the forms lived.

As indicated previously, heavy-shelled brevicones and cyrtocones with a proportionally large body chamber probably did

not possess a sufficient volume of gas in the camerae to compensate completely for the weight of the animal. Consequently, these forms are best considered as elements of the motile benthos. Upon death, putrefaction of the body probably would not have resulted in sufficient loss of weight to allow the empty shell to float. Thus, accumulations of such shells can be considered as biocoenoses. In contrast, most longicones and coiled shells were probably in a state of equilibrium during life, and loss of the soft parts would have allowed the shells to float. Accumulations of these shells consequently should be considered as thanatocoenoses. Distribution of modern *Nautilus* suggests that dead shells may float the 1,000 miles from New Caledonia or eastern Australia to New Zealand, or even the 4,500 miles from northwestern Australia or Indonesia to Madagascar. Similar dispersal can be assumed for some fossil forms.

Two classic examples may be selected to support the assumed correlation between morphology and distribution of fossil nautiloids. Elements of the "Arctic Ordovician" fauna have been described in a series of publications by FOERSTE, MILLER, and others. This fauna is widely distributed from the Canadian Arctic islands to the Mexican border. Both lithofacies and biofacies associations of the nautiloids indicate strand line or shallow water deposition. Large longicones dominate the faunas, and many of these nautiloids are in a highly fragmented state. Elsewhere, it is demonstrated that these longicones are best considered as posthumous floaters. The wide areal distribution of this "Arctic Ordovician" nautiloid fauna is compatible with its facies associations if the cephalopods are regarded as having floated into shallower water after putrefaction of the body.

The Silurian nautiloids of the Upper Mississippi Valley (5) represent a contrasting situation. Most of the 75 species described by FOERSTE were secured from the flanks of a single bioherm. Nautiloids occur sporadically but in moderate abundance in direct association with these bioherms, but they are exceedingly rare in the interreef facies. Possibly a majority of the species are brevicones with such proportionally small phragmocones that the live animals could not have been fully buoyant. Death

must have resulted in immediate settling of the shells in a biocoenose. The sporadic and localized distribution of these Silurian nautiloids is thus completely compatible with previous conclusions on mode of life of the brevicones.

## PALEOECOLOGY OF MAJOR TAXA

Morphological variation within individual nautiloid orders indicates differences in mode of life and habitat. However, the following broad generalizations for each of the groups can be devised by evaluation of the factors considered previously in this chapter.

### ENDOCERIDA

Most endocerids were longiconic orthocones with a proportionally large submarginal siphuncle; the same is true of the much smaller group included in the Intejocerida. Endocones or longitudinal lamellae were developed progressively from the apical end of the siphuncle, but cameral deposits are unknown. These longicones are judged to have maintained equilibrium between the total weight of the animal and the buoyant effect of cameral gas, and to have carried the axis of the conch in horizontal position. Color bands are exceptionally rare, but apparently were confined to the dorsum. The endocerids can be considered as nektobenthos and most were posthumous floaters. It is difficult to envisage a connection between the siphuncle and the apical camerae of forms with macrochoanitic septal necks and endocones in the adjacent siphuncle.

Adequately known representatives of the breviconic Piloceratidae and Manchuroceratidae are characterized by a proportionally small phragmocone which probably could not have contained enough gas to have compensated fully for the weight of the entire animal. They are best considered as vagrant benthos and posthumous sinkers.

### INTEJOCERIDA

Although the intejocerids are poorly known, it may be assumed that the calcareous lamellar deposits which fill the siphuncle solidly in most growth stages served the same purpose of maintaining

hydrostatic equilibrium of the shell as endocones in the Endocerida.

### ACTINOCERIDA

Practically all actinocerids are orthoconic longicones which developed voluminous cameral and siphuncular deposits. Secretion of these structures was progressive, from the apical end, so that equilibrium would have been maintained with horizontal orientation of the conch. With few exceptions, the actinocerids are inferred to have been active swimmers and posthumous floaters. Probable exceptions to these generalizations include strongly depressed forms, such as *Gonioceras* and *Lambeoceras*. These depressed conchs probably possessed such a relatively small volume of gas in the camerae that they were not fully buoyant either in life or after death.

### ELLESROCERIDA

Included within this order are forms with such diverse morphology that no single morphologic peculiarity can be considered as characteristic of the entire group. However, septa are generally more closely spaced than in other nautiloids and both cameral and volumetrically significant siphuncular deposits are absent. There is no clear indication that cameral gas was present in these ancestral nautiloids. Even if gas filled all camerae, it is doubtful whether such closely septate forms could have been fully buoyant; breviconic representatives certainly were not.

Environmental associations of the Ellesmerocerida are generally with the shallow-water shelly facies. Gastropods, trilobites, and stromatolites commonly occur with them, and a degree of fragmentation of the conchs is almost invariable.

Although each line of evidence for ellesmerocerid paleoecology is inconclusive, it is most reasonable to assume that, in general, the group was benthonic. Breviconic representatives were probably crawlers. However, the septa of the longicones may have served the same balancing function as siphuncular and cameral deposits in other nautiloids, and this group may well have been characterized by a nektobenthonic mode of life. The axis of the conch would have been horizontal for active swimmers but more nearly vertical for benthonic forms.

### ORTHOCERIDA

Almost all representatives of this order are orthoconic longicones with a proportionally small siphuncle. Voluminous cameral and siphuncular deposits are almost invariably present, at least in the apical portion of mature specimens, and concentration of these laminated structures is commonly in ventral position. Color bands are generally restricted to one surface, presumably the dorsum.

Progressive development of the deposits of the phragmocone, adorally from the apex, suggests that the orthocerids were in hydrostatic equilibrium and that the conch was maintained in horizontal position. This orientation is confirmed by available examples of color banding. Ventral concentration of cameral deposits resulted in lowering the center of gravity to achieve greater stability. Some Orthocerida underwent ontogenetic shell truncation. However, the numerical importance of this equilibrium device is not known. In view of these factors, it can be concluded that the orthocerids were active swimmers and posthumous floaters. The cephalopod coquina found locally in the Maquoketa Formation of Iowa (11) is one of the many prolific accumulations of orthocerids which clearly represent thanatocoenoses deposited in a turbid shallow-water environment.

### ASCOCERIDA

Representatives of this order are characterized by ontogenetic shell truncation of the orthoconic to cyrtoconic adapical deciduous section and development of a highly modified inflated breviconic mature ascoceroid portion (Fig. 190). Structural components of the conch were unusually thin, and cameral and siphuncular deposits are unknown. Perhaps the most notable feature of the ascoceroid portion of the conch was the concentration of the camerae, in dorsal position, above the body chamber. Three to 12 septa are present in the ascoceroid portion.

Juvenile ascocerids, which invariably are associated with mature specimens, are best considered as nektobenthos. Through periodic truncation of the apical camerae they could have maintained equilibrium with the shell in an inclined position. Mature Silurian ascocerids were almost per-

fectly adapted to an active nektonic mode of life. The compressed attenuate fusiform contours offered minimum hydrodynamic resistance, and dorsal concentration of the camerae provided maximum mobile stability. Extreme maneuverability was facilitated by formation of a deep hyponomic sinus.

Presumably the ascocerids were posthumous floaters, and small numbers of specimens are known from widely scattered localities in North America and Europe. Rarity of these nautiloids may be largely attributable to fragile construction of the conch. Specimens have been secured in moderate abundance only from the Baltic Island of Gotland, the same area which has yielded all of the undoubted deciduous conchs. Consequently, it seems probable that these occurrences represent the only known biocoenoses.

### ONCOCERIDA

Within this order are grouped the bulk of the brevicones and cyrtocones, although derivatives include some longiconic orthocones, gyrocones, torticones, serpenticones, and nautilicones. Spectacular modifications of the fully mature aperture are recorded for many forms. Both the camerae and the siphuncle are devoid of volumetrically significant mineralized deposits.

The relative sizes of the phragmocone and body chamber vary within wide limits in the breviconic orthocones and cyrtocones. However, the majority of such forms probably were not fully buoyant, owing to possession of a relatively small phragmocone, close septal spacing, and thick shell. They should be considered as benthos and posthumous sinkers. However, the persistent presence of a hyponomic sinus probably indicates that the hyponome functioned as a propulsive organ, so that a nektobenthonic mode of life is therefore plausible.

Color markings of the brevicones are invariably developed on all sides. This confirms the conclusion from studies of equilibrium, namely, that the axis of the shell was carried in inclined or vertical position. The development of even moderate curvature of the conch would have permitted horizontal disposition of the hyponome. Consequently, cyrtocones with a propor-

tionally large phragmocone may be considered as swimmers, although the conch did not constitute an efficient hydrodynamic form.

Particular problems are posed by the many oncocerids with strongly contracted apertures. Possession of a proportionally small phragmocone in most such forms marks them as benthos, although the presence of a hyponomic sinus probably indicates ability for limited propulsion as well as for respiration. Detailed buoyancy studies of some few breviconic oncocerids with exceptionally large phragmocones and restricted apertures may well indicate that these forms were floaters which lived passively as members of the plankton.

### DISCOSORIDA

Curved brevicones are characteristic of this order; both endogastric and exogastric forms may appear in the one lineage. Constricted apertures are common, and many such forms retain the prominent hyponomic sinus. Cameral and siphuncular deposits are present in some groups.

In gross conch form, the discosorids are homeomorphs of the oncocerids, and similar mode of life and habitat are likely for both (4). Most discosorids are best considered as sluggish nektobenthos, especially in view of the almost invariable benthonic associations. However, groups with a narrow siphuncle and proportionally large phragmocone, such as the Westonoceratidae, were probably in equilibrium with the sea water. They can be interpreted as active swimmers and posthumous floaters.

### TARPHYCERIDA

Included here are evolute coiled nautiloids in which cameral and siphuncular deposits are virtually absent. The Lituitidae differ in morphology from other tarphycerids and will be considered separately. Most tarphycerids exhibit some degree of divergence of the adoral portion of the mature body chamber. The peristome is characterized by a prominent hyponomic sinus at all growth stages, and the fully mature aperture commonly exhibits some degree of modification.

Qualitative comparison of the phragmocone and body chamber suggests a fairly constant proportion between the volumes

of these two parts of the conch. For example, the shell of most tarphycerids expands rapidly and possesses three to four whorls, including one-half of a volution of body chamber. However, more gradually expanded forms, such as *Hardmanoceras* and *Ophioceras* may possess six whorls, including slightly more than one volution of body chamber. Consequently, it appears that most tarphycerids lived in hydrostatic equilibrium, and were thus posthumous floaters. Presence of a deep hyponomic sinus tends to confirm interpretation of the group as active swimmers. The divergent adoral portion of the body chamber would have been oriented in horizontal position. We disagree with TEICHERT (chapter on Biostratonomy) in thinking that empty tarphycerid and barrandeocerid shells would not have floated readily.

Representatives of the tarphycerid family Lituitidae commonly have conchs with a relatively small adapical spiral and a larger straight to slightly sigmoid adoral longicone. Growth lines generally define a conspicuous hyponomic sinus. Modification of the peristome at full maturity commonly included deepening of the ocular and hyponomic sinuses and development of lap-pets. Apical buoyancy of the lituitids was balanced in at least some forms by secretion of dorsally discontinuous cameral deposits. Presumably those forms were active swimmers and posthumous floaters, not differing greatly in hydrostatic form from the orthocerids.

### BARRANDEOCERIDA

Early representatives of this order are evolute forms closely resembling the ancestral Tarphycerida. Derivatives include a variety of conch types similar to those encountered in the Lituitidae. Both cameral and siphuncular deposits are absent. Modification of the mature peristome has been recorded for only one genus. A conspicuous hyponomic sinus is commonly present.

The resemblance in gross form between the Barrandeocerida and the Tarphycerida is such that similar mode of life and habitat can be assumed. Presumably most representatives were active elements of the nektobenthos and posthumous floaters. However, crawling must have been the dominant

means of locomotion for some derivatives, such as the torticones. As noted in the preceding discussion of Tarphycerida, our interpretation of that group and of barrandeocerids differs from TEICHERT's.

### NAUTILIDA

Most of the coiled nautiloids from Devonian and younger strata are more nearly involute than the serpenticones of the older Paleozoic, and they are referred to the Nautilida. Differences in rate of expansion, whorl section, and ornament are apparent, but basic similarity to modern *Nautilus* is such that comparable habitat and mode of life can be presumed. Coiling alone was sufficient to place the center of buoyancy near the center of gravity, with the hyponome in horizontal position, so that both cameral and siphuncular deposits are absent.

All Nautilida are judged to represent nektobenthos, although effectiveness of hyponomic propulsion probably varied widely. Qualitative evaluations of buoyancy suggest that most representatives were posthumous floaters. This conclusion is supported by the widespread occurrence of many taxa. However, the body chamber of some forms, such as *Aipoceras* (Fig. 317, 1a-d), clearly was of such large size in relation to the phragmocone that the animal could not have been fully buoyant. Fossil occurrences of such forms thus approximate life sites.

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## BIOSTRATONOMY

By CURT TEICHERT

Biostratonomy is concerned with the study of all factors and processes that influence and act upon organic remains from the time of death of animals and until they come to a final resting place in a sedimentary deposit. The biostratonomy of nautiloid cephalopods<sup>1</sup>, like that of bactritids and ammonoids, is a complex and difficult subject, because the vast majority of their conchs has no modern counterpart. There has been much speculation on the possibility of widespread transportation of empty conchs of nautiloids and other chambered cephalopods (for a summary see REYMENT, 12), but little concrete information on which to base speculations is available.

GEISLER (2) immersed an undamaged and a slightly damaged shell of Recent *Nautilus* in water. Both shells floated with the body chamber downward. The damaged shell sank after 28 days, the undamaged shell 24 hours later, when enough water had penetrated the camerae.

Model experiments by REYMENT (12) have shown that the length of the body chamber has great importance for the buoyancy of conchs. An empty endocerid model conch floated if the body chamber did not exceed a quarter of the length of the phragmocone. An orthocerid type model conch floated if the body chamber was less than half the length of the phragmocone. A conch of *Nautilus pompilius* floated freely in an upright position with the body chamber downward. After 32 days it was found to have sunk only slightly in the water. However, when the body chamber was artificially enlarged to equal two-thirds of one volution, the conch sank.

The following additional results of REYMENT's experiments are of interest. (1) Evolute coiled conchs are less likely to float than highly involute ones. (2) Strongly compressed as well as strongly depressed coiled conchs tend to sink. (3) Strongly ornamented, tuberculated conchs will not

<sup>1</sup> See footnote, p. K114.

float and even moderately strongly tuberculated conchs will sink, if the tubercles are solid. (4) Apertural modifications (such as presence of ears and lobate projections) adversely affect buoyancy.

Temperature fluctuations "tend to sink a floating shell, as warm water expels air and cold water replaces the lost air when the temperature sinks." Salinity is also important. A shell of *Nautilus pompilius* sinks in water of less than normal salinity. Its downward movement may be arrested, if it meets a water layer of normal salinity at greater depth. Such conditions exist at the entrance to inland seas such as the Baltic Sea of today. In the past, conditions might have existed locally under which bottom currents of normal salinity flowing into an inland sea could have carried empty cephalopod shells to areas with surface water of low salinity where the animals could not have lived.

Along the same line KOBAYASHI (6) believed that most finds of nautilids in Tertiary rocks of Japan are necroplanktonic drifted shells. Many of them occur in sedimentary rocks formed in coastal embayments and some occur associated with fossils indicative of water temperatures that would have been too cold for the living nautilids. Similarly, STENZEL (13) believed that *Aturia* was not indigenous in the Eocene of Texas, "but floated in as dead, empty shells from the deeper parts of the Gulf of Mexico." On the other hand, in other Tertiary formations in Texas, *Aturia* was apparently indigenous.

REYMENT has demonstrated that conchs of longiconic orthocerids must have floated with the body chamber pointing downward. This may explain the common occurrence of phragmocones without body chambers, because the latter were more exposed to damage in the floating position. For certain breviconic conchs with cameral deposits (*Westonoceras*), TEICHERT (14) earlier had concluded that they may have floated with the apex directed downward.

Although much remains to be learned about the conditions influencing transportation and settling of nautiloid conchs after death, some preliminary conclusions are possible. (1) Conchs of benthonic animals with heavy cameral deposits and thick siphuncles with siphuncular deposits (e.g.,

most Endocerida and Actinocerida) are likely to become entombed at or near their natural habitat. (2) Length of the body chamber and amount of cameral deposits determine whether longiconic, stenosphonate conchs sink or float. The conchs of most Pseudorthocerataceae, of the Lamellorthoceratidae, and of similar forms can hardly have floated, whereas those of many Orthocerataceae may have done so. (3) The conchs of most early Paleozoic coiled forms (Tarphycerida, Barrandeocerida) were poor floaters and are most likely to be found not far from where they lived. (4) In evolution of the Nautilida a definite trend toward greater buoyancy of the empty conchs may be inferred, because Jurassic and later genera tend on the whole to be more involute and more globular than early Mesozoic and Paleozoic representatives of the order. (5) No experimental data and little information on the buoyancy of breviconic conchs are available from other sources. However, the distribution pattern of oncocerid and discosorid genera and families (which contain most of the brevicones) does not support the suggestion that these conchs might have floated during lengthy periods after death.

Nautilid shells infested with cementing organisms such as serpulids and certain clams have been described from Triassic rocks by WELTER (15) and by KIESLINGER (5). Irrespective of their normal buoyancy such shells cannot have floated appreciably after the animal died.

The orientation, especially of longiconic conchs, is another aspect of the biostratonomy of nautiloids. It may be used to determine the direction of ocean currents and shore-line trends at the time of the entombment of the fossils. PETRÁNEK & KOMÁRKOVÁ (10), from measurements of the orientation of nearly 1,000 orthocerid conchs in Silurian rocks of Czechoslovakia, found an overwhelming majority of them disposed in parallel position. They assumed that the apices pointed against the direction of the current. However, as pointed out by QUENSTEDT (11), orthoconic conchs with undamaged (hence, gas-filled) phragmocones must have been anchored by the heavy body chamber and the apices of such conchs would point in the direction of the current.

KAY (4) observed two orientation maxima for orthoconic cephalopod conchs in

Ordovician rocks of Ontario and Vermont, one for large specimens and the other for small conchs. The two were perpendicular to each other. KAY suggested that the large conchs were oriented normal to the contemporary shore line, whereas the small ones were parallel to it. Identical conditions were observed in Ordovician rocks of New York by CHENOWETH (1). Small orthocerids tended to be oriented parallel to ripple marks in the same beds, hence normal to the prevailing current. Large endocerid shells were found in orientation normal to the ripple marks, hence parallel to the current. CHENOWETH assumed that these shells pivoted around their apices, which would then point up-current. KRINSLEY (9) studied orthoconic conchs in Silurian rocks of Illinois and used their orientation to determine paleo-wind and -current directions. GOLDRING and FLOWER (1942) described beds containing abundant large orthoconic shells, arranged in prevailing parallel directions, from the Devonian of New York State. On the other hand, in reef flank deposits in a Silurian reef complex in Illinois, orthoconic cephalopods were found in haphazard orientation in a criss-cross pattern (3). The body chambers of conch-bearing cephalopods act as sediment traps, as first pointed out by QUENSTEDT (11) and later illustrated by means of experiments of REYMENT (12).

Experiments by KOLB (8) have shown that in the presence of a bottom current a dead *Nautilus* shell is oriented with the opening of the body chamber pointing in the direction of the current. A nautiloid shell, once in contact with sediment, is anchored down quickly and cannot be moved easily by bottom currents. Thus, most conchs of nektonic species or necroplanktonic conchs, once they sink to the bottom, are not likely to be transported any significant distances. This may not be true, however, for conchs having complex sutures (e.g., *Aturia*), which, because of greater internal rigidity provided by the folded septa, tend to have thinner shells than conchs with simple sutures (e.g., most Nautilidae). Shells of *Aturia* are almost always found without body chambers, for these are easily broken (7). It is possible that phragmocones without body chambers may be

transported more widely than shells with the body chambers intact.

Undamaged nautiloid shells, when embedded in sediment, represent empty spaces which may be filled with calcite deposited from solutions infiltrating the camerae during diagenesis. However, many shells are filled with sedimentary material, forming internal molds or steinkerns. Just how this happens is not always fully understood. GEISLER (2) has shown experimentally that only very small amounts of a watery clay suspension penetrate into the last few chambers of a *Nautilus* shell through the septal foramina, even when all connecting rings had been removed. According to the same author, however, considerable quantities of fine mud can enter camerae from the outside through very fine cracks in the outer shell.

BARRANDE has described many examples of nautiloid shells, especially orthocerids, which are partly filled with rock matrix, partly with diagenetically deposited calcite, and TEICHERT (1930) described the same condition in siphuncles of *Endoceras*. Internal sediment, of course, accumulates in the lower part of shells and siphuncles, and such specimens may, therefore, be used to establish the original position of strata in tectonically disturbed areas.

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## DESCRIPTIONS OF SUBCLASSES AND ORDERS

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## INTRODUCTORY DISCUSSION

By CURT TEICHERT and R. C. MOORE

The purpose of this short chapter is to provide a general comparison of the large groups of nautiloid cephalopods included in the three subclasses Nautiloidea, Endoceratoidea, and Actinoceratoidea, accompanied by systematic diagnoses which may serve to complement all following chapters except the final one concerned with the Bactritoidea.<sup>1</sup> This last-mentioned group is considered to stand apart because of inferred (but not yet firmly assessed) relationships which suggest linkages between it and Nautiloidea, Ammonoidea, and Coleoidea (Fig. 70).

### NAUTILOIDEA

Orders assigned to this subclass contain the preponderant majority of all described nautiloid genera. Among them are the

oldest forms known (Upper Cambrian ellesmerocerids), if we exclude the families Volborthellidae and Vologdinellidae (Lower and Middle Cambrian) which are placed by SHIMANSKIY (1962, p. 60) and BALASHOV (1962, p. 72) in an order named Volborthellida and included in the Nautiloidea. In our view, these families (and likewise the Lower Cambrian Salterellidae) are doubtful taxa which may not even belong to the class Cephalopoda. The only known living nautiloids are species of *Nautilus*, included in the order Nautilida and subclass Nautiloidea.

In forms of the conch and in many internal morphological features the Nautiloidea exhibit utmost variation. Size also ranges from a shell length of less than 2 cm. to giants 9 m. in length and 30 cm. or more in diameter at the apertural end of

<sup>1</sup> See footnote, p. K491.

the body chamber. Some orders (notably Ellesmerocerida, Orthocerida, Oncocerida) prevailingly are characterized by genera with straight or gently cyrtococonic long conchs, all with simple, straight or slightly curved sutures marking boundaries of numerous, generally short camerae of the phragmocone. Other groups (e.g., Discosorida, ascoceroid shell parts of Asco-cerida) commonly are breviconic. The conchs of Barrandeocerida are mostly cyrtococonic to gyroconic, but in some genera torticones or serpenticones appear. Well-coiled shells are confined to the Tarphycerida and Nautilida, the former with evolute or loosely coiled whorls tending to develop into a divergent terminal part of the phragmocone and body chamber; tightly coiled, highly involute shells are found only in some families of the Nautilida. Strongly curved and somewhat intricately bent sutures distinguish advanced nautilids (e.g., *Gonio-nautilus*, *Siberionautilus*, *Aturia*).

The siphuncles of genera included in orders of the Nautiloidea show wide variety in their relative size, thickness of walls, spacing of segments, nature of septal necks and connecting rings, presence or absence of internal deposits, and in position within the conch (commonly ventral or central but ranging to dorsal in some). The morphology of siphuncular structures has special importance in classification, and the same is true for cameral deposits, if present.

Features of the shell surface, whether smooth, sculptured, or varyingly ornamented may be utilized in differentiating nautiloid genera and sometimes families, especially in the orders Orthocerida and Nautilida, but external features of the conchs cannot be used to distinguish one order from another. The Discosorida and Tarphycerida rather commonly and the Oncocerida somewhat rarely are characterized by constricted or strongly sinuate apertures, whereas apertural margins in other orders generally are not deflected.

### Subclass NAUTOLOIDEA Agassiz, 1847

[*nom. transl.* TEICHERT, herein (*ex superorder* Nautiloidea SHIMANSKIY & ZHURAVLEVA, 1961, *nom. transl. ex suborder* Nautiloidea AGASSIZ, 1847)]

Small to large conchs, generally straight or moderately cyrtococonic in older, more primitive orders but loosely to tightly coiled and becoming strongly involute in younger, advanced forms. Longiconic and slightly cyrtococonic forms commonly with cameral deposits. Siphuncle variable in position within conch, slender to moderately large in diameter, with long to short segments, commonly orthochoanitic but in many cyrtchoanitic septal necks, thick or thin connecting rings, with or without siphuncular deposits (but not consisting of close-packed endocones, such as distinguish Endoceratoidea, or complex annular deposits, such as occur in Actinoceratoidea). *U.Cam.-Rec.*

### ENDOCERATOIDEA

The Endoceratoidea have medium-sized to very large conchs that are straight and longiconic in the majority of forms, but are breviconic or slightly endogastrically curved in others. The subclass is derived from the ellesmerocerids. Some early endoceratoid genera differ from contemporary genera of the Ellesmerocerida only in having endocones in the posterior part of the siphuncle, and then distinction between the two assemblages may be somewhat difficult.

The Endoceratoidea are distinguished from the Nautiloidea by the nature and relationships of the siphuncle, which in early ontogeny occupied a major part of the conch and in all growth stages housed substantial parts of the visceral mass, not just a siphuncular cord.

### Subclass ENDOCERATOIDEA Teichert, 1933

[*nom. transl.* TEICHERT, herein (*ex superorder* Endoceratoidea SHIMANSKIY & ZHURAVLEVA, 1961, *nom. transl. et correct. ex order* Endoceratoidea TEICHERT, 1933)]

Medium-sized to very large conchs, generally straight, longiconic, but including some breviconic and some slightly curved forms. Siphuncle generally medium-sized to large, ventral or subventral, rarely central, cylindrical. Septal necks ranging from nearly achoanitic to macrochoanitic, connecting rings simple or complex. Posterior part of siphuncle filled by generally close-packed endocones or with radially arranged longitudinal lamellae resembling actino-

siphonate deposits of oncocerids but more crowded. Cameral deposits absent. *L.Ord.-U.Ord.*, ?*M.Sil.*

## ACTINOCERATOIDEA

The subclass Actinoceratoidea, composed of the single order Actinocerida, includes nautiloids having medium-sized to large conchs which generally are straight and moderately slender; some are slightly curved. Body chambers tend to become contracted in the position of the aperture, reaching greatest diameter in the middle, but the apertures are uniformly entire and unmodified in shape by constrictions. The most diagnostic characters of the actinoceratoids are found in structures of the siphuncle, which are described and illustrated in the subsequent chapter devoted to this subclass and order. A systematic diagnosis of the assemblage is introduced here in company with those just given for Nautiloidea and Endoceratoidea.

## Subclass ACTINOCERATOIDEA Teichert, 1933

[*nom. transl.* TEICHERT, herein (*ex superorder* Actinoceratoidea SHIMANSKIY & ZHURAVLEVA, 1961, *nom. transl. et correct.* *ex order* Actinoceroida TEICHERT, 1933)]

Medium-sized to very large, generally straight conchs, but weakly cyrtconic in some genera. Siphuncle with cyrtchoanitic to recumbent septal necks, with segments inflated between tips of septal necks and preceding septal foramina, segments typically wider than long but in some forms longer than wide or subspherical; large siphuncles generally with broad contact of segments with ventral wall of shell, small siphuncles mostly subventral to subcentral; annular deposits within siphuncle, at adult growth stage filling all of it except central canal, radial canals, and perispatia. Episeptal and hyposeptal types of cameral deposits in many genera, circulus in some. *M.Ord.-U.Carb.*(*Penn.*).

# NAUTILOIDEA—ELLESMEROCERIDA

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## INTRODUCTION

The primitive Ellesmerocerida are considered to be inadequately known even for the purposes of basic taxonomy. Their small size and imperfect preservation, together with an apparent lack of stabilized evolutionary trends, result in many uncertainties. For example, even the genus *Ellesmeroceras* is unsatisfactory as a representative form because of poor type material.

A hundred years ago there were a few descriptions of this ancestral group, primarily by BILLINGS (6a) in 1865. WHITFIELD (207a) then made a study of the Cassin fauna of Lake Champlain. HOLM's (92a) analysis of *Bathmoceras* is a classic example of morphologic detail. RUEDEMANN's (150) monograph on cephalopods of the Champlain Basin was the first comprehensive treatment of nautiloid faunas to include numerous ellesmerocerids.

A second period of activity involving this fossil group consisted of diversified nautiloid studies by FOERSTE, mostly during the 1920's. As early as 1924, FOERSTE (54) became associated with ULRICH in an investigation of North American Lower Ordovician cephalopod faunas; portions of this comprehensive treatment were published in summary form shortly before FOERSTE's death (201). The entire collections, then submitted to MILLER for final analysis in 1939, were described by ULRICH, FOERSTE, MILLER, *et al.* (1942-44) (202-204). Numerically and geographically the materials assembled under ULRICH's direction were far greater than a combination of all others known. Nevertheless, a relatively small amount of data on shell morphology was revealed, and phylogenetic relationships were not apparent.

Within the past decade there have been important contributions by FLOWER (41,

45), CECIONI (7a), TEICHERT & GLENISTER (193), and BALASHOV (4b). These papers have provided a view of the ellesmerocerid faunas in world-wide fashion. Also, a considerable amount of new, detailed morphologic information has been presented, but the over-all view and uncertain nature of classification have not been altered greatly.

## MORPHOLOGY

Variability in both the gross form and detailed structures of the ellesmerocerids is so extreme that no single morphological peculiarity can be recognized as characterizing the entire group. Ellesmerocerids are of small or medium size, and upper Canadian representatives are comparable in this respect with the contemporaneous endocerids. Longiconic orthocones are abundant, but cyrtocones predominate. Both endogastric and exogastric conchs are common; many of them developed breviconic form, moderate curvature, and a modified mature aperture. Smooth shells are prevalent, but the Protocycloceratidae are characterized by strong annulations; a few weakly annulate genera are included in some other families.

Septa are generally closely spaced, and in plectronoceratids as many as 35 may occur in a distance equal to the corresponding dorsoventral conch diameter. The opposite extreme is encountered in some bathoceratids, where the cameral interval approximates the diameter of the conch. Almost invariably the curvature of the septal surface is uniform throughout, and in most specimens the septa are directly transverse to the long axis of the conch. Consequently, the sutures are generally straight if the conch is circular in section. Conversely, lateral lobes are present on compressed forms, whereas dorsal and ventral lobes may appear on depressed phragmocones. Strong septal flexures produce a relatively pronounced siphonal saddle or lobe in a few genera (e.g., *Bathmoceras*, *Ventroloboceras*), but imperfect preservation may result in confusion of these features with the unrelated ectosiphuncular suture.

The siphuncle of practically all ellesmerocerids is marginal or submarginal. Exceptions include the Shideleroceratidae, in which the siphuncle is central or subcentral

in position. Inclusion of this family in the Ellesmerocerida is of doubtful validity. Size of the ellesmerocerid siphuncle ranges from one-half the corresponding conch diameter (e.g., *Cochlioceras*, *Cumberloceras*, *Pachendoceras*) to one-fifteenth that measurement (e.g., *Copicerias*). Forms with the siphuncle occupying one-third to one-tenth the conch diameter predominate. An irregular series of diaphragms is commonly present in proportionally large siphuncles (e.g., *Clarkoceras*, *Eothinoceras*).

Detailed information on the structure of the ectosiphuncle is not available for most of the many taxa known only from silicified materials. Originally most of these silicified specimens were considered to be holochaanitic, but ellipochaanitic structure is now known to predominate. Short orthochaanitic septal necks are characteristic, but hemi-choanitic necks are common. More rarely the necks may be achoanitic (e.g., *Cyrtocerina*), loxochaanitic (e.g., *Desioceras*, *Loxochaanella*), cyrtochaanitic (e.g., *Plectronoceras*), subholochaanitic (e.g., *Lebetoceras*, *Multicameroceras*, *Palaeoceras*) or macrochoanitic (e.g., *Ventroloboceras*). Connecting rings are thick and structurally complex in most adequately known taxa (e.g., *Cyclostomiceras*, *Loxochaanella*, *Paracyclostomiceras*), but the protocycloceratids generally possess thin homogeneous rings. Thickening of the connecting rings reaches an extreme in the bathoceratids and cyrtocerinids, in which the rings may occupy up to half the total volume of the siphuncle.

## CLASSIFICATION AND EVOLUTION

Present knowledge of ellesmerocerid morphology is such that the validity of many taxa is not considered established. Some dozen of the included genera are monotypic, the respective type-species being based on a single specimen, and approximately half of the proposed taxa are known from such poorly preserved materials that specific comparisons and generic assignments are frustratingly difficult. A particular problem is encountered in comparing the abundant silicified materials preserved as external and internal molds with those recovered from limestone. In general,

gross form is well displayed by silicified specimens, whereas details of internal morphology, such as the structure of the ectosiphuncle, are not preserved. In contrast, most calcareous materials exhibit such details as the nature of the septal necks and connecting rings but they commonly fail to yield exact information on the form of the suture and the gross morphology. Largely as a result of these difficulties, it is believed that many of the generic and familial groupings presented to date reflect superficial similarities rather than close biologic affinities.

Because of the rudimentary state of knowledge concerning many ellesmerocerid taxa, we have refrained from listing established genera as synonyms unless obligated to do so by preponderant data. However, it is probable that many generic names accepted in the present study will be suppressed when more nearly complete information becomes available.

Despite the inadequacy of knowledge of ellesmerocerid morphology, taxonomy, and phylogeny, this group is of singular significance in nautiloid studies because it represents the rootstock from which practically all other nautiloid orders evolved directly. The earliest Ordovician represents a period of explosive diversification for the ellesmerocerids, and by Middle Ordovician times this evolution had produced the ancestral types for other relatively stable nautiloid orders.

The archaic Plectronoceratidae represent a poorly known but apparently homogeneous group which is characterized by small size and moderate expansion of the siphuncular segments. Ontogenetic progression from orthochoanitic or cyrtchoanitic to subholochoanitic has been reported for most plectronoceratid genera (FLOWER, 41). However, documentation of this assumed progression is inadequate for the Asian representatives (e.g., *Multicameroceras*, *Ruthenoceras*, *Sinoeremoceras*, *Wanwanoceras*). In addition, the two small fragments which serve as types for the single American genus (*Palaeoceras*) may not be congeneric.

The expanded siphuncular segments and thick connecting rings of the ancestral Discosorida in the Middle Ordovician suggest

relationship with the appreciably older Plectronoceratidae (FLOWER & TEICHERT, 50). However, further data are required before this possible ancestry can be considered substantiated.

Both morphologic and stratigraphic evidence indicate plectronoceratid progenitors for the Ellesmeroceratidae. This latter family includes a diverse group of smooth orthoconic longicones and compressed endogastric cyrtconic brevicones characterized by marginal siphuncle, ellipchoanitic septal necks, and thick-layered connecting rings. Future studies of the ectosiphuncles of better-preserved materials will probably demonstrate that the genera currently included in the Ellesmeroceratidae do not constitute a biologic entity.

Many primitive representatives of the order Endocerida closely resemble the contemporaneous ellesmeroceratids except for the presence of endocones. For example, the endocerid family Thylacoceratidae was originally assigned to the Ellesmerocerida by virtue of possession of a proportionally narrow siphuncle, thick, layered connecting rings, and the apparent absence of endocones (TEICHERT & GLENISTER, 193). Subsequent discovery of endocones in a small proportion of the representatives of the type-species of *Thylacoceras* now necessitates inclusion of this genus in the Endocerida. Available well-preserved representatives of other genera previously included in the Thylacoceratidae do not contain endocones and must therefore remain in the Ellesmerocerida, where the majority are currently included in the Ellesmeroceratidae. Uncertainty in ordinal assignment of some other upper Canadian taxa is also encountered where the structure of the siphuncle is unknown. The probability of polyphyletic origin of the Endocerida is indicated by appearance of endocones in forms with short septal necks, such as some Proterocameroceratidae. These ellipchoanitic endocerids may well have evolved from the ellesmerocerid family Baltoceratidae. It is probable that endocones appeared independently, by modification of diaphragms, in several ellesmerocerid stocks, when the siphuncle achieved a critical size.

The ellesmerocerid family Bassleroceratidae comprises longiconic cyrtcones with

marginal siphuncle and orthochoanitic septal necks. Genera included in this rather homogeneous family resemble some ellesmeroceratids, but differ in possession of slight to moderate exogastric curvature in contrast to the endogastric form of cyrtoconic ellesmeroceratids. Primitive representatives of the Tarphycerida so closely resemble the contemporaneous upper Canadian bassleroceratids (except for their stronger curvature) that derivation of this order from the ellesmerocerids can be considered as established. In addition, some Middle Ordovician Oncocerida belonging in the ancestral family Graciloceratidae are strikingly similar to upper Canadian bassleroceratids, from which they were derived. The graciloceratids may be distinguished from the ancestral ellesmerocerids by the possession of consistently thin and homogeneous connecting rings.

Representatives of the ellesmerocerid family Protocycloceratidae are distinguished mainly by possession of an annulate conch. Annulations probably should not be credited with major taxonomic significance, but most of the genera currently referred to the protocycloceratids are also alike in being orthoconic or only slightly cyrtoconic and in the possession of short septal necks with thin homogeneous connecting rings.

The family Baltoceratidae includes longiconic orthocones with orthochoanitic septal necks. They differ from the ancestral ellesmeroceratids in the consistent possession of a proportionally larger siphuncle and thin homogeneous connecting rings. Derivation of the ancestral Orthocerida was probably directly from the baltoceratids through Lower Ordovician representatives of the orthocerid family Troedssonellidae. As indicated elsewhere, the endocerid family Proterocameroceratidae may have evolved from the baltoceratids. Ancestry of Middle Ordovician Ascocerida is obscure but may have been from the baltoceratids or from some intermediate orthocerid or oncocerid stock.

The early Middle Ordovician genus *Eobactrites* is included within the Bactritida in the *Treatise*, but it could be referred logically to the ellesmerocerid family Baltoceratidae. The narrow siphuncular lobe is similar to those encountered in some nau-

tiloids which possess a marginal siphuncle (e.g., *Thylacoceras* of the Endocerida, and *Catoraphiceras* of the Ellesmerocerida). All other details of morphology can be duplicated in the contemporaneous Middle Ordovician baltoceratids. Inclusion of *Eobactrites* in the Bactritida depends heavily on the questionable occurrence of typical Bactritidae in the Silurian of Morocco (TERMIER & TERMIER, 1950, pl. 136, fig. 31; pl. 137, figs. 27-29), as these forms bridge the interval to the first undoubted occurrence of bactritids in the Lower Devonian.

The Bathmoceratidae constitute a group of ellesmerocerids which is characterized by spectacular thickening of the connecting rings. In other respects they resemble the Ellesmeroceratidae from which they evolved. Representatives of the Polydesmidae, the ancestral Actinocerida, resemble the bathmoceratids in the gross features of the siphuncle. Derivation of the siphuncular deposits of *Polydesmia* by differentiation within the thick connecting rings of *Bathmoceras* involves radical changes, but this suggested ancestry for the Actinocerida seemed plausible to FLOWER (50). Such an interpretation has been rejected by TEICHERT (this volume, p. K202). Relationships of the Middle and Upper Ordovician Cyrtocerinidae are uncertain, but the thick connecting rings resemble those of the Bathmoceratidae.

## GEOGRAPHIC AND STRATIGRAPHIC DISTRIBUTION

The oldest undoubted cephalopods are plectronoceratids from the late Cambrian Yingtzu Series in Asia. These small nautiloids occur at several localities, in some cases in moderate abundance as rough natural sections on weathered limestone surfaces. The strata are dated with reference to abundant associated fossils, particularly trilobites. In addition to the questionable *Shelbyoceras* and other doubtful forms, only two specimens of Cambrian cephalopods are known from America; the types of *Palaeoceras mutabile* (FLOWER, 41) are two half-inch fragments of straight shells from the Wilberns Formation (Trempealeauan) of central Texas. Sufficient detail is preserved

to give the nature of shell morphology in these ancestral forms.

Strata of earliest Ordovician age (lower Canadian) have provided nautiloids in abundance and moderate diversity, but well-preserved cephalopods in these rocks are relatively rare. Through diligent search, the characteristic Ellesmeroceratidae have been secured widely from cherts of the Gasconadian Stage throughout North America (ULRICH, *et al.*, 202-204). Many of these specimens are weathered fragmentary internal molds, unsatisfactory for detailed study; others are remarkably complete and well preserved. Almost the entire generic make-up in the lower Canadian consists of ellesmeroceratids. About a dozen genera which are found in the Gasconade Formation of the Ozarks also occur in the Oneota Dolomite of the Upper Mississippi Valley, and Chepultepec Dolomite of the southern Appalachians. An important nautiloid fauna believed to be of comparable age has been secured from limestone boulders in the upper Canadian Levis Shale near Quebec City. A few species of early Canadian age have also been secured from the Hastings Creek Limestone at the northern end of Lake Champlain. The ellesmerocerids from these dark organic limestones in southeastern Canada preserve original shell and other details.

Early lower Canadian plectonoceratids and ellesmeroceratids have been described by KOBAYASHI (101a) and others from the Wanwankou Limestone (Tremadocian) of China. In addition, a variety of ellesmeroceratids has been secured by BALASHOV (4a) from central Siberia.

Nautiloid cephalopods show a pronounced phylogenetic step following the Gasconadian of the lower Canadian. However, the grounds for distinguishing middle Canadian from upper Canadian strata on the basis of nautiloids are so obscure that these two divisions are grouped together as upper Canadian in the present study. The Gasconade was considered as "upper Ozarkian" by ULRICH (ULRICH *et al.*, 202-204), whereas he correlated the overlying Roubidoux Formation of the Ozark region and the Longview Dolomite of the southern Appalachians with the "middle Canadian." Only a few nondiagnostic ellesmerocerids occur in these two formations, but the overlying

strata contain a variety of forms, including the characteristic coiled cephalopods of the upper Canadian.

The Ellesmerocerida had assumed secondary importance as a nautiloid group by late Canadian time. However, representatives of this age are more diverse than earlier faunas and they are also based on much better-preserved materials. The bassleroceratids (exogastric cyrtocoones) and the protocycloceratids (annulate longicoones) are characteristic families.

A few ellesmerocerids are known from the type area of the Cassin Limestone (Basscom Formation) of Lake Champlain; this fauna includes some of the best-preserved upper Canadian cephalopods known and has provided much of the detailed information on the morphology of this order. Nearby Valcour Island, New York, contains a comparable fauna, and others have been secured from the St. Armand Limestone of Phillipsburg, Quebec, about 50 miles to the north of Ft. Cassin, Vermont. Well-preserved and abundant upper Canadian ellesmerocerids have also been found in Western Australia (TEICHERT & GLENISTER, 193) and in the Siberian Platform (BALASHOV, 4a). Lower Ordovician nautiloids of the Baltic Region are less well known than those abundantly represented in Middle Ordovician strata.

The distinctive family Bathmoceratidae appeared in the late Canadian and ranged through at least a portion of the Middle Ordovician. Representatives of the peculiar type-genus were originally described from the Prague area by BARRANDE (1856). The form was then recognized in the Baltic, Portugal, and Australia; it has been identified also in Argentina and China. None of the North American species is believed to be congeneric. *Eothinoceras*, a related genus, has been found in eastern New York, northwestern Australia, and central Siberia. In addition, cyrtocerinids of the North American Middle and Upper Ordovician show some affinities with the bathmoceratids.

## SYSTEMATIC DESCRIPTIONS

### Subclass NAUTILOIDEA

#### Agassiz, 1847

Diagnosis of subclass given in "Introductory Discussion" (p. K128). *U.Cam.-Rec.*

## Order ELLESMEROCERIDA

### Flower in Flower & Kummel, 1950

[*nom. correct.* FURNISH & GLENISTER, herein (*pro* Ellesmeroceratida FLOWER in FLOWER & KUMMEL, 1950, p. 606); mention of Ellesmerocerida by FURNISH, GLENISTER & HANSMAN, 1962 (p. 1342), is disregarded]

Ancestral nautiloid stock exhibiting wide morphologic variation. Primitively minute, closely septate cyrtocoines with marginal siphuncle bearing short septal necks. In general, order characterized by moderate endogastric curvature, and marginal siphuncle with irregular diaphragms, elliphoanitic septal necks, and thick complex connecting rings. Variations include annulate orthoconic longicoines, exogastric breviconic cyrtocoines, forms with thin connecting rings, and those with subcentral siphuncle. [All Cambrian and lower Canadian nautiloids as well as many upper Canadian representatives are included in this order. Younger forms rare and diverse.] *U. Cam.-U.Ord.*, ?*U.Sil.*

## Family ELLESMEROCERATIDAE

### Kobayashi, 1934

[*nom. correct.* FLOWER in FLOWER & KUMMEL, 1950, p. 606 (*pro* Ellesmeroceratidae KOBAYASHI, 1934, p. 376)] [*incl.* Cyclostomiceratidae FOERSTE, 1925, p. 14; Orthoceratidae (*partim*), Stemonoceratidae and Robsonoceratidae ULRICH, FOERSTE, MILLER & UNKLESBAY, 1944, p. 60, 29, and 73]

Orthoconic longicoines and compressed endogastric breviconic cyrtocoines characterized by marginal siphuncle, elliphoanitic septal necks and thick, layered connecting rings; irregular diaphragms common. *L.Ord.*, ?*M.Ord.*

**Ellesmeroceras** FOERSTE, 1921, p. 265 [*\*E. scheii*; OD] [= *Ellesmeroceras* FOERSTE, 1924 *et seq.* (*nom. van.*); *Ellesmeroceras* FLOWER, 1947, p. 162 (*nom. null.*); *Metaellesmeroceras* FLOWER, 1956, p. 78; *Metallesmeroceras* FLOWER, 1956, p. 78 (*nom. null.*)]. Orthoconic, gradually expanded, generally compressed; sutures form shallow lateral lobe; siphuncle marginal, about 0.2 of conch diameter; septal necks orthochoanitic to loxochaoanitic or hemichoanitic, connecting rings thick. [Type-species poorly known.] *L.Ord.*(*L.Canad.*, ?*U.Canad.*), N.Am.(widespread)-China(Manchuria)-USSR(Sib.)-?Australia(Queensl.).—FIG. 71, 3a. *E. bridgei* FLOWER, *L.Ord.*(*L.Canad.*), Alaska (Seward Penin.); enlarged sec. of ectosiphuncle (after 220a).—FIG. 71, 3b,c. *\*E. scheii*, *L.Ord.*, Can.(Ellesmere Is.), holotype, ventral and lat. views,  $\times 1.5$  (204).

**Albertoceras** ULRICH & FOERSTE, 1936, p. 261 [*\*A. walcotti*; OD]. Gradually expanded orthocoines with strongly compressed section and contracted

mature aperture; siphuncle marginal, cylindrical, about  $\frac{1}{8}$  of conch diameter; septal necks short, orthochoanitic. [Possibly distinguishable from *Eremoceras* by slight contraction of mature aperture.] *L.Ord.*(*L.Canad.*, ?*U.Canad.*), N.Am.(widespread)-USSR(Sib.).—FIG. 71, 1a,b. *A. gracillimum* ULRICH, FOERSTE, MILLER & UNKLESBAY, *L.Ord.*(*L.Canad.*), Can.(Alba.); ventral and lat. views,  $\times 3$  (204).—FIG. 71, 1c,d. *\*A. walcotti*, *L.Ord.*(*L.Canad.*), Can.(Alba.); holotype, dorsal and lat. views,  $\times 3$  (204).

**Bridgeoceras** ULRICH, FOERSTE & MILLER, 1943, p. 59 [*\*B. subannulatum*; OD]. Slightly compressed, rapidly expanded orthocoines; entire conch characterized by low, rounded annulations; sutures directly transverse, almost straight; siphuncle marginal, about 0.3 of conch diameter. [Based on single specimen.] *L.Ord.*, N.Am.(Can.).—FIG. 71, 2. *\*B. subannulatum*, Que.; 2a,b, holotype, ventral and lat. views,  $\times 1.5$  (202).

**Buehleroceras** ULRICH, FOERSTE & MILLER, 1943, p. 60 [*\*B. compressum*; OD]. Compressed straight brevicones; mature aperture strongly contracted, with subparallel ventrolateral margins and subcircular dorsal outline; growth lines forming rounded lateral salient; siphuncle tubular, septal necks hemichoanitic. *L.Ord.*(*L.Canad.*), USA (widespread).—FIG. 72, 3a-c. *\*B. compressum*, Wis.; 3a,b, holotype, lat. and dorsal views; 3c, ventral view, all  $\times 1.5$  (202).—FIG. 72, 3d,e. *B. luthi* ULRICH, FOERSTE & MILLER, Iowa; lat. and ventral views,  $\times 1.5$  (202).

**Burenoceras** ULRICH & FOERSTE, 1931, p. 208 [*\*B. pumilum*; OD]. Strongly curved, very rapidly expanded and characterized by prominent ventral flare of mature aperture. *L.Ord.*(*L.Canad.*), USA (widespread) - ?China(Manchuria).—FIG. 72, 2a,b. *B. expandum* ULRICH & FOERSTE, USA(Mo.); lat. and dorsal views,  $\times 1.5$  (202).—FIG. 72, 2c. *B. compressum* ULRICH, FOERSTE & MILLER, USA(Mo.); lat. view,  $\times 1.5$  (202).—FIG. 72, 2d,e. *\*B. pumilum*; USA(Mo.); holotype, dorsal and lat. views,  $\times 1.5$  (202).

**Caseoceras** ULRICH, FOERSTE & MILLER, 1943, p. 74 [*\*C. contractum*; OD]. Slightly curved, compressed brevicones; anterior half of body chamber gradually expanded; sutures oblique, almost straight; externally similar to *Clarkoceras*, but structure of siphuncle unknown. *L.Ord.*(*L.Canad.*), N.Am.(widespread).—FIG. 72, 1a,b. *\*C. contractum*, USA(Mich.); holotype, lat. and ventral views,  $\times 1$  (202).—FIG. 73, 1a,b. *C. nitidum* ULRICH, FOERSTE & MILLER, USA(Mich.); ventral and lat. views,  $\times 1$  (202).

**Chepuloceras** UNKLESBAY & YOUNG, 1956, p. 490 [*\*C. inelegans*; OD]. Strongly depressed longicoines with slight exogastric curvature; sutures forming shallow lateral lobe; siphuncle marginal, about 0.2 of lateral conch diameter. [Single representative possibly distorted.] *L.Ord.*(*L.Canad.*), USA(Va.).



**Clarkoceras** RUEDEMANN, 1905, p. 337 [*\*Piloceras newton-winchelli* CLARKE, 1897, p. 767; OD] [*non Clarkeoceras* WEDEKIND, 1918, p. 108] [= *Clarkeoceras* FLOWER, 1941, p. 11 (*nom. van.*)]. Compressed brevicones with moderate en-

dogastric curvature; sutures essentially straight, obliquity accentuated and pronounced in later ontogenetic stages; siphuncle about 0.3 of dorso-ventral conch diameter, submarginal to marginal; septal necks hemichoanitic, connecting rings thick;

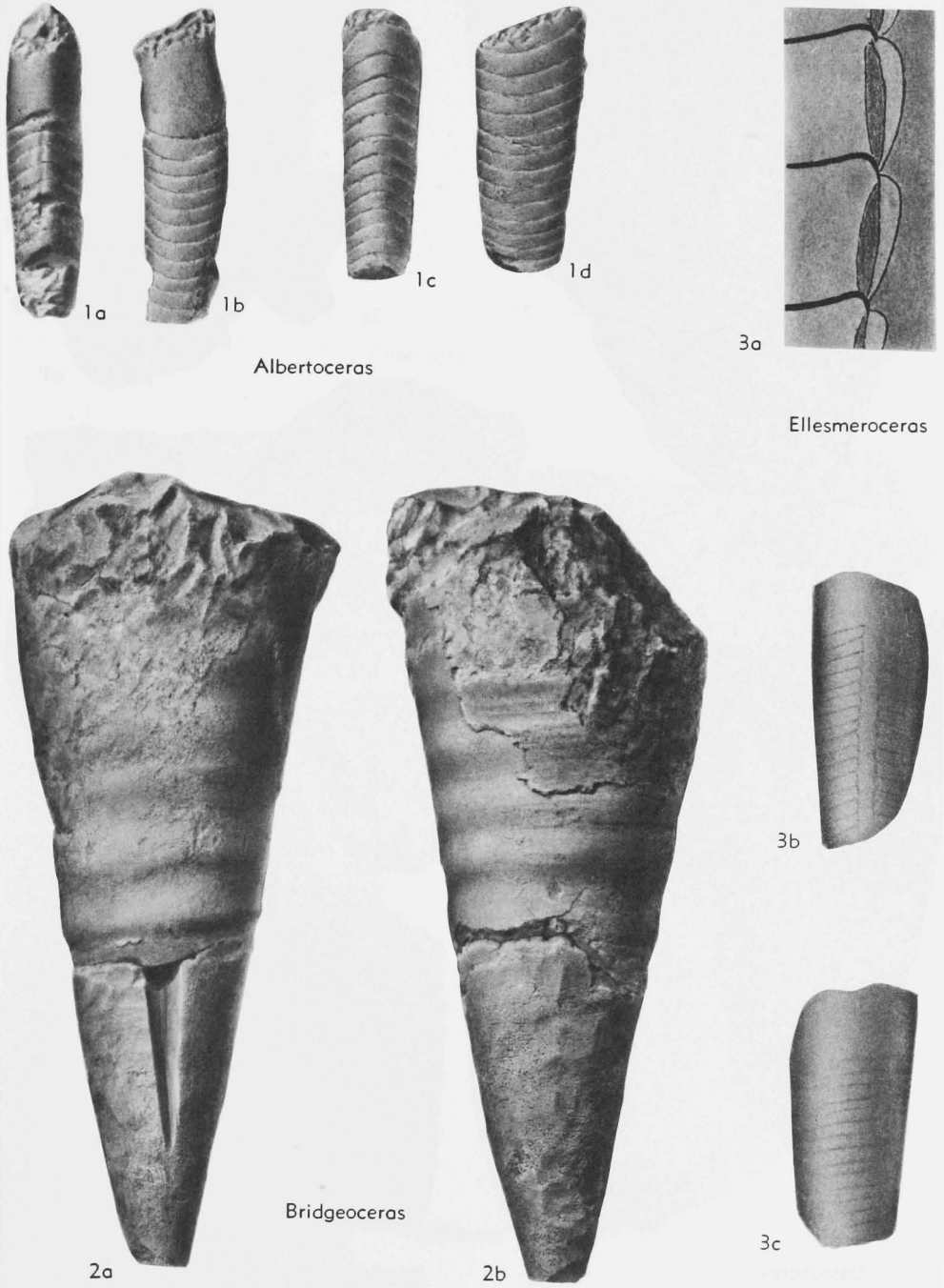


FIG. 71. Ellesmeroceratidae (p. K134).

diaphragms attenuate. *L.Ord.*(*L.Canad.*), N.Am. (widespread) - ?China(Manchuria) - USSR(Sib.).  
——FIG. 74,1a-f. \**C. newtonwinchelli* (CLARKE),

USA(Minn.); 1a,b, holotype, lat. and ventral views,  $\times 1.5$ ; 1c, holotype, sec.,  $\times 2.5$ ; 1d-f, dorsal, ventral and lat. views,  $\times 1.5$  (202).——FIG.

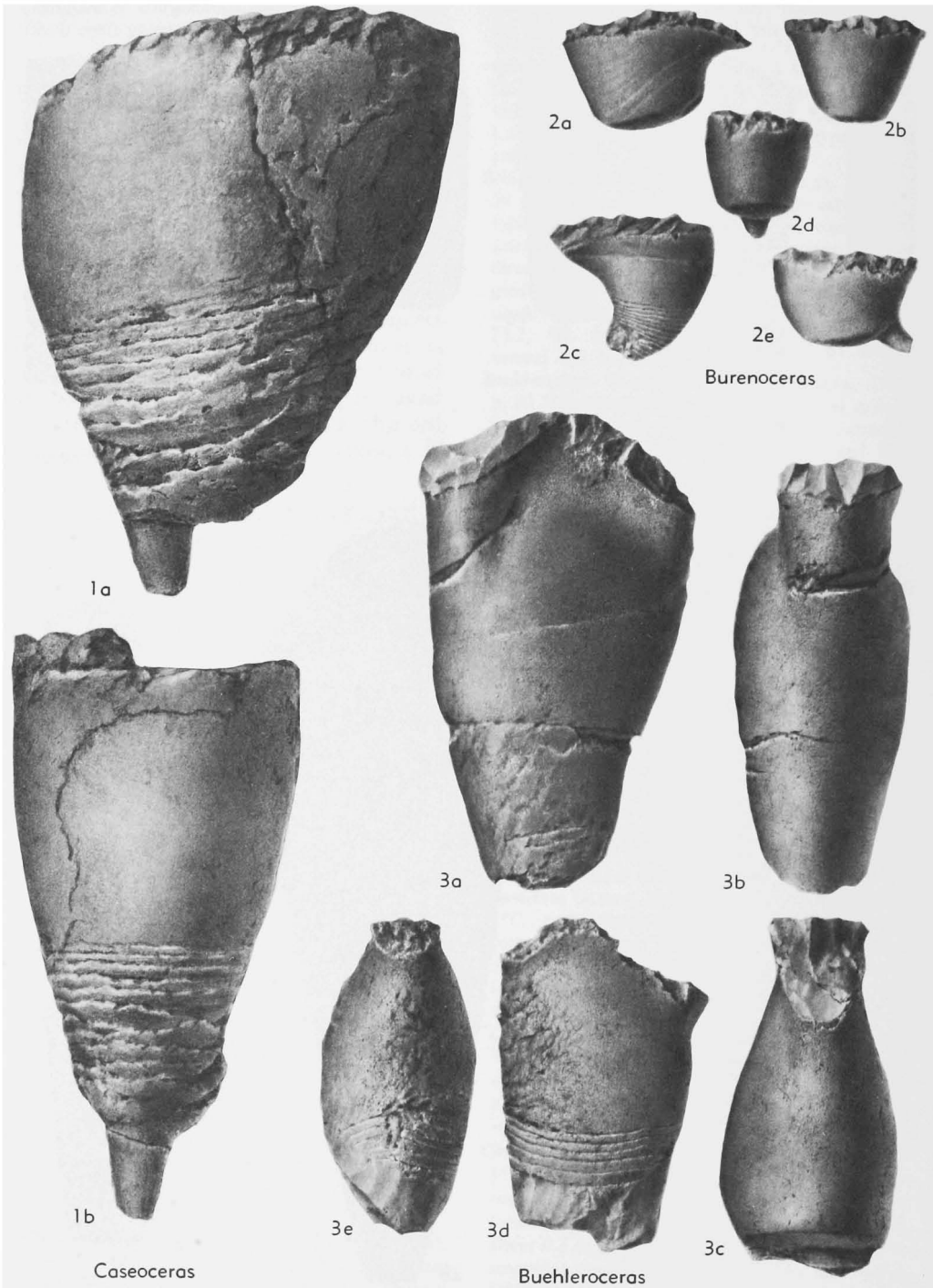


FIG. 72. Ellesmeroceratidae (p. K134).

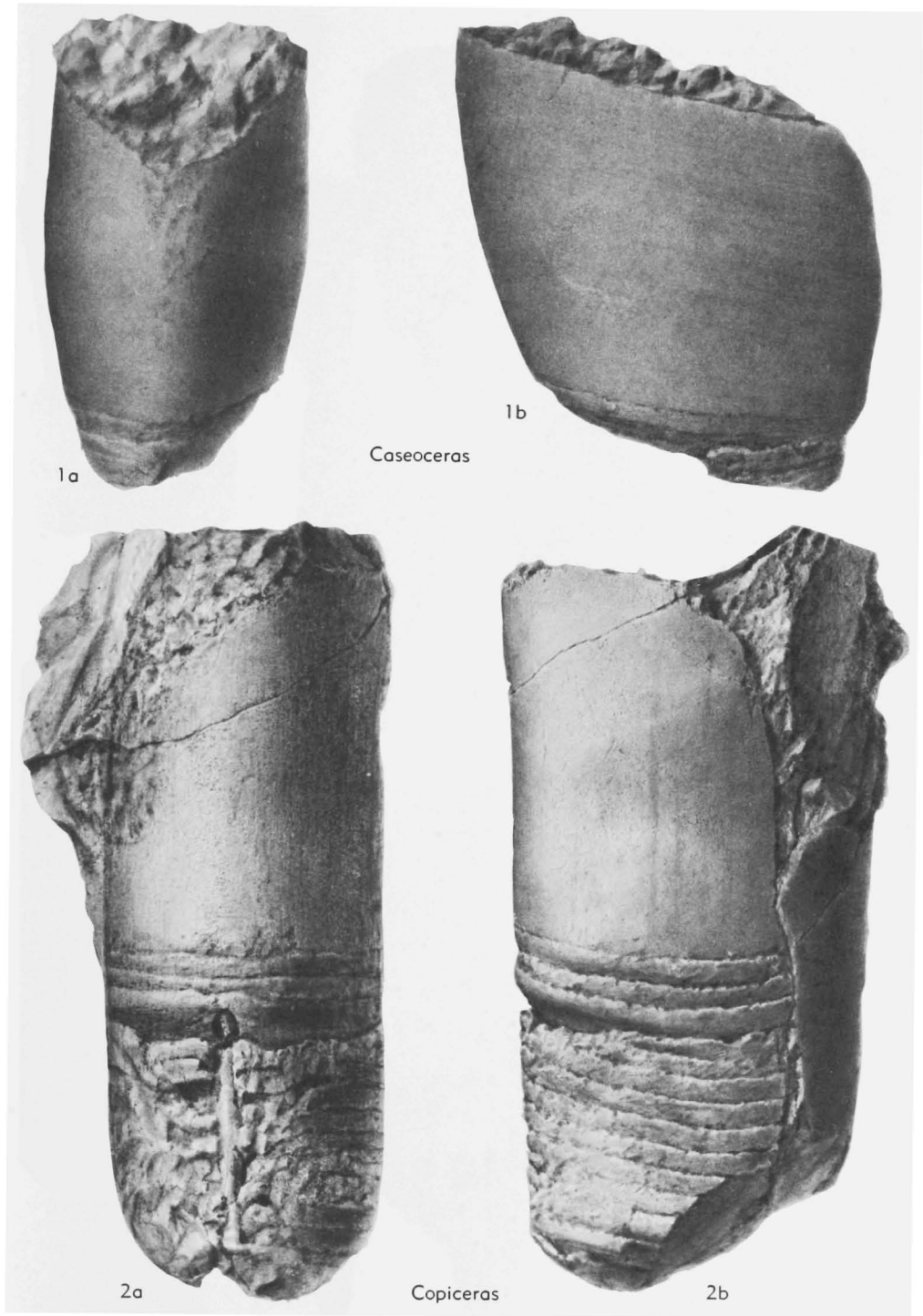


FIG. 73. Ellesmeroceratidae (p. K134, K140).

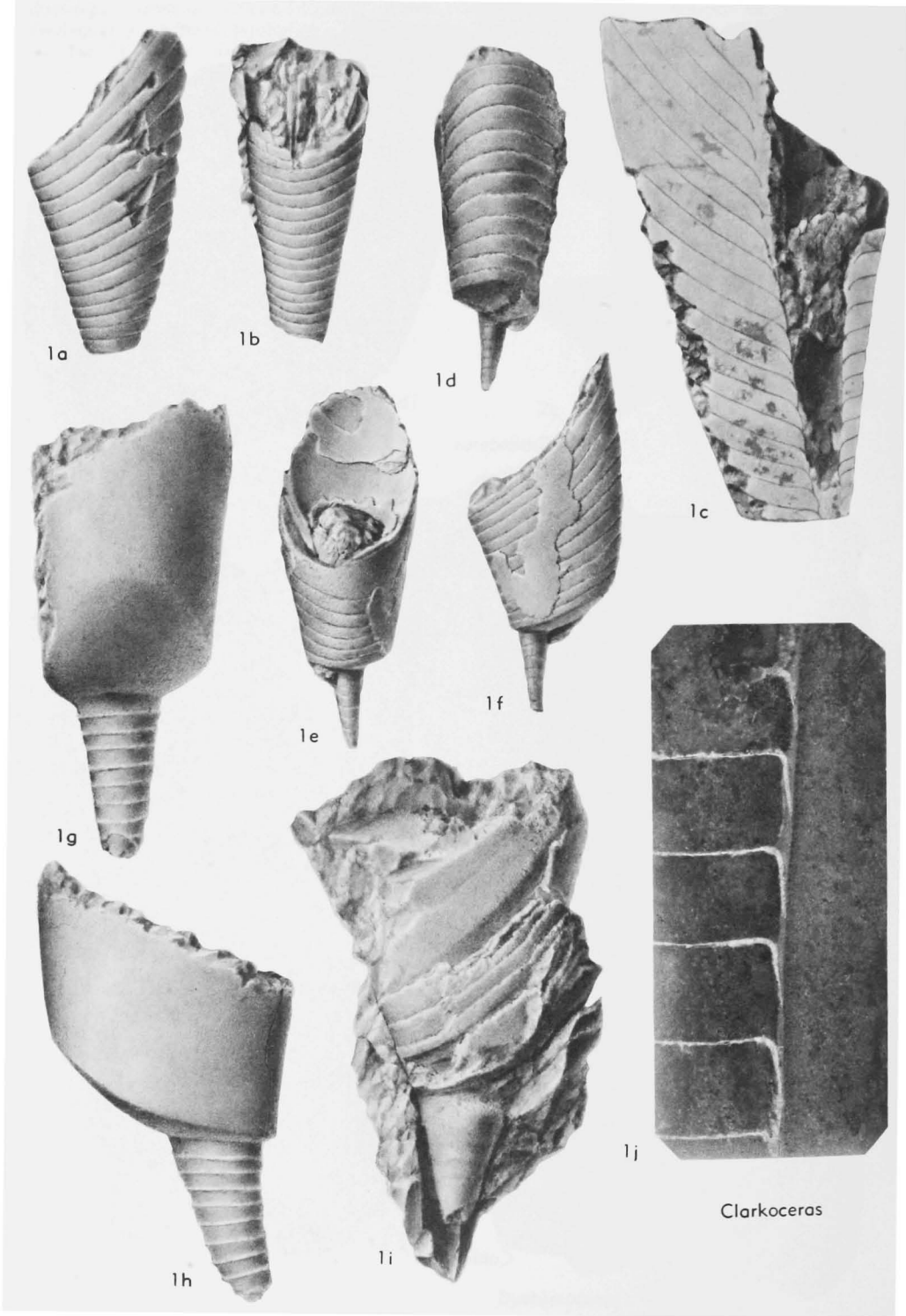


FIG. 74. Ellesmeroceratidae (p. K135-K136, K140).

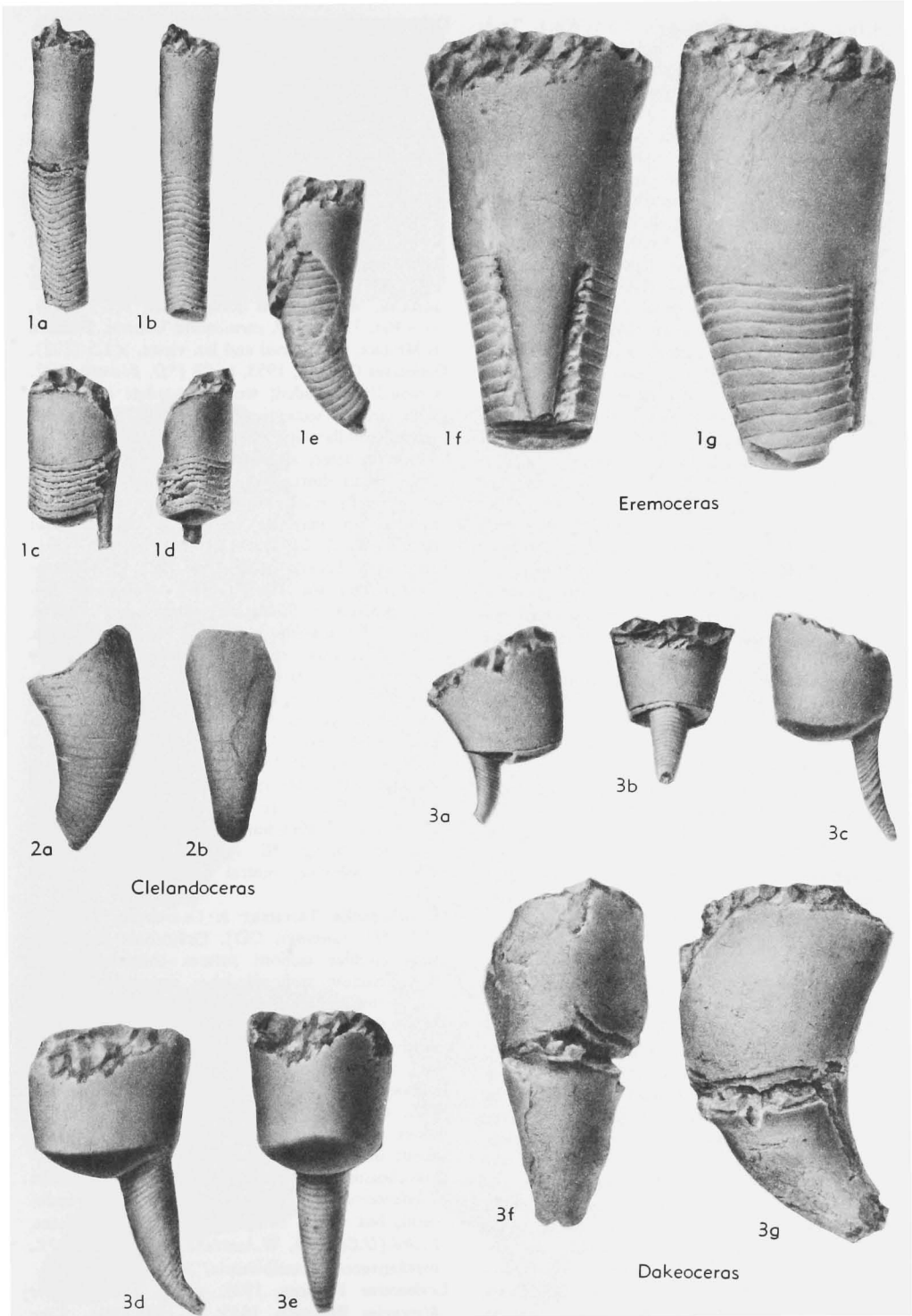


FIG. 75. Ellesmeroceratidae (p. K140).

- 74, *lg-i*. *C. luthi* (CALVIN), USA (Wis.), *lg,h*, dorsal and lat. views,  $\times 1.5$ ; USA (Iowa), *li*, lat. view, with attenuate diaphragm,  $\times 1.5$  (202). —FIG. 74, *lj*. *C. lawrencense* ULRICH, FOERSTE & MILLER, Can. (Que), sec. of ectosiphuncle,  $\times 5$  (202). [Because JOHN M. CLARKE was State Paleontologist of New York in 1905 when RUEDEMANN, as Assistant State Paleontologist, published the generic name *Clarkoceras*, it would be natural to suppose that the new generic name was dedicated to CLARKE. Examination of RUEDEMANN's paper shows no evidence at all that this assumption is correct and the name, therefore, cannot be construed to represent a *lapsus* correctable as provided by the Code (Art. 32,a,ii): ED.]
- Cleandoceras** ULRICH, FOERSTE, MILLER & UNKLESBAY, 1944, p. 134 [*\*C. elongatum*; OD]. Rapidly expanded, compressed cyrtocoines; sutures form lateral lobe; siphuncle small, cylindrical. *L.Ord.* (*L. Canad.* - *U. Canad.*), USA (Ark.-Md.-Va.). —FIG. 75, 2. *C. breve* ULRICH, FOERSTE, MILLER & UNKLESBAY, *L.Ord.* (*U. Canad.*), Ark.; 2*a,b*, lat. and dorsal views,  $\times 3$  (204).
- Conocerina** ULRICH & FOERSTE, 1936, p. 268 [*\*C. brevis*; OD] [= *Concerina* ULRICH & FOERSTE, 1936, p. 269 (*nom. null.*)]. Like *Burenoceras*, but less strongly curved and lacking mature apertural flare. *L.Ord.* (*L. Canad.*), USA (widespread). —FIG. 76, 3. *C. beani* ULRICH, FOERSTE & MILLER, USA (Wis.); lat. view,  $\times 2$  (202).
- Copicer** ULRICH, FOERSTE, MILLER & UNKLESBAY, 1944, p. 65 [*\*C. erectum*; OD] [= *Cophicer* ULRICH, FOERSTE, MILLER & UNKLESBAY, 1944, p. 221 (*nom. null.*)]. Gradually expanded compressed orthocoines; sutures directly transverse, nearly straight; siphuncle about 1/15 of conch diameter. *L.Ord.* (*U. Canad.*), USA (Ark.). —FIG. 73, 2. *\*C. erectum*; 2*a,b*, holotype, ventral and lat. views,  $\times 1.5$  (204).
- Cumberloceras** ULRICH, FOERSTE & MILLER, 1943, p. 106 [*\*C. buttsi*; OD]. Strongly curved, compressed, annulate, endogastric cyrtocoines; siphuncle approximating 0.5 of conch height. *L.Ord.* (*U. Canad.*), USA (widespread). —FIG. 76, 2. *\*C. buttsi*, Tenn.; 2*a,b*, holotype, lat. and dorsal views,  $\times 1.5$  (202).
- Cyclostomiceras** HYATT in ZITTEL, 1900, p. 530 [*\*Gomphoceras Cassinense* WHITFIELD, 1886, p. 322; OD] [= *Clostomiceras* STAUFFER, 1915, p. 142 (*nom. null.*)]; *Amphoroceras* ULRICH & FOERSTE, 1936, p. 263]. Breviconic orthocoines with circular or elliptical cross section; anterior half of mature body chamber conspicuously constricted; sutures and growth lines straight and directly transverse; siphuncle small, essentially tubular, ventral but not marginal; septal necks orthochoanitic, connecting rings thick and layered. *L.Ord.* (*U. Canad.*), N.Am. (widespread). —FIG. 76, 1. *\*C. cassinense* (WHITFIELD), USA (Vt.); 1*a*, lat. sec. of siphuncle,  $\times 10$ ; 1*b,c*, syntype, ventral and lat. views,  $\times 1$ ; 1*d*, lat. view,  $\times 1$  (202).
- Dakeoceras** ULRICH & FOERSTE, 1931, p. 209 [*\*D. normale*; SD ULRICH & FOERSTE, 1936, p. 272 (*non D. retrorsum* ULRICH & FOERSTE, 1931, p. 209, *nom. nud.*)]. Moderately rapidly expanded, compressed endogastric cyrtocoines; growth lines straight and transverse; sutures forming shallow lateral lobe; siphuncle close to venter, about 0.25 of conch diameter. *L.Ord.* (*L. Canad.*), USA (widespread). —FIG. 75, 3*a,b*. *D. retrorsum* ULRICH, FOERSTE & MILLER, Mo.; lat. and ventral views,  $\times 1.5$  (202). —FIG. 75, 3*c*. *\*D. normale*, Mo.; holotype, lat. view,  $\times 1.5$  (202). —FIG. 75, 3*d,e*. *D. magnisiphonatum* ULRICH, FOERSTE & MILLER, Mo.; lat. and dorsal views,  $\times 1.5$  (202). —FIG. 75, 3*f,g*. *D. corniculum* ULRICH, FOERSTE & MILLER, Mo.; dorsal and lat. views,  $\times 1.5$  (202).
- Desioceras** CECIONI, 1953, p. 93 [*\*D. floweri*; OD]. Gradually expanded, weakly annulate orthocoines with circular section; sutures with low, rounded ventral saddle; siphuncle marginal, about 0.3 of conch diameter; siphuncular segments contracted; septal necks short, loxochaoanitic; connecting rings exceptionally thick, structurally complex. [Poorly known but may be related to bathmoceratid *Eothinoceras*.] *L.Ord.*, S.Am. (Arg.).
- Eremoceras** HYATT, 1884, p. 282 [*\*Cyrtoceras Syphax* BILLINGS, 1865, p. 194; OD] [= *Ectenoceras* ULRICH & FOERSTE in KOBAYASHI, 1933, p. 269, 320; *Ectenolites* ULRICH & FOERSTE, 1936, p. 272]. Like *Dakeoceras* but orthoconic or weakly cyrtocoine. *L.Ord.* (*L. Canad.*), N.Am. (widespread) - China (Hopeh Prov.-Manchuria). —FIG. 75, 1*a,b*. *E. pergracile* (ULRICH, FOERSTE & MILLER), USA (Tex.); lat. and ventral views,  $\times 1.5$  (202). —FIG. 75, 1*c,d*. *E. subgracile* (ULRICH & FOERSTE), USA (Mo.); lat. and dorsal views,  $\times 1.5$  (202). —FIG. 75, 1*e*. *E. subcurvatum* (KOBAYASHI), China (Manchuria); lat. view,  $\times 3$  (202). —FIG. 75, 1*f,g*. *\*E. syphax* (BILLINGS), Can. (Que.); holotype, ventral and lat. views,  $\times 1.5$  (202).
- Hemichoanella** TEICHERT & GLENISTER, 1954, p. 192 [*\*H. canningi*; OD]. Orthoconic longicoines with circular section; sutures characterized by deep, narrow siphonal lobe; siphuncle tubular, 0.3 of conch diameter; septal necks hemichoanitic, connecting rings thick. *L.Ord.* (*U. Canad.*), W. Australia. —FIG. 77, 4. *\*H. canningi*; holotype, sec.,  $\times 5$  (193).
- Lebetoceras** TEICHERT & GLENISTER, 1954, p. 200 [*\*L. oepiki*; OD]. Gradually expanded orthocoines with circular section; siphuncle marginal, about 0.2 of conch diameter; septal necks subholochoanitic, connecting rings thick; resembles *Thylacoceras*, and possibly ancestral to that endocerid, but suture straight and endocoines absent. *L.Ord.* (*U. Canad.*), W. Australia. —FIG. 77, 2. *\*L. oepiki*; sec. of ectosiphuncle,  $\times 9$  (193).
- Levisoceras** FOERSTE, 1925, p. 11 [*\*Cyrtocera Mercurius* BILLINGS, 1865, p. 194; OD]. Like *Dakeoceras*, but more strongly curved; septal necks orthochoanitic, siphuncular segments concave;

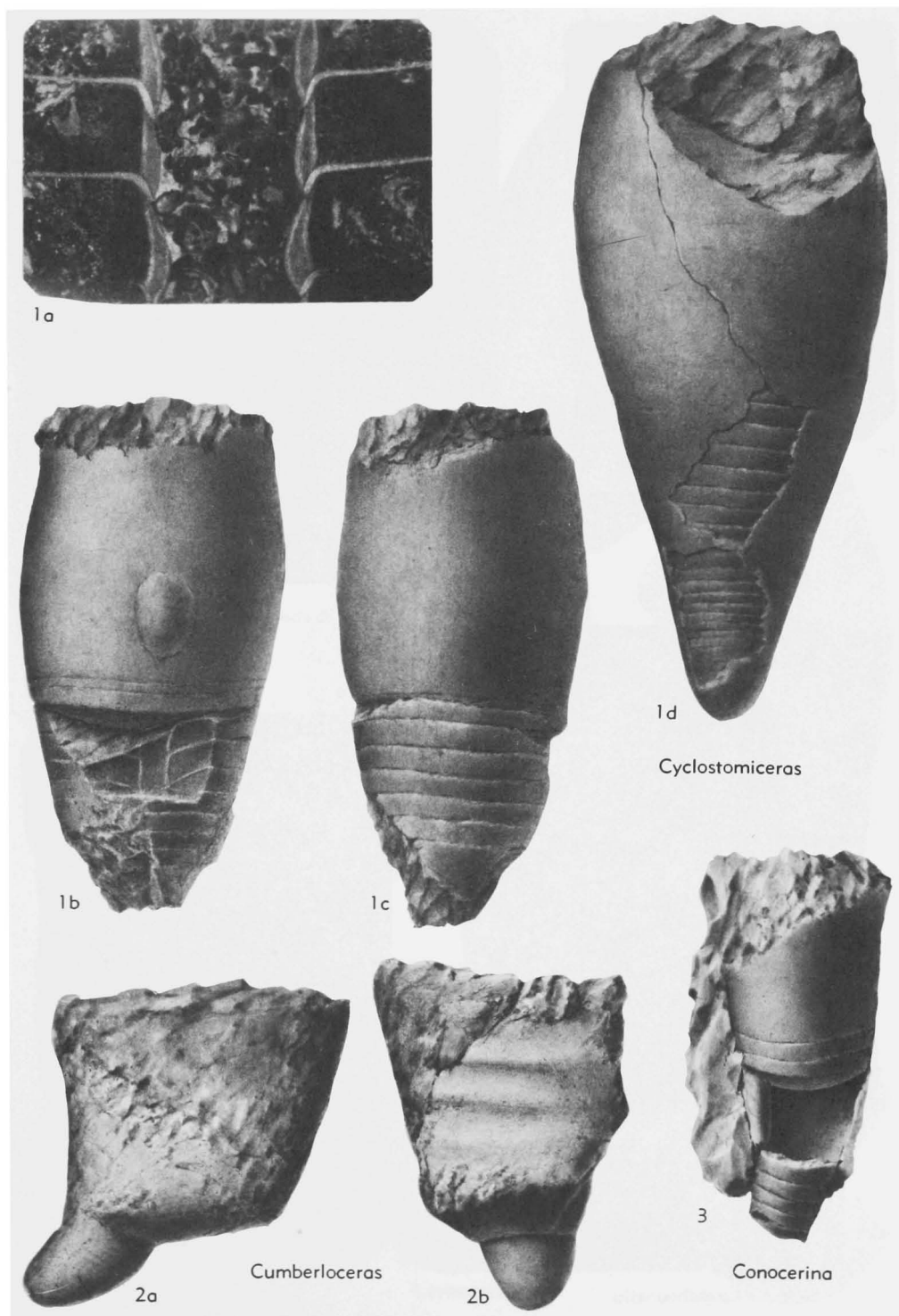


FIG. 76. *Ellesmeroceratidae* (p. K140).



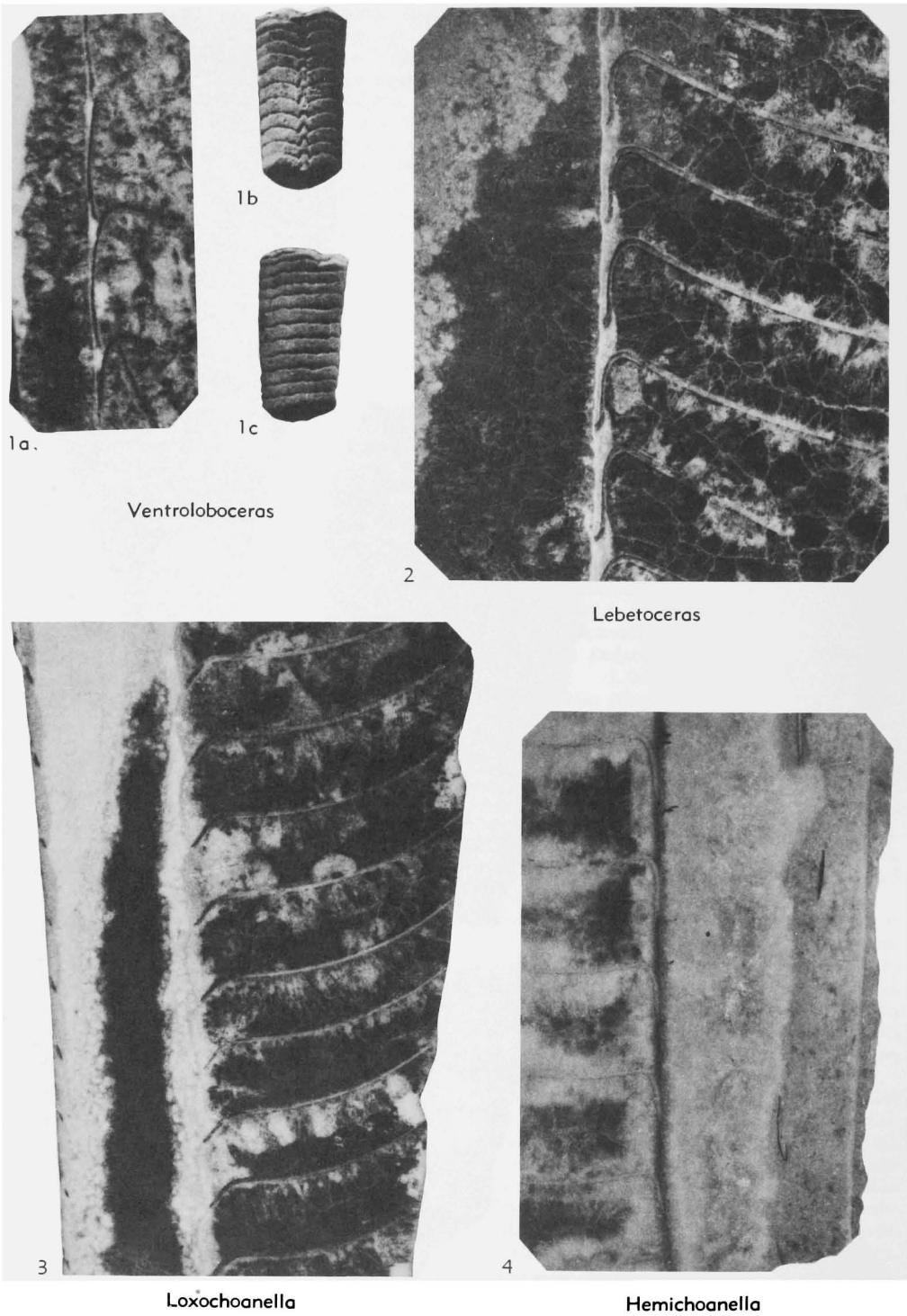


FIG. 77. Ellesmeroceratidae (p. K140, K144, K146).



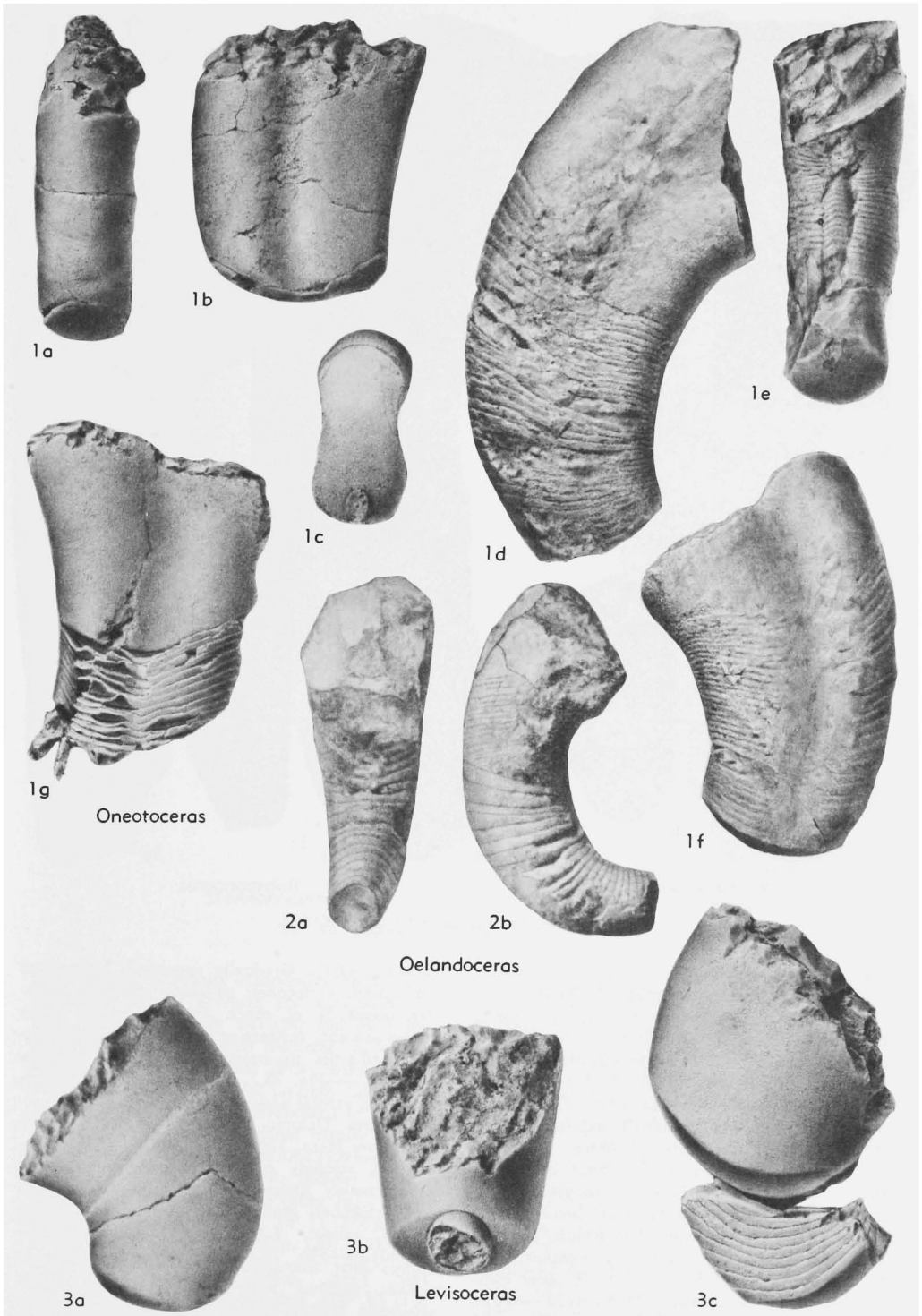


FIG. 78. Ellesmeroceratidae (p. K140-K144).

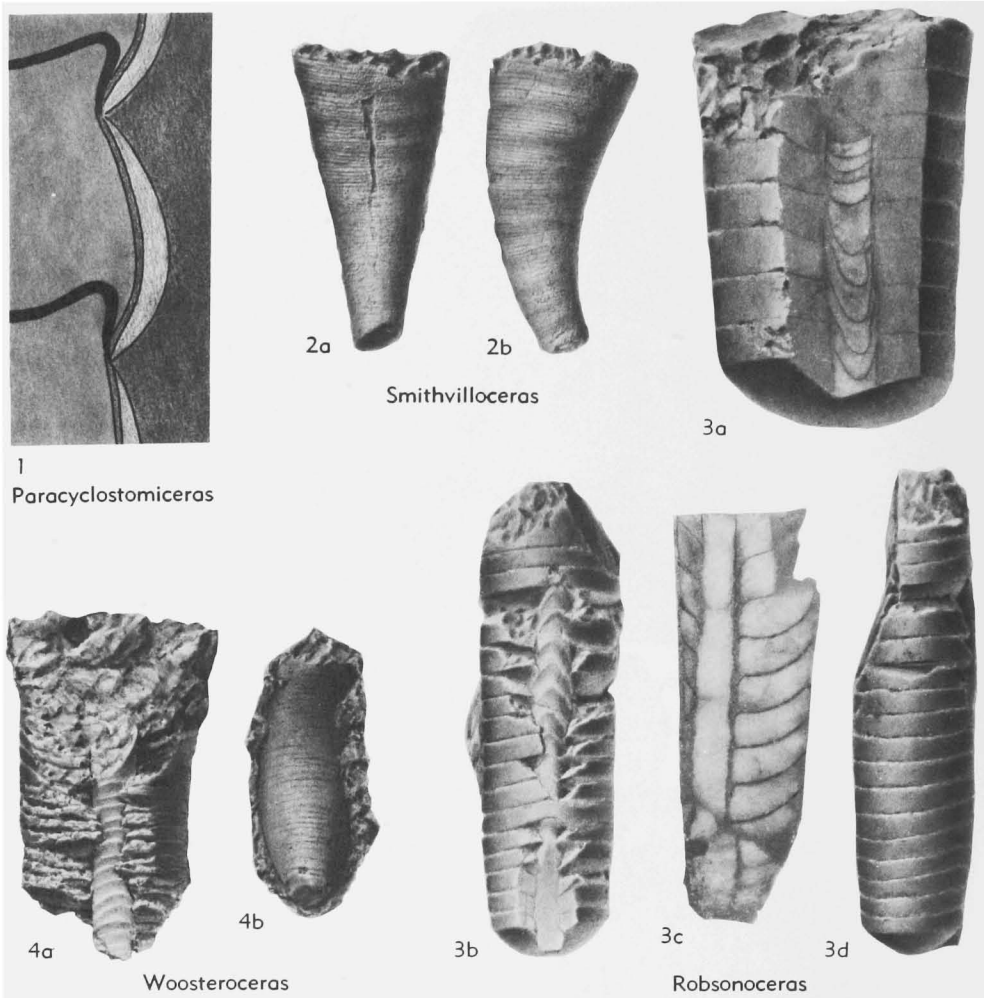


FIG. 79. Ellesmeroceratidae (p. K144-K146).

diaphragms present in at least some species. *L.Ord.* (*L.Canad.*), N.Am.(widespread)-USSR(Sib.).—FIG. 78,3a. \**L. mercurius* (BILLINGS), Can.(Que.); holotype, lat. view,  $\times 1.5$  (202).—FIG. 78,3b,c. *L. complanatum* ULRICH, FOERSTE & MILLER, USA (Mo.); ventral and lat. views,  $\times 1.5$  (202).

**Loxochoaella** TEICHERT & GLENISTER, 1954, p. 183 [\**L. warburtoni*; OD]. Gradually expanded orthocones with circular section; sutures essentially straight, ectosiphuncular suture forms high, narrow, rounded saddle; siphuncle marginal, about 0.3 of conch diameter; septal necks loxochoanitic, 0.3 to 0.5 of cameral interval in length; connecting rings thick and structurally complex, consisting of thin inner layer and thick outer component. *L.Ord.*(*U.Canad.*), W.Australia.—FIG. 77,3. \**L. warburtoni*; holotype, long. sec.,  $\times 9$  (193).

**Oelandoceras** FOERSTE, 1932, p. 170 [\**O. haellud-*

*denense*; OD]. Gradually expanded, compressed endogastric cyrtocones; siphuncle marginal, tubular, about  $\frac{1}{8}$  of conch diameter; septal necks orthochoanitic, connecting rings thin. [Ellesmerocerid affinities uncertain.] *L.Ord.*(*Arenig.*), Eu. (Baltic).—FIG. 78,2. \**O. haelluddenense*; 2a,b, holotype, ventral and lat. views,  $\times 1$  (70).

**Oneotoceras** ULRICH, 1926, p. 90 [\**Cyrtoceras loculosum* HALL, 1861, p. 42; M]. Moderately expanded, strongly compressed cyrtocones; flanks conspicuously flattened or concave, especially on body chamber; growth lines form high, rounded lateral salient. *L.Ord.*(*L.Canad.*), USA(widespread).—FIG. 78,1. \**O. loculosum* (HALL); 1a-c, Tenn., dorsal, lat. and septal views,  $\times 1$ ; 1d, Wis., holotype, lat.,  $\times 1$ ; 1e,f, Wis., ventral and lat. views,  $\times 1$ ; 1g, Minn., lat. view,  $\times 1$  (202).

**Paracyclostomiceras** CECIONI, 1953, p. 98 [\**P.*



Stenmonoceras

Quebecoceras

FIG. 80. Ellesmeroceratidae (p. K145-K146).

*floweri*; OD]. Gradually expanded orthocones with constricted mature aperture and subcircular section; suture essentially straight; siphuncle marginal, about 1/6 of conch diameter; siphuncular segments contracted; septal necks orthochoanitic, connecting rings thick and layered. Like *Cyclostomiceras*, but may be differentiated by its smaller apical angle, less constricted mature aperture and marginal siphuncle. ?*M.Ord.*(*Llanvirn.*), S. Am.(Arg.).—FIG. 79,1. \**P. floweri*; holotype, enlarged sec. of ectosiphuncle (after 7a).

**Quebecoceras** FOERSTE, 1925, p. 11 [\**Cyrtoceras Quebecense* WHITEAVES, 1898, p. 120; OD]. Gradually expanded, weakly cyrtoconic with circular cross section; growth lines forming shallow rounded lateral sinus; sutures directly transverse, almost straight; siphuncle cylindrical, septal necks probably hemichoanitic. *L.Ord.*, Can.(Que.).—

FIG. 80,2. \**Q. quebecense* (WHITEAVES); holotype, lat. view,  $\times 1.5$  (204).

**Robsonoceras** ULRICH & FOERSTE, 1933, p. 288 [\**Ellesmeroceras robsonensis* WALCOTT, 1924, p. 527; OD]. Gradually expanded orthocones with circular section; sutures directly transverse, nearly straight; siphuncle cylindrical, septal necks orthochoanitic; diaphragms widely spaced, irregular. *L.Ord.*, N.Am.(widespread).—FIG. 79,3. \**R. robsonense* (WALCOTT), Can.(B.C.); 3a, ventral view, showing irregular diaphragms,  $\times 6$ ; 3b,d, holotype, ventral and lat. views,  $\times 3$ ; 3c, sec.,  $\times 6$  (204).

**Shantungendoceras** SUN, 1937, p. 347 [\**S. conicum*; OD]. Poorly known cyrtocones, probably with marginal siphuncle. *L.Ord.*, China(Shantung Prov.).

**Smithvilloceras** ULRICH, FOERSTE & MILLER, 1943,

p. 155 [*\*S. thompsoni*; OD]. Like *Clelandoceras*, but weakly annulate. *L.Ord.*(*U.Canad.*), USA (Ark.).—FIG. 79,2. *\*S. thompsoni*; 2a,b, holotype, ventral and lat. views,  $\times 1.5$  (202).

**Stemtonoceras** ULRICH & FOERSTE, 1936, p. 288 [*\*S. elongatum*; OD]. Slender compressed cyrtocones; sutures forming shallow lateral lobe; diaphragms irregular. *L.Ord.*, USA (Pa.).—FIG. 80,1. *\*S. elongatum*; 1a,b, holotype, dorsal and lat. views,  $\times 1.5$  (204).

**Ventroloboceras** TEICHERT & GLENISTER, 1954, p. 203 [*\*V. furcillatum*; OD]. Gradually expanded orthocones with circular section; sutures characterized by broad but narrowly rounded ventral lobe; siphuncle marginal, about 1/6 of conch diameter; siphuncular segments slightly constricted; septal necks macrochoanitic, only slightly longer than cameral interval; connecting rings thick. *L.Ord.*(*U.Canad.*), W.Australia.—FIG. 77,1. *\*V. furcillatum*; holotype, 1a, sec.,  $\times 9$ ; 1b,c, ventral and lat. views,  $\times 1$  (193).

**Woosteroceras** ULRICH, FOERSTE, MILLER & UNKLESBAY, 1944, p. 30 [*\*W. trempealeauense*; OD]. Strongly curved endogastric cyrtocones with circular section; sutures straight and directly transverse; siphuncle small, cylindrical, close to venter. *L.Ord.*(*L.Canad.*), USA (Wis.-Texas-Va.).—FIG. 79,4a. *\*W. trempealeauense*, Wis.; holotype, ventral view,  $\times 3$  (204).—FIG. 79,4b. *W. cherokeeense* ULRICH, FOERSTE, MILLER & UNKLESBAY, Texas, ventral view,  $\times 1.5$  (204).

## Family ELECTRONOCERATIDAE

Kobayashi, 1935

[Electronoceratidae KOBAYASHI, 1935, p. 20] [incl. Ruthenoceratidae KORDE, 1949, p. 672]

Minute, generally compressed orthocones and endogastric cyrtocones; siphuncle marginal; septal necks variable, orthochoanitic to subholochoanitic; connecting rings thick, layered, and generally expanded between adjacent septal foramina; diaphragms reported in some. *U.Cam.-L.Ord.*

Entire group inadequately known. Imperfect preservation of the septal necks permits diverse interpretations in most forms. Connecting rings are only rarely well preserved. Ontogenetic and phylogenetic progression from expanded to tubular siphuncular segments, and ontogenetic lengthening of the septal necks from orthochoanitic to subholochoanitic has been suggested for most genera.

**Electronoceras** ULRICH & FOERSTE, 1933, p. 288 [*\*Cyrtoceras cambria* WALCOTT, 1905, p. 22; OD]. Compressed, fairly rapidly expanded endogastric cyrtocones; sutures with shallow lateral lobe; siphuncle about 0.2 of conch diameter, segments



FIG. 81. Electronoceratidae (p. K146).

expanded; septal necks variable, from orthochoanitic to hemichoanitic or cyrtchoanitic; connecting rings inadequately known but probably thick, and adnate distally. *U.Cam.*, China (Shantung Prov.-Manchuria).—FIG. 81,1a,b. *\*P. cambria* (WALCOTT), Shantung Prov.; septal and lat. views,  $\times 5$  (204).—FIG. 81,1c. *P. liaotungense* KOBAYASHI, Manchuria; sec.,  $\times 10$  (after 223b).

**Multicameroceras** KOBAYASHI, 1933, p. 273 [*\*Ellesmereoceras* (?) *multicameratum* KOBAYASHI, 1931, p. 163; OD]. Compressed orthocones with moderate rate of expansion; septa extremely closely spaced; sutures with shallow lateral lobe; siphuncle marginal and about 1/6 of conch diameter, segments expanded; septal necks hemichoanitic to subholochoanitic; irregular diaphragms possibly present. *L.Ord.*(*L.Canad.*), *?U.Canad.*), China (Manchuria)-USSR (Sib.).—FIG. 82,1. *\*M. multicameratum* (KOBAYASHI), *L.Ord.*(*L.Canad.*), Manchuria; 1a,b, lat. and septal views,  $\times 1.5$ ; 1c, sec.,  $\times 3$  (101a).

**Palaeoceras** FLOWER, 1954, p. 7 [*\*P. mutabile*; OD]. Slender compressed orthocones; lateral lobe of

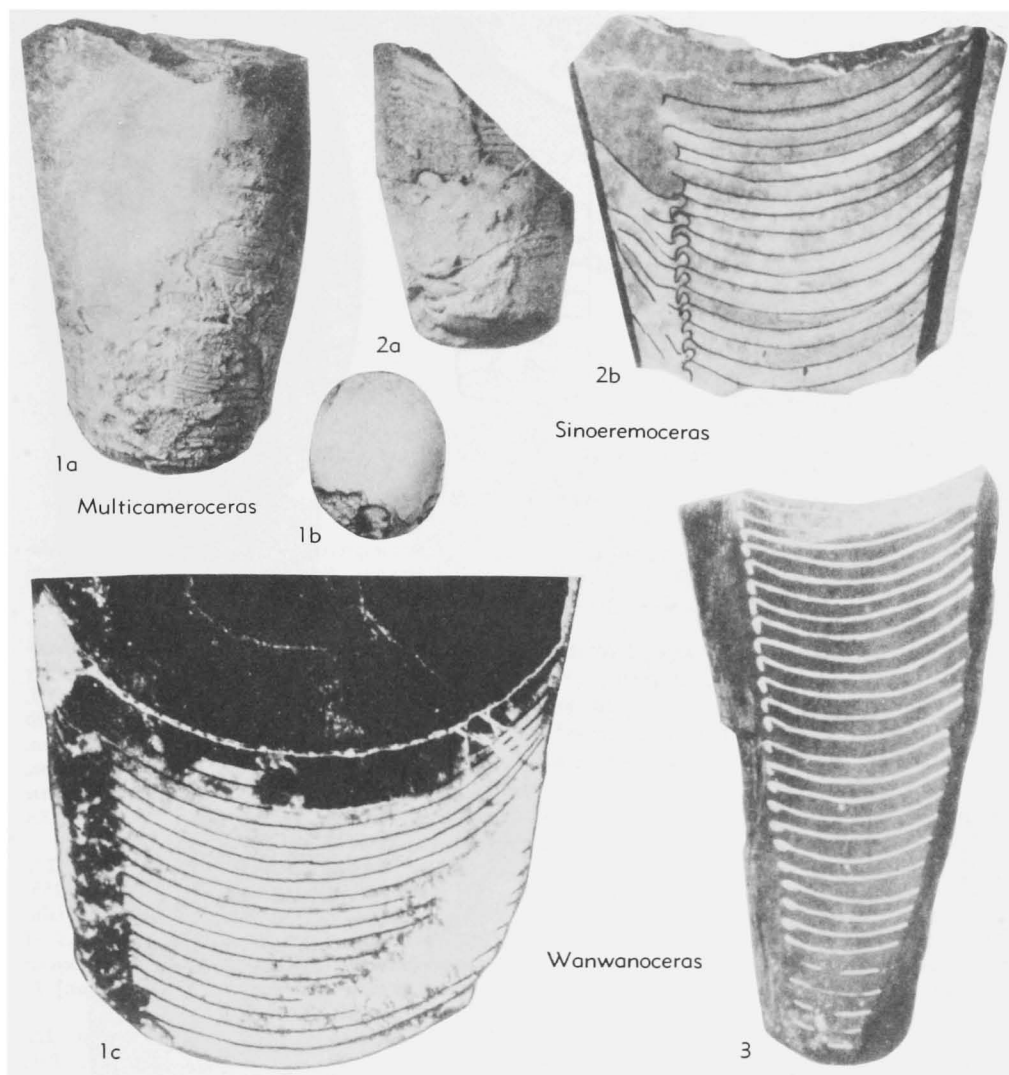


FIG. 82. Plectronoceratidae (p. K146-K147).

sutures deepest in early growth stages; siphuncle marginal, about 0.2 of conch diameter; connecting rings thick, layered; siphuncular segments inflated with orthochoanitic septal necks in early growth stages, tubular with subholochoanitic septal necks at maturity; diaphragms possibly present. *U.Cam. (Trempealeauan)*, N.Am. (Tex.).—FIG. 83,1. \**P. mutabile*; 1a, early growth stage,  $\times 6$ ; 1b, late growth stage,  $\times 4$  (after 41).

**Ruthenoceras** KORDE, 1949, p. 672 [*\*R. elongatum*; OD] [= *Angaroceras* KORDE, 1949, p. 672]. Gradually expanded cyrtocoines known from only few oblique sections of minute phragmocones; siphuncle marginal, tubular, about 0.5 of conch diameter; septal necks appear short, orthochoanitic, and connecting rings thin. ?*U.Cam.*, USSR (Sib.).

—FIG. 83,2. \**R. elongatum*, Angara Reg.; oblique sec.,  $\times 18$  (after 224a).

**Sinoeremoceras** KOBAYASHI, 1933, p. 272 [*\*Eremoceras wanwanense* KOBAYASHI, 1931, p. 164; OD] [= *Sinoceremoceras* KOBAYASHI, 1935 (*nom. van.*)]. Like *Multicameroceras*, but conch slightly cyrtocoenic. *L.Ord. (L.Canad.)*, China (Manchuria).

—FIG. 82,2. \**S. wanwanense* (KOBAYASHI); 2a, lat. view,  $\times 1.5$ ; 2b, sec.,  $\times 3$  (101a).

**Wanwanoceras** KOBAYASHI, 1933, p. 271 [*\*W. peculiare*; OD]. General conch form similar to *Sinoeremoceras*; early septal necks reported as cyrtocoanitic, but entire siphuncle may be similar to *Multicameroceras*. *L.Ord. (L.Canad.)*, China (Manchuria).—FIG. 82,3. \**W. peculiare*; sec.,  $\times 3$  (101a).

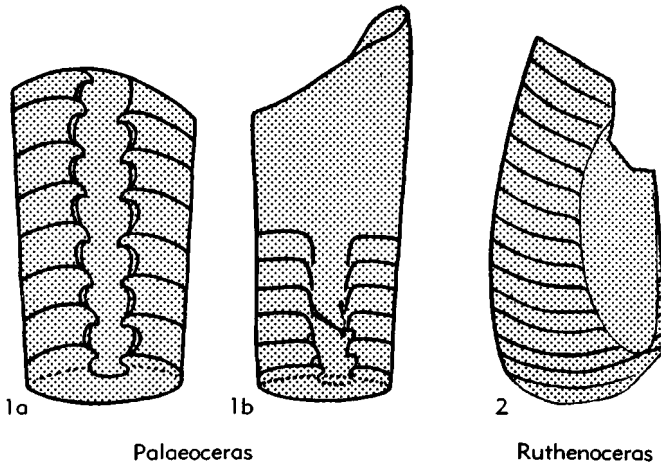


FIG. 83. Plectronoceratidae (p. K146-K147).

### Family BASSLERO CERATIDAE Ulrich et al., 1944

[Bassleroceratidae ULRICH, FOERSTE, MILLER & UNKLESBAY, 1944, p. 33]

Gradually expanded, smooth cyrtocones with slight to moderate exogastric curvature; conch strongly compressed to subcircular in section; siphuncle characteristically marginal and moderate in size, orthochoanitic. *L.Ord.*

**Bassleroceras** ULRICH & FOERSTE, 1936, p. 263 [\**Orthoceras Perseus* BILLINGS, 1865, p. 313; OD]. Smooth or weakly annulate compressed longicones with slight to moderate exogastric curvature; characterized by narrowly rounded venter; sutures forming shallow lateral lobe; siphuncle marginal or submarginal, about 0.1 of dorsoventral conch diameter, segments concave; septal necks orthochoanitic. *L.Ord.*(?*L.Canad.*-, *U.Canad.*), N. Am.(widespread) - W. Australia.—FIG. 84,1. \**B. perseus* (BILLINGS), *L.Ord.*(*U.Canad.*), Can.(Que.); holotype, 1a, lat. view,  $\times 1$ ; 1b,c, lat. and ventral views of adoral portion,  $\times 1$  (204).

**Anguloceras** UNKLESBAY & YOUNG, 1956, p. 488 [\**A. ovatum*; OD]. Gradually expanded cyrtocones with subcircular section and slight exogastric curvature; sutures essentially straight, inclined steeply backward from venter; siphuncle moderate in size, marginal. [Poorly known but apparently similar to *Bassleroceras*.] *L.Ord.*(*L.Canad.*), USA(Va.).

**Avaoceras** ULRICH, FOERSTE, MILLER & UNKLESBAY, 1944, p. 41 [\**A. elongatum*; OD] [= *Leptocyrtoceras*, *Stylocyrtoceras* ULRICH, FOERSTE, MILLER & UNKLESBAY, 1944, p. 48, 54]. Longicones with circular section and slight exogastric curvature; sutures essentially straight; siphuncle submarginal, 1/6 to 1/3 of conch diameter. *L.Ord.*(*U.Canad.*),

N.Am.(widespread).—FIG. 85,4. *A. longidomum* ULRICH, FOERSTE, MILLER & UNKLESBAY, USA(Mo.); lat. view,  $\times 1.5$  (204).

**Diaphoroceras** ULRICH, FOERSTE, MILLER & UNKLESBAY, 1944, p. 43 [\**D. avaense*; OD]. Like *Avaoceras*, but with apertural constriction at maturity and slightly compressed conch. *L.Ord.*(*U.Canad.*), N.Am.(Mo.-Okla.-Que.).—FIG. 85,2a. *D. belli* ULRICH, FOERSTE, MILLER & UNKLESBAY, Can.(Que.); lat. view showing apert. constriction,  $\times 1.5$  (204).—FIG. 85,2b,c. *D. buffaloense* ULRICH, FOERSTE, MILLER & UNKLESBAY, USA(Mo.); ventral and lat. views,  $\times 1.5$  (204).

**Dwightoceras** ULRICH & FOERSTE, 1936, p. 272 [\**Cyrtoceras? dactyloides* DWIGHT, 1884, p. 255; OD]. Slightly compressed longicones with faint exogastric curvature; siphuncle marginal, 0.3 of conch diameter. [Based on single phragmocone; similar to both *Avaoceras* and *Diaphoroceras*.] *L.Ord.*(*U.Canad.*), USA(N.Y.).

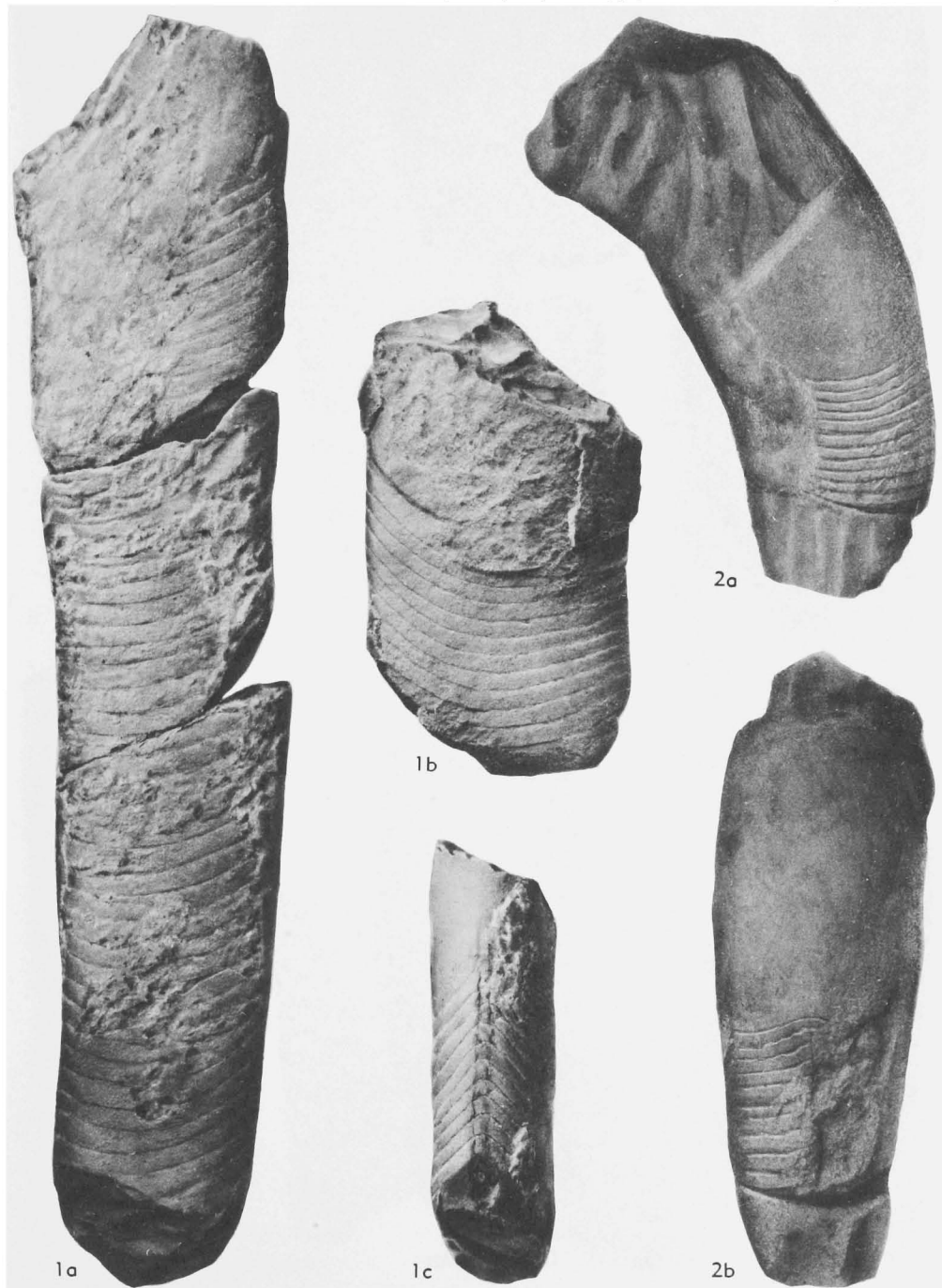
**Dyscritoceras** ULRICH & FOERSTE, 1936, p. 272 [\**Cyrtoceras Metellus* BILLINGS, 1865, p. 191; OD]. Slightly compressed longicones with moderate curvature; siphuncle small, marginal [Similar to *Avaoceras*.] *L.Ord.*, Can.(Que.).—FIG. 84,2. \**D. metellus* (BILLINGS), 2a,b, holotype, lat. and ventral views,  $\times 1.5$  (204).

**Lawrenceoceras** ULRICH, FOERSTE, MILLER & UNKLESBAY, 1944, p. 48 [\**L. collinsi*; OD] [= *Onychoceras* ULRICH & FOERSTE, 1936, p. 283 (non WUNSTORF, 1905, p. 508); *Lawrencoceras* FLOWER in FLOWER & KUMMEL, 1950, p. 611 (nom. null.)]. Gradually expanded cyrtocones with slightly depressed section and moderate exogastric curvature; siphuncle submarginal, about 0.1 of conch diameter. [Similar to *Dyscritoceras* but depressed.] *L.Ord.*(*U.Canad.*), N.Am.(widespread).—FIG. 85,1a,b. *L. confertissimum* (WHITFIELD), USA(Vt.); ventral and lat. views,  $\times 1.5$  (204).—FIG. 85,1c. \**L. collinsi*, Can.(Que.); holotype, lat. view,  $\times 1$  (204).



**Monogonoceras** ULRICH, FOERSTE, MILLER & UNKLESBAY, 1944, p. 50 [*\*M. alabamense*; OD]. Similar to *Bassleroceras*, but more narrowly

rounded ventrally. *L.Ord.(U.Canad.)*, USA (Ala.-Va.-Mo.).—FIG. 85,3. *\*M. alabamense*, USA (Ala.); holotype, lat. view,  $\times 1.5$  (204).



**Bassleroceras**

**Dyscritoceras**

FIG. 84. Bassleroceratidae (p. K148).

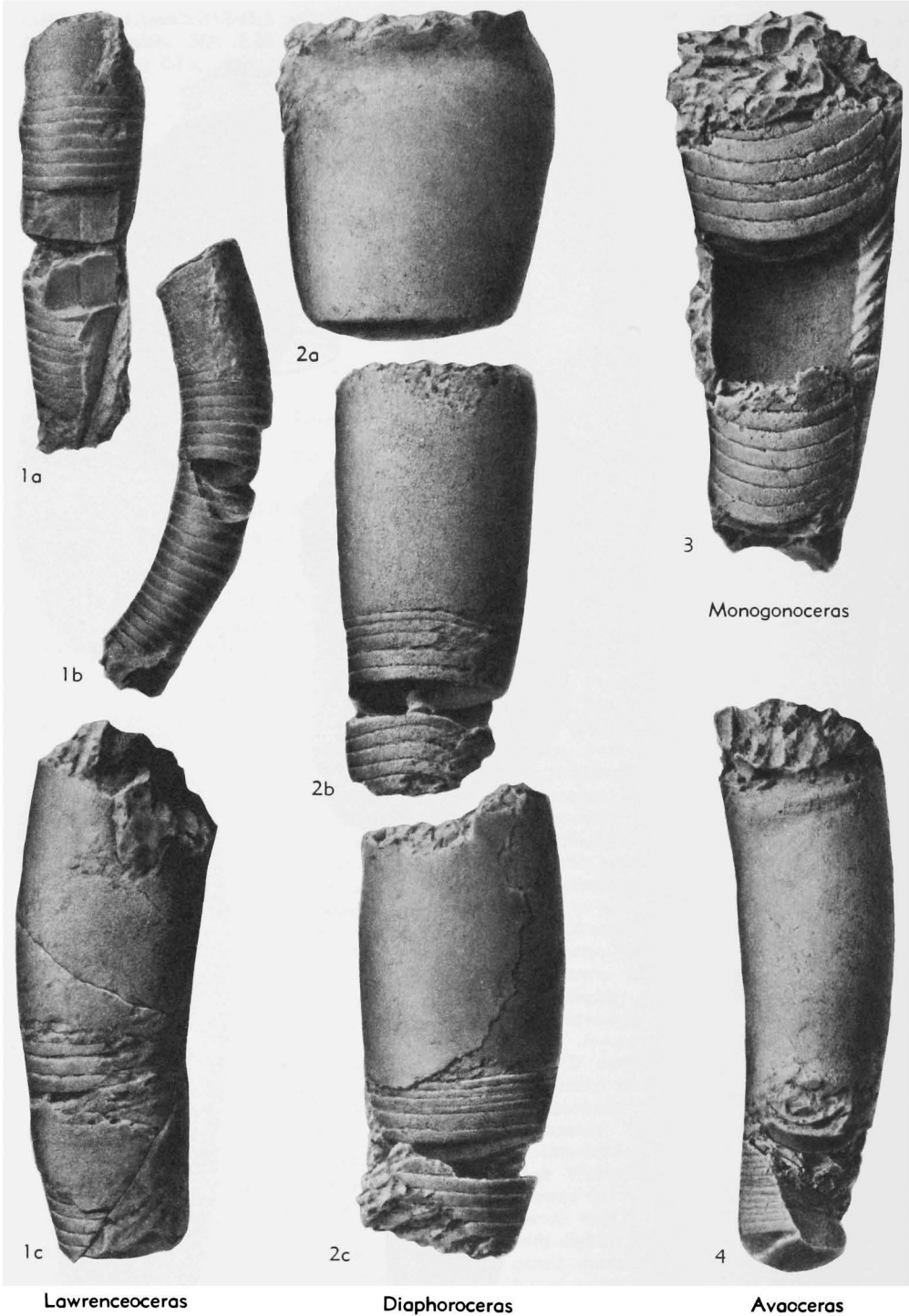


FIG. 85. Bassleroceratidae (p. K148-K149).



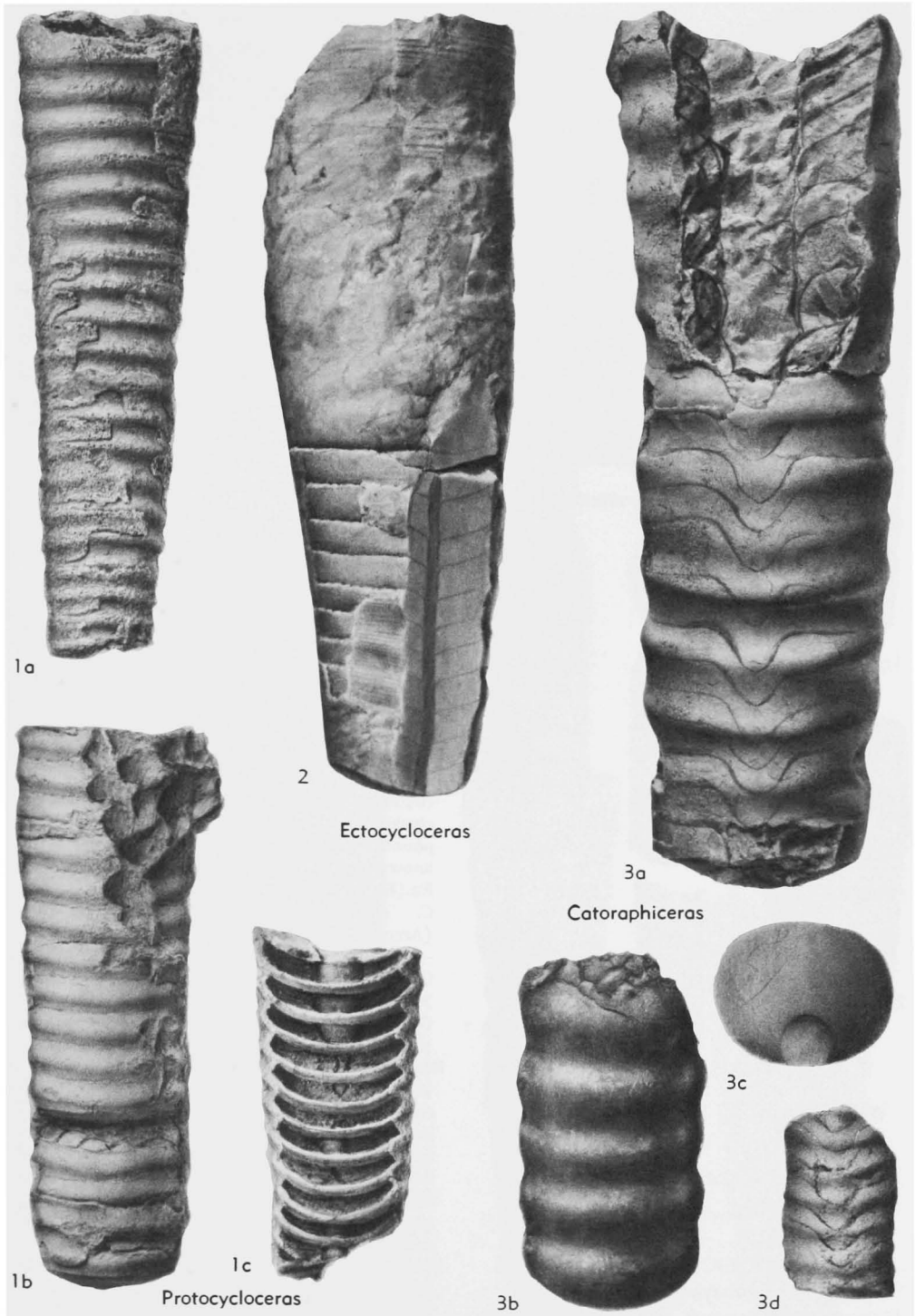


FIG. 86. Protocycloceratidae (p. K152, K154).

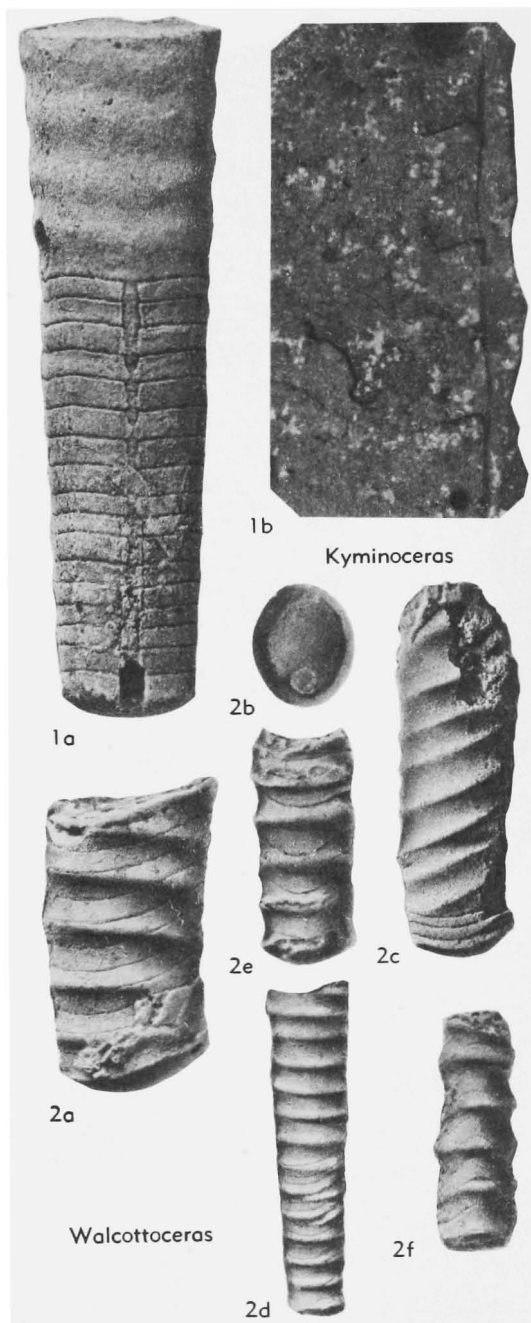


Fig. 87. Protocycloceratidae (p. K154).

### Family PROTOCYCLOCERATIDAE Kobayashi, 1935

[Protocycloceratidae KOBAYASHI, 1935, p. 746] [incl. Endocycloceratidae and Rudolfoceratidae ULRICH, FOERSTE, MILLER & UNKLESBAY, 1944, p. 30, 55; Apocrinoceratidae FLOWER in FLOWER & TEICHERT, 1957, p. 136]

Annulate longicones, either straight or with slight endogastric or exogastric curvature; siphuncle submarginal to marginal, moderate to small in size (0.1 to 0.3 of conch diameter), subcylindrical; septal necks short and characteristically orthochoanitic; connecting rings thin and homogeneous in some forms, but probably thick and layered in others. *L.Ord.*

**Protocycloceras** HYATT in ZITTEL, 1900, p. 518 [*\*Orthoceras Lamarcki* BILLINGS, 1859, p. 362; OD] [= *Orotocycloceras* KOBAYASHI, 1927, p. 183 (*nom. null.*); *Dresseroceras* ULRICH, FOERSTE, MILLER & UNKLESBAY, 1944, p. 132]. Strongly annulate orthocones with circular cross section; annulations and sutures directly transverse and essentially straight; siphuncle approximately 0.3 of corresponding conch diameter, ventral but not marginal; septal necks probably orthochoanitic, siphuncular segments tubular. *L.Ord.*(*L.Canad.-U.Canad.*), cosmop.—FIG. 86,1a,c. *\*P. lamarcki* (BILLINGS), *L.Ord.*(*U.Canad.*), *Can.*(*Ont.-Newf.*);  $\times 1.5$  (204).—FIG. 86,1b. *P. whitfieldi* RUEDEMANN, *L.Ord.*(*U.Canad.*), USA(Vt.);  $\times 1.5$  (204).

**Apocrinoceras** TEICHERT & GLENISTER, 1954, p. 221 [*\*A. talboti*; OD]. Weakly annulate orthocones with submarginal siphuncle about 0.1 of conch diameter; siphuncle characterized by weakly cyrtchoanitic septal necks and expanded siphuncular segments; connecting rings possibly thick. [Protocycloceratid affinities uncertain.] *L.Ord.*(*U.Canad.*), W.Australia.

**Catoraphiceras** ULRICH & FOERSTE, 1936, p. 266 [*\*C. lobatum*; OD]. Annulate orthocones with circular to slightly depressed cross section; suture characterized by deep rounded ventral lobe; siphuncle marginal; details of ectosiphuncle unknown. *L.Ord.*(*U.Canad.*), N.Am.(widespread)-Eu.(Est.)-USSR(Sib.)-W.Australia.—FIG. 86,3a. *C. vaginatum* (VON SCHLOTHEIM), *L.Ord.*(Arenig.), Eu.(Est.), ventral view,  $\times 1.25$  (204).—FIG. 86,3b,c. *C. colon* (WHITE), *L.Ord.*(*U.Canad.*), USA(Utah); dorsal and septal views,  $\times 1.5$  (204).—FIG. 86,3d. *\*C. lobatum*, *L.Ord.*(*U.Canad.*), USA(Tenn.); holotype, ventral view,  $\times 1.5$  (204).

**Diastoloceras** TEICHERT & GLENISTER, 1954, p. 190 [*\*D. perplexum*; OD]. Longicones with circular section and slight exogastric curvature; internal mold essentially smooth but shell surface characterized by closely spaced prominent flanges; siphuncle submarginal, about 0.1 of conch diameter; siphuncular segments expanded; septal necks achoanitic, connecting rings thin. [Affinities uncertain.] *L.Ord.*(*U.Canad.*), W.Australia.

**Ectocycloceras** ULRICH & FOERSTE, 1936, p. 275 [*\*Orthoceras Cataline* BILLINGS, 1865, p. 315; OD]. Circular to slightly compressed, annulate, moderately curved, exogastric cyrtcones; sutures essentially straight and transverse; siphuncle small,

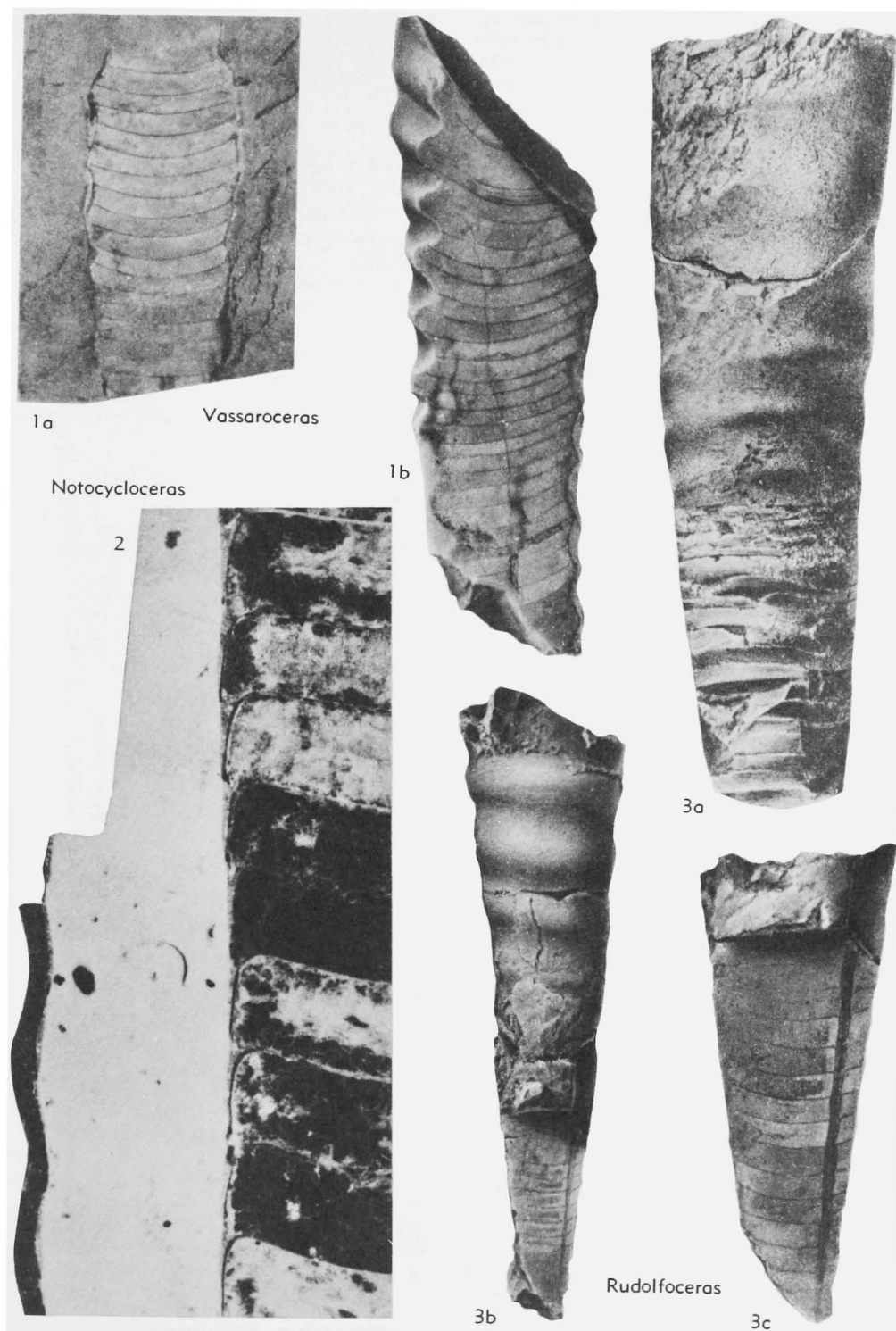


FIG. 88. Protocycloceratidae (p. K154).

situated close to ventral margin; siphuncular segments slightly expanded to constricted; septal necks orthochoanitic. *L.Ord.(U.Canad.)*, Can. (Que.)-W.Australia.—FIG. 86,2. *E. cato* (BILLINGS), *L.Ord.(U.Canad.)*, Can.(Que.); holotype,  $\times 1.5$  (204).

**Endocycloceras** ULRICH, FOERSTE, MILLER & UNKLESBAY, 1944, p. 31 [*\*E. wilsonae*; OD]. Resembles *Rudolfoceras*, but apparently curved endogastrically. *L.Ord.(L.Canad.-U.Canad.)*, N. Am.(widespread).

**Kyminoceras** TEICHERT & GLENISTER, 1954, p. 188 [*\*K. forresti*; OD]. Prominently annulate orthocones with circular or subcircular cross section; annulations transverse or sloping posteriorly from dorsum to venter; sutures weakly sinuous and directly transverse; siphuncle about 0.2 of conch diameter, either marginal or situated close to shell wall, segments approximately cylindrical; septal necks orthochoanitic, connecting rings thin, homogeneous. *L.Ord.(U.Canad.)*, N.Am.(widespread)-W.Australia.—FIG. 87,1a,b. *\*K. forresti*, W.Australia; 1a, ventral view,  $\times 3$  (Furnish & Glenister, n); 1b, sec. of ectosiphuncle,  $\times 9$  (193).

**Notocycloceras** TEICHERT & GLENISTER, 1954, p. 202 [*\*N. yurabiense*; OD]. Annulate orthocones with subholochoanitic septal necks; possibly synonymous with endocerid genus *Anthoceras*, but lack endocones. *L.Ord.(U.Canad.)*, W.Australia.—FIG. 88,2. *\*N. yurabiense*; sec.,  $\times 9$  (193).

**Rudolfoceras** ULRICH, FOERSTE, MILLER & UNKLESBAY, 1944, p. 55 [*\*Orthoceras cornu-oryx* WHITFIELD, 1886, p. 320; OD] [= *Orygoceras* RUEDEMANN, 1906, p. 449 (*non* BRUSINA, 1882)]. Orthoconic to slightly cyrtoconic exogastric annulate longicones with circular to compressed section; siphuncle submarginal, about 1/12 of conch diameter; septal necks orthochoanitic. *L.Ord.(U.Canad.)*, N.Am.(Vt.-N.Y.-Que.).—FIG. 88,3. *\*R. cornuoryx* (WHITFIELD), Vt.; 3a, topotype,  $\times 1.5$ ; 3b,c, syntype, lat. view,  $\times 1.5$ , and enlarged sec.,  $\times 3$  (204).

**Vassaroceras** ULRICH, FOERSTE, MILLER & UNKLESBAY, 1944, p. 32 [*\*Orthoceras Henrietta* DWIGHT, 1884, p. 256; OD]. Septal necks orthochoanitic. [Poorly known, may be synonym of *Endocycloceras*.] *L.Ord.(U.Canad.)*, USA(N.Y.).—FIG. 88,1. *\*V. henrietta* (DWIGHT); 1a,b, holotype and topotype,  $\times 3$  (204).

**Walcottoceras** ULRICH & FOERSTE, 1936, p. 289 [*\*Endoceras(?) monensis* WALCOTT, 1924, p. 529; OD]. Strongly annulate compressed longicones; orthoconic to gently curved endogastrically; sutures form broadly rounded lateral lobe; siphuncle submarginal, about 1/6 of dorsoventral conch diameter, cylindrical. *L.Ord.(L.Canad., ?U.Canad.)*, N.Am.(widespread).—FIG. 87,2a-d. *W. obliquum* ULRICH, FOERSTE, MILLER & UNKLESBAY, *L.Ord.(L.Canad.)*, USA (Iowa); 2a,c,d, lat. views,  $\times 1.5$ ; 2b, septal view,  $\times 3$  (204).—FIG. 87,2e,f. *\*W. monense* (WAL-

COTT), *L.Ord.(L.Canad.)*, Can.(Alba.); holotype, lat. and ventral views,  $\times 1.5$  (204).

### Family BALTOCERATIDAE Kobayashi, 1935

[Baltoceratidae KOBAYASHI, 1935, p. 751] [=Cochlioceratidae BALASHOV, 1955, p. 55]

Smooth, longiconic orthocones with moderately large marginal siphuncle, orthochoanitic septal necks and thin homogeneous connecting rings. *L.Ord.-M.Ord.*

**Cochlioceras** EICHWALD, 1860, p. 1250 [*\*Orthoceras avus* EICHWALD, 1857, p. 200; M] [= *Baltoceras* HOLM, 1897, p. 174; *Protobaltoceras* TROEDSON, 1937, p. 16]. Gradually expanded orthocones with circular section and essentially straight sutures; siphuncle tubular, marginal, 0.25 to 0.5 of conch diameter; septal necks orthochoanitic, connecting rings thin and homogeneous. *L.Ord.*

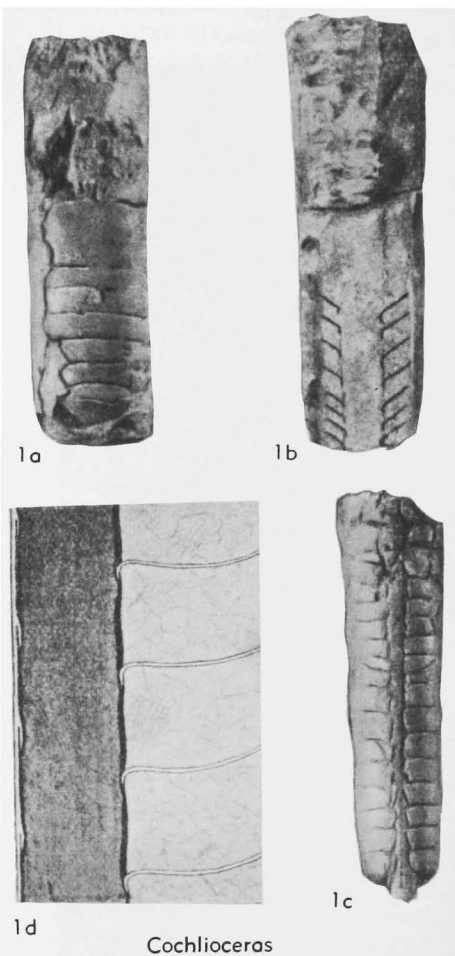


FIG. 89. Baltoceratidae (p. K154-K155).

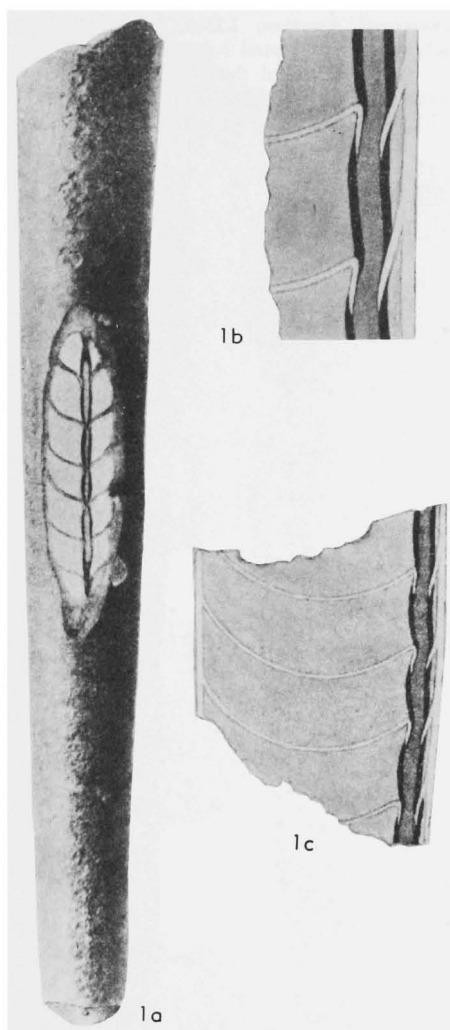


FIG. 90. *\*Bactroceras avus* HOLM (Baltoceratidae) (p. K155).

(Arenig.)-M. Ord. (Llanvirn.), Eu. (widespread)-USA (Vt.)-China (Sinkiang-Hupeh).—FIG. 89, 1a-c. *\*C. avus* (EICHWALD), L.Ord. (Arenig.), Eu. (Baltic); lat. view, lat. sec., and ventral view,  $\times 1$  (216a).—FIG. 89, 1d. *C. burchardii* (DEWITZ), M.Ord. (Llanvirn.), Eu. (Baltic); sec.,  $\times 3$  (223a). **Bactroceras** HOLM, 1898, p. 357 [*\*B. avus*; SD GLENISTER, 1952, p. 90]. Gradually expanded orthocones with circular section; siphuncle marginal, tubular, about 1/12 of conch diameter; septal necks long, orthochoanitic; connecting rings thin, homogeneous. M.Ord. (Llandeilo), Eu. (Baltic)-Australia (New S. Wales).—FIG. 90, 1. *\*B. avus*; 1a, ventral view,  $\times 1.5$ ; 1b, c, secs.,  $\times 5$ ,  $\times 2.5$  (223a).

**Murrayoceras** FOERSTE, 1926, p. 312 [*\*Orthoceras Murrayi* BILLINGS, 1857, p. 332; OD]. Gradually

expanded depressed orthocones; characterized by subtriangular section with strongly flattened venter; sutures form shallow lobe on venter and generally on dorsolateral flanks; siphuncle 0.15 to 0.3 of dorsoventral conch diameter, near venter; septal necks orthochoanitic, connecting rings thin; siphuncular segments cylindrical. M.Ord. (Chazy-Blackriver.), N.Am. (widespread).—FIG. 91, 1. *\*M. murrayi* (BILLINGS), M.Ord. (Blackriver.), Can. (Ont.); 1a-c, ventral, dorsal, septal views,  $\times 0.7$  (79).

**Ogygoceras** ULRICH, FOERSTE, MILLER & UNKLESBAY, 1944, p. 69 [*\*O. gracile*; OD]. Essentially orthoconic longicones with circular section; siphuncle marginal, about 0.25 of conch diameter; septal necks presumably orthochoanitic. [Affinities uncertain; gently sigmoid apical portion of single known representative may be pathologic.] L.Ord. (U. Canad.), USA (Ark.).—FIG. 92, 1. *\*O. gracile*; 1a, b, holotype, lat. and dorsal views,  $\times 1.5$  (204).

**Pachendoceras** ULRICH & FOERSTE, 1936, p. 283 [*\*Cameroceras huzzahense* ULRICH & FOERSTE in BRIDGE, 1931, p. 211; OD]. Large, gradually expanded orthocones with subcircular section; sutures straight; siphuncle marginal, about 0.5 of conch diameter; structure of ectosiphuncle unknown; diaphragms elongate, asymmetric. L.Ord. (L. Canad.), USA (Mo.-Va.).—FIG. 93, 1a, b. *\*P. huzzahense* (ULRICH & FOERSTE), Mo.; syntype, ventral and lat. views,  $\times 1$  (204).—FIG. 93, 1c.

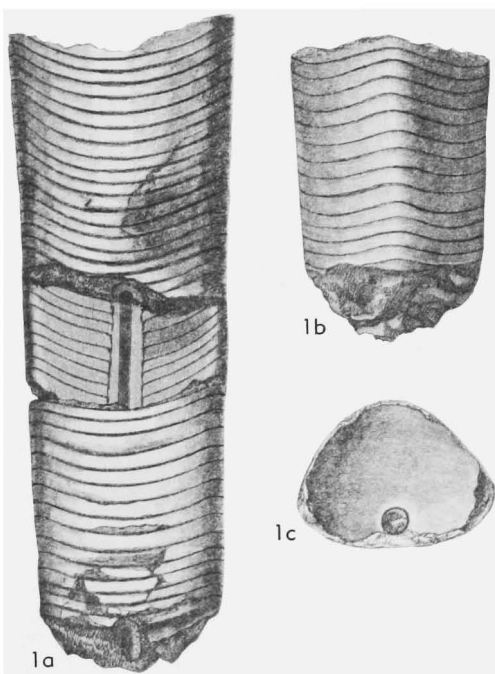


FIG. 91. *\*Murrayoceras murrayi* (BILLINGS) (Baltoceratidae) (p. K155).



FIG. 92. *\*Ogygoceras gracile* ULRICH, FOERSTE, MILLER, & UNKLESBAY (Baltoceratidae) (p. K155).

*P.?* sp., Mo.; weathered dorsoventral sec. with elongate asymmetric diaphragm,  $\times 1$  (204).

### Family BATHMOCERATIDAE

Holm, 1899

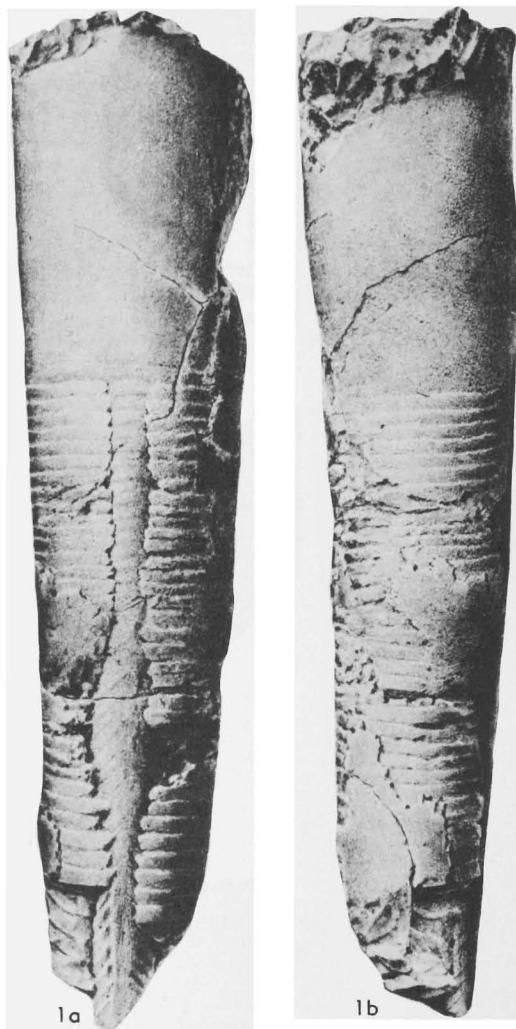
[Bathmoceratidae HOLM, 1899, p. 287] [incl. Eothinoceratidae ULRICH, FOERSTE, MILLER & UNKLESBAY, 1944, p. 130]

Essentially orthoconic longicones with large submarginal siphuncle; suture with siphuncular saddle; septal necks orthochoanitic to hemichoanitic; connecting rings greatly thickened to form flangelike extensions within siphuncle. *L.Ord.-M.Ord.*, ?*U. Sil.*

**Bathmoceras** BARRANDE, 1867, p. 74 [*\*Orthoceras complexum* BARRANDE, 1856, p. 384; SD TEICHERT, 1939, p. 388] [= *Bathmoceras* BARRANDE, 1865, p. 276 (*nom. nud.*); *Bothmoceras* BALASHOV, 1955, p. 52 (*nom. null.*)]. Orthocones and gently curved exogastric cyrtocones with circular, depressed, or compressed conch; suture with low ventral saddle; siphuncle marginal, 0.2 to 0.3 of dorsoventral conch diameter; septal necks hemichoanitic; connecting rings thick, expanded adorally as thick, obliquely truncated invaginated cones which occupy about half of total siphuncular volume. *L. Ord.* (*Arenig.*) - *M. Ord.* (*Llandeilo.*), ?*U. Sil.* (*Wenlock.*), Eu. (Czech. - Baltoscandia-Port.) - Australia (N. Terr.) - S. Am. (Arg.) - ?China. — FIG. 94, 1a-c. *\*B. complexum* (BARRANDE), M. Ord. (Llanvirn.), Eu. (Boh.); 1a,c, ventral views; 1b, septal view, all  $\times 1$  (204). — FIG. 94, 1d,e. *B.*

*linnarssoni* ANGELIN, L.Ord. (*Arenig.*), Eu. (Baltic); dorsal and ventral halves of siphuncle showing septal necks and thick connecting rings (reconst., enlarged) (after 92a).

**Eothinoceras** ULRICH, FOERSTE, MILLER & UNKLES-



**Pachendoceras**

FIG. 93. Baltoceratidae (p. K155-K156).



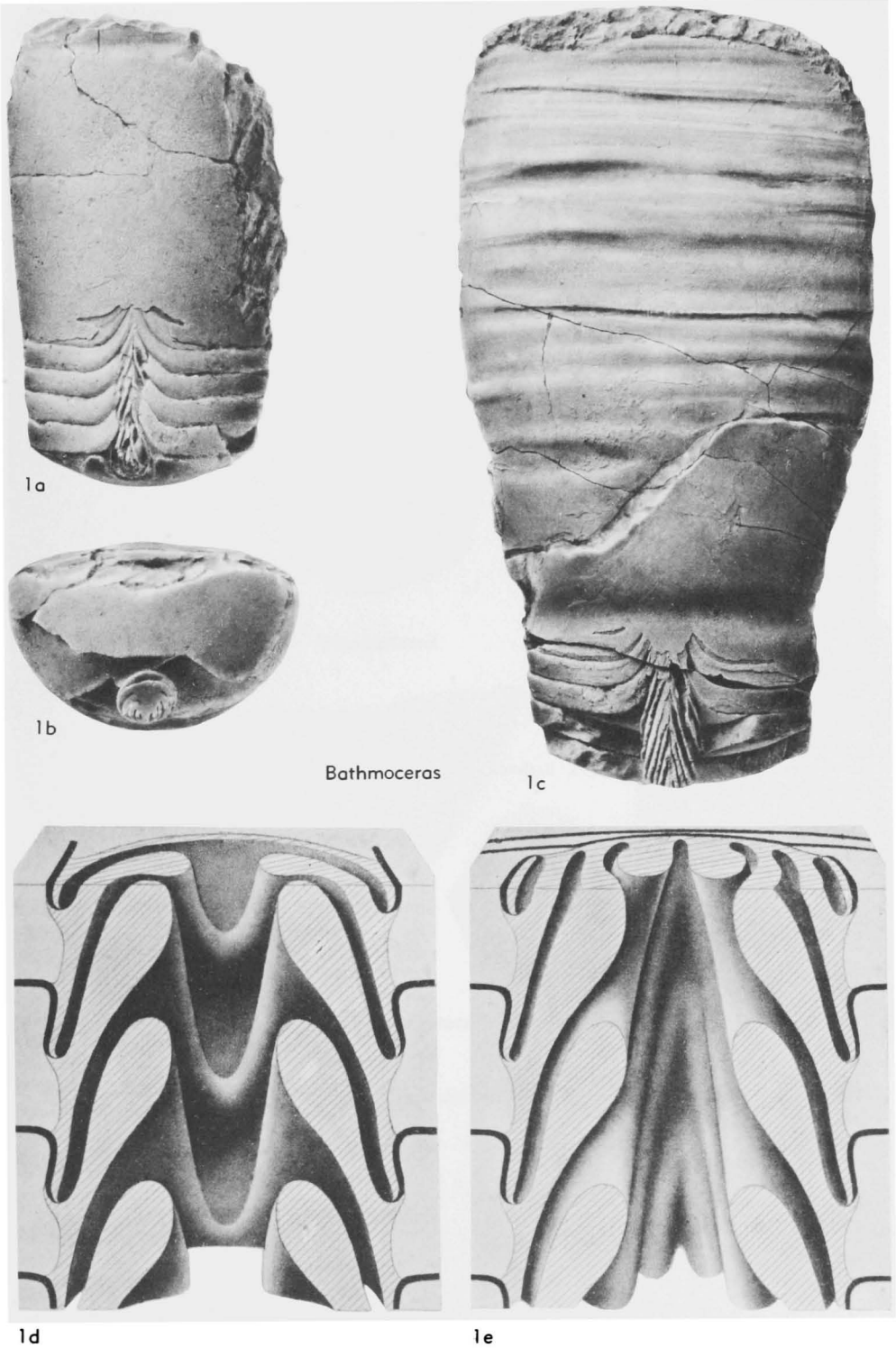


FIG. 94. Bathmoceratidae (p. K156).

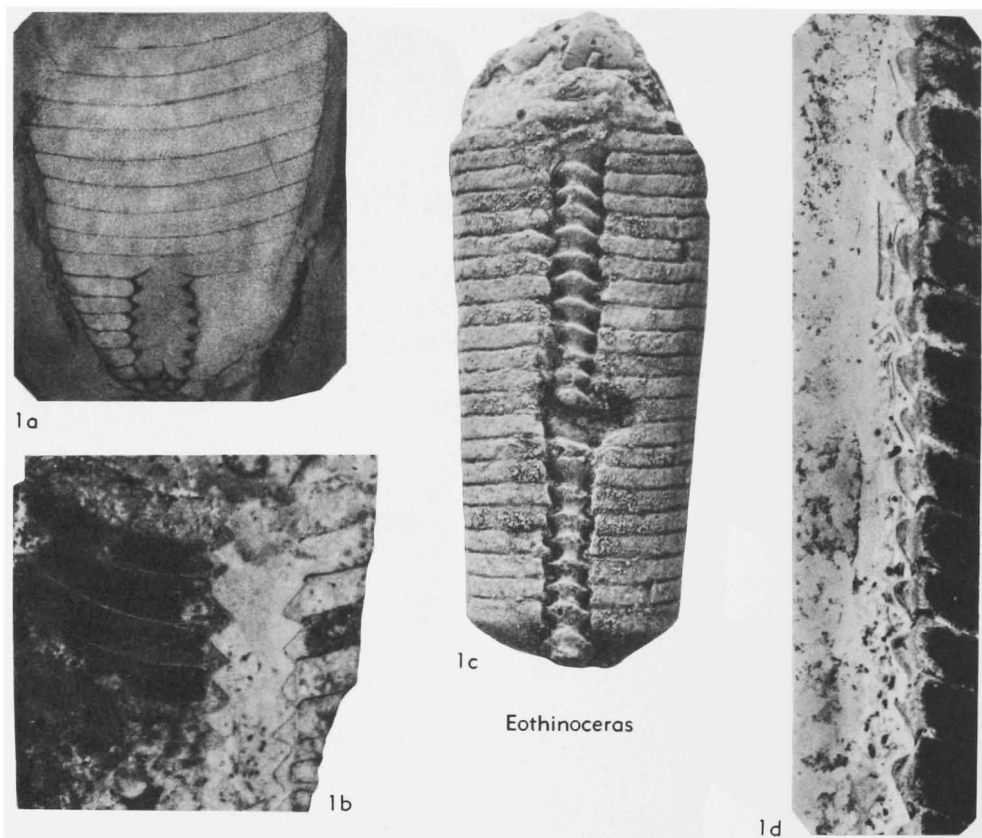


FIG. 95. Bathmoceratidae (p. K156, K158).

FIG. 96. \**Shideleroceras sinuatum* FOERSTE (Shideleroceratidae) (p. K159).

BAY, 1944, p. 131 [*E. americanum*; OD]. Gradually expanded smooth orthocones and gently exogastric cyrtocoines with subcircular cross section; sutures essentially straight, but with narrow, rounded ventral saddle; siphuncle situated close to ventral wall, 0.2 to 0.3 of conch diameter, siphuncular segments weakly concave; septal necks orthochoanitic; connecting rings thick, triangular in section with apex of triangle at about mid-length of camerae; diaphragms irregular. *L.Ord.*(*U.Canad.*), USA(N.Y.)-W.Australia-USSR (Sib.Platform).—FIG. 95,1a. \**E. americanum*, USA(N.Y.); holotype, oblique sec.,  $\times 3$  (204). —FIG. 95,1b-d. *E. maitlandi* TEICHERT & GLENISTER, W.Australia; 1b, lat. sec.,  $\times 9$  (193); 1c,d, ventral view,  $\times 3$ , and dorsoventral section of ectosiphuncle,  $\times 8$  (Furnish & Glenister, n).

#### Family CYRTOCERINIDAE Flower, 1946

[Cyrtocerinidae FLOWER, 1946, p. 585]

Endogastric cyrtocoines with large submarginal siphuncle; septal necks achoanitic, connecting rings thick and similar to those of Bathmoceratidae. *M.Ord.*-*U.Ord.*



**Cyrtocerina** BILLINGS, 1865, p. 178 [*\*C. typica*; M]. Rapidly expanded cyrtconic endogastric compressed brevicones; sutures straight; siphuncle submarginal, 0.2 to 0.3 of conch diameter; siphuncular segments concave, septal necks achoanitic; connecting rings thick, projecting inward as promi-

nent transverse flanges. *M.Ord.*(*Blackriver.*)-*U.Ord.*(*Richmond.*), N. Am. (widespread).—FIG. 96, *1a*. *\*C. typica*, *M.Ord.*(*Blackriver.*), Can. (Ont.); holotype, ventral view,  $\times 1$  (216b).—FIG. 96, *1b,c*. *C. crenulata* FLOWER, *M.Ord.*(*Blackriver.*), USA(Wis.); ventral and lat. views,  $\times 1$

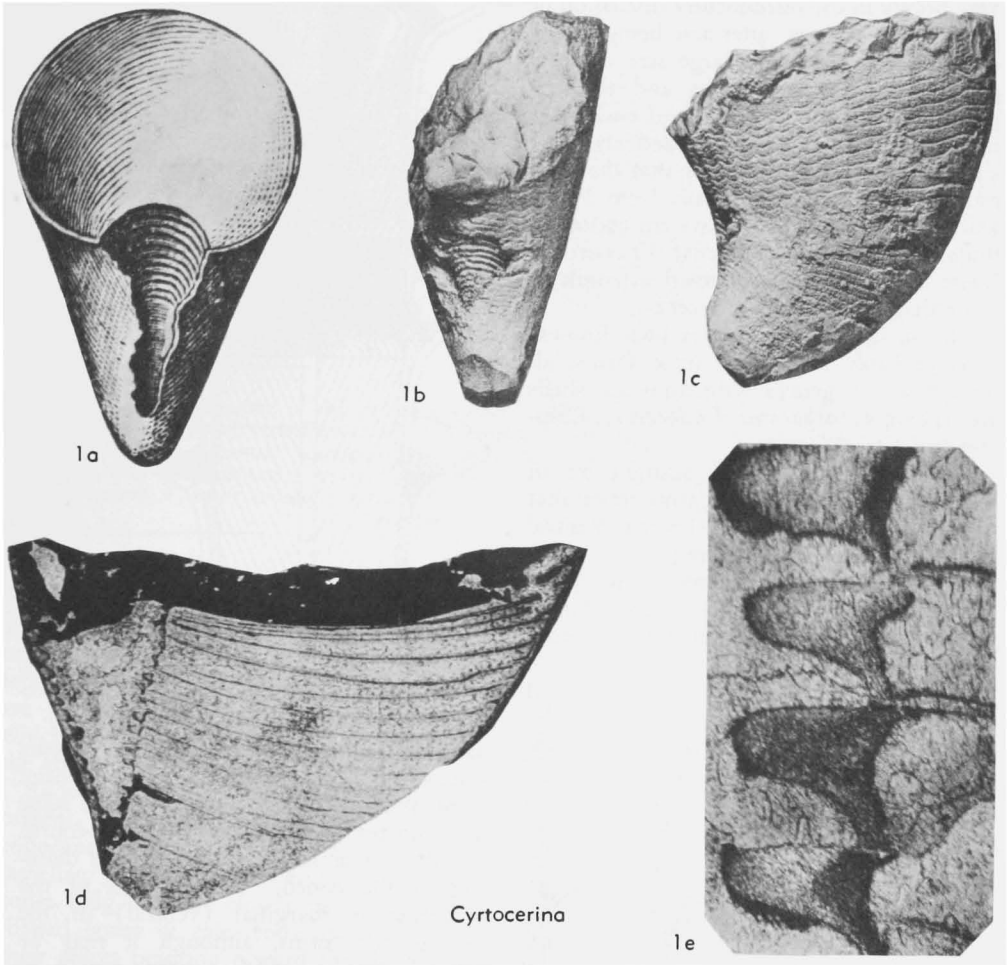


FIG. 97. Cyrtocerinae (p. K159).

(39).—FIG. 96, *1d,e*. *C. madisonensis* (MILLER), *U.Ord.*(*Richmond.*), USA(Ind.); sec.,  $\times 1$ , and ectosiphuncle,  $\times 18$  (33).

### Family SHIDELEROCERATIDAE Flower, 1946

[Shideleroceratidae FLOWER, 1946, p. 508]

Gently cyrtconic longicones with small subcentral cylindrical siphuncle; septal necks achoanitic, connecting rings thin. [Ellesmerocerid affinities doubtful.] *U.Ord.*

**Shideleroceras** FLOWER & FOERSTE in FLOWER, 1946, p. 508 [*\*S. sinuatum* FOERSTE in FLOWER, 1946, p. 510; OD]. Gradually expanded gently cyrtconic conchs with subcircular section; sutures essentially straight; siphuncle subcentral but closer to convex side, about  $\frac{1}{8}$  of conch diameter, siphuncular segments tubular; septal necks achoanitic, connecting rings thin. *U.Ord.*(*Richmond.*), USA(Ohio-Ind.).—FIG. 97, *1*. *\*S. sinuatum* FOERSTE, Ohio; *1a,b*, ventral and lat. views,  $\times 1$  (33).

## ENDOCERATOIDEA

By CURT TEICHERT

[United States Geological Survey]

## MORPHOLOGY

The endoceratoids have been described very briefly in the introductory discussion of nautiloid subclasses, attention being called chiefly to the generally large size of their prevalingly straight conchs and the important distinguishing feature of endocones in the posterior part of the relatively large siphuncle. We may add here that the largest known invertebrate fossils from Paleozoic rocks are Middle Ordovician endoceratoids belonging to the order Endocerida. Some of these conchs attained a length of more than 9 m. (nearly 30 feet).

The surface of the shell is little known. It is probably smooth in most forms, although a few genera with annulate shells are known (*Anthoceras*, *Endoceras*). Cameral deposits are absent.

The sutures are generally straight, but in some genera they have ventral lobes that usually are deep and well defined. Ventral saddles are encountered rarely.

The siphuncle is characteristically large. Only some Early Ordovician forms (Thylacoceratidae and some Proterocamerocerati-

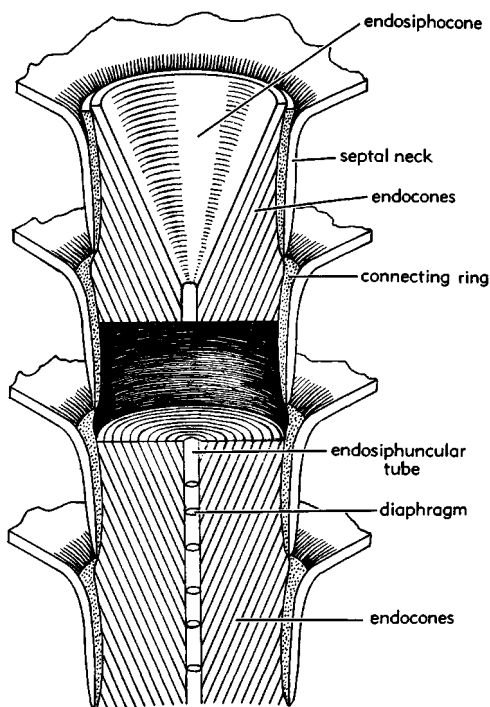


FIG. 99. Basic structural elements found in siphuncles of the Endocerida (Teichert, n).

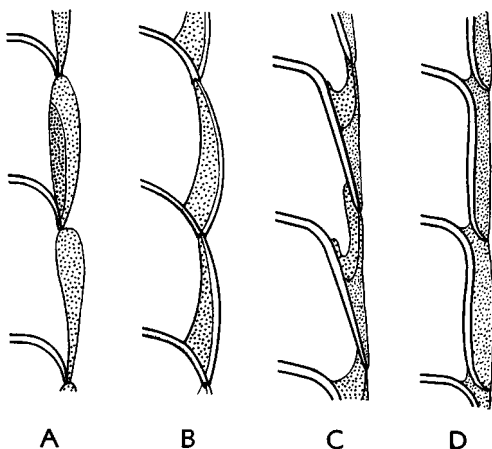


FIG. 98. Different types of septal necks and connecting rings in Endocerida: A, achoanitic necks and complex connecting ring of ellesmerocerid type; B, orthochoanitic neck and complex ring; C, hemichoanitic neck with ringless complex; D, holchoanitic neck with simple connecting ring lining inside of neck (after 34).

dae) have narrow siphuncles. In some genera the siphuncle occupies the entire apical part of the shell. In the adult stage its diameter is rarely less than one-fourth and may be as much as one-half the diameter of the conch. The position of the siphuncle is marginal (ventral) in the majority of forms, although it may be somewhat removed from the center in some; very rarely it is subcentral.

The siphuncular wall consists of septal necks and connecting rings. The septal necks are straight, ranging from almost achoanitic (*Proterocameroceras*) to macrochoanitic (*Proterovaginoceras*) (Fig. 98). Orthochoanitic and hemichoanitic forms have more or less cylindrical connecting rings that are either simple or moderately complex. Subholochoanitic forms usually have thick connecting rings. Holochoanitic

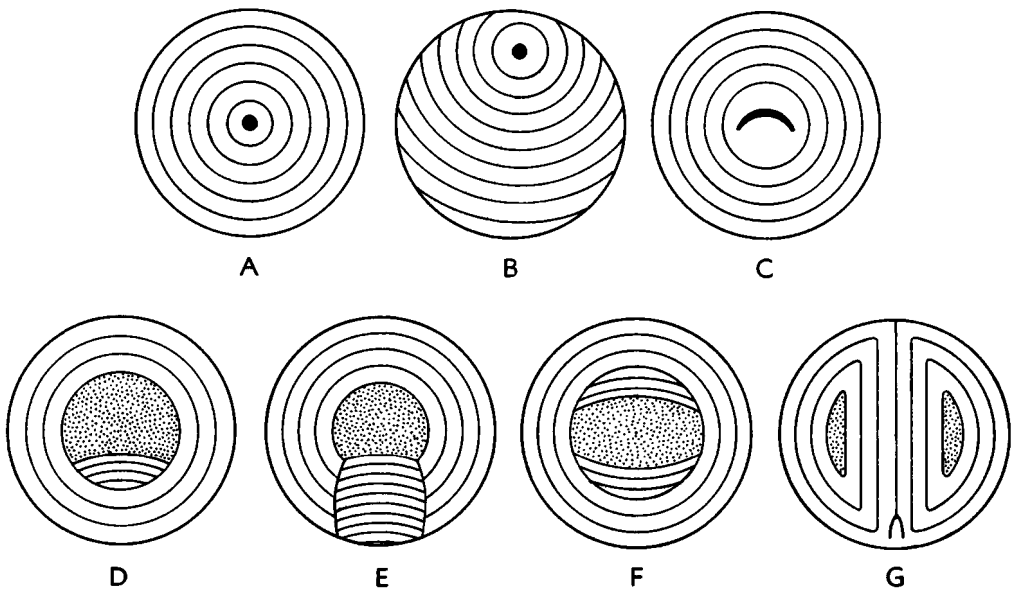


FIG. 100. Some modifications of the endocone system in Endocerida seen in cross section (black, endosiphuncular tube; stippled, endosiphocoones): A, concentric (*Cameroceras*); B, excentric (*Retroclitendoceras*, *Tasmanoceras*); C, concentric, with endosiphuncular tube of crescentic cross section (*Chazyoceras*); D, concentric, with endosiphuncular wedge (*Manchuroceras*); E, concentric, with ventral mass (*Coreanoceras*, *Emmonsoceras*); F, outer endocones concentric, inner ones elliptic (*Cameroceras*); G, double endocones (*Allotrioceras*) (Teichert, n).

and macrochoanitic forms have rudimentary connecting ring matter between the septal necks, but some have continuous connecting ring linings on the inside of the septal necks. If the connecting rings inside are continuous, they form a dark layer, which is probably what RUEDEMANN termed the endosiphuncular lining.

Endosiphuncular deposits are invariably present, most commonly in the form of **endocones**, more rarely as radially arranged lamellae, as in the Intejocerida. The endocones (Fig. 99) are closely packed funnel-shaped layers of calcareous material, with their apices pointing toward the tip of the shell and pierced by generally one, less commonly two or more tubes, called **endosiphuncular tubes**. Rarely, endosiphuncular tubes may be partitioned by transverse diaphragms. The space inside the last endocone is commonly called **endosiphocoone**. If it is filled with rock matrix, this inorganic filling is sometimes referred to as the **spiculum** (*Spiess*).

The endosiphuncular tube commonly runs slightly dorsal to the central axis of

the siphuncle. In some specialized forms (e.g., *Tasmanoceras*) (Fig. 100,B) the endocones are very asymmetrical or a complex system of multiple endocones develops as in the Chihlioceratidae and in the Allotrioceratidae (Fig. 100,G).

The endosiphocoone may be partially filled by calcareous deposits on the ventral side, or on both ventral and dorsal sides, forming the **endosiphuncular wedge** or wedges (e.g., *Manchuroceras*) (Fig. 100,D-F).

In well-preserved specimens the endocones consist of light calcite and are separated by thin dark layers that may be conchiolin films, similar to those found in the shell wall and in the septa of cephalopods. In many specimens the endocones are recrystallized during diagenesis and the space originally occupied by them is filled with structureless crystalline calcite. The form of the spiculum may then be diagnostic.

The endosiphuncular tube is usually thin and cylindrical, but in specialized forms its cross section may be flat (either depressed or compressed) or it may be half-moon or

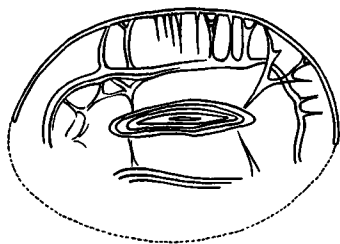


FIG. 101. Cross section of siphuncle of *Piloceras* with endosiphocoleon and endosiphofunicles (after Ruedemann, 1904).

sickle-shaped (Fig. 100,C). In a number of genera the endosiphuncular tube is traversed by widely or closely spaced, thin, concave partitions. In one family (Allotrioceratidae), more than one endosiphuncular tube is present, especially in the apical part of the siphuncle.

In some endoceratoids it has been shown that the endosiphuncular tube lies inside a dark area of depressed cross section, which possibly represents original conchiolin, and which, in a few instances, has been traced into the space of the endosiphocone. This depressed conchiolin(?) tube is called the **endosiphocoleon** (Fig. 101).

In some forms the endocones are traversed by thin, membrane-like structures that are arranged radially with respect to the endosiphuncular tube and extend from the latter to the siphuncle wall. These membranes are called **endosiphuncular blades**. In cross sections of the siphuncle, blades may vary widely in appearance in different forms. Commonly their number is either two or three, but more may be present (Fig. 102). They may be uniform throughout the entire siphuncle or, in some forms, these features may vary during ontogeny.

Other radial elements which are irregular in shape and length have been described as **secondary blades** and as **endosiphofunicles** (Fig. 101) (24), but they rarely have been observed.

The order Intejocerida is anomalous in having the siphuncle occupied by radial calcareous lamellae, rather than by endocones. These will be described in greater detail in the introduction to that order.

## ONTOGENY

Endoceratoids are characterized by the fact that from the very first stage of shell formation the siphuncle is proportionally larger than in any other cephalopod subclass. Because of the vagaries of preservation, as well as the large size of many endoceratoid genera, the ontogeny of many forms is very incompletely known, and for some genera it is not known at all. Some generic names, such as *Nanno*, have been given to specimens representing only the initial part of phragmocones, and the mature stages of such "genera" are unknown. On the other hand, many generic names have been given to forms representing only portions of mature stages of conchs, and several others are based on isolated siphuncles and the shape and size of the phragmocones of such genera remain unknown.

It is known, however, that in the earliest shell-forming stages, endoceratoids may develop in one of two ways: 1) The initial part of the shell is entirely occupied by the siphuncle (see Fig. 37,G), the first septum and camera being formed at a distance of one to several centimeters from the apex of the shell. (2) Formation of the first septum occurs close to the apex of the shell

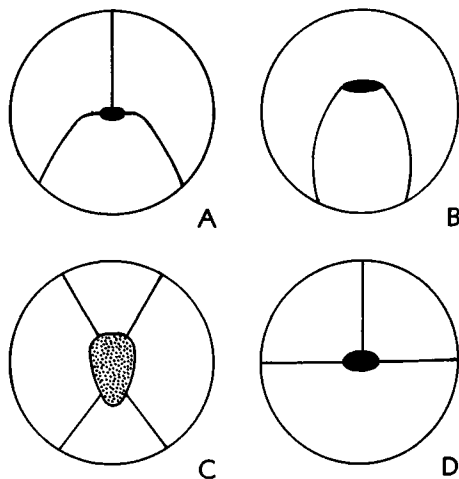


FIG. 102. Some types of arrangements of endosiphuncular blades.—A, *Cameroceras* (HOLM, 1885).—B, *Coreanoceras* (KOBAYASHI, 1936).—C, *Phragmosiphon* (FLOWER, 1956).—D, *Proterocameroceras* (RUEDEMANN, 1904) (Teichert, n).

and the entire phragmocone is camerate, as in other nautiloid orders (see Fig. 37,D).

In the first-mentioned group, the initial, noncamerate part of the conch may expand gradually or rapidly. If it expands rapidly, being entirely filled by the siphuncle, it is sharply contracted at the place where the first septum and camera are formed and the apical part of the siphuncle thus has a bulbous shape. From the point where the constriction takes place, the siphuncle retains a more or less constant diameter, whereas the conch expands very slowly in diameter. Thus, the ratio of conch diameter to siphuncle diameter increases slowly and gradually during ontogenetic growth of most endoceratoids.

In the second group, the siphuncle occupies a considerable part of the conch from the beginning but never its entire apical region. It is in contact with the inside of the ventral wall and part of the lateral walls of the conch, but the dorsal part of the apex is occupied by the first camera. It is not known with certainty whether this first chamber is homologous or analogous to the initial chamber of the actinoceratoid and nautiloid orders. The second alternative is regarded as more likely, because in forms of Group 1, where the first septum is formed at some distance from the apex, the first chamber cannot in any way be compared to the identical chamber in the nautiloid groups.

In the extreme apical part of the siphuncle, endocones are generally not clearly distinguished, and it seems that this part was filled out by rapid deposition of calcareous substance at an early growth stage. An alternative interpretation is that the endocones were thinnest in this region and so were more easily recrystallized.

In well-preserved specimens (which are few) the endosiphuncular tube can be followed through this unorganized calcareous deposit to the apex of the shell. It has been suggested that the tube pierced the apex or that a former opening is closed by a cicatrix, the true protoconch (or initial chamber) being supposedly situated outside the apex of the conch; observations that have led to these suggestions need confirmation.

## CLASSIFICATION

For many years almost all endoceratoids were united in a single family, the Endoceratidae of HYATT. For a long time knowledge of the group was almost entirely restricted to the large genera of Middle Ordovician age in Europe and North America (e.g., *Cameroceras*, *Endoceras*, *Vagino-ceras*, *Proterovaginoceras*). More recently, beginning in the 1920's, a multitude of endoceratoid forms was discovered in Lower and Middle Ordovician rocks of eastern Asia, and large and complex faunas became known from the Early Ordovician of North America, Australia, and Siberia.

The complexity of siphuncular structures, the vagaries of preservation, especially of larger forms, and the fact that genera have been based partly on fragments of mature conchs, partly on apical fragments, partly on isolated siphuncles in various states of preservation, and only in the rarest of cases on entire shells—all these factors constitute great obstacles for any attempt to formulate a natural classification of the group. That the endoceratoids constitute a taxon of ordinal rank was first suggested by TEICHERT in 1933. This suggestion gained ground, and since 1950 (49), became rather generally accepted. FLOWER (47) suggested subdivision of the order into two suborders, Proterocameroceratina, including members of the previously mentioned Group 2 (defined in the chapter on ontogeny), and Endoceratina, members of Group 1. Because of the various adverse factors cited, this subdivision, though probably taxonomically sound, is difficult to implement in practice, and many genera cannot be assigned with certainty to either suborder.

Still more recently, BALASHOV (4) made known a suborder which he named Intejoceratina. The members of this group share morphological characteristics that set them apart from all other previously known endoceratoids.

Families of the Endocerida are of very unequal scope. Almost certainly, families with many genera (e.g., Proterocameroceratidae, Endoceratidae) are not phylogenetic units. They contain many genera of unknown derivation and affinities. On the other hand, families containing only one or a few genera (e.g., Manchuroceratidae, Chihlio-

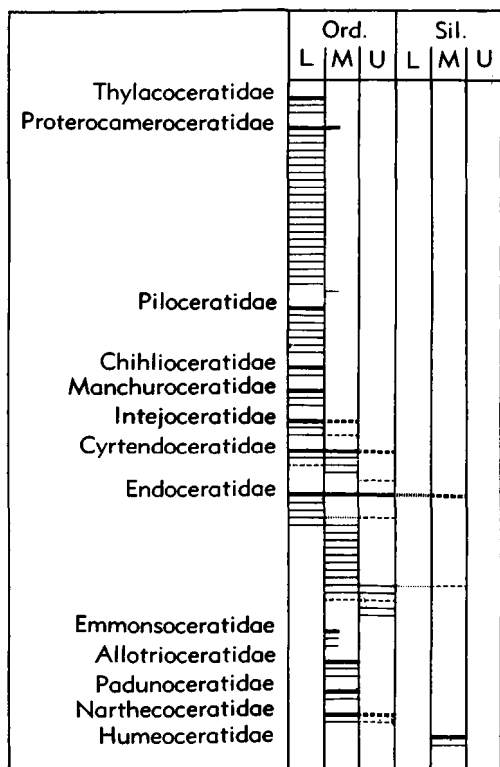


FIG. 103. Stratigraphic distribution of genera and families of Endoceratoidea (Teichert, n).

ceratidae) may be regarded as well-defined phylogenetically related groups.

## EVOLUTION

Endoceratoids developed from ellesmerocerids in Early Ordovician (Middle Canadian) time through formation of endocones (Fig. 69). The transition was gradual and probably it proceeded simultaneously in different lineages. Some ellesmerocerids developed broad siphuncles without endocones (Baltoceratidae). In other lines endocones developed in relatively narrow siphuncles (Thylacoceratidae). In this evolutionary transition zone some genera have been described that might well be classified as endoceratoids, but since no endocones have as yet been discovered in them, they are here placed with the ellesmerocerids.

The greatest diversification of the endoceratoid stock took place in the Early Ordovician (Middle to Upper Canadian) Epoch, which was a time of explosive (or eruptive)

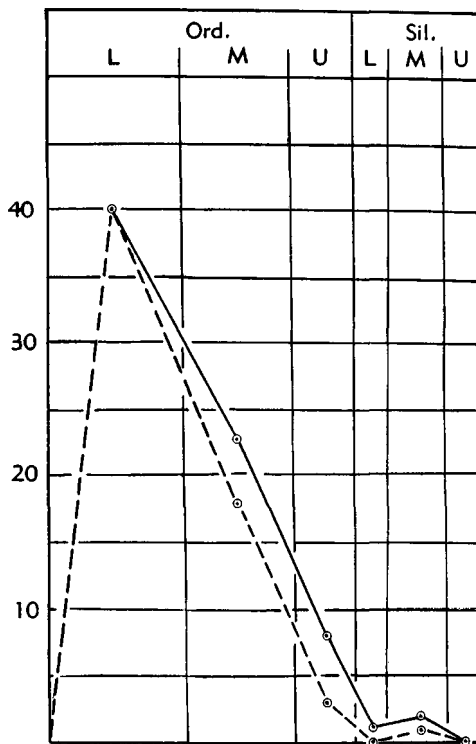


FIG. 104. Graph showing numbers of new genera of Endoceratoidea introduced in successive epochs (dashed lines) and total genera represented in each (solid lines) (Teichert, n).

nautiloid evolution (Fig. 103, 104). The Thylacoceratidae retained the primitive, comparatively narrow ellesmerocerid siphuncle to which endocones were added. The Proterocameroceratidae blossomed into a diversity of forms. While some retained the primitive orthochoanitic septal necks, these were modified in other representatives into hemichoanitic and subholochoanitic structures. Connecting rings remained complex for the most part.

Other early specializations occurred in the Manchuroceratidae, with breviconic shells, thick siphuncles, and heavy, asymmetrically disposed endocones, in the weakly cyrtoconic Piloceratidae, with holochoanitic septal necks, and in the rare Chihlioceratidae, with a multiple endocone system.

Endoceratidae with holochoanitic, and even macrochoanitic, septal necks and simple endocone systems also appeared in the late Early Ordovician. This family proved

to be the most successful one of the entire subclass.

While most Proterocameroceratidae and all Thylacoceratidae, Piloceratidae, Manchuroceratidae, and Chihlioceratidae became extinct at the end of Early Ordovician time, the Endoceratidae expanded in the Middle Ordovician. During this epoch they produced shells 15 to 30 feet long (*Camero-ceras*), the largest of any invertebrate fossils of Paleozoic times. The distribution of the family was worldwide, but giant forms are known only from North America and northern Europe.

Along with the Endoceratidae, small specialized groups also appeared in the Middle Ordovician. These were the Cyrtendoceratidae, which were strongly cyrtconic, the Emmonsoceratidae, which are large, longiconic derivatives of the Manchuroceratidae, the Allotrioceratidae, with very complex, specialized systems of endocones, and the presumably huge Narthecoceratidae, which have no known ancestors or descendants.

Only the Endoceratidae continued with certainty into the Late Ordovician and to its end. Other families (e.g., Cyrtendoceratidae, Narthecoceratidae) are doubtfully represented during the latter part of the Ordovician Period.

Presently available evidence suggests that the Endoceratidae may have survived into the Silurian (Fig. 103). A few specimens of that age have been reported from several localities in northern Canada, but none of them has been well described and all records are in need of further scrutiny.

The genus *Humeoceras* stands apart from other, scattered finds of supposedly holchoanitic conchs of Silurian age, because of its close resemblance to Early Ordovician piloceratids. The resemblance is entirely external, because details of the internal structure of *Humeoceras* are unknown. The genus is here regarded as representing a separate family that contains Middle Silurian homeomorphs of the Early Ordovician piloceratids.

## GEOGRAPHIC DISTRIBUTION

Early occurrences of endoceratoids are widespread, rich Early Ordovician faunas being known from Australia, eastern Asia, Siberia, and eastern North America. By

Middle Ordovician time, endoceratoids were well established in all continents except Africa. In most parts of the world they became extinct at the end of the Ordovician. They survived longest in North America, where they seem to have lingered on until the Middle Silurian.

## SYSTEMATIC DESCRIPTIONS

### Subclass ENDOCERATOIDEA Teichert, 1933

Diagnosis given in "Introductory Discussion" (p. K128). *L.Ord.-U.Ord.*, ?*M.Sil.*

The stratigraphic occurrence of genera included in the Endoceratoidea is shown graphically in Figure 103; the numbers of new genera introduced in successive epochs are indicated in Figure 104.

### Order ENDOCERIDA Teichert, 1933

[*nom. correct.* TEICHERT, herein, *pro* Endoceroidea TEICHERT, 1933; mention of Endocerida by FURNISH, GLENISTER, & HANSMAN, 1962 (p. 1343), is disregarded] [=Vaginati QUENSTEDT, 1836; Pleurosiphonides PICTET, 1854; Metachoanites HYATT, 1883 (ranked as subdivision of Holchoanoidea of unspecified taxonomic rank); Holchoanites HYATT, 1898 (suborder); Endoceracea SCHINDEWOLF, 1935 (suborder); Endoceracea KUHN, 1949 (order); Endoceratida FLOWER in FLOWER & KUMMEL, 1950 (order) (*non* Endoceratida HYATT, 1900, =superfamily because ranked as group of suborder Holchoanites); Endoceroida FISCHER in MOORE, LALICKER & FISCHER, 1952 (order); Endoceratina SWEET, 1958 (suborder); Endoceratida BALASHOV, 1961 (order); incl. Proterocameroceratina, Endoceratina FLOWER, 1958 (suborders)]

Breviconic, longiconic, or endogastrically curved conchs with small to large, generally marginal, more rarely subventral or central siphuncles with posterior part filled by simple or complex endocones. Septal necks ranging from nearly achoanitic to macrochoanitic. *L.Ord.(M.Canad.)-U.Ord.(Richmond.)*, ?*M.Sil.*

### Family THYLACOCERATIDAE Teichert & Glenister, 1954

Conchs straight or slightly curved, with small to medium-sized marginal siphuncles and hemichoanitic to subholchoanitic septal necks. *L.Ord.*

*Thylacoceras* TEICHERT & GLENISTER, 1952 [\**T. kimberleyense*; OD]. Gently tapering, slightly endogastric conchs, with depressed cross section; suture sinuous, with deep U-shaped lobe across venter. Siphuncle marginal, with moderate-sized septal necks which are subholchoanitic, or almost so; connecting rings thick; endosiphuncular tube thin, cylindrical. *L.Ord.(U.Canad.)*, Asia(Inner

Mongolia)-NW.Australia.—FIG. 105,1. \**T. kimberleyense*, NW.Australia; 1a, ventral,  $\times 1$ ; 1b, adoral portion of ventral side,  $\times 3$  (82).

**Talassoceras** BALASHOV, 1960 [\**T. kumyschiagense*; OD]. Small straight, gradually expanding conchs; cross section circular in early growth stages, becoming slightly compressed in adult; sutures straight, sloping slightly backward on venter; septa only slightly concave. Siphuncle broad, almost in contact with wall; septal necks hemichoanitic; spiculum short, endosiphuncular tube thin, cylindrical. *L.Ord.*, C.Asia.—FIG. 105,2. \**T. kumyschiagense*; 2a,b, dorsoventral sec.,  $\times 1$ , and lat. view,  $\times 0.7$ ; 2c, long. sec.,  $\times 5$  (4).

### Family

### PROTEROCAMEROCERATIDAE

Kobayashi, 1937

[*nom. transl.* FLOWER, 1946 (*ex* Proterocameroceratinae KOBAYASHI, 1937)]

Slender, straight or slightly cyrtconic conchs, small to medium-sized. Siphuncles small to medium-sized, marginal; septal necks ranging from nearly achoanitic to almost holchoanitic; connecting rings thick, in some forms complex; endosiphuncular structures simple or complex. *L.Ord.*(*M. Canad.*)-*M.Ord.*(*Chazy.*).

### GENERA KNOWN FROM MORE OR LESS FRAGMENTARY CONCHS, INCLUDING SIPHUNCLES, BUT MOSTLY WITH MISSING APICAL END AND BODY CHAMBER

**Proterocameroceras** RUEDEMANN, 1905 [\**Orthoceras brainerdi* WHITFIELD, 1886; OD]. Rather large straight, longicones with short camerae; sutures simple or slightly sinuous. Siphuncle large, ventral; septal necks short, forked; connecting rings thick, complex; endocones flattened, 3 endosiphuncular blades present; apical part of shell long, conical, tapering slowly. *L.Ord.*(*U.Canad.*), N.Am.-Greenl.-USSR(Sib.)-NW.Australia.—FIG. 106,1a-d. \**P. brainerdi* (WHITFIELD), Cassin Ls., USA(N.Y.-Vt.); 1a, ventral,  $\times 0.7$ ; 1b, long. sec.,  $\times 1$ ; 1c, transv. sec. of siphuncle,  $\times 3$ ; 1d, extreme adapical portion of siphuncle,  $\times 1$  (204).—FIG. 106,1e. *P. contrarium* TEICHERT & GLENISTER, NW.Australia; septal necks and connecting ring,  $\times 12$  (193).

**Anthoceras** TEICHERT & GLENISTER, 1954 [\**A. decorum*; OD]. Straight, annulate, longiconic conchs, with circular cross section. Siphuncle moderately large, marginal, with constricted segments; septal necks hemichoanitic to subholchoanitic, connecting rings thick; endocones slightly asymmetric, long. Apical end and body chamber unknown. *L.Ord.*(*M.Canad.*-*U.Canad.*), N.Am.-NW.Australia-USSR(Sib.).—FIG. 105,5. \**A. decorum*, U.Canad., NW.Australia; dorsoventral sec.,  $\times 6$  (193).

**Campendoceras** TEICHERT & GLENISTER, 1954 [\**C. gracile*; OD]. Weakly cyrtconic, slender, endogastric longicones, with circular cross section and annulate shell. Siphuncle large, marginal; septal necks subholchoanitic; endocones present. *L.Ord.*(*U.Canad.*), NW.Australia-?Eu.(Est.).—FIG. 106,2. \**C. gracile*, NW.Australia; 2a,b, lat. view, long. sec.,  $\times 1$  (193).

**Clitendoceras** ULRICH & FOERSTE, 1936 [\**C. saylesi*; OD]. Slightly cyrtconic, endogastric conchs, with compressed or circular cross section; sutures sloping forward on dorsum. Siphuncle slender, marginal; septal necks short in young, lengthening in adult; proximal endocones extended forward on ventral side; spiculum flattened ventrally. *L.Ord.*(*M.Canad.*-*U.Canad.*), N.Am.-USSR(Sib.).—FIG. 107,1a. \**C. saylesi*, Cassin Ls., USA(N.Y.); lat. view,  $\times 0.7$  (201).—FIG. 107,1b-d. *C. brevicorniferum* FLOWER, U.Canad.(El Paso Ls.), USA(W.Tex.); 1b-d, siphuncle, oblique anterodorsal view to show ventral thickening of endocones, dorsal, lat.,  $\times 0.7$  (45).

**Cotteroceras** ULRICH & FOERSTE, 1936 [\**C. compressum*; OD]. Straight, slender, compressed longicones; camerae very short, body chamber long; sutures straight, oblique, sloping adapically from dorsum to venter. Siphuncle large, marginal, structure of ectosiphuncle unknown; spiculum generally short; structure of endocones unknown. *L.Ord.*(*M.Canad.*-*U.Canad.*), N.Am.(Mo.-Minn.-Va.)-USSR(Sib.).—FIG. 107,2. \**C. compressum*, Cotter Dol., USA(Mo.); 2a,b, lat. view, fragment with part of siphuncle and spiculum,  $\times 1$  (204).

**Cyptendoceras** ULRICH & FOERSTE, 1936 [\**C. ruedemanni*; OD] [= *Cyptendocerina* ULRICH, FOERSTE, MILLER & UNKLESBAY, 1944]. Straight, slender, depressed conchs with short camerae; sutures with ventral lobe, in some conchs dorsal lobe also. Siphuncle ventral, structure unknown. *L.Ord.*(?mid. *U. Canad.*), N.Am.(widespread).—FIG. 107,5. \**C. ruedemanni*, Cassin Ls., USA(Vt.); ventral,  $\times 1$  (201).

**Lobendoceras** TEICHERT & GLENISTER, 1954 [\**L. emanuelense*; OD]. Straight, rather large conch, with circular cross section; moderately expanded; camerae short, sutures with broad, deep, ventral lobe. Siphuncle large, marginal; septal necks subholchoanitic to holchoanitic; endocones present. Body chamber and apical end unknown. *L.Ord.*(*U. Canad.*), NW.Australia-USSR(Sib.).—FIG. 107,4. \**L. emanuelense*; 4a-c, ventral, dorsal, ant. views,  $\times 0.7$  (193).

**Mcqueenoceras** ULRICH & FOERSTE, 1936 [\**M. jeffersonense*; OD]. Similar to *Clitendoceras*, but sutures with distinct ventral lobes; ventral side of endocones flattened, thickened, dorsal side thin. *L.Ord.*(*U.Canad.*), N.Am.-USSR(?Sib.).

**Meniscoceras** FLOWER, 1941 [\**M. coronense*; OD]. Straight, slender conchs, not well known. Siphuncle large, septal necks short; connecting rings



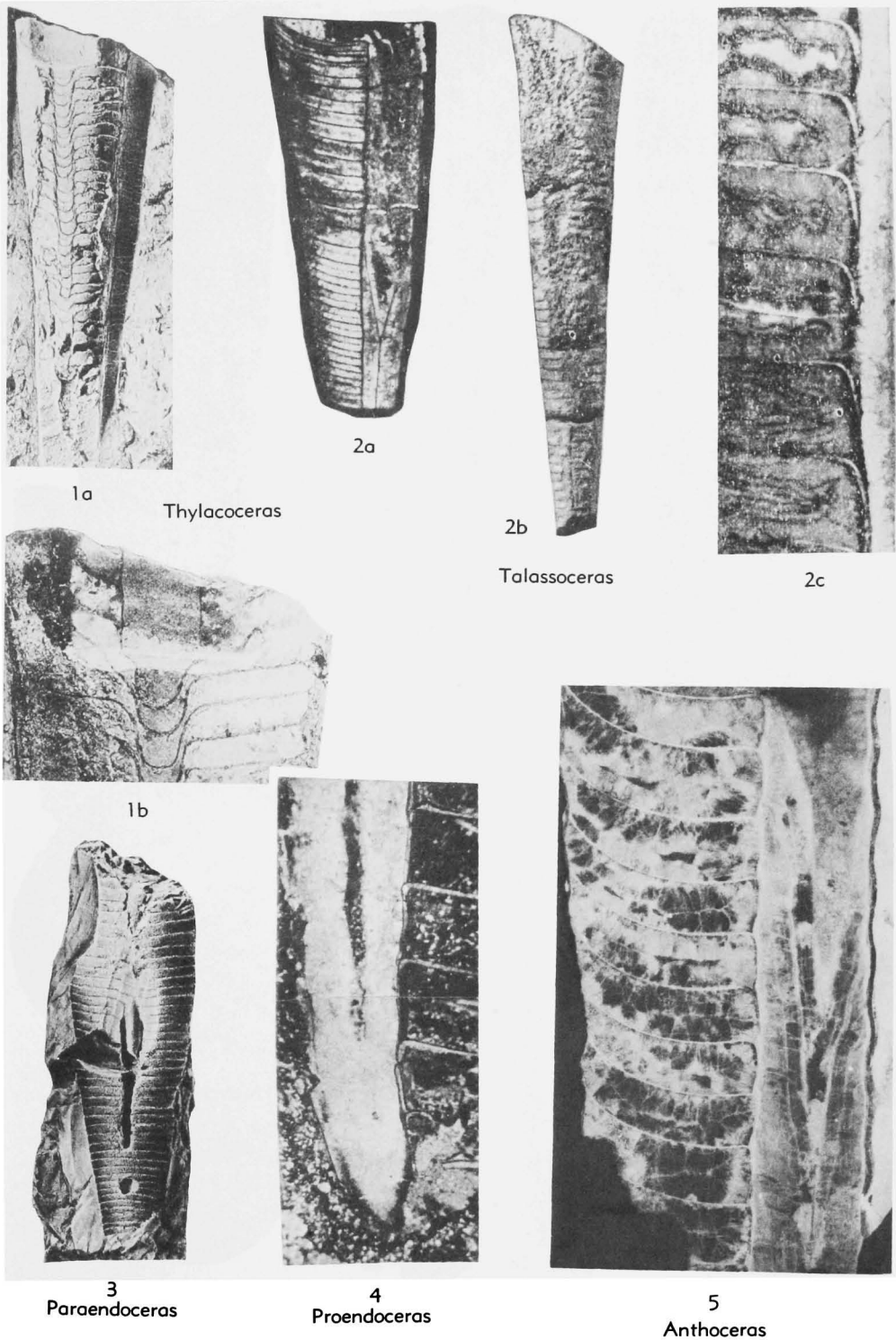


FIG. 105. Thylacoceratidae, Proterocameroceratidae (p. K165-K166, K170).

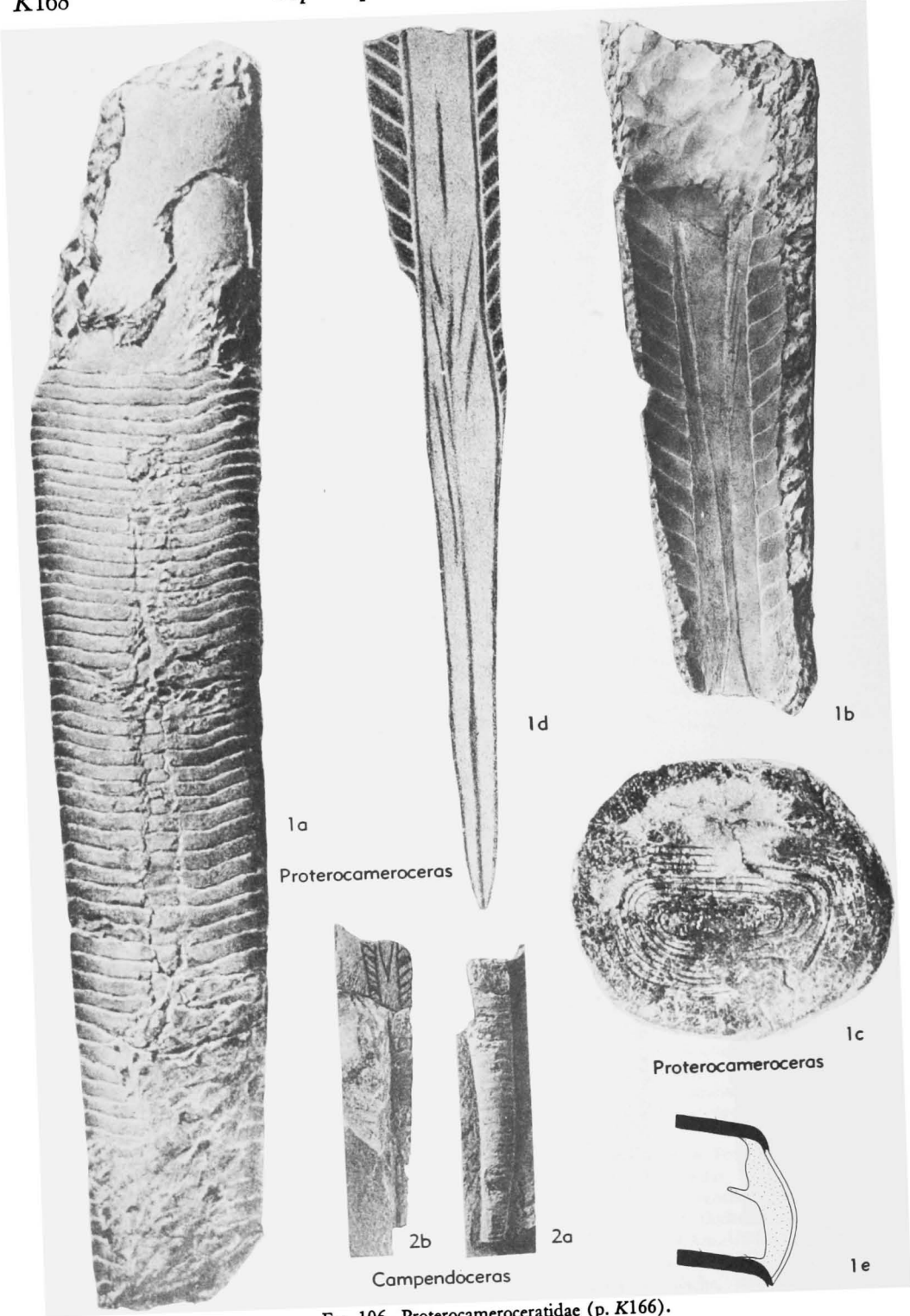


FIG. 106. Proterocameroceratidae (p. K166).

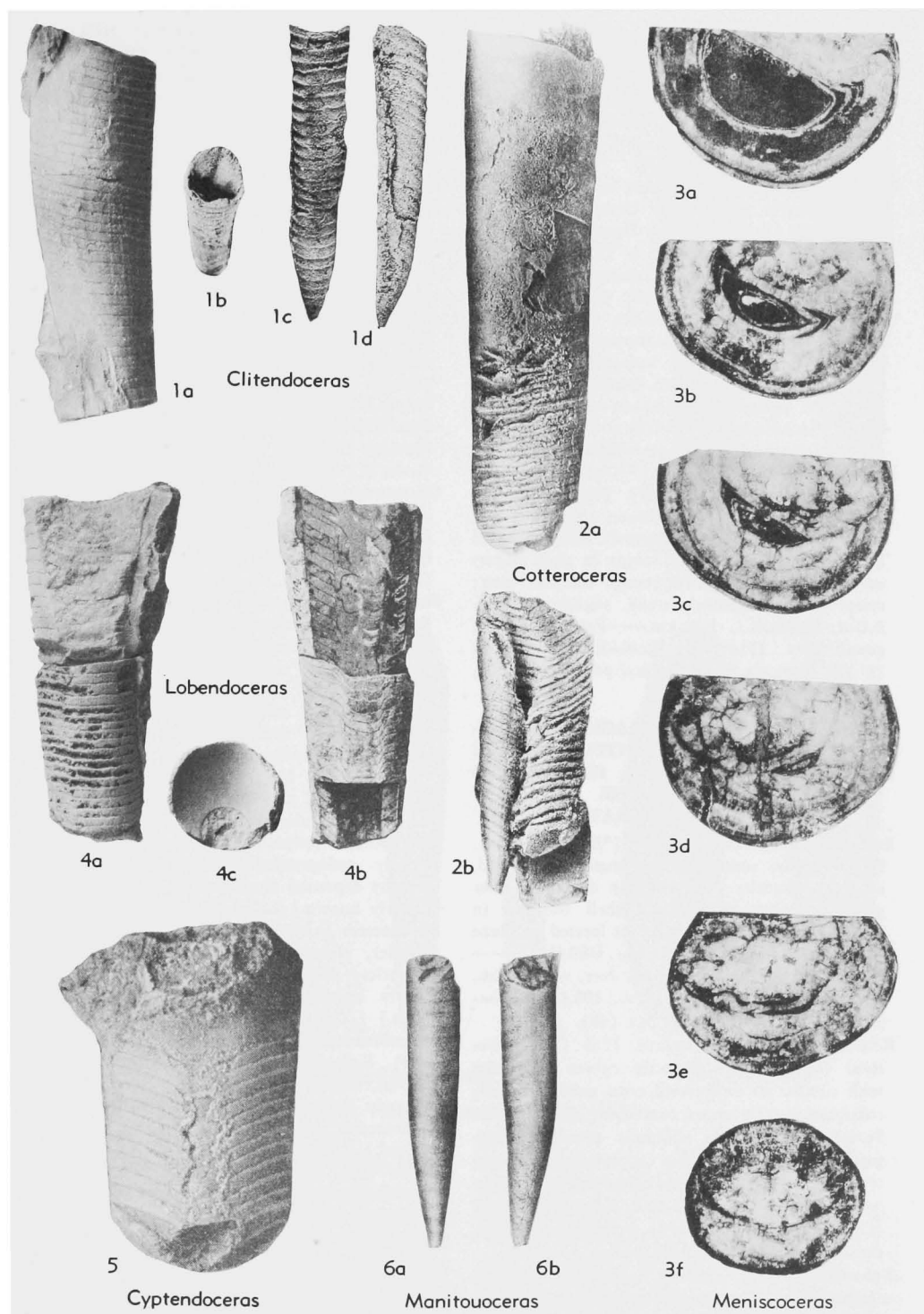


FIG. 107. Proterocameroceratidae (p. K166, K170).

thin; endocones asymmetric, dorsally flattened, concave near apex; apex of endocones and endosiphuncle flattened, endosiphuncular tube thin, tubular; 2 lateral endosiphuncular blades present. *Lou.M.Ord.(M.Chazy.)*, E.N.Am.—FIG. 107,3. \**M. coronense*, USA(N.Y.); 3a-f, successive cross sections of siphuncle,  $\times 1$  (27).

**Paraendoceras** ULRICH & FOERSTE in FOERSTE, 1936 [\**Saffordoceras jeffersonense* ULRICH & FOERSTE, 1936; OD] [= *Saffordoceras* ULRICH & FOERSTE, 1936 (obj.) (non FOERSTE & TEICHERT, 1930; *Parendoceras* ULRICH & FOERSTE, 1936 (nom. null.)). Straight, fairly rapidly enlarging conchs with small marginal siphuncles, short camerae; probably holocoanitic; endocones long; apical end and body chamber unknown. *L.Ord.(M.Canad.-U.Canad.)*, E.N.Am.-USSR(Sib.).—FIG. 105,3. \**P. jeffersonense* (ULRICH & FOERSTE), M. Canad.(Roubidoux F.), USA(Tenn.); ventral view (note spiculum slightly above middle),  $\times 1$  (201).

**Proendoceras** FLOWER, 1955 [\*“*Cameroceras*” *annuliferum* FLOWER, 1941; OD]. Straight, slender, slightly depressed conchs; sutures straight, transverse. Siphuncle tubular, ventral, narrow; septal necks very short in young, longer in adult stages; connecting rings thin in young, complex later; apical part of siphuncle small, slightly bulbous. *L.Ord.(M.Canad.)*, E.N.Am.—FIG. 105,4. \**P. annuliferum* (FLOWER), Roubidoux F., USA (N.Y.); long. sec. through apical part of siphuncle,  $\times 1$  (27).

#### GENERA KNOWN FROM FRAGMENTARY SIPHUNCLES ONLY, REPRESENTED BY PARTS FILLED WITH ENDOCONES, BELIEVED TO BELONG TO THE PROTEROCAMEROCERATIDAE

**Escharendoceras** FLOWER, 1956 [\**E. eccentricum*; OD]. Gently, somewhat asymmetrically curved, slender siphuncles with strongly depressed cross section. [Either curvature of shell was not in one plane, or siphuncle was not located in plane of symmetry.] *L.Ord.(M.Canad.)*, USA(Md.).—FIG. 108,1a-c. \**E. eccentricum*; 1a-c, ventral, lat., dorsal views,  $\times 1$  (45).—FIG. 108,1d. *E. simplex* FLOWER; adoral view,  $\times 1$  (45).

**Kirkoceras** ULRICH & FOERSTE, 1936 [\**K. arcuatum*; OD]. Large, distinctly curved siphuncles with circular to compressed cross section; rapidly enlarging in early stages, contracting aperturally. Surface of siphuncle obliquely annulated, suggesting that septal necks (or connecting rings) were slightly convex inward. [May be synonymous with *Clitendoceras*.] *L.Ord.(U.Canad.)*, USA (Colo.).—FIG. 108,2. \**K. arcuatum*; 2a-c, lat., dorsal, ventral views,  $\times 0.7$  (201).

**Lobosiphon** FLOWER, 1956 [\**L. inexpectans*; OD]. Slightly curved, compressed siphuncles; endocones with dumbbell-shaped cross section; endosiphuncular wedge on dorsal side. [Very poorly known.] *L.Ord.(U.Canad.)*, USA(Md.).

**Manitouoceras** ULRICH, FOERSTE, MILLER & UNKLESBAY, 1944 [\**M. gracile*; OD]. Straight, rather large, slender siphuncles expanding rapidly from apex; apical part with straight dorsal and slightly convex ventral outline, remainder of siphuncle nearly cylindrical; endosiphuncular blades probably present. *L.Ord.(U.Canad.)*, USA (Colo.-?Tex.).—FIG. 107,6. \**M. gracile*, Manitou Ls., USA(Colo.); 6a,b, dorsal and lat. views,  $\times 1$  (204).

?**Mysticoceras** ULRICH & FOERSTE, 1936 [\**M. vicinum*; OD]. Known from short, straight siphuncle fragments with slightly compressed cross section; rapidly expanding in extreme apical part, becoming cylindrical at short distance from apex; conch chambered from beginning, as shown by annular impression left by septal necks. [May belong to Endoceratidae.] *L.Ord.(U.Canad.)*, SE. Can.-USA(Md.).—FIG. 108,5. \**M. vicinum*, Hastings Creek F., Can.(Que.); 5a,b, lat., dorsal views,  $\times 1$  (201).

**Oderoceras** ULRICH, FOERSTE, & MILLER, 1943 [\**O. depressum*; OD]. Similar to (doubtfully distinct from) *Kirkoceras* from which it differs in broadly depressed cross section. *L.Ord.(U.Canad.)*, USA-?Can.

**Phragmosiphon** FLOWER, 1956 [\**P. septiferum*; OD]. Siphuncle externally simple, rapidly expanding, slightly compressed; endocones with subtriangular cross section, venter acute, sides flat, dorsum strongly rounded; endosiphuncular tube narrow, central, with numerous endosiphuncular blades, one pair dorsolateral and variable number lateral and ventrolateral. *L.Ord.(U.Canad.)*, USA (Md.).—FIG. 108,3. \**P. septiferum*; 3a-c, dorsal, lat., adoral views, showing subtriangular endocone and endosiphuncular blades,  $\times 1.5$  (45).

**Platysiphon** FLOWER, 1956 [\**P. expansum*; OD]. Faintly endogastrically curved siphuncles with broadly depressed cross section; endocones simple. [Poorly known.] *L.Ord.(U.Canad.)*, USA(Md.).

**Pliendoceras** FLOWER, 1956 [\**P. concavum*; OD]. Slender, endogastrically curved, compressed siphuncles; endocones long and slender. [Very poorly known, possibly synonym of *Clitendoceras*.] *L.Ord.(U.Canad.)*, USA(Md.).

**Retroclitendoceras** FLOWER, 1956 [\**R. depressum*; OD]. Siphuncle slender, slightly endogastrically curved, slightly depressed, apex blunt; endocones strongly flattened dorsally and ventrally, endosiphuncular tube close to venter. *L.Ord.(U.Canad.)*, USA(Md.).—FIG. 108,4. \**R. depressum*; 4a,b, ventral, lat. views,  $\times 1.5$ ; 4c, sec. showing transv. secs. of endocones and position of tube,  $\times 3$  (45).

**Stenosiphon** FLOWER, 1956 [\**S. sandoi*; OD]. Siphuncle slender, straight, compressed, with compressed endocones that in cross section are more narrowly rounded dorsally than ventrally; slender, central endosiphuncular tube; 1 pair of dorso-lateral endosiphuncular blades. *L.Ord.(U.Canad.)*, USA(Md.).

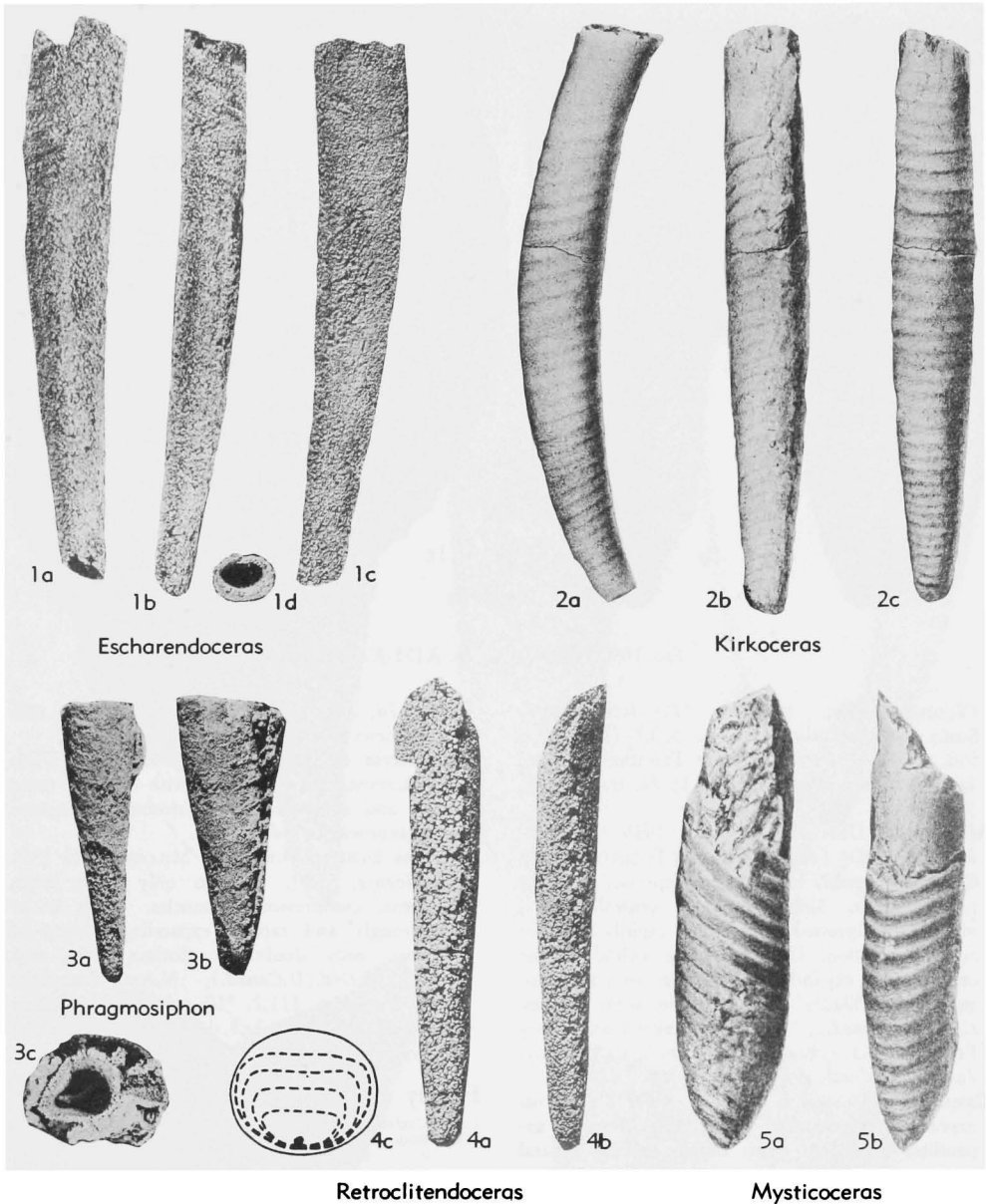


FIG. 108. Proterocameroceratidae (p. K170).

**Family PILOCERATIDAE** Miller, 1889

Breviconic, more or less strongly curved, rapidly expanding conchs with compressed cross section; body chamber may have slightly contracted aperture. Siphuncle rapidly expanding, large; septal necks, where known, holchoanitic; endocones simple, but in some forms with complex systems of

endosiphuncular blades and endosiphuncular funicles. *L.Ord. (?M.Canad.-U.Canad.)*.

**Piloceras** SALTER in MURCHISON, 1859 [*\*P. invaginatum*; OD]. Known mostly from siphuncles that are large, rapidly expanding, particularly in early stages, cyrtconic, posterior portion filled with simple endocones; conch and siphuncle compressed; septal necks holchoanitic. *L.Ord. (U. Canad.)*, N.Am. - Eu. (Scot. - Norway) - Australia

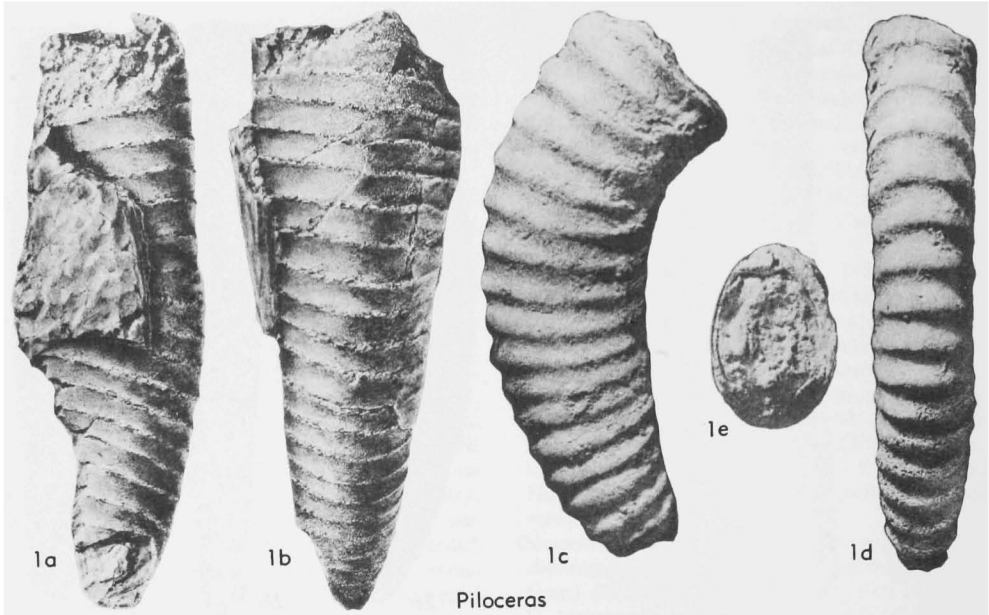


FIG. 109. Piloceratidae (p. K171-K172).

(Tasm.).—FIG. 109,1a,b. \**P. invaginatum*, Scot.; 1a,b, lat., dorsal views,  $\times 0.7$  (202).—FIG. 109,1c-e. *P. tasmaniense* TEICHERT, Tasm.; 1c,d, lat. and dorsal views,  $\times 1$ ; 1e, transv. sec.,  $\times 1$  (236).

**Allophiloceras** ULRICH & FOERSTE, 1936 [\**A. tennesseense*; OD] [= *Trundleoceras* FOERSTE, 1938]. Conch presumably breviconic, compressed, straight or nearly so. Siphuncle large, ventral, almost straight, compressed; expanding rapidly only in adapical portion, later becoming cylindrical or only slightly expanding; endocones simple; endosiphuncular blades may occur in some species. *L.Ord.*(*U.Canad.*), N.Am.-Australia(Tasm.).—FIG. 111,1. *A. canadense* (BILLINGS), Can.(Que.); 1a-c, lat., adoral, dorsal views,  $\times 0.7$  (202).

**Cassinoceras** ULRICH & FOERSTE, 1936 [\**Piloceras explanator* WHITFIELD, 1886; OD]. Rapidly expanding brevicones, with nearly straight ventral outline, except for slightly convex apical part, dorsal outline conspicuously convex and divergent from ventral one; aperture slightly contracted; siphuncle distinctly compressed, entirely filling apical portion of conch, in cross section more narrowly rounded ventrally than dorsally; simple endocones; endosiphuncular tube flattened, with widely spaced partitions; complex system of endosiphuncular blades and endosiphofunicles. *L.Ord.*(*U.Canad.*), E.N. Am.-Spitz.-Arct. O. (Bear Is.).—FIG. 110,1a-c. \**C. explanator*, Cassin Ls., USA(Vt.); 1a,b, lat. and ventral views,  $\times 0.4$ ,  $\times 0.3$ ; 1c, long. sec. (reconstr.) (202).—FIG. 110,1d-f. *C. wortheni* (BILINGS), St. George F.,

Newf.; 1d, dorsoventral sec.,  $\times 1$ ; 1e,f, lat. and ventral views of siphuncles,  $\times 1$  (202).

**Parapiloceras** OBATA, 1939 [\**P. shimizui*; OD]. Like *Piloceras* but siphuncle with circular cross section and somewhat less cyrtoconic. Phragmocone unknown. *L.Ord.*, E.Asia.

?**Utoceras** ULRICH, FOERSTE & MILLER, 1943 [\**U. coloradoense*; OD]. Known only from large, cyrtoconic, compressed siphuncles. [May be a less strongly and rapidly expanding variety of *Piloceras*; only doubtfully distinct from that genus.] *L.Ord.*(*U.Canad.*), N.Am. - ?Australia (Tasm.).—FIG. 111,2. \**U. coloradoense*, Manitou Ls., USA(Colo.); 2a,b, lat. and ventral views of siphuncle fragment,  $\times 0.5$  (202).

### Family ENDOCERATIDAE Hyatt, 1883

[incl. Cyclendoceratidae, Suecoceratidae SHIMIZU & OBATA, 1936; Endoceratinae KOBAYASHI, 1937; ?Hemipiloceratidae SHIMIZU & OBATA, 1935 (*partim*)]

Straight, generally robust, large to extremely large conchs, including the largest known Paleozoic invertebrate fossils. Siphuncle large, mostly ventral, but may be subventral to central in position. Septal necks holochoanitic to macrochoanitic; connecting rings generally thin, forming lining on internal surface of septal necks; endosiphuncular structures generally simple. In many forms apical end of siphuncle inflated to fill entire apical portion of conch. *L.Ord.*(*U.Canad.*)-*U.Ord.*(*Richmond.*), ?*M.Sil.*

**GENERA KNOWN FROM FRAGMENTARY CONCHS, INCLUDING SIPHUNCLES, WITH APICAL END AND BODY CHAMBER USUALLY UNKNOWN OR ONLY POORLY KNOWN**

*Endoceras* HALL, 1847 [*E. annulatum* HALL, 1847; SD S. A. MILLER, 1889] [= *Cyclendoceras* GRABAU & SCHIMER, 1910 (obj.)]; *Andoceras* D'ORBIGNY, 1849 (*nom. null.*). Conchs large,

straight, similar to *Cameroceras*, but with annulations varying from low and closely spaced to well elevated and distinctly apart; cross section slightly depressed; sutures straight, transverse. Siphuncle large, ventral, holochonitic; endocones subcircular in cross section; thin endosiphuncular tube; apical part unknown. *M.Ord.-U.Ord.*, N. Am.-USSR(Sib.)-E.Asia-N.Eu.—FIG. 112,2. *E.*

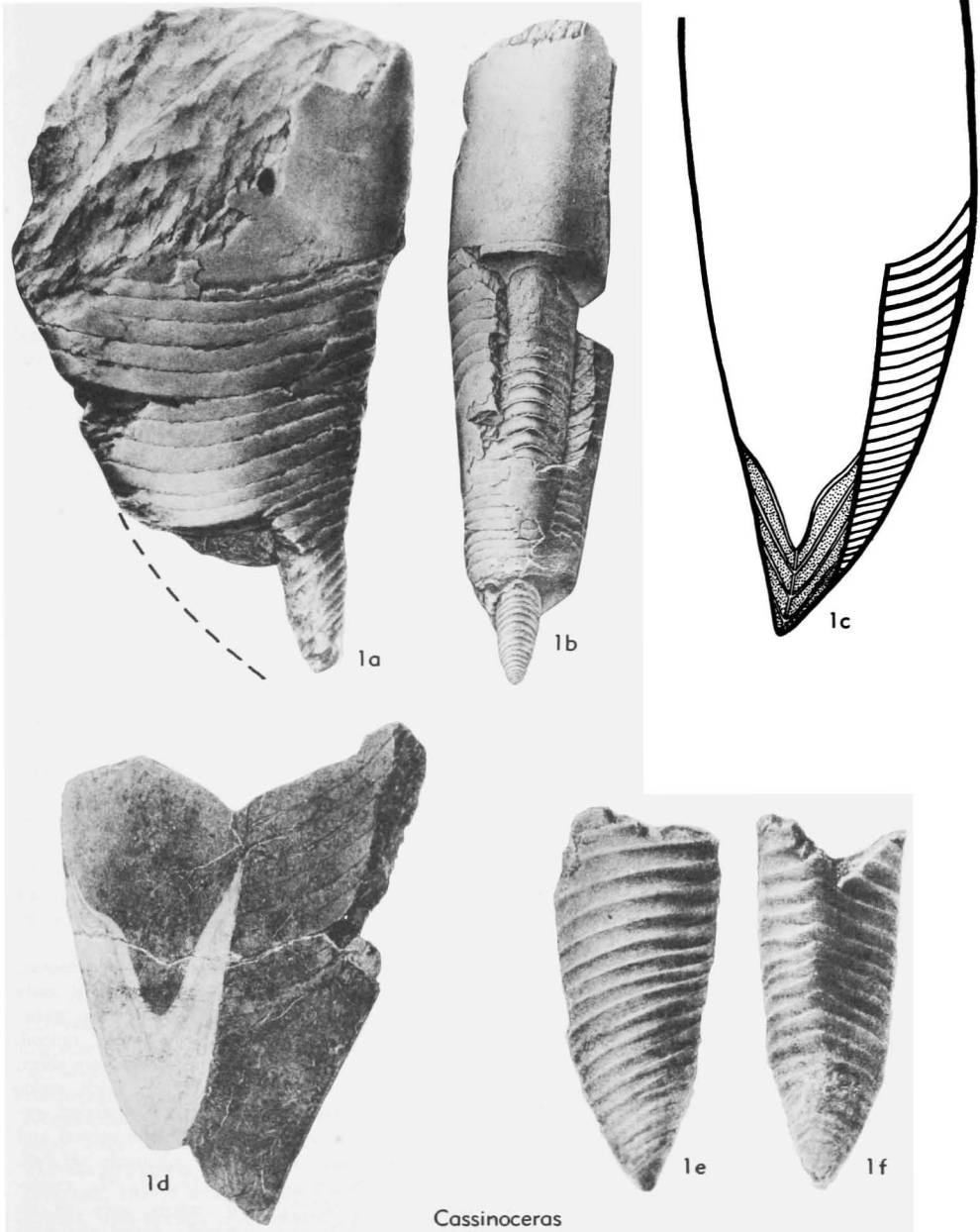


FIG. 110. Piloceratidae (p. K172).



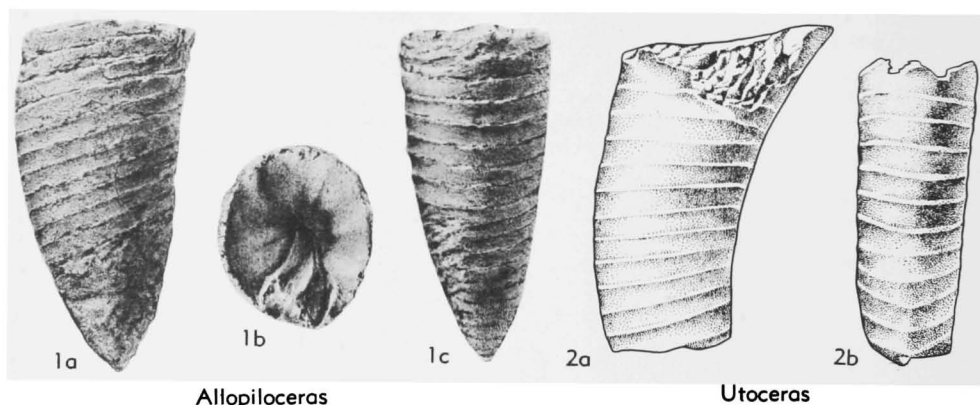


FIG. 111. Piloceratidae (p. K172).

*abundum* (MILLER), M.Ord., USA (Wyo.); 2a, ventral view,  $\times 0.6$ ; 2b,c, transv. and long secs.,  $\times 0.6$  (226).

**Cameroceras** CONRAD, 1842 [*\*C. trentonensis* (sic) (recte *\*C. trentonense*;) M] [= *Endoceras* auctt. (non HALL, 1847); *Camaroceras* OWEN, 1860 (nom. null.); *Rossicoceras* BALASHOV, 1961]. Large to extremely large, straight conchs with circular or somewhat depressed cross section; sutures simple and straight, or with very slight ventral lobe. Siphuncle as much as half diameter of conch at maturity, mostly marginal, less commonly submarginal to subcentral in position; septal necks holochaoanitic; endocones simple; endosiphuncular tube thin, situated in ventral part of siphuncle. [Nature of apical portion not known with certainty, may be identical with forms given generic names such as *Nanno* CLARKE or *Suecoceras* HOLM.] M.Ord.-U.Ord., ?M.Sil., cosmop.—FIG. 112,1. *C. vertebrale* (EICHWALD), M.Ord., Eu. (Est.); 1a,b, adoral, ventral views (part of anterior portion of phragmocone),  $\times 0.5$  (19).

**Chazyoceras** FLOWER, 1958 [*\*C. valcourense*; OD]. Large, straight, slightly depressed conchs; septa closely spaced, sutures straight, transverse. Siphuncle ventral, with bulbous apical end of *Nanno* type; septal necks holochaoanitic, covered by connecting ring substance on their inner sides; endocones of medium length, faintly crescentic in cross section; endosiphuncular tube thin, tubular, widening into cavity of appreciable size in inflated apical part of siphuncle. M.Ord. (*Chazy*.), N.Am.-Eu. — FIG. 112,3. *\*C. valcourense*, USA (N.Y.); 3a, restored long. sec.,  $\times 0.2$ ; 3b, dorsal wall of siphuncle with holochaoanitic septal neck and interior lining of connecting rings,  $\times 1$ ; 3c, transv. sec., ca.  $\times 0.3$  (47).

?**Kawasakiceras** KOBAYASHI, 1934 [*\*K. densistriatum*; OD]. Supposedly similar to *Kotoceras*, but

with weakly annulate and transversely striated shell; endosiphuncle unknown. M.Ord., Asia (Korea-Sib.).

**Kotoceras** KOBAYASHI, 1934 [*non* YABE, 1927 (nom. nud.) (= *Damesites* MATSUMOTO, 1942)] [*\*K. typicum*; OD] [= *Subvaginoceras* SHIMIZU & OBATA, 1936 (obj.)]. Large, straight, slightly depressed conchs. Camerae short. Siphuncle large, broad, ventral, with broad, flattened contact zone, depressed cross section, variable in diameter, with constricted and inflated parts equaling several camerae in length; endocones extending much farther forward ventrally than on dorsal side, their tip much closer to dorsal than ventral side, cross sections semicircular to subquadrangular; apical end and body chamber unknown. M.Ord., Asia (Korea-Inner Mongolia-Sib.). — FIG. 113,3a,b. *\*K. typicum*, Korea; 3a,b, long. and transv. secs.,  $\times 1$  (102). — FIG. 113,3c. *K. cylindricum* KOBAYASHI; long. sec.,  $\times 1.5$  (102).

**Kutorgoceras** BALASHOV, 1962 [*\*K. compressum*; OD] [= *Kutorgoceras* BALASHOV, 1961, nom. nud.]. Similar to *Proterovaginoceras* in having macrochoanitic septal necks, but differs in having thick connecting rings and very short camerae. M.Ord., USSR (Sib.).

**Lamottoceras** FLOWER, 1955 [*\*L. ruedemanni*; OD]. Large conchs, rapidly expanding in early part, later slender, with very short camerae, transverse, straight sutures. Siphuncle large, ventral, with inflated apical cone; septal necks very short, orthochaoanitic; connecting rings very thick, endocones long, subquadrangular in cross section, extending forward as long lobes on mid-ventral and mid-dorsal inner surfaces of siphuncle. M.Ord. (*Chazy*.), N.Am. — FIG. 114,3a-f. *\*L. ruedemanni*, USA (N.Y.); 3a-d, transv. secs. of siphuncles,  $\times 0.7$ ; 3e,f, siphuncle, dorsal and ventral,  $\times 0.7$  (44). — FIG. 114,3g-i. *L. franklini*



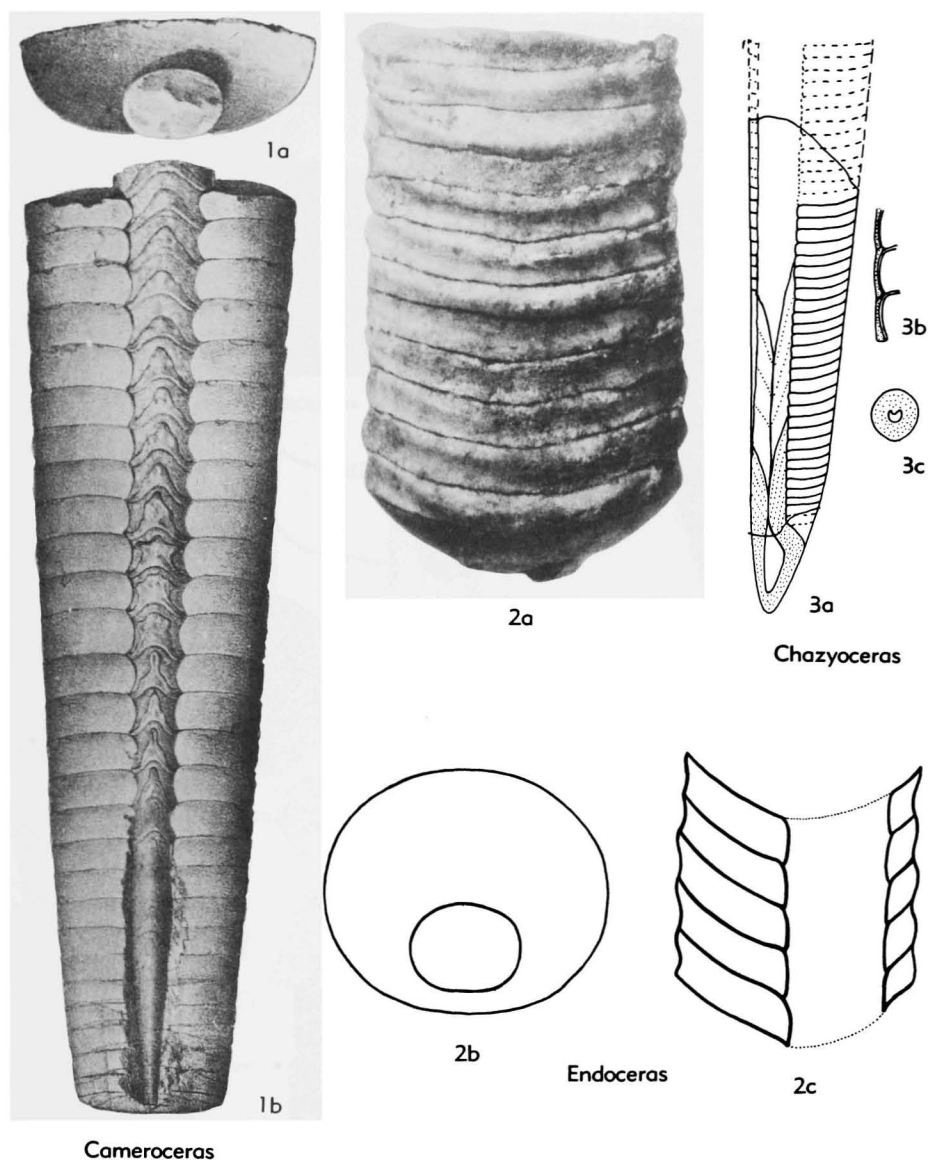


FIG. 112. Endoceratidae (p. K173-K174).

FLOWER, USA(N.Y.); 3g, septal necks, connecting rings,  $\times 2$ ; 3h,i, transv. sec. of siphuncle, long. sec. of conch,  $\times 0.45$  (47).

**Proterovaginoceras** RUEDEMANN, 1905 [*\*Endoceras belemnitiiforme* HOLM, 1885; OD] [= *Vaginoceras* AUCTT. (non HYATT, 1883); *Dideroceras* FLOWER in FLOWER & KUMMEL, 1950; *Chisiloceras* GORTANI, 1934]. Straight, medium-sized to large conchs, with circular cross section, straight sutures. Siphuncle ventral to central, with bulbous apical end of *Nanno* type occupying entire apical part

of conch; septal necks macrochoanitic, up to 2 camerae long; connecting rings lining inside of septal necks for one camera length; endocones long, slender, not well known, filling entire bulbous, apical part of siphuncle. *L.Ord.* (*M. Canad.*) - *M.Ord.* (*Trenton.*), Eu. (Norway-Sweden-Est.) - C.Asia. — FIG. 114, 1a,b. *\*P. belemnitiiforme* (HOLM), *M.Ord.*, Swed.; 1a, apical part,  $\times 0.7$ ; 1b, transv. sec. at distal part of 1a,  $\times 0.7$  (92). — FIG. 114, 1c. *P. wahlenbergi* (FOORD), *M.Ord.*, Norway; long. sec.,  $\times 1.5$  (178).

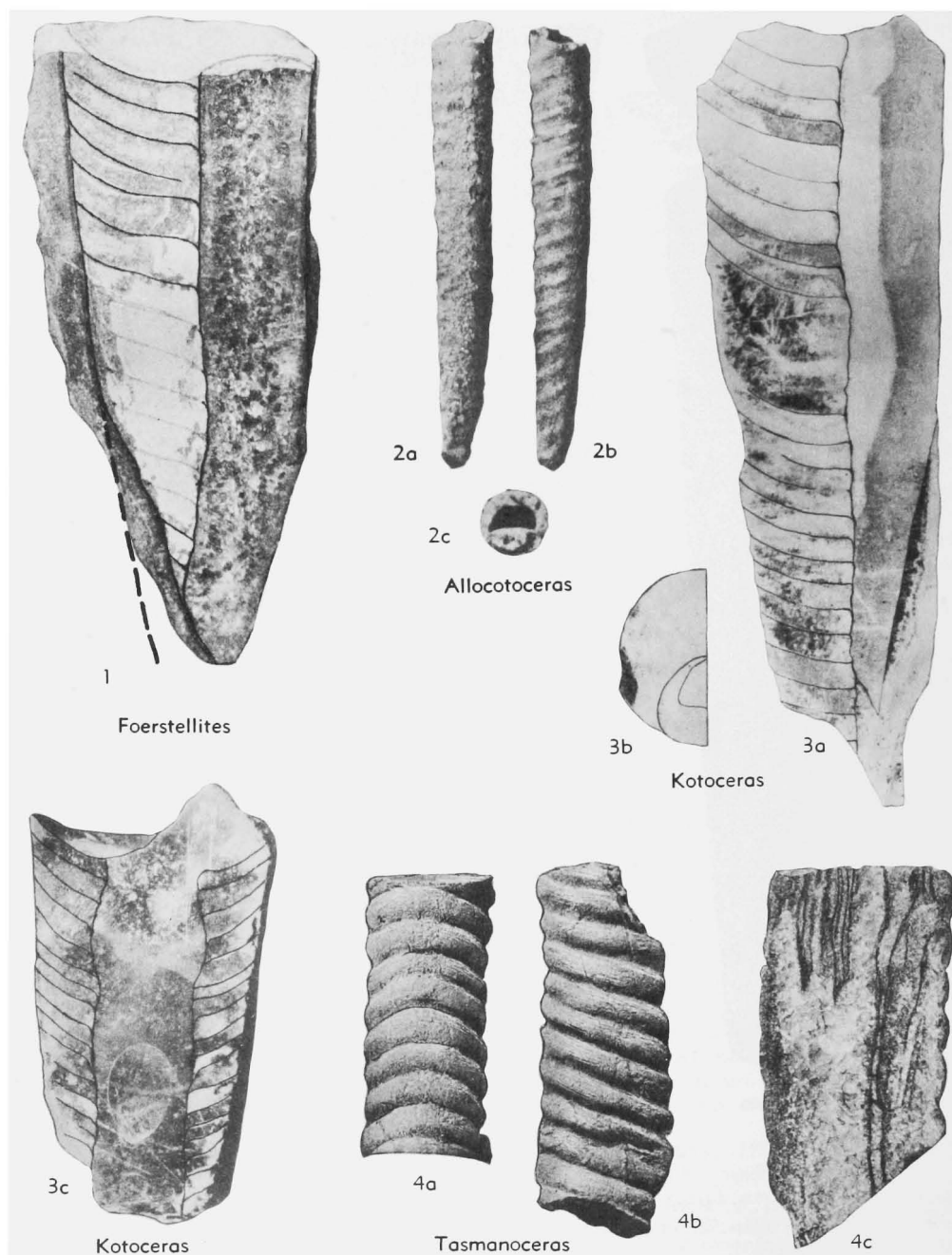


FIG. 113. Endoceratidae (p. K174, K178-K179).

**Triendoceras** FLOWER, 1958 [*\*T. montrealense*; OD]. Straight, large conchs, with slightly depressed cross section. Siphuncle ventral, holochanitic; cross section of endocones in form of isosceles triangle, with apex pointing to venter;

apex of siphuncle unknown. *L.Ord.*, ?*U.Ord.*, N. Am.(Que.-N.Y.-?Ohio)-Eu.(USSR).

**Vaginoceras** HYATT, 1883 [*\*Endoceras multitubulatum* HALL, 1847; OD]. Large conchs, like *Endoceras*, but not reaching giant size, with long,

slender endocones of compressed to cuneate cross section; 2 endosiphuncular blades; endosiphuncular tube with compressed or cuneate cross section; septal necks holochoanitic, internally lined with

thick connecting rings; *M.Ord.*, E.N.Am.-?Greenl.-Eu.(Norway)-Asia(Sib.-In. Mongolia). — FIG. 114,2. *V. sp.*, Norway; 2*a*, transv. sec. of siphuncle,  $\times 0.5$ ; 2*b*, long. sec. of conch,  $\times 0.5$  (178).

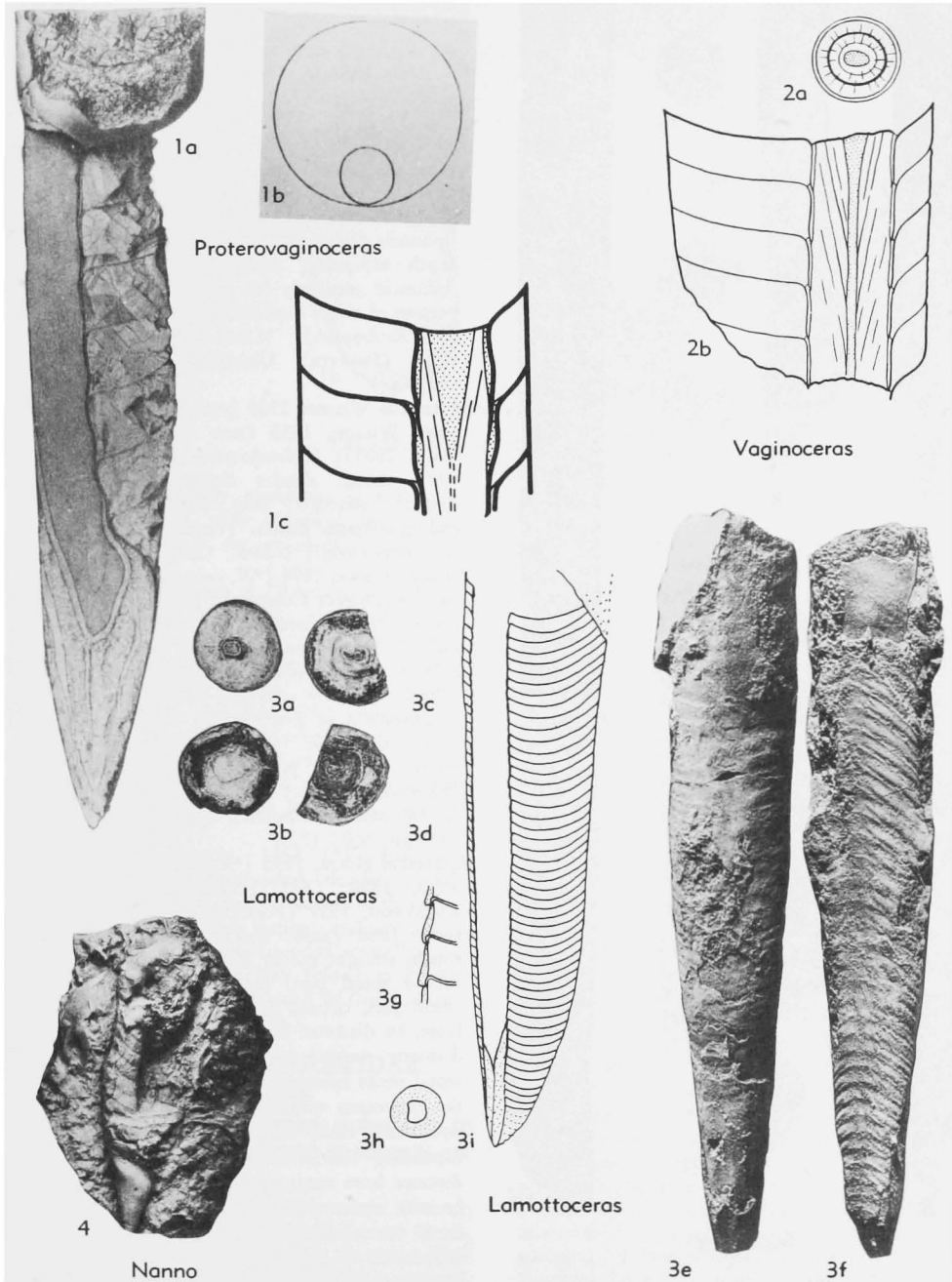


FIG. 114. Endoceratidae (p. K174-K178).

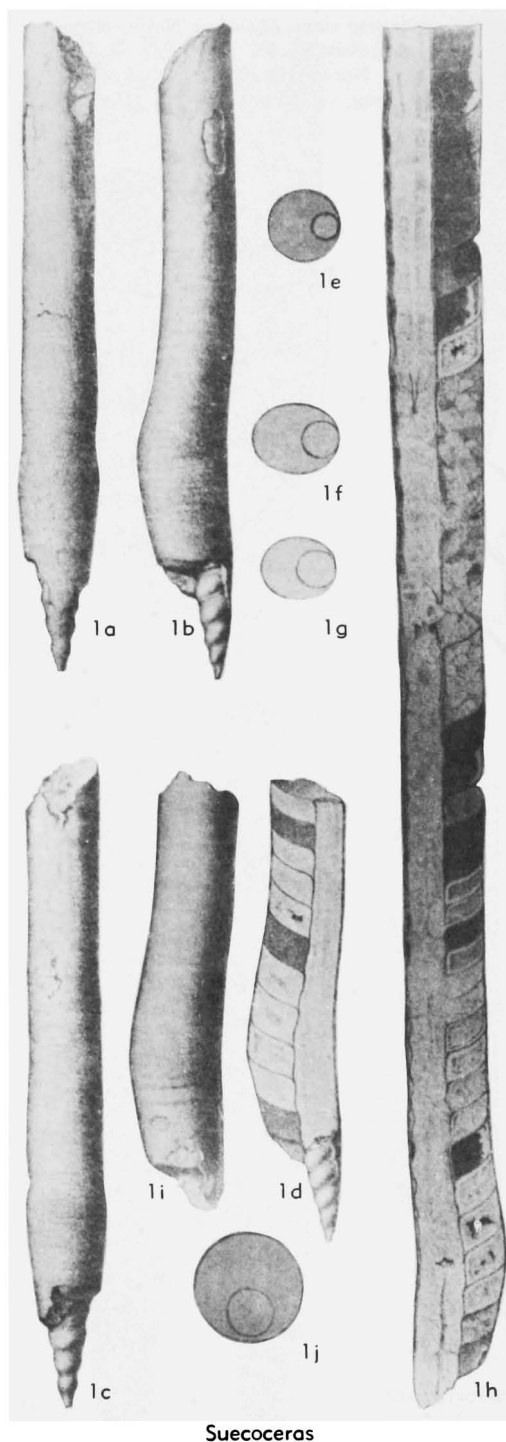


FIG. 115. Endoceratidae (p. K178-K179).

#### GENERA BASED ON SIPHUNCLES OR INITIAL PARTS OF CONCH

**Allocotoceras** TEICHERT & GLENISTER, 1953 [*\*A. insigne*; OD]. Siphuncle small, straight or gently curved, with circular cross section; septal necks holochaotic; endocones circular in cross section, with endosiphuncular wedge on dorsal side, giving endosiphuncular semicircular cross section. *L. Ord.*(*U.Canad.*), Australia(Tasm.).—FIG. 113, 2. *\*A. insigne*; 2a-c, ventral, lat., adoral views,  $\times 1$  (192).

**Foerstellites** KOBAYASHI, 1940 [*nom. subst. pro Foerstella* KOBAYASHI, 1937 (*non RUEDEMANN*, 1925)] [*\*Cameroceras? faberi* FOERSTE, 1930; OD]. Based on apical part of conch, with siphuncle filling short apical portion of it entirely; conch expanding rapidly as septa are added, siphuncle retaining its width. [Probably apical portion of either *Cameroceras* or *Vaginoceras*.] *U. Ord.*(*Richmond.*), N.Am.—FIG. 113, 1. *\*F. faberi* (FOERSTE), USA(Ind.); long. sec.,  $\times 1$  (67).

**Liskeardia** WILSON, 1939 [*nom. subst. pro Hendersonia* WILSON, 1938 (*non WAGNER*, 1905; *nec DALL*, 1905)] [*\*Hendersonia sola* WILSON, 1938; OD]. Long, slender siphuncle, longitudinally striated externally; long, slender endocones; 3 endosiphuncular blades. [Possibly junior synonym of *Cameroceras*.] *U.Ord.*, Can.(Que.).

**Nanno** CLARKE, 1894 [*\*N. aulema*; M] [= *Featherstonhaughoceras* CLARKE in BATHER, 1894 (*nom. van.*); ?*Mannoceras* LE MAITRE, 1950 (*nom. null.*)]. Established for apical conch parts that enlarge rapidly from apex; apical part of conch entirely filled by siphuncle that contracts sharply at formation of first septum, about 2 cm. from apex; siphuncle ventral; phragmocone little known. [Genus possibly a senior synonym of *Proterovaginoceras*.] *M.Ord.*, N.Am.—FIG. 114, 4. *\*N. aulema*, Blackriv., USA(Minn.); holotype, lat. view,  $\times 0.7$  (71).

**Suecoceras** HOLM, 1896 [*\*Endoceras barrandei* DEWITZ, 1880; OD] [= *Suecoceras*, *Succoceras* KOBAYASHI, 1937 (*nom. null.*); *Suecoceras* BALASHOV, 1960 (*nom. null.*)]. Very slender, long conch, straight except for slightly endogastrically curved apical part; cross section compressed in apical part, circular in adult. Siphuncle relatively large, its diameter one-half to one-third of conch diameter, ventral in young, subventral in adult; septal necks holochaotic to slightly macrochaotic; endocones extremely long and slender; endosiphuncular tube thin; apical end of siphuncle expanding slowly, first septum formed a short distance from apex; phragmocone expanding slowly with siphuncle, both contracting 2 to 3 cm. from apex, remainder of conch and siphuncle cylindrical. *M.Ord.*, Eu.(Swed.).—FIG. 115, 1. *\*S. barrandei* (DEWITZ); 1a-c, ventral, lat., dorsal views; 1d, long. sec.; 1e-g, transv. secs. of 1b at

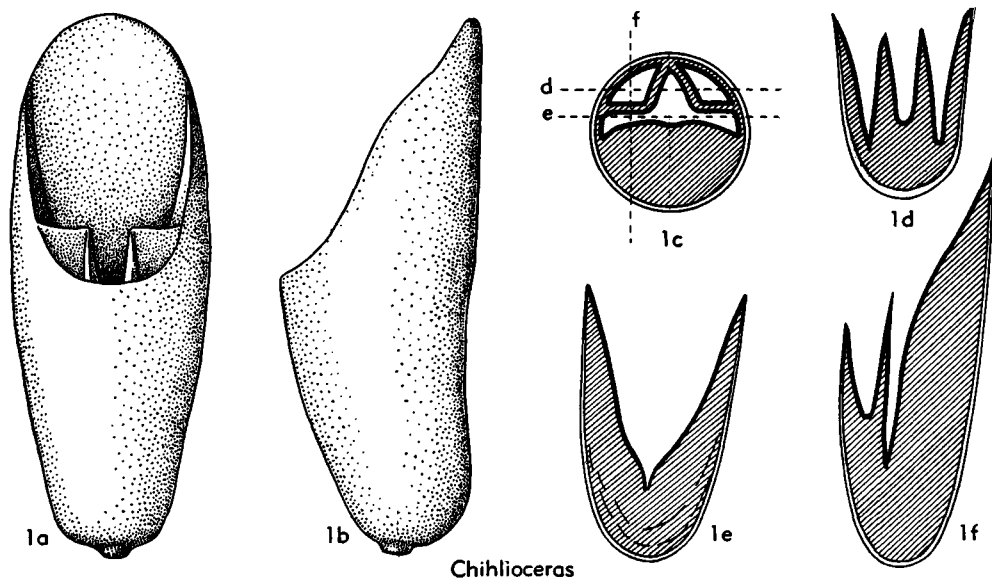


FIG. 116. Chihlioceratidae (p. K179).

positions indicated by placement of secs.; *1h,i*, long. sec. and lat. view of apical end of large specimen; *1j*, transv. sec. at adapical end of *1h*; all  $\times 1$  (92).

**Tasmanoceras** TEICHERT & GLENISTER, 1952 [*\*T. zeehanense*; OD]. Siphuncle small, slowly expanding, straight or weakly curved, with segments slightly expanded between septa; endocones asymmetrical, tending to develop in greater number on one (?ventral) side than other; endosiphuncular tube wide, nearer ?dorsal side, crossed by widely spaced diaphragms. *M.Ord.* or *U.Ord.*, Australia (Tasm.).—FIG. 113,4. *\*T. zeehanense*; *4a,b*, concave side (?vent.) and lat. views,  $\times 2$ ; *4c*, long. sec.,  $\times 3$  (191).

**Vaningenoceras** FLOWER, 1958 [*\*V. styliforme*; OD]. Siphuncle medium-sized, slender, containing long endocones, later endocones with sinuous outlines in longitudinal section; endosiphuncular tube flattened ventrally, rounded dorsally, subangular ventrolaterally. [May belong to Proteroceroceratidae. Poorly known.] *M.Ord.* (*Chazy.*), N.Am. (N.Y.-?Va.)-USSR (Sib.).

### Family CHIHLIOCERATIDAE Grabau, 1922

Known from large, broad siphuncles in which a central and 2 lateral endocones are present. *L.Ord.*

**Chihlioceras** GRABAU, 1922 [*\*C. nathani* GRABAU, 1922; SD KOBAYASHI, 1931] [= *Chilioceras* OZAKI, 1927 (*nom. null.*); *Chilioceras* FLOWER, 1947 (*nom. null.*)]. Known only from large, stout siphuncles; detailed structure of endocones un-

known; endosiphococone divided into one main, central cone of T-shaped or triangular cross section, and 2 lateral cones; lateral and dorsal alveoli may be present; last endocones prolonged ventrally into long, bladelike projection. *L.Ord.*, N.China.—FIG. 116,1. *\*C. nathani*, *1a,b*, vent. and lat. views of siphuncle (reconstr.),  $\times 0.7$ ; *1c*, transv. sec. through lower part of endosiphococone,  $\times 0.45$ ; *1d-f*, long. secs. as indicated on *1c*,  $\times 0.45$  (82).

### Family MANCHUROCRATIDAE Kobayashi, 1935

Breviconic conchs; cross section of conch and siphuncle slightly depressed. Siphuncle large, ventral, with special thickening of deposits in ventral part of siphuncle in addition to endocones. *L.Ord.* (*U.Canad.*).

**Manchuroceras** OZAKI, 1927 [*\*Piloceras wolungense* KOBAYASHI, 1931; SD KOBAYASHI, 1935] [= *Manchuriceras* KOBAYASHI, 1927 (*nom. null.*); *Manchuroceras* KOBAYASHI, 1935 (*nom. null.*); *Grabauoceras*, *Liaotungoceras* SHIMIZU & OBATA, 1936]. Medium-sized, straight or very slightly endogastrically curved brevicones. Siphuncle large, surrounded by camerae from beginning; septal necks probably long; endosiphuncular wedge on ventral side of endosiphococone, resulting in somewhat crescent-shaped cross section of latter; tri-radiate endosiphuncular blades; endosiphuncular tube dorsal of center, crossed by closely spaced partitions. *L.Ord.* (*U.Canad.*), USSR (Sib.)-E.Asia-Australia (Tasm.).—FIG. 117,1a,b. *M. excavatum* TEICHERT, Tasm.; dorsal and oral views of

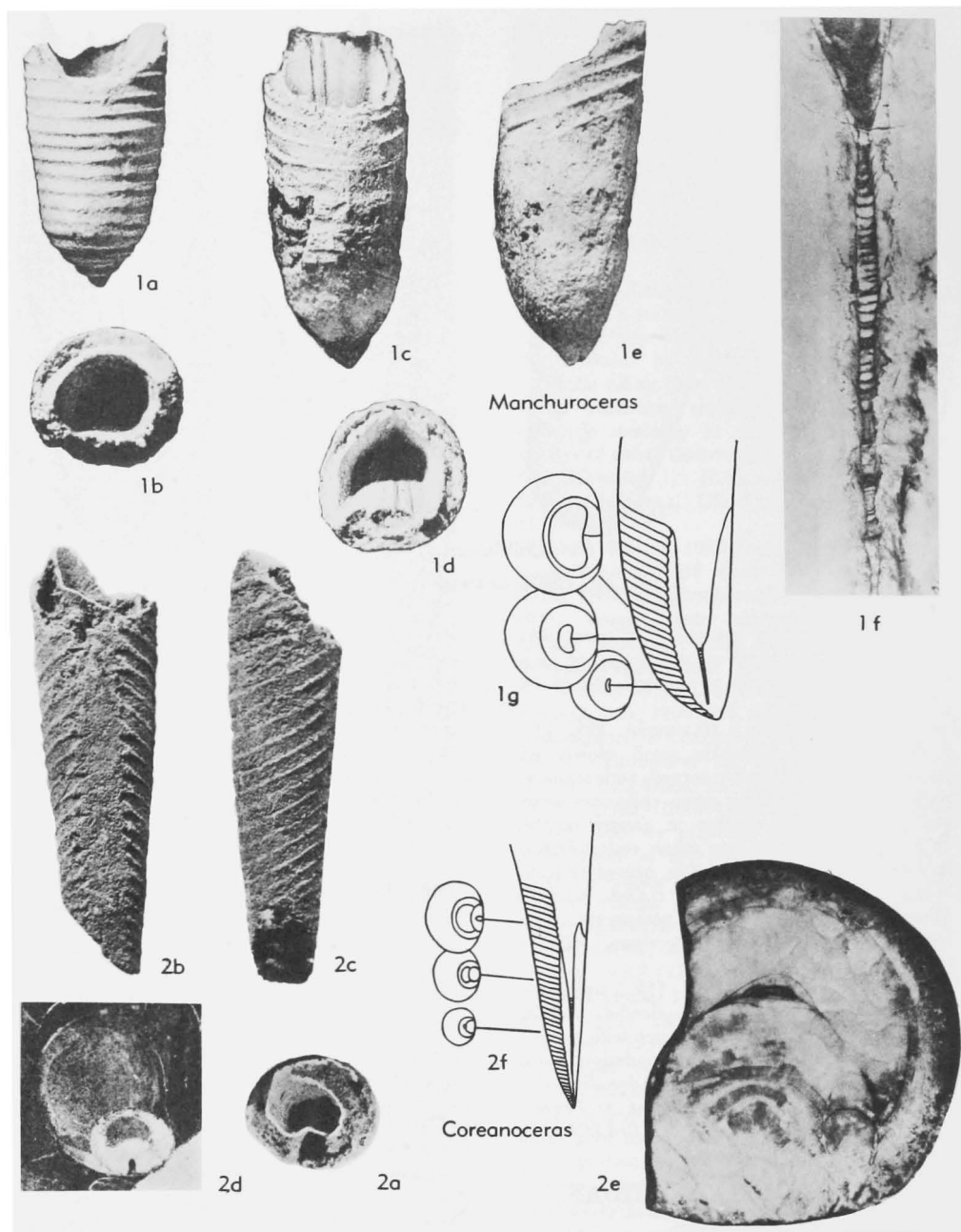


FIG. 117. Manchuroceratidae (p. K179-K181).

siphuncle,  $\times 1$  (236).—FIG. 117, 1c-e. *M. steanei* TEICHERT, Tasm.; ventral, oral, lat. views of siphuncle,  $\times 1$  (236).—FIG. 117, 1f-g. *\*M. wolungense* (KOBAYASHI), Manchuria; 1f, endosiphontube with diaphragms,  $\times 7$  (18); 1g, diagram. long. and transv. secs. (104).

*Coreanoceras* KOBAYASHI, 1931 [*\*C. kemipoense*; OD]. More slender and longiconic than *Manchuroceras*; septal necks short; endocones subconical, their ventral side convex; lateral endosiphuncular blades present, in some forms doubled; endosiphoncone with ventral elevation

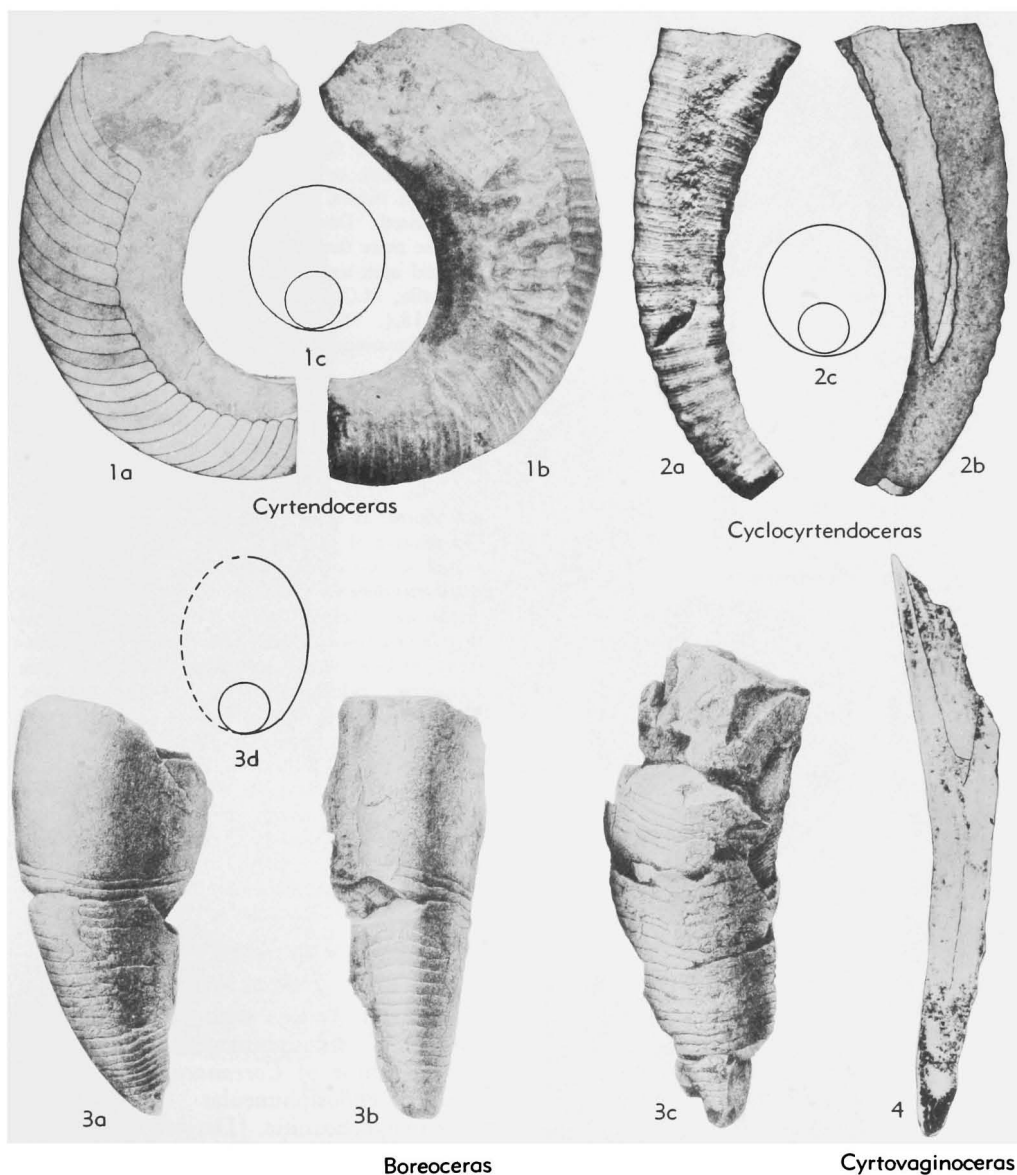


FIG. 118. Cyrtendoceratidae (p. K182).

and alveolus; endosiphuncular tube flattened. *L. Ord.* (*U. Canad.*), E. Asia-N. Am. (Md.).—FIG. 117, 2. \**C. kemipoense*, Korea; 2a-c, oral, ventral, lat. views,  $\times 0.7$ ; 2d, transv. sec. of shell and siphuncle, latter showing alveolus in endocone,  $\times 1$ ; 2e, transv. sec. of siphuncle showing ventral convexity of endocones and lat. endosiph. blades,  $\times 5$ ; 2f, diagram. long. and transv. secs. (104).

### Family CYRTENDOCERATIDAE Hyatt in Zittel, 1900

[incl. Cyrtovaginoceratidae Flower, 1958]

Cyrtconic, possibly including gyroconic, endogastric conchs with large, marginal siphuncles; septal necks holochoanitic; endocones simple, endosiphuncular tube narrow,



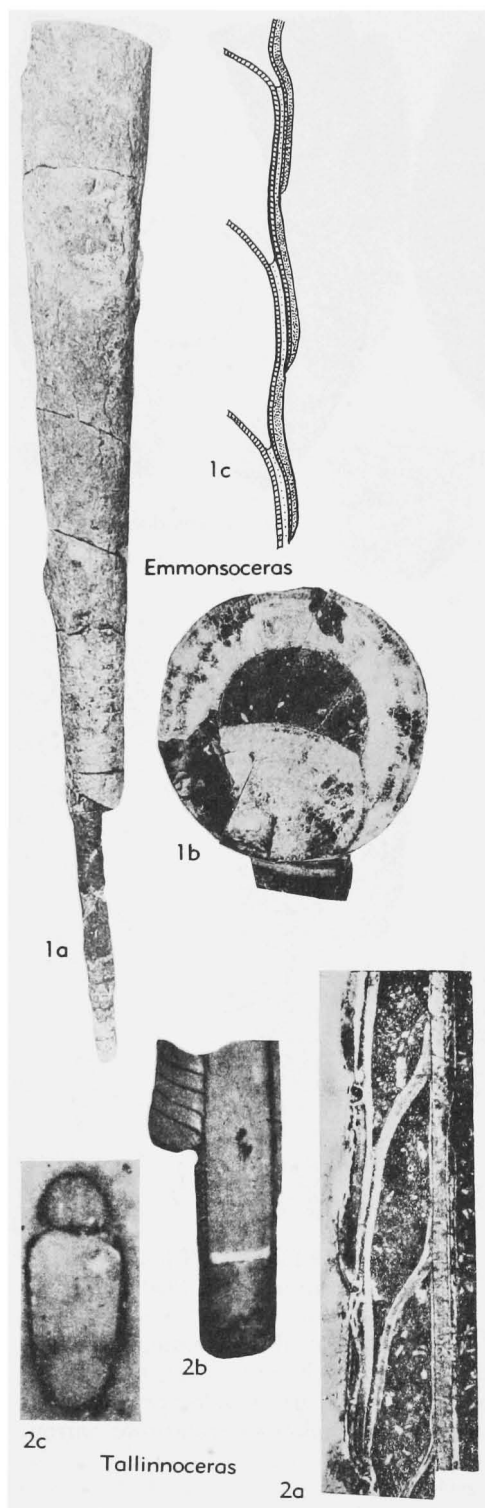


FIG. 119. Emmonsoceratidae (p. K182-K183).

cylindrical. [Probably derived from Piloceratidae.] *L.Ord.-M.Ord.*, ?*U.Ord.*

**Cyrtendoceras** REMELÉ, 1886 [*\*Endoceras* (*Cyrtocarina*) *hircus* HOLM, 1892; SM PATRUNKY, 1926]. Characters of family. Some forms with marked growth lines, or wrinkles describing lateral saddles and ventral and dorsal lobes, some slightly compressed. Dorsoventral diameter of siphuncle may be more than half that of conch. Body chamber and apex unknown. ?*L.Ord.* (*U.Canad.*), NW. Australia, *M.Ord.*, Eu. (Swed.-Est.-?Norway).—FIG. 118,1. *\*C. hircus* (HOLM), *M.Ord.*, Swed.; 1a-c, dorsoventral sec., lat. view, transv. sec.,  $\times 0.7$  (70).

**Boreoceras** MILLER & YOUNGQUIST, 1947 [*\*B. washburni*; OD]. Similar to *Cyrtendoceras*, but conch somewhat less curved, more rapidly expanding and with relatively narrower siphuncle and shorter camerae. ?*U.Ord.*, Arctic Can.—FIG. 118,3. *\*B. washburni*; 3a-c, lat., dorsal, lat. views, 3c, showing position of siphuncle,  $\times 0.7$  (227); 3d, transv. sec. of 3c,  $\times 0.7$  (Teichert, n).

**Cyclocyrtendoceras** BALASHOV, 1961 [*\*Cyrtendoceras estoniense* FOERSTE, 1932]. Conch less cyrtoconic than *Cyrtendoceras* and with circular cross section; surface weakly annulate and with fine transverse ridges. *M.Ord.*, Eu. (Est.).—FIG. 118,2. *\*C. estoniense* (FOERSTE); 2a-c, lat. view, dorsoventral and transv. sec.,  $\times 0.7$  (70).

?**Cyrtovaginoceras** KOBAYASHI, 1934 [*\*Cameroceras curvatoforme* KOBAYASHI, 1930; OD]. Weakly cyrtoconic, with long endocones, thin endosiphuncular tube, and blunt apex. *L.Ord.-M.Ord.*, E.Asia-E.N.Am.—FIG. 118,4. *C. pacificum* KOBAYASHI, *M.Ord.* (Chikusan Ls.), S.Korea; dorsoventral sec. of siphuncle,  $\times 1$  (102).

### Family EMMONSOCERATIDAE Flower, 1958

Longiconic conchs with large, marginal siphuncles; endosiphuncular deposits resembling those of *Coreanoceras* or having multiple endosiphuncular tubes; septal necks macrochoanitic. [Derived from Manchuroceratidae.] *Low.M.Ord.*

**Emmonsoceras** FLOWER, 1958 [*nom. subst. pro Hudsonoceras* FLOWER, 1956 (*non* MOORE, 1946)] [*\*Hudsonoceras aristos* FLOWER, 1956; OD]. Siphuncle nearly one-half diameter of conch; siphuncle wall composed of thin septal necks 1.5 segments long; where neck penetrates next ad-apical segment, it is separated by thin connecting ring from proximal part of preceding septal neck; anterior end of each segment faintly concave, posterior faintly convex; endosiphuncular structures similar to those in *Coreanoceras*, except that lateral endosiphuncular blades are single and no ventral alveolus occurs in endosiphococone. [Aperture and apex unknown.] *Low.M.Ord.* (*Chazy.*), N.Am.—FIG. 119,1. *\*E. aristos* (FLOWER),



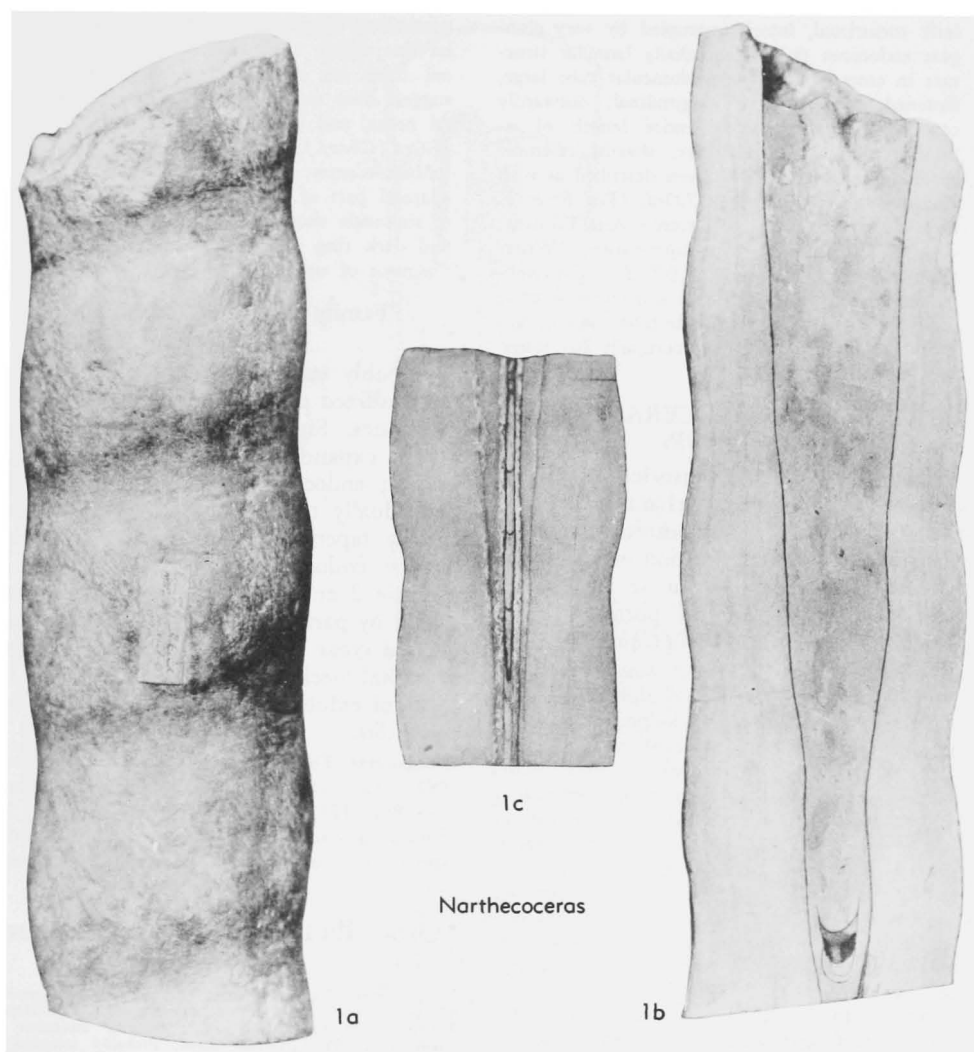


FIG. 120. Narthecoceratidae (p. K183-K184).

USA(N.Y.); 1a, lat. view of part of phragmocone and protruding part of siphuncle,  $\times 0.6$ ; 1b, transv. sec. at base of preserved part of phragmocone,  $\times 1.5$ ; 1c, diagram of siphuncle wall showing macrochoanitic necks (cross lines) and connecting rings (stippled) (47).

**Tallinnoceras** BALASHOV, 1960 [*\*T. lasnamense*; OD]. Similar to *Emmonsoceras* externally and in features of siphuncle wall; nature of endocones not well known; 3 or 4 endosiphuncular tubes present, all of which seem to possess transverse partitions; central tube larger than adventitious ones; body chamber and apical part unknown. *Low.M.Ord.* (*Lasnam F.*, =*Echinospaerites Ls.*), *Eu.(Est.)*.—FIG. 119,2. *\*T. lasnamense*; 2a, partial long. sec. of siphuncle,  $\times 4$ ; 2b, lat. view,  $\times 0.7$ ; 2c, transv. sec. of endosiphuncular tube,  $\times 37$  (4).

### Family NARTHECOCERATIDAE Flower, 1958

Known only from siphuncle fragments that are large, massive and filled with endocones; siphuncle straight, slender, very slowly increasing in diameter, and marked by narrow constrictions, between which outline of siphuncle is slightly convex. [Phragmocone and apical part of siphuncle unknown. Conchs belonging to these siphuncles must have been very large and many feet long.] *M.Ord.*, ?*U.Ord.*

**Narthecoceras** HYATT, 1895 [*\*Endoceras crassisiphonatum* WHITEAVES, 1892; OD] [=*Narhecoceras* BALASHOV, 1961 (*nom. null.*)]. Known only from large endosiphuncles with outline regu-

larly constricted, interior occupied by very elongate endocones that have radially lamellar structure in cross section; endosiphuncular tube large, flattened, with several longitudinal, outwardly convex sheaths extending entire length of siphuncle; when cut obliquely, sheaths resemble diaphragms and they have been described as such by most authors. *M.Ord.*, ?*U.Ord.* (Red River F. and equiv.), N.Am.(Can.-N.Greenl.)-Asia(Taimyr). —FIG. 120, *I*. \**N. crassisiphonatum* (WHITEAVES), Can.; *1a*, lat. view,  $\times 0.7$ ; *1b,c*, dorsoventral secs. with (1b) endocones and endosiphuncle and (1c) with endosiphuncular tube showing apparent diaphragms (in fact, obliquely cut longitudinal sheaths),  $\times 0.7$  (66).

### Family ALLOTRIOCERATIDAE

Flower, 1955

Known only from siphuncles, which are slender, medium-sized, characterized by complex endocones and multiple endosiphuncular tubes; modification of cones due to structures formed prior to endocones. Phragmocones and apical portions of siphuncles unknown. *M.Ord.*(Chazy.).

*Allotrioceras* FLOWER, 1955 [*\*A. bifurcatum*; OD]. From adoral to adapical end of siphuncle following features are observed: endosiphuncular lining present from which thick, median septum extends from one siphuncle wall to other, bifurcated at one end; adapically, space between prongs of fork become filled with calcareous deposit; in lateral spaces, on both sides of septum, 2 endocones develop, each terminating in endosiphuncular tube; in adapical part of siphuncle cones not recognizable; forked septum still present, but surrounded by dark band resembling endosiphuncular blades, along which numerous small longitudinal tubes are concentrated. *M.Ord.*(Chazy.), N.Am.—FIG. 121, *I*. \**A. bifurcatum*, USA (N.Y.); *1a-d*, transv. secs. of siphuncle, progressing from adoral to adapical end,  $\times 2$ ; *1e-k*, diagram. reconstr. and transv. secs., showing (1e) adoral part of siphuncle with siphuncular wall (1), beginning of endosiphuncular lining and forked septum (2), adoral limit of last endocone (3), and tip of last endocone (4); *1f*, showing adapical part of siphuncle (with margins of cones still faintly outlined at *j*), positions of transv. secs. marked by *g-k* in *1e* and *1f*, slightly reduced (43).

*Mirabiloceras* FLOWER, 1955 [*\*M. multitubulatum*; OD]. Center of siphuncle with triangular pillar containing tiny central tube, endocones forming complete circular ring around pillar, inner side of endocones reaching far forward nearly to apex of pillar; outer sides of pillar relatively short; adapical wedge-edge of last circular endocone forming circle in plane normal to axis of siphuncle,

continuing adapically as prominent, dark, circular line within which numerous small longitudinal tubes are arranged; traces of ectosiphuncle suggest close spacing of septa, orthochoanitic septal necks, and thin, cylindrical connecting rings. *M.Ord.*(Chazy.), N.Am. — FIG. 122, *I*. \**M. multitubulatum*, USA (N.Y.); *1a*, long. sec. of adapical part of siphuncle,  $\times 1$ ; *1b*, transv. sec. of siphuncle showing central, subtriangular pillar and dark ring with small tubes,  $\times 2$ ; *1c*, block diagrams of siphuncle, slightly reduced (43).

### ?Family HUMEOCERATIDAE

Teichert, n.fam.

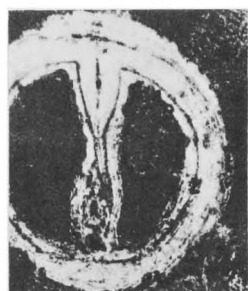
Probably large shells, only known from recrystallized parts of siphuncles containing endocones. Siphuncle large, gently curved, slowly expanding, with compressed cross section; endocones (recrystallized and not individually traceable) relatively short and rapidly tapering, as shown by cavity left by last endocone; in adapical part of siphuncle 2 endocones were developed, separated by partition along long axis of compressed cross section. Impressions of septa or septal necks not present, probably because of exfoliation of outer endoconal layers. *M.Sil.*

*Humoceras* FOERSTE, 1925 [*\*H. unguloideum*; OD]. Characters of family. *M.Sil.*, Can.(Ont.). —FIG. 123, *I*. \**H. unguloideum*; *1a-d*, lat., ?dorsal, adapical, adoral views,  $\times 0.7$ ; *1e*, another specimen showing endosiphuncle,  $\times 0.7$  (Sweet, n).

### Order INTEJOCERIDA Balashov, 1960

[*nom. correct.* TEICHERT, herein (*pro order* Intejoceratida BALASHOV, 1961, *nom. transl. ex suborder* Intejoceratina BALASHOV, 1960)] [=order Intejoceratida BALASHOV in SHIMANSKIY, 1959 (rejected name, probably intended as Intejoceratida); Interjectoceratina FLOWER, 1962 (*nom. null.*)]

Straight, longiconic, or, more rarely, slightly cyrtconic conchs with circular or slightly compressed cross section; outside of shell smooth; camerae short; sutures straight. Siphuncle large, diameter as much as one-half that of conch; marginal to central, septa achoanitic to holochaoanitic; connecting rings (in forms with short septal necks) inflated or concave between septa; long septal necks more or less cylindrical; interior of siphuncle filled with longitudinal, radially arranged, calcareous lamellae, resembling actinosiphonate deposits of Oncocerida, but more tightly packed. *L.Ord.-M.Ord.*



1a



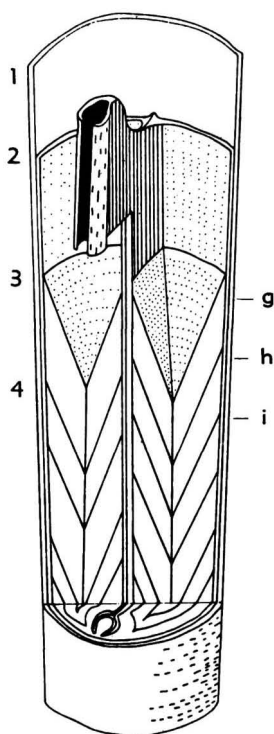
1b



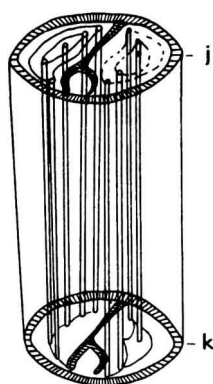
1c



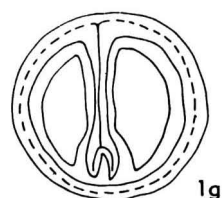
1d



1e



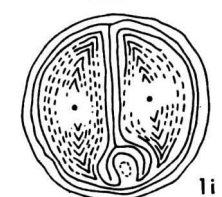
1f



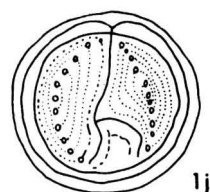
1g



1h



1i



1j



1k

# Allotrioceras

FIG. 121. Allotrioceratidae (p. K184).

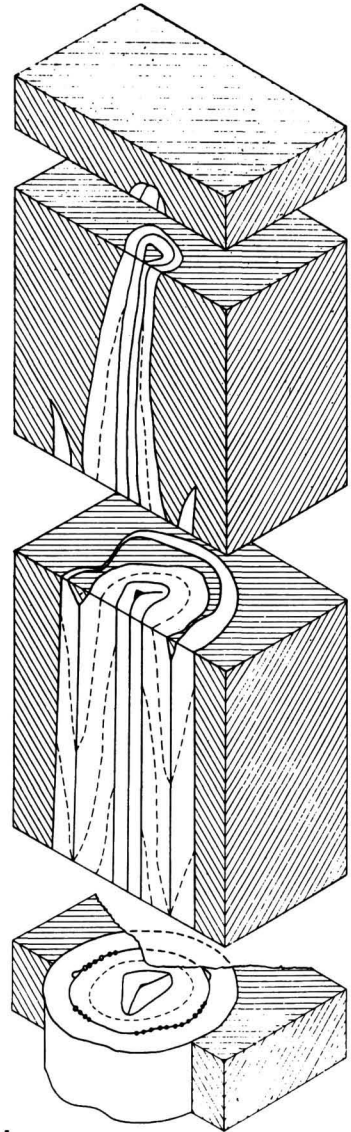


1a



1b

Mirabiloceras



1c

FIG. 122. Allotrioceratidae (p. K184).

### Family INTEJOCERATIDAE Balashov, 1960

Straight or slightly cyrtoconic conchs with circular or slightly compressed cross section; sutures straight, transverse; camerae short. Siphuncle moderately wide, central or slightly eccentric; interior of siphuncle filled with thick, longitudinal, radially arranged, calcareous lamellae; septal necks

acheanitic; connecting rings thick, convex inward. *L.Ord.*, ?*M.Ord.*

**Intejoceras** BALASHOV, 1960 [*I. angarense*; OD]. Small, straight or weakly cyrtoconic conchs with circular or slightly compressed cross section; camerae short, sutures straight. Siphuncle nearly half of conch diameter, slightly eccentric; septal necks achanitic, connecting rings thick, convex inward; in interior of siphuncle are radially and longitudinally arranged, thick, calcitic lamellae,

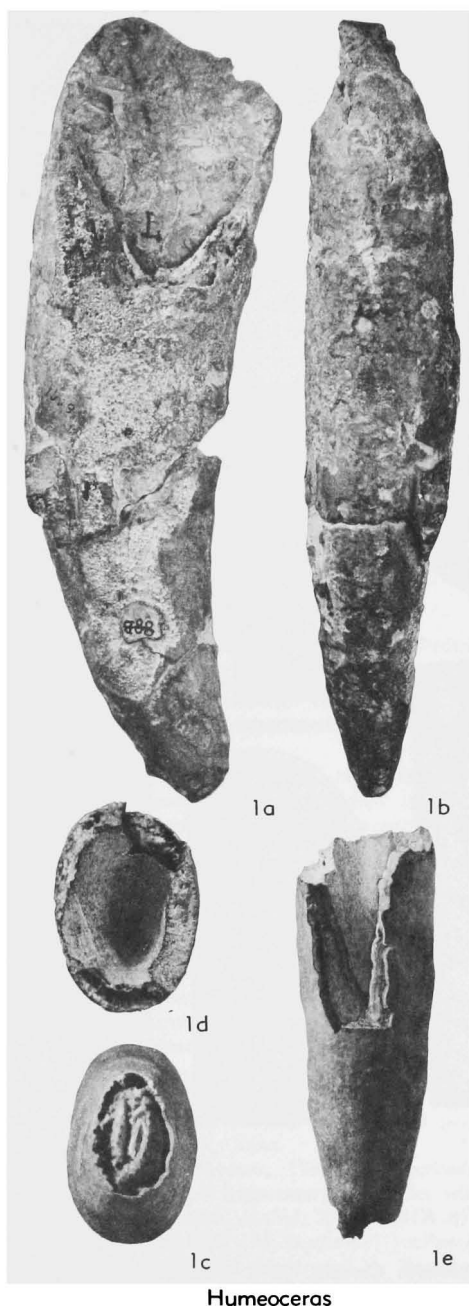


FIG. 123. Humeoceratidae (p. K184).

filling most of siphuncle except for central tube. *L.Ord.*, USSR(Sib.).—FIG. 124, 1. \**I. angarensis*; 1a, b, ventral view, long. lat. sec.,  $\times 1$ ; 1c, transv. sec.,  $\times 1.6$ ; 1d, long. sec. of ectosiphuncle with thick connecting rings,  $\times 5$  (4).

**Evencoceras** BALASHOV, 1960 [*\*E. angarensis*; OD]. Large, straight conchs with circular cross section; camerae short, sutures straight. Siphuncle about one-half of conch diameter, slightly ventral of center; septal necks achoanitic to orthochoanitic, connecting rings thick, convex inward; interior of siphuncle filled with longitudinal, radially arranged, tightly packed calcareous lamellae of irregular width and thickness; endosiphuncular tube wide, irregular in cross section, without wall. *L.Ord.*, ?*M.Ord.*, USSR(Sib.).—FIG. 124, 2a, b. \**E. angarensis*; 2a, dorsoventral sec.,  $\times 0.7$ ; 2b, transv. sec. of siphuncle,  $\times 1.3$  (4).—FIG. 124, 2c, d. *E. rozhcovense* BALASHOV; transv. sec. of siphuncle, long. sec. of siphuncle and part of phragmocone,  $\times 0.7$  (4).

### Family PADUNOCERATIDAE

Balashov, 1960

Large, straight conchs with large ventral siphuncles; septal necks holochoanitic; interior of siphuncle filled with thin radial lamellae. *M.Ord.*

**Padunoceras** BALASHOV, 1960 [*\*P. rugosaeforme*, OD]. Characters of family. Radial lamellae somewhat wavy in cross section, converging along axis nearer dorsal than ventral side; endosiphuncular tube with depressed, crescent-shaped cross section. *M.Ord.*, USSR(Sib.).—FIG. 125, 1. \**P. rugosaeforme*; 1a, dorsoventral sec. of siphuncle and part of phragmocone,  $\times 0.45$ ; 1b, c, transv. sec. of siphuncle and adapical part of siphuncle with endosiphuncular tube,  $\times 0.7$ ; 1d, diagram. reconstruction, greatly reduced (4).

### ?Family BAJKALOCERATIDAE

Balashov, 1962

Orthoconic conchs with elliptical cross section and short camerae. Siphuncle large and central or only slightly off-center. Septal necks achoanitic to hemichoanitic. Interior of siphuncle in earlier growth stages lined with calcareous deposit that seems to consist of a series of superimposed outgrowths of the connecting rings; transverse and longitudinal partitions divide this deposit into numerous individual cells. [The relationships of these forms to the Intejocerina cannot be considered as well established.] *L.Ord.*(*Arenig.*), USSR(Sib.).

**Bajkaloceras** BALASHOV, 1962 [*\*B. angarensis*; OD]. Characters of the family. *L.Ord.*(*Arenig.*), Sib.

### ENDOCERATOIDS OF UNKNOWN AFFINITIES AND UNRECOGNIZABLE GENERA

**Changkiuoceras** SHIMIZU & OBATA, 1935 [*\*C. shantungense* (*nom. nud.*)]. Insufficiently de-

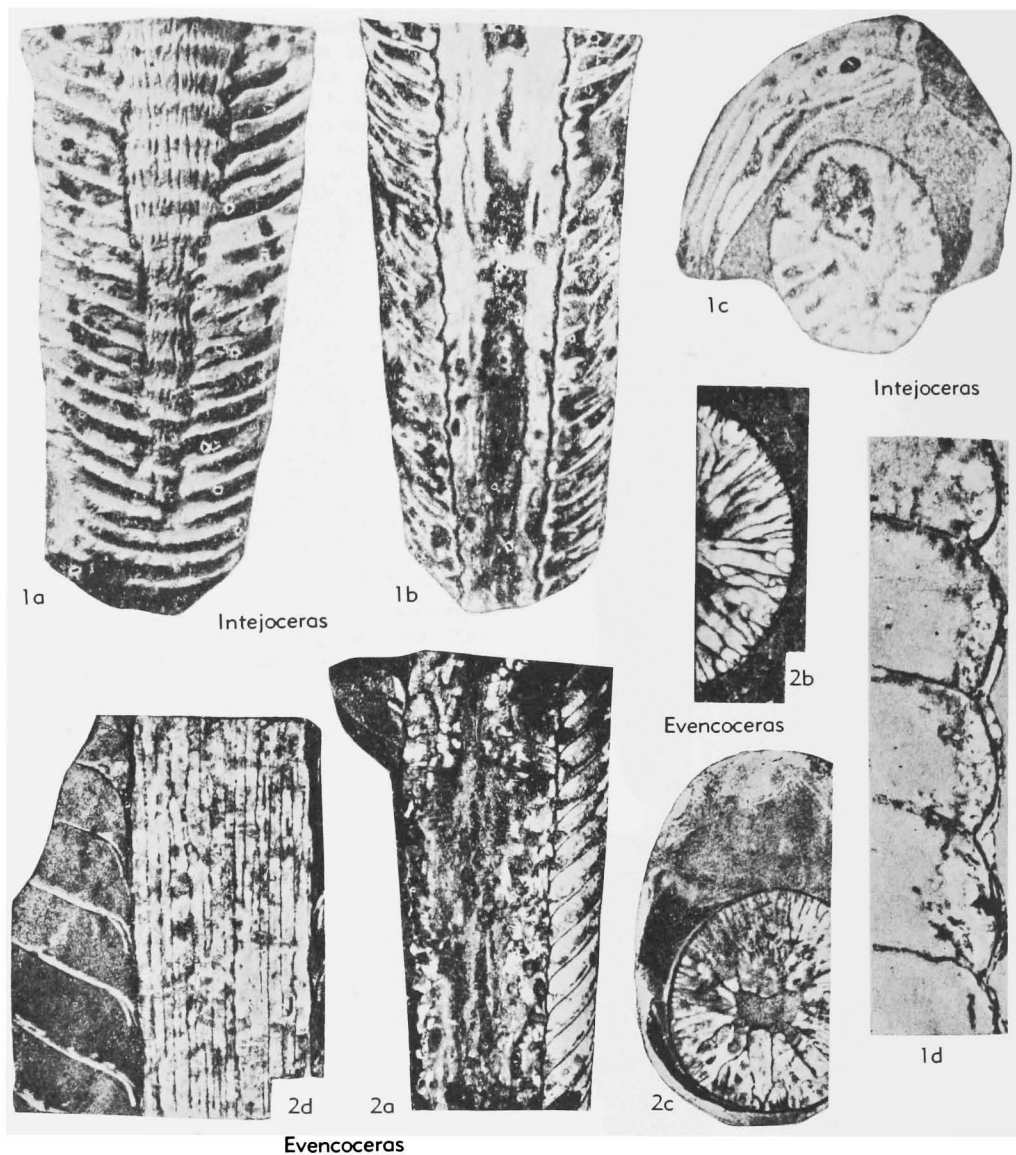


FIG. 124. Intejoceratidae (p. K186-K187).

scribed, based on undescribed type-species. *M.Ord.*, China.

**Colpoceras** HALL, 1850 [*\*C. virgatum*]. Based on siphuncle fragments. [Probably junior synonym of *Cameroeras* or *Endoceras*.] *M.Ord.*, N.Am. (N.Y.).

**Conoceras** BRONN, 1837 [*\*C. angulosus*] [= *Conoceratites* D'ARCHIAC & DE VERNEUIL, 1842 (*nom. null.*); *Conoclastites* BALASHOV, 1962 (*nom. null.*)]. Poorly described endocerid of unknown affinities. ?*Ord.*, N.Am.

**Diploceras** CONRAD, 1842 [*\*D. vanuxemi*] [*non Diploceras* SALTER, 1856 (= *Tretoceras* SALTER, 1858)]. Unrecognizable endocerid, probably belonging to Endoceratidae. *M.Ord.*, N.Am. (N.Y.).

**Hemiceratites** EICHWALD, 1840 [*\*H. angulosa*] [= *Hemiceras* EICHWALD, 1856 (*non* GUENÉE, 1852) (*obj.*); *Hemiceratites* TATE, 1868 (*nom. null.*)]. Based on abraded, fragmentary posterior parts of endocerid siphuncles. *Ord.*, Eu. (Est.).

**Hemipiloceras** SHIMIZU & OBATA, 1936 [*\*H. ellipticum*] [= *Hemipiloceras* FLOWER, 1955 (*nom.*

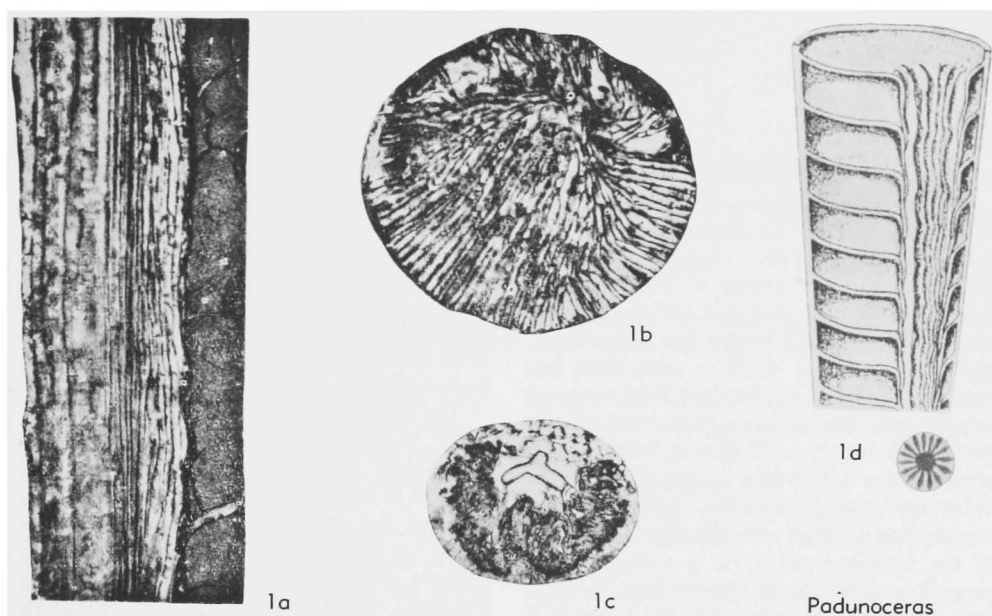


FIG. 125. Padunoceratidae (p. K187).

*null.*). Based on siphuncles of endoceratid or piloceratid affinity, perhaps similar to *Allopiloceras*. *L.Ord.*, E.Asia.

**Kailuanoceras** OBATA, 1940 [*\*K. suchuansuense*]. Based on fragment of apical portion of a siphuncle; supposed to resemble *Suecocreras*, but with more blunt apical end. *Ord.*, China.

**Kaipingoceras** SHIMIZU & OBATA, 1937 [*\*"K. elongatum, nov.=Camerocreras attenuatum (non GRABAU) in R. ENDO, 1935"*]. Unrecognizable endocerid, probably belonging to Endoceratidae or Proterocameroceratidae. *L.Ord.*, E.Asia.

**Linchengoceras** OBATA, 1940 [*\*L. nagaoui*] [= *Linchengoceras* FLOWER, 1955 (*nom. null.*)]. Based on gradually expanding apical parts of siphuncles. *M.Ord.*, China.

**Neokaipingoceras** OBATA, 1940 [*\*N. fenghuangshanense*]. Based on unrecognizable apical parts of siphuncles. *M.Ord.*, China.

**Paravaginoceras** KOBAYASHI, 1934 [*\*P. parvodepressum*]. Based on fragmentary siphuncles with depressed cross section. *M.Ord.*, Korea.

**Penhsioceras** ENDO, 1932 [*\*P. fusiforme*] [= *Penhsioceras* BALASHOV, 1961 (*nom. null.*)]. Based on

apical portion of siphuncle with slight apical swelling and somewhat asymmetrical endocones, probably belonging to Proterocameroceratidae. *L.Ord.*, E.Asia.

**Pradoceras** SAMPELAYO, 1938 [*\*P. kobayashi*]. Based on anterior part of phragmocone and body chamber; suture with significant ventral lobe; superficially similar to *Lobendoceras*; internal structure unknown. *Ord.*, Eu.(Sp.).

?**Sidemina** DE CASTELNAU, 1843 [*\*S. infundibuliforme*]. Seems to be based on one camera with large subcentral siphuncle. *Ord.*, N.Am.(Can.).

**Subpenhsioceras** SHIMIZU & OBATA, 1936 [*\*S. spindleforme*, OD]. Apical portion of siphuncle, internal structure unknown; unrecognizable. *L.Ord.*, China.

**Trifurcatoceras** OBATA, 1940 [*\*T. nakamura*]. Apical portions of rapidly expanding siphuncles; outside trifurcate near apex; affinities unknown. *M.Ord.*, E.Asia.

**Yehlioceras** SHIMIZU & OBATA, 1937 [*\*Suecocreras yehliense* GRABAU, 1922]. Apical portion of siphuncle, internal structure unknown; unrecognizable. *L.Ord.*, China.



## ACTINOCERATOIDEA

By CURT TEICHERT

[United States Geological Survey]

## MORPHOLOGY

This subclass includes cephalopods having conchs of medium to large size, generally straight and slender, though some are slightly curved. Straight shells commonly reach lengths of 2 to 3 feet (60 to 90 cm.); maximum recorded length for early Paleozoic actinoceratoid shells is somewhat less than 6 feet (180 cm.), but late Paleozoic representatives (*Rayonoceras*) are said to have reached as much as 20 feet in length. The cross section of conchs is generally subcircular to broadly elliptical, with flattened venter, but in some specialized genera (e.g., of the Gonioceratidae) it is strongly compressed and flattened. Body chambers are generally slightly contracted, reaching their maximum diameter in the middle, but apertures are entire and uncontracted.

Siphuncles are typically large, subcentral to marginal in position, though in many conchs they are intermediate. In most genera the siphuncle segments are broadly ex-

panded between septa, except in some of the Ormoceratidae, in which the segments are longer than wide.

The Actinoceratoidea contain a single order, Actinocerida, which is defined as having the same characters as those of the subclass. It is sufficient in following descriptions and discussion to write of actinocerids and Actinocerida.

The septal necks are cyrtchoanitic (Fig. 126); in the Huroniidae and Armenoceratidae they are recumbent and brims are close to or in contact with the posterior surfaces of the septa (Fig. 127). Open cyrtchoanitic necks may have a secondary calcareous deposit, known as **circulus**, filling their outer, concave side, thus strengthening the neck (Fig. 128).

In addition to the circulus, cameral deposits are common, both as episeptal and hyposeptal deposits. In the early growth stages of many conchs and in the mature stages of some, cameral deposits may occupy almost all the space of the camerae. In the vicinity of the siphuncle the episeptal deposits of some genera (e.g., *Actinoceras*) may be thickened into a **circumsiphuncular ridge**.

The most distinctive part of the actinocerid is the siphuncle. Typically it is very large and its segments are inflated between the septa. Early forms (e.g., *Polydesmia*) have siphuncular segments which are five or six times as wide as long. Among shells of later genera many have globular or elongated ellipsoidal siphuncular segments.

In genera with broadly expanded siphuncular segments, parts of the connecting rings are usually in contact with the septa along **adnation surfaces**. Usually the posterior part of the connecting ring is adnate to the anterior surface of the septum, but in some conchs (e.g., *Nybyoceras*) parts of the anterior portion of the connecting ring are in contact with the posterior surface of the anterior septum. A secondary deposit or thickening of the septum known as the **contact layer** occurs in some shells along the adnation surface on

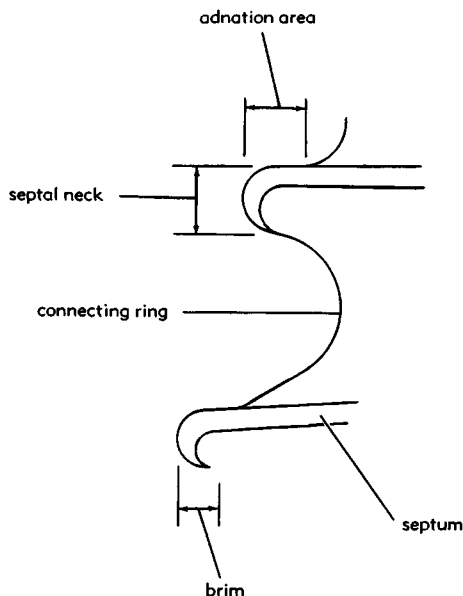


FIG. 126. Diagram of cyrtchoanitic septal neck area showing terminology (Teichert, n).





FIG. 127. Modifications of cyrtchoanitic septal neck in actinocerids: *A*, normal cyrtchoanitic; *B,C*, recumbent (armenoceratid); *D*, hook-shaped (gonioceratid, huroniid) (Teichert, n).

the anterior side of the septum (Fig. 129). The portion of the connecting ring not in contact with either of the adjacent septa is known as the **free part** of the connecting ring.

In many genera the siphuncle occupies the greater part of the initial portion of the conch. In mature parts of shells the maximum diameter of an expanded siphuncle segment may be equal to one-half or more of the diameter of the conch at the same level. In general, the siphuncle shows a tendency to decrease in diameter as the body chamber is approached. This decrease may affect both the diameter of the septal

foramen and the diameter of the siphuncular segments, and in some genera (e.g., *Actinoceras*, *Paractinoceras*, *Leurorthoceras*) which have heavy and bulky segments in the young and adult stages, the segments are increasingly slender in the anterior part of the shell.

In all typical actinocerids the siphuncle is filled with calcareous deposits, at least for the greater part of its length. A few forms are included in the order by reason of analogy, even though they are not known to possess endosiphuncular deposits (e.g., *Paractinoceras*, some species of *Ormoceras*).

In the mature stages of most actinocerids,

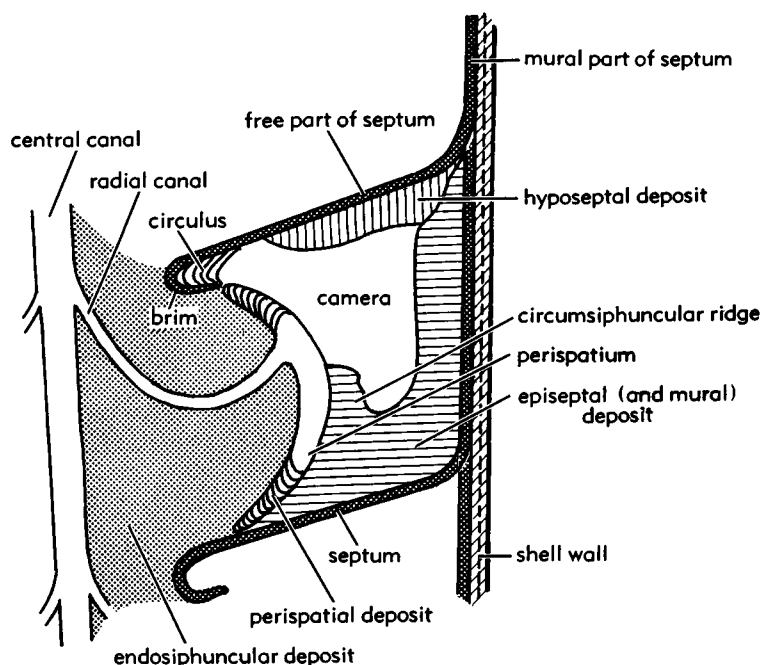


FIG. 128. Diagram of part of camera and siphuncle segment (185).

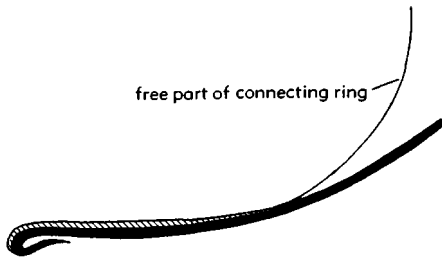


FIG. 129. Contact layer (oblique lining) in *Armenoceras* (185).

the endosiphuncular deposit is disposed in such a manner that the spaces not occupied by it form a system of more or less regularly arranged canals, believed to be a primary organic feature of the siphuncle and known as the **endosiphuncular canal system** or **endosiphuncular vascular system**. The endosiphuncular deposits are not ordinarily in contact with the inner side of the free part of the connecting ring. Between the two a narrow peripheral open space termed **perispatium** (Fig. 128), is left in the siphuncle. In some advanced growth stages the perispatium is partly occluded by later-formed **perispatial deposits** (Fig. 128).

The endosiphuncular canal system consists of a **central canal**, which runs along the whole length of the siphuncle, as a rule slightly dorsally from its central axis (Fig. 130). More rarely, the central canal is situated more eccentrically and may be situated close to the dorsal side of the siphuncle. **Radial canals** branch off from the central canal in each siphuncular segment. Their number and arrangement varies widely. In some forms they are very numerous, but in others (e.g., *Metarmenoceras*) they are relatively few and symmetrically arranged. In well-preserved specimens they are surrounded by membranes of unknown composition (Fig. 131).

In agreement with FLOWER (46), except for slight modifications, the following basic patterns in arrangement of the radial systems of actinocerid siphuncles may be distinguished (Figs. 132-134): (1) **Dendroid**, characterized by numerous fine tubes that branch complexly as they approach the wall of the siphuncle (e.g., *Polydesmia*, Fig. 132,A,B). (2) **Reticulate**, comprising a sys-

tem of double arcs modified by complex, irregular branching and by a tubular network concentrated close to the central canal (e.g., *Cyrtonyboceras*, Fig. 132,C). (3) **Arched**, having radial canals that form roughly semicircular arcs, joined to the central canal at the level of the septal foramen and extending to the perispatium at approximately mid-level of anterior and posterior segments (e.g., *Armenoceras*, many species). This type may be modified by

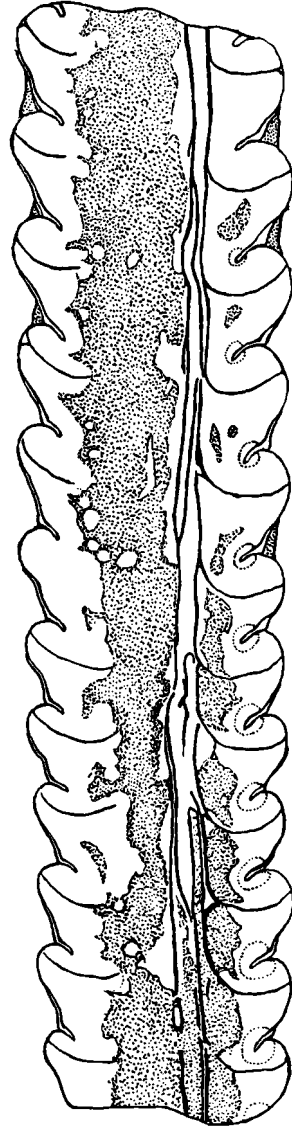


FIG. 130. Endosiphuncular canal system in *Huronella*,  $\times 1$  (185).



Fig. 131. Membranes surrounding radial canals in siphuncle of *Cyrtonybyoceras*,  $\times 5$  (185).

placement of proximal parts of the radial canals closely pressed against the central canal, bent abruptly, and extending almost straight to the perispantium (e.g., *Elrodocer*, Fig. 132,D). (4) **Curved**, characterized by radial canals that leave the central canal near the septal foramen, curving backward and then outward to join the perispantium (in some shells with minor branching) in the expanded part of the septum. In some forms curved canals issue from the central canal at a distance equaling the length of one or two segments in front of the segment whose perispantium they enter (e.g., *Actinoceras*, *Selkirkoceras*, *Lambeoceras*, *Armenoceras*, Fig. 132,E). (5) **Straight**, distinguished by simple, straight radial canals extending at right angles from the central canal to the perispantium in the mid-plane of each segment (e.g., *Deiroceras*, *Metarmenoceras*, Fig. 132,F).

The complexity of the endosiphuncular canal system of actinocerids (Fig. 133, 134) is highly suggestive of the fact that it might reflect rather accurately certain features of the soft anatomy of the actinocerid siphon. As early as 1853, SAEMANN suggested that the "canals" were tubes surrounded by membranes similar in composition to the siphuncle wall (connecting ring). Considering the size and complexity of the tubes, SAEMANN suspected that they fulfilled important organic functions.

On the other hand, BARRANDE (1855, 1877) denied the existence of a tube system in the actinocerid siphuncle. In his opinion, the central and radial canals were simply portions of the undifferentiated endosiphuncular space, not occupied by or-

ganically deposited calcareous secretions which he called "*anneaux obstrueteurs*." More recently, TROEDSSON and MUTVEI have expressed similar views.

Many students of actinocerid cephalopods (e.g., HYATT, FOERSTE, and SCHINDEWOLF), never discussed the nature and possible function of the endosiphuncular canal system.

The first detailed study of three-dimensional configurations of various types of endosiphuncular actinocerid structures was by TEICHERT (1933, 1934, 1935), who concluded that the canal system of the actinocerids represents remnants of an endosiphuncular vascular system. The radial canals do not, as had been held by some earlier observers, communicate with the camerae, but open into the perispantium, as described above. These views have been supported by FLOWER (46), who was able to offer further refinement of the classification of actinocerid endosiphuncular structures. Like TEICHERT, he considered the perispantium as the places where "interchange of metabolic products, and probably of the blood itself, could take place between the cameral and siphonal tissues."

If the endosiphuncular canal system represented only some undifferentiated siphonal residual cavity, left more or less accidentally between endosiphuncular calcareous deposits, it would be difficult to explain why this space is never entirely closed in actinocerids. Even in mature conchs, the canal system is well preserved in the most apical portions of the siphuncle. Also, the very complex endosiphuncular systems of the dendritic and reticulate types cannot be explained except as remnants of organic structures.

## ONTOGENY

Because of lack of well-preserved material, the ontogeny of actinocerids is very little known. In fact, early ontogenetic stages have been described for a few early Ordovician genera (e.g., *Actinoceras*, *Armenoceras*, and forms resembling *Kochoceras* and *Selkirkoceras*) and for the Early Carboniferous *Carbactinoceras*. All specimens on which observations of early ontogenetic stages are based are fragmentary and con-

clusions derived from them are neither convincing nor internally consistent.

It seems that in *Actinoceras* (25) and in *Armenoceras* (107) the initial chamber is

shallow, saucer-shaped, and much shorter than the succeeding camerae. Adorally, it is closed by the first septum which has achoanitic septal necks. It has been main-

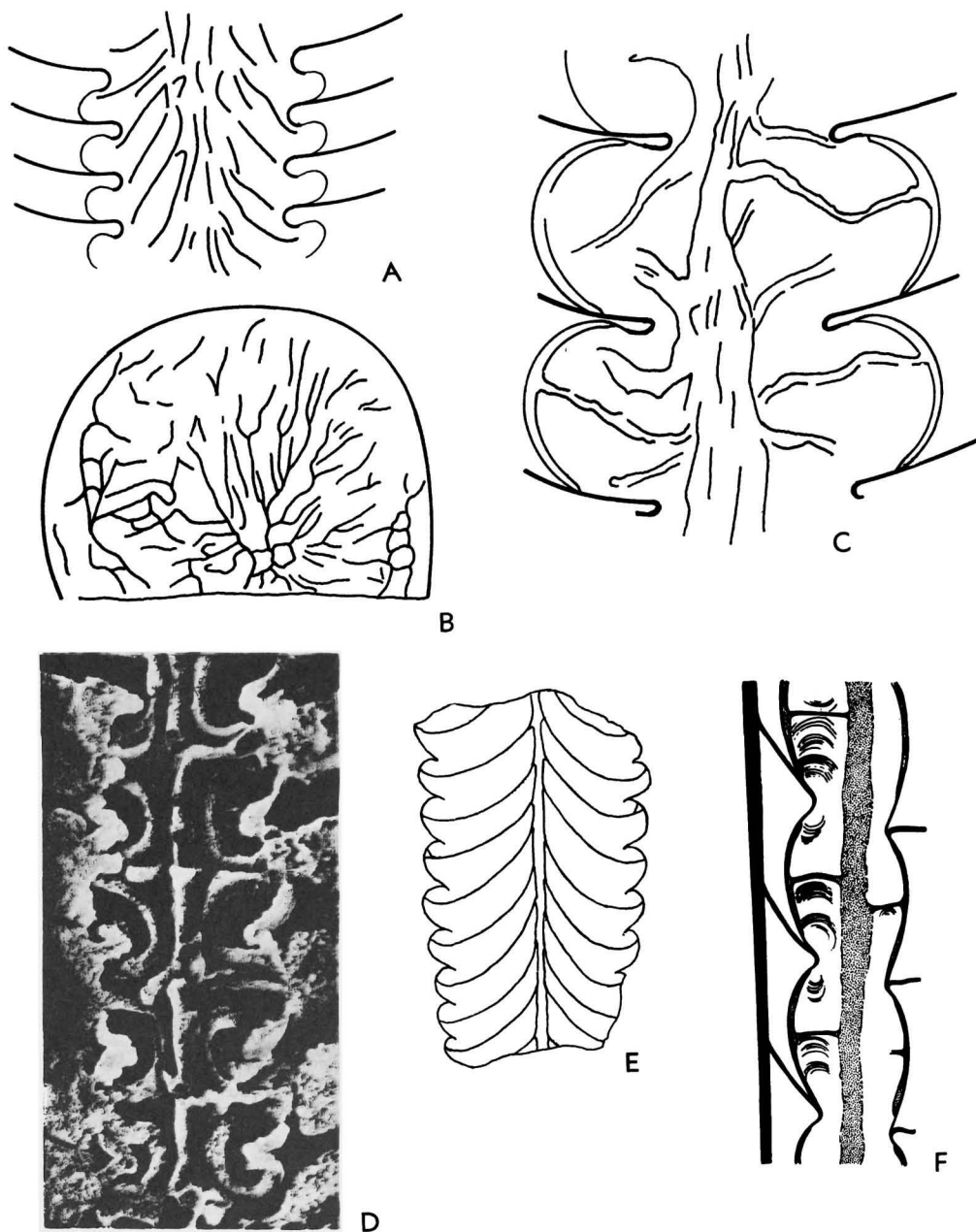


FIG. 132. Different types of endosiphuncular canal systems in actinocerids: A,B, dendritic (*Polydesmia*); C, reticulate (*Cyrtonybyoceras*); D, arched (*Armenoceras*); E, curved (*Armenoceras*); F, straight (*Deioceras*); not to scale (A-C, Teichert, n; D-F, 185).

tained that the siphuncle ends openly in the initial chamber (Fig. 135,B), but evidence offered in support of this suggestion

is not compelling, because of the fragmentary nature of the apical ends of the described specimens.

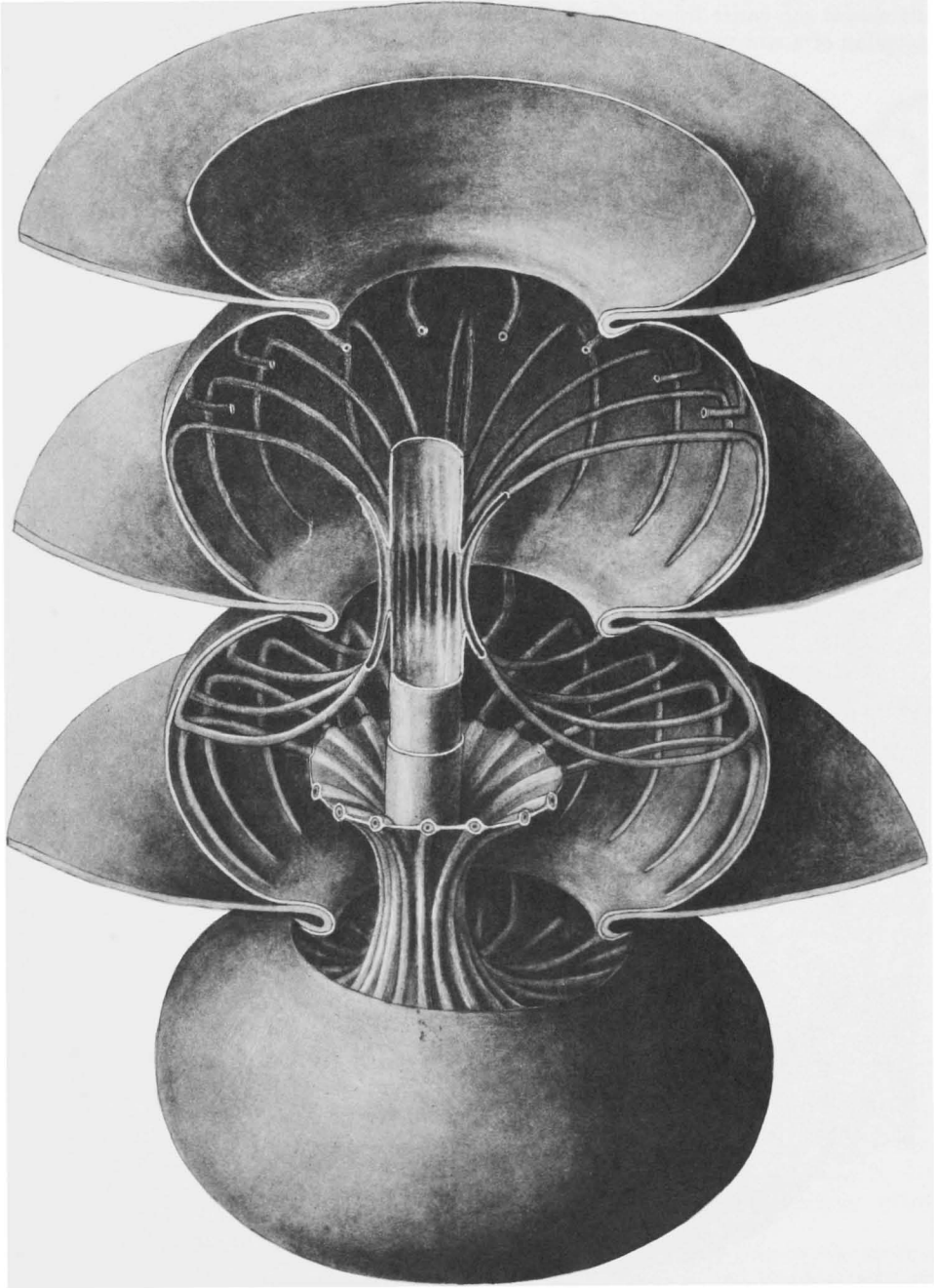


FIG. 133. Reconstruction of actinocerid siphuncles and phragmocones, with arched endosiphuncular canal system (endosiphuncular deposit partly removed) (185).

In *Kochoceras* (186) the first chamber is short-conical with a bluntly rounded apical tip and it is slightly longer than the second chamber. The first siphuncular segment fills almost the entire initial chamber, with exception of a narrow space behind the first

septum (Fig. 135,A). No evidence appears that this first preserved chamber and segment of the siphuncle were preceded by another, shallower and shorter one, as was possibly the case in *Actinoceras* and *Armenoceras* (Fig. 135,C).

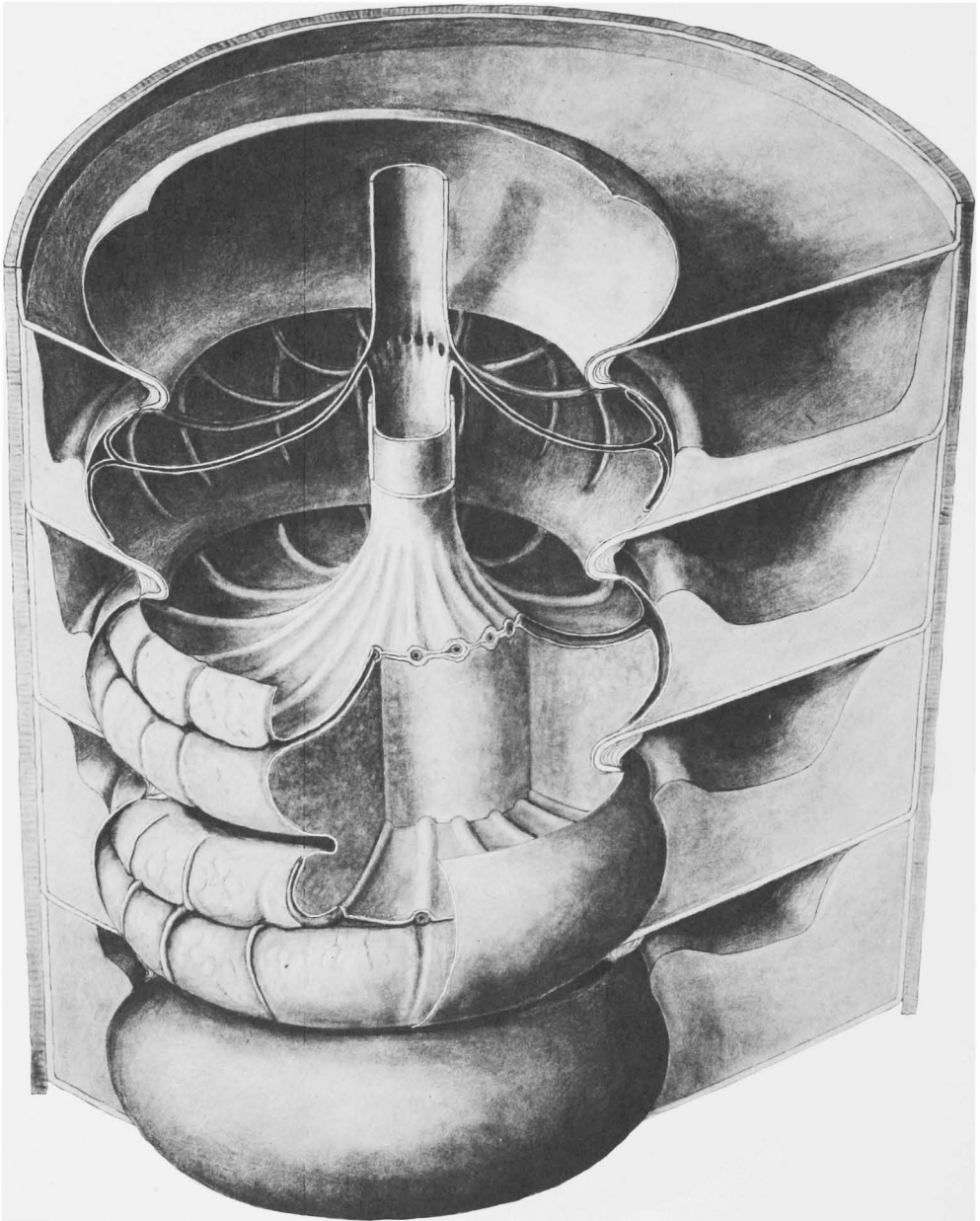


FIG. 134. Reconstruction of actinocerid siphuncles and phragmocones, with curved endosiphuncular canal system (endosiphuncular deposit partly removed), also showing hyposeptal and mural deposits (185).

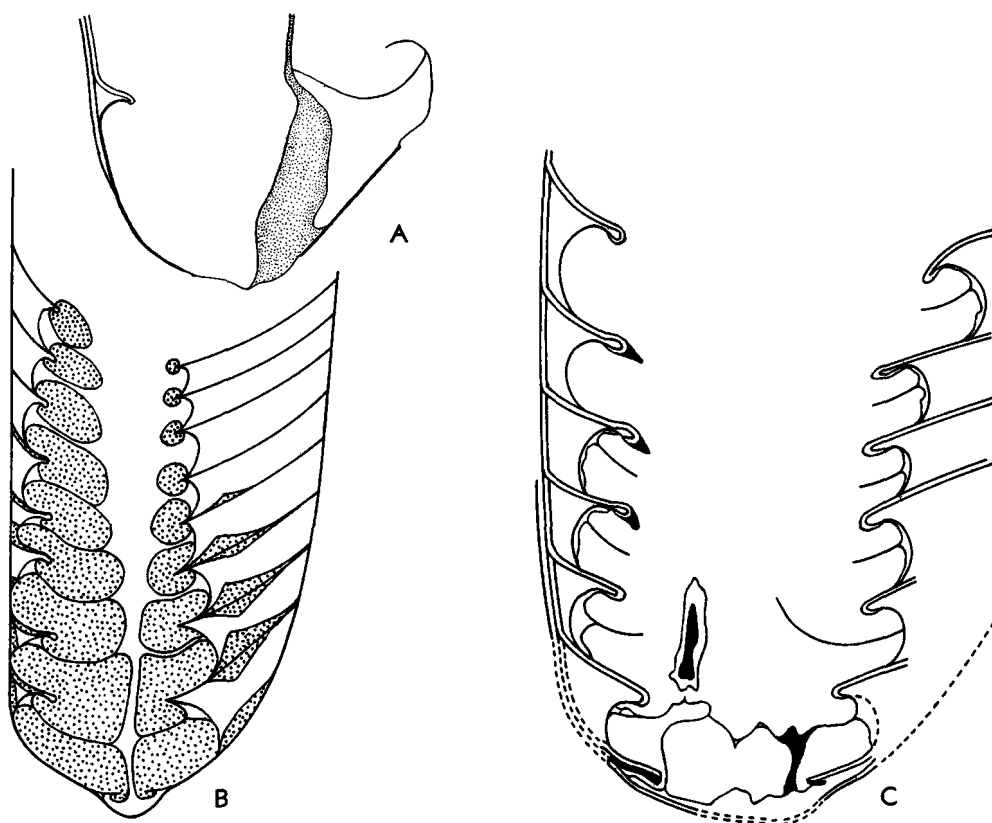


FIG. 135. Initial portions of actinocerid phragmocones and siphuncles: *A*, initial segment of *Kochoceras*, almost entirely filled by first siphuncle segment, with greatly enlarged central canal. Heavy lines: preserved connecting ring material,  $\times 1.3$  (186); *B*, initial portion of conch according to KOBAYASHI with siphuncle opening into initial camera; *C*, initial portion of conch according to FLOWER (siphuncle probably with closed caecum) (25, 107).

*Carbactinoceras* (155) and possibly other Carboniferous actinocerids have a more slowly expanding apical end, with a conical initial chamber. The siphuncle begins in this chamber with a caecum (Fig. 136), similar to structure found in stenosiphonate groups such as the *Orthocerida*, *Tarphycerida*, and *Nautilida*.

The present state of knowledge precludes generalizations in regard to the early ontogeny of actinocerids.

The first segment of the siphuncle is generally smaller, more rarely larger (e.g., *Selkirkoceras*) than the second segment. However, from the second segment onward and throughout most of the adult stages of the conch, the diameter of the siphuncular segments remains remarkably constant,

whereas the diameter of the shell expands very slowly. As full maturity is approached, the siphuncle of some actinocerids, especially the *Actinoceratidae*, in which this growth stage is best known, diminishes in diameter. In some forms, which have very broad and short siphuncle segments throughout most of the conch, these may be globular or even elongated at late stages of growth. Because this anterior part of the siphuncle usually lacks endosiphuncular deposits, fragmentary anterior parts of actinocerid shells may be difficult to distinguish from other cyrtochoanitic conchs (e.g., certain pseudorthoceratids).

The presence of a contracted aperture (e.g., in *Actinoceras*, *Gonioceras*, *Lambeoceras*, and other genera) suggests a mature, or even gerontic individual, as a rule.

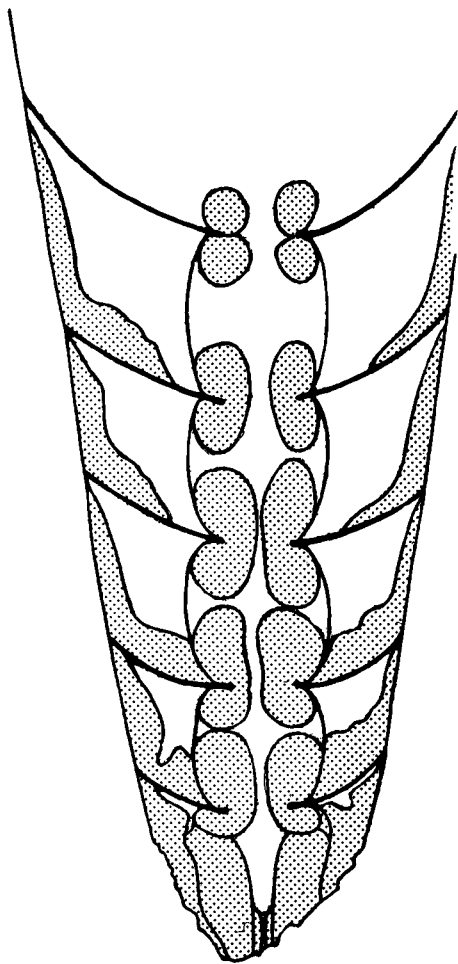


FIG. 136. Apical portion of phragmocone of *Carbactinoceras* (siphuncular and cameral deposits stippled),  $\times 7.5$  (adapted from 155).

## CLASSIFICATION

Because of the striking features of their siphuncle, some actinocerid genera are among the earliest established cephalopod taxa of this rank, and the entire order was set aside at an early date from other nautiloid groups. QUENSTEDT (1836) distinguished the huroniids as "Gigantei," separating them from forms with inflated siphuncular segments, which he called "Cochleati." DE KONINCK (1844) united the then-known genera in a group called Nummularia, because of their "nummuloid-al" siphuncular segments. SAEMANN (1852)

erected a division named Actinosiphitae for all conchs with siphuncular deposits, which included a very few having actinosiphonate deposits, now known to be of oncocerid, rather than actinocerid, lineage. HYATT (1898) was the first to set aside the actinocerid cephalopods as a subgroup of his suborder Cyrtchoanites. He called this subgroup Annulosiphonata, because of the presence of "annuli" in their siphuncles.

The group received little attention until 1930 when FOERSTE & TEICHERT (71) divided it into a number of families. The assemblage was first recognized as an order by TEICHERT in 1933 (185).

FOERSTE & TEICHERT based family units essentially on shape of the septal necks and of the siphuncular segments and they included in the actinocerids some genera (e.g., *Discosorus*, *Westonoceras*) which are now assigned to the order Discosorida.

FLOWER (46) stressed the importance for classification of features of the internal siphuncular structure. Thus, he revived the family Wutinoceratidae SHIMIZU & OBATA, 1935, to include early Middle Ordovician actinocerids with quite diversely shaped siphuncular segments but resembling each other in the complexity of the endosiphuncular canal system. However, the forms thus united are rare, generally known poorly, geographically widely scattered over the globe, and, in part, of uncertain stratigraphic correlation; therefore, it seems advisable for the present to retain the earlier morphological grouping.

## EVOLUTION

In all probability, the earliest known actinocerid genus is *Polydesmia* LORENTZ, from the Maruyama beds of eastern Asia (northern China, Manchuria) (Fig. 137). These are either of earliest Chazyan (Whiterock) age or intermediate between Late Canadian and Chazyan, without exact equivalents in North America. *Polydesmia* has a siphuncle with very broad, short segments and a complex canal system of dendritic type, although simply curved main radial canals that extend through one or two segments also are present.

Other early actinocerids are *Cyrtonybo-ceras*, in the early Chazyan of Newfoundland, and the first *Ormoceras*, found both



at this locality and in Sweden, as well as possibly in Tasmania, although in the last-mentioned area stratigraphic relationships are not clear.

The origin of these earliest actinocerids is unknown. Having cyrtocoanitic septal necks, siphuncular segments inflated in various degrees, and a well-developed siphuncular canal system, these forms are typical actinocerids, and no transitional forms exist between them and contemporaneous or earlier cephalopods. FLOWER (46 and elsewhere) regarded the ellesmerocerid *Bathmoceras* as the ancestor of the actinocerids. However, *Bathmoceras* has endosiphuncular structures that are outgrowths from the inner side of the free part of the connecting rings, whereas endosiphuncular deposits of actinocerids are never in contact with the free part of the connecting ring, but are separated from it by the perispantium. Because of this basic structural difference, it is believed that *Bathmoceras* is not in the line of ancestry of the actinocerids. The sudden appearance of the latter and the high level of organization of their earliest representatives are as mysterious and, at present, as inexplicable as the first appearance of many other highly organized invertebrates, such as the trilobites.

The following important trends characterize the evolution of the actinocerids.

(1) **Size increase.** This trend is not confined to any single lineage. Large actinocerids, several feet long, developed in the late Middle Ordovician. In the Silurian, the huroniids probably included the largest genera. No complete shells of them are known, but some very large siphuncles suggest conch lengths of possibly many feet. Among early Carboniferous forms, *Rayonnoceras* is the genus with largest conch. Early in the nineteenth century SOWERBY reported the occurrence of specimens 20 feet long, but apparently no complete conchs have ever been recovered.

(2) **Simplification of siphuncular canal system.** In the earliest actinocerids, the Polydesmiidae, the endosiphuncular canal system consists, in addition to the central canal, of a system of simply curved main radial canals and a network of dendritic or anastomosing fine canals. All Chazyan

actinocerids (e.g., *Cyrtonybyoceras*) have complex canal systems, although generally somewhat simpler than that of the Polydesmiidae, and of a type previously defined as reticulate. Most post-Chazyan actinocerids have simpler canal systems.

FLOWER (46) suggested the grouping of early actinocerids with complex canal systems in a single family (Wutinoceratidae). However, knowledge of actinocerids of Chazyan age is yet so incomplete that it seems equally possible to assume that simplification of the canal system is a case of parallel evolution in several co-existing families.

Throughout the Upper Ordovician and Silurian, canal systems of arched, curved, and straight types are found in different families. In the Silurian, a modification of the arched type developed in the more rectangular system of *Elrodoceras*, but most Silurian actinocerids have curved or straight canal systems.

In the Devonian, when actinocerids generally experienced a decline, canal systems are of the straight type as a rule, and this is also true for the canal systems of Carboniferous forms.

(3) **Decrease in width of siphuncle segments.** In mature stages of *Polydesmia* the ratio of width to length of siphuncle segments is as much as 6 to 1. In Chazyan *Cyrtonybyoceras* this ratio is 3 to 1, and in the approximately contemporaneous "*Adamsoceras*" (= *Ormoceras*) *isabellae* FLOWER, it is 1.5 to 1. Species with relatively broad siphuncular segments (width/length ratios ranging up to 5 to 1) continue into the Silurian, but are generally outnumbered by forms with much narrower siphuncle segments, such as the ormoceratids and the huroniids. Throughout the Middle and Late Ordovician, forms with broad and short siphuncle segments prevailed and are represented by many species of *Actinoceras*, *Armenoceras*, and related genera.

Devonian actinocerids generally have siphuncles with more or less globular to elongated segments. Carboniferous *Rayonnoceras* has siphuncular segments with a width/length ratio of as much as 2 to 1, but other Carboniferous actinocerids have narrower segments.

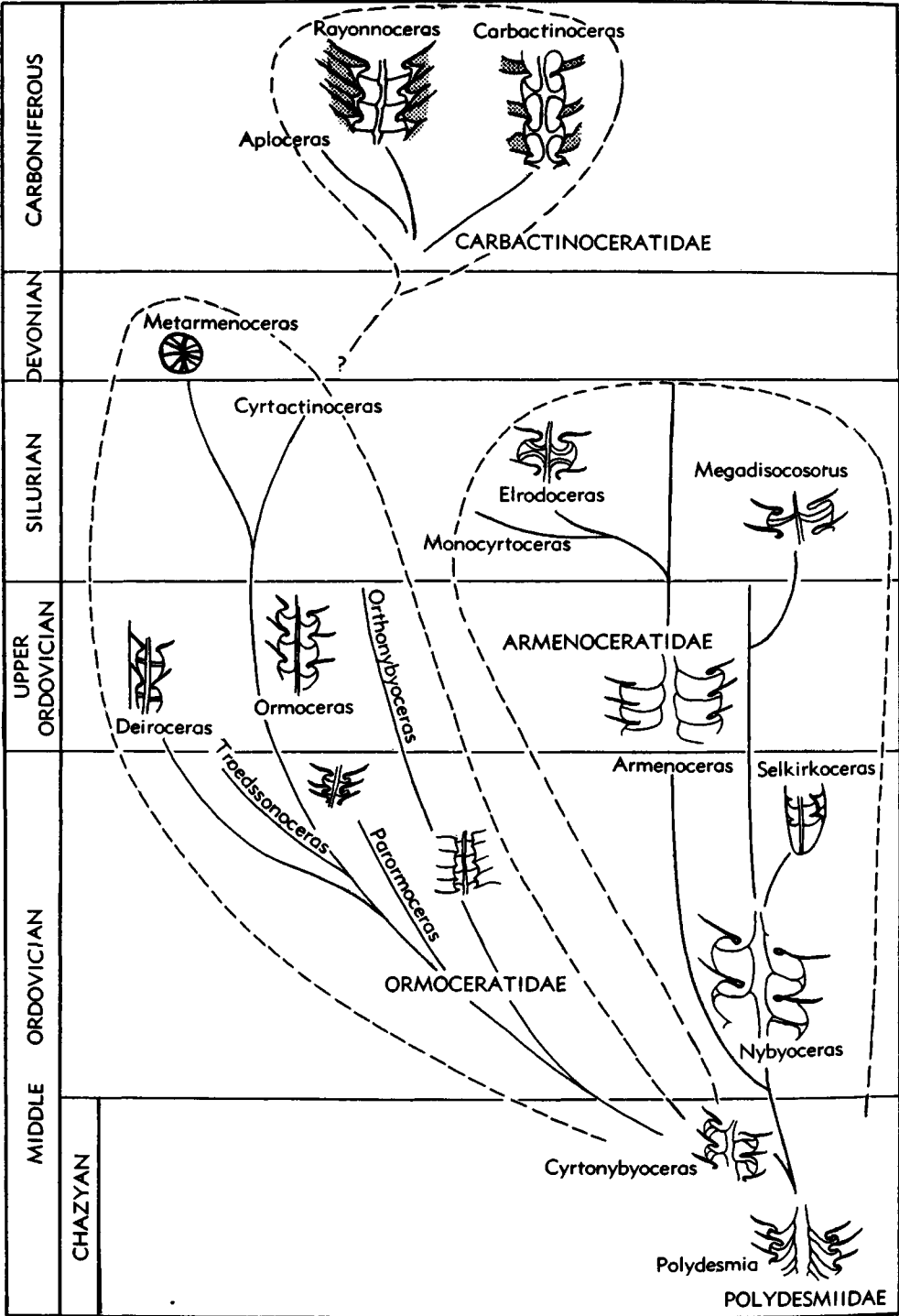


FIG. 137. Diagram showing siphuncular structures and inferred phylogenetic relationships of actinocerid families and genera (Teichert, n).

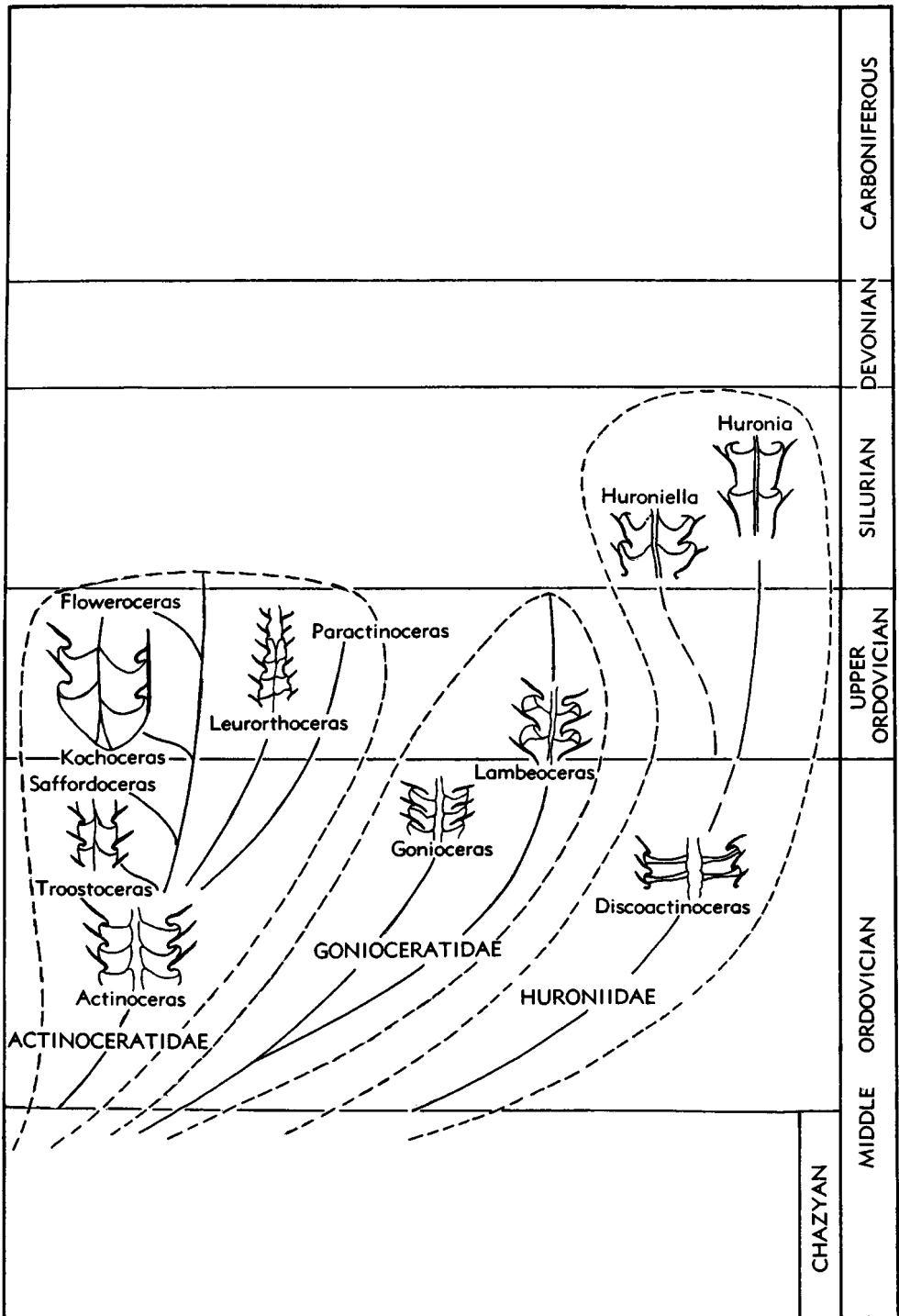


FIG. 137 (Continued).

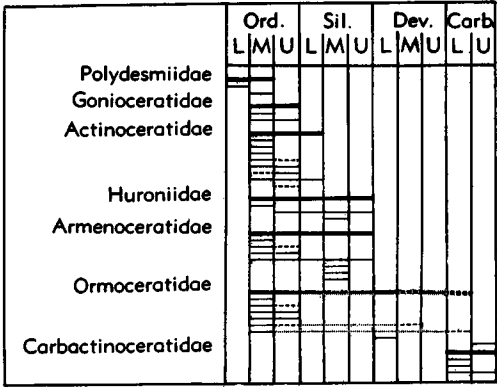


FIG. 138. Stratigraphic distribution of genera and families of Actinocerida (Teichert, n).

Thus, while decreasing width of siphuncle segments cannot be established as an evolutionary trend in any one lineage or family of actinocerids, it is a fact that the segments of the earliest actinocerids are exceptionally broad and short, and that, at least after Middle Ordovician time, actinocerids with comparatively narrower and longer siphuncle segments prevailed. No post-Silurian actinocerid had siphuncle segments with a width/length ratio greater than 2 to 1.

As regards the major feature of the evolution of the Actinoceratoidea (Fig. 137-139), it seems that the Polydesmiidae gave rise to the long-persisting Armenoceratidae through slight narrowing of the siphuncular segments, shortening of the septal necks,

and gradual simplification of the canal system. The origin of the even longer-ranging Ormoceratidae is uncertain. Most probably, they evolved independently from the Polydesmiidae through further contraction of the siphuncular segments and simplification of the canal system, at the same time retaining the primitive, long, cyrtchoanitic necks.

A third offshoot of the Polydesmiidae were the Actinoceratidae, intermediate in position between Armenoceratidae and Ormoceratidae, resembling the former in their broad siphuncular segments, the latter in their long, cyrtchoanitic septal necks.

The Armenoceratidae gave rise to the Gonioceratidae through flattening of the conch and modification of septal shape, and to the Huroniidae essentially through elongation of the siphuncular segments.

While the armenoceratid stock, with all its derivatives, did not survive the Silurian, the Ormoceratidae persisted into the Devonian and from them, in all probability, the Carbactinoceratidae developed in Early Carboniferous time. In this stock the siphuncular canal system remains simple, of the straight type, with siphuncular segments broadening in a width/length ratio of as much as 2 to 1, and in at least one genus a tendency towards considerable size increase and abundant development of siphuncular and cameral deposits is seen.

It has been suggested (SPATH, SCHINDEWOLF) that *Rayonnoceras* and other Car-

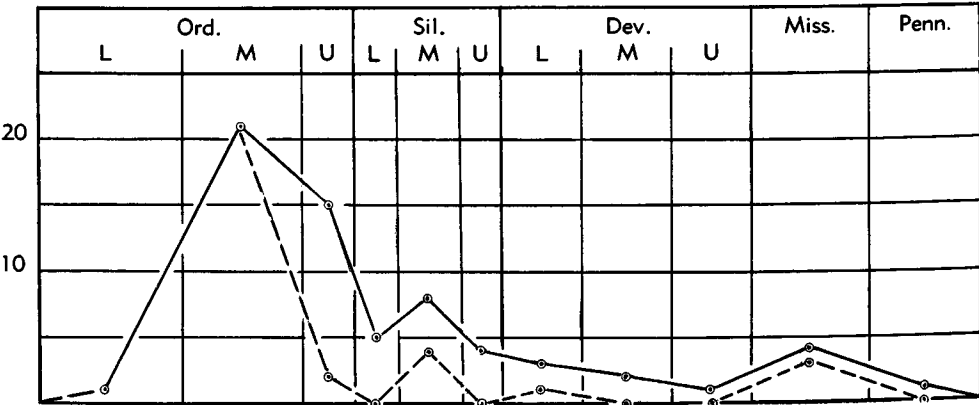


FIG. 139. Graph showing numbers of new genera of Actinocerida introduced in successive epochs (dashed lines) and total genera represented in each (solid lines) (Teichert, n).

bactinoceratidae may be unrelated to the early and middle Paleozoic actinocerids, and their origin has been sought in the pseudorthoceratids or some other orthocerid stock. Until now, this theory lacks a basis of well-substantiated facts. If proved, the development of the Carbactinoceratidae would represent one of the most remarkable examples of homeomorphic evolution among all invertebrate animals.

## GEOGRAPHIC DISTRIBUTION

In the Ordovician three main centers of actinocerid distribution are recognizable: (1) North America, including the Arctic regions and North Greenland; (2) eastern Asia; and (3) Tasmania. Maximum differentiation took place in North America. However, the actinocerid faunas of eastern Asia and Tasmania are not yet well enough known to be fully comparable.

In the Silurian, North America remained an important center of actinocerid distribution, and the order now also became important in northern Europe (Scandinavia and the Baltic regions), with isolated occurrences in central Europe. Probably, during this period actinocerids also occurred to some extent in Siberia, but not many have yet been described.

Devonian occurrences of actinocerids are rare and almost entirely restricted to North America. In the Lower Carboniferous (Mississippian), actinocerids occur sparingly in North America (USA) and in England, central Europe and USSR. In Europe they survived into the Pennsylvanian.

## SYSTEMATIC DESCRIPTIONS

### Subclass ACTINOCERATOIDEA Teichert, 1933

Diagnosis given in "Introductory Discussion" (p. K129). *M.Ord.-U.Carb.(Penn.)*.

### Order ACTINOCERIDA Teichert, 1933

[*nom. correct.* TEICHERT, herein (*pro* Actinoceroidea TEICHERT, 1933)] [=Cochleati+Gigantei QUENSTEDT, 1836; Nummularia DEKONINCK, 1844; Actinosiphitae SAEMANN, 1853 (*partim*); Annulosphonata HYATT, 1898 (subgroup of suborder); Actinoceracea SCHINDEWOLF, 1935 (suborder); Actinoceracea KINDLE & MILLER, 1939 (superfamily); Actinoceracea KUHN, 1949 (order); Actinoceratida FLOWER in FLOWER & KUMMEL, 1950 (order); Actinoceroidea FISCHER in MOORE & LALICKER & FISCHER, 1952 (order); Actinoceratina SWEET, 1958 (suborder); mention of Actinocerida by FURNISH, GLENNISTER, & HANSMAN, 1962 (p. 1343), is disregarded]

Characters of subclass. Exterior surface of shell little known, generally smooth or only weakly sculptured, rarely annulate. Aperture open or slightly constricted. *M.Ord.-U.Carb.(Penn.)*.

The stratigraphic occurrence of genera included in the Actinocerida is shown graphically in Figure 138; the numbers of new genera introduced in successive epochs are indicated in Figure 139.

### Family POLYDESMIIDAE Kobayashi, 1940

[*nom. correct.* FLOWER & KUMMEL, 1950 (*pro* Polydesmidae KOBAYASHI, 1940)]

Medium-sized, straight shells with subcircular cross section and large subcentral siphuncles. Siphuncular segments short and very broad; septal necks either short or long and connecting ring with very broad posterior adnation area; endosiphuncular radial canals numerous, steeply oblique, extending backward (adapically) through 1 or 2 segments before entering perispantium, system of very fine, anastomosing canals of dendritic pattern occurring between these canals. *L.Ord.-M.Ord.*

Polydesmia LORENZ, 1906 [*\*P. canaliculata*; M] [=Maruyamaceras KOBAYASHI, 1931; Murayamaceras TEICHERT, 1933 (*nom. null.*); Maruyamacerina KOBAYASHI, 1936]. Characters of family; septal necks equaling about one-third to one-half length of camerae. *L.Ord.*, C. & E.Asia.—FIG. 140, 1a-c. *\*P. canaliculata*, Manchuria; 1a, b, siphuncle, transv. and long. secs. (orientation unknown),  $\times 1.5$  (109); 1c, part of segment,  $\times 4$  (s, septum; c, circulus; cr, connecting ring (broken line where destroyed); rc, radial canal (Teichert, n)).—FIG. 140, 1d. *P. zuezhanshanensis* CHANG, Manchuria; transv. sec. of shell (outer line=shell, middle line=max. diam. of siphuncle, inner line=septal foramen),  $\times 1.3$  (219).

Ordosoceras CHANG, 1959 [*\*O. sphaeriforme*; OD]. Similar to *Polydesmia* in general dimensions of conch and siphuncle, but siphuncular segments inflated in mid-portion of camerae, inflated part of connecting rings not in contact with either anterior or posterior septa; episeptal and hyposeptal deposits strongly developed in camerae; endosiphuncular canal system reticulate; structure of septal necks not well known. *M.Ord.*, Inner Mongolia.—FIG. 140, 2. *O. sphaeriforme otoktiensis*; 2a, long. sec. of shell (orientation unknown),  $\times 0.7$ ; 2b, long. sec. (orientation unknown, drawn from photograph),  $\times 1.3$ ; 2c, transv. sec. (outer line=shell, middle line=siphuncular segment, inner line=septal foramen),  $\times 0.7$  (219).

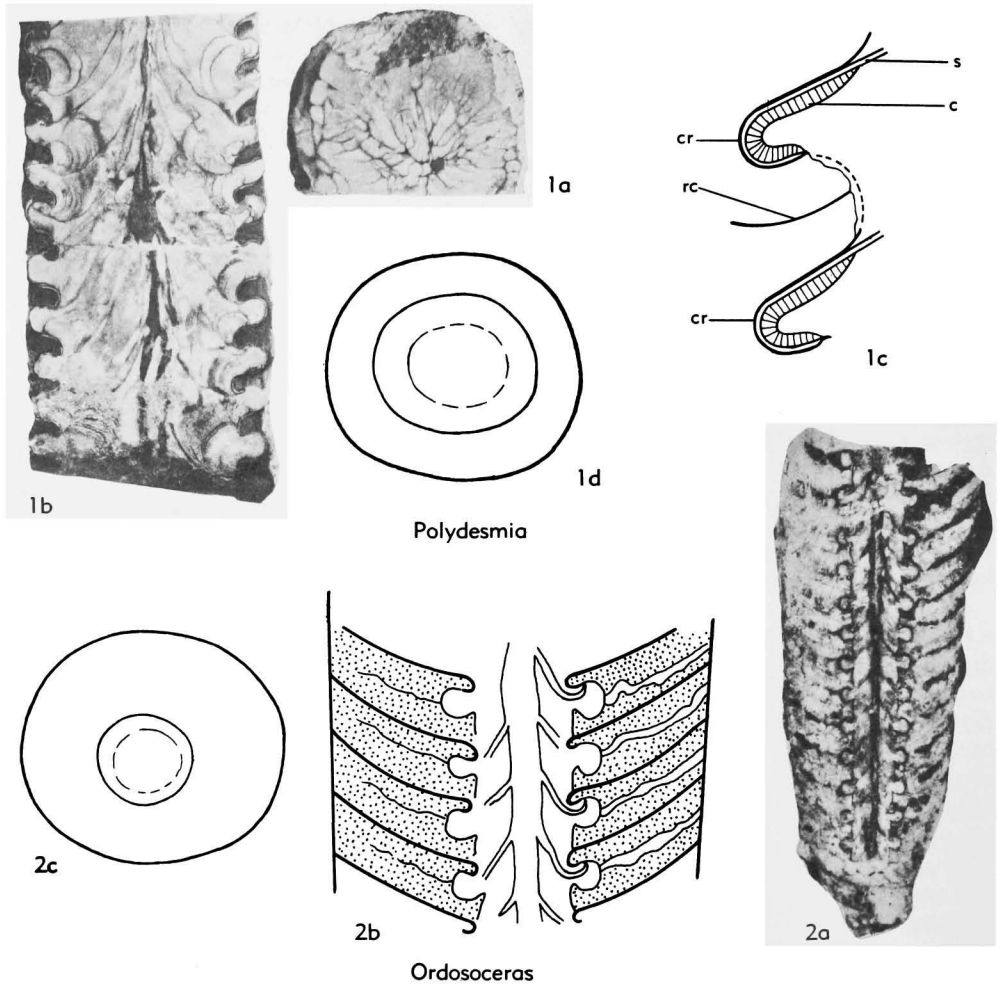


FIG. 140. Polydesmiidae (p. K203-K204).

### Family ACTINOCERATIDAE Saemann, 1853

[incl. Floweroceratidae MILLER & YOUNGQUIST, 1947; Ellinocerataceae, Ellinoceratidae BALASHOV, 1962]

Large, straight shells with blunt apex; sutures straight or only slightly sinuous. Siphuncle large, segments strongly expanded between septa; septal necks long, brims wide, endosiphuncular canals well developed, generally of curved type, remainder of endosiphuncle calcified at maturity. Cameral deposits common, generally consisting of episepal and hyposeptal deposits and in some conchs of circulus. *M.Ord.-L.Sil.*

*Actinoceras* BRONN, 1835 [\**A. bigsbyi*; *M*] [= *Actinoceratites* BRONN, 1834 (*nom. nud.*); *Conotu-*

*bularia* TROOST, 1838 (= *Conotabularia* BRONN, 1856, *nom. null.*); *Arctinoceras* DE CASTELNAU, 1843 (*nom. null.*) (*non* FLOWER & KUMMEL, 1950, *nom. nud.*); *Metactinoceras* ZHURAVLEVA, 1957]. Large, straight, somewhat fusiform shells, with tendency to decrease in diameter from anterior part of phragmocone toward aperture; cross section subcircular to circular. Siphuncle large, generally somewhat off center, tending to decrease in diameter toward adult portion of phragmocone; septal necks long, brims relatively short; narrow endosiphuncular canal in mature stage with simple radial canals. Cameral deposits common, generally of episepal and hyposeptal type; circulus present in few species. *M.Ord.-L.Sil.*, N. Am.-Greenl.-N. Eu.-USSR (Sib.)-E. Asia. — FIG. 141, I. *A. ruedemanni* FOERSTE & TEICHERT, *M. Ord.*, USA (N.Y.); 1a, b, dorsoventral sec., transv. sec.,  $\times 0.7$  (78); 1c, lat. long. sec. through si-

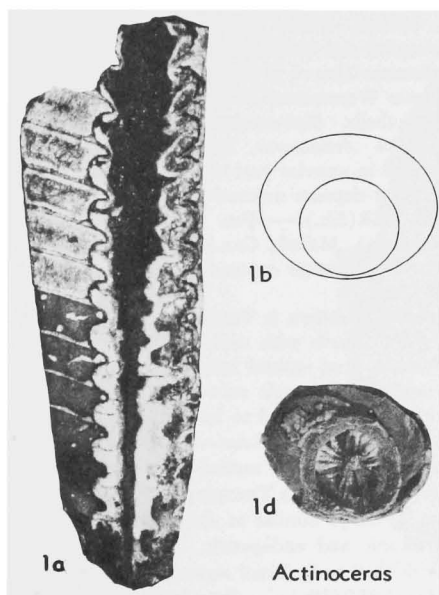


FIG. 141. Actinoceratidae (p. K204-K205).

phuncle,  $\times 1.6$  (185); 1d, apical view of septum and siphuncle with radial canals,  $\times 0.75$  (185). —FIG. 142, 1. *A. beloitense* (WHITFIELD), M.Ord., Can.(Ont.); ventral side,  $\times 0.3$  (78).

**Ellinoceras** BALASHOV, 1960 [*E. septicurvatum*; OD]. Conch small, straight, annulate; sutures strongly sinuous, each forming 14 narrow lobes

and saddles, with deep and broad ventral lobe divided by small saddle. Cameral deposits present; siphuncle subcentral, septal necks short; siphuncular segments short and broad; endosiphuncular tube wide. M.Ord., USSR(NE.Sib.).

—FIG. 143, 1. *E. septicurvatum*; 1a, b, ventral view of conch and adoral surface of septum,  $\times 1$ ; 1c, lat. long. sec.,  $\times 2.5$  (4).

**Floweroceras** MILLER & YOUNGQUIST, 1947 [*F. boreale*; OD]. Similar to *Kochoceras* but with strongly elongated initial chamber and large elongated first siphuncular segment. (?U.)Ord.,

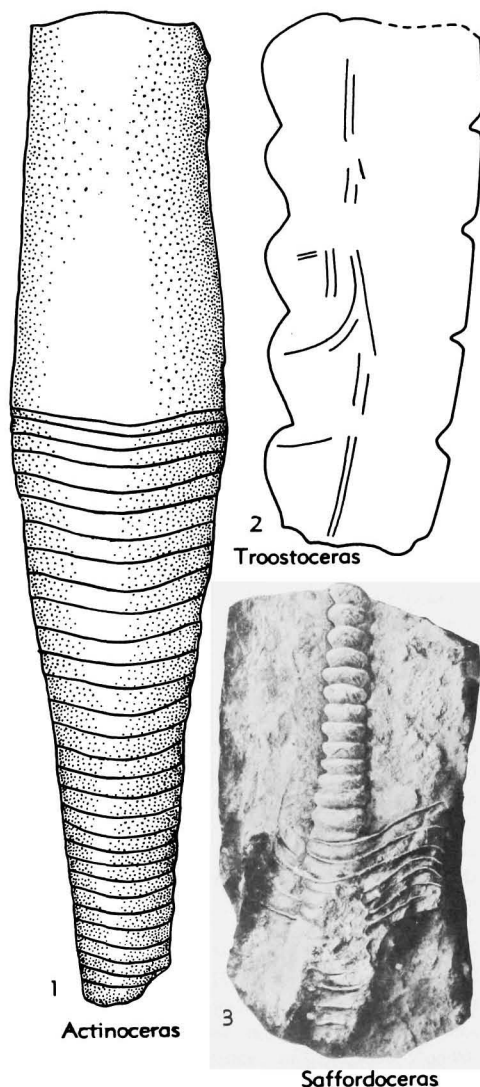
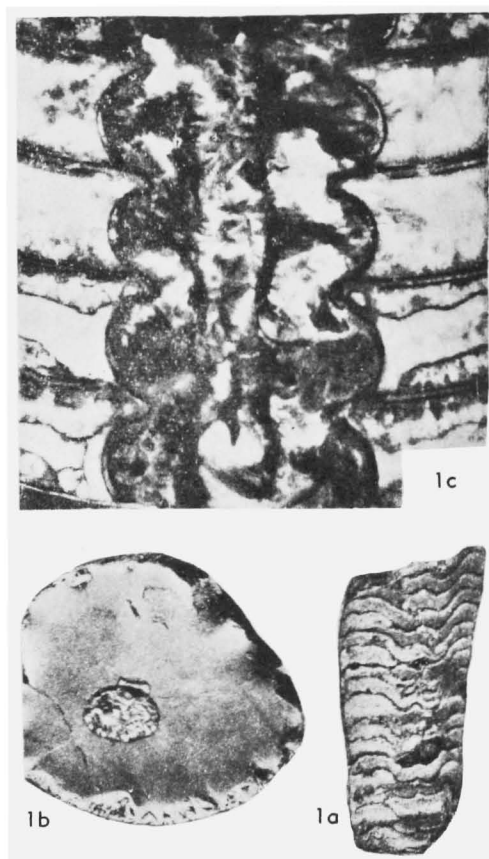


FIG. 142. Actinoceratidae (p. K204-K206).



Ellinoceras

FIG. 143. Actinoceratidae (p. K205).

Arctic Can.—FIG. 145. \**F. boreale*; dorsoventral sec.,  $\times 1$  (Teichert, n).

**Kochoceras** TROEDSSON, 1926 [\**K. cuneiforme*; OD] [= ?*Nothoceras* EICHWALD, 1860 (*non* BARBANDE, 1856)]. Similar to *Actinoceras* but shell ventrally flattened. Siphuncle marginal, in broad contact with ventral area of shell wall. *M.Ord.*-*U.Ord.*, N.Can.-Greenl.-?N.Eu.—FIG. 144, 2a-c. *K. ellipticum* TROEDSSON, *M.Ord.* or *U.Ord.*, N.Greenl.; 2a, dorsal view,  $\times 0.5$ ; 2b,c, dorsoventral and transv. secs.,  $\times 0.75$  (in Fig. 2c, outer line = shell, middle line = maximum diam. of siphuncle, inner line = septal foramen) (194).—FIG. 144, 2d. \**K. cuneiforme*, *M.Ord.* or *U.Ord.*, N.Greenl.; dorsoventral sec.,  $\times 0.75$  (194).

?**Leurorthoceras** FOERSTE, 1921 [\**L. hanseni*; OD]. Shell flattened, ventrally depressed. Siphuncle narrower than in *Actinoceras*, segments tending to be strongly elongated in mature part of phragmocone; endosiphuncular deposits simple. *M.Ord.*, ?*U.Ord.*, N.Am.-Eu.-Sib.—FIG. 144, 3. \**L. han-*

*seni*, *M.Ord.*, Arctic Can.; 3a-c, ventral view, dorsoventral and transv. secs.,  $\times 0.75$  (51).

**Paractinoceras** HYATT in ZITTEL, 1900 [\**Sactoceras canadense* WHITEAVES, 1892; OD]. Long, straight slender shells. Siphuncular segments in early stages like *Actinoceras*, becoming narrow like *Ormoceras* in anterior part of phragmocone; endosiphuncular deposits unknown. *M.Ord.* or *U.Ord.*, N.Am.-USSR(Sib.).—FIG. 144, 1. \**P. canadense* (WHITEAVES), *M.Ord.*, Can.(Man.); 1a-c, ventral view with siphuncle exposed and 2 transv. secs.,  $\times 0.5$  (206).

**Saffordoceras** FOERSTE & TEICHERT, 1930 [\**S. nelsoni*; OD]. Shells with ventral flattening; sutures with broad, deep ventral lobes and narrower lateral saddles. Siphuncle subventral, segments decreasing from about 0.3 to less than 0.2 of conch diameter. *M.Ord.*, E.N.Am.—FIG. 142, 3. \**S. nelsoni*, USA(Tenn.); ventral view,  $\times 0.7$  (78).

**Troostoceras** FOERSTE & TEICHERT, 1930 [\**T. paulocurvatum*; OD]. Similar to *Actinoceras* but slightly cyrtoconic and endogastric. Siphuncle in contact with shell wall; initial segment small. *M.Ord.*, E.N.Am.-USSR(Sib.).—FIG. 142, 2. \**T. paulocurvatum*, USA(Tenn.); dorsoventral sec. of apical portion of siphuncle,  $\times 1.5$  (Teichert, n).

### Family ARMENOCERATIDAE

Troedsson, 1926

[incl. *Wutinoceratidae* SHIMIZU & OBATA, 1935; *Nybyoceratinae* SHIMIZU & OBATA, 1935]

Large, straight or slightly curved shells. Siphuncle large, segments strongly expanded between septa; septal necks very short, with abruptly recurved long brims; endosiphuncular canals well developed, remainder of siphuncle calcified; endosiphuncular structure commonly complex. Cameral deposits rare. *M.Ord.*-*Sil.*

**Armenoceras** FOERSTE, 1924 [\**Actinoceras hearsti* PARKS, 1913; OD] [= ?*Yabeites* ENDO, 1934; *Neowutinoceras*, *Eushantungoceras* SHIMIZU & OBATA, 1935; *Shantungoceras* SHIMIZU & OBATA, 1936; *Linormoceras* KOBAYASHI & MATUMOTO, 1942; *Tunguskoceras* ZHURAVLEVA, 1957; *Kokujioceras* BALASHOV, 1962]. Medium-sized to large straight shell. Siphuncle off center, large; adnation areas broad; septal necks very short, brims wide and in contact with posterior surface of septa; endosiphuncular canals well developed, commonly complex. Cameral deposits rare. *M.Ord.*-*U.Sil.*, N.Am.-Greenl.-N.Eu.(USSR)-Asia-Australia.—FIG. 146, 1a-c. *A. arcticum* (TROEDSSON), *M.Ord.* or ?*U.Ord.*, N.Greenl.; 1a, dorsal side of weathered specimen,  $\times 0.5$ ; 1b,c, lat. long. and transv. secs.,  $\times 0.5$  (194).—FIG. 146, 1d. *A. richardsoni* (STOKES), *Ord.*, Can.; recumbent septal neck,  $\times 5$  (78). [= *Helenites* ZHURAVLEVA, 1962, p. 221].



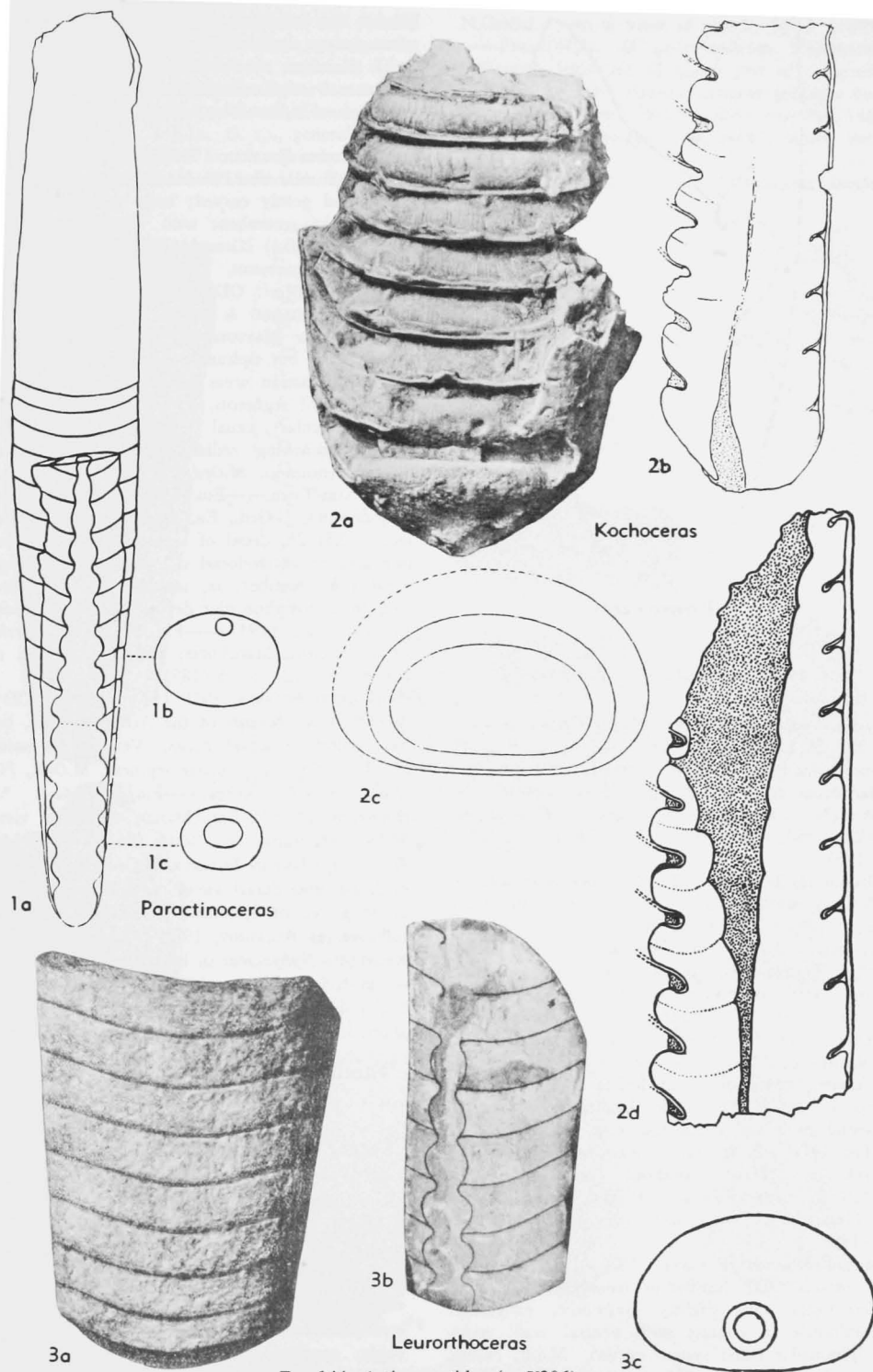
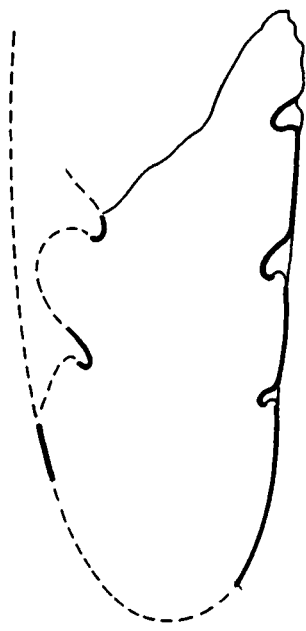


FIG. 144. Actinoceratidae (p. K206).



Floweroceras

FIG. 145. Actinoceratidae (p. K205-K206).

**Cyrtonybyoceras** TEICHERT, 1933 [*\*Orthoceras haesitans* BILLINGS, 1857; OD]. Like *Nybyoceras* but more slender and slightly curved. Endosiphuncular canal system reticulate. *M.Ord.* (*Chazy.*), N. Am. (Newf.)-E. Asia.—FIG. 146.3. *\*C. haesitans* (BILLINGS), Can. (Newf.); dorsoventral sec.,  $\times 0.5$  (185).

**Elrodoceras** FOERSTE, 1924 [*\*Cyrtoeras indianense* MILLER, 1892; OD]. Large shells, with apical part slightly curved, otherwise straight. Siphuncle narrower than in *Armenoceras*, but still wider than long; connecting rings with broad adnation areas anteriorly and posteriorly, free part of connecting rings only slightly convex between septa; endosiphuncular canal system arched. *M.Sil.*, N. Am.-Eu. (S. USSR).—FIG. 147.2a,b. *\*E. indianense* (MILLER), USA (Ind.); 2a, lat. view of conch,  $\times 0.75$  (53); 2b, detailed long. sec. of septal neck and connecting ring,  $\times 6$  (78).—FIG. 147.2c. *E. sp.*, cf. *E. abnorme* (HALL), Can. (Ont.); siphuncle without connecting rings,  $\times 0.75$  (185).—FIG. 147.2d. *E. abnorme* (HALL), USA (Wis.); detail of siphuncle,  $\times 0.75$  (185).

**Megadisocosorus** FOERSTE, 1925 [*\*M. crassisegmentatus*; OD]. Similar to *Armenoceras* but more breviconic and slightly cyrtoconic, exogastric. Siphuncle in contact with ventral wall, endosiphuncular canal system curved. *M.Sil.*, N. Am.—FIG. 147.1a,b. *\*M. crassisegmentatus*, Can.

(Ont.); 1a, lat. view of siphuncle without connecting rings,  $\times 0.7$  (55); 1b, dorsoventral sec.,  $\times 0.7$  (Teichert, n).—FIG. 147.1c. *M. crassisegmentatus orientalis* FOERSTE, Can. (Anticosti Is.); long. sec. of siphuncular segment,  $\times 1$  (Teichert, n).

**Monocytoceras** FOERSTE, 1924 [*\*M. lentidilatatum*; OD]. Siphuncle like *Elrodoceras* but entire conch evenly and gently curved; body widest at base; septal necks recumbent with very short brims. *M.Sil.*, USA (Wis.)-?Greenl.

**Nybyoceras** TROEDSSON, 1926 [*\*Actinoceras (Nybyoceras) bekkeri*; OD] [= *Wutinoceras*, *Pararmenoceras* SHIMIZU & OBATA, 1936; *Jeholoceras* KOBAYASHI & MATSUMOTO, 1942]. Similar to *Armenoceras* but siphuncle closer to ventral side of shell; adnation areas broad ventrally on posterior side of segments, dorsally on adoral side; endosiphuncular canal system reticulate to curved, branching radial canals. Cameral deposits uncommon. *M.Ord.*-*U.Ord.*, N. Am.-N. Eu.-C. & E. Asia-Tasm.—FIG. 146.2a,b. *\*N. bekkeri* (TROEDSSON), U. Ord., Eu. (Est.); 2a, dorsoventral sec.,  $\times 0.5$ ; 2b, detail of septal necks and adnation area on anterodorsal side of siphuncular segment (*ch*, chamber; *se*, septum; *sh*, connecting ring; *si*, endosiphuncular deposit; *ne*, septal neck; *fu*, brim),  $\times 2$  (194).—FIG. 146.2c. *N. foerstei* ENDO, M. Ord., Manchuria; etched long. sec. of part of siphuncle,  $\times 1.5$  (185).

**Selkirkoceras** FOERSTE, 1929 [*\*S. cuneatum*; OD]. Resembles *Kochoceras* of the Actinoceratidae, but has recumbent septal necks. Very large, broad and blunt first siphuncular segment. *M.Ord.*, ?*U. Ord.*, W. N. Am.-Korea.—FIG. 146.4a,b. *\*S. cuneatum*, M. Ord., Can. (Man.); 4a, dorsal view,  $\times 0.45$ ; 4b, transv. sec.,  $\times 0.5$  (66).—FIG. 146.4c-e. *S. tyndallense* FOERSTE, M. Ord., Can. (Man.); 4c,d, lat. and dorsal views of siphuncle,  $\times 0.45$ ; 4e, long. sec. of siphuncle,  $\times 0.45$  (66).

**Stolbovoceras** BALASHOV, 1962 [*\*S. boreale*; OD]. Resembles *Nybyoceras* in having an adnation area on posterior ventral side of siphuncle segments, but siphuncle much smaller and segments very short. *M.Ord.*, USSR (Sib.).

### Family GONIO CERATIDAE Hyatt, 1884

[incl. *Lambeoceratidae* FLOWER, 1957]

Large, straight shells, strongly depressed in cross section, with flat ventral and dorsal sides and angular flanks; sutures sinuous. Siphuncles comparatively small, subventral to subcentral. *M.Ord.*-*U.Ord.*

**Gonioceras** HALL, 1847 [*\*G. anceps*; M]. Large shells, ventral side rather flat, dorsal side moderately convex, 2 sides meeting laterally at acute angle; aperture contracted; sutures with broad dorsal and ventral lobes, more narrowly rounded

dorsolateral and ventrolateral saddles and pointed lateral lobes. Siphuncle subcentral; septal necks armenoceroid, brims very short; segments short; endosiphuncular canal system straight. Cameral deposits rare. *M.Ord.*, N.Am.-Greenl.-Eurasia (Urals-?E.Asia).—FIG. 148, *1a*. *G. sp.*, generalized reconstruction of entire conch, greatly reduced (151).—FIG. 148, *1b*. *G. holtedahli* TROEDSSON,

N.Greenl.; ventral view of conch,  $\times 0.3$  (194). —FIG. 148, *1c*. *G. groenlandicum* TROEDSSON, N.Greenl.; long. sec. of dorsal part of siphuncle and camerae with cameral deposits (oblique lining=contact layers),  $\times 1.5$  (236). — FIG. 148, *1d*. *G. wulffi* TROEDSSON, N.Greenl.; transv. sec.,  $\times 0.4$  (194).

*Lambeoceras* FOERSTE, 1917 [*Gonioceras lambii*

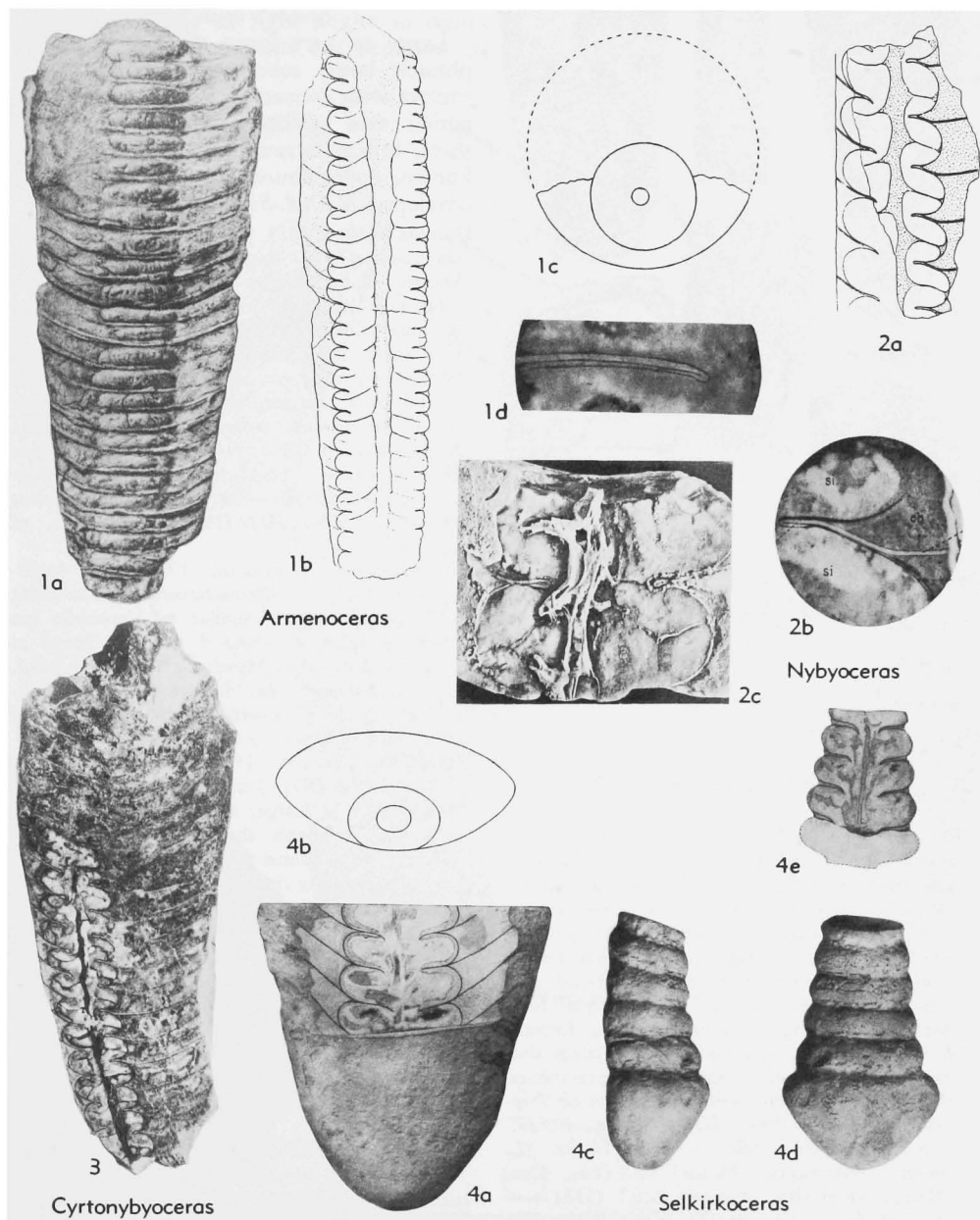


FIG. 146. Armenoceratidae (p. K206, K208).

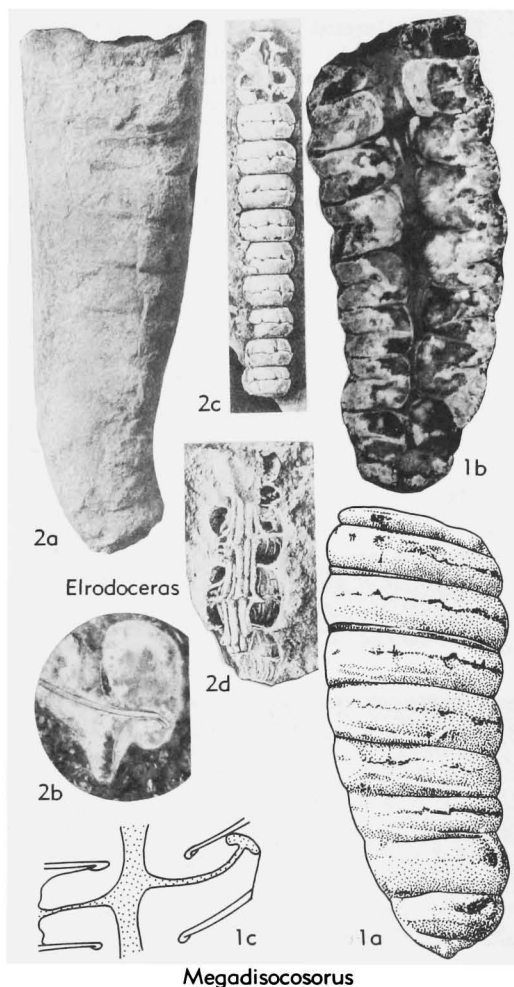


FIG. 147. Armenoceratidae (p. K208).

WHITEAVES, 1891; OD [= *G. lambei* of later authors]] [= *Hoeloceras* SWEET, 1958]. Large to very large shells, both flat sides evenly and gently convex; sutures with broad sinus across ventral and dorsal sides and acute lateral saddles. Siphuncle subventral; segments either like *Gonioceras* or with more prolonged constricted part where septa bend backward behind septal foramen; brims strongly recurved, pointing forward and outward; endosiphuncular canal system simple, known from all species except type-species. [Genus originally proposed as subgenus of *Tripteroceras* HYATT, 1884.] *M.Ord.-U.Ord.*, N.Am.-Greenl. - NE. Eu. - Sib. — FIG. 148,2a. \**L. lambii* (WHITEAVES), *M.* (or ?*U.*) *Ord.*, Can. (Man.); dorsal view of conch,  $\times 0.1$  (118). — FIG. 148,2b-e. *L. princeps* TROEDSSON, *M.* (or ?*U.*) *Ord.*, N.Greenl.; 2b, ventral view of conch,

$\times 0.18$ ; 2c, transv. sec.,  $\times 0.3$ ; 2d, siphuncle, dorsoventral sec.,  $\times 1$ ; 2e, detail of septal neck (*s*, septum; *k*, brim; *sr*, circulus; *sh*, connecting ring; *p*, perispantium; *pa*, perispantal deposit),  $\times 8$  (2b,c, 194; 2d,e, 236).

### Family HURONIIDAE Foerste & Teichert, 1930

[= *Gigantei* QUENSTEDT, 1836; incl. *Besselsoceratinae* SHIMIZU & OBATA, 1935]

Large to very large straight shells. Siphuncle large, subcentral; septa in broad contact with connecting rings, posterior adnation area of latter wide; septal necks short, brims narrow; cameral deposits unknown; endosiphuncular canal system well developed. *M.Ord.-Sil.*

**Huronia** STOKES, 1824 [\**H. bigsbei* (= *bigsbyi* of later authors); SD BASSLER, 1915]. Shell poorly known. Siphuncle very large, straight; segments long, with long cylindrical posterior part formed by long adnation area; free part of connecting ring short, slightly inflated; septal necks short, brims short and pointing forward and outward; central canal narrow, radial canals in anterior portion of segment, strongly curved. *U.Ord.-Sil.*, N.Am.-Greenl. — FIG. 149,2a. *H. paulodilata* FOERSTE, *M.Sil.*, USA (Mich.); siphuncle fragment,  $\times 0.5$  (55). — FIG. 149,2b. *H. minuens* BARRANDE, *M.Sil.*, USA (Mich.); long. sec. of siphuncle,  $\times 0.7$  (5).

**Discoactinoceras** KOBAYASHI, 1927 [\**D. multiplexum*; OD] [= *Discoactinoceras* KOBAYASHI, 1927 (*nom. null.*)]. Similar to *Huroniella* but siphuncle segments about 4 times as broad as long. *M.Ord.*, Asia (Manchuria). — FIG. 149,1. \**D. multiplexum*; 1a, dorsoventral sec. of siphuncle,  $\times 1.6$  (Teichert, n); 1b, transv. sec. of conch and siphuncle,  $\times 0.4$  (101).

**Huroniella** FOERSTE, 1924 [\**Huronia inflecta* PARKS, 1915; OD] [= *Besselsoceras* SHIMIZU & OBATA, 1935]. Large, straight shells; siphuncle subcentral; segments shorter than in *Huronia*; adnation areas funnel-shaped and narrower; free part of connecting rings longer and more strongly expanded; central and radial canals well developed. *M.Sil.*, N.Am.-Greenl.-N.Eu.-USSR (S.Urals-Sib.). — FIG. 149,3a,b. \**H. inflecta* (PARKS), USA (Mich.); 3a,b, siphuncle, lat., ventral,  $\times 0.5$  (53). — FIG. 149,3c,d. *H. persiphonata* (BILLINGS), Can. (Anticosti Is.); 3c, long. sec. of siphuncle,  $\times 0.45$ ; 3d, part of siphuncular segment (*c*, connecting ring; *s*, septum; *co*, contact layer), enlarged (185).

### Family ORMOCERATIDAE Saemann, 1853

[incl. ?*Loxoceratidae* HYATT in ZITTEL, 1900; *Sactoceratidae* TROEDSSON, 1926; ?*Eskimoceratidae* SHIMIZU & OBATA, 1936 (*partim*); *Troedssonoceratidae* KOBAYASHI, 1936; *Deiroceratidae* SHIMANSKIY, 1956]

Generally straight, medium-sized shells with circular to subcircular cross section. Siphuncle generally subcentral, one-fifth or less diameter of shell; septal necks varying from long, cyrtochoanitic to recumbent; siphuncle segments rarely broader than long, generally globular or longer than broad; endosiphuncular canal system simple, radial canals generally at right angles to central canal. Cameral deposits not common. *M. Ord.-L. Carb.*

*Ormoceras* STOKES, 1840 [*\*O. bayfieldi*; SD BASSLER, 1915] [= *Ormoceratites* D'ARCHIAC & DE VERNEUIL, 1840 (*nom. null.*); *Hormoceras* AGASSIZ, 1846 (*nom. van.*); *Sactoceras* HYATT, 1884; *Aluveroceas* BALASHOV, 1955; *Adamsoceras* FLOWER, 1957]. Medium-sized, straight shells, more or less circular in cross section. Siphuncle generally subcentral; segments almost globular; septal necks short, actinoceroid, with short brims; endosiphuncular canal system moderately complex to simple, radial canals few. Cameral deposits common, *M. Ord.-Dev.*, ?*L. Carb.*, cosmop.—FIG.

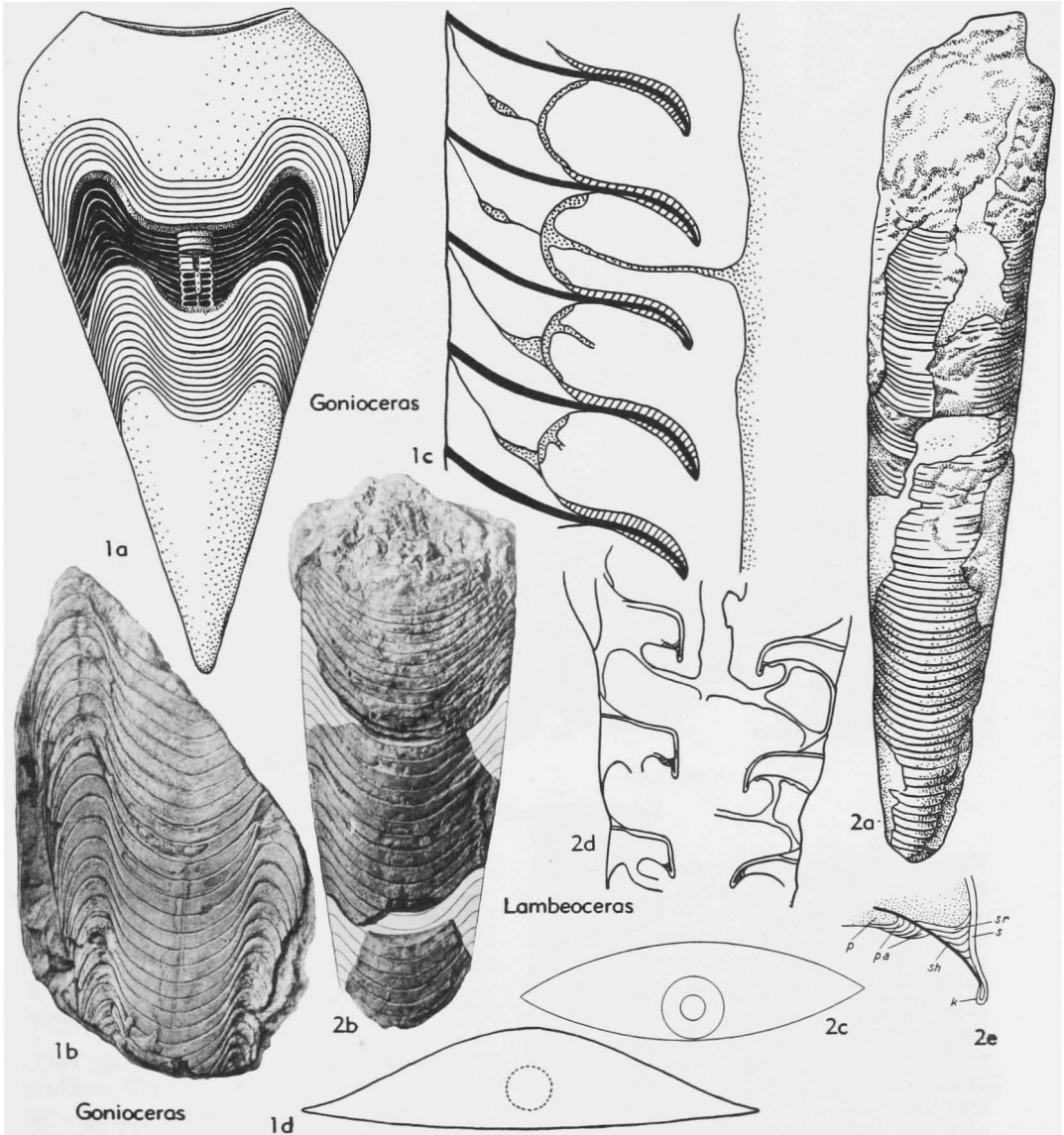


FIG. 148. Gonioceratidae (p. K208-K210).

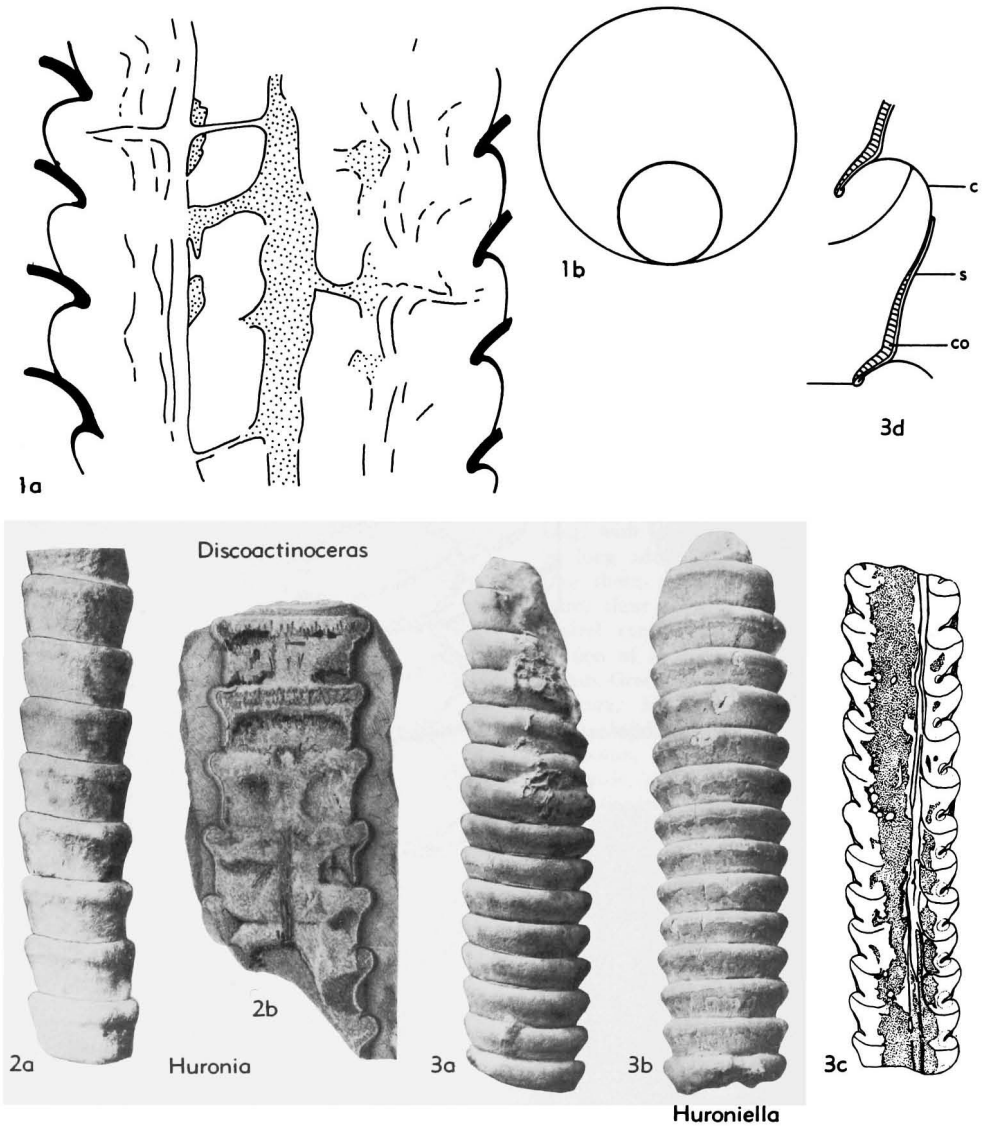


FIG. 149. Huroniidae (p. K210).

150,1a. *O. allumettense* (BILLINGS), M.Ord., Can. (Que.); ventral view of weathered conch showing siphuncle,  $\times 0.7$  (71).—FIG. 150,1b. *O. billingsi* (FLOWER), M.Ord., Can. (Newf.); dorsoventral sec.,  $\times 0.7$  (185).—FIG. 150,1c,d. *O. holmi* TROEDSSON, M.Ord., Sweden; 1c, dorsoventral sec.,  $\times 0.7$ ; 1d, detail of septal neck (*se*, septum; *sh*, connecting ring; *fu*, septal neck; *ch*, camera; *si*, central canal; *ca*, radial canals),  $\times 2.7$  (194).  
**Deiroceras** HYATT, 1884 [*\*Orthoceras python* BILLINGS, 1857; OD]. Medium-sized, straight shells with long chambers. Siphuncle subventral; segments longer than wide; septal necks compara-

tively short; endosiphuncular canal system straight, radial canals more or less perpendicular to central canal. M.Ord.-U.Ord., N.Am.-N.Eu.-Sib.; ?M. Dev., Ger.—FIG. 150,2a. *D. remotiseptum* (HALL), M.Ord., USA (N.Y.); weathered long. sec.,  $\times 0.7$  (71).—FIG. 150,2b. *D. richteri* FOERSTE & TEICHERT, M.Ord., USA (Mo.); dorsoventral sec.,  $\times 1.5$  (185).  
 ?**Eskimoceras** TROEDSSON, 1936 [*\*E. boreale*; OD]. Similar to *Orthonyboceras* but shell annulate. Endosiphuncular structure unknown. M.Ord., or ?U.Ord., N.Greenl.—FIG. 151,2. *\*E. boreale*; 2a,b, exterior, long. sec.,  $\times 0.75$ ; 2c, detail of



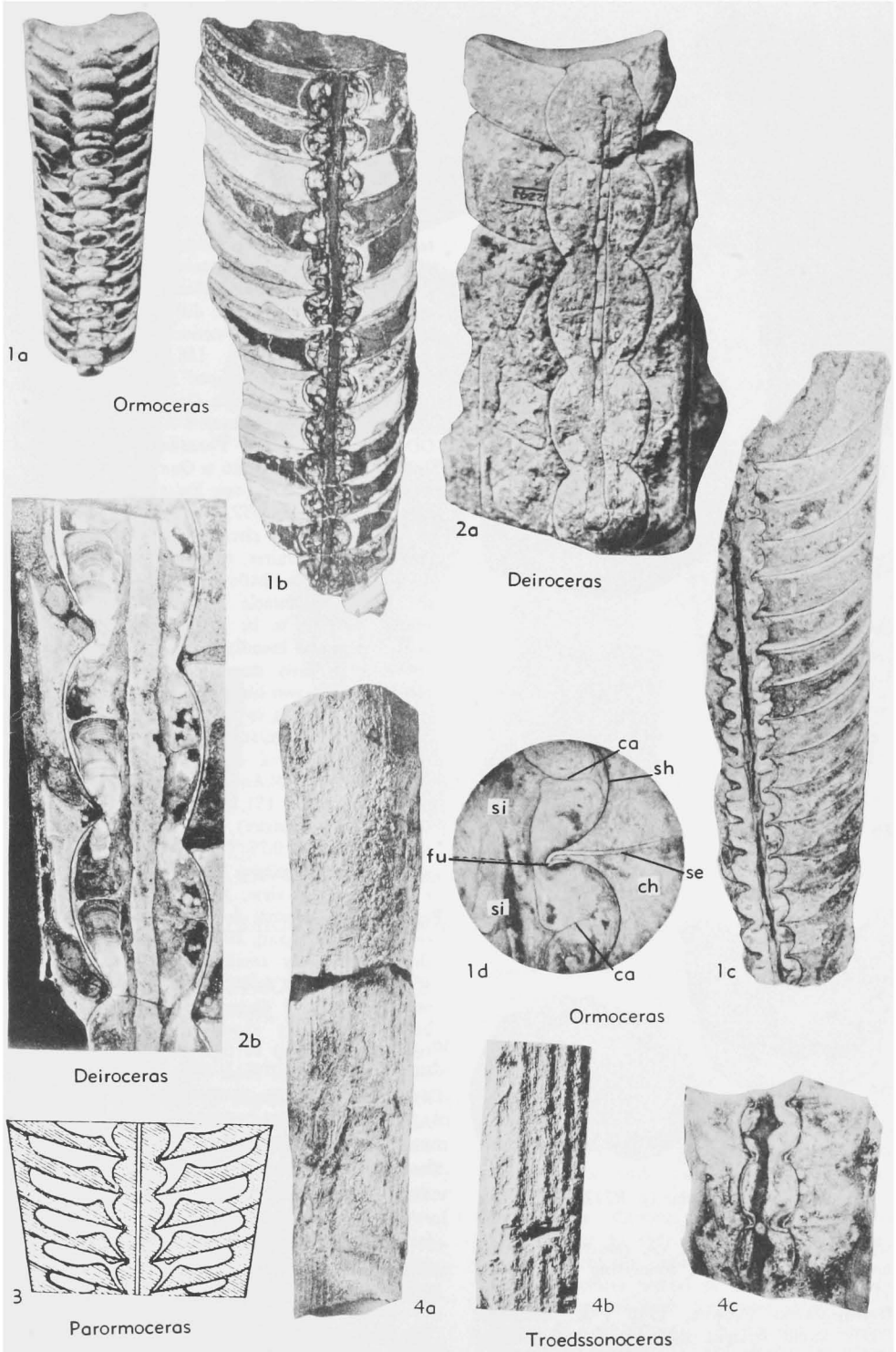


FIG. 150. Ormoceratidae (p. K211-K212, K214-K215).

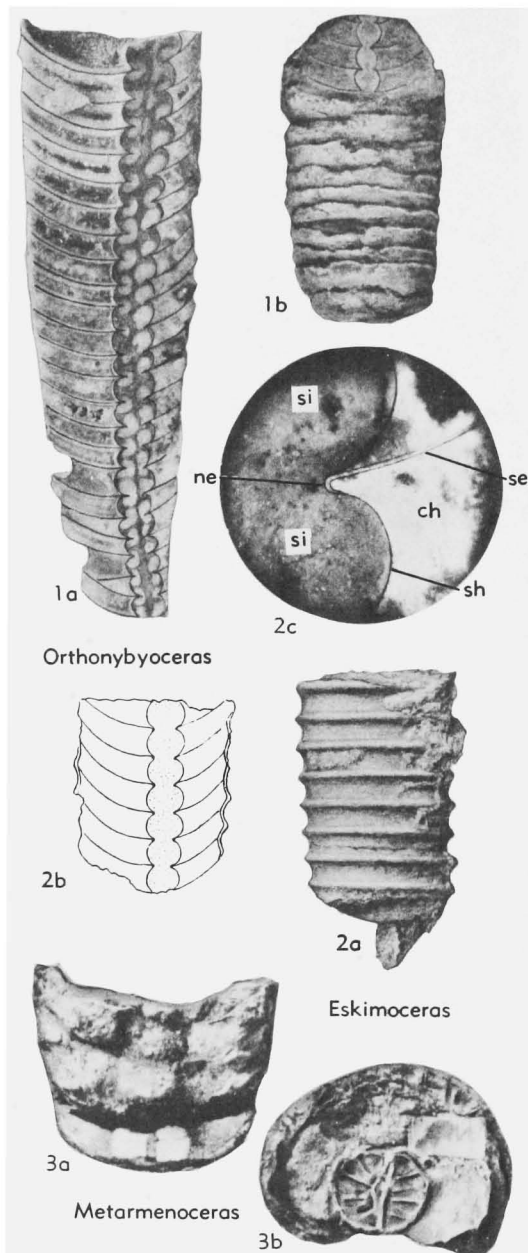


FIG. 151. Ormoceratidae (p. K212, K214).

septal neck (*se*, septum; *ch*, camera; *ne*, septal neck; *si*, siphuncle; *sh*, connecting ring),  $\times 4.5$  (194).

**Metarmenoceras** FLOWER, 1940 [*\*M. bilaterale*; OD]. Small straight shells with armenoceroide siphuncle which has compressed central canal and

bilaterally symmetrical arrangement of radial canals branching off at right angles from central canal. *L.Dev.*, Can.(Que.).—FIG. 151.3. *\*M. bilaterale*, Gaspé; 3a,b, lat. view of conch, ant. view of septal surface with siphuncle,  $\times 1$  (25). **Mstikhinoceras** SHIMANSKIY, 1961, p. 39 [*\*M. mirabile*; OD]. Short-chambered, slowly enlarging orthocones of subquadrate cross section. Sutures with broad ventral and lateral lobes and low ventrolateral saddles. Siphuncle between center and venter, slender, actinoceroide (?); details of siphuncular interior unknown. [Grossly similar externally to *Loxoceras* M'Coy, with which it is compared by SHIMANSKIY; differs from *Loxoceras* in subquadrate cross section.] *L.Carb.*(Visé.), USSR(Moskva).—FIG. 188.1. *\*M. mirabile*; 1a-c, lat., ventral, and septal views,  $\times 1$  (168a). **Orthonybyoceras** SHIMIZU & OBATA, 1935 [*\*Ormoceras? covingtonense* FOERSTE & TEICHERT, 1930; OD] [=Euorthoceras FOERSTE, 1893; *Euormoceras*, *Euhuronion* SHIMIZU & OBATA, 1936; *Treptoceras* FLOWER, 1942 (*non* EWAY, 1960); *Siberioceras* ZHURAVLEVA, 1957]. Small to medium-sized straight shells with circular to slightly depressed cross section; sutures straight, either transverse or sloping; septa shallow; septal necks short to recumbent. Siphuncle somewhat distant from venter, tending to be central or subcentral in young; segments broadly inflated, almost *Armenoceras*-like in early stages, then passing through globular *Ormoceras*-like stage to elongated *Deiroceras*-like segments in anterior part of phragmocone; endosiphuncular structures, when present, resembling those of *Ormoceras* and *Deiroceras*. *M.Ord.-U.Ord.*, N.Am.-E.Asia, probably widespread.—FIG. 151.1a. *\*O. covingtonense* (FOERSTE & TEICHERT), U.Ord., USA(Ky.); dorsoventral sec.,  $\times 0.75$  (78).—FIG. 151.1b. *O. cannonense* (FOERSTE & TEICHERT), M.Ord., USA (Tenn.); ventral view,  $\times 0.75$  (78).

**Parormoceras** SHIMIZU & OBATA, 1935 [*\*Actinoceras nanum* GRABAU, 1922; OD]. Small, straight shells, with very small siphuncle, diameter of which (except in apical region) equals less than one-sixth of shell diameter; septal necks recumbent, brims very short; greatest diameter of siphuncle segments in their anterior third where they are inflated to twice diameter of septal foramen; episepal deposits in camerae. *M.Ord.*, E. Asia.—FIG. 150.3. *\*P. nanum* (GRABAU); lat. long. sec.,  $\times 2$  (101).

**Troedssonoceras** FOERSTE, 1928 [*\*Orthoceras turbidum* HALL & WHITFIELD, 1875; OD] [=Troedssonoceras KOBAYASHI, 1936 (*nom. null.*)]. Similar to *Deiroceras* but surface of shell with longitudinal ridges and lirae, somewhat like *Kionoceras*. *M.Ord.-U.Ord.*, N.Am.—FIG. 150.4a,b. *T. baileyi* FLOWER, ?M.Ord., USA(Tenn.); 4a, lat. view,  $\times 0.7$ ; 4b, detail of shell surface,  $\times 1$  (24).—FIG. 150.4c. *\*T. turbidum* (HALL &



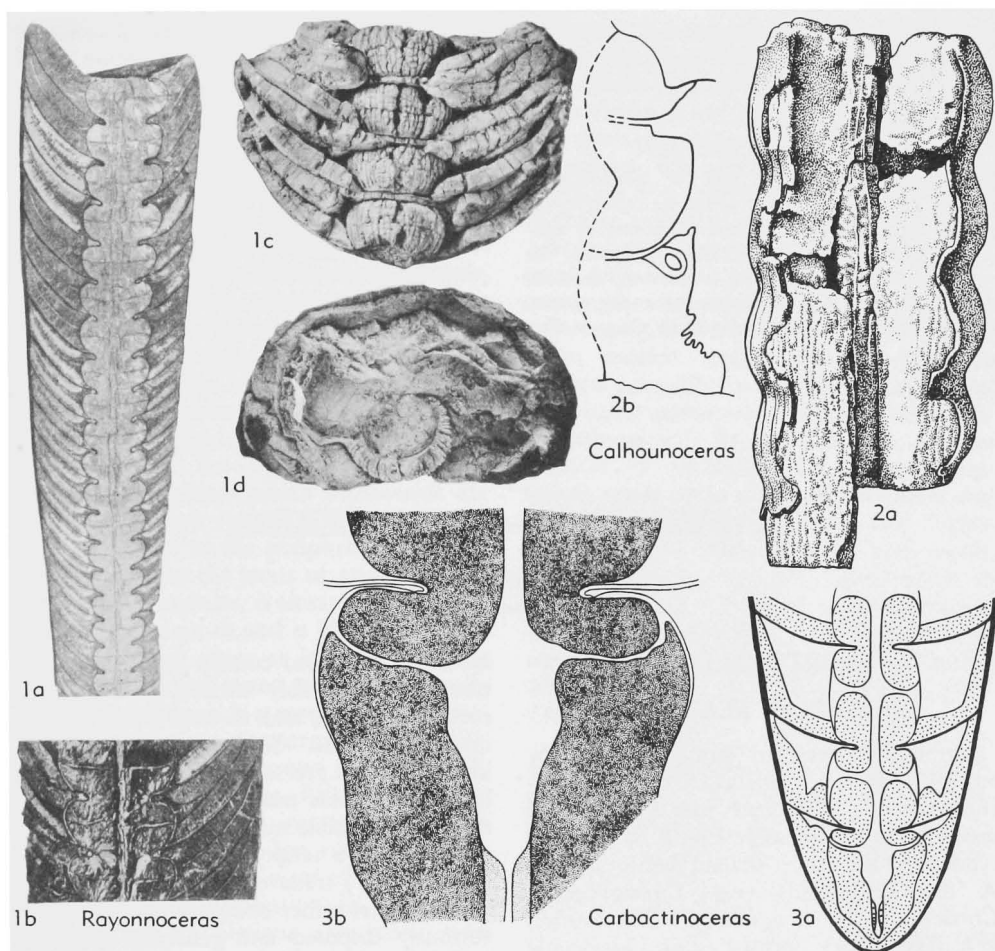


FIG. 152. Carbactinoceratidae, Family Uncertain (p. K215-K216).

WHITFIELD), U.Ord., USA(Ohio); dorsoventral sec.,  $\times 0.7$  (24).

### Family CARBACTINOCERATIDAE Schindewolf, 1943

Medium-sized to very large, straight or slightly curved shells with central to subcentral, large siphuncle, septal necks short; segments subglobular, first few tending to be narrow; endosiphuncular canal system well developed in greater part of siphuncle, with thin central and radial canals, latter perpendicular to former; greater part of siphuncle filled with solid calcareous deposit. Cameral deposits fill most chambers in large portion of phragmocone. *L.Carb. (Miss.)-U.Carb.(Penn.)*.

*Carbactinoceras* SCHINDEWOLF, 1935 [*\*C. torleyi*; OD]. Probably small, straight shells; not known

beyond earliest stages. Internal structure like *Rayonnoceras*, initial siphuncular segment elongated, canal system straight. *L.Carb. (Visé.)*, Eu. (Ger.).—FIG. 152,3. *\*C. torleyi*; 3a, lat. long. sec.,  $\times 3$ ; 3b, apical segment of siphuncle with well-developed perispantium,  $\times 13$  (155). [See also Fig. 136.]

?*Aploceras* D'ORBIGNY, 1849 [*\*Cyrtoceras verneuillianum* DE KONINCK, 1844; SD HYATT, 1884] [= *Haploceras* SAEMANN, 1853 (nom. van.)]. Like *Rayonnoceras* but cyrtoconic and smaller; shell surface with longitudinal striae. *L.Carb., W.Eu.*

*Rayonnoceras* CRONEIS, 1926 [*\*R. solidiforme*; OD]. Large to very large straight shells with large subcentrally situated siphuncle having internal structures typical of family; shell surface in some species with transverse striae. *L.Carb. (Miss.)-U. Carb. (Penn.)*, N. Am.-Eu. (Eng.-Ger.-Pol.-USSR).—FIG. 152,1a,b. *R. bassleri* FOERSTE & TEICHERT, Miss., USA(Ark.); 1a, dorsoventral

sec.,  $\times 0.7$  (78); 1*b*, portion of same,  $\times 1$  (185).  
 —FIG. 152, 1*c, d*. *R. girtyi* FOERSTE & TEICHERT, Miss., USA (Okla.); ventral and apical views,  $\times 0.7$  (185).

### Family UNCERTAIN

*Calhounoceras* TROEDSSON, 1926 [*\*C. candelabrum*; OD]. Known from large siphuncles consisting of long, slightly inflated segments separated by constrictions. Phragmocone entirely unknown. Siphuncle filled with heavy calcareous deposits; seemingly curved endosiphuncular canal system. *M.Ord.* or *U.Ord.*, N.Greenl.-Arctic Can.—FIG.

152, 2. *\*C. candelabrum*; 2*a*, portion of siphuncle,  $\times 0.7$  (194); 2*b*, long. sec. with suggestion of endosiphuncular canals,  $\times 0.9$  (186).

### UNRECOGNIZABLE GENERA which have been referred to Actinocerida

*Hopeioceras* SHIMIZU & OBATA, 1936 [*?\*H. shihlingense*]. No type-species indicated. *Ord.*, E.Asia.  
*Subtofangoceras* SHIMIZU & OBATA, 1936 [*\*Sactoceras liaotungense* ENDO, 1932]. Type-species too incompletely known for accurate diagnosis. *M.Ord.*, E.Asia.

## NAUTILOIDEA—ORTHOCERIDA

By WALTER C. SWEET

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### MORPHOLOGY

#### EXTERNAL FEATURES

Orthocerids secreted straight or weakly curved, rather gradually enlarging longiconic conchs, separated into camerae of moderate to considerable length by septa of symmetrically saucer-shaped conformation. A few orthocerids (e.g., *Chicagooceras*, *Clinoceras*, *Paraphragmites*, *Whiteavesites*, *Whitfieldoceras*) formed short breviconic shells, but no species properly referable to the Orthocerida are known to have secreted a coiled conch. Curvature of the typically longiconic shell is confined to the apical few chambers in most orthocerids, but may involve much or most of the conch in species of about 20 per cent of the genera now included in the order.

Individual orthocerid conchs may attain a length of more than 6 feet, but only a few are of any appreciable diameter; none rivals the partially contemporaneous Actinocerida or Endocerida in either conch diameter or ultimate length. Furthermore, in most orthocerids, the greatest part of conch length is composed of phragmocone; body chambers tend to be rather short.

For the most part, the orthocerid conch is of circular or nearly circular cross section, but both compressed and moderately to con-

siderably depressed conchs are known. Sutures are invariably simple, generally directly transverse, and, in only a few genera, notably sinuous. Shell surfaces in most known species are smooth, or marked only by inconspicuous transverse growth lines; a not inconsiderable minority of species, however, exhibits a variety of external sculpture, including (1) transverse or oblique annulations that are either straight or sinuous, (2) variously disposed and generally irregular "wrinkles" or plications, (3) longitudinal and transverse lirae and striae, (4) sharp-edged longitudinal ridges imparting a "fluted" appearance to the shell, and (5) longitudinal rows of nodes. Ornamentation of several of the types enumerated occur together on some conchs; on others, ontogenetic changes from one type to another, or from ornamented shells to smooth ones, have been described. Variations in sculptural details have been accorded considerable (but very uneven) taxonomic importance by some investigators; in general, however, most present-day students of nautiloids agree that surficial ornament alone is an unreliable guide to genetic relationship.

In most orthocerids, the aperture is simple and transverse to the axis of the conch; in species of several genera (e.g., *Crypt-*

*orthoceras*, *Lyecoceras*, *Plagiostomoceras*), however, the aperture is oblique and slopes posteriorly from dorsum to venter. In many orthocerid species, there is no indication of a hyponomic sinus.

The pattern of attachment of retractor and epithelial muscles is known for only a few orthocerid species. These include Swedish representatives of "*Geisonoceras*" *scabridium* (ANGELIN), "*Orthoceras*" *angulatum* WAHLENBERG, *Orthoceras regulare* (SCHLOTHEIM), *Lyecoceras goilandense* MUTVEI, and *L. longistriatum* MUTVEI. In all these species, studies indicate that periphractic elements were similar in arrangement to those of *Baltoceras burchardi* (DEWITZ), of the ellesmerocerid family Baltoceratidae, from which orthocerids are supposed to have evolved. That is, the expanded portion of the periphractic imprint, presumed to be the locus of attachment of the retractor muscles, is situated on the dorsal side of the conch and is bifid, being separated into two more or less distinct parts by a posteriorly-directed mid-dorsal notch. Nautiloids with such a pattern of retractor-muscle attachment are termed dorsomyarian. Longitudinal furrows in the body chambers of *Orthoceras*, *Bifoveoceras*, and *Ctenoceras* have been interpreted as sites of muscle attachment, but such a relationship seems unlikely in view of the fact that the periphractic impression in *Orthoceras regulare* has no obvious association with longitudinal furrows in its body chamber.

In one orthocerid species, *Brachycycloceras normale*, type of the Brachycycloceratidae, retractor muscles were apparently attached ventrolaterally. The significance of this divergence from the dorsomyarian pattern exhibited by the few other orthocerids just mentioned is not understood. However, it may well be associated with the fact that *Brachycycloceras* shed the early longiconic part of its shell during ontogeny and presumably became adapted maturely to a somewhat different mode of life.

### INTERNAL FEATURES

Although variable in many other ways, the orthocerid ectosiphuncle is invariably composed of septal necks and thin, structureless connecting rings. The latter, however, have never been observed in a few genera (e.g., *Arkonoceras*, *Leurocycloceras*),

and may have been weakly calcified or completely unmineralized in the living animal. The siphuncle is variable in position, even within a single individual, a species, or a genus. In most species, it is subcentral in position, but subventral siphuncles characterize a few genera and a position dorsal of center occurs in some species.

Septal necks are orthochoanitic and short or of only moderate length in most Orthocerataceae; in a few representatives of this superfamily, however, relatively short septal necks exhibit weak outward curvature (shown primarily by uniform convexity of their inner contours) and are termed "suborthochoanitic." In at least the mature camerae of virtually all Pseudorthocerataceae, septal necks are flexed distinctly outward and are properly designated "cyртоchoanitic." In cyртоchoanitic orthocerids, however, there is considerable variation in degree of neck curvature, and the relation between brim width and neck length is of considerable importance in discriminating some genera and many species of the Pseudorthocerataceae.

In orthochoanitic and suborthochoanitic orthocerids, connecting rings are typically cylindrical or subcylindrical, but slight inflation of siphuncular segments is not uncommon. Segments in such species, however, are invariably much longer than wide. The form of siphuncular segments in cyртоchoanitic species, however, is greatly variable; segments may be subcylindrical, with expansion confined to their anterior and posterior ends (e.g., *Dolorthoceras*), or broadly nummuloidal, with or without an area of adnation of considerable width (e.g., *Buchanoceras*, *Macroloxoceras*, *Pseudorthoceras*). In some species of the suborthochoanitic Sactorthoceratidae, mature siphuncular segments are somewhat less strongly inflated on one side than on the other, and siphuncular segments in species of the Clinoceratidae tend to be asymmetrically cyртоchoanitic. That is, septal necks in species of the latter family are more strongly curved ventrally than dorsally and segments thus tend to be planoconvex in longitudinal section, with flattened dorsal profiles.

The few studies that have been made of complete orthocerid conchs indicate that in

most cyrtochoanitic species, septal necks in early siphuncular segments are either orthochoanitic, suborthochoanitic, or less strongly cyrtochoanitic than necks in later segments of the same conch. This observation suggests, of course, that such maturely cyrtochoanitic forms were derived from an originally orthochoanitic or suborthochoanitic stock, and provides the basis for including nautiloids with both straight and curved septal necks in the same order. In a few cyrtochoanitic species (herein assembled in the family Proteoceratidae), siphuncles are cyrtochoanitic in the earliest camerae known, but tend in some to become suborthochoanitic or orthochoanitic in later camerae. Neither the phylogenetic nor the anatomic significance of such an ontogenetic sequence is known.

The siphuncles of many Orthocerida are apparently empty, but those of a considerable number of species exhibit undoubted organic endosiphuncular deposits. These are of several distinct types:

- (1) Annulosiphonate deposits, composed of small, laminated annuli beginning in the septal foramina and, in some species, encroaching during later growth anteriorly and posteriorly along the inner surfaces of the connecting rings. Such deposits characterize the Geisonoceratidae (Orthocerataceae) and several genera (e.g., *Cyrtactinoceras*, *Gorbyoceras*, *Stereospyroceras*) of the Proteoceratidae (Pseudorthocerataceae).
- (2) "Pseudorthoceroid" deposits. As in (1), annuli in the septal foramina grow primarily forward against the inner surface of connecting rings; however, in this type of deposit, these parietal masses fuse in later growth stages with the posterior portion or prolongation of deposits formed independently in the next succeeding camera. Deposits of this type may be prolonged from an endosiphuncular annulus that is complete in the septal foramen before deposits of adjacent camerae fuse ventrally (Spyroceratinae), or ventral fusion of deposits may precede development of a complete annulus in the septal foramen (Pseudorthoceratinae). Deposits of similar character have been reported in *Virgoceras* (Geisonoceratidae).
- (3) "Mysterioceroid" deposits. Endosiphuncular lining formed against connecting rings by calcareous material secreted progressively backward in each siphuncular segment from a point of origin at the tip of septal necks.
- (4) "Stereoplasmoceroid" deposits. The inner side of the ectosiphuncle of the genera of the Stereoplasmoceratidae exhibits a continuous, apparently nonsegmental lining of organic calcite. Deposits of this type are not well understood, nor have they been studied as thoroughly as is desirable. It is suspected that they may originally have been of segmental origin, as in (2) or (3) above, but that lines of junction between adjacent segmental deposits have been obscured by post mortem recrystallization. If these deposits are not of segmental origin, they were probably secreted throughout the length of the siphuncle at the same time, late in the life of the animal.
- (5) "Cayutoceroid" deposits. Annular endosiphuncular deposits like those in (1) above are covered by an inner, apparently segmental, parietal lining composed of calcareous material typically darker in color than that forming the endosiphuncular annuli. Deposits of this type characterize genera in the subfamily Cayutoceratinae (Pseudorthoceratidae).
- (6) "Troedssonelloid" deposits. Parietal deposits in the siphuncle are prolonged apically to form endocones. Known only from *Troedssonella* and *Buttsoceras* (Troedssonellidae).
- (7) "Pseudactinoceroid" deposits. Parietal endosiphuncular deposits grow principally forward from septal foramina to fuse in anterior ends of segments, and are pierced by two series of radial canals. Deposits of this type are strikingly similar to those of some Actinocerida, from which they can be distinguished by the fact that they are not separated from connect-

ing rings by a perispantium. Endosiphuncular deposits of this type characterize the Pseudorthoceratinae (Pseudorthoceratidae).

Organically secreted calcareous deposits occupy the camerae, as well as the siphuncles, of many orthocerid species, but have never been observed in the camerae of others. Although the nature, ontogenetic development, and circumferential distribution of organic cameral deposits is well known in a few orthocerid species, detailed information with respect to these structures is not yet available for a majority of the forms known to possess them. Consequently, it is difficult at this time to summarize the nature of, or to attach any general significance to, cameral deposits in orthocerid taxonomy. It should be noted, however, that peculiar cameral deposits, composed of single or distally bifid longitudinal lamellae radiating inward from the shell wall toward the siphuncle, characterize the orthoceratacean family Lamellorthoceratidae, and that the development of cameral deposits far in advance of siphuncular deposits constitutes one of the distinctive features of the pseudorthoceratacean family Proteoceratidae. Presumably, when the structure and development of cameral deposits are better known in genera of other orthocerid families, they will be of considerable taxonomic importance.

## DISTRIBUTION AND PHYLOGENY

Orthocerida are world-wide in their geographic distribution and have been reported from rocks that range in age from Early Ordovician to Late Triassic (Norian). Orthocerids are best known from, and were apparently most numerous and varied in, the pre-Carboniferous Paleozoic; Carboniferous and later orthocerids are not particularly well known, and seem to represent only a few rather generalized types. In some strata, however, late Paleozoic and early Mesozoic genera are represented by large numbers of individuals.

Representatives of both the orthochoanitic-suborthochoanitic Orthocerataceae and the cyrtchoanitic Pseudorthocerataceae have been described from the earliest Middle Ordovician rocks known to yield true ortho-

cerids. However, because orthochoanitic species are more abundant and varied than cyrtchoanitic species in both the early and late history of the order, and many cyrtchoanitic species are known to have orthochoanitic or suborthochoanitic juvenile siphuncles, it seems reasonable to conclude that early Middle Ordovician Orthoceratidae represent the root-stock of the Orthocerida. Presumably, early orthoceratids developed from similarly orthochoanitic Lower Ordovician Baltoceratidae (Ellesmerocerida) through restriction in siphuncle size and concurrent simplification of connecting ring structure.

In or before earliest Middle Ordovician time, slight morphological variation in orthocerids with tubular siphuncles probably produced suborthochoanitic Sactorthoceratidae, which, in turn, may have been the progenitors of cyrtchoanitic Middle Ordovician pseudorthocerataceans referable to the Mysterioceratidae, Proteoceratidae, and Stereoplasmoceratidae. Unknown nautiloids of the Mysterioceratidae may have given rise to the Spyroceratinae, which appear first in the Lower Silurian and represent the primitive stock of the dominantly post-Silurian Pseudorthoceratidae. On the other hand, and more probably, the Spyroceratinae may have been derived directly from as yet undescribed orthochoanitic species of the Geisonoceratidae (Orthocerataceae), some of which (e.g., *Virgoceras*) developed endosiphuncular and cameral deposits strikingly similar to those of early Silurian Pseudorthoceratidae. It is thus distinctly possible that the Pseudorthocerataceae, as herein conceived to include both Mysterioceratidae and Stereoplasmoceratidae, is polyphyletic, and contains at least two cyrtchoanitic stocks independently derived from the Orthocerataceae at different times.

Suborthochoanitic Middle Ordovician Sactorthoceratidae seem to be the most likely ancestors of Middle and Upper Ordovician Clinoceratidae, which have slender, empty, cyrtchoanitic siphuncles, the segments of which tend to be planoconvex in some species. The latter character is known also from early representatives of the Ascerida, and the Clinoceratidae may stand close to the stock from which that bizarre

group of early Paleozoic nautiloids was derived.

Annulated Middle Silurian Paraphragmitidae, with empty, suborthochoanitic to weakly cyrtochoanitic siphuncles, are reminiscent of similarly ornamented forms in the orthochoanitic Orthoceratidae, from which they may well have been derived. A similar origin, in the Orthoceratidae, may reasonably be postulated for the dominantly Devonian Lamellorthoceratidae and the Middle-Ordovician-to-Middle-Devonian Geisonoceratidae; the former differ primarily from typical Orthoceratidae in having massive cameral deposits composed of longitudinal lamellae radiating inward from the shell wall toward a central, empty, orthochoanitic siphuncle. The latter retain the orthochoanitic siphuncle, but are characterized by the formation in it of simple endosiphuncular deposits.

Derivation and relations of the early Middle Ordovician Troedssonellidae are uncertain. The suborthochoanitic, thin-walled siphuncle is of a type common to many Orthocerataceae, but the presence of endocones in this siphuncle is anomalous. Although endocones are known in the Endocerida and Discosorida (which can both be traced back to the Ellesmerocerida), endocones are not known in the Baltoceratidae, the ellesmerocerid family that probably gave rise to the orthocerids. It is thus possible that the Troedssonellidae were derived from a group other than the Baltoceratidae and may, consequently, be more closely related to the endocerids than the orthocerids. The family is herein included with the Orthocerida because the ectosiphuncle is typically orthocerid; the similarity, however, may well be the result of homeomorphy rather than close relationship.

## CLASSIFICATION

Most of the several hundred species now referred to the Orthocerida had been described before 1883, when ALPHEUS HYATT began publication of his famous studies of cephalopods. Although the internal and external biocharacters of many of these species were carefully described and recognizably illustrated, a very large number of them were based on gross conch form, features of

external sculpture, and, in a few cases, even upon characters now suspected or known to be the results of post mortem distortion. Virtually all of these species were referred to *Orthoceras*, which, of course, was interpreted very broadly; a few superficially aberrant types were recognized as representatives of distinct genera, but, for the most part, these were vaguely and incompletely diagnosed and are difficult to recognize today. All of the few attempts at suprageneric classification of these species, then, have depended largely upon the few that were originally completely described and upon later-discovered species that were described in terms of the taxonomic scheme current at the time of their discovery. To these introductory remarks it should also be added that complete conchs of only a very few orthocerid species are known. Study of probably related but now fragmentary conchs indicates, however, that both internal and external structures varied greatly from one developmental stage to the next in the same conch, and that a proper notion of specific characters and relationship can be obtained only from complete specimens. Furthermore, nearly 50 per cent of the genera herein included in the Orthocerida are monotypic—in many cases known only from a single specimen; an additional 20 per cent includes no more than three species, generally from the same geographic area and stratigraphic unit. All of these facts render suspect and highly provisional any scheme of suprageneric classification!

In 1900, when HYATT proposed his now classical suprafamilial arrangement of nautiloid cephalopods, only 21 of the more than 100 genera now included in the Orthocerida had been established. Of these, HYATT referred *Orthoceras* (in which the bulk of orthoconic nautiloids were then included) and ten others to the "division" Orthoceratida of his suborder Orthochoanites; four genera were referred to the "division" Annulosiphonata, and one (*Clinoceras*) to the "division" Actinosiphonata, both of the suborder Cyrtochoanites. Five genera, validly, if vaguely, established before 1900 (*Arthrophyllum* VON BEYRICH, *Eusthenoceras* FOORD, *Molossus* DE MONTFORT, *Sannionites* FISCHER, and *Trematoceras* EICHWALD), were understandably

omitted from HYATT's nautiloid classification. The relationships of *Eusthenoceras*, *Molossus*, and *Sannionites* are still not certainly known; the latter two are included in the Orthocerida only for the sake of convenience.

HYATT's classification of nautiloids was, with a few notable exceptions, rather generally ignored outside of North America, and at least the portion of it pertinent to the Orthocerida was not importantly modified or expanded by those who used it for 50 years after it was proposed. In 1941, however, FLOWER noted that Chazyan elliphochoanitic nautiloids familiar to him could be divided into five morphologic groups, the general characters and content of which he outlined, but for which he was reluctant to propose names. The groups he recognized are as follows:

1. Orthochoanitic nautiloids with perfectly cylindrical siphuncular segments. [This group included straight, curved, and coiled forms, and seems essentially to be HYATT's suborder Orthochoanites, expanded by 1941 by addition of genera described after 1900.]
2. Suborthochoanitic nautiloids, with straight or nearly straight septal necks, but connecting rings slightly curved, producing slightly convex siphuncular segments. No cameral deposits. [This group included only *Centroonoceras*, *Sactorthoceras*, and *Sigmorthoceras*, for which FLOWER later (1946) proposed the familial name Sactorthoceratidae.]
3. Cyrtchoanitic cephalopods with relatively small, slender siphuncular segments that become suborthochoanitic when traced posteriorly in the conch. [The cephalopods FLOWER included in this category now constitute an early stock of the Oncocerida.]
4. Cyrtchoanitic cephalopods with relatively slender segments; earliest stages unknown, but earliest ones known are cyrtchoanitic. Siphuncular outline becomes more slender anteriorly and is suborthochoanitic in latest phragmone. [FLOWER has recently (1962) referred this group to the Proteoceratidae.]
5. Primitively cyrtchoanitic species. [In-

cludes forms now referred to the Actinocerida and Discosorida.]

In another study in 1941, FLOWER implicitly restricted the content of group 1, above, by removing from it Lower Ordovician nautiloids with thickened connecting rings. In 1946, he noted inclusion of both straight and coiled forms in the residue of group 1, but hesitated to divide the group at that time because of a lack of knowledge regarding origin and phylogeny of many genera included in it. In 1950, FLOWER & KUMMEL separated the thin-ringed coiled forms included in group 1 (and in HYATT's "divisions" Plectoceratida, Pleuronautilida, Ryticeratida, Rhadinoceratida, Hercoceratida, Koninckoceratida, and Digonioceratida of the suborder Orthochoanites) and distributed them among several newly created nautiloid orders. Furthermore, they combined the residue of FLOWER's 1941 group 1 with his group 2 as the family Michelinoceratidae (a name proposed by FLOWER in 1945), and included this family, the Stereoplasmoceratidae (group 4 above), the Pseudorthoceratidae (which FLOWER monographed in 1939), the Clinoceratidae (established in 1946, but based on concepts first elaborated in 1941), and the newly established Paraphragmitidae in a new nautiloid order, for which the name Michelinoceratida was proposed.

Studies by various specialists since 1950 have introduced several important new genera, have considerably extended the ranges of certain orthocerid families, and have provided more extensive descriptions of many genera included in the family Michelinoceratidae of 1950. FLOWER's arrangement of 1950, however, has generally been retained, although there has been debate as to the proper name for the order and about its status in the hierarchy of nautiloid classification. Perhaps the most significant discoveries have had to do with the range and relationships of cyrtchoanitic forms referred to the various subfamilies of the Pseudorthoceratidae established by FLOWER in 1939. In 1950, no representatives of the Pseudorthoceratidae were known from pre-Devonian rocks. Subsequently, however, new genera of both the Cayutoceratinae and Spyroceratinae (=Dolorthoceratinae of FLOWER, 1939) have been de-

scribed from Silurian strata, and a newly described family (Mysterioceratidae) includes pseudorthoceratid-like early Middle or Upper Ordovician species or both. It thus appears possible that the pseudorthoceratid stock may have been well developed, if primitive and poorly represented, in the earliest strata from which orthocerid (=michelinoceratid) nautiloids have so far been reported.

The order Orthocerida,<sup>1</sup> as herein conceived, is essentially the Michelinoceratida of FLOWER (in FLOWER & KUMMEL, 1950), with names for several taxa revised to conform to requirements set forth in recently issued recommendations of the International Commission on Zoological Nomenclature, and with subdivision of the order into two superfamilies (Orthocerataceae and Pseudorthocerataceae) to accommodate the two principal morphological groups ("Michelinoceratidae" and Stereoplasmoceratidae-Pseudorthoceratidae) referred to the Michelinoceratida by FLOWER, in 1950. Relationship between these two groups has not yet been satisfactorily established, and the arrangement herein adopted may ultimately be shown to be unreasonable; for the present, however, it lends emphasis to the inclusion of orthochoanitic and cyrtochoanitic forms in the same order, and underscores the essentially equivalent antiquity of both structural types in the Orthocerida.

### STATUS OF ORTHOCERA, ORTHOCEROS, ORTHOCERATITES, AND ORTHOCERUS

In the late 18th and early 19th centuries, the generic names *Orthocera*, *Orthoceros*, *Orthoceratites*, and *Orthocerus*, together with *Orthoceras*, were used indiscriminately and partly interchangeably for all kinds of orthoconic cephalopods, as well as for Foraminifera and certain pelecypods. Only *Orthoceras*, much restricted in scope, is included in the systematic portion of this chapter; the status of the other names listed above is as follows:

- (1) *Orthocera* MODEER, 1789 [*\*Nautilus radícula* LINNÉ, 1758; SD MELVILLE, 1959]. With the designated type-species, *Orthocera*, regardless of past usage, is an unused senior objective synonym of *Nodosaria* LAMARCK, 1816 (122, p. 22), and thus unavailable for cephalopods or other animals.
- (2) *Orthoceros* BRÜNNICH, 1771 [*\*Orthoceratites regularis* SCHLOTHEIM, 1820; SD ULRICH, FOERSTE, MILLER, & UNKLESBAY, 1944]. Senior objective synonym of *Orthoceras* BRUGUIÈRE, 1789. MELVILLE (122) has applied to the International Commission on Zoological Nomenclature to use its plenary powers to suppress *Orthoceros* for the purposes of the Law of Priority, but not for those of the Law of Homonymy, particularly so as to preserve the name *Orthoceras* in its accustomed sense. No action has yet been announced on MELVILLE's application, but the name *Orthoceros* does not appear in either the text or synonymies in the following systematic list of Orthocerida genera, for it is felt that the sense of the pending application is sound and that the Commission will eventually take appropriate steps to correct matters in accord with the procedure requested.
- (3) *Orthoceratites* LAMARCK, 1799. No nominal species was included in this genus by LAMARCK (who apparently used it for a hippurite) and, although many nautiloid species have been described in terms of it, no species have subsequently been referred to *Orthoceratites* by anyone who attributed the name to LAMARCK. Although the name could be removed from the list of valid generic names in any one of several devious ways, Cox (14) has applied to the International Commission on Zoological Nomenclature to use its plenary powers to suppress the name for purposes of the Law of Priority. No action has yet been announced on Cox's application, but it is assumed that the Commission will ultimately regard it favorably. For this reason, the name does not appear, even in synonymy, in the fol-

<sup>1</sup>OSKAR KUHN, in a synoptic classification of 1940, seems to have been the first to propose an order-group name for a category including the Orthoceratidae. In that work, KUHN grouped the Orthoceratidae and other straight nautiloid cephalopods in a suborder Orthoceracea; later, in a text published in 1949, he raised this group to ordinal status. Thus, KUHN's name Orthoceracea (herein emended to Orthocerida) clearly has priority over the more widely used name Michelinoceratida, proposed for essentially the same group of nautiloids by FLOWER in FLOWER & KUMMEL, 1950.



lowing descriptions of Orthocerida.  
(4) *Orthocerus* KING, 1844. In so far as can be determined, this name has never been stabilized by indication or description of a named type-species. The fossil to which KING referred is not known and the genus was originally so inadequately characterized that it does not seem desirable to stabilize it by designating a type-species.

SYSTEMATIC DESCRIPTIONS

Subclass NAUTILOIDEA Agassiz, 1847

Diagnosis given in "Introductory Discussion" (p.K128). *U.Cam.-Rec.*

Order ORTHOCERIDA Kuhn, 1940

[*nom. transl.* KUHN, 1949 (to Ordnung Orthoceracea); *nom. correct.* SWEET, herein (*pro* Orthoceracea KUHN, 1940 (sub-order)) [=Orthoceratida HYATT in ZITTEL, 1900 ("Division" of order); Orthoceracea SCHINDEWOLF, 1942 ("Stamm")];

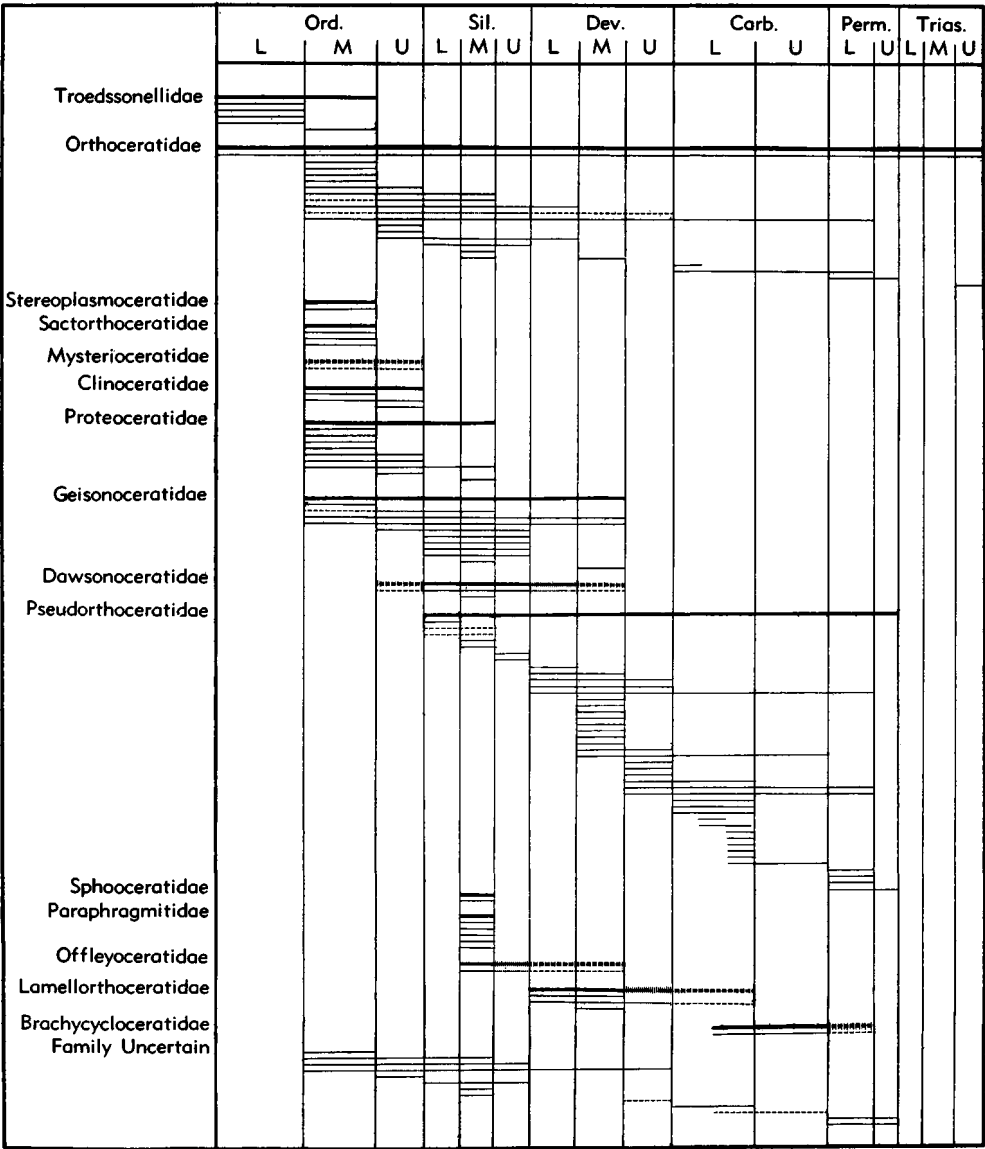


FIG. 152A. Stratigraphic distribution of genera and families of Orthocerida (Sweet, n).

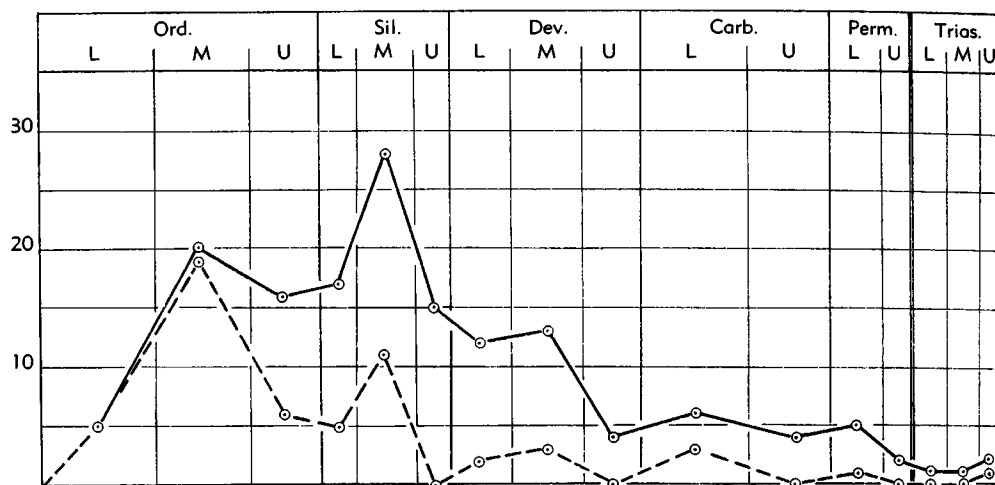


FIG. 152B. Graph showing numbers of new genera of Orthocerida introduced in successive epochs (dashed lines) and total genera represented in each (solid lines) (Sweet, n).

Michelinoceratida FLOWER in FLOWER & KUMMEL, 1950 (order); Michelinoceroida FISCHER in MOORE, LALICKER, & FISCHER, 1952 (order); Orthoceratida BALASHOV, 1956 (order); Michelinoceratina SWEET, 1958 (suborder); Sinoceratida KOBAYASHI, 1958 (order); Orthocerotida ZHURAVLEVA, 1959 (order)] [Mention of Orthocerida by FURNISH, GLENISTER, & HANSMAN, 1962 (p. 1343), is disregarded]

Straight-to-curved but never coiled nautiloids with smooth or elaborately ornamented shells, typically well-developed cameral deposits, and siphuncles with orthochoanitic, or secondarily cyrtochoanitic septal necks and thin connecting rings, either empty or occupied by parietal or annulosiphonate deposits. [The Orthocerida almost certainly developed from the Balto-ceratidae of the Ellesmerocerida.] *L.Ord.-U.Trias.*

The stratigraphic occurrence of genera included in the Orthocerida is shown graphically in Figure 152A; the numbers of new genera introduced in successive epochs are indicated in Figure 152B.

### Superfamily ORTHOCERATACEAE M'Coy, 1844

[*nom. transl.* SWEET, herein (ex Orthoceratidae M'Coy, 1844)] [=Orthocerocea KINDLE & MILLER, 1939 (superfam.); Orthocerotoidea SHIMANSKIY, 1951 (superfam.)]

Straight or slightly curved, smooth or ornamented, orthochoanitic to suborthochoanitic conchs, generally with circular cross section. Includes some secondarily cyrtochoanitic forms. *L.Ord.-U.Trias.*

### Family ORTHOCERATIDAE M'Coy, 1844

[=Orthocerotidae TEICHERT & MILLER in KINDLE & MILLER, 1939]

Smooth or elaborately ornamented, generally subcircular in cross section and with central or subcentral siphuncle that is typically free of endosiphuncular deposits. *L.Ord.-U.Trias.*

#### Subfamily ORTHOCERATINAE M'Coy, 1844

[*nom. transl.* SWEET, herein (ex Orthoceratidae M'Coy, 1844)]

Body chamber marked by 2 to 5 longitudinal furrows. *M.Ord.*

*Orthoceras* BRUGUIÈRE, 1789, p. xvi [*\*Orthoceras regularis* SCHLOTHEIM, 1820; SD MILLER, DUNBAR & CONDRA, 1933] [= *Ortaoceras* MEEK, 1861 (*nom. null.*)]. Slightly expanding, almost cylindrical orthocones or faintly exogastric cyrtocones with empty, subcentral to slightly ventral cylindrical orthochoanitic siphuncle. Body chamber transversely constricted at mid-length and marked by single longitudinal dorsal and 2 longitudinal ventral depressions. Surface ornamented by a network of fine lirae; internal surface faintly striated longitudinally, with prominent conchal furrow on venter; muscle attachment dorsomyarian. *M.Ord.*, Eu. (Est.-Lith.-USSR-Sweden). — FIG. 153.1. *\*O. regulare* (SCHLOTHEIM), Est.; 1a, long. sec. through siphuncle,  $\times 1$ ; 1b, right lat. view of body chamber,  $\times 0.5$  (195).

*Bifoveoceras* BALASHOV, 1956, p. 237 [*\*Orthoceras bifoveatum* NOETLING, 1884, p. 111; OD]. Like *Orthoceras*, but with 2 lateral longitudinal de-

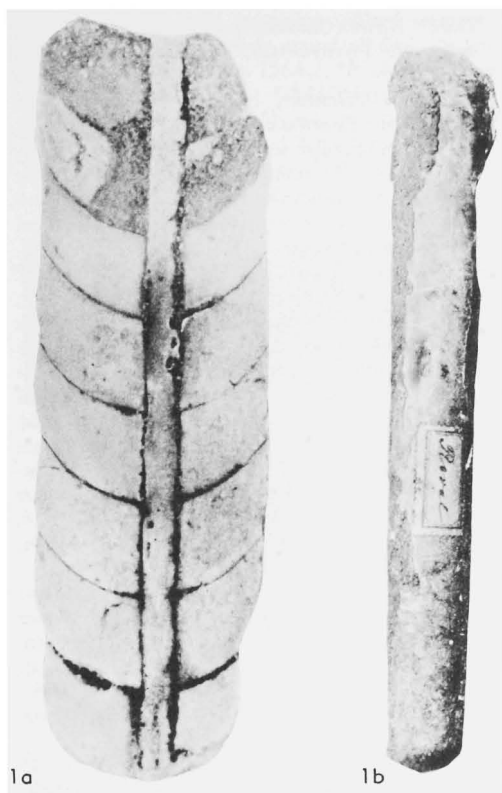


FIG. 153. \**Orthoceras regulare* (SCHLOTHEIM)  
(Orthoceratidae—Orthoceratinae) (p. K224).

pressions on body chamber and more coarsely sculptured test. *M.Ord.*, Eu.(Est.-Sweden).—FIG. 154,1. \**B. bifoveatum* (NOETLING), Sweden; 1a, long. sec. through siphuncle; 1b, ventral view of body chamber,  $\times 1$  (195).

?*Ctenoceras* NOETLING, 1884, p. 115 [\**C. schmidtii*; M] [=?*Palaeocycloceras* SHIMIZU & OBATA, 1936, p. 20]. Subcylindrical to faintly exogastric conchs of somewhat compressed section. Surface with prominent sinuous annulations and growth lines forming broad salients on ventral side. Body chamber with 1 dorsal and 2 ventral impressions. Siphuncle small, subcentral, or between center and venter; orthochoanitic; necks short and straight, connecting rings faintly expanded at anterior ends of segments. Siphuncle of some species (not type) with apparently continuous parietal lining; no cameral deposits known. [Endosiphuncular deposits suggest relation to *Stereoplasmoceratidae*, but orthochoanitic siphuncle, apparent lack of cameral deposits, and impressions in body chamber suggest relationship to *Orthoceras*.] *M.Ord.*, Eu.(Est.-Norway-Sweden)-?Asia(?China).—FIG. 155,1. \**C. schmidtii*, Est.; 1a-c, ventral, dorsal, lat. views,  $\times 0.75$  (144).—FIG. 155,2. *C. sp.* SWEET, Norway; long. sec.,  $\times 2$  (178).

#### Subfamily MICHELINOCERATINAE Flower, 1945

[*nom. transl.* SWEET, herein (ex *Michelinoceratidae* FLOWER, 1945)] [=?*Sinoceratidae* SHIMIZU & OBATA, 1935; *Michelinocerotidae* KOBAYASHI, 1958]

Smooth or indistinctly ornamented *Orthoceratidae* with central or eccentric orthochoanitic, empty siphuncle and generally with well-developed cameral deposits. [FLOWER (May, 1961) has reported "... the first of the true *Michelinoceratidae*" from rocks of latest Canadian (Early Ordovician) age. No genera or species are described, however.] *L.Ord.-U.Trias.*

*Michelinoceras* FOERSTE, 1932, p. 51 [\**Orthoceras michelini* BARRANDE, 1866; OD]. Long, slender, subcylindrical orthocones of circular section and with long camerae and very long body chamber. Siphuncle central or eccentric by no more than its own diameter, empty. Septal necks straight; connecting rings homogeneous, cylindrical. Well-developed hyposeptal and episepal deposits in camerae. [FOERSTE (71) recognized that *Orthoceras*, based on *O. regulare* (SCHLOTHEIM), is of very limited scope, and can no longer accommodate a majority of the orthochoanitic orthocones

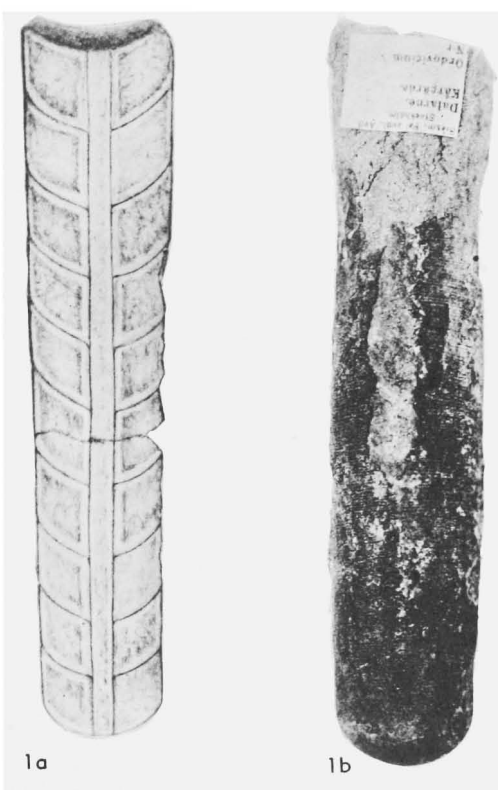


FIG. 154. \**Bifoveoceras bifoveatum* (NOETLING)  
(Orthoceratidae—Orthoceratinae) (p. K224-K225).

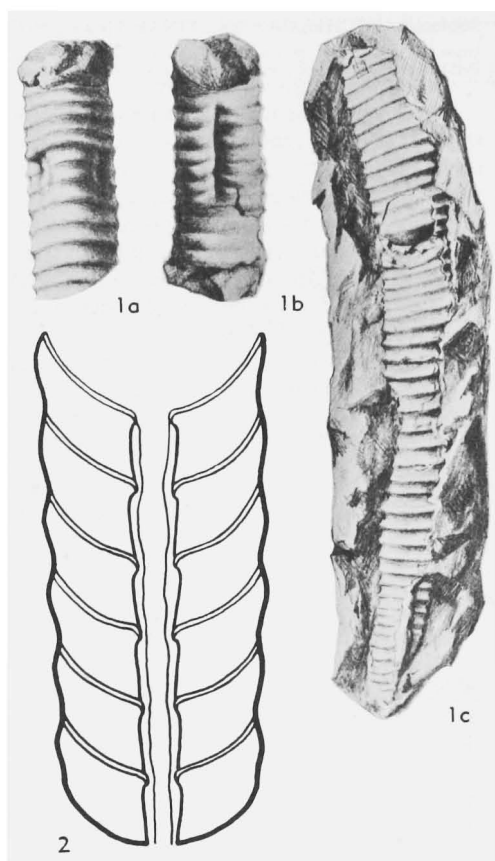


FIG. 155. \**Ctenoceras schmidtii* NOETLING (Orthoceratidae—Orthoceratinae) (p. K225).

with cylindrical siphuncles previously referred to it. For these species, all of which are probably not related, FOERSTE proposed the name *Michelinoceras*. True *Michelinoceras* is known from Lower, Middle, and Upper Ordovician, Silurian, and Devonian rocks. Carboniferous, Permian, and Triassic species referred to the genus are relatively few in number and, for the most part, not well known internally. However, until such time as these late Paleozoic and early Mesozoic species have been studied more thoroughly, they are perhaps best included in *Michelinoceras sensu lato*. That practice is followed here.] *L.Ord.-U.Trias.(Norian)*, N. Am.-Eu.-Asia-Australia, widespread. —FIG. 156.3. \**M. michelini* (BARRANDE), M.Sil., Eu. (Czech.); long. sec.,  $\times 1$  (5).

**Arkonoceras** FLOWER, 1945, p. 701 [\**Orthoceras arkonense* WHITEAVES, 1898, p. 406; OD]. Slender, compressed orthocones of somewhat subquadrate section. Camerae deep; sutures with dorsal and ventral saddles and lateral lobes. Siphuncle midway between center and venter; necks long, straight, connecting rings not known. *M.*

*Dev.*, N. Am. (Ohio-Ont.). —FIG. 157.1. \**A. arkonense* (WHITEAVES), Ont.; long. sec.,  $\times 2.5$  (32).

**Balticoceras** TEICHERT, 1940, p. 590 [\**Trematoceras discors* EICHWALD, 1857, p. 201; OD]. Orthocones of subcircular section; broadly flattened ventral side, evenly rounded dorsal side. Siphuncle marginal, orthochoanitic. *U.Ord.*, Eu. (Est.). —FIG. 156.2. \**B. discors* (EICHWALD); 2a-c, dorsal, ventral, post. views,  $\times 1$  (19).

**Bitauinioceras** SHIMIZU & OBATA, 1936, p. 27 [\**Orthoceras bitauiniense* HANIEL, 1915, p. 141; OD]. Gradually expanding, circular orthocones with straight transverse sutures. Test surface with a few shallow rounded transverse constrictions and many prominent transverse lirae of unequal size. Siphuncle subcentral, small; orthochoanitic, with short, straight necks and cylindrical rings. *Perm.*, USA (Tex.)-Mex. (Coahuila)-Sicily-Timor-USSR (S. Urals). —FIG. 156.1. *B. coahuilense* MILLER & YOUNGQUIST, Mex. (Coahuila); 1a,b, long. secs.,  $\times 7.5$ ,  $\times 3$ ; 1c,d, lat., septal views,  $\times 2.25$  (136).

**Eotripteroceras** FLOWER, 1943, p. 71 [\**E. minutum*; OD]. Smooth, depressed orthocones with venter flatter than dorsum, sutures with dorsal and ventral lobes. Siphuncle ventral of center, cylindrical; both siphuncle and camerae empty. *M.Ord.*, USA (N.Y.). —FIG. 157.3. \**E. minutum*; 3a,b, long. sec., septal view,  $\times 2$  (31).

**Hesperoceras** MILLER & YOUNGQUIST, 1947, p. 115 [\**H. laudoni*; OD]. Orthocones of subrectangular cross section. Sutures straight and transverse on narrow conch sides, but forming broad shallow rounded lobes on wide sides. Siphuncle small, central; internal structure unknown. *L. Miss.*, USA (N. Mex.). —FIG. 157.2. \**H. laudoni*; 2a,b, ?ventral, ?lat. views,  $\times 2$  (135).

**Plagiostomoceras** TEICHERT & GLENISTER, 1952, p. 741 [\**Orthoceras pleurotomum* BARRANDE, 1866, pl. 224; OD]. Long slender orthocones with circular to slightly depressed cross section. Sutures straight or slightly oblique; may develop faint lateral lobes. Septa moderately concave. Aperture strongly oblique, sloping adapically from antisiphuncular side. In lateral view, aperture somewhat sinuous, sloping more strongly on side and flattening on both antisiphuncular and siphuncular sides. Surface with growth lines and weak ridges parallel to aperture. Siphuncle central or eccentric, orthochoanitic. *U.Ord.-L.Dev.*, Eu. (Czech.)-Australia. —FIG. 156.5. \**P. pleurotomum* (BARRANDE), M.Sil., Czech.; 5a-c, long. sec., septal view, lat. view,  $\times 1$  (5).

**Pleurorthoceras** FLOWER, 1962, p. 35 (publ. Oct. 12) [\**Orthoceras clarkesvillense* FOERSTE, 1924, p. 220; OD] [= *Shimizuoceras* ZHURAVLEVA, 1962, p. 85 (publ. Dec. 17) (*nom. subst. pro Foersteoceras* SHIMIZU & OBATA, 1936; *non* RUEDEMANN, 1925) (type, *Orthoceras selkirkense* WHITEAVES, 1892)]. Like *Michelinoceras* externally, but siphuncle sub-

orthochoanitic, with somewhat inflated segments. Cameral deposits entirely mural. *U.Ord.*, N.Am. (Ohio-Manit.).—FIG. 156A, I. \**P. clarkesvillense* (FOERSTE), Richmond., USA (Ohio); 1a, apical part of specimen,  $\times 1$ ; 1b, ant. part of phragmone of 1a, lacking cameral deposits,  $\times 1$  (47a).

?*Sinoceras* SHIMIZU & OBATA, 1935, p. 6 [\**Orthoceras chinense* FOORD, 1888, p. 100]. Like *Micheli-*

*noceras*, but camerae shorter and septal necks nearly one-third camera length. Surface unknown in genoholotype, but in presumably conspecific forms, surface marked either by very fine irregular striae or by sinuous transverse growth bands, patterns of which are not known in detail. Connecting rings unknown; camerae apparently with thick episeptal and hyposeptal deposits. [Doubt-

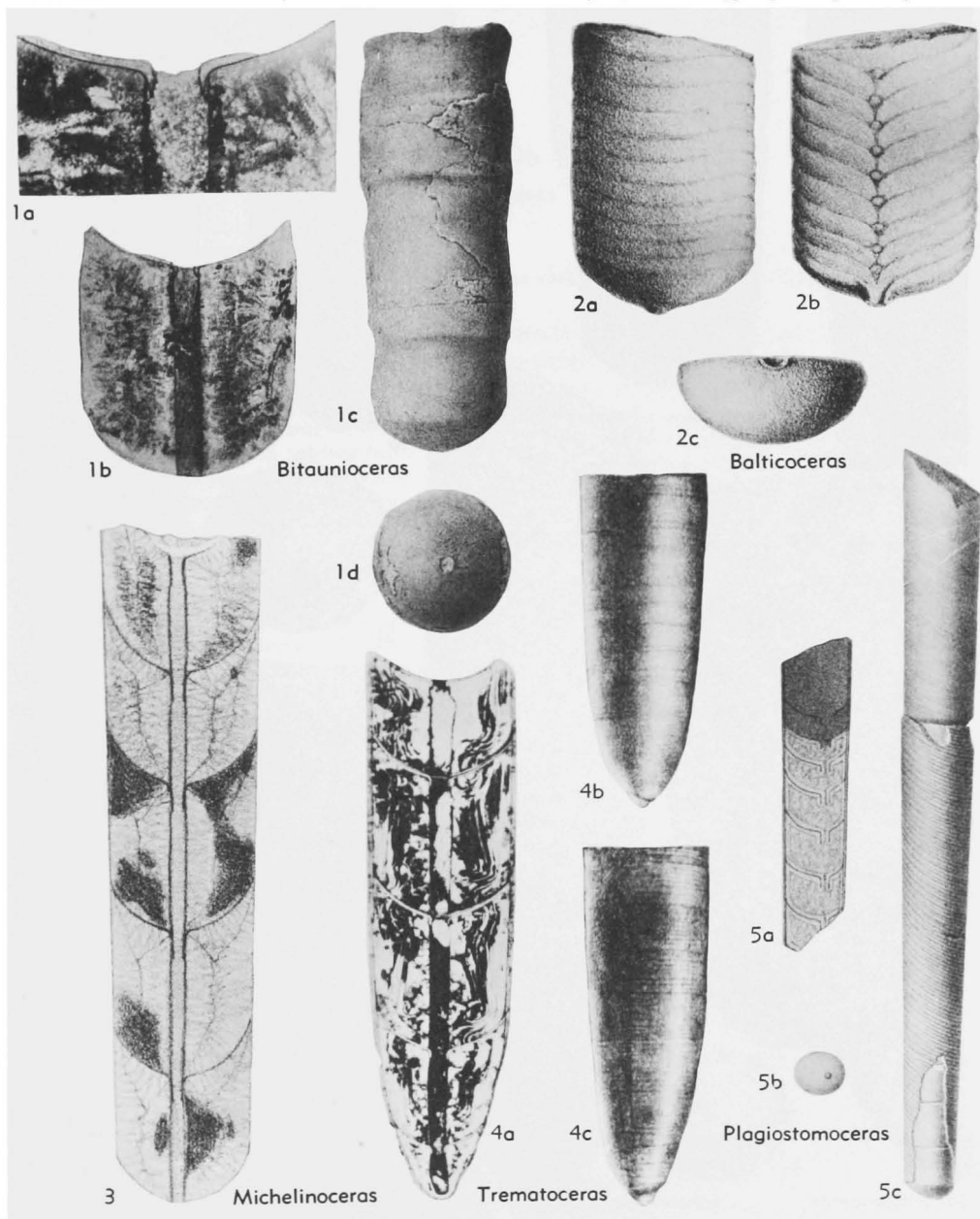


FIG. 156. Orthocerataceae (Orthoceratidae—Michelinoceratinae) (p. K225-K226, K229).

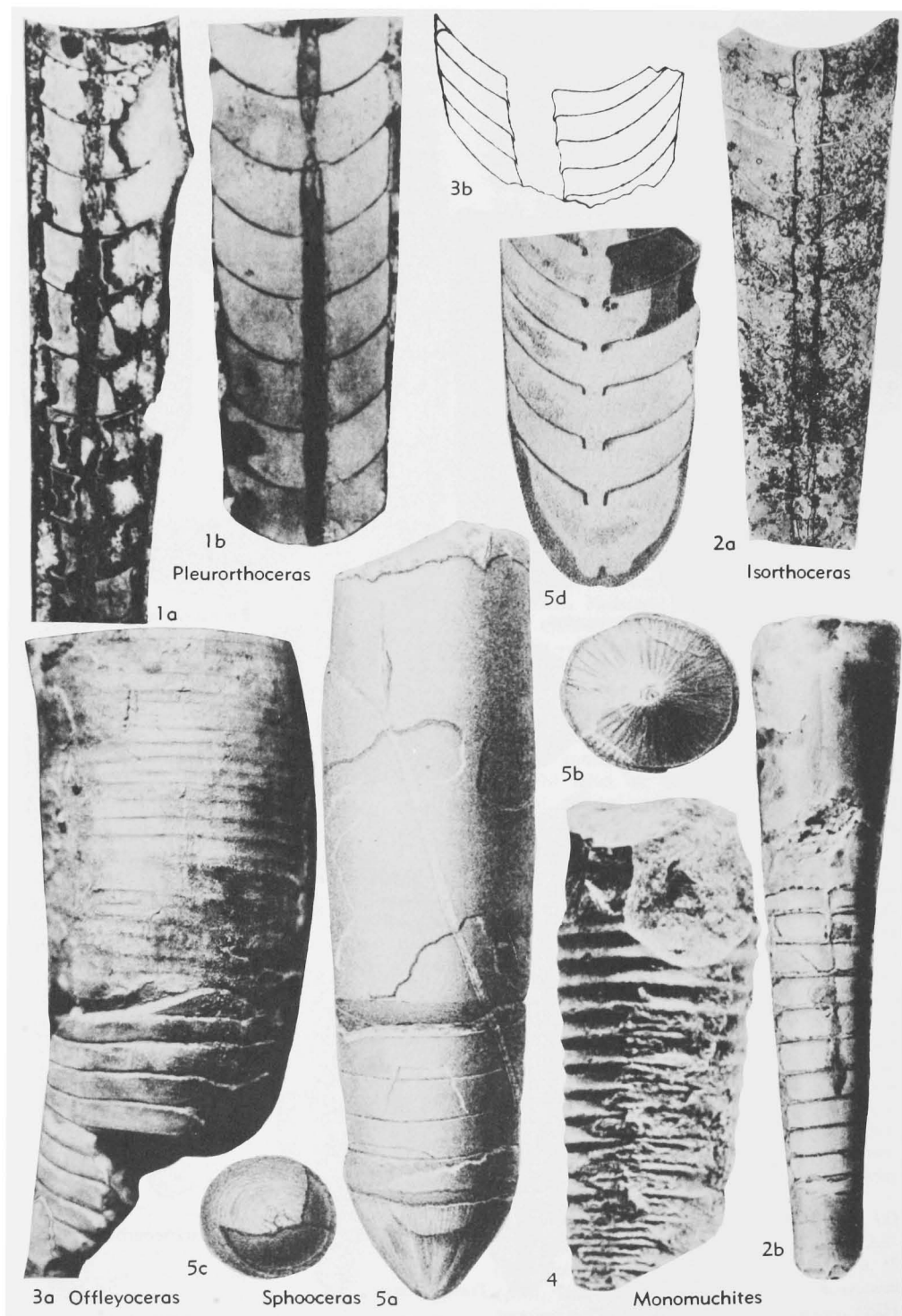
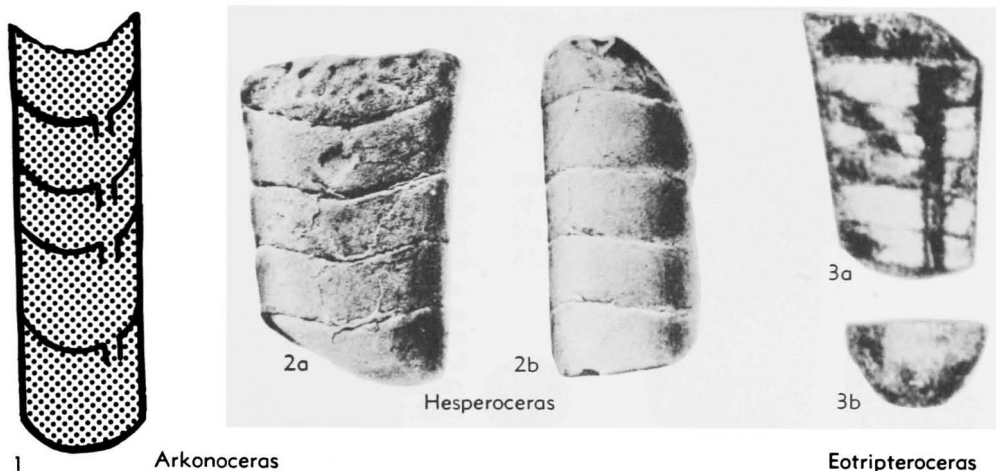


FIG. 156A. Orthocerataceae (Orthoceratidae-Michelinoceratinae) (p. K226-K227); (Proteoceratidae) (p. K256-K259); (Offleyoceratidae) (p. K242); (Sphooceratidae) (p. K232).



Arkonoceras

Eotripteroceras

FIG. 157. Orthocerataceae (Orthoceratidae—Michelinoceratinae) (p. K226).

fully distinct from *Michelinoceras*; stratigraphic derivation of type uncertain. FOORD regarded type-species as possibly Devonian; YÜ, SHIMIZU & OBATA, and KOBAYASHI record it from the Middle Ordovician. Content and status of Sinoceratidae SHIMIZU & OBATA uncertain pending better stratigraphic and morphologic data concerning certain topotypes of type-species.] ?*M.Ord.*, ?*Dev.*, China. —FIG. 158. \**S. chinense* (FOORD); long. sec.,  $\times 0.5$  (211).

**Trematoceras** EICHWALD, 1851, p. 124 [*\*Orthoceratites elegans* MÜNSTER, 1841; SD SCHINDEWOLF, 1933, p. 18] [*non Trematoceras* WHITFIELD, 1882 (= *Tylorthoceras* MILLER, 1932); *non Trematoceras* HYATT, 1884 (= *Ammonellipsites* PARKINSON, 1822)]. Slender, subcylindrical orthocones with long chambers, simple straight transverse sutures, and smooth or faintly cancellated shell surface. Siphuncle central, orthochoanitic, empty; necks short, connecting rings perfectly cylindrical or only faintly expanded in camerae, which are occupied by prominent lamellar episeptal and mural deposits, former so arranged as to produce star- or petal-shaped impressions radiating outward from septal foramen on internal molds of septal faces. *U.Trias.*, Aus.-Kazakh. —FIG. 156, 4a. *T. cf. politum* (KLIPSTEIN); long. sec.,  $\times 6$  (154). —FIG. 156, 4b, c. \**T. cf. elegans* (MÜNSTER); apical parts of 2 specimens,  $\times 10$  (154).

#### Subfamily KIONOCERATINAE Hyatt in Zittel, 1900

[*nom. transl.* SWEET, herein (*ex* Kionoceratidae HYATT in ZITTEL, 1900)] [= *Ohioceratidae* SHIMIZU & OBATA, 1935 (*partim*)]

Conchs with more or less well-developed longitudinal surficial ornament of lirae, ribs, ridges, or combinations of these, with or without subordinate transverse ornament of

similar nature, or with faint transverse annulations. *M.Ord.-L.Perm.*

**Kionoceras** HYATT, 1884, p. 275 [*\*Orthoceras doricum* BARRANDE, 1868, pl. 269; OD]. Slender to rapidly expanding, apically curved, longitudinally fluted orthocones of circular to subcircular section. Surface ornament of prominent longitudinal ribs separated by concave interspaces and, in most species, less conspicuous longitudinal and transverse lirae or striae. Early-formed part of test may be faintly annulated. Siphuncle central to subcentral, empty in Silurian type-species and in most Ordovician species, but with annulosiphonate deposits in some questionably congeneric Silurian and later species; necks straight, or suborthochoanitic, segments cylindrical or weakly expanded within camerae. *M.Ord.-L.Perm.*, N.Am.-Eu.-Asia-Australia. —FIG. 159, 1. \**K. doricum* (BARRANDE), M.Sil., Eu. (Czech.); 1a-c, long. sec., lat., apical views,  $\times 1$  (5).

**Ohioceras** SHIMIZU & OBATA, 1935, p. 6 [*\*Cyrtoceras myrice* HALL & WHITFIELD, 1875, p. 149; OD]. Slightly curved, uncompressed to faintly depressed longicones; surface with low, broad longitudinal ribs separated by distinct shallow grooves. Siphuncle subcentral, probably orthochoanitic; segments of presumably conspecific topotype cylindrical or nearly so. *M.Sil.*, USA (Ohio). —FIG. 159, 5. \**O. myrice* (HALL & WHITFIELD); lat. view,  $\times 1$  (62).

**Parakionoceras** FOERSTE, 1928, p. 313 [*\*Orthoceras originale* BARRANDE, 1868, pl. 267; OD]. Faintly curved, uncompressed, exogastric longicones with relatively long camerae and straight transverse sutures. Surface with sharp-edged longitudinal ribs separated by broader concave interspaces. Siphuncle slightly eccentric, empty; necks short, directed obliquely toward siphuncle axis (loxochoanitic); connecting rings somewhat inflated at



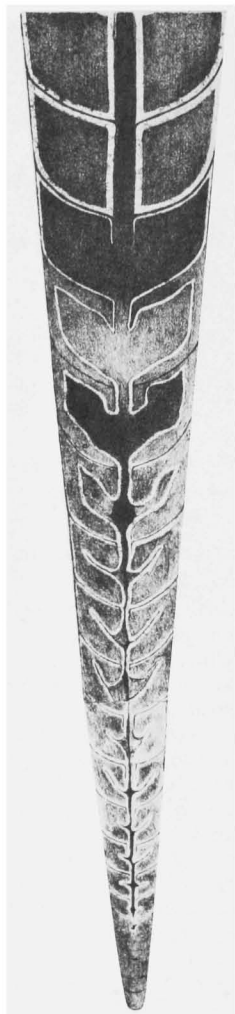


FIG. 158. *\*Sinoceras chinense* (FOORD) (Orthocera-  
tidae—Michelinoceratinae) (p. K227, K229).

septal necks, otherwise essentially cylindrical. Cameral deposits well developed. *M.Sil.*, Eu. (Czech.).—FIG. 159.3. *\*P. originale* (BARRANDE); 3a-c, lat., septal views, long. sec.,  $\times 0.75$  (5).

**Polygrammoceras** FOERSTE in TWENHOFEL, 1928, p. 244 [*\*P. twenhofeli*; OD]. Orthocones with straight transverse sutures and circular cross section. Surface with longitudinal ribs, bars, or striae separated by narrow grooves or shallow flat linear spaces. Siphuncle empty, between center and venter; segments expanded within camerae, truncated adapically and adorally. *M.Ord.-L.Dev.*, N. Am. (Iowa-Minn.-N.Y.-Anticosti Is.-Ont.-Que.)-Eu. (Eng.-Czech.-Norway-USSR-Sweden)-Asia (Outer Mongolia).—FIG. 159.4. *\*P. twenhofeli*, U.Ord.,

Can. (Anticosti Is.); 4a,b, long. sec., lat. view,  $\times 0.7$  (60).

**Thoracoceras** FISCHER DE WALDHEIM, 1844, p. 755 [*\*T. vestitum*; OD] [= *Melia* FISCHER DE WALDHEIM,<sup>1</sup> 1829 (obj.); *Mellia* FISCHER DE WALDHEIM, 1844 (obj.); *Mellia* HERRMANNSEN, 1847 (nom. null.) (non *Mellia* SCHMIDT, 1920, nec MEYRICK, 1934); *Thoracoceras* MARSHALL, 1877 (nom. null.)]. Compressed orthocones marked by prominent longitudinal rounded grooves separated by angular ridges; each rib bearing single row of small blunt spines along its apex. Septa simple, saucer-shaped; sutures straight and transverse. Siphuncle small, submarginal; internal structure unknown. *Carb.* (Miss.-Penn.)-*L.Perm.*, USA (?Ariz.-?Kans.-Mo.-?Tex.)-Eu. (C. USSR-Belg.).—FIG. 159.2. *\*T. vestitum*, *Carb.*, C.USSR (Karowa); 2a,b, lat., septal views,  $\times 0.75$  (128).

#### Subfamily LEUROCYCLOCERATINAE Sweet, n. subfam.

Transversely annulated, with or without subordinate longitudinal striae or lirae. *M. Ord.-Sil.*

**Leurocyloceras** FOERSTE, 1928, p. 272 [*\*L. raymondi*; OD]. Slender, circular or slightly compressed orthocones with asymmetrically curved septa and straight transverse or slightly oblique sutures. Surface with low annulations, in some species so broad and flat that interspaces are only narrowly incised striae on otherwise smooth exterior. Siphuncle eccentric, orthochoanitic, empty; necks unusually long and straight, connecting rings unknown. Moderate episepal and strong hyposeptal deposits; in advanced stages, these deposits may join through septal foramen with those of adjacent camerae to enclose septal necks completely. ?*M.Ord.*, *U.Ord.*, Eu. (Est.); *M.Sil.*, N.Am. (Ill.-Ind.-N.Y.-Ohio-Wis.-Ont.)-Eu. (Czech.). — FIG. 160.1b-d. *\*L. raymondi*, *M.Sil.*, USA (Wis.); ventral, dorsal, lat. views,  $\times 0.5$  (62).—FIG. 160.1a. *L. bruceana* (WILLIAMS), *M.Sil.*, Can. (Ont.); 1a, schematic long. sec., enlarged (22).

**Anaspyroceras** SHIMIZU & OBATA, 1935, p. 4 (emend. FLOWER, 1943, p. 114) [*\*Orthoceras anellus* CONRAD, 1843, p. 334; OD]. Externally like *Spyroceras* (Spyroceratinae), but with simple transverse sutures and orthochoanitic siphuncle. Siphuncle central or eccentric, empty; necks short, connecting rings probably cylindrical. Cameral deposits not known. *M.Ord.-U.Ord.*, N.Am. (Iowa-Minn.-Miss.-N.Y.-Ohio-Ont.).—FIG. 161.1. *\*A. anellus* (CONRAD), *M.Ord.*, N.Y.; 1a-c, surface detail, enlarged; septal, lat. views,  $\times 1$  (83).

**Bohemites** ZHURAVLEVA, 1962, p. 84 [*\*Orthoceras*

<sup>1</sup> In addition to FISCHER DE WALDHEIM, ten other authors before and after 1829 have established generic taxa named *Melia*. References to these may be found in NEAVE, *Nomenclator Zoologicus*, v. 3, 1940, and no good purpose would be served by listing them here.



*aculeatum* BARRANDE, 1877; OD]. *Sil.*, Eu. [Czech. (Bohemia)].

**Metaspyroceras** FOERSTE, 1932, p. 48 [\**Spyroceras ruedemanni* FOERSTE, 1928, p. 281; OD] [=*Hypospyroceras*, *Eospyroceras* SHIMIZU & OBATA, 1935]. Like *Anaspyroceras*, but annulations and sutures oblique rather than straight; sutures typically sloping adorally on one side, annulations on other. *M.Ord.-M.Sil.*, N.Am.(Ill.-Minn.-Ohio-Wis.-Wyo.-Anticosti-Ont.-Que.). — FIG. 161,2.

\**M. ruedemanni* (FOERSTE), *M.Sil.*, USA(Ohio); 2a-g, several specimens,  $\times 0.75$  (62).

**Family SPHOOCERATIDAE Flower, 1962**

Siphuncle subcentral, tubular; septa deep; ontogenetic decollation of posterior portion of shell recognized by 3-layered conical callosus that seals apical end of mature conch. *M.Sil.*

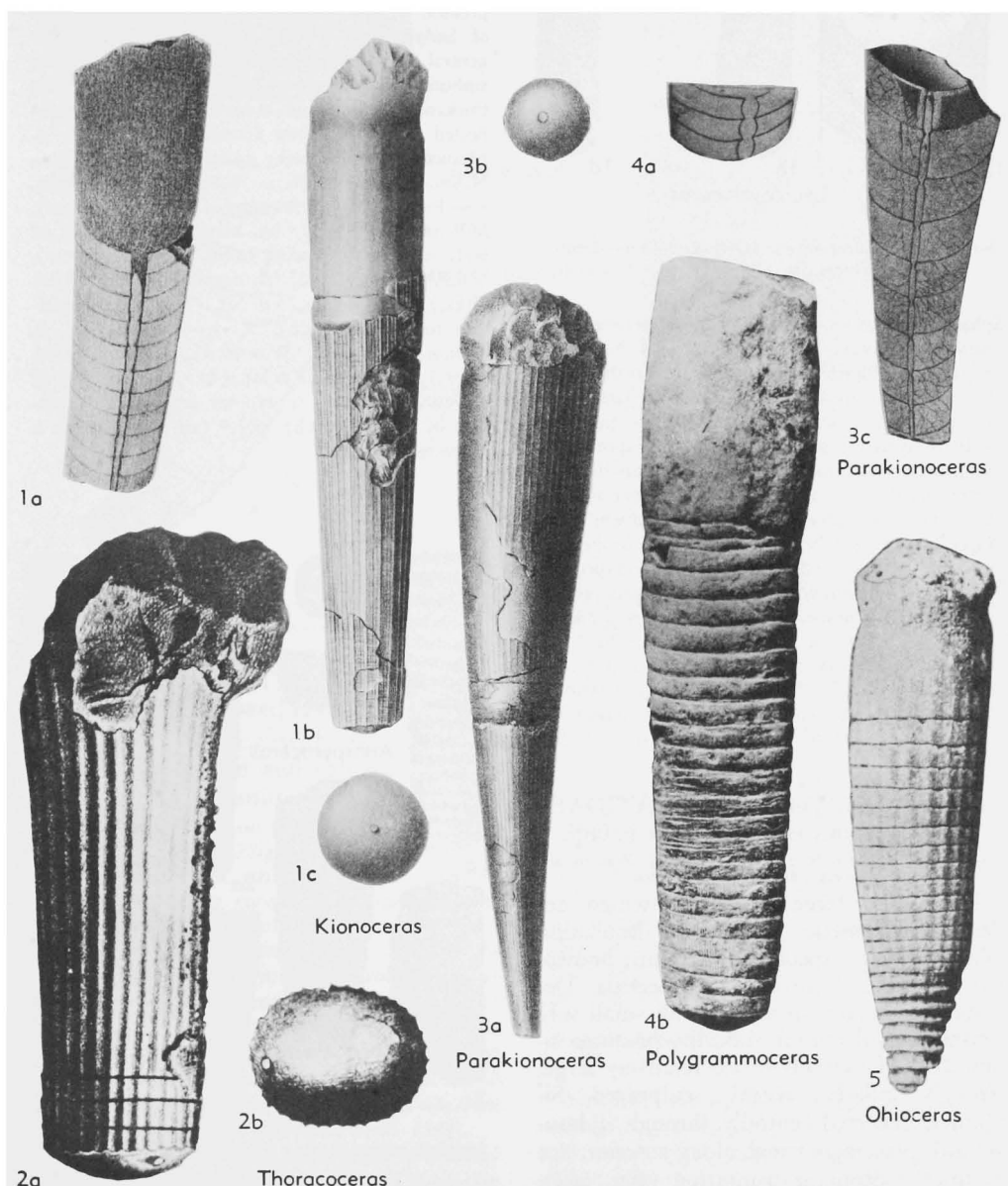


FIG. 159. Orthocerataceae (Orthoceratidae—Kionoceratinae) (p. K229-K230).

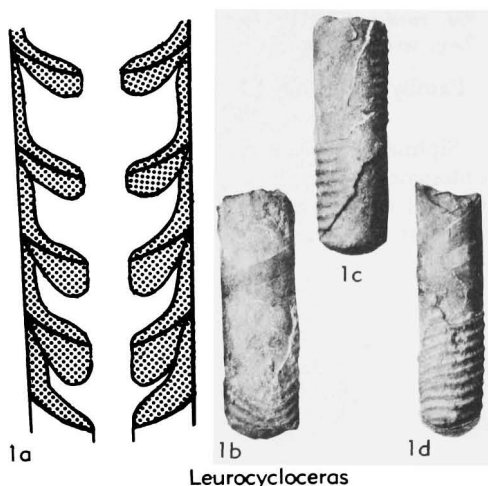


FIG. 160. Orthocerataceae (Orthoceratidae—Leurocycloceratinae) (p. K230).

**Sphooceras** FLOWER, 1962, p. 33 [*\*Orthoceras truncatum* BARRANDE, 1868, pl. 341; OD]. Gradually expanding orthocones with subcentral orthochoanitic siphuncle and long chambers separated by conical septa. Apical end of all known specimens with 3-layered conical callus sealing siphuncular termination and smoothing contour of shell. Inner layer of callus smooth; intermediate layer marked by striae that radiate outward from apex; outer layer ornamented by concentric striae broken on opposite sides of conch by lines of V-shaped invaginations in individual striae. Deciduous portion of conch not known. Septal necks short, straight; connecting rings not known. Neither cameral nor siphuncular deposits reported. *M.Sil.*, Eu.(Czech.). —FIG. 156A,5. *\*S. truncatum* (BARRANDE); 5a,b, lat. and apical end of specimen; 5c, apical end of another specimen; 5d, med. long. sec.; all  $\times 1$  (5).

### Family BRACHYCYCLOCERATIDAE Furnish, Glenister & Hansman, n. fam.

[Materials for this family prepared by W. M. FURNISH and B. F. GLENISTER, State University of Iowa]

Moderately large nautiloids which undergo ontogenetic truncation; decollation takes place at a specialized septum; homeomorphic with Ordovician Ascocerida. Deciduous longicone annulate, with small subcentral to subventral suborthochoanitic siphuncle. Mature brevicone relatively large, strongly inflated, weakly sculptured. Siphuncle deflected ventrally, through siphuncular displacement canal, along anterior face of thick septum of truncation (Fig. 162). *U.Miss.-U.Penn.*, ?*L.Perm.*

**Brachycycloceras** MILLER, DUNBAR & CONDRA, 1933, p. 105 [*\*B. normale*; OD]. Moderately large, circular to quadrate, consisting of orthoconic to gently cyrtoconic exogastric longiconic deciduous portion and larger breviconic truncated mature conch. Deciduous part strongly annulate; surface sculpture on mature shell relatively weak. Mature aperture oblique, with ventral salient traversed by shallow hyponomic sinus. Muscle scars prominent and bilobate, broadest ventrolaterally. Dorsal and dorsolateral internal thickening of mature shell present, as transverse callus, at about mid-length of body chamber. Siphuncle subcentral to subventral and small; septal necks suborthochoanitic; siphuncular segments slightly expanded. At thickened septum of truncation, siphuncle deflected ventrally, along anterior face through siphuncular displacement canal. *U.Miss.-U.Penn.*, N.Am.-?USSR(S.Urals); ?*L.Perm.*, W.Australia. —FIG. 163,1. *B. bransoni* (MILLER & OWEN), M.Penn., USA(Mo.); lat. view internal mold of body chamber (showing callus and muscle scar),  $\times 0.7$ . —FIG. 163,2. *\*B. normale*, U.Penn., USA (Tex.); 2a,c, vent.; 2b,d, lat. (2c,d retain transition to mature conch),  $\times 1.4$ . —FIG. 163,3. *B. curtum* (MEEK & WORTHEN), U.Penn., USA (Tex.); 3a, vent.; 3b,c, lat. (3a,b, are ant. part of deciduous portion, 3c exposes septum of truncation of mature conch),  $\times 1.4$  (all figs. Furnish & Glenister, n).

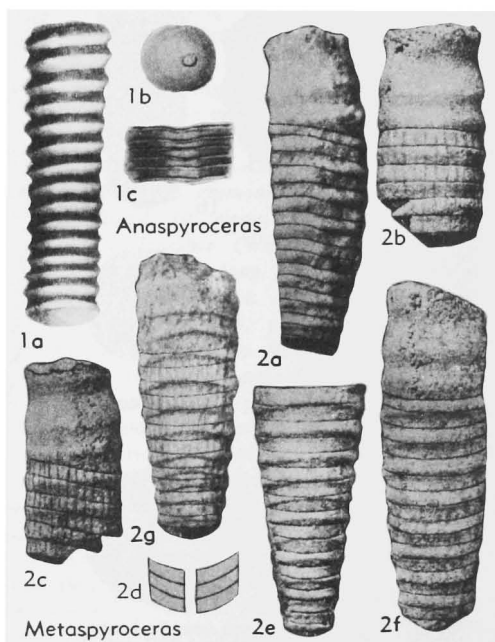


FIG. 161. Orthocerataceae (Orthoceratidae—Leurocycloceratinae) (p. K230-K231).

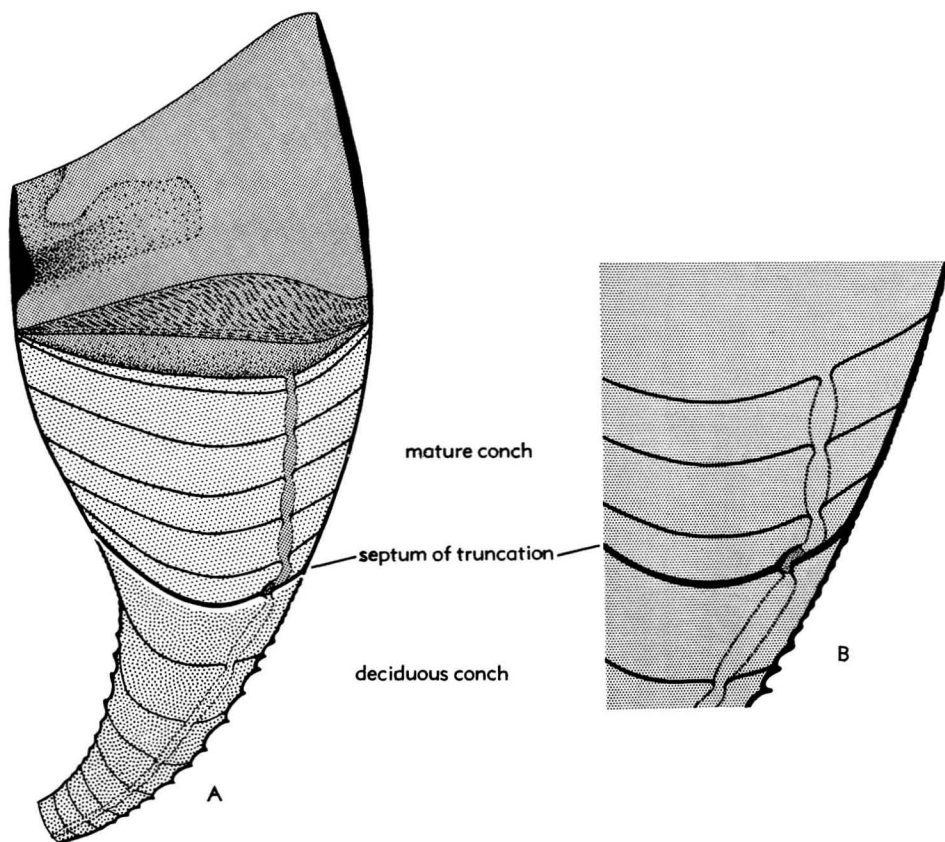


FIG. 162. *Brachycycloceras* (Brachycycloceratidae), composite diagrammatic dorsoventral section with phragmocone based on *B. curtum* and body chamber on *B. bransoni*; A, approx.  $\times 0.4$ ; B, enlarged portion of A showing details of siphuncular displacement canal (p. K232).

### Family SACTORTHOCERATIDAE Flower, 1946

Suborthochoanitic, with subcentral siphuncle. Siphuncle and camerae typically free of organic deposits. *M.Ord.*

*Sactorthoceras* KOBAYASHI, 1934, p. 407 [*\*S. gonioseptum*; OD] [=?*Sigmorthoceras* KOBAYASHI, 1934]. Smooth or striated, closely camerated, straight or slightly curved longicones with slender subcentral empty suborthochoanitic siphuncle expanded slightly within camerae. No cameral deposits. [*Sigmorthoceras* differs from *Sactorthoceras* only in having longitudinally sigmoid conch curvature, a feature of doubtful derivation and uncertain generic significance.] *M.Ord.*, USA (N.Y.)-Asia (Korea)-Eu. (Norway).—FIG. 164, 1. *\*S. gonioseptum*, Korea; 1a-c, long. sec., schematic long. sec. (enlarged), lat. view,  $\times 0.5$  (102).

*Centroonoceras* KOBAYASHI, 1934, p. 417 [*\*Ooceras?* *tokunagai* KOBAYASHI, 1927, p. 202; OD] [=?*Cyrtotoönoceras* FLOWER, 1939]. Like *Sactorthoceras* but cyrtconic; subcentral siphuncle subortho-

choanitic, with elongate, subfusiform segments that are generally straighter on dorsum than venter. No cameral deposits known. *M.Ord.*, USA (N.Y.)-Asia (Korea). — FIG. 165, 1. *\*C. tokunagai* (KOBAYASHI), Korea; diagram. dorsoventral sec.,  $\times 0.7$  (101).

*Sigmocycloceras* KOBAYASHI, 1934, p. 424 [*\*Protocycloceras?* *rogenense* KOBAYASHI, 1927, p. 183; OD]. Similar to *Sactorthoceras*, but conch longitudinally sigmoid and transversely annulated. Internal characters not well known; siphuncle probably suborthochoanitic. *M.Ord.*, Asia (Korea). — FIG. 165, 2. *\*S. rogenense* (KOBAYASHI); diagram. lat. long. sec.,  $\times 0.7$  (101).

### Family LAMELLOTHOCERATIDAE Teichert, 1961

Straight or slightly endogastric, transversely crenulate, with slender, cylindrical, subcentral orthochoanitic siphuncle free of organic deposits. Camerae with simple or distally bifurcating longitudinal episepal, or rarely hyposeptal lamellae arranged in

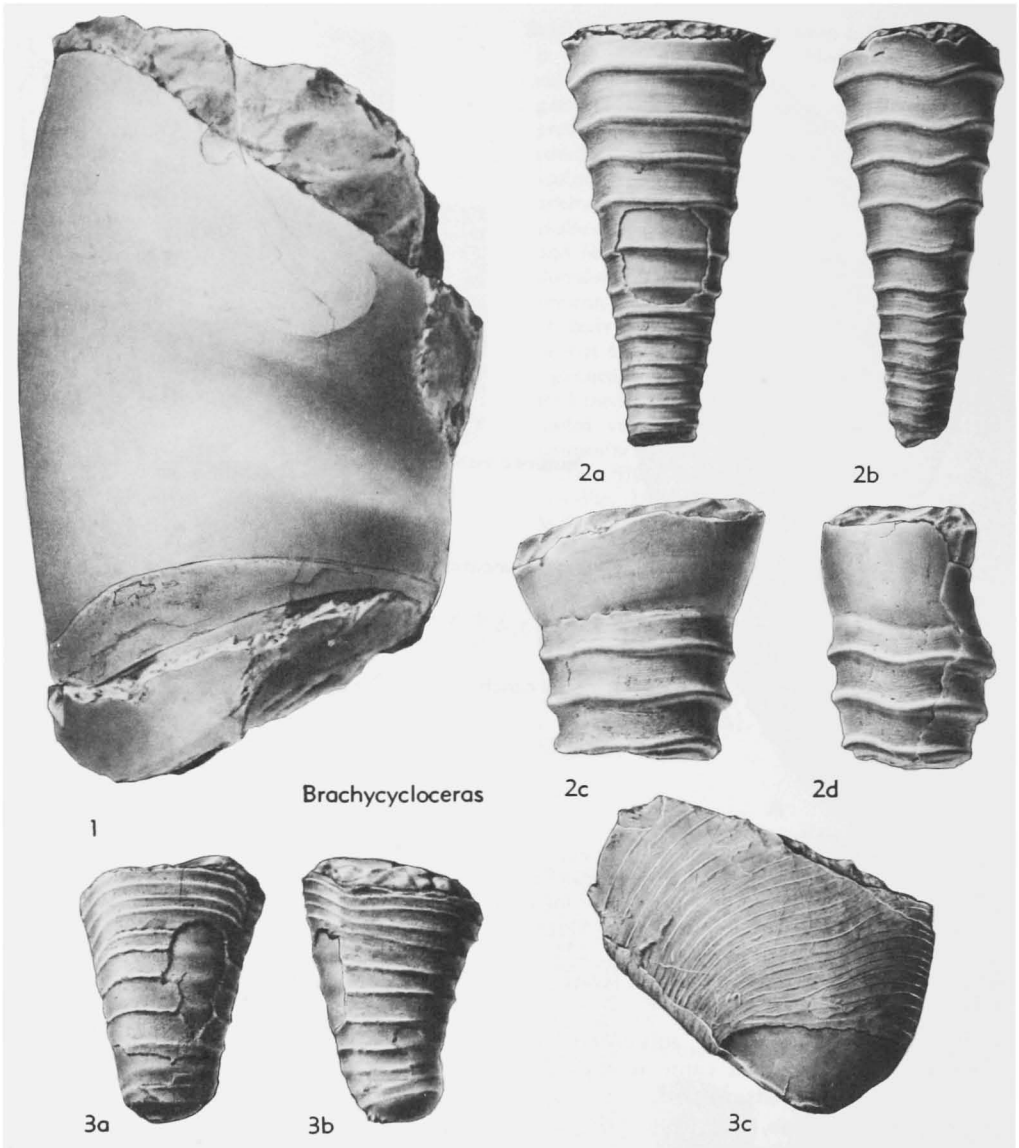


FIG. 163. Orthocerataceae (Brachycycloceratidae) (p. K232).

radial pattern with respect to siphuncle; posterior part of conch may be completely filled by radial lamellae. *L.Dev.-M.Dev.*, ?*L.Carb.*

**Lamellorthoceras** TERMIER & TERMIER, 1950, p. 78 [*\*L. vermiculare*; OD] [= *Lamelloceras* MUTVEI, 1956 (*nom. null.*)]. Similar to *Arthrophyllum* but with tendency to develop both radiating episeptal and hyposeptal lamellae that tend to be wavy, twisted, or to have bifurcating inner edges. Cameral deposits may occupy all chambers of phragmocone and may not coalesce apically. *L.Dev.-M.Dev.*, Afr. (Algeria-Morocco).—FIG. 166, 1b.

*\*L. vermiculare*, M.Dev., Morocco; transv. sec.,  $\times 2.5$  (190).—FIG. 166, 1a. *L. gracile* TERMIER & TERMIER, Dev. (Siegen.), Morocco; lat. view of exfoliated specimen,  $\times 2$  (190). [= *Coralloceras* ZHURAVLEVA, 1962.]

**Arthrophyllum** BEYRICH, 1850, p. 10 [*\*Orthoceratites crassus* ROEMER, 1843; SD ROEMER, 1852]. Slender, uncompressed, gradually expanding orthocones or faintly endogastric longiconic cyrtocones. Surface with closely spaced sinuous transverse crenulations forming broad dorsal and ventral salients and lateral sinuses. Septa shallow;

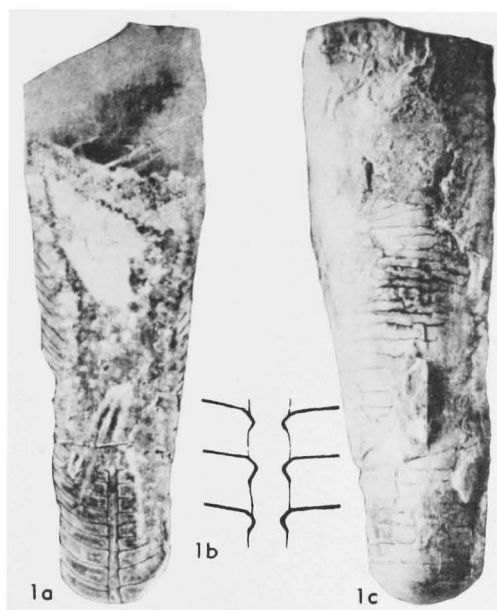


FIG. 164. \**Sactorthoceras gonioseptum* KOBAYASHI (Sactorthoceratidae) (p. K233).

sutures straight, transverse. Weak conchal furrow on venter. Siphuncle slender, between center and venter, orthochoanitic; segments cylindrical, empty. Camerae with episepal deposits forming numerous simple longitudinal lamellae radiating inward from outer walls of chamber and increasing in bulk adapically so as to fill apical chambers completely. *L.Dev.*, ?*L.Carb.*, Eu.(Fr.-Ger.-Turkey).—FIG. 166,2. *A. kahlebergense* (DAHMER), *Dev.*(U.Coblentz.), Ger.; 2a, transv. sec.,  $\times 2$ ; 2b, lat. view,  $\times 1$  (190).

**Gorgonoceras** ZHURAVLEVA, 1961, p. 93 [*\*G. visendum*; OD]. Like *Arthrophylum*, but surface with faint longitudinal ribs and eccentric siphuncle with continuous endosiphuncular lining on venter. Camerae with numerous longitudinal lamellae radiating inward from outer walls; a ventral lamella is much thicker than the others and is distally bifid. *M.Dev.*(*Eifel.*), USSR(Sverdlovsk district).—FIG. 167,1. *\*G. visendum*; 1a,b, transv. sec., lat. view,  $\times 2$  (214a).

### Family TROEDSSONELLIDAE Kobayashi, 1935

[=Buttsoceratidae FLOWER in FLOWER & KUMMEL, 1950]

Suborthochoanitic, with continuous endosiphuncular lining of parietal deposits prolonged adapically to form endocones. *L.Ord.-M.Ord.*

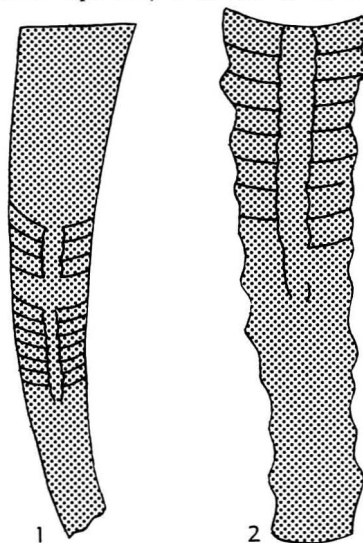
**Troedssonella** KOBAYASHI, 1935, p. 746 [*\*Polygrammoceras endoceroides* TROEDSSON, 1932, p. 30; OD]. Slender, uncompressed, longitudinally striated orthocones. Siphuncle between center and

venter, suborthochoanitic; necks short, connecting rings faintly expanded, with continuous endosiphuncular lining of parietal deposits prolonged adapically to form endocones. Camerae with thin mural and hyoseptal deposits. *M.Ord.*, Eu. (Sweden).—FIG. 168,1. *\*T. endoceroides* (TROEDSSON); 1a, lat. view,  $\times 1$ ; 1b, long. sec.,  $\times 2$  (196).

**Buttsoceras** ULRICH & FOERSTE, 1933, p. 288 [*\*Orthoceras adamsi* BUTTS, 1926, expl. pl. 18; OD] [=?*Oxfordoceras* ULRICH, FOERSTE, MILLER, & UNKLESBAY, 1944]. Slender uncompressed orthocones with large subcentral tubular siphuncle. Septal necks short, straight; connecting rings thin. Lamellar endosiphuncular lining thickens posteriorly, filling siphuncle or leaving narrow tubular cavity that may be crossed by diaphragms. Lobate, bilaterally symmetrical hyoseptal and episepal deposits concentrated ventrally in camerae. *L.Ord.* (*U. Canad.*), N. Am.(Ala.-Texas-Utah - Idaho - N. Mex.-Que.).—FIG. 168A,2. *\*B. adamsi* (BUTTS); 2a, holotype, weathered sec.,  $\times 1.5$ ; 2b, weathered sec. with tube in siphuncle,  $\times 1.5$ ; 2c,d, lat. and septal views,  $\times 1.5$ ; 2e, sec.,  $\times 3$  (204).

?**Glenisteroceras** FLOWER in FLOWER & TEICHERT, 1957, p. 137 [*\*G. obscurum*; OD]. Weakly annulate orthocones with circular section and large central siphuncle; septal necks weakly cyrtchoanitic, connecting rings thick, siphuncular segments expanded. [Based on single immature phragmocone of 5 mm. diameter; structures and affinities uncertain.] *L.Ord.*(*U. Canad.*), USA(N.Y.).

**Oxfordoceras** ULRICH, FOERSTE, MILLER, & UNKLESBAY, 1944, p. 70 [*\*O. billingsi*; OD]. Smooth orthocones with circular section; characterized by subcentral siphuncle, about 0.25 of conch diam-



Centroonoceras      Sigmocycloceras  
FIG. 165. Orthocerataceae (Sactorthoceratidae) (p. K233).

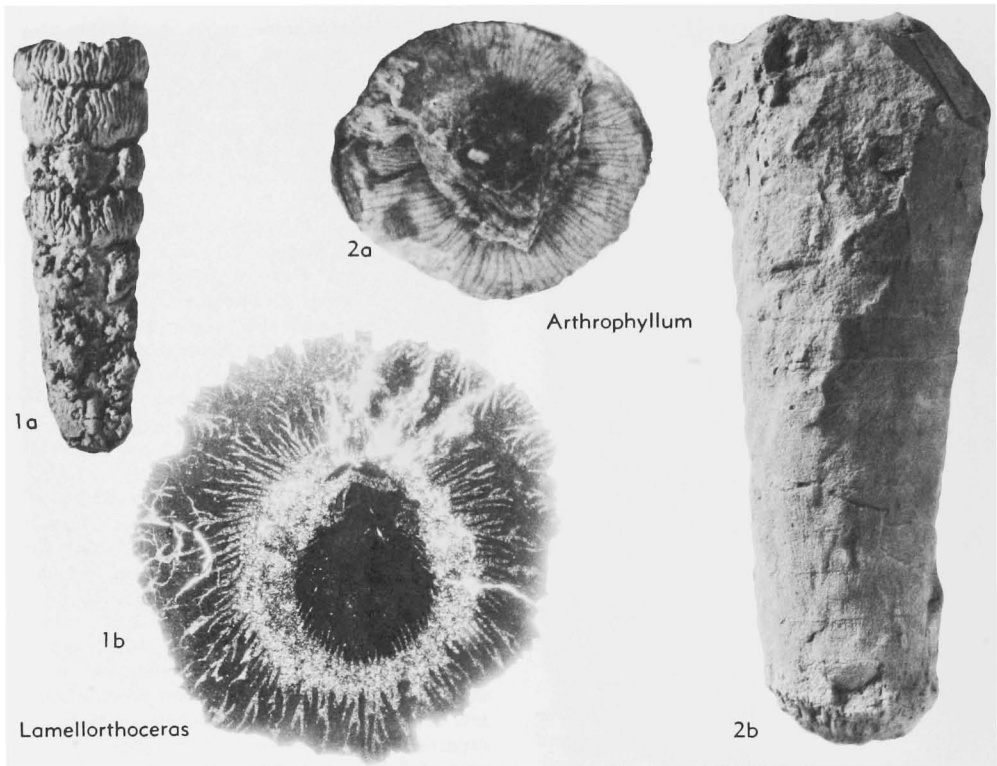


FIG. 166. Orthocerataceae (Lamellorthoceratidae) (p. K234-K235).

eter; siphuncular segments slightly contracted. *L. Ord.* (*U. Canad.*), Can. (Ont.).—FIG. 168A, I. \**O. billingsi*; holotype,  $\times 1.5$  (204). [FLOWER (47a) now regards *Oxfordoceras* as a synonym of *Buttso-ceras* ULRICH & FOERSTE, 1933.-WCS.]

?*Wolungoceras* KOBAYASHI, 1931, p. 166 [\**W. foerstei*; M]. Slender orthocones with circular section; siphuncle subcentral, about 0.3 of conch diameter; septal necks presumably orthochoanitic. *L. Ord.*, Asia (Manchuria) - ?USA (Md.).

#### Family GEISONOCERATIDAE Zhuravleva, 1959

Orthoconic or cyrtoconic conchs of sub-circular cross section, with orthochoanitic to suborthochoanitic siphuncle occupied by endosiphuncular annuli restricted to septal foramen or growing anteriorly against connecting rings; in advanced species, endosiphuncular annuli fusing with those of adjacent segments to form continuous siphuncular lining. *M. Ord.*-*M. Dev.*

*Geisonoceras* HYATT, 1884, p. 275 [\**Orthoceras rivale* BARRANDE, 1866, pl. 209; OD]. Slowly enlarging orthocones or cyrtocones of circular to subcircular cross section and with straight transverse or slightly oblique sutures. Siphuncle sub-

central; necks short and straight, connecting rings expanding slightly within camerae. Small adorally attenuated annulosiphonate deposits in adapical

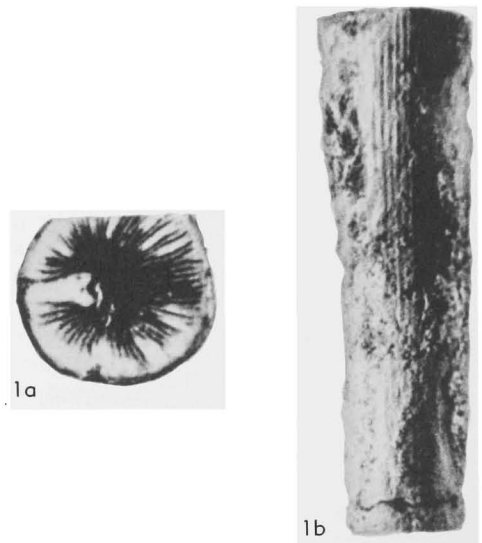


FIG. 167. \**Gorgonoceras visendum* ZHURAVLEVA (Lamellorthoceratidae) (p. K235).





FIG. 168. \**Troedssonella endoceroideis* (TROEDSSON) (Troedssonellidae) (p. K235).

siphuncular segments; camerae with episeptal and hyposeptal deposits. Surface with broad transverse bands, between which are fine growth lines. Aperture transverse, with slight hyponomic sinus. *M.Ord.-M.Dev.*, N.Am.-Eu.-Asia.—FIG. 169,6. \**G. rivale* (BARRANDE), M.Sil., Eu.(Czech.); 6a,b, lat. view, dorsoventral sec.,  $\times 0.5$  (5).

**Columenoceras** BARSKOV, 1960 [\**Orthoceras columen* BARRANDE, 1874; OD]. *Sil.*, Czech.(Bohemia). ?**Geisonocerina** FOERSTE, 1935, p. 22 [\**Orthoceras wauwatosense* WHITFIELD, 1882, p. 297; OD]. Like *Geisonoceras* externally but differs in absence of periodic thickening of transverse lirae and striae. Internal features unknown; genus probably artificial in its present state. *U.Ord.-M.Dev.*, N.Am.-Eu.-Australia.—FIG. 169,5. \**G. wauwatosense* (WHITFIELD), M.Sil., USA(Wis.);  $\times 1$  (62).

**Harrisoceras** FLOWER, 1939, p. 475 [\**H. orthoceroideis*; OD]. Circular or slightly depressed orthocones with straight transverse sutures, moderate to deep camerae. Surface smooth, even growth lines unknown. Siphuncle generally large, orthochoanitic, with central tube and annulosiphonate deposits in form of simple annuli in septal foramen which may constrict mature siphuncle in-

terior to 0.3 of its width. Deposits developed against necks, never against rings. Cameral deposits episeptal and hyposeptal, never massive. Mature body chamber with internal thickening just before aperture. ?*M.Ord.*, Eu.(Est.); *M.Sil.*, N. Am.(Ill.-Ind.-E.Can.)-Eu.(Czech.)-Sib.—FIG. 169,8. \**H. orthoceroideis*, M.Sil., USA(Ind.); long. sec.,  $\times 2.5$  (23).

**Joachimoceras** BARSKOV, 1960 [\**Orthoceras micro-megas* BARRANDE, 1874; OD]. *Sil.*, Czech.(Bohemia).

**Jonesoceras** BARSKOV, 1960 [\**Orthoceras jonesi* BARRANDE, 1874; OD]. *Sil.*, Czech.(Bohemia).

**Mesnaquaceras** FLOWER, 1955, p. 820 [\**M. curvisseptatum*; OD]. Slender compressed orthocones with low distant surficial annulations. Camerae long, septa deeply curved, sutures straight and transverse. Siphuncle subventral, orthochoanitic; necks straight, connecting rings expanding slightly within camerae. Endosiphuncular annuli growing adorally along siphuncle wall from origin in septal foramina, but not fusing to form continuous endosiphuncular lining. Thin episeptal and hyposeptal cameral deposits. *M.Ord.*(*Chazy*), USA(Vt.).—FIG. 169,1. \**M. curvisseptatum*; 1a,b, ventral view, dorsoventral sec.,  $\times 0.75$  (44). [FLOWER (47a) now includes this genus in the Proteoceratidae.]

**Protokionoceras** GRABAU & SHIMER, 1910, p. 58 [\**Orthoceras medullare* HALL, 1868; OD]. Moderately expanding orthocones of subcircular section and straight transverse sutures. Surface with cancellate markings produced by intersecting longitudinal and transverse striae or lirae. Siphuncle and cameral deposits in at least some species similar to those of *Geisonoceras*; these structures not well known in type-species. *M.Ord.-M.Dev.*, N. Am.(Ill. - Ind.-Me.-Mich.-N.Y.-Pa.-Wis.-Anticosti-Ont.-Que.)-Eu. (Norway)-Australia.—FIG. 169,7. \**P. medullare* (HALL), M.Sil., USA(Wis.); lat. view,  $\times 0.3$  (62).

**Striacoceras** FLOWER, 1936, p. 28 [\**Orthoceras typum* SAEMANN, 1854, p. 164; OD]. Slender orthocones of circular section, with straight, transverse or slightly oblique sutures. Surface of early stages with equidistant transverse and longitudinal lirae; in later stages longitudinal lirae disappearing and transverse ones broadening so as to become flat and impressed upon otherwise smooth surface. Internal mold with 3 ventral carinae. Siphuncle orthochoanitic, eccentric, empty; necks short and straight, connecting rings expanding slightly in camerae. Episeptal and mural cameral deposits well developed. [Included with *Geisonoceratidae* because of strong similarity of early stage ornamentation with that of adult *Protokionoceras*.] *M.Dev.*, USA (N.Y.) - USSR (Novaya Zemlya).—FIG. 169,3. *S. typum beta* FLOWER, USA(N.Y.);  $\times 0.75$  (20).

**Temperoceras** BARSKOV, 1960 [\**Orthoceras temperans* BARRANDE, 1874, OD]. *Sil.*, Czech.(Bohemia).

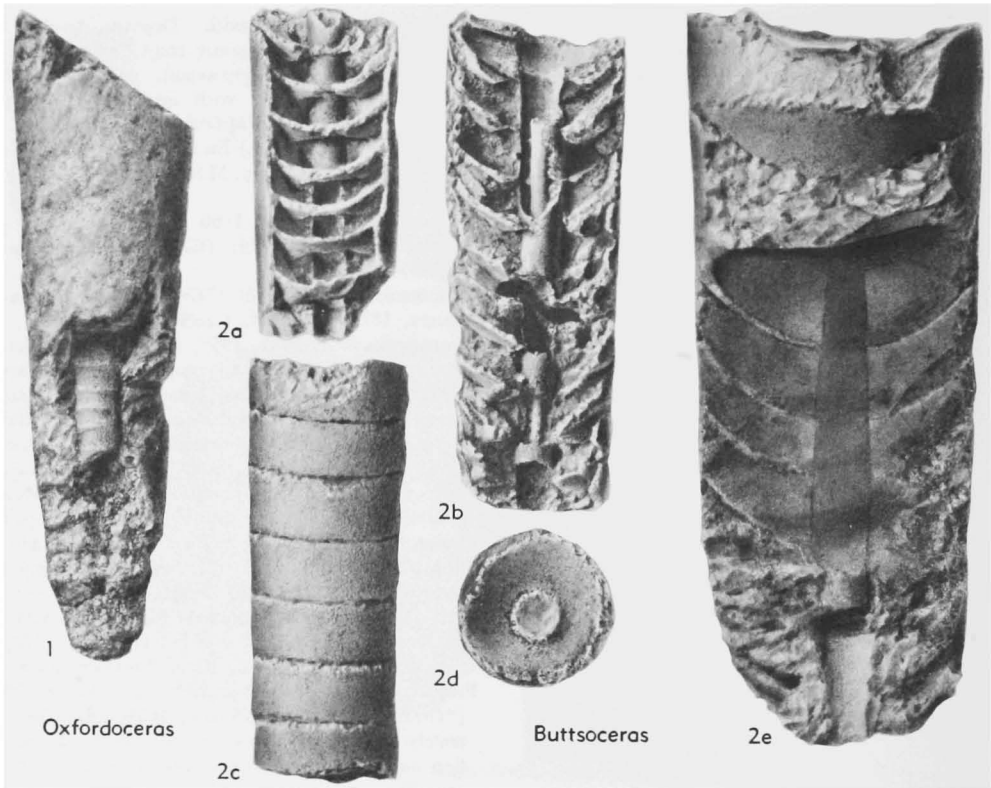


FIG. 168A. Orthocerataceae (Troedssonellidae) (p. K235-K236).

**Virgoceras** FLOWER, 1939, p. 162 [*\*Orthoceras palemon* BARRANDE, 1870, pl. 394; OD]. Uncompressed orthocones with straight transverse sutures and surface marked by fine oblique or transverse and (in some species) longitudinal lines. Siphuncle central or subcentral, orthochoanitic; siphuncular deposits of annulosiphonate deposits fusing to form continuous siphuncular lining. *M.Sil.*, USA (Ind.)-Eu.(Czech.).—FIG. 169,2. *\*V. palemon* (BARRANDE), Czech.; 2a,b, dorsoventral sec., lat. view,  $\times 0.75$  (5).

#### Family DAWSONOCERATIDAE Flower, 1962

Siphuncle subcylindrical, with short, recumbent septal necks; siphuncular segments abruptly constricted at septal foramina. ?*U. Ord.*, *L.Sil.-U.Sil.*, ?*M.Dev.*

**Dawsonoceras** HYATT, 1884, p. 276 [*\*Orthoceras annulata* SOWERBY, 1818, p. 77; OD] [= *Cedarvilleoceras* SHIMIZU & OBATA, 1935]. Straight to slightly curved orthocones with circular to sub-circular transverse section, straight transverse sutures and shell with conspicuous transverse annulations. Surface markings consist typically of

scalloped or festooned transverse lirae but may include secondary longitudinal lirae. Siphuncle subcentral, septal necks short, recumbent; segments occupied by small annulosiphonate deposits. Camerae with mural deposits. ?*U.Ord.*, Eu.(Est.); *L.Sil.-U.Sil.*, N.Am.-Eu.-Asia-Australia; ?*M.Dev.*, Can.(Ont.).—FIG. 170,1b,c. *\*D. annulatum* (SOWERBY), M.Sil., Eng.(Shrops.); detail of shell surf. (enlarged), lat. view,  $\times 0.4$  (61).—FIG. 170,1a. *D. sp.*; diagram of shell interior, enlarged (22).

**Dawsonocerina** HORNÝ, 1956 [*\*Orthoceras dulce* var. *omega* BARRANDE, 1868, pl. 294; OD]. Like *Dawsonoceras*, at least externally, but edges of transverse growth bands minutely crenulated. Crenulations aligned in each growth band to produce weak longitudinal lirae that are more conspicuous than crenulations. *M.Sil.*, Eu.(Czech.).—FIG. 169,4. *\*D. omega* (BARRANDE); 4a-c, lat. view,  $\times 0.5$ , with moderately and much enlarged views of shell surface (5).

#### Family CLINOCERATIDAE Flower, 1946

Faintly curved longiconic cyrtocones of fusiform or subfusiform shape, with no



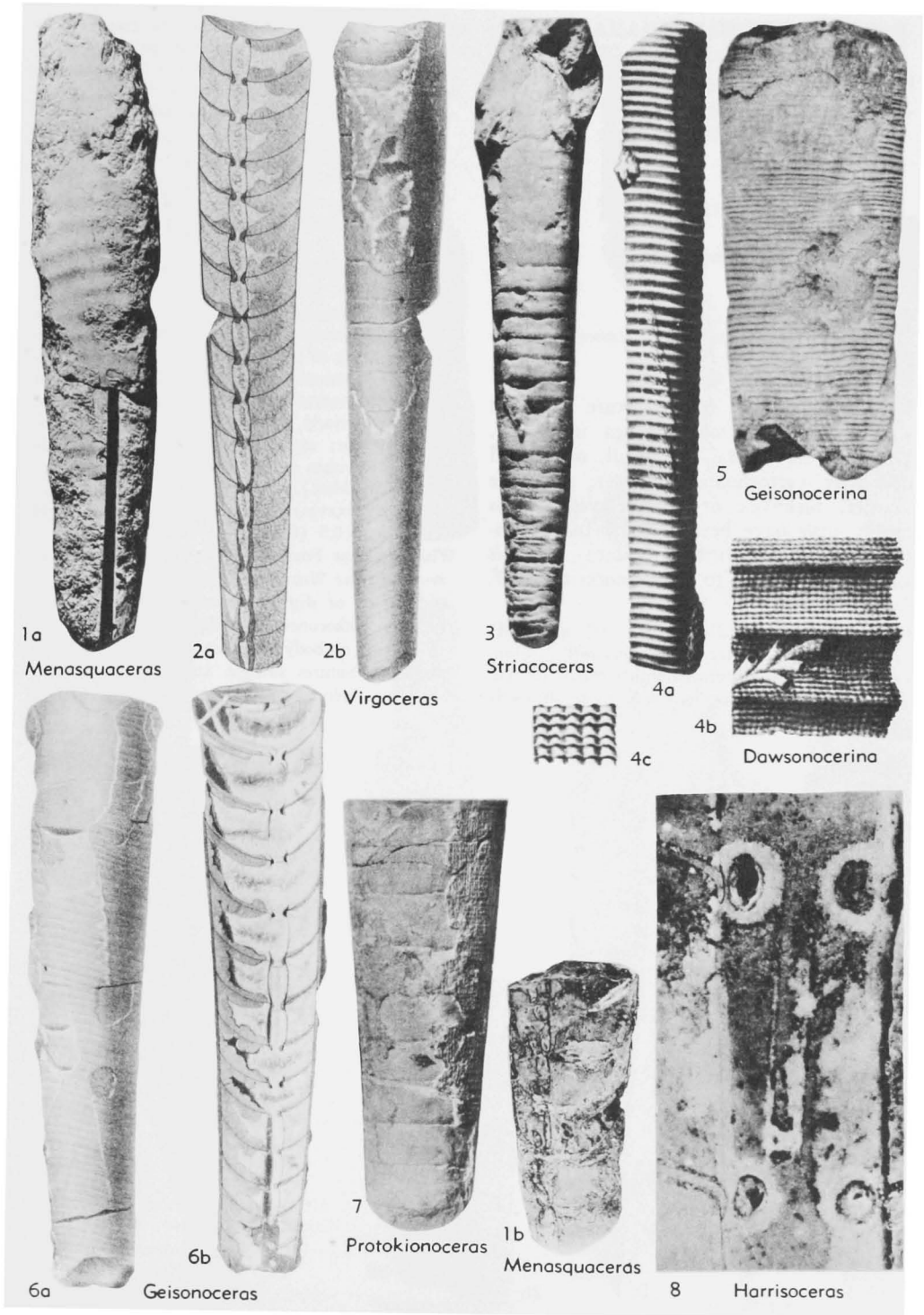


FIG. 169. Orthocerataceae (Geisonoceratidae) (p. K236-K238); (Dawsonoceratidae) (p. K238).

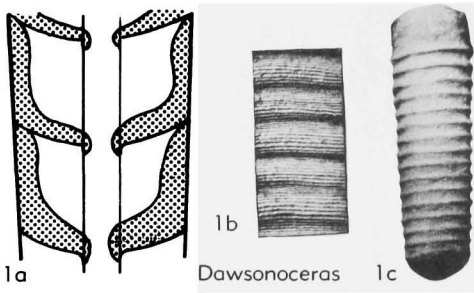


FIG. 170. Orthocerataceae (Dawsonoceratidae) (p. K238).

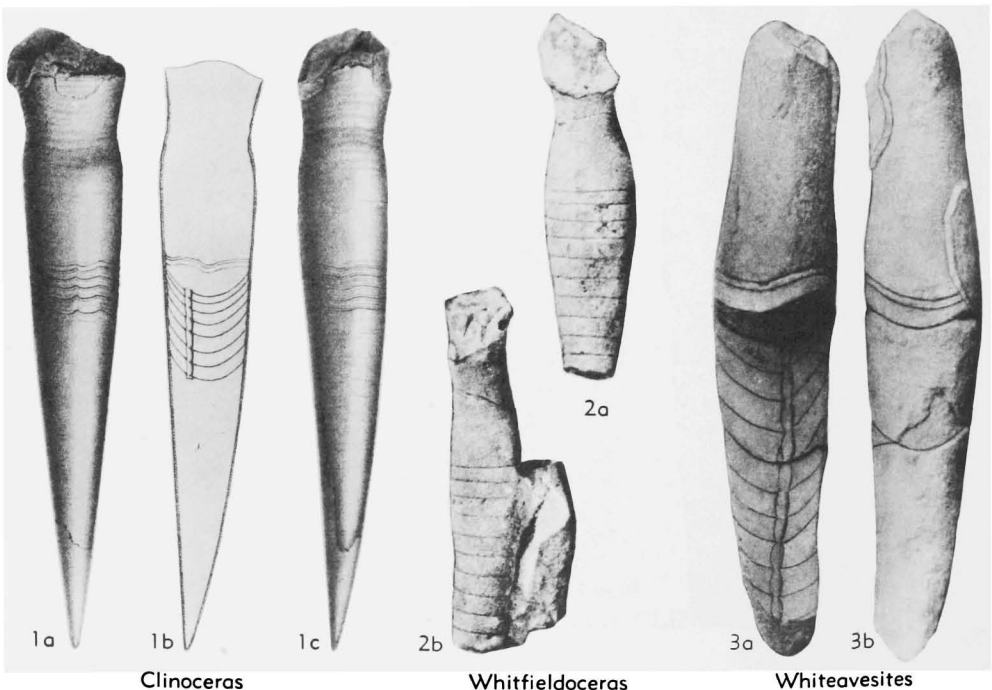
hyponomic sinus, but aperture inclined slightly forward from dorsum to venter. Siphuncle subcentral, or dorsal, or ventral of center, cyrtochoanitic, empty; segments slender, biconvex or planoconvex. [This family may have been derived from *Centrocnoceras* (Sactorthoceratidae) and is probably ancestral to the Ascocerida.] *M. Ord.-U.Ord.*

*Clinoceras* MASCKE, 1876, p. 49 [*\*C. dens*; *M*] [= *Clynoceras* DEWITZ, 1879 (*nom. null.*)]. Elongate, subfusiform cyrtocones with virtually straight to slightly concave dorsum and more distinctly

convex venter; conch constricted in anterior part of body chamber, then expanding to aperture. Surface marked by sinuous growth lines, forming pair of ventral and lateral sinuses. Siphuncle dorsal of center, cyrtochoanitic; segments slightly expanded ventrally, flat or faintly concave dorsally, apparently empty. [Type-species from drift boulders in East Prussia.] *M.Ord., N.Eu.* (?Sweden).—FIG. 171,1. *\*C. dens*; 1a-c, ventral view, dorsoventral sec., right lat. view,  $\times 0.75$  (120).

*Whiteavesites* FOERSTE, 1929, p. 167 [*\*Orthoceras winnipegense* WHITEAVES, 1892, p. 12; OD]. Elongate, depressed, fusiform orthocones or faintly curved cyrtocones. Conch expands gradually to posterior part of body chamber, then contracts to aperture. Sutures with lateral lobes and broad dorsal and ventral saddles. Siphuncle ventral of center posteriorly, dorsal of center anteriorly, cyrtochoanitic; segments biconvex, only slightly expanded within camerae, apparently empty. *U. Ord., Can. (Man.)*.—FIG. 171,3. *\*W. winnipegense* (WHITEAVES); 3a,b, dorsoventral sec., right lat. view,  $\times 0.5$  (66).

*Whitfieldoceras* FOERSTE, 1932, p. 49 [*\*Oncoceras mumiaeforme* WHITFIELD, 1882, p. 58; OD]. Uncompressed or slightly depressed, apically curved fusiform orthocones, expanding gradually to posterior part of body chamber, then contracting to aperture. Sutures straight and transverse; septa shallow. Siphuncle central or slightly ventral of



Clinoceras

Whitfieldoceras

Whiteavesites

FIG. 171. Orthocerataceae (Clinoceratidae) (p. K240-K241).

center, cyrtocoanitic; segments expanding within camerae, apparently empty. *M.Ord.-U.Ord.*, N.Am. (Iowa-Minn.-N.Y.-Wis.-Wyo.-Baffin Is.-Ont.).—  
FIG. 171,2. \**W. mumiaeforme* (WHITFIELD), *M. Ord.*, USA(Wis.); 2*a,b*, dorsal, right lat. views,  $\times 1$  (71).

**Family PARAPHRAGMITIDAE Flower  
in Flower & Kummel, 1950**

Annulated orthocones, cyrtococones, and  
brevicocones with subcentral suborthochoanitic,  
empty siphuncle. *M.Sil.*

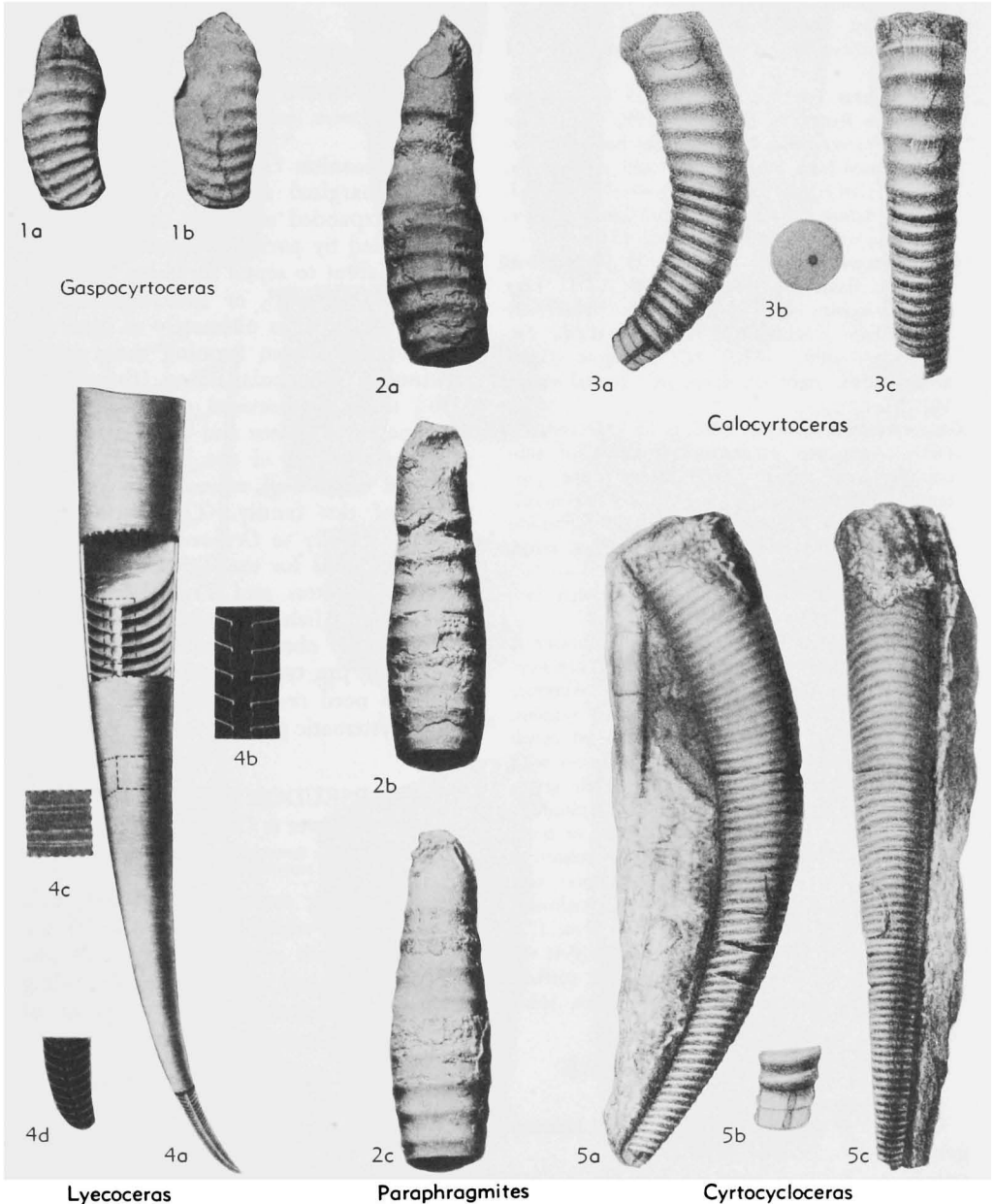


FIG. 172. Orthocerataceae (Paraphragmitidae) (p. K242).

**Paraphragmites** FLOWER, 1943, p. 254 [*\*P. asco-ceroides*; OD]. Curved annulated exogastric brevicones of subcircular section. Conch expanding to mid-length of body chamber, then contracting to aperture. No hyponomic sinus. Surface with fine transverse lirae and striae in addition to more prominent transverse annulations. Siphuncle subcentral or slightly dorsal from center, cyrtochoanitic; segments broadly expanded, empty. *M.Sil.*, Can.(Nova Scotia).—FIG. 172,2. *\*P. asco-ceroides*; 2a-c, left lat., ventral, dorsal views,  $\times 1$  (29).

**Calocyrtoceras** FOERSTE, 1936, p. 59 [*\*Cyrto-ceras cognatum* BARRANDE, 1866, pl. 199; OD]. Like *Gaspocyrtoceras* and *Cyrtoycloceras* but shell surface striated both longitudinally and transversely. *M.Sil.*, Can.(Que.)-Eu.(Czech.).—FIG. 172,3. *\*C. cognatum* (BARRANDE), Eu.(Czech.); 3a-c, right lat., septal, ventral views,  $\times 1$  (5).

**Cyrtoycloceras** FOERSTE, 1936, p. 58 [*\*Cyrto-ceras urbanum* BARRANDE, 1866, pl. 198; OD]. Like *Gaspocyrtoceras*, but shell surface transversely rather than longitudinally striated. *M.Sil.*, Eu.(Czech.).—FIG. 172,5. *\*C. urbanum* (BARRANDE); 5a-c, right lat., long. sec., ventral views,  $\times 1$  (5).

**Gaspocyrtoceras** FOERSTE, 1936, p. 56 [*\*G. cooperi*; OD]. Annulated exogastric cyrtocones of subcircular cross section. Annulations slope posteriorly toward venter forming shallow hyponomic sinus. Surface longitudinally striated. Siphuncle slender, slightly ventral of center; internal structure unknown. *M.Sil.*, N.Am.(Wis.-Que.).—FIG. 172,1. *\*G. cooperi*, Can.(Que.); 1a,b, left lat., ventral views,  $\times 1$  (75).

**Lycoceras** MUTVEL, 1957, p. 248 [*\*L. goilandense*; OD]. Slender endogastric cyrtocones of subcircular to slightly depressed cross section. Aperture oblique, not contracted; peristome faintly sinuous, with hyponomic sinus on concave side of conch and septal furrow on convex side. Sutures with broad dorsal lobe and single broad saddle across sides and venter. Surface with faint longitudinal striae and weak transverse annulations, or both. Siphuncle slightly dorsal of center; suborthochoanitic to weakly cyrtochoanitic, empty; segments expand within camerae. Muscle attachment dorsomyarian. *M.Sil.*, Eu.(Sweden).—FIG. 172,4. *\*L. goilandense*; 4a, left lat. view,  $\times 0.4$ ; 4b, sec. of siphuncle,  $\times 0.8$ ; 4c, detail of test surface,  $\times 0.8$ ; 4d, dorsoventral sec. of conch apex,  $\times 1.5$  (143).

### Family OFFLEYOCERATIDAE Flower, 1962

Characters of the type and only known genus. *M.Sil.*, ?*L.Dev.*, ?*M.Dev.*

**Offleyoceras** FOERSTE, 1928, p. 315 [*\*Orthoceras arcticum* FOORD, 1888, p. 38; OD]. Transversely banded or faintly annulated orthocones with large

excentric, apparently holochoanitic siphuncle, structural details of which are not adequately known. *M.Sil.*, ?*L.Dev.*, ?*M.Dev.*, N.Am.(Arctic)-Eu.(Novaya Zemlya).—FIG. 156A,3. *\*O. arcticum* (FOORD), *Sil.*(?Wenlock), N.W.Greenl.(Kennedy Channel); 3a, lat. ext. view of type, venter at right,  $\times 0.5$  (61); 3b, dorsoventral sec. of basal part of type, through siphuncle,  $\times 0.5$  (62).

## Superfamily PSEUDORTHOCERATACEAE Flower & Caster, 1935

[*nom. transl.* SWEET, herein (*ex* Pseudorthoceratidae FLOWER & CASTER, 1935)]

Cyrtochoanitic Orthocerida with subcentral to marginal siphuncle of broadly to weakly expanded segments that are empty or occupied by parietal deposits that begin in or adjacent to septal foramina and grow forward, backward, or both, against connecting rings, so as ultimately to fuse with adjacent deposits in forming more or less continuous siphuncular lining. [SHIMANSKIY (161) notes that several orthocerids from the Triassic of Timor and China have characters reminiscent of the Pseudorthoceratidae and may well represent undescribed genera of this family. These species, referred originally to *Orthoceras*, herein provide the record for the Triassic occurrence of *Michelinoceras* and *Trematoceras* (Orthoceratidae, Michelinoceratinae). Although SHIMANSKIY's observations have considerable merit, the types of all the species he mentions need re-examination before their proper systematic position is clear.] *M.Ord.-Perm.*

### Family PSEUDORTHOCERATIDAE Flower & Caster, 1935

[=Mooreoceratidae SHIMANSKIY, 1951; Shikhanoceratidae SHIMANSKIY, 1956]

Cyrtochoanitic orthocones and longiconic cyrtocones, in which endosiphuncular annuli develop into continuous parietal endosiphuncular lining, each deposit extending forward or backward from its point of origin to join the next. *L.Sil.-Perm.*

### Subfamily PSEUDORTHOCERATINAE Flower & Caster, 1935

[*nom. transl.* FLOWER, 1939 (*ex* Pseudorthoceratidae FLOWER & CASTER, 1935)]

Conchs in which siphonal deposits fused ventrally to form continuous lining before appearing on dorsum. *M.Dev.-L.Perm.*

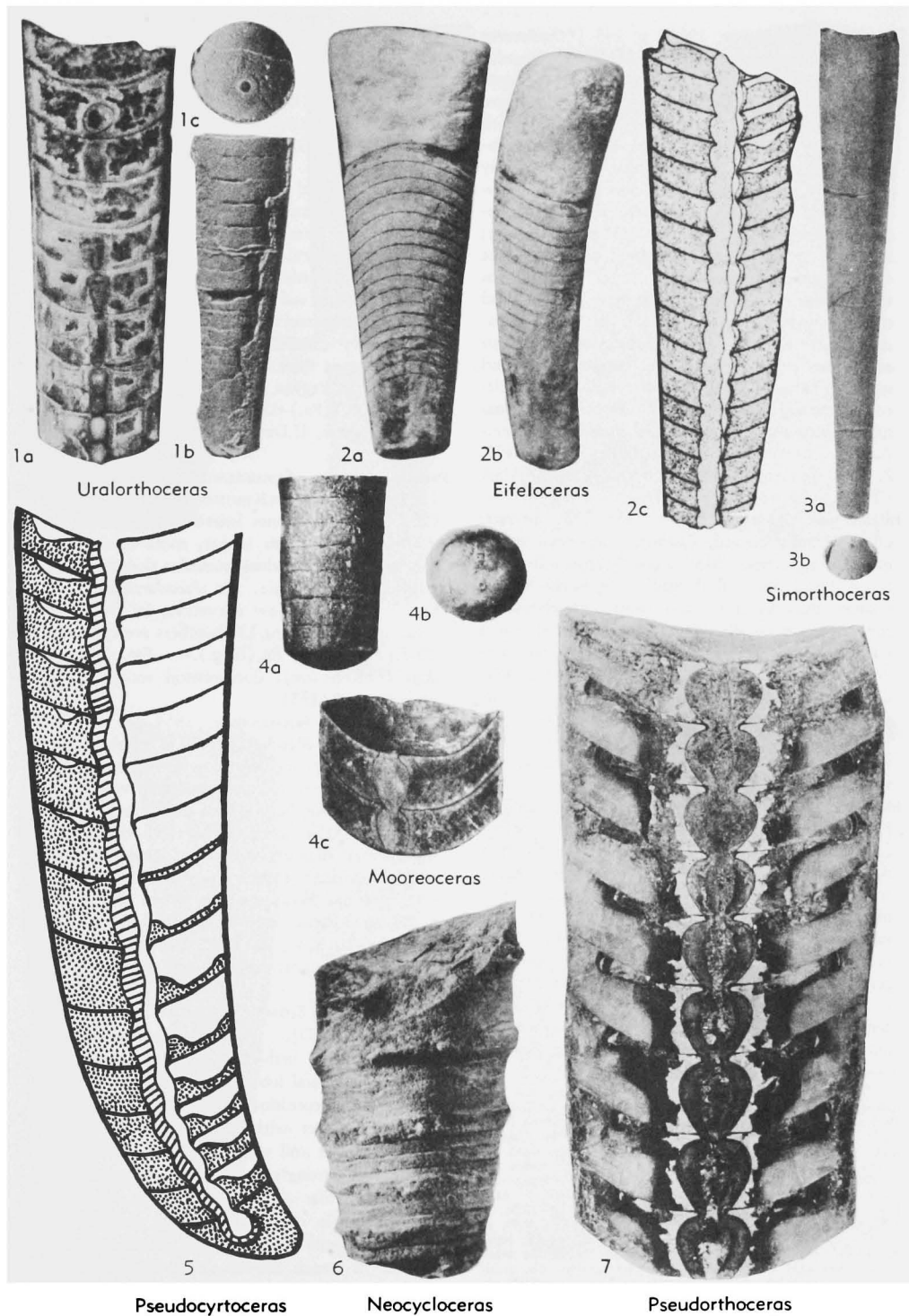


FIG. 173. Pseudorthocerataceae (Pseudorthoceratidae—Pseudorthoceratinae) (p. K242, K244).

**Pseudorthoceras** Girty, 1911,<sup>1</sup> p. 143 [*\*Orthoceras knoxense* McChesney, 1859, p. 69; OD]. Slender uncompressed orthocones with very slight exogastric curvature in apical 2 chambers. Sutures straight and transverse; septa moderate in depth and evenly curved. Siphuncle central or subcentral; segments changing shape ontogenetically from early suborthochoanitic stage through orthochoanitic then cyrtchoanitic stages with progressively longer brims and more inflated segments; in adult segments, brim and neck subequal, area of adnation being equal to half or less of brim width, free part of connecting ring convex, and segments pyriform to subglobular in shape. Endosiphuncular deposits fusing along venter to form continuous lining before being continuous around septal foramen. Camerae with well-defined circumferentially lobate mural deposits. Internal molds with septal and conchal furrows. *U.Dev.-L.Perm.*, N.Am.-Eu.-Asia-Australia.—FIG. 173, 7. *\*P. knoxense* (McChesney), *L.Perm.*, USA (Tex.); long. sec.,  $\times 5$  (136).

**Eifeloceras** Foerste, 1929, p. 283 [*\*E. kayseri*; OD]. Slightly curved, distinctly depressed endogastric longicones, with sinuous sutures forming broad dorsal and ventral saddles. Siphuncle nearer dorsum than venter; necks short, cyrtchoanitic; connecting rings moderately inflated and lined with parietal deposits that are thick and well developed ventrally but thin and inconspicuous dorsally. Septa curve only dorsoventrally; no lateral curvature. Camerae with thick deposits. *M. Dev.*, Eu.(Ger.).—FIG. 173, 2. *\*E. kayseri*; 2a,b, ventral, lat. views,  $\times 1$  (29); 2c, diagram. dorso-ventral sec.,  $\times 4$  (157).

**Moeroceras** Miller, Dunbar, & Condra, 1933, p. 85 [*\*M. normale*; OD]. Smooth-surfaced orthocones, uncompressed in early stages, typically (but not invariably) depressed in later stages. Early sutures straight and transverse; later ones normally sloping forward on dorsum and having faint lateral saddles and dorsal and ventral lobes. Septa very shallow, even in early stages. Early siphuncle central, later ventral from center; segments typically pyriform, with greatest diameter in front of center. Siphuncular deposits like *Pseudorthoceras*, not known to fuse on dorsum. Cameral deposits

concentrated ventrally. Both conchal and septal furrows on internal saddle. *U.Dev.-L.Perm.*, N. Am.-Eu.-Asia-Australia.—FIG. 173, 4. *\*M. normale*, *M.Penn.*, USA (Kansas); 4a,b, lat., septal views,  $\times 1$ , 4c, long. sec.,  $\times 2$  (128).

?**Neocycloceras** Flower & Caster, 1935, p. 14 [*\*N. obliquum*; OD]. Slender uncompressed to very slightly depressed orthocones with large, sinuous, slightly oblique surficial annulations. Sutures more oblique than annulations, projected adapturally on venter; sutural obliquity increasing with age. Sutures with broad low dorsal saddle, high conspicuous ventral saddle, and lateral lobes. Siphuncle between center and venter; segments nummuloidal, occupied by continuous lamellar endosiphuncular deposit that is thickest at widest part of siphuncle and thin in region of necks. *U.Dev.-L.Carb.*(*U. Miss.*), USA (Pa.)-Afr.(Morocco).—FIG. 173, 6. *\*N. obliquum*, *U.Dev.*, USA (Pa.); lat. view,  $\times 1$  (48).

**Pseudocyrtoceras** Schindewolf, 1943, p. 241 [*\*Cyrtoceras acus* deKoninck, 1880, p. 28; OD]. Compressed cyrtcones internally similar to *Pseudorthoceras* but with longer, more conical initial chamber and no endosiphuncular deposits on dorsal side of siphuncle. [In *Pseudorthoceras*, only first 2 chambers show curvature; in *Pseudocyrtoceras*, at least the first 12 chambers are cyrtconic.] *Carb.*(*Tournais.*), Eu.(Belg.).—FIG. 173, 5. *\*P. acus* (deKoninck); dorsoventral sec. through siphuncle,  $\times 4$  (155).

?**Simorthoceras** Shimanskiy, 1954, p. 108 [*\*S. gracile*; OD]. Slender, depressed, slightly curved longiconic cyrtcones with low camerae and slightly concave septa. Surface with transverse growth lines. Siphuncle ?subventral, small; necks strongly cyrtchoanitic, connecting rings cylindrical. Endosiphuncular deposits unknown; cameral deposits well developed. [Questionably referred to *Pseudorthoceras* because of presumed close relation to *Uralorthoceras*, itself a doubtful representative of this subfamily.] *L.Perm.*, USSR(S.Urals).—FIG. 173, 3. *\*S. gracile*; 3a,b, ventral, septal views,  $\times 1$  (161).

?**Uralorthoceras** Shimanskiy, 1951, p. 14 [*\*U. tzwetaevae*; OD]. Slightly depressed, smooth, apically curved orthocones; sutures with slight dorsal and ventral lobes, body chamber with slight longitudinal depressions and faint transverse constrictions; venter with conchal furrow. Siphuncle between center and venter, slender; segments subcylindrical, strongly contracted at septal necks. Endosiphuncular deposits said to be pseudorthoceroïd; details of distribution in siphuncle not clear from type description or illustration. Initial portion of conch curved, with acuminate apex, as in *Pseudorthoceras*. *L.Perm.*, USSR(S.Urals).—FIG. 173, 1. *\*U. tzwetaevae*; 1a, long. lat. sec.,  $\times 3.8$ ; 1b,c, right lat., septal views,  $\times 2$  (161).

<sup>1</sup> In addition to that for *Pseudorthoceras* Girty, 1911, the following entry appears in Neave, *Nomenclator Zoologicus*, 1940, v.3, p. 1002: "*Pseudorthoceras* Hoernes & Aninger [sic], 1880, Gast. Meeres-Ablag. Mioc. Medit.-Stude Oest.-Ungar., Lief. 2, 142-Moll." The full, correct title of the work referred to is: R. Hoernes & M. Aninger, *Die Gastropoden der Meeres-Ablagerungen der ersten und zweiten Mediterran-Stufe in der Österreichisch-Ungarischen Monarchie*; Abh. K.K. Geol. Reichsanstalt, Bd. 12, H. 1, June 1, 1879, p. 1-52, pls. 1-6; 2d Lief., *ibid.*, Bd. 12, H. 2, Dec. 31, 1880, p. 53-112, pls. 7-12; 3d Lief., *ibid.*, Bd. 12, H. 3, Jan. 15, 1882, p. 113-152, pls. 13-16. Careful search of the entire work cited shows that the name *Pseudorthoceras* does not occur in it. Furthermore, p. 142 belongs to Lief. 3, which appeared in 1882, not in 1880. The citation of "*Pseudorthoceras* Hoernes & Aninger, 1880" in Neave, 1940, is thus indicated to be erroneous, which signifies that Girty's publication of this name in 1911 is valid.—C. TEICHERT.

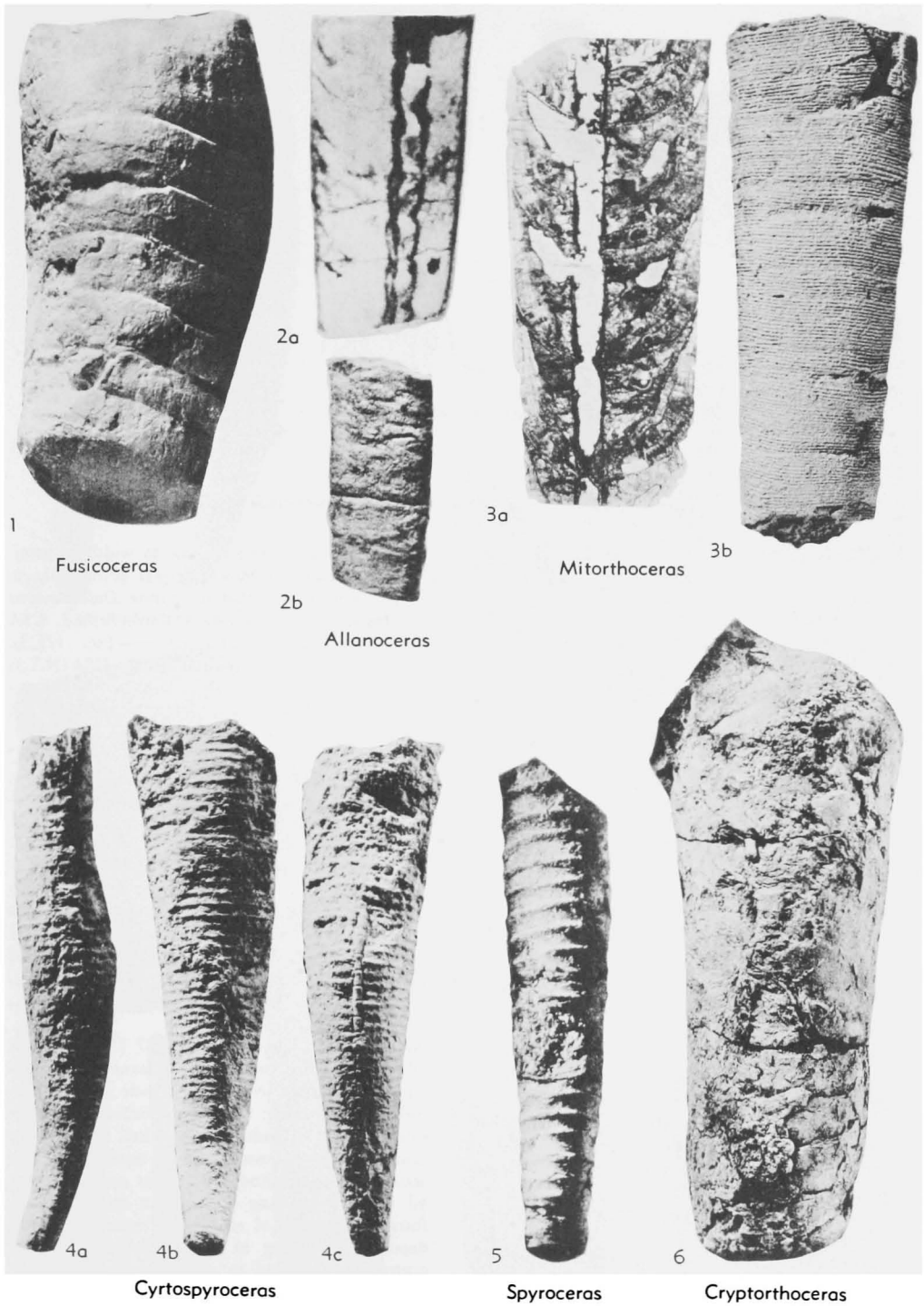


FIG. 174. Pseudorthocerataceae (Pseudorthoceratidae—Spyroceratinae) (p. K246, K248-K250).



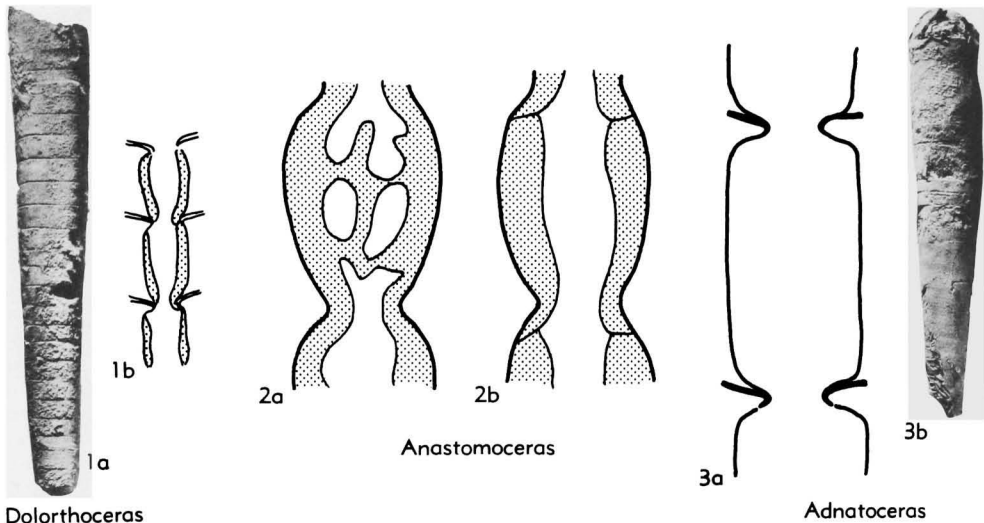


FIG. 175. Pseudorthocerataceae (Pseudorthoceratidae—Spyroceratinae) (p. K246, K249).

#### Subfamily SPYRO CERATINAE Shimizu & Obata, 1935

[*nom. transl.* SWEET, herein (*ex* Spyroceratidae SHIMIZU & OBATA, 1935)] [=Dolorthoceratinae FLOWER, 1939]

Simple Pseudorthoceratidae characterized by development of complete endosiphuncular annulus before segmental deposits fuse ventrally. Siphuncular segments uniformly slender, longer than wide, with expansion typically localized near their anterior and posterior ends. ?*L.Sil.*, *M.Sil.*-*Perm.*

**Spyroceras** HYATT, 1884, p. 276 [*\*Orthoceras crotalum* HALL, 1861, p. 50; OD] [= *Spiroceras* AHLFELD & BRANIŠA, 1960 (*non* QUENSTEDT, 1858) (*nom. null.*)]. Annulated orthocones with straight transverse sutures, transverse or slightly oblique surficial annulations, and faintly cyrtoconic apices. Surface variously ornamented, but longitudinal lirae conspicuous from earliest stage. Siphuncle central or slightly ventral from center; segments and endosiphuncular deposits like those of immature *Dolorthoceras*; in mature segments, brims and necks subequal, longer than width of adnation area. Cameral deposits mural; both cameral and siphuncular deposits developing later than in other Pseudorthoceratidae, hence confined to more apical regions of conch. *Dev.*, N.Am. (widespread)-Eu. (Czech.-Eng.-Ger.).—FIG. 174, 5. *\*S. crotalum* (HALL), M.Dev., USA (N.Y.);  $\times 1.5$  (22).

**Adnatoceras** FLOWER, 1939, p. 120 [*\*Orthoceras spissum* HALL, 1879, p. 287; OD] [= *Adnathoceras* SHIMANSKIY, 1954 (*nom. null.*)]. Like *Dolorthoceras*, but siphuncular segments abruptly expanded at septal foramen, parallel-sided, and

area of adnation equal at least to width of brim. In some species, siphuncle reverts gerontically to simpler outline like that of mature *Dolorthoceras* or *Anastomoceras*. *M.Dev.*-*U.Carb.* (Penn.), USA (Alaska-N.Y.-Tex.)-Eu. (Belg.).—FIG. 175, 3a. *A. naplense* FLOWER, U.Dev., USA (N.Y.); diagram. outline of ectosiphuncle,  $\times 4$  (22).—FIG. 175, 3b. *\*A. spissum* (HALL), M.Dev., USA (N.Y.);  $\times 0.5$  (22).

**Allanoceras** BARSKOV, 1959, p. 57 [*\*A. inusitatum*; OD]. Uncompressed smooth-surfaced orthocones. Siphuncle between center and venter, suborthochoanitic, with brims not developed; segments expanding only slightly within camerae. Annulo-siphonate endosiphuncular deposits growing forward dorsally to form continuous lining of uniform thickness; ventrally, deposits inflated in adapical part of segment, but thinner in forward part of segment. Episeptal, hyposeptal, and mural deposits in camerae. *U.Sil.*, USSR (S.Ferghana).—FIG. 174, 2. *\*A. inusitatum*; 2a, b, long. sec., lat. view,  $\times 1$  (6).

**Anastomoceras** FLOWER, 1939, p. 87 [*\*A. mirabile*; OD]. Orthocones with straight transverse sutures and circular cross section. Siphuncle slender, central, cyrtocchoanitic; segments fusiform to subcylindrical; brim width less than half neck length. Connecting rings join preceding septum with no area of adnation. Endosiphuncular annuli in septal foramen growing forward in each segment, fusing with those of succeeding segment; further deposition resulting in longitudinally perforated central core attached to parietal deposits by irregular radial pillars. *L.Dev.*, USA (N.Y.).—FIG. 175, 2. *\*A. mirabile*; diagram. views of siphuncular segments in older (2a) and younger (2b) parts of conch,  $\times 9$  (22).



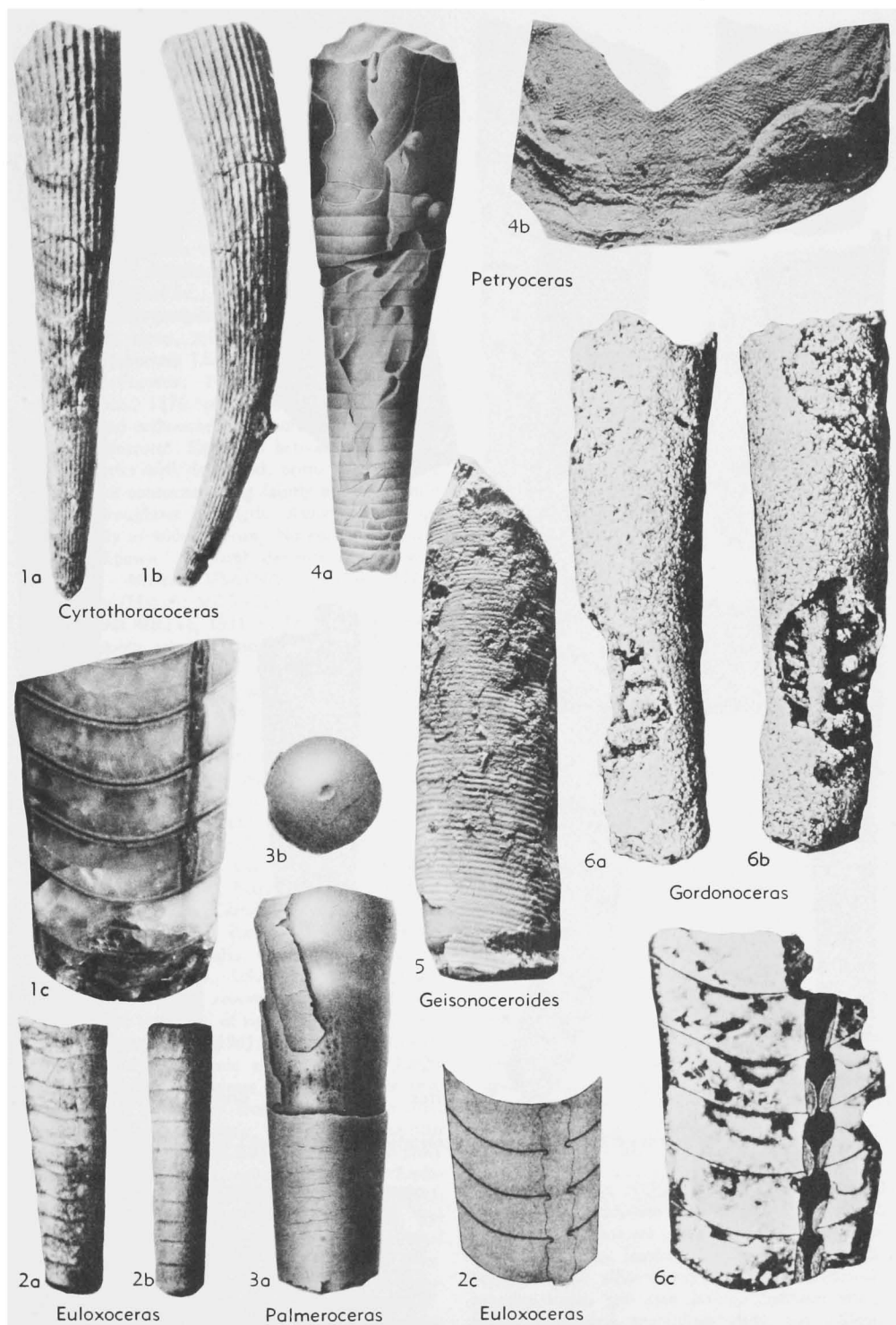


FIG. 176. Pseudorthocerataceae (Pseudorthoceratidae—Spyroceratinae) (p. K249-K250).

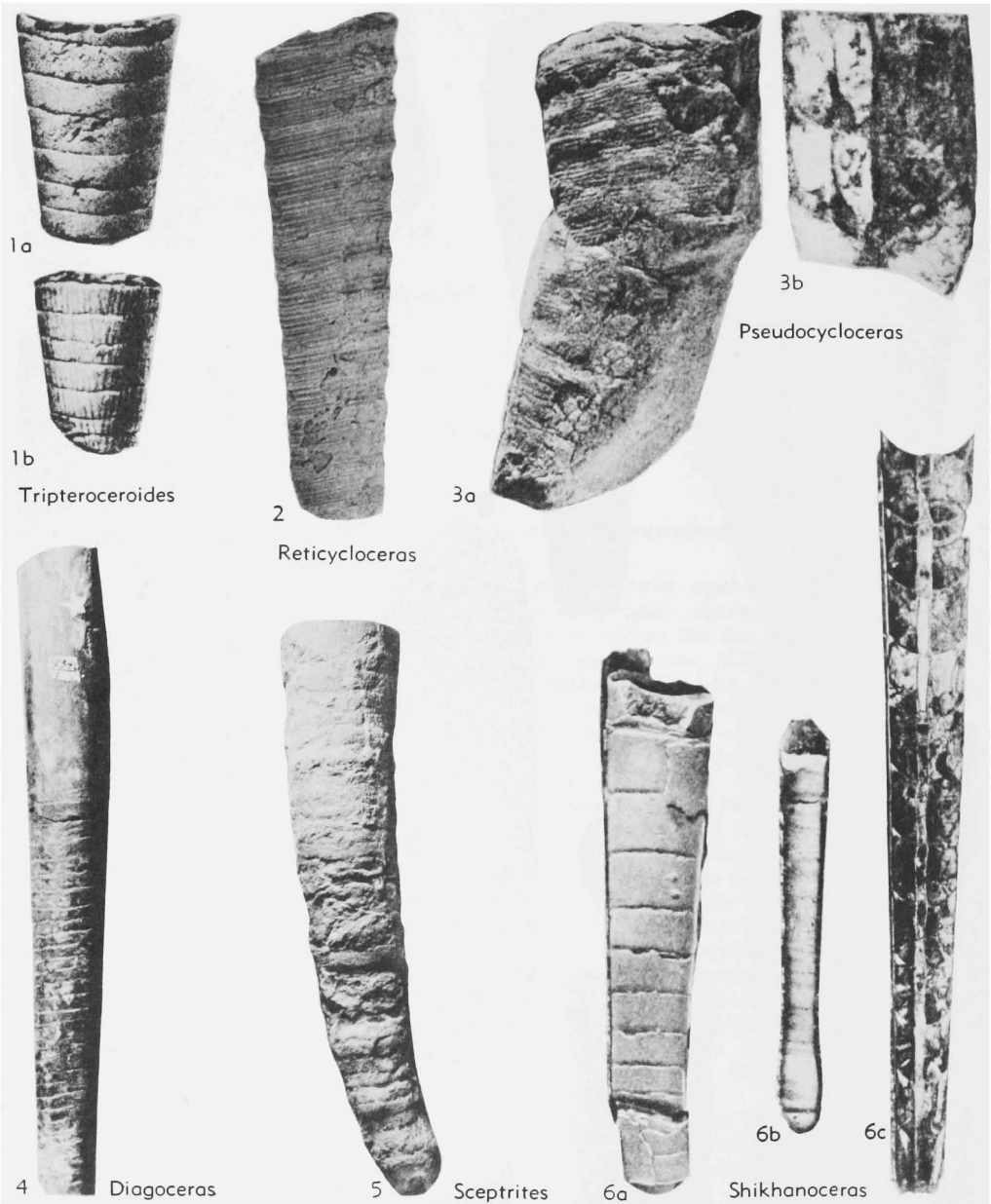


FIG. 177. Pseudorthocerataceae (Pseudorthoceratidae—Spyroceratinae) (p. K249-K251).

**Cryptorthoceras** FLOWER, 1939, p. 131 [*\*C. productum*; OD]. Depressed orthocones with oblique aperture turned abruptly toward venter so that dorsum is arched over normal apertural position. Dorsal apertural margin broadly arched, lateral parts rounded, central part like dorsal side laterally, but with prominent hyponomic sinus. Sutures straight. Siphuncle slightly ventral from

center; segments slender, faintly expanding; width of brim and adnation area equal and less than neck length in adult segments. No endosiphuncular deposits known. *M.Dev.*, USA (N.Y.).—FIG. 174, 6. *\*C. productum*;  $\times 1$  (22).

?**Cyrtospyroceras** FLOWER, 1938, p. 50 [*\*C. reimanni*; OD]. Like *Spyroceras*, but with cyrtconic conch apex and ventral siphuncle: *M.Dev.*, USA

(N.Y.).—FIG. 174,4. \**C. reimanni*; 4a-c, lat., dorsal, ventral views,  $\times 0.75$  (21).

**Cyrtothoracoceras** TURNER, 1954, p. 300 [*\*Cyrtoceras tuberculatum* M'COY, 1844, p. 11; OD]. Longitudinally fluted cyrtocoines with strong longitudinal ridges carrying closely spaced nodes on their crests and separated by concave longitudinal interspaces without longitudinal lirae. Siphuncle small, submarginal, faintly cyrtocoanitic; segments subcylindrical, but rather abruptly expanded at each end, hence wider than septal foramina. Cameral and siphuncular deposits unknown. *L. Carb. (Tournais.-Visé.)*, G.Brit. (Isle of Man).—FIG. 176,1. *C. wrighti* TURNER, U.Viséan; 1a,b, ventral, lat. views,  $\times 0.7$  (199); 1c, dorsoventral sec.,  $\times 4$  (courtesy J.S. Turner).

**Diagoceras** FLOWER, 1936, p. 23 [*\*Orthoceras aptum* HALL, 1876, pl. 38; OD]. Uncompressed or depressed orthocoines with sutures directed forward on dorsum. Siphuncle between center and venter; necks well developed, brims rudimentary, free part of connecting ring faintly and uniformly convex throughout its length. Adnation area approximately as wide as brim. No endosiphuncular deposits known. Cameral deposits mural, well developed. *M.Dev.*, USA (N.Y.).—FIG. 177,4. \**D. aptum* (HALL);  $\times 0.5$  (22).

**Dolorthoceras** MILLER, 1931, p. 419 [*\*D. circulare*; OD]. Smooth, uncompressed or slightly depressed orthocoines with straight transverse or slightly oblique sinuous sutures and probably trilobate hyponomic sinus. Early ectosiphuncle orthocoanitic, central; later cyrtocoanitic, slightly ventral from center in most species, with necks becoming more strongly curved and rings more inflated. In adult stage, neck length and brim width normally equal, but rings adnate only in early part of adult siphuncle. Endosiphuncular annuli growing forward and normally completed around septal foramen before ventral fusion of adjacent deposits. Cameral deposits mural; heavier ventrally than dorsally. *L.Dev.-L.Perm.*, N. Am.-Eu.-Asia-Australia. — FIG. 175,1a. *D. exile* (HALL), *M.Dev.*, USA (N.Y.);  $\times 0.7$  (22). — FIG. 175,1b. *D. revertum* FLOWER, *M.Dev.*, USA (N.Y.); long. sec. of siphuncle,  $\times 3.3$  (22).

?**Eridites** ZHURAVLEVA, 1961, p. 55 [*\*E. astrovae*; OD]. Faintly cyrtocoine smooth-surfaced longicoines of circular transverse section. Sutures simple, sloping posteriorly from dorsum to venter. Siphuncle slightly eccentric, height about one-fifth conch height. Segments longer than wide, slightly inflated; septal necks suborthochoanitic. Endosiphuncular annuli apparently incomplete; developed into fused parietal deposits ventrally, but absent dorsally. Cameral deposits well developed ventrally, seemingly absent dorsally. *M.Sil. (Wenlock.)*, USSR (Podolia).—FIG. 178,1. \**E. astrovae*; long. sec., venter on right,  $\times 1$  (214b).

**Euloxoceras** MILLER, DUNBAR, & CONDRA, 1933, p. 97 [*\*E. greenei*; OD]. Longitudinally costate

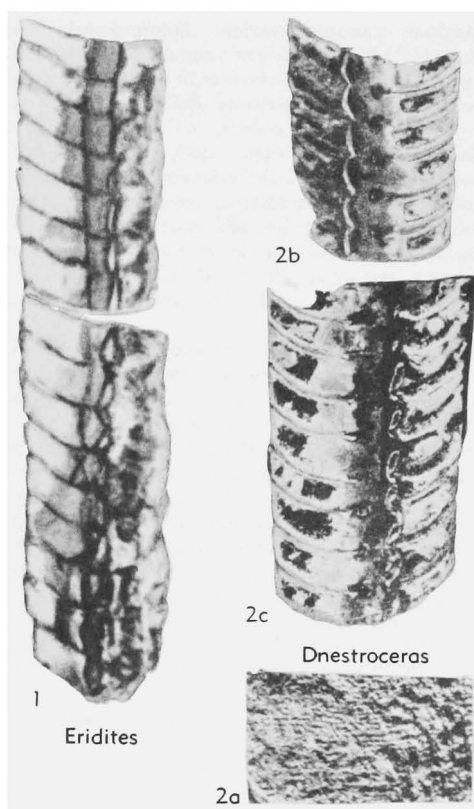


FIG. 178. Pseudorthocerataceae (Pseudorthoceratidae—Spyroceratinae, Cayutoceratinae) (p. K249, K251).

orthocones with uncompressed early stage. Laterally compressed later stage and oval or subquadrangular cross section. Sutures with prominent lateral lobes and dorsal and ventral saddles, crests of which may be straight or possess rudimentary lobes. Siphuncle between center and dorsum; segments subcylindrical, but contracted abruptly at septal foramen. Brim width more than twice neck length; width of adnation area less than that of brim, but greater than neck length. Free part of connecting ring transverse at either end, continuing expansion of siphuncle; turn to longitudinal part abrupt and greater part of ring either cylindrical or faintly concave. Relatively thick endosiphuncular deposits like those of *Dolorthoceras*, slightly better developed ventrally than dorsally. Cameral deposits episepal and hyoseptal, markedly heavier ventrally than dorsally. Well-defined septal furrow on dorsum. *U. Miss. - Penn.*, USA (Mo.-Okla.-Tex.). — FIG. 176,2. \**E. greenei*, Okla.; 2a, ventral view,  $\times 1$ ; 2b, lat. view,  $\times 1$ ; 2c, long. sec.,  $\times 2$  (128).

**Fusicoceras** FLOWER, 1939, p. 137 [*\*F. erienne*; OD]. Faintly exogastric brevicoines of subtri-

- angular transverse section. Sutures with low broad dorsal lobe, deeper ventral lobe. Siphuncle subventral, like *Dolorthoceras* in outline and form of endosiphuncular deposits. *M.Dev.*, USA(N.Y.).—FIG. 174,1. \**F. erienae*;  $\times 1$  (22).
- Geisonoceroidea** FLOWER, 1939, p. 113 [\**G. woodae*; OD]. Like *Dolorthoceras*, but with simple aperture and transverse ornament of slightly oblique rounded ridges and equal concave interspaces. Fine ornament varies; may consist of fine distant transverse striae. *M.Dev.-U.Dev.*, USA(N.Y.).—FIG. 176,5. \**G. woodae*, *M.Dev.*;  $\times 0.75$  (22).
- Gordonoceras** TEICHERT & GLENISTER, 1953, p. 39 [\**G. bondi*; OD]. Moderately large, smooth, uncompressed cyrtocoines with straight transverse sutures, long camerae, and shallow concave septa. Siphuncle small, subcylindrical, midway between center and venter; necks cyrtochaonic, with narrow brims. Endosiphuncular deposits consisting of annuli in septal foramen that grow forward along connecting rings; not known to fuse with deposits of adjacent camerae. Mural deposits in camerae best developed ventrally. *L.Sil.* or *M.Sil.*, Tasm.—FIG. 176,6. \**G. bondi*; 6a, lat. view,  $\times 1$ ; 6b, ventral view,  $\times 1$ ; 6c, dorsoventral sec.,  $\times 2$  (192). [FLOWER (47a) now includes this genus in the Proteoceratidae.]
- Lopingoceras** SHIMANSKIY, 1962, p. 90 [\**Orthoceras lopingense* STOYANOW, 1909; OD]. *Perm.*, Eu. (Yugo.-Aus.-USSR)-Asia(China).
- Mitrothoceras** GORDON, 1960, p. 135 [\**M. perfilosum*; OD]. Small orthocoines ornamented by gently sinuous transverse lirae separated by concave to flat interspaces. Septa moderately concave; sutures straight and transverse or slightly oblique. Siphuncle subcentral, cyrtochaonic; segments subcylindrical, rings slightly contracted at necks; endosiphuncular annuli growing anteriorly from necks and fusing with succeeding deposits. Camerae with well-developed lamellar episeptal and less well-developed hyposeptal deposits slightly thicker on venter than dorsum. Both conchal and septal furrows present. *L.Miss.-U.Miss.*, USA(Alaska-Ark.-Calif.-Miss.-Okla.-Tex. - Utah) - Eu. (Ire.-Ger.).—FIG. 174,3. \**M. perfilosum*, *Miss.*, USA (Ark.-Utah); 3a, long. sec.,  $\times 5$ ; 3b, lat. view,  $\times 3$  (81).
- Palmeroceras** FLOWER, 1936, p. 58 [\**Orthoceras justis* HALL, 1879, p. 281; OD]. Orthocoines with straight transverse sutures and circular cross section; shell surface with fine cancellate markings. Aperture trilobate; body chamber with series of internal constrictions. Siphuncle central, cyrtochaonic; brim width nearly twice neck length; width of adnation area nearly equals that of brim; free part of connecting ring abruptly curved at anterior and posterior ends, slightly convex over mid-portion. Endosiphuncular and cameral deposits unknown. *M.Dev.*, USA(N.Y.).—FIG. 176,3. \**P. justis* (HALL); 3a,b, lat., septal views,  $\times 0.5$  (22).
- Petryoceras** FLOWER, 1939, p. 117 [\**Orthoceras thyestes* HALL, 1879, p. 306; OD]. Similar to *Dolorthoceras*, but surface marked by fine bands of short, oblique, zigzag striae and lirae. No trace of hyponomic sinus. *U.Dev.*, USA(N.Y.).—FIG. 176,4; \**P. thyestes* (HALL); 4a, lat. view,  $\times 0.3$  (87); 4b, shell surface,  $\times 1$  (22).
- Pseudocycloceras** BARSKOV, 1959, p. 56 [\**P. karanglense*; OD]. Uncompressed to slightly depressed, annulated orthocoines with secondary surficial growth bands or ridges. Siphuncle large, suborthochoanitic, between center and venter; segments subcylindrical, only slightly expanded within camerae, somewhat contracted at septal necks, occupied by parietal deposits growing forward from point of origin in septal foramina. Parietal deposits heavy ventrally, but not forming continuous lining; dorsally thin, but forming continuous or nearly continuous siphuncular lining. Camerae with episeptal and mural deposits. *M.Sil.*, USSR(S.Ferghana).—FIG. 177,3. \**P. karanglense*; 3a, lat. view,  $\times 2$ ; 3b, long. sec.,  $\times 2.5$  (6).
- Reticycloceras** GORDON, 1960, p. 134 [\**R. croneisi*; OD]. Maturely annulated orthocoines with earliest stages nonannulated and ornamented by fine transverse and longitudinal lirae to form delicate network. Longitudinal lirae disappearing at short distance in front of apex, but transverse lirae continuing through length of conch. Siphuncle subcentral, suborthochoanitic to weakly cyrtochaonic; connecting rings subcylindrical, flat- to faintly convex-sided, slightly compressed at mid-length, abruptly contracted at ends of each segment. Siphuncular deposits continuous, heavier ventrally than dorsally; thick mural deposits in camerae. *L.Carb.(U.Miss.)*, USA(Ark.-Okla. - Utah) - Eu. (Belg.-Eng.).—FIG. 177,2. \**R. croneisi*, USA (Ark.); lat. view,  $\times 3$  (81).
- Sceptrites** FLOWER, 1939, p. 133 [\**Orthoceras sceptrum* HALL, 1888, p. 26; OD]. Probably smooth, slightly compressed, ?endogastric cyrtocoines with straight transverse early sutures and later sutures with slight lateral lobes. Siphuncle subcentral, empty; segments apparently similar to immature *Dolorthoceras* in shape. Mural cameral deposits concentrated against concave side of conch. *M.Dev.*, USA (Ohio-N.Y.)-Australia(Victoria). — FIG. 177,5. \**S. sceptrum* (HALL), USA(N.Y.); lat. view,  $\times 0.5$  (22).
- Shikhanoceras** SHIMANSKIY, 1954, p. 116 [\**S. sphaerophorum*; OD]. Laterally compressed, slowly enlarging orthocoines with thin irregular surficial striae and slightly sinuous transverse sutures. Embryonic stage straight, with hemispherical initial chamber and inflated first 6 chambers. Siphuncle subcentral; necks short, weakly cyrtochaonic; connecting rings cylindrical, but wider than septal foramen. Cameral deposits absent or

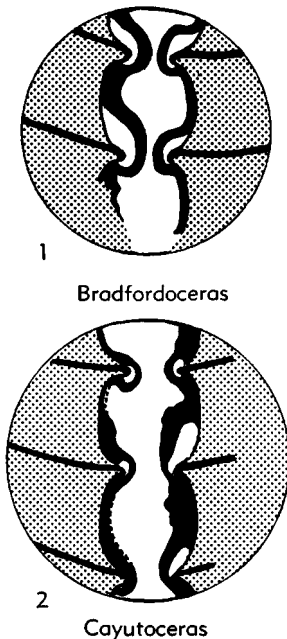


FIG. 179. Pseudorthocerataceae (Pseudorthoceratidae—Cayutoceratinae) (p. K251).

weakly developed, simple. *L.Perm.*, USSR (S. Urals).—FIG. 177,6. \**S. sphaerophorum*; 6a, lat. view,  $\times 2$ ; 6b, embryonic stage of conch,  $\times 8.5$ ; 6c, long. sec.,  $\times 7.5$  (161).

**Tripteroceroides** MILLER & FURNISH, 1940, p. 358 [\**T. knighti*; OD]. Depressed, apically curved orthocones with venter flatter than dorsum and surface with dorsally convergent longitudinal lirae. Sutures with slight ventral and dorsal lobes and lateral saddles. Siphuncle subventral, slender, cyrtchoanitic; segments subcylindrical, sharply contracted at septal foramen. Endosiphuncular and cameral deposits unknown. *L.Carb.* (Miss.), USA (Ky.)-?Eu. (Ire.).—FIG. 177,1. \**T. knighti*, USA (Ky.); 1a,b,  $\times 1$  (130).

#### Subfamily CAYUTOCERATINAE Flower, 1939

Siphuncular deposits differentiated into an outer layer of discrete calcareous annuli and an inner dark-colored layer of fused segmental deposits forming a continuous endosiphuncular lining. *L.Sil.-Dev.*

**Cayutoceras** FLOWER, 1939, p. 155 [\**C. casteri*; OD]. Uncompressed or slightly depressed smooth-surfaced orthocones with straight transverse sutures and evenly curved septa. Siphuncle slender, central to slightly ventral from center; segments subovate, longer than wide, with brim width and neck length equal and width of adnation area less than half brim width. Endosiphuncular an-

nuli in septal foramen possibly extending forward, but not fusing with those of adjacent camerae; annuli covered by continuous dark-colored lining of probable segmental origin; both deposits thicker ventrally than dorsally, but appearing dorsally before dark inner lining becomes continuous ventrally. *U.Dev.*, USA (N.Y.)-Armenia-Australia.—FIG. 179,2. \**C. casteri*, USA (N.Y.); diagram. long. sec. of siphuncle,  $\times 6$  (22).

**Arpaoceras** ZHURAVLEVA, 1962, p. 89 [\**A. raphaeli*; OD]. *Dev.*, Eu. (Armenian SSR).

**Bradfordoceras** FLOWER & CASTER, 1935, p. 32 [\**B. transversum*; OD]. Slightly depressed orthocones with shallow septa and slightly oblique sutures with lateral saddles and shallow ventral and deeper dorsal lobes. Surface with obscure growth lines; aperture with broad, shallow hyponomic sinus. Siphuncle ventral from center; mature segments pyriform or globular in shape. Endosiphuncular deposits like *Cayutoceras*. *U.Dev.*, USA (Pa.).—FIG. 179,1. \**B. transversum*; diagram. long. sec. of siphuncle,  $\times 3.3$  (22).

**Buchanoceras** TEICHERT & GLENISTER, 1952, p. 742 [\**B. graviventrum*; OD]. Large, gradually enlarging uncompressed to slightly depressed orthocones with straight transverse sutures and moderately deep septa. Siphuncle slightly eccentric; segments nummuloidal, occupied by *Cayutoceras*-like deposits restricted largely to ventral side. Camerae with thick hyoseptal and episeptal deposits. *L.Dev.* - *M.Dev.*, Australia (Victoria). — FIG. 180,1. \**B. graviventrum*, *M.Dev.*; long. sec. of siphuncle,  $\times 3.5$  (181).

?**Dnestroceras** ZHURAVLEVA, 1961, p. 56 [\**D. incertum*; OD]. Straight to faintly curved longicones of compressed section. Surface with fine transverse striae inclined toward venter. Sutures straight or slightly sinuous, inclined toward dorsum. Siphuncle eccentric, wide; septal necks cyrtchoanitic, connecting rings moderately inflated. Endosiphuncular annuli more strongly developed ventrally than dorsally; growing anteriorly, fusing to form continuous endosiphuncular lining. Episeptal, hyoseptal, and mural deposits well developed in ventral portions of camerae. [Details of endosiphuncular deposits not entirely clear from type description or illustration, hence not certainly a cayutoceratinid.] *U.Sil.* (U.Ludlov.), USSR (Podolia).—FIG. 178,2. \**D. incertum*; 2a, segment of surface,  $\times 6$ ; 2b,c, dorsoventral secs.,  $\times 1$ , venter on left and right, respectively (214b).

**Metastromatoceras** ZHURAVLEVA, 1957, p. 678 [\**M. formosum*; OD]. Like *Stromatoceras*, but straight, uncompressed, and with subcentral rather than distinctly eccentric siphuncle. Cameral deposits episeptal and mural; both cameral and endosiphuncular deposits concentrated ventrally. [Nature of endosiphuncular deposits not entirely clear from type description or illustration.] *L.Sil.*, USSR.—FIG. 180,3. \**M. formosum*; long. sec. of siphuncle,  $\times 1$  (212).

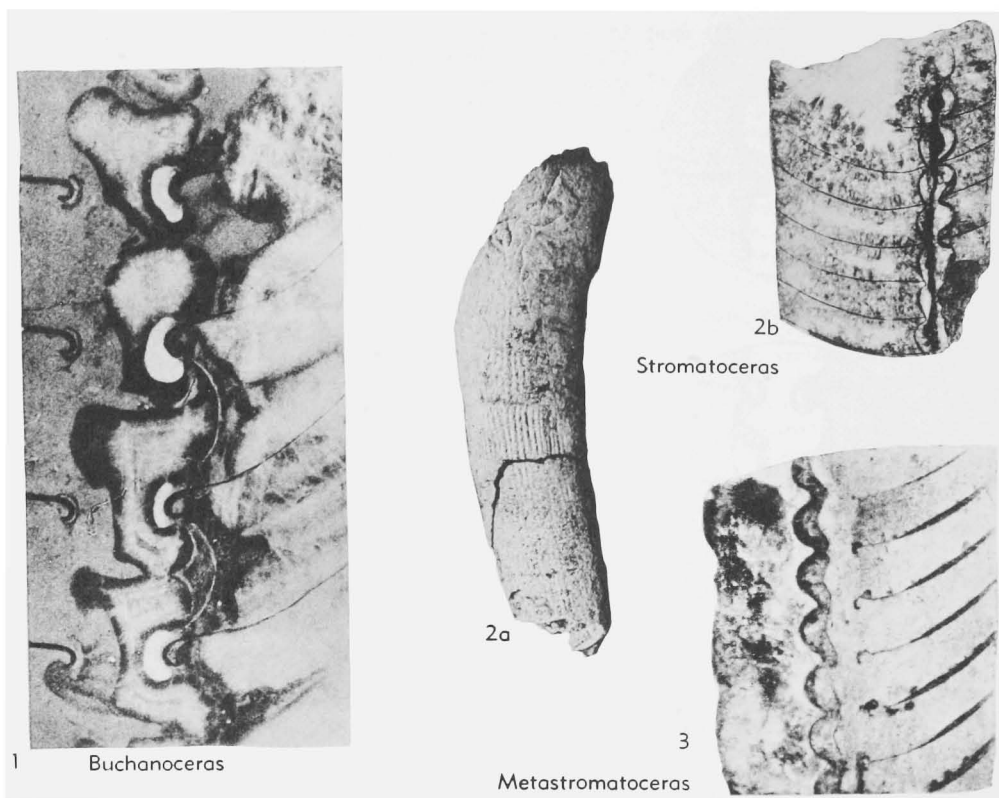


FIG. 180. Pseudorthocerataceae (Pseudorthoceratidae—Cayutoceratinae) (p. K251-K252).

**Stromatoceras** TEICHERT & GLENISTER, 1953, p. 36 [*\*S. eximium*; OD] [= *Stromotoceras* TEICHERT & GLENISTER, 1953 (*nom. null.*)]. Slowly enlarging, uncompressed to slightly depressed cyrtocones ornamented by regular longitudinal ribs and irregular transverse annulations. Sutures with lateral saddles separated by dorsal and ventral lobes. Siphuncle between center and venter; segments nummuloidal, occupied by endosiphuncular deposits of *Cayutoceras* type. Mural deposits in camerae. *L.Sil.* or *M.Sil.*, Tasmania.—FIG. 180, 2. *\*S. eximium*; 2a,b, left lat. view, dorsoventral sec. of siphuncle,  $\times 0.5$  (192). [FLOWER (47a) now includes this genus in the Proteoceratidae.]

**Subfamily PSEUDACTINOCERATINAE**  
**Schindewolf, 1943**

[*nom. transl.* SWEET, herein (*ex* Pseudactinoceratidae SCHINDEWOLF, 1943)] [= *Macroloxoceratinae* FLOWER, 1957]

Conchs with broadly expanded, typically spherical siphuncular segments with brim width greater than neck length and connecting rings commonly extensively adnate to septa. Parietal endosiphuncular deposits growing mainly forward, fusing in anterior ends of segments; deposits thick in expanded part of segment and pierced by 2

series of radial canals, one terminating in anterior part of ring close to tip of neck, other ending just anterior to beginning of adnation area. Anterior and posterior canals appearing to join in anterior third of segment. [Distinguished from actinocerids primarily by slender early siphuncle segments and by lack of separation of endosiphuncular deposits from connecting rings by a perispatium.] *U.Dev.-L.Carb.*

**Pseudactinoceras** SCHINDEWOLF, 1943, p. 233 [*\*P. promiscuum*; OD]. Slightly depressed longiconic cyrtocones with large siphuncle between center and venter. Early siphuncular segments suborthochoanitic; later segments strongly cyrtchoanitic, nummuloidal, broader than long. Segments with annulosiphonate parietal deposits growing more prominently forward than backward; canals slightly anterior of segment center. Camerae with thick hyposeptal and episeptal deposits on venter; only thin episeptal deposits on dorsum. *L.Carb.* (*Visé.*), Eu.(Ger.).—FIG. 181, 5. *\*P. promiscuum*; dorsoventral sec. of conch apex,  $\times 6$  (155).

?**Bergoceras** FLOWER, 1939, p. 155 [*\*Cyrtoceras antelope* DEKONINCK, 1880, p. 36; OD]. Slightly curved cyrtocones with subcentral siphuncle. Si-

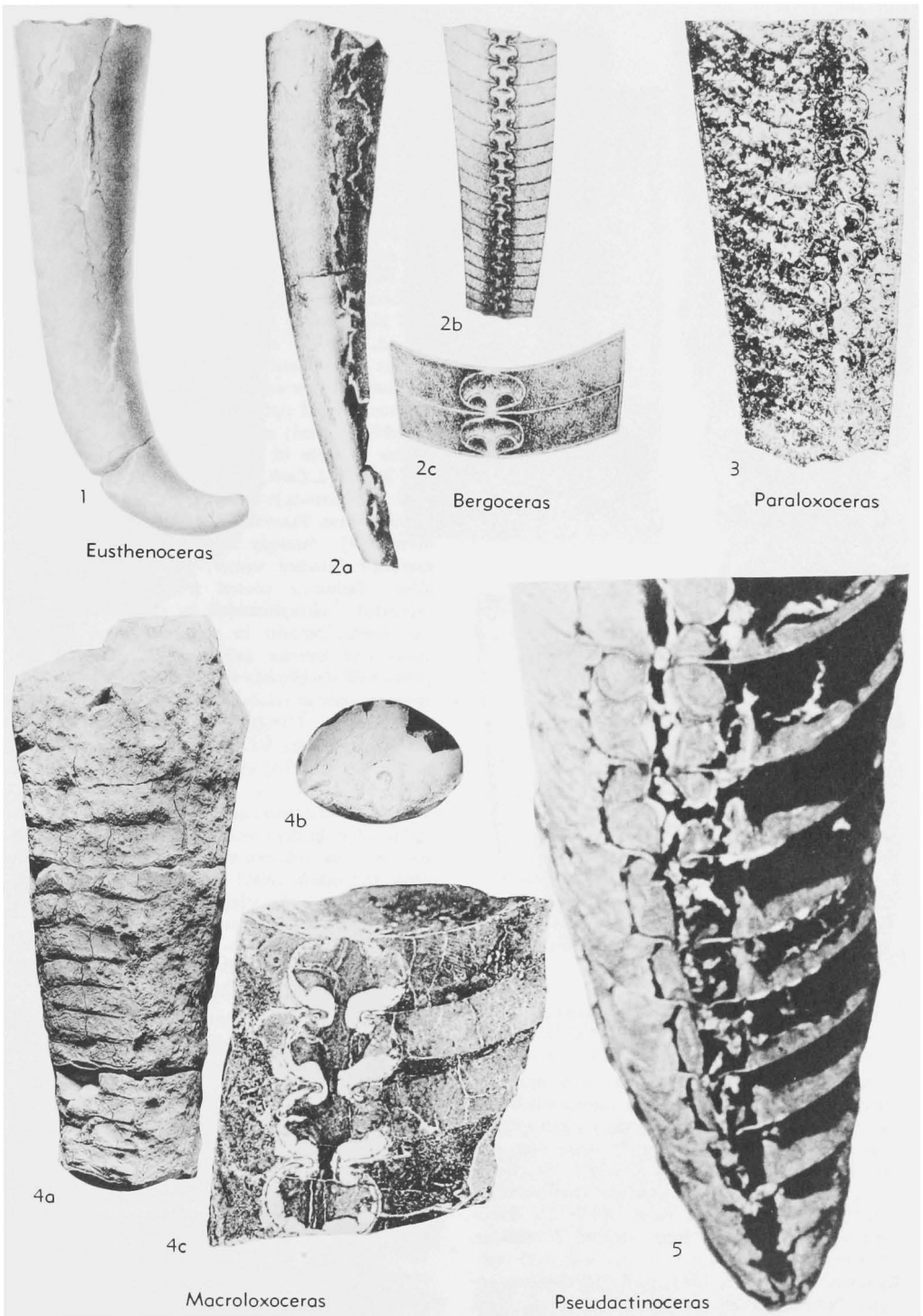


FIG. 181. Pseudorthocerataceae (Pseudorthoceratidae—Pseudactinoceratinae) (p. K252, K254).



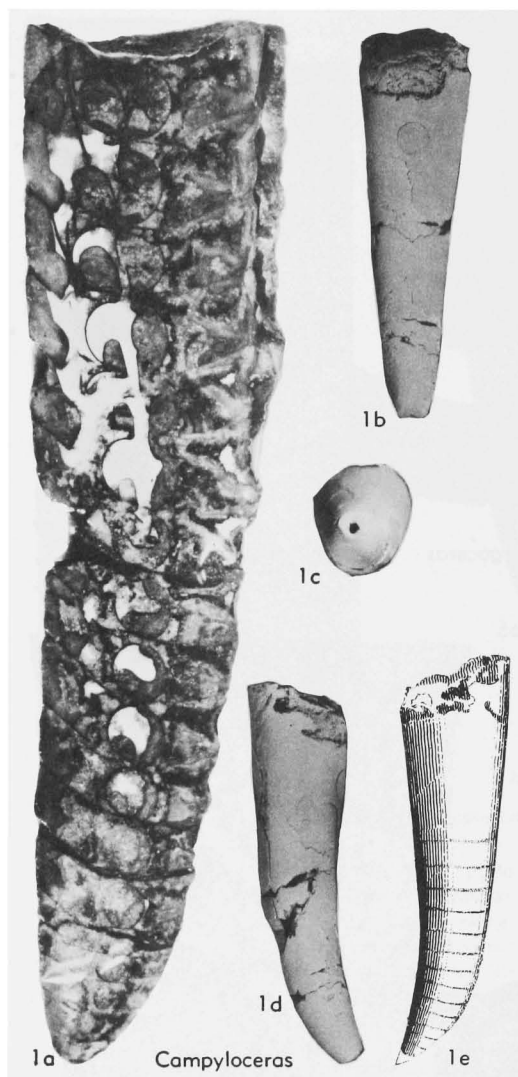


FIG. 182. Pseudorthocerataceae (Pseudorthoceratidae —Pseudactinoceratinae) (p. K254).

phuncle segments broadly expanded, occupied by thick endosiphuncular deposits; radial canals unknown, for all described specimens are immature and deposits occupy only slightly more than apical half of segments. *L.Carb.(Visé.)*, Eu.(Belg.-Ire.).—FIG. 181,2. \**B. antelope* (DEKONINCK), Eu.(Belg.); 2a, left lat. view,  $\times 0.5$ ; 2b, dorsoventral sec.,  $\times 1$ ; 2c, long. sec. of 2 camerae,  $\times 0.5$  (22).

*Campyloceras* M'Coy, 1844, p. 6 [\**Orthoceras unguis* PHILLIPS, 1836, p. 238; SD TURNER, 1954, p. 300]. Slender, smooth, longiconic cyrtocones of subcircular transverse section and with straight or slightly sinuous sutures. Siphuncle central,

cyrtochoanitic; segments subspherical through known parts of conch, occupied by parietal deposits like those of *Macroloxoceras*, but less well developed on dorsal side of siphuncle than on ventral side. Camerae with well-developed episepal and mural deposits. *L.Carb.(Visé.)*, Eu. (Eng.-Scot.-Ire.-Belg.).—FIG. 182,1a. *C. sp. cf. C. unguis* (PHILLIPS), Scot.; dorsoventral sec.,  $\times 4$  (courtesy J. S. Turner, Leeds).—FIG. 182,1b-e. \**C. unguis* (PHILLIPS), Eng.-Scot.; dorsal, apical, left, and right lat. views,  $\times 1$  (courtesy Brit. Mus. Nat. Hist.).

\**Eusthenoceras* FOORD, 1898, p. 98 [\**Cyrtoeras hulli* DEKONINCK, 1881, p. 50; OD]. Large, depressed, apically curved, exogastric cyrtocones. Sutures with dorsal saddles; siphuncle subcentral or between center and venter, cyrtochoanitic. Shape and structure of siphuncle unknown, its segments probably inflated; may be occupied by deposits similar to those of *Pseudactinoceratinae*, but not well known. *L.Carb.*, Eu.(Ire.).—FIG. 181,1. \**E. hulli* (DEKONINCK); lat. view,  $\times 0.3$  (80).

*Macroloxoceras* FLOWER, 1957, p. 67 [\**M. magnum*; OD]. Strongly depressed orthocones with markedly flattened venter; sutures with ventral lobes. Siphuncle ventral from center, broadly expanded and spheroidal in shape, with long free brims; deposits in siphuncle show discrete apical and anterior radial canals. Episepal deposits well developed; smaller hyposeptal deposits apparent only in relatively early parts of phragmocone. *U.Dev.*, USA (Colo.-N.Mex.).—FIG. 181, 4. \**M. magnum*, USA (Colo.); 4a,b, dorsal and septal views,  $\times 0.3$ ; 4c, long. sec. of siphuncle,  $\times 1$  (46).

*Paraloxoceras* FLOWER, 1939, p. 153 [\**P. konincki*; OD]. Slightly depressed orthocones with straight sutures. Endosiphuncular deposits like *Macroloxoceras*, but canals united in central part of deposit. *L.Carb.(Visé.)*, Eu.(Belg.).—FIG. 181,3. \**P. konincki*; dorsoventral sec.,  $\times 1.3$  (22).

### Family MYSTERIOCERATIDAE Sweet, n. fam.

Conchs characterized by cyrtochoanitic mature siphuncle with segments occupied by parietal deposits that originate immediately behind septal necks and grow backward to preceding septal neck, where they fuse with anterior part of preceding deposit to form continuous lining. *M.Ord.* or *U. Ord.*

*Mysterioceras* TEICHERT & GLENISTER, 1953, p. 33 [\**M. australe*; OD]. Slowly enlarging, uncompresssed, smooth-surfaced orthocones with moderately large, subcentral siphuncle. Septal necks short and cyrtochoanitic, with very narrow brims; connecting rings faintly inflated, segments longer than wide. Siphuncular lining produced by parie-



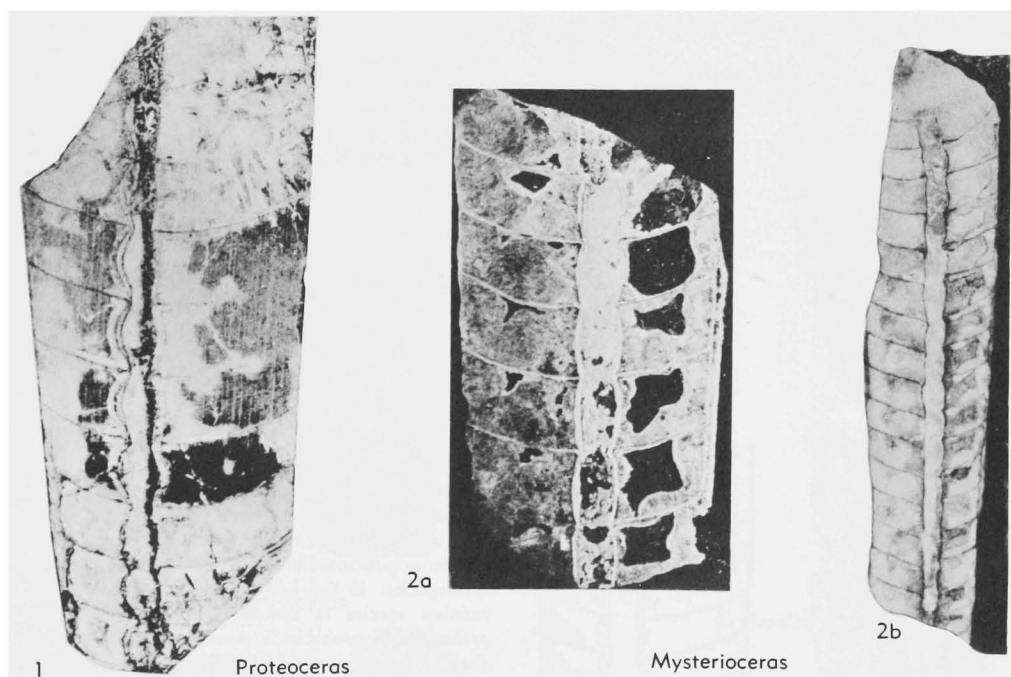


FIG. 183. Pseudorthocerataceae (Mysterioceratidae) (K254-K255); Proteoceratidae (p. K256).

tal deposits that develop first along connecting rings immediately behind septal necks, then grow adapically and adorally so that deposits of adjacent segments fuse in adapical portions of segments to produce continuous sheath lining siphuncle. Cameral deposits mural and episeptal, well developed. *M.Ord.* or *U.Ord.*, Tasm.-Eu. (USSR).—FIG. 183,2. \**M. australe*; 2a,b, dorsoventral secs.,  $\times 3$ ,  $\times 1.5$  (192).

### Family STEREOPLASMOCERATIDAE Kobayashi, 1934

Smooth cyrtochoanitic orthocones. Camerae typically with well-developed organic deposits; siphuncle empty, or with continuous, apparently nonsegmental, lining. Siphuncular segments moderately to broadly expanded. [Type genus, of which *Stereoplasmocerina* KOBAYASHI, 1936, is considered a synonym, not well known. The nonsegmental lining, by which the family is most adequately distinguished, may be an effect of preservation in cyrtochoanitic orthocerids of diverse origin.] *M.Ord.*

*Stereoplasmoceras* GRABAU, 1922, p. 65 [*\*S. pseudoseptatum*; OD] [= *Stereoplasmocerina* KOBAYASHI, 1936]. Smooth, longiconic orthocones of subcircular section but with somewhat flattened

venter. Siphuncle relatively large, subcentral or between center and venter, cyrtochoanitic; empty, or with continuous apparently nonsegmental organic lining; segments moderately to considerably expanded within camerae. Camerae with hyposeptal and episeptal, or with episeptal and mural deposits invariably well developed. *M.Ord.*, Eu. (Norway)-Asia (China-Korea-S. Manchuria). —FIG. 184,1. *S. longicameratum* SWEET, Norway; 1a, diagram. dorsoventral sec.,  $\times 1.3$ ; 1b, lat. view,  $\times 0.7$  (178).—FIG. 184,2. *S. tofangoense* (KOBAYASHI), S. Manchuria; long. sec.,  $\times 1$  (105). —FIG. 184,3. *S. approximatum* (SWEET), Norway; diagram. dorsoventral sec.,  $\times 1.3$  (178).

### Family PROTEOCERATIDAE Flower, 1962

[=Hammelloceratidae SHIMIZU & OBATA, 1935]

Smooth or annulated orthocones and exogastric cyrtocones with expanded cyrtochoanitic siphuncular segments in early stages and narrower, subcylindrical, orthochoanitic segments in late stages. Siphuncular deposits consist of annuli that develop into parietal deposits by growth forward, backward, or in both directions, from septal foramen. Cameral deposits well developed in most genera. *M.Ord.-M.Sil.*

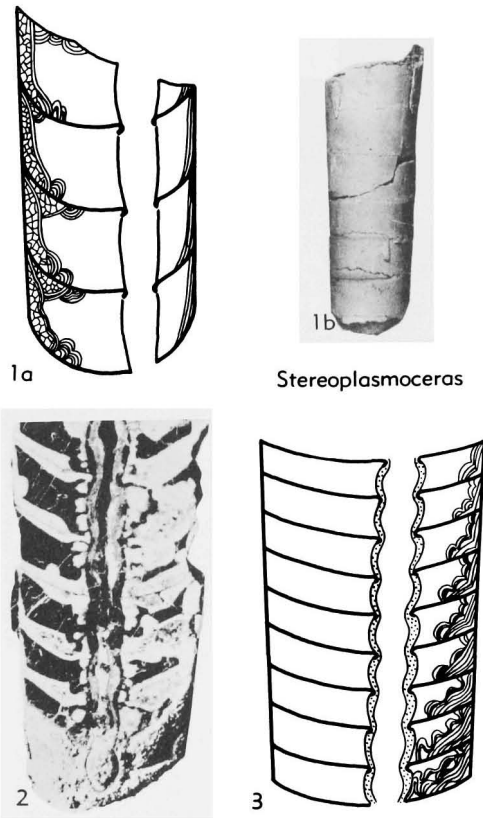


FIG. 184. Pseudorthocerataceae (Stereoplasmoderataceae) (p. K255).

**Proteoceras** FLOWER, 1955, p. 821 [*\*Oonoceras perkinsi* RUEDEMANN, 1906, p. 499; OD]. Smooth, slender, apically curved orthocones with straight transverse sutures. Siphuncle excentric in young, more nearly central in later stages; early segments expanded, with short recurved septal necks and no adnation area; later segments orthochoanitic, cylindrical. Endosiphuncular deposits parietal or annular, thick in front of and behind septal neck, but wanting over most constricted part of septal foramen. Mural deposits elaborate in some forms, better developed dorsally than ventrally. Adoral parts of phragmocone may lack both cameral and siphuncular deposits. *M.Ord.*, N.Am.(Vt.-N.Y.-Que.)-Eu.(Balt.).—FIG. 183,1. *\*P. perkinsi* (RUEDEMANN), USA(N.Y.); dorsoventral sec., venter on left,  $\times 2$  (44).

**Cyrtactinoceras** HYATT in ZITTEL, 1900, p. 528 [*\*Cyrtoceras rebelle* BARRANDE, 1866, pl. 164; OD] [= *Cyrtactinoceras* KOBAYASHI, 1927 (*nom. null.*)]. Slender depressed exogastric cyrtococones with ventral hyponomic sinus and straight sutures that slope forward on dorsum. Siphuncle subventral, cyrtchoanitic; segments inflated, longer

than wide, becoming more slender anteriorly. Annular siphuncular deposits growing forward and backward from point of origin in septal foramina. *M.Sil.*, Eu.(Czech.-Ger.).—FIG. 185,2. *\*C. rebelle* (BARRANDE), Eu.(Czech.); 2a, left lat. view,  $\times 1$ ; 2b, long. sec.,  $\times 3$ ; 2c, transv. sec.,  $\times 1$  (5).

?**Ephippiorthoceras** FOERSTE, 1924, p. 86 [*\*Orthoceras formosum* BILLINGS, 1857, p. 317; OD]. Uncompressed to slightly compressed orthocones with inconspicuous ornament of transverse or longitudinal striae and lirae, or both, or rather coarse oblique plications. Sutures forming broad lateral lobes and dorsal and ventral saddles; camerae of moderate length. Siphuncle subcentral to subventral, cyrtchoanitic; segments moderately to considerably expanded, occupied in at least some species by circumferentially continuous parietal deposits originating in septal foramina and extending adorally along connecting rings. Camerae of some species with episeptal and mural deposits that are heavier ventrally than dorsally. [Details of the siphuncular interior are not known in the type-species; if the internally better-known Tasmanian species is indeed congeneric, *Ephippiorthoceras* is probably a pseudorthoceratid rather than a proteoceratid.] *M.Ord.-M.Sil.*, N.Am.(Colo.-Iowa-S.Dak.-Wyo.-Anticosti Is.-Baffin Is.-Man.-Ont.)-Eu.(Norway)-Tasm. — FIG. 185,1. *\*E. formosum* (BILLINGS), U.Ord., Can.(Anticosti Is.); 1a,b, lat. view, dorsoventral sec.,  $\times 1$  (63).

**Gorbyoceras** SHIMIZU & OBATA, 1935, p. 4 [*\*Orthoceras gorbyi* MILLER, 1894, p. 322; OD] [= *Hamelloceras*, *Porteroceras* SHIMIZU & OBATA, 1935]. Annulated orthocones with longitudinal markings. Siphuncle subcentral, cyrtchoanitic; segments weakly to broadly expanded with small endosiphuncular annuli in septal foramina in early parts of phragmocone. Mural cameral deposits developed much farther anteriorly than endosiphuncular deposits. *M.Ord.-U.Ord.*, widespread. — FIG. 185,4. *G. duncaniae* FLOWER, U.Ord., USA(Ohio); lat. view,  $\times 0.75$  (33).

**Isorthoceras** FLOWER, 1962, p. 32 [*\*Orthoceras sociale* HALL in MILLER, 1877, p. 245; OD]. Smooth orthocones with subcircular transverse section. Siphuncle subcentral; early segments barrel-shaped, slender, expanding abruptly at septal foramina; later segments subcylindrical. Endosiphuncular annuli grow forward and backward, joining those of adjacent segments to form continuous parietal lining of nearly uniform thickness throughout segments. *M.Ord.-U.Ord.*, N.Am.(Iowa-Ky.-Tenn.).—FIG. 156A,2. *\*I. sociale* (HALL), U. Ord.(Maquoketa Sh.), USA(Iowa); 2a, long. sec.,  $\times 4$ ; 2b, lat. ext.,  $\times 1$  (277).

?**Metephippiorthoceras** ZHURAVLEVA, 1957, p. 679 [*\*M. helenae*; OD]. Uncompressed annulated orthocones with short camerae and sutures with low dorsal and ventral saddles. Siphuncle slender, submarginal, cyrtchoanitic; segments nummul-

oidal, connecting rings broadly adnate to adapical side of anterior septum on ventral side in each segment. No deposits known in siphuncle or camerae. *U.Ord.*, USSR.—FIG. 185,5. \**M. hel-*

*enae*; 5a,b, septal view, dorsoventral sec.,  $\times 2$  (212).

**Monomuchites** WILSON, 1961, p. 24 [\**M. costalis*; OD]. Gradually expanding, uncompressed ortho-

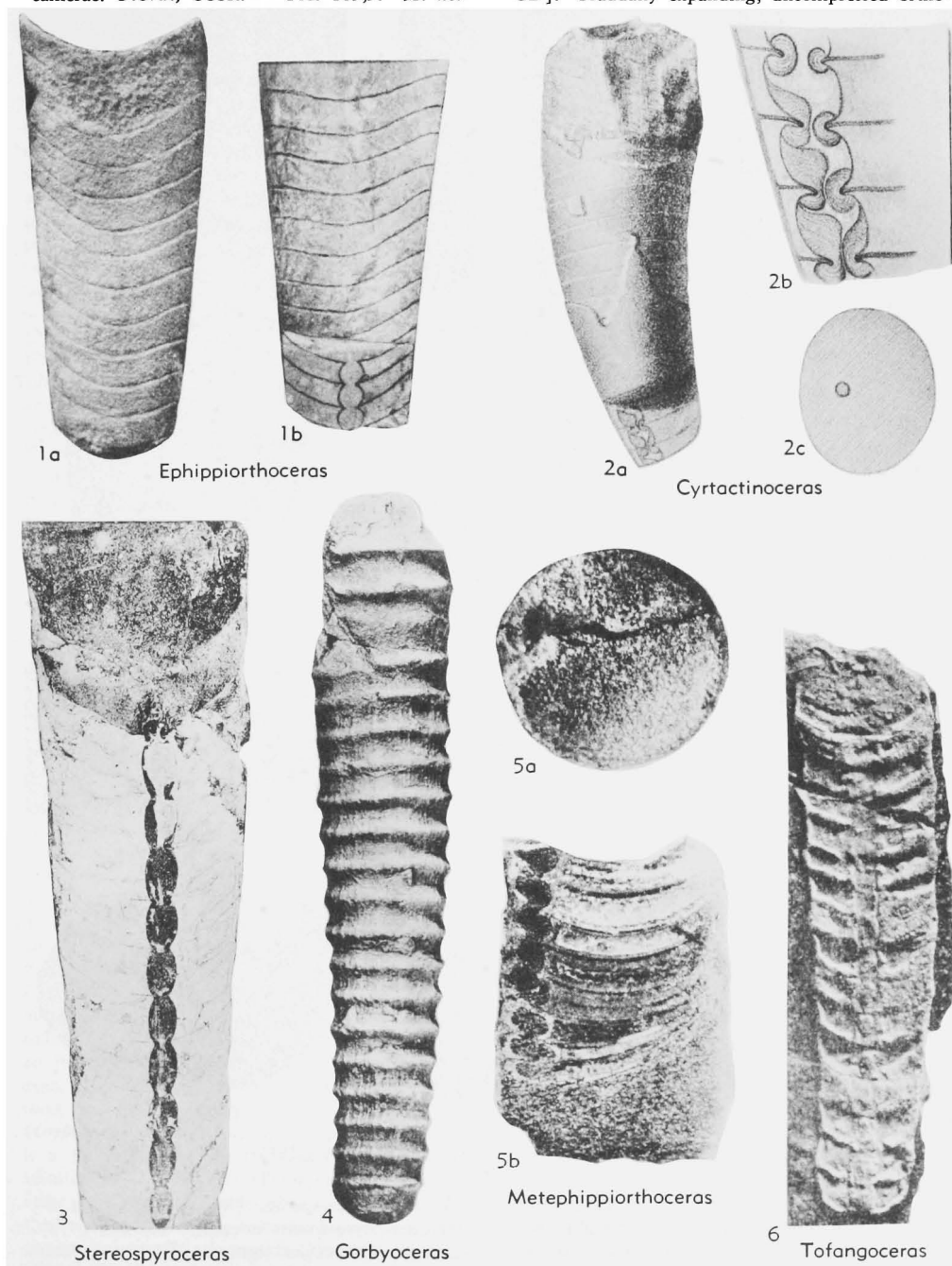


FIG. 185. Pseudorthocerataceae (Stereoplasmoceratidae) (p. K256-K259).

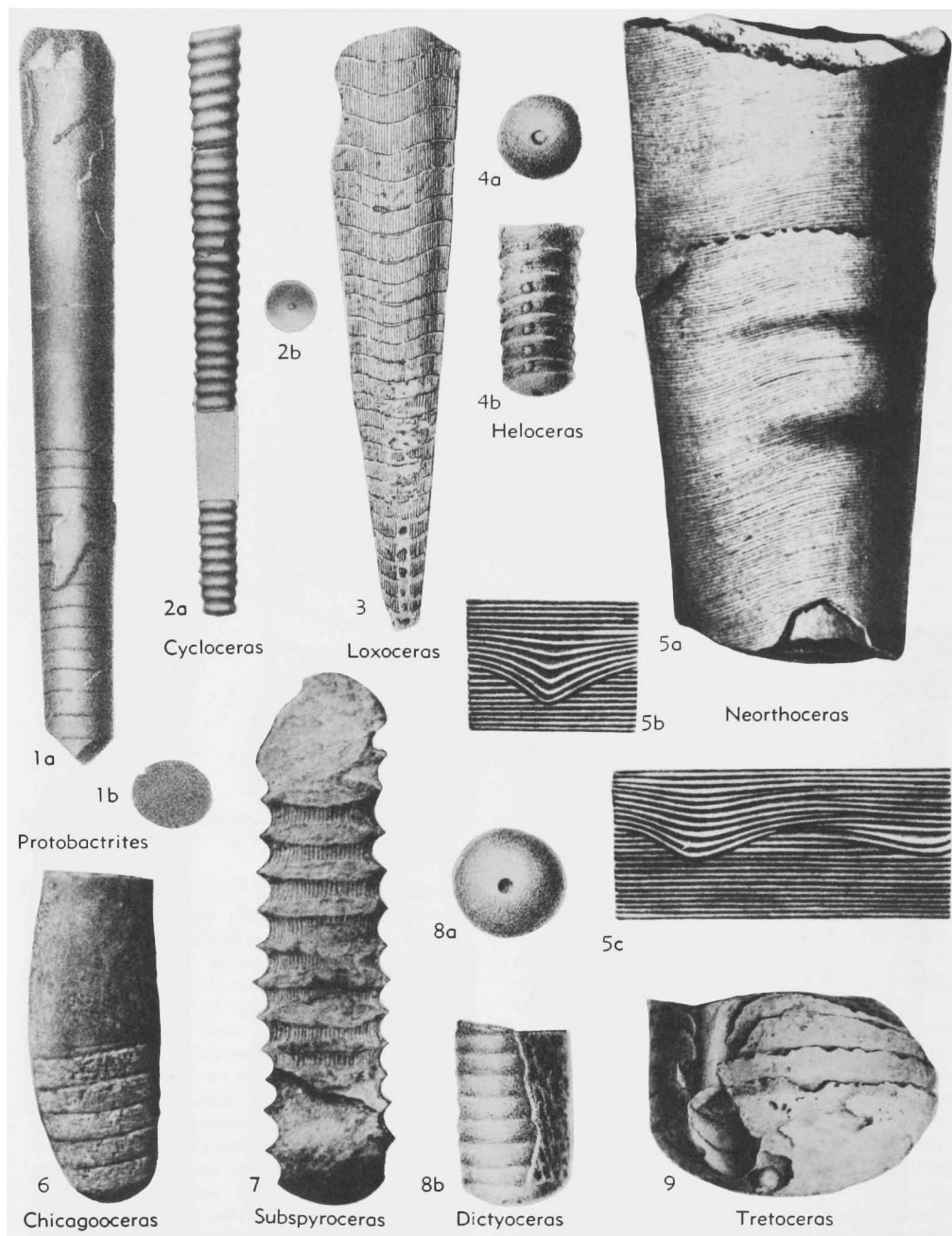


FIG. 186. Orthocerida, Family Uncertain (p. K259-K261).

cones with straight transverse sutures and exterior marked by one transverse annulation at mid-length of each chamber. Siphuncle subcentral, small; septal necks short, slightly recurved; connecting rings faintly expanded, apparently occupied by segmental organic deposits, the nature of which is not

clear in the type-species. [WILSON states that siphuncle of type-species is empty. FLOWER (47a) states that siphuncular segments of *Monomuchites* are broadly expanded in young, slender in adult, and occupied by annuli similar to those of other genera which he includes in the Proteoceratidae.

Neither of these characters is evident in the description or illustration of the type-species.] *M. Ord.*, N.Am.(N.Y.-Que.-Ont.).—FIG. 156A,4. \**M. costalis*, Leray Ls., Ont.; annulated ext., paratype,  $\times 1$  (Wilson, 1961).

**Stereospyroceras** FLOWER, 1955, p. 827 [\**S. champlainense*; OD]. Straight or faintly curved conchs, prominently annulated and longitudinally lined in young; annulations reduced in mature shells of some species. Siphuncle eccentric, suborthochoanitic or weakly cyrtchoanitic in early stages, segments tending to become planoconvex and finally subcylindrical in late stages. Siphuncular deposits annular, irregular, thick, produced primarily anteriorly, but also posteriorly from origin in septal foramina. Camerae with episepal and mural deposits developed far in advance of siphuncular deposits. *M.Ord.*, USA(Vt.)-Eu.(Norway).—FIG. 185.3. \**S. champlainense*, USA(Vt.); long. sec.,  $\times 0.75$  (44).

**Tofangoceras** KOBAYASHI, 1927, p. 189 [\**T. pauciannullatum*; OD] [= *Pseudeskimoceras*, *Kogenoceras* SHIMIZU & OBATA, 1936; *Tofangocerinina* KOBAYASHI, 1936; *Toufangocerinina* BALASHOV, 1959 (*nom. null.*)]. Like *Stereoplasmoceras*, but superficially annulated. *M.Ord.*, USA(N.Y.)-Asia(S. Manchuria - Korea - Siberia). — FIG. 185.6. \**T. pauciannullatum*, Korea; nat. long. sec.,  $\times 1$  (101).

### SUPERFAMILY AND FAMILY UNCERTAIN

**Chicagoceras** FOERSTE & SAVAGE, 1927, p. 47 [\**C. welleri*; OD]. Faintly curved brevicones, uncompressed adapically, depressed anteriorly; flattened dorsally, attaining maximum gibbosity at adapical end of body chamber. Sutures straight but sloping slightly adapically from dorsum to venter. Siphuncle small, slightly ventral of center; probably orthochoanitic and cylindrical in form. [Resembles many Silurian Aceistoceratidae (Oncocherida), but differs probably in orthochoanitic siphuncle.] *M.Sil.* N.Am.(Ill.-Ont.).—FIG. 186, 6. \**C. welleri*, USA(Ill.); lat. view,  $\times 1$  (77).

**Cycloceras** M'COY, 1844, p. 6 [\**Orthocera annularis* FLEMING, 1815, p. 203; SD BASSLER, 1915, p. 325] [= ?*Perigrammoceras* FOERSTE, 1924; *Cycloceras* CRONEIS, 1926 (*nom. null.*)]. Annulated, subcylindrical orthocones with no longitudinal ornamentation. [Type-species is based on an internal mold of a body chamber on which even position of siphuncle is indiscernible. The most common species referred to *Cycloceras* (*Orthocera sulcata* FLEMING, *non* MODEER, 1797) is a *Reticyclocheras*, but this has no bearing on affinities of *C. annularis* (FLEMING). No species other than the type-species should be referred to *Cycloceras* until its type is better known, and the proper content of Cycloceratidae HYATT in ZITTEL, 1900, will likewise remain unknown until that time. *Perigrammoceras* FOERSTE (\**Orthoceras laevigatum* FOORD, 1897) has been considered

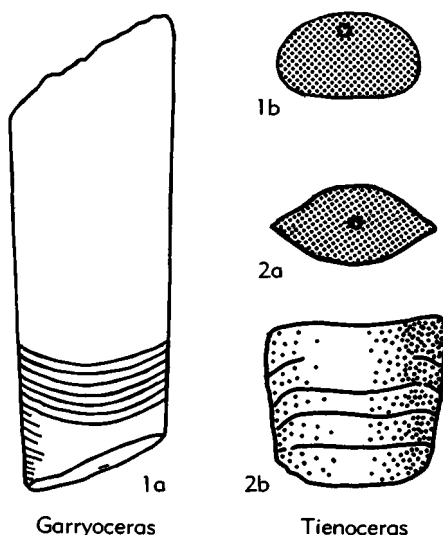


FIG. 187. Orthocerida, Family Uncertain (p. K259-K260).

synonymous with *Cycloceras* by MILLER, DUNBAR, & CONDRA, and others since 1933. It has a central siphuncle, the structure of which is unknown, and external characters similar to those of the fragmentary type of *Orthocera annularis* FLEMING. Validity or invalidity of the suggested synonymy will depend on establishment of identity or lack of identity of internal structures in type-species of the two genera.] *L.Carb.*(Visé.) or *U.Carb.*(Namur.), Eu.(Scot.-Ire.).—FIG. 186,2. *C.? laevigatum* (FOORD), *L.Carb.*, Ire.; 2a,b, lat., septal views,  $\times 0.5$  (80).

**Dictyoceras** EICHWALD, 1860, p. 1263 [\**Orthoceras porosum* EICHWALD, 1857; M]. Uncompressed annulated orthocones, with annulations at posterior ends of each chamber. Test exterior with porous, spongy layer thought to be original. Siphuncle central; internal structure unknown. *Sil.*, Eu.(Est.).—FIG. 186,8. \**D. porosum*; 8a,b, septal, lat. views,  $\times 1$  (19).

**Donacoceras** FOERSTE, 1925, p. 68 [\**D. timiskamingense*; OD]. Large, straight or faintly curved longicones known only from isolated siphuncles, which are composed of weakly inflated presumably empty segments and probably very short straight or slightly curved septal necks. [This genus may be a valid taxon for many orthocerids with similar ectosiphuncles; however, it will be unrecognizable until more is known of the conch and endosiphuncular structure.] *M.Sil.*, Can.(Ont.-Que.).

**Garryoceras** FOERSTE, 1928, p. 42 [\**Orthoceras semiplanatum* WHITEAVES, 1892, p. 81; OD]. Strongly depressed orthocones with flattened dorsum, more narrowly rounded venter. Camerae short; sutures sloping adapically from dorsum to

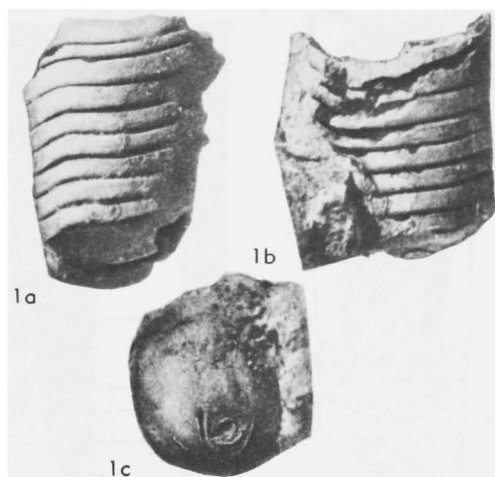


FIG. 188. \**Mstikhinoceras mirabile* SHIMANSKIY, Actinocerida (Ormoceratidae) (p. K214).

venter and forming broad shallow dorsal lobes. Siphuncle small, subventral, subcylindrical in form. [Detailed morphology of conch interior unknown; gross form suggests relationship to Valcouroceratidae (Oncocerida), but siphuncle is too small and apparently is cylindrical.] *U.Ord.*, Can.(Man.).—FIG. 187,1. \**G. semiplanatum* (WHITEAVES); 1a,b, dorsal, septal views,  $\times 0.7$  (65).

**Heloceras** EICHWALD, 1860, p. 1262 [\**H. tuberculatum*; M]. Small, slender, cylindrical orthocones with transverse annulations and a longitudinal row of hemispherical tubercles along one side. Siphuncle relatively large, subcentral; internal structure unknown. *M.Ord.-M.Sil.*, Eu.(Est.-Czech.).—FIG. 186,4. \**H. tuberculatum*; 4a,b, septal, lat. views,  $\times 1$  (19).

**Loxoceras** M'COY, 1844, p. 6 [\**Orthocera breyni* FLEMING, 1828, p. 238; SD BASSLER, 1915, p. 767] [= *Breynioceras* FOERSTE, 1929 (obj.)]. Smooth orthocones with transverse septa forming broad ?ventral lobe. Siphuncle between center and ?venter. [According to MARTIN, who first described the type-species, and FLEMING, who stabilized it, the siphuncle is “. . . simple, small, and cylindrical”; but, according to FOORD (1888, p. 193), it is composed of segments that are “. . . considerably inflated between the septa.” Until the type of *Orthocera breyni* is located and restudied, *Loxoceras* will remain unrecognizable and content of the family Loxoceratidae HYATT in ZITTEL, 1900 will remain uncertain.] *L.Carb.*, Eu.(Eng.).—FIG. 186,3. \**L. breyni* (FLEMING); lat. view,  $\times 1$  (55).

**Molossus** DEMONTFORT, 1808, p. 350 [\**Orthoceratites gracilis* BLUMENBACH, 1803; M]. Type and only known species based on flattened and stretched fragment of slender orthoconic conch,

the internal and external details of which are unknown. ?*Dev.*, Eu.(Ger.).

**Neorthoceras** SHIMIZU & OBATA, 1936, p. 18 [\**Orthoceras verbeeki* HANIEL, 1915; OD]. Moderately expanding orthocones of subcircular cross section, with straight transverse sutures and deeply concave septa. Surface with low, fine, rounded, sinuous transverse growth bands forming salient on ?ventral side. Siphuncle subcentral; internal structure unknown. *Perm.*, Malay Arch.(Timor).—FIG. 186,5. \**N. verbeeki* (HANIEL); 5a, slightly compressed conch with shell preserved,  $\times 1$ ; 5b,c, details of sculpture,  $\times 3$  (88).

**Protobactrites** HYATT in ZITTEL, 1900, p. 518 [\**Orthoceras styloideum* BARRANDE, 1866, pl. 365; OD] [= *Protobactolites* KOBAYASHI, 1934 (nom. null.)]. Long slender orthocones or faintly curved longicones of circular or subcircular cross section. Surface with transverse and in some species longitudinal striae. Siphuncle eccentric; structure unknown but possibly cylindrical in shape. Aperture oblique to long axis; natural truncation of shell may have taken place. [Genus is unrecognizable until internal information is available.] *M.Ord.-Sil.*, ?USA (Ohio) - Eu. (Czech. - Sweden) - USSR (Pskov).—FIG. 186,1. \**P. styloideum* (BARRANDE), *M.Sil.*, Czech.; 1a,b, lat. view, transv. sec.,  $\times 1$  (5).

**Sannionites** FISCHER DE WALDHEIM, 1829, p. 325 [\**S. crepitaculum*; SM FISCHER DE WALDHEIM, 1837, p. 126]. Orthocone, apparently with thick cameral deposits. Age unknown, USSR.

**Subsphyroceras** SHIMIZU & OBATA, 1935, p. 4 [\**Spyroceras middlevillense* FOERSTE, 1928, p. 178; OD]. Slender orthocones with prominent transverse annulations and longitudinal lirae. Internal features unknown. [No species other than the type can be referred to this genus until its interior is known; the name has page preference over *Anaspyroceras* SHIMIZU & OBATA, 1935, of which it may ultimately be proved a synonym.] *M.Ord.*, USA(N.Y.).—FIG. 186,7. \**S. middlevillense* (FOERSTE); lat. view,  $\times 1$  (62).

**Tienoceras** CHAO, 1954, p. 28 [\**T. lenticulare*; OD]. Slightly enlarging, smooth, depressed orthocones of lenticular cross section, with mid-portions of dorsum and venter flattened or depressed and with longitudinal depressions in dorso- and ventrolateral sides. Sutures with mid-ventral, mid-dorsal, and sharp lateral lobes separated by narrow dorso- and ventrolateral saddles. Siphuncle small, subcentral; internal structure not known. *Perm.*, China(Hunan).—FIG. 187,2. \**T. lenticulare*; 2a,b, septal, ventral or dorsal views,  $\times 1$  (9).

**Tretoceras** SALTER, 1858, p. 179 [nom. subst. pro *Diploceras* SALTER, 1856, non CONRAD, 1842] [\**Orthoceras bisiphonatum* SOWERBY in MURCHISON, 1839, p. 642; M] [= *Tritoceras* WOODWARD, 1868 (nom. null.)]. Depressed orthocones with

closely spaced septa and ?2 siphuncles, one a large marginal subcylindrical tube, the other a small moniliform structure about halfway between center and venter. Neither surface nor interior nor real nature of ?2 siphuncles well known. [FOERSTE (1928, p. 267; 1930, p. 123) suspected symbiotic relationship between this cephalopod and an organism that is responsible for the internal tube. FLOWER (1952, p. 33-34) admitted FOERSTE's view is possible, but noted that 4 species

with similar internal structure are known. He regarded *Tretoceras* as a probably valid genus deserving of recognition as a distinct family or even higher nautiloid group, although he mistakenly believed that all 4 species were of the same age.] *M.Ord.*, Eu.(Eng.) [Similar specimens are known from *M.Ord.*, USA(Tenn.)-Eu.(Czech.), *M.Sil.*, Can.(Anticosti Is.), and *Dev.*, Eu.(Ger.)].—FIG. 186,9. \**T. bisiphonatum* (SOWERBY), Eu.(Eng.); ?ventral view,  $\times 1$  (173).

## NAUTILOIDEA—ASCOCERIDA

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### INTRODUCTION

The Ascocerida are comparatively small nautiloids which are confined to Ordovician and Silurian strata. Representatives are known from Europe and North America, but most of the well-preserved material is from Upper Silurian strata of the Baltic Island of Gotland and beds of similar age in the Province of Bohemia, Czechoslovakia. Numerous scattered localities in North America have yielded ascocerids in small numbers, but the preservation of these specimens almost invariably is imperfect. The poor preservation of most representatives is related to their unusually thin septa. Largely because of the rarity of well-preserved material, little has been added to our understanding of basic ascocerid morphology since the classic studies of BARRANDE (1846-77) and LINDSTRÖM (118a). The latter study presented an admirably thorough understanding of morphology and ontogeny. We have examined LINDSTRÖM's types and find his lithographs reliable in all details. Some additional information has been derived from thin section preparations of Gotland material, however.

The Ascocerida possess several unusual morphological features which, in combination, are unique. Of particular taxonomic significance is the radical change in conch morphology which was associated with ontogenetic shell truncation. The progressive development of saddle-like dorsal camerae and strongly sigmoidal confluent septa

is even more remarkable. This trend culminated in the attainment of centrally "windowed" or lacunose cameral partitions in advanced ascoceratids. The mature ascocerid siphuncle is also distinctive; it may consist of only a few strongly nummuloidal segments in the ventroposterior portion of the phragmocone, and so correspond to only one-tenth the total length of the mature conch.

Possession of these unusual morphological features renders the Ascocerida a highly distinctive nautiloid group, which is readily separable from other orders. Ascocerids are indeed "très-bizarres" (BARRANDE, 1846).

### PREVIOUS INVESTIGATIONS AND CLASSIFICATION

In his first note on the discovery of the ascocerids, BARRANDE (1846) recognized their distinctive nature and erected a separate genus to include them. During the following 30 years, this author included detailed studies of the group in his extensive faunal analysis of the Bohemian Silurian. BARRANDE (5) described the shell morphology and published fine lithographs of a variety of forms. Although he also erected a familial grouping in 1867, his conclusions on morphological relationships have not been substantiated, for he regarded the ascoceroid body chamber as analogous to the endocerid siphuncle, and the ascocerid group generally was considered to be primi-



tive rather than complex. Nevertheless, BARRANDE had a fair comprehension of natural shell truncation, though none of his ascocerid material actually displays the transitional stage from the deciduous cyrtocone. These early attempts at interpretation and classification pursued various courses, and BARRANDE was aided to a considerable extent by contemporary paleontologists, notably H. G. BRONN (*vide* LINDSTRÖM, 1890, p. 18).

Over a period of years many accounts of the ascocerids have been given, most of them now of little significance. BILLINGS (1857, 1862, 1866) recognized Ordovician representatives of the family which were clearly identifiable as near relatives of the Silurian forms. HYATT (93) clarified some generalizations but also outlined unsound relationships on the basis of apertures. FOORD (79) presented a logical summary based on fairly extensive material.

By far the most important contribution yet made to our knowledge of this group is that of LINDSTRÖM (118a). His study embraced numerous specimens perfectly preserved in dense limestone. He was able to secure several shells which retain part of the deciduous cyrtoconic conch on the inflated ascoceroid portion. Serial sections and models made it possible to construct a three-dimensional view of practically all details of the entire conch. Carefully prepared figures include the only original illustrations of the radically different deciduous shell. LINDSTRÖM also had a clear idea of function in shell morphology.

FOERSTE's descriptions during the 1920's recorded more primitive Ordovician genera and involved restudy of BILLINGS' materials. MILLER (123) presented a comprehensive discussion of the group. Three of LINDSTRÖM's species and one of BILLINGS' were designated as types of new genera. MILLER also proposed a major subdivision of the group, named Schuchertoceratidae, based primarily upon existence of a "basal septum." Experience has shown that this structure occurs in ascocerid species which otherwise are diverse, as well as in association with normal ascoceratids which in other respects are almost indistinguishable. The presence of a simple septum in the mature conch, therefore, provides an illogical basis for familial subdivision.

FLOWER's (26) discussion of ascocerid phylogeny is highly speculative. His visualization of "prebasal siphuncular segments" has not been borne out by examination of better-preserved materials. Also, it now appears probable that his identification of "plano-convex siphuncular segments" was based upon vagaries of preservation. In view of the importance he attached to these supposed structures, the association of *Hebetoceras* with the true ascocerids is even less well founded. No single distinctive feature of the order can be recognized, but the family Hebetoceratidae is retained as a separate ascocerid group for convenience.

## MORPHOLOGY AND ONTOGENY

The conch secreted by an individual ascocerid consists of two distinct portions which rarely are found joined together. The juvenile, or deciduous, conch has been recognized with certainty only in Silurian Ascoceratinae, although probable deciduous conchs of the Silurian Choanoceratidae are recorded. Typically, the deciduous portion consists of a slender cyrtocone which underwent periodic truncation. The cumulative length of the decollated sections in extreme individuals probably approached 200 mm., although most were much shorter. A specialized septum of truncation forms the apical end of the breviconic mature, or ascoceroid, portion of the conch. Decollation normally occurred along this septum, but several specimens retain part of the deciduous conch attached to the ascoceroid portion. The largest recorded ascoceroid conch has a length of 150 mm., but some fully mature representatives are slightly less than 20 mm. long. Evidence derived from the Silurian collections of Gotland suggests that the cumulative length of the decollated sections ranged from slightly more than that of the corresponding mature ascoceroid conch to more than twice the length of the fully mature conch.

The external shell of the Ascocerida is consistently thinner than that of most other orthocones and cyrtocones of comparable size. Shell thickness rarely exceeds 1 mm. in even the largest representatives, except where thickening occurs along the constricted area near the mature aperture. The



septa of both the deciduous portion and the mature conch are also extremely thin. Few specimens exhibit septa which are thicker than 0.2 mm., and septal thickness of most forms approximate 0.1 mm. The septum of truncation is the one exception to these generalizations; commonly its thickness is two or three times that of adjacent septa and is approximately equal to the thickness of the external shell. Rarity of satisfactory preservation of the internal structures of the ascocerids is attributable to their delicate construction. Fragmentation of internal structures by predators, or during subsequent habitation by other organisms, seems probable.

The extreme changes in conch morphology during the ontogeny of the Ascocerida necessitate separate consideration of each of the three stages of growth. The longiconic deciduous portion is taken to represent the conch of juvenile growth stages, and the brevicone housed the mature animal. Gerontism is marked by the secretion of adventitious transverse septa within the mature body chamber.

#### DECIDUOUS CONCH

The longiconic portion has been recognized with certainty in only four species, *Ascoceras manubrium* (see Fig. 192,3c-e; 193,1f-h), *A. lagena* (see Fig. 193, 1i,j), *Parascoceras fistula* (see Fig. 192,1c,d; 196, 1b), and *P. decipiens* (see Fig. 192,1a,b). All are Ascoceratinae and were described by LINDSTRÖM (118a) from the Silurian of Gotland. KESLING's (98a) report of the deciduous longicone of Ordovician Ascocerida has not been authenticated.

*Parascoceras decipiens* is the only ascocerid in which the apex of the deciduous conch is known adequately. The shell corresponding to the first camera is devoid of ornament. Length of this first camera is more than that of the two succeeding chambers. The first segment of the siphuncle is more inflated than subsequent segments, and, unlike other segments of the deciduous conch, is in contact with the ventral shell wall for most of its length. Cross sections of the deciduous conch are approximately circular. All known species exhibit prominent growth lines or transverse lirae, and some forms are annulate. Longitudinal lirae are also present in some species.

Rate of expansion of the deciduous conch was extremely slow and uniform. Most species are gently cyrtconic, although reversal of curvature near the apex in some forms results in a weakly sigmoid outline. The tubular siphuncle is situated about midway between the conch axis and the venter. Septa are uniformly simple throughout the deciduous conch. They are somewhat oblique, extending farther forward dorsally; sutures are straight. Length of the camerae may approximate one and one-half times the corresponding conch diameter. Septal interval increases anteriorly in irregular cycles; initiation of a new cycle is marked by short camerae, in which the length is as little as one-third that of the preceding camera.

Septal necks are short and orthochoanitic. Some species exhibit a unique adoral flange around the septal foramen. These flanges appear to be continuous with the septum, and they provide an area of adnation for the connecting ring. Only slight expansion of the connecting ring occurs between adjacent foramina.

#### MATURE ASCOCEROID CONCH

The great majority of Ascocerida are represented only by the mature, or ascoceroid, conch. Typically, this consists of an expanded exogastric brevicone, although uniform expansion characterizes the Choanoceratidae and Hebetoceratidae. Smooth, lirate, reticulate, and strongly annulate forms are known.

The apical end of the mature ascoceratid conch is formed by a specialized septum of truncation. Thickness of this septum approximates that of the corresponding lateral walls of the mature shell and commonly is more than three times the thickness of adjacent septa in both the deciduous and mature conchs. Many Silurian Ascoceratidae possess an adoral flange around the foramen of the septum of truncation (Fig. 189,1; see Fig. 193,1f,h). These foraminal flanges appear to be identical with those of the deciduous conch. Other Silurian ascoceratids seem to lack a flange (Fig. 189,2), but some forms resemble known Ordovician representatives in possessing a siphuncular displacement canal (Fig. 189,3,4; see Fig. 193,3b,c). This canal is a short oblique tube which deflected the siphuncle ven-

trally across the adoral face of the septum of truncation. A mineralized plug probably closed the foramen through the septum of truncation prior to decollation of the deciduous conch.

The fully mature conch of the Ascoceratidae generally consists of an expanded posterior portion, to which the phragmocone is confined, and a shorter, contracted cylindrical anterior part, the neck. The posterior portion is usually depressed in Ordovician Ascoceratidae, although it may be approximately equidimensional. Silurian ascoceratids differ in that they are almost invariably compressed. The neck is generally circular in section; it is short and indistinct in Ordovician ascoceratids but approximates one-third of the total length of the ascoceroid conch in most Silurian representatives.

Spectacular modifications are seen in fully mature representatives of *Glossoceras* (Fig. 190,C; see Fig. 196,2) and may occur, as yet undescribed, in other Ascoceratinae. The modified fully mature aperture of *Glossoceras* is trilobate, consisting of a prominent dorsal salient, deep ocular sinuses, and a shallow hyponomic sinus. Such apertural irregularities were developed only near the extreme margins of fully mature shells. Elsewhere, the aperture was approximately straight and transverse. HYATT's (93) reference to a *Mesoceras*-like aperture in *Billingsites* has been found to represent an irrelevant break on the posterior end of one type-specimen. Shell thickening near the aperture and close to the base of the neck has been observed in fully mature representatives of several taxa and was probably a characteristic feature.

Secretion of the septum of truncation coincided approximately with formation of the constriction at the base of the neck. Subsequent decollation of the remaining deciduous conch did not occur, in one Silurian ascoceratid specimen observed, until the mature number of ascoceroid septa had appeared. Hundreds of other well-preserved mature specimens in the Silurian lack any remnant of the longicone. Also, Ordovician representatives with less than the mature number of segments fail to retain any trace of the deciduous conch. Whether this latter situation indicates post-

mortem fragmentation or relatively early ontogenetic truncation is not known.

As few as three camerae may be present in the mature ascoceratid conch; the average is about five, but 12 are known in extreme forms. The number is nearly constant for a given species. Several ascoceratid genera possess a simple basal septum, which is parallel to the septum of truncation. The suture corresponding to this basal septum is straight but oblique. Subsequent septa in the Probillingsitinae are also subparallel to the septum of truncation but tend to become more acutely oblique and to develop gently sigmoidal sutures. Sutures of all but the basal septum of the Ascoceratinae are strongly oblique and sigmoidal. In fully mature individuals, the last camera extends forward to the base of the neck. As a result of this unique distribution of the ascoceroid septa, the camerae are restricted almost entirely to the dorsal portion of the brevicone, above the ventrally situated body chamber.

The septa of all Probillingsitinae are separate and entire. Ordovician Ascoceratinae commonly have portions of adjacent septa in contact, but in no specimen belonging to this group is there an indication that secretion was not continuous across the entire septum. This is not true of Silurian forms, as these younger representatives invariably possess at least one "windowed" or lacunose septum. A lacuna (see Fig. 193, 1a-e) is a dorsal discontinuity in a septum and is bounded by the line along which the septum is in contact with its predecessor. No lacunae extend as far as the shell wall, and accordingly the whole of each camera is in direct contact with the corresponding siphuncular segment. However, septa generally are so closely spaced around the lateral margins of the lacunae that the sutures in that vicinity are in close mutual proximity. Sutures may appear confluent laterally in poorly preserved fossils, but better specimens show that each suture maintains its identity. Only the adoral septum of *Lindstroemoceras* is lacunose. The basal septum, if present, and the succeeding first ascoceroid septum of other Silurian Ascoceratidae are entire, but the remaining ascoceroid septa invariably are lacunose.

As noted by numerous authors, the si-

siphuncle in advanced ascocerids appears so distinctive as to deserve special taxonomic treatment in itself (Mixochoanites of Hyatt). Several features, collectively, are unique to the order. As a morphological feature, the mature ascoceroid siphuncle was degenerate but remained thoroughly functional; enlarged dorsal buoyant sections of the camerae retained vital communication with the reduced posteroventral siphuncle. The rudimentary siphuncular deposits which existed were probably not important physiologically. However, it is apparent that even the best-preserved specimens from Gotland lack sufficient detail to discern all structures with certainty.

Within the first ascoceroid camera, considerable variation is observed in outline and relative size of the siphuncle. Also, the several genera display marked differences in length of the initial segment. For example, in *Probillingsites* (Fig. 189,4) length of the first element is approximately equal to that of the next three segments collectively; also, the apical portion of the siphuncle is in contact with the ventral shell wall and is prominently asymmetrical. In the next phylogenetic stage, represented by *Schuchertoceras newberryi* (Fig. 189,3), the first chamber is associated with a basal septum which is more widely spaced than septa which follow. FLOWER (26) has sought to recognize vestiges of three cyrtchoanitic segments in this elongate portion of *S. thomasi* MILLER (= *S. iowaense* FLOWER, *nom. van.*). Direct examination of the single type indicates that the siphuncle of this specimen is poorly preserved but probably resembles that of *S. newberryi*, with no constrictions or indication of segments.

Prominent segmentation of the first siphuncular segment does occur in some representatives of *Parascoceras* figured by LINDSTRÖM (118a). *P. pupa* displays a prominently inflated section directly in contact with the ventral wall and a reduced oblique portion with dorsal invagination which appears analogous to the displacement canal in other forms. Other species (e.g., *P. decipiens*, *P. sipho*) have the long first segment displaced ventrally but in-folded on the ventral side. These strictures have been interpreted by LINDSTRÖM (118a) and others as possible vestiges of a basal

septum which had been resorbed. The existence of these phantom septa is doubted, but such striking irregularities of the siphuncle in otherwise similar conchs suggest that no fundamental significance is to be attached to them. A reversion to simple adventitious septa in the gerontic conch of *P. decipiens* also substantiates the idea that major changes in the ascoceroid siphuncle involved no great alteration in the soft parts of the creature.

The siphuncle of typical *Ascoceras* is characterized by strongly inflated segments. In extreme cases (Fig. 189,1) connecting rings approach the restricted boundaries within the posteroventral part of the phragmocone. Septal necks are extremely varied, in terms of the stability usually accorded this feature as an important morphological structure in nautiloid systematics. Recumbent foraminal brims are apparently present in all mature Ascoceratidae and Choanoceratidae; all likewise have simpler cyrtchoanitic or orthochoanitic growth stages. The Ordovician genus *Schuchertoceras* passes from a moderately inflated segment in the basal camera to a strongly inflated portion, within the ascoceroid conch. The change from a nearly cylindrical siphuncle in Silurian deciduous conchs to a strongly inflated basal ascoceroid portion substantiates FLOWER's (26) basic concept of reduction and omission of ontogenetic stages.

In addition to a secondary cylindrical calcareous deposit which apparently sealed the basal ascoceroid foramen before truncation, siphuncular deposits occur on the necks in the Ascoceratidae and Choanoceratidae (Fig. 189,3; see Fig. 196,3a). Even with the best-preserved specimens available for study, doubt still exists as to which portion is fortuitous and which is intrinsic. None of the well-preserved sections, however, reveal a "planoconvex" siphuncular outline interpreted by FLOWER (26) to be characteristic of Ordovician genera.

## ADVENTITIOUS SEPTA

LINDSTRÖM (118a) figured a few ascocerid specimens in which the secretion of a normal sequence of mature septa was succeeded by a series which constitutes a simple orthoconic phragmocone. One specimen (see Fig. 193,3a,b) possesses four such

septa which had been secreted in the posterior part of the body chamber after the regular phragmocone with ascoceroid septa was established. Comparable types of modification are known in other cephalopod groups, but nothing so spectacular as a reversion to a simple type after creation of the specialized ascoceroid conch. The implications of such a feature as adventitious septa were discussed by ULRICH *et al.* (203), and the phenomenon was concluded to be pathologic, rather than to represent normal gerontism. The term "gerontopathologic" would care for all modifications of this nature. In no way are these rare shells comparable to drastic mature apertural modifications designated as "gerontic" by HYATT (1894) and by CLARKE (1899). It seems logical that physiological adjustment at maturity might assume the guise of shell juvenility. The variations in shell secretion during later stages in the life span of modern *Nautilus* have never been explored.

LINDSTRÖM (118a) interpreted the unique post-mature phragmocone merely as an indication that the body of the animal occupied the entire chamber. MILLER (123) regarded the structure as of questionable significance, beyond indicating a close relationship between cytochoanitic and orthochoanitic conchs; however, he employed the term "senile" for this stage. FLOWER (26) stated that the adventitious septa signify "telescoping of an ontogenetic stage to a position other than that which it ordinarily occupies. . . the normal ontogenetic sequence of the ascoceroid is reversed."

### PHYLOGENY

The most distinctive feature of the ascocerids, namely, a decollated breviconic conch with dorsally oblique camerae, is clearly recognizable in ancestral forms. Representatives from the Middle Ordovician to the Upper Silurian provide an orthogenetic group with few irregular members.

Status of the Hebetoceratidae, proposed as a primitive ascocerid gens by FLOWER (26), remains uncertain. Better-preserved material, however, should be sought. The unspecialized nature of known early ontogenetic stages in *Ascoceras* suggests that the ancestral strain may not be identifiable in forms which lack a specialized septum of truncation.

*Probillingsites*, from the Middle and Upper Ordovician, conforms in every respect to the concept of a primitive ascocerid. It is also possible to trace a phylogenetic series within the genus. Only the Upper Ordovician forms reveal a pronounced siphuncular displacement canal, strongly differentiated first and second ascoceroid camerae, a flattened ventral surface, and more strongly oblique, slightly sigmoid sutures at the fully mature stage.

*Schuchertoceras* represents a major evolutionary step only with respect to the change in the nature of the siphuncle between the first and second ascoceroid camerae. Also, the second ascoceroid septum is prominently sigmoid in contrast to the simple basal septum. Retention of this vestigial structure, the basal septum, in Late Silurian forms is probably of little significance. MILLER (123) proposed that independent stocks originating in the Middle Ordovician led to a parallel development of *Parascoceras* and *Ascoceras* by Late Silurian time; in the light of their close similarity, except for a basal septum, such a development seems unlikely.

*Billingsites* is fundamentally a *Schuchertoceras* lacking the basal camera. The two genera are found in direct association and can be distinguished only by the apical suture. As might be expected, however, younger species of *Billingsites* display some advanced features in form of the conch and septa.

All of the Silurian Ascoceratidae appear to have possessed at least one lacunose septum at full maturity; such a feature is not known in any Ordovician form. This adaptation provided greater stability and a saving in shell material. Lacunae became progressively enlarged and fully developed by the second septum in advanced forms.

The general conch shape of the ascocerids evolved from a simple depressed subglobular shell to an attenuate, laterally compressed fusiform conch, an effective response for stable mobility. An extended neck in later Silurian representatives contrasts strongly with the short flange on Ordovician shells.

Too little is known of the trilobate *Glossoceras*-type aperture to generalize, as most specimens are fragmented. However, ancestral Ordovician genera may have had

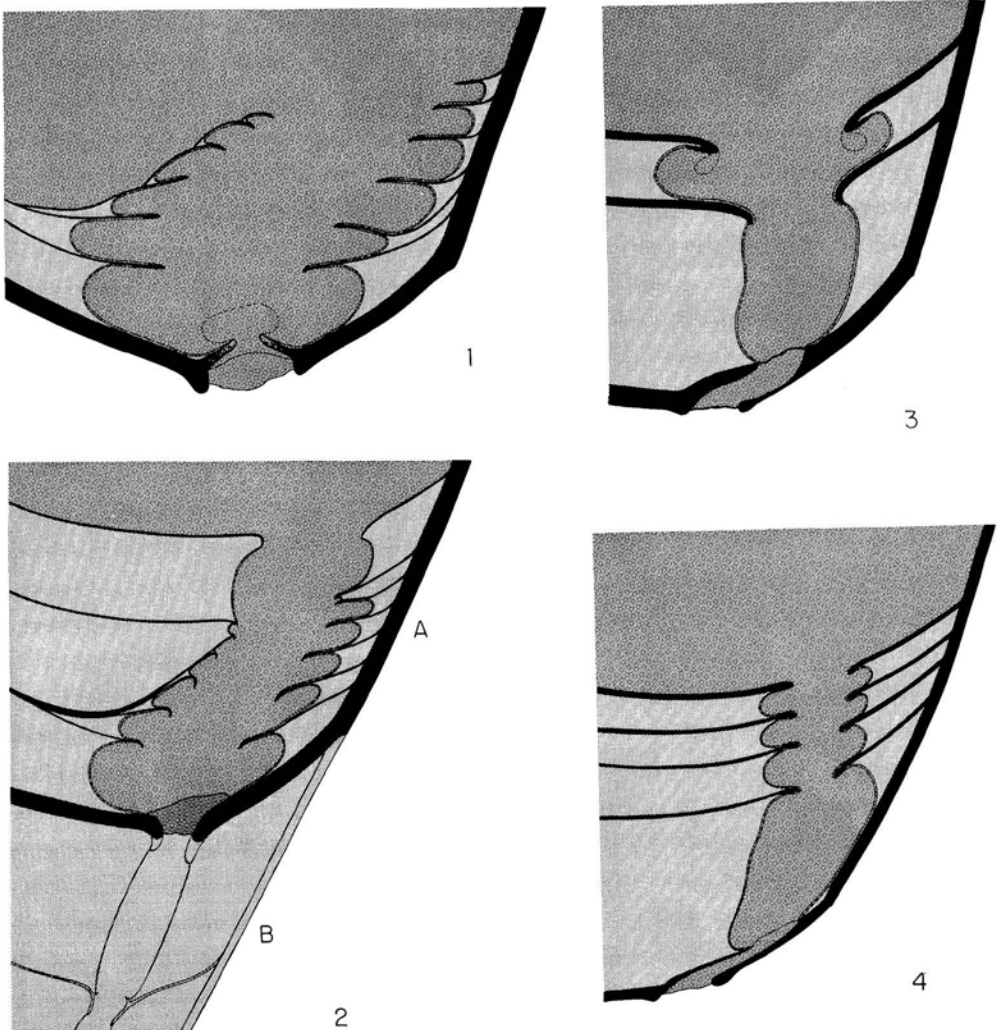


FIG. 189. Diagrammatic cross sections of apical portions of mature Ascoceratidae illustrating morphological details within siphuncle; 1,2, *Ascoceras* (A, ascoceroid segment with gerontic septa; B, deciduous segment); 3, *Schuchertoceras*; 4, *Probillingsites* (p. K273, K275-K276) (Furnish & Glenister, n).

a simple circular opening at full maturity. The modified margin, with re-entrants for eyes and propulsive organ, provided maximum protection while permitting the protrusion of tentacles and hyponome.

The family Choanoceratidae is poorly represented, yet sufficiently removed from typical *Ascoceras* to obscure relationships. The group did not develop an inflated ascoceroid conch, and the septal lacunae are ventral in position. Some of the similarities to typical ascocerids may therefore be superficial or indicate early divergence from the parent stock.

## GEOGRAPHIC AND STRATIGRAPHIC DISTRIBUTION

The ascocerids are sufficiently distinctive in appearance for most discoveries, even the chance finding of a single specimen, probably to have become a matter of record. These unique cephalopods have been found in numerous localities in the Ordovician and Silurian of Europe and North America, but largely in areas of most intensive search. Very rarely are more than a few such shells known from a single locality; for example,

FLOWER (33) stated that only about 20 individuals have been secured from the entire type Cincinnatian area. A most noteworthy exception is the ascocerid collection assembled and described by LINDSTRÖM from the Upper Silurian cephalopod-bearing limestones of Gotland. LINDSTRÖM (118a) stated that these beds locally contain a variety of cephalopod shells, and he illustrated (1890, pl. 1, fig. 17) one slab with more than 20 small mature *Parascoceras fistula* packed into an area of 30 sq. cm. Still, the large assemblage of material in Stockholm was made possible only by intensive effort and thorough familiarity with collecting localities; these collections have not been duplicated, even to a small degree, in the ensuing 75 years.

Most of the authentic records of Middle and Upper Ordovician ascocerids refer to North American specimens. A few individuals have been secured from Mohawkian strata of the eastern United States and southeastern Canada; others are known from the Upper Mississippi Valley. Older (Chazyan) Hebetoceratidae from the state of New York may be sufficiently well known to establish them as an ancestral stock; these forms do conform to a stratigraphic occurrence and a level of generalized evolution which is to be expected for primitive ascocerids.

Upper Ordovician ascocerids are relatively well represented in the "Boreal" molluscan-coralline fauna of western United States and central and northern Canada. In the shelf areas of the Eastern Interior and the Maritime Provinces, ascocerids also occur with a brachiopod-bryozoan-trilobite assemblage. In neither occurrence are these peculiar cephalopods a conspicuous faunal element.

Molluscan faunas in Lower Silurian (Llandoveryan) strata of Europe and America are less well represented than those of the younger Silurian (Wenlockian and Ludlovian). For this reason, perhaps, the ascocerids are better known in rocks of Late Silurian age. Ludlovian strata in Gotland and Bohemia have produced the greatest number of specimens and largest diversity of ascocerid species; LINDSTRÖM (118a) described 14 species from rocks of this age. Other regions have produced only isolated

specimens. Seemingly, the greatest diversity and numbers of individuals existed immediately preceding extinction during Late Silurian time.

## PALEOECOLOGY

Many authors have speculated on the paleoecology and life habits of the Ascocerida during their various ontogenetic stages (LINDSTRÖM, 118a; TOBIEN, 193b; FLOWER, 46a; KESLING, 98a). Most students agree that the fully mature ascocerid was a facile swimmer, but wide difference of opinion prevails as to the habits and habitats of early growth stages. Perhaps the most pertinent evidence bearing on this problem is the mutual association of all growth stages. The only localities from which deciduous ascocerid conchs have been identified with certainty are those of the Silurian of Gotland. Each of the several Baltic localities which have yielded juvenile ascocerids is also the source for mature ascocerid conchs. It is most improbable that these associations represent chance post-mortem accumulations, as the delicate shells almost certainly would have been destroyed by appreciable transportation after death of the animals. Failure to recognize the distinctive juvenile portions of the ascocerid phragmocone in localities beyond the confines of Gotland is probably a function of both their rarity and fragility. Disintegration of the deciduous shell presumably began, prior to decollation, with the blockage of the siphuncle. Indeed, it is possible that disintegration of nonvital shell was in an advanced stage before decollation occurred, and that known juvenile conchs represent remains of animals which died before maturity was achieved. Irrespective of these considerations, evidence from known occurrences suggests that juvenile and mature forms occupied the same habitat, as is the case in modern *Nautilus*.

Mature Silurian ascoceratids were almost perfectly adapted for an active nektonic mode of life. Of particular significance was concentration of the gas-filled camerae in a dorsal position, above the body chamber. This arrangement placed the center of buoyancy in a stable position directly above

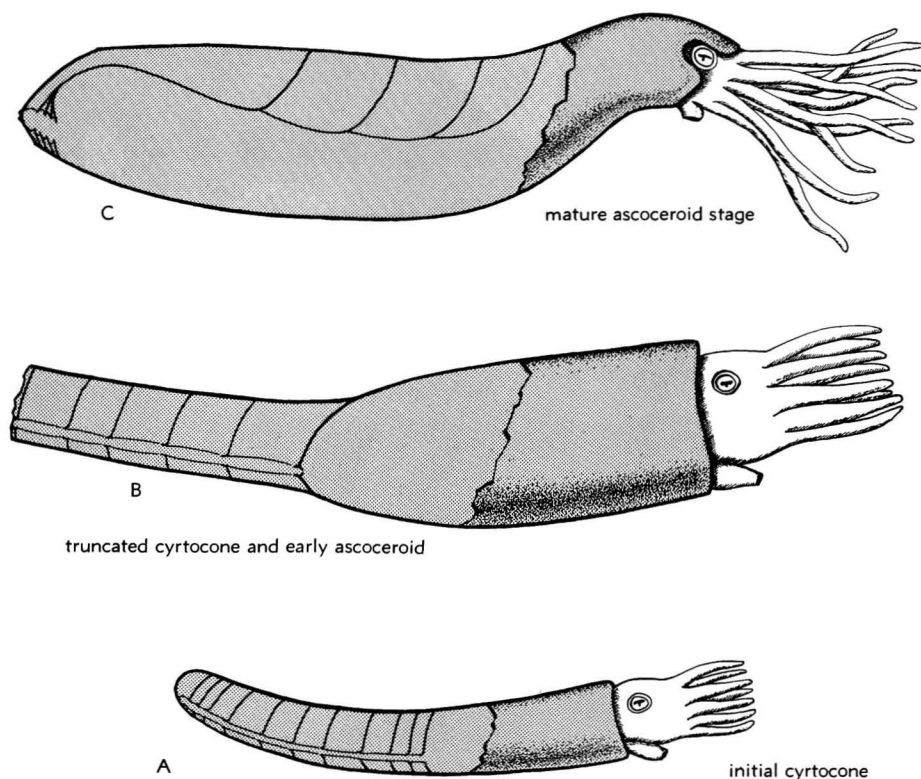


FIG. 190. Ontogenetic series of *Glossoceras lindstroemi* MILLER, U.Sil.(Ludlov.), Sweden(Gotl.); three growth stages, partly restored, in representative ascoceratid; apical portions shown as in section; soft parts schematic;  $\times 2.5$  (p. K273) (Furnish & Glenister, n).

the center of gravity with the conch in a horizontal swimming position. The compressed, attenuate, fusiform contours of almost all Silurian ascoceratids offered minimum hydrodynamic resistance and maximum stability during backward movement. Even the contours of the septum of truncation merge into the mature shell, providing a bluntly rounded leading margin for the conch. Presence of a well-developed hyponomic sinus in at least some fully mature Silurian ascoceratids may be taken to indicate effective adaptation for jet propulsion.

More detailed information on the morphology of the deciduous ascoceratid conch is required before speculation on life habits of the juvenile forms is warranted. Problems are increased by the presumed repeated decollation of the conch. However, if we are correct in assuming that all ontogenetic stages lived in direct association, then a nektonic or nektobenthonic habit can

be attributed to the juvenile ascoceratids.

Progressive development of a nektonic habit is assumed for the Ordovician Ascoceratidae. Available information on the Choanoceratidae and Hebetoceratidae does not provide a trustworthy basis for speculation.

## SYSTEMATIC DESCRIPTIONS

### Subclass NAUTILOIDEA

Agassiz, 1847

Diagnosis given in "Introductory Discussion" (p. K128). *U.Cam.-Rec.*

### Order ASCOCERIDA Kuhn, 1949

[*nom. correct.* FURNISH & GLENISTER, herein (*pro* Ascoceracea KUHN, 1949, order, *partim*)] [=Mixochoanites HYATT in ZITTEL, 1900 (suborder); Ascoceracea KUHN, 1940 (suborder) (*nom. nud.*); Ascoceratida FLOWER in FLOWER & KUMMEL, 1950 (order); Ascoceratina SWEET, 1958 (suborder); ?Ecdyceratida FLOWER, 1962 (order) (*partim*); mention of Ascocerida by FURNISH, GLENISTER, & HANSMAN, 1962 (p. 1341), is disregarded]

Bizarre nautiloids which underwent

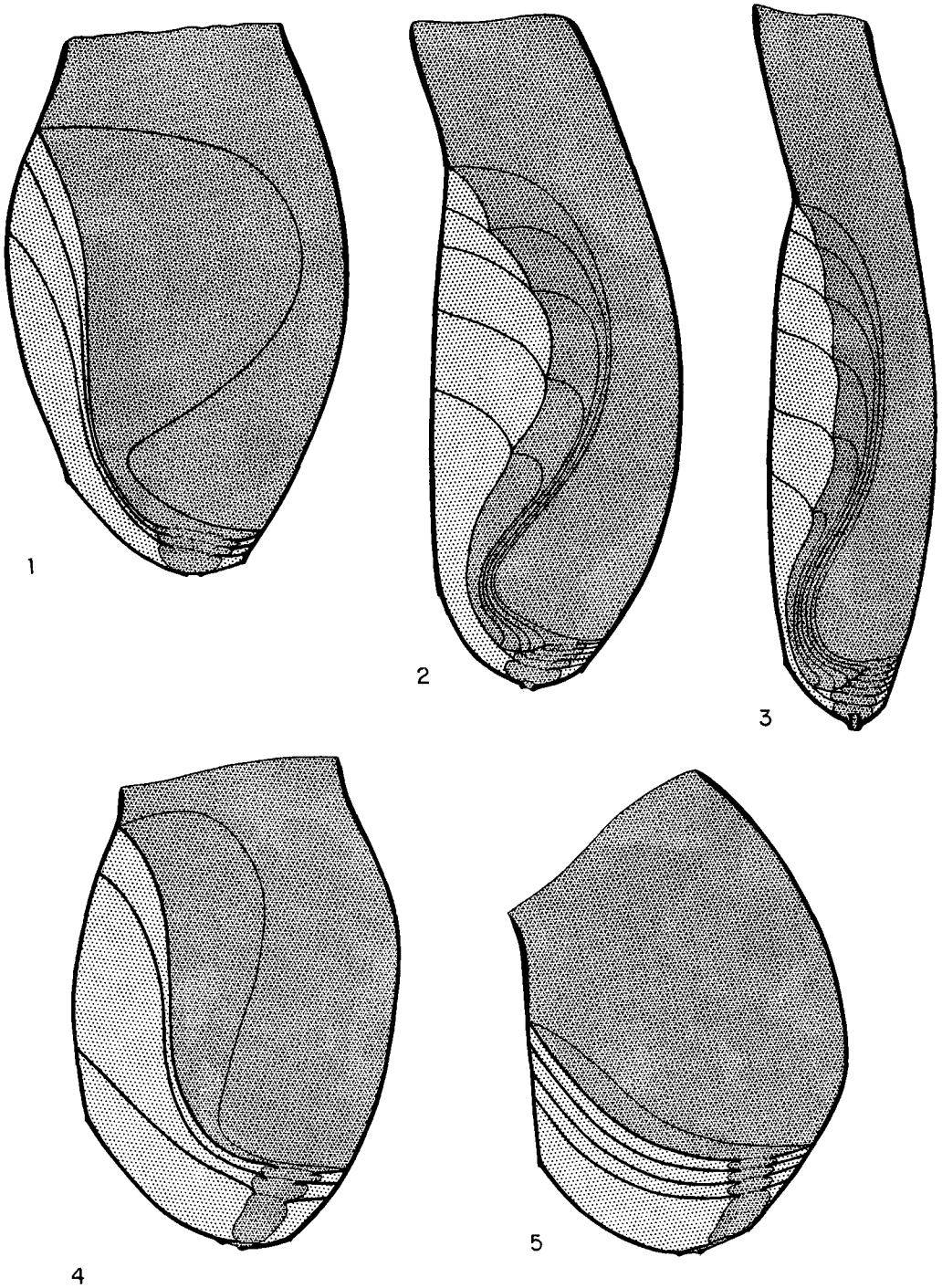


FIG. 191. Diagrammatic cross sections of Ascoceratidae; 1, *Billingsites*; 2,3, *Ascoceras*; 4, *Schuchertoceras*; 5, *Probillingsites* (lines within body chamber represent septal margins as viewed within a hollow conch) (p. K273, K275-K276) (Furnish & Glenister, n).



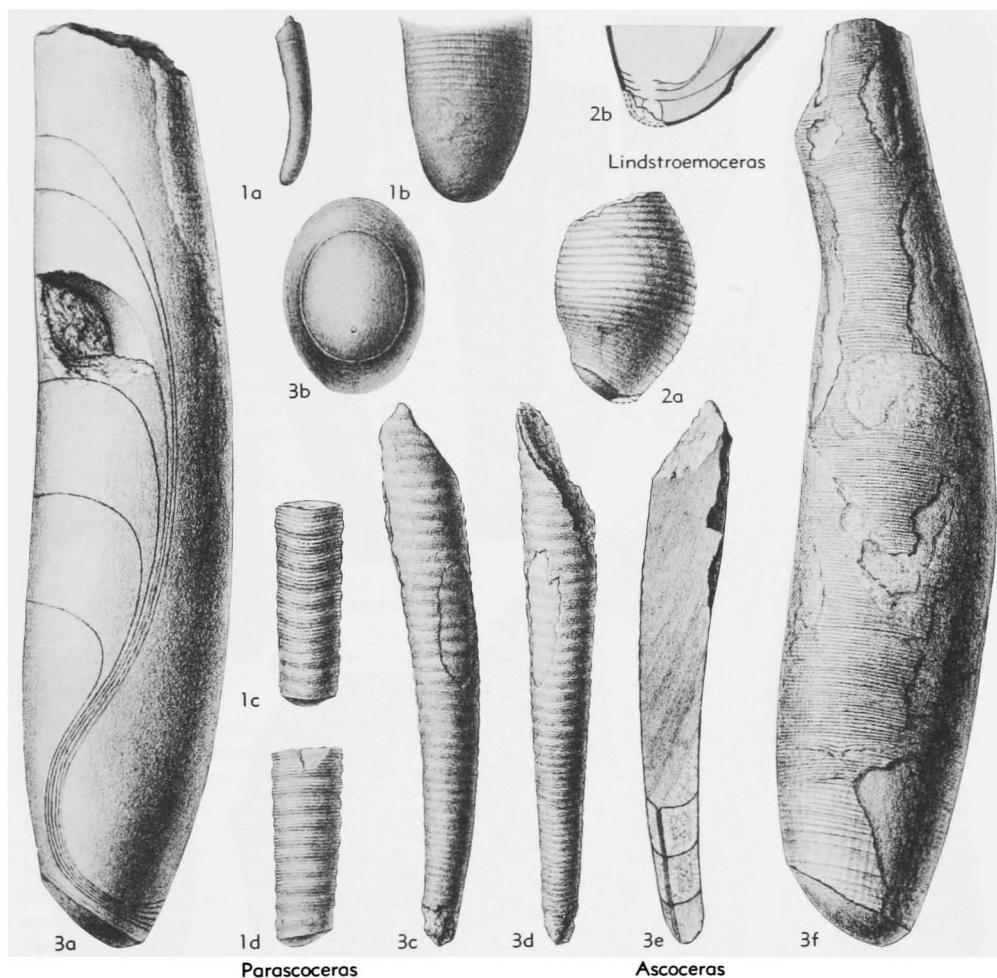


FIG. 192. Ascoceratidae (Ascoceratinae) (p. K273-K275).

periodic truncation of conch; primitively, slender orthocones and cyrtocones with slightly inflated siphuncle and orthochoanitic to suborthochoanitic septal necks; more advanced forms consisting of slender orthoconic to cyrtoconic adapical deciduous section and inflated breviconic adoral ascoceroid portion; siphuncle ventral, subcentral to submarginal in position; deciduous section characterized by long camerae and orthochoanitic septal necks, mature ascoceroid portion recognized by possession of neck and few camerae. *M.Ord.-U.Sil.*

# Family ASCOCERATIDAE Barrande, 1867

[*nom. correct.* HYATT, 1884 (*pro* Ascoceratides BARRANDE, 1867)] [*incl.* Schuchertoceratidae MILLER, 1932]

Conch consisting of longiconic, deciduous early growth stages which underwent periodic truncation, and inflated breviconic mature ascoceroid section. *M.Ord.-U.Sil.*

## Subfamily ASCOCERATINAE Barrande, 1867

[*nom. transl.* FURNISH & GLENISTER, herein (*ex* Ascoceratides BARRANDE, 1867, and Ascoceratidae HYATT, 1884)] [*incl.* Schuchertoceratidae MILLER, 1932]

Exogastric ascoceroid stage characterized by development of neck, ocular and hyponomic sinuses at full maturity, dorsally lacunose septa and sigmoid sutures; siphuncle situated close to venter; siphuncular segments nummuloidal; septal necks cyrtochoanitic, generally with recumbent brims; deciduous stage cyrtoconic to orthoconic, with long but variable camerae, almost straight sutures, orthochoanitic septal

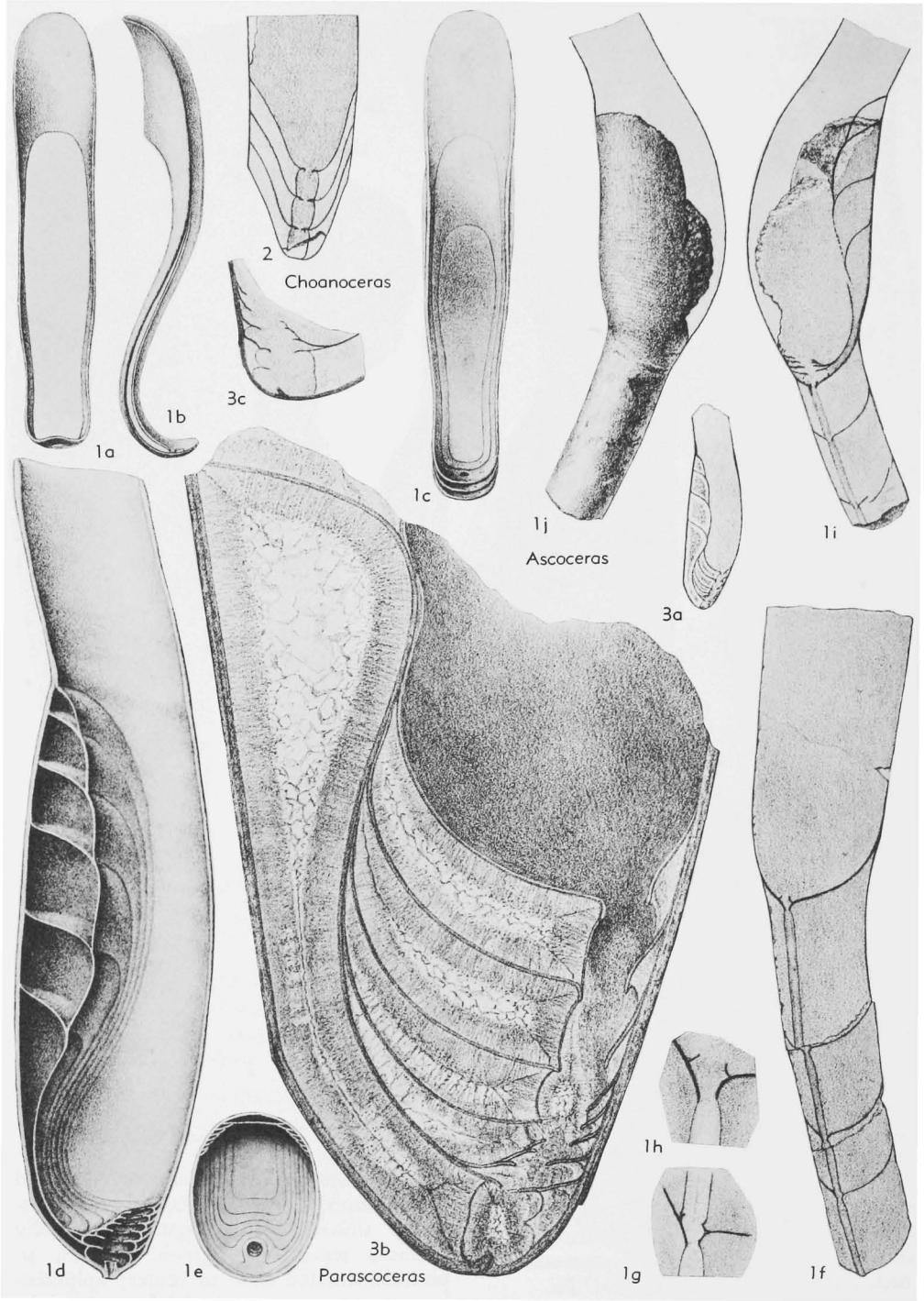


FIG. 193. Ascoceratidae (Ascoceratinae) (p. K273-K275); Choanoceratidae (p. K276-K277).

necks and tubular siphuncular segments, slightly constricted at septal foramina. *M. Ord.-U.Sil.*

**Ascoceras** BARRANDE, 1847, p. 901 [*\*A. bohemicum* BARRANDE, 1855; SD BARRANDE, 1855, p. 174] [= *Cryptoceras* BARRANDE, 1846 (*nom. nud.*) (non *Cryptoceras* D'ORBIGNY, 1849); *Asoceras* MITCHELL, 1890 (*nom. null.*)]. Ascoceroid stage moderately inflated and compressed, with long cylindrical neck; mature aperture unknown; shell surface smooth except for fine lirae; no basal septum; siphuncle decreasing in absolute size adorally; 4 to 7 camerae normally present in mature conch, as many as 12 known in extremes; longiconic deciduous portion of conch weakly annulate. *M.Sil.-U.Sil.*, Eu.-N.Am.—FIG. 189,2; 191,2. *A. collare* LINDSTRÖM, U.Sil. (Ludlov.), Sweden(Gotl.); 189,2, partially restored diagram. long. sec. of siphuncle,  $\times 8$ ; 191,2, diagram. long. sec.,  $\times 2$  (118a).—FIG. 189,1; 191,3; 192,3; 193,1a-h. *A. manubrium* LINDSTRÖM, U.Sil. (Ludlov.), Sweden(Gotl.); 189,1, diagram. long. sec. of siphuncle,  $\times 3$  (Furnish & Glenister, n); 191,3, diagram. long. sec.,  $\times 1$  (118a); 192,3a,b,f, lat. view of internal mold, septal view, and lat. view of specimen with shell retained,  $\times 1$  (118a); 192,3c-e, lat., ventral views, and long. sec. of deciduous portion,  $\times 1$  (118a); 193,1a-e, diagrams showing lacunose septa (1a,b, ventral, lat. views of single septum; 1c, ventral view of 3 septa) and inner views of body chamber (1d, long., 1e, adapical),  $\times 1$  (118a); 193,1f-h, long. sec. of attached deciduous conch,  $\times 1$ , and secs. of enlarged portions of siphuncle,  $\times 2.5$  (118a).—FIG. 193,1i,j. *A. lagena* LINDSTRÖM, U.Sil. (Wenlock.), Sweden (Gotl.); long. sec. retaining part of deciduous conch and lat. view,  $\times 1$  (118a).

**Aphragmites** BARRANDE, 1865, pl. 94, expl. [*\*Ascoceras Buchi* BARRANDE, 1855; SD MILLER, 1932, p. 47]. Like *Ascoceras*, but strongly annulate. *U.Sil.*, Eu.(Boh.).—FIG. 194,1. *\*A. buchi* (BARRANDE); 1a-c, dorsal, lat., septal views,  $\times 1.5$  (5).

**Billingsites** HYATT, 1884, p. 278 [*\*Ascoceras Canadense* BILLINGS, 1857, p. 310; OD] [= *Billingoceras* HYATT, 1884, *nom. null.*]. Ascoceroid stage strongly inflated, depressed, with short, slightly contracted neck; fully mature aperture unknown; shell surface smooth or with moderate transverse sculpture; basal septum absent, ascoceroid septa generally entire, but possibly weakly lacunose; 6 ascoceroid septa present in extreme forms, but 3 common at maturity; siphuncle expanded adorally. Deciduous portion unknown. *U.Ord.*, N.Am.-Eu.—FIG. 191,1; 195,3. *\*B. canadensis* (BILLINGS), U.Ord. (Richmond.), Que. (Anticosti Is.); 191,1, diagram. long. sec.,  $\times 1$ ; 195,3a,b, ventral, lat. views, holotype,  $\times 1$  (3a,b, 63); 195,3c,d, lat., dorsal views,  $\times 1$  (3c, 60; 3d, 63).

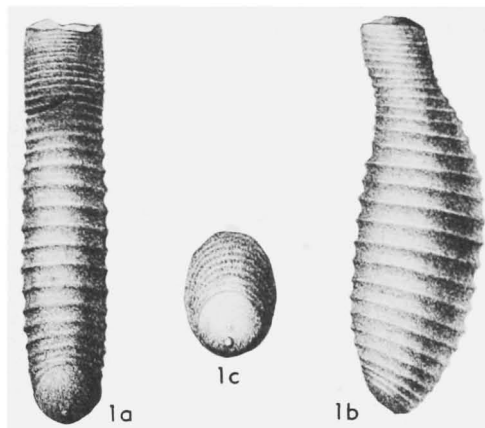


FIG. 194. *Aphragmites buchi* (BARRANDE), Ascoceratidae (Ascoceratinae) (p. K273).

**Glossoceras** BARRANDE, 1865, pl. 94, expl. [*\*Ascoceras (G.) gracile*; OD]. Like *Ascoceras* but with trilobate aperture characterized by prominent dorsal salient, deep ocular sinuses and shallow hyponomic sinus. [May represent mature *Ascoceras* in which aperture is preserved.] *M.Sil.-U.Sil.*, Eu.—FIG. 190; 196,2. *G. lindstroemi* MILLER, U.Sil. (Ludlov.), Sweden(Gotl.); 190, A-C, ontogenetic series,  $\times 2.5$ ; 196,2a-f, fully mature conchs; 2a, lat. view, aperture,  $\times 6$ , 2b, long. sec.,  $\times 1$ , 2c-e, lat., ventral, apert. views,  $\times 1$ , 2f, sec. of siphuncle,  $\times 6$  (118a).

**Lindstroemoceras** MILLER, 1932, p. 32 [*\*Ascoceras dolium* LINDSTRÖM, 1890, p. 21; OD]. Similar to *Aphragmites* but with basal septum; ascoceroid stage small, slightly compressed, strongly inflated but constricted at neck; mature aperture and length of neck unknown; shell annulate; basal septum and 3 ascoceroid septa present at maturity, only last septum lacunose; siphuncle slightly expanded adorally; first siphuncular segment moderately inflated, succeeding segments nummuloidal. Deciduous stage unknown. *U.Sil.*, Eu.—FIG. 192,2. *\*L. dolium* (LINDSTRÖM), U.Sil. (Wenlock.), Sweden(Gotl.); 2a, lat. view,  $\times 1.5$ ; 2b, long. sec.,  $\times 2$  (118a).

**Parascoceras** MILLER, 1932, p. 34 [*\*Ascoceras fistula* LINDSTRÖM, 1890, p. 22; OD] [= *Pseudascoceras* MILLER, 1932, p. 37 (= *Pseudoscoceras* FLOWER, 1941, *nom. null.*)]. Like *Ascoceras* but may have basal septum; ascoceroid stage subcylindrical, slightly compressed; neck long and cylindrical; shell surface coarsely lirate; 3 or 4 lacunose ascoceroid septa generally present at maturity. Deciduous stage orthoconic or slightly curved, circular in cross section, weakly annulate, and with small siphuncle situated close to venter. *U.Sil.*, Eu. (Gotl.).—FIG. 192,1c,d; 196,1. *\*P. fistula* (LINDSTRÖM),

U.Sil.(Wenlock.); 192,1c,d, ventral, lat. views of annulate deciduous conch,  $\times 2$ ; 196,1a,b, lat. view, long. sec. with probable conspecific deciduous conch in body chamber,  $\times 1$  (118a).—FIG. 192, 1a,b; 193,3. *P. decipiens* (LINDSTRÖM), U.Sil. (Ludlov.); 192,1a,b, apical portion,  $\times 1$ ,  $\times 6$ ;

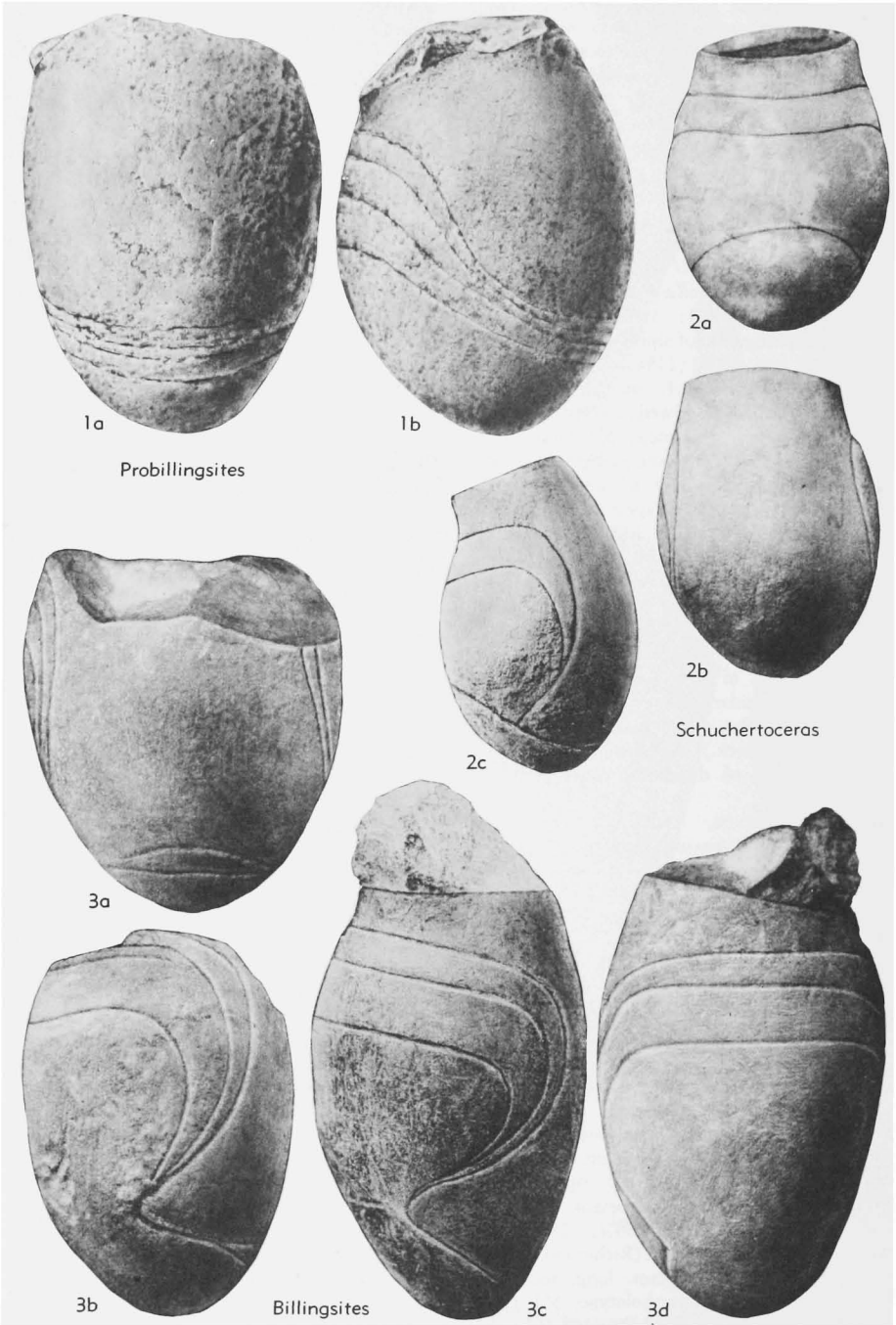


FIG. 195. Ascoceratidae (Ascoceratinae, Probillingsitinae) (p. K273, K275-K276).

193,3a,b; long. sec. showing 4 gerontic septa,  $\times 1$ ,  $\times 10$ ; 193,3c, long. sec., normal siphuncle,  $\times 6$  (118a).

**Schuchertoceras** MILLER, 1932, p. 28 [\**Ascoceras anticostiense* BILLINGS, 1866, p. 60; OD]. Like

*Billingsites* but with basal septum; slight median contraction in long, inflated first siphuncular segment. *U.Ord.*, N.Am.-Eu.—FIG. 191,4; 195,2. \**S. anticostiense* (BILLINGS), *U.Ord.*(Richmond.), Que.(Anticosti Is.); 191,4; diagram. long. sec. re-

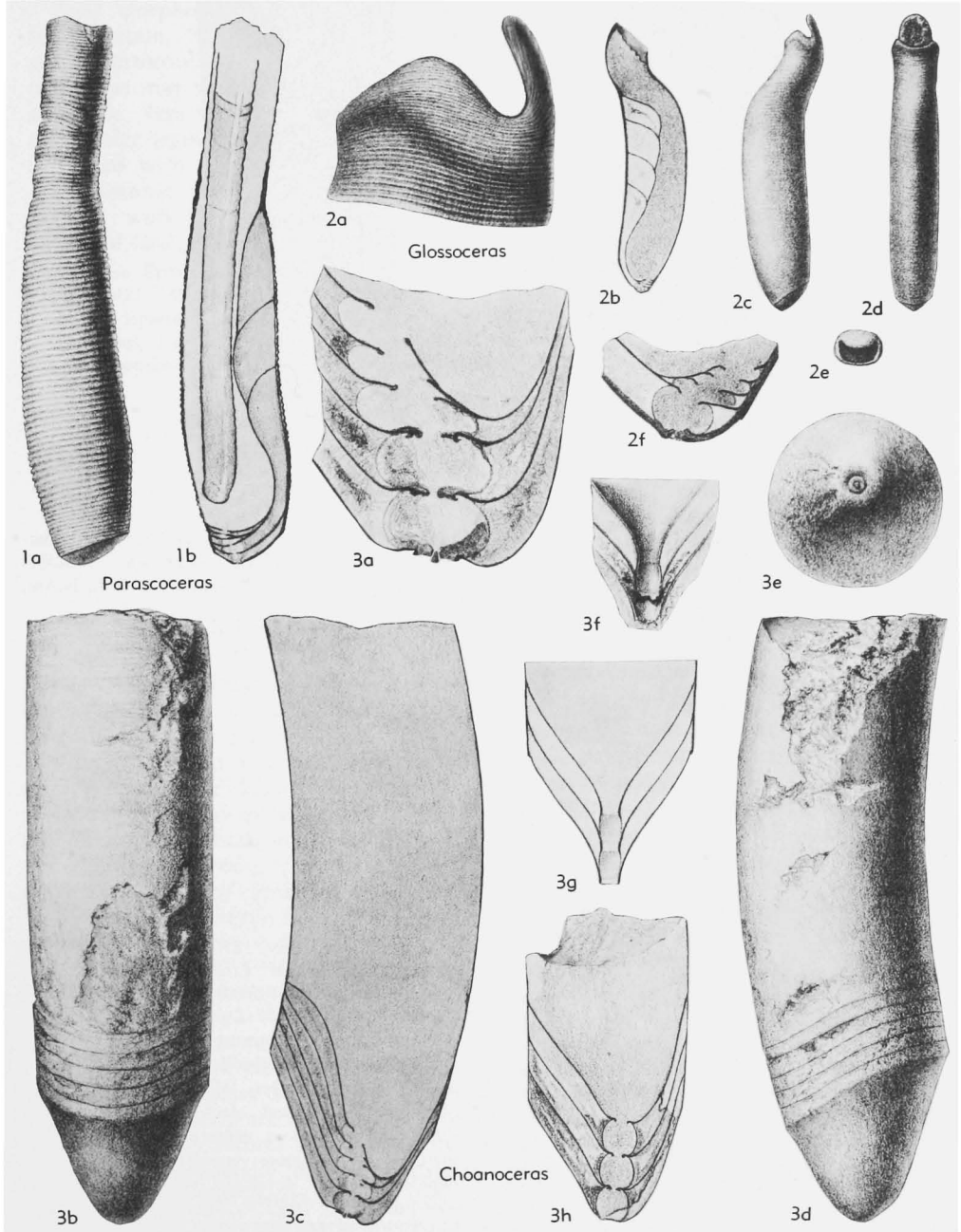


FIG. 196. Ascoceratidae (Ascoceratinae), Choanoceratidae (p. K273-K277).

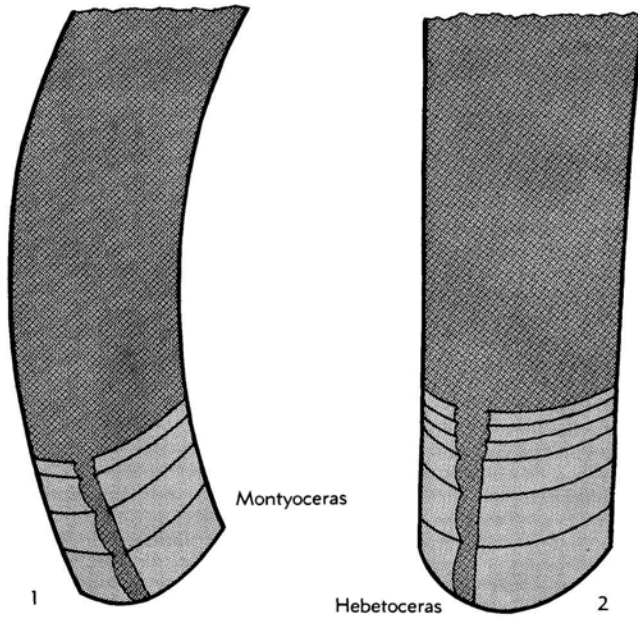


FIG. 197. Hebetoceratidae (p. K277).

stored,  $\times 1$ ; 195,2a-c, dorsal, ventral, lat. views of neoholotype,  $\times 1$  (2a,b, 63; 2c, 60).—FIG. 189, 3. *S. newberryi* (BILLINGS), U.Ord.(Richmond.), Arctic Can.(Devon Is.); diagram. long. sec.,  $\times 9$  (Furnish & Glenister, n).

#### Subfamily PROBILLINGSITINAE Flower, 1941

Mature portion breviconic, with indistinct short neck; septa neither lacunose nor confluent; mature sutures generally oblique and slightly sinuous, but sigmoid in advanced forms. Deciduous section unknown. *M.Ord.-U.Ord.*

**Probillingsites** FOERSTE, 1928, p. 317 [*\*P. welleri*; OD]. Mature portion obese, subcircular in cross section but flattened ventrally, with as many as 5 camerae; siphuncular segments constricted at septal foramina to less than half maximum diameter; connecting rings adnate above and below septa; first siphuncular segment with almost straight dorsal margin in section, its length approximating that of other adoral segments combined. *M.Ord.-U.Ord.*, N.Am.-?Eu.—FIG. 189, 4; 191,5. *P. sutherlandi* SWEET & MILLER, U.Ord., Arctic Can.(Cornwallis Is.); 189,4, siphuncle with displacement canal,  $\times 3.5$ ; 191,5; diagram. sec.,  $\times 1.5$  (Furnish & Glenister, n).—FIG. 195,1. *P. pronis* MILLER & YOUNGQUIST, U.Ord., USA (Iowa); 1a,b, ventral, lat. views,  $\times 1.5$  (136).

**Shamattawaceras** FOERSTE & SAVAGE, 1927, p. 31 [*\*S. ascoceroides*; OD]. Poorly known. Appar-

ently similar to *Probillingsites*, but with flattened venter; siphuncle unknown. [Possibly senior synonym of *Probillingsites*.] *U.Ord.*, N.Am.

#### Family CHOANOCERATIDAE Miller, 1932

Conch slightly curved, with gradual rate of expansion, apertural modifications unknown; septa forming deep asymmetrical cones; adoral septa lacunose over part of area between siphuncle and venter; sutures straight; siphuncle subcentral, siphuncular segments gradually changing from slightly expanded in early growth stages to nummuloidal at maturity; mature septal necks cyrtocochanitic and recumbent. *U.Sil.*

**Choanoceras** LINDSTRÖM, 1890, p. 34 [*\*C. mutabile*; OD] [= *Choaniceras* LINDSTRÖM, 1888 (*nom. nud.*); *Choniceras* LINDSTRÖM, 1888 (*nom. null.*); *Coanoceras* FLOWER, 1941 (*nom. null.*)]. Form of deciduous juvenile stages uncertain; mature conch gently curved exogastrically, longitudinally lirate; mature body chamber large in proportion to phragmocone retained after truncation; sutures sloping adorally from venter; 3 adoral septa of mature forms lacunose ventrally; annulosiphonate deposits weakly developed. *U.Sil.*, Eu.(Gotl.).—FIG. 193,2; 196,3. *\*C. mutabile*, U.Sil.(Wenlock.); 193,2, 196,3f-h, long. secs. of presumed conspecific deciduous portions,  $\times 1$  (193,2, 196,



3*h*),  $\times 3$  (196,3*f,g*); 196,3*a*, long. sec., mature siphuncle,  $\times 3$ ; 196,3*b-e*, ventral view, long. sec., lat. view, septum of truncation,  $\times 1$  (118*a*).

### Family HEBETOCERATIDAE Flower, 1941

[incl. Ecdyceratidae FLOWER, 1961]

Shell morphology and ascocerid affinities uncertain. Slender orthocones and exogastric cyrtocones in which periodic natural truncation may have occurred; septa entire; siphuncle ventral, commonly subcentral; siphuncular segments ranging from slightly expanded with ?plano-convex outline and orthochoanitic septal necks to moderately inflated with open cyrtochoanitic septal necks. *M.Ord.*, ?*U.Ord.*

**Hebetoceras** FLOWER, 1941, p. 545 [*\*H. mirandum*; OD]. Mature section of conch smooth, slender, depressed, orthoconic, with as many as 6 camerae; hyponomic sinus probably present; sutures simple, with slight anterior inclination

dorsally; adapical septa strongly arched, adoral septa less convex; siphuncle midway between conch axis and venter, slightly expanded adorally; adapical siphuncular segments flat dorsally, weakly expanded ventrally, with orthochoanitic septal necks; adoral segments biconvex, with suborthochoanitic to open cyrtochoanitic septal necks. *M.Ord.*, N.Am.—FIG. 197,2. *\*H. mirandum*, Chazy, USA(N.Y.); diagram. long. sec.,  $\times 1.5$  (after 26).

**Ecdyceras** FLOWER, 1941, p. 546 [*\*E. sinuiferum*; OD] [= *Pachecdyeras* FLOWER, 1947, p. 429; *fide* FLOWER, 1962, p. 1]. Doubtful hebetoceratid affinities; superficially like *Hebetoceras* but more depressed and typically with deep, rounded dorsal and ventral lobes, adoral siphuncular segments unknown. *M.Ord.*, ?*U.Ord.*, N.Am.

**Montyoceras** FLOWER, 1941, p. 539 [*\*M. arcuatum*; OD]. Like *Hebetoceras* but cyrtoconic, exogastric, and with all siphuncular segments plano-convex. *M.Ord.*, N.Am.—FIG. 197,1. *\*M. arcuatum*, Chazy, USA(N.Y.); diagram. long. sec.,  $\times 1.5$  (after 26).

## NAUTILOIDEA—ONCOCERIDA

By WALTER C. SWEET

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### MORPHOLOGY

#### GENERAL CHARACTERS

Primitive oncocerid conchs were cyrtocones. From these, however, virtually straight shells came to be developed, some of them with inflated body chambers and contracted apertures (brevicones), the peristomes of which, in many species, are elaborately sinuous. From primitive cyrtocones also developed rapidly or gradually enlarging longiconic cyrtocones, orthocones, gyrocones, torticones, serpenticones, and nautilicones. Primitively, the conch was compressed and exogastric; in more specialized later groups, however, slightly to markedly endogastric curvature developed and conchs of depressed section are numerous in several large families. Sutures are almost invariably simple, generally directly transverse, and, in only a few genera, notably sinuous. Smooth shells, or ones marked only by a pattern of fairly closely spaced transverse

growth lines, are the rule; however, a surficial pattern of posteriorly imbricating growth band lamellae, in some genera giving rise to surficial annulation, is not uncommon in many Silurian species, and a few oncocerids exhibit longitudinal ribs or ridges normal to growth lines or bands, producing a cancellated or reticulated surface pattern. True annulation of the shell (involving its inner as well as its outer surfaces) is known in the Oncocerida, but is not common.

ZHURAVLEVA (214) has figured and described the initial, or embryonic, stages of four species of Devonian Oncocerida, representing the families Brevicoceratidae, Acleistoceratidae, and perhaps Polyelasmoceratidae. Her outline drawings are shown in Fig. 198 and need not be described again here. From these few specimens, ZHURAVLEVA concludes that Devonian Oncocerida built an embryonic phragmocone (within the egg) consisting of one or two chambers,

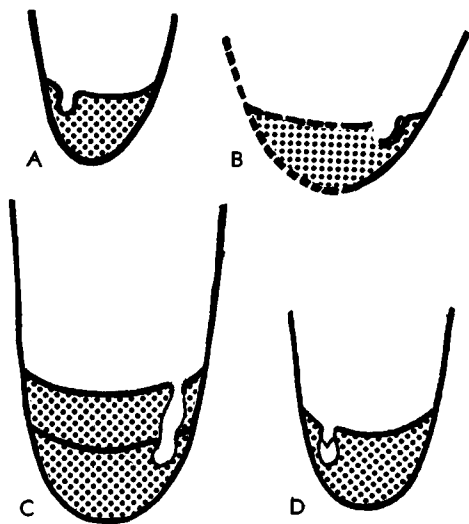


FIG. 198. Diagrammatic dorsoventral sections through the embryonic conchs of four Devonian oncocerids: A,D, *Anglicornus* sp.,  $\times 5$ ,  $\times 6$ ; B, *Paracleistoceras* sp.,  $\times 12$ ; C, *Turoceras schnyrevae* ZHURAVLEVA,  $\times 6$  (214).

set off externally from the postembryonic phragmocone by finer sculpture, a weak constriction, or thickening of the external shell layer. Internally, these embryonic chambers are somewhat longer than the first postembryonic chambers, but are not separated from the latter by a constriction, as in representatives of other nautiloid orders investigated by her. The siphuncle begins in the first, cap-shaped chamber; it is closed adapically, bulbous, and adjacent to, or partially contiguous with, the ventral wall of the conch.

Primitively and commonly, the siphuncle of the Oncocerida is located in the ventral portion of the conch; in most genera it is submarginal or marginal in position. The earliest siphuncular stages have not been studied or figured for most species; however, in early Middle Ordovician forms, the earliest segments known are characterized by short, orthochoanitic septal necks and straight, thin-walled, tubular connecting rings (32, 33). Later in development of primitive forms, and probably throughout the conch of advanced forms, the septal necks are cyrtochoanitic on at least one side of the siphuncle, and the connecting rings are variously inflated to produce a siphuncu-

lar outline that has been described as "beaded," "nummuloidal," "ellipsoidal," "cylindroid," "ovoid," or "moniliform." Ordinarily, the connecting rings are thin and not divided into distinguishable lamellae or other structures. However, in "actinosiphonate" forms, the connecting rings in at least the later siphuncular segments are thickened and their inner surfaces produced into a series of radially disposed longitudinal lamellae (*lamelles rayonnantes*).

In several stocks of the Oncocerida, relatively more rapid secretion of shell material dorsally than ventrally resulted in slight to marked endogastric curvature. In these forms, the siphuncle ordinarily retains its submarginal, ventral position and typically oncocerid structure, including the development of actinosiphonate deposits in some of them. In one genus, *Archiacoceras*, the siphuncle has been shown to be dorsal and marginal in position (31); it is possible, but rather improbable, that several other oncocerid genera thought to be endogastric are actually exogastric forms with dorsal siphuncles. This has not been demonstrated.

Cameral deposits are virtually unknown in the Oncocerida, although they may occur, of course, in any number of genera for which internal information is currently lacking. In many genera, however, the surface of steinkerns is marked by a series of longitudinal grooves and ridges, indicating that the interior of the cameral walls was of irregular circumferential thickness. This may indicate that "incipient" cameral deposits were rather persistently present throughout the order; or, these longitudinal markings may be associated in many forms with loculi in a narrow, distinctive "basal zone," extending transversely about the conch at the posterior end of the mature body chamber and probably representing the loci of secretion of excess shell material by the adult animal in the zone of epithelial muscle attachment.

The loci of attachment of the shell, or retractor muscles of the cephalopodium are known for only a few oncocerids (*Oncoceras*, *Beloitoceras*, *Diestoceras*, and possibly *Poterioceras*) (15, 180). In these forms, muscles were functionally attached along lunate areas immediately to each side of the ventral mid-line. For the present, at least,



it may then be assumed that the primary pattern of muscle attachment in the Oncocerida was ventromyarian.

### ACTINOSIPHONATE DEPOSITS

Many species now included in the Oncocerida possess endosiphuncular structures in the form of more or less longitudinal lamellae projecting inward toward the siphuncular axis from the inner surfaces of the connecting rings. Although the origin and mode of formation of these structures vary considerably, they are termed collectively, actinosiphonate deposits. Only a few actinosiphonate species have been studied in detail, but at least the following five types of actinosiphonate structures have been recognized (16, 31). (1) Deposits formed as simple **thickenings of the connecting rings**, produced toward the siphuncular axis in **radially arranged longitudinal lamellae**. Such deposits form initially in the region of the septal foramen; rays may then extend adorally, in some species through several siphuncular segments (e.g., *Valcouroceras*, *Augustoceras*, *Minganoceras*). (2) Deposits apparently of segmental origin as in (1), but **rays alternately bladeliike and distally bifid** (e.g., *Actinomorpha*, *Polyelasmoceras*). (3) Deposits of segmental origin as in (1) and (2), but rays in one segment aligned and fused with those of adjacent segments to form **lamellae continuous through a number of siphuncular segments** (e.g., *Archiacoceras*). (4) Deposits of irregular, complex processes produced from a **lining in the siphuncular foramen**. The lining is reminiscent of that in some Discosorida; development of actinosiphonate processes from it, however, is not (e.g., *Danoceras*, *Diestoceras*). (5) Deposits consisting of a **siphuncular lining and short, simple processes arising from it in the septal foramen**. Typically, these processes bifurcate distally, are always discrete, and are never markedly complex (e.g., *Brevioceras*, *Eleusoceras*, *Foersteoceras*, *Mitroceras*, other Brevioceratidae).

In addition, in at least one Devonian genus (*Xenoceras*) the connecting ring is thickened in the septal foramen to form a bulbous, pendent process, superficially similar to discosorid bullettes, but apparently different in origin and internal structure.

Presumably, this represents a degenerate or highly modified actinosiphonate structure, characterized by connecting ring thickening and by the absence of discrete longitudinal lamellae.

Actinosiphonate deposits are bizarre. Collectively and superficially, they are so similar in appearance that, until fairly recently, nautiloids with such structures were thought to form a distinct and closely related genetic unit. However, even HYATT (97) and FOERSTE (57), who referred these nautiloids to a division "Actinosiphonata" of the suborder Cyrtoceroanites, found it difficult to exclude from this division closely related forms distinguished only by the absence of actinosiphonate deposits. Although true actinosiphonate structure seems limited to species of oncocerid affinities, not all oncocerids exhibit such structures. Several lines of reasoning suggest that the deposits are not only polyphyletic in origin within the Oncocerida, but otherwise peculiar in their appearance in species known to possess them. That is, actinosiphonate deposits include at least the five (or six) distinct types outlined above; their distribution among individuals of actinosiphonate species is erratic (only late mature or gerontic conchs exhibit them consistently and immature forms may have empty siphuncles); and many species with such structures can be shown to be closely related in other ways to nonactinosiphonate species. Consequently, it has been suggested that actinosiphonate deposits were formed fairly rapidly in pre-existing siphuncular spaces of the gerontic or near-gerontic individuals of advanced, specialized species, probably not greatly different otherwise from contemporaneous, nonactinosiphonate oncocerids (31). The presence of such deposits in siphuncles of all genera in several families (e.g., Valcouroceratidae, Diestoceratidae, Hemiphragmoceratidae, Brevioceratidae, Jovellaniidae, Nothoceratidae, Archiacoceratidae, Polyelasmoceratidae) and late genera of other families of Oncocerida (e.g., Oncoceratidae, Acleistoceratidae, ?Karoceratidae), suggests closely similar conformation in the entire order of the siphuncular tissues by or within which these deposits were secreted.

## DISTRIBUTION AND PHYLOGENY

Representatives of the Oncocerida are conspicuous as fossils in Ordovician, Silurian, and Devonian faunal assemblages in North America, Europe, Australia, and some parts of Asia (where they are not, however, well known). The order continues, in much smaller numbers, into the Lower Carboniferous, but is apparently not known from the Upper Carboniferous or Permian. Apparently, oncocerids reached the peak of their abundance and diversity in the widespread warm seas of the Middle Silurian, although Middle Devonian assemblages are comparable in numbers of genera described, and few Middle and Upper Ordovician nautiloid faunas are without representatives of at least one oncocerid family.

Four families of Oncocerida (Graciloceratidae, Oncoceratidae, Tripteroceratidae, Valcouroceratidae) appear simultaneously in early Middle Ordovician rocks in North America, and a few representatives of the latter three families are known from virtually contemporaneous strata in northern Europe. The Graciloceratidae, with thin-walled, empty, orthochoanitic siphuncles, are the most primitive of the Oncocerida; they are difficult to distinguish from Lower Ordovician Bassleroceratidae (Ellesmerocerida), from which they were almost certainly derived, and from which they differ only in having thin, rather than thickened, connecting rings. From the Graciloceratidae, three persistent oncocerid groups were produced: (1) the Oncoceratidae, primitively breviconic and retaining in their early camerae the orthochoanitic to suborthochoanitic siphuncle of the Graciloceratidae, but later developing cyrtochoanitic necks and moderately to considerably expanded siphuncular segments; (2) the Tripteroceratidae, longicones with small siphuncles similar to those of the Oncoceratidae; and (3) the Valcouroceratidae, cyrtoconic brevicones of depressed, subtriangular section and cyrtochoanitic siphuncle, occupied, at least in adults, by complex actinosiphonate deposits. The Graciloceratidae, Tripteroceratidae, and Valcouroceratidae appear to be confined to the Middle and Upper Ordovician; the

Oncoceratidae continue (via *Oonoceras* and others) into the Silurian, at which time the family underwent a second great expansion.

Ordovician *Oncoceras* (Oncoceratidae) seems the most likely ancestor for the faintly endogastric Ordovician Diestoceratidae, although the possibility remains that this small, peculiar group may have been derived from the Discosorida through modification of discosorid bullettes to produce short, irregular actinosiphonate rays, closely approximating those of the Oncocerida (50). A similar origin for the endogastric Silurian Hemiphragmoceratidae (from *Oncoceras*) and the exogastric Silurian Trimeroceratidae, is the only one that now seems at all likely. Nevertheless, the Trimeroceratidae, with slender, empty siphuncles are difficult to associate positively with the Oncocerida, and it has been suggested that this strange group may also have been derived from the Discosorida, one family of which (Mandaloceratidae) exhibits the tendency for reduction of the siphuncle from broadly expanded segments with thick rings to slender segments with thin rings (50).

From *Oonoceras* (Oncoceratidae), of the Middle Silurian, developed the compressed, torticonic *Oxygonioceras*, which is considered to be the point of origin of the dominantly Devonian Brevicoceratidae. It is probable that *Oonoceras* was also ancestral to Silurian *Perimecoceras* and *Blakeoceras*, concavosiphonate and actinosiphonate forms that, in the late Silurian or early Devonian, gave rise to the similarly concavosiphonate and actinosiphonate cyrtocones, nautilicones, and torticones of the Nothoceratidae (42). A similar origin in Silurian *Oonoceras* or *Oocerina* can be logically postulated for the endogastric Silurian *Codoceras* and *Danaoceras*, which, in turn, seem ancestral to the largely Devonian Polyelasmoceratidae, a group of relatively large, actinosiphonate, endogastric oncocerids.

Some part of the small group of depressed Ordovician Oncoceratidae, or perhaps a form like *Oncoceras*, was the progenitor of a large group of depressed, exogastric Silurian oncocerids typified by *Amphicyrtoceras* and here regarded as early Acleistoceratidae. The Devonian Acleisto-

ceratidae seem to have been derived from the Oncoceratidae by way of the *Amphicyrtoceras* stock, which may have given rise, as well, to other Devonian oncocerids (Poterioceratidae, Karoceratidae), the origins of which are as yet obscure.

The most logical ancestors of the Silurian and Devonian Jovellaniidae are Ordovician Valcouroceratidae; however, no bridge is known between the two groups at present. The origins of the anomalous Devonian Archiacoceratidae and the Devonian and Mississippian Tripleuroceratidae, a probably artificial group, are quite unknown.

### CLASSIFICATION

With a few important exceptions and a number of additions based on more adequate knowledge of early Paleozoic nautiloids than was available 60 years ago, the concept of an order Oncocerida is virtually that of the division "Actinosiphonata" of HYATT's suborder Cyrtoceroidea (97). Although HYATT seems to have regarded cyrtoceroidean septal necks and actinosiphonate lamellae within the siphuncle as primary characters of his Actinosiphonata, he also included in this division genera and groups of genera not known to be actinosiphonate, but closely related in other ways to actinosiphonate forms. In his many studies of nautiloid cephalopods, primarily between 1924 and 1938, FOERSTE concerned himself very little with suprageneric taxonomy. However, in several places, he, too, seems to have experienced difficulty in separating actinosiphonate cephalopods from others not known to be actinosiphonate—hence, at least indirectly, he may be said to have supported HYATT's inclusion of both types in the same general suprageneric or suprafamilial categories. TEICHERT, on the other hand, held that known actinosiphonate cephalopods should be grouped together in an ordinal category (for which he proposed the name "Cyrtoceroidea" in 1933), distinguished from other orders of shell-bearing cephalopods by the presence of actinosiphonate deposits (185, 187). Oncocerida without actinosiphonate deposits were grouped in a separate order, Gomphoceroidea, by TEICHERT. In 1939, TEICHERT subdivided his order Cyrtoceroidea into nine

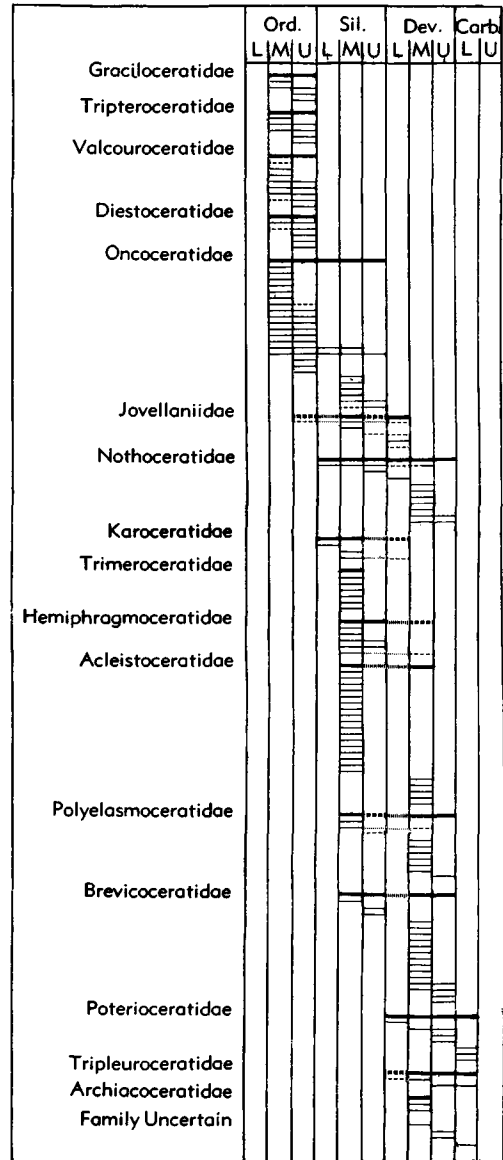


FIG. 198A. Stratigraphic distribution of genera and families of Oncocerida (Sweet, n).

families (four of them new at the time), the characters of which may be deduced from the nature of the nominate genus of each. These families are Jovellaniidae, Diastoceratidae, Oocerinidae, Karoceratidae, Cyrtoceratidae, Archiacoceratidae, Phragmoceratidae, Ptenoceratidae, and Nothoceratidae.

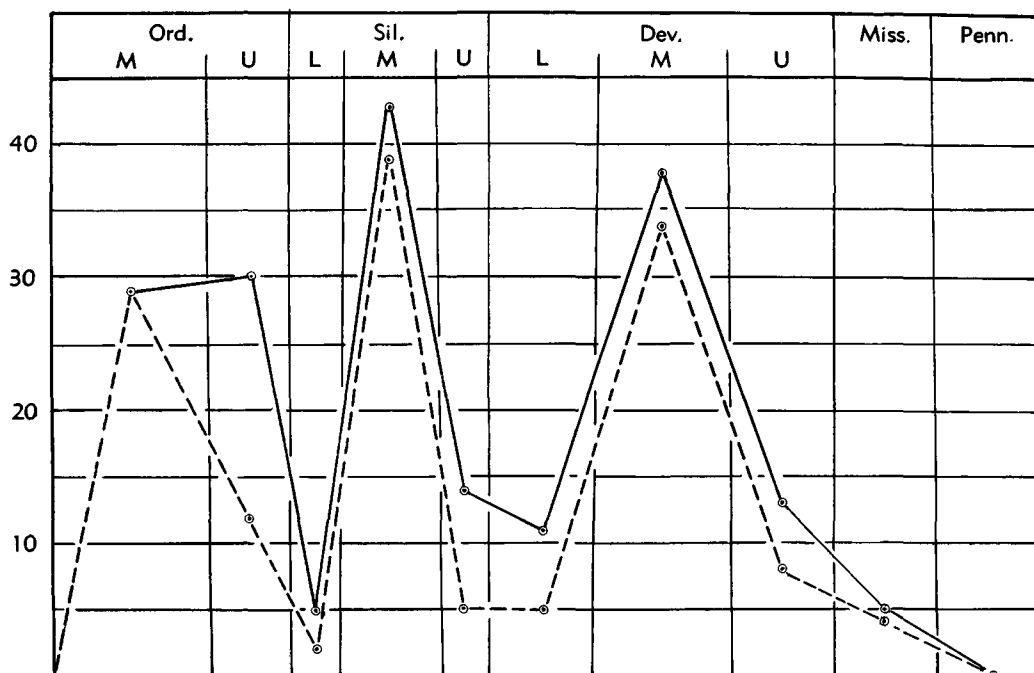


FIG. 198B. Graph showing numbers of new genera of Oncocerida introduced in successive epochs (dashed lines) and total genera represented in each (solid lines) (Sweet, n).

FLOWER's studies of the form and distribution of actinosiphonate deposits in a number of early Paleozoic nautiloids resulted in the conclusion (discussed above) that the occurrence of such structures is entirely too erratic to be of primary taxonomic value (31, 33). That is, actinosiphonate deposits seem to be formed only in the larger species of many genera, and, even then, they frequently seem to be adult or perhaps gerontic features. Hence, even within genera, the distribution and presence or absence of actinosiphonate siphuncles may be an unreliable guide to relationship. As a consequence of this, FLOWER included most actinosiphonate nautiloids with quite a number of otherwise similar nonactinosiphonate forms, at first in a superfamily Oncoceroidea, later in an order Oncoceratida (33, 49, 50). Thus, FLOWER's concept of the Oncocerida (essentially the one followed herein) is parallel to, if somewhat more elaborate than, HYATT's of 1900, in that both the Oncocerida and the "Cyrtchoanites Actinosiphonata" include both actinosiphonate and nonactinosiphonate nautiloids, with

relationships between the groups deduced primarily from similarities or differences in other structures.

## SYSTEMATIC DESCRIPTIONS

### Subclass NAUTILOIDEA Agassiz, 1847

Diagnosis given in "Introductory Discussion" (p. K128). *U.Cam.-Rec.*

### Order ONCOCERIDA Flower in Flower & Kummel, 1950

[*nom. correct.* SWEET, herein (*pro* Oncoceratida FLOWER in FLOWER & KUMMEL, 1950; *emend.* FLOWER in FLOWER & TEICHERT 1957; mention of Oncocerida by FURNISH, GLENISTER, & HANSMAN, 1962 (p. 1343), is disregarded) [=Actinosiphonata HYATT in ZITTEL, 1900 (division of suborder), Cyrtoceroidea, Gomphoceroidea TEICHERT, 1933 (orders); Cyrtoceroidea, Gomphoceroidea SCHINDEWOLF, 1935 (suborders); Oncoceroidea FLOWER, 1946 (superfamily); Cyrtoceroidea KUHN, 1949 (order, *partim*); Oncoceroidea FISCHER in MOORE, LALICKER, & FISCHER, 1952 (order); Oncoceratina SWEET, 1958 (suborder)]

Primitively compressed exogastric cyrtocones and brevicones, from which developed a number of straight, torticonic, gyroconic, and nautiliconic forms, many with depressed section and endogastric curvature. Siphuncle on the ventral side of center; sep-

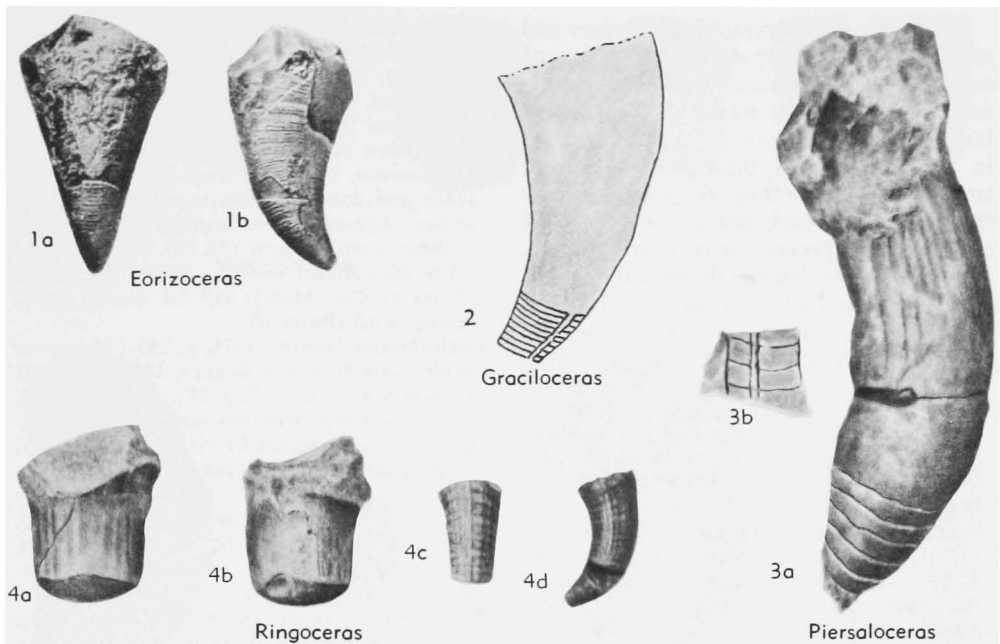


FIG. 199. Graciloceratidae (p. K283).

tal necks tubular or suborthochaoanitic in early stages and primitive forms, cyrtchoanitic in adults and probably throughout conch of derived forms. Siphuncular segments generally slender, but may be large and considerably inflated. Connecting rings typically thin, but may be thickened in adult or gerontic individuals and variously produced to form actinosiphonate deposits (33, 49, 50). *M.Ord.-L.Carb.(Miss.)*.

The stratigraphic occurrence of genera included in the Oncocerida is shown graphically in Figure 198A; the numbers of new genera introduced in successive epochs are indicated in Figure 198B.

#### Family GRACILO CERATIDAE Flower in Flower & Kummel, 1950

Exogastric cyrtocoines with tubular, thin-walled, orthochaoanitic siphuncle, which is empty and marginal or subventral (49, 50). [Probably derived from Bassleroceratidae (Ellesmerocerida), but differing primarily in having thin, homogeneous connecting rings.] *M.Ord.-U.Ord.*

**Graciloceras** FLOWER, 1943, p. 72 [*\*G. longidomum*; OD]. Conch slender, compressed, regularly expanding; body chamber much longer than phragmocone. Siphuncle subventral (31, 33). *M.*

*Ord.-U.Ord.*, N.Am.—FIG. 199, 2. *\*G. longidomum*, *M.Ord.*, USA(N.Y.); long. sec., venter right,  $\times 1$  (31).

**Eorizoceras** FLOWER, 1943, p. 69 [*\*E. platyceroides*; OD]. Conch apically curved, adorally straight, rapidly expanding, faintly compressed; ephebic section ovoid, sutures straight, slightly oblique; shell exterior with transverse bands and finer longitudinal markings; no hyponomic sinus. Siphuncle small, ventral (31). *M.Ord.*, N.Am.—FIG. 199, 1. *\*E. platyceroides*, USA(N.Y.); 1a, b, venter and lat. (venter left),  $\times 1$  (31).

**Piersaloceras** TEICHERT, 1930, p. 282 [*\*P. gageli*; OD]. Like *Graciloceras*, but larger, not distinctly compressed, siphuncle well removed from venter; surface with weak longitudinal ribs crossed by thick, ripple-shaped flutings (183). *U.Ord.*, Eu.(Est.).—FIG. 199, 3. *\*P. gageli*; 3a, b, lat. (venter right) and long. sec.,  $\times 1$  (183).

**Ringoceras** STRAND, 1934, p. 24 [*\*R. praecurvum*; OD]. Small, strongly curved, depressed; surface with longitudinal ribs and fine, irregular transverse striae. Siphuncle subventral; internal structure not known (176). *U.Ord.*, Eu.(Norway).—FIG. 199, 4. *\*R. praecurvum*; 4a-d, dorsal, lat. (venter left), ventral, lat. (venter right),  $\times 1$  (176).

#### Family ONCOCERATIDAE Hyatt, 1884

[Incl. Maelonoceratidae HYATT, 1884 (=Melonoceratidae HYATT, 1894); Oncoceratidae, Rizoceratidae HYATT in ZITTEL, 1900; Oocerinidae TEICHERT, 1939; Oonoceratidae FLOWER, 1942]

Exogastric, ventromyarian brevicones and cyrtocoines with empty siphuncles on ventral side of center. Siphuncles suborthochoanitic and tubular in early stages of early forms, but cyrtchoanitic with expanded segments in later stages and throughout conch of later forms. Connecting rings thin. Conch typically compressed, but a few species of circular or depressed section are known. Actinosiphonate deposits developed in a few advanced forms (33, 49). *M.Ord.-U.Sil.*

**Oncoceras** HALL, 1847, p. 197 [*\*O. constrictum*; OD] [= *Oncoceras* TATE, 1868 (*nom. null.*)]. Compressed, curved brevicones, gibbous behind body chamber and contracting to aperture. At gibbous region, convexity of ventral profile typically increased; dorsal profile concave adapically, convex over gibbous region. Siphuncle small, ventral; segments ovoid to scalariform, generally longer than wide. Septal necks short, recurved (33, 83). *M.Ord.-U.Ord.*, N.Am.-Eu.—FIG. 200, 3. *\*O. constrictum*, M.Ord., USA (N.Y.); *3a,b*, lat. (venter right), septum (venter up),  $\times 1$  (53). *?Asaphiceras* FOERSTE, 1928, p. 314 [*\*A. schucherti*; OD]. Compressed, straight to faintly cyrtoconic shells with slight dorsal gibbosity on adoral part of phragmocone. Siphuncle large, ventral, empty; segments moderately expanded within camerae. Reported to be achoanitic, but probably cyrtchoanitic with short, strongly recurved necks (60). *M.Sil.*, N.Am.—FIG. 203, 3. *\*A. schucherti*, Can. (Anticosti Is.); *3a,b*, lat. (venter left), ventral,  $\times 0.5$  (60).

**Beloitoceras** FOERSTE, 1924, p. 244 [*\*Oncoceras pandion* HALL, 1861, p. 45; OD]. Like *Oncoceras*, but less inflated and gibbous on body chamber rather than on phragmocone; dorsal profile may be concave adapically, but is straighter or slightly convex over parts of body chamber. Siphuncle small, ventral (33, 53). *M.Ord.-U.Ord.*, N.Am.-Eu.—FIG. 200, 4. *\*B. pandion* (HALL), M.Ord., USA (Wis.); *4a,b*, lat. (venter right), ventral,  $\times 1$  (208).

**Centrorizoceras** FOERSTE, 1930, p. 22 [*\*C. slocomi*; OD]. Like *Rizoceras*, but conch slightly curved and siphuncle subventral. Internal structure unknown (68). *M.Sil.*, N.Am.—FIG. 202, 5. *\*C. slocomi*, USA (Ill.); lat. (venter left),  $\times 1$  (68).

**Cyrtorizoceras** HYATT in ZITTEL, 1900, p. 529 [*\*Cyrtoceras minneapolis* CLARKE, 1897, p. 808; OD] [= *Cyrtorizoceras* CLARKE & RUEDEMANN, 1903 (*nom. null.*)]. Compressed cyrtocoines; dorsal and ventral profiles diverging constantly adorally; sides converging slightly over body chamber. Aperture with deep hyponomic sinus; surface obscurely or prominently costate. Siphuncle subventral, slender; segments slightly expanded, probably empty (33, 93). [Described Silurian species probably homeomorphs of Ordovician type.] *M.*

*Ord.*, *?U.Ord.*, N.Am. (N.Y.-Wis.-?Que.)-?Eu. (?Est.-?Norway).—FIG. 200, 2. *\*C. minneapolis* (CLARKE), M.Ord., USA (Wis.); *2a-c*, lat. (venter left), dorsal, ventral,  $\times 1$  (57).

**Digenoceras** FOERSTE, 1935, p. 43 [*\*Oxygonioceras? latum* FOERSTE, 1929, p. 218; OD]. Similar to *Oonoceras*, but conch more compressed, both venter and dorsum acutely angular in transverse section. Siphuncle cyrtchoanitic; segments subfusiform, probably empty (33, 73). *U.Ord.*, N.Am. (Wyo.-Man.-Arctic).—FIG. 200, 6. *\*D. latum* (FOERSTE), Can. (Arctic); *6a,b*, lat. (venter right), ventral,  $\times 0.5$  (Sweet, n).

**Dunleithoceras** FOERSTE, 1924, p. 245 [*\*Cyrtoceras dunleithense* MILLER & GURLEY, 1896, p. 30; SD FOERSTE & SAVAGE, 1927, p. 53]. Strongly curved, slowly enlarging cyrtocoines with subcircular section, rounded longitudinal ridge on venter, and submarginal siphuncle of unknown internal structure (53). *M.Ord.-U.Ord.*, N.Am. (Ill.-Ont.).—FIG. 201, 5. *\*D. dunleithense* (MILLER & GURLEY), M.Ord., USA (Ill.); *5a,b*, lat. (venter left), apert. (venter left),  $\times 1$  (138). [= *Dunleithoceras* BALASHOV, 1962 (*nom. null.*)].

**Ehlersoceras** FOERSTE, 1932, p. 50 [*\*E. huronense*; OD]. Slightly curved, depressed, longiconic cyrtocoines. Siphuncle small, subventral; interior not known. Transverse surficial striae slope posteriorly toward venter on sides (71). *M.Ord.*, N.Am.—FIG. 203, 2. *\*E. huronense*, Can. (Ont.); *2a,b*, lat. (venter left), ventral,  $\times 1$  (71).

**Ekwanoeras** FOERSTE & SAVAGE, 1927, p. 51 [*\*E. breviconicum*; OD]. Rapidly enlarging cyrtocoines of subcircular section. Siphuncle central, cyrtchoanitic; segments cylindroid, actinosiphonate (77). *M.Sil.*, N.Am. (?Ohio-Ont.).—FIG. 202, 3. *\*E. breviconicum*, Can. (Ont.); *3a,b*, lat. (venter left), ventral,  $\times 1$  (77).

**Kentlandoceras** FOERSTE, 1932, p. 49 [*\*K. schrocki*; OD]. Like *Loganoceras*, but less curved and with submarginal ventral siphuncle. Adapical part of siphuncular segment almost in contact, or in actual contact with venter (33, 71). *M.Ord.*, N.Am. (Ind.-Wis.-Ont.).—FIG. 201, 3. *\*K. schrocki*, USA (Ind.); *3a,b*, lat. (venter left), ventral,  $\times 1$  (71).

[FOERSTE's original spelling "*schrocki*" is clearly incorrect since it is attributed (p. 74) to "ROBERT R. SCHROCK" (*recte* SHROCK). Change of the specific name to "*schrocki*" is a subsequent spelling (herein) classed as a justified emendation (Rules, Art. 33a, ii) which is to be cited as of FOERSTE, 1932.]

**Loganoceras** FOERSTE, 1932, p. 49 [*\*Cyrtoceras regulare* BILLINGS, 1857, p. 314; OD]. Smooth, strongly curved cyrtocoines of circular section. Siphuncle empty, probably cyrtchoanitic, ventral of center; dorsal profile of siphuncular segments scalariform (71). *M.Ord.*, N.Am.—FIG. 201, 7. *\*L. regulare* (BILLINGS), Can. (Ont.); *7a,b*, lat. (venter left), dorsal,  $\times 1$  (71).

**Maelonoceras** HYATT, 1884, p. 280 [*\*Phragmoceras praematurum* BILLINGS, 1860, p. 173; OD] [= *Cyrtoceras* (*Meloceras*) FOORD, 1888 (*nom.*

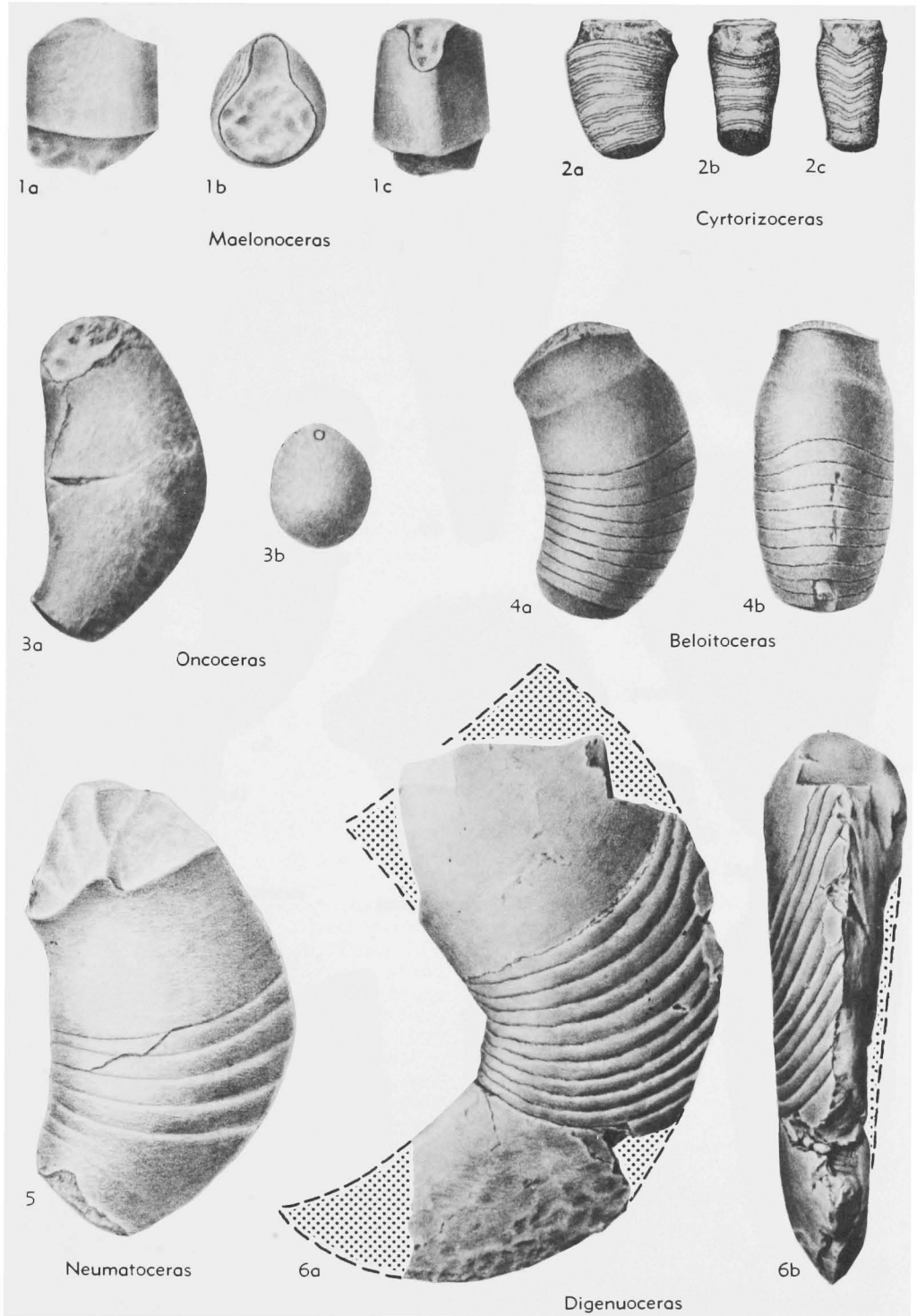


FIG. 200. Oncoceratidae (p. K284, K288).

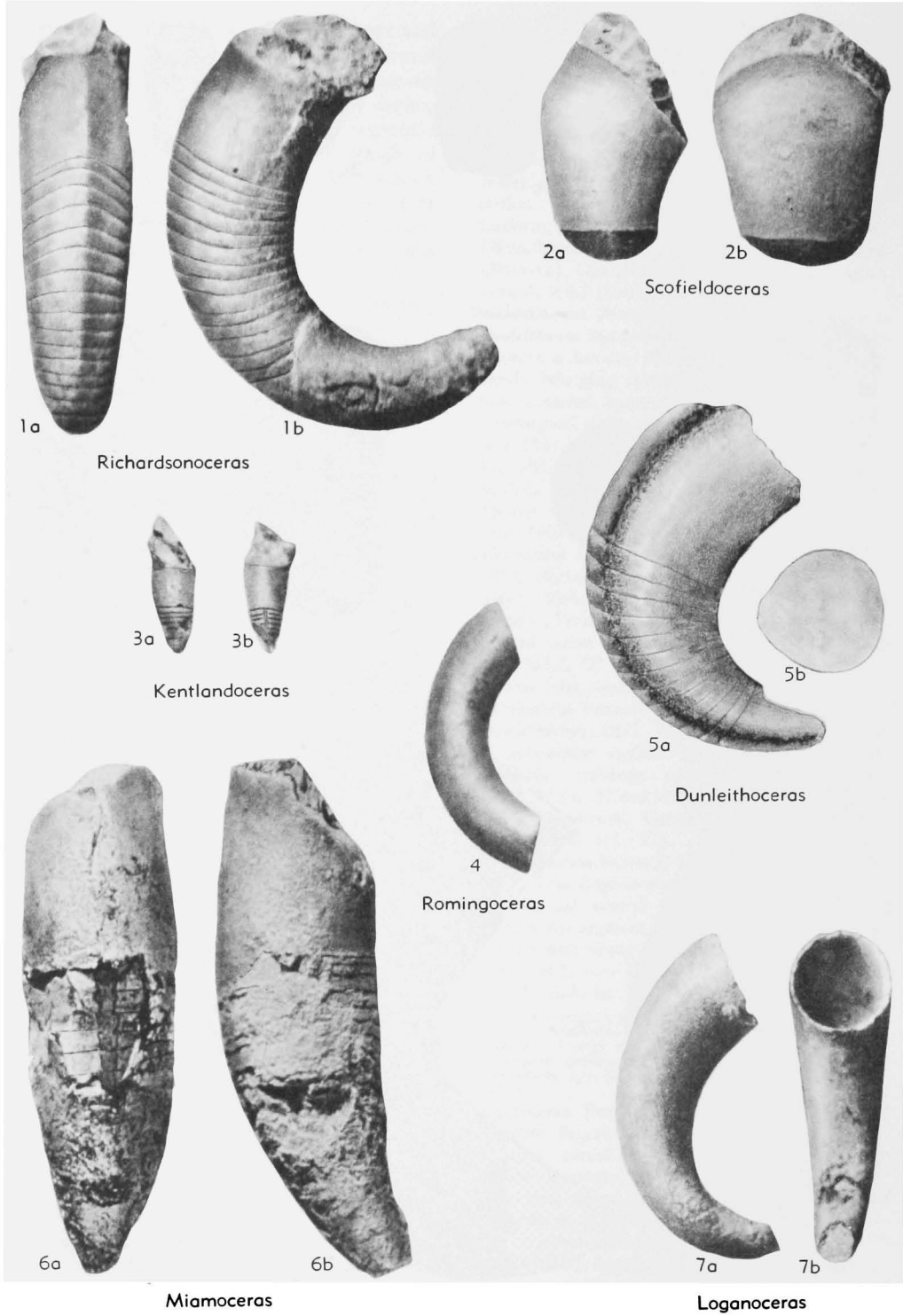


FIG. 201. Oncoceratidae (p. K284, K288).



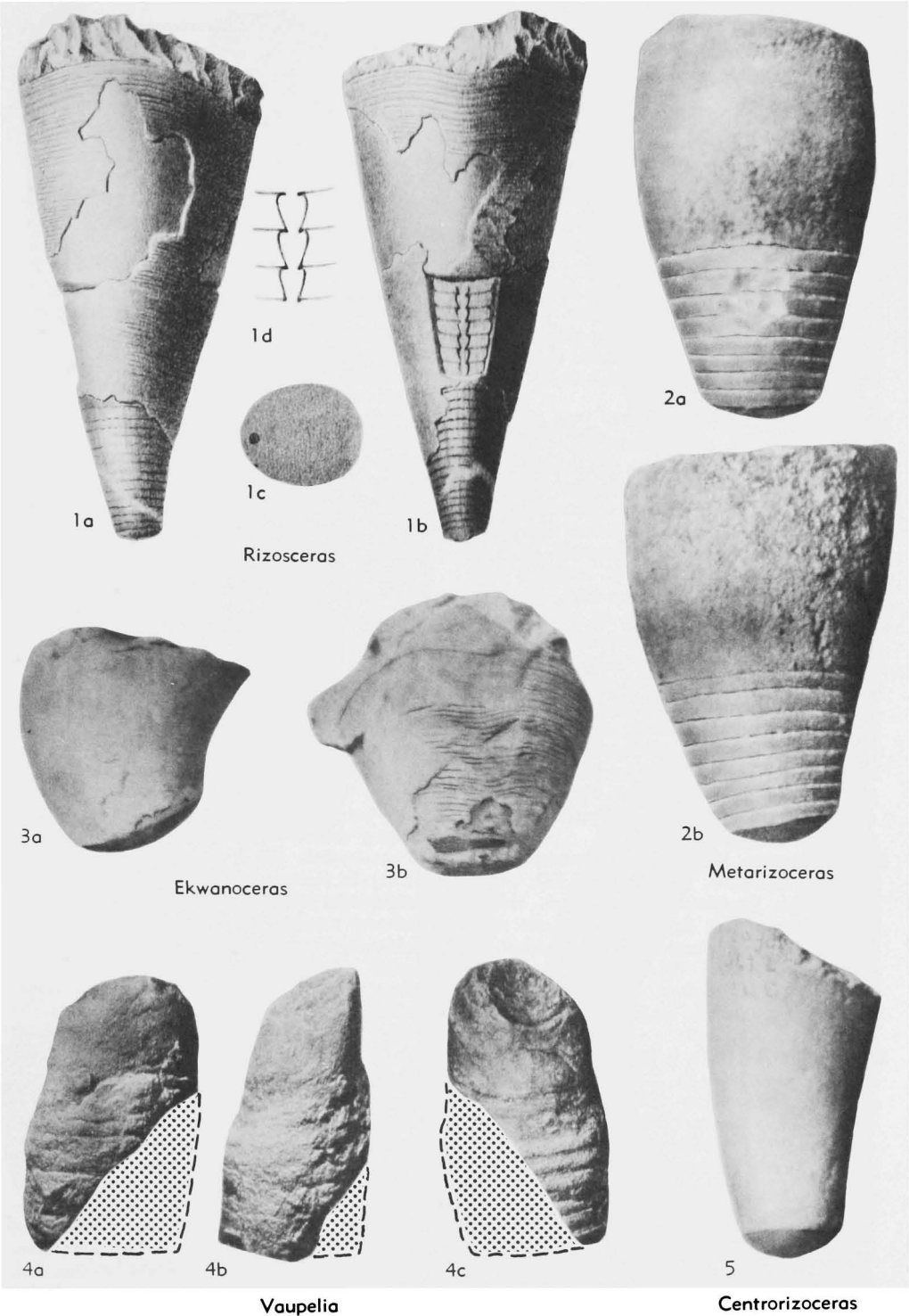


FIG. 202. Oncoceratidae (p. K284, K288).

- null.*; *Melonoceras* HYATT, 1894 (*nom. null.*). Faintly gibbous cyrtocoines with subparallel dorsal and ventral profiles but adorally converging sides on body chamber. Aperture partially visored, pear-shaped, with hyponomic sinus. Siphuncle small, ventral (33, 93). *M.Ord.*, N.Am.(Ont.). —FIG. 200.1. \**M. praematurum* (BILLINGS); *1a-c*, lat.(venter left), apert.(venter up), ventral,  $\times 1$  (53).
- Metarizoceras** FOERSTE, 1930, p. 23 [\**M. savagei*; OD] [= *Cyclorizoceras* FOERSTE, 1930]. Slightly curved, compressed, rapidly enlarging brevicones with faintly gibbous dorsal profile and adorally converging sides over body chamber. Siphuncle subventral, cyrtchoanitic; segments oblong rather than fusiform in outline (68). *M.Sil.*, N.Am. —FIG. 202.2. \**M. savagei*, USA(Ill.); *2a,b*, ventral, lat.(venter left),  $\times 1$  (68).
- Miamoceras** FLOWER, 1946, p. 317 [\**M. shideleri*; OD]. Compressed, rapidly enlarging cyrtocoines, with slight adapical curvature and tubular body chamber with faintly convergent sides. Siphuncle ventral, cyrtchoanitic; segments subcardioid, rings thickened near septal necks. Aperture with hyponomic sinus; surface features unknown (33). *U.Ord.*, N.Am. —FIG. 201.6. \**M. shideleri*, USA (Ohio); *6a,b*, ventral, lat.(venter left),  $\times 1$  (33).
- Neumatoceras** FOERSTE, 1935, p. 31 [\**N. gibberosum*; OD]. Compressed brevicones with maximum height behind posterior end of body chamber; dorsal profile straight, concave, or very slightly convex; ventral profile geniculate on phragmocone. Siphuncle subventral, segments almost cylindrical (33, 73). [May include unrelated extremely gibbous species of both *Beloitoceras* and *Oncoceras*.] *M.Ord.-U.Ord.*, N.Am.-Eu. —FIG. 200.5. *N. nutans* FOERSTE, *U.Ord.*, USA(Wyo.); lat.(venter right),  $\times 1$  (orig., after 73).
- Oocerina** FOERSTE, 1926, p. 321 [\**Cyrtoceras lentigradum* BARRANDE, 1866, pl. 137; OD] [= ?*Oocenia* DECHASEAUX, 1941 (*nom. null.*)]. Like *Oonoceras*, but siphuncular segments nummuloidal, actinosiphonate (33, 57). ?*M.Sil.-U.Sil.*, Eu.(Czech. - S.USSR) - ?N.Am.(?Ont.). —FIG. 203.1. \**O. lentigradum* (BARRANDE), *U.Sil.*, Czech.; *1a-c*, ventral, lat.(venter left), septum (venter left),  $\times 0.75$  (5).
- Oonoceras** HYATT, 1884, p. 280 [\**Cyrtoceras acinaces* BARRANDE, 1866, pl. 118; SD BASSLER, 1915, p. 877] [= *Cyrtoceras* (*Ooceras*) FOORD, 1888 (*nom. null.*); *Ooceras* HYATT in ZITTEL, 1900 (*nom. null.*); *Exomegoceras* MILLER & CARRIER, 1942]. Slender compressed cyrtocoines of slight curvature and gradual enlargement. Sutures with lateral lobes; camerae and body chamber short; aperture with hyponomic sinus. Siphuncle close to venter, cyrtchoanitic, empty; segments either slightly or broadly expanded within camerae (28, 33, 93). *M.Ord.-M.Sil.*, N.Am.-Eu. —FIG. 203.5. \**O. acinaces* (BARRANDE), *M.Sil.*, Eu.(Czech.); *5a-d*, ventral, lat.(venter left), septum(venter left), dorsal,  $\times 0.5$  (5). [= *Exomegoceras* BALASHOV, 1962 (*nom. null.*).]
- Paroocercina** ZHURAVLEVA, 1961, p. 57 [\**P. podolskensis*; OD]. Like *Oocerina*, but with hyponomic sinus. *M.Sil.-U.Sil.*, Eu.(Czech.-USSR). —FIG. 204.1. \**P. podolskensis*, *U.Sil.*, USSR (Podolia); *1a-c*, left lat., ventral, dorsovent. sec. (venter right),  $\times 1$ ; *1d*, lat. sec. of siph.,  $\times 1.5$  (214b).
- Richardsonoceras** FOERSTE, 1932, p. 50 [\**Cyrtoceras simplex* BILLINGS, 1857, p. 313; OD]. Gradually enlarging cyrtocoines like *Beloitoceras*, but not gibbous adorally, body chamber not contracted adorally, siphuncle somewhat larger than that of *Beloitoceras* (33, 71). [Only superficially distinct from *Oonoceras*.] *M.Ord.-U.Ord.*, N.Am. —FIG. 201.1. \**R. simplex* (BILLINGS), *M.Ord.*, Can.(Ont.); *1a,b*, ventral, lat.(venter left),  $\times 1$  (71).
- Rizoceras** HYATT, 1884, p. 276 [\**Orthoceras indocile* BARRANDE, 1866, pl. 185; OD] [= *Rizoceras* HYATT in ZITTEL, 1900, *et auctt.*]. Compressed, rapidly enlarging, straight to faintly cyrtconic conchs with hyponomic sinus and distinct, faintly rugose transverse surficial ornament. Siphuncle ventral, marginal, cyrtchoanitic, cardioid in dorsoventral section (33, 93). *M.Ord.-U.Sil.*, N.Am.-Eu. —FIG. 202.1. \**R. indocile* (BARRANDE), *M.Sil.*, Eu.(Czech.); *1a-c*, lat.(venter left), ventral, septum(venter left),  $\times 1$ ; *1d*, partial long. sec.,  $\times 2.5$  (5).
- Romingoceras** FOERSTE, 1932, p. 50 [\**R. josephianum*; OD] [= *Romingoceras* FOERSTE, 1933 (*nom. null.*)]. Slowly enlarging, strongly curved, depressed cyrtocoines or ?gyrocones of ovoid transverse section. Siphuncle small, ventral; segments oblong, longer than high. Transverse surficial striae curve slightly backward mid-ventrally, indicating shallow hyponomic sinus (71). *M.Ord.*, N.Am. —FIG. 201.4. \**R. josephianum*, Can.(Ont.); lat.(venter left),  $\times 1$  (71).
- Scofieldoceras** FOERSTE, 1932, p. 50 [\**Cyrtoceras shumardi* CLARKE, 1897, p. 810; OD] [= *Schofieldoceras* FLOWER, 1941 (*nom. null.*)]. Short, rapidly enlarging, depressed cyrtocoines, probably strongly curved. Ventral profile of body chamber geniculate. Siphuncle small, subventral (71). *M.Ord.*, N.Am. —FIG. 201.2. \**S. shumardi* (CLARKE), USA(Minn.); *2a,b*, lat.(venter left), ventral,  $\times 1$  (71).
- ?**Vaupelia** FLOWER, 1946, p. 479 [\**V. russelli*; OD]. Depressed, cyrtconic brevicones with gibbous phragmocone, somewhat contracted body chamber, relatively long camerae, and large, ventral, cyrtchoanitic siphuncle. Siphuncular segments broadly nummuloidal, empty; septal necks recumbent dorsally, orthchoanitic to suborthchoanitic ventrally (33). [Relations with other oncocerids obscure.] *U.Ord.*, N.Am. —FIG. 202.4. \**V. russelli*, USA(Ohio); *4a-c*, ventral, lat. (venter right), dorsal,  $\times 1$  (33).
- Zitteloceras** HYATT, 1884, p. 284 [\**Cyrtoceras hal-*

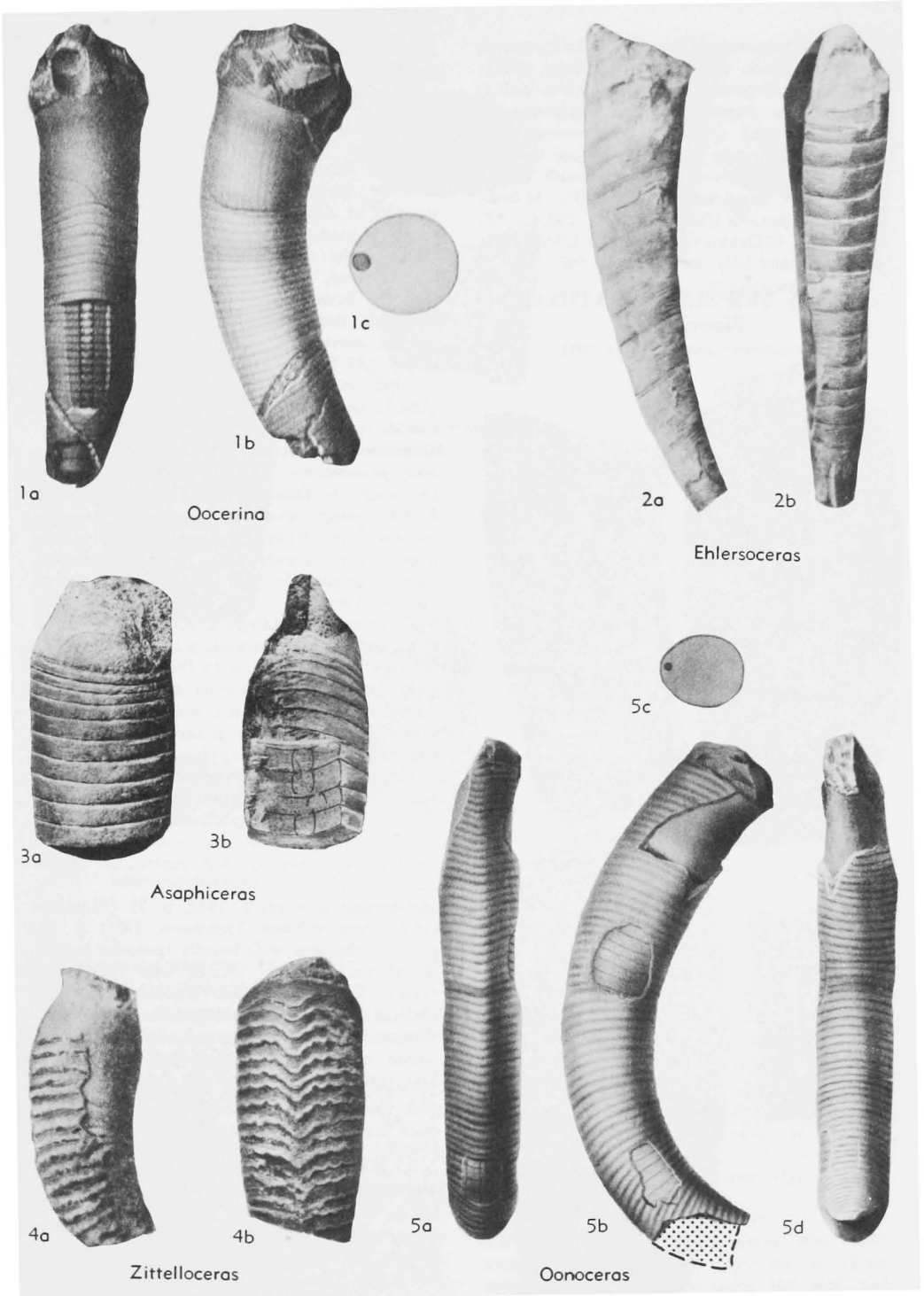


FIG. 203. *Oncoceratidae* (p. K284, K288, K290).

*lianum* D'ORBIGNY, 1850, p. 1 (= *Cyrtoceras lamellosum* HALL, 1847, non DEVERNEUIL, 1842); OD] [= *Zittloceras* ZITTEL, 1884 (*nom. null.*); *Laphamoceras* FOERSTE, 1932]. Subcircular or slightly depressed cyrtocones with ventral, suborthochoanitic, empty siphuncle; surface typically with crenulate transverse frills, or with distant noncrenulate annulations (33, 71, 93). *M.Ord.-U.Ord.*, N.Am.-Eu.(Scot.).—FIG. 203, 4. \**Z. hallianum* (D'ORBIGNY), *M.Ord.*, USA(N.Y.); 4a,b, lat.(venter left), ventral,  $\times 1.5$  (62).

### Family TRIPTEROCERATIDAE Flower, 1941

[= *Allumettoceratidae* FLOWER, 1945]

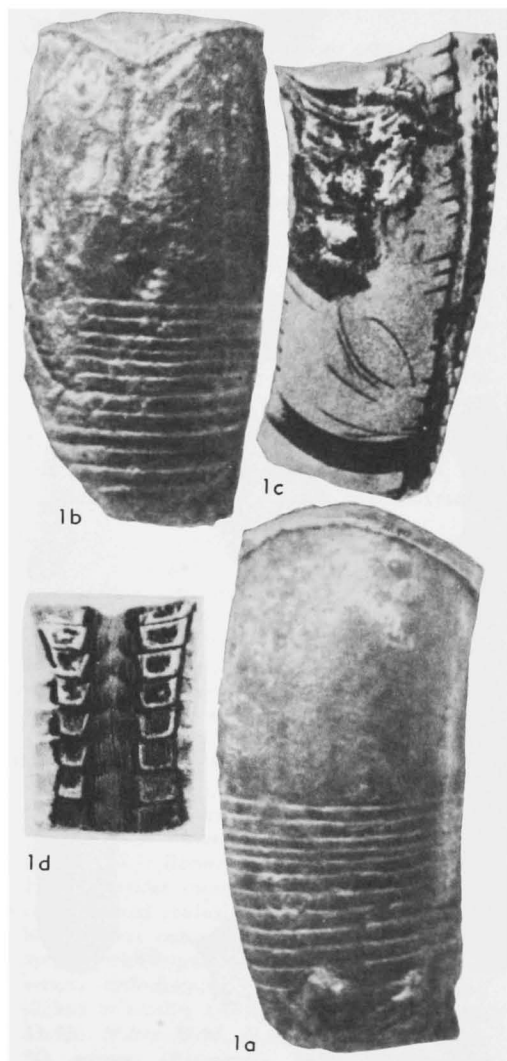


FIG. 204. \**Paroocera podolskensis* ZHURAVLEVA (*Oncoceratidae*) (p. K288).

Depressed, straight to faintly exogastric longicones with flattened venter and empty, ventral, suborthochoanitic to cyrtchoanitic siphuncle (32, 33, 49). *M.Ord.-U.Ord.*

**Tripteroceras** HYATT, 1884, p. 287 [\**Orthoceras hastatum* BILLINGS, 1857, p. 333; OD] [= *Trypteroceras* ZITTEL, 1884 (*nom. null.*)]. Small, straight, or slightly exogastric conchs of broadly depressed triangular section; venter broad and flat, lateral angles acute, dorsum divided by median ridge or keel; dorsolateral regions flat or slightly concave. Sutures with dorsal and ventral lobes. Siphuncle small, ventral; segments slightly expanded, interior not well known, but apparently empty (33, 93). *M.Ord.*, N.Am.-?Eu.(Norway).—FIG. 205, 3. \**T. hastatum* (BILLINGS), Can. (Ont.); 3a-c, ventral, septum (venter down), lat. (venter right),  $\times 1$  (53).

**Allumettoceras** FOERSTE, 1926, p. 311 [\**Tripteroceras pauquetense* FOERSTE, 1924, p. 233; OD]. Orthocones or faintly exogastric cyrtocones with flattened venter, broadly arched dorsum, narrowly rounded sides. Early siphuncle suborthochoanitic; later stages cyrtchoanitic, with subspherical, empty segments (33, 57). *M.Ord.-U.Ord.*, N.Am.-Eu.(Est.-Norway).—FIG. 205, 2. \**A. pauquetense* (FOERSTE), *M.Ord.*, Can.(Ont.); 2a,b, septum (venter down), ventral,  $\times 1$  (53).

**Hadoceras** STRAND, 1934, p. 68 [\**H. septocurvatum*; OD] [= *Hadeoceras* FLOWER & KUMMEL, 1950 (*nom. null.*)]. Orthocones with broadly arched venter and more highly arched dorsum. Sutures with dorsal and mid-ventral saddles and ventrolateral lobes. Siphuncle cyrtchoanitic, between venter and center; segments expanded within camerae, faint ?annulosiphonate deposits in septal foramen (176). *U.Ord.*, Eu.—FIG. 205, 4. \**H. septocurvatum*, Norway; 4a,b, ventral, lat. (venter left),  $\times 1$  (176).

**Rasmussenoceras** FOERSTE, 1932, p. 51 [\**Lambeoceras? leveannulatum* TROEDSSON, 1926, p. 50; OD]. Orthocones with broadly lenticular section, sharp lateral angles; sutures with dorsal and ventral lobes, subangular lateral saddles. Siphuncle small, ventral, suborthochoanitic to orthochoanitic; segments empty, expanded only slightly within camerae. Early stages with faint dorsal keel, suggesting derivation from *Tripteroceras* (33, 71). *M.Ord.-U.Ord.*, N.Am.-Greenl.—FIG. 205, 1. \**R. leveannulatum* (TROEDSSON), *U.Ord.*, Greenl.; 1a,b, ventral, septum (venter down),  $\times 0.5$  (194).

**Tripterocerina** FOERSTE, 1935, p. 49 [\**T. kirki*; OD]. Like *Tripteroceras*, but dorsum fluted as well as keeled (33, 73). *U.Ord.*, N.Am.—FIG. 205, 5. \**T. kirki*, USA(Wyo.); ventral,  $\times 0.75$  (73).

### Family VALCOUROCERATIDAE Flower, 1945

[Incl. *Manitoulinoceratidae* SHIMANSKIY, 1956]

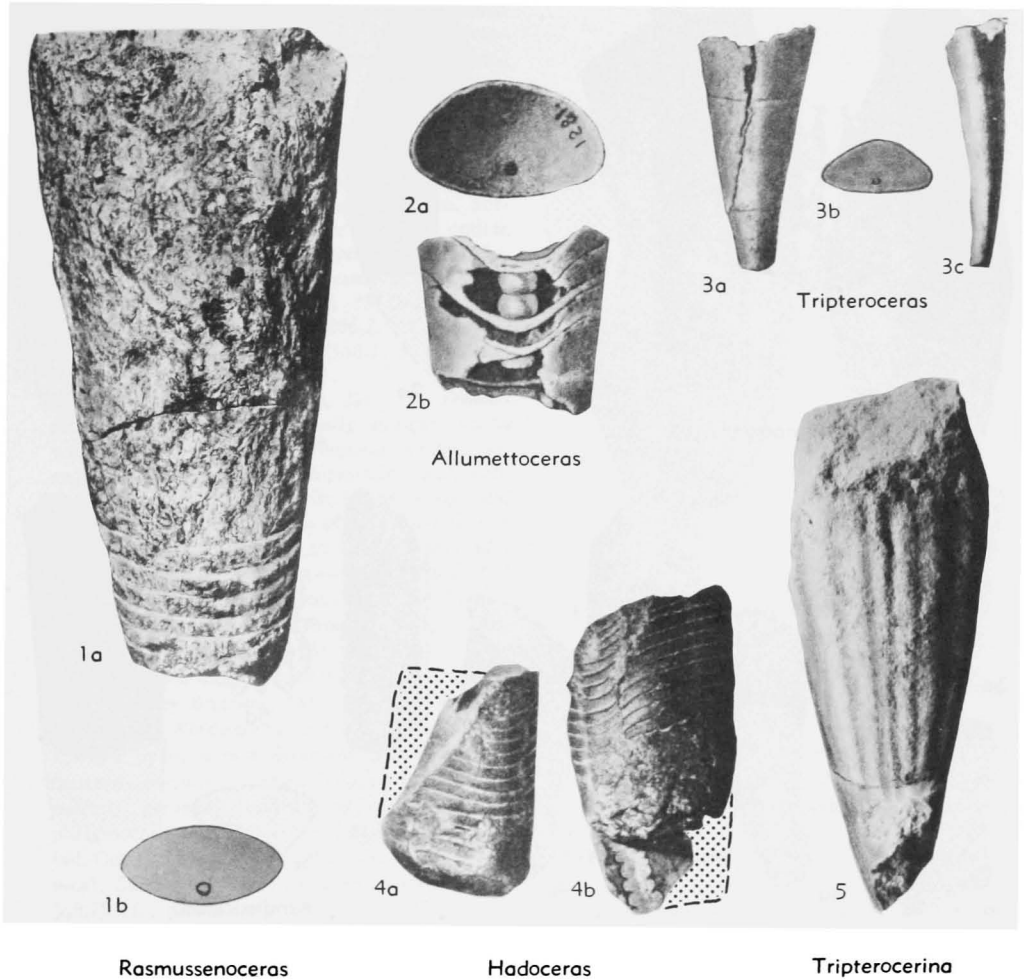


FIG. 205. Tripteroceratidae (p. K290).

Exogastric cyrtocoines and brevicoines with ventral, actinosiphonate siphuncle, and conch that changes ontogenetically from compressed to depressed or subtriangular section (32, 33, 49). *M.Ord.-U.Ord.*

*Valcouroceras* FLOWER, 1943, p. 43 [*\*V. bovinum*; OD]. Like *Minganoceras*, but more curved, body chamber more gibbous, sutures oblique. Compressed in early stages, later flattened dorsally, then depressed and subtriangular; may be compressed at adapical end of body chamber. Early stages of siphuncle suborthochoanitic, ventral, empty; later segments more inflated, with thicker rings and actinosiphonate deposits (31, 33). *M. Ord.*, N.Am.-?Eu. (?Norway).—FIG. 206, 7. *\*V. bovinum*, USA (N.Y.); 7*a*, lat. (venter right),  $\times 0.56$ ; 7*b-d*, partial long. sec.,  $\times 3$ ; 7*e*, transv.  $\times 0.56$ ; 7*f*, partial long. sec.,  $\times 3$ ; 7*g*, transv.  $\times 3$ ; 7*h*, partial long. sec.,  $\times 3$ ; 7*i*, transv.  $\times 3$ ; 7*j*, partial long. sec.,  $\times 3$ ; 7*k*, transv.  $\times 3$ ; 7*l*, partial long. sec.,  $\times 3$ ; 7*m*, transv.  $\times 3$ ; 7*n*, partial long. sec.,  $\times 3$ ; 7*o*, transv.  $\times 3$ ; 7*p*, partial long. sec.,  $\times 3$ ; 7*q*, transv.  $\times 3$ ; 7*r*, partial long. sec.,  $\times 3$ ; 7*s*, transv.  $\times 3$ ; 7*t*, partial long. sec.,  $\times 3$ ; 7*u*, transv.  $\times 3$ ; 7*v*, partial long. sec.,  $\times 3$ ; 7*w*, transv.  $\times 3$ ; 7*x*, partial long. sec.,  $\times 3$ ; 7*y*, transv.  $\times 3$ ; 7*z*, partial long. sec.,  $\times 3$ ; 7*aa*, transv.  $\times 3$ ; 7*ab*, partial long. sec.,  $\times 3$ ; 7*ac*, transv.  $\times 3$ ; 7*ad*, partial long. sec.,  $\times 3$ ; 7*ae*, transv.  $\times 3$ ; 7*af*, partial long. sec.,  $\times 3$ ; 7*ag*, transv.  $\times 3$ ; 7*ah*, partial long. sec.,  $\times 3$ ; 7*ai*, transv.  $\times 3$ ; 7*aj*, partial long. sec.,  $\times 3$ ; 7*ak*, transv.  $\times 3$ ; 7*al*, partial long. sec.,  $\times 3$ ; 7*am*, transv.  $\times 3$ ; 7*an*, partial long. sec.,  $\times 3$ ; 7*ao*, transv.  $\times 3$ ; 7*ap*, partial long. sec.,  $\times 3$ ; 7*aq*, transv.  $\times 3$ ; 7*ar*, partial long. sec.,  $\times 3$ ; 7*as*, transv.  $\times 3$ ; 7*at*, partial long. sec.,  $\times 3$ ; 7*au*, transv.  $\times 3$ ; 7*av*, partial long. sec.,  $\times 3$ ; 7*aw*, transv.  $\times 3$ ; 7*ax*, partial long. sec.,  $\times 3$ ; 7*ay*, transv.  $\times 3$ ; 7*az*, partial long. sec.,  $\times 3$ ; 7*ba*, transv.  $\times 3$ ; 7*bb*, partial long. sec.,  $\times 3$ ; 7*bc*, transv.  $\times 3$ ; 7*bd*, partial long. sec.,  $\times 3$ ; 7*be*, transv.  $\times 3$ ; 7*bf*, partial long. sec.,  $\times 3$ ; 7*bg*, transv.  $\times 3$ ; 7*bh*, partial long. sec.,  $\times 3$ ; 7*bi*, transv.  $\times 3$ ; 7*bj*, partial long. sec.,  $\times 3$ ; 7*bk*, transv.  $\times 3$ ; 7*bl*, partial long. sec.,  $\times 3$ ; 7*bm*, transv.  $\times 3$ ; 7*bn*, partial long. sec.,  $\times 3$ ; 7*bo*, transv.  $\times 3$ ; 7*bp*, partial long. sec.,  $\times 3$ ; 7*bq*, transv.  $\times 3$ ; 7*br*, partial long. sec.,  $\times 3$ ; 7*bs*, transv.  $\times 3$ ; 7*bt*, partial long. sec.,  $\times 3$ ; 7*bu*, transv.  $\times 3$ ; 7*bv*, partial long. sec.,  $\times 3$ ; 7*bw*, transv.  $\times 3$ ; 7*bx*, partial long. sec.,  $\times 3$ ; 7*by*, transv.  $\times 3$ ; 7*bz*, partial long. sec.,  $\times 3$ ; 7*ca*, transv.  $\times 3$ ; 7*cb*, partial long. sec.,  $\times 3$ ; 7*cc*, transv.  $\times 3$ ; 7*cd*, partial long. sec.,  $\times 3$ ; 7*ce*, transv.  $\times 3$ ; 7*cf*, partial long. sec.,  $\times 3$ ; 7*cg*, transv.  $\times 3$ ; 7*ch*, partial long. sec.,  $\times 3$ ; 7*ci*, transv.  $\times 3$ ; 7*cj*, partial long. sec.,  $\times 3$ ; 7*ck*, transv.  $\times 3$ ; 7*cl*, partial long. sec.,  $\times 3$ ; 7*cm*, transv.  $\times 3$ ; 7*cn*, partial long. sec.,  $\times 3$ ; 7*co*, transv.  $\times 3$ ; 7*cp*, partial long. sec.,  $\times 3$ ; 7*cq*, transv.  $\times 3$ ; 7*cr*, partial long. sec.,  $\times 3$ ; 7*cs*, transv.  $\times 3$ ; 7*ct*, partial long. sec.,  $\times 3$ ; 7*cu*, transv.  $\times 3$ ; 7*cv*, partial long. sec.,  $\times 3$ ; 7*cw*, transv.  $\times 3$ ; 7*cx*, partial long. sec.,  $\times 3$ ; 7*cy*, transv.  $\times 3$ ; 7*cz*, partial long. sec.,  $\times 3$ ; 7*da*, transv.  $\times 3$ ; 7*db*, partial long. sec.,  $\times 3$ ; 7*dc*, transv.  $\times 3$ ; 7*dd*, partial long. sec.,  $\times 3$ ; 7*de*, transv.  $\times 3$ ; 7*df*, partial long. sec.,  $\times 3$ ; 7*dg*, transv.  $\times 3$ ; 7*dh*, partial long. sec.,  $\times 3$ ; 7*di*, transv.  $\times 3$ ; 7*dj*, partial long. sec.,  $\times 3$ ; 7*dk*, transv.  $\times 3$ ; 7*dl*, partial long. sec.,  $\times 3$ ; 7*dm*, transv.  $\times 3$ ; 7*dn*, partial long. sec.,  $\times 3$ ; 7*do*, transv.  $\times 3$ ; 7*dp*, partial long. sec.,  $\times 3$ ; 7*dq*, transv.  $\times 3$ ; 7*dr*, partial long. sec.,  $\times 3$ ; 7*ds*, transv.  $\times 3$ ; 7*dt*, partial long. sec.,  $\times 3$ ; 7*du*, transv.  $\times 3$ ; 7*dv*, partial long. sec.,  $\times 3$ ; 7*dw*, transv.  $\times 3$ ; 7*dx*, partial long. sec.,  $\times 3$ ; 7*dy*, transv.  $\times 3$ ; 7*dz*, partial long. sec.,  $\times 3$ ; 7*ea*, transv.  $\times 3$ ; 7*eb*, partial long. sec.,  $\times 3$ ; 7*ec*, transv.  $\times 3$ ; 7*ed*, partial long. sec.,  $\times 3$ ; 7*ee*, transv.  $\times 3$ ; 7*ef*, partial long. sec.,  $\times 3$ ; 7*eg*, transv.  $\times 3$ ; 7*eh*, partial long. sec.,  $\times 3$ ; 7*ei*, transv.  $\times 3$ ; 7*ej*, partial long. sec.,  $\times 3$ ; 7*ek*, transv.  $\times 3$ ; 7*el*, partial long. sec.,  $\times 3$ ; 7*em*, transv.  $\times 3$ ; 7*en*, partial long. sec.,  $\times 3$ ; 7*eo*, transv.  $\times 3$ ; 7*ep*, partial long. sec.,  $\times 3$ ; 7*eq*, transv.  $\times 3$ ; 7*er*, partial long. sec.,  $\times 3$ ; 7*es*, transv.  $\times 3$ ; 7*et*, partial long. sec.,  $\times 3$ ; 7*eu*, transv.  $\times 3$ ; 7*ev*, partial long. sec.,  $\times 3$ ; 7*ew*, transv.  $\times 3$ ; 7*ex*, partial long. sec.,  $\times 3$ ; 7*ey*, transv.  $\times 3$ ; 7*ez*, partial long. sec.,  $\times 3$ ; 7*fa*, transv.  $\times 3$ ; 7*fb*, partial long. sec.,  $\times 3$ ; 7*fc*, transv.  $\times 3$ ; 7*fd*, partial long. sec.,  $\times 3$ ; 7*fe*, transv.  $\times 3$ ; 7*ff*, partial long. sec.,  $\times 3$ ; 7*fg*, transv.  $\times 3$ ; 7*fh*, partial long. sec.,  $\times 3$ ; 7*fi*, transv.  $\times 3$ ; 7*fj*, partial long. sec.,  $\times 3$ ; 7*fk*, transv.  $\times 3$ ; 7*fl*, partial long. sec.,  $\times 3$ ; 7*fm*, transv.  $\times 3$ ; 7*fn*, partial long. sec.,  $\times 3$ ; 7*fo*, transv.  $\times 3$ ; 7*fp*, partial long. sec.,  $\times 3$ ; 7*fq*, transv.  $\times 3$ ; 7*fr*, partial long. sec.,  $\times 3$ ; 7*fs*, transv.  $\times 3$ ; 7*ft*, partial long. sec.,  $\times 3$ ; 7*fu*, transv.  $\times 3$ ; 7*fv*, partial long. sec.,  $\times 3$ ; 7*fw*, transv.  $\times 3$ ; 7*fx*, partial long. sec.,  $\times 3$ ; 7*fy*, transv.  $\times 3$ ; 7*fz*, partial long. sec.,  $\times 3$ ; 7*ga*, transv.  $\times 3$ ; 7*gb*, partial long. sec.,  $\times 3$ ; 7*gc*, transv.  $\times 3$ ; 7*gd*, partial long. sec.,  $\times 3$ ; 7*ge*, transv.  $\times 3$ ; 7*gf*, partial long. sec.,  $\times 3$ ; 7*gg*, transv.  $\$

?*Actinomorpha* FLOWER, 1943, p. 53 [*\*A. pupa*; OD]. Compressed brevicones with venter more narrowly rounded transversely than dorsum; gibbous at adoral end of phragmocone. Siphuncle ventral, with broad, slightly expanded, cyrtochaonic segments in which are continuous, branched or pectinate actinosiphonate deposits. Aperture with distinct hyponomic sinus; surface with closely spaced, low, irregular growth lines (31). ?*M.Ord.*, N.Am.(Wis. or Minn.).—FIG. 207, I. \**A. pupa*; 1*a, b*, lat. (venter right), ventral,  $\times 0.75$  (31).

**Augustoceras** FLOWER, 1946, p. 343 [*A. shideleri*; OD]. Slender, fusiform cyrtocones with subtriangular transverse section, short camerae, oblique sutures, slight hyponomic sinus, and shell with fine transverse, faintly rugose growth lines. Siphuncle subventral, cyrtoconeanitic, with fusiform segments and simple actinosiphonate deposits (33).

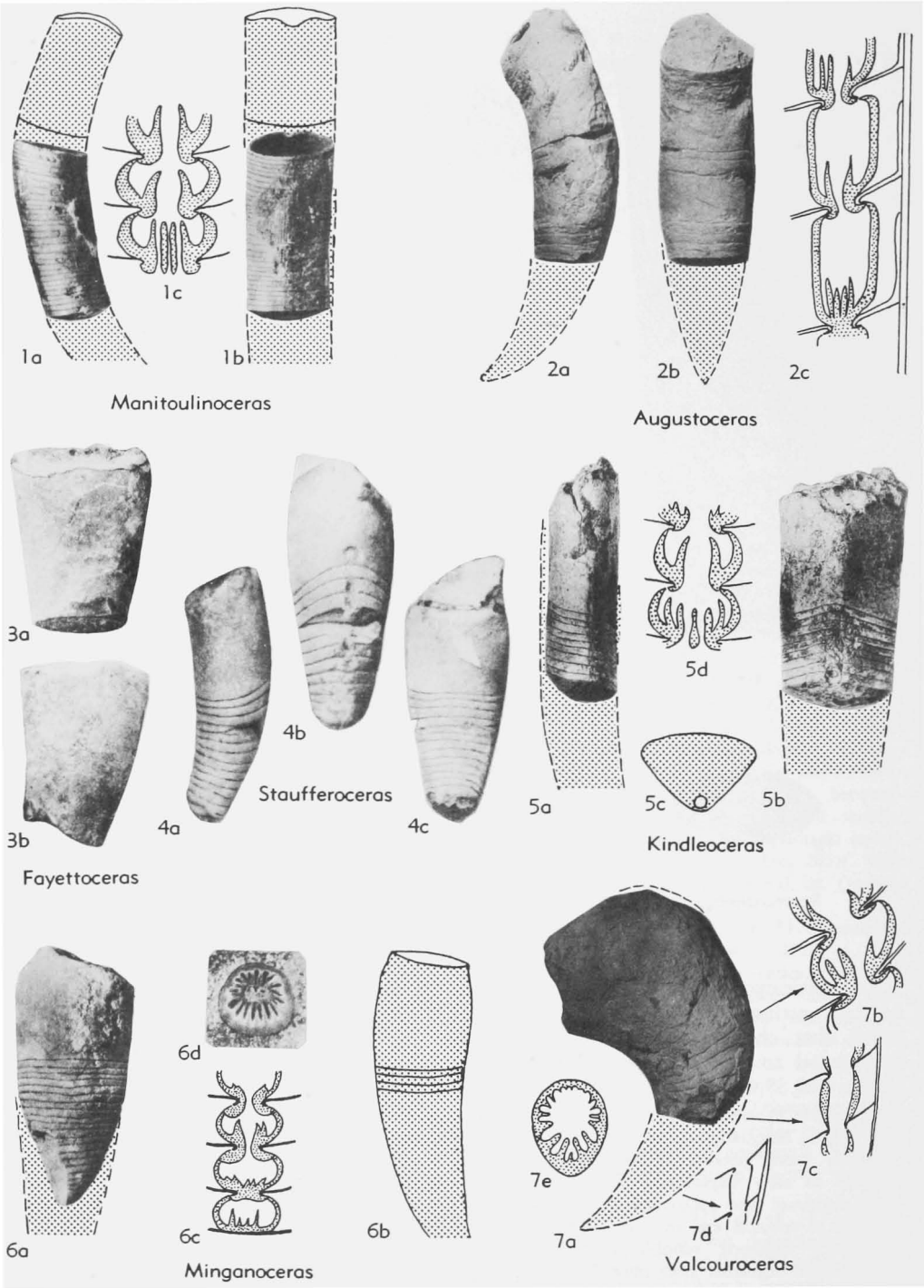


FIG. 206. Valcouroceratidae (p. K291, K293).

*M.Ord.-U.Ord.*, N.Am.(Ky.-Ohio).—FIG. 206,2. \**A. shideleri*, M.Ord., USA(Ky.); 2*a,b*, lat. (venter right), dorsal,  $\times 0.56$ ; 2*c*, partial long. sec.,  $\times 4.5$  (33).

**Fayetoceras** FOERSTE, 1932, p. 50 [\**Cyrtoceras thompsoni* MILLER, 1894, p. 323; OD]. Depressed cyrtocones with ventral cyrtchoanitic siphuncle of elongated, ovoid segments strongly contracted at septal necks. Internal structure unknown. Surface transversely striated; striae probably outline faint hyponomic sinus on venter (33, 71). [Referred to Valcouroceratidae because of superficial similarity to *Manitoulinoceras*.] ?*M.Ord.*, *U.Ord.*, N.Am.(Ind.-?Wis.).—FIG. 206,3. \**F. thompsoni* (MILLER), *U.Ord.*, USA(Ind.); 3*a,b*, dorsal, lat. (venter right),  $\times 0.75$  (71).

**Kindleoceras** FOERSTE, 1924, p. 226 [\**K. reversatum*; OD]. Curved or virtually straight conchs with flattened dorsum, subangular venter, triangular transverse section. Siphuncle small, ventral, cyrtchoanitic, with thickened rings and actinosiphonate deposits, rays of which are shorter and more numerous than in *Augustoceras* (33, 54). *M.Ord.-U.Ord.*, N.Am.—FIG. 206,5. \**K. reversatum*, *U.Ord.*, Can.(Ont.); 5*a-c*, lat. (venter left), ventral, transv. sec. (venter down),  $\times 0.75$ ; 5*d*, partial long. sec.,  $\times 3$  (33, 54).

**Manitoulinoceras** FOERSTE, 1924, p. 230 [\**Cyrtoceras lysander* BILLINGS, 1865, p. 161; OD]. Siphuncle like *Kindleoceras*, but shell more curved, aperture open, section depressed with somewhat flattened dorsum. Actinosiphonate deposits apparently gerontic, confined to early parts of phragmocone (33, 54). *U.Ord.*, N.Am.(Ky.-Ohio-Ind.-Ont.).—FIG. 206,1. \**M. lysander* (BILLINGS), Can.(Ont.); 1*a,b*, lat. (venter left), ventral  $\times 0.75$ ; 1*c*, partial long. sec.,  $\times 4.5$  (33, 54).

**Minganoceras** FOERSTE, 1938, p. 104 [\**Cyrtoceras subtrubrinatum* BILLINGS, 1857, p. 312; OD]. Slender, depressed cyrtocones with venter more narrowly rounded than dorsum; siphuncle cyrtchoanitic with simple actinosiphonate deposits (33, 76). *M.Ord.*, N.Am.—FIG. 206,6. \**M. subtrubrinatum* (BILLINGS), *M.Ord.*, Que.(Mingan Is.); 6*a-c*, ventral, lat. (venter left), partial long. sec.,  $\times .35$ ; 6*d*, siphuncle (venter down),  $\times 0.4$  (33, 76).

**Staufferoceras** FOERSTE, 1932, p. 50 [\**Cyrtoceras featherstonhaughi* CLARKE, 1897, p. 807; OD]. Like *Manitoulinoceras* in section, but gibbous adorally; internal structures unknown. Deep camerae and rapid expansion suggest early stages of *Manitoulinoceras*, for which reason this genus is referred to the Valcouroceratidae (33, 71). *M.Ord.-U.Ord.*, N.Am.(Ohio-Minn.).—FIG. 206,4. \**S. featherstonhaughi* (CLARKE), *M.Ord.*, USA (Minn.); 4*a-c*, lat. (venter right), ventral, dorsal,  $\times 1$  (71).

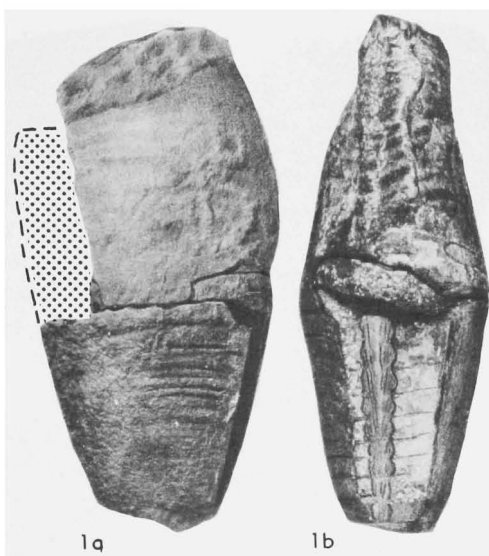


FIG. 207. \**Actinomorpha pupa* FLOWER (?Valcouroceratidae) (p. K291).

### Family DIESTOCERATIDAE Foerste, 1926

Compressed, straight to faintly endogastric brevicones with marginal, cyrtchoanitic siphuncle in which are discrete, irregular actinosiphonate deposits (32, 33, 49, 57). *M.Ord.-U.Ord.*

**Diestoceras** FOERSTE, 1924, p. 262 [\**Gomphoceras indianense* MILLER & FABER, 1894, p. 137; OD]. Conch with greatest height and width at adoral end of phragmocone, contracting to aperture; peristome straight, transverse, with hyponomic sinus. Siphuncle ventral, cyrtchoanitic; segments subquadrate in longitudinal section, usually scalariform in outline; thin annulosiphonate rings in septal foramen produce distinctive irregular linear processes extending adapically and adorally, but not forming rays continuous from segment to segment (31, 33, 53). *M.Ord.-U.Ord.*, N.Am.-Eu.—FIG. 208,5. \**D. indianense* (MILLER & FABER), *U.Ord.*, USA(Ind.); 5*a,b*, lat. (venter right), ventral,  $\times 0.5$ ; 5*c*, partial long. sec. (venter left),  $\times 2$  (33, 53).

**Danoceras** TROEDSSON, 1926, p. 101 [\**D. ravni*; OD] [= *Hyperoceras* FOERSTE, 1928]. Conch slightly contracted at aperture. Siphuncle cyrtchoanitic; necks recumbent, segments elongate, subtrapezoidal in longitudinal section; endosiphuncular deposits like *Diestoceras*; not well developed in known species (33, 194). ?*M.Ord.*, *U.Ord.*, Eu. (Est.) - Greenl. - USSR (Sib., Taimyr Penin.).—FIG. 208,4. \**D. ravni*, *M.Ord.* or *U.*



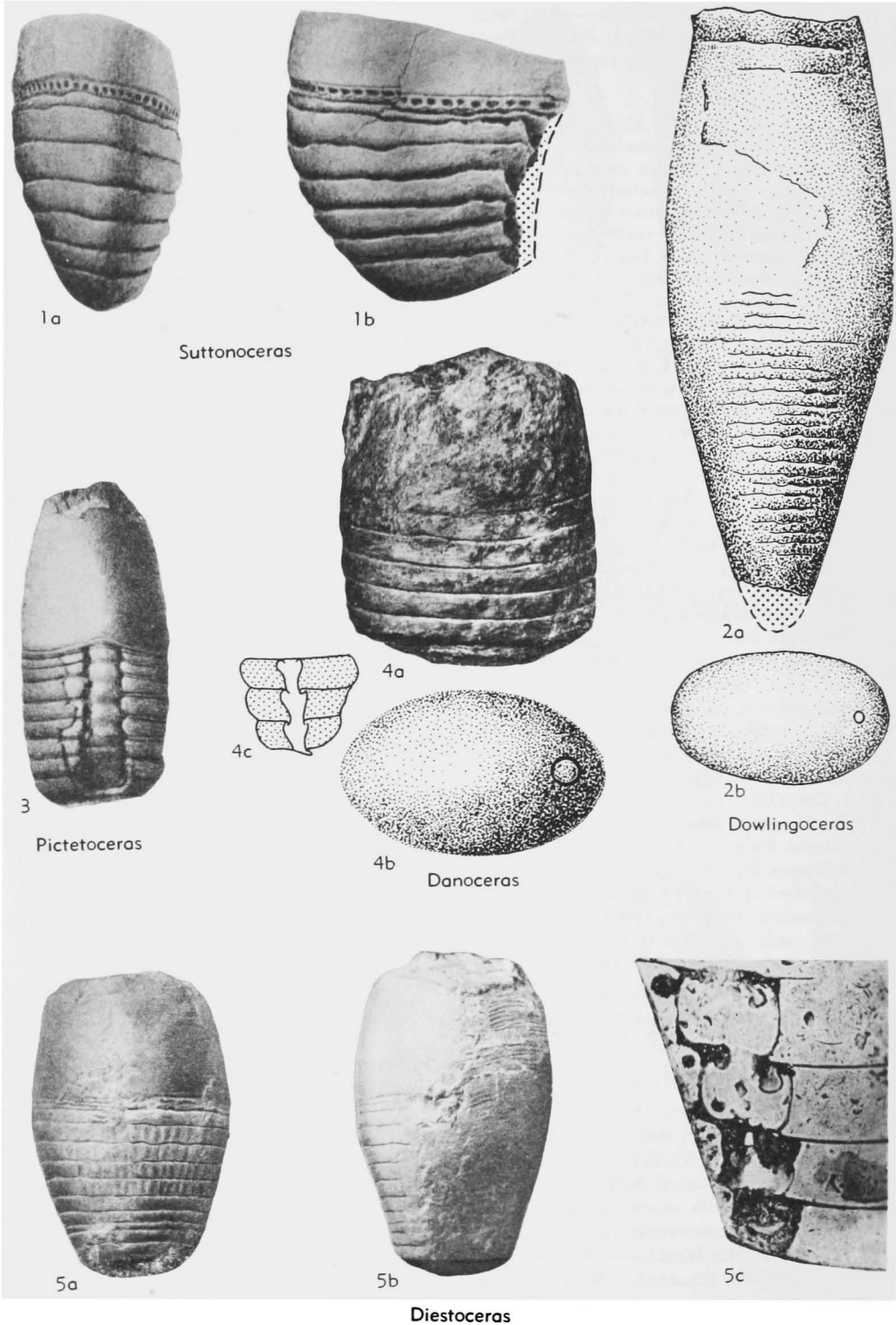


FIG. 208. Diestoceratidae and Genus Dubium (p. K293, K295, K319).



Ord., Greenl.; 4a-c, lat. and septum (venter right), partial long. sec.,  $\times 1$  (194).

**Dowlingoceras** FOERSTE, 1928, p. 43 [*\*Poterioceras gracile* WHITEAVES, 1892, p. 87; OD]. Somewhat like *Diestoceras* in form, but more slender, more compressed, and with relatively much smaller siphuncle that is only slightly inflated within camerae; internal structure of siphuncle unknown (65). [Referred to *Diestoceratidae* on basis of external similarity to *Diestoceras*.] *U.Ord.*, N.Am.-?Eu.(?Est.-?Norway).—FIG. 208,2. *\*D. gracile* (WHITEAVES), Can.(Man.); 2a,b, lat. and septum (venter right),  $\times 1$  (Sweet, n).

?**Lyckholmoceras** TEICHERT, 1930, p. 301 [*\*L. estoniae*; OD]. Large, faintly endogastric cyrtocones with slightly compressed cross section, venter more narrowly rounded than dorsum; aperture with hyponomic sinus; septal necks slightly cyrtochaonic; connecting rings thin; actinosiphonate deposits not known (183). *U.Ord.*, Eu. (Est.-Norway).—FIG. 209,1. *\*L. estoniae*, Est.; 1a,b, lat. (venter left), ventral,  $\times 0.7$  (183).

**Suttonoceras** MILLER & YOUNGQUIST, 1947, p. 13 [*\*S. rossorum*; OD]. Slightly curved, endogastric brevicones with adorally contracted body chamber, straight sutures, and nummuloidal submarginal actinosiphonate siphuncle. Interior of siphuncle unknown (134). [May be a synonym of *Diestoceras*.] *U.Ord.*, N.Am.—FIG. 208,1. *\*S. rossorum*, Can.(Arctic); 1a,b, dorsal, lat. (venter right),  $\times 0.75$  (134).

### Family HEMIPHRAGMOCERATIDAE Foerste, 1926

Compressed, endogastric brevicones, curved adapically, straight adorally, with ventral, nummuloidal, actinosiphonate siphuncle and elaborately visored aperture. Actinosiphonate deposits continuous from one segment to the next. Mature peristome with hyponomic sinus on spoutlike process, paired lateral sinuses, and mid-dorsal salient (49, 57). *M.Sil.-U.Sil.*, ?*M.Dev.*

**Hemiphragmoceras** HYATT in ZITTEL, 1900, p. 531 [*\*Phragmoceras pusillum* BARRANDE, 1865, pl. 52; OD] [= *Hemiphragmoceras* COSSMANN, 1900 (nom. null.)]. Similar to *Tetrameroceras*, but peristome with single pair of dorsolateral sinuses, distal extremities of which curve adventrally (57, 97). *M.Sil.*, Eu.(Czech.). ?*M.Dev.*, USSR(Sib., Taimyr Penin.).—FIG. 210,3. *\*H. pusillum* (BARRANDE), M.Sil., Czech.; 3a,b, lat. and apert. (venter right),  $\times 1$  (5).

**Conradoceras** FOERSTE, 1926, p. 361 [*\*C. pseudoconradi*; OD] [non *Conradoceras* FOERSTE, 1928 (= *Reedsoceras* FOERSTE, 1929)]. Like *Tetrameroceras*, but straighter; mature peristome with hyponomic sinus and 2 pairs of broad dorsolateral emarginations, largest of which is produced lat-

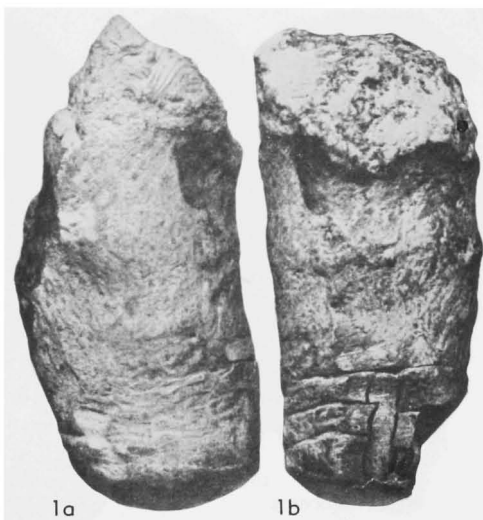


FIG. 209. *\*Lyckholmoceras estoniae* TEICHERT (?*Diestoceratidae*) (p. K295).

erally, whereas smaller is directed ventrolaterally (57). *M.Sil.*, Eu.—FIG. 210,4. *\*C. pseudoconradi*, Czech.; 4a-c, lat. and apert. (venter left), long. sec.,  $\times 1$  (5).

**Hexameroceras** HYATT, 1884, p. 278 [*\*Phragmoceras Panderi* BARRANDE, 1865, pl. 48; OD] [= *Septameroceras* HYATT, 1884 (subj.); *Octameroceras* HYATT in ZITTEL, 1900 (subj.); *Hep-tameroceras* ZITTEL, 1884 (nom. null.); *Hexamoceras* MITCHELL, 1890 (nom. null.)]. Similar to *Tetrameroceras*, but mature peristome with 3 pairs of dorsolateral sinuses and narrow mid-dorsal salient (57, 93). *M.Sil.-U.Sil.*, N.Am.-Eu.—FIG. 210,1. *\*H. panderi* (BARRANDE), M.Sil., Eu. (Czech.); 1a,b, lat. and apert. (venter right),  $\times 0.75$  (5).

**Octamerella** TEICHERT & SWEET, 1962, p. 611 [*\*Octameroceras callistomoides* FOERSTE, 1926; OD]. Like *Tetrameroceras*, but straighter; mature peristome with 4 pairs of dorsolateral sinuses and broad mid-dorsal salient (57, 97). *M.Sil.*, N.Am. (Ont.)-Eu.(Czech.).—FIG. 210,2. *\*O. callistomoides* (FOERSTE), Czech.; 2a,b, lat. and apert. (venter left),  $\times 1$  (5). [See 193a.]

**Tetrameroceras** HYATT, 1884, p. 277 [*\*Phragmoceras bicinctum* BARRANDE, 1865, pl. 51; OD]. Dorsal and ventral profiles convex, body chamber inflated, with contracted, visored aperture; peristome with long hyponomic sinus, 2 pairs of dorsolateral sinuses, and mid-dorsal salient. Siphuncle with convex segments and continuous actinosiphonate deposits (57, 93). *M.Sil.-U.Sil.*, N. Am.-Eu.—FIG. 210,5. *\*T. bicinctum* (BARRANDE), M.Sil., Eu.(Czech.); 5a,b, lat. and apert. (venter left),  $\times 1$  (5).

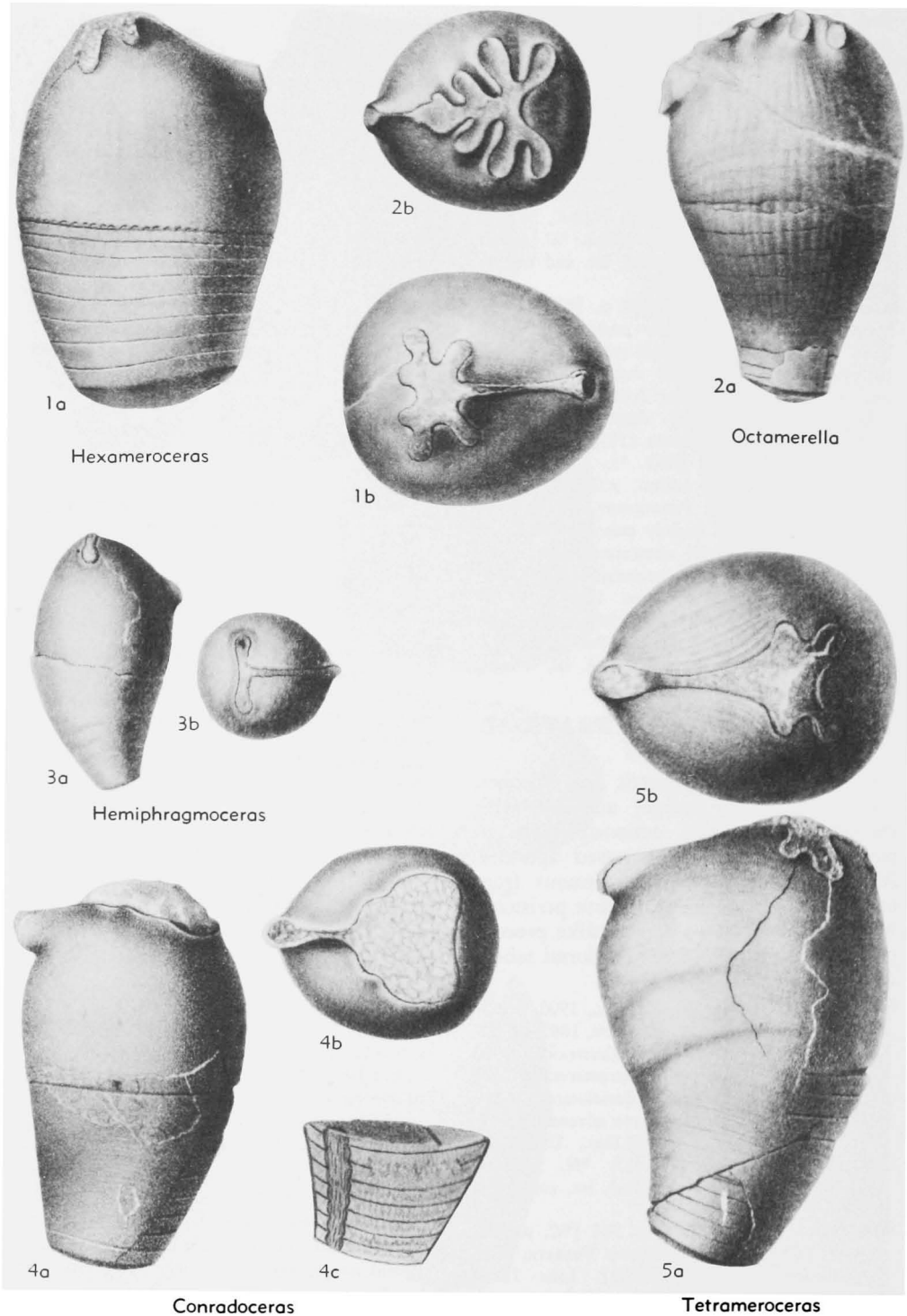


FIG. 210. Hemiphragmoceratidae (p. K295).

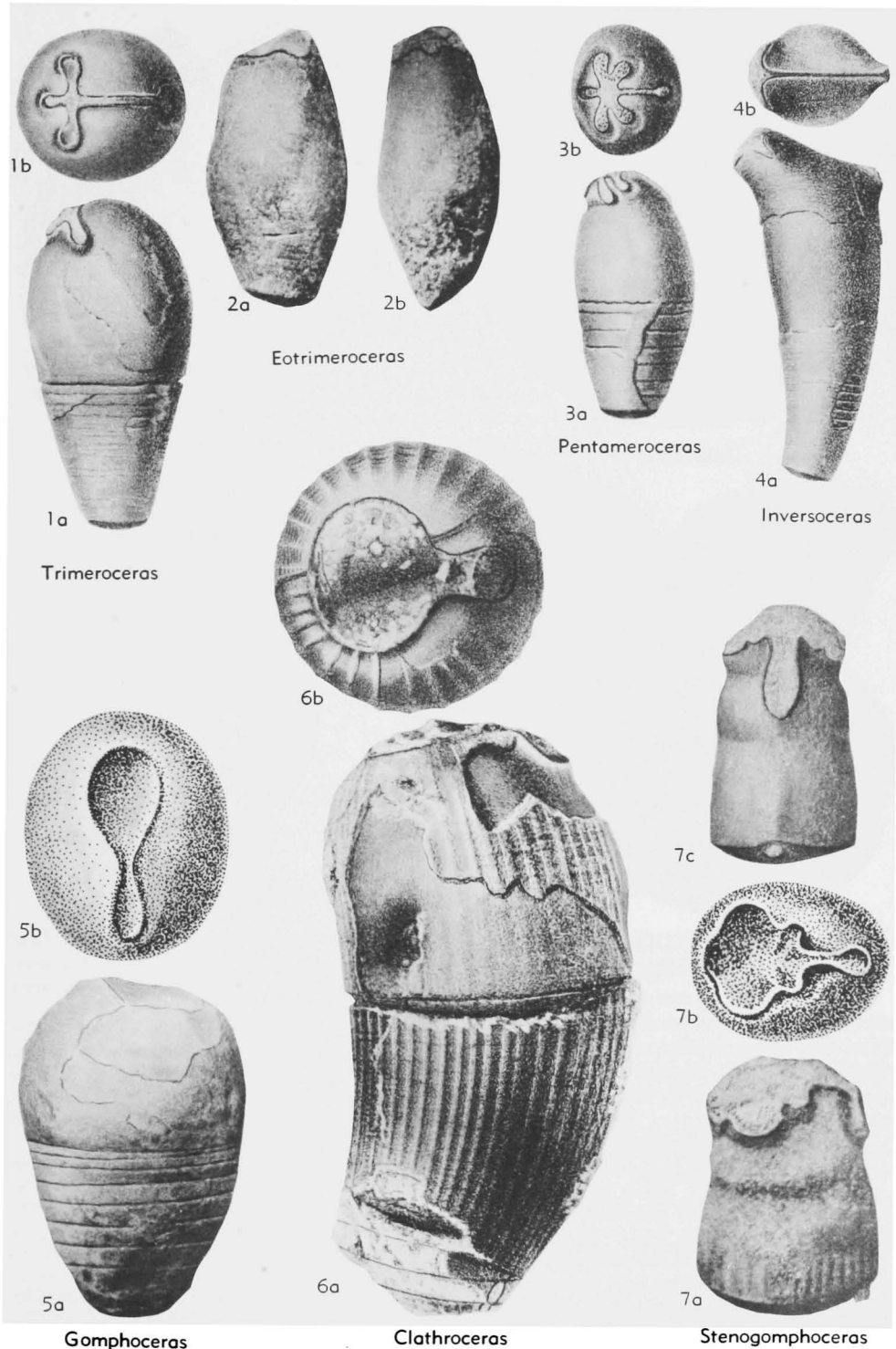


FIG. 211. Trimeroceratidae and Genus Dubium (p. K298-K299, K318).

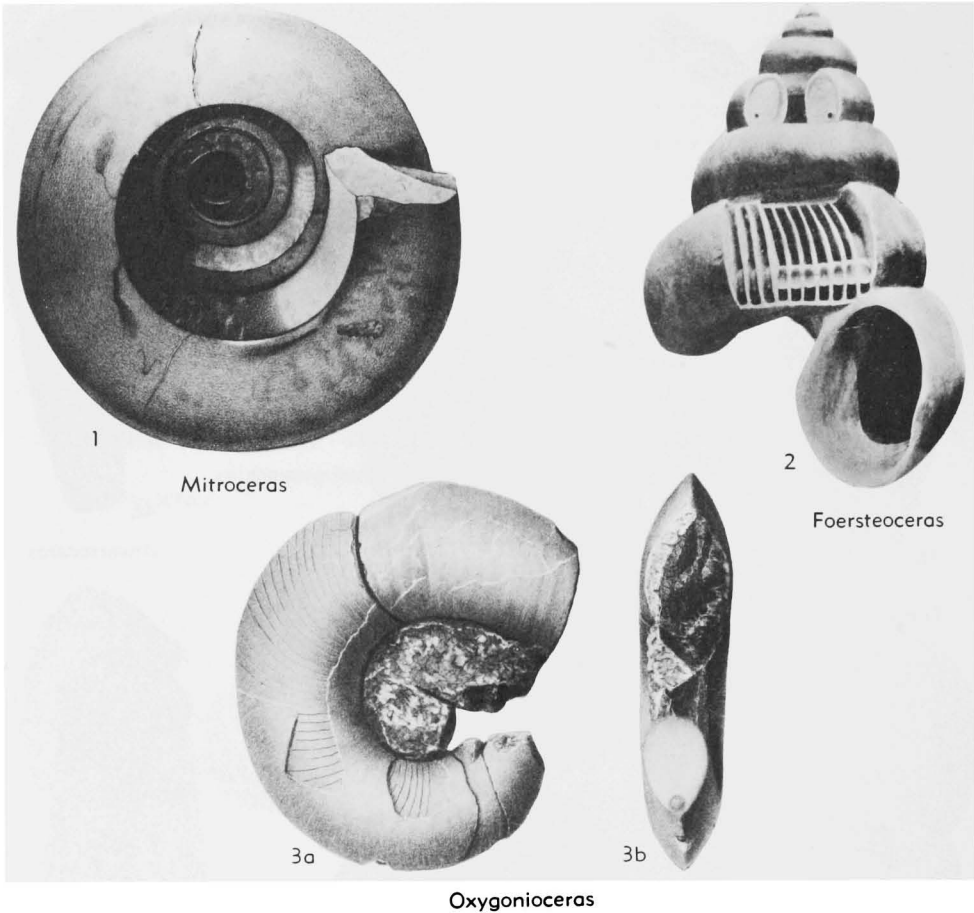


FIG. 212. Torticonic Brevicercerataidae (p. K301).

### Family TRIMEROCERATIDAE Hyatt in Zittel, 1900

Exogastric, mostly compressed brevicones, superficially similar to Hemiphragmocerataidae, but with slender, empty siphuncles. Aperture visored; mature peristome with median dorsal sinus (49, 97). *M.Sil.*

**Trimeroceras** HYATT, 1884, p. 278 [*\*Gomphoceras staurostoma* BARRANDE, 1865, pl. 73; OD]. Straight brevicones with inflated body chamber; peristome with hyponomic sinus, slitlike median element, narrow dorsolateral and mid-dorsal sinuses (57, 93). *M.Sil.*, Eu.—FIG. 211, 1. *\*T. staurostoma* (BARRANDE), Czech.; 1a,b, lat. and apert. (venter right),  $\times 1$  (5).

**Clathroceras** FOERSTE, 1926, p. 354 [*\*Phragmoceras sulcatum* BARRANDE, 1865, pl. 47; OD]. Ribbed brevicones with transverse aperture; mature peristome with subcircular hyponomic sinus,

ventrolateral salients, and broad, circular dorsal sinus (57). *M.Sil.*, Eu.—FIG. 211, 6. *\*C. sulcatum* (BARRANDE), Czech.; 6a,b, lat. and apert. (venter right),  $\times 1$  (5).

**Eotrimeroceras** FOERSTE, 1928, p. 319 [*\*E. jupiterense*; OD]. Like *Trimeroceras*, but lateral and dorsal sinuses in dorsal half of peristome less distinctly developed (60). *M.Sil.*, N.Am.—FIG. 211, 2. *\*E. jupiterense*, Can. (Anticosti Is.); 2a,b, lat. (venter right), ventral,  $\times 1$  (60).

**Inversoceras** HEDSTRÖM, 1917, p. 7 [*\*Phragmoceras perversum* BARRANDE, 1865, pl. 53; OD]. Slender brevicones with faintly gibbous body chamber and visored aperture sloping adapically from dorsum to venter, with spoutlike dorsal and ventral processes; mature peristome with hyponomic sinus, narrow, slitlike median element, and broad dorsal sinus, smooth contour of which is broken laterally by deep, V-shaped emarginations (57, 68). *M.Sil.*, Eu. (Czech.-Sweden)-N.Am. (Wis.). — FIG. 211,

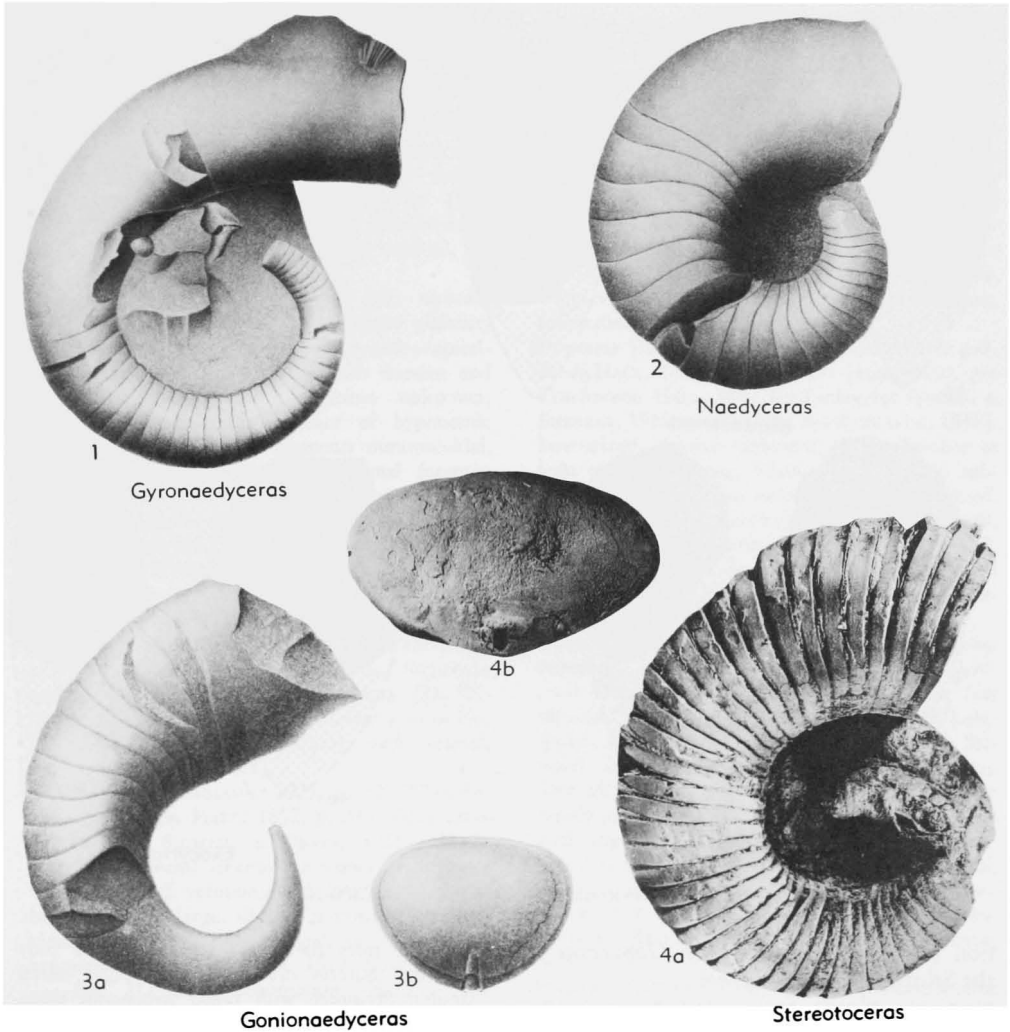


FIG. 213. Coiled Brevicoceratidae (p. K301-K302).

4. *\*I. perversum* (BARRANDE), Eu.(Czech.); 4a,b, lat. and apert. (venter right),  $\times 1$  (5).

**Pentameroceras** HYATT, 1884, p. 278 [*\*Gomphoceras mirum* BARRANDE, 1865, pl. 82; OD]. Straight to faintly exogastric brevicones with compressed, depressed, or virtually circular transverse section; body chamber inflated; aperture visored; peristome with hyponomic and mid-dorsal sinuses and 2 pairs of narrow dorsolateral sinuses (57, 93). *M.Sil.*, N.Am.-Eu.—FIG. 211,3. *\*P. mirum* (BARRANDE), Eu.(Czech.); 3a,b, lat. and apert. (venter right),  $\times 1$  (5).

**Stenogomphoceras** FOERSTE, 1930, p. 367 [*\*S. chadwicki*; OD]. Straight or faintly exogastric brevicones; body chamber contracted adorally, constricted at mid-length; peristome like *Pentamero-*

*ceras*, but lateral sinuses not produced into narrow, arcuate lobes (67). *M.Sil.*, N.Am.(Ill.-?Ohio).—FIG. 211,7. *\*S. chadwicki*, USA(Ill.) 7a-c, lat. and apert. (venter right), ventral,  $\times 1$  (67).

### Family BREVICOCERATIDAE Flower, 1941

[Incl. Naedyceratidae SHIMANSKIY & ZHURAVLEVA, 1956; Mitroceratinae ZHURAVLEVA, 1962] [=Trochoceratidae S. A. MILLER, 1877 (based on *Trochoceras* HALL, 1852, non BARRANDE, 1848) (non Trochoceratidae ZITTEL, 1884, based on *Trochoceras* BARRANDE, 1848, non HALL, 1852)]

Exogastric (or, rarely, endogastric) gyrocones, torticones, and brevicones, tending to develop vestigial, irregular actinosiphonate deposits and subtriangular transverse sec-

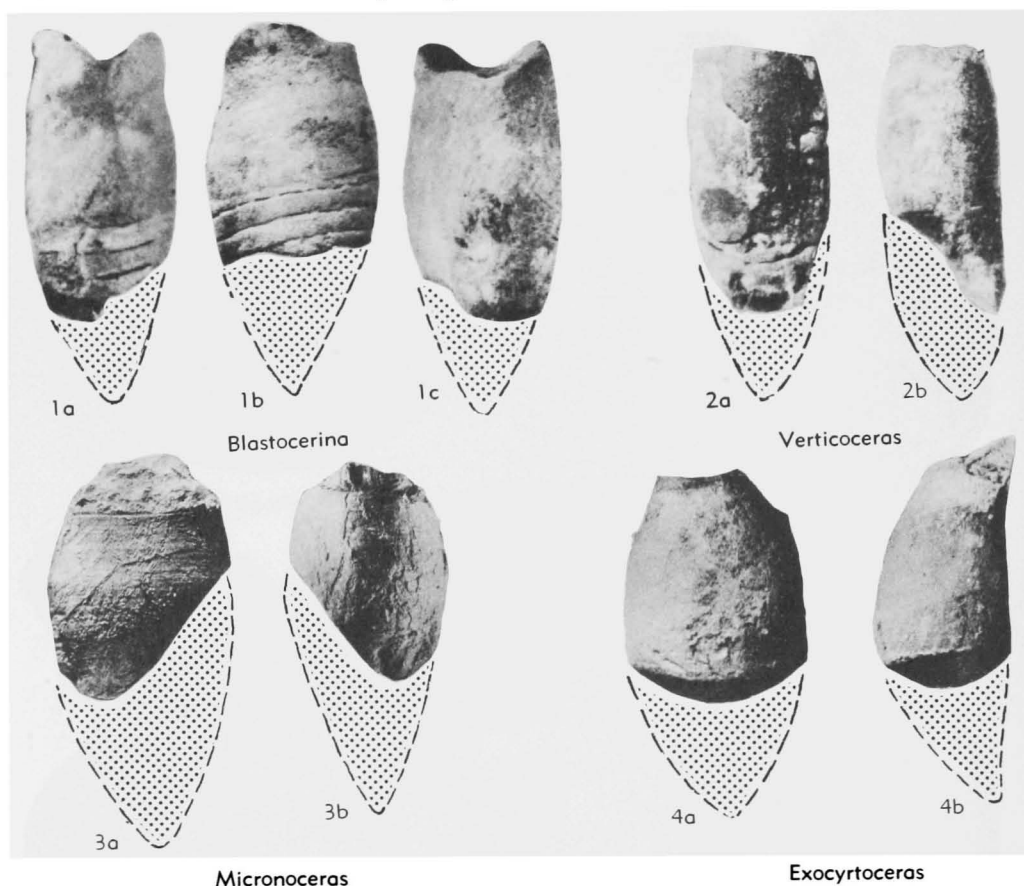


FIG. 214. Breviconic Brevicoceratidae (p. K300-K302).

tion (32, 49). [Derived from *Oonoceras* in the Silurian.] *M.Sil.-U.Dev.*

**Brevicoceras** FLOWER, 1938, p. 24 [*\*B. casteri*; OD]. Depressed brevicones with flattened dorsum, more narrowly rounded venter; ventral profile convex, dorsal profile concave adapically, convex over adoral part of phragmocone and adjacent body chamber, straight or faintly concave just behind aperture; sides convex, diverging to place of maximum dorsal gibbosity, contracting adorally. Sutures with ventral and dorsal lobes, lateral saddles. Aperture transverse, little constricted, not visored; peristome with dorsal and ventrolateral salients and small mid-ventral hyponomic sinus. Siphuncle ventral, slender, nummuloidal, with irregular actinosiphonate deposits (21). *M.Dev.*, N.Am. (N.Y.-Mich.-Iowa-Ont.).—FIG. 215, 1a. *B. pompeyense*, USA (N.Y.); transv. sec.,  $\times 0.5$  (21).—FIG. 215, 1b, c. *\*B. casteri*, USA (N.Y.); ventral, lat. (venter left),  $\times 0.5$  (21).

**Aletoceras** FLOWER, 1938, p. 35 [*\*A. gracile*; OD]. Slightly depressed brevicones, gibbous in adoral part of phragmocone and adapical half of body

chamber, sides flaring in adoral part of body chamber. Sutures straight or with slight lateral saddles. Peristome with broad hyponomic sinus, ventrolateral salients, dorsolateral sinuses, and probably broad mid-dorsal salient. Siphuncle ventral, empty, with nummuloidal, slightly scalariform segments (21). *M.Dev.*, N.Am.—FIG. 215, 5. *\*A. gracile*, USA (N.Y.); 5a, b, ventral, lat. (venter left),  $\times 1$  (21).

**Anglicornus** FLOWER & CASTER, 1935, p. 52 [*\*A. anneliesae*; OD]. Slightly depressed brevicones with maximum gibbosity slightly in front of posterior end of body chamber; dorsum more gibbous than venter. Peristome with hyponomic sinus, rounded ventrolateral salients. Siphuncle ventral, segments fusiform, internal structure unknown (21, 48, 214). *U.Dev.*, N.Am. (Pa.-N.Y.).—FIG. 215, 2. *\*A. anneliesae*, USA (Pa.); 2a, b, lat. (venter right), ventral,  $\times 1$  (48).

**Blastocerina** FLOWER, 1940, p. 447 [*Blastoceras cylindrostomum* FLOWER & CASTER, 1935, p. 51; OD] [= *Blastoceras* FLOWER & CASTER, 1935 (non FITZINGER, 1860)]. Brevicones with slightly more

- convex venter than dorsum and greatest gibbosity in adapical third of body chamber; body chamber subcylindrical or only slightly contracted adorally from this. Sutures produced adaperturally on dorsum. Peristome with broad hyponomic sinus, ventrolateral salients, dorsolateral sinuses and mid-dorsal salient. Siphuncle probably near venter; position and internal structure unknown (48). *U.Dev.*, N.Am.—FIG. 214,1. \**B. cylindrostoma* (FLOWER & CASTER), USA(Pa.); 1a-c, ventral, lat. (venter left), dorsal,  $\times 1$  (48).
- Eleusoceras** FLOWER, 1938, p. 55 [\**E. nicholsi*; OD]. Straight brevicones with greatest gibbosity posterior of body chamber, uncompressed adapically; slightly depressed adorally, with dorsum and venter equally rounded. Aperture unknown; growth lines indicating absence of hyponomic sinus. Siphuncle ventral; segments nummuloidal, with actinosiphonate deposits in septal foramen not continuous from segment to segment (21, 32). *M.Dev.*, N.Am.—FIG. 215,6. \**E. nicholsi*, USA (N.Y.); dorsal,  $\times 0.75$  (21).
- Exocyrtoceras** FLOWER, 1938, p. 37 [\**E. exoticum*; OD]. Slightly curved, depressed brevicones and more strongly curved torticones with rounded venter and flattened dorsum. Aperture transversely elliptical; without hyponomic sinus. Siphuncle ventral, narrowly cyrtchoanitic, empty (21, 32). *M.Dev.*, N.Am.(N.Y.-Ohio-Mich.-Ont.).—FIG. 214,4. \**E. exoticum*, USA(Ohio); 4a,b, ventral, lat. (venter left),  $\times 1$  (21).
- Foersteoceras** RUEDEMANN, 1925, p. 62 [\**Trochoceras turbinatum* HALL, 1852, p. 335; OD] [non *Foersteoceras* SHIMIZU & OBATA, 1936]. High-spined, mitriform, dextral torticones with 5 or more depressed volutions and long body chamber. Siphuncle large, slightly nummuloidal, marginal; with secondary, vestigial, or rudimentary actinosiphonate deposits (33, 152). *U.Sil.*, N.Am.—FIG. 212,2. \**F. turbinatum* (HALL), USA (N.Y.); outer whorl contour, ventral,  $\times 0.5$  (152).
- Gonionacdyoceras** FLOWER, 1945, p. 716 [\**Trochoceras pandion* HALL, 1876, pl. 48; OD]. Strongly curved cyrtocones with asymmetric, subtriangular transverse section; dorsum obliquely flattened, venter with rounded to angular ridge not in plane of siphuncle. Sutures with dorsal lobes, umbilical saddles sharper on left than right, lateral lobes, and rounded ventral saddle. Siphuncle ventral, cyrtchoanitic, actinosiphonate (32). *M.Dev.*, N.Am.—FIG. 213,3. \**G. pandion* (HALL), USA (N.Y.); 3a,b, lat. (venter convex), septum (venter down),  $\times 0.75$  (87).
- Gyronaedyoceras** FLOWER, 1945, p. 716 [\**Gyroceras validum* HALL, 1876, pl. 51; OD]. Compressed gyrocones of about 2 volutions; whorl section asymmetrical, subtriangular, with broadly rounded to subangular venter and flat dorsum; sutures essentially straight and transverse. Siphuncle ventral, cyrtchoanitic, with discrete actinosiphonate deposits (32). *M.Dev.*, N.Am.(N.Y.-Wis.).—FIG. 213,1. \**G. validum* (HALL), USA(N.Y.); lat. (venter convex),  $\times 0.33$  (87).
- Micronoceras** FLOWER, 1938, p. 46 [\**M. delphicolum*; OD]. Small, slightly curved, depressed brevicones enlarging to body chamber mid-length, then gradually contracting adorally to round or faintly subtriangular aperture. Siphuncle ventral; segments elongate and only slightly expanded; interior unknown (21, 32). *M.Dev.*, N.Am.(N.Y.-Ohio-Ind.).—FIG. 214,3. \**M. delphicolum*, USA(N.Y.); 3a,b, opposite sides of same specimen, orientation uncertain,  $\times 1$  (21).
- Mitroceras** HYATT, 1894, p. 503 [\**Trochoceras gebhardi* HALL, 1852, p. 335; OD] [nom. subst. pro *Trochoceras* HALL, 1852 (= *Tachoceras* GRABAU & SHERZER, 1910, nom. null.), non BARRANDE, 1848]. Low-spined, dextral torticones; body chamber at least one whorl long, whorls subcircular to subquadrate in transverse section, slightly impressed. Siphuncle ventral, marginal, nummuloidal, small; with rudimentary actinosiphonate deposits (32, 152). *U.Sil.*, N.Am.—FIG. 212,1. \**M. gebhardi* (HALL), USA(N.Y.); outer whorl contour, ventral,  $\times 0.5$  (84).
- Naedyoceras** HYATT, 1884, p. 281 [\**Trochoceras eugenium* HALL, 1861, p. 108; OD] [= ?*Gyroceras* OWEN, 1844; ?sr. syn. of *Naedyoceras* (see MILLER, DUNBAR, & CONDRA, 1933, p. 90)]. Low-spined, loosely coiled, dextral torticones with flattened dorsum and subtriangular whorl section little affected by asymmetry of coil; body chamber faintly gibbous; mature aperture contracted. Sutures with slight lateral lobes, broad ventral and umbilical saddles, and dorsal lobe. Siphuncle ventral, cyrtchoanitic, actinosiphonate (32, 93). *M.Dev.*, N.Am.(N.Y.-Wis.-Ohio).—FIG. 213,2. \**N. eugenium* (HALL), USA(N.Y.); venter convex,  $\times 0.5$  (87).
- Ovoceras** FLOWER, 1936, p. 64 [\**Gomphoceras (Apioceras) oviforme* HALL, 1860, p. 105; OD]. Small, erect, depressed brevicones, expanding adorally beyond adapical end of body chamber, then contracting to aperture. Peristome with prominent hyponomic sinus, ventrolateral salients, lateral sinuses and straight or faintly emarginate dorsum. Siphuncle ventral; interior unknown (20, 21). *M.Dev.*, N.Am.(N.Y.-Ind.-Eu.(Ger.)).—FIG. 215,3. \**O. oviforme* (HALL), USA(N.Y.); 3a,b, apert. (venter down), dorsal,  $\times 0.75$  (20).
- Oxygonioceras** FOERSTE, 1925, p. 62 [\**Trochoceras oxynotum* BARRANDE, 1865, pl. 14; OD]. Compressed, loosely coiled, dextral torticones, with rounded dorsum and angular or subangular venter in transverse section; sutures with broad lateral lobes. Siphuncle ventral; segments broadly nummuloidal, subscalariform, empty (29, 32, 55). *M.Sil.*, N.Am.-Eu.(Eng.-Czech.).—FIG. 212,3. \**O. oxynotum* (BARRANDE), Eu.(Czech.); 3a,b, lat. (venter convex), dorsal,  $\times 0.5$  (5).



**Stereotoceras** FLOWER, 1950, p. 12 [*\*S. oppletum*; OD]. Smooth, depressed gyrocones with dorsum much flatter than venter. Sutures straight ventrally, but with dorsal lobes; surface with transverse growth lines outlining mid-ventral hyponomic sinus. Siphuncle ventral, nummuloidal, with discrete, irregular actinosiphonate deposits concentrated at septal foramina (37). *M.Dev.*, N. Am.-Eu. (Czech.); *U.Dev.*, N. Am. (N.Y.).—FIG. 213.4. *\*S. oppletum*, *M.Dev.*, USA (N.Y.); *4a,b*, lat. (venter convex), septum (venter down),  $\times 0.5$  (37).

**Verticoceras** FLOWER, 1936, p. 72 [*\*V. erectum*; OD]. Virtually straight, depressed, endogastric brevicones with greatest gibbosity in adapical part of body chamber. Aperture slightly contracted, round except for hyponomic sinus. Siphuncle ventral (20, 21, 32). *M.Dev.-U.Dev.*, N. Am.—FIG. 214.2. *\*V. erectum*, *M.Dev.*, USA (N.Y.); *2a,b*, ventral, lat. (venter right),  $\times 1$  (20).

**Wissenbachia** FOERSTE, 1926, p. 319 [*\*Phragmoceras orthogaster* SANDBERGER & SANDBERGER, 1852, p. 150; OD]. Compressed brevicones; ventral profile uniformly convex, dorsum faintly concave; venter more narrowly rounded than dorsum. Sutures and aperture straight and transverse; peristome with broad hyponomic sinus, rounded ventrolateral salients, ?dorsal sinus. Siphuncle ventral, nummuloidal, actinosiphonate (21, 57). *M.Dev.*, Eu. (Czech.-Ger.)-N. Am. (N.Y.).—FIG. 215.4. *\*W. orthogaster* (SANDBERGER & SANDBERGER), Ger.; *4a,b*, lat. (venter right), ventral,  $\times 1$  (57).

### Family JOVELLANIIDAE Foord, 1888

Longiconic cyrtocones and orthocones with large, ventral, actinosiphonate siphuncles and subtriangular to depressed transverse section; venter typically angular or more acutely rounded than dorsum (22, 41). [Probably developed from Valcouroceratidae in Upper Ordovician or Silurian.] *?U.Ord.*, *M.Sil.-L.Dev.*

**Jovellania** BAYLE, 1879, p. 91 [*\*Orthoceratites buchi* DEVERNEUIL, 1850, p. 778; OD] [= *Trigonodema* LAPORTE, 1843 (ICZN pend.); *Jovellania* MITCHELL, 1890 (*nom. null.*)]. Like *Mixosiphonoceras*, but not so strongly depressed; shell annulated (16, 57, 79). *L.Dev.*, Eu. (Fr.-Ger.).—FIG. 216.6. *\*J. buchi* (DEVERNEUIL), Fr.; *6a,b*, long. sec. and septum (venter left),  $\times 1$  (57).

**Herkimeroceras** FOERSTE, 1926, p. 288 [*\*Cyrto-ceras subrectum* HALL, 1859, p. 342; OD]. Virtually straight, faintly gibbous, compressed, venter slightly more narrowly rounded than dorsum. Siphuncle ventral, marginal; segments nummul-

oidal to scalariform, actinosiphonate (57). *?U.Sil.* or *?L.Dev.*, N. Am.—FIG. 216.4. *\*H. subrectum* (HALL), USA (N.Y.); *4a,b*, lat. (venter left), ventral,  $\times 0.75$  (57).

**Laumontoceras** FOERSTE, 1926, p. 305 [*\*Orthoceras laumonti* BARRANDE, 1866, pl. 235; OD]. Uncompressed orthocones with central, cylindroid siphuncle slightly contracted at septal necks, with discrete, discontinuous actinosiphonate deposits (57). *?L.Dev.*, Eu.—FIG. 216.3. *\*L. laumonti* (BARRANDE), Fr.; *3a,b*, lat. (venter left), long. sec. (venter right),  $\times 0.5$  (5).

**Mixosiphonoceras** HYATT, 1900, p. 529 [*\*Cyrto-ceras desolatum* BARRANDE, 1877, p. 135; OD]. Slowly enlarging, longiconic cyrtocones or orthocones with subtriangular depressed section; dorsum flat, venter subangular. Siphuncle between center and venter, segments cylindroid, only moderately contracted at septal foramen, actinosiphonate (57, 97). *?U.Ord.*, Eu. (Norway); *M.Sil.*, Eu. (Czech.); *?L.Dev.*, Eu. (Sp.).—FIG. 216.2. *\*M. desolatum* (BARRANDE), M. Sil., Czech.; *2a-c*, septum (venter down), ventral, long. sec. (venter right),  $\times 0.5$  (5).

**Projovellania** HYATT in ZITTEL, 1900, p. 529 [*\*Cyrto-ceras athleta* BARRANDE, 1877, p. 116; OD]. Like *Mixosiphonoceras* and *Jovellania*, but compressed, rather than depressed (57, 97). *M. Sil.*, Eu.—FIG. 216.1. *\*P. athleta* (BARRANDE), Czech.; *1a-c*, ventral, lat. and septum (venter left),  $\times 0.33$  (5).

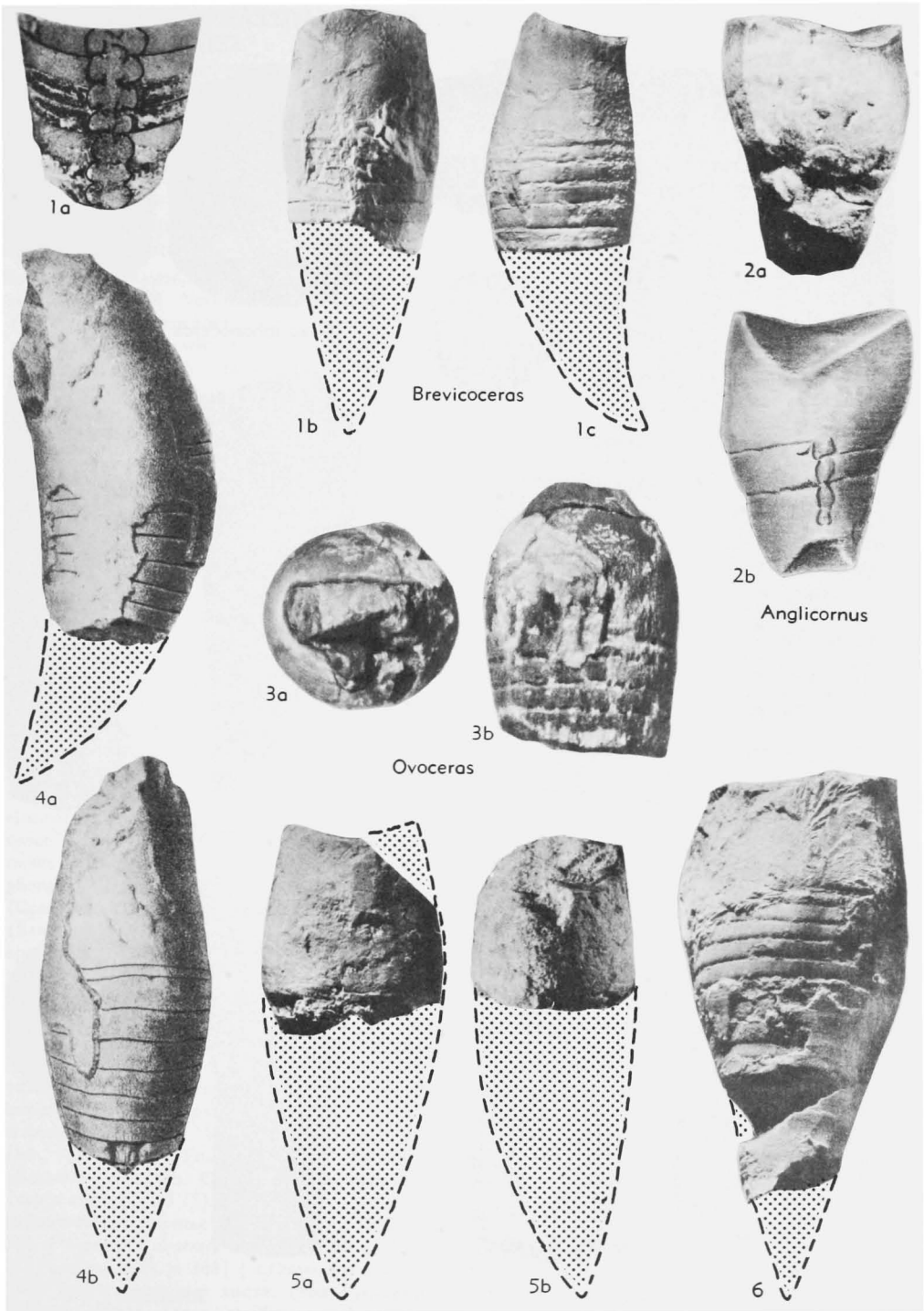
### Family TRIPLEUROCERATIDAE Foerste, 1926

Longiconic orthocones with rounded triangular transverse section; venter flattened, dorsum narrowly rounded or angular. Sutures with narrow dorsal saddles and lateral lobes. Siphuncle on ventral side of center, cyrtochoanitic, in some forms occupied by actinosiphonate deposits (57, 167). *?L.Dev.*, *M.Dev.-L.Carb.* (Miss.).

**Tripleuroceras** HYATT, 1884, p. 289 [*\*Orthoceras archiaci* BARRANDE, 1868, pl. 251; OD]. With characters of family. Siphuncle ventral, marginal, actinosiphonate (57, 93, 167). *?L.Dev.*, Eu. (Ger.); *M.Dev.*, Eu. (Czech.-USSR)-N. Am. (Ont.).—FIG. 216.5. *\*T. archiaci* (BARRANDE), M. Dev., Czech.; *5a,b*, ventral, long. sec. (venter right),  $\times 0.3$  (5).

**Psiaoceras** SHIMANSKIY, 1957, p. 531 [*\*Gomphoceras hesperis* EICHWALD, 1860; OD]. Like *Tripleuroceras*, but siphuncle smaller, apparently not actinosiphonate (167). *U.Dev.-L.Carb.*, Eu.—FIG. 217.1. *\*P. hesperis* (EICHWALD), L. Carb., USSR; *1a-c*, dorsal, lat. (venter right), septum (venter down),  $\times 0.5$  (19).





Wissenbachia

Aletoceras

Eleusoceras

FIG. 215. Breviconic Brevicoceratidae (p. K300-K302).

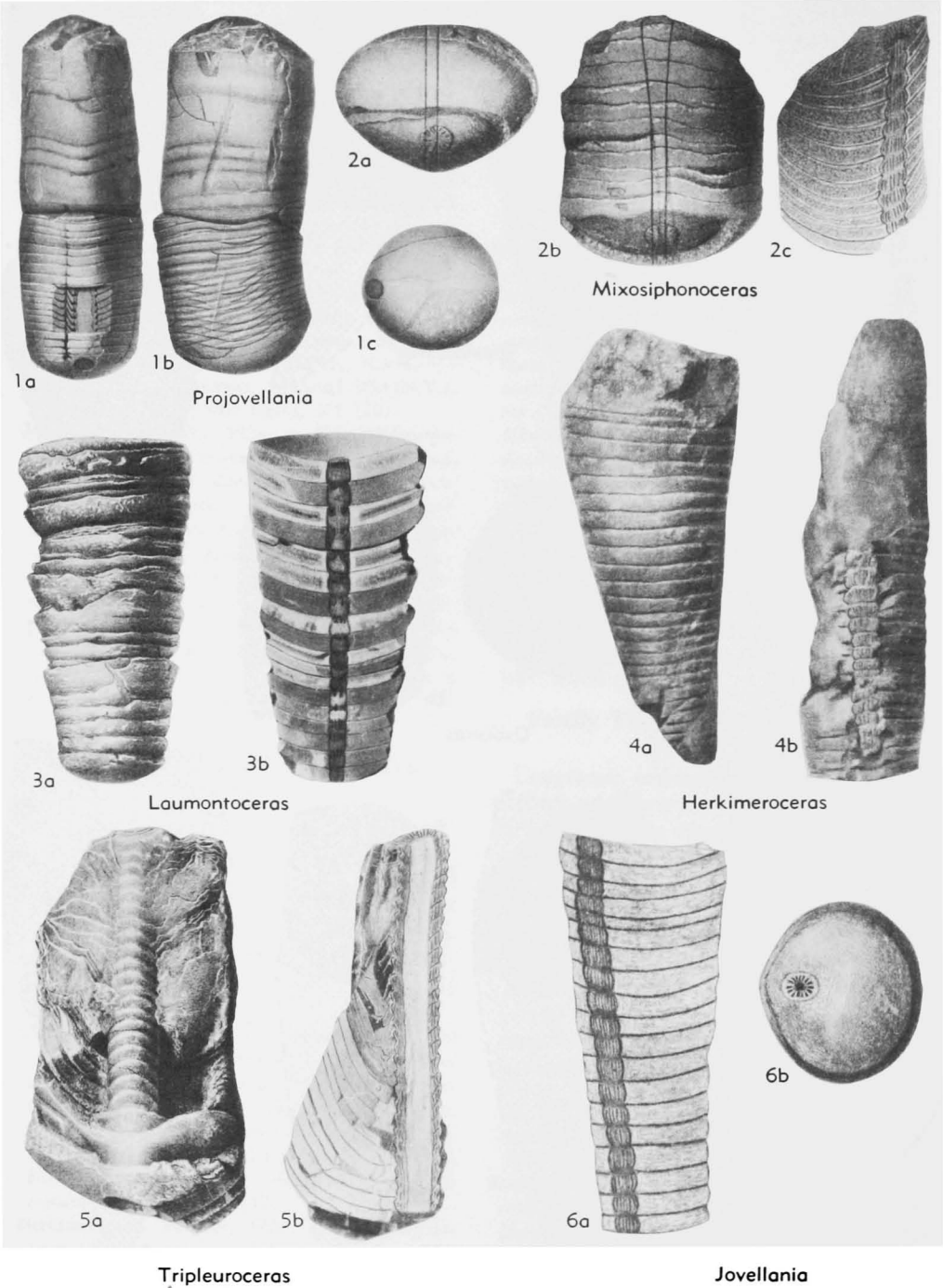


FIG. 216. Jovellaniidae, Tripleuroceratidae (p. K302).

# Family NOTHOCERATIDAE Fischer, 1882

[=Nothoceratidae TEICHERT, 1939 (jr. syn. homonym)]  
[Incl. Cyrtoceratidae CHAPMAN, 1857; Cranoceratidae SHIMANSKIY, 1957; Bolloceratidae ZHURAVLEVA, 1962]

Depressed (or primitively compressed), exogastric or endogastric brevicones, nautilicones, and torticones with contracted or visored apertures and ventral, generally concavosiphonate siphuncle occupied by actinosiphonate deposits (42, 49, 183). *Sil.-U.Dev.*

**Nothoceras** BARRANDE, 1856, p. 317 [*\*N. bohemicum*; OD] [*non Nothoceras* EICHWALD, 1860 (= *?Kochoceras* TROEDSSON, 1926)]. Evolute, exogastric nautilicones with depressed, dorsally impressed whorls; body chamber half a volution long, contracted laterally to aperture. Siphuncle ventral, marginal; segments concavosiphonate, (5, 57). *M.Dev.*, Eu.—FIG. 218.1. *\*N. bohemicum*, Czech.; 1a,b, lat. (venter convex), ventral,  $\times 0.3$  (5).

**Blakoceras** FOERSTE, 1926, p. 322 [*\*Cyrtoceras empiricum* BARRANDE, 1877, p. 141; OD]. Like *Perimeoceras*, but phragmocone enlarging more rapidly, body chamber shorter, and siphuncular diameter proportionately greater. Siphuncle concavosiphonate, with discontinuous actinosiphonate deposits (42, 57). *Sil.*, Eng.; *M.Dev.*, Eu.(Czech.). —FIG. 218.5. *\*B. empiricum* (BARRANDE), M. Dev., Czech.; lat. (venter right),  $\times 0.3$  (5).

**Bolloceras** FOERSTE, 1926, p. 351 [*\*Phragmoceras rex* BARRANDE, 1865, pl. 101; OD]. Compressed endogastric brevicones with adorally contracted body chamber. Aperture T-shaped, with transversely slitlike dorsal element, narrow median element, and slightly expanded liplike hyponomic spout. Siphuncle large, ventral, marginal; segments cylindrical to concavosiphonate, actinosiphonate (21, 50, 57). *M.Dev.-U.Dev.*, Eu. (Czech.)-N.Am.(N.Y.). —FIG. 218.2. *\*B. rex* (BARRANDE), M.Dev., Eu.(Czech.); 2a-c, lat., apert., and septal views (venter right),  $\times 3$ ; 2d, ventral,  $\times 3$  (5).

**Conostichoceras** FOERSTE, 1926, p. 341 [*\*Cyrtoceras palinurus* BARRANDE, 1877, p. 37; OD]. Similar externally to *Turnoceras*, but lateral profiles slightly convex, converging near aperture. Siphuncle ventral; segments nummuloidal in adapical half of camera, but with concave profiles in adoral half; actinosiphonate (57). *M.Dev.*, Eu.(Czech.); *U.Dev.*, Australia.—FIG. 218.6. *\*C. palinurus* (BARRANDE), M.Dev., Czech.; 6a,b, ventral, lat. (venter right),  $\times 0.3$  (5).

**Cyrtoceratites** D'ARCHIAC & DEVERNEUIL, 1842, p. 348 [*\*Cyrtocera depressa* BRONN, 1835, p. 101; SD FLOWER, 1950, p. 368] [= *Cranoceras* HYATT, 1884 (obj.); *Cyrtoceras* AUCTT. (*non Cyrtoceras* CONRAD, 1838)]. Large, rapidly expanding, depressed cyrtocones with short body chamber contracted to aperture, and subtriangular to sub-

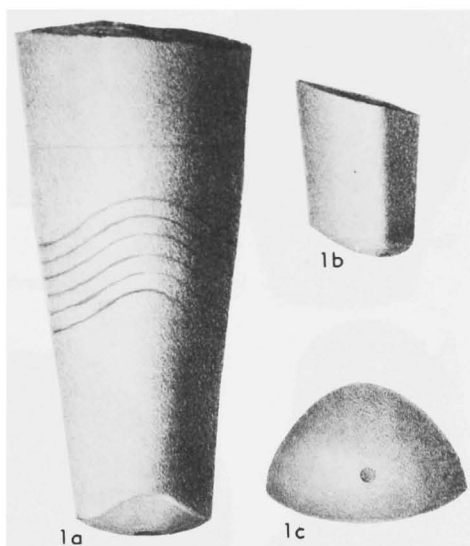


FIG. 217. *\*Psiaoceras hesperis* (EICHWALD)  
(Tripleuroceratidae) (p. K302).

reniform transverse section; dorsum broadly concave, venter more narrowly rounded, at least adorally. Siphuncle large, ventral; segments concavosiphonate, actinosiphonate (37, 57, 200). *M.Dev.*, Eu.—FIG. 219.3. *\*C. depressus* (BRONN), Ger.; 3a,b, dorsal, lat. (venter left),  $\times 0.75$ ; 3c, dorsoventral sec. (venter right),  $\times 1$  (1, 57).

**Lorieroceras** FOERSTE, 1926, p. 382 [*\*Trochoceras lorieri* BARRANDE, 1870, pl. 460; OD]. Loosely coiled, sinistral, turbinate torticones with depressed whorls. Siphuncle ventral, marginal; segments fusiform in outline, inflated adapically, contracted adorally in each camera; actinosiphonate (42, 57). *L.Dev.*, Eu.—FIG. 218.3. *\*L. lorieri* (BARRANDE), Fr.; lat. (venter convex),  $\times 0.75$  (5).

**Metaphragmoceras** FLOWER, 1938, p. 64 [*\*Phragmoceras verneuli* BARRANDE, 1865, pl. 66; OD]. Compressed endogastric brevicones with dorsally inflated body chamber and visored aperture. Dorsal profile abruptly expanded toward dorsum. Peristome with hyponomic sinus, narrow median element, and subquadrate dorsal sinus developed strongly oblique to axis of conch. Siphuncle actinosiphonate, compressed; form of segments not known (21). *M.Dev.*, Eu.(Czech.)-N.Am.(N.Y.). —FIG. 218.4. *\*M. verneuli* (BARRANDE), Czech.; 4a,b, lat. and apert. (venter right),  $\times 0.2$  (5).

**Paraconradoceras** FOERSTE, 1926, p. 362 [*\*Phragmoceras rigescens* BARRANDE, 1877, p. 238; OD]. Brevicones of subcircular or faintly lachrymiform section, probably slight endogastric curvature, and adorally contracted body chamber. Aperture visored; peristome with pentalobate dorsal element,

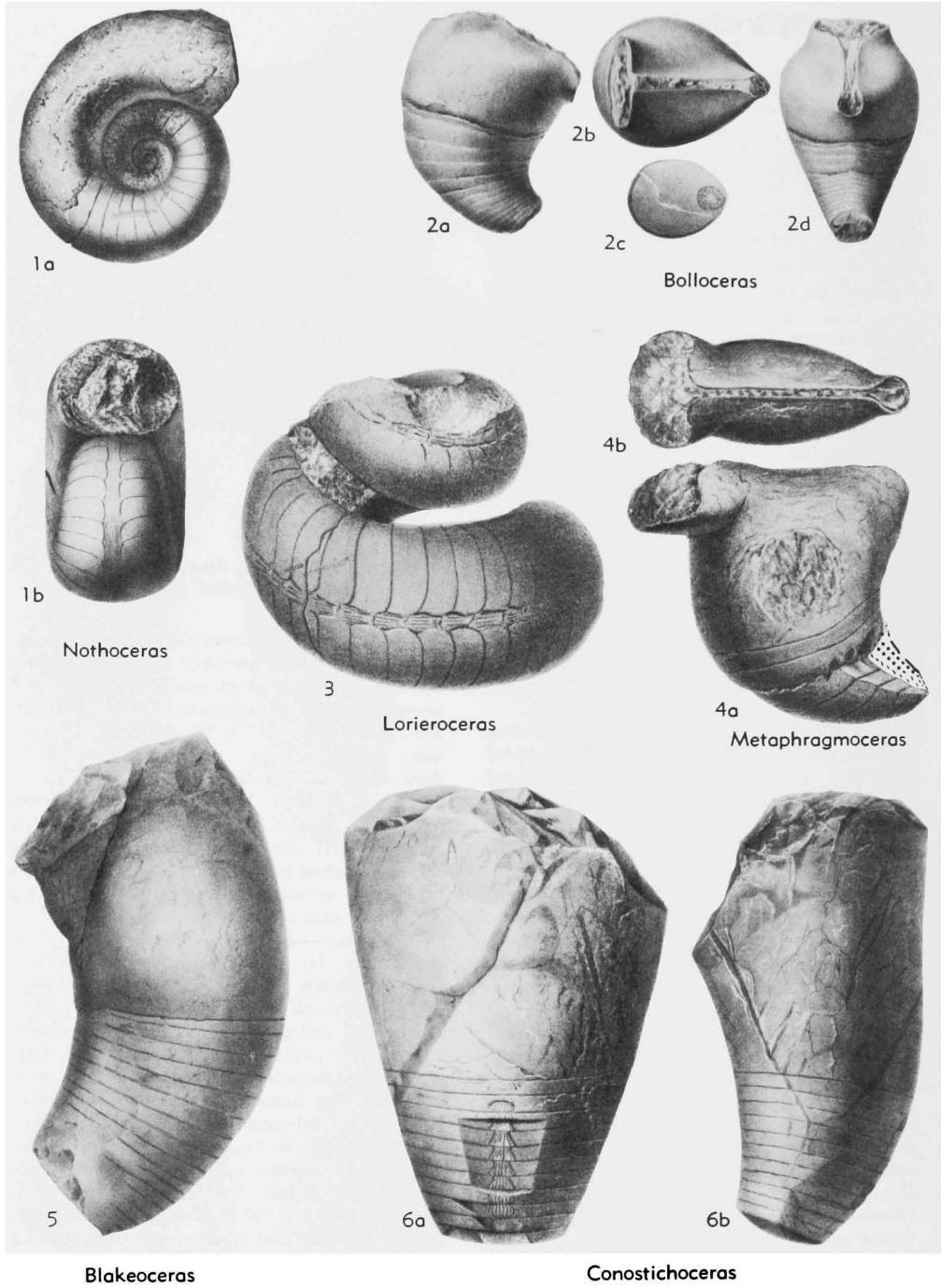


FIG. 218. Nothoceratidae (p. K305).

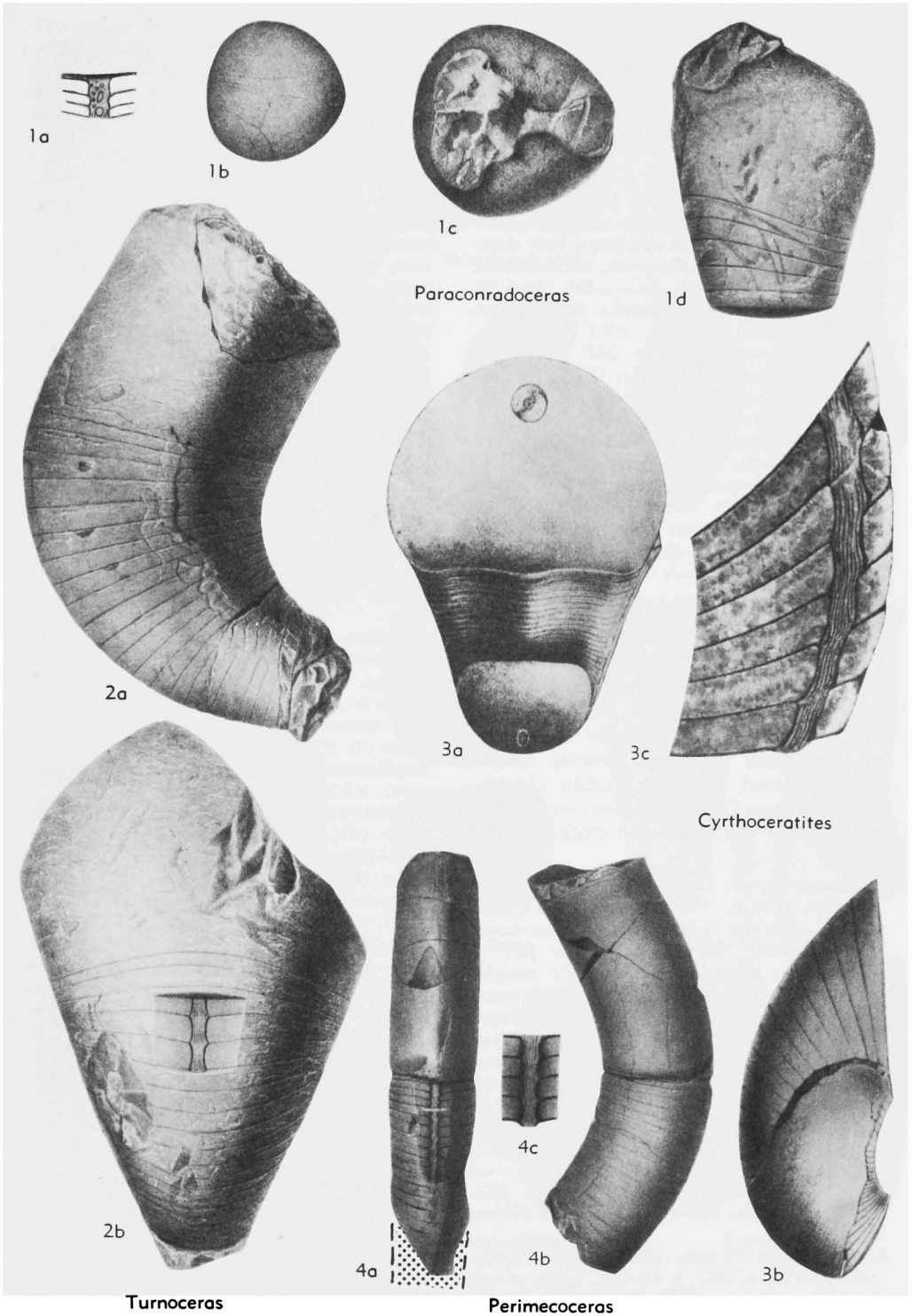


FIG. 219. Nothoceratidae (p. K305, K308).

short median element, subcircular ventral sinus not developed on hyponomic spout. Siphuncle ventral, marginal; segments concavosiphonate, actinosiphonate (5, 21). *M.Dev.*, Eu.—FIG. 219, 1. \**P. rigescens* (BARRANDE), Czech.; 1a-d, long. sec., septal, apert., and lat. views (venter right),  $\times 0.5$  (5).

**Perimecoceras** FOERSTE, 1926, p. 322 [\**Cyrtoceras contrastans* BARRANDE, 1877, p. 129; OD]. Slowly enlarging compressed cyrtocoines similar to *Oonoceras* (Oncoceratidae), but with longer body chamber and ventral, concavosiphonate, actinosiphonate siphuncle (42, 57). *U.Sil.*, Eu.—FIG. 219, 4. \**P. contrastans* (BARRANDE), Czech.; 4a-c, ventral, lat. (venter right), long. sec.,  $\times 0.5$  (5).

**Turnoceras** FOERSTE, 1926, p. 342 [\**Cyrtoceras turnus* BARRANDE, 1877, p. 46; OD]. Depressed exogastric cyrtocoines with flattened dorsum, uncontracted aperture, no hyponomic sinus; sides straight, diverging regularly to aperture; dorsal and ventral profiles convex over phragmocone, but abruptly straightened and subparallel over body chamber. Siphuncle ventral; segments concavosiphonate, actinosiphonate (57). *M.Dev.*, N.Am. (N.Y.)-Eu.(Czech.).—FIG. 219, 2. \**T. turnus* (BARRANDE), Czech.; 2a,b, lat. (venter left), ventral,  $\times 0.3$  (5).

#### Family ACLEISTOCERATIDAE Flower in Flower & Kummel, 1950

Depressed (or rarely compressed, at least in early stages) exogastric brevicoines and cyrtocoines; siphuncle broadly expanded, actinosiphonate in some Devonian species (49). [Derived through Silurian *Amphicyrtoceras* from Ordovician *Oonoceras*, independently of the *Oonoceras* stock.] *M.Sil.*, *M.Dev.*

**Acleistoceras** HYATT, 1884, p. 277 [\**Apioceras olla* SAEMANN, 1854, p. 163; OD]. Straight to slightly curved, subcircular to faintly depressed brevicoines with maximum diameter in anterior part of phragmocone. Dorsal profile virtually straight, ventral profile convex to aperture. Aperture transverse, subtriangular, with well-developed hyponomic sinus. Siphuncle subventral, cyrtochaonic; segments broadly expanded, nummuloidal, scalariform, empty in some species, thought to be actinosiphonate in others (21, 57, 93). *M.Dev.*, N.Am. (widespread).—FIG. 222, 3a-c. \**A. olla* (SAEMANN), USA(Ohio); 3a-c, lat. (venter right), apert. (venter down), ventral,  $\times 0.56$  (57).—FIG. 222, 3d. *A. nummulatum* FOERSTE, USA (Mich.); long. sec. (venter right),  $\times 0.75$  (Sweet, n).

**Amphicyrtoceras** FOERSTE, 1924, p. 255 [\**Cyrtoceras orcas* HALL, 1862, p. 43; OD]. Large, curved brevicoines with convex ventral profile; dorsal profile concave adapically, convex over body cham-

ber, concave adorally; sides diverging adapically, converging adorally. Aperture transverse, with broad hyponomic sinus. Siphuncle subventral, cyrtochaonic, empty; segments subcylindrical, abruptly contracted at septal foramen (53). *M.Sil.*, N.Am. (Ohio-Ill.-Wis.-Que.)-?Eu. (?Czech.).—FIG. 220, 9a,b. \**A. orcas* (HALL), USA(Wis.); ventral, lat. (venter left),  $\times 0.6$  (57).—FIG. 220, 9c. *A. laterale* (HALL), USA(Wis.); partial long. sec.,  $\times 0.64$  (57).

**Anomeioceras** FOERSTE, 1930, p. 89 [\**A. compressum*; OD]. Similar to *Byronoceras*, but early stages compressed, later stages uncompressed; conch more strongly curved and slightly contracted toward aperture. Siphuncle subventral, like *Amphicyrtoceras* (68). *M.Sil.*, N.Am.(Ill.-Ohio).—FIG. 220, 10. \**A. compressum*, USA(Ill.); 10a,b, ventral, lat. (venter right),  $\times 0.75$  (68).

**Austinoceras** FOERSTE, 1934, p. 139 [\**A. turgidulum*; OD]. Slightly depressed to faintly compressed breviconic cyrtocoines, contracted adapically, with concave dorsal and geniculate ventral profiles. Siphuncle subventral, empty; segments expanded within camerae, but abruptly contracted at septal foramen (72). *M.Sil.*, N.Am. (Ill.-Ohio).—FIG. 220, 5. \**A. turgidulum*, USA (Ohio); 5a,b, ventral, lat. (venter left),  $\times 0.75$  (72).

**Byronoceras** FOERSTE & SAVAGE, 1927, p. 82 [\**B. longidomum*; OD]. Slightly depressed, slowly expanding, moderately curved conchs. Siphuncle similar to *Amphicyrtoceras*, but segments elongate oval, apparently moderately inflated (77). *M.Sil.*, N.Am.(Ill.-?Ohio-?Can.).—FIG. 220, 4. \**B. longidomum*, USA(Ill.); 4a,b, ventral, lat. (venter right),  $\times 0.75$  (77).

**Chadwickoceras** FOERSTE, 1930, p. 93 [\**C. fusiforme*; OD]. Similar externally and internally to *Amphicyrtoceras*, but straight; dorsum flatter than venter (68). *M.Sil.*, N.Am.—FIG. 220, 11. \**C. fusiforme*, USA(Ill.); 11a,b, ventral, lat. (venter right),  $\times 0.4$  (68).

?**Clionysiceras** FOERSTE, 1930, p. 40 [\**C. petilum*; OD]. Subcircular to slightly depressed cyrtocoines with faintly gibbous body chamber and oblique sutures sloping adorally from dorsum to venter. Siphuncle ventral, cyrtochaonic, abruptly expanded within camerae (68). *M.Sil.*, N.Am.—FIG. 221, 4. \**C. petilum*, USA(Ill.); 4a,b, ventral, lat. (venter right),  $\times 1$  (68).

**Crateroceras** FOERSTE & SAVAGE, 1927, p. 84 [\**C. raymondi*; OD]. Like *Amphicyrtoceras*, but with short body chamber that is gibbous at mid-length rather than adapically. Siphuncular segments similar to, but shorter than *Amphicyrtoceras* (77). *M.Sil.*, N.Am.(Wis.-?NW.Can.).—FIG. 220, 8. \**C. raymondi*, USA(Wis.); 8a,b, ventral, lat. (venter right),  $\times 0.75$  (77).

**Ectocyrtoceras** FOERSTE, 1930, p. 79 [\**E. marginatum*; OD]. Similar to *Amphicyrtoceras*, but maxi-

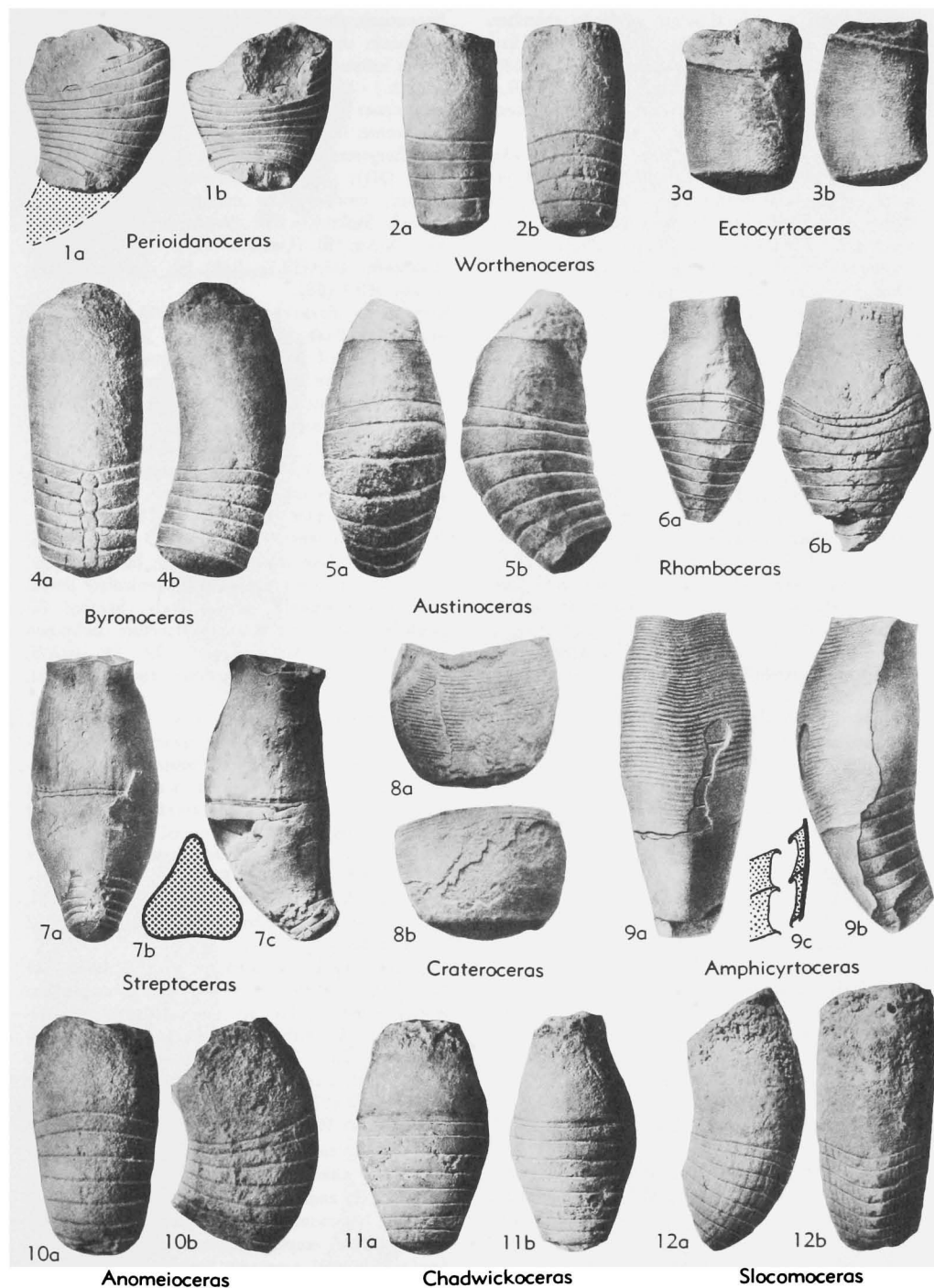


FIG. 220. Silurian Acleistoceratidae (p. K308, K310, K312).



- mum gibbosity at mid-length of body chamber, which has uninflated dorsal profile; dorsum flattened. Siphuncle ventral; interior unknown (68). *M.Sil.*, N.Am.(Ill.-Ont.-?Ohio).—FIG. 220,3. \**E. marginatum*, USA (Ill.); 3a,b, dorsal, lat. (venter left),  $\times 0.75$  (68).
- Euryrizoceras** FOERSTE, 1930, p. 81 [\**E. chadwicki*; OD]. Depressed cyrtocones with regularly divergent dorsum and venter, but adorally convergent sides on body chamber. Dorsum flattened on body chamber. Siphuncle like *Amphicyrtoceras*, but segments less elongated (68). *M.Sil.*, N.Am.(Ill.-Ohio).—FIG. 221,2. \**E. chadwicki*, USA (Ill.); 2a,b, lat. (venter left), ventral,  $\times 0.75$  (68).
- Galtoceras** FOERSTE, 1934, p. 169 [\**Cyrtoceras arcticameratum* HALL, 1852, p. 349; OD]. Depressed, slender, elongate cyrtocones with subventral, empty, cyrtochoanitic siphuncle, with segments somewhat expanded within camerae but abruptly contracted at septal foramen (72). *M.Sil.*, N.Am.(N.Y.-Ont.).—FIG. 221,6. \**G. arcticameratum* (HALL), USA (N.Y.); 6a-c, lat. and transv. sec. (venter left), ventral,  $\times 0.75$  (72).
- Gonatocyrtoceras** FOERSTE, 1926, p. 343 [\**Cyrtoceras heteroclytium* BARRANDE, 1866, pl. 118; OD]. Depressed breviconic cyrtocones, with geniculate ventral and lateral profiles. Aperture transverse, elliptical, without hyponomic sinus. Siphuncle small, subventral; internal structure unknown (57). *M.Dev.*, N.Am.(Ill.-Eu.(Czech.)).—FIG. 222,1. \**G. heteroclytium* (BARRANDE), Czech.; 1a-c, dorsal, lat. (venter left), ventral,  $\times 0.75$  (5).
- ?**Grimsbyoceras** FOERSTE, 1934, p. 129 [\**Cyrtoceras clitus* BILLINGS, 1866, p. 85; OD]. Slightly depressed cyrtocones of moderate curvature and expansion, with adorally convergent sides and distinct hyponomic sinus. Siphuncle ventral, marginal; segments fusiform (72). *M.Sil.*, N.Am.(Ont.-Ohio).—FIG. 221,5. \**G. clitus* (BILLINGS), Can.(Ont.); 5a,b, ventral, lat. (venter right),  $\times 1.25$  (72).
- Hercocyrtoceras** FOERSTE, 1927, p. 313 [\**Oncoceras amator* BILLINGS, 1866, p. 59; OD]. Depressed irregularly annulated cyrtocones, ornamented by raised longitudinal and transverse ridges, with V-shaped hyponomic sinus defined laterally by 2 longitudinal ridges. Position and structure of siphuncle unknown (60). *M.Sil.*, N.Am.(Nova Scotia-Que.).—FIG. 221,1. \**H. amator* (BILLINGS), Que.; 1a,b, ventral, lat. (venter left),  $\times 1$  (60).
- Paracleistoceras** FOERSTE, 1926, p. 335 [\**Phragmoceras devonians* BARRANDE, 1865, pl. 107; OD]. Curved brevicones with flattened dorsum, uncompressed subtriangular adapical region, and depressed adapertural section. Maximum diameter in body chamber. Dorsal profile concave adapically, faintly convex over body chamber; ventral profile markedly convex throughout entire length. Aperture transverse, subtriangular, with hyponomic sinus and broad ventrolateral salients. Siphuncle ventral, marginal, cyrtochoanitic; segments inflated, actinosiphonate (57). *M.Dev.*, Eu.(Czech.) - ?N.Am. (?Ont.).—FIG. 222,4. \**P. devonians* (BARRANDE), Czech.; 4a,b, apert. and lat. (venter left),  $\times 0.25$  (5).
- Periodanoceras** FOERSTE, 1930, p. 92 [\**P. rotundatum*; OD]. Like *Amphicyrtoceras*, but uncompressed, more rapidly enlarging, more strongly curved. Siphuncle like *Amphicyrtoceras* (68). *M.Sil.*, N.Am.(Ill.-?Que.).—FIG. 220,1. \**P. rotundatum*, USA (Ill.); 1a,b, lat. (venter right), dorsal,  $\times 0.4$  (68).
- Poteriocerina** FOERSTE, 1926, p. 343 [\**Cyrtoceras lumbosum* BARRANDE, 1877, p. 33; OD]. Depressed, curved brevicones, gibbous in phragmone. Aperture subelliptical, transverse; without hyponomic sinus or sinuous peristome. Siphuncle ventral, marginal, cyrtochoanitic; segments not greatly inflated, actinosiphonate (57). *M.Dev.*, N.Am.(Man.-N.Y.-Mich.-Eu.(Czech.)).—FIG. 222,2. \**P. lumbosum* (BARRANDE), Czech.; 2a,b, dorsal, lat. (venter right),  $\times 0.25$  (5).
- Rhomboceras** FOERSTE, 1934, p. 165 [\**R. welchi*; OD]. Conch like *Amphicyrtoceras*, but straighter, more rapidly enlarging, with subgeniculate lateral profiles and adorally tubular body chamber. Siphuncle subventral; internal structure unknown (72). *M.Sil.*, N.Am.—FIG. 220,6. \**R. welchi*, USA (Ohio); 6a,b, lat. (venter right), ventral,  $\times 0.56$  (72).
- Slocmoceras** FOERSTE, 1930, p. 85 [\**S. retrorsum*; OD]. Similar to *Amphicyrtoceras*, but longitudinally ribbed, not strongly depressed, only slightly contracted adorally, without hyponomic sinus. Siphuncular segments like *Amphicyrtoceras*, but not so strongly elongated; dorsal profile of segment straight, ventral profile moderately convex (68). *M.Sil.*, N.Am.—FIG. 220,12. \**S. retrorsum*, USA (Ill.); 12a,b, lat. (venter right), ventral,  $\times 0.56$  (68). [= *Slokoceras* BALASHOV, 1962 (nom. null.).]
- Streptoceras** BILLINGS, 1866, p. 88 [\**S. janus*; SD S.A.MILLER, 1889, p. 454]. Conch similar to *Amphicyrtoceras*, but aperture distinctly triangular in outline, with flaring margins (57). *M.Sil.*, N.Am.—FIG. 220,7. \**S. janus*, Can.(Ont.); 7a-c, dorsal, transv. sec. (venter up), lat. (venter left),  $\times 0.38$  (57).
- ?**Tumidoceras** FLOWER, 1949, p. 78 [\**T. lentum*; OD]. Compressed, exogastric cyrtocones with fusiform body chamber, contracted to aperture; venter obscurely angulate, dorsum somewhat flattened. Shallow hyponomic sinus. Siphuncle subventral, cyrtochoanitic, empty; adapical segments slender, fusiform, adoral segments broadly nummuloidal, wider than long (36). *M.Dev.*, N.Am.—FIG. 221,3. \**T. lentum*, USA (Mich.); lat. (venter left),  $\times 0.33$  (36).
- Worthenoceras** FOERSTE, 1930, p. 76 [\**W. elonga-*



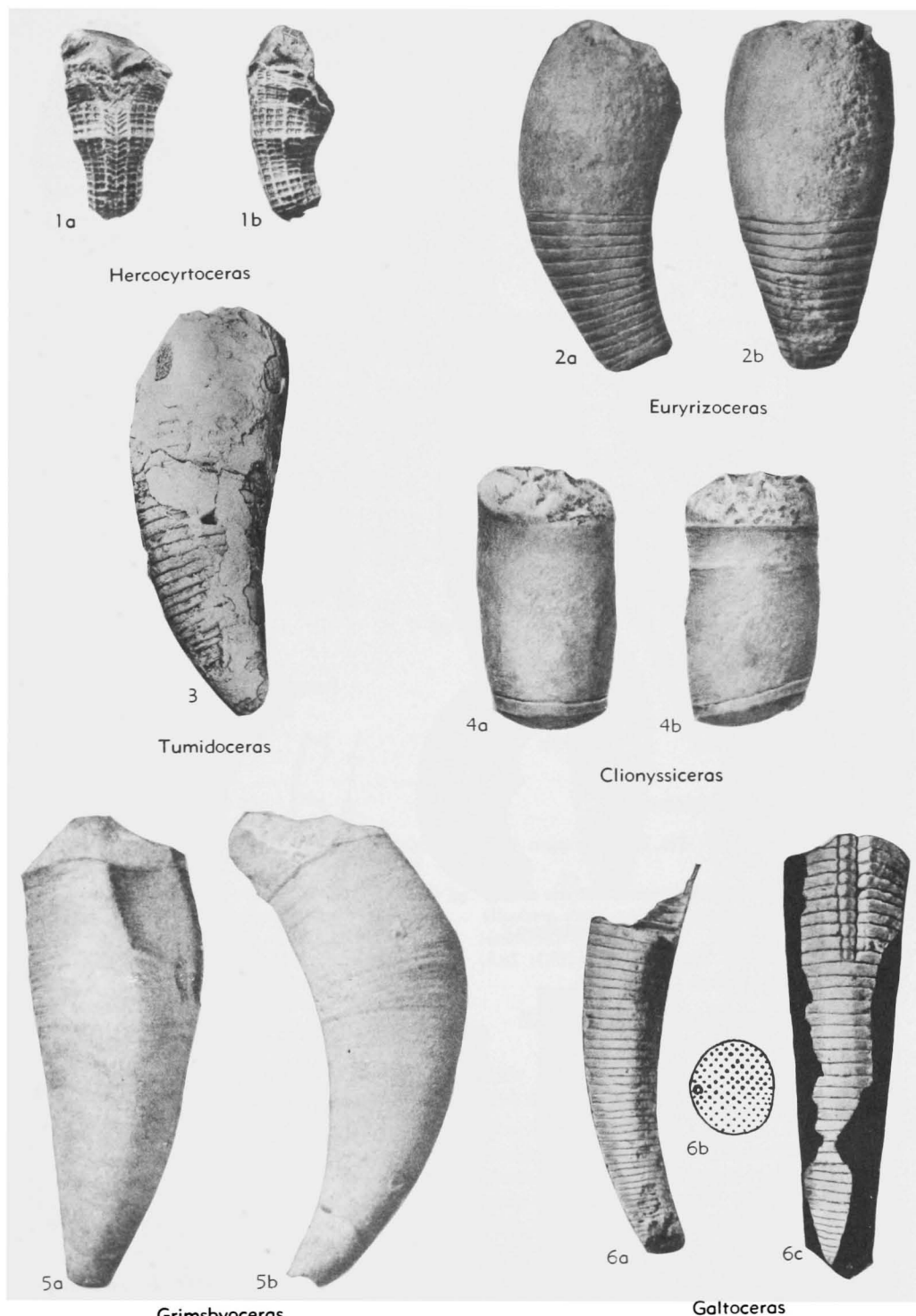


FIG. 221. *Acleistoceratidae* (p. K308, K310).

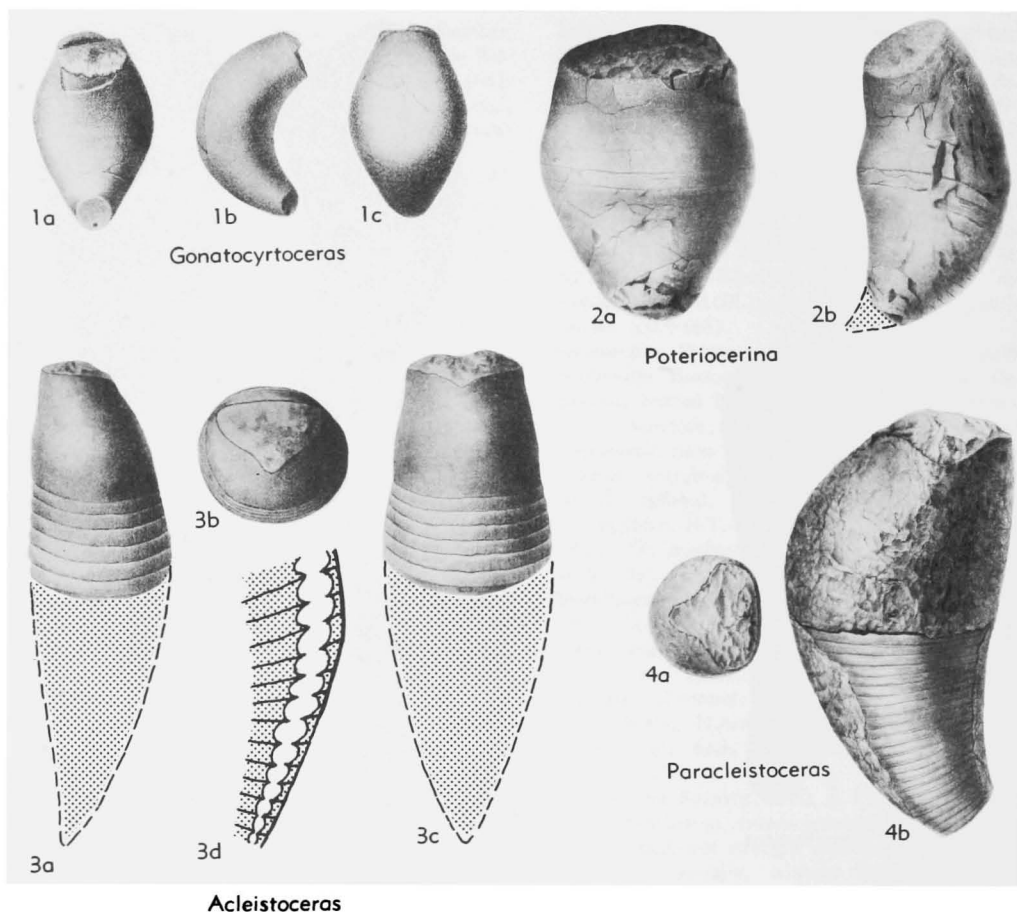


FIG. 222. Devonian Acleistoceratidae (p. K308, K310).

tum; OD]. Like *Amphicyrtoceras*, but less strongly depressed, only faintly gibbous, more gradually enlarging (68). *M.Sil.*, N.Am.(Ill.-?Wis.-?Ohio). —FIG. 220,2. \**W. elongatum*, USA (Ill.); 2a,b, lat. (venter left), ventral,  $\times 0.75$  (68).

#### Family ARCHIACOCERATIDAE Teichert, 1939

Compressed, exogastric cyrtocones, with large, actinosiphonate, dorsal siphuncle (49, 187). *Dev.*

*Archiacoceras* FOERSTE, 1926, p. 346 [\**Phragmoceratites subventricosus* D'ARCHIAC & DEVERNEUIL, 1842, p. 351; OD]. Compressed, exogastric cyrtocones with slightly concave dorsal profile, more strongly convex ventral profile, septal furrow on concave side. Large siphuncle on concave dorsal side; actinosiphonate rays, developed from thickened connecting rings, projecting toward siphuncle center; rays independent in each segment, but aligned and fused with rays in adjacent segments

(31, 57). *M.Dev.*, Eu.—FIG. 223,1. \**A. subventricosus* (D'ARCHIAC & DEVERNEUIL), Ger.; 1a,b, lat. and septum (venter left),  $\times 1$ ; 1c, partial long. sec.,  $\times 2$  (1, 31).

?*Cyrtoceratites* GOLDFUSS, 1830, p. 226 [\**Orthoceratites flexuosus* SCHLOTHEIM, 1820; OD] [= *Cyrtocera* GOLDFUSS, 1832 (obj.); *Cirrhoceratites* DESHAYES in CUVIER, 1838 (?); *Cyrtoceras* KING, 1844 (obj.); ?*Campulites* DESHAYES in LAMARCK, 1845]. Compressed, rapidly expanding cyrtocone with siphuncle on concave side; neither body chamber nor siphuncular structure known (37, 200). [May be senior subjective synonym of *Archiacoceras* FOERSTE, 1926.] *M.Dev.*, Ger.

*Devonocheilus* SHIMANSKIY, 1962, p. 108 [\**Phragmoceras? timanicum* HOLZAPFEL, 1899; OD]. *Dev.*, N.USSR (Timan).

#### Family KAROCERATIDAE Teichert, 1939

Compressed, exogastric cyrtocones and orthocones with slender ventral siphuncle;

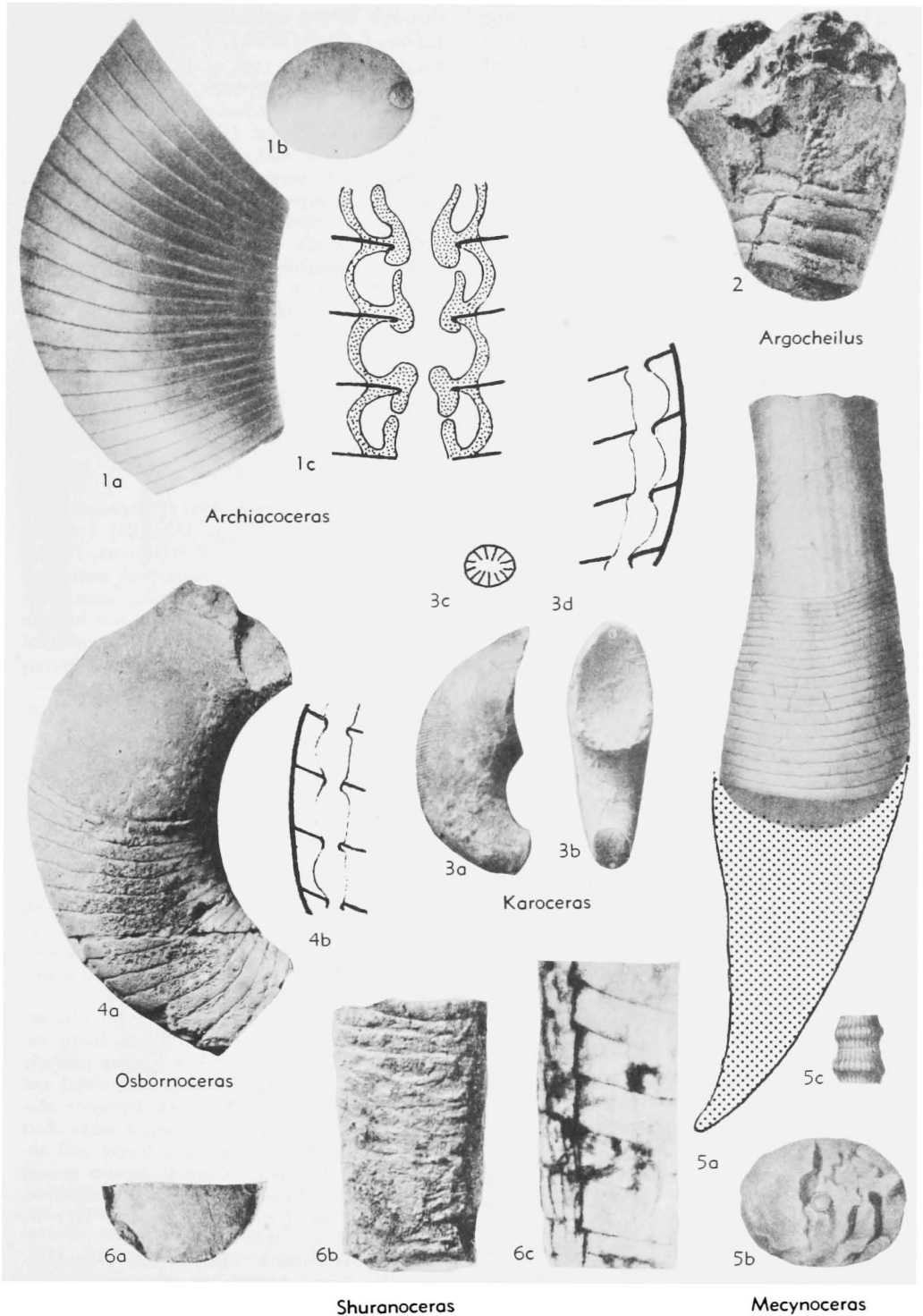


FIG. 223. Archiacoceratidae (p. K312); Karoceratidae (p. K314); Poterioceratidae (p. K314-K315).

septal necks cyrtchoanitic, connecting rings inflated ventrally but straight dorsally. Siphuncle empty, except in *Karoceras*, which is actinosiphonate (187). *L.Sil.-M.Sil.*, ?*L.Dev.*

Genera included in this family are related in general shape, and in conformation of siphuncle. However, none of them can be said to be well known and the grouping herein suggested may well be highly artificial.

**Karoceras** ROUSSANOFF, 1909, p. 169 [*\*Cyrtoceras laminare* BARRANDE, 1877; OD]. Compressed, exogastric cyrtocoones of subvoid section, with hyponomic sinus. Siphuncle slender, ventral, actinosiphonate; septal necks cyrtchoanitic, connecting rings inflated ventrally, straight dorsally (57, 148). *M.Sil.*, ?*L.Dev.*, Eu.(Czech.-?Novaya Zemlya). —FIG. 223,3. *K.?* *typicum* FOERSTE, ?*L.Dev.*, USSR(Novaya Zemlya); 3a,b, lat. (venter left), dorsal,  $\times 0.5$  (57); 3c-d, dorsoventral sec. of siphuncle, long. sec.,  $\times 1$  (57).

**Osbornoceras** FOERSTE, 1936, p. 265 [*\*O. swinnertoni*; OD]. Large, compressed, moderately enlarging cyrtocoones with narrowly rounded venter, more broadly rounded dorsum. Body chamber contracting laterally and dorsoventrally to aperture, which has deep hyponomic sinus. Siphuncle slender, ventral, cyrtchoanitic, empty; segments elongate, moderately expanded ventrally, virtually straight dorsally (74). *L.Sil.*, N.Am.(Ohio-?Man.). —FIG. 223,4. *\*O. swinnertoni*, USA(Ohio); 4a, lat. (venter left),  $\times 0.5$ ; 4b, dorsoventral sec.,  $\times 1$  (74).

**?Shuranoceras** BARSKOV, 1959, p. 59 [*\*S. dolmatovi*; OD]. Smooth, compressed, slowly enlarging orthocoones with submarginal, empty, ventral siphuncle. Siphuncular segments subtrapezoidal, longer than wide, faintly expanded ventrally, straight dorsally; septal necks long and recumbent dorsally, shorter and not recumbent ventrally (6). *M.Sil.*, USSR(Ferghana). —FIG. 223,6. *\*S. dolmatovi*; 6a-c, septal and lat. (venter right), dorsoventral sec. (venter left),  $\times 1$  (6).

### Family POTERIOCERATIDAE

Foord, 1888

Subcircular to compressed, exogastric cyrtocoones with no hyponomic sinus, submarginal to subcentral siphuncle with subquadrate or nummuloidal segments and septal necks more strongly curved dorsally than ventrally. Some forms actinosiphonate or with annulosiphonate masses thought to be incipient or reduced actinosiphonate deposits. [Relationship uncertain; perhaps derived from Silurian Acleistoceratidae or from Ordovician Oncoceratidae (?*Vaupelia*)

through as yet unknown Silurian species.] *L.Dev.-L.Carb.*(*Miss.*).

**Poterioceras** M'COY, 1844, p. 10 [*\*Orthocera fusiformis* J.D.E.C. SOWERBY, 1829, p. 167; SD FOERSTE, 1924, p. 254] [= *Calchasiceras* SHIMANSKIY, 1957; ?*Ampheroopsis* CRICK, 1904; *Ampheroopsis* MUTVEI, 1957 (*nom. null.*)]. Compressed or subcircular, exogastric, breviconic cyrtocoones with convex ventral and sigmoid dorsal profiles. Body chamber inflated dorsally, then contracted adorally; peristome circular or faintly ellipsoidal in outline, without hyponomic sinus. Siphuncle empty, ventral, marginal in early stages, only slightly on ventral side of center at maturity. Septal necks cyrtchoanitic, at least in some species more strongly curved dorsally than ventrally (57, 93, 160). *L.Carb.*(*Miss.*), N.Am.-Eu., widespread. —FIG. 224,5a-c. *\*P. fusiforme* (SOWERBY), Eu. (Ire.); ventral, lat. and septum (venter right),  $\times 0.5$  (93). —FIG. 224,5d. *P. latiseptatum* FOORD, Eu.(Ire.); dorsoventral sec., enlarged (orig., from 160).

**?Argocheilus** SHIMANSKIY, 1961 [*\*Argoceras chinense* SHIMANSKIY, 1957, p. 532; OD] [= *Argoceras* SHIMANSKIY, 1957 (*non* STEINMANN, 1925)]. Like *Welleroeras*, but straighter, with more sinuous sutures and broad ?hyponomic sinus. Suborthochoanitic to cyrtchoanitic siphuncle between center and venter; segments empty, subcylindrical (167). [May be slightly endogastric; type description and figure confusing.] *L.Carb.*, China. —FIG. 223,2. *\*A. chinense* (SHIMANSKIY); lat. (venter right),  $\times 1$  (167).

**Cyrtogomphus** FLOWER, 1938, p. 43 [*\*C. curvatus*; OD]. Depressed exogastric breviconic cyrtocoones with poterioceratid inflation of body chamber and no hyponomic sinus. Siphuncle subventral, cyrtchoanitic, empty; segments subspherical, septal necks more strongly curved dorsally than ventrally (21, 160). *M.Dev.-U.Dev.*, N.Am.(N.Y.-Ont.)-Eu. (Ger.-Pol.). —FIG. 224,1a-c. *\*C. curvatus*, M. Dev., USA(N.Y.); 1a,b, lat. (venter right), ventral,  $\times 0.5$ ; 1c, transv. long. sec.,  $\times 2.5$  (21). —FIG. 224,1d. C. sp., U.Dev., Ger.; dorsoventral sec.,  $\times 3$  (160).

**Lysagoroceras** SCHÖNENBERG, 1952, p. 394 [*\*L. angustum*; OD]. Slender, subcircular to faintly depressed longiconic cyrtocoones, expanding regularly but slightly to aperture. Sutures with dorsal and ventral lobes and lateral saddles. Siphuncle subventral, cyrtchoanitic, empty; septal necks short and suborthochoanitic ventrally, longer and abruptly curved dorsally. Cameral deposits present (160). *U.Dev.*, Eu. —FIG. 224,3. *\*L. angustum*, Pol.; 3a,b, lat. (venter left), ventral,  $\times 1$ ; 3c, dorsoventral sec.,  $\times 2.5$  (160).

**?Mecynoceras** FOERSTE, 1926, p. 332 [*\*Gomphoceras rex* PACHT, 1858, p. 78; OD]. Compressed, gibbous cyrtocoones with convex venter, dorsum inflated near mid-length of phragmocone, body

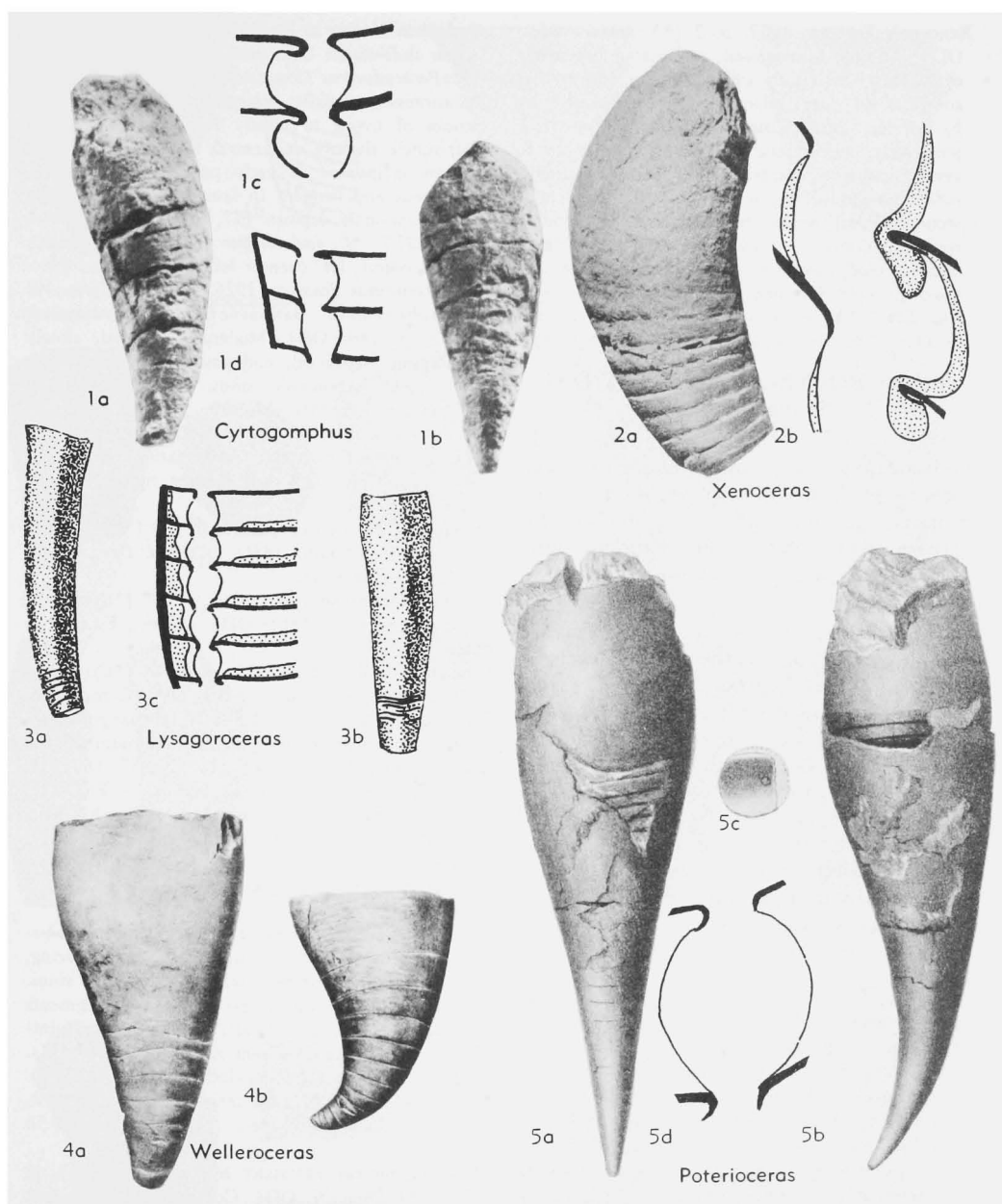


FIG. 224. Poterioceratidae (p. K314-K316).

chamber long, tubular. Siphuncle large, subcentral, cyrtchoanitic; segments abruptly inflated in annular ring near mid-length, actinosiphonate (57). *U.Dev.*, S.USSR.—FIG. 223,5. \**M. rex* (PACHT); 5a-c, lat. and septum (venter right), 2 segments of siphuncle,  $\times 0.75$  (57).

**Welleroceras** MILLER & FURNISH, 1938, p. 174 [\**W. liratum*; OD]. Compressed or subcircular, rapidly

expanding breviconic cyrtocoines, with smooth to faintly lirate shell, no hyponomic sinus, simple transverse sutures. Siphuncle small, subcentral, cyrtchoanitic, empty; septal necks in some species less strongly curved ventrally than dorsally (129). *L.Carb.(Miss.)*, N.Am.-Eu.—FIG. 224,4. \**W. liratum*, USA(Mo.); 4a,b, ventral, lat. (venter right),  $\times 0.3$  (129).

**Xenoceras** FLOWER, 1952, p. 2 [*\*X. oncoceroides*; OD]. Slightly compressed, exogastric, breviconic cyrtocoques with faintly inflated body chamber that contracts to subcircular aperture unmarked by hyponomic sinus. Sutures straight and transverse posteriorly, but sloping adorally from dorsum to venter anteriorly. Siphuncle subventral; segments inflated, subquadrate, scalariform in dorsoventral section. Septal necks straight ventrally, strongly recurved dorsally; connecting rings thick, produced dorsally but not ventrally into pendent deposits in septal foramen (38). *L.Dev.*, N.Am.—FIG. 224,2. *\*X. oncoceroides*, USA (N.Y.); 2a, lat. (venter left),  $\times 1$ ; 2b, dorsoventral sec.,  $\times 4$  (38).

### Family POLYELASMOCERATIDAE

Shimanskiy, 1956

Slightly compressed or somewhat depressed, rapidly expanding, endogastric cyrtocoques of lachrymiform to subtriangular transverse section. Siphuncle cyrtocoanitic, between center and venter; segments nummuloidal for most part, actinosiphonate. *M.Sil.-U.Dev.*

The ancestry of this family is uncertain. *Danaoceras* (M.Sil.) is the most generalized genus and may represent the stock from which its contemporary, *Codoceras*, and Devonian genera developed. The siphuncle of *Danaoceras* is not unlike that of several species of *Oonoceras* or *Oocerina* and it is possible that endogastric *Danaoceras* evolved from the latter through formation of a rapidly expanding, breviconic conch that grew more rapidly dorsally than ventrally.

**Polyelasmoceras** TEICHERT & GLENISTER, 1952, p. 745 [*\*P. aduncum*; OD]. Rapidly expanding, strongly curved, slightly depressed, endogastric cyrtocoques with long body chamber, no hyponomic sinus, subtriangular transverse section. Siphuncle orthocoanitic, close to concave margin; segments moderately expanded, area of adnation wide. Actinosiphonate lamellae simple, continuous, not normally bipectinate (191). *M.Dev.*, Australia.—FIG. 225,8. *\*P. aduncum*; 8a, lat. (venter left),  $\times 0.4$ ; 8b, transv. sec. of siphuncle,  $\times 1.5$ ; 8c, dorsoventral sec. (venter on left),  $\times 1.25$  (191).

**Brachydomoceras** TEICHERT & GLENISTER, 1952, p. 746 [*\*B. erectum*; OD]. Large, uncompressed, straight brevicones with short body chamber, unconstricted aperture, hyponomic sinus. Siphuncular segments like *Macrodomoceras*, but actinosiphonate lamellae simple, not bipectinate (191). *M.Dev.*, Australia.—FIG. 225,4. *\*B. erectum*; 4a, lat. (venter left),  $\times 0.56$ ; 4b, dorsoventral sec.,  $\times 2.2$  (191).

**Codoceras** HYATT in ZITTEL, 1900, p. 532 [*\*Cyrtoceras indomitum* BARRANDE, 1866, pl. 162; OD]. [= *Paracodoceras* COSSMANN, 1901 (*nom. van.*)]. Compressed, rapidly enlarging, endogastric cyrtocoques of ovoid to faintly lachrymiform section. Siphuncle slightly on ventral side of center; segments cylindroid in early part of conch, nummuloidal and broader in later parts, occupied by actinosiphonate deposits (57, 97). *M.Sil.*, Eu.—FIG. 225,7. *\*C. indomitum* (BARRANDE), Czech.; 7a,b, ventral, lat. (venter left),  $\times 0.4$  (5).

**Coelocytroceras** FOERSTE, 1926, p. 349 [*\*Cyrtoceras ventralisinnatum* SANDBERGER & SANDBERGER, 1852, p. 146; OD]. Moderately curved, slowly enlarging, depressed, endogastric cyrtocoques with prominent hyponomic sinus. Siphuncle ventral, marginal; segments obliquely globular in form, actinosiphonate (57). *M.Dev.*, Eu.—FIG. 225,5. *\*C. ventralisinnatum* (SANDBERGER & SANDBERGER), Ger.; 5a,b, lat. (venter right), ventral,  $\times 0.56$  (57).

**Cycloptites** ZHURAVLEVA, 1962, p. 110 [*\*Pachtoceras cyclops* VENYUKOV, 1886; OD]. *U.Dev.*, USSR (Russian Platform).

**Cyrtocheilus** SHIMANSKIY, 1962, p. 109 [*\*Cyrtoceras obliquum* FOORD, 1888; OD]. *M.Dev.*, Eu. (Ger.)-China.

**Danaoceras** FOERSTE, 1926, p. 346 [*\*Cyrtoceras danai* BARRANDE, 1866, pl. 161; OD]. Compressed, endogastric cyrtocoques of faintly subtriangular section. Siphuncle actinosiphonate, submarginal, not known to expand broadly adorally (57, 188). *M.Sil.*, Eu. (Czech.); ?*M.Dev.*, N.Am.—FIG. 225,9. *\*D. danai* (BARRANDE), M.Sil., Czech.; 9a-c, lat. and septum (venter right), ventral,  $\times 0.4$  (5).

**Evlanoceras** ZHURAVLEVA, 1962, p. 109 [*\*Pachtoceras evlanensis* NALIVKIN, 1947; OD]. *U.Dev.*, USSR (Russian Platform).

**Hipparionoceras** FLOWER, 1945, p. 719 [*\*H. iowaense*; OD]. Rapidly enlarging, adorally flaring, endogastric cyrtocoques with hyponomic sinus. Siphuncle subventral, cyrtocoanitic; segments elongate, contracted adorally and adapically, faintly scalariform in dorsoventral section, empty (32). *M.Dev.*, N. Am. (N.Y.-Pa.-Ind.-Iowa)-Eu. (Czech.). —FIG. 225,1. *\*H. iowaense*, USA (Iowa); 1a,b, ventral, dorsoventral sec. (venter left),  $\times 0.56$  (32).

**Macrodomoceras** TEICHERT & GLENISTER, 1952, p. 747 [*\*M. howitti*; OD]. Compressed, endogastric cyrtocoques of subtriangular section, like *Danaoceras*, but sutures have shallow bluntly pointed ventral saddles. Siphuncle ventral, marginal, with continuous thick, bipectinate actinosiphonate lamellae interspersed among more numerous short, simple lamellae (191). *M.Dev.*, Australia.—FIG. 225,2. *\*M. howitti*; 2a,b, ventral, lat. (venter right),  $\times 0.56$ ; 2c, dorsoventral sec.,  $\times 2.2$  (191).

**Pectinoceras** TEICHERT & GLENISTER, 1952, p. 745 [*\*Phragmoceras subtrigonum* M'COY, 1876, pl.

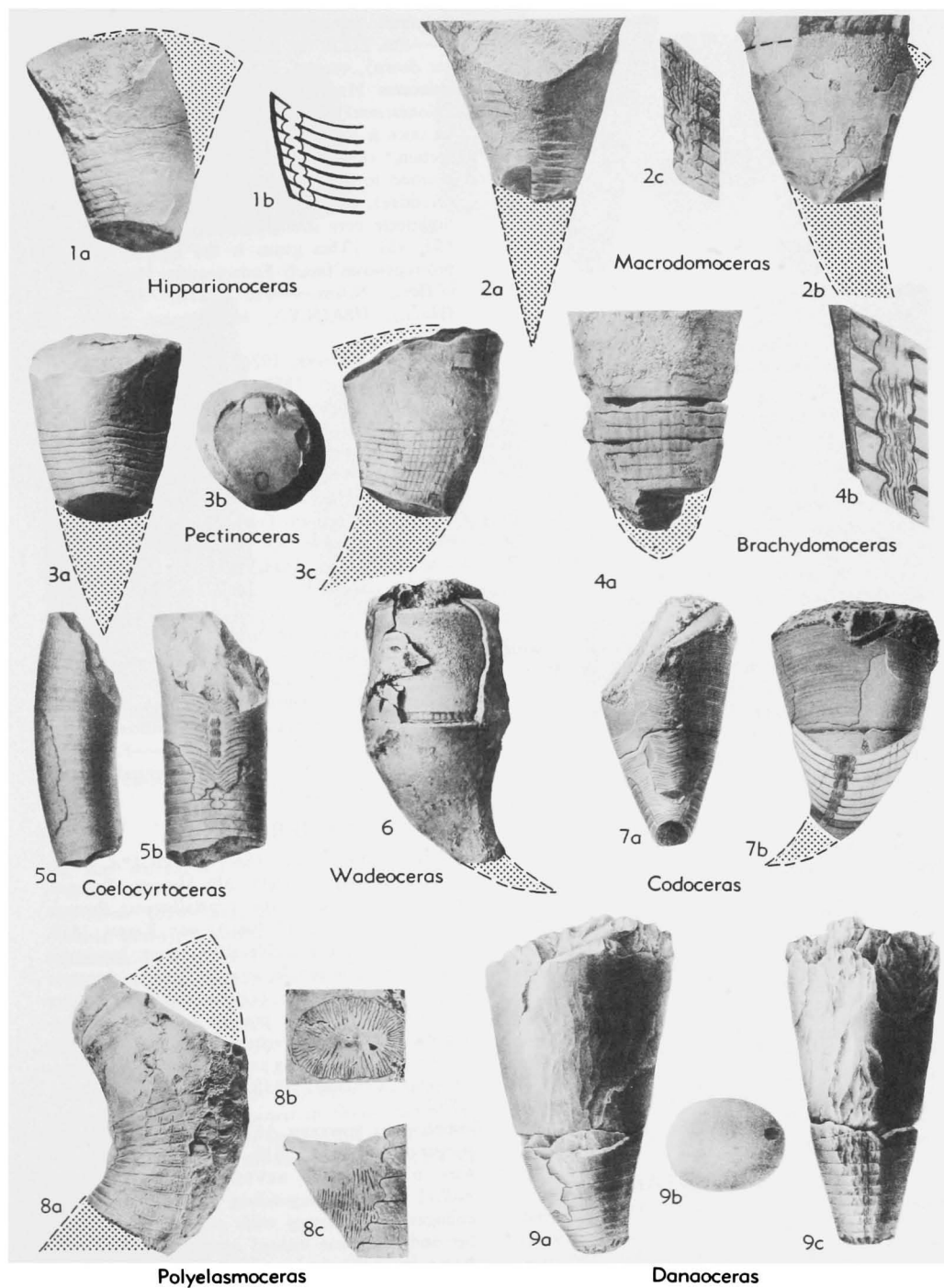


FIG. 225. Polyelasmoceratidae (p. K316, K318).



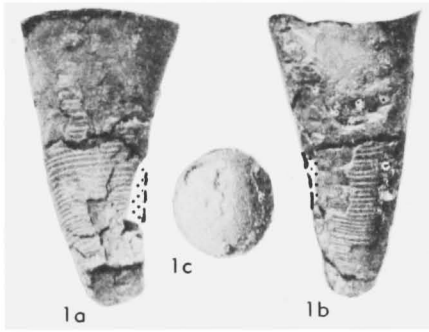


FIG. 226. \**Turoceras schnyrevae* ZHURAVLEVA (?Polyelasmoceratidae) (p. K318).

35; OD]. Compressed, endogastric cyrtocoones of subtriangular section, similar to *Danaoceras*, but siphuncular diameter greater. Lamellae of endosiphuncular actinosiphonate deposits bipectinate, apparently continuous from segment to segment (191). *M.Dev.*, Australia.—FIG. 225,3. \**P. subtrigonomum* (M'Coy); 3a-c, ventral, septum (venter down), lat. (venter left),  $\times 0.4$  (188).

?*Turoceras* ZHURAVLEVA, 1959, p. 46 [\**T. schnyrevae*; OD]. Like *Danaoceras* and *Codoceras* externally, but siphuncle slender, submarginal, with shape in dorsoventral section similar to *Macrodomoceras*, *Brachydomoceras*. No siphuncular deposits known (214). [Included tentatively with Polyelasmoceratidae because of conch shape, endogastric curvature, and general similarity in siphuncular conformation to genera mentioned.] *U.Sil.*, USSR.—FIG. 226,1. \**T. schnyrevae*; 1a,b, lat. (venter right), lat. (venter left),  $\times 1$ ; 1c, septum (venter down),  $\times 3$  (214).

*Wadeoceras* TEICHERT, 1939, p. 111 [\**W. australe*; OD] [= *Waderoceras* CRESPIN, 1960 (*nom. null.*)]. Compressed, cyrtoconic brevicones with visored phragmoceroid peristome. Siphuncle near concave side, cyrtochaonic externally, concave internally, occupied by actinosiphonate deposits in septal foramen, not continuous from segment to segment (187, 188). [Orientation of type uncertain; described as endogastric, but may be exogastric, with dorsal siphuncle—hence referable to Archiacoceratidae, rather than Polyelasmoceratidae (22).] *U.Dev.*, W.Australia.—FIG. 225,6. \**W. australe*; lat. (venter right),  $\times 0.38$  (188).

### Family UNCERTAIN

*Antonoceras* SHIMANSKIY, 1957, p. 531 [\**A. balaschovi*; OD]. Depressed orthocone or faintly curved cyrtocone, with short chambers and long, tubular body chamber. Sutures with deep dorsal and ventral lobes and lateral saddles. Siphuncle between center and venter, cyrtochaonic; segments "beaded," apparently empty (167). [This genus is the type of the monotypic family Antono-

ceratidae SHIMANSKIY, 1957.] *L.Carb.*, C.USSR.—FIG. 227,4. \**A. balaschovi*; 4a,b, septum (venter down), ventral,  $\times 1$  (167).

*Eudoceras* HYATT, 1884, p. 287 [\**Trochoceras?* (*Gonioceras?*) *pandum* HALL, 1857, p. 403; SD CLARKE & RUEDEMANN, 1903, p. 587]. Similar in section, sutural configuration, and siphuncular position to Ordovician *Rasmussenoceras* (Triptero-ceratidae), but expanding sideward more rapidly. Siphuncle very small, ventral; structure unknown (33, 93). [This genus is the type of the quite heterogeneous family Eudoceratidae HYATT, 1884.] *M.Dev.*, N.Am.—FIG. 227,2. \**E. pandum* (HALL), USA(N.Y.); lat. (venter right),  $\times 1$  (87).

*Pachtoceras* FOERSTE, 1926, p. 328 [\**Gomphoceras rotundum* PACT, 1858, p. 84; OD]. Slightly compressed, probably straight brevicones, with ad-orally contracted body chamber. Siphuncle between center and venter, cyrtochaonic; segments elongate, subcylindrical, actinosiphonate (57). *U.Dev.*, S.USSR.—FIG. 227,1. \**P. rotundum* (PACT); 1a,b, ventral, septum (venter up),  $\times 1$ ; 1c, 2 segments of siphuncle,  $\times 4$  (57).

*Sycoceras* PICTET, 1854, p. 645 [\**Gomphoceras ficus* ROEMER, 1850, p. 38; SD FOERSTE, 1926, p. 329] [= *Sycoceras* ZITTEL, 1884 (*nom. null.*)]. Straight brevicones of circular section; maximum height and width near adoral end of phragm-cone, contracting to aperture. Surface with prominent transverse ornament, but no true annulation. Siphuncle small, ?ventral, marginal; internal structure not known (57). *U.Dev.*, Eu.—FIG. 227,3. \**S. ficus* (ROEMER), Ger.; 3a,b, ventral, septum (venter down),  $\times 1$  (57).

### GENERA DUBIA

*Apioceras* FAHRENKOHLE, 1844, p. 779 [\**A. trochoides* FAHRENKOHLE, 1844; SD MILLER, DUNBAR, & CONDRA, 1933, p. 40] [= *Bolboceras* FISCHER in FAHRENKOHLE, 1844 (obj.), *non* KIRBY, 1819, Coleopt.]. Unrecognizable short, stout, breviconic orthocones with simple, straight sutures. Aperture and interior unknown (189). [Until type-species is restudied, it is not possible to determine systematic position. Perhaps synonymous with *Poterioceras*; apparently intended to replace *Gomphoceras* SOWERBY, 1839.] *L.Carb.* or *U.Carb.*, USSR.

*Gomphoceras* SOWERBY, 1839, p. 621 [\**Orthoceras pyriforme* SOWERBY, 1839; OD] [= *Gomphocera-tites* D'ARCHIAC & DEVERNEUIL, 1842 (*nom. null.*)]. Rapidly expanding, straight to faintly endogastric brevicones with gibbous body chamber and transverse visored aperture; mature peristome incompletely known, but with hyponomic sinus on low, spoutlike process and perhaps broadly rounded, undivided dorsal sinus (57, 67, 189). [Until dorsal element of peristome and internal features are known, genus is unrecognizable and systematic position in doubt. This genus is type



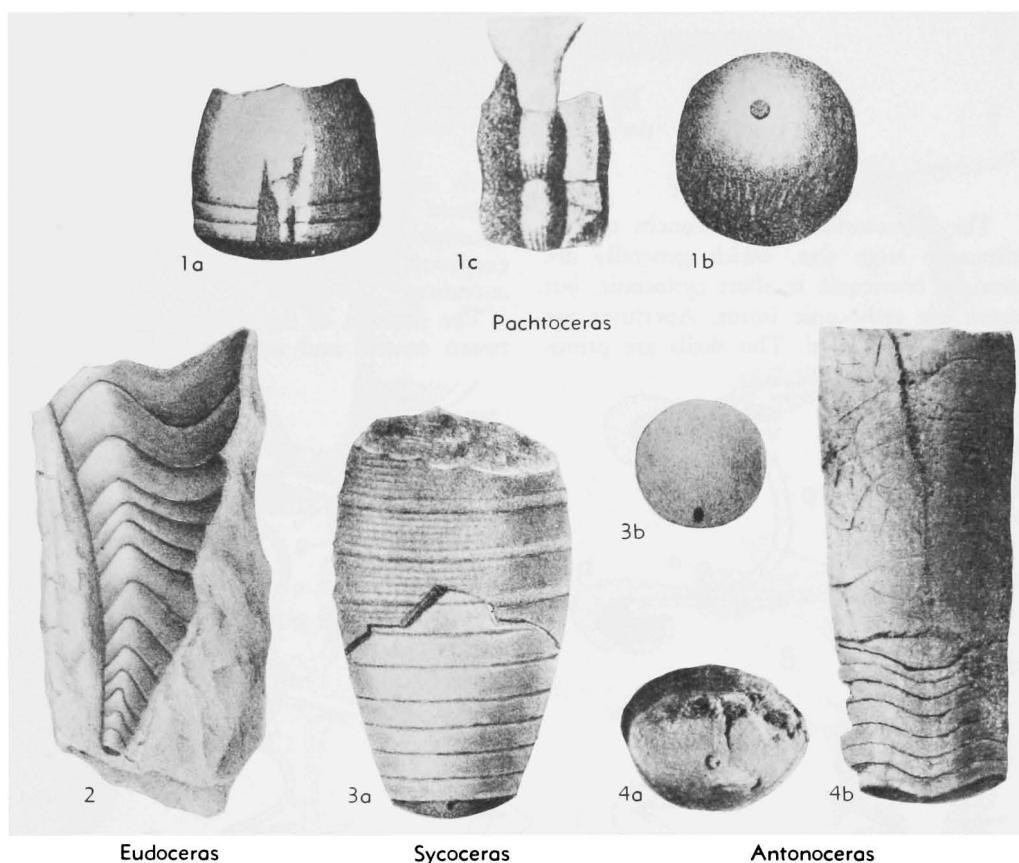


FIG. 227. Oncocerida, Family Uncertain (p. K318).

of the unrecognizable family Gomphoceratidae PICTET, 1854.] *M.Sil.*, Eu.—FIG. 211,5. \**G. pyriforme* (SOWERBY), Eng.; 5a,b, ventral, apert. (venter down),  $\times 0.5$  (57).

**Nelimenia** LAPORTE, 1843, p. 33 [\**N. incognita*; OD] [= *Nolimenia* LAPORTE, 1843 (*nom. null.*)]. Unrecognizable brevicones resembling *Beloitoceras* (7). *M.Ord.*, Can.(Que.).

**Pictetoceras** FOERSTE, 1926, p. 327 [\**Gomphoceras eichwaldi* DEVERNEUIL, 1845, p. 357; OD]. Like *Diestoceras*, of which it may be a synonym. Internal structure not known in detail, hence disposition uncertain (57). *Ord.*, USSR.—FIG. 208, 3. \**P. eichwaldi* (DEVERNEUIL); ventral,  $\times 1$  (57).

**Trigonodema** LAPORTE, 1843, p. 27. Originally proposed for species of *Orthoceras* with triangular cross section, but no type-species has ever been designated. Strictly interpreted, *Trigonodema* is probably a senior objective synonym of *Jovellania* BAYLE, 1879. Application to ICZN for suppression of *Trigonodema* is pending (SWEET, 1962).

**Wetherbyoceras** FOERSTE, 1926, p. 323 [\**Cyrtoceras conoidale* WETHERBY, 1881, p. 78; OD]. Type-species, of which holotype is lost, probably congeneric with those now referred to *Augustoceras*. In absence of types, only type-species can be referred here and identity of genus is obscure (33). *U.Ord.*, N.Am.(Ky.-Ohio-Tenn.).

## NAUTILOIDEA—DISCOSORIDA

By CURT TEICHERT

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## MORPHOLOGY

The Discosorida include conchs of medium to large size, which generally are straight breviconic to short cyrtconic, but some are orthoconic forms. Apertures are open or constricted. The shells are primi-

tively endogastric, but exogastric in specialized families (e.g., *Westonoceratidae*, *Mandaloceratidae*); exceptional types in the exogastric stocks may revert to endogastric curvature.

The position of the siphuncle varies between central and marginal, although in

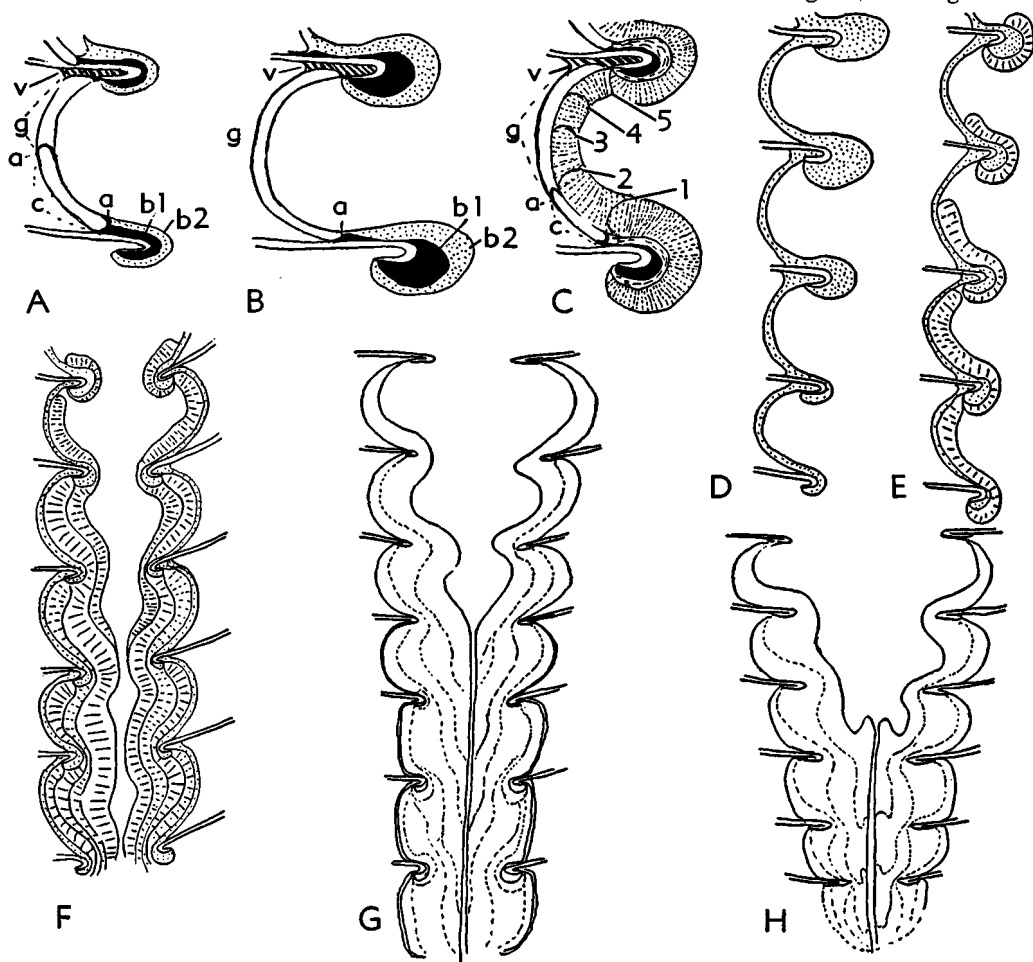


FIG. 228. Longitudinal sections showing typical discosorid siphuncle structures.—A. *Ruedemannoceras* (v, vinculum; g, granular zone; a, amorphous band; c, conchiolinous zone: b1, b2, inner and outer layers of bullette).—B. *Cyrtogomphoceras* (lettering as in A).—C. *Westonoceratidae*, generalized (1, 2, 3, 4, 5, successive forward limits of parietal deposits that begin at septal foramina and gradually become extended adorally; lettering as in A).—D. Generalized diagram of connecting rings showing adoral increase in size of bullettes.—E. Growth pattern in *Westonoceratidae*, combining bullettes which increase in size adorally, with parietal deposits decreasing from young to mature.—F. Growth pattern of *Fabroceras*, with thick rings, bullettes, and parietal deposits extending into endocoones.—G. Siphuncle of *Tuyloceras*, showing early segments like those of *Fabroceras*, with succeeding segments broader, bullettes smaller, and rings thinner.—H. Siphuncle of *Discosorus*, with elevation at bottom of endosiphocoone (50).

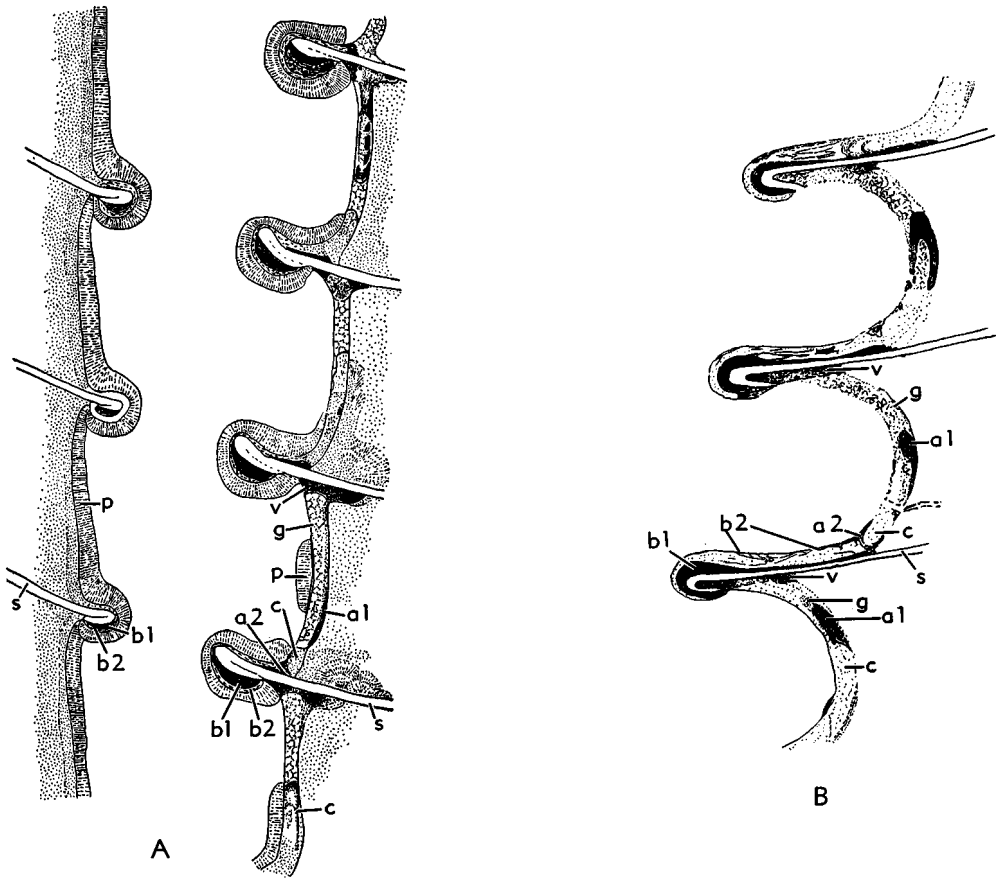


FIG. 229. Siphuncle wall of discoridids.—A. Ventral wall (at left) and dorsal wall (at right) of *Westonoceras* sp., showing greater development of parietal deposits on ventral than dorsal side (a1, a2, first and second amorphous layers; b1, b2, inner and outer layers of bullette; c, conchiolinous zone; g, granular zone; p, parietal deposits; s, septum; v, vinculum).—B. Dorsal wall of siphuncle of *Ruedemannoceras boycii* (WHITFIELD) showing variation in extent and expression of parts (lettering as in A) (50).

most forms it is intermediate. In all except some specialized end members of stocks, it consists of broadly expanded segments. The septal necks are short, cyrtchoanitic, strongly recurved, with brims close to or touching the posterior surface of the septa.

Discosorid genera are characterized either by thick, complex connecting rings or by specialized endosiphuncular deposits, or a combination of both (Fig. 228).

The structural differentiation of the connecting rings is best exhibited in early unspecialized forms like *Ruedemannoceras* (Fig. 229,B). Here, each connecting ring is attached to the posterior surface of the septum, just beyond the tip of the strongly recurved septal neck; the region of the con-

necting ring in the vicinity of the septum consists of dense, amorphous calcite and is called the **vinculum**. The anterior half of the connecting ring just behind the vinculum is made of coarsely granular calcite (or possibly a mixture of calcite and conchiolin) called the **granular zone**. The posterior half of the free part of the connecting ring contains a zone of fine yellowish material so suggestive of conchiolin that it is called the **conchiolinous zone**. This lies between two narrow bands, curved with the concave sides facing the conchiolinous zone like two parentheses; these are termed the **amorphous bands**.

The tip of the ring that curves around the cyrtchoanitic septal neck is divided

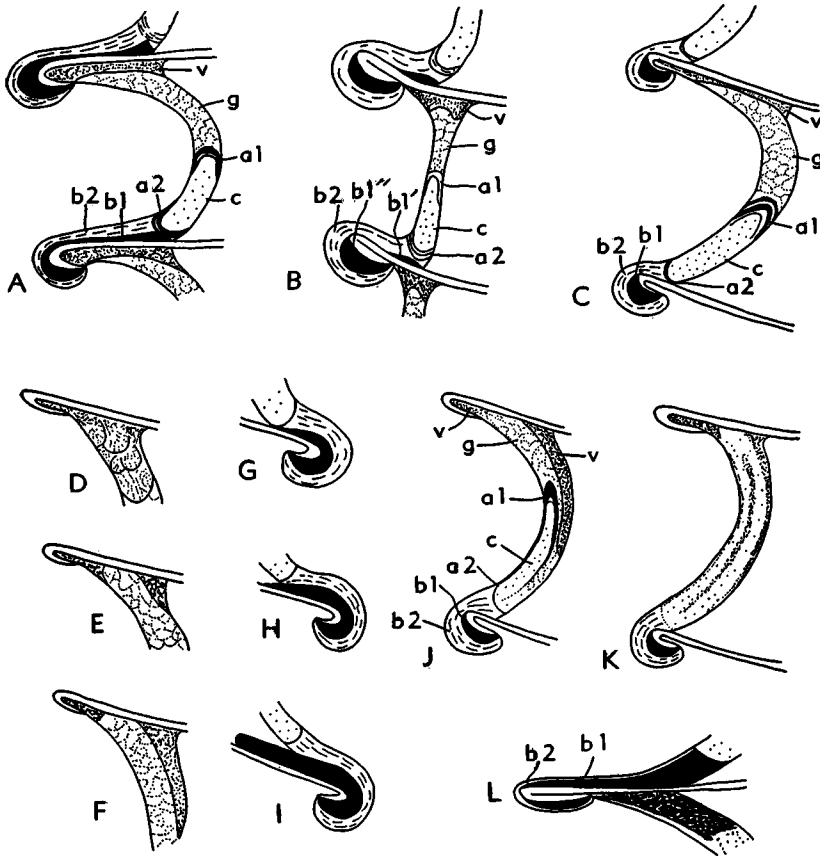


FIG. 230. Structures within discosorid connecting rings.—A. *Ruedemannoceras boycei* (WHITFIELD) (a1, a2, first and second amorphous layers; b1, b2, inner and outer layers of bullette; c, conchiolinous zone; g, granular zone; v, vinculum).—B. *Westonoceras* sp., similar to A but with bullette inflated and differentiated into smaller anterior (b1') and larger posterior (b1'') portion (other lettering as in A).—C. *Faberoceras* sp., with small vinculum, zonation of connecting ring comparable to that in A and B, bullette small (lettering as in A).—D, E, F. Variations in vinculum of *Faberoceras*.—G, H, I. Variations in bullette on ventral side of *Faberoceras*.—J. Modification of connecting ring structure in *Faberoceras* (lettering as in A).—K. Banded condition of connecting ring as observed in late stages of *Faberoceras* and *Alpenoceras*; only bullettes retain identity.—L. Recumbent septal neck and portion of connecting ring in *Discosorus*, with indications of cingulum (lettering as in A) (50).

into an outer zone (next to the neck) consisting of dense amorphous material and an inner zone (facing the cavity of the siphuncle) composed of lamellae paralleling the curving surface of the ring. These two layers, which are true extensions of the connecting ring, taken together constitute the **bullette**. True bullettes are found only in discosorids. Similar structures in oncocerids are not layered. In *Ruedemannoceras* the bullettes have the same thickness as the connecting rings, but in many later genera (e.g., *Cyrtogomphoceras*, *Westonoceras*, Fig. 229, 230) they are swollen.

**Parietal deposits** are present in many

Middle and Late Ordovician and Silurian discosorids (Fig. 231). They grow at first as annular deposits in the region of the septal foramen, then extend forward on the inside of the connecting ring. If they extend across more than one segment of the siphuncle they acquire the character of **endocones**, which are typical especially of some *Westonoceratidae* and *Lowoceratidae* and of the *Discosoridae*. Through the center of the part of the siphuncle that is filled by endocones runs an **endsiphuncular canal**, which in *Alpenoceras* is partitioned by transverse diaphragms (Fig. 231).

Some discosorids are known to possess a

**central tube** within the siphuncle (not to be confused with the endosiphuncular canal of forms possessing endocones). Central tubes have been observed in species of *Madiganella*, *Pseudogomphoceras*, and *Westonoceras*.

Cameral deposits are known in many discosorids, but are generally thin, except in the two genera *Ruedemannoceras* and *Westonoceras*, in which they are more prominent.

## ONTOGENY

Almost without exception the apical ends of representatives of Discosorida are unknown, or else too poorly preserved for study. It is probable that many Discosorida have a somewhat blunt apical end, that their initial chamber is cup-shaped and the siphonal caecum bulbous. At present it is not known whether the complex structure of the connecting rings in discosorids is a feature acquired during ontogeny or if it exists also in early ontogenetic stages.

## CLASSIFICATION

Only a few discosorids were known prior to about 1925, and the few genera described at that time were scattered among unrelated groups. *Discosorus* was regarded as an actinocerid, *Phragmoceras* was grouped with unrelated cyrtchoanitic forms, and *Glyptodendron* was at first believed to be the remains of a plant. Most of the genera now recognized have been established since 1924, but the true taxonomic affinities of many of these have remained uncertain until comparatively recent years (50).

Principal features by which discosorids are distinguished are differences in the structure of the connecting rings, in the presence or absence of endosiphuncular structures, and in the differentiation of these structures into bullettes, parietal deposits, endocones, and so on, when present. The order includes many shell forms that are homeomorphic with oncocerids, the siphuncular structure of which is quite different, however.

## EVOLUTION

The Discosorida are judged to have been derived from ellesmerocerids, from which

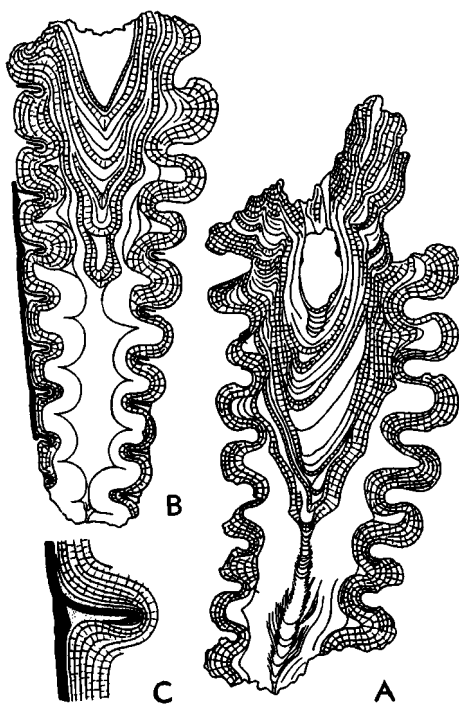


FIG. 231. Siphuncle structures of *Alpenoceras*; A, Endocones and endosiphuncular canal with transverse partitions; B, Endocones and parietal deposits; C, Detail of recumbent septal neck in B (156).

early discosorids differ in having more highly differentiated connecting rings (e.g., *Ruedemannoceras*). Such forms developed in the early Middle Ordovician. Very soon they gave rise to the strongly diversified Cyrtogomphoceratidae, which flourished from the Middle Ordovician to the Early Silurian. The principal evolutionary trends are observed to be an increase in size of the shells, development of conchs with dominantly compressed cross sections, strong development of bullettes, and shifting of the siphuncle to a marginal position (Fig. 232).

The Cyrtogomphoceratidae gave rise to the Silurian Phragmoceratidae by developing greatly contracted apertures and further compression of the conchs. Earlier, the Westonoceratidae must have branched off, or else they represent an independent offshoot of the Ruedemannoceratidae. They are characterized by complex connecting rings and complex endosiphuncular deposits that develop into large bullettes and parietal de-

posits, which in some forms (e.g., *Winnipegoceras*, *Faberoceras*) are fused into continuous endocones. In the Discosoridae the endocones become the predominant endosiphuncular structures, forming deposits that to some extent are homeomorphic with the endosiphuncular deposits of certain endocerids.

In the Lowoceratidae, which, no doubt, are also derived from the Westonoceratidae, bullettes are found only in early growth stages. Adult stages have broadly expanded segments with indications of endocones.

The Silurian Mandaloceratidae and their possible derivatives, the Mesoceratidae, are of doubtful origin and affinities. They may have been derived from Middle Ordovician Ruedemannoceratidae (50) (Figs. 233, 234).

The Discosorida, though never numerous, had two marked evolutionary peaks: one, when they first appeared in the Middle Ordovician, the second in the Middle Silurian, when the important families Discosoridae and Phragmoceratidae flourished (Fig. 233, 234A, 234B).

## GEOGRAPHIC DISTRIBUTION

The earliest discosorids, members of the family Ruedemannoceratidae (e.g., *Ruedemannoceras*, *Franklinoceras*), appeared in the Appalachian geosyncline in early Middle Ordovician (Chazyan) time. During the Middle and Late Ordovician, discosorids spread across North America and northern Europe and several genera are also known from rocks of this age in Australia and Tasmania. Genera of the Cyrtogomphoceratidae are widespread, though never abundant as individuals, in North America and northern Europe. The Westonoceratidae are almost entirely restricted to North America, including the Arctic regions.

In the Silurian, true Discosoridae are entirely restricted to North America, exclusive of the Arctic regions, whereas the essentially contemporaneous Phragmoceratidae are widespread both in North America and in northern and central Europe. In

Europe rich phragmoceratid assemblages are known in Gotland and in the Bohemian basin in Czechoslovakia. In the latter area the Mandaloceratidae also flourished. This family has few representatives elsewhere.

Devonian discosorids are so far known only from Michigan, and from the Eifel region of western Germany. In both places they are represented by the genus *Alpenoceras*, of the family Discosoridae, the last survivor of the discosorid stock.

No discosorids are known from South America, Africa, and Asia.

## SYSTEMATIC DESCRIPTIONS

### Subclass NAUTILOIDEA Agassiz, 1847

Diagnosis given in "Introductory Discussion" (p. K128). *U.Cam.-Rec.*

### Order DISCOSORIDA Flower in Flower & Kummel, 1950

[*nom. correct.* BASSE, 1952 (*pro Discosoroidea* FLOWER in FLOWER & KUMMEL, 1950)] [=Discosoroidea FLOWER, 1940 (*superfam.*); Discosoroidea FISCHER in MOORE, LALICKER & FISCHER, 1952 (*order*)]

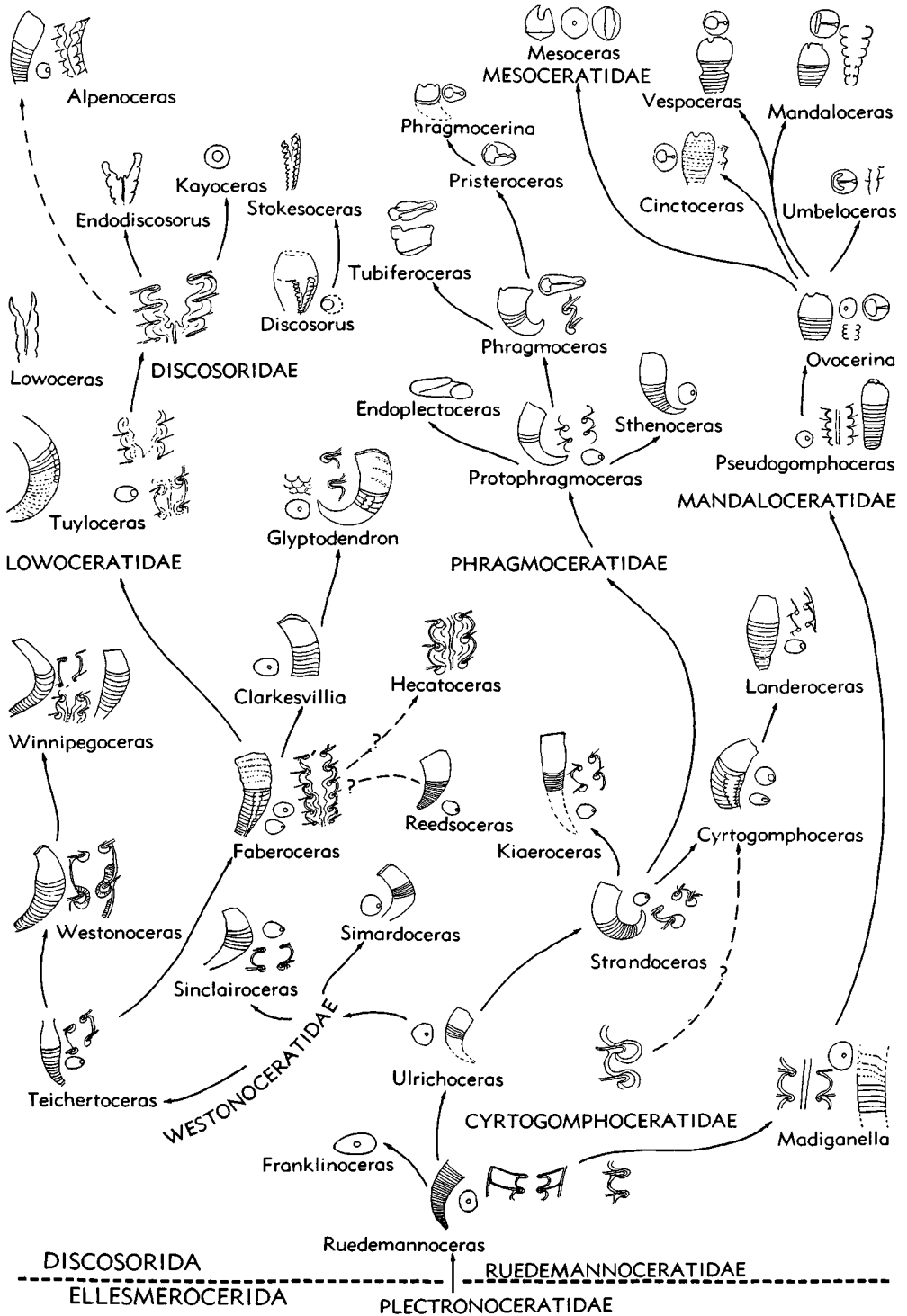
Medium-sized to large brevicones, short cyrtocones, and some orthocones, with open or constricted aperture; endogastric, rarely exogastric; siphuncle generally with broadly expanded segments, central to marginal; connecting rings generally thick, complex; endosiphuncular deposits in some forms. *M.Orð.* (*Chazy.*) *M.Dev.*, ?*U.Dev.*

The stratigraphic occurrence of genera included in the Discosorida is shown graphically in Figure 234A; the numbers of new genera introduced in successive epochs are indicated in Figure 234B.

### Family RUEDEMANNOCERATIDAE Flower, 1940

Conchs consisting of medium- to large-sized endogastric cyrtocones and near orthocones with unconstricted apertures bearing shallow hyponomic sinus. Siphuncle located slightly adventrally from center, with siphuncular bulbs in early stages that in later

FIG. 232. (*Facing page.*) General evolutionary pattern of the Discosorida. Essential features of the genera are shown, and except for the torticonic *Endoplectoceras*, internal molds, cross sections and siphuncles are oriented with the venter to the left. In some places more than one possibility is indicated, favored interpretation being indicated by solid arrows and less probable alternatives by broken-line arrows. Details of structure and relationship are discussed in the text (50, mod.).



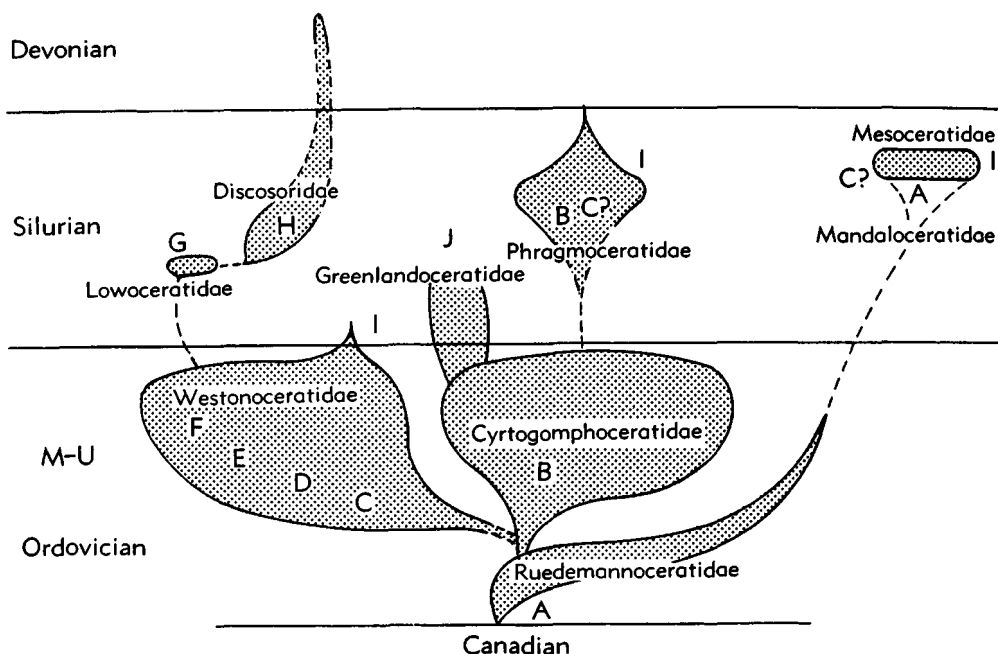


FIG. 233. Diagram of phylogeny of Discosorida, showing distribution of forms differentiated by evolution of siphuncular structures.—A. Thick rings, bullettes not swollen, no annular deposits.—B. Thick rings, bullettes swollen, no annular deposits.—C. Parietal annulosiphonate deposits added to B.—D. Bullettes markedly enlarged in anterior siphuncle segments.—E. Bullettes and parietal deposits clearly developed.—F. Annulosiphonate deposits extended in growth through a series of segments, forming endocones.—G. Young as in F, adoral segments with thin homogenous rings.—H. Thin rings, no evident bullettes, simple endocones throughout.—I. Simplification of internal structure by reduction of bullettes and thinning of rings, essentially as in G and H, but without endocones.—J. Connecting rings thin, with complex, uniform, interior lining which has bullette-like swellings (50, mod.).

stages change to broadly expanded segments with strongly recurved septal necks; connecting rings thick, with vinculum, granular and conchiolinous zones, 2 amorphous bands and 2 layers of bullettes well differentiated; bullette uniform in thickness with remainder of ring. Sutures either straight, tending to slope forward from venter to dor-

sum, or with faint sinuate lobes on venter. In cross section, venter either broadly flattened or more broadly rounded than dorsum. *M.Ord.*

**Ruedemannoceras** FLOWER, 1940 [*Cyrtoceras boycei* WHITFIELD, 1886; OD]. Conchs small to medium in size; cross section wider than high, venter slightly flattened; sutures closely spaced, sloping

FIG. 234. Stratigraphic occurrence of Discosorida (50, mod.). Approximate stratigraphic and geographic positions indicated by numbers, as follows.—(1) M.Ord.(mid.Chazy.-up.Chazy.), USA(N.Y.).—(2) M.Ord.(Murfreesboro), USA(Tenn.).—(3) M.Ord., C.Australia-Tasmania.—(4) M.Ord.(Platteville), USA(Iowa-Ill.-Wis.-Minn.).—(5) M.Ord.(Simard), Can.(Que.).—(6) M.Ord.(Terrebonne-Cobourg-Stewartville), Can.(Que.-Ont.)-USA(N.Y.-Mich.-Minn.).—(7) M.Ord.(Cynthiana-Catheys), USA(Ky.-Tenn.).—(8) M.(?U.)Ord.(Red River-Bighorn), N.USA-Can.-Greenl.—(9) M.(?U.)Ord.-?Sil., N. Am.-Eu.—(10, 11) U.Ord.(Eden), USA(Ohio-Ky.).—(12) U.Ord., Norway.—(13) U.Ord.(Leipers), USA(Ky.-Tenn.).—(14) U.Ord.(Maysville), USA(Ohio-Ky.-Ind.).—(15) U.Ord.(Richmond), USA(Ohio-Ky.-Ind.).—(16) L.Sil.(Brassfield), USA(Ohio).—(17) M.Sil.(Clinton), USA(Mich.)-Can.—(18) M.Sil.(Clinton), USA(N.Y.-Ohio-Ind.-Iowa)-Que.(Anticosti Is.).—(19) M.Sil.(Etage E<sub>2</sub>), Czech.—(20) M.Sil.(Racine-Guelph), E.N.Am.—(21) M.Sil., Sweden(Gotl.).—(22) U.Sil.(Bertie), USA(N.Y.).—(23) U.Sil.(Manlius), USA(N.Y.).—(24) L.Dev.(Etage Ff<sub>2</sub>), Czech.—(25) M.Dev.(Win-nipegosis), Can.(Man.).—(26) M.Dev.(Alpena) USA(Mich.).—(27) M.(?U.)Dev. (*Stringocephalus* Ls., ?*Orthoclymenia* Zone, Ger. (This figure serves as stratigraphic key for Fig. 232).



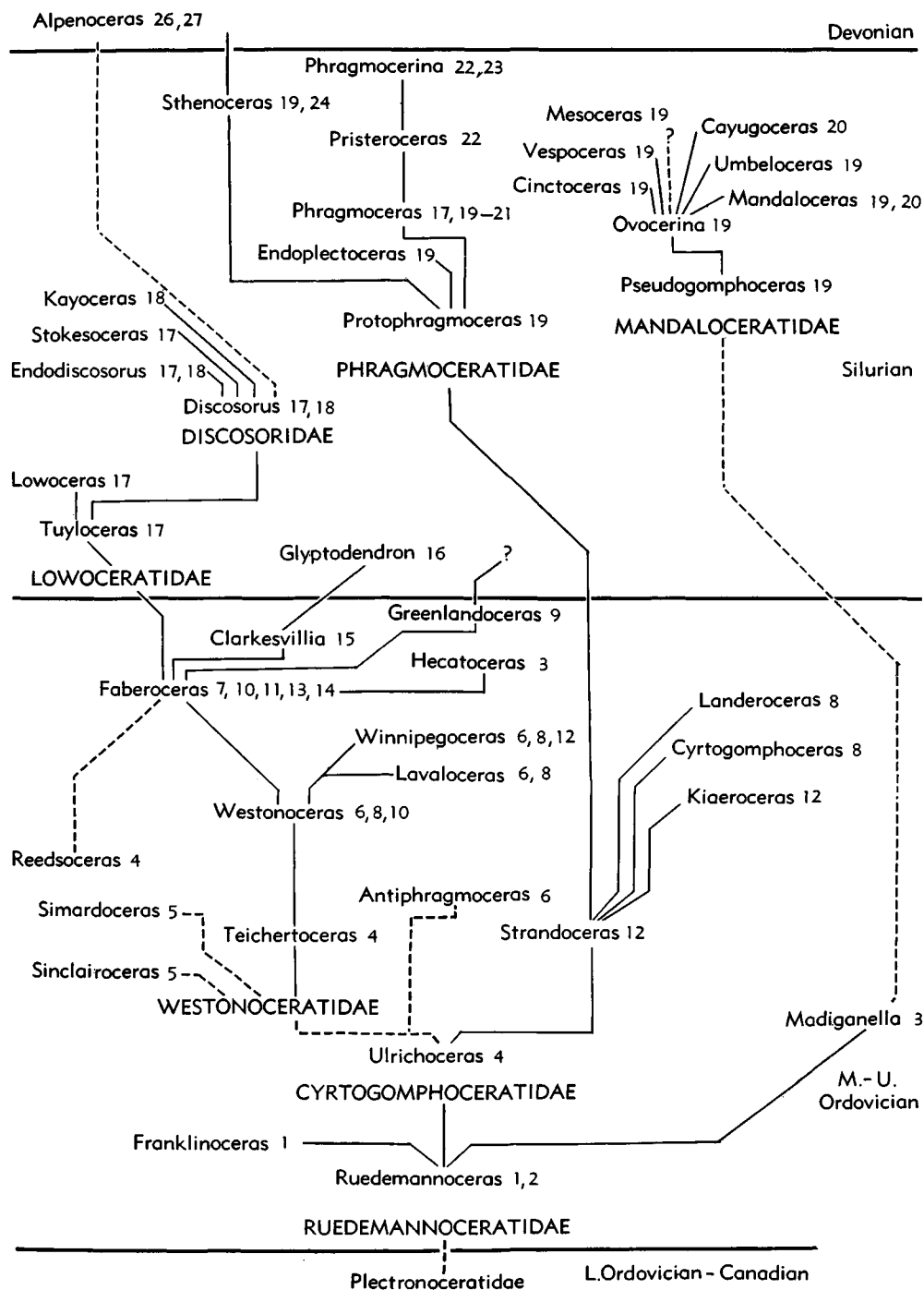


FIG. 234. (Explanation on facing page.)

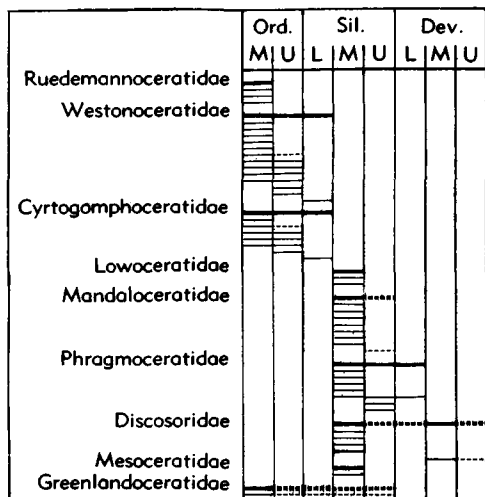


FIG. 234A. Stratigraphic distribution of genera and families of Discosorida (Teichert, n).

forward from venter to dorsum, without definite lobes; early portion of conch essentially straight; shell surface smooth; siphuncle slightly offset toward venter; early segments bulb-shaped, with short septal necks, expanding in later stages and brims becoming longer; connecting rings thick, with all primitive structures developed as described for order; cameral deposits strongly developed. *M.Ord.*, E.N.Am., Eu.(?Norway).—FIG. 235,1. \**R. boycii* (WHITFIELD), Chazy, USA (N.Y.); 1a, dorsoventral sec. of conch, venter on left,  $\times 1.3$ ; 1b, long. sec. of siphuncle,  $\times 4.5$ ; 1c, lat. view of conch, venter on left,  $\times 1.3$  (50).

**Franklinoceras** FLOWER, 1957 [*\*F. elongatum*; OD]. Similar to *Ruedemannoceras* but with strongly compressed cross section and straight sutures. *M.Ord.*, N.Am.(N.Y.).

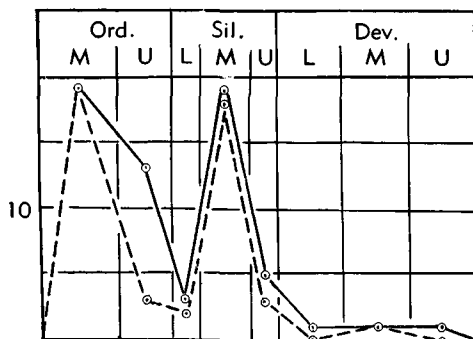


FIG. 234B. Graph showing numbers of new genera of Discosorida introduced in successive epochs (dashed lines) and total genera represented in each (solid lines) (Teichert, n).

**Madiganella** TEICHERT & GLENISTER, 1952 [*\*M. magna*; OD]. Shells large, slender, straight or nearly straight; siphuncle with broad, expanded segments and short, strongly recurved septal necks; connecting rings thick, with few differentiated structures; hard, calcified narrow tube almost invariably present within siphuncle. Growth lines of shell indicate presence of hyponomic sinus on concave side. *M.Ord.*, C.Australia.—FIG. 235,2. \**M. magna*; 2a, dorsoventral sec.,  $\times 0.7$ ; 2b, detail of siphuncle with central tube,  $\times 2.7$  (50, 191).

### Family CYRTOGOMPHOCERATIDAE Flower, 1940

Conchs dominantly medium-sized to large, compressed endogastric cyrtocones with siphuncle close to ventral side. Siphuncular segments short, broadly expanded; connecting rings thick, their apical end expanded into markedly swollen bullettes. *M.Ord.-L.Sil.*

**Cyrtogomphoceras** FOERSTE, 1924 [*\*Oncoceras magnum* WHITEAVES, 1890; OD]. Large endogastric brevicones, fusiform in profile, expanding rapidly, gibbous over anterior end of phragmone or base of body chamber, which contracts conically; aperture with ventral hyponomic sinus; cross section of conch generally strongly compressed, though circular in some forms; sutures with faint lateral lobes, sloping increasingly forward on dorsum in later growth stages; siphuncle large, slightly removed from venter, short segments broadly expanded; septal necks short, with strongly recurved brims; connecting rings thickened, bullettes swollen, but generally poorly seen; cameral deposits absent. *M.Ord.-U.Ord.*, N.Am.-Greenl.; *Sil.*, Eu.(Est.).—FIG. 236,1a-c. *C. nutatum* FOERSTE & SAVAGE, M.(or U.?) *Ord.*, Can. (Hudson Bay); 1a-c, dorsal, lat., ventral views,  $\times 0.5$  (50).—FIG. 236,1d. *C. turgidum* (TROEDSSON), *Ord.*(Cape Calhoun beds), N. Greenl.; portion of connecting ring with large bullette, adapical (lower) one with 2 layers,  $\times 4$  (50).—FIG. 236,1e,f. *C. sp.*, *Ord.* (Mt. Silliman beds), Baffin Is.; 1e, long. sec. of ventral side of siphuncle showing details of necks, thick connecting rings, and bullettes,  $\times 2$ ; 1f, partial view of same, showing apparent secondary thickening on outside of connecting rings, enlarged (184).

**Kiaeroceras** STRAND, 1934 [*\*K. frognoeyense*; OD]. Shells slender, almost straight; anterior portion of body chamber slightly contracted; some forms with slightly flaring aperture; cross section compressed, venter narrowly rounded; sutures with faint lateral lobes; siphuncle close to venter, septal necks short, connecting rings thickened, with prominent bullettes; interior of siphuncle empty. *U.Ord.*, N.Eu.—FIG. 237,1a-c. \**K. frognoeyense*, Norway; 1a, lat. view of conch; 1b, ventral view

of body chamber; *1c*, transv. sec.; all  $\times 0.2$  (50). FIG. 237, *1d,e*. *K. heroeyense* STRAND, Norway; *1d*, transv. sec. of conch,  $\times 0.2$ ; *1e*, siphuncle wall with bullettes,  $\times 2$  (50).

**Konglungenoceras** SWEET, 1959 [*\*K. norvegicum*; OD]. Strongly compressed, endogastric shells with contracted apertures; siphuncle with complex connecting rings lacking bullettes; endosiphuncular deposits in apical portion of siphuncle, consisting of heavy parietal laminae extended apically into endocones, similar to those in *Discosorus* and *Alpenoceras*. *L.Sil.*, Eu. (Norway).—FIG. 237, 2. *\*K. norvegicum*; *2a,b*, long. and transv. secs. of conch,  $\times 0.5$ ; *2c*, connecting ring, with vinculum and parietal deposits, enlarged (179).

**Landeroceras** FOERSTE, 1935 [*\*Diestoceras prolatum* MILLER, 1932; OD]. Similar to *Cyrtogomphoceras* but shell straight. *M.* (or ?*U.*) *Ord.* (Bighorn Dol.), W.N.Am.

**Parryoceras** SWEET & MILLER, 1957 [*\*P. euchari*; OD]. Similar to *Strandoceras* but differing in broadly expanded siphuncular segments and straight to only slightly convex ventral outline; inside of mature shell with strong thickening just behind aperture so that pronounced constriction marks internal mold near oral end of body chamber. *M.Ord.-U.Ord.*, N.Am. (Can., Arctic)-Eu. (Norway).—FIG. 238, 1. *\*P. euchari*, *M.* (or ?*U.*) *Ord.*, Arctic; *1a*, lat. view of holotype,  $\times 0.5$ ; *1b,c*, lat. and dorsal views,  $\times 0.5$ ; *1d*, dorsoventral sec. (235).

**Strandoceras** FLOWER, 1940 [*\*Protophragmoceras tyriense* STRAND, 1933; OD]. Generally strongly compressed endogastric cyrtocones, with body chamber straighter and more slender than phragmocone; venter narrowly rounded; sutures with shallow lateral lobes; aperture open, shallow hyponomic sinus on venter; siphuncle close to venter, with large broadly rounded segments, necks with short brims; connecting rings thick. *M.Ord.-U.Ord.*, N.Eu.—FIG. 236, 3. *\*S. tyriense* (STRAND), *U.Ord.*, Norway; *3a,b*, lat. and ventral views of conch,  $\times 0.5$  (10); *3c,d*, siphuncle wall with large bullettes, long. sec. of part of siphuncle,  $\times 1.8$  (50).

**Ulrichoceras** FOERSTE, 1928 [*\*U. beloitense*; OD]. Shell cyrtoconic, endogastric; fairly rapidly expanding to middle of body chamber, then contracting toward aperture; cross section slightly depressed, subtriangular; dorsal and ventrolateral sides strongly rounded; sutures faintly sinuate, describing broad lobes on ventral side; broad hyponomic sinus on venter; siphuncle located between center and venter, segments short, not strongly contracted at septal foramen, broadly rounded; connecting rings thickened, with inflated bullettes. *M.Ord.*, USA (Wis.).—FIG. 236, 2. *\*U. beloitense*; *2a,b*, lat. and ventral views of

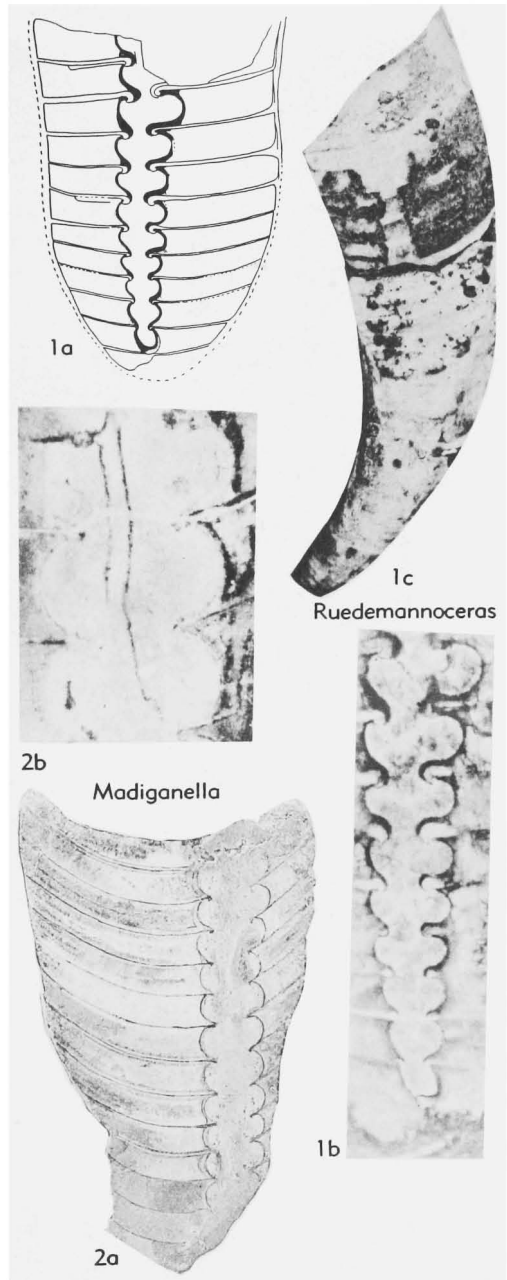


FIG. 235. Ruedemannoceratidae (p. K326, K328).

conch, apex and aperture restored,  $\times 0.5$ ; *2c*, siphuncle wall with inflated bullette,  $\times 2.7$ ; *2d*, transv. sec. of conch near base,  $\times 0.5$ ; *2e*, portion of siphuncle, with bullettes, enlarged (50).

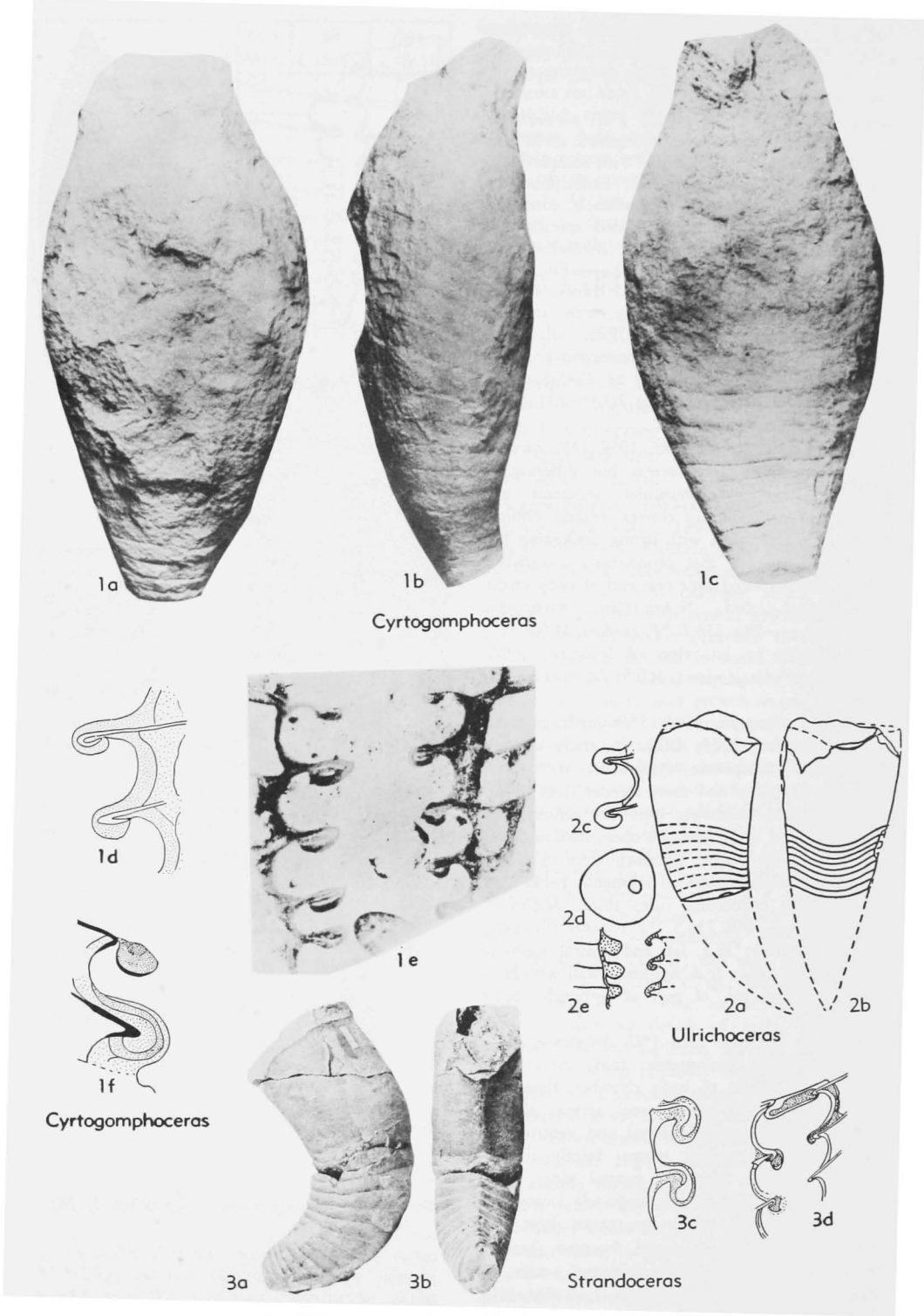


FIG. 236. Cyrtogomphoceratidae (p. K328-K329).

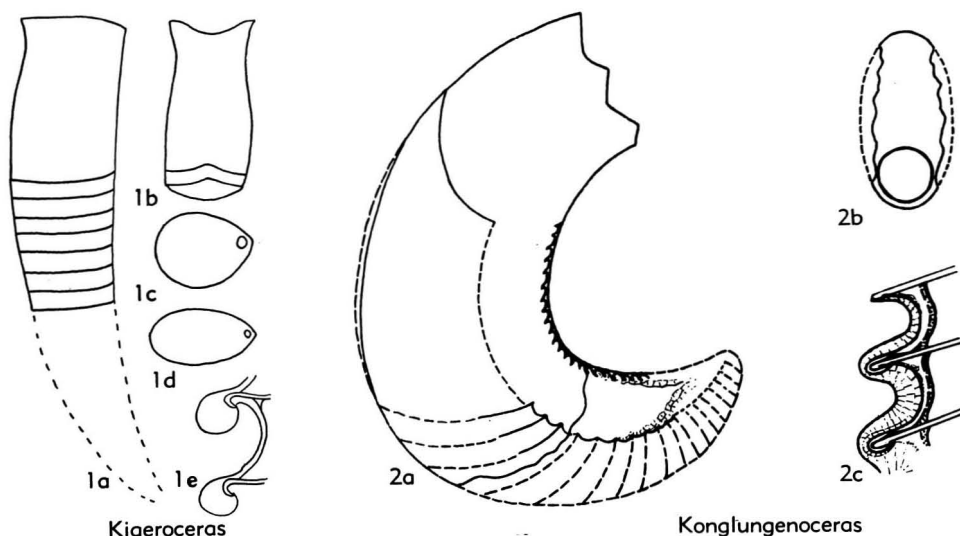


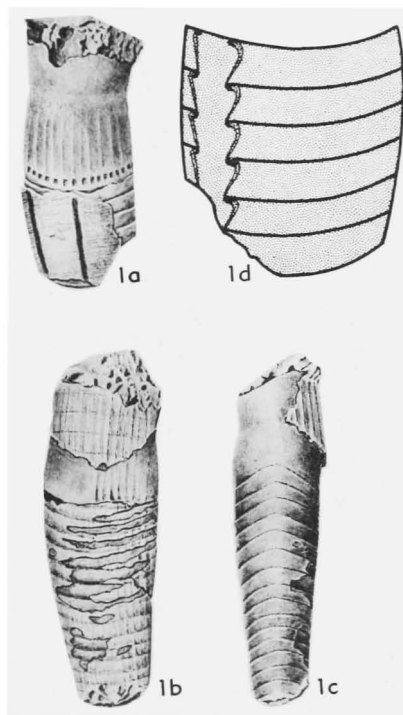
FIG. 237. Cyrtogomphoceratidae (p. K328-K329).

### Family WESTONOCERATIDAE Teichert, 1933

Conchs mostly compressed exogastric cyrtocones, medium- to large-sized, with moderately sized siphuncles; apertures constricted or open. Connecting rings thin to moderately thick; bullettes inflated; parietal deposits in interior of siphuncle, forming endocones in advanced genera. Cameral deposits present in some genera. *M.Ord.-L.Sil.*

**Westonoceras** FOERSTE, 1924 [*\*Cyrtoceras manitobense* WHITEAVES, 1890; OD] [= *Westenoceras* FOERSTE, 1924 (obj.), ICZN Opin. 593; *Thuleoceras* TROEDSSON, 1926]. Compressed, humped exogastric cyrtocones; early part of conch slender, gently exogastric to straight, rapidly expanding, convexity of ventral profile increasing; greatest gibbosity along anterior part of phragmocone and posterior part of body chamber; in cross section dorsum broadly rounded, venter narrow; sutures with lateral lobes; siphuncle close to ventral wall, segments strongly expanded, box-shaped; septal necks strongly recumbent, rings thick; parietal deposits initiated at septal foramina, growing forward and commonly forming continuous lining within siphuncle; cameral deposits invariably present. *M.Ord.-U.Ord.*, N.Am.-Greenl.-N.Eu.—FIG. 239, 1a. *\*W. manitobense* (WHITEAVES), *M.(or ?U.)Ord.*, Can.(Man.); dorsolat. view,  $\times 0.5$  (59). —FIG. 239, 1b. *W. sp.*; diagrammatic representation of shape and distribution of cameral deposits, enlarged (185). —FIG. 239, 1c. *W. sp.*, *Ord.*,

Baffin Is.; dorsoventral sec. of phragmocone showing cameral deposits and remnants of central tube in anterior part of siphuncle,  $\times 1.5$  (long. sec. of siphuncle of same specimen, Fig. 229, A) (50).

FIG. 238. *\*Parryoceras euchari* SWEET & MILLER (Cyrtogomphoceratidae) (p. K329).

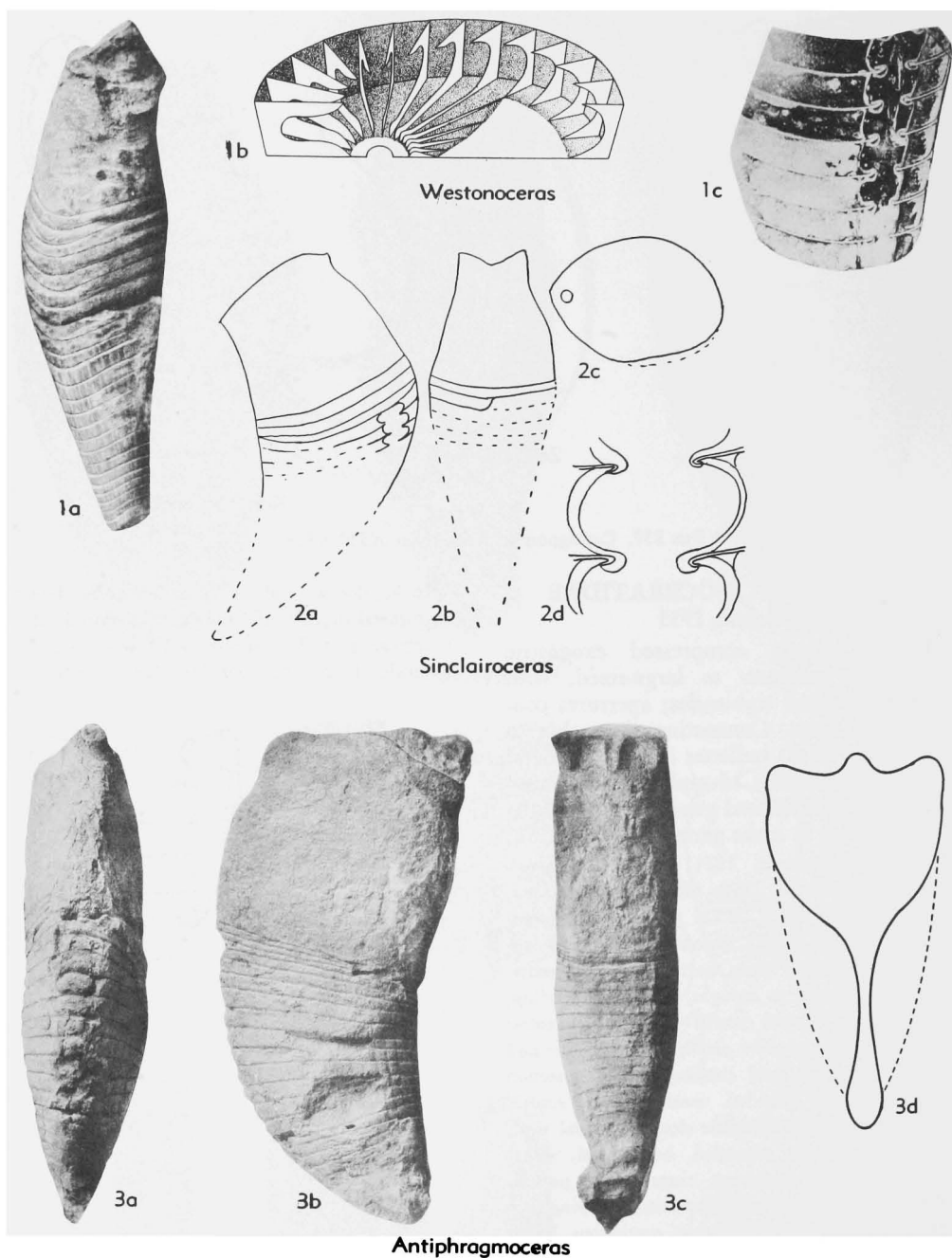


FIG. 239. Westonoceratidae (p. K331-K332, K334).

**Antiphragmoceras** FOERSTE, 1925 [*\*A. ulrichi*; OD]. Rather large exogastric, weakly cyrtconic conch, strongly compressed and with flattened dorsum; body chamber with constriction behind aperture (may be internal only); aperture

T-shaped as in *Phragmoceras*; siphuncle large, with strongly expanded segments. *M.Ord.*(Trenton.), E.N.Am.—FIG. 239,3. *\*A. ulrichi*, USA (Tenn.); 3a-c, dorsal, lat., ventral views,  $\times 0.45$ ; 3d, apert. view,  $\times 0.7$  (55).

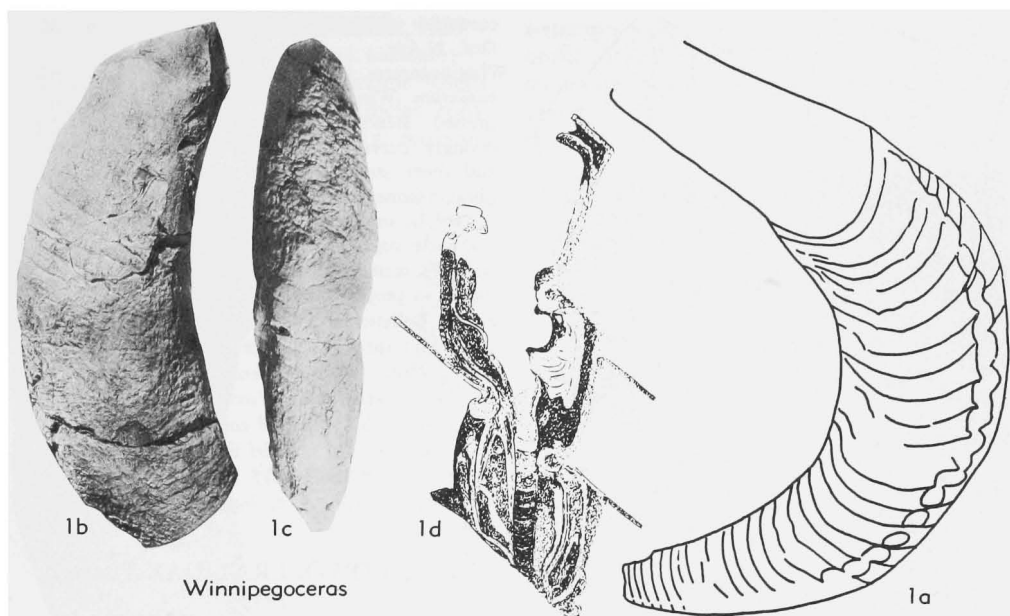


FIG. 240. Westonoceratidae (p. K334).

**Broeggeroceras** SWEET, 1958 [*\*B. contractum*; OD]. Similar to (possibly identical with) *Simardoceras* but with transversely elliptical to almost circular cross section. *M.Ord.*, ?*U.Ord.*, Eu.(Norway).

**Clarkesvillia** FLOWER, 1946 [*\*C. halei*; OD]. Differs from *Fabroceras* in prominent flattening of venter, from *Glyptodendron* in more ventrally placed siphuncle. *U.Ord.*, USA(Ohio).

**Fabroceras** FLOWER, 1946 [*\*F. multicinctum*; OD]. Large exogastric, compressed cyrtocoines, slender and gently enlarging from apex to aperture; sutures with faint lateral lobes; siphuncle close to venter in young, more central in later stages; segments broadly expanded, with parietal deposits, discrete or forming endocoines; shell surface in mature specimen with transverse costae. *M.Ord.-U.Ord.*, N.Am.-?Eu.—FIG. 242,1. *\*F. multicinctum*, *U.Ord.*, USA(Ky.); 1a, lat. view of conch showing transv. ridges,  $\times 0.45$ ; 1b, dorsoventral sec. of siphuncle, showing thick rings, small bullettes, parietal deposits which begin to form endocoines, and central tube in posterior portion,  $\times 6$  (50); 1c, details of siphuncle walls, enlarged (50).

**Glyptodendron** CLAYPOLE, 1878 [*\*G. eatonense*; M] [= *Cyrtoceras* (*Glyptoceras*) FOERSTE, 1893 (obj.)]. Large compressed cyrtocoines, dorsum narrowly rounded, greatest width in ventrolateral region; sutures sloping forward from dorsum, with faint ventral lobes; siphuncle slightly on

ventral side of center; segments subspherical in young, equally broad but shorter in adult; connecting rings thick, bullettes vestigial; no endosiphuncular deposits known; shell surface with scalelike shallow pits arranged in oblique intersecting rows; obscure costae in adult stage prominent close to ventrolateral angles and fading away dorsolaterally; aperture sloping backward from dorsum to ventrolateral angles. *L.Sil.*, USA(Ohio). —FIG. 242,3. *G. subcompressum* (BEECHER) (= *\*G. eatonense*); 3a, lat. view of conch with surface markings,  $\times 0.45$ ; 3b, long. sec. of ant. part of siphuncle,  $\times 1.1$ ; 3c,d, restorations, holotype (3c), composite based on 2 hypotypes (3d),  $\times 0.2$  (50).

**Hecatoceras** TEICHERT & GLENISTER, 1952 [*\*H. longinquum*; OD]. Probably endogastric, almost straight cyrtocoines; shell not known; siphuncle filled with calcareous deposits which form heavy endocoines; segments broadly expanded, probably with thick connecting rings. *U.Ord.*, Australia (Tasm.). —FIG. 242,2a-c. *\*H. longinquum*; 2a, ventral view of siphuncle fragment,  $\times 1.5$  (192); 2b,c, dorsoventral sec. of siphuncle, 2c showing thick connecting rings and parietal deposits,  $\times 1$ ,  $\times 3$  (191, 192). —FIG. 242,2d. *H. obliquum* TEICHERT & GLENISTER; dorsoventral sec. of siphuncle,  $\times 3$  (192).

**Lavaloceras** FLOWER, 1952 [*\*L. geniculatum*; OD]. Nearly straight exogastric brevicoines; cross section not quite as broad as *Simardoceras*. *M.Ord.*, N.Am. (E.Can.).

**Reedsoceras** FOERSTE, 1929 [*nom. subst. pro Con-*

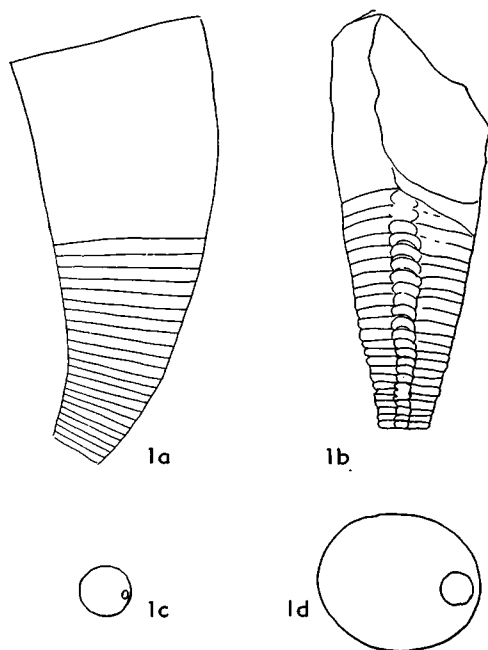


FIG. 241. \**Reedsoceras macrostomum* (HALL)  
(Westonoceratidae) (p. K333-K334).

*radoceras* FOERSTE, 1928 (*non* FOERSTE, 1926)] [*\*Cyrtoceras macrostomum* HALL, 1847; OD]. Large exogastric cyrtocones with rapidly expanding, uncontracted aperture; sutures straight; siphuncle ventral, with very short, broad segments that are broadly rounded; structure of siphuncular wall unknown. *M.Ord.-U.Ord.*, E.N.Am.—FIG. 241, *1*. \**R. macrostomum* (HALL), *M.Ord.*, USA (N.Y.); *1a,b*, lat., ventral views of conch,  $\times 0.45$ ; *1c,d*, transv. secs. of phragmocone near apex and body chamber at its base,  $\times 0.45$  (50).

*Simardoceras* FLOWER, 1957 [*\*S. simardense*; OD]. Similar to *Winnipegoceras* and *Sinclairioceras* but with broad, almost compressed cross section; aperture less strongly contracted than in *Sinclairioceras*. *M.Ord.*, Can.(Que.).

*Sinclairioceras* FLOWER, 1952 [*\*S. hahae*; OD]. Compressed exogastric brevicones, dorsal outline only slightly concave, ventral outline strongly convex, strongly humped in anterior part of phragmocone; body chamber contracted, with slight apertural flare; aperture sloping from dorsum to venter, with slight hyponomic sinus; sutures almost straight; siphuncle close to venter, segments broadly expanded; connecting rings thick. *M.Ord.*, Can.(Que.).—FIG. 239, 2. \**S. hahae*; *2a-c*, lat., ventral views, long. sec. of conch,  $\times 0.5$ ; *2d*, details of siphuncle, enlarged (50).

*Teichertoceras* FOERSTE, 1933 [*\*T. husseyi*; OD]. Differs from *Westonoceras* mainly in endogastric

curvature of earlier portion of phragmocone. *M.Ord.*, N.Am.

*Winnipegoceras* FOERSTE, 1928 [*\*Cyrtoceras laticurvatum* WHITEAVES, 1895; OD]. Large compressed slender exogastric cyrtocones, mostly strongly curved and slowly expanding; gibbous and more strongly curved near anterior end of phragmocone; body chamber slender, gently contracted in some forms; sutures with lateral lobe; siphuncle slightly removed from venter, segments strongly contracted at septal foramen, generally longer in proportion to diameter than in *Westonoceras*; bullettes swollen; parietal deposits and other siphuncular deposits rarely preserved. *M.Ord.-U.Ord.*, N.Am.-Greenl.-N.Eu.—FIG. 240, *1a*. \**W. laticurvatum* (WHITEAVES), Red River F., Can.(Man.); long. sec. of conch,  $\times 0.5$  (50).—FIG. 240, *1b-d*. *W. sinclairi* FLOWER, *M.Ord.* (Black River Gr.); Can.(Que.); *1b,c*, lat. and dorsal views,  $\times 0.5$  (39); *1d*, long. sec. of siphuncle,  $\times 4$  (50).

#### Family LOWOCERATIDAE Flower, 1940

Conchs consisting of slender exogastric cyrtocones; young shells with thick connecting rings and swollen bullettes; adult forms with siphuncle segments more rounded, less swollen bullettes, and thin connecting rings; endocones within siphuncle. *M.Sil.*

*Lowoceras* FOERSTE & SAVAGE, 1927 [*\*L. southamptonense*; OD]. Like *Tuyloceras*, but with endocones in the siphuncle similar to those of *Discosorus*, but without bullettes. *M.Sil.*, N.Am.(N.Can.).—FIG. 243, *1*. \**L. southamptonense*, *Sil.*, Can.(Southampton Is.); *1a,b* (holotype), vert. sec. (venter on left) showing endocones without bullettes, opposite side showing exterior of siphuncle,  $\times 1$  (50).

*Tuyloceras* FOERSTE & SAVAGE, 1927 [*\*T. percurvatum*; OD]. Strongly compressed exogastric brevicone with venter more narrowly rounded than dorsum, enlarging moderately in diameter to middle of body chamber, very gently contracting over mature body chamber toward aperture; sutures trending strongly adapically from dorsum to venter; siphuncle at short distance from venter; segments changing during ontogeny from slender subquadrate (in dorsoventral section), with thick rings and swollen bullettes to more expanded segments of more rounded section, with thin ring and bullettes not swollen. *M.Sil.*, N.Am.(N.Can.).—FIG. 244, *1*. \**T. percurvatum*; *1a,b*, lat. and ventral views,  $\times 0.7$ ; *1c*, dorsoventral sec. through siphuncle showing septal necks, connecting rings, and bullettes,  $\times 2.8$  (50).



Family DISCOSORIDAE Miller, 1889

[=Discosoridae TEICHERT, 1931 (jr. syn. homonym)]

Endogastric, generally breviconic shells (complete shells rare but siphuncles common). Siphuncles with broadly rounded

segments that expand rapidly in width ad-orally; septal necks short, brims long, recumbent; connecting rings poorly known, generally thin; bullettes never swollen; endocones within siphuncle, leaving endo-

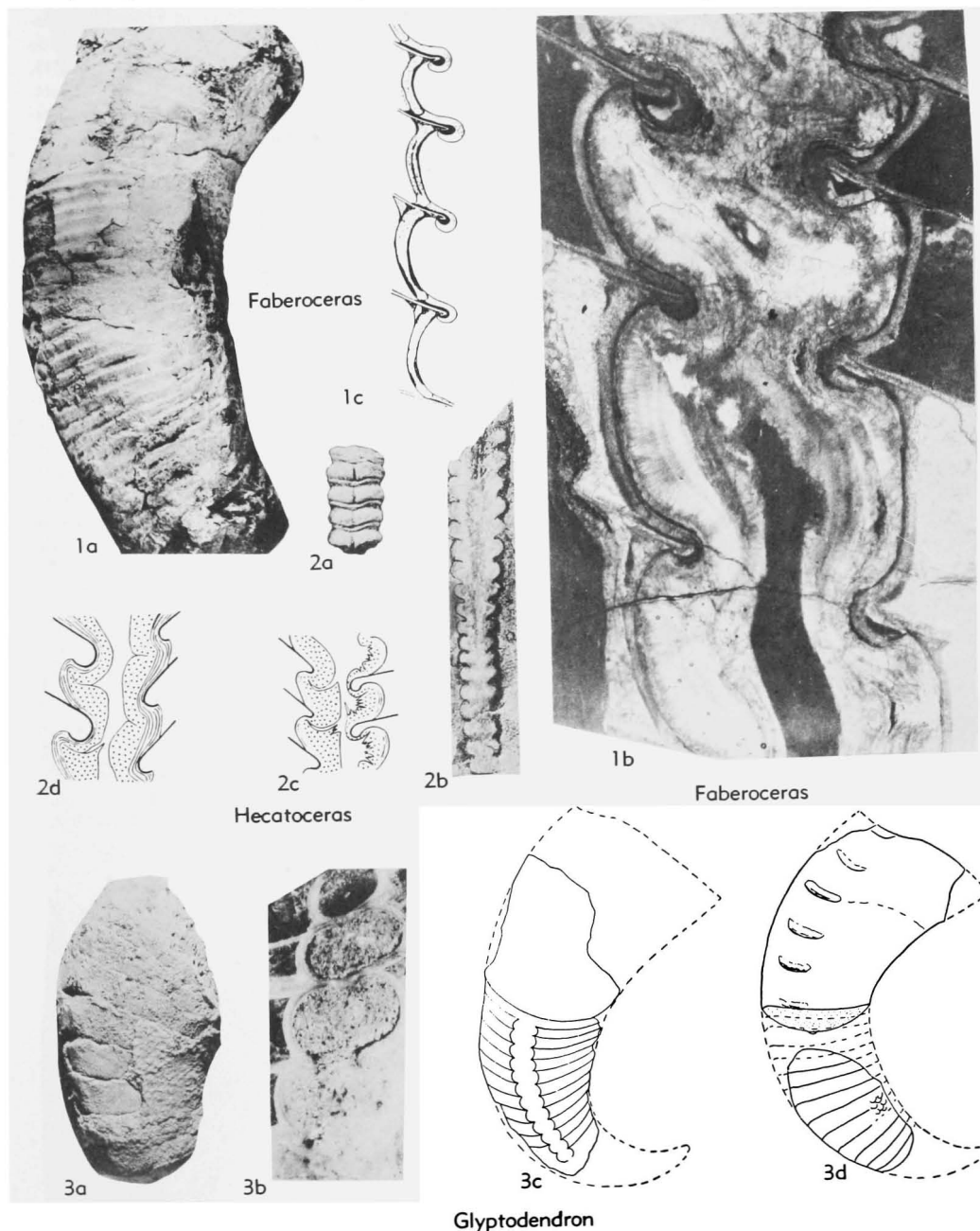


FIG. 242. Westonoceratidae (p. K333).



FIG. 243. \**Lowoceras southamptonense* FOERSTE & SAVAGE (Lowoceratidae) (p. K334).

siphuncular tube, which may contain diaphragms. *M.Sil.-M.Dev.*, ?*U.Dev.*

*Discosorus* HALL, 1852 [\**D. conoideus*; M]. Mostly known from isolated siphuncles composed of

broadly rounded, strongly expanded segments, increasing very rapidly in size; septal necks recumbent, with long brim in contact with free part of connecting ring; interior of siphuncle occupied by endocones, leaving endosiphuncular tube, with elevated protuberance of endocone material surrounding aperture of tube. Phragmocone short, rapidly expanding, generally little known. *M.Sil.*, Arct.N.Am.-E.N.Am.—FIG. 245, 1a. \**D. conoideus*, USA(N.Y.); dorsoventral sec. of siphuncle showing traces of endocone, elevation, and endosiphuncular tube,  $\times 1.3$  (50).—FIG. 245, 1b,c. *D.* sp., cf. *D. ehlersi* FOERSTE, Can.; ventral and lat. views of siphuncle,  $\times 0.7$  (50).—FIG. 245, 1d. *D.* sp., Can.; dorsoventral sec. of siphuncle showing thickened connecting rings and elevation at bottom of endosiphuncular cavity,  $\times 0.7$  (181).—FIG. 245, 1e,f. *D. austini* FOERSTE, Ohio; ventral and lat. views of siphuncle with part of body chamber,  $\times 0.3$  (50).

*Alpenoceras* FOERSTE, 1927 [\**A. ulrichi*; OD] [= *Endodiscosorus* (*Endostokesoceras*), *Discosorus* (*Neodiscosorus*) SCHINDEWOLF, 1944]. Shell ?endogastric, moderately breviconic, expanding fairly rapidly to body chamber, which contracts faintly at aperture; cross section slightly depressed; sutures straight and transverse; growth lines showing moderate hyponomic sinus on concave side of conch; siphuncle close to ventral (concave) side,

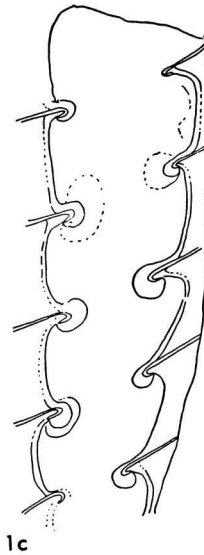


FIG. 244. \**Tuyloceras percurvatum* FOERSTE & SAVAGE (Lowoceratidae) (p. K334).

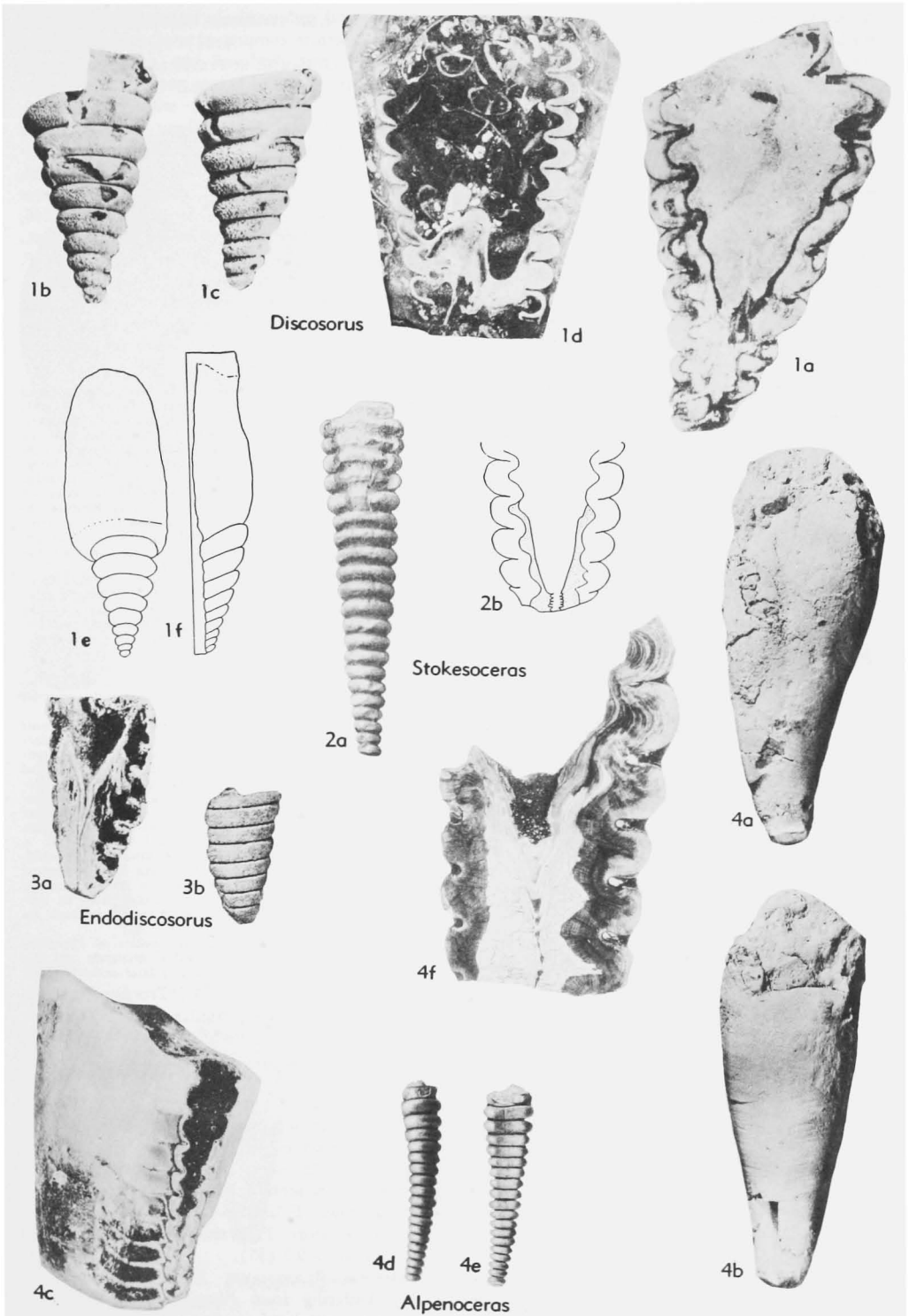


FIG. 245. Discosoridae (p. K336, K338).

segments broadly expanded, connecting rings thick, supplemented by secondary thickening on their outer side; endosiphuncular deposits similar to those of *Discosorus*. *M.Dev.*, ?*U.Dev.*, USA (Mich.)-Can.-Eu.(Ger.).—FIG. 245,4a-c. \**A. ulrichi*, *M.Dev.*, Mich.; 4a,b, lat. and ventral views of conch, growth lines indicating hyponomic sinus,  $\times 0.5$ ; 4c, dorsoventral sec.,  $\times 1.5$  (50).—FIG. 245,4d-f. *A. eifelense* SCHINDEWOLF, *M.Dev.*, Ger.; 4d,e, lat. and ventral views of siphuncle,  $\times 0.7$ ; 4f, long. sec. of siphuncle showing parietal deposit and endocones which are closed posteriorly,  $\times 2.7$  (156).

**Endodiscosorus** TEICHERT, 1931 [\**E. foerstei*; OD]. Similar to *Discosorus* but sides of siphuncular segments flattened; siphuncle enlarging more rapidly initially, more slender anteriorly; endocones massive, with smooth anterior cavity and without median elevation such as found in *Discosorus*. *M.Sil.*, USA (Mich.-Iowa)-Can. (Lake Timiskaming-Lake Huron).—FIG. 245,3. \**E. foerstei*, Can. (Lake Timiskaming); 3a, dorsoventral sec. of siphuncle showing endosiphuncular canal, endocones partly weathered out,  $\times 1$ ; 3b, lat. view of siphuncle,  $\times 0.7$  (185).

**Kayoceras** FOERSTE, 1934 [\**Discosorus?* *biconoideus* THOMAS, 1915; OD]. Differs from *Discosorus* in more central position of siphuncle; breviconic, contracting slightly toward aperture. *M.Sil.*, USA (Iowa).

**Stokesoceras** FOERSTE, 1924 [\**S. romingeri*; OD]. Similar to *Discosorus* but much more slender and relatively straight. Anterior end of endosiphuncular tube showing annulate structure. *M.Sil.*, N. Am. (USA-N.-Can.)-Eu. (Est.).—FIG. 245,2a. \**S. romingeri*, USA (Mich.); ventral view of siphuncle,  $\times 0.7$  (220).—FIG. 245,2b. *S. engadinense* FOERSTE, USA (Mich.); long. sec. of siphuncle showing annular structure of endosiphuncular tube,  $\times 0.9$  (50).

## Family PHRAGMOCERATIDAE

Miller, 1877

[=Phragmoceratidae HYATT in ZITTEL, 1900 (jr. syn. homonym)]

Cyrtconic, endogastric, compressed shells with strongly contracted aperture, modified in various ways. Siphuncles with broadly expanded segments, thick connecting rings, and small to vestigial bullettes. *M.Sil.-L.Dev.*

**Phragmoceras** BRODERIP in SOWERBY in MURCHISON, 1839 [=BRODERIP in MURCHISON, 1834 (*nom. nud.*)] [\**P. arcuatum* SOWERBY, 1839; SD S.A. MILLER, 1889] [=Phragmocera BRAUN, 1840 (obj.) (*nom. van.*); Phragmoceratites D'ARCHIAC & DEVERNEUIL, 1842 (obj.) (*nom. van.*); Phragmoceras BROWN, 1848 (obj.) (*nom. van.*)]. Generally large, rapidly expanding conchs, differing from *Protophragmoceras* in greatly constricted

aperture and comparatively larger siphuncle; main part of aperture compressed oval to subtriangular and lesser part produced into narrow long slit that widens ventrally into narrow ovate lobe (hyponomic sinus); sutures with lateral lobes, general course normal to shell curvature. Siphuncle close to ventral side, with broadly expanded segments; connecting rings thick, undifferentiated, with bullettes; interior of siphuncle may have parietal deposits. *M.Sil.*, N. Am.-Eu.—FIG. 246, 1a,b. *P. lamellosum* HEDSTRÖM, Eu. (Sweden); lat., ventral views,  $\times 0.45$  (90).—FIG. 246,1c. *P. farsimen* HEDSTRÖM, Sweden (Gotl.); dorsoventral sec. showing siphuncle with internal deposits,  $\times 0.7$  (90).—FIG. 246,1d. *P. transversale* HEDSTRÖM, Sweden (Gotl.); long. sec. of siphuncle showing large bullettes,  $\times 3.5$  (50).

[Type-species of *Phragmoceras*.—In his paleontological contributions to MURCHISON'S "Silurian System" (1839), J. DE C. SOWERBY credited several new genera to BRODERIP, by simply inserting BRODERIP'S name in parentheses after the generic name. J. C. BRODERIP was a British zoologist, a contemporary of SOWERBY and an associate of WILLIAM BUCKLAND. Among genera thus credited by SOWERBY to BRODERIP is the discosorid *Phragmoceras*. Although SOWERBY does not characterize the nature of the contribution by BRODERIP to knowledge of this genus, it has always been tacitly assumed that the generic characteristics stated by SOWERBY were obtained by him from BRODERIP and as a result BRODERIP has been cited as the author of *Phragmoceras*.

SOWERBY definitely assigned three species to *Phragmoceras*, namely, *P. arcuatum*, *P. ventricosum*, and *P. compressum*. The first and the third of these species are new and are to be credited to SOWERBY. After *P. ventricosum*, however, SOWERBY added "(*Orthoceratites ventricosus?* STEININGER, Mém. soc. géol. France, v. 1 [1834]. . .)" and the description of the species is followed by the remark, "If the fossil described by STEININGER be the same as our species the artist [of STEININGER'S illustration] has apparently reversed the curvature of the septa."

WOODWARD (1868) selected *Orthoceratites ventricosus* STEININGER as the type-species of *Phragmoceras*. If this selection were regarded as valid, *Phragmoceras* would be an unrecognizable genus, based on a cephalopod fragment of Devonian age. However, since SOWERBY assigned *O. ventricosus* STEININGER only doubtfully to *Phragmoceras*, it is ineligible for designation as the type-species of *Phragmoceras* (Rules, Art. 67h). *P. ventricosum* SOWERBY, from Silurian rocks of England, may be regarded rightly as a separate species but the transfer of STEININGER'S *O. ventricosus* (1834) to *Phragmoceras* by WOODWARD (1868) operated to make SOWERBY'S *P. ventricosum* (1839) a junior secondary homonym, which by provision of the Rules must be permanently rejected. SOWERBY'S *P. ventricosum* is here re-named as *P. broderipi* TEICHERT.

The first valid selection of a type-species of *Phragmoceras* was by MILLER (1889) who cited *P. arcuatum* and this designation has been accepted as valid by later authors (50).]

**Endoplectoceras** FOERSTE, 1924 [\**Trochoceras secula* BARRANDE, 1865; OD]. Similar to *Protophragmoceras*, differing in greater slenderness of shell and very faint trochoceroïd coiling. *M.Sil.*, Eu. (Czech.).

?**Phragmocerina** FLOWER, 1948 [\**Gomphoceras osculum* RUEDEMANN, 1916; OD]. Slightly compressed brevicones, endogastric in early stages, straight in later ones; apertural plane essentially parallel to last septum; siphuncle small, its structure unknown. *U.Sil.*, USA (N.Y.).—FIG. 246,2. *P. litchfieldensis* FLOWER; 2a-c, ventral, lat., apert. views,  $\times 0.7$  (35).

**Pristeroceras** RUEDEMANN, 1925 [\**P. tumidum*; OD]. Differing from *Phragmoceras* in strongly crenulated margin of aperture. *U.Sil.*, USA (N.Y.).

—FIG. 246,4. \**P. tumidum*; 4a,b, lat., apert. views,  $\times 0.5$ ,  $\times 1$  (181).

**Protophragmoceras** HYATT in ZITTEL, 1900 [\**Cyrtoceras murchisoni* BARRANDE, 1866; OD]. Com-

pressed endogastric cyrtocoones, enlarging evenly and gradually from apex to aperture, which is unrestricted; sutures swinging forward on convex dorsum, with lateral lobes; growth lines indi-

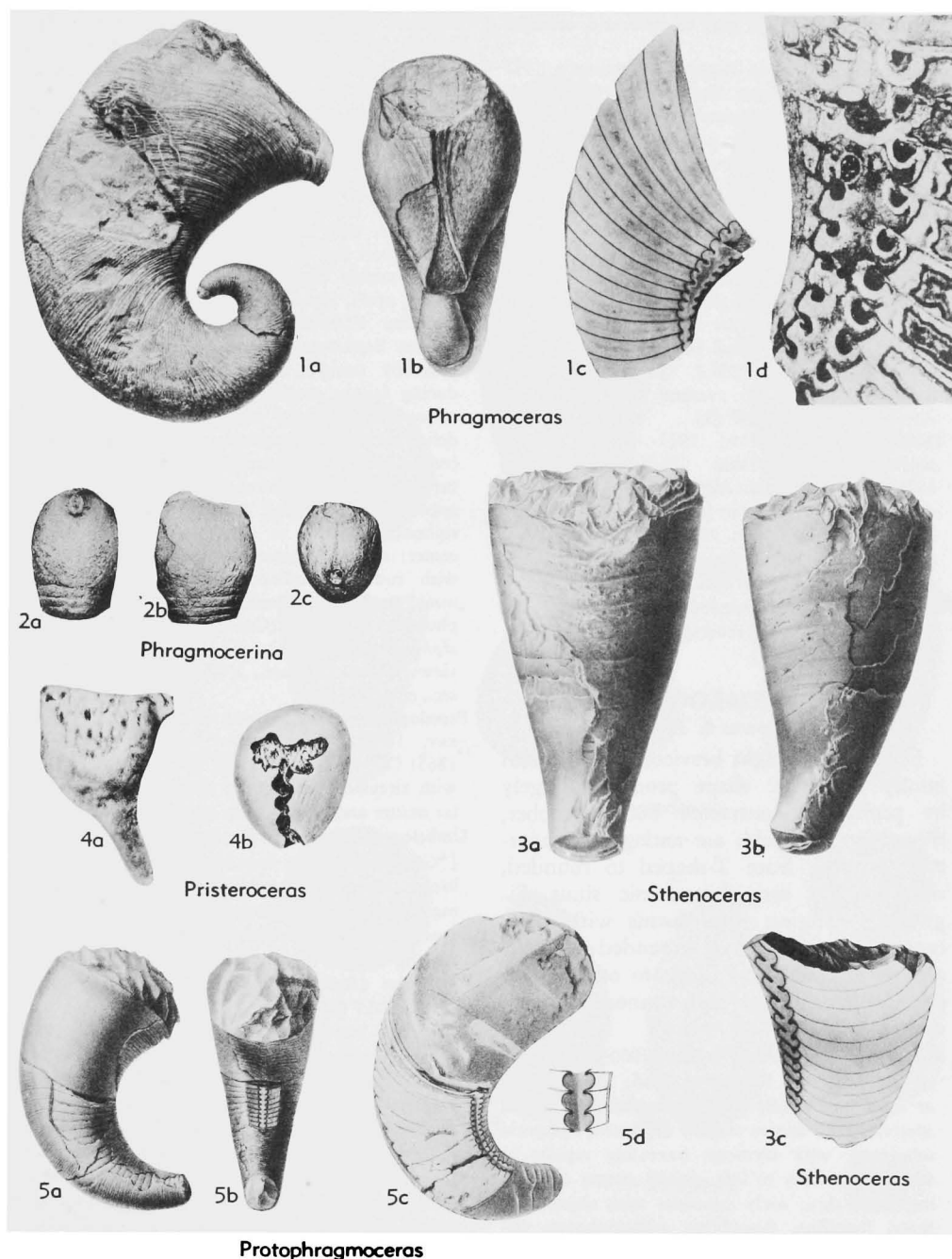


FIG. 246. Phragmoceratidae (p. K338-K340).

cating deep and sharp hyponomic sinus; siphuncle close to venter, segments short, broad; connecting rings thick. *M.Sil.*, Eu.(Czech.).—FIG. 246,5. \**P. munchisoni* (BARRANDE); 5a,b, lat., ventral views,  $\times 0.45$ ; 5c, dorsoventral sec. of another specimen,  $\times 0.45$ ; 5d, part of siphuncle, enlarged (5).

**Sthenoceras** FLOWER in FLOWER & TEICHERT, 1957 [*\*Cyrtoceras aduncum* BARRANDE, 1866; OD]. Large, smooth, endogastric shells with slight hyponomic sinus, early part of shell expanding moderately rapidly, curvature and rate of expansion both reduced in later stages, mature body chamber tending to become nearly straight, with slightly convex sides and aperture very slightly contracted; cross section broad, with dorsal side slightly flattened; sutures mostly straight and transverse, some with slight lateral lobes; siphuncle close to venter, segments slightly to broadly expanded, thick rings, small bullettes. *M.Sil.-L.Dev.*, Eu.(Czech.).—FIG. 246,3. \**S. aduncum* (BARRANDE), L.Dev.; 3a,b, ventral, lat. views; 3c, dorsoventral sec.,  $\times 0.45$  (5).

**Tubiferoceras** HEDSTRÖM, 1917 [*\*Phragmoceras proboscideum* HEDSTRÖM, 1917; SD FOERSTE, 1926]. Differing from *Phragmoceras* in that dorsal sinus of aperture is projected beyond dorsal side of shell to form tubular extension; shell straighter than *Phragmoceras* and more rapidly expanding; structure of siphuncle unknown. *M.Sil.*, USA (Ind.-Wis.)-Eu.(Sweden).—FIG. 247,1. *T. prominens minus* (HEDSTRÖM), Sweden (Gotl.); lat. view,  $\times 0.45$  (90).

## Family MANDALOCERATIDAE

### Flower in Flower & Teichert, 1957

Essentially straight breviconic shells with faintly exogastric shape produced largely by profile of contracted body chamber, though some species are endogastric; apertures varying from T-shaped to rounded, with narrow, long hyponomic sinus. Siphuncles ranging from forms with short broad, rounded, strongly expanded segments and thick connecting rings to others with slender segments and thin connecting rings. *M.Sil.*, ?*U.Sil.*

**Mandaloceras** HYATT in ZITTEL, 1900 [*\*Gomphoceras bohemicum* BARRANDE, 1865; M]. Straight or cyrtoconic shells with constricted T-shaped aperture; cross section slightly depressed; siphuncle subcentral, with segments increasing rapidly in width from early to late growth stages; connecting rings thin; early segments with deposits at septal foramina, resembling actinosiphonate deposits. *M.Sil.*, N.Am.-Eu.(Eng.-Czech.).—FIG. 247,3. *M. verneuli* (BARRANDE), Czech.; 3a,b,

ventral, apert. views, 3c, dorsoventral sec.,  $\times 0.5$  (5).

?**Cayugoceras** FLOWER, 1947 [*\*Gomphoceras? semiclausum* BARRANDE, 1865; OD]. Similar to *Ovocerina* but siphuncle contracted to small subtriangular aperture. Structure of siphuncle unknown. *U.Sil.*, Eu.(Czech.)-N.Am.(N.Y.).—FIG. 247,4. \**C. semiclausum* (BARRANDE), Czech.; 4a-d, dorsal, apert. lat., apical views,  $\times 0.7$  (5).

**Cinctoceras** FLOWER in FLOWER & TEICHERT, 1957 [*\*Gomphoceras imperiale* BARRANDE, 1865; OD]. Large, straight brevicones, with constricted T-shaped aperture; shell with numerous, low, sharp transverse costae; cross section tending to be depressed, with flattened dorsum. Siphuncle segments short and broad. *M.Sil.*, Eu.—FIG. 247,2. \**C. imperiale* (BARRANDE), Czech.; 2a-d, ventral, dorsal, apert. views, dorsoventral sec.,  $\times 0.45$  (5).

**Ovocerina** FLOWER, 1947 [*\*Gomphoceras marsupium* BARRANDE, 1865; OD]. Small breviconic, generally straight, contraction of aperture producing faintly exogastric aspect owing to greater convexity of ventral side, smaller species more definitely curved, exogastric; cross section slightly compressed; sutures straight and transverse; aperture either broadly round or transversely extended, approaching T-shaped aperture of *Mandaloceras*; siphuncle slightly to dorsal or ventral side of center; segments generally very broad and short, with rounded outlines; connecting rings thin; some species with vesicular structures inside siphuncle. *M.Sil.*, Eu.(Czech.).—FIG. 247,5. *O. alphas* (BARRANDE); 5a-d, lat., ventral, apert. views, dorsoventral sec.,  $\times 0.5$ ; 5e, siphuncle, long. sec., enlarged (5).

**Pseudogomphoceras** FLOWER in FLOWER & TEICHERT, 1957 [*\*Gomphoceras rigidum* BARRANDE, 1865; OD]. Like *Ovocerina* but large, longiconic, with circular cross section; siphuncle with vesicular matter and central tube. *M.Sil.*, Eu.(Czech.).

**Umbeloceras** FLOWER in FLOWER & TEICHERT, 1957 [*\*Gomphoceras spei* BARRANDE, 1865; OD]. Small brevicones, slightly exogastric, cross section ranging from slightly compressed to slightly depressed; aperture T-shaped, with the 2 lateral branches curving toward venter. *M.Sil.*, Eu.—FIG. 248,1. \**U. spei* (BARRANDE), Czech.; 1a,b, lat., apert. views,  $\times 0.7$  (5).

**Vesporoceras** FLOWER in FLOWER & TEICHERT, 1957 [*\*Gomphoceras vespa* BARRANDE, 1865; OD]. Medium-sized straight brevicones with broad annular expansion in anterior part of phragmone, followed by constriction at base of body chamber, latter expanding normally at first and having open or constricted aperture; siphuncle midway between center and venter, segments moderately to strongly expanded. *M.Sil.*, Eu.—FIG. 248,2. \**V. vespa* (BARRANDE), Czech.; 2a-c, lat., dorsoventral sec., ventral views,  $\times 0.5$  (5).

?Family MESOCERATIDAE Hyatt,  
1884

Body chamber straight, short, strongly  
contracted anteriorly; aperture consisting of  
broad, long transverse slit; cross section

slightly depressed; sutures simple, trans-  
verse. Siphuncle subcentral. *M.Sil.*

*Mesoceras* BARRANDE, 1877 [*\*M. bohemicum*; M].  
Characters of family; known only from body  
chamber. *M.Sil.*, Eu.(Czech.).—FIG. 248,3. *\*M.*

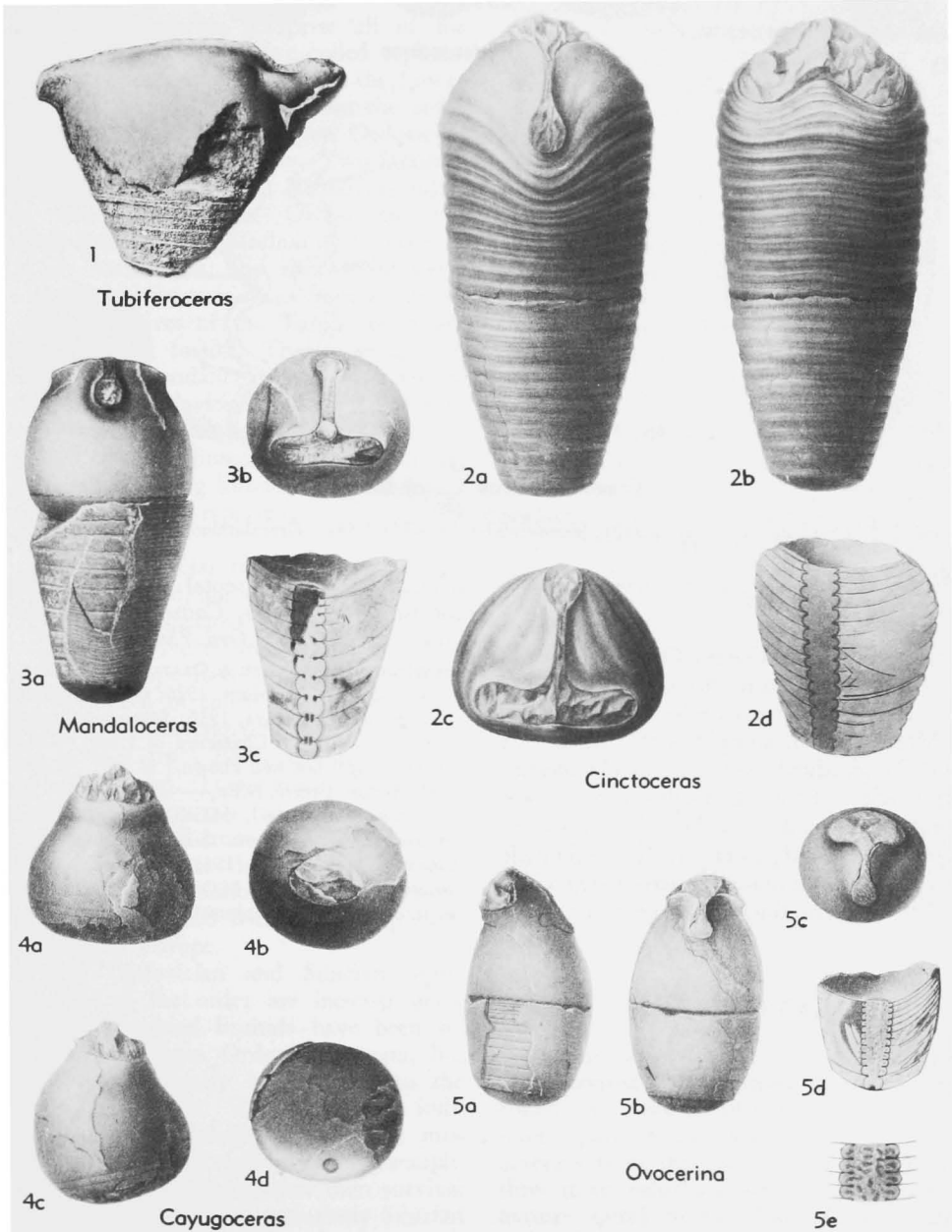


FIG. 247. Phragmoceratidae, Mandaloceratidae (p. K340).

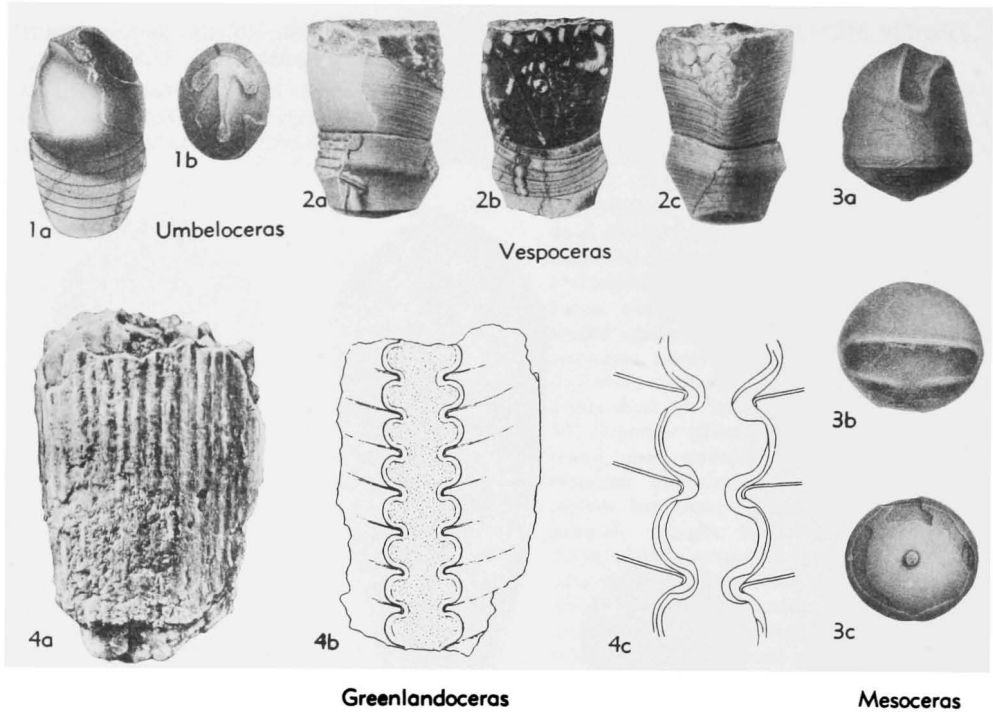


FIG. 248. Mandaloceratidae (p. K340); Mesoceratidae (p. K341-K342); Greenlandoceratidae (p. K342).

*bohemicum*; 3a-c, lat., apert. views, bottom of body chamber,  $\times 0.5$  (5).

?Family **GREENLANDOCERATIDAE**  
Shimizu & Obata, 1935

[=Striatoceratidae FLOWER, 1939]

Medium-sized, straight shells; outer side with longitudinal ridges, as in *Kionoceras*. Siphuncle subcentral, medium-sized; segments subglobular to broadly expanded; septal necks short; inner surface of siphuncle lined with continuous calcareous deposit of rather uniform thickness except for slight

thickening around septal necks, typically consisting of 2 layers. Cameral deposits unknown. *M.Ord.*, ?*U.Ord.*-?*Sil.*

**Greenlandoceras** SHIMIZU & OBATA, 1935 [\*?*Sactoceras lineatum* TROEDSSON, 1926; OD] [=Striatoceras SHIMIZU & OBATA, 1935; *Sactocerina* KOBAYASHI, 1936 (obj.)]. Characters of family. [These forms are still not well known.] *M.Ord.*, ?*U.Ord.*-?*Sil.*, N.Am.-Greenl.-N.Eu.—FIG. 248, 4a, b. \**G. lineatum* (TROEDSSON), *M.Ord.*, N.Greenl.; 4a, b, external views, long. sec. showing siphuncle with internal lining,  $\times 0.7$  (194).—FIG. 248, 4c. *G. striatum* (TROEDSSON), *M.Ord.*, N.Greenl.; details of internal lining of siphuncle,  $\times 1$  (236).



## NAUTILOIDEA—TARPHYCERIDA

By W. M. FURNISH and BRIAN F. GLENISTER

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## INTRODUCTION

The Tarphycerida comprise all of the earliest and most primitive coiled cephalopods; they are known best from the Lower Ordovician (late Canadian), but the order persists through the younger Ordovician and into the Upper Silurian. Two families, the Tarphyceratidae and Estonioceratidae, are exclusively Lower Ordovician, the Trocholitidae are predominantly Lower and Middle Ordovician, and the Ophidioceratidae are known only from Silurian strata.

Representatives of the Tarphycerida are relatively rare fossils. Their variety and comparative abundance in the North American Lower Ordovician probably signifies only intensive search and widespread development of a molluscan facies. However, judging by existing knowledge, such forms may also be well represented in Australia and Siberia.

Middle Ordovician tarphycerids are widespread and varied, but in the Balto-Scandian Region the associated straight nautiloids predominate. Nevertheless, the plains of northern Europe have provided numerous fine specimens of coiled genera from drift boulders ("Diluvialgeschieben"), presumably derived from Baltic countries or the Baltic depression. To a considerable degree, studies of the lituitids have been based on specimens secured from erratics. The Lituitidae also represent the only known case of provincial distribution in the order; none have been identified with certainty outside of northern Europe.

Upper Ordovician and Silurian representatives of the order are inconspicuous. A few undoubted lituitids have been secured from Upper Ordovician strata, but generally the family is restricted to the Middle Ordovician. The long range indicated for the Trochilitidae could be misleading, for a dorsal siphuncle may exemplify repetitive evolution, rather than survival of a stable lineage. An exclusively Silurian family, the Ophidioceratidae, has been variously regarded by taxonomists but shows several features characteristic of some

tarphycerids—evolute conch, divergent body chamber, and complex aperture.

Many tarphycerid taxa are based upon fragmentary or imperfectly preserved type material. Also, little intensive study of internal shell morphology has been undertaken. Nevertheless, the taxonomy seems to be at least as well founded as for comparable groups. In a few noteworthy examples fine preservation of these Lower Paleozoic cephalopods is found to reveal all details (e.g., upper Canadian fauna of the Cassin Limestone in Champlain basin).

Recognition of several tarphycerid genera preceded the last century; *Lituites* was a pre-Linnéan taxon validated 200 years ago. Significant contributions which are still valuable references include BARRANDE (1865, 1867), ANGELIN & LINDSTRÖM (1880), REMELÉ (1880), NOETLING (1882, 1884), LINDSTRÖM (1890), and SCHRÖDER (1891). In North America, HYATT (1894) and RUEDEMANN (1906) presented comprehensive detail; more recently FOERSTE (e.g., 1930) studied a variety of representatives of this order. ULRICH, FOERSTE, MILLER & FURNISH (1942) described known Lower Ordovician forms. Modern studies of the classic Balto-Scandian province include those of STRAND (1934) and SWEET (1958) on Upper and Middle Ordovician faunas in the Oslo area; SWEET's studies of the Lituitidae are most authoritative. BALASHOV (1953, 1962) has recorded faunas from the eastern Baltic and the Siberian Platform. TEICHERT & GLENISTER (1952-54) described coiled Ordovician forms from Australia.

## MORPHOLOGY

Representatives of the Tarphycerida generally consist of a relatively small, loosely coiled or evolute, planospiral conch, in which part of the mature body chamber diverges from the preceding whorl. About three to six volutions may be present in the mature spiral conch. Some fully mature coiled forms (e.g., *Moreauoceras*) attain a conch diameter of only 20 mm., whereas a number of other upper Canadian genera

exceed 150 mm. at maturity. The divergent orthocone of uncoiled derivatives (e.g., *Lituites*) may exceed 300 mm. in length. A single imperfectly known torticone (*Aethoceras*) is included in the order. Whorls of the spiral portion of the conch are generally in contact and exhibit slight to moderate dorsal impression (Tarphyceratidae, Trocholitidae, Ophidioceratidae). However, looser coiling is characteristic of the Estonioceratidae and the whorl section in this family is rounded to flat dorsally. The spiral portion of most Lituitidae is relatively small in comparison with the associated adoral orthocone. An extreme is encountered in the lituitid genus *Rhynchorthoceras*, in which the entire conch is straight, except for the weakly cyrtconic apical portion (Fig. 267,2). With the possible exception of typical *Wichitoceras*, even the most tightly coiled forms are believed to possess a narrow umbilical perforation.

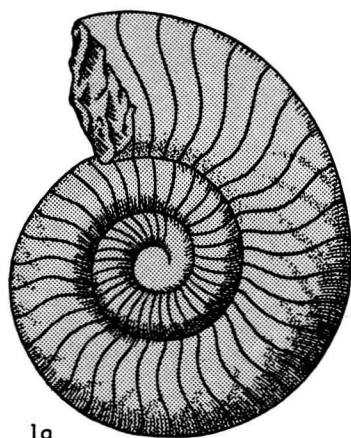
Morphological changes in late growth stages comprise whorl divergence and modification of the aperture. Divergence of the whorl for a short distance, but at an obtuse angle, and apertural contraction at full maturity are involved in formation of the subterminal aperture (Fig. 251,1). This feature is reported in the literature only for the tarphyceratid genera *Moreauoceras* and *Pilotoceras*; however, it is known to be developed in the trocholitid *Graftonoceras* and may be fairly common in other Tarphyceratidae and Trocholitidae. The body chamber of most Tarphyceratidae, Estonioceratidae, and Trocholitidae is approximately one-half a volution in length; many representatives of these families exhibit divergence of most or all of the mature body chamber, although the extent of divergence is not constant within a genus. A somewhat longer and more strongly divergent body chamber characterizes the Ophidioceratidae. It is noteworthy that the length of the mature body chamber may exceed an entire volution in the Ophidioceratidae and in some Trocholitidae (e.g., *Hardmanoceras*).

Representatives of the Lituitidae characteristically consist of a relatively small adapical spiral portion and a weakly sigmoid to straight adoral orthocone. The mature orthocone of the typical genus may exceed 300 mm. in length and the accom-

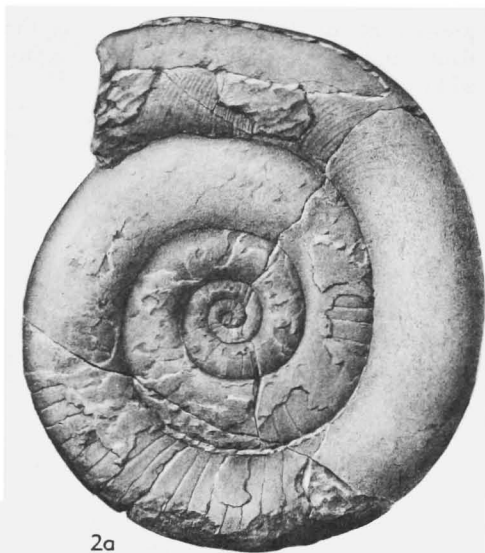
panying spiral portion may have a maximum diameter of only 20 mm. (Fig. 266, 1a).

Practically all adequately known Tarphycerida developed some degree of modification of the fully mature aperture. In the Tarphyceratidae, Estonioceratidae, and Trocholitidae, the outlines of the mature aperture are subparallel to those of earlier ontogenetic stages and form a deep, rounded hyponomic sinus and lateral salients. Modification at full maturity in representatives of these families consists of slight subterminal whorl constriction and weak terminal flare. Immature Ophidioceratidae resemble all other tarphycerids, except some lituitids, in the simple form of the aperture. However, the growth lines of the terminal few millimeters of the fully mature ophidioceratid body chamber diverge to form a pronounced pair of dorsolateral ocular sinuses and a narrow lingulate dorsal salient in association with the hyponomic sinus (Fig. 269). The form of the growth lines in the Lituitidae varies markedly during ontogeny of individual specimens and within the family as a whole, but serves as an important basis for generic distinction. The characteristic tarphycerid hyponomic sinus is commonly associated with sinuous growth lines in immature lituitids. However, the configuration of the aperture changed rapidly at maturity. Fully mature representatives of *Lituites* possess two pairs of prominent lappets in conjunction with a dorsal salient and hyponomic and ocular sinuses (Fig. 266, 1d-f). As in the Ophidioceratidae, the apertural crenulations may become conspicuous only near the terminal portion of the mature conch. Other lituitid genera are characterized by variable but simpler apertures.

The tarphycerid whorl cross section is variable for the order as a whole but is moderately stable for a given family and provides one basis for familial definition. Even in the upper Canadian, the whorl sections vary from strongly compressed to moderately depressed. The compressed whorl section of the Estonioceratidae is generally associated with rounded to flat dorsal whorl outline and loose coiling. Equidimensional whorl sections and slight to moderate dorsal impression characterize the Tarphycera-



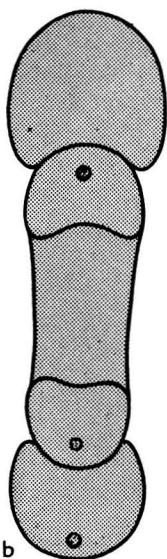
1a



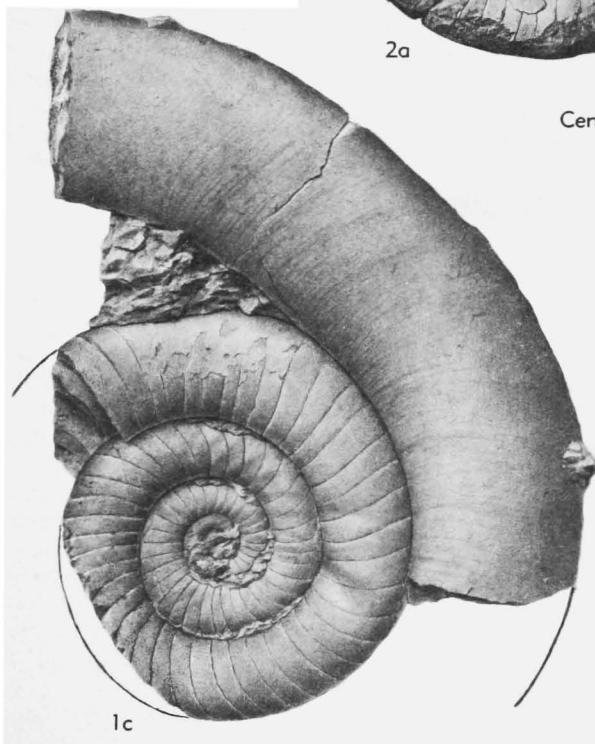
2a

Tarphyceras

Centrotarphyceras



1b



1c



2b

FIG. 249. Tarphyceratidae (p. K354-K355).

tidae, whereas the whorls of the Trocholiti-  
dae are depressed and moderately im-  
pressed. Greater variation is encountered  
in the Lituitidae and Ophidioceratidae.  
However, the lituitid spiral is generally  
compressed and rounded to weakly im-  
pressed dorsally, whereas the adoral ortho-

cone is more nearly circular in section, al-  
though commonly compressed.

Tarphycerid septa appear to maintain a  
constant radius of curvature, so that the  
form of the suture is simply a reflection of  
whorl cross section. Forms with circular  
section possess straight sutures, whereas im-

pression of the dorsum or flattening of the flanks and venter produced shallow rounded lobes.

Position of the siphuncle varied during ontogeny, but it is used as a basis for generic and even familial distinction. All Tarphycerida possess a subventral siphuncle in the first few camerae, but migration during ontogeny resulted in situation of the mature siphuncle in any axial position between the dorsal and ventral shell margins. The Tarphyceratidae and Estonioceratidae are characterized by ventral position of the mature siphuncle, the Trocholitidae by dorsal position, and the Lituitidae and Ophidioceratidae by a subcentral siphuncle.

Orthochoanitic septal necks are apparently common to all Tarphycerida. Adequately known Canadian forms possess thick, layered connecting rings similar to those of the Ellesmerocerida. Layering of the connecting ring is probably common to later Ordovician representatives, although the connecting rings of the lituitids are thinner than those of typical Tarphycerida. The Ophidioceratidae of the Silurian appear to differ from other Tarphycerida in the possession of thin connecting rings in which no evidence of layering has been observed.

It has been suggested (178) that part of the connecting ring in some Lituitidae was resorbed to allow access to the camerae for the siphuncular tissues. Confirmation of the primary nature of such observed features must await further documentation, as must the reported presence of endosiphuncular deposits (178, 203) (Fig. 13, A-C).

The periphraet, or area of muscle attachment at the base of the fully mature body chambers has been documented for some forms (143, 178) (Fig. 13); such features have not been observed for most tarphycerid taxa. The expanded portion of the periphraet is located on the ventral side of the conch in those tarphyceratids and trocholitids in which it has been observed. However, this area of supposed retractor attachment is dorsally situated in the lituitids.

Preservation of most recorded Lower Ordovician Tarphycerida precludes detailed studies of internal structures. However, possible cameral deposits have been reported (203) in a few well-preserved representatives of the Tarphyceratidae (*Campbello-*

*ceras*, *Centrotarphyceras*) and the Trocholitidae (*Curtoceras*). Interpretation of these deposits as being of primary origin is supported by a degree of regularity in progressive development and symmetry. However, the deposits completely sheathe the connecting ring in some examples, thus posing the problem of supply for the cameral mantle. Confirmation of the primary nature of these deposits must thus await availability of additional information.

Voluminous cameral deposits of a generalized type (Fig. 266, 1b), but with some unique features, are known for the lituitid genera *Lituities*, *Ancistroceras*, and *Rhynchorthoceras* (HOLM, 1885; REMELÉ, 1890; SCHINDEWOLF, 1942; SWEET, 1958). As with cameral deposits in other nautiloids, those of the Lituitidae formed progressively from the apical end of the conch. The ultimate few camerae of the orthocone in some specimens may be devoid of primary deposits. These same specimens exhibit a fairly regular adapical increase in the proportion of the camerae filled by deposits, so that the adapical camerae of the orthocone and those of the spiral portion of the conch are almost completely filled. Episeptal and hyposeptal deposits were secreted; the two types of deposit meet along a somewhat irregular truncated conical surface, the pseudoseptum. Both types of deposit are continuous ventrally and laterally in any single camera but do not meet dorsally, where they leave a wedge-shaped hiatus. Discrete laminated deposits have been observed within this dorsal hiatus, forming the "vertical lamella" or "dorsal wall," but their primary nature has not been established beyond doubt. Laminae of the dorsal wall may be traced ventrally around the outer margins of the siphuncle and into the endosiphuncle, through ventral perforations in the connecting ring. Again, it is uncertain whether the endosiphuncular deposits and the perforations of the connecting ring are primary structures.

## CLASSIFICATION AND PHYLOGENY

The Tarphycerida appear to be a closely related relatively unspecialized group of cephalopods. A single distinguishing char-

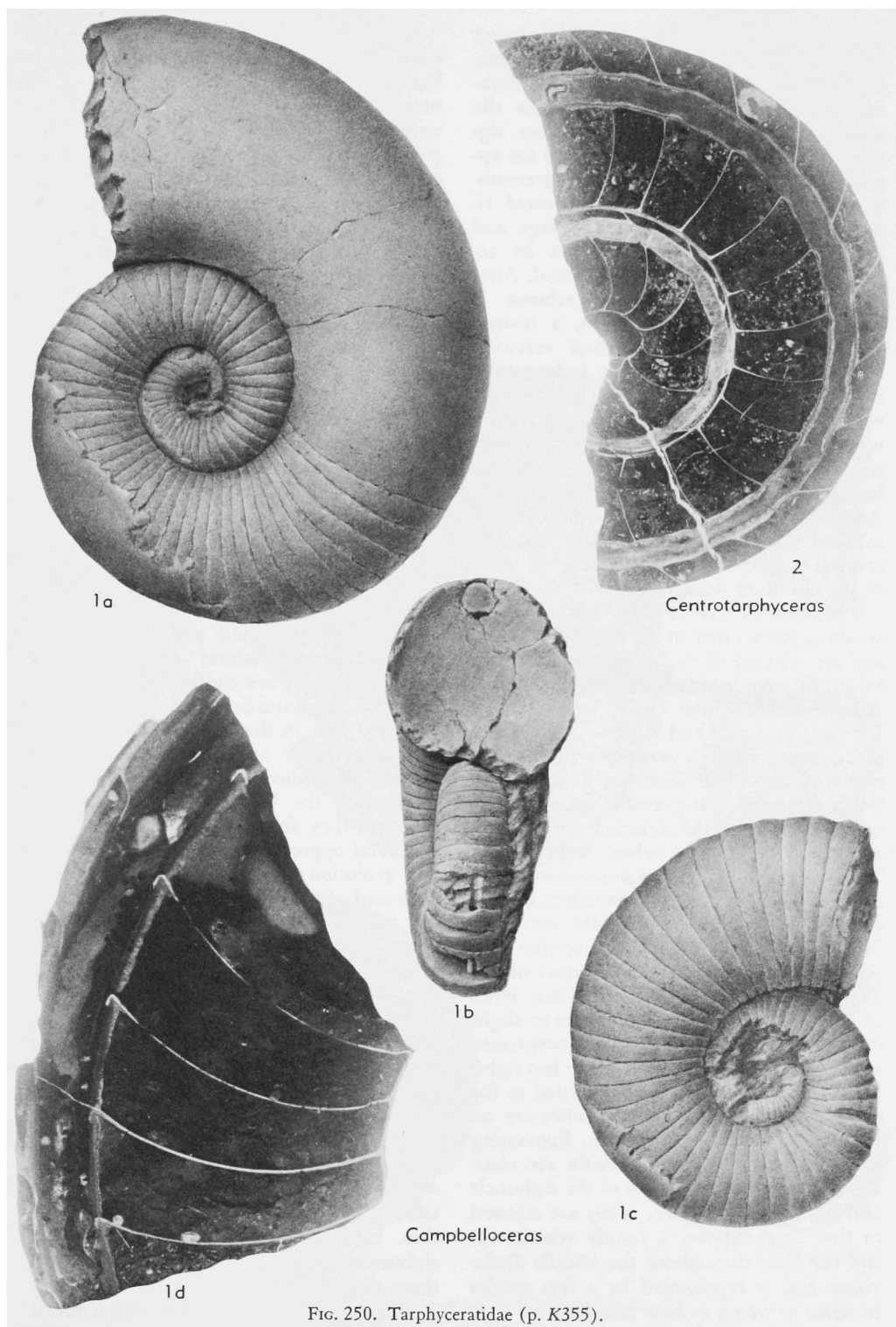


FIG. 250. Tarphyceratidae (p. K355).

acteristic, the spiral conch, is an adaptation which separates the order from its ancestors. Cyrtconic members of the Bassleroceratidae (Ellesmerocerida) anticipate the closed tarphycerid coil, and no other significant changes in shell morphology are apparent in the early transitional representatives. The relatively large tarphycerid siphuncle, with thick connecting rings and orthochoanitic septal necks, must be regarded as primitive and conventional. Also, the intraordinal classification scheme is based primarily on shell form, a feature which involves no fundamental variation from the prototype. In like fashion, the only direct descendants of the early Ordovician tarphycerids, in addition to stocks within the order, were probably the very similar Barrandeocerida, an important faunal element of the Middle Ordovician. Apparently none of the later tarphycerids in the Trocholitidae, Lituitidae, or Ophidioceratidae contributed to further evolution in the nautiloid lineage.

The ancestral Lower Ordovician Tarphycerida appeared first in the upper Canadian and are referred to the families Tarphyceratidae, Estonioceratidae, and Trocholitidae. All are closely similar in the general coiled form of the conch and possession of a simple aperture, characterized by a deep hyponomic sinus. Subdivision into families and lower taxonomic categories is based largely on the position of the siphuncle at maturity and the form of the whorl section. The Tarphyceratidae and Estonioceratidae are distinguished by ventral situation of the siphuncle. Differentiation of the two families is by reference to whorl section and tightness of coiling. Representatives of the Tarphyceratidae commonly possess equidimensional whorls with moderate to slight dorsal impression, whereas the compressed whorls of the Estonioceratidae are less tightly coiled and thus exhibit a rounded to flat dorsal whorl section. Both families are restricted to the upper Canadian. Remaining Lower Ordovician Tarphycerida are characterized by dorsal position of the siphuncle and by impressed whorls. They are referred to the Trocholitidae, a family which was still common throughout the Middle Ordovician and is represented by a few species in strata as young as Late Silurian.

Derivation of the coiled Tarphycerida from the cyrtconic ellesmerocerid family Bassleroceratidae is indicated by close morphological similarity; although the early tarphycerids were approximate contemporaries of the upper Canadian bassleroceratids. Ancestry from the Bassleroceratidae through the Estonioceratidae can be considered as established. Both families are characterized by rounded, compressed whorl sections, simple septa, ventral submarginal siphuncle, and thick, layered connecting rings. Evolution of the estonioceratids involved only the modification of the exogastric bassleroceratid cyrtcone into the loosely coiled tarphycerid spiral. Tighter coiling in turn produced the equidimensional dorsally impressed whorls of the Tarphyceratidae, whereas migration of the siphuncle to a dorsal position yielded the Trocholitidae.

Representatives of the Lituitidae exhibit greater variability in gross form of the conch and configuration of the aperture, but most are characterized by possession of an adapical spiral portion and a straight to slightly sigmoid adoral orthocone. Undoubted lituitids are confined to the Ordovician of the Balto-Scandian Region. They appeared first in the late Early Ordovician Arenigian Stage and are characteristic of the Middle Ordovician. Lituitids also range throughout the Upper Ordovician (178), although they are rare in that series.

Several opposing views on the derivation and evolution of the Lituitidae have been presented. SCHINDEWOLF (1942) suggested that the lituitid spiral developed by proterogenesis in an orthocerid ancestor. FLOWER (41, 49) initially placed the family in the coiled Barrandeocerida and indicated derivation from the Barrandeoceratidae. He later (44) expressed the belief that the Lituitidae evolved from the Tarphyceratidae. Thorough evaluation of existing and new information by SWEET (178) finally demonstrated that the lituitids must have evolved from either the Trocholitidae or the Tarphyceratidae. As in the case of the Estonioceratidae, stratigraphic evidence is inconclusive. However, details of the lituitid ectosiphuncle are practically identical with those of typical tarphycerids, as is the gross form of the lituitid spiral. The characteristic

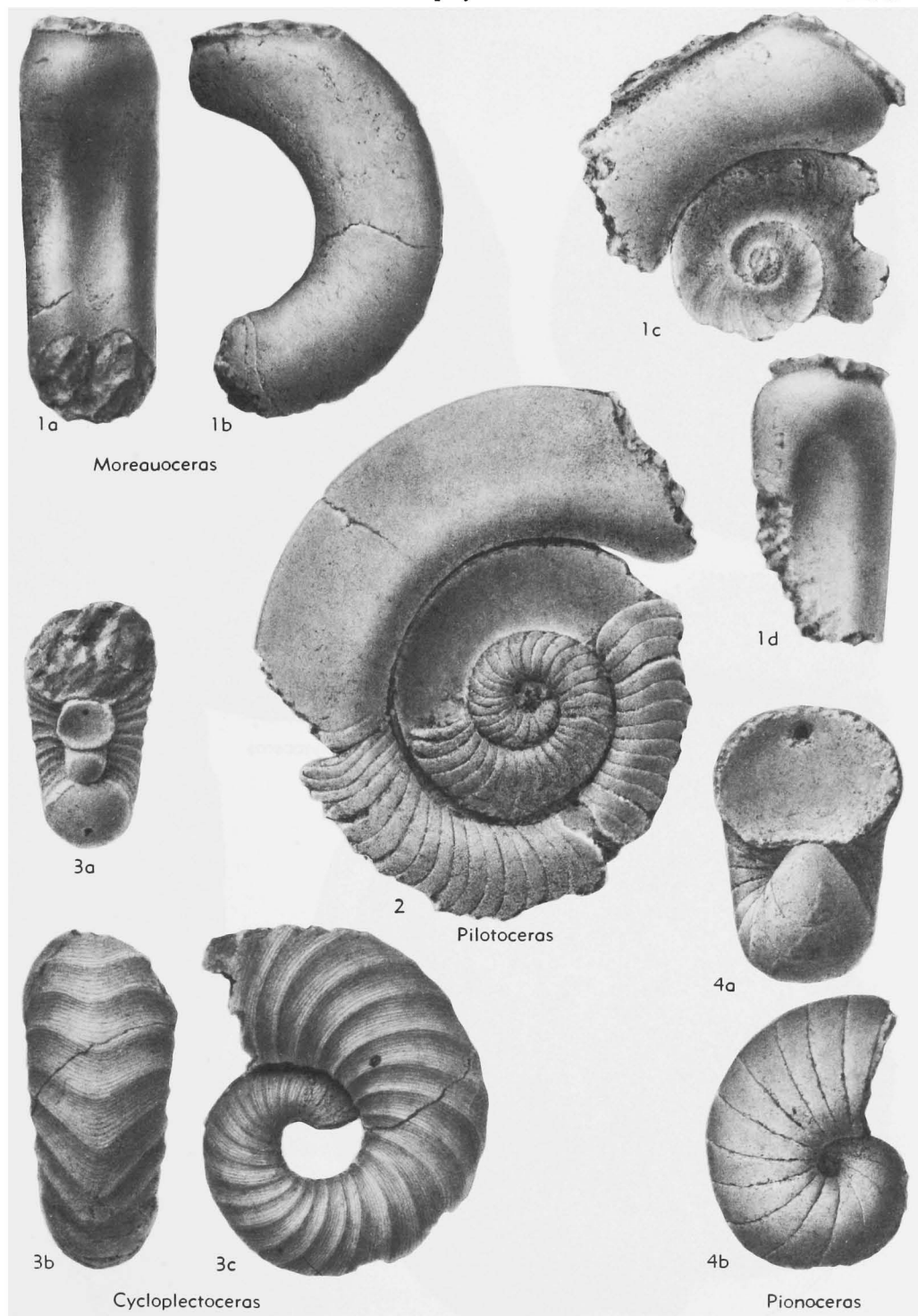


FIG. 251. *Tarphyceratidae* (p. K355, K357).



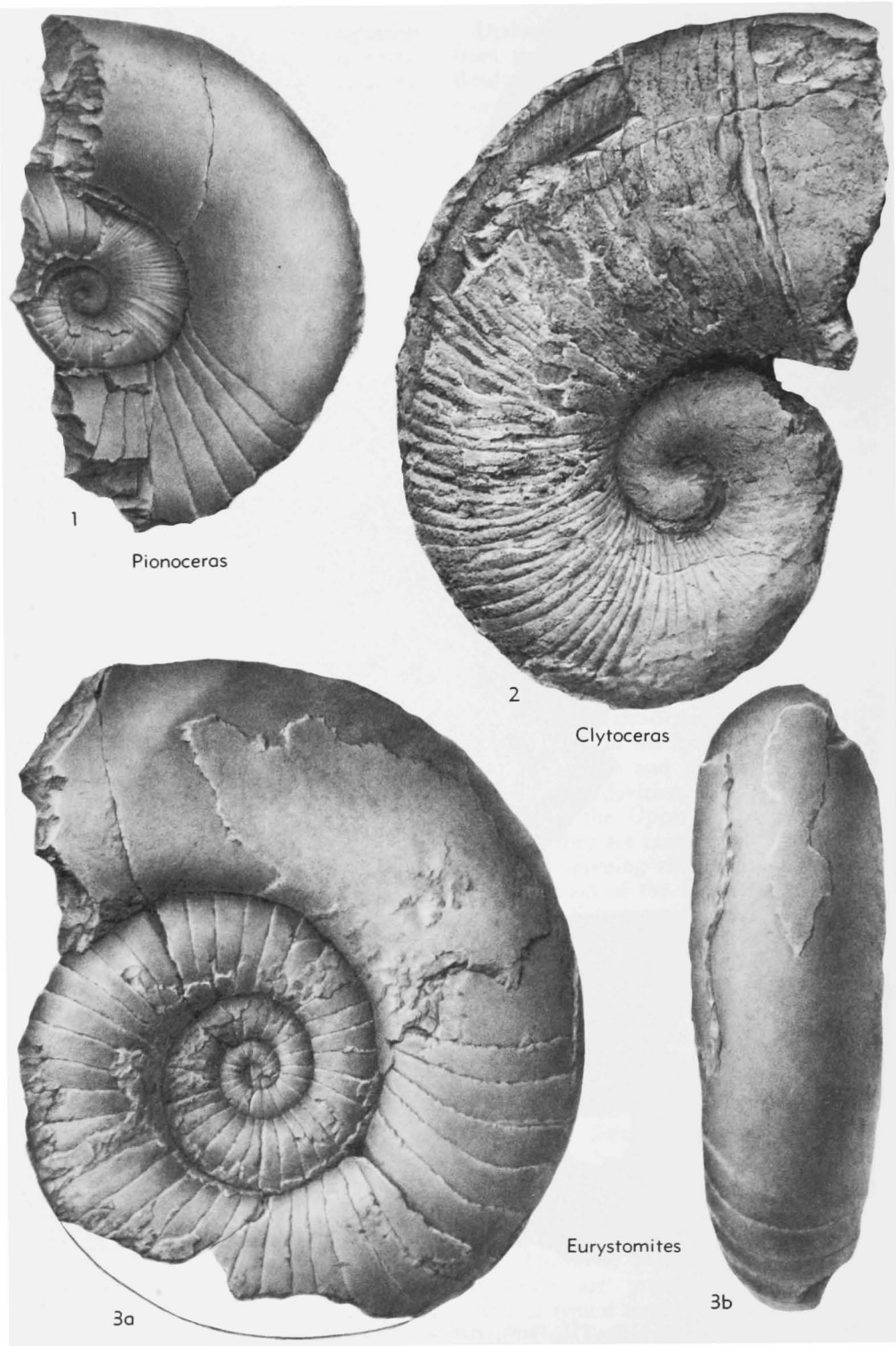


FIG. 252. Tarphyceratidae (p. K355, K357); Estonioceratidae (p. K358-K359).



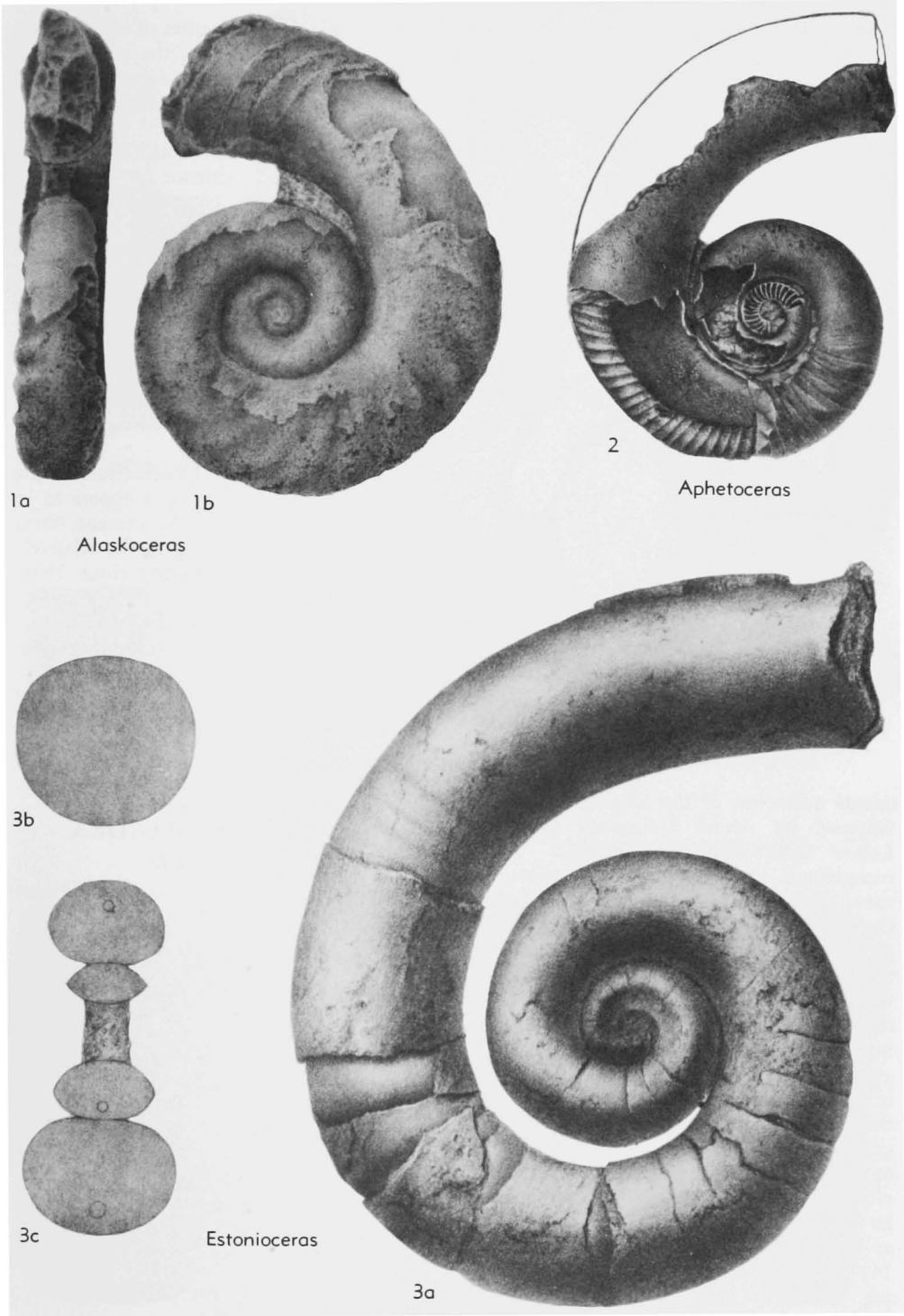


FIG. 253. Estonioceratidae (p. K357-K358).

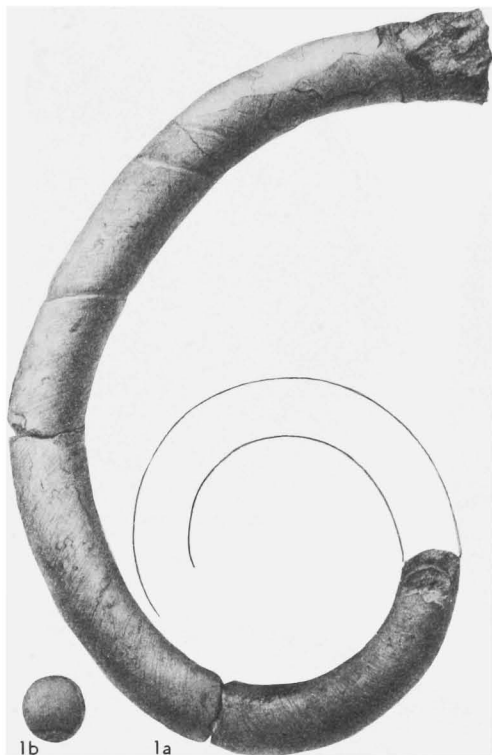


FIG. 254. \**Tragoceras falcatum* (VON SCHLOTHEIM)  
(Estonioceratidae) (p. K359).

adoral orthocone of the Lituitidae was anticipated by whorl divergence of many Lower Ordovician Tarphycerida. Other conspicuous morphological differences between the Lituitidae and ancestral Lower Ordovician tarphycerids comprise the complex lituitid aperture, the dorsal loci of retractor muscles, and the development of voluminous cameral deposits in some lituitid species. Extreme ontogenetic modification in the form of the growth lines is apparent in lituitids, and no single pattern is common to the family. Consequently, the complex nature of the apertural margin should not be considered as an indication of a basic biologic difference. Characteristically, the loci of retractor muscle attachment in the Tarphycerida are in ventral position, as in most other evolute coiled shells (Fig. 14) (143). However, those nautiloids which are essentially straight at maturity generally possess dorsal attachment loci. Consequently, it is logical to conclude (178) that these apparent differences within the

Tarphycerida are a function of conch form and living habits. Again, the cameral deposits of lituitids simply represent a response to the problem of equilibrium, posed by modification of the lituitid conch away from the ancestral tarphycerid form.

Despite the clear evidence for lituitid ancestry, evolutionary patterns within the family are not readily apparent. This stems, at least in part, from the relative rarity of available materials and the absence of detailed stratigraphic information for many taxa. SWEET (178) has suggested that the group exhibits considerable plasticity in gross form, even at the specific level, and that evolutionary trends can be established more readily by reference to ontogeny of the aperture.

Relationships of the Ophidioceratidae are uncertain, but closest affinities appear to be with the Tarphycerida. At present, there is no indication of layering in the relatively thin ophidioceratid connecting rings. However, general conch form is closely similar to that of some Trocholitidae, and derivation from this Ordovician family seems probable. Similarity of the modified fully mature ophidioceratid aperture to that of some lituitids is considered homeomorphic.

## SYSTEMATIC DESCRIPTIONS

### Subclass NAUTILOIDEA Agassiz, 1847

Diagnosis given in "Introductory Discussions" (p. K128). *U.Cam.-Rec.*

### Order TARPHYCERIDA Flower in Flower & Kummel, 1950

[*nom. correct.* FURNISH & GLENISTER, herein (*pro Tarphyceratida* FLOWER in FLOWER & KUMMEL, 1950, p. 615, order)]  
[=Tarphyceratina SWEET, 1958, p. 92 (suborder); mention of Tarphycerida by FURNISH, GLENISTER, & HANSMAN, 1962 (p. 1342), is disregarded]

Coiled conchs with varying degrees of adoral divergence; septa simple, siphuncle unstable in position; septal necks orthochoanitic, connecting rings layered; aperture characterized by prominent hyponomic sinus; fully mature aperture commonly modified. *L.Ord.-U.Sil.*

### Family TARPHYCERATIDAE Hyatt, 1894

[Tarphyceratidae HYATT, 1894, p. 433]

Smooth or ribbed conchs with slight to

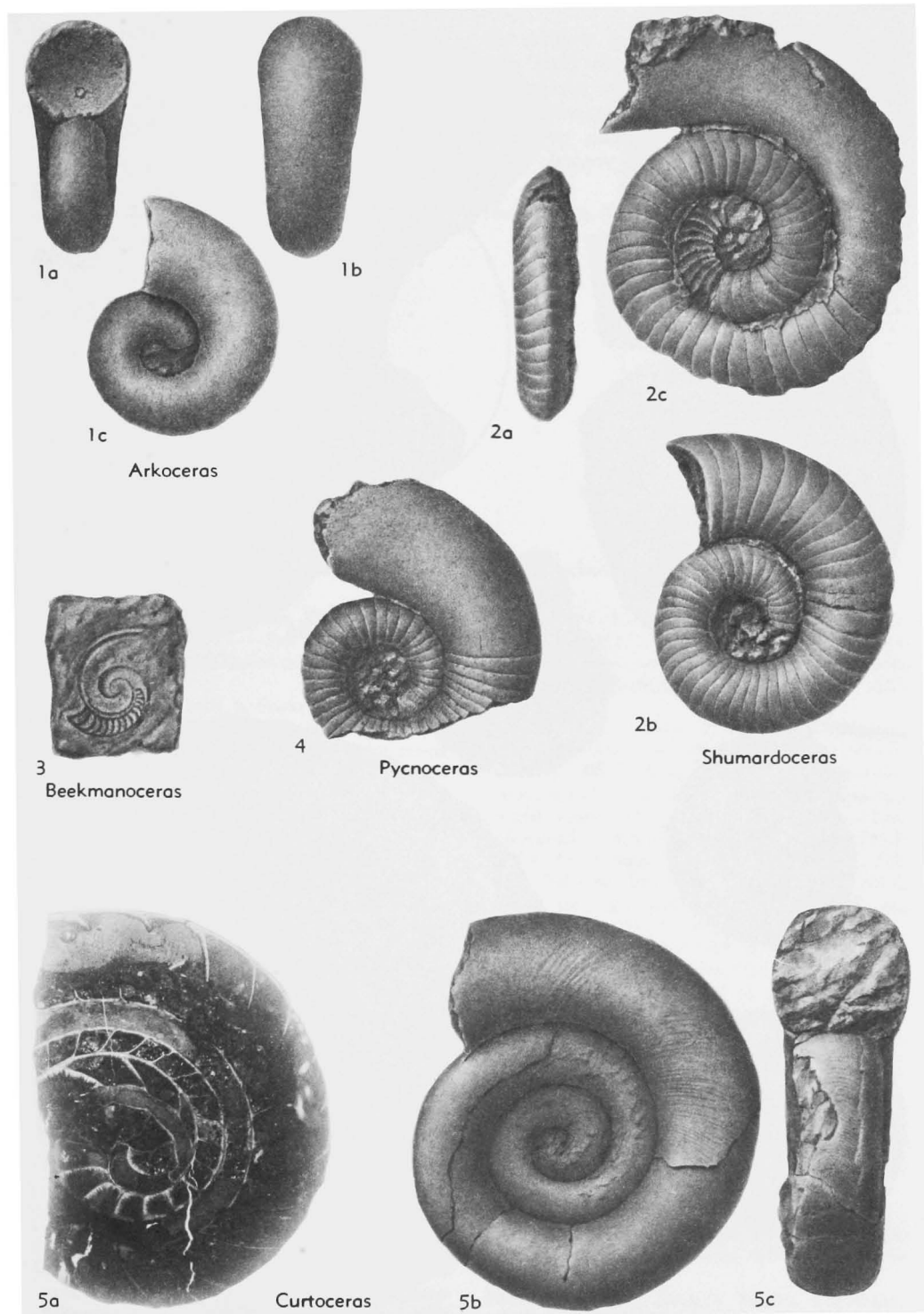


FIG. 255. Estonioceratidae (p. K359); Trocholitidae (p. K360).

moderate dorsal impression of whorls; ad-oral portion generally divergent from preceding volution in fully mature specimens; growth lines forming broadly rounded deep hyponomic sinus; whorl section generally equidimensional; siphuncle ventral, submarginal to subcentral. *L.Ord.*

**Tarphyceras** HYATT, 1894, p. 433 [*\*T. prematurum*;

OD] [=?*Remeleceras* HYATT, 1894, p. 525; *Remeleoceras* HYATT in ZITTEL, 1900, p. 526 (*nom. van.*)]. Rate of expansion moderate; whorls rounded ventrally and laterally, deeply impressed (1/5) dorsally, siphuncle ventral to subcentral. *L.Ord.*(*U.Canad.*), N.Am.(wide-spread).—FIG. 249, *1a,b*. *T. aucoini* HYATT, Can.(Newf.); syntypes, lat., cross sec.,  $\times 1.3$  (96).—FIG. 249, *1c*. *T. chadwickense* ULRICH,

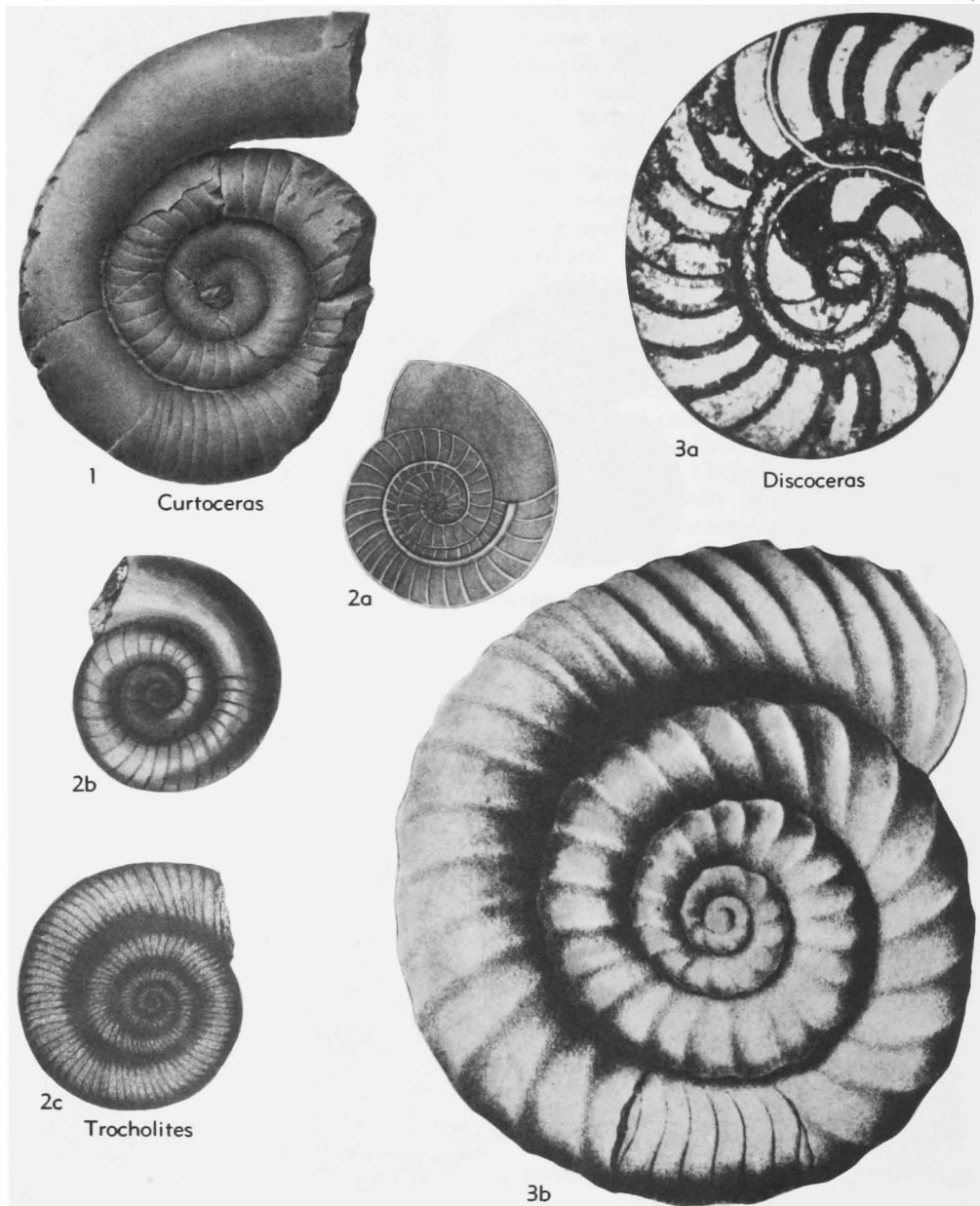


FIG. 256. Trocholitidae (p. K359-K360).

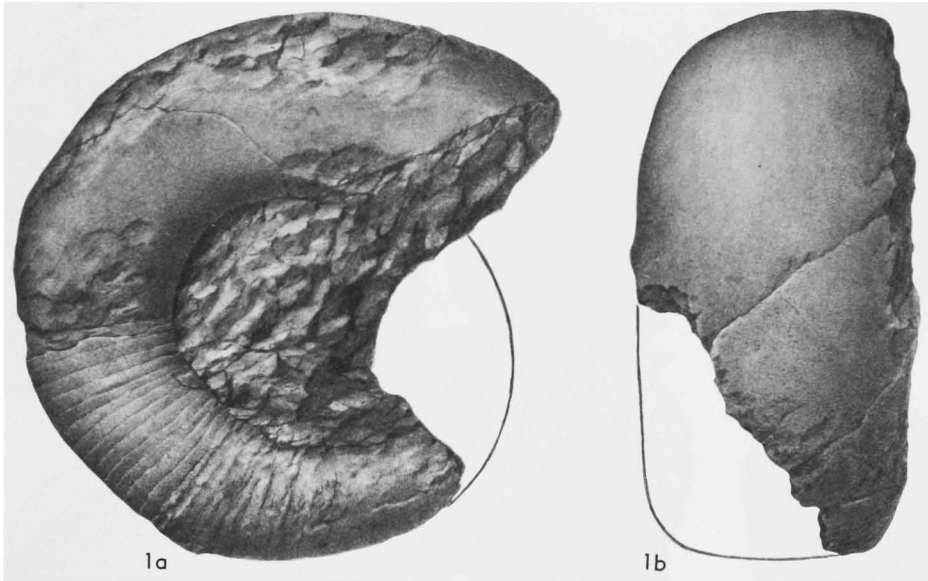


FIG. 257. \**Litoceras versutum* (BILLINGS) (Trocholitidae) (p. K361).

FOERSTE, MILLER & FURNISH, USA(Mo.); holotype, lat.,  $\times 0.8$  (203).—FIG. 262,2. \**T. prematurum*, Can.(Newf.); holotype, whorl sec.,  $\times 2$  (203).

**Campbelloceras** ULRICH & FOERSTE, 1936, p. 265 [*Eurystomites Virginiana* HYATT, 1894, p. 444; OD]. Whorl section circular, slightly impressed; siphuncle close to venter at all growth stages. Differs from *Tarphyceras* in more rapid expansion, shallower impressed zone, and proportionally larger submarginal siphuncle. *L.Ord.*(*U. Canad.*), N.Am. (widespread).—FIG. 250,1; 262,4. \**C. virginianum* (HYATT), USA(Va.); 250,1a-c, holotype and hypotype, lat., apert. and lat. views,  $\times 1$ ; 262,4, holotype, whorl sec.,  $\times 1.3$  (203).—FIG. 250,1d; 265,4. *C. rotundum* (HYATT), USA(Vt.); thin sec.; diagram of 250,1d; both  $\times 5$  (203).

**Centrotarphyceras** ULRICH & FOERSTE, 1936, p. 267 [*Lituites Seelyi* WHITFIELD, 1886, p. 330; OD]. Like *Tarphyceras*, but more gradually expanded, and mature siphuncle subcentral; typically with flattened venter and flanks. *L.Ord.*(*U. Canad.*), N. Am.(widespread).—FIG. 249,2; 250,2; 262,3; 265,1. \**C. seelyi* (WHITFIELD), USA(Vt.); 249,2a,b, syntype and topotype, lat., septal views,  $\times 0.5$ ,  $\times 0.7$ ; 262,3, whorl sec. (same as 249,2b),  $\times 1.3$ ; 250,2, 265,1, thin sec.; diagram of 250,2,  $\times 5$ ,  $\times 11$  (203).

**Cycloplectoceras** ULRICH, FOERSTE, MILLER & FURNISH, 1942, p. 33 [*C. miseri*, OD]. Like *Campbelloceras* in gross form, whorl section, and position of siphuncle, but characterized by pronounced

ribs. *L.Ord.*(*U. Canad.*), USA(widespread).—FIG. 251,3; 262,7. \**C. miseri*, USA(Ark.); 251,3a, paratype, septal view; 251,3b,c, holotype, ventral, lat. views;  $\times 3$ ; 262,7, holotype, whorl sec.,  $\times 2.5$  (203).

**Eurystomites** SCHRÖDER, 1891, p. 26 [*Nautilus Kelloggi* WHITFIELD, 1886, p. 328; SM HYATT, 1894, p. 441]. Closely similar to *Centrotarphyceras*, especially in whorl section, but siphuncle nearer venter and expansion more rapid. *L.Ord.*(*U. Canad.*), N.Am.(widespread).—FIG. 252,3; 262,5. \**E. kelloggi* (WHITFIELD), USA(Vt.); 252,3a,b, holotype, lat., ventral views,  $\times 0.7$ ; 262,5, whorl sec.,  $\times 1$  (203).—FIG. 264,2. *E. sp.*, USA(Okla.); thin sec.,  $\times 5$  (203).

**Moreauceras** CULLISON, 1944, p. 68 [*M. milleri*; OD]. Like *Campbelloceras*, but more gradually expanded and characterized by subterminal fully mature aperture. *L.Ord.*(*U. Canad.*), USA(Mo.).—FIG. 251,1. \**M. milleri*; 1a,b, fully mature body chamber, dorsal, lat. views,  $\times 3$ ; 1c,d, holotype, lat., dorsal views,  $\times 3$  (226a).

**Pilotoceras** CULLISON, 1944, p. 68 [*P. brunei*; OD]. Gradually expanded; characterized by cordate mature whorl section with narrowly rounded venter, flat flanks, and slight but distinct dorsal impression; siphuncle subventral. Like *Shumardoceras*, but impressed. [Based on single specimen.] *L.Ord.*(*U. Canad.*), USA(Mo.).—FIG. 251,2; 262,6. \**P. brunei*; holotype, lat. view, whorl sec., both  $\times 3$  (226a).

**Pionoceras** ULRICH, FOERSTE, MILLER & FURNISH, 1942, p. 64 [*Nautilus Pomponius* BILLINGS, 1862, p. 26; OD]. Moderately rapidly expanded conchs

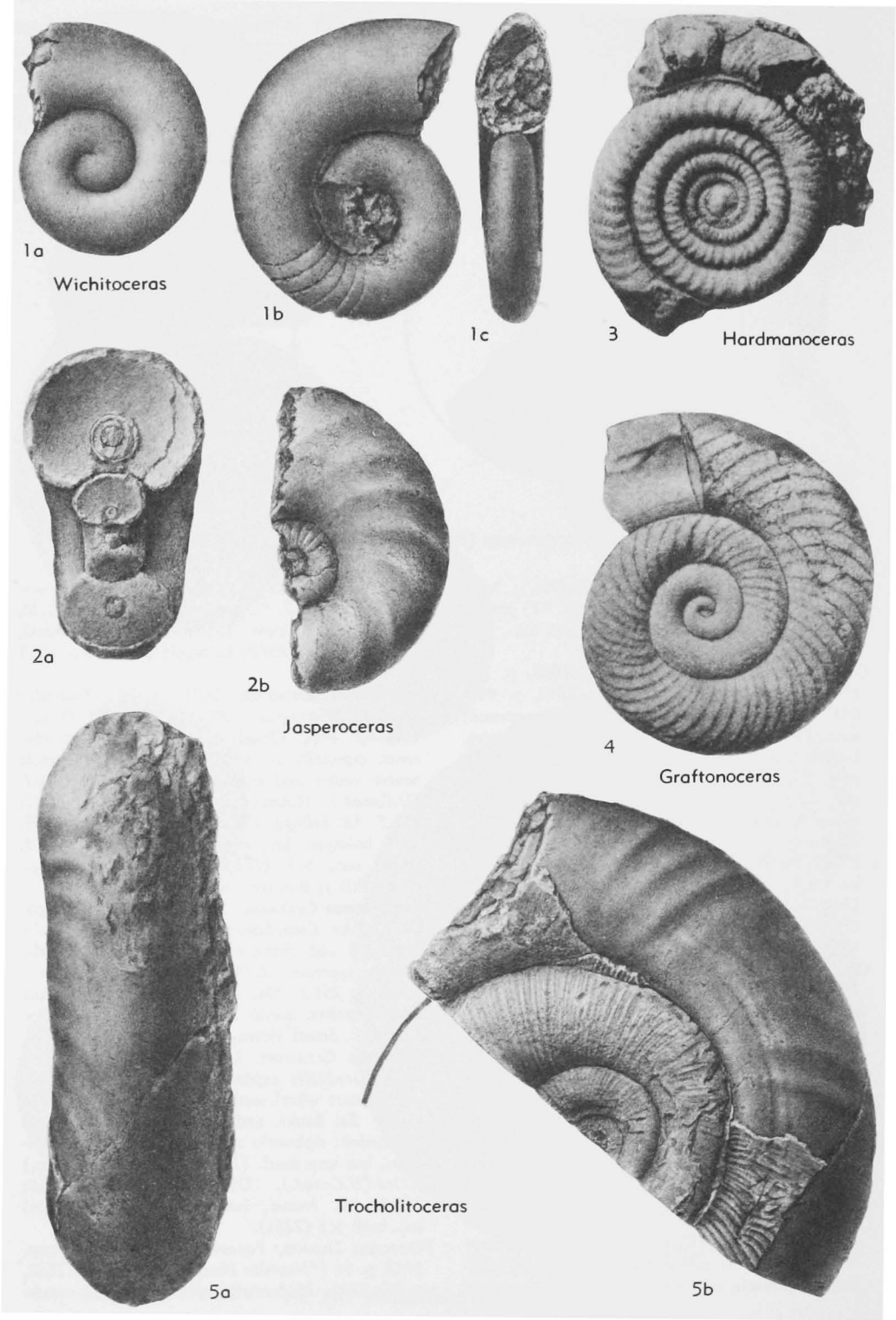


FIG. 258. Trocholitidae (p. K360-K362).

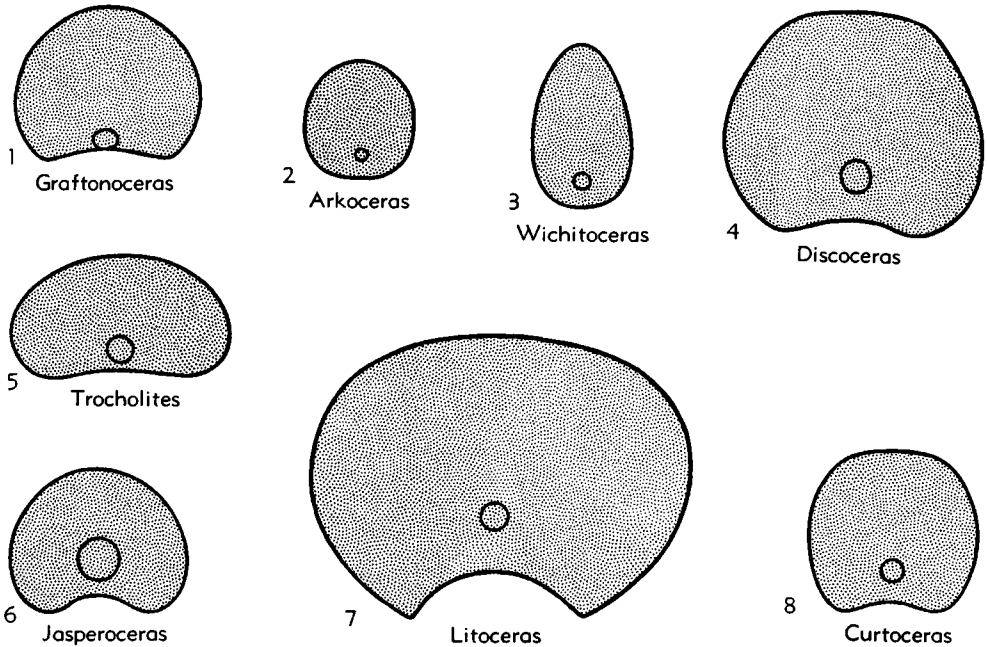


FIG. 259. Trocholitidae (p. K359-K362).

characterized by depressed subtrapezoidal whorls; siphuncle subventral. *L.Ord.*(*U.Canad.*), N.Am. (widespread).—FIG. 252,1; 262,1. \**P. pomponius* (BILLINGS), Can.(Que.); 252,1, lat. view,  $\times 0.7$ ; 262,1, neoholotype, whorl sec.,  $\times 1$ .—FIG. 251,4. *P. smithvillense* ULRICH, FOERSTE, MILLER & FURNISH, USA(Ark.); 4a,b, syntype, septal and lat. views,  $\times 2.5$  (203).

**Seelyoceras** ULRICH & FOERSTE, 1936, p. 286 [*\*Cyrtoeras Raei* WHITFIELD, 1889, p. 58; OD]. Depressed, annulate, strongly curved nautiloids with ventral marginal siphuncle. [Affinities uncertain; based on single fragment.] *L.Ord.*(*U.Canad.*), USA(N.Y.).

### Family ESTONIOCERATIDAE Hyatt in Zittel, 1900

[Estonioceratidae HYATT in ZITTEL, 1900, p. 526] [=Deltoceratidae ULRICH, FOERSTE, MILLER, & FURNISH, 1942, p. 14 (partim)]

Smooth or ribbed conchs characterized by loose coiling and divergence at full maturity; growth lines form broad, deep hyponomic sinus; whorls generally compressed, but broadly rounded to flat dorsally; siphuncle ventral, generally submarginal. Similar to Tarphyceratidae, but more loosely coiled and lacking dorsal impression. *L.Ord.*

**Estonioceras** NOETLING, 1883, p. 275 [*\*Lituites lamellosus* HISINGER, 1837, p. 27; OD] [=*Fal-*

*cilitites* REMELÉ, 1886, p. 467 (type, *Lituites Decheni* REMELÉ, 1880, p. 233; OD)]. Early volutions in contact, with depressed fusiform whorl section; ultimate volution divergent, mod-

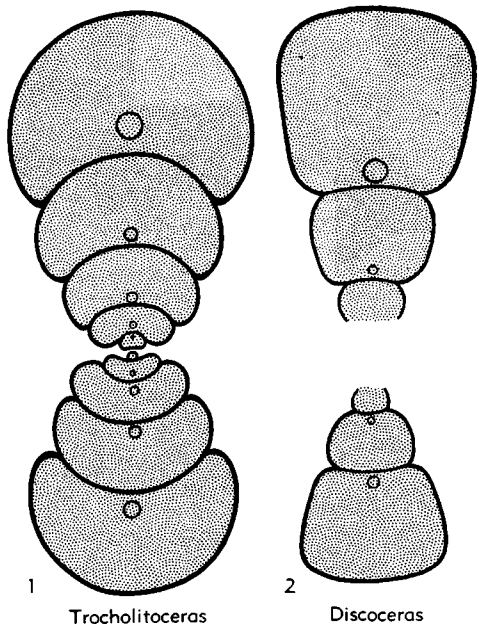


FIG. 260. Trocholitidae (p. K360-K361).



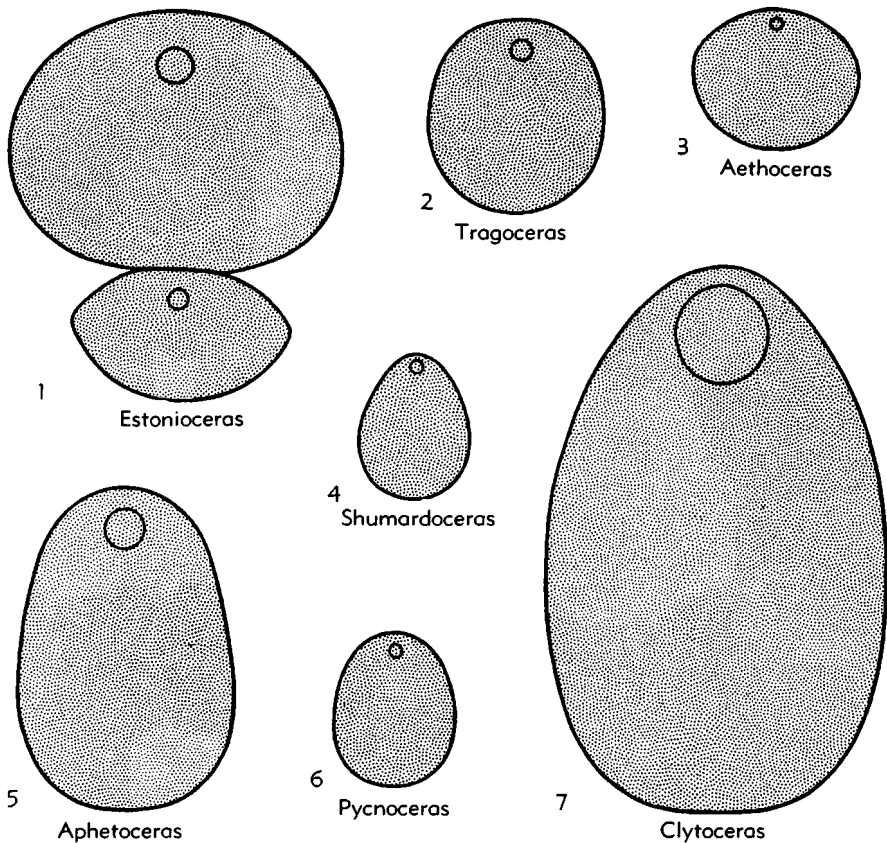


FIG. 261. Estonioceratidae (p. K357-K359).

erately depressed, rounded; siphuncle subventral to subcentral. *L.Ord.*(*Arenig.*), Eu.(Balto-Scandia).—FIG. 253,3; 261,1. *E. ariense* (SCHMIDT); 253,3a-c, lat. view and cross secs. of body chamber and phragmocone,  $\times 0.7$ ; 261,1, whorl secs.,  $\times 1.3$  (160a).

**Aethoceras** TEICHERT & GLENISTER, 1954, p. 227 [*\*A. caurus*; OD] [= *Aetoceras* BALASHOV, 1962, p. 78]. Gradually expanded, loosely coiled, low-spired, dextral torticones; whorls slightly depressed, subcircular in section; siphuncle ventral, submarginal; ribs attenuate as delicate flanges, with length approximating radius of whorl section. Coiling unique for Tarphycerida, comparable flanges unknown in other Ordovician nautiloids. [Based on single specimen; affinities uncertain.] *L.Ord.*(*U.Canad.*), W.Australia.—FIG. 261,3. *\*A. caurus*; holotype, whorl sec.,  $\times 3.5$  (193).

**Alaskoceras** MILLER & KUMMEL, 1945, p. 126 [*\*Plectoceras* *sewardense* FLOWER, 1941, p. 32; OD]. Moderately expanded, ribbed, with divergent mature body chamber; whorl section slightly compressed, broadly rounded ventrally, more nar-

rowly rounded dorsally; siphuncle marginal at maturity; septal necks short, orthochoanitic, almost achoanitic; connecting rings thick, layered. ?*L.Ord.*, USA(Alaska).—FIG. 253,1. *\*A. sewardense* (FLOWER); 1a,b, holotype, apert. and lat. views,  $\times 0.7$  (226b).

**Aphetoceras** HYATT, 1894, p. 447 [*\*A. americanum*; SD ULRICH, FOERSTE, MILLER & FURNISH, 1942, p. 16]. Conch loosely coiled, gradually expanded, and commonly with weak ribs; early volutions in contact or nearly so, mature ultimate whorl widely divergent; whorl section compressed, oval; siphuncle subventral in all growth stages. *L.Ord.*(*U.Canad.*), N.Am.(widespread)-W.Australia.—FIG. 261,5. *\*A. americanum*, Can. (Newf.); holotype, whorl sec.,  $\times 1.3$  (203).—FIG. 253,2. *A. evolutum* ULRICH, FOERSTE, MILLER & FURNISH, USA(Mo.); holotype, lat. view,  $\times 1$  (203).—FIG. 265,2. *A. attenuatum* HYATT, Can.(Que.); diagram. sec.,  $\times 5$  (203).

**Clytoceras** ULRICH, FOERSTE, MILLER & FURNISH, 1942, p. 25 [*\*C. capax*; OD]. Conch rapidly expanded, strongly compressed, characterized by elliptical whorl section and large subventral si-



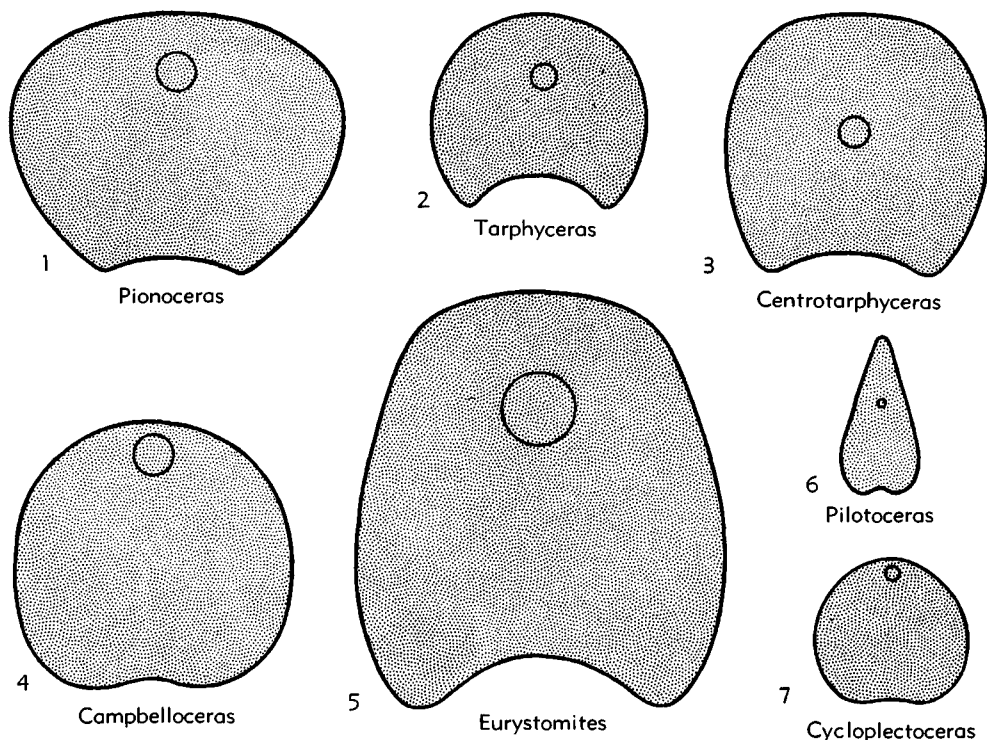


FIG. 262. Tarphyceratidae (p. K354-K355, K357).

phuncle. *L.Ord.(U.Canad.)*, USA(Ark.).—FIG. 252,2; 261,7. \**C. capax*; holotype, lat. view; whorl sec.;  $\times 0.7$ ,  $\times 1$  (203).

**Eichwaldoceras** BALASHOV, 1955, p. 45 [*\*E. volchovense*; OD]. Poorly known. Apparently like *Tragoceras*, but more rapidly expanded, and with marginal siphuncle. *L.Ord.(Arenig.)*, Eu.(Balto-Scandia).

**Pycnoceras** HYATT, 1894, p. 455 [*\*P. apertum*; OD] [= *Pyrenoceras* CRESPIN, 1960, p. 84 (*nom. null.*)]. Like *Campbelloceras*, but conch much smaller at full maturity, less rapidly expanded, and whorls flat or very slightly impressed dorsally. *L.Ord.(U.Canad.)*, N. Am.(widespread)-W.Australia.—FIG. 261,6. \**P. apertum*, Can.(Newf.); holotype, whorl sec.,  $\times 2.5$  (203).—FIG. 255,4. *P. rotundatum* ULRICH, FOERSTE, MILLER & FURNISH, USA(Mo.); syntype, lat. view,  $\times 1.5$  (203).

**Shumardoceras** ULRICH & FOERSTE, 1936, p. 288 [*\*Lituites complanata* SHUMARD, 1863, p. 107; OD]. Conch small, volutions in contact except for extreme adoral portion at full maturity; whorl section strongly compressed, characterized by flattened flanks and narrowly rounded to subangular venter; siphuncle subventral. *L.Ord.(U.Canad.)*, USA(Mo.).—FIG. 255,2; 261,4; 264,3. \**S. complanatum* (SHUMARD); 255,2a-c, ventral and lat. views,  $\times 3$ ; 261,4, whorl sec.,  $\times 3.5$ ; 264,3, lat. view, gerontic septa,  $\times 3$  (203).

**Tragoceras** REMELÉ, 1890, p. 35 [*\*Orthoceratites falcatus* VON SCHLOTHEIM, 1820, p. 53; M] [= *Aegoceras* REMELÉ, 1880, p. 244 (obj.) (*non* WAAGEN, 1869); *Planctoceras* SCHRÖDER, 1891, p. 41 (obj.)]. Like *Estonioceras*, but whorls compressed; similar to *Aphetoceras* and possibly synonymous. *L.Ord.(Arenig.)*, Eu.(Balto-Scandia).—FIG. 254,1; 261,2. \**T. falcatum* (VON SCHLOTHEIM); 254,1a,b, lat., septal views,  $\times 0.5$ ; 261,2, whorl sec.,  $\times 1.3$  (160a).

### Family TROCHOLITIDAE Chapman, 1857

[Trocholitidae CHAPMAN, 1857, p. 115] [*incl.* Beekmanoceratidae ULRICH, FOERSTE, & MILLER, 1943, p. 155; Trocholithidae LEONHARD & BRONN, 1858, p. 617 (*nom. null.*)]

Smooth to strongly ribbed conchs with whorls in contact except for divergence in part of fully mature body chamber; growth lines forming deep, broad hyponomic sinus; whorls generally depressed and moderately impressed dorsally; siphuncle dorsal, marginal to subcentral. Distinguished by combination of dorsal siphuncle and simple hyponomic sinus. *L.Ord.-U.Sil.*

**Trocholites** CONRAD, 1838, p. 118 [*\*T. ammonius*; OD] [= *Palaeonutilus* REMELÉ, 1880, p. 246 (type, *P. hospes* REMELÉ, 1880, p. 249; SD

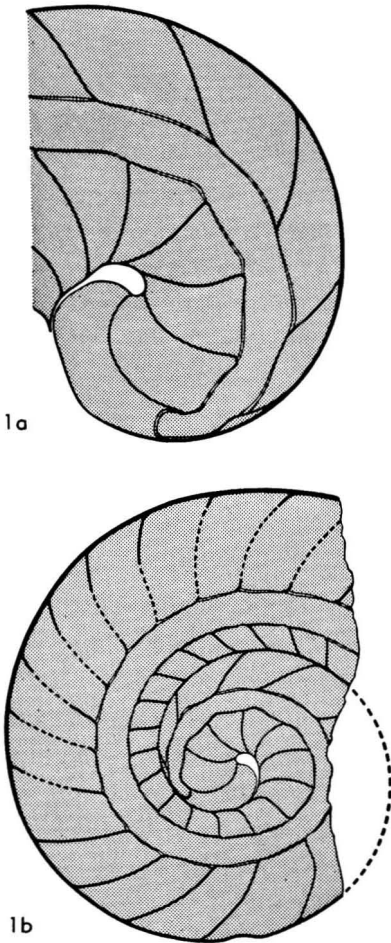


FIG. 263. \**Curtoceras eatoni* (WHITFIELD)  
(Trocholitidae) (p. K360).

FOERSTE, 1930, p. 285); *Palaeoclymenia* REMELÉ, 1881, p. 13 (type *Trocholites planorbiformis* CONRAD, 1842, p. 274; M); *Trocholithes* LEONHARD & BRONN, 1858, p. 617 (*nom. null.*). Conch gradually expanded, weakly ribbed; whorls strongly depressed, weakly impressed, rounded across venter and flanks; siphuncle subdorsal. *M.Ord.* (*Chazy.*) - *U.Ord.* (*Richmond.*), N. Am. (widespread) - Eu. (Balto-Scandia).—FIG. 256,2; 259,5. \**T. ammonius*, *M.Ord.* (Trenton.), USA (N.Y.); 256,2a-c, long. sec., and lat. views,  $\times 0.7$ ; 259,5, whorl sec.,  $\times 1.3$  (83).

**Arkoceras** ULRICH, FOERSTE, MILLER & FURNISH, 1942, p. 68 [\**A. exiguum*; OD] [= *Arcoceras* BALASHOV, 1962, p. 79 (*nom. null.*)]. Conch moderately rapidly expanded, with whorls in contact but not impressed dorsally; characterized by slightly compressed oval whorl section and sub-

dorsal siphuncle. Like *Curtoceras*, but whorls rounded dorsally. *L.Ord.* (*U.Canad.*), N. Am. (Ark.-Que.) - W. Australia. —FIG. 255,1; 259,2. \**A. exiguum*, USA (Ark.); 255,1a-c, syntypes, apert., ventral, lat. views,  $\times 3$ ; 259,2, whorl sec.,  $\times 2.5$  (203).

**Beckmanoceras** ULRICH & FOERSTE, 1936, p. 264 [\**Cyrtendoceras* (?) *priscum* RUEDEMANN, 1906, p. 430; OD]. Minute gyrocones with circular section and dorsal, marginal siphuncle. Affinities uncertain, morphology obscure. *L.Ord.* (*U.Canad.*), USA (N.Y.). —FIG. 255,3. \**B. priscum* (RUEDEMANN); lat. view,  $\times 1$  (150).

**Curtoceras** ULRICH, FOERSTE, MILLER & FURNISH, 1942, p. 69 [\**Lituites Eatoni* WHITFIELD, 1886, p. 331; OD]. Conch gradually expanded, with half of fully mature body chamber divergent from preceding volution; whorl section approximately equidimensional, moderately impressed; smooth or with weak ribs; siphuncle ventral in initial chamber, subdorsal after one volution. *L.Ord.* (*U.Canad.*) - *M.Ord.* (*Caradoc.*), N. Am. (widespread) - Eu. (Balto-Scandia). —FIG. 255,5; 256,1; 259,8; 263,1; 264,1c. \**C. eatoni* (WHITFIELD), *L.Ord.* (*U.Canad.*), USA (Vt.); syntypes and topotypes; 255,5a-c, thin sec., lat., ventral views,  $\times 5$ ,  $\times 1.5$ ,  $\times 1.5$ ; 256,1, lat. view,  $\times 1$ ; 259,8, whorl sec.,  $\times 1.3$ ; 263,1a,b, diagram. secs. (same as 264,1c, 255,5a,  $\times 11$ ,  $\times 5$ ; 264,1c, thin sec.,  $\times 10$  (203). —FIG. 264,1a,b; 265,3. *C. internastriatum* (WHITFIELD), *L.Ord.* (*U.Canad.*), USA (Vt.); syntype and topotypes; 264,1a, thin sec., 265,3a, diagram of 264,1a,  $\times 5$ ,  $\times 11$ ; 264,1b, ventrolateral view, Runzelschicht and shell,  $\times 4$ ; 265,3b, diagram. sec.,  $\times 11$  (203).

**Discoceras** BARRANDE, 1867, p. 177 [\**Clymenia antiquissima* EICHWALD, 1842, p. 33; SD SCHRÖDER, 1891, p. 159] [*non Discoceras* HYATT, 1867, p. 76, *nec* KOSSMAT, 1895, p. 179, *nec* SICARD, 1909, p. 103] [= *Schroederoceras* HYATT, 1894, p. 458 (type, *Lituites angulatus* SAEMANN, 1852, p. 166; SD BASSLER, 1915, p. 1148); *Eurasiaticoceras* SHIMIZU & OBATA, 1935, p. 5 (type, *Discoceras eurasiaticum* FRECH, 1911, p. 5; OD)]. Gradually expanded ribbed or smooth forms characterized by slight to moderate impression and subquadrate whorl section; siphuncle central in initial half-volution, marginodorsal in succeeding 1.5 to 2 whorls, subdorsal at maturity; connecting rings thick, layered. *M.Ord.* (*Llandeil.*) - *U.Ord.* (*Ashgill.*), Eu. (Balto-Scandia) - Can. (Baffin Is.) - China (Yunnan-Hopeh Prov.) - India (Punjab). —FIG. 256,3b; 260,2. \**D. antiquissimum* (EICHWALD), *M.Ord.*, Eu. (Baltic); lat. view, cross sec.,  $\times 1.7$  (219a, 176). —FIG. 259,4. *D. angulatum* (SAEMANN), *U.Ord.* (*Ashgill.*), Eu. (Norway); holotype, whorl sec.,  $\times 1.3$  (203). —FIG. 256,3a. *D. boreale* SWEET, *M.Ord.*, Eu. (Norway); thin sec.,  $\times 2.5$  (178).

**Graftonoceras** FOERSTE, 1925, p. 59 [\**Lituites Graftonensis* MEEK & WORTHEN, 1870, p. 51;

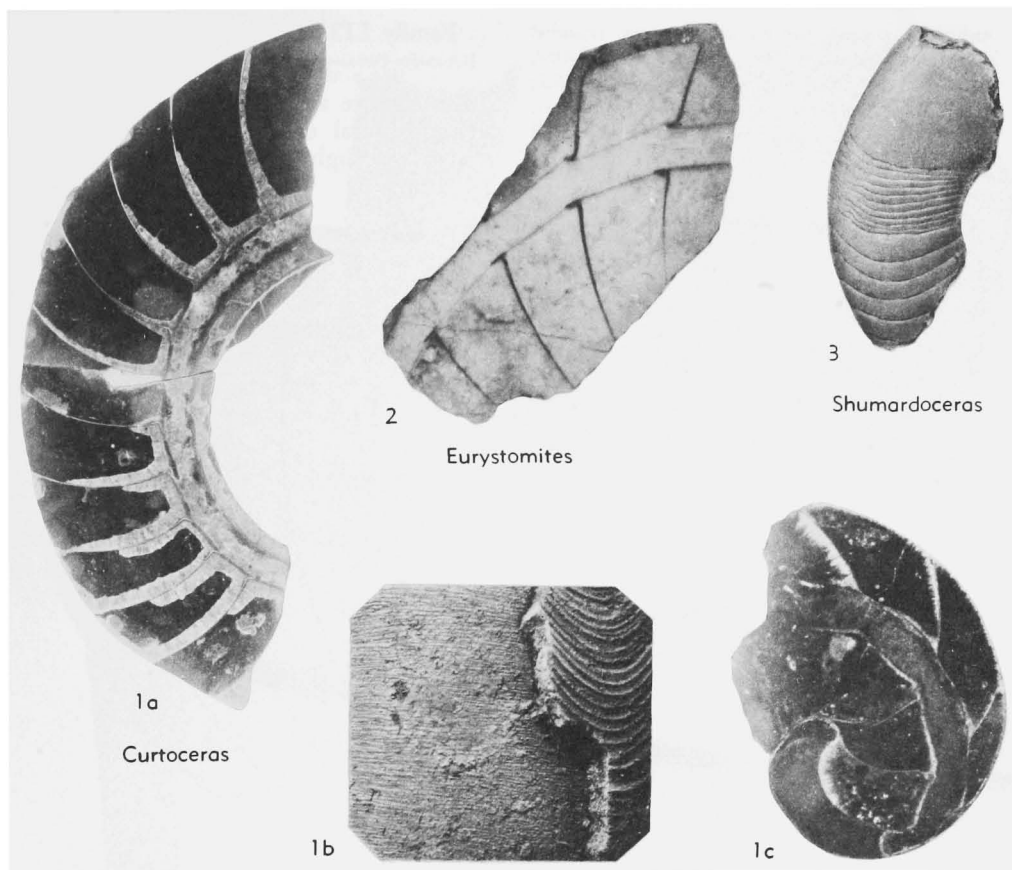


FIG. 264. Tarphyceratidae (p. K355); Estonioceratidae (p. K359); Trocholitidae (p. K360).

OD]. Like *Trocholites*, but less strongly depressed and with subterminal aperture. *U.Sil. (Niagar.)*, USA (widespread)-Australia (New S. Wales).—FIG. 258, 4; 259, 1. \**G. graftonense* (MEEK & WORTHEN), USA (Ohio); lat. view, whorl sec.,  $\times 1$ ,  $\times 1.3$  (55).

**Hardmanoceras** TEICHERT & GLENISTER, 1952, p. 748 [\**H. lobatum*; OD]. Like *Discoceras*, but prominently ribbed and with strongly depressed whorls; body chamber  $1\frac{1}{2}$  volutions, ultimate portion slightly divergent. *L.Ord. (U.Canad.)*-? *M.Ord. (Chazy.)*, W. Australia.—FIG. 258, 3. \**H. lobatum*, *L.Ord. (U.Canad.)*; lat. view,  $\times 1$  (193).

**Jasperoceras** ULRICH, FOERSTE, MILLER & FURNISH, 1942, p. 76 [\**J. costatum*; OD]. Conch subglobular, rapidly expanded, weakly ribbed; whorls strongly depressed, uniformly rounded across venter and flanks; siphuncle relatively large, subdorsal. [Known from single representative.] *M.Ord. (Chazy.)*, USA (Ark.).—FIG. 258, 2a, b; 259, 6. \**J. costatum*; holotype, septal, lat. views; whorl sec.;  $\times 1.5$ ,  $\times 1.3$  (203).

**Litoceras** HYATT, 1883, p. 268 [\**Nautilus versutus*

BILLINGS, 1865, p. 259; OD] [= *Litoceras* HYATT, 1894, p. 474 (type, *L. whiteavsi* HYATT, 1894, p. 475; OD); *Litoceres* HYATT, 1894, p. 476 (nom. null.)]. Apparently similar to *Pionoceras*, but siphuncle subcentral. *L.Ord. (U.Canad.)*-*M.Ord. (Chazy.)*, Can. (Newf.).—FIG. 257, 1. \**L. versutum* (BILLINGS), *L.Ord. (U.Canad.)*; 1a, b, holotype, lat., ventral views,  $\times 0.6$  (203).—FIG. 259, 7. *L. whiteavsi* HYATT, ? *M.Ord. (Chazy.)*; syntype, whorl sec.,  $\times 0.7$  (203).

**Trocholitoceras** HYATT, 1894, p. 480 [\**T. walcotti*; OD]. Conch weakly ribbed; like *Trocholites*, but deeply impressed, and with siphuncle close to dorsum in all but innermost volution. *L.Ord. (U.Canad.)*, N. Am. (widespread)-Australia (Tasm.-?Victoria).—FIG. 258, 5. \**T. walcotti*, USA (Vt.); 5a, b, holotype, ventral, lat. views,  $\times 1$  (203).—FIG. 260, 1. *T. latum* ULRICH, FOERSTE, MILLER & FURNISH, Can. (Que.); syntype, cross sec.,  $\times 1.2$  (203).

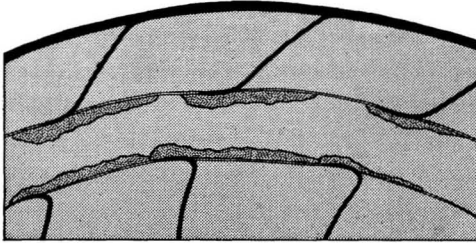
**Wichtoceras** ULRICH, FOERSTE, MILLER & FURNISH, 1942, p. 83 [\**W. compressum*; OD]. Smooth, gradually expanded; whorls in contact but not

impressed, strongly compressed, narrowly rounded ventrally; siphuncle dorsal, submarginal. *L.Ord.* (*U.Canad.*), N.Am.(widespread).—FIG. 258,1; 259,3. \**W. compressum*, USA(Ark.); syntypes; 258,1a-c, lat. and apert. views,  $\times 3$ ; 259,3, whorl sec.,  $\times 3.5$  (203).

### Family LITUITIDAE Phillips, 1848

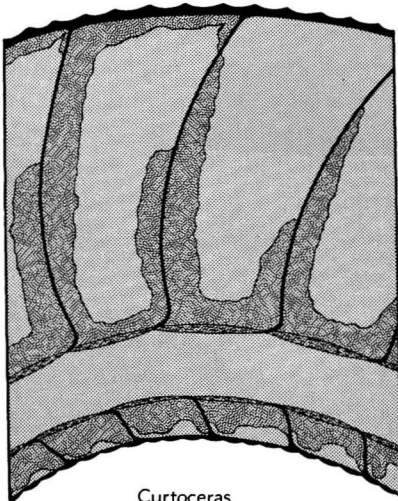
[Lituitidae PHILLIPS, 1848, p. 246] [=Lituidae NOETLING, 1884, p. 129 (*non* GRAY, 1847, p. 206)]

Annulate to smooth conchs consisting of adapical spiral or cyrtconic portion and straight to slightly sigmoid adoral ortho-



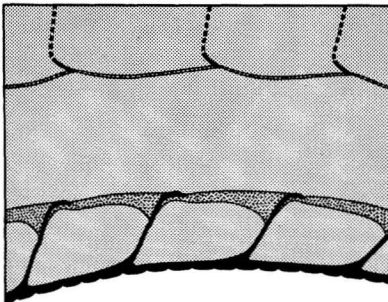
1

Centrotarphyceras

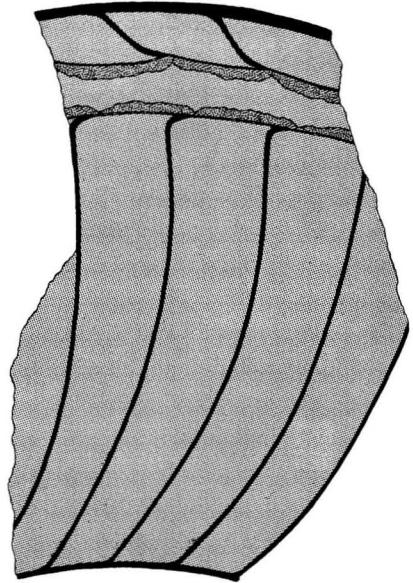


3a

Curtoceras

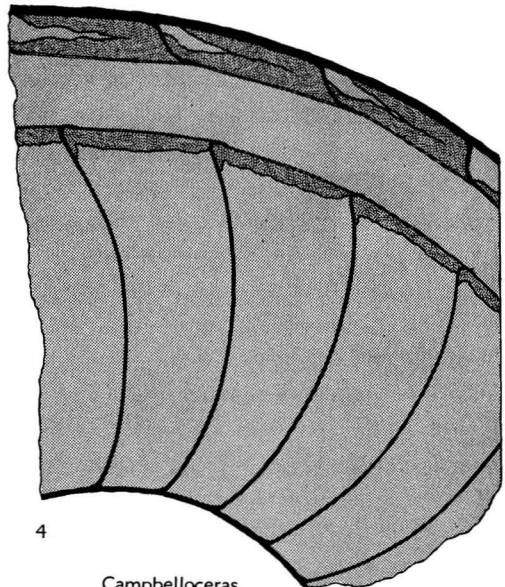


3b



2

Aphetoceras



4

Campbellloceras

FIG. 265. Tarphyceratidae (p. K355); Estonioceratidae (p. K358); Trocholitidae (p. K360).

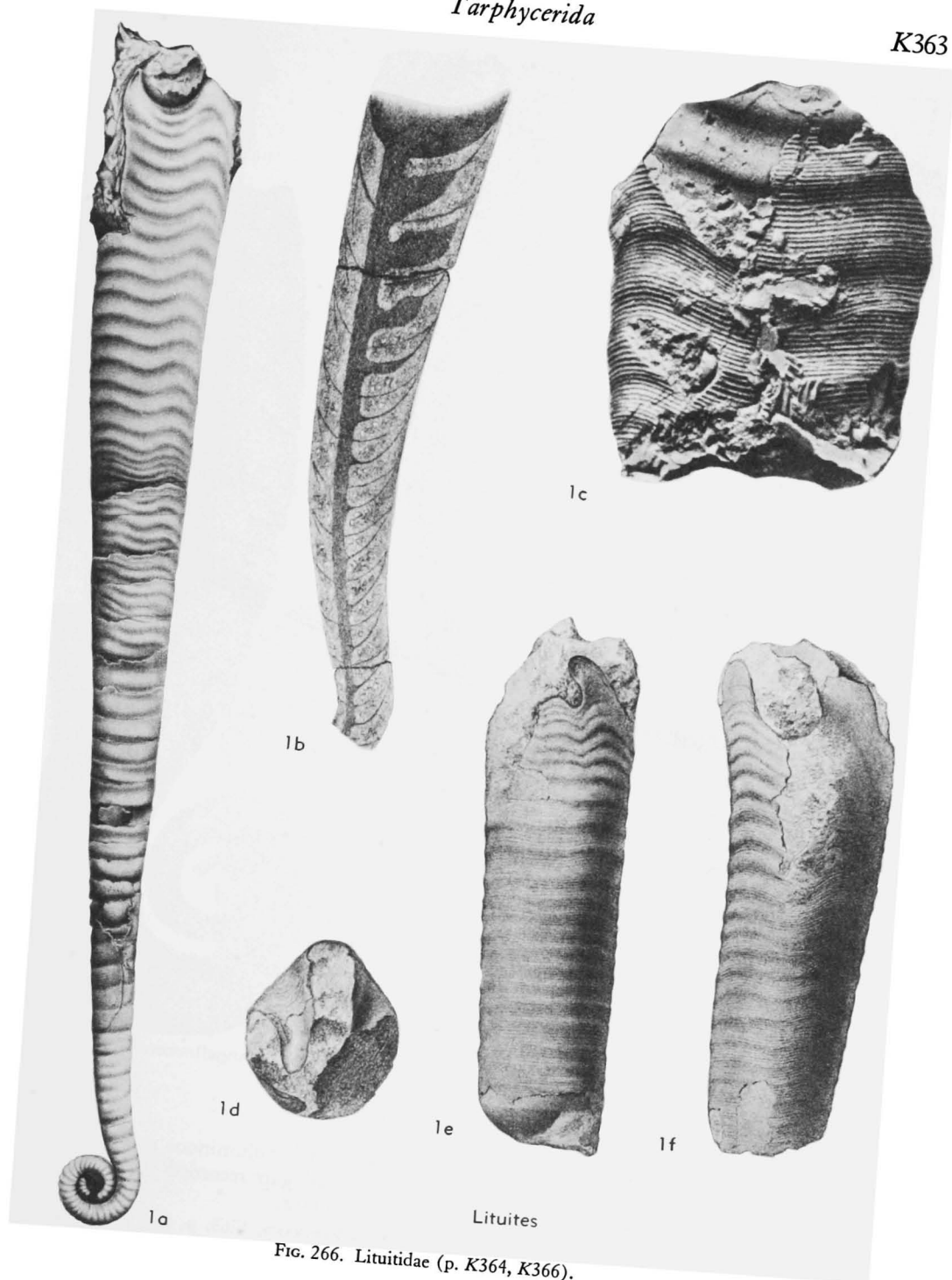


FIG. 266. Lituitidae (p. K364, K366).

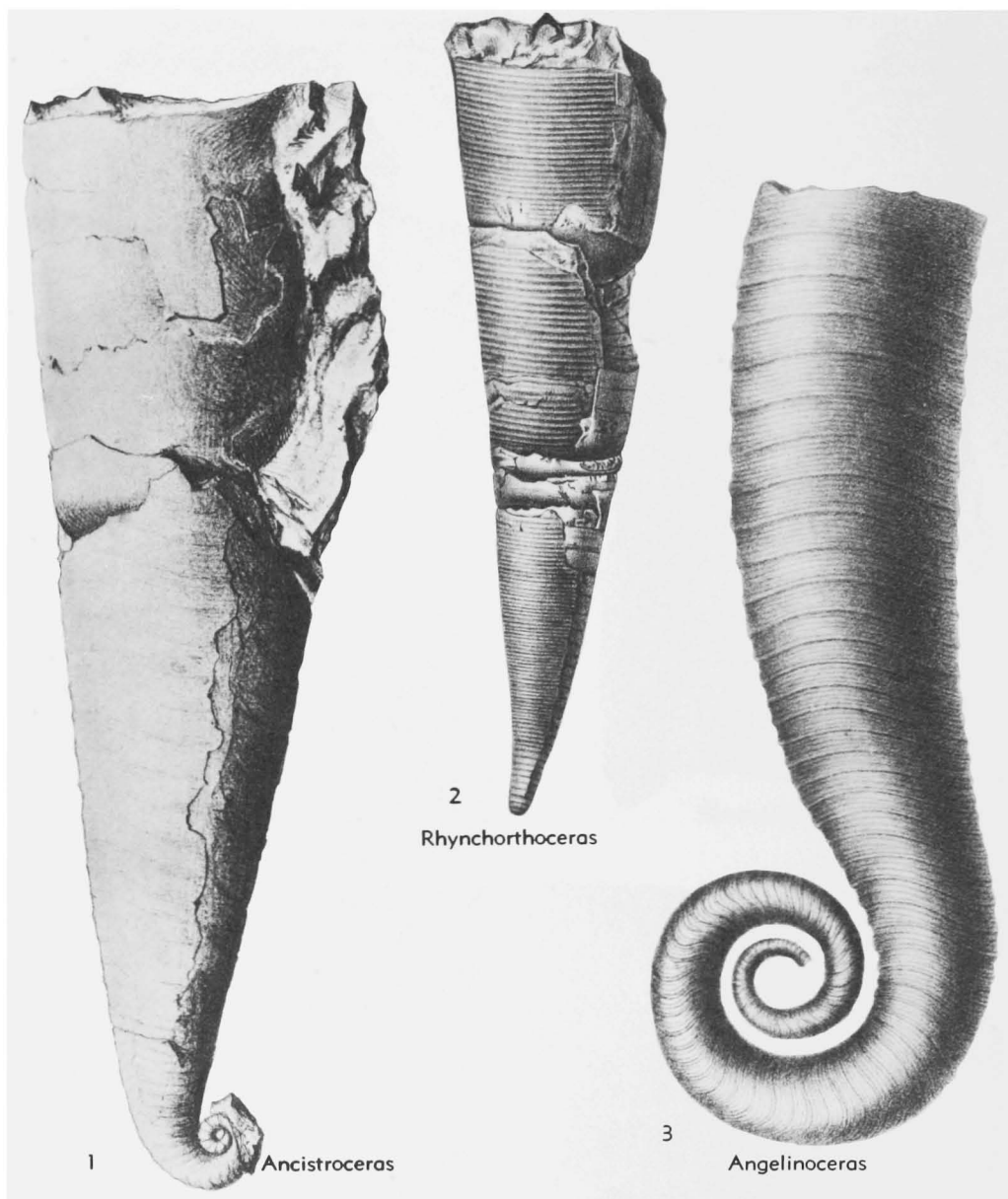


FIG. 267. Lituitidae (p. K366-K367).

cone; coiled portion generally with compressed whorls in contact; whorls rounded or weakly impressed dorsally; orthocone with circular or compressed cross section; growth lines variable in outline but mostly sinuous and with conspicuous ventral sinus; fully mature aperture characterized by lapets with deep hyponomic and ocular sinuses; siphuncle subcentral, connecting

rings layered; voluminous cameral deposits with dorsal gap recorded in some genera. *L.Ord.-U.Ord.*

*Lituites* BERTRAND, 1763, p. 89 [*\*Orthocera lituus* MODEER, 1796, p. 152; SM DE MONTFORT, 1808, p. 279] [= *?Hortolus* DE MONTFORT, 1808, p. 282 (type, *H. convolvans* DE MONTFORT, 1808, p. 283; OD); *Spirulites* PARKINSON, 1811, p. 110 (no type-species given, OD or SD)]. *Lituites* GESNER, 1758,



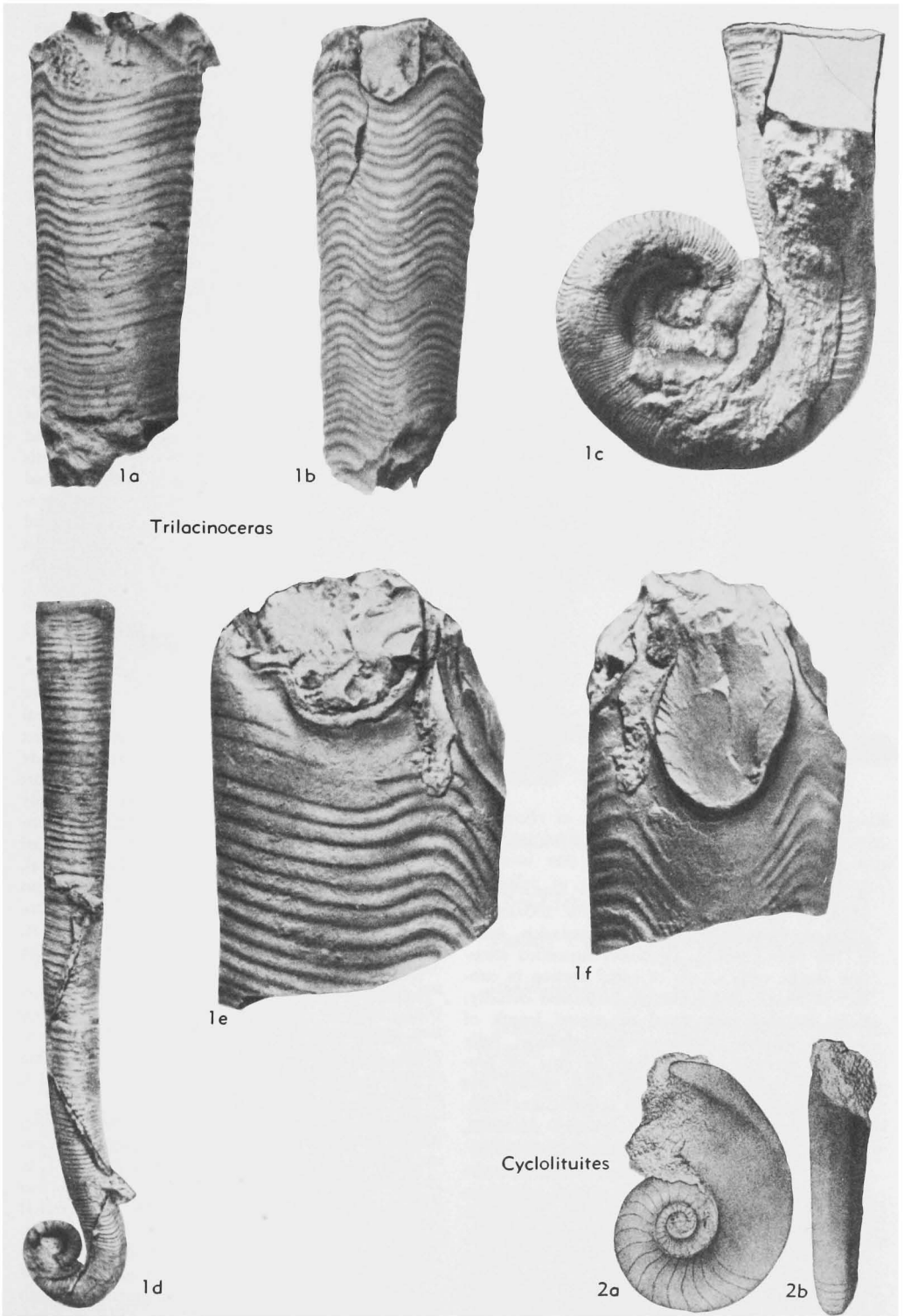


FIG. 268. Lituitidae (p. K366-K367).

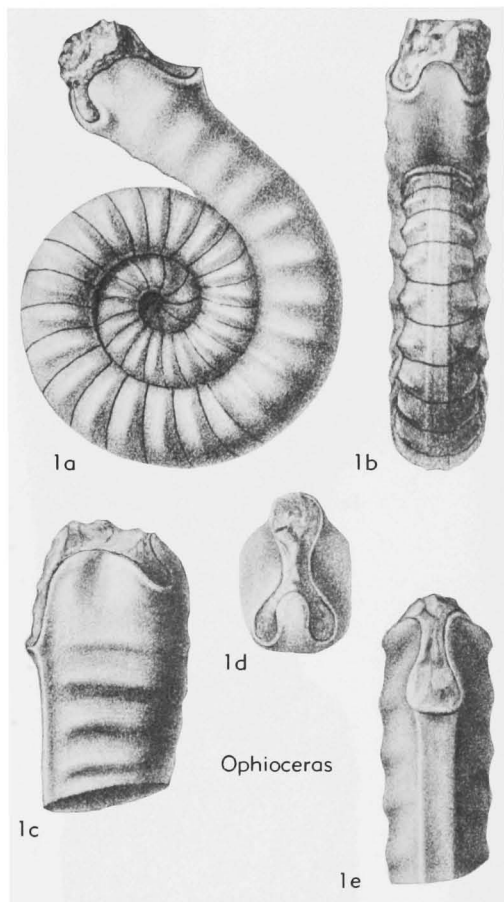


FIG. 269. Ophidioceratidae (p. K367-K368).

p. 46 (*nom. nud.*); *Lithuites* VON SCHLOTHEIM, 1820, p. 59 (*nom. null.*); *Lituitus* D'ORBIGNY, 1826, p. 71 (obj.); *Litulies* REICHENBACH, 1828, p. 100 (*nom. null.*). Gradually expanded annulate conchs with whorls of spiral portion in contact or loosely coiled but not impressed dorsally; body chamber may equal or exceed length of weakly sigmoid orthoconic phragmocone; fully mature aperture characterized by pair of pronounced ventrolateral lappets and similar but shorter dorsolateral lappets; dorsal sinus generally divided by low salient; siphuncle subdorsal. *M.Ord.*(*Llanvirn.-Caradoc.*), Eu.(Balto-Scandia).—FIG. 266,1a-c. \**L. lituus* (MODEER); 1a, Pleist. drift, Eu.(Ger.), fully mature specimen, lat. view,  $\times 0.5$  (227a); 1b, Llanvirn., Eu.(Sweden), long. sec. with cameral deposits,  $\times 1$  (223a); 1c, *M.Ord.*(Llandeil.), Eu.(Norway), lat. view,  $\times 1$  (178).—FIG. 266,1d-f. *L. toernquisti* HOLM, Llanvirn., Eu.(Sweden); apert. view (dorsum down), dorsal view, lat. view (venter on

right) of fully mature body chamber,  $\times 1$  (223a). **Ancistroceras** BOLL, 1857, p. 87 [*\*Lituites* (*A.*) *undulatum*; M] [= *Strombolituites* REMELÉ, 1881, p. 189 (obj.)] [*non Ancistroceras* REMELÉ, 1881, p. 187]. Conch weakly annulate, consisting of 1.5 to 2 contiguous or slightly separated compressed whorls and rapidly expanded orthocone (apical angle about 30 degrees) with circular section; growth lines sinuous with pronounced hyponomic sinus adapically, almost straight adorally. Orthocone similar to *Rhynchorthoceras* but more rapidly expanded, like *Holmiceras* but lacking sigmoid outline. *L.Ord.* (*Arenig.*)-*M.Ord.* (*Caradoc.*), Eu.(Balto-Scandia).—FIG. 267,1. \**A. undulatum* BOLL, Pleist. drift, Eu.(Ger.); lat. view,  $\times 1$  (144).

**Angelinoceras** HYATT, 1894, p. 508 [*\*Lituites latus* ANGELIN in ANGELIN & LINDSTRÖM, 1880, p. 9; SD SWEET, 1958, p. 131]. Conch consisting of relatively large, loosely coiled spiral portion and rapidly expanded sigmoid orthocone; whorls strongly compressed throughout; weak ribs and growth lines forming deep ventral sinus and pronounced lateral salient in spiral portion, broad low lateral salient on orthocone. Like *Lituites* but less tightly coiled and with more rapidly expanded orthocone. *M.Ord.*(*Llanvirn.-Caradoc.*), Eu.(Balto-Scandia).—FIG. 267,3. \**A. latum* (ANGELIN), Llanvirn., Sweden; lat. view,  $\times 1$  (215a).

**Cyclolituites** REMELÉ, 1886, p. 467 [*\*Lituites applanatus* REMELÉ, 1880, p. 240; OD]. Ribbed or smooth, small spiral conchs which lack typical lituitid orthocone; whorls coiled, and in contact except for slight divergence of terminal body chamber; whorl section compressed to circular; mature body chamber with ventral flare; fully mature aperture characterized by pair of asymmetric ventrolateral lappets and less pronounced dorsolateral and dorsal salients; siphuncle dorsal, subcentral. Like *Lituites*, but fully mature forms lack orthocone. *M.Ord.*(Llandeil.), Eu.(Balto-Scandia).—FIG. 268,2. *C. lynceus* HOLM, Sweden; 2a,b, lat., ventral views of fully mature specimen,  $\times 1$  (223a).

**Holmiceras** HYATT, 1894, p. 512 [*\*Lituites praecurrens* HOLM, 1891, p. 30; M] [= *Holmoceras* FLOWER, 1955, p. 250 (*nom. van.*)]. Like *Ancistroceras*, but with loosely coiled spiral portion and weakly sigmoid orthocone. *L.Ord.*(*Arenig.*), Eu.(Balto-Scandia).

**Rhynchorthoceras** REMELÉ, 1881, p. 480 [*\*Lituites Breynii* BOLL, 1857, p. 88; SD FURNISH & GLENISTER, herein] [= *Ancistroceras* REMELÉ, 1881, p. 187 (obj.)] (*non* BOLL, 1857); *Rhynchoceras* REMELÉ, 1881, p. 480 (obj.) (*nom. correct.*); *Rhynchorthoceras* HYATT, 1894, p. 511 (*nom. null.*). Essentially orthoconic longicones with slight curvature near apex and moderate rate of expansion; body chamber may approximate length of phragmocone; siphuncle large (1/6 of conch



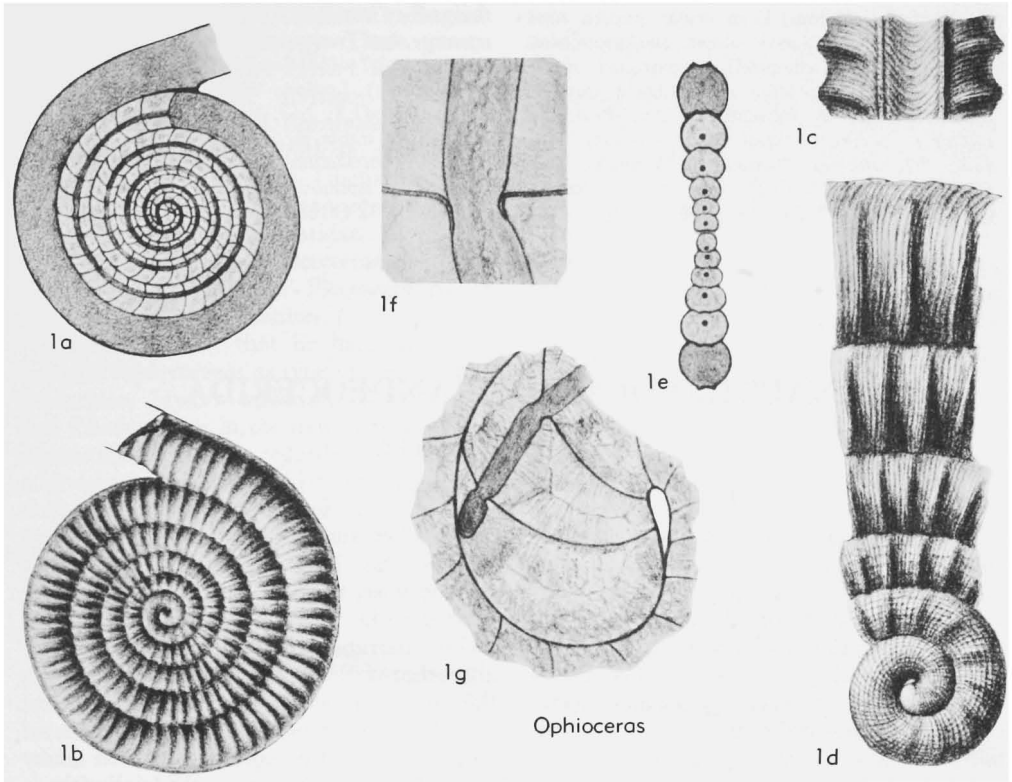


FIG. 270. Ophidioceratidae (p. K367-K368).

diameter), subcentral; faint ribs and growth lines sinuous, forming shallow ventral and lateral sinuses. Like *Ancistroceras*, but lacking coiled apical portion. *M.Ord.*(*Llanvirn.-Caradoc.*), Eu. (Balto-Scandia-Pol.).—FIG. 267,2. *R. beyrichii* REMELÉ, Pleist. drift, Pol.; lat. view,  $\times 0.5$  (229a).

**Trilacnocras** SWEET, 1958, p. 147 [*\*Lituites discors* HOLM, 1891, p. 26; OD]. Like *Lituites*, but smaller and with less complex aperture; fully mature aperture characterized by pronounced pair of ventrolateral lappets, deep hyponomic sinus, and high dorsal salient; conch similar to *Angelinocras*, but fully mature aperture not known in that genus. *M.Ord.*(*Llanvirn.-Caradoc.*), Eu. (Balto-Scandia).—FIG. 268,1a-d. *\*T. discors* (HOLM), *M.Ord.*(*Llandeil.*), Norway; 1a,b, lat. (venter on left) and ventral views of mature body chamber,  $\times 1$ ; 1c, lat. view,  $\times 1.5$ ; 1d, lat. view,  $\times 0.75$  (178).—FIG. 268,1e,f. *T. norvegicum* SWEET, *M.Ord.*(*Llandeil.*), Norway; lat. (venter to right) and ventral views of fully mature body chamber,  $\times 1$  (178).

**Tyrioceras** STRAND, 1934, p. 49 [*\*T. kjerulfi*; OD]. Poorly known large orthocones which resemble

lituitids in configuration of growth lines; conch compressed; growth lines forming subdued ventrolateral and dorsolateral salients; body chamber similar to *Rhynchorthoceras*. *M.Ord.*(*Caradoc.*)-*U.Ord.*(*Ashgill.*), Eu. (Balto-Scandia).

### Family OPHIDIOCERATIDAE Hyatt, 1894

[Ophidioceratidae HYATT, 1894, p. 513] [=Ophidioceratidae STRAND, 1934, p. 46]

Strongly ribbed, coiled conchs with divergent adoral portion of mature body chamber; whorls depressed to compressed, only slightly impressed; siphuncle subcentral, connecting rings thin; fully mature aperture characterized by deep hyponomic and ocular sinuses. *U. Sil.*

**Ophioceras** BARRANDE, 1865, expl. pl. 45 [*\*Lituites (O.) simplex* BARRANDE, 1865, expl. pl. 97; SD FURNISH & GLENISTER, herein] [*non Ophioceras* HYATT, 1867, p. 75] [=Ophidioceras BARRANDE, 1867, p. 174 (obj.); *Euophioceras* MILLER, 1932, p. 17 (obj.)]. Small, evolute conchs with 3 to 6 volutions; venter bicarinate, flat; growth lines

forming ventral sinus; deep ocular sinuses, separated by narrow dorsal salient, and prominent hyponomic sinus characterize contracted, fully mature aperture; position of siphuncle variable from subdorsal to subventral. *U.Sil.* (Wenlock-Ludlov.), N.Am.-Eu. (widespread).—FIG. 269, *1a,b*. \**O. simplex* BARRANDE, Wenlock., Eu. (Czech.); lat. and ventral views of fully mature specimen,  $\times 2.7$  (5).—FIG. 269, *1c-e*. *O. rudens*

BARRANDE, Wenlock., Eu. (Czech.); fully mature aperture, lat. (venter on left), apert., and ventral views,  $\times 2.7$  (5).—FIG. 270, *1a-e*. *O. rota* (LINDSTRÖM), Ludlov., Eu. (Gotl.); *1a,b*, sec. and lat. view,  $\times 1.3$ ; *1c,d*, ventral and lat. views of *1b*,  $\times 4$ ; *1e*, transv. sec.,  $\times 1.3$  (118a).—FIG. 270, *1f,g*. *O. reticulatum* (ANGELIN), Wenlock., Eu. (Gotl.); *1f*, siphuncle sec.,  $\times 20$ ; *1g*, sec. of initial camerae,  $\times 12$  (118a).

## NAUTILOIDEA—BARRANDEOCERIDA

By WALTER C. SWEET

[The Ohio State University]

Early barrandeocerids are closely coiled, compressed serpenticones, with open umbilici, slender whorls that are only faintly, if at all, impressed dorsally, and with a distinct tendency to uncoil during formation of late stages of the conch. From this fundamental type developed cyrtocones, gyrocones, torticones, lituicones, and even essentially straight brevicones, many of broad, depressed transverse section.

Primitive barrandeocerids are modestly, but distinctly, ornamented by transverse costae, at least on inner whorls, and growth lines that form a hyponomic sinus on the venter. Some derived species are very prominently costate, and several develop a pattern of longitudinal lirae, as well. Other derived species entirely lose the prominent costation (or longitudinal markings, or both); or, in a third group, costation is confined to early parts of the conch. Thus, many virtually smooth forms are included in the order.

In all but one genus, the aperture is terminal, simple, and unmodified. In *Catyrophoceras* (Lechritrochoceratidae), the aperture is restricted to a dumbbell-shaped opening by broad lateral lappets in the mature peristome.

Sutural patterns are simple and related primarily (if not entirely) to the shape of the transverse section of the conch or whorl. Species with essentially circular whorl or conch sections have straight, transverse sutures, whereas those with compressed (or depressed) transverse sections may develop

slight lobes and saddles. No particular importance has been attached, taxonomically or otherwise, to sutural patterns in the Barrandeocerida.

The barrandeocerid siphuncle is invariably thin-walled and empty. Primitively, the siphuncle seems to be slender, central or subcentral in position, orthochoanitic in structure, and tubular in shape. In many derived species, however, the siphuncle is displaced toward the venter (or even slightly toward the dorsum) in adult conchs and, at least in mature camerae, septal necks may be cyrtchoanitic around all or part of the periphery of the septal foramen. In these "secondarily cyrtchoanitic" species, siphuncular segments are typically slightly to considerably inflated, although inflation may be abrupt at the septal necks and the segment essentially cylindrical throughout most of its length.

Cameral deposits have not been noted in the Barrandeocerida, and the pattern of retractor and epithelial muscle attachment is known for only a few species, all referable to the Apsidoceratidae. In these species, retractor muscles were attached along expanded bosses of shell material on either side of the ventral mid-line; hence they may be said to be "ventromyarian" (180).

## CLASSIFICATION

Of the 36 genera now included in the Barrandeocerida, only 11 were known to HYATT (97) when he prepared the classi-

fication of nautiloids for Zittel's English *Text-book of Palaeontology*. These genera were not assembled by HYATT in any one family or subordinal 'division,' but were scattered among several. *Barrandeoceras* was referred to the Tarphyceratidae, and *Plectoceras* and *Sphyradoceras* (including both *Peismoceras* and *Systrophoceras*) were placed in the Plectoceratidae. Both the Tarphyceratidae and Plectoceratidae were included in the 'division' Plectoceratida, of the suborder Cyrtchoanites.

Despite the fact that he had earlier regarded *Nephriticeras* as type of the Nephriticeratidae, HYATT included *Nephriticeras* and *Rhadinoceras* in the new family Rhadinoceratidae, which he regarded as typical of a 'division' Rhadinoceratida, of the suborder Orthochoanites. Because of their inflated siphuncular segments, *Uranoceras* and *Gigantoceras* made up HYATT's Uranoceratidae, which, even though uranoceratid siphuncles were and are known to be empty, were included in the 'division' Annulosphonata, of the suborder Cyrtchoanites.

Neither *Apsidoceras* HYATT, 1884, nor the heterogeneous family Apsidoceratidae, of which it was made type in 1884, were mentioned by HYATT in 1900. *Triplooceras* HYATT, 1884, referred to the Rutoceratidae at the time of its establishment, was similarly ignored in the 1900 nautiloid classification.

Between 1924 and 1936, FOERSTE named and described 18 barrandeocerid genera, some of which he referred to HYATT's families, others of which he included in newly established or partially revised families embodying his own taxonomic concepts. FOERSTE, however, concerned himself very little with suprafamilial classification and, in later years, seems to have paid relatively little attention even to familial taxonomy.

In 1941, FLOWER (26) recognized five "morphological groups" among Chazyan and later elliphochoanitic nautiloids, of which the first (containing orthochoanitic forms with perfectly cylindrical siphuncular segments) included both orthochoanitic orthocones and coiled genera later referred to the Barrandeocerida. Also in 1941, FLOWER (27) discovered that two types of siphuncular structure occur in coiled nautiloids included by HYATT (97) in the Tarphycera-

tidae. One group, including *Tarphyceras* itself, exhibits thick, complex connecting rings, whereas the other (represented by *Barrandeoceras*) has thin-walled connecting rings. As a result of this difference, the Tarphyceratidae were restricted to thick-walled forms like *Tarphyceras*.

In 1946, FLOWER (33) noted two strikingly different nautiloid groups in the assemblage of orthochoanitic forms characterized by tubular, thin-walled siphuncles. One group includes orthocones (and is, for the most part, the present order Orthocerida); the other is made up largely of curved or coiled forms, and constitutes the nucleus of the present Barrandeocerida. In 1946, however, FLOWER was uncertain whether the orthocones and curved forms constituted a natural group, or whether internal differences indicated two homeomorphic lines.

In 1950, FLOWER (49) elaborated upon the subdivision of orthochoanitic cephalopods predicted in his study of 1946; that is, he referred the dominantly straight forms to the Michelinoceratida (now Orthocerida), and the dominantly curved and coiled forms to the Barrandeoceratida (now Barrandeocerida). As conceived in 1950, the Barrandeocerida included the families Barrandeoceratidae, Plectoceratidae, Uranoceratidae, Lechritrochoceratidae, Rhadinoceratidae (=Nephriticeratidae), Apsidoceratidae, and Lituitidae. Subsequently, SWEET (178) has shown that the Lituitidae have a siphuncular structure strikingly like that of the Trocholitidae (Tarphycerida), and they are now included in that order. Otherwise, the classification adopted herein is that of FLOWER in FLOWER & KUMMEL, 1950 (49).

## DISTRIBUTION AND PHYLOGENY

Knowledge of the distribution and phylogenetic development of the Barrandeocerida is based largely upon described collections from just a few Ordovician, Silurian, and Devonian localities. Many genera are monotypic; others are represented by several species, but, for the most part, all species of these genera are from the same formations in a single geographic area. Furthermore, only a few species are known well enough

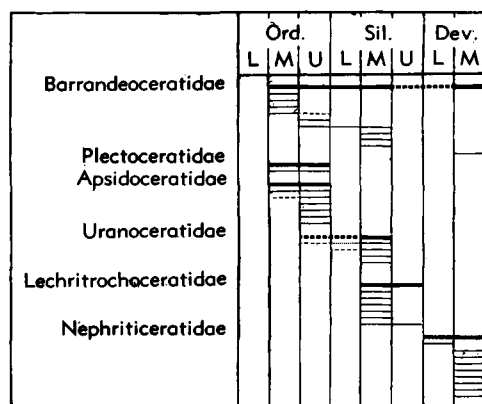


FIG. 270A. Stratigraphic distribution of genera and families of Barrandeocerida (Sweet, n).

internally to be properly evaluated phylogenetically. Thus, paucity of knowledge both of geographic and stratigraphic distribution and small range of specific diversity prohibit very meaningful analysis of barrandeocerid phylogeny.

Described barrandeocerids are largely North American (including Greenland), but a few species have been reported from northern and central Europe and from Australia. The order appears first in the early Middle Ordovician and ranges into the Middle Devonian.

The earliest barrandeocerids (all referable to the Barrandeoceratidae) are closely similar in form and external ornamentation to late Early and early Middle Ordovician Tarphycerida (e.g., *Aphetoceras*), from which they differ primarily in having thin, rather than thickened, connecting rings. Thus, there can be little doubt but that the Tarphycerida are ancestral to the Barrandeocerida.

FLOWER (40) has suggested that compressed, costate, closely coiled *Barrandoceras*, of the early Middle Ordovician, gave rise to gyroconic or cyrtoconic, costate *Centrocyrtoceras*, of the later Middle and Late Ordovician. Through reduction in surficial ornament, *Centrocyrtoceras* may have given rise in the Middle Ordovician to smooth-shelled, loosely coiled *Paquettoceras*; through development of somewhat more prominent gyroconic coiling and more pronounced surface ornament, the same genus was probably also the progenitor of Late

Ordovician through Middle Silurian *Bickmorites*.

*Bickmorites* (Barrandeoceratidae) was almost certainly the point of origin of the less prominently costate, but more conspicuously uncoiled Uranoceratidae (Late Ordovician through Middle Silurian) as well as of dextral, costate torticones included in the Silurian Lechritrochoceratidae.

The oldest known genus of the Nephriticeratidae, *Sphyradoceras*, of the Early or Middle Devonian Schoharie Formation of New York, is a sinistral torticone, the early stages of which are gyroconic and closely similar to the conch of adult *Bickmorites*. This suggests an origin of the Nephriticeratidae in *Bickmorites* (Barrandeoceratidae) (42). *Sphyradoceras* is the logical ancestor of cyrtoconic Middle Devonian *Baeopleuroceras*, which, among known Nephriticeratidae, is the most likely progenitor of more regularly coiled Middle Devonian *Nephriticeras*, *Rhadinoceras*, and others, as well as of the essentially straight brevicone, *Endoplanoceras*.

Origin of the cyrtocoeanitic late Middle and Late Ordovician Apsidoceratidae is unknown, and no very likely ancestral species have been described among Ordovician Barrandeoceratidae. The family is included in the Barrandeocerida (rather than in the Oncocerida), for it is thought to include species characterized by secondarily cyrtocoeanitic siphuncles and because attempts to trace it to primitively cyrtocoeanitic ancestors have been fruitless (33). An orthocoeanitic origin of the family is suggested largely because there are virtually no Middle Ordovician cyrtocoeanitic, curved nautiloids

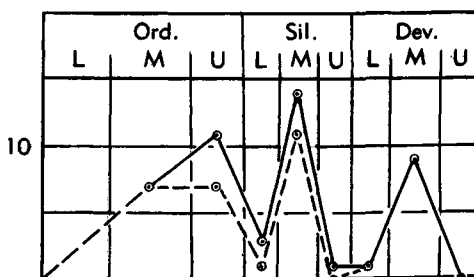


FIG. 270B. Graph showing numbers of new genera of Barrandeocerida introduced in successive epochs (dashed lines) and total genera represented in each (solid lines) (Sweet, n).

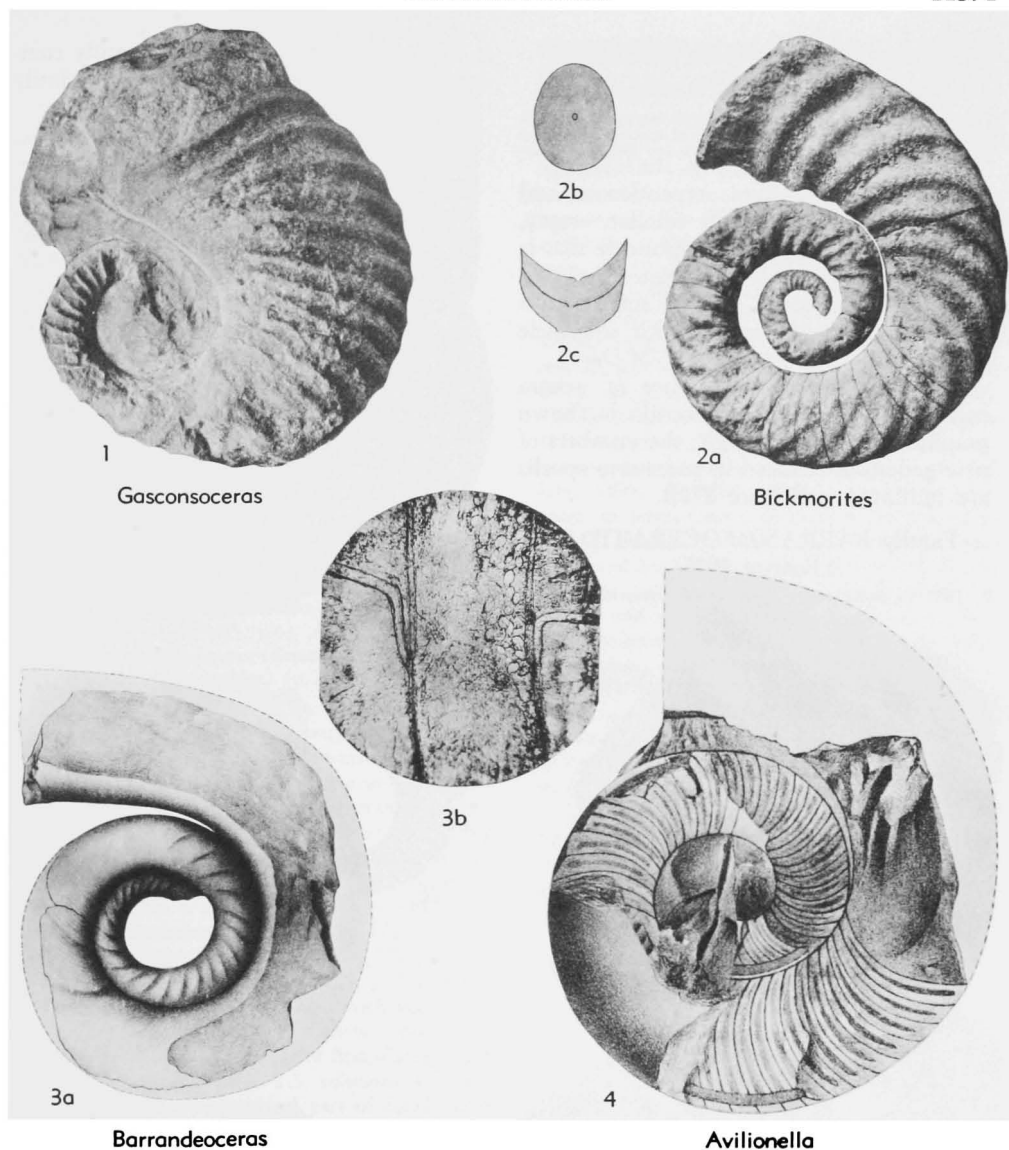


FIG. 271. Barrandeoceratidae (p. K372-K373).

with subcentral siphuncles, such as characterize the Apsidoceratidae, nor is there any ontogenetic indication in the family of origin in cephalopods with ventral siphuncles. On the other hand, the slender early siphuncular stages of *Charactoceras* (Fig. 279,2b) suggest an origin in some stock of suborthochoanitic or orthochoanitic cephalopods.

*Plectoceras*, type of the monotypic Ordovician Plectoceratidae, was probably derived

from externally similar coiled Barrandeoceratidae, from which it differs primarily in having a subventral siphuncle and a more strikingly costate shell.

## SYSTEMATIC DESCRIPTIONS

### Subclass NAUULOIDEA Agassiz, 1847

Diagnosis given in "Introductory Discussion" (p. K128). *U.Cam.-Rec.*

## Order BARRANDEOCERIDA Flower in Flower & Kummel, 1950

[*nom. correct.* SWEET, herein (*pro* Barrandeoceratida FLOWER in FLOWER & KUMMEL, 1950); mention of Barrandeocerida by FURNISH, GLENISTER, & HANSMAN, 1962 (p. 1342), is disregarded] [=Barrandeoceratina SWEET, 1959 (suborder)]

Cyrtocoines, gyrocoines, serpenticoines, and torticoines, with primitively tubular, empty, orthochoanitic, thin-walled siphuncle that is central, ventral, or between center and dorsum or venter; many derived species with wholly or partially cyrtchoanitic siphuncle and inflated segments. *M.Ord.-M.Dev.*

The stratigraphic occurrence of genera included in the Barrandeocerida is shown graphically in Figure 270A; the numbers of new genera introduced in successive epochs are indicated in Figure 270B.

### Family BARRANDEOCERATIDAE Foerste, 1925

[Incl. Bickmoritidae FOERSTE, 1925; Centrocyrtoceratidae KOBAYASHI, 1934]

Coiled barrandeocerids, dominantly compressed; siphuncle subcentral, secondarily ventral. *M.Ord.-M.Dev.*

**Barrandeoceras** HYATT, 1884, p. 299 [\**Nautilus natator* BILLINGS, 1859, p. 466; OD] [=Barrandioceras ZITTEL, 1884, *nom. null.*; Barrandoceras FLOWER, 1955, *nom. null.*]. Large, subdiscoidal, laterally compressed serpenticoines with volutions in contact but not dorsally impressed; body chamber separated from preceding whorl adorally; whorls oval in cross section and somewhat more narrowly rounded ventrally than dorsally; growth lines forming deep ventral sinus; prominent lateral ribs parallel to growth-lines present at least on inner volutions of conch; sutures with lateral lobes. At maturity, siphuncle is small, orthochoanitic, and subcentral in position. *M.Ord.*, N.Am.(N.Y.-Ont.-Que.).—FIG. 271, 3a. \**B. natator* (BILLINGS), USA(N.Y.);  $\times 0.3$  (150). —FIG. 271, 3b. *B. sp.*, USA(N.Y.); long. sec. through siphuncle,  $\times 4.7$  (26).

?**Antiplectoceras** FOERSTE & SAVAGE, 1927, p. 58 [\**Discoceras*(?) *shamattawaense* PARKS, 1915, p.

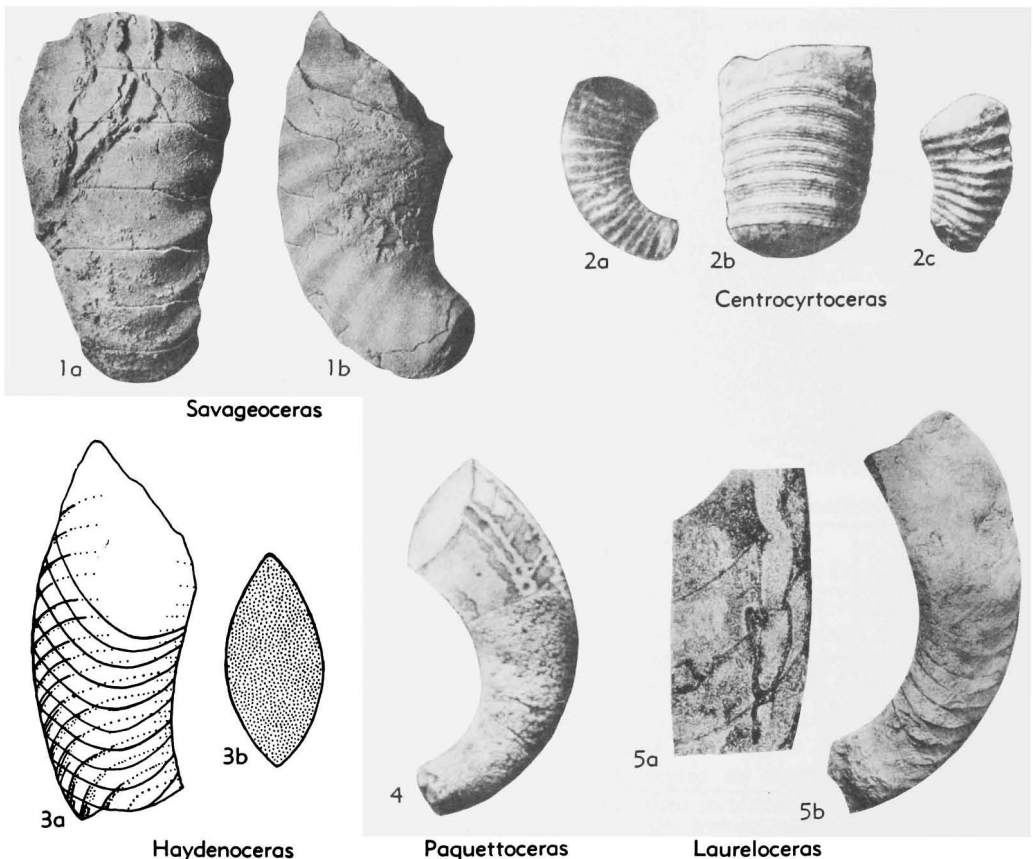


FIG. 272. Barrandeoceratidae (p. K373-K374).

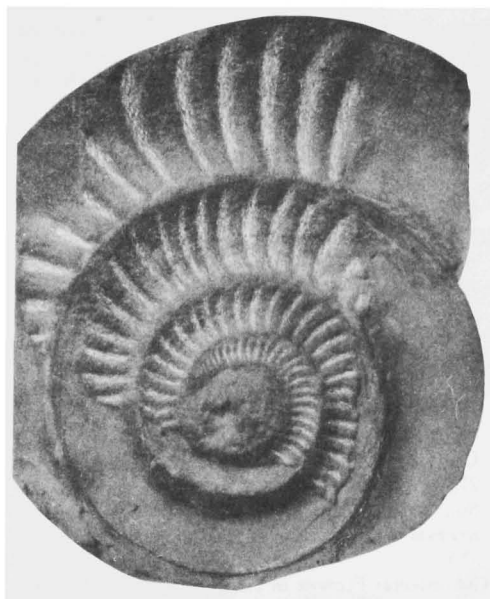


FIG. 273. \**Antiplectoceras shamattawaense* (PARKS) (?Barrandeoceratidae) (p. K372-K373).

31; OD]. Slender-whorled, compressed, annulate serpenticones of 4 or more volutions that are oval in cross section, with venter more acutely rounded than dorsum. Surface marked by transverse ribs that define broad lateral sinuses and probably somewhat more narrowly rounded and less distinct dorsal and ventral salients. Internal structures unknown. *U.Ord.*, Can.(Ont.).—FIG. 273. \**A. shamattawaense* (PARKS);  $\times 1$  (77).

*Avilionella* FLOWER, 1952, p. 56 [\**Tarphyceras multicameratum* RUEDEMANN, 1906, p. 472; OD]. Closely coiled compressed conchs with very small umbilical perforation and shallow dorsal impressed zone from completion of first whorl; conch becomes gyroconic after 1.5 volutions in some species; in all species, adoral part of conch more loosely coiled than adapical. Surface smooth with faintly fasciculate growth lines that slope adapically from dorsum to venter. Siphuncle subventral, tubular; connecting rings thin. *M.Ord.*, N.Am. (N.Y.-Ont.).—FIG. 271,4. \**A. multicamerata* (RUEDEMANN), USA(N.Y.);  $\times 0.7$  (150).

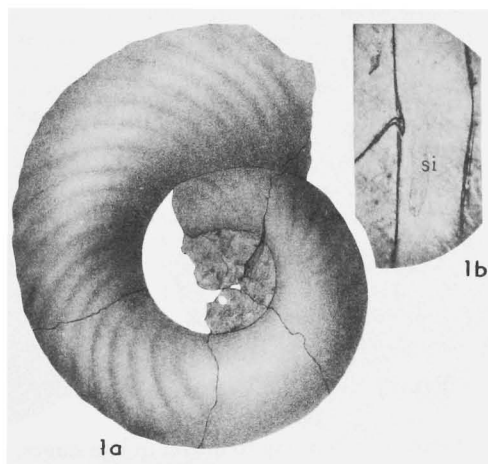
*Bickmorites* FOERSTE, 1925 p. 47 [\**Lituites bickmoreanus* WHITFIELD, 1885, p. 191; OD] [= *Tyrrelloceras* FOERSTE, 1925; *Goniotrochoceras* FOERSTE, 1928; *Leuronotoceras* FOERSTE, 1928]. Slender gyrocones of circular or slightly compressed section, describing several volutions; mature body chamber straight and tubular in some species. Surface with prominent ribs adapically inclined to form hyponomic sinus on venter, and with finer transverse and longitudinal markings in gerontic specimens. Sutures transverse, with

slight lateral lobes. Siphuncle slightly ventral of center, orthochoanitic. *U.Ord.-M.Sil.*, N.Am. (widespread)-?Eu. (Norway).—FIG. 271,2. \**B. bickmoreanus* (WHITFIELD), *M.Sil.*, USA(Ind.); 2a-c, right lat. view, transv. sec., long. sec. through siphuncle, all  $\times 0.3$  (55).

*Centrocyrtoceras* FOERSTE, 1926, p. 366 [\**Cyrtoceras annulatum* HALL, 1847 (= *Cyrtoceras subannulatum* D'ORBIGNY, 1850, obj.); OD]. Cyrtocones or gyrocones of subcircular section and with straight transverse sutures. Surface with transverse annulations and finer lirae and striae that slope slightly adapically on venter. Siphuncle subcentral; segments cylindrical or subcylindrical. *M.Ord.*, N. Am.(N.Y.-Tenn.-Wis.-Ont.); ?*U.Ord.*, ?Eu.(Norway).—FIG. 272,2. \**C. annulatum* (HALL), *M.Ord.*, USA(N.Y.); 2a-c,  $\times 1$  (57).

*Gasconsoceras* FOERSTE, 1936, p. 61 [\**G. pulchellum*; OD]. Rapidly enlarging annulated gyrocones or serpenticones of slightly compressed to slightly depressed section. Surface with fine transverse and longitudinal striae and transverse ribs that are prominent laterally and dorsally, but weaker and adapically deflected ventrally to form deep hyponomic sinus. Siphuncle between center and venter; internal character unknown. *M.Sil.*, Can.(Que.-Cornwallis Is.).-Tasm. — FIG. 271,1. *G. obesum* FOERSTE, Que.(Gaspé);  $\times 0.7$  (75).

*Haydenoceras* FLOWER, 1949, p. 75 [\**H. acutum*; OD]. Gradually expanding, strongly compressed cyrtocones of cuneate cross section; dorsum strongly rounded, venter acutely angled. Sutures with lateral lobes, subangular ventral saddle and lower, more rounded dorsal saddle. Surface with rugose growth lines, costate in adults, and sloping obliquely toward apex from dorsum to venter.



### Plectoceras

FIG. 274. Plectoceratidae (p. K374).

Siphuncle tubular, subcentral. *M.Dev.*, USA (Nev.).—FIG. 272,3. \**H. acutum*; 3a,b,  $\times 0.7$  (36).

**Laureloceras** FLOWER, 1943, p. 97 [\**L. cumingsi*; OD]. Slender compressed smooth-shelled cyrtocones or gyrocones with venter more narrowly rounded than dorsum. Sutures transverse, but may develop broad lateral lobes. Siphuncle subventral; necks straight, connecting rings somewhat expanded within camerae; no cameral or siphuncular deposits. *M.Sil.*, N.Am.(Ind.-Tenn.-?Ont.).—FIG. 272,5. \**L. cumingsi*, USA(Ind.); 5a, "enlarged," 5b,  $\times 0.4$  (31).

**Paquettoceras** FOERSTE, 1932, p. 51 [\**P. allumetense*; OD]. Like *Centrocyrtoceras*, but not annulated. *M.Ord.*, Can.(Ont.).—FIG. 272,4. \**P. allumetense*;  $\times 1$  (71).

?**Savageoceras** FOERSTE, 1930, p. 41 [\**S. transversale*; OD]. Depressed rapidly expanding cyrtocones of subtrapezoidal section; ventral side wider and flatter than dorsal; sides converging toward dorsum. Sutures with slight lateral and ventral lobes and ventrolateral saddles. Surface with transverse striae and riblike annulations that are low and vaguely defined dorsally and ventrally, but increase in prominence toward ventrolateral shoulders where they are most conspicuous. Siphuncle central; interior unknown. *M.Sil.*, USA (Ill.).—FIG. 272,1. \**S. transversale*; 1a,b,  $\times 0.4$  (68).

### Family PLECTOCERATIDAE Hyatt in Zittel, 1900

Coiled, costate barrandeocerids, with subventral adult siphuncle. *M.Ord.-U.Ord.*

**Plectoceras** HYATT, 1884, p. 268 [\**Nautilus jason* BILLINGS, 1859, p. 464; OD] [= *Metaplectoceras* FOERSTE, 1935]. Costate serpenticones of subcircular whorl section; large umbilical perforation, whorls in contact and impressed by end of first volution; adorally, phragmocone loses impressed zone and mature body chamber is free. Surficial costae sloping adapically from dorsum to venter, where they form hyponomic sinus. Sutures straight or with lateral lobes. Siphuncle subventral, orthochoanitic; necks short and straight, connecting rings thin, structureless. *M.Ord.-U.Ord.*, N. Am. (N. Y.-Wis.-Wyo.-Que.-Ont.-Labrador)-Greenl.—FIG. 274,1a. \**P. jason* (BILLINGS), *M.Ord.*, USA(N.Y.);  $\times 0.4$  (150).—FIG. 274,1b. \**P. foerstei* TROEDSSON, *M.Ord.*, Greenl.; long. sec. through siphuncle,  $\times 2.7$  (194).

### Family URANOCERATIDAE Hyatt in Zittel, 1900

Gyroconic, tending to uncoil in late stages; early stages of a few species annulated, later stages of all smooth or faintly cancellated or striated; septal necks straight in many spe-

cies, but distally recumbent on one side or around entire siphuncular periphery in others; connecting rings thin, subcylindrical, markedly contracted immediately adjacent to septal foramen. ?*U.Ord.*, *M.Sil.*

**Uranoceras** HYATT, 1884, p. 298 [\**Cyrtoceras uranum* BARRANDE, 1866, pl. 196; OD]. Loosely coiled, rapidly expanding, compressed gyrocones of 1.5 or 2 subquadrate whorls. Sutures with lateral lobes and dorsal and ventral saddles. Surface smooth or with distinct transverse growth lines or growth bands that form hyponomic sinus on venter. Siphuncle large, slightly ventral from center; necks orthochoanitic to suborthochoanitic; connecting rings thin, cylindrical, strongly contracted immediately before junction with necks. ?*U.Ord.*, Can.(Anticosti Is.)-Eu.(Sweden); *M.Sil.*, USA (Ill.-Ind.-?Ohio-Wis.)Eu.(Czech.). — FIG. 275,1a-c. *U. hercules* (WINCHELL & MARCY), *M.Sil.*, Wis., Ill.;  $\times 0.3$  (55).—FIG. 275,1d. \**U. uranum* (BARRANDE), *M.Sil.*, Eu.(Czech.);  $\times 0.7$  (5).

**Cliftonoceras** FLOWER in FLOWER & TEICHERT, 1957, p. 141 [\**C. quadratum*; OD]. Smooth, compressed gyrocones with flattened venter, rounded dorsum, and greatest width ventral from center. Sutures with lateral lobes, broad dorsal saddles; ventral sutures either straight or forming slight lobes. Siphuncle subventral, separated by more than diameter of septal foramen from ventral wall; segment sides subparallel in middle, but contracting as they approach septal foramen; necks straight ventrally, recumbent dorsally; thin connecting rings adnate dorsally at anterior end and ventrally at posterior end of each segment. *L.Sil.* or *M.Sil.*, USA(Tenn.); *M.Sil.*, USA(Ind.).—FIG. 275,2. \**C. quadratum*, USA(Tenn.); 2a-c,  $\times 0.5$  (50).

**Cumingsoceras** FLOWER in FLOWER & KUMMEL, 1950, p. 613 [\**Gyroceras elrodi* WHITE, 1882, p. 356; OD]. Compressed, rapidly expanding gyrocones of about 1.5 narrowly separated whorls. Sutures straight and transverse dorsally and ventrally, but with slight lateral lobes. Surface faintly cancellated by slight longitudinal lines and growth lines that define deep ventral hyponomic sinus. Siphuncle small, subcentral; necks recumbent, connecting rings unknown. *M.Sil.*, USA(Ind.-Ill.).—FIG. 275,4. \**C. elrodi* (WHITE), USA(Ind.); 4a-c,  $\times 0.3$  (55).

**Jolietoceras** FOERSTE, 1925, p. 54 [\**J. senescens*; OD]. Compressed, annulate litiucones, gyroconic in early stage, straight, more compressed, more rapidly expanding in later stage. Sutures straight and transverse; surficial annulations sloping strongly to posterior from dorsum to venter on coiled segment of conch, but lacking on straight segment. Siphuncle central; interior unknown. *M.Sil.*, USA (Ill.-Wis.).—FIG. 275,3. \**J. senescens*, USA(Ill.); 3a,b,  $\times 0.3$  (55).



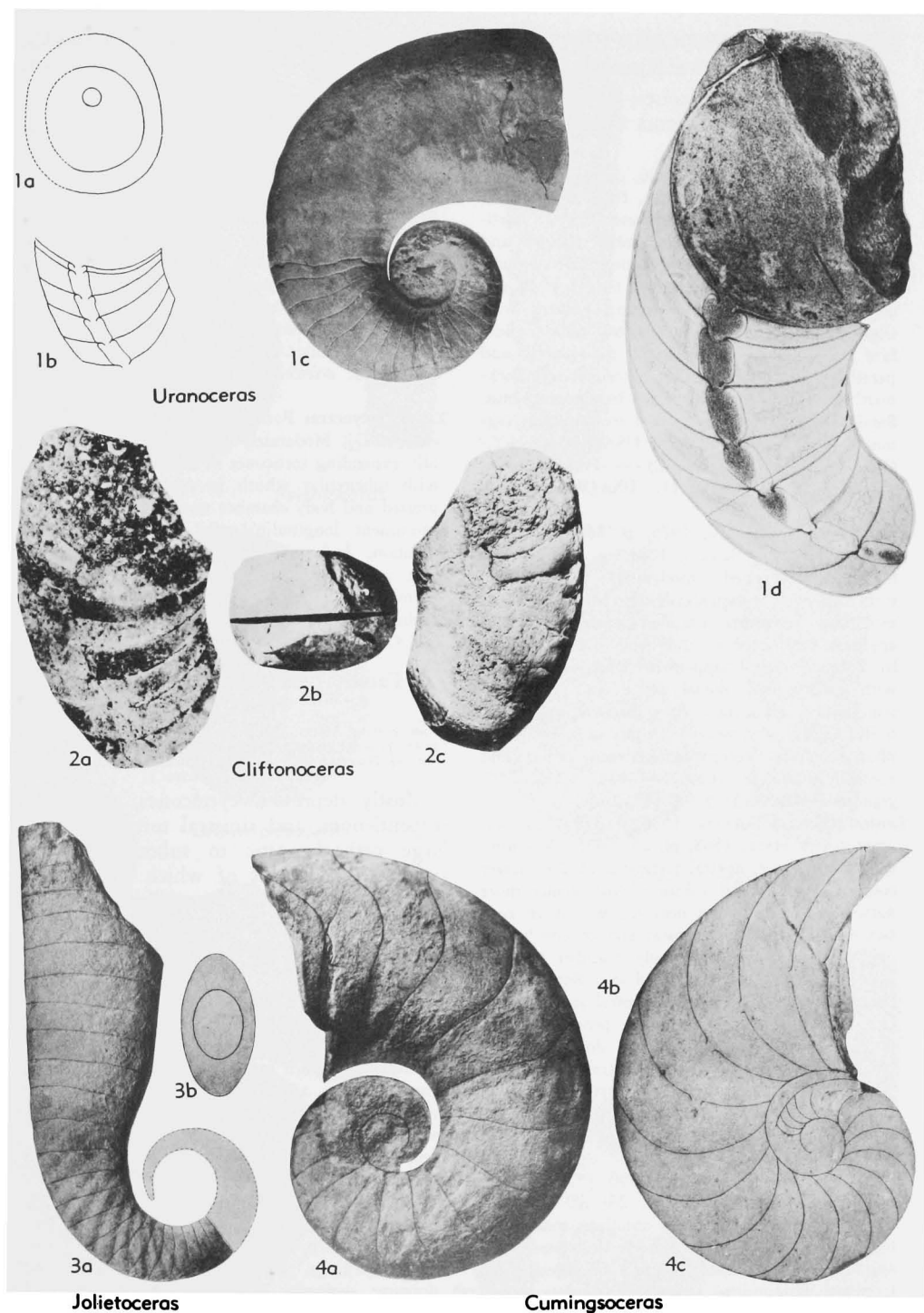


FIG. 275. Uranoceratidae (p. K374).

### Family LECHRITROCHOCERATIDAE Flower in Flower & Kummel, 1950

Dextral costate torticones; siphuncle ventral from center, segments cylindrical. *M. Sil.-U.Sil.*

**Lechritrochoceras** FOERSTE, 1926, p. 367 [*\*Trochoceras desplainensis* MCCHESENEY, 1860, p. 68; OD]. Low-spined, prominently costate dextral torticones of about 2 volutions; umbilicus open and dorsally impressed except in adoral part of outer volution where conch exhibits tendency to uncoil; whorls circular in section. Sutures with slight lateral lobes and low ventral saddles. Surface with relatively prominent annulations and parallel transverse striae that curve strongly backward on venter to define deep hyponomic sinus. Small siphuncle slightly ventral from center; segments cylindrical. *M.Sil., USA (Ill.-Ind.-N.Y.-Ohio-Tenn.-Wis.)-Eu. (Czech.)*.—FIG. 276,5. *\*L. desplainense* (MCCHESENEY), USA (Wis.); 5a,b,  $\times 1$  (57).

**Catyrephoceras** FOERSTE, 1926, p. 368 [*\*Trochoceras giganteum* BLAKE, 1882, p. 223; OD]. Slightly compressed, moderately asymmetrical torticones with subquadragonal whorls in contact, body chamber uncoiled adorally; mature aperture constricted to dumbbell-shaped opening by 2 broad lateral lappets in peristome. Surface with longitudinal dorsal striae and transverse annulations and growth lines that are weak ventrally, outlining hyponomic sinus on venter. Siphuncle slightly eccentric, between center and venter. *M.Sil., Eu. (Eng.)*.—FIG. 276,2. *\*C. giganteum* (BLAKE);  $\times 0.7$  (57).

**Leurotrochoceras** FOERSTE, 1926, p. 373 [*\*Trochoceras aeneas* HALL, 1868, pl. 25; OD]. Very low-spined, gyroconic, dextral torticones of 2 or fewer compressed, flat-sided volutions with venter more narrowly rounded than dorsum; whorls in contact only at extreme adapical end of conch, but neither phragmocone nor body chamber diverges very broadly from preceding whorls. Sutures with lateral lobes and dorsal and ventral saddles. Surface with transverse annulations prominent ventrally, less so laterally, and faint dorsally, annulations forming prominent ventral hyponomic sinus. Siphuncle between center and venter; segments cylindrical. *M.Sil., USA (Iowa-Ill.)*.—FIG. 276,3. *\*L. aeneas* (HALL), USA (Iowa);  $\times 0.7$  (37).

**Peismoceras** HYATT, 1894, p. 500 [*\*Trochoceras optatum* BARRANDE, 1865, pl. 23; SD FOERSTE, 1926]. Slightly compressed, annulate, moderately torticonic gyrocones with whorls in contact only apically, body chamber distinctly divergent. Surface with longitudinal striae and annulations and growth lines that curve adapically on venter to form prominent hyponomic sinus; annulations less prominent toward aperture. Sutures with slight ventral saddles. Siphuncle large, subventral;

segments cylindrical. *M.Sil.-U.Sil., Eu. (Czech.)*.—FIG. 276,1. *\*P. optatum* (BARRANDE); 1a-d,  $\times 0.45$  (5).

**Systrophoceras** HYATT, 1894, p. 502 [*\*Trochoceras arietinum* BARRANDE, 1865, pl. 17; SD FOERSTE, 1926]. Slender-whorled, annulate, faintly torticonic gyrocones of about 2 whorls; whorls depressed, ventrally flattened, free to apex, with large umbilical perforation. Sutures with slight lateral lobes and faint ventral saddles. Surficial annulations and growth lines sloping adapically from dorsum to venter, forming prominent hyponomic sinus. Dorsum longitudinally striated; annulations faint ventrally. Siphuncle slightly ventral from center. *M.Sil., Eu. (Czech.)*.—FIG. 276,6. *\*S. arietinum* (BARRANDE); 6a-d,  $\times 0.45$  (5).

**Trochodictyoceras** FOERSTE, 1926, p. 372 [*\*T. slocomi*; OD]. Moderately asymmetrical, rather rapidly expanding torticones of less than 2 volutions, with subcircular whorls in contact but not impressed and body chamber uncoiled. Surface with prominent longitudinal ribs, at least on early volution, and prominent transverse annulations that curve backward from dorsum to venter, forming prominent ventral hyponomic sinus. Siphuncle unknown. *M.Sil., USA (Ill.)*.—FIG. 276,4. *\*T. slocomi*; 4a,b,  $\times 0.7$  (57).

### Family NEPHRITICERATIDAE Hyatt, 1894

[*nom. correct.* SWEET, herein (*ex Nephritidae* HYATT, 1894)] [=Rhadinoceratidae HYATT in ZITTEL, 1900, incl. Sphyradoceratidae FOERSTE, 1926 (*partim*); Rhadinoceracea KINDLE & MILLER, 1939 (*superfam.*)]

Mostly depressed cyrtocones, gyrocones, serpenticones, and sinistral torticones with large orthochoanitic to suborthochoanitic siphuncle, segments of which tend to be somewhat inflated; siphuncle subcentral or displaced slightly toward either dorsum or venter. *L.Dev.-M.Dev.*

**Nephriticeras** HYATT, 1884, p. 300 [*\*Nautilus bucinum* HALL, 1860, p. 104; OD] [=?*Cyrtoceras* CONRAD, 1838, p. 117 (may be valid sr. subj. syn.)]. Depressed serpenticones of 1.5 or 2 volutions that are in contact and shallowly impressed along adoral part of phragmocone and adjacent part of body chamber; aperture transverse; peristome with broad dorsal and ventral recesses. Sutures in early stages with dorsal and ventral saddles; in later stages with broad shallow dorsal and ventral lobes; or sutures virtually straight, or retaining slight ventral saddles. Surface with sharp, longitudinal lirae and fine transverse markings. Siphuncle between center and dorsum; segments tubular to faintly expanded within camerae. *M.Dev., N.Am. (N.Y.-Pa.-?Md.-?Iowa-Ind.-Mo.-?Ont.)*.—FIG. 277,5. *\*N. bucinum* (HALL), USA (N.Y.); 5a-c,  $\times 0.7$  (87). [Topotypes of the inadequately diagnosed type-

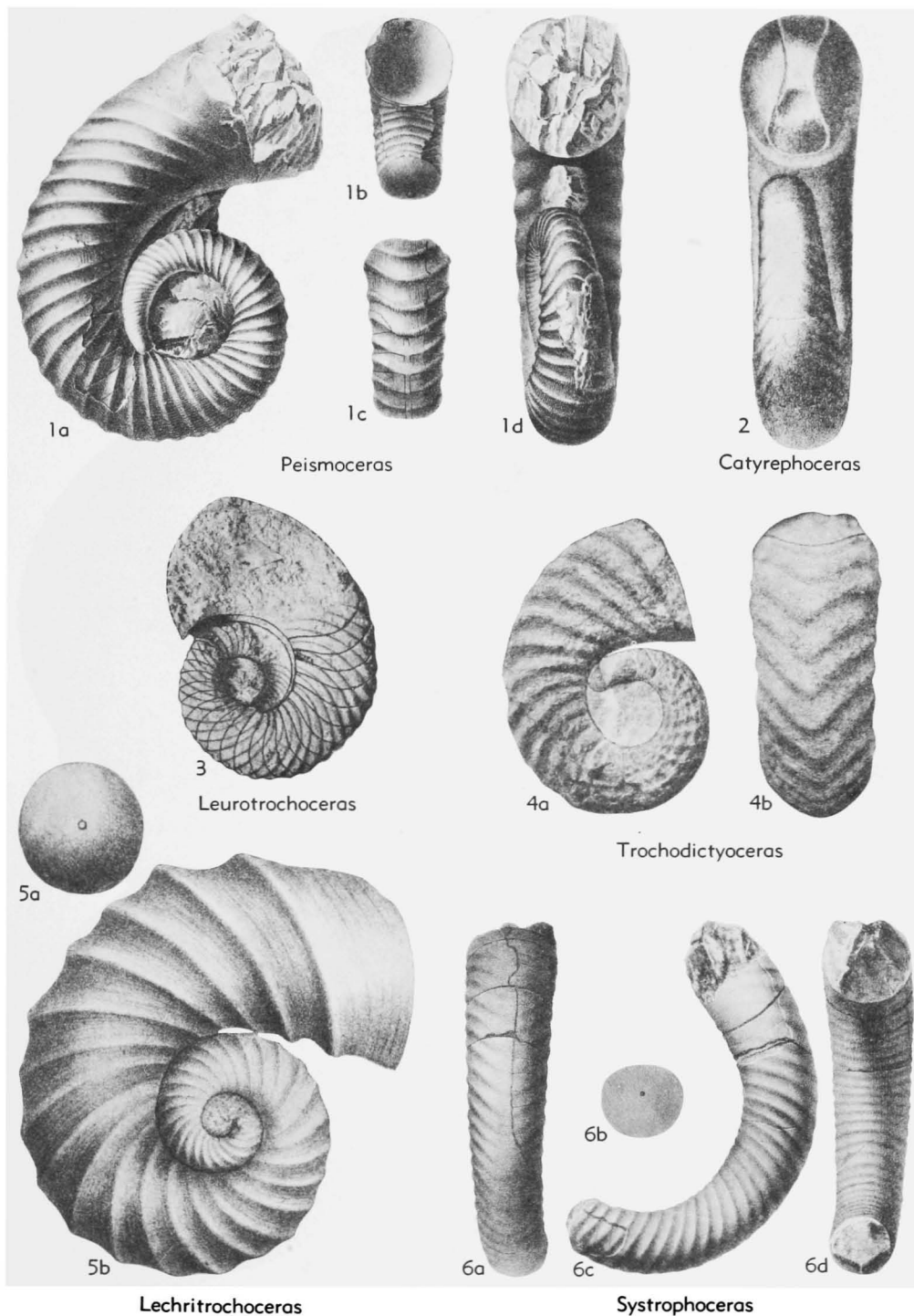


FIG. 276. Lechritrochoceratidae (p. K376).

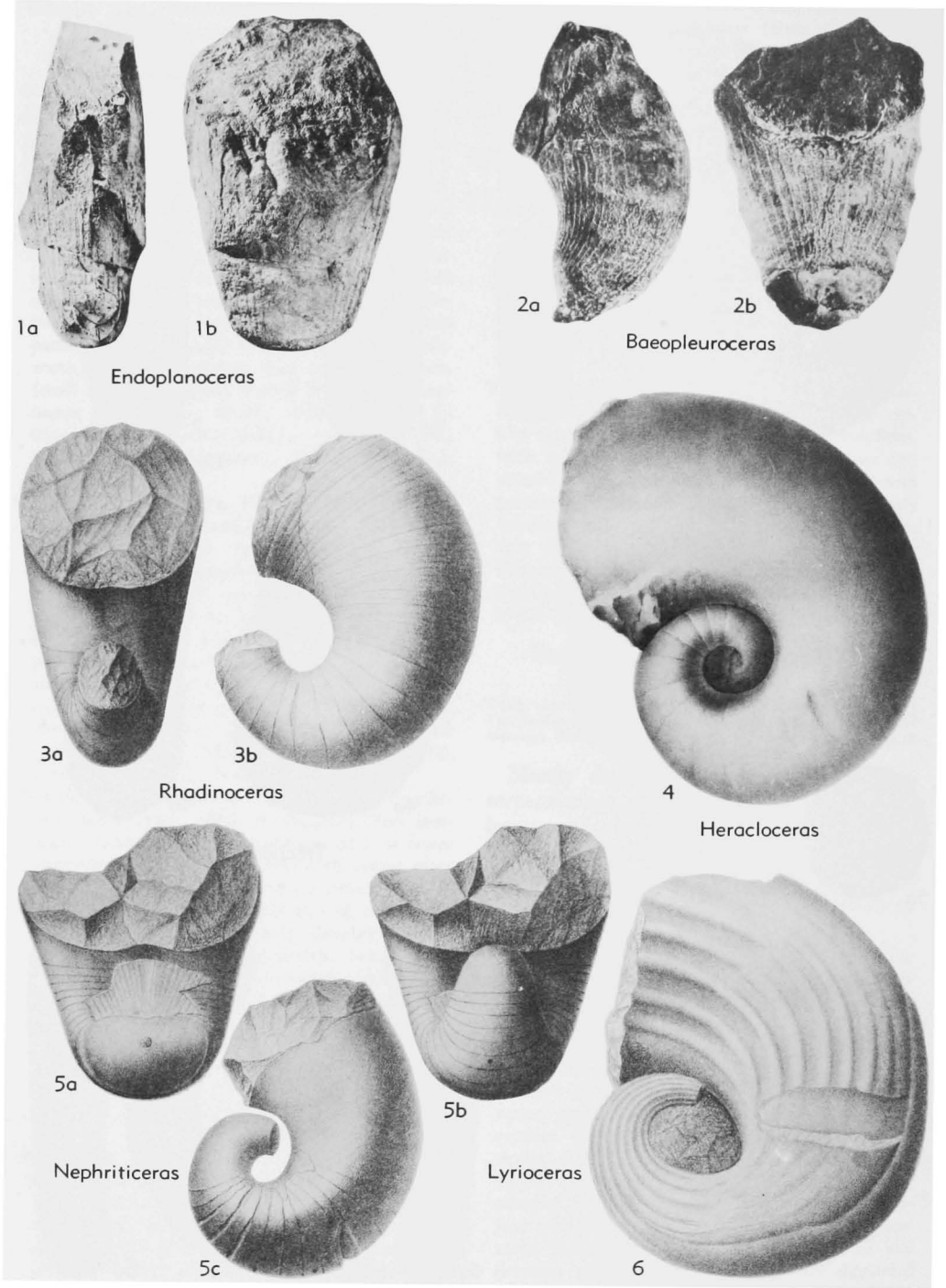


FIG. 277. Nephriticeratidae (p. K376, K380).

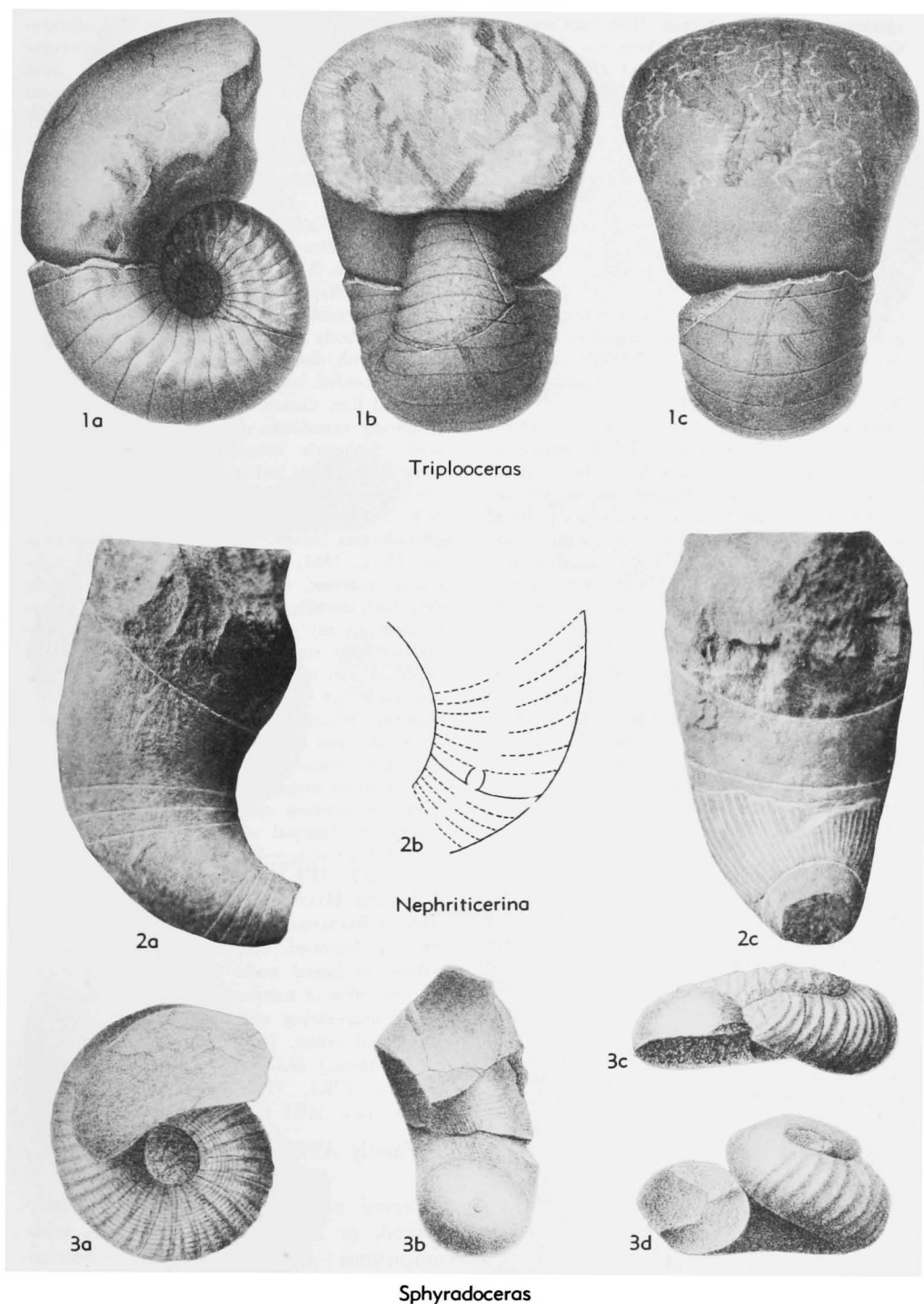


FIG. 278. Nephriticeratidae (p. K380).

species of *Cyrtoceras* CONRAD, 1838 (= *Cyrtoceras* CONRAD, 1838, *nom. null.*; *Certoceras* VANUXEM, (*nom. null.*), illustrated by HALL (86, 87) have, since 1894, been referred to *Nephriticeras*. If these specimens are conspecific with the types of *C. maximum* CONRAD, then *Nephriticeras* is a junior subjective synonym of *Cyrtoceras* and must be suppressed in its favor. However, FLOWER (37) expresses doubt about the specific identity of HALL's specimens and the never-figured and inadequately described type(s) of CONRAD's *C. maximum*. This doubt will probably always remain, hence it seems best to regard *Cyrtoceras* CONRAD, 1838, as a valid, but unrecognizable genus of Devonian nautiloids that may, but cannot be proven to be the oldest available name for the many well-known species now assigned to *Nephriticeras* HYATT, 1884.]

**Baeopleuroceras** WILLIAMS in COOPER & WILLIAMS, 1935, p. 851 [*\*B. incipiens*; OD] [= *Baepleuroceras* MILLER, 1939 (*nom. null.*)]. Short, rapidly expanding, depressed cyrtocones, curved through at least 90 degrees. Surficial annulations deflected adapically on venter to form hyponomic sinus. Body chamber one-half length of conch. Siphuncle subcentral; segments slightly expanded within camerae. *M.Dev.*, N.Am.(N.Y.-Pa.-Ont.).—FIG. 277,2. *\*B. incipiens*, USA(N.Y.); *2a,b*,  $\times 1$  (13).

**Endoplanoeceras** FLOWER, 1938, p. 53 [*\*E. gomphus*; OD]. Depressed, rapidly enlarging, faintly cyrtoconic conchs with longitudinal lirae and faintly contracted aperture. Siphuncle between center and concave (?dorsal) side; form of segments unknown. *M.Dev.*, USA(N.Y.).—FIG. 277,1. *\*E. gomphus*; *1a,b*,  $\times 0.3$  (21).

**Heracloceras** TEICHERT, 1940, p. 590 [*nom. subst. pro Gigantoceras* HYATT in ZITTEL, 1900 (*non* HOLLAND, 1893)] [*\*Gyroceratites* (*Nautilus?*) *inelegans* MEEK, 1871, p. 89; OD]. Large, compressed, rapidly expanding gyrocones of 2 or 3 virtually contiguous volutions and body chamber half a volution long. Sutures with shallow lateral lobes and low dorsal and ventral saddles. Surface of inner volutions with faint transverse ribs. Siphuncle slightly eccentric, between center and venter; necks suborthochoanitic or cyrtocochanitic; shape of segments unknown. *M.Dev.*, N.Am.(Mich.-Ky.-Ohio-Ont.).—FIG. 277,4. *\*H. inelegans* (MEEK), USA(Ohio);  $\times 0.25$  (121).

**Lyrioceras** FOERSTE, 1927, p. 193 [*\*Gyroceras liratum* HALL, 1860, p. 104; OD]. Obscurely annulate gyrocones or serpenticones of about 2 volutions; early whorls subcircular, later ones depressed. Surface with fine transverse striae, widely spaced, faint transverse annulations, and bold longitudinal ribs that are prominent dorsally and laterally but faint ventrally. Siphuncle central or subcentral. *M.Dev.*, N. Am. (Mich. - N.Y. - ?Pa. - ?Ont.).—FIG. 277,6. *\*L. liratum* (HALL), USA (N.Y.);  $\times 0.7$  (87).

**Nephriticerina** FOERSTE, 1927, p. 194 [*\*N. alpenensis*; OD]. Depressed, rapidly enlarging cyrtocones with oblique aperture sloping adapically from venter to dorsum, and surface with prominent longitudinal ribs and fine transverse lines. Siphuncle central or slightly displaced toward dorsum; segments inflated within camerae. *M.Dev.*, N. Am. (Md.-Mich. - N.Y. - Ohio - Pa. - ?Nev. - Man. - Ont.).—FIG. 278,2. *\*N. alpenensis*, USA (Mich.); *2a-c*,  $\times 0.7$  (58).

**Rhadinoceras** HYATT, 1894, p. 530 [*\*Nautilus cornulum* HALL, 1876, pl. 60; SD FOERSTE, 1927]. Similar to *Nephriticeras*, but whorls subcircular and less rapidly enlarging; without impressed zone and body chamber tending to become free. Surface with distinct transverse lamellose growth bands crowded into folds toward apertural margin, and fine, distant, irregular, longitudinal lirae producing cancellated pattern on some parts of shell. Siphuncle between center and dorsum; form of segments unknown. *M.Dev.*, USA(N.Y. - ?Wis.).—FIG. 277,3. *\*R. cornulum* (HALL), N.Y.; *3a,b*,  $\times 0.7$  (87).

**Sphyradoceras** HYATT, 1884, p. 298 [*\*Trochoceras clio* HALL, 1861, p. 108; OD]. Relatively high-spired, annulate, sinistral torticones with slightly depressed, dorsally impressed whorls; early phragmocone rapidly expanding, gyroconic, laterally nodose; later stages torticonic and lateral nodes modified into transverse annulations; annulations prominent on phragmocone, absent on body chamber; annulations and growth lines transverse on dorsum and in dorsolateral zones, but forming distinct hyponomic sinus on venter. Surface also bears distinct longitudinal raised lines. Siphuncle central or between center and dorsum; segments moniliform, internal structure unknown. *L.Dev.*, USA(N.Y.).-Can.—FIG. 278,3. *\*S. clio* (HALL), Schoharie F.; *3a-d*,  $\times 1$  (87).

**Triplooceras** HYATT, 1884, p. 285 [*\*Nautilus insperatus* BARRANDE, 1877; OD]. Coiled conchs of about 2 depressed, dorsally impressed volutions; 3 rows of lateral nodes formed in early stages at intersection of transverse and longitudinal lirae, nodes disappearing adorally. Siphuncle between center and venter. [Said by FLOWER (10) to be cyrtocochanitic.] *M.Dev.*, USA(N.Y.).-Eu.(Czech.).—FIG. 278,1. *\*T. insperatum* (BARRANDE), Czech.; *1a-c*,  $\times 0.7$  (5).

### Family APSIDOCERATIDAE Hyatt, 1884

Curved or coiled, smooth, transversely marked, or laterally costate, conchs with conspicuous hyponomic sinus. Section primitively triangular, with rounded dorsum and flattened venter; later section much broader, impressed dorsally in tightly coiled forms. Sutures with lateral lobes in primi-

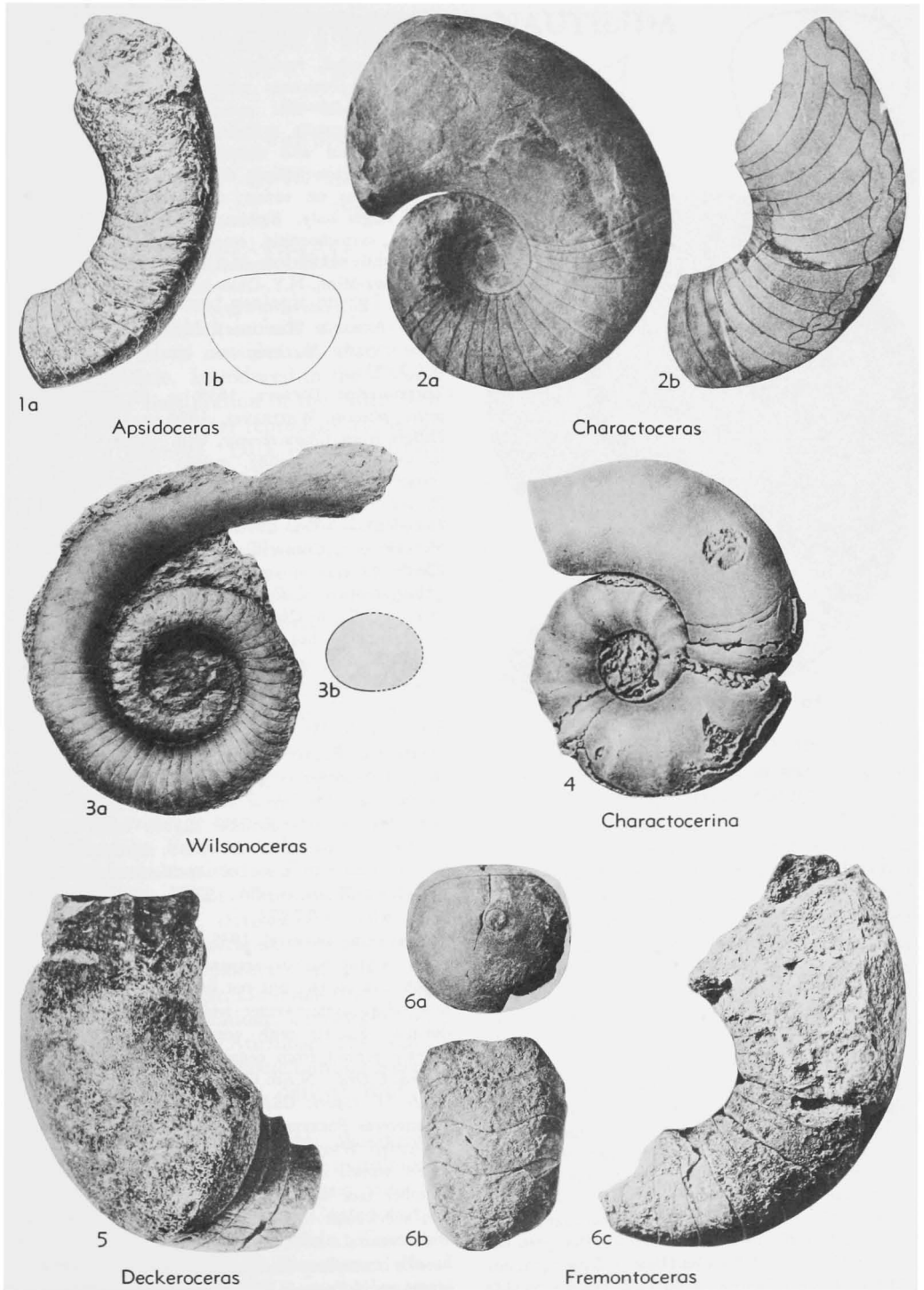


FIG. 279. Apsidoceratidae (p. K382).



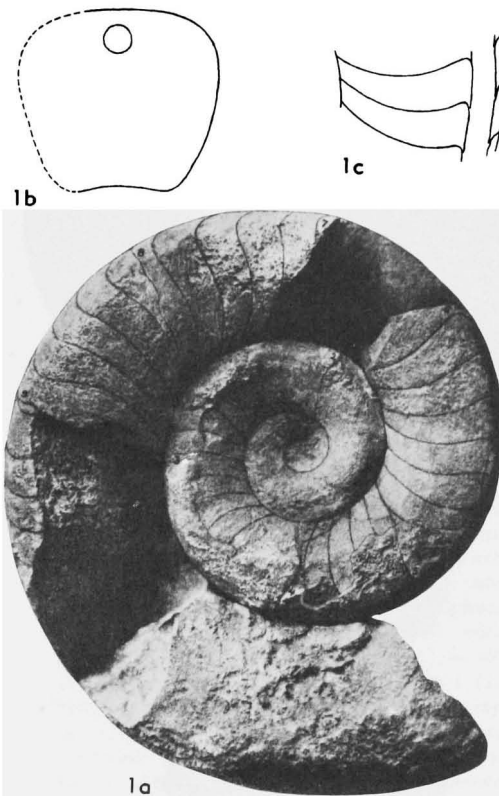


FIG. 279A. *\*Chidleyenoceras chidleyense* (FOERSTE)  
(Apsidoceratidae) (p. K382).

tive forms; no lateral lobes but broad ventral lobe in more advanced species with broader section. Siphuncle cyrtochoanitic, empty; segments variously expanded and siphuncle variable in position, but never close to either dorsum or venter. *M.Ord.*-*U.Ord.*

**Apsidoceras** HYATT, 1884, p. 289 [*\*Gyroceras* (*Lituites*) *magnificum* BILLINGS, 1857, p. 307; OD]. Conch curved or loosely coiled; whorls free, subtriangular, with rounded dorsum and flattened venter. Sutures primitively with lateral lobes, but ventral lobe weak or wanting; more specialized species with strongly developed ventral lobe but reduced lateral lobes. Siphuncle between center and venter, cyrtochoanitic, empty; segments relatively slender. [Supposedly phylogerontic species contract gradually over a considerable part of the conch.] ?*M.Ord.*, Can.(Que.); *U.Ord.*, Can. (Anticosti Is.-L.Cornwallis Is.-Man.-Ont.)-Greenl.-Eu.(Norway).—FIG. 279,1. *A. elegans* TROEDSSON, *U.Ord.*, Greenl.; 1a,b,  $\times 0.3$  (194).

**Charactoceras** FOERSTE, 1924, p. 234 [*\*Trochoceras?* *baeri* MEEK & WORTHEN, 1865, p. 263; OD]. Closely coiled, rapidly expanding, dorsally impressed serpenticones with flattened venter and rounded sides that converge toward dorsum. Sutures essentially straight laterally, but forming broad ventral and dorsal lobes. Surface with transverse growth lines that form distinct hyponomic sinus on venter, and transverse ribs in early stages only. Siphuncle between center and venter, cyrtochoanitic, empty; segments expanding slightly within camerae. *U.Ord.*, N.Am.(Colo.-Ind.-Iowa-Minn.-N.Y.-Ohio-Anticosti Is.-Baffin Is.)-Greenl. - Eu.(Est. - Norway).—FIG. 279,2. *\*C. baeri* (MEEK & WORTHEN), USA(Ohio); 2a, lat. view,  $\times 0.4$ ; 2b, long. sec. through siphuncle,  $\times 0.7$  (53).

**Charactocerina** FOERSTE, 1935, p. 85 [*\*Eurystomites plicatus* WHITEAVES, 1896, p. 396; OD]. Differs from *Charactoceras*, with which it agrees in section and coiling, mainly in presence of costae in dorsolateral regions of conch. *U.Ord.*, N. Am.(?Ind. - Wyo. - Cornwallis Is. - Man.) - Eu. (Sweden).—FIG. 279,4. *C. eximia* SWEET & MILLER, Can.(Cornwallis Is.);  $\times 0.7$  (182).

?**Chidleyenoceras** SHIMIZU & OBATA, 1935, p. 368 [*\*Eurystomites chidleyense* FOERSTE, 1928, p. 58; OD]. Similar to *Charactocerina* in gross form and ornamentation, but whorls less strongly depressed; siphuncle large, subventral, apparently orthochoanitic with tubular segments. *M.Ord.*, N.Am.(Can.). —FIG. 279A,1. *\*C. chidleyense* (FOERSTE), Labrador; 1a,  $\times 0.45$ ; 1b,c, diagram. secs. (61).

**Deckeroceras** FOERSTE, 1935, p. 92 [*\*D. adaense*; OD]. Cyrocones or gyrocones of more rounded section than *Apsidoceras* but with ventral sutural lobe. Mature body chamber slightly inflated. Siphuncle between center and venter; segments similar in outline to those of *Apsidoceras*. *U.Ord.*, USA(Iowa-Okla.).—FIG. 279,5. *\*D. adaense*; USA(Okla.);  $\times 0.7$  (73).

**Fremontoceras** FOERSTE, 1935, p. 89 [*\*F. loperi*; OD]. Gyrocones or serpenticones with whorls possibly in contact but not impressed; whorl section subquadrate; venter wider and flatter than dorsum. Sutures with ventral lobes. Siphuncle slightly ventral from center; structure unknown. *M.Ord.*-*U.Ord.*, N.Am.(Colo.-N.Y.-Que.).—FIG. 279,6. *\*F. loperi*; USA(Colo.); 6a-c,  $\times 0.4$  (73).

**Wilsonoceras** FOERSTE, 1929, p. 180 [*\*Trochoceras mccharlesi* WHITEAVES, 1890, p. 81; OD]. Conch coiled, whorls in contact but not impressed, body chamber free and widely divergent; whorl section subcircular to slightly depressed, but sutures with ventral lobes of *Apsidoceras*. Siphuncle broadly cyrtochoanitic, slightly eccentric, between center and dorsum. *U.Ord.*, N.Am.(Wyo.-Baffin Is.-Man.).—FIG. 279,3. *W. squawcreekense* MILLER, Baffin Is.; 3a,b,  $\times 0.16$  (137).



## NAUTILOIDEA—NAUTILIDA

By BERNHARD KUMMEL

[Museum of Comparative Zoölogy, Harvard College]

with Systematic Descriptions as Indicated

By W. M. FURNISH and BRIAN F. GLENISTER

[State University of Iowa, Iowa City]

## CLASSIFICATION

The evolution and geologic history of the nautiloid taxa which include modern *Nautilus* has received considerable attention in the past decade. Introduced in the *Treatise* is a revised classification of the order Nautilida, which *Nautilus* represents as the last surviving member. Data on the relationships and history of the group are discussed.

One of the most interesting aspects of the history of nautiloid studies is the dominance of one man, ALPHEUS HYATT. The classification presented by HYATT in the 1900 edition of the Zittel's "Text-book of Palaeontology" is still in vogue among several modern students of nautiloid cephalopods (MILLER, DUNBAR & CONDRA, 1933; MILLER & YOUNGQUIST, 1949; SCHMIDT, 1951), even though most students readily agree that HYATT's five main divisions were far from satisfactory. The first serious attempt to present a new classification of the comprehensive assemblage termed Nautiloidea was published by FLOWER & KUMMEL (1950). Their scheme consisted of 75 families placed in 14 orders. Their Nautilida began with the Liroceratidae, derived from the Barrandeoceratida [Barrandeocerida], and included the Ehippioceratidae, Paranautilidae, Clydonautilidae, Gonionautilidae, Nautilidae, Paracenoceratidae, Cymatoceratidae, Hercoglossidae, and Aturiidae. The Nautilidae and other post-Triassic families were interpreted to have been derived from the Paranautilidae.

In the FLOWER & KUMMEL classification the remaining curved to coiled nautiloids of the Devonian through Triassic were included in three orders—Centroceratida, Rutoceratida and Solenochilida. These authors made clear that their proposed classification was a "progress report" that could serve as a working hypothesis and stimulant to other students.

A tendency toward reducing the number of orders of "Nautiloidea" in recent years is discernible—a natural result of accumulation of more data and reflection on the older schemes. The principal difficulty has been that the origin and relationships of the various "orders" of Devonian to Recent coiled nautiloids are not well known. Derivation of the Nautilida, Solenochilida, Centroceratida, and Rutoceratida from the Barrandeoceratida by FLOWER & KUMMEL was inferred with considerable misgivings, since no concrete evidence for this relationship was available, but it followed a traditional interpretation.

In recent years FLOWER (40, 42) has strongly advocated the view that the Rutoceratidae are derived not from coiled Silurian ancestors but from cyrtconic and breviconic genera of the order Oncoceratida [Oncocerida]. The best syntheses to date of the Rutoceratidae are by FLOWER (32, 42) but the complete evidence for the derivation of the group from the Oncocerida has not as yet been published.

My own studies lead to complete agreement with FLOWER on this interpretation.

That the late Paleozoic Tainoceratidae and Koninckioceratidae stem from the Rutoceratidae is now widely accepted.

On the basis of a very detailed examination of the initial whorls of *Centroceras* (M. Dev.), FLOWER (40) came to the conclusion that the Centroceratidae most likely stemmed from the Tetragonoceratidae (here included in the order Nautilida). The nature of the evidence, however, did leave room for other interpretations and he advocated retaining the two families in separate orders. Interpretations of the origin of post-Triassic nautiloids were completely revised when I demonstrated (114), that the origin of the Nautilidae was in the family Syringonautilidae (order "Centroceratida," here included in Nautilida) and not

in the Paranautilidae (=Liroceratidae) as previously advocated.

Mounting evidence thus seems to support conclusions that (1) a majority of the Devonian-through-Triassic nautiloids belong to one of two main evolving lines, the rutoceratid or the centroceratid stocks,<sup>1</sup> and (2) the rutoceratids arose from cyrtoconic and breviconic Oncocerida and the centroceratids most probably from the rutoceratid stock (through Tetragonoceratidae). This leaves two groups whose ancestry is still somewhat puzzling, the liroceratids and the aipoceratids. SHIMANSKIY (166) suggested an origin of the liroceratids from the Rutoceratidae, but the evidence, to be discussed later, is not very convincing. At the same time, no close connection has been found to link the liroceratids with the Barandeocerida. No one has yet presented evidence to give any concrete indication of the origin of the aipoceratids (formerly known as solenochilids). The general consensus seems to be that the ancestors of this group are to be found in the Rutoceratidae (42, 116).

Paleontological evidence directs attention to four main stocks of Devonian-through-Triassic curved to coiled nautiloids, all of which became extinct by the close of the Triassic (Fig. 280). The post-Triassic nautiloids form an additional homogeneous unit. Two of the Paleozoic stocks can be tied directly or indirectly to the Oncocerida. The two remaining stocks are judged to have the same origin (through the Ruto-

ceratidae) not so much on the basis of any direct evidence as from a lack of any other known potential ancestral group. Any system of classification should reflect as nearly as possible an actual or inferred phylogeny. In the case at hand it seems inescapable that we are dealing with a fairly homogeneous group of families, each of which represents distinct adaptive trends. Overemphasis on the differences between the main stocks only tends to obscure the overall similarity and probable common origin of the groups. It is for this reason that I advocate that all these groups of Devonian-to-Recent coiled nautiloids should be placed in a single order, Nautilida. Each of the main evolving stocks, then, can be grouped as a superfamily, namely the Tainocerataceae, Trigonocerataceae, Aipocerataceae, Clydonautilaceae, and Nautilaceae. Each of these superfamilies are morphologically distinct, and, in spite of numerous cases of homeomorphy, it is generally possible to assign families and genera on the basis of fundamental conch patterns and geologic distribution.

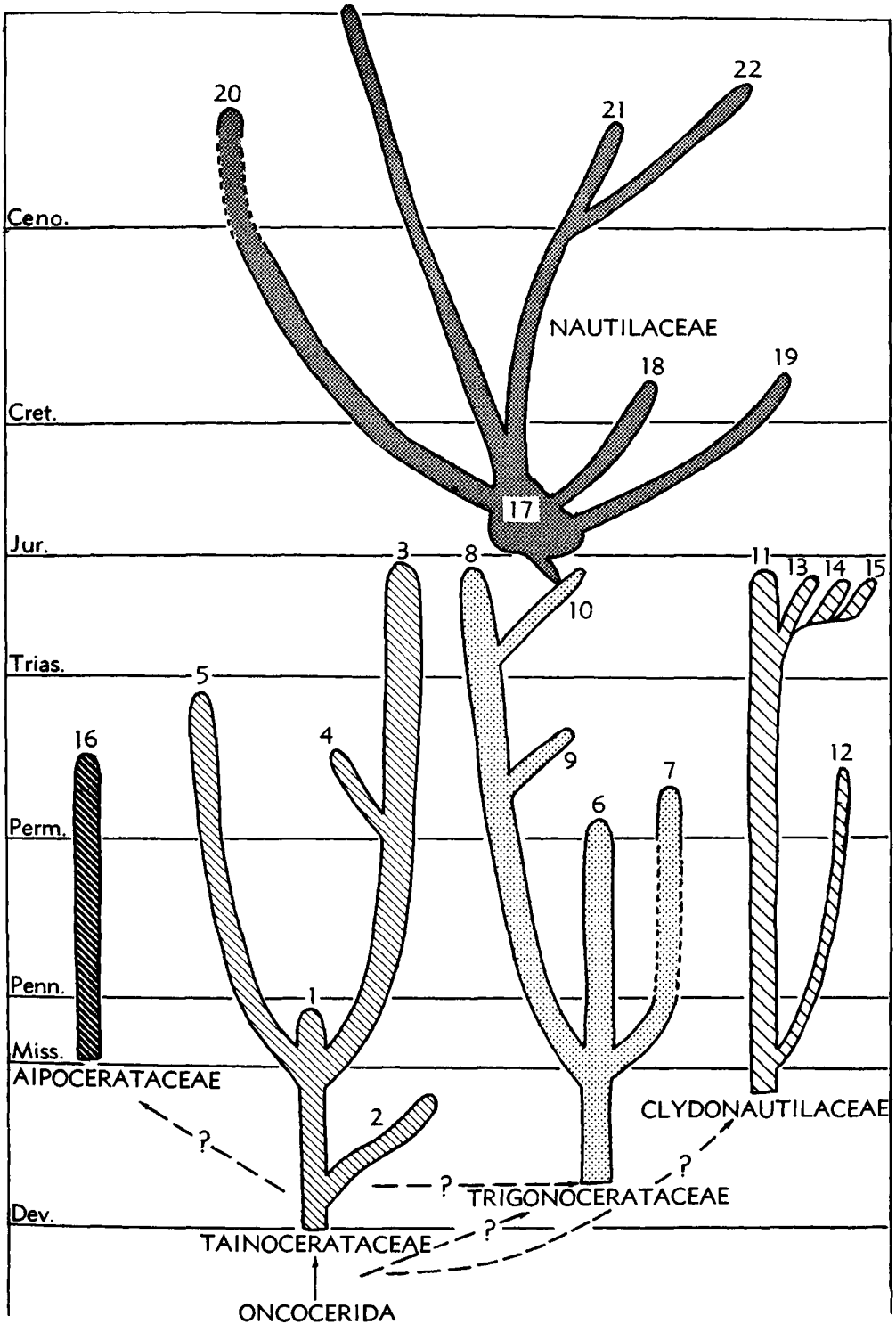
Within the better-studied families of the Nautilida one can recognize one, or at times two, genera with a basic conch pattern that is generally simple and unspecialized in any way. These genera are the longest-ranging of any in the family, have the largest number of described species, and the greatest geographic distribution. The large numbers of "species" I interpret as merely a reflection of their greater abundance. The evolutionary history of these genera shows only slow change in general. Most of the remaining genera within the family groups can most easily be understood as offshoots of the main evolving line. These offshoots generally differ from the parent stock in only one feature, or, less commonly, two

<sup>1</sup> Application of the Law of Priority has necessitated changes in nomenclature in four out of five nautilid superfamilies. The Tainocerataceae are essentially the "rutoceratid stock," whereas the Trigonocerataceae correspond closely to the Centroceratida of FLOWER & KUMMEL. The Clydonautilaceae are the "liroceratids" and the Aipocerataceae the "solenochilids" of earlier, and even more recent, literature. The reasons for these nomenclatural adjustments will be apparent from the systematic descriptions of the superfamilies.

FIG. 280. (Facing page.) Phylogeny of the Nautilida (Kummel, n).

- |                       |                                |                      |
|-----------------------|--------------------------------|----------------------|
| 1. Rutoceratidae      | 9. Permoceratidae <sup>1</sup> | 16. Solenochilidae   |
| 2. Tetragonoceratidae | 10. Syringonautilidae          | 17. Nautilidae       |
| 3. Tainoceratidae     | 11. Liroceratidae              | 18. Paraceratidae    |
| 4. Rhiphaeoceratidae  | 12. Ephippioceratidae          | 19. Pseudonautilidae |
| 5. Koninckioceratidae | 13. Clydonautilidae            | 20. Cymatoceratidae  |
| 6. Centroceratidae    | 14. Gonionautilidae            | 21. Hercoglossidae   |
| 7. Trigonoceratidae   | 15. Siberionautilidae          | 22. Aturiidae        |
| 8. Grypoceratidae     |                                |                      |

<sup>1</sup> L.Perm. instead of U.Perm.



characters. It is generally expressed by the addition of some ornamental feature, by a tendency toward greater involution or toward greater compression, or by modification of the sutures. As a general rule, genera derived from the main evolving stock have few species and restricted geographic distributions.

The principal criteria useful for establishing affinities between genera and between families are (1) conch pattern, which includes shape of whorls, degree of involution, nature of sutures, presence or absence of ornamentation, (2) stratigraphic range, and (3) ontogeny. None of these criteria can be used singly, but one must balance the data in terms of the whole. Elaboration of these points will be made in discussions of each superfamily group.

Before proceeding it is desirable to notice recent arrangements of nautilid families published by other authors.

A most significant contribution to the systematics of the Nautilida has been made by V. N. SHIMANSKIY (1957). In his scheme this order is divided into five suborders and 11 superfamilies as follows (numbers in parentheses preceding family names correspond to numbers shown in Figure 281):

### *Classification of Nautilida by Shimanskiy*

#### Order NAUTILIDA

##### Suborder RUTOCERATINA

###### Superfamily Rutocerataceae

- (1) Rutoceratidae HYATT, 1884
- (2) Neptunoceratidae SHIMANSKIY, 1957

###### Superfamily Solenochilaceae

- (3) Litogyroceratidae SHIMANSKIY, 1957
- (4) Solenochilidae HYATT, 1893
- (5) Scyphoceratidae RUZHENTSEV & SHIMANSKIY, 1954
- (6) Dentoceratidae RUZHENTSEV & SHIMANSKIY, 1954

##### Suborder TAINOCERATINA

###### Superfamily Tainocerataceae

- (7) Tetragonoceratidae FLOWER, 1945
- (8) Mosquoceratidae RUZHENTSEV & SHIMANSKIY, 1954
- (9) Tainoceratidae HYATT, 1883
- (10) Pleuronautilidae HYATT in ZITTEL, 1900

###### Superfamily Encoilocerataceae

- (11) Encoiloceratidae SHIMANSKIY & ERLANGER, 1955

###### Superfamily Temnocheilaceae

- (12) Temnocheilidae MOJSISOVICS, 1902
- (13) Gzheloceratidae RUZHENTSEV & SHIMANSKIY, 1954

###### Superfamily Rhiphaeocerataceae

- (14) Rhiphaeoceratidae RUZHENTSEV & SHIMANSKIY, 1954
- (15) Actubonautilidae RUZHENTSEV & SHIMANSKIY, 1954

##### Suborder CENTROCRATINA

###### Superfamily Tribolocerataceae

- (16) Triboloceratidae HYATT, 1884

###### Superfamily Centrocerataceae

- (17) Centroceratidae HYATT in ZITTEL, 1900
- (18) Thrinoceratidae RUZHENTSEV & SHIMANSKIY, 1954
- (19) Permoceratidae MILLER & COLLINSON, 1953
- (20) Domatoceratidae MILLER & YOUNGQUIST, 1949
- (21) Grypoceratidae HYATT in ZITTEL, 1900
- (22) Syringonautilidae MOJSISOVICS, 1902

##### Suborder LIROCRATINA

###### Superfamily Lirocerataceae

- (23) Koninckioceratidae HYATT, 1893
- (24) Liroceratidae MILLER & YOUNGQUIST, 1949
- (25) Ephippioceratidae MILLER & YOUNGQUIST, 1949
- (26) Paranautilidae KUMMEL, 1950

###### Superfamily Clydonautilaceae

- (27) Gonionautilidae KUMMEL, 1950
- (28) Siberionautilidae POPOV, 1951
- (29) Pseudonautilidae HYATT in ZITTEL, 1900
- (30) Clydonautilidae HYATT in ZITTEL, 1900

##### Suborder NAUTILINA

###### Superfamily Nautilaceae

- (31) Nautilidae D'ORBIGNY, 1840 [*recte* DE BLAINVILLE, 1825]
- (32) Hercoglossidae SPATH, 1927
- (33) Aturidae HYATT, 1894 [*recte* Aturiidae HYATT, 1894]
- (34) Cymatoceratidae SPATH, 1927

SHIMANSKIY outlined the basis for recognizing the larger systematic units as follows: (1) basic morphological distinctness, (2) differing ontogenetic development as seen in related and co-ordinated groups, (3) chronological distinctness or interrelatedness, (4) specialized paths of development for the group as a whole. SHIMANSKIY's phylogenetic diagram showing his interpretation of the interrelationships of the families (Fig. 281) differs from mine (Fig. 280) in a number of significant areas. SHIMANSKIY's scheme includes five suborders, 11 superfamilies, and 34 families, whereas my arrangement recognizes only five superfamilies and 24 families. The superfamilies of my classification are comparable to SHIMANSKIY's suborders; reduction in the number of families results from placing many in synonymy.

Multiplication of taxonomic units tends to obscure relationships.

Conversely, as illustrated in WIEDEMANN'S (1960) classification of a large assemblage

of Cretaceous nautiloids from Spain, too inclusive grouping together of forms also obscures significant distinctions and relationships. WIEDEMANN concluded that only

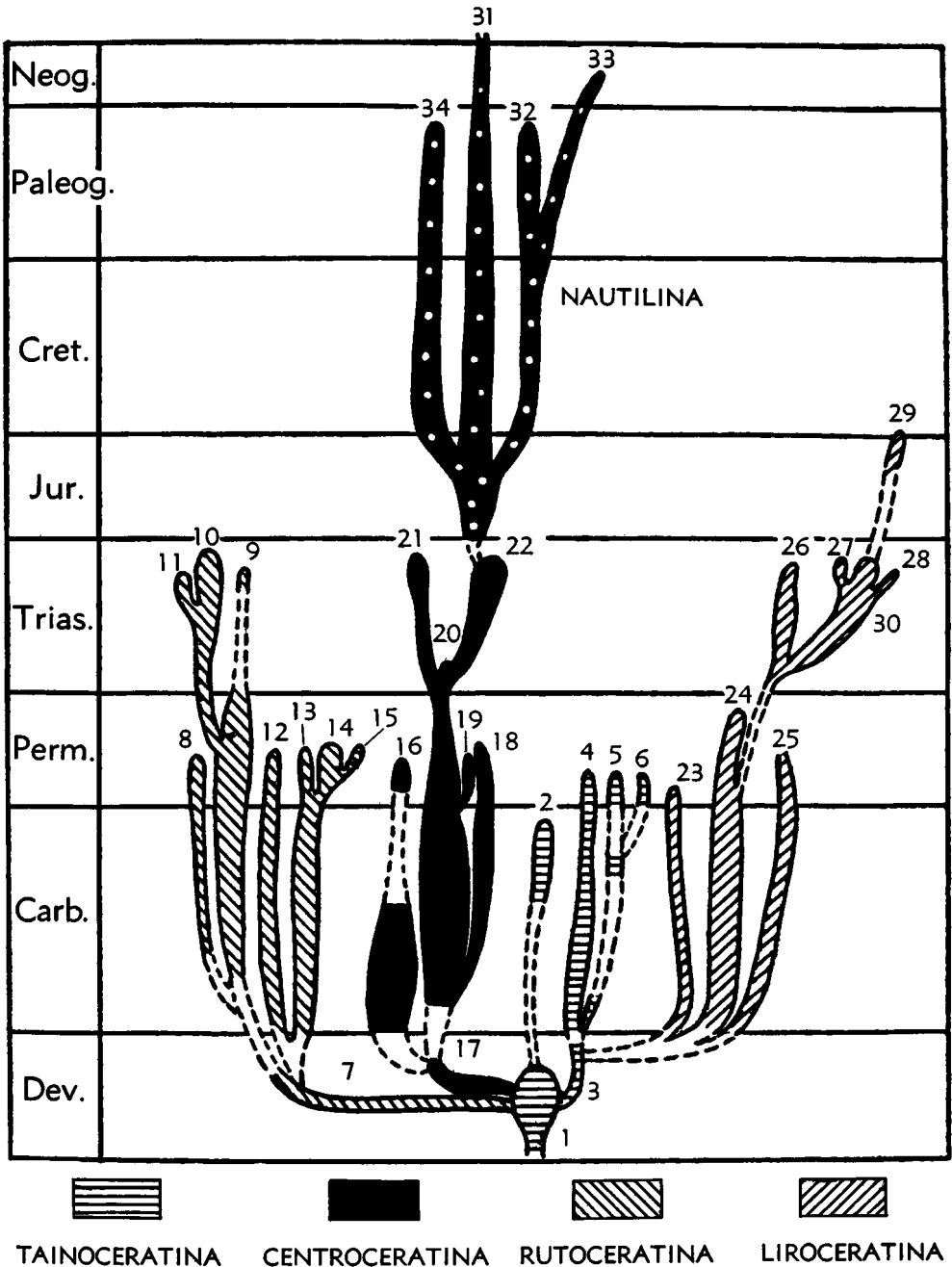


FIG. 281. Phylogeny of the Nautilida as interpreted by V. N. SHIMANSKIY. Suborders are distinguished by patterns and numbers serve for identification of families as given in the list showing SHIMANSKIY'S classification of Nautilida (166).

suture patterns are trustworthy guides for classification and thus he assigned to the subfamily Nautilinae *Hercoglossa* and *Aturia*, as well as *Nautilus* and other Nautilidae.

## PHYLOGENY

In essence, the evolutionary history of curved and coiled nautiloids from Devonian to Recent is marked by the differentiation of four well-defined stocks of Devonian-through-Triassic age; followed by near extinction of all toward the close of the Triassic, and then a renewed but weak radiation in the Jurassic encompassing the superfamily Nautilaceae (113, 115) (Fig. 280).

The Devonian-through-Triassic stocks are each characterized by their own basic conch form. Smooth, convolute to involute shells with straight-to-highly-sinuuous sutures typify the Clydonautilaceae. Straight-to-curved or loosely coiled, evolute shells with wings, frills, spines, nodes, or ribs are characteristic of the Tainocerataceae. Evolute-to-involute, generally compressed conchs, mostly unornamented, distinguish the Trigonocerataceae. Finally, the shells with siphuncles in extreme ventral position are set apart in the Aipocerataceae.

The post-Triassic nautiloids exhibit considerable adaptive variation in conch shape, size, suture pattern, and surface characters but clearly are a closely related stock classified as the superfamily Nautilaceae.

## TAINOCERATACEAE

The stem from which most, if not all, of the Devonian-to-Triassic nautiloids are derived is the family Rutoceratidae. This group, summarized by FLOWER (32, 42), is mainly of Devonian age (Fig. 282) and comprises, for the most part, gyrocones with depressed sections, simple sutures, and surface ornament consisting of wings, spines, nodes, ribs, and varices. Within the family are forms with tightly coiled conchs (e.g., *Anomaloceras*, M.Dev.), and others which are nearly straight (e.g., *Casteroceras*, M.Dev.; *Tylorthoceras*, M.Dev.), and forms with torticonic coiling (e.g., *Trochoceras*, L.Dev.-M.Dev.). In most genera the siphuncle is tubular and ventral in position. A few of the more primitive conchs have

cyrtocoanitic siphuncles, some even containing actinosiphonate deposits. These have been interpreted by FLOWER (42, p. 254) as relict features retained from their ancestors in the Oncocerida. The family contains a heterogeneous group of 23 genera.

The Tetragonoceratidae are a small family of only three genera ranging from gyrocones to coiled shells with slight impressed zones. The whorl section is mostly tetragonal, with a narrow dorsum and wider venter (Fig. 282, K, N). Nodes may develop on the flanks and shoulders. FLOWER & KUMMEL (49) believed that the group was derived from *Hercoceras* (M.Dev.) of the Rutoceratidae and gave rise to the Centrococeratidae (42).

Probably the most abundant and widespread of the late Paleozoic coiled nautiloids are members of the Tainoceratidae. This family is characterized by generally evolute conchs with ornamentation consisting of nodes, ribs, or spines and with sutures characterized by shallow lobes. The facility of making taxonomic separations largely based on shell ornamentation has led to introduction of an excessive number of tainoceratid generic and specific names. The group has been thoroughly reviewed by me (113) and recently has received much attention from RUZHENTSEV & SHIMANSKIY (153) and SHIMANSKIY (166). It is in this nautiloid assemblage that greatest divergence of views is encountered.

One of the principal factors which has led SHIMANSKIY to increase greatly the number of taxa in this group is his thesis that nature of the embryonic whorl is the most critical indicator of phylogenetic relationships. The rigidity with which this concept is applied by its author to classification leads to the grouping together of quite diverse forms, on the one hand, and more seriously, to wide separation of otherwise obviously closely related forms, on the other. Countless attempts have been made to set up systematic schemes among the cephalopods on the basis of a single character; needless to say all have failed.

Our knowledge of the embryology and earliest growth stages of modern *Nautilus* is extremely limited. It is known only from observations by WILLEY (209, 210), which

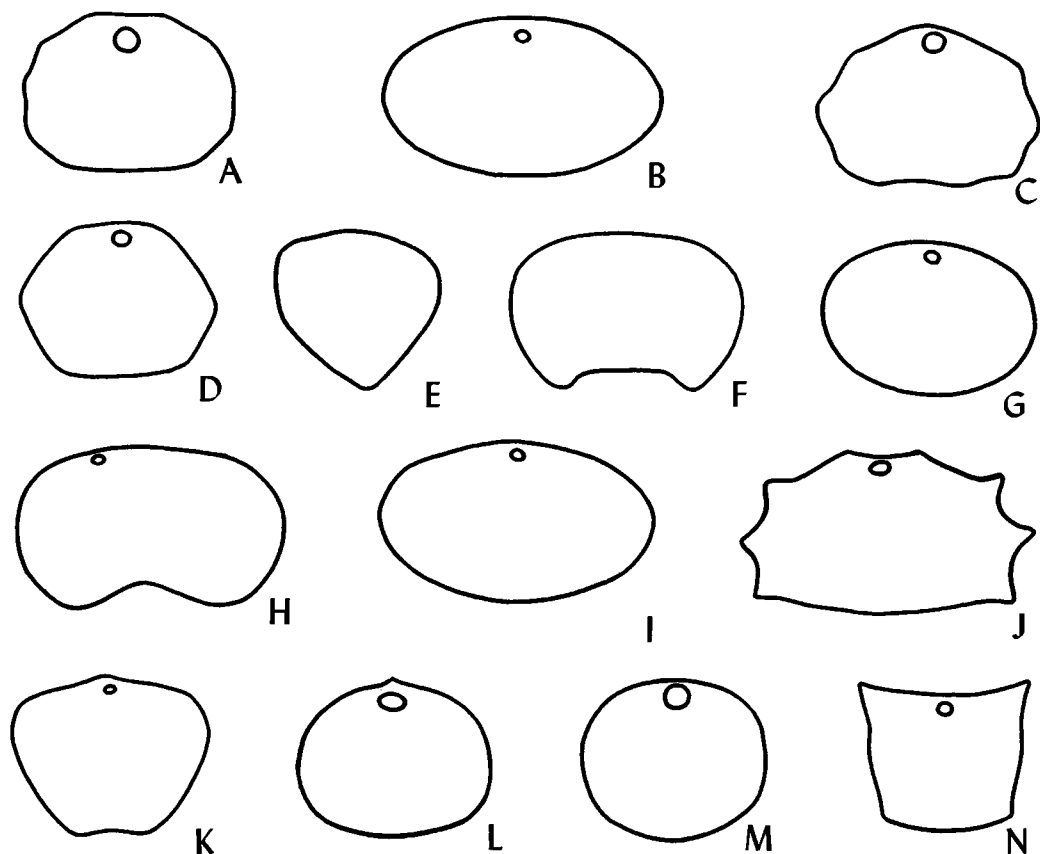


FIG. 282. Whorl sections of representative genera of the Rutoceratidae and Tetragonoceratidae.—A. *Hindeoceras canadense* (WHITEAVES) (1891, pl. 9, fig. 1b); height, 38 mm.—B. *Rutoceras ornatus* (D'ARCHAIC & DE VERNEUIL) (1842, pl. 28, fig. 52); height, 31 mm.—C. *Adelphoceras bohemicum* BARRANDE (1870, pl. 459, fig. 5); height, 38 mm.—D. *Homoadelphoceras devonians* (BARRANDE) (1866, pl. 240, fig. 17); height, 19 mm.—E. *Halloceras undulatum* (HALL) (1879, pl. 53, fig. 4); height, 30 mm. (deformed).—F. *Hercoceras mirum* (BARRANDE) (1854, pl. 43, fig. 3); height, 23 mm.—G. *Ptenoceras alatum* (BARRANDE) (1865, pl. 44, fig. 13); height, 18 mm.—H. *Anomaloceras anomalum* (BARRANDE) (after Hyatt, 1894, pl. 8, fig. 16); height, 10 mm.—I. *Pleuonoceras nodosa* (BRONN) (1837, pl. 1, fig. 4b); height, 17 mm.—J. *Tetranodoceras transversum* (HALL) (after Flower, 1936, fig. 2); height, 17 mm.—K. *Nassauoceras subtuberculatus* (SANDBERGER & SANDBERGER) (1852, pl. 12, fig. 3d); height, 30 mm.—L. *Goldringia cyclops* (HALL) (1879, pl. 104, fig. 2); height, 49 mm.—M. *Ptyssoceras alienum* (BARRANDE) (1866, pl. 127, fig. 3); height, 22 mm.—N. *Tetragonoceras gracile* (WHITEAVES) (1891, pl. 8, fig. 26); height, 15 mm. (Kummel, n.).

STENZEL has summarized in the chapter on "Living Nautilus." The first volution is supposed to originate during the development inside the egg. The differences in this embryonic stage are in the degree of curvature or coiling of the first volution. *Encoiloceras* (U.Trias.), a ribbed nautiloid from the Alps and probably Hungary, has the largest umbilical perforation of any known Triassic nautiloid. This genus has been considered by most authors to be no

more than another ribbed nautiloid related to *Pleuromytilus* (Perm.-Trias.). SHIMANSKIY (166), on the other hand, has introduced a new family and superfamily for this one genus and species on the basis of its widely umbilicate first volution. The Gzheloceratidae and Mosquoceratidae, both of RUZHENTSEV & SHIMANSKIY (153) are composed of forms with the typical conch pattern and ornamentation of the Tainoceratidae and Koninckioceratidae, but ac-

cording to their authors they show slight differences in size and shape of the first volutions.

It is difficult to accept size and shape of the first volution as a principal criterion for definition of families and for indicating evolutionary affinities. Owing to almost complete lack of knowledge of this growth stage in modern *Nautilus* and general sparseness of such data relating to fossil nautiloids, we have no measure of how much intrageneric or intraspecific variation should be expected. It is well known that among ammonoids and other invertebrate groups the amount of variation can be just as great in juvenile or embryonic stages as in mature stages. The effects on the developing shell of temperature, depth of water, salinity, turbulence, size of the egg, amount of yolk, and feeding habits of the female are completely unknown, but one would suspect that they have some bearing on the problem.

The multiplication of genera in the Tainoceratidae results mainly from using ornamentation as the main criterion for separation of genera. It is true that upper Paleozoic and Triassic nautiloids seldom appear in the fossil record in such large numbers as the ammonoids, and that studies on variation of nautiloids, therefore, are seldom possible; at the same time most students of the group are reluctant to stray beyond a strictly typological approach. Examination of a large number of specimens and synthesis of world literature on the group permits recognition of two principal evolutionary lines within the family. The first, exemplified by *Metacoceras* (Penn.-Perm.) and *Mojsvaroceras* (Trias.), is characterized by forms with subquadrate conchs and nodes on the ventral or umbilical shoulders or both; the second group, exemplified by *Pleuromutilus*, has ribs as its main ornamentational feature. All remaining members of the Tainoceratidae can best be understood as offshoots of these two main evolutionary lines.

*Metacoceras* has the same relationship to *Mojsvaroceras* as *Domatoceras* (Penn.-Perm.) has to *Grypoceras* (Trias.) of the Grypoceratidae. *Mojsvaroceras* is a direct descendant of *Metacoceras*, differing only in the presence of an annular lobe and a

tendency towards greater involution. More than 50 species have been assigned to *Metacoceras*, the principal criterion for their differentiation being the nature of ornamentation. As one would expect, the nodes vary in shape, size, numbers, and prominence. Distinction of species on the basis of slight differences in nodes is highly questionable; when the same criterion is used for separation of genera it is even more unrealistic. An example of such procedures is furnished by the Mosquoceratidae RUZHENTSEV & SHIMANSKIY (153) in which the authors include three new genera, *Mosquoceras*, *Leonardocheilus*, and *Articheilus*. These were separated from the Tainoceratidae because the embryonic chamber is "large, thick, and rapidly expanding," in contrast to a "smaller" embryonic chamber in members of the Tainoceratidae. Adult individuals, however, are difficult to distinguish from other well-known genera, except that the nodes are longitudinal-oblong, rather than rounded or pyramidal as in the Tainoceratidae. This distinction in form of nodes is found to be utterly without significance when one examines the range of variations within and between the more common genera and species of the Tainoceratidae. *Mosquoceras* is a synonym of *Metacoceras*. *Leonardocheilus* was introduced by RUZHENTSEV & SHIMANSKIY (153) for *Temnocheilus inaequilaterale* MILLER & YOUNGQUIST (136)—the type and only species assigned to the genus—from the Leonard Formation, Glass Mountains, Texas. The single specimen upon which this species was established has nodes on only one side of the conch and is clearly a pathological specimen, as suggested by MILLER & YOUNGQUIST (136, p. 95). *Leonardocheilus* is a synonym of *Temnocheilus* (Miss.-Perm.) of the Koninckioceratidae. Finally *Articheilus*, another monotypic form, is based on a species that can be accommodated very well in the genus *Temnocheilus*.

The remaining members of the nodose Tainoceratidae maintain the basic conch pattern of *Metacoceras* and *Mojsvaroceras* but have additional or modified features of ornamentation (Fig. 283). Conchs include forms with a double row of nodes on the venter (*Tainoceras*, Perm.-Trias.), longitudinal ribs on the venter (*Aulametaco-*



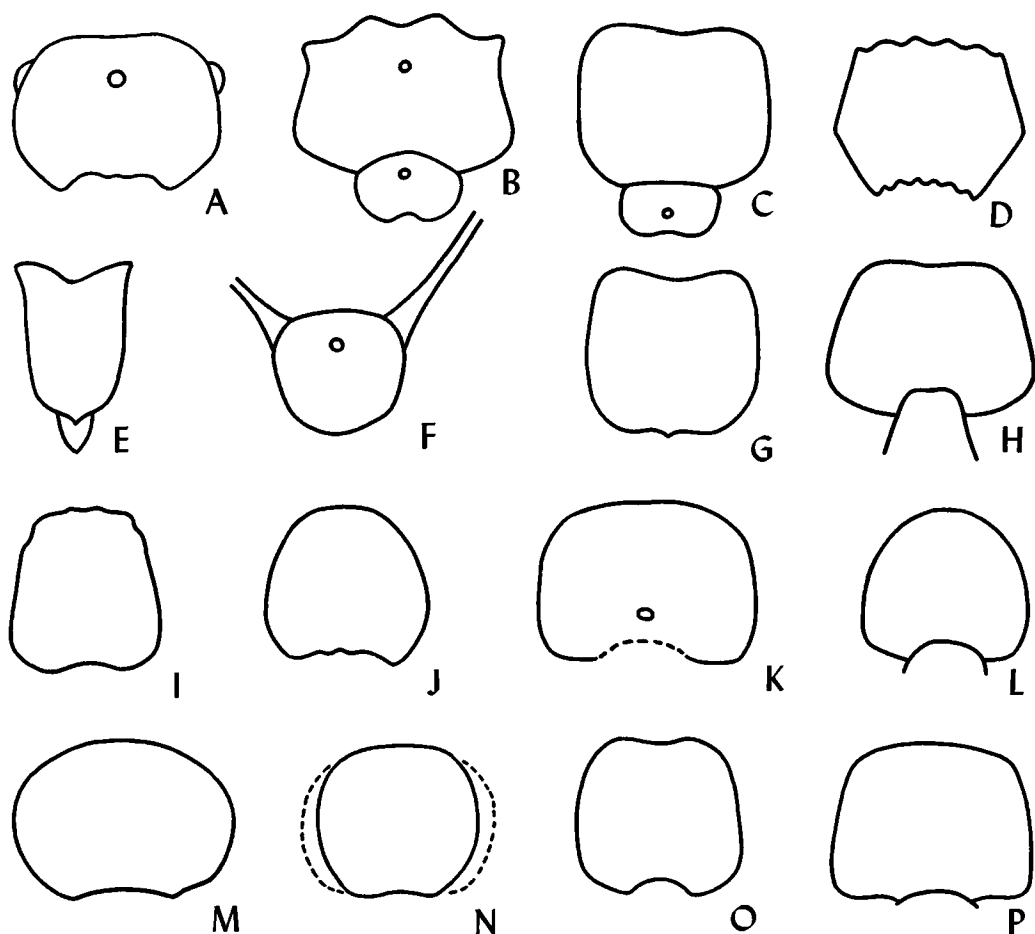


FIG. 283. Whorl sections of representative genera of the Tainoceratidae.—A. *Metacoceras dubium* HYATT (1891, fig. 35); height, 43 mm.—B. *Tainoceras wyomingense* MILLER & THOMAS (1936, fig. 3A); height, 34 mm.—C. *Tainionautilus transitorius* (WAAGEN) (1879, pl. 6, fig. 4); height, 38 mm.—D. *Aulametacoceras mckeei* MILLER & UNKLESBAY (1942, fig. 1A); diameter, ca. 185 mm.—E. *Tirolonautilus crux* (STACHE) (1877, pl. 6, fig. 1c); height, 26 mm.—F. *Cooperoceras texanum* MILLER (1945, fig. 1B); height, 10 mm.—G. *Thuringionautilus jugatonodosus* (ZIMMERMANN) (1892, pl. 27); height, 52 mm.—H. *Germanonautilus breueri* (HAUER) (after Mojsisovics, 1902, pl. 9, fig. 2b); diameter, 118 mm.—I. *Pleuronautilus trinodosus* MOJSISOVICS (1882, pl. 85, fig. 1b); diameter, 90 mm.—J. *Trachynautilus subgemmatus* MOJSISOVICS (1882, pl. 85, fig. 2b); diameter, 24 mm.—K. *Anoploceras ampezzanus* (LORETZ) (after Mojsisovics, 1882, pl. 84, fig. 1c); diameter, 102 mm.—L. *Phaedrysmocheilus subaratus* (KEYSERLING) (after Mojsisovics, 1886, pl. 16, fig. 1b); diameter, 52 mm.—M. *Holconautilus semicostatus* (BEYRICH) (after Mojsisovics, 1882, pl. 86, fig. 1b); diameter, 92 mm.—N. *Encoiloceras superbus* (MOJSISOVICS) (1873, pl. 4, fig. 1b); diameter, 97 mm.—O. *Enoploceras wulfeni* MOJSISOVICS (1902, pl. 10, fig. 1b); diameter, 127 mm.—P. *Phloioceras gemmatum* MOJSISOVICS (1873, pl. 3, fig. 1b); diameter, 140 mm. (Kummel, n).

ceras, M.Perm.-U.Trias.), concave venters aligned by retrograde ribs and sinuous longitudinal nodes on the ventral shoulder (*Tirolonautilus*, U.Perm.), rows of nodes on the venter and lateral area (*Tylonautilus*, L.Carb.-Perm.), complete loss of ornamentation (*Germanonautilus*, Trias.), unusually

large spines (*Cooperoceras*, L.Perm.), and a sulcus on the venter (*Thuringionautilus*, U.Trias.).

The ribbed genera of the Tainoceratidae are best understood as offshoots of *Pleuronautilus*. Here again the presence or absence of ribs, and where present, their pat-

tern, direction, and strength, are extremely variable. Several attempts have been made to separate as distinct genera forms with what appear to be distinctive rib patterns. All such attempts merely tend to confuse and hide a rather simple basic adaptive type of conch with ribs as the main form of ornamentation.

All ribbed Permian nautiloids and the majority of ribbed Triassic conchs, in my opinion, can be interpreted best as species of a variable genus, *Pleuromutilus*. I would place in the synonymy of *Pleuromutilus* the upper Paleozoic forms, *Shansinutilus* YABE & MABUTI (1935), *Huanghoceras* GRABAU in YIN (1933), *Tungkuanceras* HAYASAKA (1947) and *Pseudofordiceras* RUZHENTSEV & SHIMANSKIY (153). *Gzheloceras* (U. Carb.-L.Perm.) is like *Pleuromutilus* but lacks an annular lobe, and on this basis probably should be accepted as a separate genus. *Hexagonites* HAYASAKA (1947), *Hunanoceras* CHAO (9), and *Tanchiashanites* CHAO (9), all from the Permian of China, are so inadequately described and illustrated that one can only accept them tentatively until further data become available.

The ribbed nautiloids underwent a great evolutionary radiation in the Triassic. The new adaptive types were expressed in conchs with wide umbilici and foldlike ribs (*Encolloceras*), with depressed whorl sections (*Anoploceras*), with more quadrate nodose whorl sections (*Enoploceras*), with ventral saddles (*Holconutilus*), outer whorls becoming smooth and ovate (*Phaedrysmocheilus*), with longitudinal ribs (*Phloioceras* and *Trachynutilus*), and with ribs extending onto the venter ending at a median sulcus (*Tainionutilus*) (Fig. 283). All these Triassic genera are represented by relatively few species and comprise a fairly homogeneous group which can best be interpreted as direct or indirect descendants of *Pleuromutilus*. Some authors favor grouping these ribbed forms into a family called Pleuromutilidae. There may be justification for this but close relationship to the nodose Tainoceratidae is thereby obscured. It seems best to keep the ribbed and nodose forms together in one family and, if desired, to recognize subfamilies.

One small group of Permian nautiloids described by RUZHENTSEV & SHIMANSKIY

(153) as the family Rhiphaeoceratidae is most interesting. This assemblage, which includes four genera known only from Lower Permian rocks of the southern Urals, has conchs of quite variable whorl section which bear ribs and have sutures with a deep dorsal lobe. It is this last feature, the deep dorsal lobe, that sets these forms apart.

The second evolutionary line, which evolved from the Rutoceratidae, can be most conveniently brought together in the family Koninckioceratidae. Whereas the Tainoceratidae have a basic conch pattern characterized by a subquadrate whorl section, and a surface with nodes or ribs or both, the Koninckioceratidae have depressed, more or less rounded whorl sections in which the dorsum is usually much narrower than the venter (Fig. 284). The maximum width of the whorls varies from near the ventral area of the conch to about the mid-position of the whorl section. Ornamentation, when present, generally consists of nodes.

Nine of the 11 genera of the Koninckioceratidae have depressed conchs with maximum width about midway between the venter and dorsum. These forms, each quite distinctive, differ primarily in whorl shape. *Edaphoceras* (Miss.) has a lenticular whorl section with no dorsal impressed zone; *Millkoninckioceras* (Miss-Perm.) has a subelliptical whorl section with a shallow impressed zone; *Lophoceras* (L. Carb.) has subangular flanks and ventral areas, which on the venter disappear on the mature body chamber; in *Planetoceras* (Miss-Penn.) the flanks and ventral areas are broadly convex to flattened. All of the above forms are smooth, devoid of any ornamentation except for growth lines. Some related forms with much the same conch form have ornamentation—for example, *Endolobus* (U.Miss.-L.Perm.) has a subelliptical whorl section with prominent nodes on the flanks; *Tylo-discoceras* (Miss.) has much the same pattern, except that, in addition, there is a conspicuous, broad ventral sulcus; in *Valhallites* (Miss.-L.Perm.) prominent longitudinal striae are present also. Another group of this assemblage has a more subtrapezoidal whorl section, *Temnocheilus* being the best example. In this genus the venter is broad, slightly convex, with sharp-

ly rounded to angular ventral shoulders bearing nodes, and convex flanks which converge toward the dorsum. *Knightoceras* (U.Miss.-Penn.) has much the same conch pattern but lacks nodes. *Subvestinautilus* (L.Carb.) is another nontuberculate koninckioceratid. *Foordiceras* (Perm.) has a temnocheilid conch with ribs on the flanks that terminate at nodes on the ventral shoulders.

The unsettled and as yet tentative nature of classification of the Nautilida is nowhere better illustrated than in the Koninckioceratidae in which 11 genera are brought together. SHIMANSKIY (166) placed these same 11 genera in seven families, six superfamilies, and four suborders. In the Koninckioceratidae SHIMANSKIY places *Koninckioceras*, *Lophoceras*, and, with doubt, *Planetoceras* and *Potoceras*; he put the family in his superfamily Lirocerataceae. This unusual procedure is apparently based on the assumption that *Potoceras* is of Devonian age and the predecessor of both the Liroceratidae and Koninckioceratidae. As pointed out in discussion of the Clydonautilaceae, *Potoceras*, Late Devonian or Early Carboniferous age, is no more than a slightly evolute *Liroceras* (Miss.-Perm.) with no similarity to any member of the Koninckioceratidae as recognized here. All the Koninckioceratidae are evolute forms with broad, open umbilici, whereas the Trigonocerataceae are typically tightly involute, globular conchs, completely different adaptive types.

*Librovitschiceras* SHIMANSKIY (166) was placed by its author in the family Litogyroceratidae (a subjective synonym of Rutoceratidae), suborder Rutoceratina, but *Knightoceras* was placed in the Triboloceratidae (=Trigonoceratidae), suborder Centroceratina. These two genera differ really only in position of the siphuncle, that in *Librovitschiceras* being close to the venter, but not marginal as in *Litogyroceras* (M.Dev.); the siphuncle of *Knightoceras* is generally reported to be more or less central in position. Without doubt, *Librovitschiceras* is a synonym of *Knightoceras*. *Librovitschiceras* is monotypic, and my records show seven species assigned to *Knightoceras* from Pennsylvanian and Permian rocks of Russia and North America. In

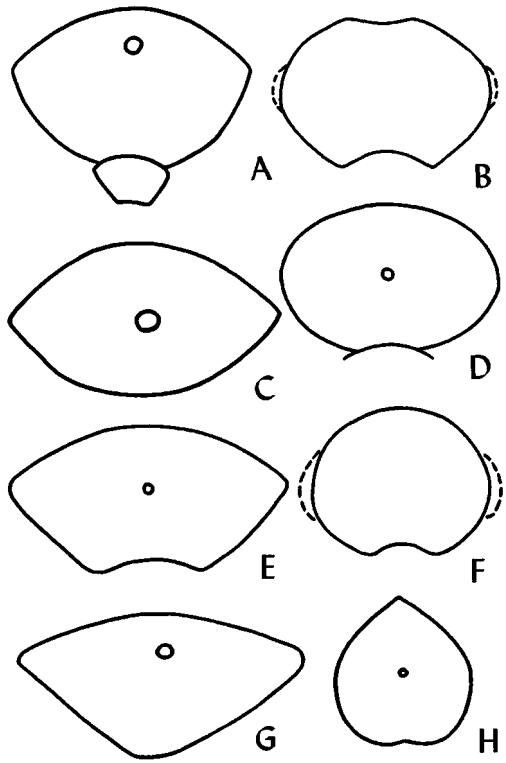


FIG. 284. Whorl sections of representative genera of the Koninckioceratidae.—A. *Knightoceras kempae* MILLER & YOUNGQUIST (1949, fig. 4); height, 12 mm.—B. *Tylodiscoceras nosowi* COLLINSON (1956, fig. 2A); diameter, 250 mm.—C. *Edaphoceras niotensis* (MEEK & WORTHEN) (1873, fig. 3); height, 17 mm.—D. *Millkoninckioceras konincki* (MILLER & KEMP) (after deKoninck, 1878, p. 105); height, 40 mm.—E. *Temnocheilus* sp. MILLER & OWEN (1934, fig. 2B); height, 24 mm.—F. *Tylodiscoceras nosowi* COLLINSON (1956, fig. 2B); diameter, 145 mm.—G. *Subvestinautilus crassimarginatus* (FOORD) (1900, pl. 22, fig. 5c); diameter, 115 mm.—H. *Lophoceras pentagonus* (SOWERBY) (after deKoninck, 1878, pl. 13, fig. 5b); height, 52 mm. (Kummel, n).

species of *Knightoceras* the position of the siphuncle is "subcentral," where known, more often closer to the venter than dorsum. In *Knightoceras kempae* MILLER & YOUNGQUIST (136) from the Lower Permian of Texas, the conch is 12 mm. high and the siphuncle is 2.5 mm. from the venter (21 percent of whorl height). In the type and only species of *Librovitschiceras*, *Nautilus atuberculatus* TSVETAeva, 1888, at a conch height of 20 mm. the siphuncle is 3 mm. from the venter (15 percent of

whorl height). Here is a case in which two genera are placed, on one hand, in two different suborders and, on the other, are considered to be synonyms.

*Tylosioceras* is known from only three specimens, assigned to two species, from the Mississippian of Kentucky. MILLER & COLLINSON (125), authors of the genus, did not dwell at length on its relationships. At that time the authors had only one specimen. Later COLLINSON (11) studied an additional specimen of the type-species and described another species, *T. nosowi*, in which the ventral depressed zone is developed only on the mature part of the conch, which "may be taken to indicate that *T. nosowi* is more primitive than the genotype and that *Tylosioceras* arose from *Endolobus*" (Fig. 283,B,C). With this conclusion I am in complete agreement. *Tylosioceras* is nothing more than an *Endolobus* with a ventral furrow, yet SHIMANSKIY placed these genera in separate superfamilies (*Tylosioceras* in the Tainocerataceae and *Endolobus* in the Temnocheilaceae). Two monotypic genera from the Permian of the southern Urals are considered to be synonyms of *Endolobus*; these are *Heurekoceras* RUZHENTSEV & SHIMANSKIY (153), family Gzheloceratidae, and *Actubonautilus* RUZHENTSEV & SHIMANSKIY (153), family Actubonautilidae.

### CLYDONAUTILACEAE

The origin of the Clydonautilaceae is still unknown. FLOWER & KUMMEL (37, Fig. 1) suggested an ancestry in the Barandeocerida but cited no evidence to support this suggestion. Later, FLOWER (42) concluded that "while it is not impossible that the dominantly late Paleozoic Liroceratidae and their derivatives may have developed from this general stock (Barandeoceratida), as yet no close connection can be found. It is necessary to turn to other stocks of the nautiloids to find the origin of the dominant groups of younger coiled cephalopods." SHIMANSKIY (166) suggested that the origin of this stock lies within his family Litogyroceratidae, pointing to similarities in shell structure of the Devonian *Anomaloceras* and *Potoceras*, which FLOWER (40, p. 521) considered to be the first representative of the Liroceratidae. To

some extent *Syrreghmatoceras*, referred by SHIMANSKIY to the Litogyroceratidae, shares in these similarities. *Potoceras* recently has been illustrated for the first time and re-described by me (KUMMEL, 1962). HYATT's type-specimen, which is the only one known, is unaccompanied by record of its source but is thought probably to have come from the Iberger Kalk (U.Dev.) of Germany or possibly from Viséan (L.Carb.) rocks of Belgium.

At any rate, *Potoceras* is nothing more than a slightly evolute *Liroceras*. Whether it is the oldest representative of the Liroceratidae is doubtful. It is difficult to visualize *Anomaloceras*, with its off-center siphuncle, as ancestral to the Liroceratidae.

Evolutionary radiation within the Clydonautilaceae is expressed by modifications of the involute, smooth conch and elaboration of the suture patterns. The Liroceratidae are a long-lived stock, appearing in the Lower Carboniferous, or possibly Devonian, and dying out toward the close of the Triassic Period. The smooth, tightly involute, essentially straight-sutured *Liroceras* (L.Carb.-Perm.), which is the most common and widely distributed genus is interpreted as the main evolving stock (Fig. 285,J). No distinct pattern of change in conch shape is recognizable throughout its geologic range.

The Triassic *Paranautilus* is identical with *Liroceras* except for a tendency to develop a more compressed conch; it is a direct evolutionary continuation of the late Paleozoic *Liroceras* (Fig. 285,L).

Other members of the Liroceratidae are distinguished mainly by slight modifications of conch form. *Hemiliroceras* (L. Perm.), *Potoceras* (?U.Dev.-?L.Carb.), and *Bistrialites* (L. Carb.) are more evolute than *Liroceras* and have deep umbilici. The first two are quite similar in conch form, but the sutures of *Hemiliroceras* have a deep dorsal lobe, that is lacking in *Potoceras* (Fig. 285,I). *Bistrialites* has spiral lines in the region of the umbilical shoulders. Three species of *Bistrialites* are known, two of *Hemiliroceras*, and only one of *Potoceras*. Exceptionally rapid expansion of the whorls occurred twice in the history of the Liroceratidae. *Permonautilus* (U.Perm.) has, in addition to a rapidly ex-

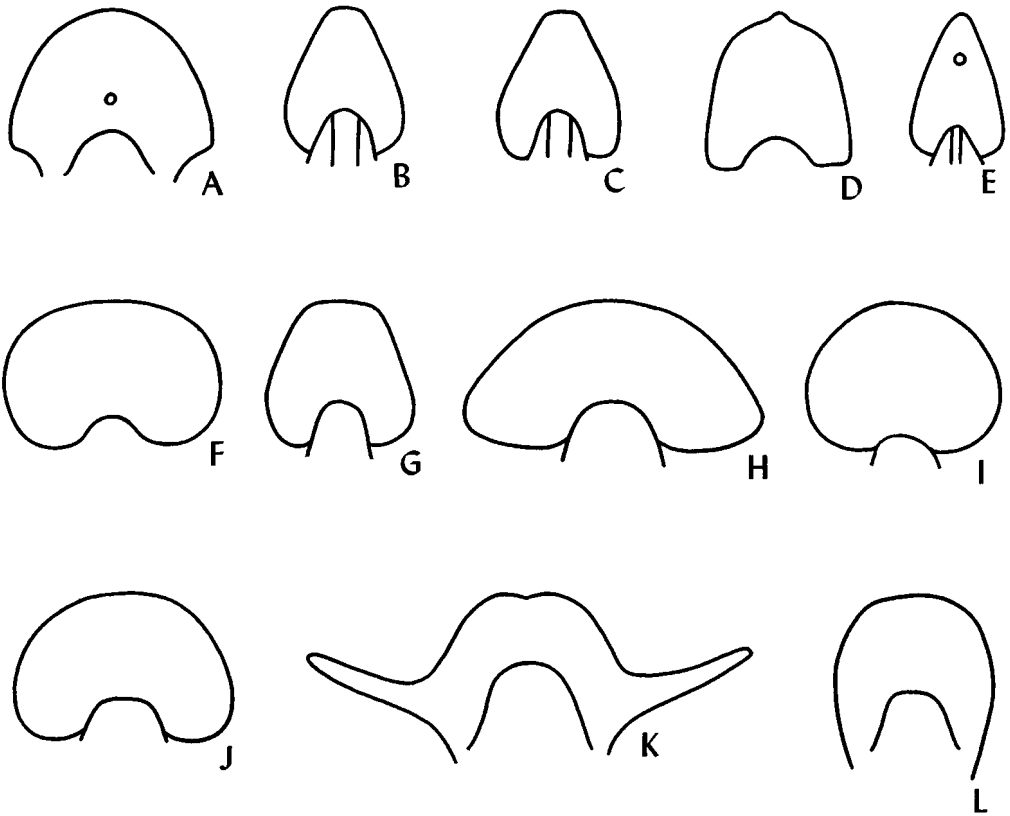
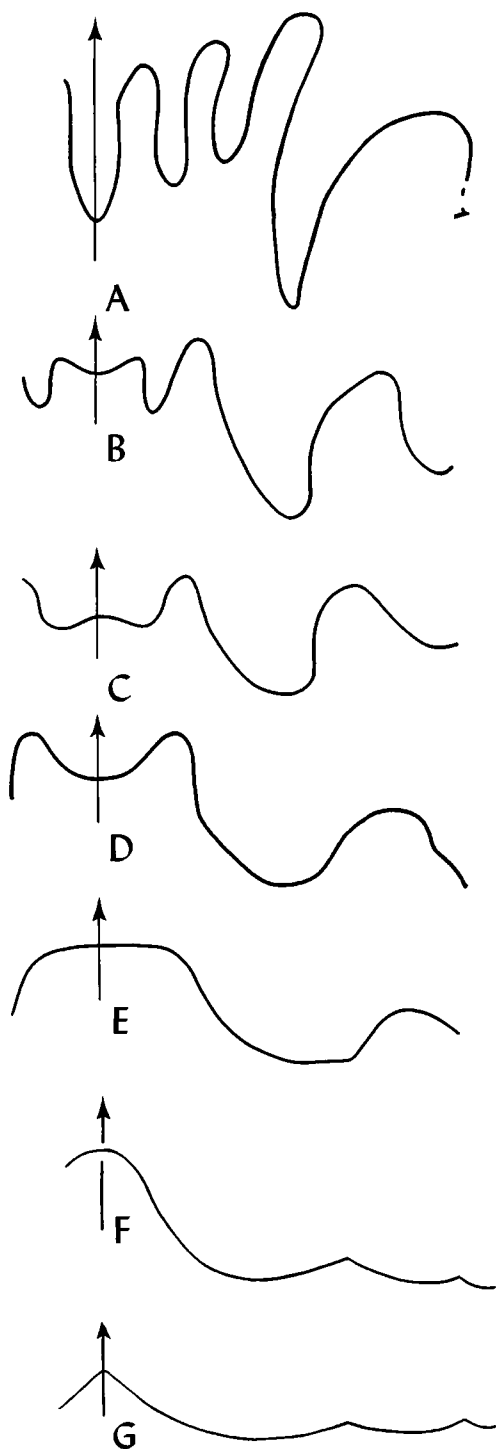


FIG. 285. Whorl sections of representative genera of the Clydonautilaceae.—A. *Styrionautilus styriacus* Mojsisovics (1873, pl. 14, fig. 7b); diameter, 74 mm.—B. *Proclydonautilus griesbachi* Mojsisovics (1896, pl. 22, fig. 1b); diameter, 87 mm.—C. *Clydonautilus biangularis* Mojsisovics (1896, pl. 22, fig. 2b); diameter, 83 mm.—D. *Callaionautilus turgidus* KIESLINGER (1927, pl. 5, fig. 1b); diameter, 108 mm.—E. *Gonionautilus securis* (DITTMAR) (after Mojsisovics, 1902, pl. 1, fig. 1b); diameter, 108 mm.—H. *Sibyllonautilus fergusonii* KUMMEL (1953, fig. 37); diameter, 49 mm.—I. *Hemiliroceras inflatum* RZUHENTSEV & SHIMANSKIY (1954, pl. 12, fig. 2a); diameter, 35 mm.—J. *Liroceras liratum* (GIRTY) (after Miller, Dunbar, & Condra, 1937, pl. 6, fig. 3); diameter, 29 mm.—K. *Permonautilus cornutus* (GOLOVKINSKY) (after Miller & Youngquist, 1949, pl. 54, fig. 1); diameter, 103 mm.—L. *Paranautilus simonyi* (HAUER) (after Mojsisovics, 1902, pl. 1, fig. 2b); diameter, 76 mm. (Kummel, n).

panding conch, long spines formed by greatly extended umbilical shoulders (Fig. 285,K). *Sibyllonautilus* (M.Trias.-U.Trias.) (Fig. 285, H) is a form with greatly expanded conch but without spines. *Coelogastroroceras* (Penn.-Perm.) is characterized by a median sulcus on the venter. The slightly evolute *Peripetoceras* (U.Miss.-Perm.) and tightly involute *Indonautilus* (M.Trias.-U.Trias.) have flattened ventral and lateral areas (Fig. 285,F,G). Finally, *Condraoceras* (Penn.-L.Perm.) may be thought of as a compressed *Liroceras*. It is of special significance that only *Liroceras*

and its successor *Paranautilus* are fairly well represented in the fossil record and nearly world-wide in distribution; other genera of the family being known only from few species or monotypic and much more restricted both geographically and in geologic range.

The Ehippioceratidae maintain the basic conch form of *Liroceras* but the sutures are modified in the ventral area. *Ehippioceras* (Miss.-L.Perm.) has a V-shaped ventral saddle, *Megaglossoceras* (Penn.) a broad, tongue-shaped ventral saddle (Fig. 286, F,H). *Ehippioceras* is fairly well repre-



sented in Mississippian through Permian strata in North America, Europe and China. *Megaglossoceras* is only known from Pennsylvanian strata of the United States.

In the Late Triassic three stocks that evolved from the Liroceratidae (*Paranautilus*) attained the highest elaboration in suture of any known nautiloids. These are the families Clydonautilidae, Gonionautilidae and Siberionautilidae; they are included by SHIMANSKIY (1966) in his superfamily Clydonautilaceae distinguished from his superfamily Lirocerataceae on the basis of more elaborate sutures observed in the first-mentioned group. No question arises as to close relationship of these groups, for the clydonautilids, gonionautilids, and siberionautilids clearly were derived from the liroceratids. Here all are placed in a single superfamily, which on the basis of priority (publication date of the first-proposed among included families) must bear the name Clydonautilaceae.

The principal modifications of sutures in the Clydonautilidae are in the ventral region. What appears to be a linear series extends from *Styrionautilus* (M.Trias.-U. Trias.), with a straight ventral saddle (Fig. 286,E), to *Proclydonautilus* (U.Trias.), which has a lobe in the ventral saddle (Fig. 286,D), and *Clydonautilus* (U.Trias.), which has a small saddle in the lobe of the ventral saddle (Fig. 286,C). The basic pattern of the suture is maintained in each of these genera, although it is accompanied by considerable variation in the shape of the conch (113). *Cosmonautilus* (U. Trias.) and *Callaionautilus* (U.Trias.) have sutures like that of *Proclydonautilus*, but in addition have nodes on ventral shoulders on early volutions of the conch that gradually disappear on the mature volutions. In *Callaionautilus* a median keel with large

FIG. 286. Sutures of representative genera of the Clydonautilaceae.—A. *Siberionautilus multilobatus* POPOV (1951, fig. 2a).—B. *Clydonautilus noricus* MOJSISOVICS (1873, pl. 11, fig. 2).—C. *C. biangularis* MOJSISOVICS (1896, pl. 22, fig. 2C).—D. *Proclydonautilus griesbachi* (MOJSISOVICS) (1896, pl. 22, fig. 1c).—E. *Styrionautilus discoidalis* (WELTER) (1914, pl. 31, fig. 8).—F. *Megaglossoceras pristinum* MILLER & OWEN (1934, fig. 1C).—G. *Ephippioceras ferratum* (Cox) (after Miller & Owen, 1934, fig. 1A) (Kummel, n).

nodes develops on the outer volution. These are the only two genera in the Clydonautilaceae that have ornamentation; in every other morphological feature they are intimately related to *Proclydonautilus* and similar forms. It is believed completely wrong to interpret these nodes as indicating any relationship with the Tainoceratidae. *Gonio-nautilus* and *Siberionautilus* are known from only one and two species respectively and their sutures represent the acme in sutural development among the nautiloids (Fig. 286, A,B).

Elaborate sutures are found in only a few other late Paleozoic-to-Recent nautiloid stocks. Among the Tainocerataceae the suture never develops more than shallow lobes. In the Trigonocerataceae, only the genus *Permoceras* (Permoceratidae), a monotypic form from the Upper Permian of Timor, has a highly differentiated suture with a deep V-shaped ventral lobe and lateral lobe. This suture is remarkably similar to that of the Upper Jurassic *Pseudonautilus*. This last genus is the name-giver of the family *Pseudonautilidae* and is believed to represent a stock that evolved from *Cenoceras* in the Middle Jurassic. SHIMANSKIY (166) placed this family in the Clydonautilaceae, seemingly because a ventral lobe is developed in the early stages of *Xenocheilus* (U.Jur.-L.Cret.). The significance of this early developed lobe is not clear to me. SHIMANSKIY also included *Pseudaganides* (Jur.) and *Hercoglossoceras* (a synonym of *Pseudaganides*, in my opinion) in the "Hercoglossidae."

To the best of my knowledge no Rhaetic nautiloids have yet been recorded. No member of the Tainocerataceae survived the wave of extinctions at the end of the Triassic, and the same is true of the Trigonocerataceae. The nautiloid faunas of the Lias throughout the world are composed of forms that in my judgment belong to a single but highly variable genetic group. The homogeneity and similarity of all Liassic nautiloids, indeed, is one of the most remarkable features in the history of this group. Nearly all Liassic nautiloids are believed to belong to the genus *Cenoceras* (U. Trias.-M.Jur.). The variability in this group is expressed in the sutures, shape of the conch, degree of involution, and de-

tails of shell ornamentation (115). The Paracenoceratidae, Cymatoceratidae, and Pseudonautilidae are believed to have their ancestry within the *Cenoceras* complex. One of the earliest recognizable radiations from *Cenoceras* is the Liassic *Pseudaganides kochi*, which belongs to a stock of fairly wide geographic distribution and abundant in the geologic record; 37 species of this genus have been described. *Pseudonautilus* (U.Jur.-L.Cret.) is most easily understood as an offshoot of *Pseudaganides* (Jur.) in which the sutural elaboration has gone one step farther. We may interpret the relationship between *Hercoglossa* (?L.Cret., Paleoc.-Eoc.) and *Aturoidea* (U.Cret.-Eoc.) in much the same way.

Sinuosity of the suture developed in isolated cases in other stocks. For example, in the Cymatoceratidae, *Paracymatoceras* (U. Jur.-L.Cret.) and *Heminautilus* (L.Cret.) have fairly elaborate sutures with prominent lobes and saddles.

Late Cretaceous and Cenozoic nautiloids with sinuous sutures are included in the Hercoglossidae. The gross morphological features of this family are so similar to those of the Pseudonautilidae that it is difficult to recognize significant differences between them. Their separation rests mainly on the fact that the predominantly Jurassic Pseudonautilidae can be traced from the *Cenoceras* complex, whereas the Hercoglossidae stem from *Eutrephoceras* (U.Jur.-Mio.) through *Cimomia* (U.Jur.-Oligo.), of the Nautilidae and are mainly late Cretaceous and early Cenozoic in age. It is difficult to avoid the conclusion that they are heterochronous homeomorphs.

### AIPOCERATACEAE

In terms of numbers of genera this is the smallest superfamily of the Nautilida, as well as probably the least known. The group is characterized by ventral position of the siphuncle, generally smooth conchs, and nearly straight sutures. Although the origin of the group is uncertain, the assemblage can be best understood as one of the major lineages of the Nautilida. Only the genus *Solenochilus* (Miss.-Perm.) has been recorded a moderate number of times in the literature. *Aipoceras*, *Oncodoceras*, and *Asymptoceras*, all Mississippian, have

been almost unnoticed since their introduction.

Recently RUZHENTSEV & SHIMANSKIY (153) described a very interesting and diverse Lower Permian fauna of nautiloids from the southern Urals. In their collections were unique cyrtoceraconic forms with reduced phragmocones and large body chambers; these they placed in a new family, named Scyphoceratidae. Another group, Dentoceratidae, also defined as a new family, completely lacks a phragmocone in mature specimens. The authors understandably expressed doubt as to phylogenetic relations of these assemblages but placed them close to the Solenochilidae, more for lack of any other plausible comparable group than on any firm morphological affinities.

A great amount of additional data is needed before the Aipocerataceae will be well understood. Judging, however, from the over-all shell morphology of the few known genera I suspect that additional data will tend to strengthen the proposed relationship of this superfamily to others of the Nautilida.

### TRIGONOCERATACEAE

The Trigonocerataceae are another long-ranging superfamily of coiled nautiloids. Though generally not as abundant as the Tainocerataceae or Clydonautilaceae, they do form a significant part of the record from Devonian through Triassic time and are believed to be the group from which the Nautilidae arose. The origin of the assemblage, however, is still far from settled. The leading student of its older representatives has been FLOWER (49) who suggested that origin of the group was possibly in the Tetragonoceratidae. Later, on the basis of detailed studies of the ontogeny (especially earliest volution) of *Centroceras* (M.Dev.), FLOWER (40) reaffirmed this suggestion. He freely admitted, however, that the data were such as to be open to other interpretations and the question was by no means settled. After KUMMEL (114) presented evidence indicating that the origin of the Nautilaceae was probably in the Syringonautilidae (of the Trigonocerataceae), FLOWER (42) suggested combining these two superfamilies (orders in his classification).

In view of the scant nature of the evidence linking the centroceratids with the rutoceratids, FLOWER justifiably holds that the two groups should be kept separate, at least for the time being. FLOWER & TEICHERT (50) indicated on a diagram separate origins for the Centrocerataceae (=Trigonocerataceae) and Rutocerataceae (=Tainocerataceae) from the Oncocerida; SHIMANSKIY (166), on the other hand, appears to be more certain that his Centroceratina stem from his Rutoceratina but he presents no evidence.

The root of the Trigonocerataceae is the family Centroceratidae, comprising only five genera, three from the Devonian and two of Early Carboniferous age. *Centroceras* appears to be the ancestral form, having a basic conch pattern from which various modifications gave rise to other genera of the family. The conch of *Centroceras* is tarphyceraconic, with no real impressed zone, the whorls tetragonal in section, with angular ventral and umbilical shoulders.

*Carlloceras* (U.Dev.), a monotypic genus, is essentially a *Centroceras* with slightly impressed zone and somewhat rounded ventral and umbilical shoulders (Fig. 287, Q). Likewise, *Strophiceras* (M.Dev.), another genus known only from its type-species, is little more than a *Centroceras* in which the tubercles on the ventral shoulders are prolonged into ribs over the venter, terminating in pairs of nodes along a narrow mid-ventral line (Fig. 287, U). *Homaloceras* (M.Dev.) is a large cyrtoconic to gyroconic form that FLOWER (1952) believed to be a possible descendant of *Centroceras* (Fig. 287, T). The two remaining genera of the Centroceratidae have conch forms that anticipate the common upper Paleozoic *Domatoceras* (Penn.-Perm.) and *Stenopoceras* (Penn.-L.Perm.). These are *Diorugoceras* (Fig. 287, R) and *Phacoceras* (Fig. 287, S), both from the Lower Carboniferous of Europe. Much needs to be done with this family group; three of the genera (*Strophiceras*, *Carlloceras*, and *Diorugoceras*) are known only from the type-species and the other two from few species, *Centroceras* having the greatest geographic distribution.

The Trigonoceratidae, aside from being



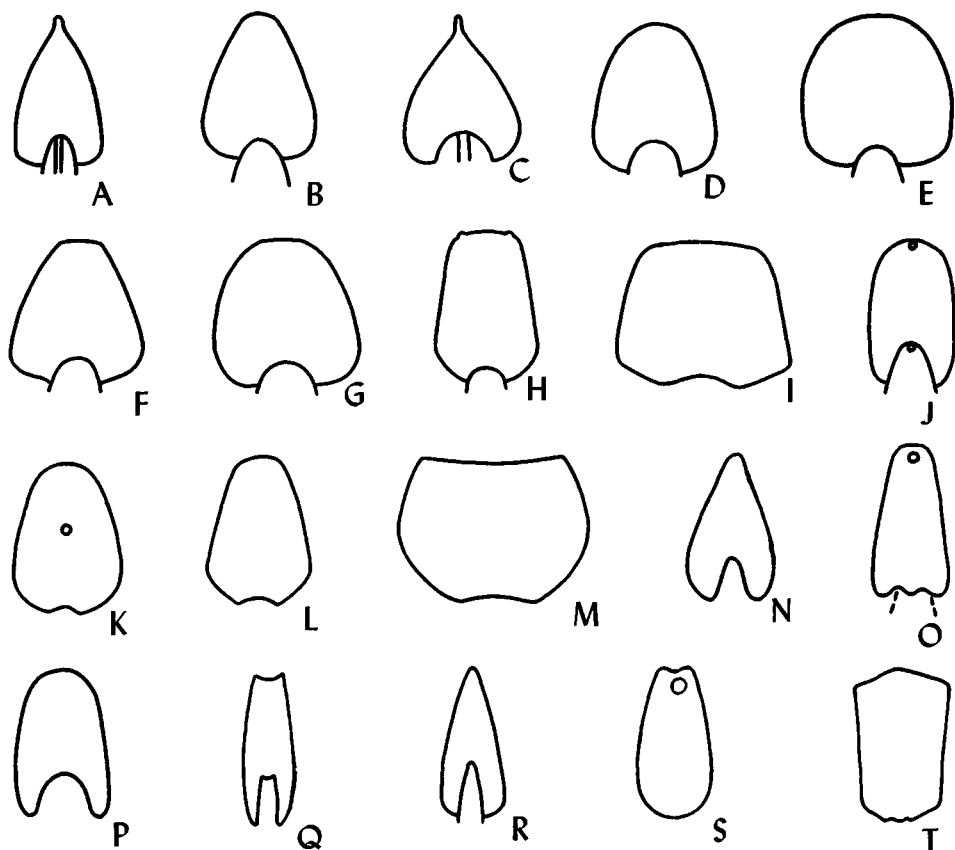


FIG. 287. Whorl sections of representative genera of the Centroceratidae, Grypoceratidae, and Syringonautilidae.—A. *Oxynautilus acutus* (HAUER) (after Mojsisovics, 1902, pl. 3, fig. 1b); diameter of conch, 138 mm.—B. *Juvavionautilus heterophyllus* (HAUER) (after Mojsisovics, 1902, pl. 4, fig. 2b); diameter, 128 mm.—C. *Gryponautilus galeatus* MOJSISOVICS (1873, pl. 12, fig. 1); diameter, 390 mm.—D. *Clymenonautilus ehrlichi* (MOJSISOVICS) (1873, pl. 6, fig. 9b); diameter, 55 mm.—E. *Syringoceras credneri* MOJSISOVICS (1902, pl. 6, fig. 1b); diameter, 110 mm.—F. *Grypoceras mesodicum* (QUENSTEDT) (after Mojsisovics, 1873, pl. 8, fig. 1b); diameter, 150 mm.—G. *Parastenopoceras khvorovae* RUZHENTSEV & SHIMANSKIY (1954, pl. 9, fig. 4b); diameter, 33.5 mm.—H. *Virgaloceras noduliferum* (REED) (after Schindewolf, 1954, fig. 52); height, 47 mm.—I. *Stearoceras simplex* (HYATT) (after Miller & Youngquist, 1949, fig. 18); height, 68 mm.—J. *Menuthionautilus kieslingeri* (COLLINGNON) (1933, fig. 4); height, 55 mm.—K. *Domatoceras umbilicatum* HYATT (1891, fig. 17); height, 73 mm.—L. *Pselioceras ophioneus* (WAAGEN) (1879, pl. 5, fig. 2b); height, 48 mm.—M. *Titanoceras ponderosum* (MEEK) (after Miller & Unklesbay, 1942, fig. 1J); height, 61 mm.—N. *Stenopoceras whitei* (MILLER & YOUNGQUIST) (1949, fig. 22A); height, 37 mm.—O. *Paradomatoceras applanatum* DELÉPINE (1937, fig. 2A); height, 24 mm.—P. *Carilloceras garlandensis* FLOWER & CASTER (1935, pl. 2, fig. 14); height, 14 mm.—Q. *Diorugoceras planidorsatum* (PORTLOCK) (1843, pl. 35, fig. 1b); diameter, 90 mm.—R. *Phacoceras oxytostomus* (PHILLIPS) (after deKoninck, 1878, pl. 17, fig. 3b); diameter, 68 mm.—S. *Homaloceras planatum* WHITEAVES (1891, pl. 8, fig. 1d); height, 42 mm.—T. *Strophiceras binodosum* (SANDBERGER & SANDBERGER) (1852, pl. 12, fig. 4b); height, 37 mm. (Kummel, n).

a puzzle as to origins and history, have led to a great deal of taxonomic confusion. The genera now included in this family were originally included by HYATT in the Trigonoceratidae HYATT, 1884, Rineoceratidae HYATT, 1893, and Triboloceratidae HYATT, 1884. Combination of these families into

one was first suggested by FLOWER (49). Since that time MILLER & GARNER (1953) and SHIMANSKIY (166) have followed the same procedure. FLOWER (49) believed Triboloceratidae to be a preferred name for the combined family, a procedure followed by SHIMANSKIY (166). MILLER & GARNER

(131), however, presented convincing evidence that *Triboloceras* HYATT, 1884, is a synonym of *Vestinautilus* RYCKHOLT, 1852, and that "the only valid name for this family is Rineceratidae HYATT, 1893." This is erroneous since Trigonoceratidae clearly has priority over Rineceratidae.

The Trigonoceratidae now include 18 genera, of which one (*Apogonoceras*) is known from Lower Permian strata of the southern Urals, the remainder being confined to the Mississippian (Lower Carboniferous) of North America and Europe. The range of variation in conch form and ornament within the family is very great (Fig. 288). Included are forms with smooth, compressed evolute conchs (e.g., *Aphelaeceras*, Fig. 288,E, and *Mesochasmoceras*); smooth, depressed conchs (e.g., *Diodoceras*, Fig. 288,I); strongly lirate conchs with variable whorl shape (e.g., *Apogonoceras*, *Discitoceras*, *Epistroboceras*, *Lispoceras*, *Maccoyoceras*, *Pararinoceras*, *Rineceras*, *Stroboceras*, *Thrincoceras*, *Vestinautilus*); loosely coiled conchs, whorls not in contact (e.g., *Chouteauoceras*); conchs with nearly goniatitic sutures (e.g., *Subclymenia*); and conchs in which the ornamentation is very weak (e.g., *Leuoceras*, Fig. 288,I).

Very little work has been done to date on the trigonoceratid genera. The hypothesis of a derivation of this family from the Centroceratidae is based mainly on negative evidence; no other group is known that displays positive resemblance.

The principal late Paleozoic and Triassic descendants of the Centroceratidae are the Grypoceratidae. Within this family we have displayed in the clearest possible manner the existence of a single main evolving stock, wide in geographic distribution and large in number of species, from which forms more specialized in adaptation were derived.

The upper Paleozoic representative of the main grypoceratid stock is *Domatoceras*, and the Triassic member, which is a direct evolutionary continuation of *Domatoceras*, is *Grypoceras*. In 1953, I suggested that relationships of these genera are close enough to warrant classifying *Domatoceras* (HYATT, 1891) as a subgenus of *Grypoceras* (HYATT, 1883). I now believe this to be undesirable and, even though I strongly

maintain the close and special relationships of these two forms, treat them as separate genera.

*Domatoceras* is an abundant nautiloid in late Paleozoic rocks and is practically worldwide in distribution. It shows a great range of variation in the Pennsylvanian and Permian, but the variations appear to be random, lacking stratigraphic significance. As previously mentioned, *Grypoceras* is considered to be a direct offshoot of *Domatoceras* which it replaced in the Triassic. The main changes are toward a rounding of the venter and a greater degree of involution (Fig. 287,F). Scythian species of *Grypoceras* (e.g., *G. brahmanicum*, *G. hexagonalis*, *G. milleri*) have rectangular whorl sections with rounded ventral and umbilical shoulders and somewhat flattened flanks. These species are actually difficult to distinguish from several Pennsylvanian and Permian species of *Domatoceras*. Middle and Late Triassic species of *Grypoceras* show more rounding of the venter and greater involution.

The sutures of *Domatoceras* generally have rather moderate ventral and lateral lobes, those of *Grypoceras* being somewhat deeper and having annular lobes (Fig. 289,E). This relationship is very similar to that between *Metacoceras* and *Mojsvaroceras* of the Tainoceratidae. *Plummeroceras* (L.Perm.) is an aberrant offshoot of *Domatoceras* that maintained the typical evolute conch of the latter but its sutures acquired a very deep, rounded ventral lobe, similar to that of some Triassic species of *Grypoceras* (Fig. 289,E). *Paradomatoceras* (U. Carb.) has a concave venter on the earlier volutions and sutures with a shallow, pointed ventral lobe (Fig. 289,D). *Epidomatoceras* (L.Carb.) has sutures with a deeper, pointed ventral lobe and lirae on ventral margins of the conch (Fig. 289,C).

The three last-mentioned genera maintain the general conch pattern of *Domatoceras* but show certain modifications, mainly in the sutures. They are either monotypic or represented by few species with restricted geographic distributions. A trend toward greater involution is found in *Parastenopoceras* (L.Perm.) (Fig. 287,H), *Stenopoceras* (Penn.-L.Perm.) (Fig. 287,O), *Menuthionutilus* (L.Trias.) (Fig. 287,K),

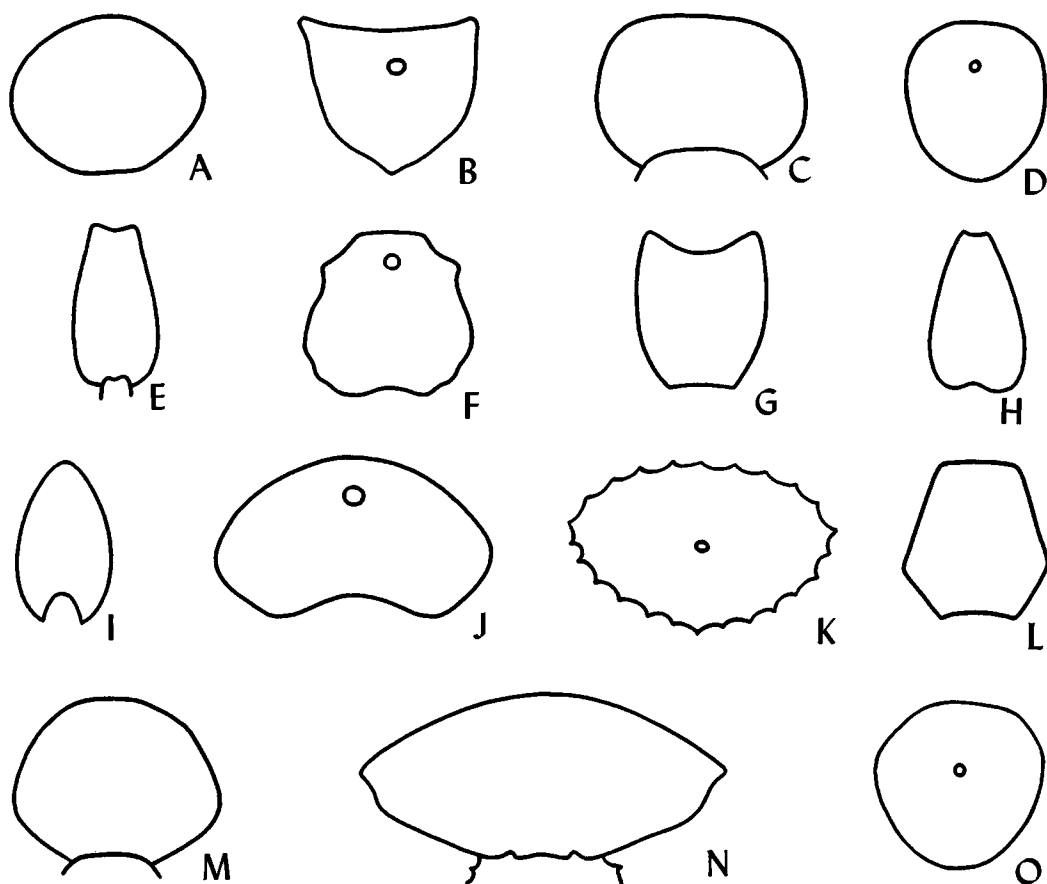


FIG. 288. Whorl sections of representative genera of the Trigonoceratidae.—A. *Lispoceras trivolve* HYATT (based on holotype); diameter, 38 mm.—B. *Trigonoceras paradoxicum* (SOWERBY) (after Miller, Dunbar, & Condra, 1933, fig. 19); height, 27 mm.—C. *Thrinoceras depressum* HYATT (1893, fig. 10); diameter, 128 mm.—D. *Chouteauoceras americanum* (MILLER & FURNISH) (after Miller & Garner, 1953, fig. 1B); height, 14 mm.—E. *Aphelaeceras difficilis* (DEKONINCK) (1878, pl. 26, fig. 5b); diameter, 59 mm.—F. *Stroboceras hartii* (DAWSON) (after Miller & Garner, 1953, fig. 1H); height, 6.5 mm.—G. *Subclymenia gibbosa* HYATT (based on holotype); diameter, 59 mm.—H. *Epistroboceras stubblefieldi* TURNER (1954, new photograph of holotype); diameter, 45 mm.—I. *Leuroceras aplanatum* HYATT (based on holotype); diameter, 81 mm.—J. *Diodoceras avonensis* (DAWSON) (1868, fig. 124); diameter, 39 mm.—K. *Rineceras propinquum* (DEKONINCK) (1880, pl. 33, fig. 52); height, 18 mm.—L. *Macrococeras discors* (M'COY) (1844, pl. 3, fig. 5); diameter, 71 mm.—M. *Discitoceras costellatus* (M'COY) (1844, pl. 2, fig. 4); diameter, 30 mm.—N. *Vestinautilus koninckii* (D'ORBIGNY) (after deKoninck, 1878, p. 138); height, 20 mm.—O. *Apogonoceras remotum* RUZHENTSEV & SHIMANSKIY (1954, pl. 11, fig. 8a); diameter, 40 mm. (Kummel, n).

and *Gryponautilus* (U.Trias.) (Fig. 287,C). *Stenopoceras* has a highly involute and compressed conch with a generally narrow venter that may be rounded, subacute, or even concave. It is connected with *Domatoceras* through such involute species as *D. kleihegei* and *D. moorei*. *Parastenopoceras* is best interpreted as an inflated, slightly evolute *Stenopoceras*. The even more evolute

*Pselioceras* (L.Perm.) can be interpreted in much the same way.

*Menuthionautilus*, which has a rapidly expanding, smooth, and involute conch, is another offshoot of *Domatoceras*. The venter is flattened on the early whorls but becomes broadly convex on the mature portion of the conch. The conch form, sutures, and ontogeny appear to indicate a close re-

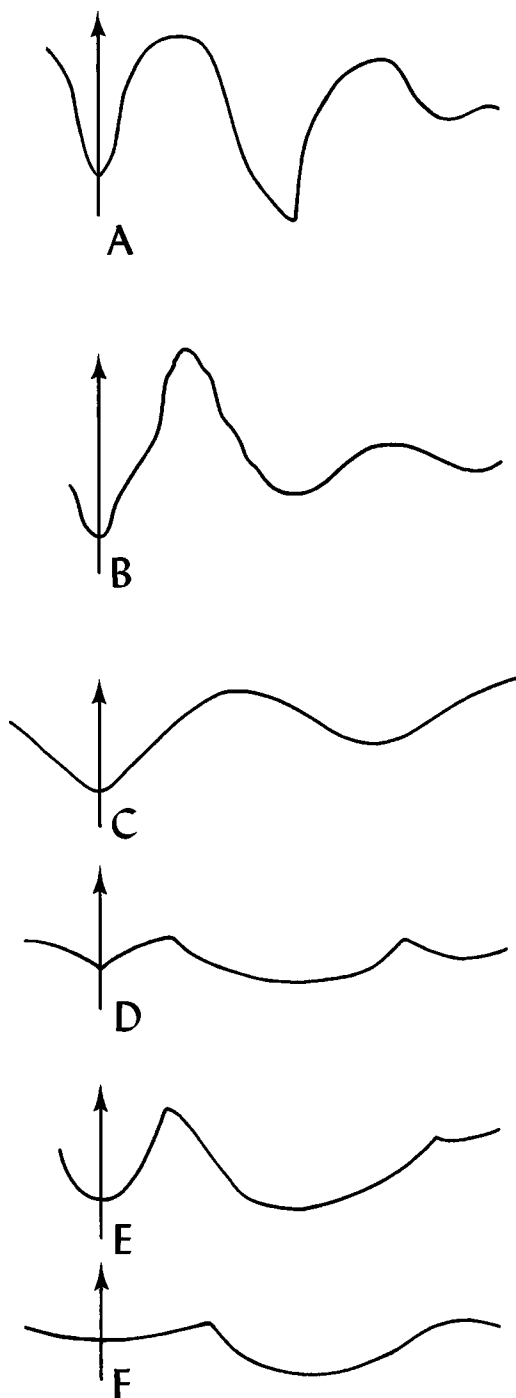


FIG. 289. Sutures of representative members of the Trigonocerataceae.—A. *Permoceras bitauniense* (Haniel) (after Miller & Collinson, 1953, fig. 1A). —B. *Subclymenia evoluta* (Phillips) (after de-

relationship to *Domatoceras*. Along with the greater involution of the conch there was a shifting of the siphuncle to an extreme ventral position. The parent stock, *Domatoceras*, shows a great deal of variation in position of the siphuncle. Some of the more involute species (e.g., *D. kleihegei*) have the siphuncle only 12.5 per cent of the whorl height from the venter. Shifting of the siphuncle to an extreme ventral position is a relatively rare occurrence in late Paleozoic and Triassic nautiloids.

Unique among nautiloids is a pattern of ornamentation consisting of a continuous line of elongate nodes along the umbilical seam (e.g., *Virgaloceras*). The cross section of the outer volution (Fig. 287,H) is domatoceratid in aspect except for a narrow ridge along the ventral shoulder. The inner volutions are more elliptical in cross section (e.g., *Pselioceras*).

A number of late Paleozoic nautiloids are characterized by more or less quadrate whorl sections in which the ventral and umbilical shoulders are subangular to rounded. These forms are generally brought together in the loosely defined genus *Stearoceras* (L.Penn.-L.Perm.), which includes a group of species that obviously needs much additional study. Tentatively these forms are considered as related and parallel to *Domatoceras*.

The origin of the Syringonaulitidae is much less obvious than is that of the other families of Triassic nautiloids. A possible origin in the Grypoceratidae (114) is suggested by similarity of the basic conch patterns found in some groups of these two families (Fig. 287), plus the lack of another possible ancestral group, since the Tainocerataceae, Aipocerataceae, and Clydonaulitaceae are completely ruled out on morphological grounds.

The most important evolutionary lines in Pennsylvanian and Permian Grypoceratidae are represented by *Domatoceras* and

Koninck, 1880, pl. 45, fig. 5c).—C. *Epidomato-ceras maccoyi* TURNER (1954, fig. 1a).—D. *Paradomatoceras applanatum* DELÉPINE (1937, fig. 2C). —E. *Plummeroceras plummeri* KUMMEL (1953, fig. 27).—F. *Domatoceras umbilicatum* HYATT (after Turner, 1954, fig. 1c) (Kummel, n).

*Stearoceras*, which show a wide divergence in conch shape and have transitional forms between them. It is in these transitional forms that one can find nautilids with essential morphological features requisite to a syringonauilid ancestry. *Syringoceras* (M. Trias.-U.Trias.) and *Syringonauutilus* (M. Trias.-U.Trias.) differ only in position of the siphuncle. The geologic history of these two genera has interesting and contrasting patterns. *Syringonauutilus*, which has an almost centrally located siphuncle, is represented by most of its species near the beginning of its recorded history and declines rapidly in numbers of species until its extinction in the Late Triassic (Norian). *Syringoceras*, which has a nearly marginal siphuncle, on the other hand, furnishes record of a great evolutionary explosion toward the close of its history in the Carnian.

In the Late Triassic three aberrant genera (*Juvavionauutilus*, *Oxynauutilus*, *Clymenonauutilus*) probably evolved from *Syringonauutilus*. The first two have conch patterns similar to those found in the ancestral Paleozoic family Grypoceratidae, *Juvavionauutilus* being morphologically similar to *Domatoceras* and *Oxynauutilus* to *Stenopoceras* (Fig. 287,A,B,L,O). *Clymenonauutilus* is vaguely convergent with the Clydonauilidae in its suture pattern but has the conch shape of a typical *Syringonauutilus* (Fig. 287,D).

### NAUTILACEAE

The near extinction of the nautiloids toward the close of the Triassic is strikingly illustrated by the great contrast between Devonian-Triassic and the Jurassic-Recent nautiloids. The earliest Jurassic marine deposits contain a very homogeneous nautiloid fauna of nearly worldwide distribution. In so far as nautiloids are concerned, there must have existed in the transition from Triassic to Jurassic what amounts to an ecologic vacuum evidenced by the extinction of all Triassic stocks. A single derivative of the Syringonauilidae survived this transition (114), and in the early Jurassic (Lias) a new evolutionary radiation took place. SHIMANSKIY (166) has allied the Jurassic Pseudonauilidae with the earlier Clydonauilidae, an interpretation I cannot accept, as already discussed. Elements of the early Jurassic stock are quite clearly re-

lated to one another very closely, but at the same time they show a wide adaptive range in terms of conch shape, size, sutures, and shell characters (115, Fig. 8, 9, 10). All these features reflect and express the new adaptive radiation that was taking place at this time, initiated in a single genus, *Cenoceras*. The earliest species of *Cenoceras* (*C. trechmanni*), from Upper Triassic (Carnian) strata of New Zealand, was derived from the Syringonauilidae (114). In the Lias a worldwide fauna of involute to evolute, strigate-to-smooth nautilid forms thus is recognized with a wide range in whorl shapes. From this homogeneous but plastic stock several distinct evolutionary lines arose from diverse parts of the complex, characterized by specialization of one or more morphological features (Fig. 290). From this *Cenoceras* complex arose the persisting, stable stock (*Eutrephoceras*) that gave rise to the other members of the Nautilidae. Likewise the Paracenoceratidae, Pseudonauilidae, and the Cymatoceratidae are believed to have originated directly from the *Cenoceras* complex.

No author seems to feel the need of separating at a higher than family level within the Nautilaceae such forms as *Eutrephoceras* (U.Jur.-Mio.), of the family Nautilidae, from *Aturoidea* (U.Cret.-Eoc.), family Hercoglossidae, which has a highly elaborate suture.

*Eutrephoceras* has a worldwide distribution and a range in time from the Late Jurassic to the mid-Cenozoic. It and *Cymatoceras* (U.Jur.-Oligo.) are the most common post-Triassic nautiloids. Some 90 so-called species of *Eutrephoceras* have been described. The genus generally has a tightly involute, subglobular, smooth conch with nearly straight sutures (Fig. 290,E). It is a perfect heterochronous homeomorph of *Liroceras*. This basic, very simplified, conch type became modified in some species either by greater compression, by depression, or by slightly looser coiling. The variants, however, on the basis of the available record, appear to be completely random in their chronologic and geographic distribution. The long geologic range and pattern of morphological variation seen in this genus is very reminiscent of the *Liroceras-Paranauutilus* line, which ranges from Car-

boniferous through Triassic. *Carinonautilus* (U.Cret.) and *Obinautilus* (Oligo.) are monotypic forms, the latter seeming to be a highly compressed descendant of *Eutrephoceras*, as is *Nautilus*. *Carinonautilus* and *Strionautilus* (L.Cret.) are very difficult to interpret. They are placed in the Nautilidae for want of any better indication of affinities. *Pseudocnoceras* (Cret.) appears to be a compressed descendant of *Eutrephoceras* with a slightly open umbilicus.<sup>1</sup>

The Paracenoceratidae are a small family of four genera characterized by specialization of the venter. The main stock of the family, *Paracenoceras* (M.Jur.-L.Cret.), is nearly world-wide in distribution and has by far the largest number of species. The other genera, *Somalinautilus* (M.Jur.-U. Jur.), *Aulaconautilus* (U.Jur.), and *Tithonoceras* (U.Jur.), are more highly specialized forms with few known species. In *Paracenoceras* the whorl section is subtrapezoidal, generally with a broad, sulcate venter (Fig. 290,F). *Somalinautilus* has angular ventral shoulders but a broad arched venter. *Aulaconautilus* has four or more longitudinal ridges on the venter. In this respect it is homeomorphous with *Aulame-tacoceras* of the Permian and Triassic (Fig. 290,G). *Tithonoceras* has prominent, rounded ventrolateral keels with a sulcate venter.

One of the most successful and diverse groups to stem directly or via intermediate forms from the *Cenoceras* complex is the Cymatoceratidae. This family of 10 genera, ranging from the Jurassic to the mid-Cenozoic, is characterized by rib-bearing conchs and is the only group of post-Triassic nautiloids to have ornamentation, aside from *Aulaconautilus* of the Paracenoceratidae. Radiation within the Cymatoceratidae is reflected by shape of the conch, sutures and ornamentation. The main evolving stock, *Cymatoceras*, has an involute, rounded conch with only a slightly sinuous suture (Fig. 290,L). Most other genera of this family are believed to represent various specialized groups derived from *Cymatoceras*. *Paracymatoceras* (U.Jur.-L.Cret.) has more

sinuous sutures, much like those of *Hercoglossa*, and even in this feature is gradational with *Cymatoceras*. Forms differentiated on the basis of conch shape include *Heminautilus* (L.Cret.), *Deltocymatoceras* (U.Cret.), *Epicymatoceras* (U.Cret.), and *Cymatonautilus* (M.Jur.-U.Jur.) (Fig. 290). *Heminautilus* has a compressed, involute conch with highly sinuous sutures. *Deltocymatoceras* is a homeomorph of *Deltoidonautilus* with a sagittate whorl section. *Epicymatoceras* has an evolute, highly compressed conch with a subrectangular whorl section. *Cymatonautilus* has a concave venter and concave lateral areas. Genera differentiated on the basis of modification of ribbing pattern include *Eucymatoceras* (L.Cret.), *Anglonautilus* (L.Cret.-U.Cret.), *Procymatoceras* (M.Jur.), and *Syrionautilus* (U.Cret.). In *Eucymatoceras* the ribs form prominent V-shaped salients on the venter and flanks. In *Anglonautilus* coarse folds occur on the venter, whereas *Procymatoceras* has a rapidly expanding, robust conch with ribs mainly on the lateral areas. *Syrionautilus* has peculiarly shaped ribs with wide interspaces like those of *Proclydonautilus spirolobus* of the Triassic. The most widespread and characteristic nautiloids of the Cretaceous are members of the Cymatoceratidae.

The only direct offshoot from the Nautilidae is the family Hercoglossidae, which first appeared in the Jurassic, had a very modest Cretaceous record, and became very abundant and widespread in the early Cenozoic. The Hercoglossidae are involute, smooth nautilicones with main evolutionary emphasis on modification of the sutures (Fig. 291). A progressive series can be distinguished, leading from *Cimomia* (U.Jur.-Oligo.) to *Hercoglossa* (?L.Cret., Paleoc.-Eoc.) to *Aturoidea* (U.Cret.-Eoc.), and then to *Aturia* (Paleoc.-Mio.) of the Aturidae. It seems clear that *Cimomia* arose from *Eutrephoceras*, although the transition from one to the other is not easy to decipher. The only significant difference between these genera is in degree of sinuosity of the sutures, *Eutrephoceras* having straight or nearly straight sutures, whereas sutures of *Cimomia* have distinct lobes and saddles on the lateral areas. Intergrading forms occur. The time ranges of the two genera are ap-

<sup>1</sup> SHIMANSKIY (1966) included 15 genera in the Nautilidae, of which *Bisiphytes*, *Digonioceras*, *Ophionautilus*, and *Sphaeronautilus* are believed to be synonyms of *Cenoceras* (KUMMEL, 1956). Three other genera (*Paracenoceras*, *Somalinautilus*, *Tithonoceras*) are here kept in the Paracenoceratidae of SPATH. *Paleliulia* SHIMANSKIY (1954) is a synonym of *Pseudaganides*.

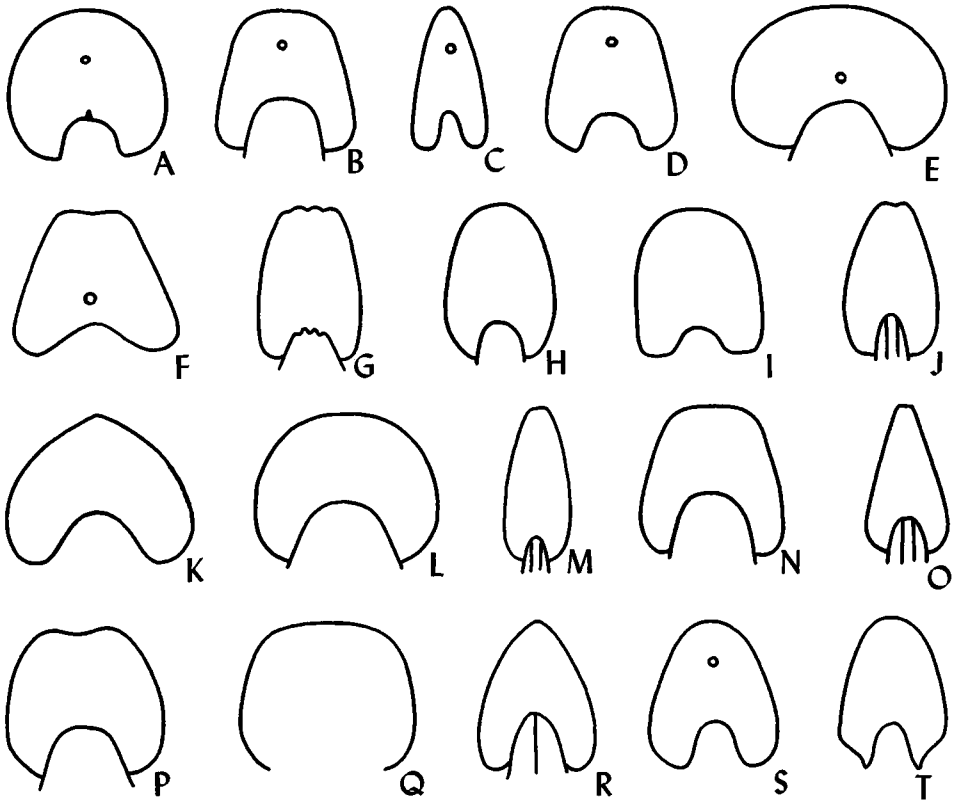


FIG. 290. Whorl sections of representative genera of the Nautilaceae.—A. *Cenoceras striatus* (SOWERBY) (after Pia, 1914, pl. 8); diameter, 110 mm.—B. *Pseudaganides kutchensis* (WAAGEN) (1873, pl. 3, fig. 4b); diameter, 46 mm.—C. *Pseudaganides gravesiana* (D'ORBIGNY) (after Pia, 1914, pl. 10); diameter, 240 mm.—D. *Pseudonautilus geinitzi* (OPPEL) (after Miller & Collinson, 1953, fig. 1); height, 30 mm.—E. *Eutrophoceras dekayi* (MORTON) (after Stenzel, 1940, fig. 115); diameter, 46 mm.—F. *Paracenoceras hexagonum* (SOWERBY) (after Spath, 1935, fig. 4d); height, 56 mm.—G. *Aulaconautilus sexcarinatus* (PICHET) (1867, pl. 10, fig. 1b); diameter, 107 mm.—H. *Nautilus pompilius* LINNÉ (after Miller, 1949, fig. 4); diameter, 150 mm.—I. *Pseudocenoceras largilliertianus* (D'ORBIGNY) (based on plesiotype in Kummel, 1956, pl. 10, fig. 3, 4); diameter, 62 mm.—J. *Carinonautilus ariyalurensis* SPENGLER (1910, pl. 14, fig. 1a, c); diameter, 87 mm.—K. *Deltocymatoceras rugatus* (FRITSCH & SCHLÖNBACH) (1872, pl. 15, fig. 2); height, 80 mm.—L. *Cymatoceras sharpei* (SCHLÜTER) (1876, pl. 46, fig. 6); diameter, 168 mm.—M. *Epicymatoceras vaelsensis* (BINCKHORST) (1861, pl. 5c, fig. 2b); diameter, 105 mm.—N. *Procymatoceras baberi* (MORRIS & LYCETT) (1850, pl. 1, fig. 1a); diameter, 82 mm.—O. *Heminautilus saxbii* (MORRIS) (based on holotype); diameter, 85 mm.—P. *Paracymatoceras asper* (OPPEL) (after Zittel, 1868, pl. 3, fig. 1a); diameter, 83 mm.—Q. *Anglonautilus undulatus* (SOWERBY) (after Kummel, 1956, fig. 26); height, 40 mm.—R. *Deltoidonautilus triangularis* (DEMONTEFORT) (after d'Orbigny, 1840, pl. 12, fig. 2); diameter, 200 mm.—S. *Hercoglossa orbiculata* (TUOMEY) (after Miller, 1947, fig. 12); height, 174 mm.—T. *Aturoidea parkinsoni* (EDWARDS) (after Miller, 1951, fig. 15A); height, 180 mm.

proximately the same, *Cimomia* appearing slightly later in time.

### CONVERGENCE, DIVERGENCE, AND PARALLELISM IN EVOLUTION

The shell of any member of the Nautilida is a very simple structure consisting of

phragmocone, body chamber, septa, and siphuncle. The relationships of these parts to one another and to the whole shell, and relationships of the shell to features of environment and the mode of life of individuals are unfortunately very poorly understood, even for the modern *Nautilus*. It is assumed by most students that the shell reflects a more or less specific adaptation to

a particular mode of life and environmental niche. Some experimental work has been done on the relative streamlining of cephalopod shells (H. SCHMIDT, 1930; KUMMEL & LLOYD, 1955) and on buoyancy of the shells (TRUEMAN, 1941; REYMENT, 1958). Most of these studies have substantiated generally held views as to the relative streamlining of various types of cephalopod shells. KUMMEL & LLOYD (116) presented experimental data to show that involute shells are generally better streamlined than evolute ones but that evolute, compressed shells also have favorable streamlining. Widely umbilicate shells with depressed whorl sections are much less streamlined, as, of course, are coarsely ornamented forms. Shape of the shell, degree of involution, and the like undoubtedly influenced ease of movement of individuals.

The shell of a nautiloid is essentially a straight-to-coiled tapering tube or cone and as such is limited in the range of possible modifications in shape. The cross section of such a tapering shell conforms basically to one of four primary patterns: modified square, rectangle, circle, or triangle.

In the preceding discussion of the classification and evolution of the Nautilida it was pointed out that in many of the main evolutionary lineages (families and superfamilies) a certain basic shell pattern predominated, that the largest number of species, widest geographic distribution, and longest geologic ranges are found among genera having this "basic shell pattern," and that most other genera of a particular evolutionary line possess special adaptations comprising modifications of the basic pattern. Thus, within the Tainoceratidae, the subquadrate whorl section of *Metaceras* and *Mojsvaroceras* determines the main pattern for this family, as does the subrectangular whorl section of *Domatoceras* and *Grypoceras* for the Grypoceratidae, and the subglobular whorl section for the Liroceratidae. Whereas the mid-Paleozoic-through-Triassic nautiloids have, for the most part, distinctive shell shapes in each of the main evolving lines (superfamilies) this does not apply to the Nautilaceae of Jurassic-to-Recent age. In this group extensive mixing of shell shapes is found within a single family (e.g., Cymatoceratidae).

Although a correlation can be seen between shell form and evolutionary lineage in most groups, many examples of unrelated genera are found to develop similar shell forms. If the form of a nautiloid shell is an adaptive character, then convergence in shell form is easily understood.

One of the more specialized types of shells has convergent flanks and narrowly rounded-to-acute venters, and presumably the streamlined conch thus achieved permitted greater ease of movement. This type of conch appears in several evolutionary lines at least once and, in some, several times. Each acquisition of this type can be fairly well traced from ancestral forms characterized by subrectangular, or ovate whorl sections, or both. No conchs with highly convergent flanks are known in the Tainocerataceae or Aipocerataceae but they are common in the Trigonocerataceae, Clydonautilaceae, and Nautilaceae.

The oldest known true oxycone is the centroceratid *Phacoceras*, from the Lower Carboniferous of Europe. The other members of the Centroceratidae have compressed conchs, but in each case the venter is flat, concave, or slightly arched. The Centroceratidae are believed to stem from the Tetragonoceratidae, or possibly directly from the Oncocerida, both of these groups having quadrate to oval whorl sections as the dominant pattern. The Centroceratidae gave rise to the Trigonoceratidae and Grypoceratidae. No true oxycones are recognized in the Trigonoceratidae but conchs with whorl sections approaching this type characterize *Aphelaeceras* (Miss.), *Epistroboceras* (L.Carb.), and *Leuroceras* (L. Carb.). True oxycones are to be found in the Grypoceratidae in *Stenopoceras* (Penn.-L.Perm.), *Gryponautilus* (U.Trias.), and in the Syringonautilidae in *Oxynautilus* (U. Trias.). In *Stenopoceras* only a few species have an acute or narrowly rounded venter (e.g., *S. whitei* MILLER & YOUNGQUIST, *S. sp.* MILLER, 1945). Other species have narrow, concave venters (e.g., *S. smithi* MILLER & UNKLESBAY and *S. abundum* MILLER & THOMAS) or narrow, arched venters (e.g., *S. cooperi* MILLER & UNKLESBAY, *S. dumblei* (HYATT)). One specimen of *S. abundum* figured by MILLER & YOUNGQUIST (136) has a narrow arched venter, rather



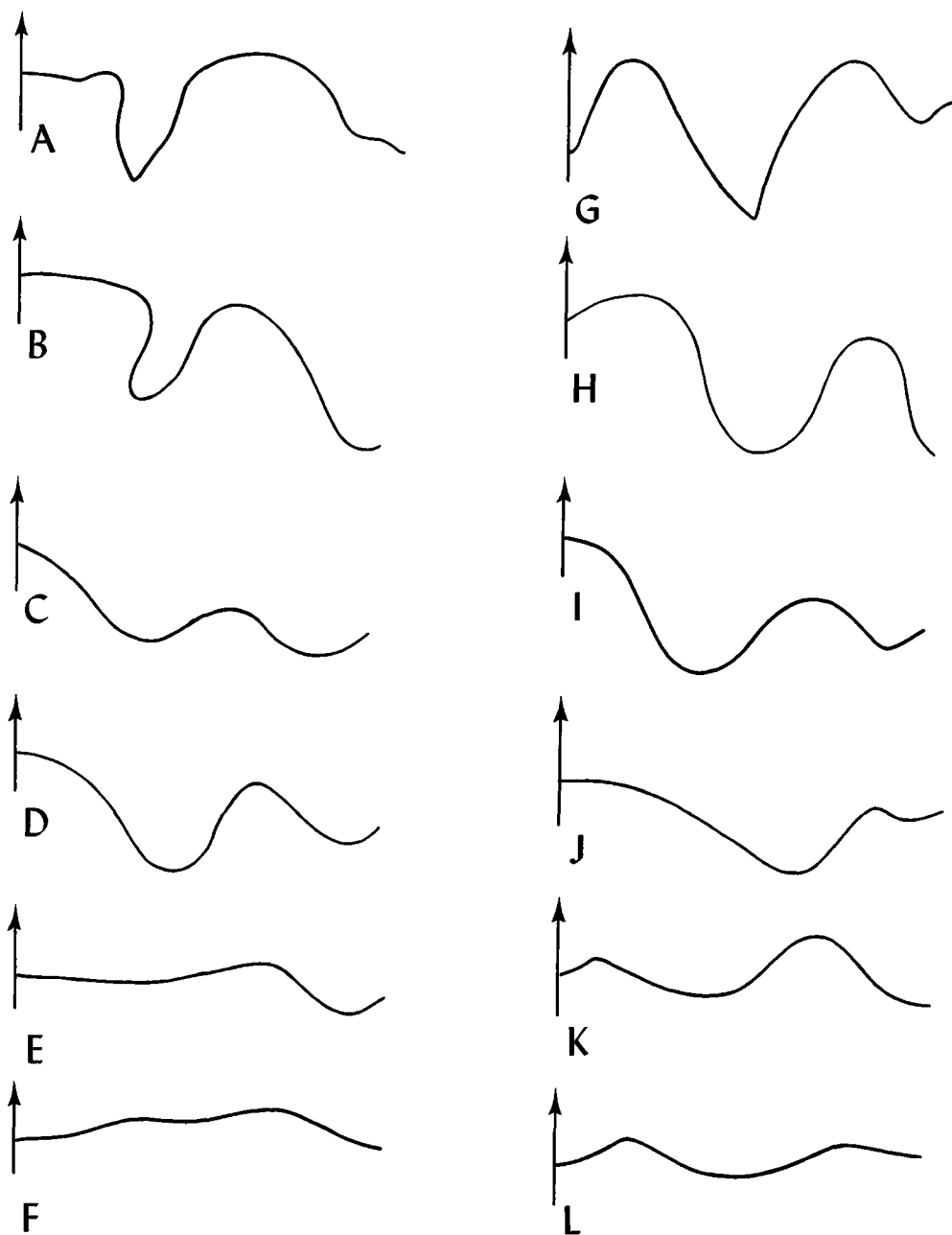


FIG. 291. Sutures of representative genera of the Nautilaceae.—A. *Aturia luculoensis* MILLER (1945, fig. 3C).—B. *Aturoidea paucifex* (COPE) (after Miller & Thompson, 1935, pl. 65, fig. 2).—C. *Deltoidonautilus sowerbyi* (WETHERELL) (after Stenzel, 1940, fig. 124).—D. *Hercoglossa orbiculata* (TUOMEY) (after Stenzel, 1940, fig. 117).—E. *Cimomia landanensis* (VINCENT) (after Miller, 1947, fig. 7a).—F. *Eutrophoceras deKayi* (MORTON) (after Reeside, 1924, fig. 1d).—G. *Pseudonautilus geinitzi* (OPPEL) (1868, pl. 2, fig. 7).—H. *Pseudaganides brunhuberi* (LOESCH) (1914, fig. 5c).—I. *Paracymatoceras texanum* (SHUMARD) (after Miller & Harris, 1945, fig. 3A).—J. *Nautilus pompilius* LINNÉ (after Miller, 1949, fig. 4).—K. *Heminautilus etheringtoni* DURHAM (1946, fig. 3C).—L. *Paracenoceras hexagonum* (SOWERBY) (after Spath, 1935, fig. 4e).

than a concave one, such as occurs in the type. *Stenopoceras* is descended from *Domatoceras*, which has, basically, a subrectangular whorl section, through such species as *Domatoceras kleihegei* and *D. moorei*. *Stenopoceras* is the only Paleozoic offshoot of the *Domatoceras-Grypoceras* lineage that evolved toward oxycone shells. The acquisition of this type of conch form invariably accompanied a trend toward greater involution. In the Triassic, the oxycone trend did not attain fulfillment in *Grypoceras* although in that genus clear tendency toward involution with rounding and narrowing of the periphery is seen. As previously mentioned, *Grypoceras* is considered to be a direct evolutionary continuation of *Domatoceras*. The culmination of the oxycone trend in *Grypoceras* itself is best shown by *G. obtusum* of Norian age. Oxyconic shape was attained in *Gryponautilus*, an upper Triassic offshoot of *Grypoceras*. Of interest is the tightly involute nature of the conch, with converging whorl sides and a broad, more or less flattened venter; it is only on the outermost mature whorls (as in the type species, *G. galeatus*) that the venter becomes acute, almost keel-like.

The oxycone trend is also expressed in the Syringonautilidae, derivatives of the Paleozoic *Domatoceras* complex (114). In this line it reaches its acme of development in the genus *Oxynautilus*. At the same time an approach to the oxycone type of whorl section can be recognized in several species of *Juvavionautilus*. *Oxynautilus* is very much like *Stenopoceras*, and *Juvavionautilus* is much like many species of *Domatoceras*.

The number of species involved in these trends towards oxycone shells is small. *Oxynautilus* is monotypic, *Phacoceras* has three species, and *Stenopoceras* eight species. Only one species of *Gryponautilus* shows the acute venter.

In the Trigonocerataceae near-oxycone and oxycone conchs appeared more or less throughout the history of the superfamily. One of the most unexpected groups to produce them is the Clydonautilaceae, in which this development was common in the Late Triassic, although unknown in the earlier history of the several families

comprising the group. The Liroceratidae, mainly Paleozoic, have oval, involute whorl sections or modifications of them. The Triassic *Paranautilus* is a direct evolutionary extension of the late Paleozoic *Liroceras*. The principal difference between these genera is a tendency in *Paranautilus* toward greater compression, a tendency that reached its acme in *P. meridionus* from the Upper Triassic of Timor. Both genera and other closely related forms of the Liroceratidae have simple, nearly straight sutures. *Paranautilus* gave rise to a highly successful group of Upper Triassic families that maintained a tightly involute conch but developed highly differentiated sutures with deep lobes and saddles. In this radiation, the basic pattern of the sutures remained fairly constant within each generic group even though conch shapes became highly varied (113, Fig. 38, 40). One trend was in the direction of whorls having strongly convergent flanks and narrow venters (e.g., *Styrionautilus discoidalis*, *Proclydonautilus ermollii*, *P. buddhaicus*, *Clydonautilus timorensis*, *Gonionautilus securis*, *Cosmonautilus dilleri*, which are among the most common Upper Triassic nautiloids).

The tendency toward development of oxycone conchs is widespread in the Nautilaceae. In the *Cenoceras* complex it is expressed in such forms as *C. araris* and *C. fischeranus*. In the Pseudonautilidae, *Pseudaganides gravesianus* and *P. sinuatus* are good examples. The range of variation in shape of the whorl section of *Pseudaganides* is from quadrate (*P. brunhuberi*), to oval (*P. schneidi*), to subrectangular (*P. frickenensis*), to triangular (*P. gravesianus*). Also, the degree of sinuosity of the sutures seems correlatable with degree of variability of the whorl sections. This relationship is best seen in genera of the Upper Triassic Clydonautilidae and in the Jurassic Pseudonautilidae.

In the Cymatoceratidae an acute venter is found only in one genus, *Deltocymatoceras* (U.Cret.). An approach to this type of venter, however, is seen in *Heminautilus* (L.Cret.), which has a narrow, concave to flattened venter. The main pattern of the whorl section in the Cymatoceratidae

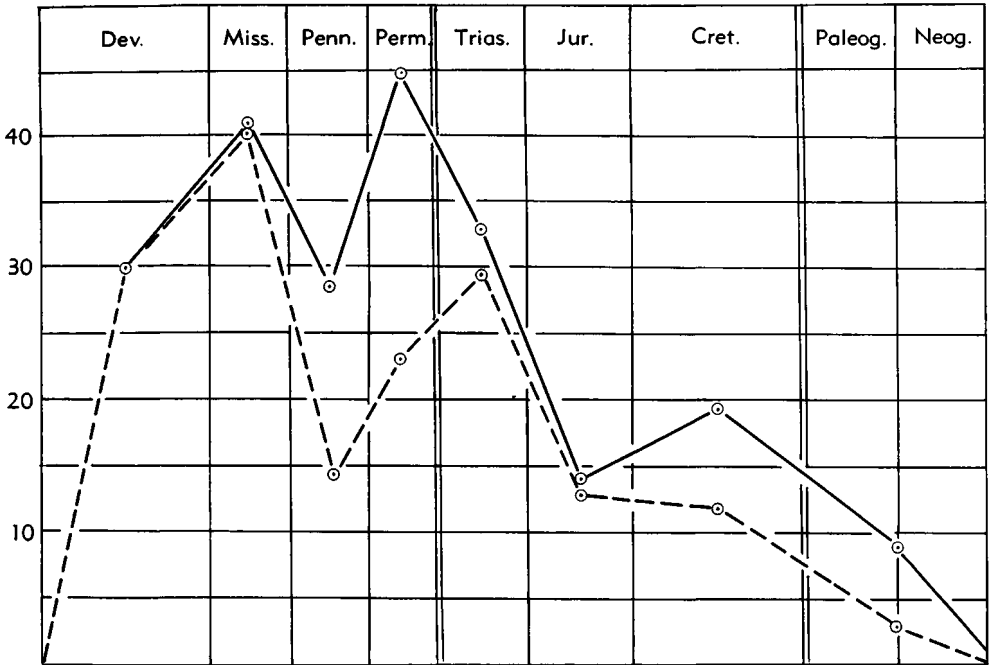


FIG. 292. Total number of nautilid genera (solid lines) and new genera (dashed lines), by periods.

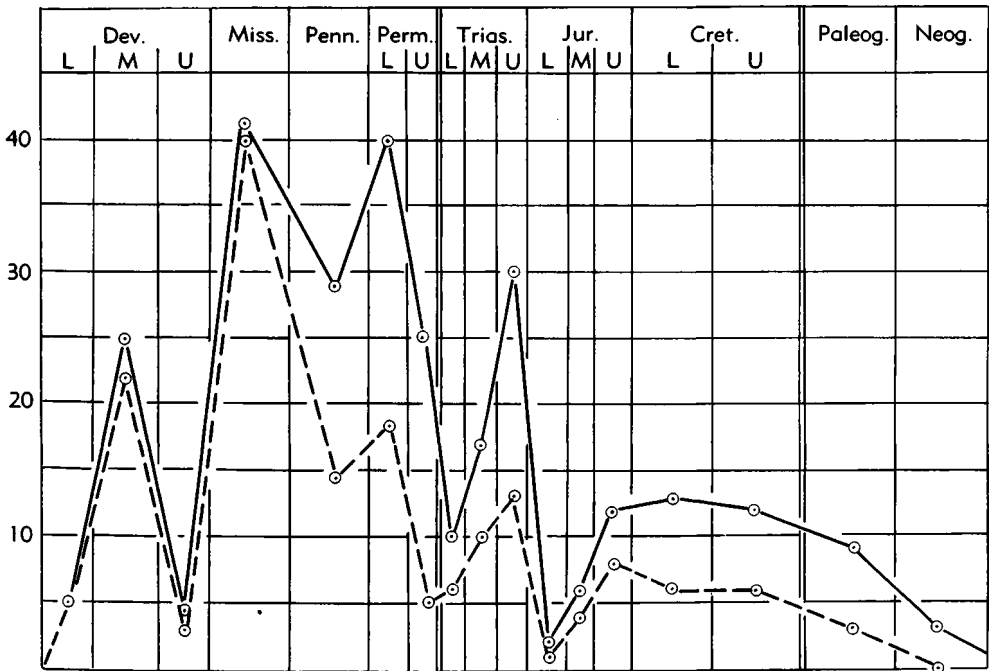


FIG. 293. Total number of nautilid genera (solid lines) and new genera (dashed lines) by epochs. [Permoceratidae should be shown as L.Perm., not U.Perm.]

is oval, with some tendency toward flattening of the venter and flanks.

Forms with acute venters in the Hercoglossidae are included in *Deltoidonautilus* (U.Cret.-Oligo.), in which the whorl section ranges from depressed (e.g., *Deltoidonautilus* sp. HAAS & MILLER, 1952) to highly compressed (e.g., *D. rogeri* MILLER, 1951).

The time distribution of the species with acute or nearly acute venters supports the conclusion that these adaptations originated in different stocks at different times. Among the Lower Carboniferous forms, only *Phacoceras* has a truly acute venter, although *Aphelaeceras*, *Epistroboceras*, and *Leuroceras* have narrowly rounded to flattened or concave venters. In Pennsylvanian through Middle Permian forms, only certain species of *Stenopoceras* attained an acute venter. During the Late Permian, Early and Middle Triassic, no species with acute venters are known. It was during the Late Triassic that a number of such forms again appeared, belonging to the Gryptoceratidae (*Gryponautilus*), Syringonautilidae (*Oxy-nautilus*), Clydonautilidae (*Styrionautilus*, *Proclydonautilus*, *Clydonautilus*) and Gonionautilidae (*Gonionautilus*).

In the Trigonocerataceae acute whorl sections appeared in the early history of the group and again at the close; in the Clydonautilaceae this type of conch only appeared at the close; in the Nautilaceae it appeared both in the early and late middle history of the superfamily.

Ornamentation does not figure prominently in evolution of the Nautilida, being largely confined to the Tainocerataceae and to the Cymatoceratidae among the Nautilaceae. As in shape of whorl sections, variety of ornamentation is limited and particular patterns appear in quite unrelated groups. For example, longitudinal ribs on the venter first appear in the Permian *Aulametaceras*, which also has a Triassic species; the same type of ribbing appears in *Aulaconautilus* of Jurassic age (family *Paraceneratidae*). The mature umbilical spines of the solenochilids are proportionally longer than those of *Cooperoceras* (L.Perm.). Ribs characterize *Pleuro-*

*nautilus* and related genera of the Permian and Triassic. They appeared again, but in very different form, in the predominantly Cretaceous Cymatoceratidae.

Homeomorphy in sutural development is probably the most striking example of adaptive convergence in the Nautilida. The sutures of the Tainocerataceae and Aipocerataceae are quite simple, with shallow lobes and saddles. In two families, the Clydonautilidae (Clydonautilaceae) and the Hercoglossidae (Nautilaceae), what appears to be a linear series of progressive elaboration of sutures produced deep lobes and saddles. Sutures of this general type appeared also in the Trigonocerataceae, Pseudonautilidae, and the Cymatoceratidae.

Among known examples of homeomorphy in sutures one of the most perfect is that of the Permian grypoceratid *Permoceras* and the late Jurassic pseudonautilid *Pseudonautilus* (Fig. 288,A; 291,G). The former genus is allied to *Domatoceras* in general shape of the conch, and there are transitional types of sutures intermediate between those of *Domatoceras* and *Permoceras* (Fig. 291). For example, *Plummeroceras* has a deep, rounded ventral lobe and an equally deep lateral lobe, *Epidomatoceras* a broad V-shaped ventral lobe, and *Paradomatoceras*, a similar but shallower V-shaped ventral lobe. In general, other members of the Grypoceratidae have sutures with shallow lobes and saddles. *Pseudonautilus* seems best understood as a specialized descendant of *Pseudaganides*. The hercoglossid type of suture appeared in two members of the Cymatoceratidae. In one (*Paracymatoceras*) the whorl section is oval; in the other (*Heminautilus*) it is highly compressed, with convergent flanks and narrow venter.

## SYSTEMATIC DESCRIPTIONS

### Subclass NAUTILOIDEA Agassiz, 1847

Diagnosis given in "Introductory Discussion" (p. K128). *U.Cam.-Rec.*

FIG. 294. (Facing page.) Stratigraphic distribution of genera and families of Nautilida (Kummel, n). [Permoceratidae should be shown as L.Perm., not U.Perm.]

	Dev.			Miss.	Penn.	Perm.			Trias.			Jur.			Cret.		Paleog.	Neog.
	L	M	U			L	U	L	M	U	L	M	U	L	U			
Rutoceratidae																		

Order NAUTILIDA Agassiz, 1847

[*nom. correct.* SHIMANSKIY, 1957 (*pro order* Nautiloidea AGASSIZ, 1847, *nom. transl.* HYATT, 1883, *ex suborder* Nautiloidea, 1847); mention of Nautilida by FURNISH, GLENISTER, & HANSMAN, 1962 (p. 1342), is disregarded] [incl. Nautilida (*ex* Nautiloidea) SPATH, 1927; Nautilacea SCHINDEWOLF, 1935 (*suborder*); Nautilacea KUHN, 1949 (*order*); Rutoceratida, Centroceratida, Solenochilida FLOWER in FLOWER & KUMMEL, 1950 (*orders*); Nautilina, Liroceratina, Tainoceratina, Centroceratina, and Rutoceratina SHIMANSKIY, 1957 (*suborders*)]

Curved to coiled conchs representing majority of mid-Paleozoic to Recent nautiloids. [Tainocerataceae and Trigonocera-

taceae derived directly or indirectly from Oncocerida; origin of Clydonautilaceae and Aipocerataceae uncertain, probably from Rutoceratidae. Nautilidae stem from Syringonautilidae.] *L.Dev.-Rec.*

The total number of nautilid genera and new genera introduced in successive periods are shown graphically in Figure 292. The total number of nautilid genera and new

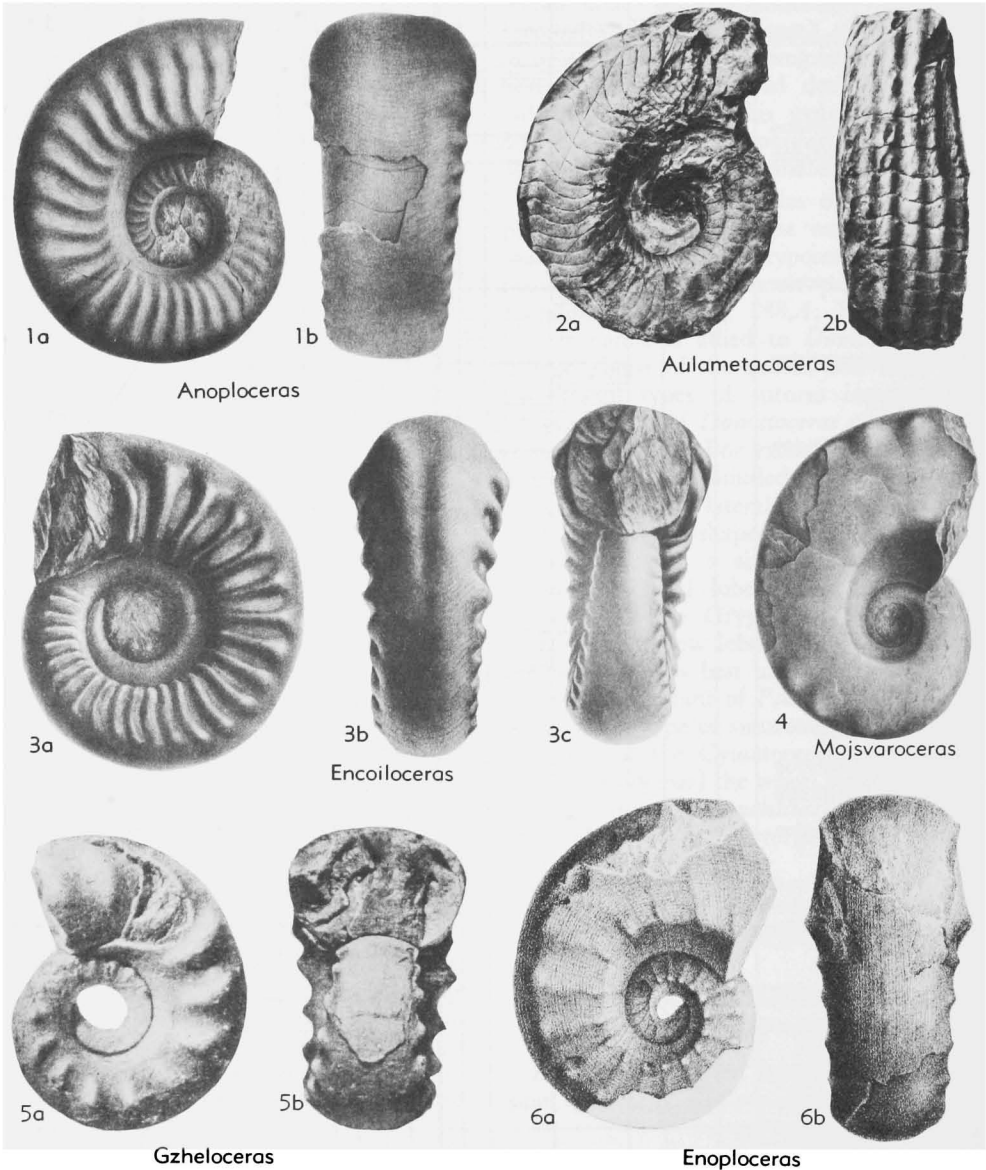


FIG. 295. Tainocerataceae (Tainoceratidae) (p. K413-K414).

genera introduced in successive epochs are indicated in Figure 293.

The stratigraphic occurrence of genera included in the Nautilida is shown graphically in Figure 294.

## Superfamily TAINOCERATACEAE Hyatt, 1883

[*nom. transl.* KUMMEL, herein (ex Tainoceratidae HYATT, 1883)] [incl. Koninckioceratida, Hercoceratida, Rhyticeratida HYATT, 1900 (divisions of suborder); Hercoceracea, Ryticeracea KINDLE & MILLER, 1939 (superfam.) (*partim*); Rutoceratida FLOWER in FLOWER & KUMMEL, 1950 (order); Tainocerataceae, Tainoceratina, Encoilocerataceae, Temnocheilaceae, Rhiphaocerataceae, Rutocerataceae, Rutoceratina SHIMANSKIY, 1957 (suborders)]

Straight to loosely coiled shells with depressed to quadrate whorl sections, rarely with compressed whorl sections. Early forms with straight to loosely coiled conch bearing wings, spines, ribs, nodes, or frills; later forms with more tightly coiled conch bearing nodes or ribs or both; some forms essentially smooth. Siphuncle generally near-ventral in early forms but variable in position (usually central) in later forms. Suture with very shallow lobes on venter and flanks, annular lobe present in many forms. *L.Dev.-Trias.*

### Family TAINOCERATIDAE Hyatt, 1883

[incl. Gyroceratinae MOJSISOVICS, 1882 (*partim*); Pleuronautilidae HYATT in ZITTEL, 1900; Temnocheilidae MOJSISOVICS, 1902; Mosquoceratidae, Gzheloceratidae RUZHENTSEV & SHIMANSKIY, 1954; Encoiloceratidae SHIMANSKIY & ERLANGER, 1955; Tainoceratinae SHIMANSKIY, 1957; Pleuronautilinae SHIMANSKIY, 1959]

Includes nearly all nautiloids of late Paleozoic and Triassic age that bear ornamentation consisting of ribs or nodes, or both. Conch generally evolute, large; whorls quadrate to rectangular in outline. Suture only slightly sinuous, siphuncle usually near center (113). *L.Carb.(Miss.)-Trias.*

**Tainoceras** HYATT, 1883 [*\*Nautilus quadrangulus* MCCLESNEY, 1860; OD]. Like *Metaceras* but with a double row of nodes on venter (134). *U.Carb.(Penn.)-Trias.*, N.Am.-Asia.—FIG. 298, 5. *T. clydenae* MILLER & KEMP, L.Perm., USA (Tex.); 5*a,b*,  $\times 0.7$  (134).

**Anoploceras** HYATT in ZITTEL, 1900 [*\*Nautilus ampezzanus* LORETZ, 1875; OD]. Like *Pleuro-nautilus* but with depressed whorl section, broad, slightly concave venter; conspicuous lateral ribs that project adorally near umbilical shoulder (113). *M.Trias.(Anis.)-U.Trias.(Carn.)*, Eu.

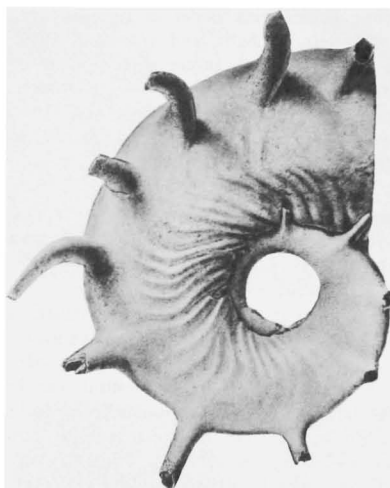


FIG. 296. *\*Cooperoceras texanum* MILLER (Tainoceratidae) (p. K413).

(Alps-Rumania).—FIG. 295, 1. *\*A. ampezzanum* (LORETZ), Carn., Alps; 1*a,b*,  $\times 0.4$  (140).

**Aulametaceras** MILLER & UNKLESBAY, 1942 [*\*A. mckeei*; OD]. Like *Metaceras* but with several longitudinal grooves and ridges on venter. *L.Perm.-U.Trias.(Carn.)*, N.Am.-Eu.(Alps).—FIG. 295, 2. *\*A. mckeei*, L.Perm., USA (Ariz.); 2*a,b*,  $\times 0.2$  (134).

**Cooperoceras** MILLER, 1945 [*\*C. texanum*; OD]. Evolute; whorl section subcuneiform, flattened ventrally and laterally, flanks converging dorsally; narrow, shallow, median groove on venter; umbilicus, wide, open, perforate; at maturity conch bears sinuous lateral ribs and long, slender, hollow, paired ventrolateral spines that project ventrolaterally and are recurved; suture with rounded ventral, lateral and dorsal lobes; siphuncle, small, subcentral, orthochoanitic (134). *L.Perm.*, N.Am.-Eu.(Urals).—FIG. 296. *\*C. texanum*, USA (Tex.);  $\times 0.4$  (134).

**Encoiloceras** HYATT in ZITTEL, 1900 [*\*Nautilus superbus* MOJSISOVICS, 1873; OD]. Evolute, widely umbilicate conchs with large umbilical perforation; whorl section subquadrate, with arched venter, flanks with thick foldlike ribs that thicken at ventral shoulder; suture with shallow ventral, lateral and dorsal lobe, and annular lobe; siphuncle close to dorsum (113). *U.Trias.(Carn.)*, Eu.(Alps-Hung.).—FIG. 295, 3. *\*E. superbum* (MOJSISOVICS), Alps; 3*a-c*,  $\times 0.5$  (139).

**Enoploceras** HYATT in ZITTEL, 1900 [*\*Nautilus wulfeni* MOJSISOVICS, 1873; OD]. Moderately involute, with subquadrate whorl section, wider than high; venter, flanks and umbilical wall flattened; ventral and umbilical shoulders generally sharply rounded; umbilicus deep, with small per-

- foration; flanks with nodes at umbilical or ventral shoulders, or both, and with radial ribs and sinuous growth lines; suture with shallow ventral and lateral lobes, and annular lobe; siphuncle subcentral (113). *Trias.*, Eu.(Alps)-Asia(India)-E. Indies(Timor)-N.Am.(Idaho).—FIG. 295,6. \**E. wulfeni* (Mojsisovics), U.Trias.(Carn.), Alps; 6a,b,  $\times 0.7$  (139).
- Germanonautilus** MOJSISOVICS, 1902 [\**Nautilus bidorsatus* SCHLOTHEIM, 1832; OD] [= *Monilifer fritsch*, 1906 (obj.)]. Nautiliconic, moderately involute; whorl section subquadrate, generally wider than high; venter broad, flattened, commonly slightly concave; flanks converging ventrally; umbilical shoulders sharply rounded; shell smooth; suture with shallow ventral and broad, deeper lateral lobes, and annular lobe; siphuncle approximately central in position with strongly nummuloidal segments (113). *Trias.*, N.Am.-Eu.-Asia (Japan-Himalayas-Israel) - Afr.(Egypt). — FIG. 297,3. *G. breunneri* (Mojsisovics), U.Trias. (Carn.), Alps; 3a,b,  $\times 0.4$  (139).
- Gzheloceras** RUZHENTSEV & SHIMANSKIY, 1954 [\**G. uralense*; OD]. Evolute, with elliptical to subquadrate whorl sections; ribs on flanks; like *Pleuonautilus*, but lacking annular lobe (153). *U.Carb.-L.Perm.*, USSR.—FIG. 295,5. \**G. uralense*, L.Perm.; 5a,b,  $\times 1$  (153).
- Hexagonites** HAYASAKA, 1947 [\**H. chechiangensis*; OD]. Very evolute, whorl section hexagonal in outline, with 6 rows of tubercles, pairs on ventrolateral, on lateral, and on dorsolateral angles; dorsum almost straight; suture with shallow lobes; based on incomplete, crushed specimen (89). *Perm.*, E.Asia(China).—FIG. 298,4. \**H. chechiangensis*, Chechiang;  $\times 0.7$  (89).
- Holconautilus** MOJSISOVICS, 1902 [\**Nautilus semicostatus* BEYRICH, 1867; SD DIENER, 1915]. Like *Pleuonautilus* but with ventral saddles rather than lobes (113). *M.Trias.(Anis.)-U.Trias.(Carn.)*, Eu.-E.Indies(Timor).—FIG. 297,4. \**H. semicostatus*, Anis., Alps; 4a,b,  $\times 0.5$  (140).
- Hunanoceras** CHAO, 1954 [\**H. globosum*; OD]. Evolute, globose, with wide funnel-shaped umbilicus, broad depressed whorl sections; venter broadly rounded, emerging onto rounded lateral areas and bearing 2 rows of elongate nodes which disappear adorally; umbilical shoulder marked by raised ridge, umbilical wall high and steeply inclined; suture with shallow ventral and lateral lobes; siphuncle subcentral (9). *Perm.*, China (Hunan).
- Metacoceras** HYATT, 1883 [\**Nautilus* (*Discus*) *sangamonensis* MEEK & WORTHEN, 1861; OD] [= *Mosquoceras* RUZHENTSEV & SHIMANSKIY, 1954]. Moderately evolute, with subquadrate whorl section, bearing nodes on ventral or umbilical shoulders or both; suture with shallow ventral and lateral lobes, no annular lobe; siphuncle small, subcentral, and orthochoanitic (113). *U.Carb.(Penn.)-Perm.*, cosmop.—FIG. 297,2. *M. inconspicuum* HYATT, Perm., USA(Kans.);  $\times 0.5$  (134).
- Mojsvaroceras** HYATT, 1883 [\**Temnocheilus neumayri* MOJSISOVICS, 1882; OD] [= *Mojsisoceras* VON ZITTEL, 1884 (nom. van.?)]. Like *Metacoceras* but with annular lobe and slightly more involute. A direct evolutionary descendant of *Metacoceras* (113). *Trias.*, Eu.-Asia(Tethys)-W. N.Am.—FIG. 295,4. \**M. neumayri* (Mojsisovics), M.Trias.(Anis.), Alps;  $\times 0.3$  (140).
- Parametacoceras** MILLER & OWEN, 1934 [\**P. bellatulum*; OD]. Tarphyceraconic, evolute; whorl section subquadrate; umbilicus large, perforate; with sinuous growth lines that trace deep rounded hyponomic sinus on venter; flanks bearing short transverse ribs on mature portion of conch; suture with shallow ventral, lateral, and dorsal lobes; siphuncle small, subcentral, orthochoanitic (133). *U.Carb.(Penn.)*, N.Am. - Eu.(USSR - Belg.). — FIG. 297,1. \**P. bellatulum*, USA(Mo.); 1a-c,  $\times 1.3$  (133).
- Phaedrysmocheilus** SHIMANSKIY & ERLANGER, 1955 [\**Nautilus subaratus* KEYSERLING, 1860; OD]. Involute nautiliconic, early volutions slightly depressed, rounded, mature volutions slightly compressed, whorl section ovate with convex flanks, arched venter; umbilical shoulders sharply rounded, umbilical walls sloping so as to form deep funnel-shaped umbilicus; suture only slightly sinuous; early volutions with lateral ribs which are absent on living chamber (141). *L.Trias.*, USSR. — FIG. 297,5. \**P. subaratum* (KEYSERLING), Sib.; 5a,b,  $\times 0.8$  (141).
- Phloioceras** HYATT, 1884 [\**Nautilus gemmatus* MOJSISOVICS, 1873; OD]. Conch with longitudinal nodose ridges on flanks and venter (113). *M. Trias.(Ladin.)-U.Trias.(Nor.)*, N.Am.(Nev.-Alaska)-E. Indies(Timor)-Asia(Himalayas)-Eu.(Alps). — FIG. 298,7. \**P. gemmatum* (Mojsisovics), U. Trias.(Carn.), Alps; 7a,b,  $\times 0.3$  (139).
- Pleuonautilus** MOJSISOVICS, 1882 [\**P. trinodosus*; SD MOJSISOVICS, 1902] [= *Shansinautilus* YABE & MABUTI, 1935; *Huanghoceras* GRABAU IN YIN, 1933; *Tungkuoceras* HAYASAKA, 1947; *Basleonautilus*, *Pseudofoordiceras* RUZHENTSEV & SHIMANSKIY, 1954]. Evolute, widely umbilicate, perforate; whorl section subquadrate, flanks with straight or sinuous ribs that may bear nodes; venter smooth; suture forming shallow ventral and lateral lobes, and annular lobe; siphuncle small, approximately central (113). *Perm.-Trias.*, N.Am., Eu.-Asia-E.Indies.—FIG. 297,6. \**P. trinodosus* MOJSISOVICS, M.Trias.(Anis.), Alps; 6a,b,  $\times 0.5$  (140).
- Tainionautilus** MOJSISOVICS, 1902 [\**Nautilus transistorius* WAAGEN, 1879; SD DIENER, 1915]. Evolute; whorl section subquadrate with flattened ventral area and flanks; umbilicus wide, deep, probably perforate; lateral areas of early volu-



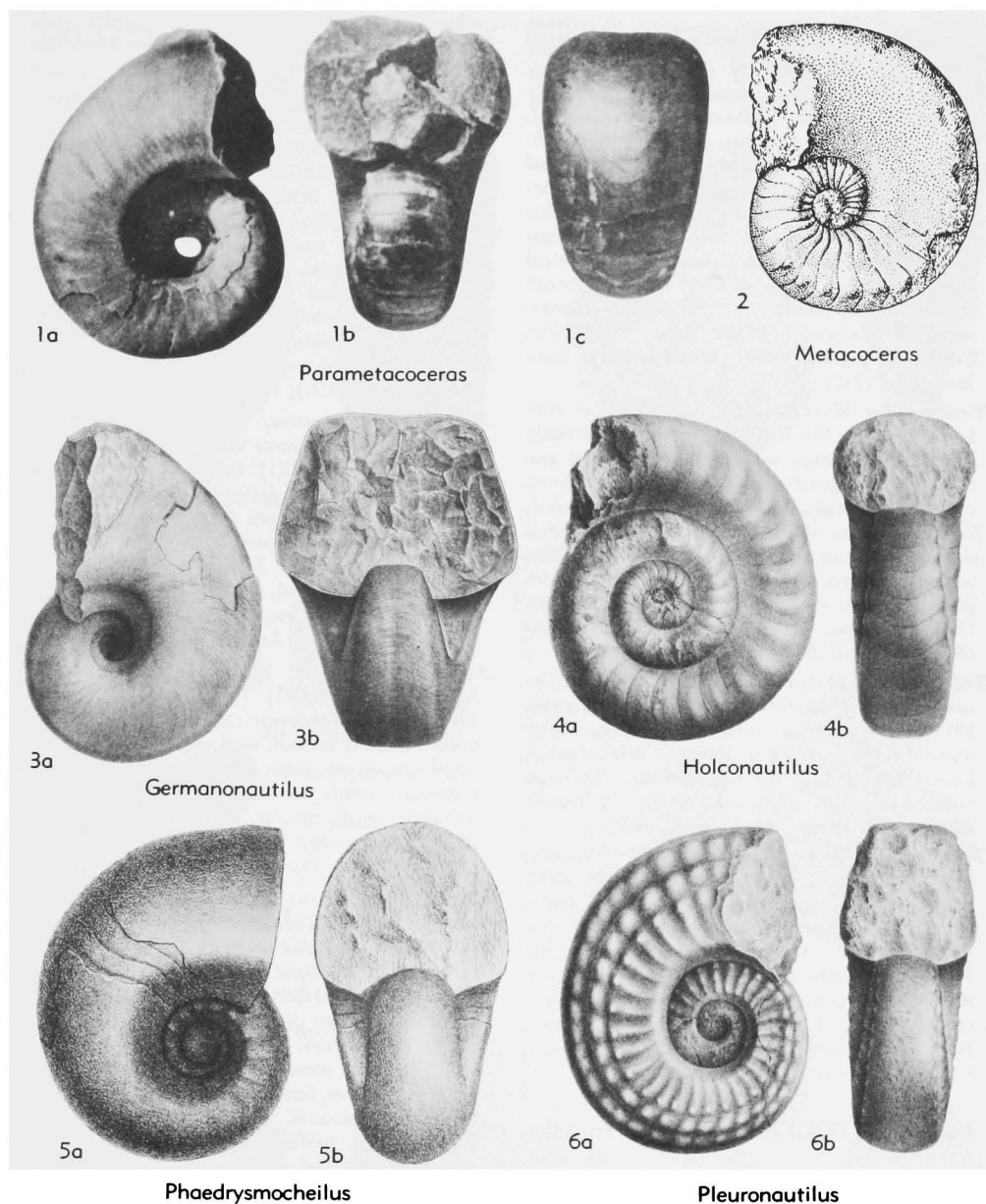


FIG. 297. Tainocerataceae (Tainoceratidae) (p. K414).

tions bearing radial folds, umbilical shoulder forming conspicuous carinae; lateral areas of outer volutions with curved retrograde folds, one set beginning on umbilical shoulders and an intervening set beginning above umbilical shoulder; folds cross ventral shoulders and end at smooth, median sulcus on venter; suture only slightly sinuous; siphuncle small, subventral (113). *U.*

*Perm.-L.Trias.*, Eu.(Alps) - Asia(Pak.). — FIG. 298,1. \**T. transitorius* (WAAGEN), U.Perm., Pak. (Salt Range); 1a,b,  $\times 0.3$  (205).

*Tanchiashanites* CHAO, 1954 [\**T. marginalis*; OD]. Evolute, umbilicus large, shallow; whorls compressed, subrectangular; flanks with sinuous ribs; venter flat and with sharp or raised, carinate ventrolateral shoulders; suture with shallow ven-

tral and lateral lobe; siphuncle small, subventral (9). *Perm.*, China(Hunan).

**Thuringionautilus** MOJSISOVICS, 1902 [*\*Trematodiscus jugatonodosus* ZIMMERMANN, 1892; OD]. Large, moderately involute; whorl section subquadrate, with slightly convex flanks and broad venter with deep furrow, ventral shoulders narrowly rounded to subangular, umbilical shoulders broadly rounded; ventral shoulders with longitudinal nodes that slope diagonally backward on venter toward ventral furrow, which is smooth but with sharp borders; suture slightly sinuous; siphuncle subdorsal (113). *U.Trias.*, Eu.—FIG. 298.3. *\*T. jugatonodosus* (ZIMMERMANN), *Ger.*; *3a-c*,  $\times 0.3$  (242).

**Tirolonautilus** MOJSISOVICS, 1902 [*\*Nautilus crux* STACHE, 1877; SD KUMMEL, 1954]. Moderately involute nautilicones with compressed whorl section, rapidly expanding flanks, which are convex, subparallel; umbilical shoulders broadly rounded; venter concave, with flared subangular ventral shoulders, narrow sinus along mid-part of venter, ventral shoulders with sinuous longitudinal nodes that curve in toward ventral sinus; flanks smooth (113). *U.Perm.*, Eu.—FIG. 298.2. *\*T. crux* (STACHE), Alps; *2a,b*,  $\times 0.7$  (234).

**Trachynautilus** MOJSISOVICS, 1902 [*\*Pleuronautilus subgemmatus* MOJSISOVICS, 1882; SD DIENER, 1915]. Longitudinal ridges on flanks, venter smooth (113). *M.Trias.(Anis.)-U.Trias.(Carn.)*, Eu.—FIG. 298.8. *\*T. subgemmatus* (MOJSISOVICS), Anis., Alps; *8a,b*,  $\times 1.3$  (140). [= *Trachinautilus* SHIMANSKIY, 1962 (*nom. null.*).]

**Tylonautilus** PRINGLE & JACKSON, 1928 [*\*Nautilus (Discites) nodiferus* ARMSTRONG, 1866; OD]. Evolute, with subquadrate whorl section; venter with median smooth sulcus bordered by 2 thin lirae followed by 3 rows of nodes on venter and 3 rows of nodes on flanks, radially arranged; suture with ventral and lateral lobes; siphuncle central (216). *L.Carb.*, Eu.(Scot.-Pol.), *Perm.*, Japan.—FIG. 298.6. *\*T. nodiferus* (ARMSTRONG), *L.Carb.*, Scot.; *6a,b*,  $\times 0.7$  (216).

### Family RUTCERATIDAE Hyatt, 1884

[=Trochoceratidae ZITTEL, 1884 (based on *Trochoceras* BARRANDE, 1848, *non* HALL, 1852), *non* Trochoceratidae S.A. MILLER, 1877 (based on *Trochoceras* HALL, 1852, *non* BARRANDE, 1848); Hallooceratidae HYATT in ZITTEL, 1900 + Ryticeratidae HYATT in ZITTEL, 1900 (*nom. null.*); incl. Hercoceratidae HYATT, 1884, Adelphoceratidae FOERSTE, 1926, Litogyroceratidae SHIMANSKIY, 1956, Ptenoceratidae TEICHERT, 1939]

Longiconic, curved and coiled shells characterized by development of wings, frills, and spines which are either hollow and spoutlike or solid. Conchs typically cyrtoconic and gyroconic, a few forms with slight impressed zones; siphuncle invariably ventral, generally orthochoanitic and empty; a few forms cyrtchoanitic; some known to

have actinosiphonate deposits (32). *L.Dev.-L.Carb.*

**Rutoceras** HYATT, 1884 [*\*Cyrtoceras jason* HALL, 1879; OD] [= *Kophinoceras* HYATT, 1884; *Cophinoceras* HYATT in ZITTEL, 1900 (*nom. null.*); *Cophinaceras* HYATT in ZITTEL, 1900 (*nom. null.*); *Ryticeraceras* HYATT in ZITTEL, 1900 (*nom. null.*)]. Gyroconic, with ventral cyrtchoanitic siphuncle; with spoutlike spines flanking venter and 2 lateral series of spines which may be suppressed in region of mature living chamber; spoutlike spines imperfectly connected by short, generally incomplete frills (93). *M.Dev.*, N.Am.-?S.Am.(Bol.) - Eu.—FIG. 299.7. *\*R. jason* (HALL), USA(N.Y.); *7a,b*,  $\times 0.2$  (223).

**Adelphoceras** BARRANDE, 1870 [*\*A. bohemicum*; OD] [*non Adelphoceras* GIRTY, 1909 (= *Girtyoceras* WEDEKIND, 1918)]. Conch apparently slightly tortedonic but this is questionable; whorl section depressed, oval, with shallow impressed zone on dorsal concavity; aperture strongly contracted, T-shaped; flanks with 2 rows of spines on each side; siphuncle ventral, containing actinosiphonate deposits (32). *M.Dev.*, Eu.—FIG. 299.8. *\*A. bohemicum*, Czech.; *8a,b*,  $\times 0.2$ ; *8c*,  $\times 0.7$  (5).

**Anomaloceras** HYATT, 1884 [*\*Nautilus anomalus* BARRANDE, 1865; OD] [= *Hyatticeras* COSSMAN, 1900 (obj.); *Alpheiceras* COSSMAN, 1900 (obj.)]. Coiled, evolute, smooth, with wide open umbilicus, slight impressed zone; whorl section elliptical, depressed; suture forming shallow ventral lobe; siphuncle, small, tubular, slightly off center (93). *M.Dev.*, Eu.—FIG. 299.1. *\*A. anomalum* (BARRANDE), Czech.; *1a,b*,  $\times 0.5$  (5).

**Casteroceras** FLOWER, 1936 [*\*Cyrtoceras alternatum* HALL, 1879 (*nom. subst. pro C. undulatum* HALL, 1876, *non* VANUXEM, 1842); OD]. Slender, cyrtoconic, with slight curvature which is greater adapically than adapturally; cross section slightly depressed, exterior divided distinctly into 10 faces in the type-species, though number may vary; internal molds preserving ventral face, but preservation of other faces varying within species; suture slightly sinuous, with narrow dorsal saddle, broad ventral saddle separated by lateral lobes; septa uniformly and very slightly curved; siphuncle close to ventral wall, narrow, orthochoanitic; test thick, bearing irregular transverse undulating lirae, which are crossed by a few coarse, large, poorly defined longitudinal lirae; at intervals of about every other camera interior bears ring of nodose expansions (one under each lira), above which lirae are projected into short spines; nodes decreasing adorally; shallow hyponomic sinus present (20). *M.Dev.*, N.Am.(USA-Can.)-Eu.(Eng.).—FIG. 299.5. *\*C. alternatum* (HALL), Dev., USA(N.Y.); *5a,b*,  $\times 0.4$  (223).

**Centrolitoceras** FLOWER, 1945 [*\*C. perplexum*; OD]. Gyroconic, consisting probably of 2 volu-

tions when complete; cross section slightly depressed but with venter and dorsum equally rounded; suture straight, transverse; siphuncle tubular, adjacent to venter; surface in early stages

marked by transverse frills or annulations which show no trace of a hyponomic sinus; at termination of first volution, annulations have weakened and disappeared, leaving surface with only coarse

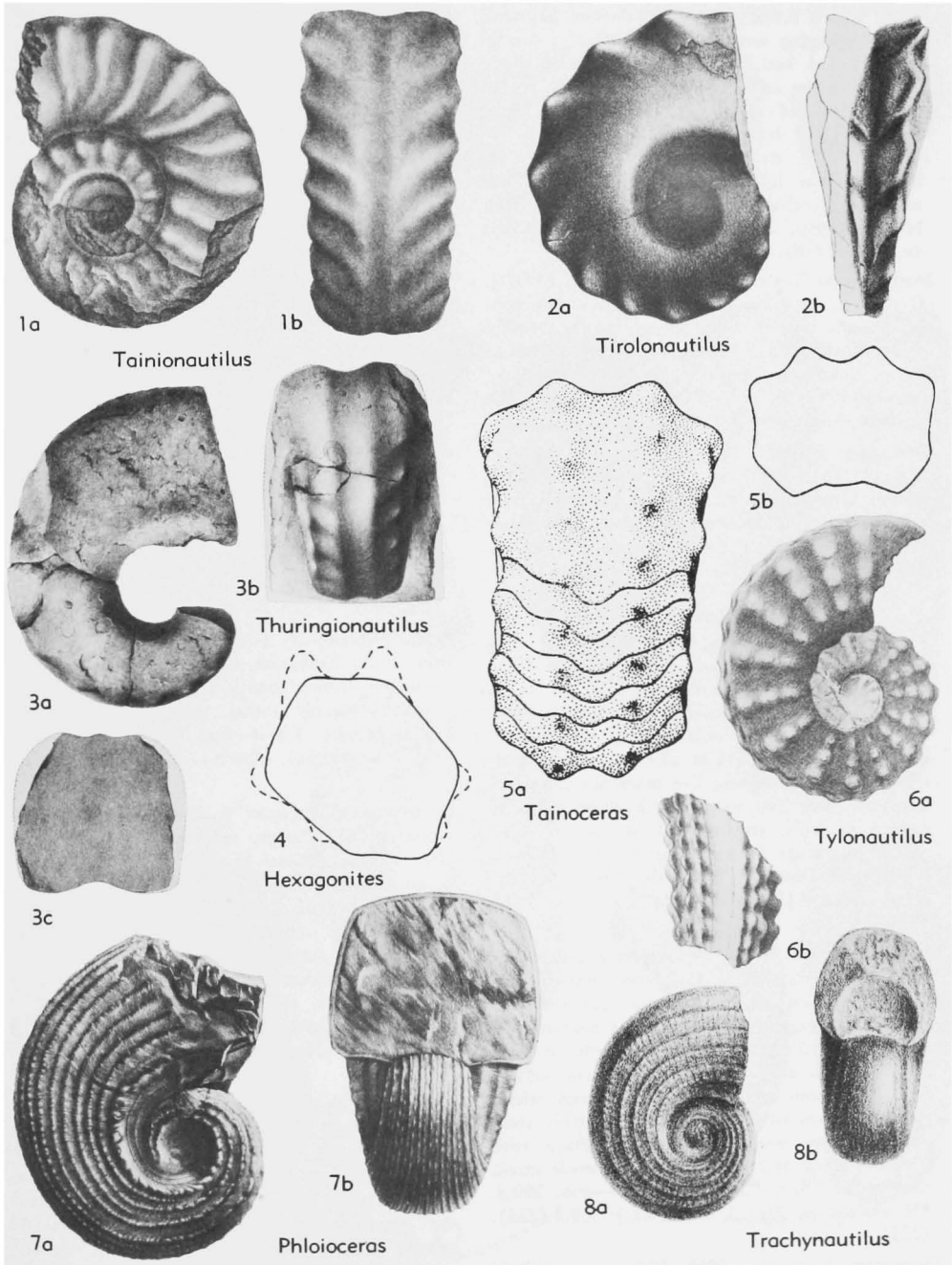


FIG. 298. Tainocerataceae (Tainoceratidae) (p. K414-K416).

- growth lines (32). *M.Dev.*, N.Am.(Can.).—FIG. 299,2. \**C. perplexum*, Man.; 2a-c,  $\times 1$  (Kummel, n).
- Diademoceras** FLOWER, 1949 [*\*D. palmeri*; OD]. Gyroconic, probably with not more than 2 volutions, whorls broadly depressed, dorsum flattened, sides converging ventrally and meeting in strongly developed keel; conch ornamented by single series of spines on each side; other surface markings consist of transverse striae which form well-developed hyponomic sinus on venter; sutures straight, transverse ventrally but forming broad shallow lobe on dorsum; siphuncle close to venter, orthochoanitic, empty (36). *M.Dev.*, N.Am.—FIG. 299,4. \**D. palmeri*; USA(N.Y.); 4a,b,  $\times 0.4$  (36).
- Duerleyoceras** TURNER, 1954 [*\*D. gaylense*; OD]. Gyroconic, cross section subcircular, ornamented with single row of nodes on each flank, together with transverse and longitudinal lirae; outline of suture unknown; siphuncle apparently dorsal of center (198). *L.Carb.*, Eu.—FIG. 299,3. \**D. gaylense*, Eng.; 3a-c (holotype),  $\times 2$  (Kummel, n).
- Goldringia** FLOWER, 1945 [*\*Gyroceras cyclops* HALL, 1861; OD] [= ?*Polycronites* TROOST, 1840]. Gyroconic, with 1 or 2 volutions, free; cross section slightly broader than high, dorsum more flattened than venter, which typically is narrowly rounded, thus producing faintly subtriangular cross section; suture essentially straight, transverse; siphuncle ventral, tubular, free of any known organic deposits; surface of shell produced at regular intervals into crenulate frills, each frill bent downward on venter so as to form well-defined hyponomic sinus; frills continuous around shell, only slightly shorter dorsally than ventrally (if at all), no spoutlike or spinous lateral processes; five markings consist of transverse lirae and striae which show crenulate pattern of frills, accompanied by fainter longitudinal markings in some forms (32). *M.Dev.*, N.Am.(N.Y.-Ohio-Ind.).—FIG. 299,6. \**G. cyclops* (HALL), USA(N.Y.); 6a,  $\times 0.2$ ; 6b,  $\times 0.5$  (223).
- Halloceras** HYATT, 1884 [*\*Cytroceras undulatum* VANUXEM, 1842; OD]. Gyroconic, whorls subtriangular in section, venter broad, rounded, lateral areas divergent, dorsum forming narrow apex of section; frills at varices of growth, at their junction with shell wall describing not only a hyponomic sinus but pair of lateral sinuses, which represent bases of regions in which frills were produced into winglike processes; suture with shallow ventral and lateral lobes; siphuncle small, near venter (32). *L.Dev.*, N.Am.—FIG. 300,3. \**H. undulatum* (HALL), USA(N.Y.);  $\times 0.3$  (223).
- Hercoceras** BARRANDE, 1865 [*\*Gyroceras mirum* BARRANDE, 1854; OD]. Involute, torticonic, impressed zone distinct; whorl sections depressed, lateral areas converging dorsally, shoulders rounded; aperture of mature forms reduced, slitlike; sutures transverse; siphuncle close to venter; lateral areas with row of lunate projections, as in *Pyssoceras*, but smaller in size (32). *M.Dev.*, Eu.—FIG. 300,2. \**H. mirum* (BARRANDE), Czech.; 2a,b,  $\times 0.5$ ; 2c,  $\times 1$  (5).
- Hindeoceras** FLOWER, 1945 [*\*Gyroceras canadense* WHITEAVES, 1891; OD]. Gyroconic, large, with about 2 volutions; cross section with dorsum broadly flattened to slightly concave, sides strongly rounded, venter well arched; pairs of spines on surface (reflected by nodes on internal mold) which give cross section a faintly faceted appearance; spines and nodes variable in number, one pair flanking flattened ventral face and at least 4 lateral pairs present in addition, in typical forms with rows of spines spaced about equally around circumference crossing dorsum, though spines decrease in size from venter to dorsum and dorsally may be so small as to disappear as nodes on internal mold; suture simple ventrally, tending to develop broad shallow lobes on dorsum; siphuncle close to venter, tubular, and free from organic deposits; surface of shell bearing spines at regular rhythmic intervals, representing varices of growth; rugose transverse markings are also present; well-developed hyponomic sinus on narrow flat ventral face (32). *M.Dev.*, N.Am.(Can.).—FIG. 300,1. \**H. canadense* (WHITEAVES), Man.; 1a,b,  $\times 0.3$ ; 1c,  $\times 0.5$  (241).
- Homoadelphoceras** FOERSTE, 1926 [*\*Gyroceras devonicans* BARRANDE, 1866; OD]. Like *Adelphoceras* but dorsum convex, without impressed zone; conch gyroconic rather than faintly torticonic (57). *M.Dev.*, Eu.—FIG. 300,4. \**H. devonicans* (BARRANDE), Czech.; 4a,  $\times 0.3$ ; 4b,  $\times 1$  (5).
- Litogyroceras** TEICHERT & GLENISTER, 1952 [*\*L. spirale*; OD]. Large, exogastric gyrocones with free whorls, distance between them gradually increasing from apical to oral part of conch; whorl section subcircular, flattened dorsally; shell surface smooth; siphuncle small, very near venter; septa highly concave, camerae deep; suture consisting of shallow dorsal lobe, pair of shallow lateral saddles, and deep narrow ventral lobe; septal necks orthochoanitic (191). *M.Dev.*, SE. Australia.—FIG. 300,7. \**L. spirale*; 7a,b,  $\times 0.3$  (191).
- Muiroceras** FLOWER, 1949 [*\*M. tuberosum*; OD]. Conch strongly curved, nearly gyroconic when complete, rapidly expanding, depressed in section; dorsum more flattened than venter, expanded more rapidly transversely than vertically in growth; sutures faintly oblique, rising on venter to form low saddles, not known dorsally; siphuncle composed of broad, short nummuloidal segments, barrel-shaped, about as wide as long; no organic deposits; surfaces of shell faintly

marked with transverse growth lines, modified on sides to form rounded tubercles, as in bases of alate expansions of *Ptenoceras* and its allies (36). *M.Dev.*, Alaska.—FIG. 301,4. \**M. tuberosum*; 4a-c,  $\times 0.7$  (Kummel, n).

*Pluronoceras* FLOWER in FLOWER & KUMMEL,

1950 [*\*Spirula nodosa* BRONN, 1837; OD] [= *Spirulites* QUENSTEDT, 1846 (obj.), *non* PARKINSON, 1811, *nec* KRUEGER, 1823]. Gyroconic, shell thin, with only faint growth lines and longitudinal lirae, sides of shell expanded into pair of hollow nodose lateral expansions of shell; intermediate be-

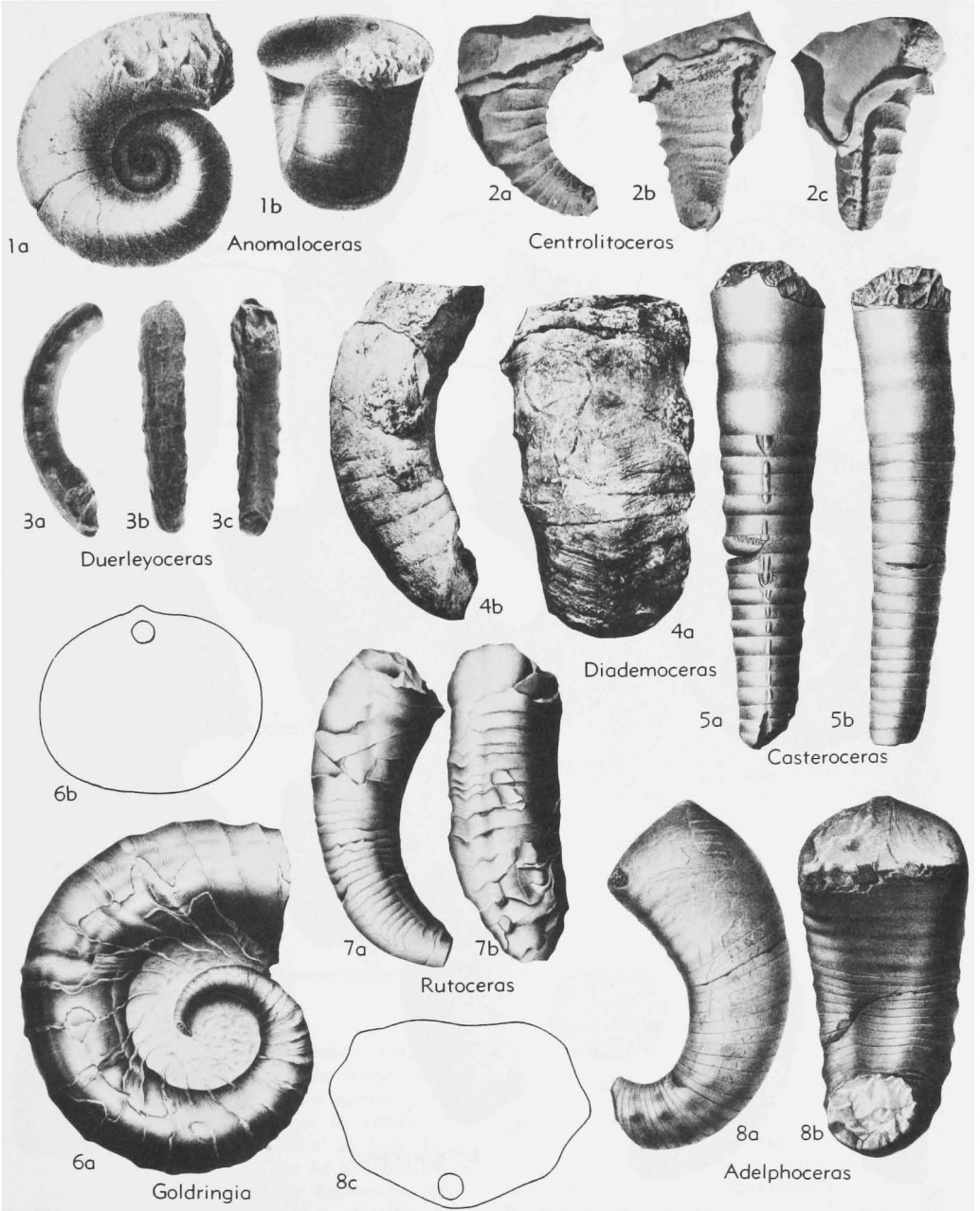


FIG. 299. Tainocerataceae (Rutoceratidae) (p. K416-K418).

tween *Ptenoceras* and *Hindeoceras* (49). *M.Dev.*, Eu.—FIG. 300,8. \**P. nodosum* (GOLDFUSS), Ger.; 8a,b,  $\times 0.8$  (218).

**Ptenoceras** HYATT, 1894 [\**Gyroceras alatum* BAR-

RANDE, 1865; SD FOERSTE, 1926]. Gyroconic, volutions separated by interval of 2 or 3 mm.; whorl sections depressed, elliptical; transverse striae on surface of shell strongly recurved on

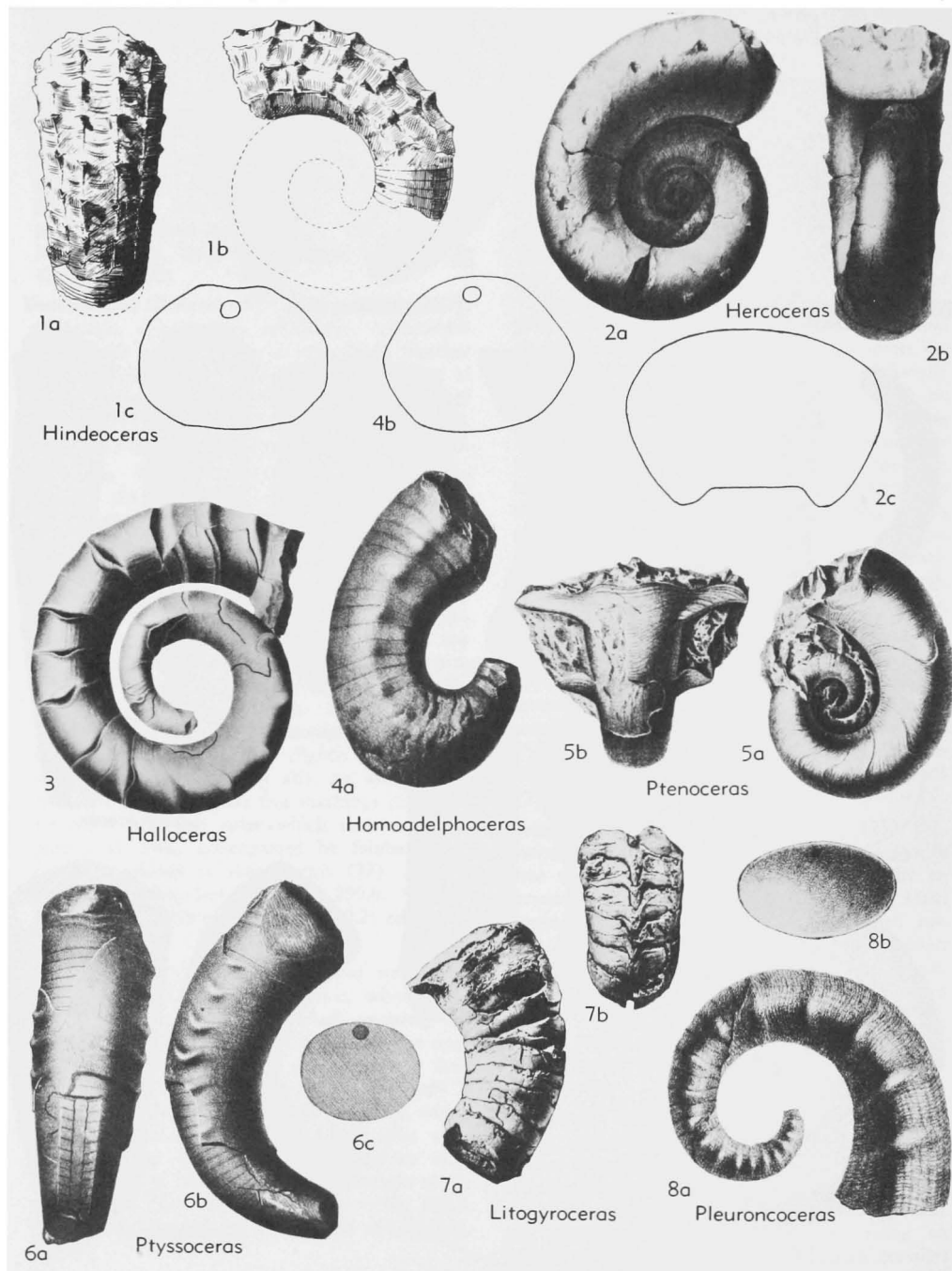


FIG. 300. Tainocerataceae (Rutoceratidae) (p. K418-K421).

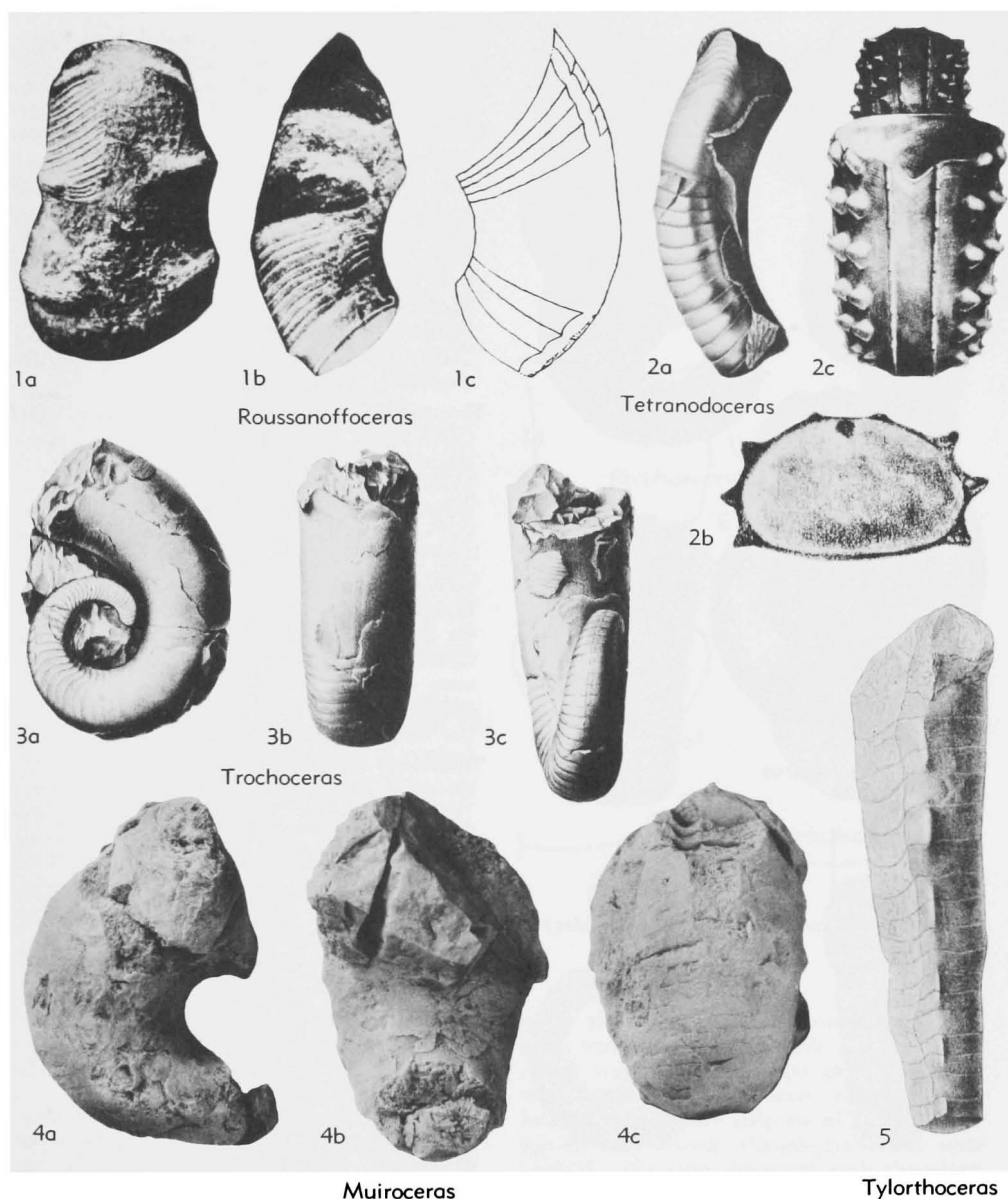


FIG. 301. Tainocerataceae (Rutoceratidae) (p. K418-K419, K421-K422).

flanks, forming deep sinuses; lateral margins of aperture bearing 2 long, narrow wings, similar but smaller pair of wings behind aperture; suture nearly straight; siphuncle close to venter, with deposits which appear annular in longitudinal section and may or may not be actinosiphonate (96). *L.Dev.-M.Dev.*, N.Am.-Eu.—FIG.300,5. \**P. alatum* (BARRANDE), L.Dev., Czech.; 5a,b,  $\times 0.5$  (5).

*Ptyssoceras* HYATT, 1884 [\**Cyrtoceras alienum*

BARRANDE, 1866; OD]. Cyrtoconic, whorl sections depressed, oval; flanks with rows of short transverse lunate ridges, their concave margins facing upward. Sutures straight, transverse. Siphuncle close to venter (93). *Dev.*, N.Am.-Eu.—FIG. 300,6. \**P. alienum* (BARRANDE), Czech.; 6a-c,  $\times 0.7$  (5).

*Roussanoffoceras* FOERSTE, 1925 [\**R. depressum*; OD] [= *Roussanoffoceras* COOPER & WILLIAMS, 1935 (*nom. null.*)]. Conch strongly curved



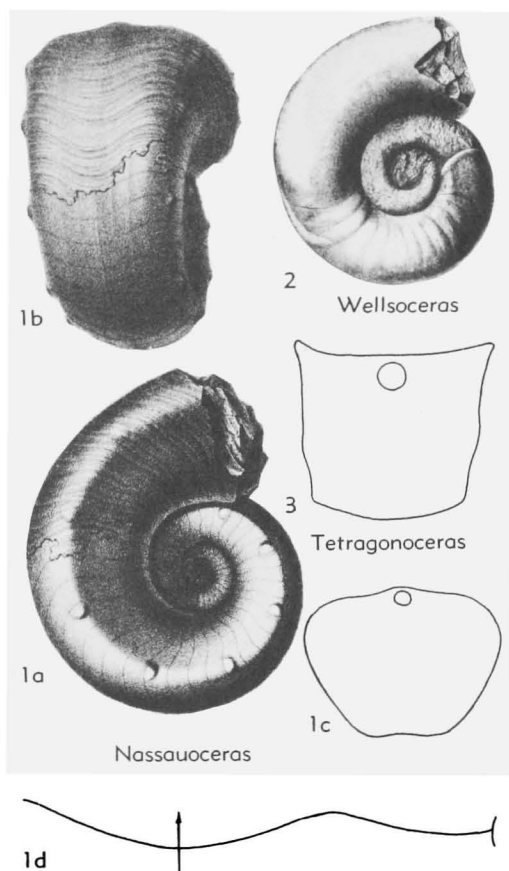


FIG. 302. Tainocerataceae (Tetragonoceratidae)  
(p. K423).

lengthwise, apparently gyroconic, possibly cyrtoconic; strongly depressed, with elliptical cross section, enlarging rapidly; siphuncle near venter, not well known; transverse ribs on lateral areas of conch may be complete ventrally but reduced there and absent dorsally; growth lines inscribe moderately deep hyponomic sinus (56). ?*L.Dev.*, USSR (Novaya Zemlya).—FIG. 301,1. \**R. depressum*; 1a-c,  $\times 0.7$  (56).

**Syrreghmatoceras** SVERBILOVA, 1957 [\**S. arcuatum*; OD] [= *Surreghmatoceras* SVERBILOVA, 1957 (nom. null.)]. Cyrtoconic, possibly gyroconic, whorl section depressed, elliptical, no dorsal impressed zone; sutures straight; siphuncle near venter; conch with faint longitudinal ribs; like *Anomaloceras* in conch form, but with siphuncle in median position, and faint ornamentation on shell (177). *U.Dev.*, Eu. (USSR).

**Tetranodoceras** FLOWER, 1936 [\**Cyrtoceras transversum* HALL, 1860; OD]. Gyrocones with much-depressed whorl section; dorsum transverse, scarce-

ly elevated, not distinctly separated from flanks, which are slightly convex and converge toward venter; venter set off by nodes in early volutions and well-defined angular shoulder in later stages; conch with 4 pairs of tubercles or blunt spines, which are hollow on early whorls but become solid on mature whorls; shell thick, with surface markings of fine longitudinal lirae and coarse transverse undulating striae; hyponomic sinus; suture transverse except for broad shallow dorsal lobe; siphuncle small, tubular, near venter (20). *M.Dev.*, N.Am. (N.Y.-Ill.).—FIG. 301,2. \**T. transversum* (HALL), USA (N.Y.); 2a,  $\times 0.3$  (223a); 2b, diagram transv. sec.,  $\times 1.3$ ; 2c, surface (reconstr.),  $\times 0.5$  (20).

**Threoceras** FLOWER, 1945 [\**T. inexpectans*; OD]. Conch coiled, whorls broad, subtriangular, venter keeled, at least on outer whorl, ventral area adjacent to keel flattened, lateral area strongly rounded; umbilical wall broadly arched, dorsal area with prominent impressed zone; sides of shell with single pair of large nodes on extreme lateral portion. Suture transverse ventrally and laterally, though slightly modified by nodes; slight saddle instead of lobe in impressed zone; septa and siphuncle not known; surface of shell with transverse markings which slope adapically on venter, forming deep sinus directly in line with ventral keel (32). *M.Dev.*, N.Am. (Ohio).

**Trochoceras** BARRANDE in VON HAUER, 1848 [\**T. davidsoni* BARRANDE, 1865; SD HYATT, 1894] [non *Trochoceras* HALL, 1852 (= *Mitroceras* HYATT, 1894)]. Like *Ptenoceras*, but lacking siphuncular deposits and having a torticonic form of coiling; whorl section of phragmocone ovate, of living chamber quadrangular; coiling of conch sinistral, only slightly torticonic; conch with 2 pairs of winglike processes, one at aperture, the other toward base of living chamber; suture with shallow ventral and lateral lobes; siphuncle at venter, segments fusiform (96). *L.Dev.-M.Dev.*, Eu.—FIG. 301,3. \**T. davidsoni* BARRANDE, *M.Dev.*, Czech.;  $\times 0.3$  (5).

**Tylorthoceras** MILLER, 1932 [\**Trematoceras ohioense* WHITFIELD, 1882; OD] [= *Trematoceras* WHITFIELD, 1882 (non EICHWALD, 1851, nec HYATT, 1884)]. Shell straight, whorl section depressed; siphuncle ventral, tubular, empty; venter marked by pair of longitudinally elongated spines which recur at regular intervals (123). *M.Dev.*, N.Am. (N.Y.-Ohio).—FIG. 301,5. \**T. ohioense* (WHITFIELD), USA (Ohio);  $\times 0.7$  (241).

### Family TETRAGONOCERATIDAE Flower, 1945

Shells coiled, gyroconic or with slightly impressed zones, quadrangular in section, flanks diverging from umbilical to ventral shoulders and widest close to venter. Nodes



may be developed on flanks and shoulders. Sutures typically with lateral lobes, and may possess ventral and dorsal lobes as well; these are best developed in more compressed forms. Siphuncle tubular, typically close to the venter (32). *M.Dev.*

**Tetragonoceras** WHITEAVES, 1891 [*\*T. gracile*; OD]. Gyroconic; whorl section quadrate, venter broader than dorsum; ventral shoulder angular, finely crenulate; suture with slight lateral and ventral lobes separated by subangular saddles; siphuncle ventral, tubular (205). *M.Dev.*, N.Am. (Can.).—FIG. 302,3. *\*T. gracile*, Man.;  $\times 2$  (205).

**Nassauceras** MILLER, 1932 [*\*Nautilus sub tuberculatus* SANDBERGER & SANDBERGER, 1852; OD]. Evolute, with wide, deep umbilicus and weakly impressed zone; whorl section subtrigonal, with broad, low arched venter, rounded ventral shoulders, and convex flanks converging dorsally; conch with nodes on ventral shoulders; suture with shallow ventral and lateral lobe; siphuncle near venter (32). *M.Dev.*, Eu.—FIG. 302,1. *\*N. sub tuberculatum* (SANDBERGER & SANDBERGER), Ger.; 1a-c,  $\times 0.7$ ; 1d,  $\times 1.5$  (231).

**Wellsoceras** FLOWER, 1945 [*\*Gyroceras columbiense* WHITFIELD, 1882; OD]. Shell coiled, whorls in contact until mature living chamber is reached, which is free; cross section slightly wider than high, faintly subquadrangular; dorsal face convex and in some forms not clearly defined laterally, though umbilical shoulders are strongly rounded; flanks slightly convex, tending to converge very slightly toward venter, which is slightly arched; all shoulders rounded; suture straight, transverse ventrally or with very slight ventral lobe, well-developed lateral lobe; broad, low saddle on dorsum, which is slightly flattened but not impressed; siphuncle halfway between center and ventral wall, presumably tubular; type-species free of nodes, but related species with 2 series of lateral nodes, on inner whorls (32). *M.Dev.*, N.Am. (Ohio-Ind.-Ont.).—FIG. 302,2. *\*W. columbiense* (WHITFIELD), USA (Ohio);  $\times 0.3$  (241).

### Family RHIPHAEOCERATIDAE

Ruzhentsev & Shimanskiy, 1954

Evolute conchs with perforate umbilicus; whorl section oval, subquadrate, subtrapezoidal, bearing ribs. Suture with ventral saddle, usually only slight lateral lobe and deep funnel-shaped dorsal lobe (153). *L. Perm.*

**Rhiphaoceras** RUZHENTSEV & SHIMANSKIY, 1954 [*\*R. venustum*; OD]. Evolute, perforate, with low elliptical whorl section; shoulders broadly rounded; umbilicus wide; flanks bearing faint,

narrow radial ribs. Suture with low, broad ventral saddle, straight on whorl sides, and with deep dorsal lobe; growth lines forming deep sinus on

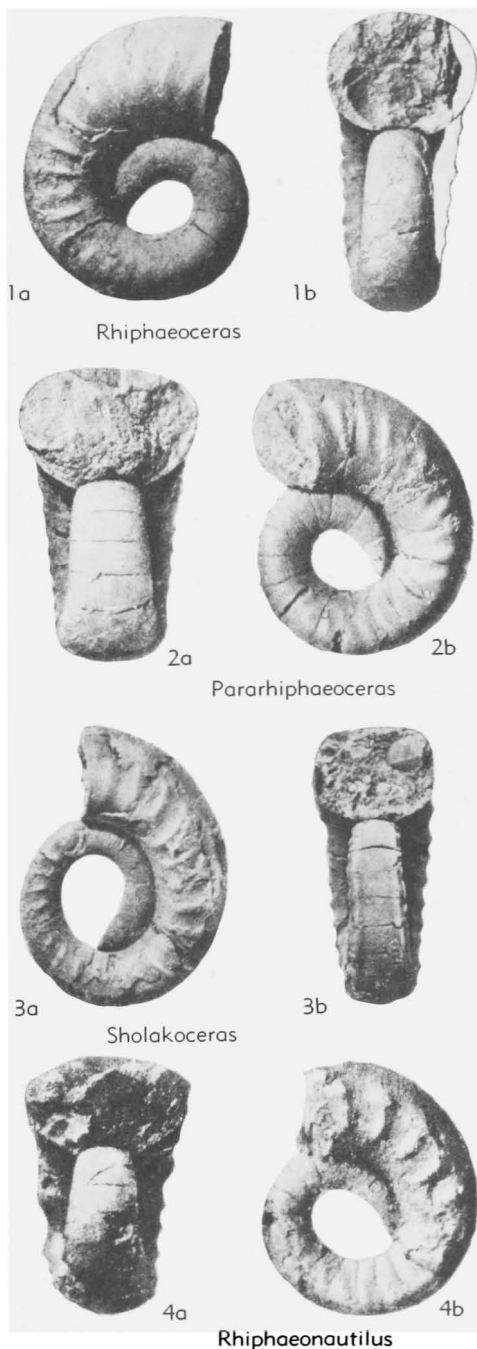


FIG. 303. Tainocerataceae (Rhiphaeoceratidae) (p. K423-K424).

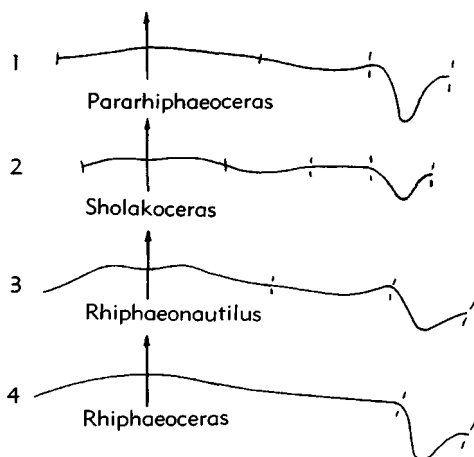


FIG. 304. Tainocerataceae (Rhiphaoceratidae) (p.K423-K424).

venter (153). *L.Perm.*, USSR (S. Urals).—FIGS. 303,1; 304,4. \**R. venustum*; 303,1a,b,  $\times 1$ ; 304,4,  $\times 2$  (153).

**Pararhiphaoceras** RUZHENTSEV & SHIMANSKIY, 1954 [*\*Temnocheilus multituberculatum* WAAGEN var. *tastubensis* KRUGLOV, 1928; OD]. Evolute, perforate, with subtrapezoidal whorl section; venter broad, low, smooth, ventral shoulder rounded, flanks sloping toward umbilicus with no noticeable umbilical shoulder, flanks with short, oblique ribs; suture with broad ventral saddle containing very shallow lobe in center, straight on flanks, and deep funnel-shaped dorsal lobe (153). *L.Perm.*, SE. USSR.—FIG. 303,2; 304,1. \**P. tastubense* (KRUGLOV); 303,2a,b,  $\times 1$ ; 304,1,  $\times 2$  (153).

**Rhiphaeonautilus** RUZHENTSEV & SHIMANSKIY, 1954 [*\*R. curticostratus*; OD]. Evolute, perforate; whorl section subtrapezoidal, with broad arched venter, distinctly rounded ventral shoulder, narrow lateral area, indistinct umbilical shoulder, broad sloping umbilical wall, lateral area bearing short, inflated ribs; suture forms broad ventral saddle with slight, shallow lobe and deep funnel-shaped dorsal lobe (153). *L.Perm.*, USSR (S. Urals).—FIGS. 303,4; 304,3. \**R. curticostratus*; 303,4a,b,  $\times 1$ ; 304,3,  $\times 0.8$  (153).

**Sholakoceras** RUZHENTSEV & SHIMANSKIY, 1954 [*\*S. bisulcatum*; OD]. Evolute, perforate; whorl section subquadrate, with flattened lateral and ventral areas, rounded ventral and umbilical shoulders, ventral shoulder with narrow rounded ridge on earlier volutions which disappear in maturity, lateral areas bearing short, slightly oblique ribs; suture with broad ventral saddle marked with very shallow lobe, very shallow lateral lobe and deep funnel-shaped dorsal lobe (153). *L.Perm.*,

S.USSR.—FIGS. 303,3; 304,2. \**S. bisulcatum*; 303,3a,b,  $\times 1$ ; 304,2,  $\times 3$  (153).

### Family KONINCKIOCERATIDAE Hyatt in Zittel, 1900

[*nom. correct.* HYATT in ZITTEL, 1913 (*pro Koninckioceratida* HYATT in ZITTEL, 1900)] [Based on *Koninckioceras* HYATT, 1884, and although this nominal genus is considered to be synonym of *Millkoninckioceras* KUMMEL, 1963, the family name is retained in accordance with Article 40 of the Rules (1961)] [= *Temnocheilidae* MOYSSISOVICH, 1902 (*partim*), *Koninckioceracea* KINDLE & MILLER, 1939 (*superfam.*) (*partim*); *Temnocheilaceae* SHIMANSKIY, 1957 (*superfam.*) (*partim*); incl. *Aktubonautilidae* RUZHENTSEV & SHIMANSKIY, 1954 (*partim*); *Knightoceratinae* SHIMANSKIY, 1962]

Evolute conchs with depressed whorls, not deeply impressed dorsally, sutures only slightly sinuous, siphuncle subcentral, flanks typically converging toward dorsum; ornamentation, when present, consisting of nodes along ventral shoulder or in middle of lateral areas or elongate nodes on ventral part of lateral area (134). *L.Carb.*(*Miss.*)-*Perm.*

**Millkoninckioceras** KUMMEL, 1963 [*\*Koninckioceras konincki* MILLER & KEMP, 1947; OD] [= ?*Koninckioceras* HYATT, 1884 (unrecognizable type-species); ?*Koninckioceras* HYATT in ZITTEL, 1900 (*nom. null.*)]. Evolute, widely umbilicate, smooth conch; whorl section depressed, elliptical, venter broadly rounded, flanks also rounded; dorsal impressed zone slight; umbilicus large and perforate. Suture essentially straight; siphuncle small, subcentral (134). *L.Carb.*(*Miss.*)-*Perm.*, N. Am.-Eu.—FIG. 305,5. \**M. konincki* (MILLER & KEMP), *L.Carb.*, Eu.; 5a,b,  $\times 0.4$  (134).

**Edaphoceras** HYATT, 1884 [*\*Nautilus* (*Temnocheilus*) *niotensis* MEEK & WORTHEN, 1873; OD]. Evolute, with whorls in contact but not embracing, large funnel-shaped umbilicus; whorl sections depressed, fusiform, with subangular lateral area merging onto broadly rounded venter and dorsum; suture with distinct ventral and dorsal lobe, subangular saddles; siphuncle small, approximately central (93). *Miss.*, N. Am.—FIG. 306,2. \**E. niotense* (MEEK & WORTHEN), USA (Ill.); 2a,b,  $\times 0.7$  (225).

**Endolobus** MEEK & WORTHEN, 1865 [*\*Nautilus spectabilis* MEEK & WORTHEN, 1860 (= *N. Endolobus*) *perampus* MEEK & WORTHEN, 1865]; SD MEEK & WORTHEN, 1866] [= *Aktubonautilus*, *Heurekoceras* RUZHENTSEV & SHIMANSKIY, 1954]. Nautilonic, evolute; whorl section subelliptical, broadly rounded ventrally, narrowly rounded laterally, slightly impressed dorsally; umbilicus wide, deep, presumably perforate; flanks of conch bearing low nodes; external suture only slightly sinuous, dorsal suture with prominent lobe; siphuncle small, subcentral, orthochoanitic (134). *L.Carb.* (*U. Miss.*)-*L. Perm.*, N. Am. (Tex.-N. Mex.-Kans.-Ark.-Ind.-Pa.-Ky.-Alaska)-Eu. (USSR). — FIG.

305,1. \**E. spectabilis* (MEEK & WORTHEN), U. Miss., USA (Ill.); 1a,b,  $\times 0.4$  (134).

**Foordiceras** HYATT, 1893 [*\*Nautilus goliathus* WAAGEN, 1879; OD]. [= *Foordoceras* GIRTY, 1908 (nom. null.)]. Involute nautilicone with

moderately broad, deep umbilicus; whorl section trapezoidal, with broad arched venter, convex lateral areas that slope dorsally, ventral shoulders rounded, umbilical shoulders more broadly rounded, umbilical wall broad and steep; flanks with

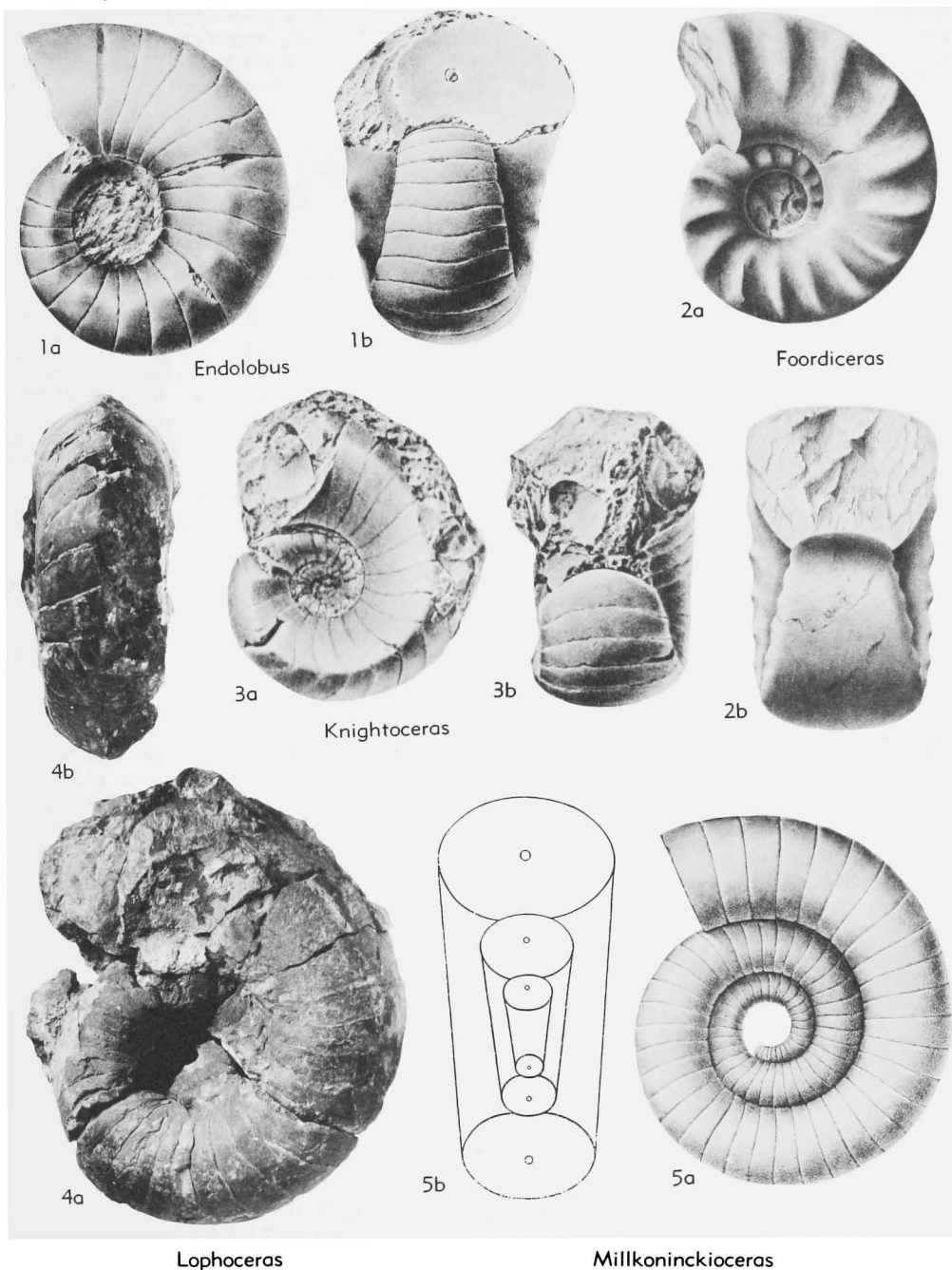


FIG. 305. Tainocerataceae (Koninckioceratidae) (p. K424-K427).

transverse elongated nodes on ventral shoulders that disappear by mid-part of lateral area; suture slightly sinuous; position of siphuncle not known (113). *Perm.*, Eu.(USSR-Sicily)-Asia(Pak.)-E. Indies.—FIG. 305,2. \**F. goliathum* (WAAGEN), Pak. (Salt Range); 2*a,b*,  $\times 0.3$  (205).

**Knightoceras** MILLER & OWEN, 1934 [\**K. missouriense*; OD] [= *Librovitschiceras* SHIMANSKIY, 1957]. Nautilonic, subglobular, rapidly expand-

ing; whorls depressed, sublenticular in cross section, broadly rounded ventrally and dorsally, subangular laterally, impressed zone small, inconspicuous; umbilicus broad, deep; with deep rounded hyponomic sinus on venter. Suture with shallow ventral lobe, angular saddle on subangular lateral zone, essentially straight on umbilical wall; siphuncle small, subcentral (132). *L.Carb.*(*U. Miss.*), N.Am.(Mo.-Iowa-Alaska)-Eu.(USSR).—

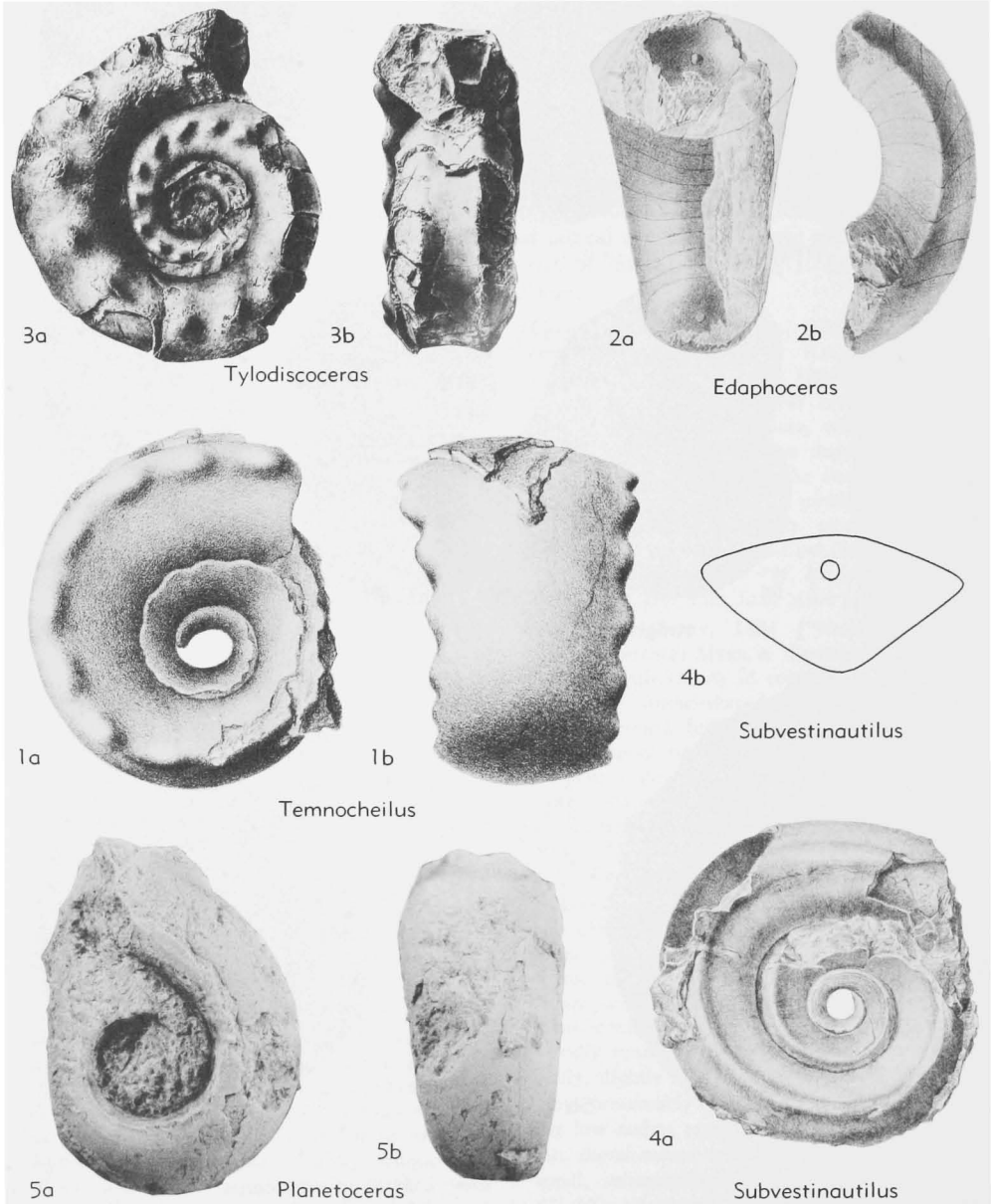


FIG. 306. Tainocerataceae (Koninckioceratidae) (p. K424, K427).

FIG. 305,3. *K. abundum* MILLER, LANE, & UNKLEBAY, M.Penn., USA (Mo.); 3a,b,  $\times 0.7$  (132). [KUMMEL judges firmly that *Librovitschiceras* is a junior synonym of *Knightoceras*, whereas FURNISH & GLENISTER accept this genus as belonging in the family Aipoceratidae (p. K441, Fig. 318,1).]

**Lophoceras** HYATT, 1893 [*\*Nautilus pentagonus* J. SOWERBY, 1819; OD] [non *Lophoceras* PARONA & BONARELLI, 1895 (1897); nec VON HOEPEN, 1933 (ammonites)]. Evolute, large, with slight impressed zone; whorl section in early volutions rounded, then developing obtuse angular ventral area and venter, that on venter disappearing adorally on mature body chamber; suture with subangular ventral saddle, broad shallow lateral lobe, dorsal lobe, and possibly an annular lobe; conch smooth except for growth lines (95). *L. Carb.*, Eu.—FIG. 305,4. *\*L. pentagonum* (SOWERBY), Eng.; 4a,b,  $\times 0.25$  (Kummel, n).

**Planetoceras** HYATT, 1893 [*\*P. retardatum*; OD]. Evolute, widely umbilicate, tarphyceronic, adoral part of living chamber not in contact with preceding whorl; whorl section depressed, venter broad, convex, ventral shoulders rounded, flanks slightly convex, steeply sloping; deep, tongue-shaped hyponomic sinus; suture with very slight ventral and lateral lobes; siphuncle ventral of center (59). *L. Carb. (Miss.)-U. Carb. (Penn.)*, N. Am.-Eu. (Belg.-Ire.).—FIG. 306,5. *\*P. retardatum*, *L. Carb.*, Belg.; 5a,b,  $\times 1$  (Kummel, n).

**Subvestinautilus** TURNER, 1954 [*\*Vestinautilus crassimarginatus* FOORD, 1900; OD]. Evolute, whorl section depressed, trapezoidal, venter convex throughout development; suture with broadly rounded ventral lobe, deeper lateral lobe; annular lobe may be present; umbilical shoulder carinate in youth but rounded or marked by longitudinal rib in maturity; spiral ornament on umbilical walls in early whorls (199). *L. Carb.*, Eu. (Ire.-Isle of Man).—FIG. 306,4. *\*S. crassimarginatus* (FOORD), Ire.; 4a,  $\times 0.4$ ; 4b,  $\times 0.7$  (80).

**Temnocheilus** M'COY, 1844 [*\*Nautilus (Temnocheilus) coronatus* M'COY, 1844; SD HYATT, 1884] [= *Pseudotemnocheilus*, *Articheilus*, *Leonardocheilus* RUZHENTSEV & SHIMANSKIY, 1954]. Evolute, with large, open, perforate umbilicus; whorl section subtrapezoidal, flattened ventrally and laterally, slightly impressed dorsally; lateral zones convergent dorsally; deep hyponomic sinus on venter; ventrolateral shoulders bearing single row of longitudinally elongate nodes; sutures with ventral, lateral, and dorsal lobes; siphuncle small, subcentral, orthochoanitic (128). *L. Carb. (Miss.)-Perm.*, N. Am. (Ill.-Ky.-Mo.-Kans.-Tex.-Colo.)-Eu. (Ire.-Eng.-USSR).—FIG. 306,1. *\*T. coronatus* (M'COY), *L. Carb.*, Ire.; 1a,b,  $\times 0.7$  (80).

**Tylodiscoceras** MILLER & COLLINSON, 1950 [*\*T. unicum*; OD]. Large, discoidal, and nautilonic, only slightly involute; whorls depressed, rounded laterally, concave ventrally; umbilicus large, open,

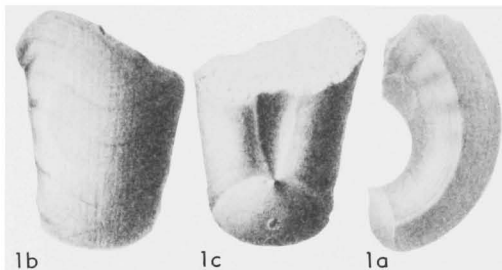


FIG. 307. *\*Valhallites ornatus* (GIRTY) (Koninckiocerataceae) (p. K427).

and probably perforate, umbilical shoulders rounded; test thick, bearing single row of large rounded lateral nodes; suture with shallow broadly rounded ventral, lateral, and presumably dorsal lobes, separated by narrowly rounded saddles (125). *Miss.*, N. Am. (Ky.-Tenn.).—FIG. 306,3. *\*T. unicum*, Ky.; 3a,b,  $\times 0.2$  (125).

**Valhallites** SHIMANSKIY, 1959 [*\*Endolobus ornatus* GIRTY, 1911; OD]. Evolute, rapidly expanding, with depressed, elliptical whorl section; venter broadly convex, lateral area acute, umbilical wall, broad, convex, dorsal area shallow; suture with shallow ventral, lateral, and dorsal lobes and annular lobe; conch bearing short radial ribs, sinuous growth lines, and prominent longitudinal striae; siphuncle, slightly ventral of center (221). *L. Carb. (Miss.)-L. Perm.*, N. Am. (Ark.)-Asia (Sib.).—FIG. 307,1. *\*V. ornatus* (GIRTY), *Miss.*, USA (Ark.); 1a-c,  $\times 1$  (221).

## Superfamily TRIGONOCERATACEAE Hyatt, 1884

[*nom. transl.* KUMMEL, herein (*ex* Trigonoceratidae HYATT, 1884)] [= Centroceratida FLOWER in FLOWER & KUMMEL (order) 1950; Centroceratina SHIMANSKIY, 1957 (suborder); Centrocerataceae SHIMANSKIY, 1962 (superfam.).]

Gyroconic to nautilonic, whorls primitively quadrate, venter narrow to acute, dorsum broad; section may develop a concave venter, or may become broad and rounded. Some forms with strongly lirate surfaces (49). *Dev.-Trias.*

## Family TRIGONOCERATIDAE Hyatt, 1884

[incl. Triboloceratidae HYATT, 1884, Rinceratidae HYATT, 1893 (= Rhinceratidae HYATT in ZITTEL, 1900, *nom. null.*), Thrinoceratidae RUZHENTSEV & SHIMANSKIY, 1954, Tribolocerataceae SHIMANSKIY, 1957] [= Neothrinoceratidae, Subclymeniidae, Apheloceratinae SHIMANSKIY, 1962]

Loosely coiled to evolute, with oval to subquadrate, depressed to compressed whorl sections, generally bearing longitudinal ridges which may decrease with growth. Suture typically only slightly sinuous. Si-

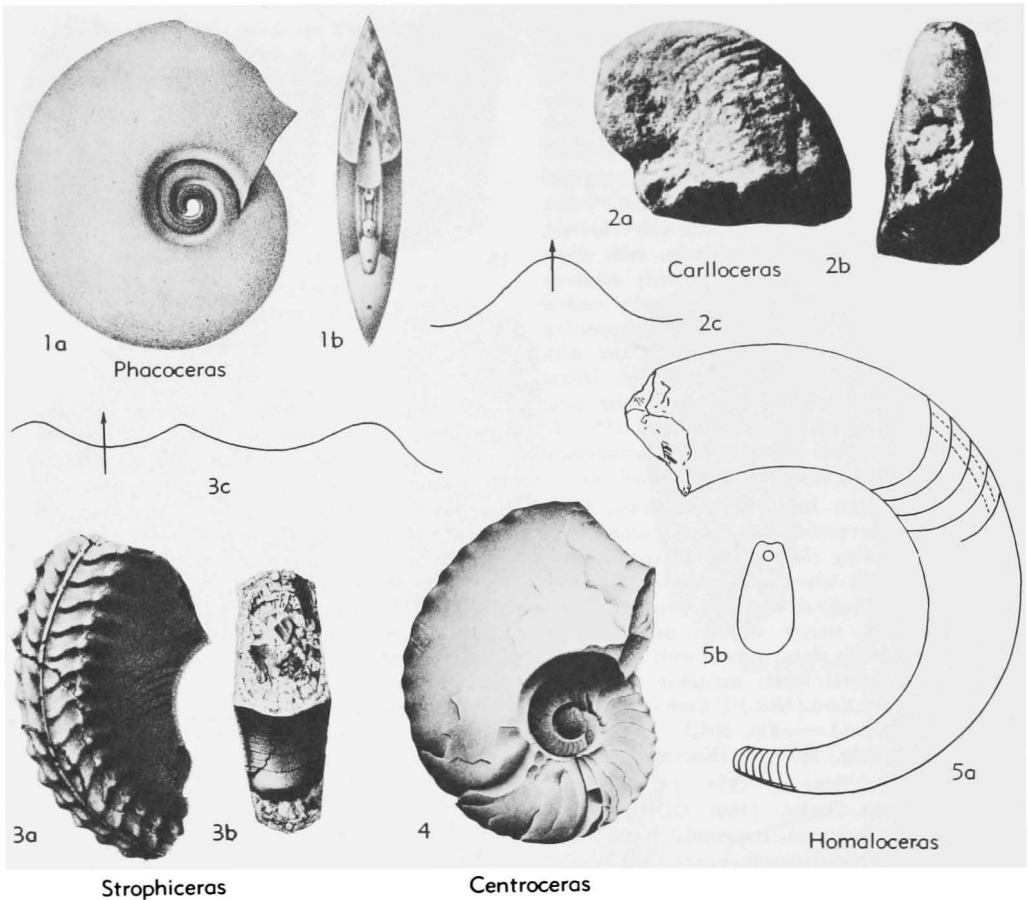


FIG. 308. Trigonocerataceae (Centroceratidae) (p. K432).

phuncle small, subcentral, orthochoanitic (32). *L.Carb.*(*Miss.*)-*L.Perm.*

**Trigonoceras** M'COY, 1844 [*\*Orthocera paradoxa* SOWERBY, 1825; OD] [= *Nautiloceras* D'ORBIGNY, 1849]. Known only from fragmentary specimens, which appear to be cyrtoconic or very loosely coiled gyroconic forms with subtriangular cross section, venter broadly concave, shoulders angular and lateral areas broad, convex; siphuncle above center, orthochoanitic (128). *L.Carb.*, Eu. (Eng.-Belg.-Ger.).—FIG. 310,1. *\*T. paradoxicum* (SOWERBY), Eng.;  $\times 0.7$  (233).

**Aphelaeceras** HYATT, 1884 [*\*Nautilus (Discites) disciformis* MEEK & WORTHEN, 1873; SD MILLER & GARNER, 1953] [= *Apheloceras* HYATT, 1893 (*nom. null.*)]. Evolute, compressed, with wide umbilicus, small impressed zone; whorl section subrectangular, with convex lateral areas converging toward concave venter; ventral shoulders subangular; umbilical shoulders broadly rounded; suture with narrow ventral lobe, broad lateral

lobe; siphuncle barely ventral from center (93). *L.Carb.*(*Miss.*), N.Am.-Eu.—FIG. 310,6. *A. difficile* (DEKONINCK), Belg.; 6a,b,  $\times 0.7$  (224).

**Apogonoceras** RUZHENTSEV & SHIMANSKIY, 1954 [*\*A. remotum*; OD]. Gyroceraconic, very loosely coiled; whorl section at maturity rounded. Sculpture of sharp longitudinal ribs; suture nearly straight; siphuncle subcentral (42). [Type and only specimen is very fragmentary.] *L.Perm.*, SE. USSR.

**Chouteauceras** MILLER & GARNER, 1953 [*\*Rineceras americanum* MILLER & FURNISH, 1939; OD]. Loosely coiled, volutions not in contact except perhaps slightly at maturity; whorl section ovate, higher than wide, more rounded dorsally than ventrally, not impressed dorsally; conch with numerous longitudinal ridges and fine transverse growth lines; suture with broad rounded lateral lobes and dorsal and ventral saddles; siphuncle small, subcentral (131). *Miss.*, N.Am.(Mo.-Mich.).—FIG. 310,3. *\*C. americanum* (MILLER & FURNISH), Mo.;  $\times 1$  (131).



**Diodoceras** HYATT in ZITTEL, 1900 [*\*Nautilus avonensis* DAWSON, 1868; OD]. Evolute, widely umbilicate, with moderate impressed zone; whorl section depressed, with broadly arched venter merging into obtusely rounded flanks, broad, sloping, slightly convex umbilical wall; suture only slightly sinuous; siphuncle near venter. *Miss.*, N. Am.(Can.).—FIG. 310,9. *\*D. avonense* (DAWSON), Nova Scotia; 9a,b,  $\times 0.7$  (Kummel, n).

**Discitoceras** HYATT, 1884 [*\*Nautilus (Discites) costellatus* M'COY, 1844; OD] [= *Discites* M'COY, 1844 (non SCHLOTHEIM, 1813, nec DEHAAN, 1825)]. Widely umbilicate nautilicone with shallow impressed zone; whorl section depressed, with broadly rounded venter and rounded ventral shoulders, flanks flattened, converging ventrally, umbilical shoulders subangular, umbilical wall broad, slanting, slightly convex; septa sinuous (details unknown); siphuncle approximately central; test bearing longitudinal ridges separated by spaces greater than twice their own width; ridges covering venter and lateral areas but not umbilical wall (93). *L.Carb.*, NW.Eu.—FIG. 310,2. *\*D. costellatum* (M'COY), Ire.; 2a-c,  $\times 0.8$  (119).

**Epistroboceras** TURNER, 1954 [*\*E. stubblefieldi*; OD]. Evolute, highly compressed, with converging convex flanks, narrow concave venter, and angular, carinate ventral shoulders; flanks with spiral ribs, sulci and lirae of varying prominence; ventral lobe of suture shallow, lateral lobe deeper and broadly rounded; siphuncle subventral (199). *L.Carb.*, W.Eu.—FIG. 310,5. *\*E. stubblefieldi*, Isle of Man; 5a-c,  $\times 1$  (199).

**Leuroceras** HYATT, 1893 [*\*L. aplanatum*; OD]. Compressed, involute, smooth, nautilicone; whorl section elliptical, higher than wide, flanks broadly convex, converging on rounded venter; umbilical shoulders broadly rounded; whorls cover about 0.7 of preceding whorls. Living chamber half a volution in length; suture with rounded ventral saddle, broad shallow lateral lobe, and possibly dorsal lobe with small annular lobe; siphuncle near venter; inner whorls bearing longitudinal ridges (95). *L.Carb.*, Eu.(Belg.-Eng.).—FIG. 310,7. *\*L. aplanatum*, Belg.; 7a,b,  $\times 0.7$  (Kummel, n).

**Lispoceras** HYATT, 1893 [*\*L. trivolve*; OD]. Evolute, with subelliptical whorl section on outer whorl where venter is broadly rounded, grading imperceptibly into flanks; umbilical shoulder subangular; umbilical wall broad, sloping; earlier volutions more rounded in cross section; conch bearing fine longitudinal lirae and growth lines which form prominent sinus on venter; suture with shallow ventral and lateral lobes; siphuncle just ventral of center (95). *L.Carb.*, W.Eu.—FIG. 310,4. *\*L. trivolve*, Belg.; 4a-c,  $\times 0.7$  (Kummel, n).

**Maccoyceras** MILLER, DUNBAR, & CONDRA, 1933 [*\*Nautilus (Discites) discors* M'COY, 1844; OD].

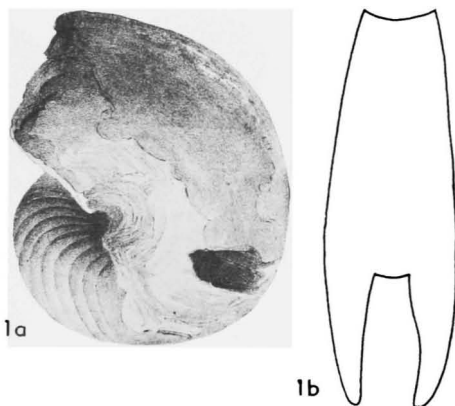


FIG. 309. *\*Diorugoceras planidorsatum* (PORTLOCK) (Centroceratidae) (p. K432).

Evolute, volutions only slightly impressed; whorl section hexagonal, with flattened venter, converging flanks, prominent umbilical shoulder, and sloping umbilical wall; conch bearing prominent transverse lirae; suture with shallow ventral and lateral lobes; siphuncle small, ventral of center of whorl (128). *L.Carb.*(*Miss.*), N.Am.(Mich.)-Eu.—FIG. 310,8. *\*M. discors* (M'COY), Ire.; 8a,b,  $\times 0.7$ ,  $\times 1$  (119).

**Mesochasmoceras** FOORD, 1900 [*\*Nautilus (Discites) latidorsatus* M'COY, 1844; OD]. Very evolute, smooth, compressed, with broad open umbilicus; early whorls nearly ovate in cross section, later whorls subrectangular, with broad slightly convex flanks, subangular ventral shoulders, concave venter, and umbilical shoulders broadly rounded; suture unknown; siphuncle near center (80). *L.Carb.*, Eu.—FIG. 311,1. *\*M. latidorsatum* (M'COY), Ire.; 1a,b,  $\times 0.5$  (80).

**Pararincoceras** TURNER, 1954 [*\*Nautilus luidi* FLEMING, 1828; OD]. Evolute, with large perforate umbilicus (tarphophioceraconic); whorls no longer making contact at adoral end of conch; whorl section depressed, elliptical, widest at mid-part of whorl, venter broadly rounded; conch bearing prominent longitudinal striae and radial growth lines and lirae, with nodes at their intersection; suture with shallow ventral and lateral lobes; siphuncle subcentral (199). *L.Carb.*, NW. Eu.(Ire.-Isle of Man-Eng.).—FIG. 311,2. *\*P. luidi* (FLEMING), Eng.; 2a-c,  $\times 1.5$  (Kummel, n).

**Rincoceras** HYATT, 1893 [*\*Gyroceras propinquum* DEKONINCK, 1880; SD FOORD, 1900] [= *Rhincoceras* HYATT in ZITTEL, 1900]. Evolute, volutions in contact but not deeply impressed at maturity; whorl section elliptical, depressed, ventral or dorsal zones (or both) tending to be flattened or even slightly concave; conch bearing prominent longitudinal ridges, which may be spinose; camerae short; sutures slightly sinuous; siphuncle small, subcentral, orthochoanitic (95). *L.Carb.*

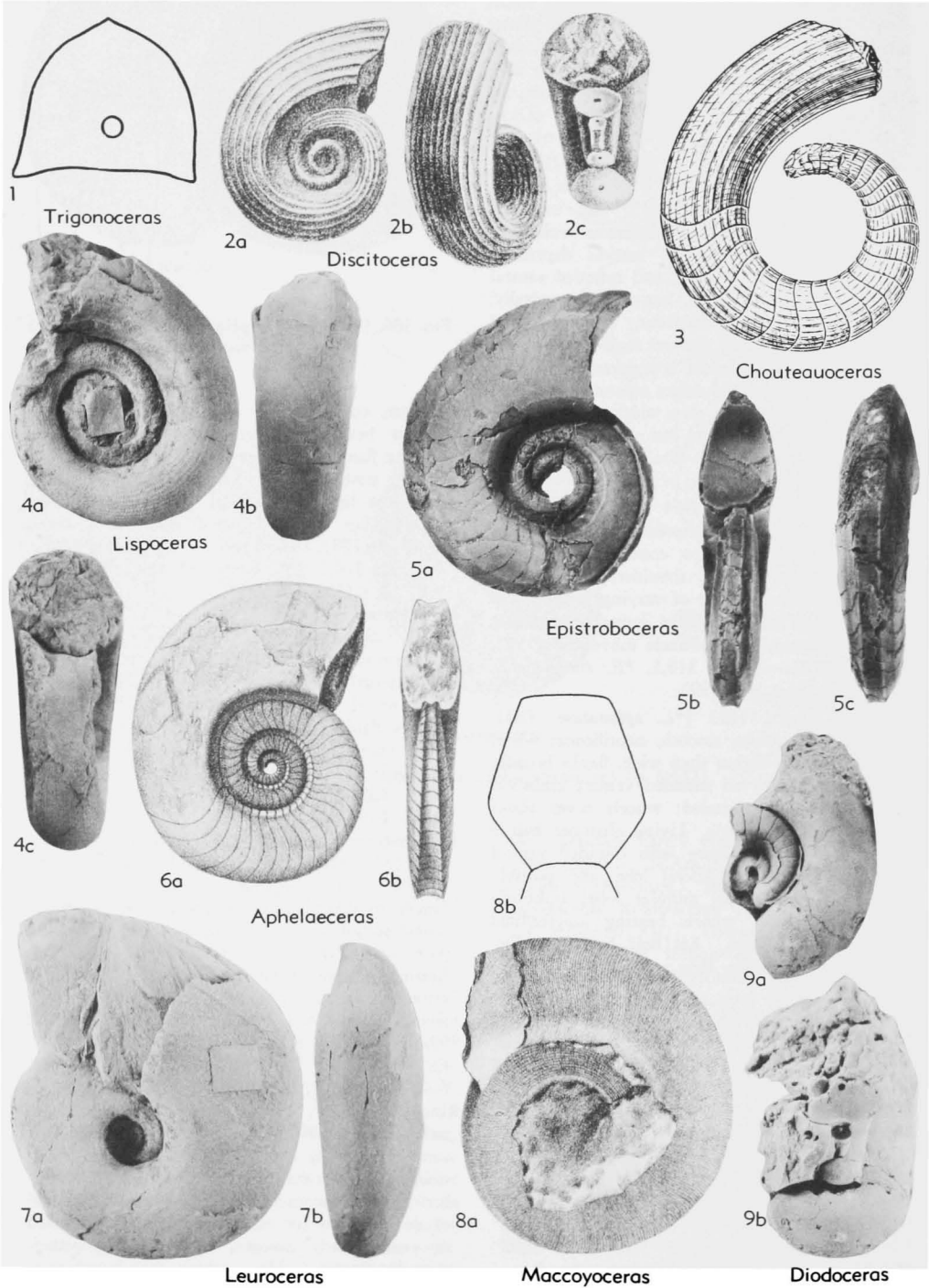


FIG. 310. Trigonocerataceae (Trigonoceratidae) (p. K428-K429).



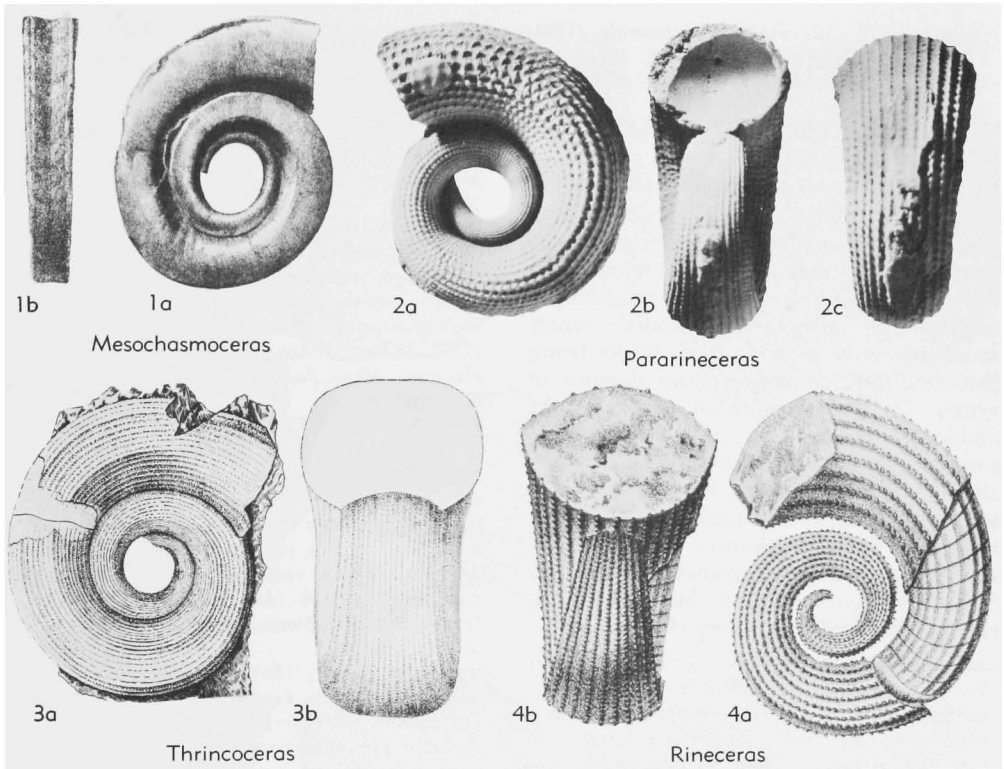


FIG. 311. Trigonocerataceae (Trigonoceratidae) (p. K429, K431).

(Miss.), N.Am.-Eu.—FIG. 311.4. \**R. propinquum* (DEKONINCK), Belg.; 4a,b,  $\times 0.8$  (224).

**Stroboceras** HYATT, 1884 [\**Gyroceras hartii* DAWSON, 1868; OD]. Evolute, indented very little, outer whorls losing contact; whorl section variable, generally higher than wide, converging toward venter; conch bearing prominent ventral ridges and grooves; suture slightly sinuous; siphuncle small, ventral of center (131). *L.Carb.* (Miss.), N.Am.-Eu.—FIG. 312.1a. \**S. hartii* (DAWSON), U.Miss., Nova Scotia;  $\times 5$  (131).—FIG. 312.1b. *S. stygiale* (DEKONINCK), *L.Carb.*, Belg.;  $\times 1$  (131).—FIG. 312.1c.d. *S. sulcatum* (SOWERBY); 1c, U.Miss., USA (Ky.) [=“*Discitoceras sulcatum* SOWERBY” MILLER & FURNISH],  $\times 3$ ; 1d, *L.Carb.*, Ire.,  $\times 3$  (131).—FIG. 312.1e. *S. bisulcatum* (DEKONINCK), *L.Carb.*, Belg.;  $\times 1.7$  (131).

**Subclymenia** D'ORBIGNY, 1849 [\**Goniatites evolutus* PHILLIPS, 1836; SM D'ORBIGNY, 1850]. Evolute, compressed, with perforate umbilicus; whorl section subquadrate, flanks subparallel, slightly convex, venter concave, ventral shoulders subangular; conch bearing growth lines and longitudinal lirae on ventral area of flanks and on ventral shoulders; suture with deep, funnel-shaped ventral lobe, subangular saddle on ventral shoulder,

with annular lobe; siphuncle near venter (95). *L.Carb.*, Eu.(Eng.-Ire.-Belg.).—FIG. 312.2. *S. oculata* HYATT, Belg.; 2a,b,  $\times 1$ ; 2c,  $\times 0.7$  (224).

**Thrincoceras** HYATT, 1893 [\**T. depressum*; SD SCHMIDT, 1951] [=Neothrincoceras RUZHENTSEV & SHIMANSKIY, 1954]. Evolute, not greatly impressed; whorl section robust, subquadrate, depressed; venter broad, flattened, ventral and umbilical shoulders rounded; flanks only slightly convex; umbilicus wide, perforate; conch bearing prominent longitudinal ridges both on venter and flanks. Suture slightly sinuous; siphuncle just ventral of center (95). *L.Carb.*(Miss.)-*L.Perm.*, N. Am.-Eu.—FIG. 311.3. \**T. depressum*, USA (Ky.); 3a,b,  $\times 0.3$  (95).

**Vestinautilus** RYCKHOLT, 1852 [\**Nautilus konincki* D'ORBIGNY, 1850; SD HYATT, 1884] [=Triboloceras HYATT in ZITTEL, 1884]. Evolute, volutions in contact except at early and very late ontogenetic stages; umbilicus large, perforate; whorl section variable, generally semicircular and flattened ventrally on immature volutions, sublenticular at full maturity; conch bearing longitudinal ridges, most of which become obsolete at maturity; camerae short; sutures sinuous, tending to form ventral and in some cases, dorsal and lateral lobes; si-

phuncle small, subcentral, orthochoanitic (199). *L.Carb.*(Miss.), N.Am. - Eu.—FIG. 312,3. \**V. konincki* (D'ORBIGNY), Eu.; 3a-c,  $\times 0.6$  (224).

### Family CENTRO CERATIDAE Hyatt in Zittel, 1900

[=Phacoceratidae SHIMANSKIY, 1962]

Shells gyroconic to tarphyceraconic and nautilicone in coiling, characterized by a quadrangular cross section in which ventral and umbilical shoulders are sharply angular and only rarely rounded; venter much narrower than dorsum, flanks being flattened and converging from dorsum to venter. Hyponomic sinus on venter. Flanks divided in center by a crest, best seen in early stages of *Centroceras*, where it is also elevated on a slight ridge, so that transverse sections are faintly hexagonal. Growth lines transverse dorsally. Sutures with lobes on venter and sides, but transverse dorsally. Siphuncle tubular, close to but not in contact with venter (32). *M.Dev.-L.Perm.*

**Centroceras** HYATT, 1884 [\**Goniatis marcellensis* VANUXEM, 1842; OD]. Tarphyceraconic, consisting of few, rapidly expanding volutions; umbilicus perforate, wide; slightly impressed zone near base of mature living chamber; whorl sections tetragonal, with sharp ventral and umbilical shoulders; dorsum broad, convex in young, nearly straight in mature portions; lateral areas oblique, convergent toward narrow, scarcely convex venter; whorls compressed; suture with shallow ventral lobe and broad lateral lobe having subacute saddles on shoulders, dorsal portion nearly transverse except in mature portion where broad shallow lobe occurs; siphuncle tubular, near venter; living chamber half a volution in length; ornamentation consists of alternating striae and lirae which are more or less fasciculate; ventral shoulders of early volutions bear small nodes (93). *M.Dev.*, Eu.(Ger.)-N.Am.(N.Y.-Ohio-Can.). —FIG. 308,4. \**C. marcellense* (VANUXEM), USA(N.Y.);  $\times 0.3$  (223).

**Cariloceras** FLOWER & CASTER, 1935 [\**C. garlandensis*; OD] [= *Carloceras* SHIMANSKIY, 1957 (nom. null.)]. Moderately involute nautilicone; whorl section trapezoidal, compressed, ventral and lateral areas nearly flat, with slight dorsal impressed zone; shoulders slightly rounded; suture with ventral saddle and broad lateral lobe. Siphuncle small, near venter; surface of internal mold smooth (48). *U.Dev.*, N.Am.—FIG. 308, 2. \**C. garlandense*, Pa.; 2a-c,  $\times 1$  (48).

**Diorugoceras** HYATT, 1893 [\**Nautilus planidorsatus*, PORTLOCK, 1843; OD]. Nautilicone, very involute, with small umbilicus, compressed; whorl section with slightly convex broad lateral areas

that converge toward concave venter; ventral shoulders angular, umbilical shoulders broadly rounded; conch smooth, as far as known; suture with broad, deep lateral lobe, nature of ventral and dorsal lobe unknown; position of siphuncle unknown (95). *L.Carb.*, Eu.—FIG. 309,1. \**D. planidorsatus* (PORTLOCK), Ire.; 1a,  $\times 0.5$ ; 1b,  $\times 1$  (229).

**Homaloceras** WHITEAVES, 1891 [\**H. planatum*; OD]. Cyrtoconic to gyroconic; whorl section compressed, venter narrow and concave, flanks broadly convex, dorsal areas convex; suture only slightly sinuous; siphuncle tubular, near venter (207). *M.Dev.*, N.Am.(Can.). —FIG. 308,5. \**H. planatum*, Man.; 5a,b,  $\times 0.3$  (207).

**Phacoceras** HYATT, 1884 [\**Nautilus oxystomus* PHILLIPS, 1836; OD]. [= *Phaceras* TEICHERT & GLENISTER, 1952 (nom. null.)]. Moderately involute, highly compressed, lenticular; venter acute, conch widest at umbilical shoulder; surface smooth except for growth lines; suture with broad shallow lobe on flanks and ventral saddle; siphuncle slightly ventral from center (93). *L. Carb.* (Eu.)-*L. Perm.* (Australia). —FIG. 308,1. \**P. oxystomus* (PHILLIPS), *L.Carb.*, Eu.; 1a,b,  $\times 0.7$  (224).

**Strophiceras** HYATT, 1884 [\**Gyroceras binodosum* SANDBERGER & SANDBERGER, 1850; OD] [= *Strophiceras* ZITTEL, 1884 (nom. null.)]. Probably gyroceraconic (type known from fragment only); whorl section subrectangular, higher than wide; flanks flattened, convergent toward venter; both dorsal and ventral areas slightly arched, venter with ridge along center line, aligned by diagonally elongated nodes which decrease toward ventral shoulder; enlarged longitudinal nodes on ventral shoulder which show their effect slightly on otherwise smooth flanks. Suture with ventral, lateral and dorsal lobes. Siphuncle very near venter (93). *M.Dev.*, Eu.—FIG. 308,3. \**S. binodosum* (SANDBERGER & SANDBERGER), Ger.; 3a,b,  $\times 0.7$ ; 3c,  $\times 1$  (231).

### Family GRYPOCERATIDAE Hyatt in Zittel, 1900

[incl. Gryponautilidae MOJSISOVICS, 1902; Domatoceratidae MILLER & YOUNGQUIST, 1949] [=Grypoceratinae SHIMANSKIY, 1962]

Evolute to involute, generally smooth, compressed showing some modification of venter from flattened to subangular, or bearing keel. Ornamentation not common but some forms with nodes or carinae. Suture with distinct ventral and lateral lobes. Position of siphuncle variable, one form having siphuncle at venter (115). *L.Carb.-Trias.*

**Grypoceras** HYATT, 1883 [\**Nautilus mesodicus* QUENSTEDT, 1845; OD]. Like *Domatoceras*, but tending toward more involution and rounding of ventral shoulders; suture with annular lobe (115).

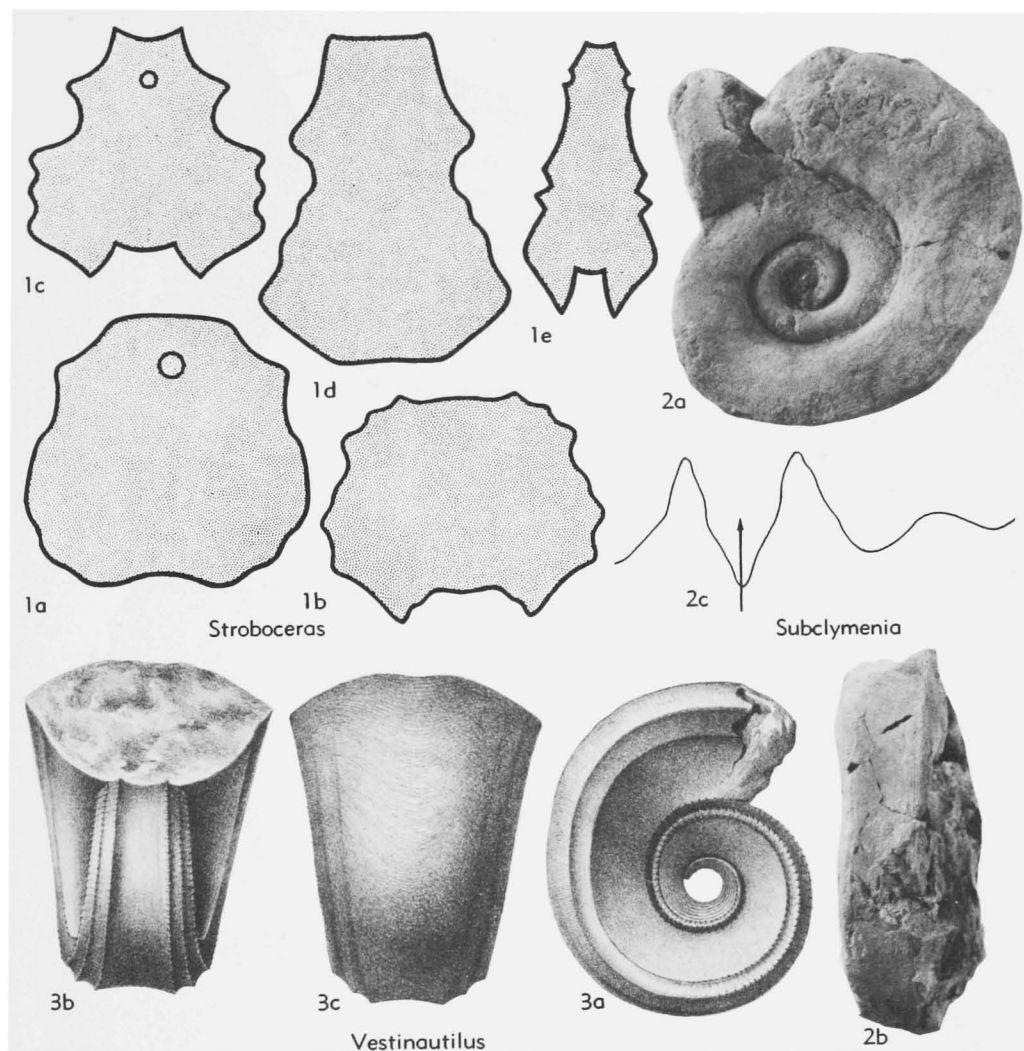


FIG. 312. Trigonocerataceae (Trigonoceratidae) (p. K431-K432).

*Trias.*, Eu.-Asia (Himalayas)-N. Am. (Idaho-Nev.-Calif.).—FIG. 313,2. \**G. mesodicum* (QUENSTEDT), Nor., Alps; 2a,b,  $\times 0.3$  (139).

**Domatoceras** HYATT, 1891 [\**D. umbilicatum*; SD MILLER, DUNBAR & CONDRA, 1933] [= *Stenodomatoceras*, *Penascoceras*, *Permodomatoceras* RUZHENTSEV & SHIMANSKIY, 1954; *Pseudomatoceras* MILLER, DUNBAR & CONDRA, 1933]. Subdiscoidal, nautilonic, generally evolute; whorl section flattened ventrally and laterally, generally only slightly impressed dorsally; shoulders typically narrowly rounded to subangular, flanks typically convergent ventrally, with maximum width just above umbilical shoulders; growth lines indicate deep hyponomic sinus on venter; some forms have low ventrolateral or dorsolateral nodes (or both) in late

maturity; suture with broad rounded ventral, lateral, and dorsal lobes, separated by subangular saddles; siphuncle subcentral (113). *U. Carb.* (Penn.)-Perm., N.Am.-Eu.-Afr.-Asia (China)-E. Indies-Australia.—FIG. 313,1. \**D. umbilicatum*, Penn., USA (Kans.); 1a,b,  $\times 0.3$ ; 1c,  $\times 1$  (134).

**Epidomatoceras** TURNER, 1954 [\**Nautilus planotergatus* M'Coy, 1844; OD]. Like *Domatoceras* but ventral shoulders rounded on living chamber, angular on phragmocone; slight narrow sulcus separating ventrolateral margin from series of lirae on ventral margins; suture with sharp angular ventral lobe and broad rounded lateral lobe; siphuncle subcentral (199). *L. Carb.*, Eu.—FIG. 313,5. *E. maccoyi* TURNER, Ire.; 5a,b,  $\times 0.7$ ; 5c,  $\times 1.5$  (199).

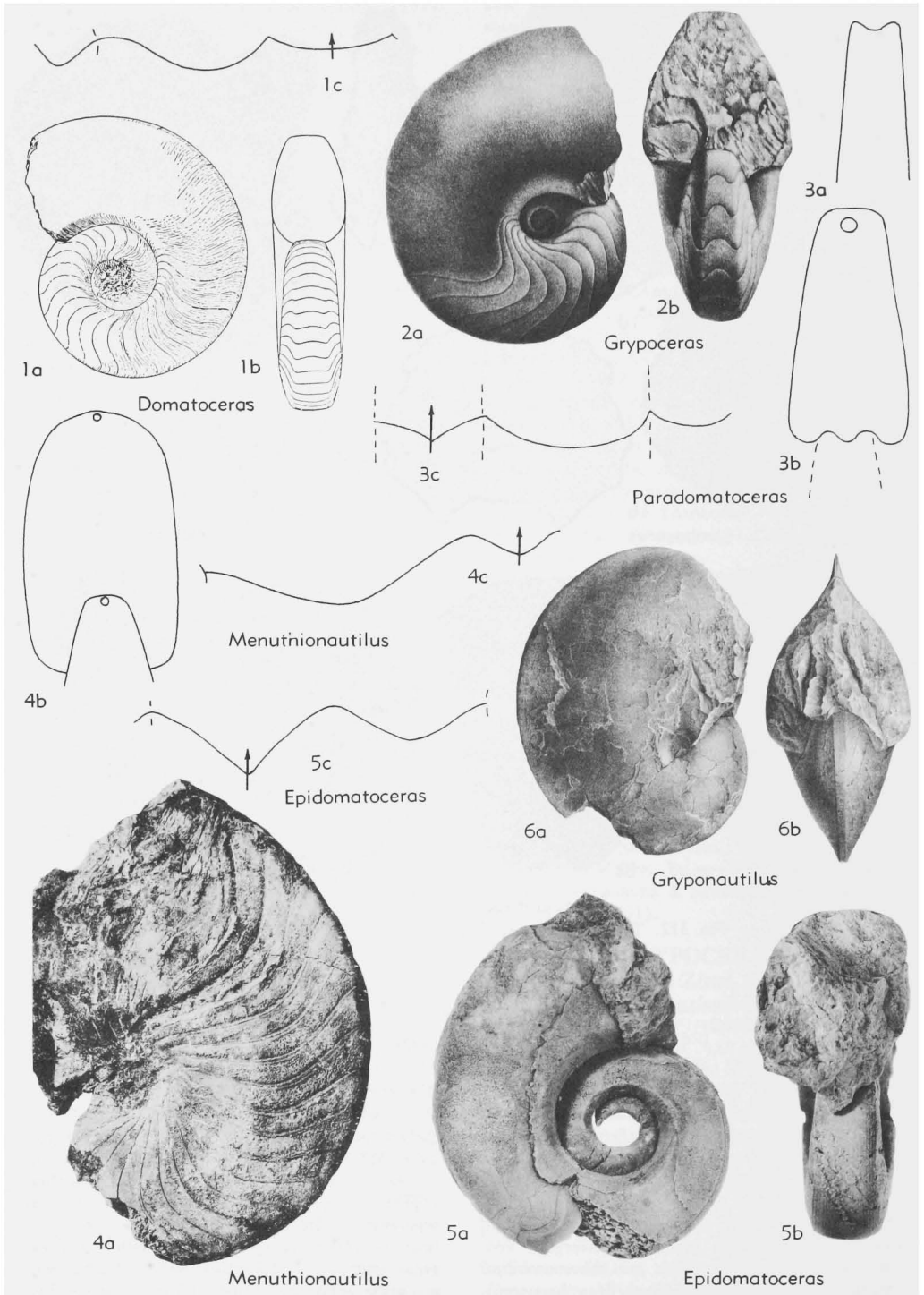


FIG. 313. Trigonocerataceae (Grypoceratidae) (p. K433, K435-K436).

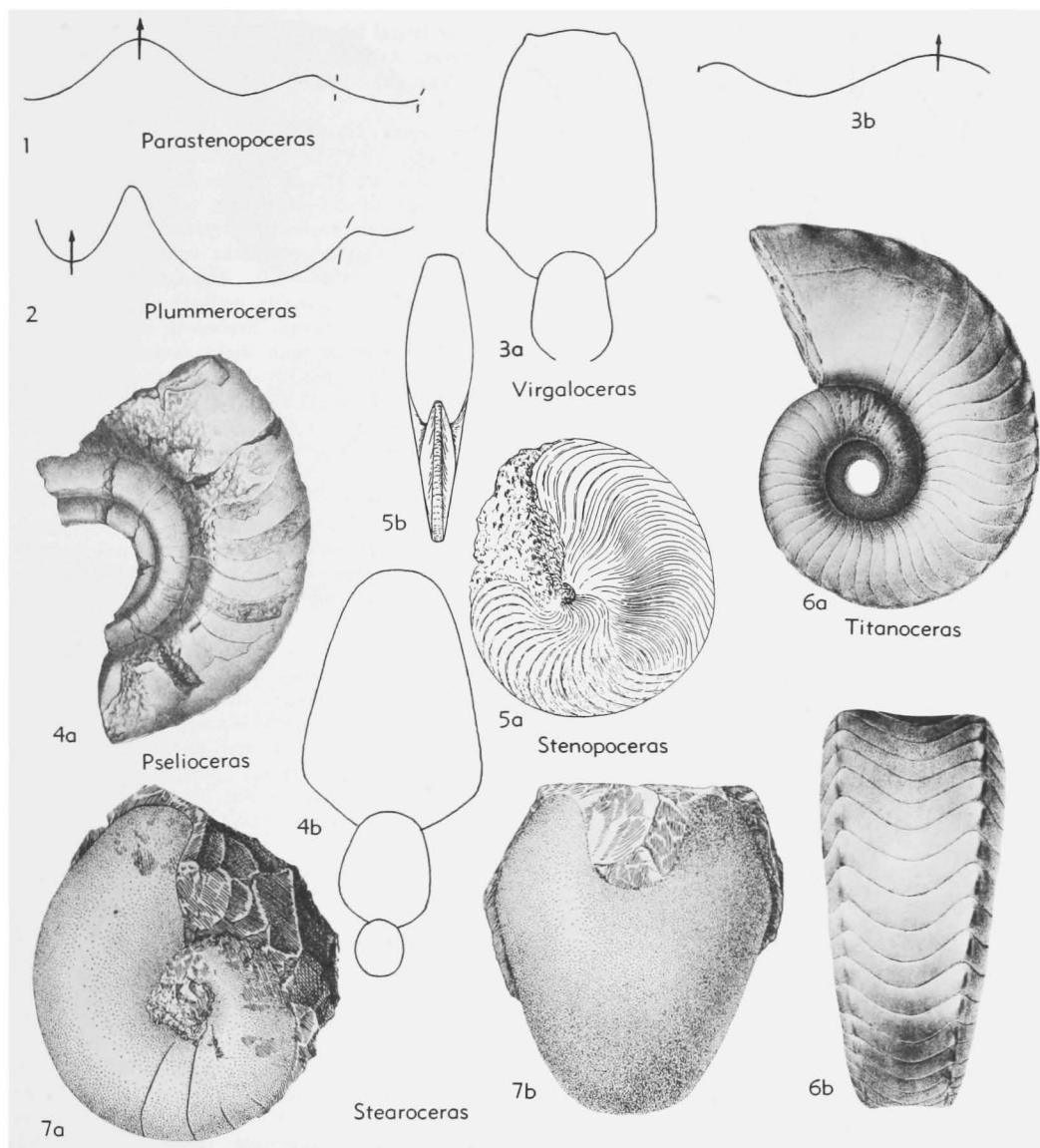


FIG. 314. Trigonocerataceae (Grypoceratidae) (p. K436).

**Gryponautilus** MOJSISOVICS, 1902 [*\*Nautilus galeatus* MOJSISOVICS, 1873; SD DIENER, 1915]. Involute, inflated conch that at maturity has a narrowly rounded keel-like venter; inner whorls have broad concave to convex truncated venters and inflated lateral areas with row of nodes along angular ventral shoulders; suture with shallow ventral and lateral lobe and annular lobe (113). *U.Trias.* (Carn.-Nor.), Eu. (Alps, USSR)-Asia (Himalayas, Indonesia)-N.Am. (Calif.).—FIG. 313, 6. *\*G. galeatum* (MOJSISOVICS), Carn., Alps; 6a, b,  $\times 0.2$  (139).

**Menuthionautilus** COLLIGNON, 1933 [*\*Nautilus (Menuthionautilus) kieslingeri*; OD]. Involute, rapidly expanding, smooth; whorl sections compressed, venter broadly convex on mature whorls, inner whorls with flattened venter; flanks broadly convex; umbilicus very small, umbilical shoulders rounded, umbilical walls steep; suture with shallow ventral lobe and broad lateral lobe; siphuncle against venter (113). *L.Trias.* (Scyth.), Afr. (Madag.)-Eu. (USSR)-Asia (Pak.).—FIG. 313, 4. *\*M. kieslingeri*, Madag.; 4a,  $\times 0.4$ ; 4b, c,  $\times 0.7$  (10).

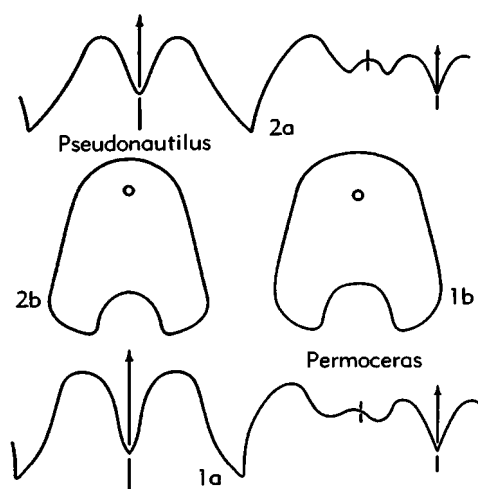


FIG. 315.1. *\*Permoceratidae bitauniense* (Haniel) (Permoceratidae) (p. K437). [FIG. 315.2. Homeomorphic form, *Pseudonautilus geinitzi* (Oppel) (Pseudonautilidae) (p. K451).]

**Paradomatoceras** DELÉPINE, 1937 [*\*P. applanatum*; OD]. Conch much like that of *Domatoceras*, compressed, evolute; whorl section subrectangular, with flattened flanks converging toward flattened venter, ventral shoulder narrowly rounded, umbilical shoulders more broadly rounded; inner whorls with subparallel flanks and concave venter bordered by distinct carina; suture with shallow pointed ventral lobe, broad shallow lateral lobe, angular saddle on umbilical shoulder and shallow lobe on umbilical wall; siphuncle in near ventral position (17). *U.Carb.*, Eu.(Holl.)-N.Afr.-(Morocco).—FIG. 313.3. *\*P. applanatum*; 3a,b, Holl.,  $\times 1.5$ ; 3c, Morocco,  $\times 1.5$  (17).

**Parastenopoceras** RUZHENTSEV & SHIMANSKIY, 1954 [*\*P. khvorovae*; OD]. Involute, smooth, slightly inflated; whorl sections semielliptical, flanks broadly convex, venter rounded, with distinct umbilical shoulders and nearly vertical umbilical wall; suture with ventral saddle, large lateral lobe, lateral saddle on umbilical shoulder, and shallow dorsal lobe (153). [Conchs have the appearance of an inflated, evolute *Stenopoceras*.] *L.Perm.* (Artinsk.), S.USSR.—FIG. 314.1. *\*P. khvorovae*;  $\times 2$  (153).

**Plummeroceras** KUMMEL, 1953 [*\*Grypoceras (Plummeroceras) plummeri*; OD]. Like *Domatoceras*, but more evolute and suture with deep ventral lobe (113). *L.Perm.*, USA(Tex.).—FIG. 314.2. *\*P. plummeri*;  $\times 0.5$  (113).

**Pselioceras** HYATT, 1884 [*\*Nautilus ophioneus* WAAGEN, 1879; OD]. Evolute, smooth, whorls little embracing, umbilicus perforate; whorl section ovoid, flanks slightly convex, converging ventrally, venter rounded, umbilical shoulders broadly rounded; suture straight over venter, with shal-

low lateral lobe; siphuncle above center (113). *L. Perm.*, Asia(Pak.).—FIG. 314.4. *\*P. ophioneus* (WAAGEN), Salt Range; 4a,  $\times 0.3$ ; 4b,  $\times 0.7$  (205).

**Stearoceras** HYATT, 1893 [*\*Endolobus gibbosus* HYATT, 1891; OD] [= *Parapenascoceras*, *Neodomatoceras* RUZHENTSEV & SHIMANSKIY, 1954]. Involute, rapidly expanding, volutions few; whorl sections subtrapezoidal, depressed, flattened laterally and ventrally; flanks convergent ventrally; impressed zone small; umbilicus moderate in size, deep, presumably perforate, umbilical walls steep; conch smooth; hyponomic sinus deep and rounded; suture with slight ventral, lateral, and dorsal lobes, and small V-shaped annular lobe (134). *U.Carb.*(*L.Penn.*)-*L.Perm.*, N.Am.-Asia (China)-Australia-Eu.(USSR).—FIG. 314.7. *\*S. gibbosum* (HYATT), *L.Penn.*, USA(Tex.); 7a,b,  $\times 0.4$  (134).

**Stenopoceras** HYATT, 1893 [*\*Phacoceras dumblei* HYATT, 1891; OD]. Subdiscoidal, rapidly expanding adaperturally, compressed, flattened laterally, deeply involute; venter narrow, flattened or slightly concave; umbilical shoulders low, broadly rounded; growth lines indicate deep hyponomic sinus; suture with deep ventral saddle, broad lateral lobe, smaller rounded dorsolateral saddle in regions of umbilical shoulder, similar lobe near umbilical seam, deep V-shaped dorsal lobe; siphuncle small, on ventral side of center (134). *U.Carb.*(*Penn.*)-*L.Perm.*, N.Am.-Eu.(USSR)-Asia (China)-Australia.—FIG. 314.5. *\*S. dumblei* (HYATT), *L.Perm.*, USA(Kans.); 5a,b,  $\times 0.3$  (134).

**Titanoceras** HYATT, 1884 [*\*Nautilus ponderosus* MEEK, 1872; OD]. Moderately evolute, thick, subdiscoidal; whorl section subquadrate, wider than high, slightly impressed dorsally, flattened to slightly convex laterally, subangular ventrolaterally, concave ventrally; umbilicus large, open, perforate; at full maturity ventral shoulders bear relatively small longitudinally elongate nodes; suture with broad, rounded ventral, lateral, and dorsal lobes; siphuncle not known (134). *U.Carb.* (*Penn.*)-*L.Perm.*, N. Am.-W. Australia.—FIG. 314.6. *\*T. ponderosum* (MEEK), USA(Neb.); 6a,b,  $\times 0.2$  (134).

**Virgaloceras** SCHINDEWOLF, 1954 [*\*Gastrioceras? noduliferum* REED, 1944; OD]. Like *Domatoceras*, but with row of nodes on umbilical wall against umbilical seam and ventral saddle rather than ventral lobe in suture (158). *U.Perm.*, Asia.—FIG. 314.3. *\*V. noduliferum* (REED), Pak. (Salt Range); 3a,b,  $\times 0.6$  (158).

### Family PERMOCERATIDAE Miller & Collinson, 1953

Involute, compressed, smooth; whorl section higher than wide, subrectangular, with flattened flanks, rounded venter, and ventral

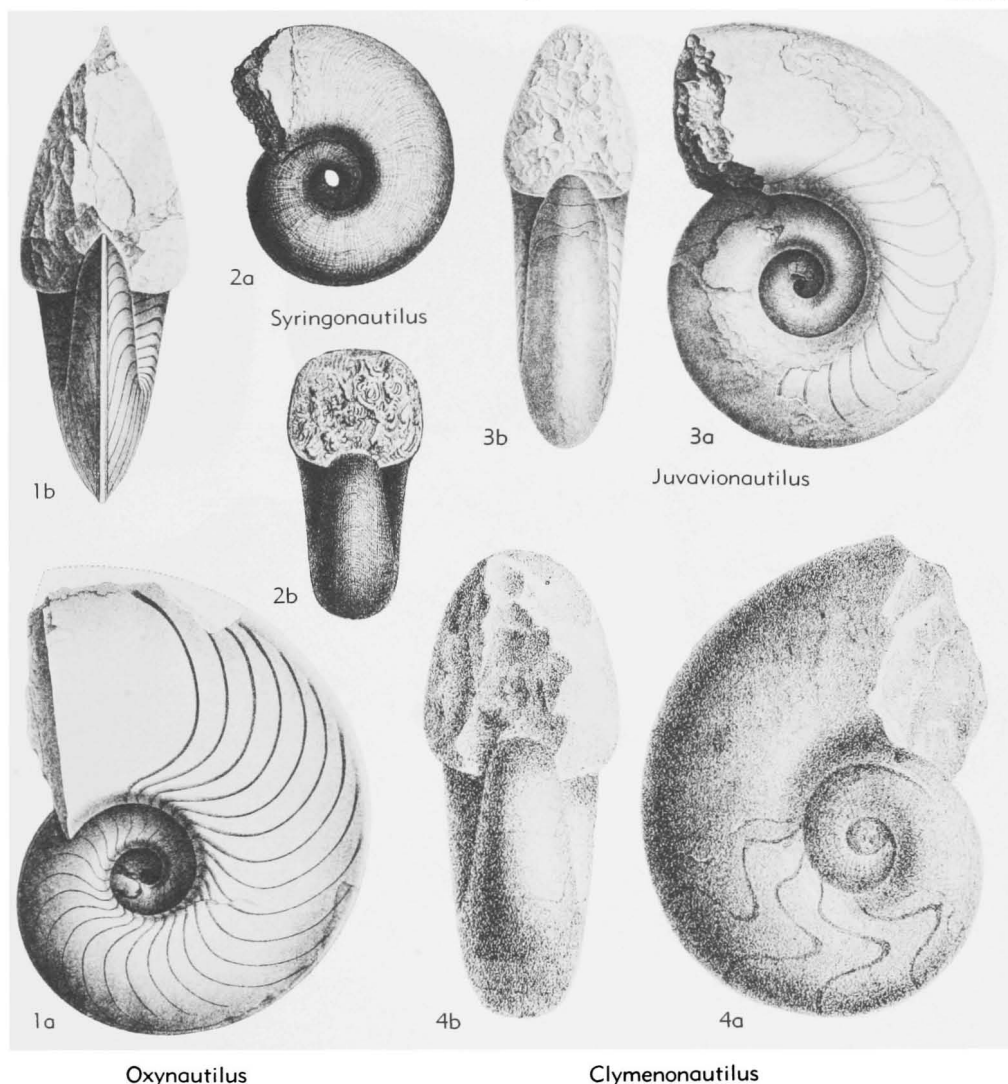


FIG. 316. Trigonocerataceae (Syringonautilidae) (p. K439-K440).

and umbilical shoulders rounded. Suture with deep, narrow, pointed ventral lobe, large, asymmetrical pointed lateral lobe, small lobe above umbilical seam and another inside seam, deep V-shaped dorsal lobe. Siphuncle subcentral, closer to venter than dorsum (126). [*Permoceras* is a homeomorph of *Pseudonautilus* of the Jurassic.] *L.Perm.*

**Permoceras** MILLER & COLLINSON, 1953 [*\*Nautilus* (*Aganides*) *bitauniensis* HANIEL, 1915; OD]. *L. Perm.*, E.Indies.—FIG. 315, 1a,b. *\*P. bitauniense* (HANIEL), Timor,  $\times 0.7$  (126). [Compare Figs.

315, 2a,b, and 332, 2, *Pseudonautilus geinitzi* (OPPEL), U.Jur.(Tithon.), Eu.;  $\times 0.7$  (126).]

#### Family SYRINGONAUTILIDAE Mojsisovics, 1902

[=Syringonautilinae SHIMANSKIY, 1962; Clymenonautilinae SHIMANSKIY, 1962]

Evolute conchs with rounded to sagittate whorl sections; siphuncle variable in position. Surface smooth except for growth lines and fine lirae in some forms. Suture generally only slightly sinuous (113). [This group is believed to be derived from the



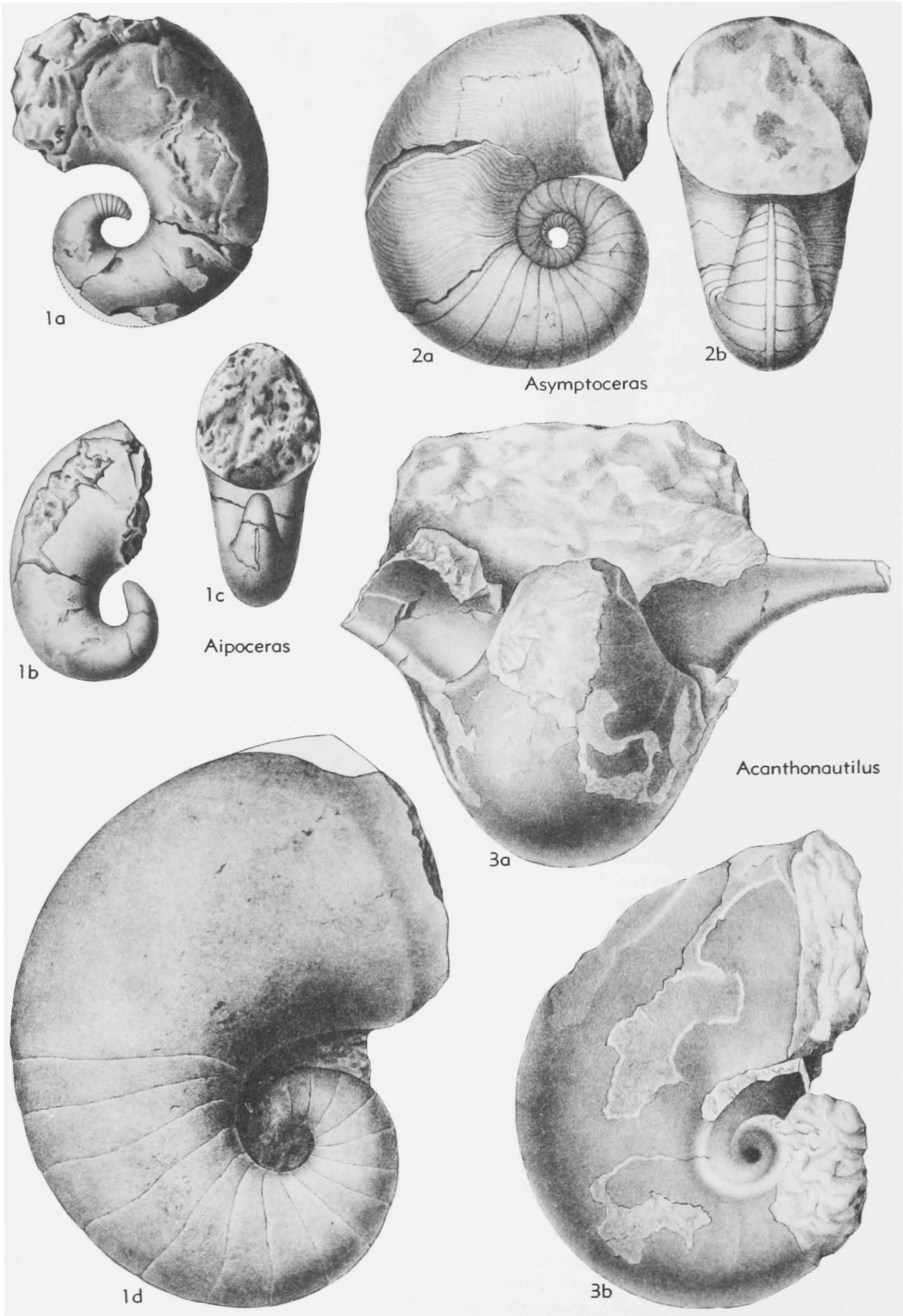


FIG. 317. Aipocerataceae (Aipoceratidae) (p. K440-K441); (Solenochilidae) (p. K441-K442).



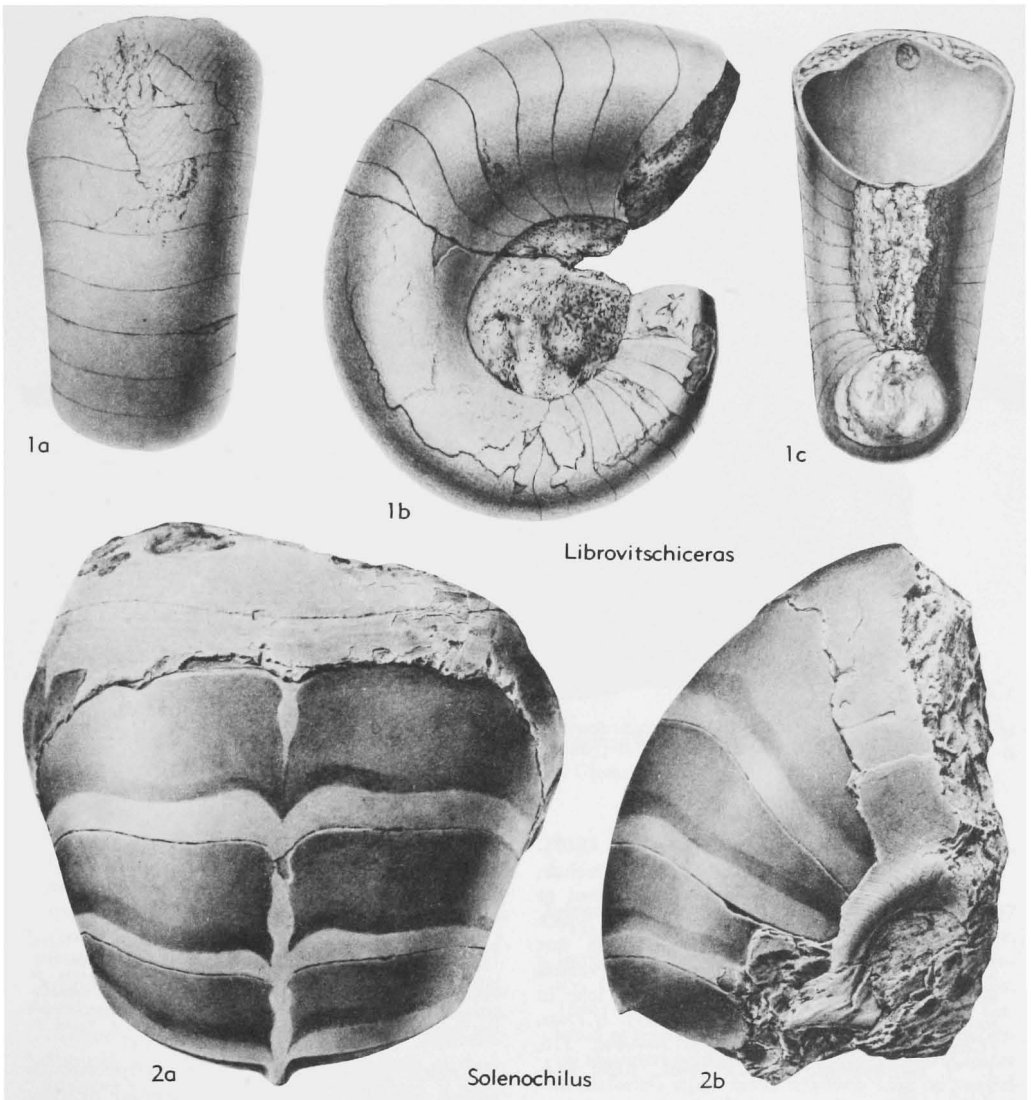


FIG. 318. Aipocerataceae (Aipoceratidae, Solenochilidae) (p. K441).

Gypoceratidae and ancestral to the Nautilidae.] *M.Trias.*(*Anis.*)-*U.Trias.*(*Nor.*).

**Syringonautilus** MOJSISOVICS, 1902 [*\*Nautilus lilianus* MOJSISOVICS, 1882; SD DIENER, 1915]. Evolute, rapidly expanding conch with perforate umbilicus; whorl section suboval, with well-rounded shoulders, and convex venter and lateral areas; conch bearing fine lirae; suture with faint ventral saddle, shallow lateral lobe, and annular lobe; siphuncle subcentral (113). *M.Trias.*(*Anis.*)-*U.Trias.*(*Nor.*), Eu.(Alps-Spitz.)-Asia (India-Japan).—FIG. 316.2. *\*S. lilianus* (MOJSISOVICS), *Anis.*, Alps; 2a,b,  $\times 0.8$  (140).

**Clymenonautilus** HYATT in ZITTEL, 1900 [*\*Nautilus ehrlichi* MOJSISOVICS, 1873; OD] [= *Clymenionautilus* DIENER, 1915 (*nom. null.*)]. Conch rapidly expanding, evolute, with perforate umbilicus; whorls higher than wide, enclosing third of preceding whorl; ventral and umbilical shoulders rounded, whorl sides flattened; surface of outer whorls smooth, inner whorls with fine lirae; suture straight over venter, with deep, tongue-shaped lateral lobe; position of siphuncle not known (113). *U.Trias.*(*Nor.*), Eu.—FIG. 316.4. *\*C. ehrlichi* (MOJSISOVICS), Alps; 4a,b,  $\times 1.0$  (139).

**Juvavionautilus** MOJSISOVICS, 1902 [*\*Nautilus het-*

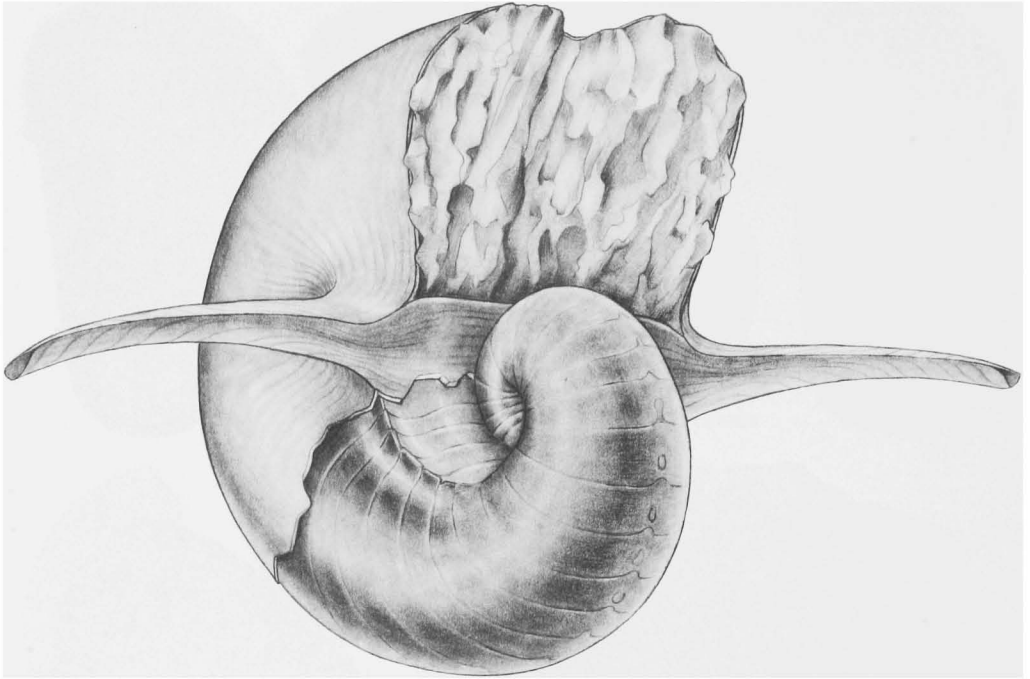


FIG. 319. *\*Solenochilus springeri* (WHITE & ST. JOHN) (Aipocerataceae-Solenochilidae) (p. K441).

*erophyllus* HAUER, 1849; SD DIENER, 1915]. Widely umbilicate, slowly expanding, evolute, perforate conch; whorl section with flattened to broadly rounded ventral area and flanks which converge toward venter; maximum width just above umbilical shoulder; suture with ventral saddle, broad lateral lobe; small ventral lobe in some forms; siphuncle subcentral (113). *U.Trias.* (*Carn.-Nor.*), Eu.-E.Indies (Timor).—FIG. 316, 3. *\*I. heterophyllus* (HAUER), *Nor.*, Alps; 3a,b,  $\times 0.4$  (139).

*Oxynautilus* MOJSISOVICS, 1902 [*\*Nautilus acutus* HAUER, 1846; OD]. Compressed, involute, lenticular conch having narrow to acute venter with or without keel; whorls expanding rapidly, much higher than wide; greatest width just above umbilical shoulder; suture with narrowly rounded to pointed ventral saddle, broad lateral lobe, small lobe on umbilical wall and small saddle on umbilical shoulder, and annular lobe; siphuncle subcentral (113). *U.Trias.* (*Nor.*), Eu. (Alps)-N.Am. (Calif.).—FIG. 316, 1. *\*O. acutus* (HAUER), Alps; 1a,b,  $\times 0.4$  (139).

*Syringoceras* HYATT, 1894 [*\*Ammonites? granulosostriatus* KLIPSTEIN, 1843; OD]. Like *Syringonautilus*, but with near-marginal siphuncle (113). *M. Trias.* (*Anis.*) - *U. Trias.* (*Nor.*), Eu. - E.Indies (Timor)-N.Am. (Nev.-Calif.).

### Superfamily AIPOCERATACEAE Hyatt, 1883

[*nom. transl.* SHIMANSKIY, 1962 (*ex Aipoceratidae* HYATT, 1883)] [= *Solenochelidae* HYATT, 1893; *Solenochilida* MILLER, DUNBAR, & CONDRA, 1933; *Solenochilida* FLOWER in FLOWER & KUMMEL, 1950 (order); *Solenochilaceae* SHIMANSKIY, 1957 (*ex Solenochelidae* HYATT, 1893)] [Materials for this superfamily prepared by W. M. FURNISH & BRIAN F. GLENISTER, State University of Iowa]

Conch rapidly expanding, cyrtconic to coiled, whorls rounded to flattened or possibly impressed dorsally; shell surface smooth to ribbed; modified mature aperture known in most forms; sutures nearly straight; siphuncle marginal and ventral; septal necks orthochoanitic on ventral surface and orthochoanitic to cyrtchoanitic on dorsal side. *L.Carb.* (*Miss.*)-*L.Perm.*

### Family AIPOCERATIDAE Hyatt, 1883

[= *Solenochelidae* HYATT, 1893 (*partim*); *Solenochilidae* MILLER, DUNBAR, & CONDRA, 1933 (*partim*)]

Loosely coiled or whorls faintly impressed; shell surface smooth; mature aperture modified. *L.Carb.* (*Miss.*)-*U.Carb.*

*Aipoceras* HYATT, 1884, p. 296 [*\*Gyroceras gibberosum* DEKONINCK, 1880, p. 6; OD]. Loosely

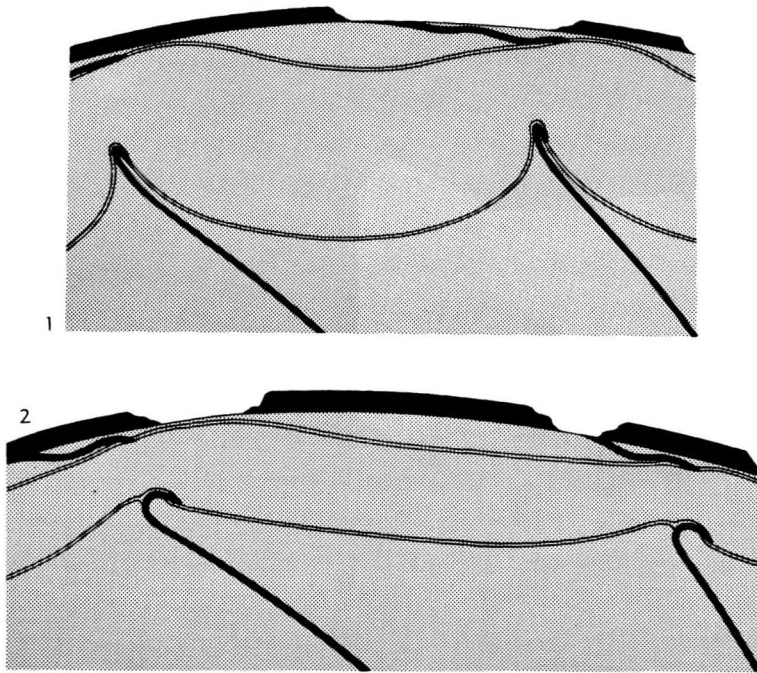


FIG. 320. Diagrammatic cross sections of siphuncles in Aipocerataceae (Solenochilidae).—1. *Solenochilus springeri* (WHITE & ST. JOHN) (White & St. John, 1868).—2. *Acanthonautilus collectus* (MEEK & WORTHEN) (Furnish & Glenister, n).

coiled, whorls laterally compressed. *L. Carb.* (Miss.), Eu.-N.Am.—FIG. 317, 1a-c. \**A. gibberosum* (DEKONINCK), *L. Carb.* (Tournais.), Belg.; two specimens,  $\times 0.5$  (224).—FIG. 317, 1d. *A. pinhookense* MILLER & FURNISH, *L. Miss.* (Kinderhook.), USA (Mo.); lat.,  $\times 0.4$  (129).

*Asymptoceras* RYCKHOLT, 1852, p. 6 [\**Nautilus cyclostomus* PHILLIPS, 1836, p. 232; OD] [= *Oncodoceras* HYATT, 1893]. Similar to *Aipoceras*, but tightly coiled and with only part of body chamber divergent from preceding whorl. *L. Carb.* (Miss.), Eu.-N.Am.—FIG. 317, 2. \**A. cyclostomum* (PHILLIPS), *L. Carb.* (Viséan), Belg.; 2a, b, lat., apert.,  $\times 0.7$  (deKoninck, 1878).

*Librovitschiceras* SHIMANSKIY, 1957, p. 109 [\**Nautilus atuberculatus* TSVETAeva, 1888, p. 13; OD]. Affinities uncertain; triangular-shaped whorls in contact; deep ventral sinus; siphuncle slightly removed from venter. *U. Carb.*, Eu.—FIG. 318, 1. \**L. atuberculatum* (TSVETAeva), *U. Carb.* (Westphal.), USSR (Moscow); 1a-c, vent., lat., septal,  $\times 1$  (237).

#### Family SOLENOCHILIDAE Hyatt, 1893

[*nom. correct.* MILLER, DUNBAR, & CONDR, 1933 (*pro Solenocheilidae* HYATT, 1893)]

Like Aipoceratidae, but all representatives with whorls in contact and with prominent umbilical spines at maturity. Connecting

rings conspicuously inflated in some forms. *L. Carb.* (*U. Miss.*)-*L. Perm.*

*Solenochilus* MEEK & WORTHEN, 1870, p. 47 [\**Nautilus (Cryptoceras) Springeri* WHITE & ST. JOHN, 1868, p. 124; OD] [= *Cryptoceras* D'ORBIGNY, 1850 (*non* LATREILLE, 1804, *nec* BARRANDE, 1846; *Solenochilus* HYATT, 1884)]. Whorls flattened or possibly slightly impressed; angular umbilical shoulders expanded into prominent lateral spines at maturity; septal necks relatively long on ventral surface and recumbent cyrtocochanitic on dorsal side; ectosiphuncular suture biconvex. *U. Carb.* (*L. Penn.*)-*L. Perm.*, cosmop.—FIGS. 319, 320, 1, 321. \**S. springeri* (WHITE & ST. JOHN); 319, M. Penn. (Bendian), USA (Ark.), oblique view, composite,  $\times 0.5$  (Furnish & Glenister, n); 320, 1, U. Penn. (Missourian), USA (Kans.), diagram. cross sec., siphuncle,  $\times 5$  (Furnish & Glenister, n); 321, U. Penn. (Missourian), USA (Iowa), outline,  $\times 0.5$  (after White & St. John, 1868).—FIG. 318, 2. *S. greenensis* STURGEON, M. Penn. (Desmoinesian), USA (Ohio); 2a, b, vent., lat.,  $\times 1$  (Sturgeon & Miller, 1948).

*Acanthonautilus* FOORD, 1896, p. 42 [\**A. bispinosus*; OD]. Like *Solenochilus*, but septal necks less strongly curved and siphuncle only slightly expanded. *L. Carb.* (*U. Miss.*), Eu.-N.Am.—FIG. 317, 3. \**A. bispinosus*, *L. Carb.* (Viséan), Ire;

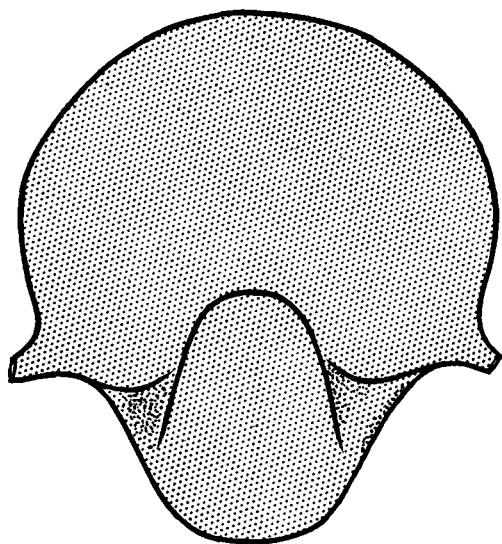


FIG. 321. \**Solenochilus springeri* (WHITE & ST. JOHN) (Aipocerataceae-Solenochilidae) (p. K441).

3a,b, apert., lat.,  $\times 0.5$  (80).—FIG. 320, 2. *A. collectus* (MEEK & WORTHEN), U.Miss. (Meramec.), USA (Ind.); diagram. cross sec., siphuncle,  $\times 5$  (Furnish & Glenister, n).

### Family SCYPHOCERATIDAE Ruzhentsev & Shimanskiy, 1954

[incl. *Dentoceratidae* RUZHENTSEV & SHIMANSKIY, 1954]

Cyrtconic or possibly loosely coiled in phragmocone; shell smooth or ribbed; connecting rings slightly expanded. *L.Perm.*

*Scyphoceras* RUZHENTSEV & SHIMANSKIY, 1954, p. 135 [\**S. dionysi*; OD]. Conch ribbed; phragmocone relatively small and sharply curved. *L.Perm.*, USSR (Urals).—FIG. 322, 2. \**S. ellipticum* RUZHENTSEV & SHIMANSKIY, *L.Perm.* (Artinsk.), S.Urals; 2a,b, vent., lat.,  $\times 1.3$  (153).

*Dentoceras* RUZHENTSEV & SHIMANSKIY, 1954, p. 141 [\**D. magnum*; OD] [= *Dentoceras* SHIMANSKIY, 1951, *nom. nud.*]. Affinities uncertain; conch conical, slightly curved; phragmocone proportionally small; siphuncle close to venter. *L.Perm.*, USSR (Urals).—FIG. 322, 3. *D. latum* RUZHENTSEV & SHIMANSKIY, *L.Perm.* (Artinsk.), S.Urals; 3a,b, lat., vent.,  $\times 0.7$  (153).

*Mariceras* RUZHENTSEV & SHIMANSKIY, 1954, p. 138 [\**M. ferum*; OD]. Like *Scyphoceras*, but less curved and smooth. *L.Perm.*, N.Am.-USSR.—FIG. 322, 1d,e. \**M. ferum*, *L.Perm.* (Artinsk.), USSR (S.Urals); vent., lat.,  $\times 1$  (153).—FIG. 322, 1a-c, *M. sp.*, *L.Perm.* (Leonard.), USA (Ariz.); lat., apert., vent.,  $\times 0.7$  (Furnish & Glenister, n).

*Venatoroceras* RUZHENTSEV & SHIMANSKIY, 1954, p. 139 [\**V. verae*; OD]. Like *Scyphoceras*, but

conch smooth and phragmocone relatively large; may be immature solenochilid. *L.Perm.*, USSR.—FIG. 322, 4. \**V. verae*, Artinsk., S.Urals; 4a,b, vent., lat.,  $\times 1$  (153).

## Superfamily CLYDONAUTILACEAE Hyatt in Zittel, 1900

[*nom. transl.* SHIMANSKIY, 1957 (ex *Clydonautilidae* HYATT in ZITTEL, 1900)] [= *Lirocerataceae* SHIMANSKIY, 1957; *Liroceratina* SHIMANSKIY, 1962]

Generally smooth, involute, globular to occluded conchs. Sutures nearly straight in early forms but one branch of later forms developing highly differentiated sutures (113). ?*U.Dev.*, *L.Carb.-Trias.*

### Family CLYDONAUTILIDAE Hyatt in Zittel, 1900

Involute, generally smooth, globular to compressed nautilids with very small or occluded umbilicus. Group characterized by differentiation of suture with prominent lobes and saddles (113). *M.Trias.-U.Trias.*

*Clydonautilus* MOJSISOVICS, 1882 [\**Nautilus noricus* MOJSISOVICS, 1873; OD]. Suture like that of *Proclydonautilus* but with small median saddle in ventral lobe (113). *U.Trias.* (Carn.-Nor.), Eu.-Asia (India)-E.Indies (Timor).—FIG. 323, 4. \**C. noricus* (MOJSISOVICS), Nor., Alps; 4a,b,  $\times 0.4$ ; 4c,  $\times 0.2$  (139).

*Callaionautilus* KIESLINGER, 1924 [\**C. turgidus*; OD]. Like *Proclydonautilus* in early volutions, with nodes on ventral shoulders that disappear adorally, later whorls becoming more oval in cross section and median keel appearing on venter where large nodes develop; shallow furrow aligns both sides of median nodose keel; suture like that of *Proclydonautilus*; position of siphuncle unknown (113). *U.Trias.*, E.Indies.—FIG. 323, 3. \**C. turgidus*, Timor; 3a,b,  $\times 0.4$ ; 3c,  $\times 1$  (99).

*Cosmonautilus* HYATT & SMITH, 1905 [\**C. dilleri*; OD]. Suture like that of *Proclydonautilus*; early whorls of conch bear nodes on ventral shoulders which disappear on later whorls; mature conch smooth, involute as in other members of family (113). *U.Trias.* (Carn.-Nor.), N.Am. (Calif.-Mex.)-Asia (India)-E.Indies (Timor).—FIG. 323, 2. \**C. dilleri*, Carn., USA (Calif.);  $\times 0.4$  (232).

*Proclydonautilus* MOJSISOVICS, 1902 [\**Nautilus griesbachi* MOJSISOVICS, 1896; SD HYATT & SMITH, 1905] [= *Procladonautilus* SHIMANSKIY & ERLANGER, 1955 (*nom. null.*)]. Suture consisting of broad, shallow to deep ventral lobe that divides large ventral saddle; large lateral lobe on flanks followed by smaller lateral saddle and second lateral lobe; annular lobe generally lacking (113). *U.Trias.* (Carn.-Nor.), N.Am.-Eu.-Asia (India)-E.

Indies (Timor)-N.Z.—FIG. 323, 1. \**P. griesbachi* (Mojsisovics), India; 1a, b,  $\times 0.5$ ; 1c,  $\times 0.7$  (142). *Styrionautilus* Mojsisovics, 1902 [\**Nautilus styria-*

*cus* Mojsisovics, 1873; OD]. Ventral saddle straight, lateral lobe deep, acutely rounded, lateral saddle larger and developed from the small um-

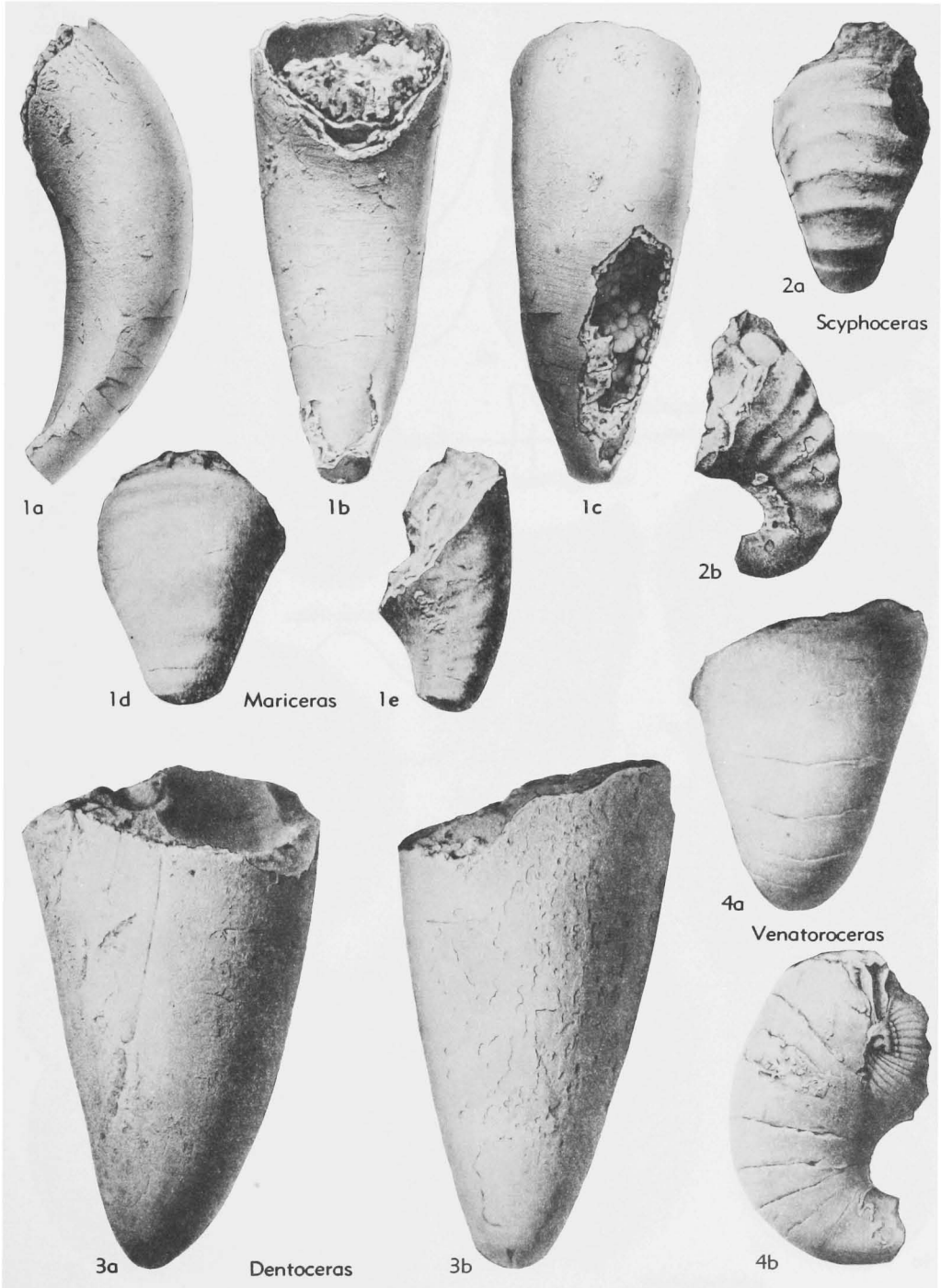


FIG. 322. Aipocerataceae (Scyphoceratidae) (p. K442).

bilical saddle of *Paranautilus*, no annular lobe; siphuncle subcentral (113). *M.Trias.(Anis.)-U.Trias.(Nor.)*, N.Am.(Nev.)-Eu.-E.Indies(Timor). —FIG. 323,5a,b. \**S. styriacus* (MOJSISOVICS), Carn., Alps;  $\times 1$  (139). —FIG. 323,5c. *S. discoidalis* (WELTER), U.Trias., Timor;  $\times 1.5$  (239).

**Family LIROCERATIDAE**  
**Miller & Youngquist, 1949**

[=Coloceratidae HYATT, 1893; incl. Paranautilidae KUMMEL, 1950]

Involute nautilicones, generally with occluded, smooth conchs; whorls usually de-

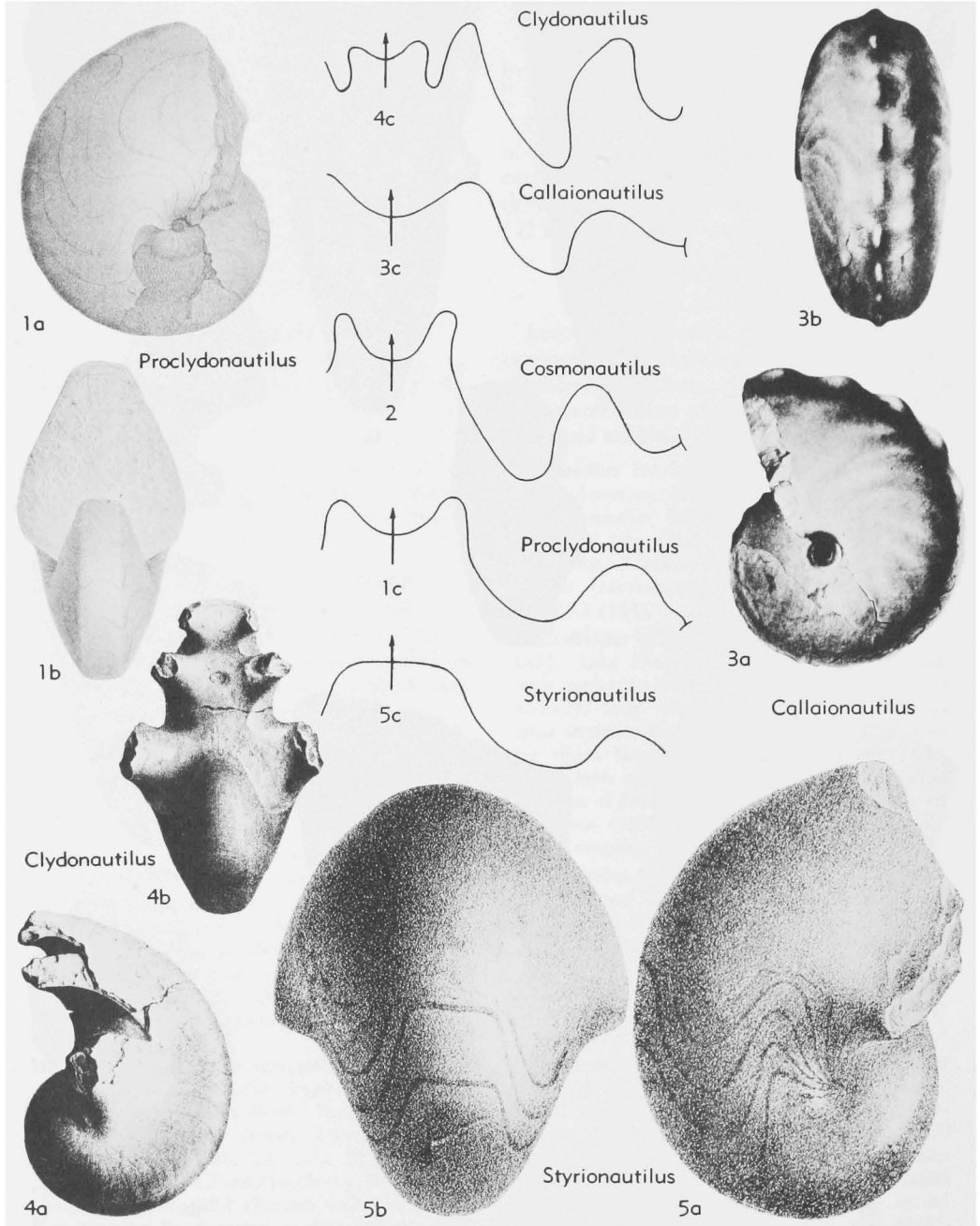


FIG. 323. Clydonautilaceae (Clydonautilidae) (p. K442-K444).



pressed, broadly rounded. Suture only slightly sinuous. Siphuncle usually more or less central (134). ?*U.Dev.*, *L.Carb.*(*Miss.*)-*Trias.*

*Liroceras* TEICHERT, 1940 [*\*Coloceras liratum* GIRTY, 1911; *\_OD*] [= *Coloceras* HYATT, 1893

(*non* NITZSCH, 1882)]. Nautiliconic, subglobose, rapidly expanding; whorl section reniform, broadly rounded ventrally, more narrowly rounded laterally, impressed dorsally; umbilicus small, at maturity; suture essentially straight; position of siphuncle variable, not marginal (134). *L.Carb.* (*Miss.*)-*Perm.*, N. Am.-Eu.-Asia(China)-E. Indies.

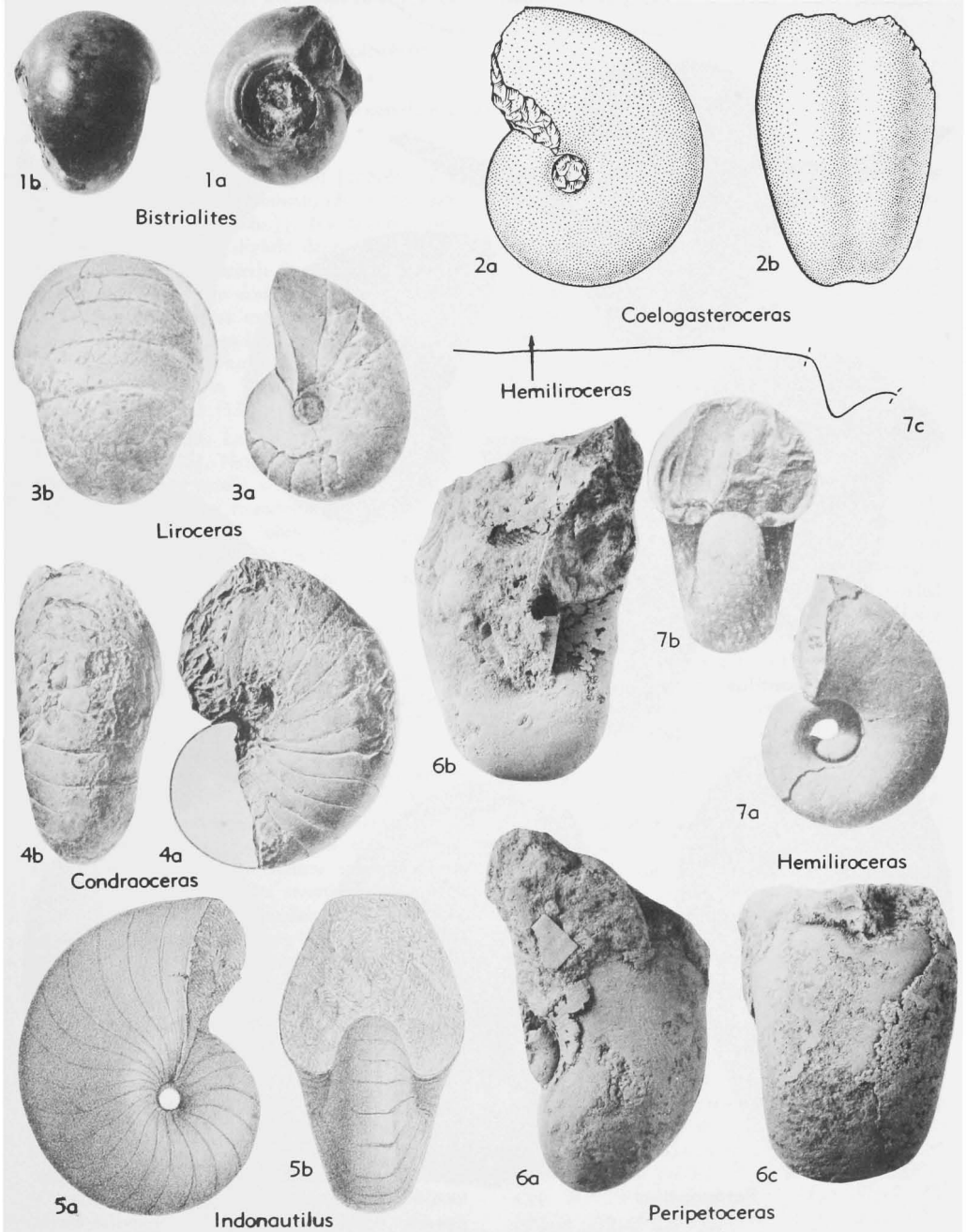


FIG. 324. Clydonautilaceae (Liroceratidae) (p. K445-K447).

—FIG. 324,3. \**L. liratum* (GIRTY), Penn., USA (Okl.); 3a,b,  $\times 1$  (134).

**Alexandronautilus** SHIMANSKIY, 1962 [\**Coloceras abichi* KRUGLOV]. [Considered by author to be a subgenus of *Permonautilus*.] *U. Perm.*, USSR (Caucasus).

**Bistrialites** TURNER, 1954 [\**Nautilus bistrialis* PHILLIPS, 1836; OD]. Involute, globose, whorl

section reniform, large funnel-shaped umbilicus; surface smooth except for spiral ornament in region of umbilical shoulder; suture simple, lacking annular lobe (199). *L. Carb.*, Eu.—FIG. 324, 1. \**B. bistrialis* (PHILLIPS), Eng.; 1a,b,  $\times 1.5$  (199).

**Coelogasteroceras** HYATT, 1893 [\**C. coxi* GORDON, 1960 (*nom. subst. pro Nautilus canaliculatus* Cox,

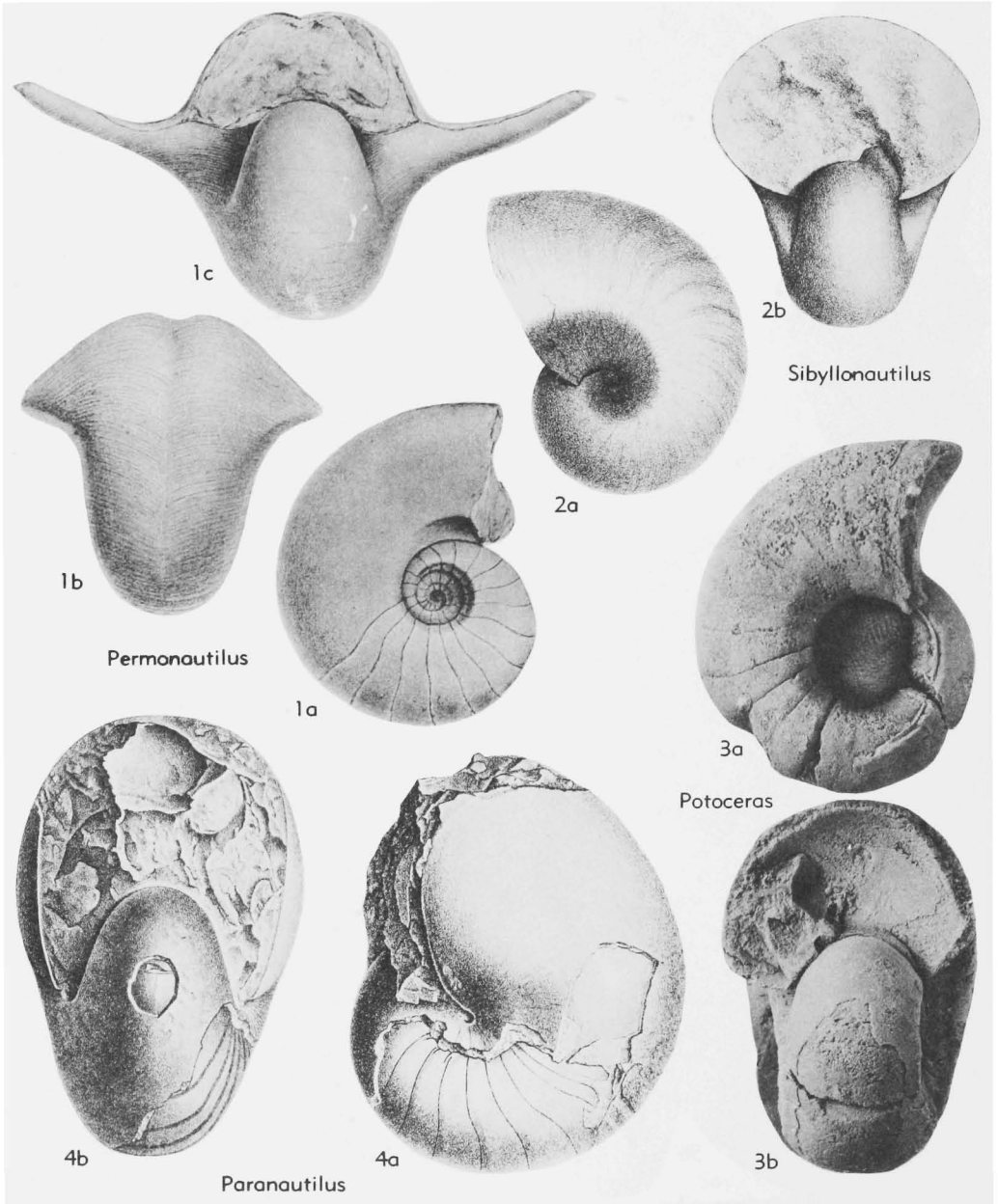


FIG. 325. Clydonautilaceae (Liroceratidae) (p. K447).



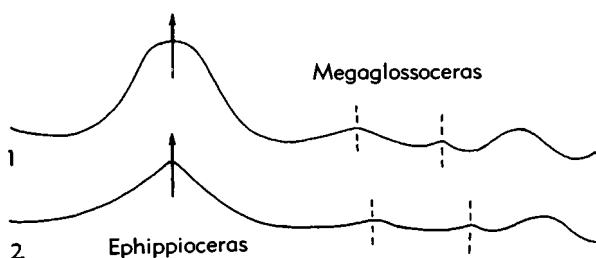


FIG. 326. Clydonautilaceae (Ephippioceratinae) (p. K448).

1858, *non* EICHWALD, 1857); OD] [= *Solenoceras* HYATT, 1884 (obj.) (*non* CONRAD, 1860); *Conradi-ceras* COSSMANN, 1900 (obj.)]. Nautilonic, subglobular; whorl section slightly depressed, laterally flattened, ventrally grooved; flanks convergent toward venter, maximum width just outside umbilical shoulder; umbilicus moderately small; suture with shallow ventral and lateral lobes; siphuncle subcentral (134). *Penn.-Perm.*, N.Am.—FIG. 324,2. *C. mexicanum* (GIRTY), L.Perm., USA (Wyo.); 2*a,b*,  $\times 0.7$  (134).

**Condraoceras** MILLER, LANE, & UNKLESBAY, 1947 [*\*C. primum*; OD]. Nautilonic, involute, compressed, umbilicus small; whorl section subcircular, umbilical shoulder rounded; suture with shallow ventral and lateral lobes; siphuncle small, subcentral (132). *Penn.* (N.Am.)-L.Perm. (Eu.). —FIG. 324,4. *\*C. primum*, Penn., USA (Kans.); 4*a,b*,  $\times 0.5$  (132).

**Hemiliroceras** RUZHENTSEV & SHIMANSKIY, 1954 [*\*H. inflatum*; OD]. Like *Liroceras*, but evolute, with wide deep, perforate umbilicus and deep funnel-shaped dorsal lobe (153). L.Perm. (*Artinsk.*), Eu.(USSR).—FIG. 324,7. *\*H. inflatum*; 7*a,b*,  $\times 1$ ; 7*c*,  $\times 1.5$  (153).

**Indonautilus** MOJSISOVICS, 1902 [*\*Nautilus krafftii* MOJSISOVICS, 1902 (= *N. sp. indet.* ex *N. aff. mesodici* MOJSISOVICS, 1896); OD]. Compressed, involute nautilicone with small or occluded umbilicus; whorl section subrectangular, with slightly convex flanks converging ventrally, venter flattened, ventral shoulders rounded to subangular, umbilical shoulders broadly rounded; suture essentially straight over venter, broad shallow lateral lobe, no annular lobe; siphuncle subdorsal (113). *M.Trias.* (*Anis.*)-*U.Trias.* (*Nor.*), N. Afr. (Egypt)-Asia (Himalayas-Israel)-E. Indies.—FIG. 324,5. *\*I. krafftii* (MOJSISOVICS), Nor., Himalayas; 5*a,b*,  $\times 0.8$  (142).

**Paranautilus** MOJSISOVICS, 1902 [*\*Nautilus simonyi* HAUER, 1849; OD]. Very involute to occluded smooth conch, as in *Liroceras*, but tending to be more compressed (113). *M.Trias.* (*Anis.*)-*U.Trias.* (*Nor.*), N.Am.-Eu. (Alps-Yugo.)-Asia (Pak.-Himalayas)-E. Indies.—FIG. 325,4. *\*P. simonyi* (HAUER), Nor., Alps; 4*a,b*,  $\times 0.7$  (139).

**Peripetoceras** HYATT, 1894 [*\*Nautilus freieslebeni* GEINITZ, 1843; OD] [= *Cyclonautilus* HIND, 1911; *Periptoceras* CHAO, 1954 (*nom. null.*); *Nannoceras* HYATT, 1894 (*nom. null.*)]. Smooth, involute conch with deep small umbilicus; whorl section with flattened venter, rounded ventral shoulders, convergent slightly convex flanks, rounded umbilical shoulder, steep convex umbilical wall; suture with slight ventral and lateral lobes; siphuncle small, dorsal of center. L.Carb. (*U. Miss.*)-Perm., Eu. (Eng.-Ger.-USSR)-Asia (China). —FIG. 324,6. *\*P. freieslebeni* (GEINITZ), Perm., Eng.; 6*a-c*,  $\times 1.4$  (Kummel, n).

**Permonautilus** KRUGLOV, 1933 [*\*Nautilus cornutus* GOLOVINSKY, 1868; OD]. Involute, globular, with deep umbilicus; whorl section depressed, venter broadly rounded with median sulcus on most adoral whorl; umbilical shoulders subangular, adoral portion of umbilical shoulder extended laterally to form long spinelike processes; suture only slightly sinuous; siphuncle subcentral (134). [Genus may be synonym of *Acanthonautilus* FOORD but the position of the siphuncle in that genus is not known.] *U.Perm.*, USSR.—FIG. 325,1. *\*P. cornutus* (GOLOVINSKY); 1*a,b*,  $\times 0.7$ ; 1*c*,  $\times 0.4$  (134).

**Potoceras** HYATT, 1894 [*\*P. dubium*; OD]. Involute, smooth conch, with deep umbilicus; whorl section suboval, with broadly arched venter and broadly rounded ventral shoulders which grade imperceptibly onto convex lateral areas; umbilical shoulders more sharply rounded, umbilical wall steep; suture straight except for slight lateral lobe, and broad, low, V-shaped dorsal lobe and minute annular lobe. ?*U.Dev.*, Eu. (Ger.); ?*L. Carb.*, Eu. (Belg.). —FIG. 325,3. *\*P. dubium*; 3*a,b*,  $\times 1.4$  (Kummel, n).

**Sibyllonautilus** DIENER, 1915 [*\*Nautilus sibyllae* MOJSISOVICS, 1886; OD] [= *Tumidonautilus* DIENER, 1915]. Tightly involute, globular, like average *Paranautilus*, characterized by extraordinary expansion of adoral part of conch; suture essentially straight; position of siphuncle not known (113). *M.Trias.* (*Anis.*)-*U.Trias.* (*Nor.*), N.Am. (Nev.-B.C.)-Eu. (Alps-Spitz.). —FIG. 325,2. *\*S. sibyllae* (MOJSISOVICS), Anis., Spitz.; 2*a,b*,  $\times 0.7$  (141).

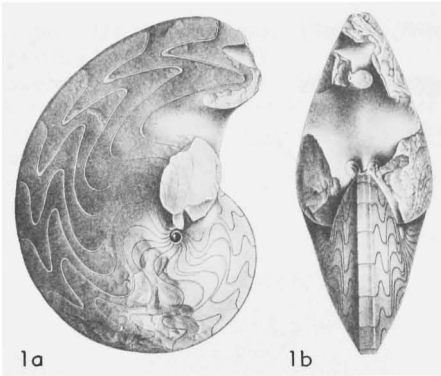


FIG. 327. \**Gonionutilus securis* (VON DITTMAR)  
(Gonionautilidae) (p.K448).

### Family EPHIPPIOCERATIDAE Miller & Youngquist, 1949

[=Ephippioceratidae SCHMIDT, 1951 (jr. syn. homonym);  
Ephippioceratidae SHIMANSKIY, 1956 (jr. syn. homonym)]

Conch as in typical representatives of *Liroceratidae* but suture forming deep ventral and dorsal saddles (134). *L.Carb.(Miss.)-L.Perm.*

*Ephippioceras* HYATT, 1884 [\**Nautilus ferratus* Cox, 1858; OD]. Nautiliconic, subglobose, smooth or slightly costate, rapidly expanding adorally; whorl sections reniform, broadly rounded ventrally and laterally, impressed dorsally; umbilicus closed at maturity; suture with V-shaped, narrowly rounded ventral saddle, broadly rounded lateral lobe; siphuncle small, subcentral (128). *L.Carb.(Miss.)-L.Perm.*, N. Am.-Eu.-Asia(China). —FIG. 326,2. \**E. ferratum* (Cox), Penn., USA (Mo.);  $\times 0.7$  (133). [= *Arthuroceras* SHIMANSKIY, 1962.]

*Megaglossoceras* MILLER, DUNBAR & CONDR, 1933 [\**Nautilus montgomeryensis* WORTHEN, 1884; OD]. Like *Ephippioceras* except that ventral saddle is broad, tongue-shaped (128). *Penn.*, N. Am. (Kans.-Neb.-Colo.-Mo.). —FIG. 326,1. *M. pristinum* MILLER & OWEN, USA (Mo.);  $\times 0.7$  (133).

### Family GONIONAUTILIDAE Kummel in Flower & Kummel, 1950

Involute, smooth, compressed conch, angular ventral shoulders, flattened venter. Suture like that of *Clydonautilus* but with more highly developed median saddle and double-pointed annular lobe (113). *U.Trias.*

*Gonionautilus* MOJSISOVICS, 1902 [\**Nautilus securis* VON DITTMAR, 1866; OD]. Characters of family. *U.Trias.(Nor.)*, Eu.(Alps)-N. Am.(Nev.). —FIG. 327,1. \**G. securis* (VON DITTMAR), Alps; 1a,b,  $\times 0.4$  (139).

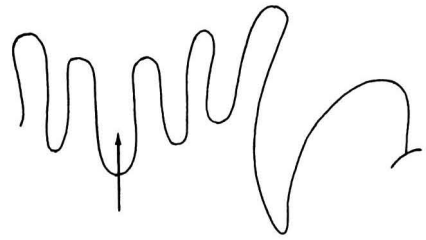


FIG. 328. \**Siberionautilus multilobatus* POPOV  
(Siberionautilidae) (p. K448).

### Family SIBERIONAUTILIDAE Popov, 1951

Involute, globular, flanks flattened, converging toward venter which is rounded; umbilical shoulders distinct. Surface marked by fine radial ribs. Suture highly differentiated, goniatitic in character. Siphuncle central (145). *U.Trias.*

*Siberionautilus* POPOV, 1951 [\**S. multilobatus*; OD]. Characters of family. *U.Trias.(Carn.)*, USSR(Sib.). —FIG. 328. \**S. multilobatus*;  $\times 0.5$  (145).

### Superfamily NAUTILACEAE de Blainville, 1825

[*nom. transl.* SHIMANSKIY, 1957 (ex family Nautilacea DE BLAINVILLE, 1825)] [incl. Digonicoceratida HYATT in ZITTEL, 1900 (div. of suborder)]

Involute, generally smooth, with sinuous plications or ribs in some groups; whorl section compressed to depressed. Sutures straight to strongly sinuous. Siphuncle central or dorsal (49). *U.Trias.-Rec.*

### Family NAUTILIDAE de Blainville, 1825

[*nom. correct.* BRODERIP, 1839 (pro family Nautilacea DE BLAINVILLE, 1825)] [= Nautilacées LAMARCK, 1809 (vernacular)] [incl. Eutrophoceratidae, MILLER, 1951]

Involute or slightly evolute, generally smooth, with compressed to depressed whorl sections. Sutures straight to sinuous (115). *U.Trias.-Rec.*

*Nautilus* LINNÉ, 1758 [\**N. pompilius*; SD DEMONTFORT, 1808]. Smooth, nautiliconic, involute to occluded; suture consisting of broad rounded ventral saddle, broad lateral lobe, small saddle in vicinity of umbilical shoulder, shallow lobe on umbilical wall, small saddle near umbilical seam, broad shallow dorsal lobe and annular lobe; siphuncle subcentral (124). *Oligo.-Rec.*, SW.Pac.-E.Indies-Australia-Eu.(USSR). —FIG. 329,1; 330,1. \**N. pompilius*, Rec., SW.Pac.; 329,1a,b, apert. and lat. views of artificial internal mold prepared by dissolving paraffin-filled shell in hydrochloric acid,  $\times 0.7$  (A. K. Miller); 330,1a-c,  $\times 0.5$  (124).

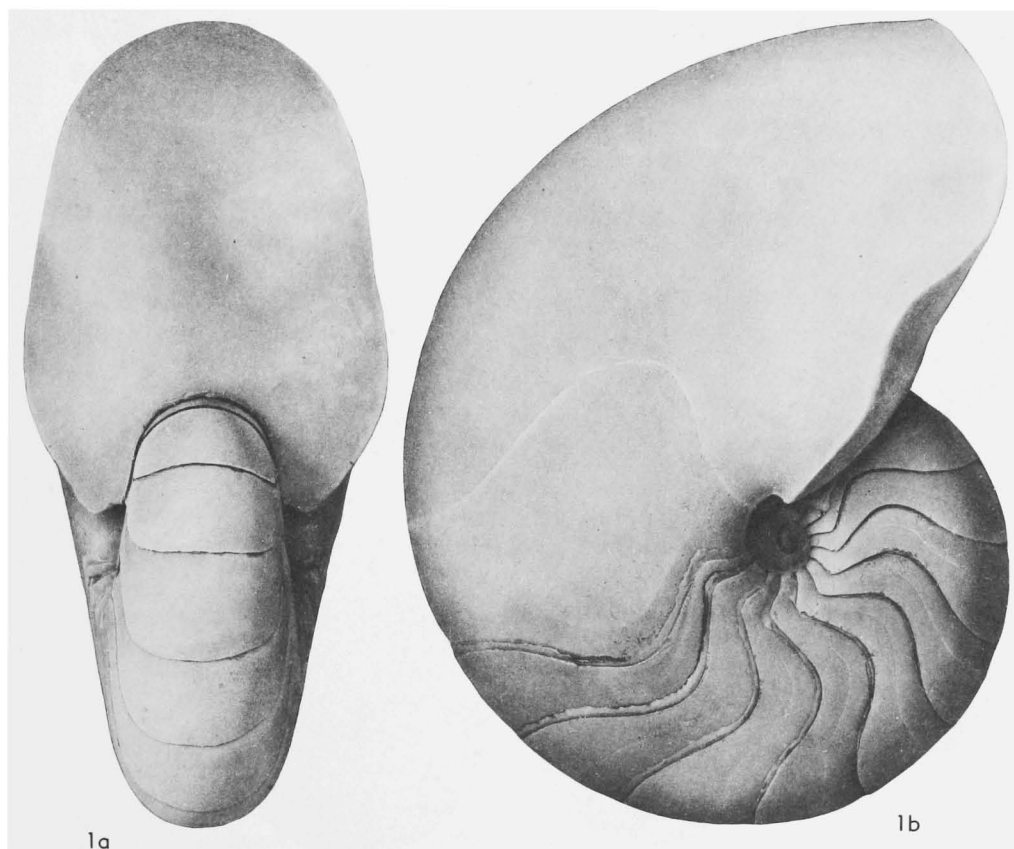
**Carinonautilus** SPENGLER, 1910 [*\*C. ariyalurensis*; OD]. Nautiliconic, very involute, compressed; whorl section higher than wide; umbilicus small and shallow; flanks broadly convex, converging toward venter, ventral shoulders aligned by distinct furrow; venter with prominent rounded keel that is broader on adoral part of living chamber and divided by median furrow; umbilical shoulders broadly rounded; suture only slightly convex; surface smooth except for growth lines; position of siphuncle unknown (115). *U.Cret.*, Asia (India).—FIG. 330,4. *\*C. ariyalurensis*; 4a-c,  $\times 0.4$  (115).

**Cenoceras** HYATT, 1884 [*\*Nautilus intermedius* SOWERBY, 1816 (non D'ORBIGNY, 1843; OD) [= *Digonioceras* HYATT, 1894; *Nautilites* ZIETEN, 1830 (non PALLAS, 1771); *Ophionautilus*, *Sphaeronautilus* SPATH, 1927]. Evolute to involute, compressed lenticular to globose, depressed venter and flanks rounded to flattened; test generally bearing fine longitudinal lines and growth lines; suture generally with shallow ventral and lateral lobes;

position of siphuncle variable but never at extreme dorsal or ventral position (115). *U.Trias.-M.Jur.*, cosmop.—FIG. 331,1. *\*C. intermedius* (SOWERBY), L.Jur., Eu.; 1a,b,  $\times 0.5$  (115).

**Eutrephoceras** HYATT, 1894 [*\*Nautilus Dekayi* MORTON, 1834; OD]. Nautiliconic, generally subglobular; whorl section reniform, broadly rounded ventrally and laterally; aperture marked ventrally by broad shallow rounded hyponomic sinus; umbilicus small to occluded; surface smooth; suture only slightly sinuous; annular lobe may be present; siphuncle small, variable in position (115). *U.Jur.-Mio.*, cosmop.—FIG. 330,2a,b. *E. laverdei* DURHAM, L.Cret., S.Am.(Colom.);  $\times 0.3$  (226).—FIG. 330,2c. *E. aff. \*E. dekayi* (MORTON), U.Cret., USA(S.Dak.);  $\times 1$  (226).

**Obinautilus** KOBAYASHI, 1954 [*\*O. pulchra*; OD]. Discoidal, very involute, umbilicus almost closed, whorls rapidly expanding, compressed, parallel, slightly convex; venter rounded, with broad, shallow furrow having subangular margins; ventral shoulders broadly rounded merging with flanks;



Nautilus

FIG. 329. *\*Nautilus pompilius* LINNÉ (Nautilidae) (p. K448).

test bearing radial ribs (or bunched growth lines) separated by narrow, shallow grooves; suture and position of siphuncle not known (111). *Oligo.*, Japan.—FIG. 330,3. \**O. pulcher*; 3a,b,  $\times 0.4$  (111).

**Pseudocnoceras** SPATH, 1927 [*\*Nautilus largilliertianus* D'ORBIGNY, 1840; OD]. Nautilonic, compressed, smooth; whorl section subrectangular, venter broad, flattened, ventral shoulders

rounded; flanks flattened, subparallel; umbilical shoulders rounded, umbilical wall nearly vertical; suture essentially straight across venter, with broad, shallow lateral lobe; siphuncle subcentral (115). *Cret.*, Eu. (Crimea) - N. Afr. (Libya).—FIG. 330,6. \**P. largilliertianum* (D'ORBIGNY), Eu.; 6a,b,  $\times 0.7$  (115).

**Strionautilus** SHIMANSKIY, 1951 [*\*Nautilus pondi-cherriensis* BLANFORD, 1866; OD]. Involute, com-

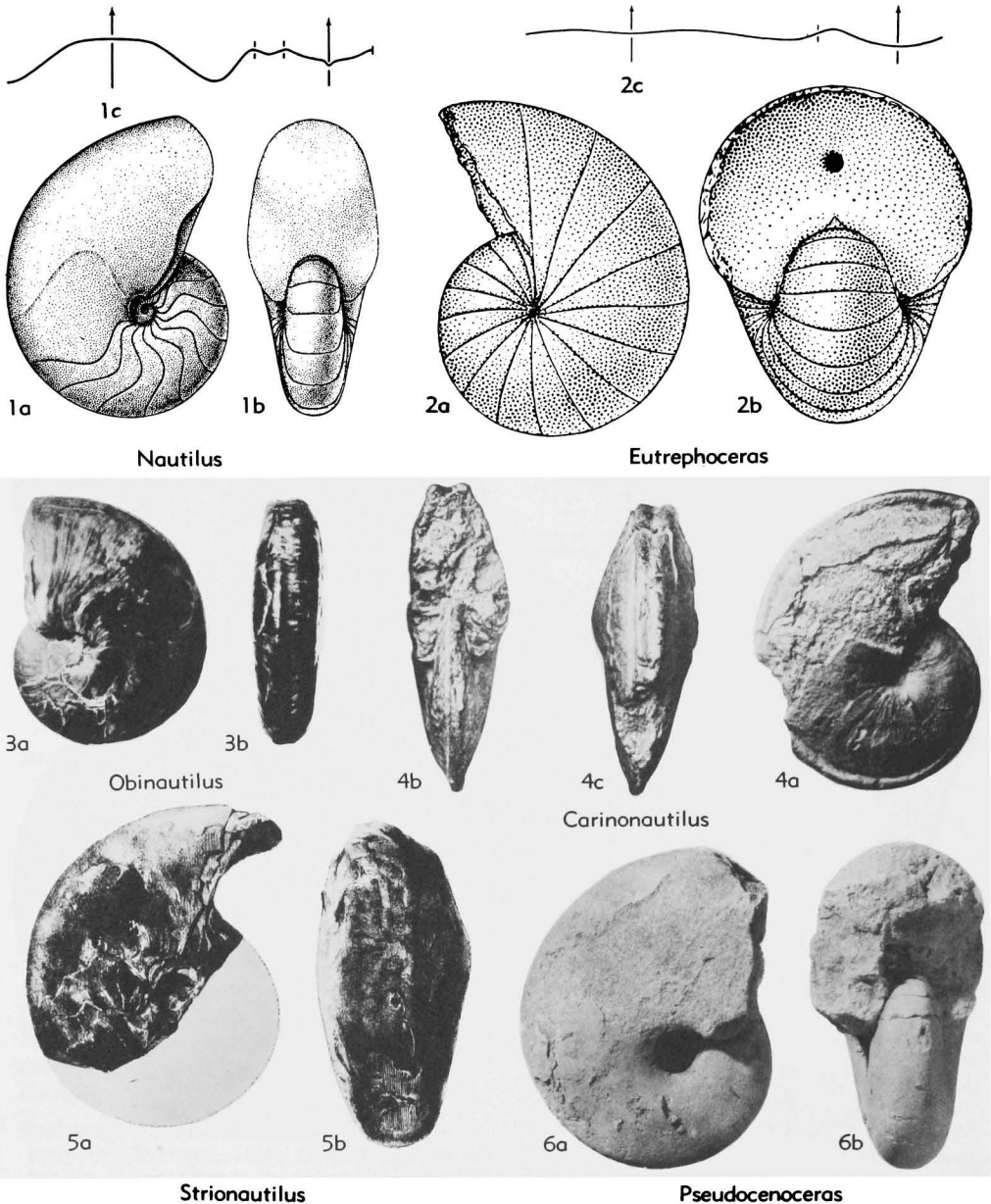


FIG. 330. Nautilaceae (Nautilidae) (p. K448-K451).

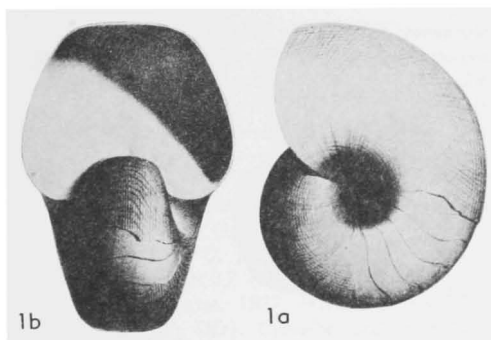


FIG. 331. *Cenoceras intermedius* (SOWERBY)  
(Nautilidae) (p. K449).

pressed nautilicone; whorl section subrectangular, with flattened venter and whorl sides; ventral and umbilical shoulders subangular; umbilicus small but deep; suture poorly known but appears to have ventral and lateral lobes; siphuncle subcentral; surface with fine longitudinal lirae (217). *L.Cret.*, Eu.(USSR)-Asia(India). — FIG. 330,5. \**S. pondicherriensis* (BLANFORD), India; 5a,b,  $\times 0.4$  (217).

### Family PSEUDONAUTILIDAE Shimanskiy & Erlanger, 1955

[=Pseudaganidinae KUMMEL, 1956]

Involute nautilicones, generally compressed, characterized by highly sinuous “goniatitic” suture; siphuncle generally between center and venter (115). *Jur.-L.Cret.*

**Pseudonautilus** MEEK, 1876 [*\*Nautilus geinitzi* OPPEL in ZITTEL, 1868; OD]. Nautiliconic, involute, compressed; whorl section higher than wide, flanks flattened; venter low and broadly arched; umbilicus small and deep; suture with deep narrow ventral lobe, large V-shaped lateral lobe, followed by rounded saddle with small second lateral lobe just above umbilical seam, dorsal lobe deep and pointed; siphuncle subventral (115). [This genus is an almost perfect homeomorph of the Permian *Permoceras* MILLER & COLLINSON.] *U.Jur.-L.Cret.*, Eu.-N.Afr.(Tunisia). — FIG. 315,2a,b; 332,2. \**P. geinitzi* (OPPEL), *U.Jur.*(Tithon.), Eu.; 315,2a,b,  $\times 0.7$ ; 332,2a,b,  $\times 0.4$  (228).

**Pseudaganides** SPATH, 1927 [*\*Nautilus kutchensis* WAAGEN, 1873; OD] [= *Hercoglossoceras* SPATH, 1927; *Paracymatoceras* (Palelialia) SHIMANSKIY, 1955, non *Paracymatoceras* SPATH, 1927]. Nautiliconic, umbilicus very small; whorl section generally subrectangular to compressed, with flattened converging flanks; venter flattened to rounded; suture with ventral lobe and broad deep lateral lobe; siphuncle central to subcentral (115). *Jur.*, Eu.-Asia(Pak.). — FIG. 332,1. \**P. kutchensis* (WAAGEN), *U.Jur.*, Pak.; 1a,b,  $\times 0.7$  (238).

**Xenocheilus** SHIMANSKIY & ERLANGER, 1955 [*\*Nautilus ulixis*; OD]. Like *Pseudonautilus* but ventral shoulders subangular; ventral and lateral lobes rounded rather than acute (164). *U.Jur.-L.Cret.*, Eu.(Fr.-Crimea)-N.Afr.(Algeria).

### Family PARACENOCERATIDAE Spath, 1927

Generally involute, characterized by differentiation of venter, generally associated with increase of sinuosity of suture line and presence of ventral lobe. [Family believed to be derived from various parts of the Lower Jurassic *Cenoceras* complex. *Paracenoceras* has most species and widest distribution, other genera being known by few species. Family largely confined to eastern hemisphere (115).] *M.Jur.-L.Cret.*(Alb.).

**Paracenoceras** SPATH, 1927 [*\*Nautilus hexagonus* SOWERBY, 1826; OD]. Robust, involute, smooth; whorl section subtrapezoidal; flanks flattened, convergent toward broad venter that may be flattened, truncate or sulcate; ventral shoulders rounded; umbilicus small, umbilical shoulders rounded, umbilical walls steep; suture with slightly sinuous ventral and lateral lobes, plus small saddle at umbilical shoulders and wall; position

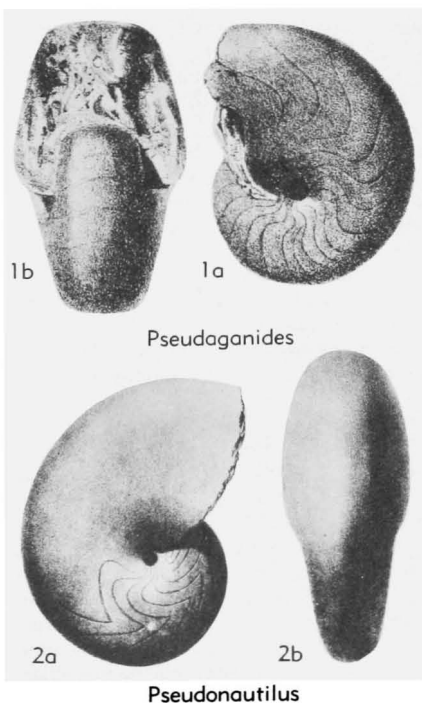


FIG. 332. Nautilaceae (Pseudonautilidae) (p. K451).

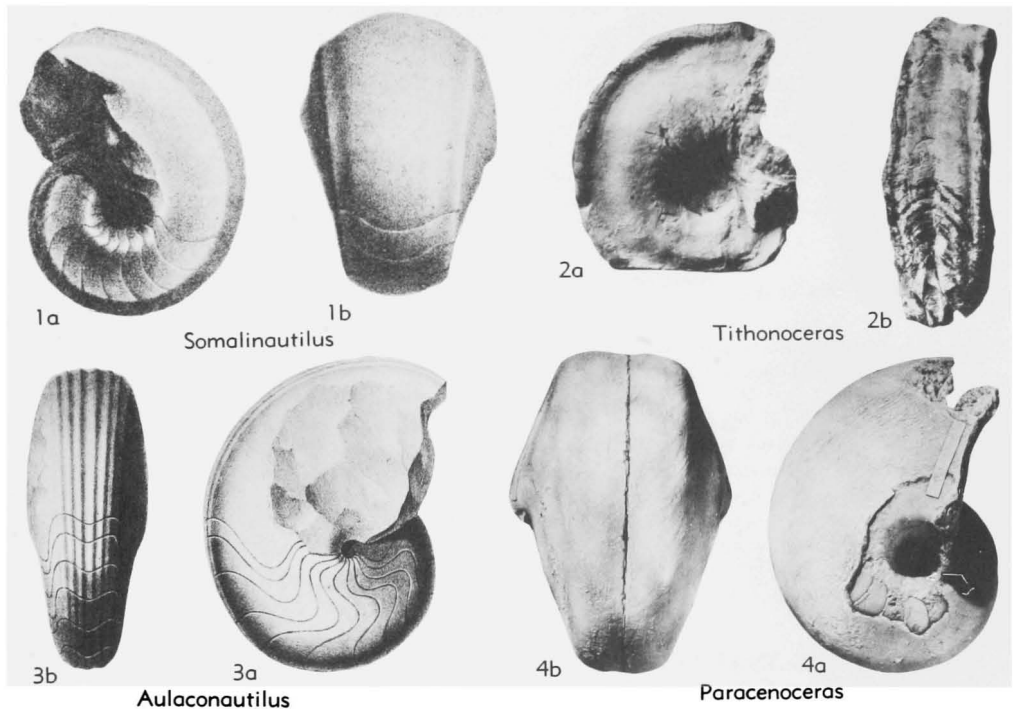


FIG. 333. Nautilaceae (Paracenoceratidae) (p. K451-K452).

of siphuncle variable, siphuncle beaded with short funnels (115). *M.Jur.-L.Cret.(Alb.)*, Eu.-E.Afr.-N. Afr.-Asia (Pak.)-W.Indies (Cuba).—FIG. 333, 4. \**P. hexagonum* (SOWERBY), U.Jur., Eu.; 4a,b,  $\times 0.4$  (115).

**Aulaconautilus** SPATH, 1927 [*\*Nautilus sexcarinatus* PICTET, 1867; OD]. Nautilonic, involute, generally compressed; flanks smooth, convex, and converging ventrally; ventral shoulders rounded, venter broad, low, with longitudinal ribs; umbilicus very small, umbilical shoulders rounded; suture sinuous, with shallow ventral lobe, broad deep lateral lobe, and saddle at umbilical shoulders; position of siphuncle unknown (115). *U. Jur.*, Eu.—FIG. 333,3. \**A. sexcarinatus* (PICTET), 3a,b,  $\times 0.5$  (115).

**Somalinautilus** SPATH, 1927 [*\*Nautilus antiquus* DACQUÉ, 1910; OD (= *N. bisulcatus* DACQUÉ, 1905, non DE KONINCK, 1878)] [= *Somaliceras* SPATH, 1927 (*nom. null.*)]. Involute, depressed, rapidly expanding, whorls wider than high; venter slightly arched, ventral shoulders subangular, adjoined on venter by distinct furrow; flanks concave adjacent to ventral shoulder, convex toward umbilicus; umbilical shoulders sharply rounded, umbilical wall steep; surface with sinuous growth lines and in places longitudinal striae; suture with shallow ventral lobe, generally angular saddle at ventral shoulder, broad shallow, lat-

eral lobe, low saddle on umbilical wall; siphuncle subcentral (115). *M.Jur.-U. Jur.*, Eu. (Eng.-Fr.)-Afr. (Somali.). — FIG. 333,1. \**S. antiquus* (DACQUÉ), U.Jur. (Kimm.), Somali; 1a,b,  $\times 0.7$  (115).

**Tithonoceras** RETOWSKI, 1894 [*\*T. zitteli*; OD]. Evolute, compressed, smooth; whorl section subrectangular, higher than wide; venter broad, flattened, with shallow median furrow; ventral shoulders inflated, forming smooth keel-like ridge which is aligned on venter and flanks by furrows that on flanks are broadly concave, occupying nearly half of flanks; umbilical shoulder broadly rounded; suture sinuous, with ventral and lateral lobes; position of siphuncle unknown (115). *U. Jur. (Tithon.)*, Eu. (Crimea).—FIG. 333,2. \**T. zitteli*; 2a,b,  $\times 0.3$  (230).

### Family CYMATOCERATIDAE Spath, 1927

[= *Heminautilinae* SHIMANSKIY, 1962]

Involute nautilicones bearing ribs; conch shape highly variable, suture only so to limited extent. Members of this family are most common Cretaceous nautiloids. [Origin of family uncertain, possibly stemming from Lower Jurassic *Cenoceras* complex (115).] *M.Jur.-Oligo.*

**Cymatoceras** HYATT, 1884 [*\*Nautilus pseudoelegans* D'ORBIGNY, 1840; OD] [= *Neocymatoceras* KOBAYASHI, 1954]. Involute, generally subglobular with rounded whorl section but this feature variable; degree of involution varying from occluded to slightly evolute conchs; suture only slightly sinuous; position of siphuncle variable; surface with conspicuous ribs that cover whorl sides and venter (115). *U. Jur.-Oligo.*, cosmop. —FIG. 334,4. *\*C. pseudoelegans* (D'ORBIGNY), Cret., Eu.; 4a,b,  $\times 0.2$  (115).

**Anglonautilus** SPATH, 1927 [*\*Nautilus undulatus* SOWERBY, 1813; OD]. Cymatoceratid with large

foldlike undulations on venter which decrease rapidly on flanks; suture with shallow ventral and lateral lobes; siphuncle subcentral (115). *L. Cret. (Hauteriv.)-U. Cret. (Cenom.)*, Eu. (Eng.-Fr.-Crimea). —FIG. 334,3. *\*A. undulatus* (SOWERBY), L. Cret., Eng.; 3a,b,  $\times 0.4$  (115).

**Cymatonautilus** SPATH, 1927 [*\*Nautilus julii* D'ORBIGNY, 1850; OD]. Widely umbilicate, robust, whorls subquadratic, slightly wider than high; flanks flattened, with broad lateral groove; venter flattened and with median groove; conch bearing sinuous ribs that obliquely cross suture and form deep ventral sinus; suture with shallow

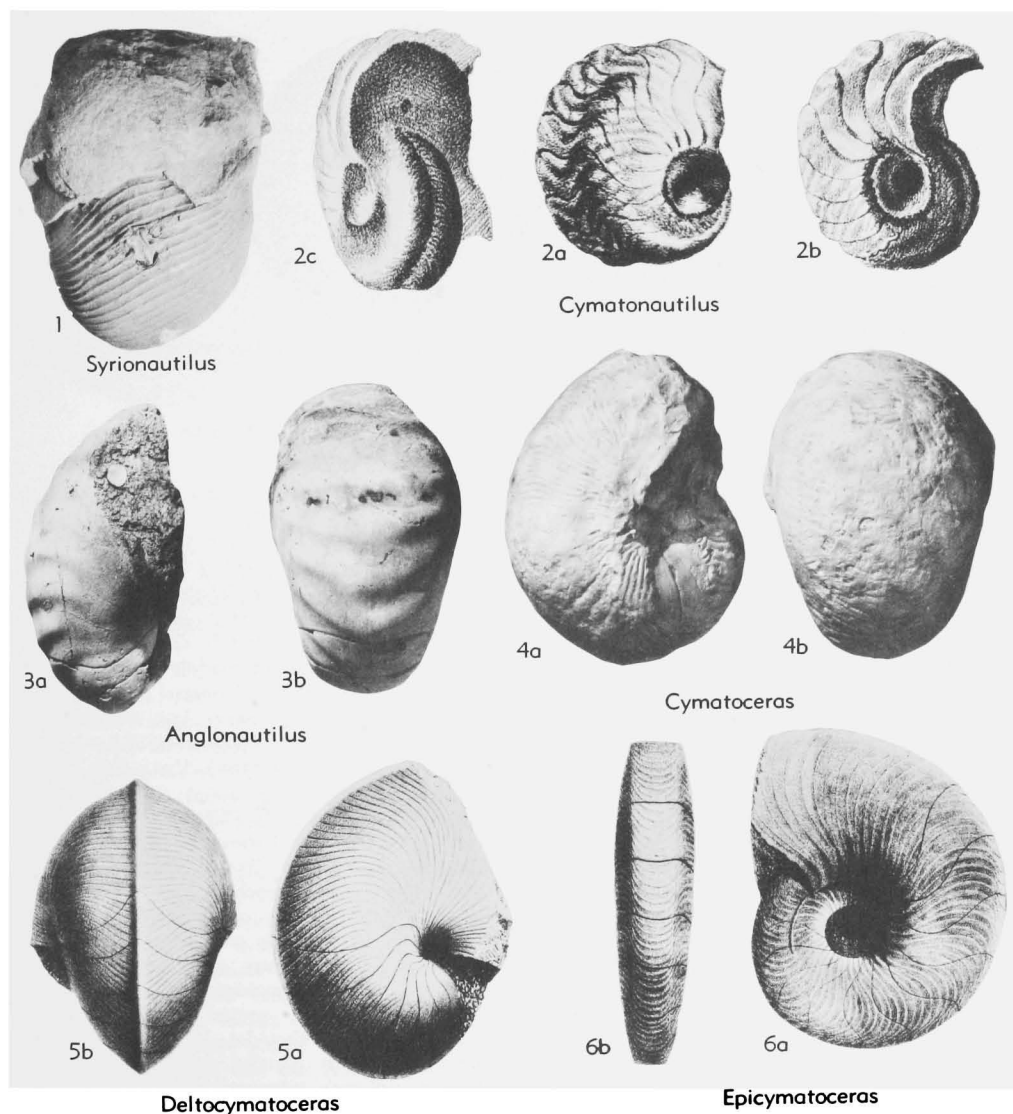


FIG. 334. Nautilaceae (Cymatoceratidae) (p. K453-K455).



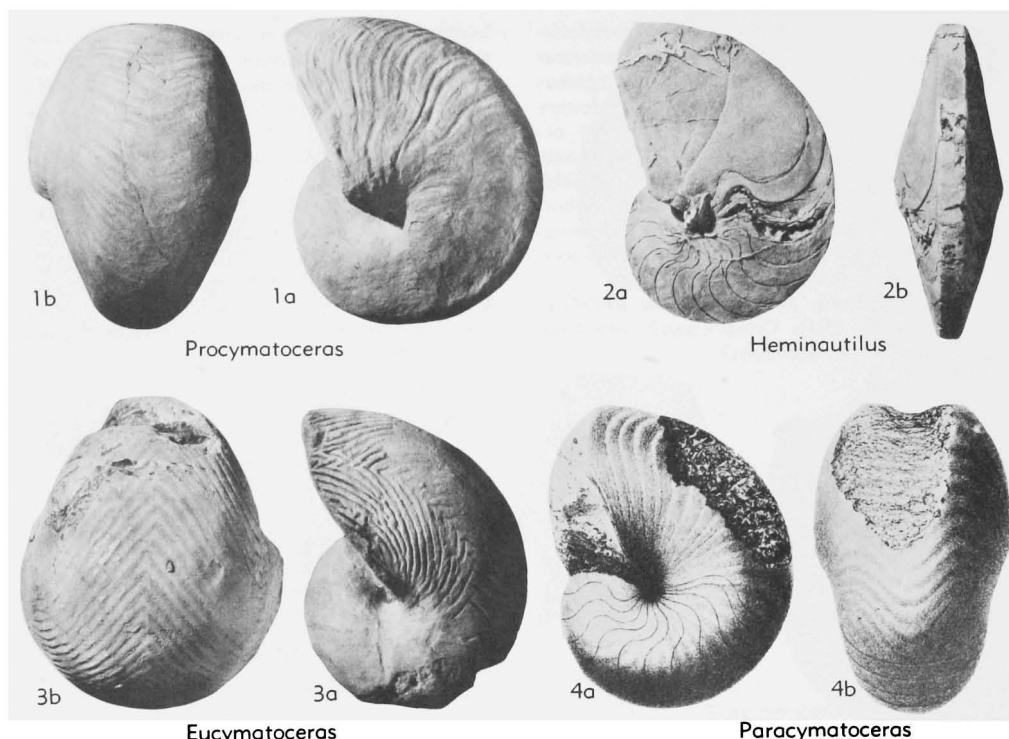


FIG. 335. Nautilaceae (Cymatoceratidae) (p. K454-K455).

ventral lobe and broad concave lateral lobe; siphuncle subcentral (115). *M.Jur.-U.Jur.*, Eu.(Fr.-Aus.).—FIG. 334,2. \**C. julii* (D'ORBIGNY), *U. Jur.*(Callov.), Fr.; 2a-c,  $\times 0.7$  (222).

**Deltocymatoceras** KUMMEL, 1956 [*\*Nautilus leiotropis* SCHLÜTER, 1876; OD]. Involute, with broadly arched strongly convergent whorl sides; venter marked by slight rounded, smooth, keel-like ridge; no distinct ventral shoulders; flanks bearing prominent cymatoceratid ribs that bifurcate near middle of whorl sides, ribs not crossing venter; suture with narrow, somewhat pointed ventral saddle, broad shallow lateral lobe, and prominent saddle on umbilical shoulder; position of siphuncle unknown (115). *U.Cret.*, Eu.—FIG. 334,5. \**D. leiotropis* (SCHLÜTER), Ger.; 5a,b,  $\times 0.2$  (115).

**Epicymatoceras** KUMMEL, 1956 [*\*Nautilus vaelsensis* BINCKHORST, 1861; OD]. Widely evolute, greatly compressed; whorl section subquadrate, nearly twice as high as wide; ventral shoulders angular, venter narrow and flattened; flanks only slightly inflated; umbilical shoulders broadly arched; suture with shallow ventral lobe and shallow lateral lobe; position of siphuncle unknown; surface bearing fine sinuous ribs that curve backward toward ventral shoulders and

form slight sinus on venter (115). *U.Cret.* (Maastricht.), Eu.(Ger.-Belg.).—FIG. 334,6. \**E. vaelsensis* (BINCKHORST), Ger.; 6a,b,  $\times 0.4$  (115). **Eucymatoceras** SPATH, 1927 [*\*Nautilus plicatus* FITTON, 1835; OD]. Subglobular, involute, umbilicus closed, whorl section rounded, broader than high; suture only slightly sinuous; siphuncle small, subcentral; surface bearing prominent ribs that form deep, angular V-shaped ventral sinus and on whorl sides, similar but asymmetrical salient (115). *L.Cret.*, Eu.(Eng.-USSR).—FIG. 335,3. \**E. plicatum* (FITTON), Eng.; 3a,b,  $\times 0.4$  (115).

**Heminautilus** SPATH, 1927 [*\*Nautilus saxbii* MORRIS, 1848; OD] [= *Vorticoceras* SCOTT, 1940; *Platynautilus* YABE & OZAKI, 1953]. Involute, compressed, whorls much higher than wide; flanks flattened, strongly converging toward narrow, flattened or slightly concave venter; ventral shoulders angular, venter on earlier volutions rounded; umbilical shoulders broadly rounded; suture sinuous, with ventral lobe, subangular saddle on ventral shoulder, broad deep lateral lobe and narrowly rounded saddle on umbilical shoulder; siphuncle subcentral; surface with sinuous ribs that curve strongly adorally over ventral half of whorl sides; ribbing may be weak or ab-



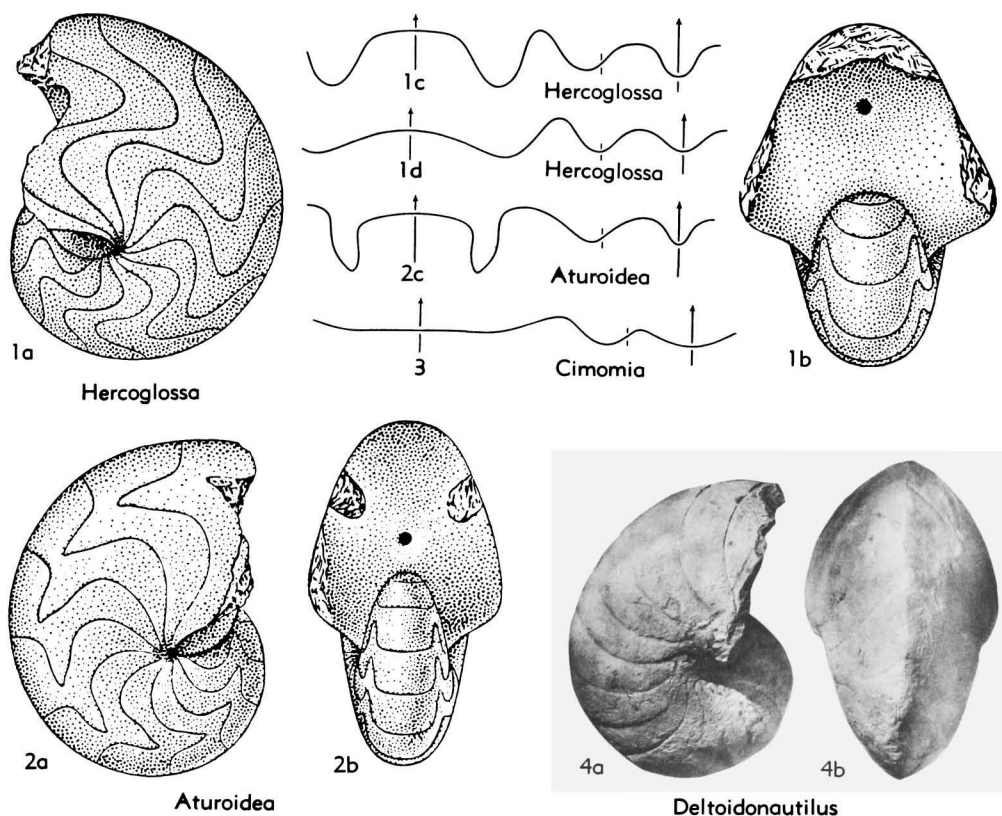


FIG. 336. Nautilaceae (Hercoglossidae) (p. K456).

sent on immature forms (115). *L.Cret.*, N.Am. (Ark.) - Eu. (Eng.-Fr.-Switz.) - N. Afr. (Egypt) - Asia (Israel - Japan) - S.Am. (Colom.). — FIG. 335, 2. \**H. saxbii* (MORRIS), *L.Cret.* (Apt.), Eng.; 2a, b,  $\times 0.5$  (115).

**Paracymatoceras** SPATH, 1927 [*\*Nautilus asper* OPPEL in ZITTEL, 1868; OD]. Like *Cymatoceras* but suture more sinuous, with deep, broadly rounded lateral lobe, and second lobe on umbilical wall (115). *U.Jur.-L.Cret.*, Eu. (Crimea) - Asia (India) - Afr. (Madag.) - E. Indies - N. Am. (Mex.-Tex.). — FIG. 335, 4. \**P. asperum* (OPPEL), *U.Jur.*, Eu.; 4a, b,  $\times 0.5$  (228).

**Procymatoceras** SPATH, 1927 [*\*Nautilus subtruncatus* MORRIS & LYCETT, 1850; OD]. Tightly involute, large, rapidly expanding conch; flanks and center flattened on living chamber, shoulders rounded; earlier volutions more rounded in cross section; whorl section subquadrate, with flanks converging toward venter; sutures only slightly sinuous, with shallow ventral and dorsal lobes; surface with sinuous ribs that form broad sinus on venter, ribs appearing to be fasciculate growth lines that may not be homologous to ribs of typical *Cymatoceras*; ribbing most distinctive on

living chamber (115). *M.Jur.*, Eu. (Eng.-Fr.) - Afr. (Ethiopia). — FIG. 335, 1. \**P. subtruncatum* (MORRIS & LYCETT), Eng.; 1a, b,  $\times 0.4$  (115).

**Syrionautilus** SPATH, 1927 [*\*Nautilus libanoticus* FOORD & CRICK, 1890; OD] [= *Syrinautilus* SHIMANSKIY, 1949, *nom. null.*]. Like *Cymatoceras* but with acute ribs separated by interspaces wider than rib width (115). *U.Cret.* (Senon.), Asia (Syria-Israel) - S.USSR. — FIG. 334, 1. \**S. libanoticus* (FOORD & CRICK), Syria;  $\times 0.6$  (115).

### Family HERCOGLOSSIDAE Spath, 1927

Smooth, involute nautilicones characterized by differentiation of suture; whorl sections generally rounded except in *Deltoidonautilus* where it is triangular in outline. An increasing grade of sutural complexity is observed from *Cimomia* to *Hercoglossa* to *Aturoidea*. *Deltoidonautilus* has a suture like that of *Hercoglossa*. *Cimomia* is believed to be an offshoot of *Eutrophoceras*, with which it appears to intergrade (124). *U.Jur.-Oligo.*

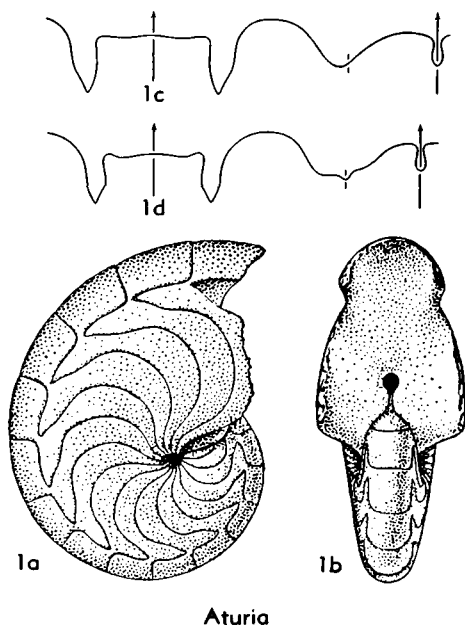


FIG. 337. Nautilaceae (Aturiidae) (p. K457).

**Hercoglossa** CONRAD, 1866 [*\*Nautilus orbiculatus* TUOMEY, 1856; SD HYATT, 1883; neotype, MILLER & THOMPSON, 1933] [= *Enclimatoceras* HYATT, 1883; *Woodringia* STENZEL, 1940]. Nautiliconic, subglobular to subdiscoidal; whorls flattened to broadly rounded laterally, narrowly rounded ventrally, deeply impressed dorsally; umbilicus small, umbilical shoulders rounded; surface smooth; suture with broad rounded ventral saddle, deep rounded lateral lobe, similar lateral saddle, shallower and rather broad rounded lobe on or near umbilical wall, and broad rounded internal lateral saddle that extends to deep narrowly rounded dorsal lobe; siphuncle small, variable in position but never marginal (124). ?*L. Cret.*, *Paleoc.-Eoc.*, cosmop.—FIG. 336, 1a-c. \**H. orbiculata* (TUOMEY), *Paleoc.*, Ala. (124); 1a,b,  $\times 0.5$ ; 1c,  $\times 0.2$  (226). — FIG. 336, 1d. *H. harrisi* MILLER & THOMPSON, *Paleoc.*, Trinidad;  $\times 0.5$  (226).

**Aturoidea** VREDENBURG, 1925 (ICZN pend.) [*\*Nautilus parkinsoni* EDWARDS, 1849; SD MILLER & THOMPSON, 1935] [= *Paraturia* SPATH, 1927 (obj.)]. Nautiliconic, occluded, sublenticular; whorls compressed, flattened laterally, rounded ventrally, impressed dorsally, umbilical shoulders rounded; suture with broad, high, blunt ventral saddle, aligned by deep, narrow asymmetrical lateral lobe, broad, high, rounded asymmetrical lateral saddle, broad rounded lobe with center near umbilical seam, broad rounded saddle on side of impressed zone and large rounded V-shaped dor-

sal lobe; siphuncle subcentral (124). *U.Cret.-Eoc.*, N. Am. (Calif.-N.J.)-S. Am. (Peru)-Eu. (Eng.-Aus.)-Afr. (Libya - Angola) - Asia (India)-Australia. — FIG. 336, 2a,b. *A. olssoni* MILLER, *Eoc.*, Peru;  $\times 0.4$  (124). — FIG. 336, 2c. *A. paucifex* (COPE), *L.Eoc.*, USA (N.J.);  $\times 0.5$  (226).

**Cimomia** CONRAD, 1866 [*\*Nautilus burtini* GALEOTTI, 1837; OD] [= *Nautilus (Javanoceras)* MARTIN, 1932; *Cymomia* CONRAD, 1866 (*nom. null.*); *Cymmomea* CONRAD, 1868 (*nom. null.*); *Cimonia* FISCHER, 1882 (*nom. null.*)]. Subglobular to subdiscoidal, nautiliconic; whorls broadly rounded laterally and ventrally; umbilicus small, umbilical shoulders low, broadly rounded; surface smooth except for growth lines; suture with broad, shallow, rounded ventral saddle, broad, shallow lateral saddle near umbilical shoulder, and broad, rounded lobe on umbilical wall; siphuncle small, variable in position but never marginal (124). [Genus is a morphologically transitional form between *Eutrophoceras* and *Hercoglossa*.] *U.Jur.-Oligo.*, cosmop.—FIG. 336, 3. *C. vincenti* MILLER, *Paleoc.*, Afr.;  $\times 0.5$  (226).

**Deltoidonautilus** SPATH, 1927 [*\*Nautilus Sowerbyi* SOWERBY, 1843; OD] [= *Lissoniceras* BENAVIDES-CÁCERES, 1956; *Teichertia* GLENISTER, MILLER, & FURNISH, 1956; ?= *Angulithes* DEMONTFORT, 1808 (*nom. dub.*); *Angulites* SHIMANSKIY, 1957 (*nom. null.*)]. Nautiliconic, involute, compressed, with small inconspicuous umbilicus; whorl section sagittate, with narrowly rounded to angular ventral zone; lateral areas converging toward venter; deeply impressed dorsal zone. Growth lines forming deep hyponomic sinus; suture with broad narrowly rounded to acute ventral saddle, large lateral lobe, small lateral saddle and lobe on umbilical wall, dorsal lobe which may be very narrow; siphuncle near dorsum (115). *U.Cret.-Oligo.*, cosmop.—FIG. 336, 4. *D. triangularis* (DEMONTFORT), *U.Cret.*, Fr.; 4a,b,  $\times 0.3$  (115).

[Type-species of *Deltoidonautilus*.—When SPATH (1927, p. 22) proposed the genus *Deltoidonautilus*, he cited as type-species "*Nautilus sowerbyi* Wetherell, 1836, in J. de C. Sowerby, 1843, p. 35, pl. dcxxvii, figs. 1-3." WETHERELL (1836, p. 466) merely announced the discovery in the London Clay (Eocene) of a new species of "*Nautilus*" referred to as "minute cephalopodous Mollusca." He did not name the fossils but wrote: "The great zeal which Mr. J. de C. Sowerby has always evinced in the advancement of science has induced me to give his name to a new species of *Nautilus* which I have discovered at the railroad." It is clear from the published discussion that the fossils in question are Foraminifera. SOWERBY (1843) described a nautiloid cephalopod—not a foraminifer—from the London Clay under the name "*Nautilus Sowerbyi*," attributing the species to WETHERELL, 1836, and giving a reference to p. 466 in the article already mentioned which actually relates to unnamed foraminifers. SOWERBY's nautiloid is an involute shell with a siphuncle near the dorsal side of the conch but not in contact with it; the whorl section has slightly convex flanks and broadly rounded venter (SOWERBY, 1843, pl. 627, fig. 2, 3), although his accompanying description (p. 35) states that the aperture is triangular. Since the cited figures (2, 3) represent immature growth stages, it is reasonable to assume that the "triangular" shape of the aperture does not develop until the adult stage is reached.

Since WETHERELL did not actually name a species "*sowerbyi*," and since this specific name, if published in

1836, would have been attached to a foraminifer, the name "*Nautilus Sowerbyi*," as used for a nautiloid cephalopod, must be attributed to SOWERBY (1843) himself and not to WETHERELL, as erroneously recorded by SOWERBY. (References—WETHERELL, N. T., "Observations on some of the fossils of the London Clay . . .": *Philos. Mag. & Jour. Sci.*, v. 9, p. 462-469, 1836, London and Edinburgh. SOWERBY, J. DE C., *The mineral conchology of Great Britain*, v. 7, 1843, London.)—CURT TEICHERT.]

### Family ATURIIDAE Chapman, 1857

[*nom. correct.* KUMMEL, herein (*pro* Aturidae CHAPMAN, 1857)] [=Aturidae SPATH, 1927; Aturiaceae HYATT, 1894 (*nom. transl.* SHIMANSKIY, 1962, *superfam.*)]

Smooth, very involute to occluded, discoidal conch, flattened laterally, rounded ventrally, with deep impressed zone; suture with broad, flattened ventral saddle, narrow pointed lateral lobe, broadly rounded lateral saddle, broad lobe on umbilical slope

and dorsal area, and broad saddle on dorsal area divided by deep, narrow lobe; siphuncle moderate in size, subdorsal and located in infundibuliform dorsal adapical flexure of septa. *Paleoc.-Mio.*

Aturia BRONN, 1838 [*\*Nautilus aturi* BASTEROT, 1825; SD HERMANNSEN, 1846 (p. 90)] [=?*Pelagus* DEMONTFORT, 1808; *Nautilopsis* CONRAD, 1847; *Megasiphonia* D'ORBIGNY, 1849; *A.(Sphenaturia)* IHERING, 1921; *A.(Nilaturia)*, *A.(Brazaturia)* STENZEL, 1935]. Characters of family. *Paleoc.-Mio.*, cosmop.—FIG. 337, *1a,b.* *A. angustata* (CONRAD), *Mio.*, USA (Wash.);  $\times 0.4$  (124).—FIG. 337, *1c.* *A. alabamensis* (MORTON), *U.Eoc.*, Afr.;  $\times 1$  (226).—FIG. 337, *1d.* *A. curvilineata* (MILLER & THOMPSON), *Mio.*, S.Am.(Venez.);  $\times 0.3$  (226).

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COMPOSITE LIST PREPARED BY CURT TEICHERT, BERNHARD KUMMEL, W. C. SWEET, W. M. FURNISH, BRIAN F. GLENISTER, AND R. C. MOORE

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[The title-page shows 1900 as the publication date and the English Catalog gives it more precisely as January, 1900. Actually, a first part of this volume, containing pages 1-352, was published in 1896 and sold as a book (at the price of \$2.50, according to the American Catalog), one copy of which is in the New York Public Library. A notice of it was given in the September-October 1896 issue of the *Journal of Geology* (v. 4, p. 733). Advance copies of the entire volume, containing pages 353-706, as well as those previously published, seem to have been made available to some individuals in 1899, for this date is given in a review by C. R. Keyes that was included in the January-February 1900 issue of the *Journal of Geology* (v. 8, p. 81). Keyes wrote: "After an interval of more than three years since the appearance of Part I, the invertebrate portion of ZITTEL's *Palaontology* is at last brought to a conclusion." A review signed "W." (probably signifying H. S. WILLIAMS) in the *American Journal of Science* in 1900 (v. 9, p. 388) cites the publi-

cation date as 1900. The records of Macmillan & Company, Ltd., as reported in a letter (24 October 1961) to Mr. KURT LAUMANN, Long Island City, N.Y., show that the first part of the ZITTEL textbook was published in 1896 and the second part in January 1900; the whole volume bears the publication date of 30 January 1900. The chapter on Cephalopoda, which contains contributions by HYATT, forms a portion of the second part of the textbook, and accordingly, new taxa published therein by him are correctly referred to as "HYATT in ZITTEL, 1900." CURT TEICHERT & R. C. MOORE.]

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- (223a) Holm, Gerhard, 1885, 1891, 1897, 1898
- (223b) Kobayashi, Teiichi, 1935
- (224) Koninck, L. G. de, 1880
- (224a) Korde, K. B., 1949
- (225) Meek, F. B., & Worthen, A. H., 1873
- (226) Miller, A. K., 1932; 1935; 1947
- (226a) Miller, A. K., & Cullison, J. S., 1946
- (226b) Miller, A. K., & Kummel, Bernhard, 1945
- (227) Miller, A. K., & Youngquist, W. L., 1947, 1949
- (227a) Noetting, Fritz, 1882
- (228) Oppel, Albert, 1868
- (229) Portlock, J. E., 1843
- (229a) Remelé, Adolf, 1882
- (230) Retowski, O., 1894
- (231) Sandberger, G., & Sandberger, F., 1850-54
- (232) Smith, J. P.
- (233) Sowerby, James, 1825
- (234) Stache, G., 1877
- (235) Sweet, W. C., & Miller, A. K., 1957
- (236) Teichert, Curt, 1924; 1934; 1935; 1947
- (237) Tsvetaeva, Marie, 1888
- (238) Waagen, W. H., 1873
- (239) Welter, O. A., 1914
- (240) Whiteaves, J. F., 1891
- (241) Whitfield, R. P., 1882
- (242) Zimmerman, E., 1892

## RHYNCHOLITES

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## INTRODUCTION

Rhyncholites, as etymology of the name indicates, are stone (fossil) beaks. A considerable variety of organic remains fits such a designation, and so it is necessary to specify the particular category of fossil beaks which has been differentiated by usage under this term. The objects are identified as jaw parts of cephalopods, since many of them closely resemble the calcareous parts of the upper and lower jaws of modern *Nautilus pompilius* and allied species of this genus. The certainty that some known kinds of rhyncholites, perhaps a majority of them, are skeletal elements secreted by nautiloids cannot be accepted as indication that only nautiloids are represented by this group of fossils. A number of workers, including JELETZKY, who is a *Treatise* author working on Coleoidea, have held the opinion that some rhyncholites belong to belemnites and that upon more detailed study and comparison of these fossils with the beaks of Recent coleoid cephalopods, their relationships will become apparent. The systematic position of rhyncholites is discussed in a section of the present chapter under "Relationships."

It was BIGUET (1819, p. 58) who first published the name "*Rhyncolite*." Plainly he used it both as a vernacular term (e.g., *le Rhyncolite*, *les Rhyncolites*) and also as part of binominal designations, both vernacular and with Latin specific names, for five different kinds of fossil beaks which he described briefly (e.g., *Rhyncolite mouette*, *R. Larus*, p. 58). The Latin specific names given by BIGUET unquestionably are valid as "indications" in zoological nomenclature, and in our view BIGUET's "*Rhyncolite*" qualifies as a generic name because this author consistently applied the principles of binominal nomenclature (Zool. Code, 1961, Art. 11,c) and employed the Latin- or Greek-derived name coined by him as a noun in the nominative singular, as required by zoological rules (Art. 11,f).

It is true that the spelling "*Rhynco*-" is neither correctly transliterated from the Greek "*rhynchos*" (neuter gender), meaning snout or beak, nor accurately transcribed from the Latin "*rhynchus*" (masculine gender, Art. 30,a,1), derived from Greek. Adjectival specific names published by BIGUET uniformly have masculine endings, as is correct for agreement with a generic name terminating in -lite (Greek, *lithos*, masculine).

*Rhyncolite*, as a generic name, is not emendable to *Rhyncholite*, on the ground of improper transliteration or latinization of *Rhyncolite*, because imperfection of this sort is rejected as an inadvertent error subject to correction (Art. 32,a,ii); also, it cannot be changed to *Rhyncholites*, *Rhyncholithes*, *Rhyncholithus*, or other spelling and attributed to BIGUET. The spelling "*Rhyncolyte*," found in one place (p. 58), seems clearly to be inadvertent. Accordingly, we propose to recognize *Rhyncolite* BIGUET, 1819, as a generic name and to employ the spelling rhyncholite (pl., rhyncholites) as the inclusive vernacular designation for all sorts of cephalopod jaw parts (beaks). The fact that the name *Rhyncolite* is open to criticism on etymological grounds is well counterbalanced by the advantage of clear distinction between *Rhyncolite* (nominal genus) and rhyncholite (common noun).

## HISTORICAL REVIEW

Rhyncholite fossils had been observed for a number of years before they were given formal names and were either described simply as "beaks of birds" or "duck's beaks," because of their resemblance to these known objects; they were called "histerolites" or "glossopetrae" by some pre-Linnean authors.

In 1819, FAURE BIGUET described five species of what he termed "rhyncholites," but he figured only one. These fossils were included in a work on belemnites because BIGUET considered them to belong to this group. BIGUET's specimens seem to have

come from Triassic rocks of southeastern France.

VON SCHLOTHEIM (1820) published a rhyncholite (conchorhynch) description and figure under the name *Lepadites avirostris*, thinking the form was related to barnacles. Thus he mistakenly extended the use of the generic name *Lepadites* BLUMENBACH, 1803, which was in reality introduced for fossil cirripeds, to include conchorhynchs. However, BLUMENBACH (1803, p. 21, pl. 2) gave only the name "*sepiarum rostra*" to two kinds of rhyncholites which he described and figured.

GAILLARDOT (1824) described and figured these same two types of rhyncholites (probably M. Trias., France) (Fig. 338), which he did not undertake to name, designating them merely as "first species" (pl. 22, fig. 3-14) (later named *Conchorhynchus* by DE BLAINVILLE, 1827) and "second species" (pl. 22, fig. 15-26), the original *Rhyncholite* of BIGUET. GAILLARDOT believed that these fossils belonged to cephalopods closely related to *Sepia*. His drawings were excellent and seemingly very accurate.

D'ORBIGNY (1825, p. 212, 215) used the generic name *Rhyncholites* which he incorrectly ascribed to BIGUET, referring it to arrowhead-shaped forms, as BIGUET had done. He described four species with Latinized names, two of which were figured (Trias.-Jur., France, Germany). D'ORBIGNY's "Division 1, espèces à capuchon," were the *Rhyncholite*-type which he believed belonged to the genus *Nautilus*. His "Division 2, espèces sans capuchon," were what was later named *Conchorhynchus*.

In 1827, DE BLAINVILLE divided the rhyncholites known to him into two genera based upon a distinct difference in form. That equivalent to BIGUET's *Rhyncholite* he named *Rhyncholithes* (Fig. 339,1) (GAILLARDOT's fig. 15-26, pl. 22), and the other he defined as the new genus *Conchorhynchus* (Fig. 339,2) (GAILLARDOT's fig. 3-14, pl. 22, and D'ORBIGNY's 1825 *Rhyncholites Gaillardoti*). DE BLAINVILLE apparently thought that these were structures belonging to belemnites.

ZIETEN (1830), MÜNSTER (1829), and MERIAN (1835) used the generic name *Rhyncholites* and the latter two named new species, although MERIAN's is a *nomen*

*nudum*. ROEMER (1836), followed by QUENSTEDT (1852), and OOSTER (1863), published descriptions of additional rhyncholites of Jurassic age. HAGENOW (1842) and MÜLLER (1847) were first to describe rhyncholites of Cretaceous age.

ROEMER (1854) and BÖHM (1912) have described the only nautiloid mandibles known from beds of Paleozoic age in Germany; later BRADY (1955) reported similar occurrences from Lower Permian rocks of the USA (Arizona).

In an important paper published in 1847, D'ORBIGNY named a third new genus belonging to this group of fossils, *Rhynchoteuthis*, with about a half dozen species (all of Cretaceous age), some new and some reassigned from the old genus *Rhyncholite*. The next new genus included in this group was *Palaeoteuthis* described by D'ORBIGNY in 1850, with but a single species.

Another new genus, *Scaptorhynchus* BELLARDI, 1871 (Miocene, Italy), is strikingly different from all previous ones (Fig. 344,2).

Lengthy papers by TILL (1906, 1907, 1908, 1909, 1910, 1911) contained the new genera *Hadrocheilus*, *Leptocheilus*, *Akidocheilus*, *Gonatocheilus*, and *Mesocheilus* and numerous reassignments of former genera and species. As some authors before him had done, TILL reduced to subgeneric status some of the previously recognized genera of rhyncholites [e.g., *Temnocheilus* (*Rhyncholithes hirundo* BIGUET) and *Nautilus* (*Rhyncholithes giganteus* D'ORBIGNY)], thus linking the names with recognizable nautiloid conchs.

RÜGER (1921), Moos (1924), and BESSLER (1938) made significant contributions to the knowledge of rhyncholites of Jurassic age in Germany.

SHIMANSKIY (1947, 1949, 1959) further revised genera and species, including those of TILL, naming new genera, subgenera, and species.

RUTTE (1962) recently has reported on some exceptionally well-preserved nautiloid mandibles in the Middle Triassic (Muschelkalk) of Germany. His consideration of the possibility that what he called *Rhyncholithes* (= *Rhyncholite*) is the upper jaw of *Germanonautilus bidorsatus* and *Conchorhynchus* is its lower jaw (Fig. 340) led

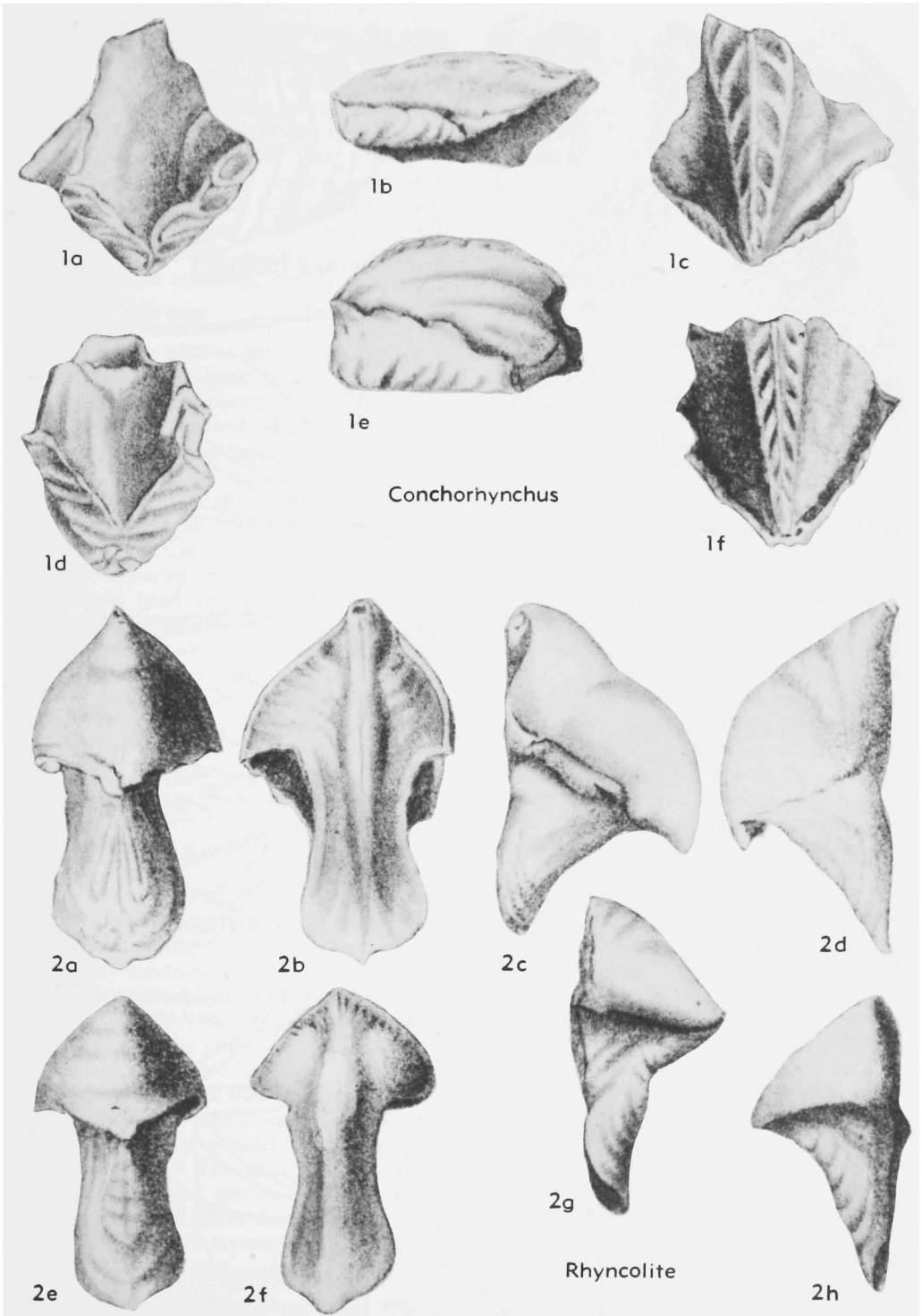


FIG. 338. Rhyncholites figured and described by GAILLARDOT (1824); 1a-f, "*première espèce*," the new genus *\*Conchorhynchus* of DE BLAINVILLE, 1827; 2a-h, "*seconde espèce*," the original *\*Rhyncolite* of BIGUET, 1819; all  $\times 2$  (18) (p. K477-K478).

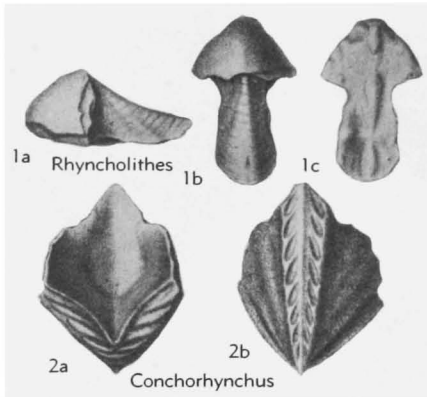


FIG. 339. Rhyncholithes figured and described by DE BLAINVILLE (1827) showing his nomenclature; 1a-c, *Rhyncholithes* (= *Rhyncholite* BIGUET, 1819); 2a,b, *Conchorhynchus*;  $\times 0.75$  (7).

to the judgment that this is very probably correct, though complete proof has not yet been produced.

MÜLLER (1851), EUDES-DESLONGCHAMPS (1858), ROLLE (1862), and LAUBE (1868, 1870) described supposed nautiloid mandibles as the genera *Peltarion*, *Cyclidia*, *Scaphanidia*, and *Rhynchidia*; these were subsequently determined to be gastropod opercula by ZITTEL (1884), VINCENT (1900), and TILL (1906-10).

## MORPHOLOGY

A description of the main morphological features observed in a study of rhyncholithes is introduced advantageously by observing characters of the upper and lower jaws of living *Nautilus* (Fig. 341, 341A). These have been described by STENZEL in a foregoing chapter on "Living Nautilus" (p. K61, Fig. 44A).

Rhyncholithes vary in size rather widely, since their length or width ranges from 2 or 3 mm. to more than 50 mm.

### UPPER JAW

The upper jaw of living *Nautilus* may be compared to a flaring cape which is broadly open toward the front (anteroventral side) and hooded at the top, this hood bearing a turned-back rim or collar that projects above the rounded sides and back (dorsal side) of the cape. The hood is sharply pointed at its peak which forms

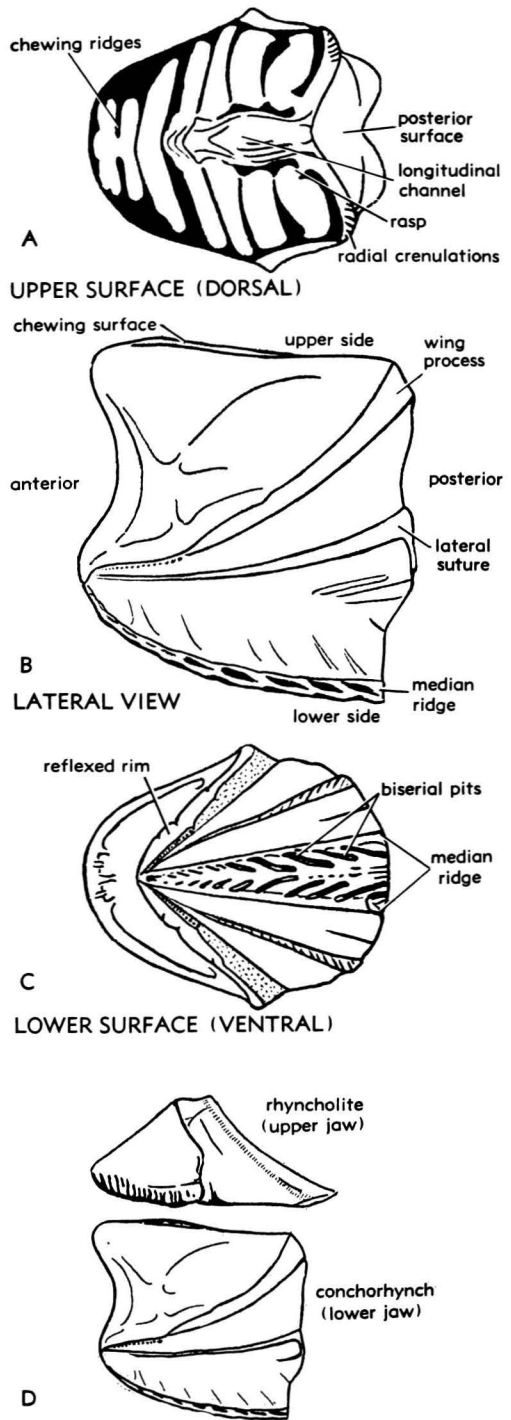


FIG. 340. Diagrams of lower jaw (conchorhynch) in three views (A-C) and of both jaws in side view (D), representing features of cephalopod mandible (41).



the main biting part of the jaw. Its outer portion consists of hard, smooth, shiny calcareous shell substance which covers a relatively soft, somewhat spongy inner calcareous layer. The calcareous structure has a shaftlike prolongation that extends a short distance into the concave interior of the curved upper jaw. All remaining parts, including the reflexed collar, are horny and dark-colored. Their surface is marked by fine striations running parallel to the jaw margins.

Fossil rhyncholites that correspond most closely to jaw parts of living *Nautilus* represent the calcified beak region, but the adjoined horny structures, or "wings," are only rarely preserved. Fossils similar to those described and named by BIGUET (5), now interpreted to represent upper beaks, may be classed as **rhyncholites** in the narrow sense, because it is they which were so named by BIGUET.

Such rhyncholites consist of a rhomboid or deltoid head (termed the **hood**) fixed on a distinctly narrower **shaft** (Fig. 342). The anterior tip of the hood, which constitutes the biting extremity of the jaw, may be irregular or broken in fossil forms. In side view, the shaft appears triangular in outline, with two long sides formed by the dorsal and ventral surfaces and a short side marking the junction of the shaft with the head. The shaft is transversely convex on the dorsal side and gently concave on the ventral side.

According to TILL (48, p. 657), numerous rhyncholites which he considered to represent the upper beaks of cephalopods (probably nautiloids other than *Nautilus*) are distinguished by a hood that is notched on the posterior side opposite the pointed tip, by an angular cross section of the shaft, instead of a rounded one, and by differentiation of the convex side of triple prolongations, one in a median position and the other two nearly parallel or diverging in lateral position. The definition of genera and of numerous species has been based on variations of these features which are presumed to have taxonomic significance.

### LOWER JAW

The calcareous part of the lower jaw in living *Nautilus* also bears fine, concentric striae. It is more arcuate and has greater

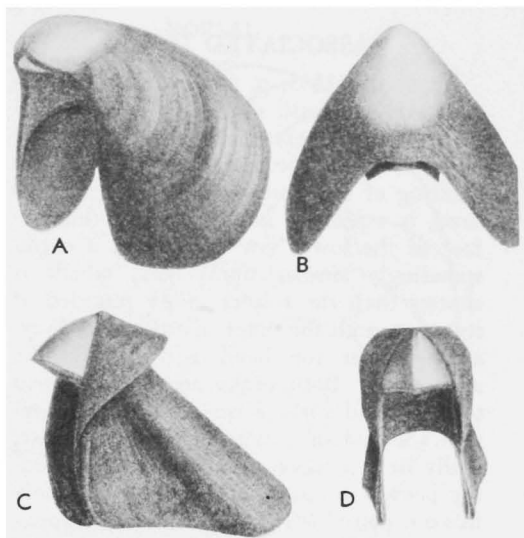


FIG. 341. Mandibles of living *Nautilus*. A,B, lower jaw, lat. and ventral views; C,D, upper jaw, lat. and ventral views,  $\times 1$  (47).

breadth and depth than the upper jaw. Its anterior cutting surface is dentated and its posterior extremity opposite the beak is concave. The beak is calcareous, as in the upper jaw, but the calcareous matter is deposited on both sides of a thin layer of horny substance (also concentrically laminated), which would tend to disintegrate in the course of fossilization. Hence, the lower jaws (beaks) occur less commonly as fossils.

A type of rhyncholite that was first described and illustrated by BLUMENBACH (1803) and later named *Conchorhynchus* by DE BLAINVILLE (1827) is inferred to be the preserved part of a lower jaw. Such rhyncholites are termed **conchorhynchs**. They have a broadly scalloped, arcuate outline or a nearly quadrangular shape, without any extension that is interpretable as a shaft (Fig. 339,2). Rhyncholites of this sort, which are extremely rare as compared with those judged to have been structures of upper jaws, resemble a rather thin shell (conch). Some Mesozoic conchorhynchs are distinguished by corrugated margins on the concave side adjacent to the pointed beak and on the convex side by a median keel bordered by acute-angled, short lateral ridges in approximately paired or slightly alternating opposed position.

### ASSOCIATED JAWS

MÜNSTER (1843, p. 69) recorded the occurrence of a fossil showing the lower and upper jaws preserved in contact with one another. This specimen, found after the printing of the plate and therefore not figured, is especially interesting. To the surface of the lower jaw is attached a correspondingly similar upper jaw, which is shorter than the former, more rounded at its point, with the outer side not as convex, and without the band with feather-like channeling. Both beaks are firmly joined together and form a quadrangular projection. Should this, as seems to be the case, really be a junction of the two corresponding jaws, it is remarkable that there is only this one paired jaw among at least 150 specimens studied and that no free upper jaw was found among so many lower jaws.

### DIMORPHISM

TILL (49, p. 586; 50, p. 424) has suggested the possible occurrence of sexual dimorphism in species of *Hadrocheilus*, because he observed that otherwise very similar forms, found in the same locality, differ only in the length of the shaft.

### ONTOGENY

The ontogeny of rhyncholites is little known. TILL (50, p. 413) found that in one species of *Hadrocheilus* the small, presumably younger, specimens are flatter, but are similar in all other proportions to the larger specimens. In another species of the same genus (p. 423) a stronger curvature of the hood seems to occur during ontogeny, accompanied by a broadening of the shaft furrow, and a rounding of the shaft edges.

### CLASSIFICATION

Rhyncholites present the same sorts of problems to paleontologists as those which are encountered in studies of conodonts, otoliths, and discrete fragments of several groups of animals found as isolated fossils. That some rhyncholites are remains of genera classifiable in the order Nautilida (although none certainly belonging to *Nautilus*) can hardly be doubted. Several

records of such an association have been reported (see chapter on "Biostratonomy"). Classification and nomenclature of rhyncholites in terms of parataxa would be suited for work on these fossils but cannot be accepted in the *Treatise* because (1) parataxa have not been sanctioned by international Rules and (2) authors have consistently treated rhyncholites as objects appropriate for recognition as natural taxa. Among these, at the generic level, are some rhyncholites which were presumed to belong to *Nautilus*, *Temnocheilus* (*recte Peripetoceras*), *Germanonautilus*, *Somalinnautilus*, *Cenoceras*, *Hercoglossa*, *Pseudonnautilus*, *Aturia*, and numerous others as questionably identified forms. BÖHM (9) referred a late Permian rhyncholite (*Conchorhynchus*) to the nautiloid species *Temnocheilus Freieslebeni* (GEINITZ) (= *Peripetoceras freieslebeni*), because this was the only nautiloid known in strata containing the rhyncholite. The rhyncholite was then designated as *Temnocheilus* (*Conchorhynchus*) *Freieslebeni* GEINITZ. Another rhyncholite distinguished as *Conchorhynchus avirostris* (SCHLOTHEIM), from the Triassic, was similarly referred to *Nautilus* or *Temnocheilus bidorsatus* VON SCHLOTHEIM (subsequently made the type-species of *Germanonautilus* by MOJSISOVICS, 1902). It is noteworthy that these identifications rest solely on assumptions that the Permian and Triassic rhyncholites cited must belong to the indicated species previously described on the basis of conchs, because the latter happen to be the only nautiloids known to occur in proximity with the rhyncholite fossils. Obviously, such evidence has value only as support for a guess.

Accordingly, rhyncholites having morphological resemblance to the jaw parts of living *Nautilus* are herein designated by the generic name *Rhyncholite* BIGUET, but this name is not considered to be a synonym of *Nautilus*. The fossils classed as rhyncholites are assigned to no family and are not definitely included in the order Nautilida, even though some seem to belong there. CHENU (1859) established a family, Palaeoteuthidae, to include all rhyncholites known up to that time, as well as the "genre aptychus," in addition. In view of the difficulties experienced in determining the relationships between various groups of

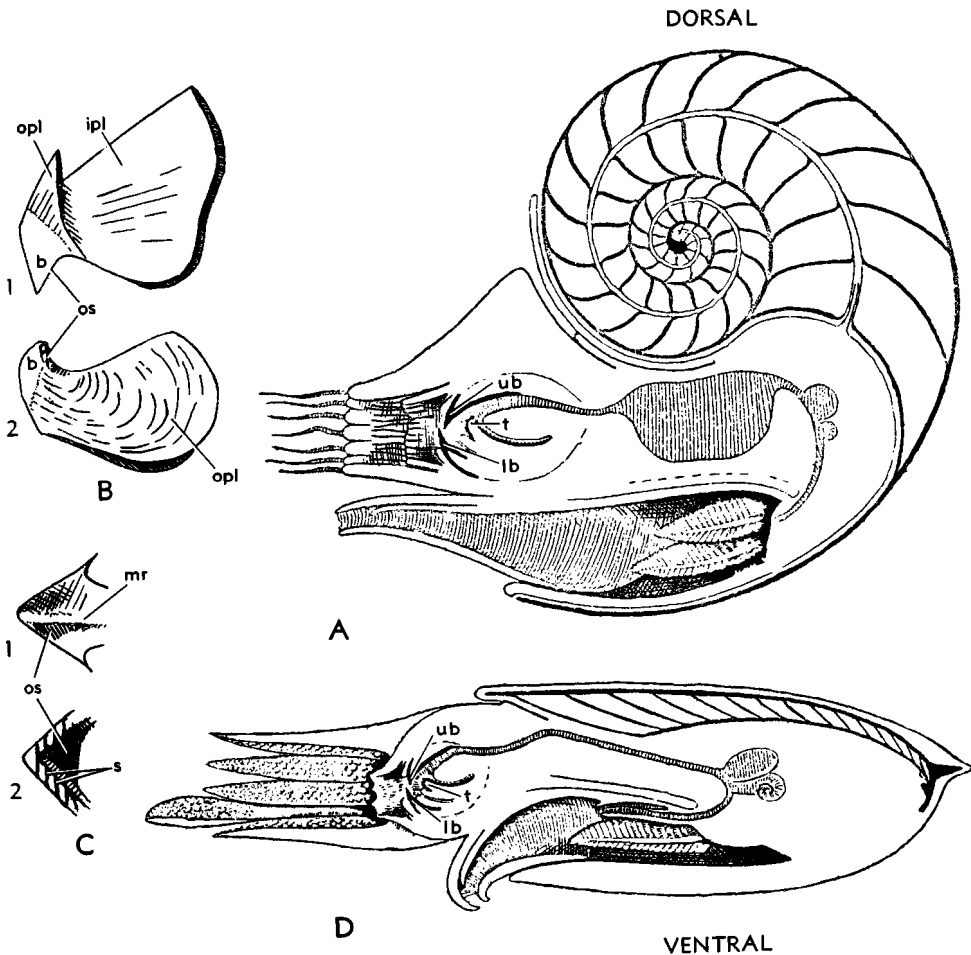


FIG. 341A. A. Schematic median sec. of *Nautilus pompilius* showing placement of upper and lower beaks in relationship to body organs; *ub*, upper beak, *lb*, lower beak, *t*, tongue (Compare Fig. 44A).—B. Jaws of *N. pompilius*, lat. view; 1, upper jaw showing beak (*b*), occludent surface (*os*), outer plate (*opl*) (exposed), and inner plate (*ipl*) (covered by muscle tissue and cartilage); 2, lower jaw showing beak (*b*), occludent surface (*os*), and outer plate (*opl*) (inner plate on lower jaw is completely covered by outer plate).—C. Enlarged diagrammatic representation of occludent surfaces of upper and lower beaks, 1, showing median ridge (*mr*) on upper beak, 2, showing serrations (*s*) on lower beak (occludent surface, *os*).—D. Schematic median sec. of *Sepia* sp. showing position of beaks for comparison with those in *Nautilus* (letter symbols as in A); (adapted from 27a) (p. K470).

rhyncholites and between them and shell-bearing cephalopods, we judge that grouping of rhyncholites into one or more families would be an artificial procedure.

## RELATIONSHIPS

The most detailed discussion of systematic relationships of the fossils known as rhyncholites has been published by SHIMANSKIY (45). He noted that some nominal genera considered by their authors

to be rhyncholites almost certainly belong to mollusks other than cephalopods (e.g., Gastropoda, Amphineura) and these may be dismissed from attention. The description of a conchorhynch-type of rhyncholite by VON SCHLOTHEIM (1820) under the name *Lepadites avirostris* can be accepted as validly establishing this species, but the reference of it to BLUMENBACH'S (1803) nominal genus of cirripeds can be regarded as merely an interesting, curious mistake. BIGUET (1819), DE BLAINVILLE (1827), and

ZIETEN (1830) were of the opinion that rhyncholites were hard parts located somewhere in the soft body of supposed dibranchiate cephalopods, for the fossils were found in belemnite-bearing Mesozoic strata and their dark color and apparently fibrous microcrystalline structure resembled characters of belemnoid rostra. GAILLARDOT (1824) interpreted the rhyncholites studied by him as almost surely fossilized jaw parts of *Sepia*-type cephalopods, if not of *Sepia* itself.

D'ORBIGNY (1825) was first to suggest that some rhyncholites may belong to the "genus *Nautilus*," and stated (1847) that some (*Rhynchoteuthis*) had been placed by him in the belemnites ("Céphalopodes Acétabulifères"). Although ammonoids are extremely abundant in many Triassic, Jurassic, and Cretaceous deposits which yield rhyncholites, none of the latter have ever been found in an ammonoid conch.

OWEN (1832, *Memoir on the Pearly Nautilus*, p. 21), after an excellent description of the jaws of modern *Nautilus*, concluded: There are, however, certain fossils called *Rhyncholites*, formerly considered to be the beaks of fossil birds, but recognized by Blumenbach as appertaining rather to the Cephalopods, although evidently differing from all the recent genera then known. M. d'Orbigny having invariably met with a large kind of these *Rhyncholites* in the same stratum with the fossil shell of a large *Nautilus* (*Nautilus gigas*), suspected from the circumstance that they might be the mandibles of that species (see his Memoir in the *Ann. des Sci. Nat.*, v. [5], p. 241, pl. 6). The calcareous extremities of the mandibles of *Nautilus pompilius*, and peculiarities of their form, especially the flattened superior surface of the upper mandible, fully confirm that conjecture, and at the same time show that a small portion only of the beak is represented by the fossil.

In 1849, D'ORBIGNY (*Cours Élémentaire de Paléontologie et Géologie*, p. 281) grouped some genera of rhyncholites (e.g., *Conchorhynchus*, *Rhynchoteuthis*, *Palaeoteuthis*) in a separate category of his classification of cephalopods, placing them neither in the so-called dibranchiates nor in the tetrabranchiates. On the other hand, in 1843, this author (*Paléontologie Française, Description des Mollusques et Rayonnes Fossiles, Terrains Jurassiques*, p. 163, pl. 39, 40) had unqualifiedly assigned *Rhyncholites gigantea* D'ORBIGNY, 1825, to *Nautilus giganteus* D'ORBIGNY, 1825, and

illustrated rhyncholites as "*Bec de Nautilus giganteus*" and "*Bec de Nautilus lineatus* Sow."

FOORD (1891, *Catalogue of fossil Cephalopoda*, p. 364), in agreement with OWEN, wrote:

The resemblance between the calcareous extremity of the upper mandible of *Nautilus pompilius* . . . and the corresponding fossil mandibles . . . will not be disputed. There seems to be, therefore, sufficient evidence upon which to rest the assumption that the fossil mandibles referred to belonged to the genus *Nautilus*. They do, indeed, vary in detail; but such variations may be significant of specific, rather than of generic differences in the animals to which the beaks belonged, or they may be due simply to difference in age.

TILL (1906, and later comprehensive papers) divided the rhyncholite genera and species studied by him into "*Nautilus-Schnäbel*" and "*Nicht-Nautilus-Schnäbel*" or "*Nicht-Nautilus-Rhyncholithen*."

RÜGER (40) expressed doubts about the suggested affinity of rhyncholites with genera of Nautilidae. He pointed out that rhyncholites appear in significant numbers first in Triassic rocks at a time when nautiloid cephalopods were declining, and that a discrepancy generally exists between the number of rhyncholites and the number of nautilid shells in rocks of this age. RÜGER suggested that the so-called "*Nautilus* beaks" of TILL did not belong to nautilids, ammonites, or belemnites, but to an unknown cephalopod group from which no other parts have been found preserved. These hypothetical cephalopods were interpreted to have been comparatively rare in numbers of individuals, though diversified into many genera and species. For the Lower Jurassic rhyncholites studied by him, RÜGER concluded that their bearers had no shells and were adapted to a benthonic life.

Opposed to RÜGER's views, Moos (25) pointed out that TILL's "*Nautilus* beaks" are highly peculiar and specialized organs which admittedly are very similar to the beaks of modern *Nautilus*. He found it difficult to believe that such specialized structures would have developed independently in two entirely different lineages of cephalopods.

BESSLER (4) believed that *Hadrocheilus* beaks did not belong to ammonoids or belemnites, because if they did they could

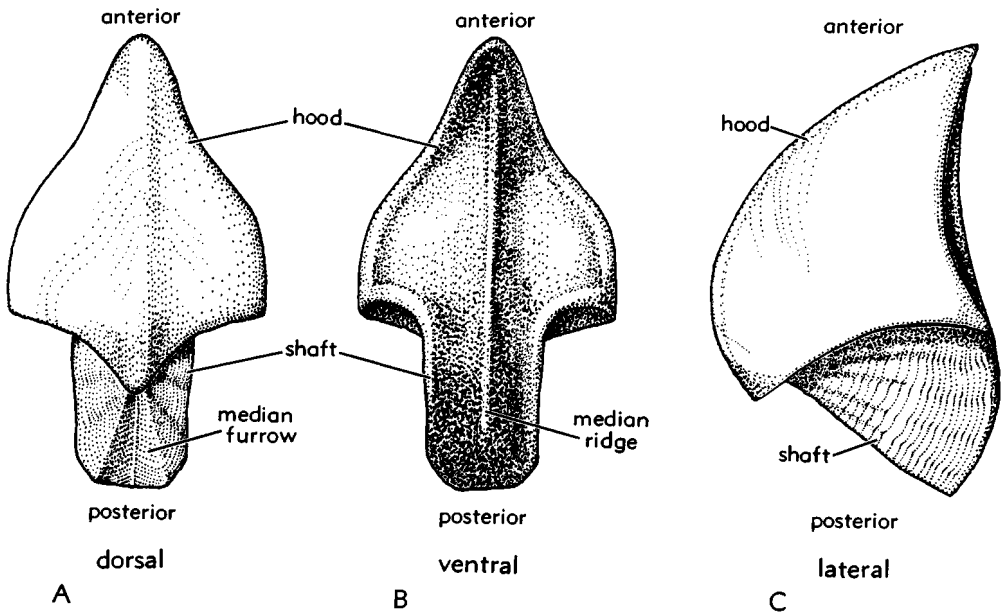


FIG. 342. Rhyncholite terminology. A, dorsal view; B, ventral view; C, lateral view (Teichert, Moore, & Zeller, n).

be expected to be much more common in Jurassic deposits. The first appearance of *Hadrocheilus* coincides approximately with that of the Chitinotheutidae. However, this group is restricted to the Middle Lias, whereas *Hadrocheilus* persists into the Upper Cretaceous. He also expressed the opinion that the “not-*Nautilus* beaks” belong to cephalopods lacking other hard parts and with soft body parts as yet unknown. He concluded (apparently in agreement with RÜGER, 40, and Moos, 25) that the present distribution of “not-*Nautilus* beaks” may be assumed to indicate the approximate range of distribution of the animals to which they belonged and that their relative abundance probably indicated population density.

SHIMANSKIY (45) undertook to analyze evidence for and against four hypotheses with respect to the relationships of rhyncholites. These were that (1) only nautiloids are represented by these sorts of fossil remains; (2) only external-shelled, supposed tetrabranchiate cephalopods (nautiloids and ammonoids) produced rhyncholites; (3) in addition to nautiloids and possibly ammonoids, some supposed dibranchiates (belemnoids) gave rise to rhyncholites; and

(4) nautiloids and some unknown types of shell-less cephalopods are the animals to which rhyncholites belonged.

Among suggestive observations reviewed by SHIMANSKIY is the reported occurrence of some 250 belemnoid rostra in the stomach contents of a Liassic fish without a single associated rhyncholite. Clearly, these ingested belemnites must have lacked fossilizable jaw parts. Also, it must be significant that in none of the rather numerous ammonoid conchs which have been discovered with aptychi remaining in the apertural region has a rhyncholite been found. The record of a fossil collection from a single Jurassic locality (Verkhni-Rechensk) in the USSR in which some 10,000 belemnoid rostra, 2,000 ammonoids, and miscellaneous other remains are associated with 150 rhyncholites, but in which no specimen of nautiloid is found, lacks significance, especially in view of the much-too-small size of the belemnoid rostra in comparison with the moderately robust rhyncholites. It is sufficient to report SHIMANSKIY's conclusion that only negative evidence can be adduced for support of any of the hypotheses advanced by him, but he was able to exclude probabilities that rhyncholites are hard parts

of cephalopods other than nautiloids and soft-bodied forms without an external or internal skeleton. That is to say, ammonoids and belemnoids were not thought by him to be organisms represented by remains classed as rhyncholites. An effort to correlate the known stratigraphic distribution of different sorts of rhyncholites with nautiloid genera having like range is interesting and suggestive, but not more than that. The known facts are best accommodated by the interpretation that rhyncholites were formed by unknown cephalopods, some of which probably belong to the Nautilida. These unknown cephalopods are classifiable in terms of genera and species based on the characters of their rhyncholite remains.

### STRATIGRAPHIC AND GEOGRAPHIC DISTRIBUTION

The great majority of all rhyncholites are known from rocks of Mesozoic age in France, southern Germany, southern Poland, and the southern part of the European USSR. They are generally rare fossils and occurrences of more than a few individuals in any one locality are unusual.

In pre-Mesozoic rocks rhyncholites do exist, but they are even more rare, only three specimens having been made known from the Carboniferous and Permian Systems: *Tillicheilus? sella* (ROEMER), doubtfully recorded from the Lower Carboniferous of Germany, *Rhynchoteuthis kaibabensis* BRADY from the Lower Permian of Arizona (USA), and an unnamed *Conchorhynchus?* from the Upper Permian Kupferschiefer of Germany. The specimens described from the Permian of Arizona are the more remarkable in that they are the only rhyncholites so far recorded from the Western Hemisphere. A suggestion made by TILL (48, p. 148) that *Aptychus? knoxvillensis* STANTON (1895) from the Cretaceous of California may be a rhyncholite is rejected by us.

The only rhyncholites of Mesozoic age known outside of Europe are *Hadrocheilus kossmati* TILL (50) and *Rhynchoteuthis sonii* SAHNI & JAIN (41a) from the Upper Cretaceous of southern India and *Hadrocheilus costatus* TILL from the Lower Cretaceous of Algeria (46a). In addition,

rhyncholite- and conchorhynch-type beaks have been described from the Eocene of Egypt (51).

The reasons for the geographically restricted distribution of rhyncholites are not clear, but perhaps this distribution pattern is more apparent than real. Additional finds in Asia may be expected which would materially affect the present picture.

### PALEOECOLOGY

GASIOROWSKI (19) found rhyncholites in the Jurassic-Cretaceous Klippe zone of the Carpathian Mountains to be restricted to rocks thought to have been deposited in deep water; among these rocks are radiolarites and nodular limestones with and without calpionellids. From these observations one might conclude that the cephalopods from which the rhyncholites came were essentially eupelagic. It is interesting to compare this observation with reports of mass occurrences of cephalopod beaks in the deeper parts of the Arabian Sea and the Gulf of Aden, where up to 15,000 beaks per square meter have been dredged up (14).

On the other hand, many jaw-bearing cephalopods undoubtedly lived in shallow water as shown by the occurrence of rhyncholites in the German Muschelkalk.

BRADY (10, p. 102), in discussing a collection of specimens of *Rhynchoteuthis* from the Kaibab Limestone of southern Arizona (USA), wrote:

David Nicol (1944, p. 553) describes the strata from which the material here described was collected as 'thin bedded dolomites, dolomitic sandstone . . .' and believes that they represent deposits in shallow, landlocked and somewhat hypersaline seas, and that the nautiloids were swept into these sediments by waves or currents. He recognized, however, the possibility that they may be true facies fossils, species which had adapted themselves to conditions somewhat abnormal for such cephalopods.

It is significant that all of the specimens in question were collected in the particular horizon near the top of the formation from which almost all the nautiloids of the Kaibab have come.

### BIOSTRATONOMY

After the death of a jaw-bearing cephalopod, the jaws and soft parts would sink to

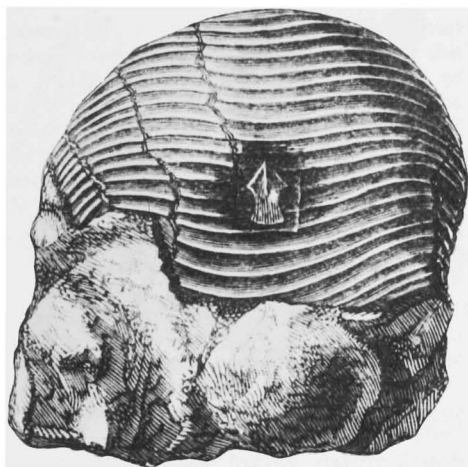


FIG. 343. *Somalinautilus libanoticus* (FOORD & CRICK), U.Cret., Lebanon, with rhyncholite preserved in ventral side of body chamber,  $\times 1$  (17) (p. K477).

the bottom and, if the cephalopod possessed a shell, this very likely would become separated from the jaws. Several nautilid shells with rhyncholites embedded in the matrix filling their body chambers are on record, but few of these specimens have ever been described adequately. Thus, BUCKLAND (12) mentioned "a specimen of a fossil *Nautilus* from the Lias of Lyme Regis [England] in which the external open chamber contains a rhyncholite." FOORD (17) reported that the British Museum possessed five specimens of *Nautilus* (*recte Somalinautilus*) *libanoticus* from the Upper Cretaceous of Lebanon (of which he figured one<sup>1</sup>), "exhibiting the mandibles associated with the shell, and in each example there is a brownish stain surrounding the mandible caused, no doubt, by the decay of animal matter." All beaks are exposed on the surface of the internal mold on the ventral side of the body chamber (Fig. 343). Additional information is lacking. As far as one can judge, all five "mandibles" are upper jaw parts and no lower jaw parts are present. TILL (51) referred to "*Nautilus*" shells with rhyncholites in their body chambers deposited in the Senckenberg Museum, Germany, but he failed to give age(s) and localities.

As a rule it may be expected that the jaws and soft parts attached to them would sink

slowly through the water. If currents existed in the water body, they would carry the slowly sinking cephalopod remains a variable distance. Lower beaks of the *Conchorhynchus* type, as shown by RUTTE (41), have horny parts that are larger than those of upper beaks; thus, the two jaws might become separated on their downward journey to the sea floor.

TILL (47) has observed that, on drying, the calcareous part of an upper beak of Recent *Nautilus* broke away from the horny parts, whereas the calcareous part of the lower beak disintegrated into small particles. This observation may account for the fact that remains of lower beaks (conchorhynchus) are much rarer as fossils than those of upper beaks (rhyncholites). RUTTE (41) found that specimens of *Conchorhynchus* in marl were embedded either lying on their sides or with the median ridge pointing upward.

TILL (50) reported that in rhyncholites of *Rhynchoteuthis* type (with dorsal furrow) the hood breaks away easily from the shaft. The posterior edges of such hoods are almost always broken. Chipping and breaking during transportation and sedimentation may considerably affect the shape of rhyncholites.

Possible horizontal transportation of cephalopod jaw parts after death of the animal, as previously suggested, must have been relatively small. Therefore, the present distribution of rhyncholites in deposits of any given age may be presumed to coincide approximately with the range of the cephalopods to which they belonged. Furthermore, since rhyncholites are not easily destroyed during sedimentation or diagenesis, abundance of these fossils in sedimentary rocks may reflect the relative population density of their bearers (4, 25, 40).

## SYSTEMATIC DESCRIPTIONS

### Class CEPHALOPODA Cuvier, 1797

### Order and Family UNCERTAIN

[Arrangement of genera is in chronological order of their description]

**Rhyncholite** BIGUET, 1819, p. 58 [\**R. hirundo*; SD TEICHERT, MOORE & ZELLER, herein] [= *Rhyncholites* D'ORBIGNY, 1825, p. 212; *Rhyncholithes* DE

<sup>1</sup> According to L. R. Cox (personal communication), preserved in the British Museum (Natural History).

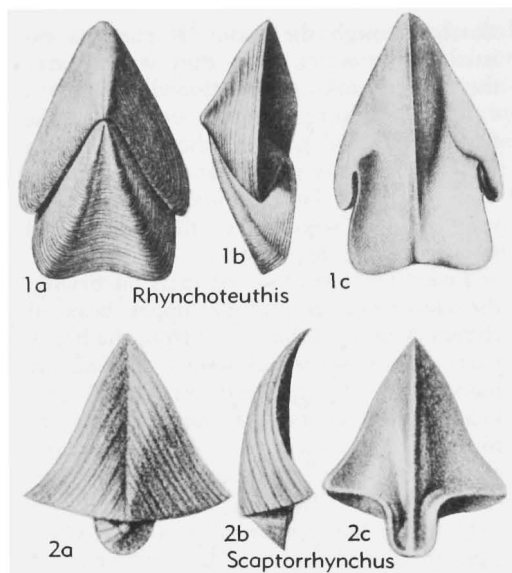


FIG. 344. Rhyncholites. 1, *Rhynchoteuthis astieriana* D'ORBIGNY,  $\times 1$  (32). 2, *\*Saptorrhynchus miocenicus* BELLARDI,  $\times 2$  (2) (p. K478-K479).

BLAINVILLE, 1827, p. 114 (obj., type, *R. hirundo*—*lapsus pro R. hirundo*—BIGUET, 1819, p. 59); *Rhyncholites* ZIETEN, 1830, p. 49 (type, *R. hirundo* BIGUET, 1819; SD TEICHERT, MOORE & ZELLER, herein); *Rhyncholites* MÜNSTER, 1829, p. 70 (nom. null.) (type, *R. duplicatus*; M); *Rhyncholithus* BRONN, 1853, p. 180 (obj., type, *R. hirundo* BIGUET, 1819; SD TEICHERT, MOORE & ZELLER, herein); *Rhyncholythes* BELLARDI, 1873, pl. 3 (nom. null.); *Rhombocheilus* SHIMANSKIY, 1947, p. 1476 (obj.); *Nautilorhynchus* FRIČ, 1910, p. 15 (nom. null.); *Longocapuchones* SHIMANSKIY, 1947, p. 1476 (type *Rhyncholites gigantea* D'ORBIGNY, 1825, p. 215)]. Inferred upper beak with relatively broad rhomb-shaped hood, elevated median upper part rounded to keel-like, lower surface gently concave, shaft convexly rounded dorsally, concave ventrally, triangular in side view. *M.Trias.-Mio.*, Eu.-Afr.(Egypt).—FIG. 338,2. *\*R. hirundo*, *M.Trias.*, Eu.(Fr.); 2a-h, upper (dorsal), lower (ventral), and lateral views of 2 specimens,  $\times 2$  (18).

**Conchorhynchus** DE BLAINVILLE, 1827, p. 115 [*\*C. ornatus* (= *Lepadites avirostris* VON SCHLOTHEIM, 1820, p. 169; “première espèce” GAILLARDOT, 1824, p. 485; *Rhyncholites Gaillardoti* D'ORBIGNY, 1825, p. 219; *Rhyncholites Gaillardoti* ZIETEN, 1830, p. 49; *Sepia Gaillardoti* KEFERSTEIN, 1834, p. 53; *Conchorhynchus avirostris* BRONN, 1837; OD(M)] [= *Onchorhynchus* OPPENHEIM, 1906, p. 346 (nom. null.); *Conchorhynchus* TILL, 1906, p. 91 (nom. null.)]. Inferred lower beak, subrhombic in outline, thin, upper (dorsal) side gently concave, surface sloping to shallow median

furrow, edges near tip corrugated; lower (ventral) side transversely slightly convex, mid-line marked by keel with short side ridges that diverge at acute angle from keel. *U.Perm.-M.Trias.*, Eu.; ?*L. Tert.(Eoc.)*, Eu.(Belg.)-Afr.(Egypt).—FIG. 338, 1. *\*C. avirostris* (VON SCHLOTHEIM), *M.Trias*, Eu. (Fr.); 1a-f, upper (dorsal), lat., and lower (ventral) views of 2 specimens,  $\times 2$  (18).

[The Zoological Code (Art. 30,a,i,3) classes generic names with endings in -us, based on latinized Greek words of feminine or neuter gender (e.g., -rhynchus, -cheilus), as having masculine gender.]

**Rhynchoteuthis** D'ORBIGNY, 1847, p. 593 [*\*R. astierianus* D'ORBIGNY, 1847, p. 598; SD TEICHERT, MOORE & ZELLER, herein] [= *Rhyncholites* AUCTT. (non CHUN, 1903, p. 716); *Rhynchotenthis* COLLINGE, 1893 (nom. null.); *Rhynchoteuthis* TILL, 1906, p. 133 (nom. van.)]. Head arrowhead-shaped, strongly notched opposite point and set off from shaft by relatively deep and narrow indentation, upper (dorsal) side with median part narrowly rounded, lower (ventral) side marked by keel that extends onto shaft, which is moderately broad and short, with dorsal side marked by diverging curved ridges having well-rounded summits, median area shallowly depressed, sides steep-sloping, ventral side of shaft divided into 2 gently concave areas. [SHIMANSKIY's (44, p. 1476) designation of *R. astierianus* as the type-species of *Hadrocheilus* TILL, 1907, is invalid because this species was not listed by TILL among forms originally assigned by him to *Hadrocheilus*.] *L.Perm.*, N.Am.(Ariz.); *L.Jur.(Lias.)-U.Cret.(Senon.)*, Eu.; *U.Cret.(Cenoman.)*, Asia(India).—FIG. 344,1. *\*R. astieriana*, *L.Cret.(Apt.)*, Eu.(Fr.); 1a-c, dorsal, lat., ventral views,  $\times 1$  (32).

**Palaeoteuthis** D'ORBIGNY, 1849, p. 281 [*\*P. Honoratianus* D'ORBIGNY, 1849 (1850), p. 327; SM] [non *Palaeoteuthis* ROEMER, 1855; nec AMEGHINO, 1889] [= *Palaeotheutis* TILL, 1906, p. 91 (nom. van.)]. Hood triangular, somewhat rounded at anterior tip; median furrow on dorsal side extending almost one-half distance from tip to base; shaft broad and short; prominent median ridge extending along entire ventral surface. *M. Jur.(Callov.)*, Eu.(Fr.).—FIG. 344A. *\*P. honoratianus*; 1a-c, dorsal, lat., and ventral views,  $\times 4$  (14a).

[Original description (in D'ORBIGNY's *Cours Élémentaire*, 1849, p. 281): “*Palaeoteuthis*, d'Orb., 1847. Bec voisin des *Rhynchoteuthis* mais bien plus étroit, très-pointu, lancéolé en avant, sans ailes latérales, pourvu seulement d'un talon postérieur, plus large que reste. Une seule espèce connue est de l'étage callovien.” No illustration was given and no species was named. Subsequently, in the *Prodrome de Paléontologie*, bearing date of 1849 but published in 1850, a nearly identical description was given (33, p. 327), accompanied by the notation: “*Honoratianus* d'Orb., 1847. La seule espèce connue. France, Chaudon (Basses-Alpes).” This is thus the type by subsequent monotypy. The type was redescribed and illustrated by COTTREAU (14a, 14b) in the *Annales de Paléontologie* (t. 8, fasc. 4, 1913; t. 14, fasc. 4, 1925). The type-specimen (no. 3154) still exists in the d'Orbigny Collection in the Muséum National d'Histoire Naturelle (personal communication from Mme. S. Freneix, Muséum National d'Histoire Naturelle, Paris, to L. R. Cox.)]



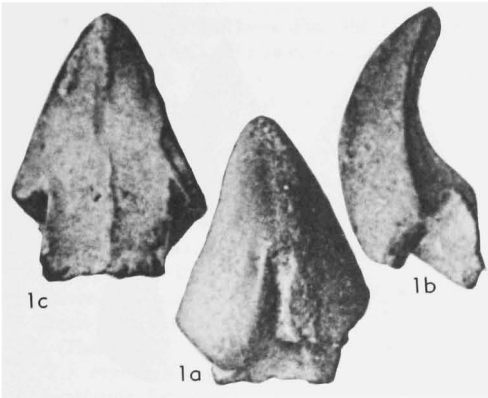


FIG. 344A. \**Palaeoteuthis honoratianus* D'ORBIGNY,  $\times 4$  (14a).

**Scaptorhynchus** BELLARDI, 1871, p. 12 [\**S. miocenicus*, 1873, p. 42; SM] [= *Scaptorhynchus* ZITTEL, 1885, p. 387 (*nom. null.*)]. Hood thin, narrowly triangular, lateral margins slightly sinuate, posterior edge knife-sharp, slightly sinuate, bowing outward near tip and inward near posterolateral corners, dorsal side convex but with narrow longitudinal furrow, ventral side concave except for straight, prominent median keel; shaft narrow and very short, on dorsal side separated from hood by suture-like depression but on ventral side continuous with hood and its keel. *Mio.*, Eu.(Italy).—FIG. 344,2. \**S. miocenicus*;

2a-c, dorsal, lat., ventral sides of upper beak,  $\times 2$  (2). [See note under *Conchorhynchus*.]

**Hadrocheilus** TILL, 1907, p. 568 [\**H. Theodosiae*, p. 586; SD TEICHERT, MOORE & ZELLER, herein] [As noted under *Rhynchoteuthis*, SHIMANSKIY's (44, p. 1476) designation of *R. astierianus* D'ORBIGNY, 1847, as type-species of *Hadrocheilus* is invalid]. Head arrow-like, posterior margin strongly notched, dorsal side with moderately steep slopes from rounded median ridge, ventral side gently concave, with narrow keel that extends onto shaft; shaft large and wide, dorsal side clearly divided into 3 areas by diverging slightly curved ridges that extend from center of notch in hood to posterolateral extremities of shaft, median area gently concave. *Jur.-Cret.*, Eu.-USSR; *L.Cret.*, Afr.(Algeria). [See note under *Conchorhynchus*.]

**H. (Hadrocheilus)**. Longitudinal profile wavy on lower (ventral) side. *Jur.-Cret.*, Eu.(Ger.-USSR).

—FIG. 345,1. \**H. (H.) theodosiae*, U.Jur. (Tithon.), Crimea; 1a-c, dorsal, lat., ventral views,  $\times 2$  (48).

**H. (Arcuatobeccus)** SHIMANSKIY, 1947, p. 1476 [\**Hadrocheilus procerus* TILL, 1907, p. 606; OD]. Ventral side of hood somewhat concave. *Jur.-L.Cret.*, Eu.(Fr.-USSR).—FIG. 345,2. \**H. (A.) procerus* TILL, *L.Cret.*(Neocom.), Fr.; 2a-c, dorsal, lat., ventral sides,  $\times 2$  (48).

**H. (Convexiterbeccus)** SHIMANSKIY, 1947, p. 1476 [\**Hadrocheilus convexus* TILL, 1907, p. 576; OD]. Longitudinal profile uniformly convex on

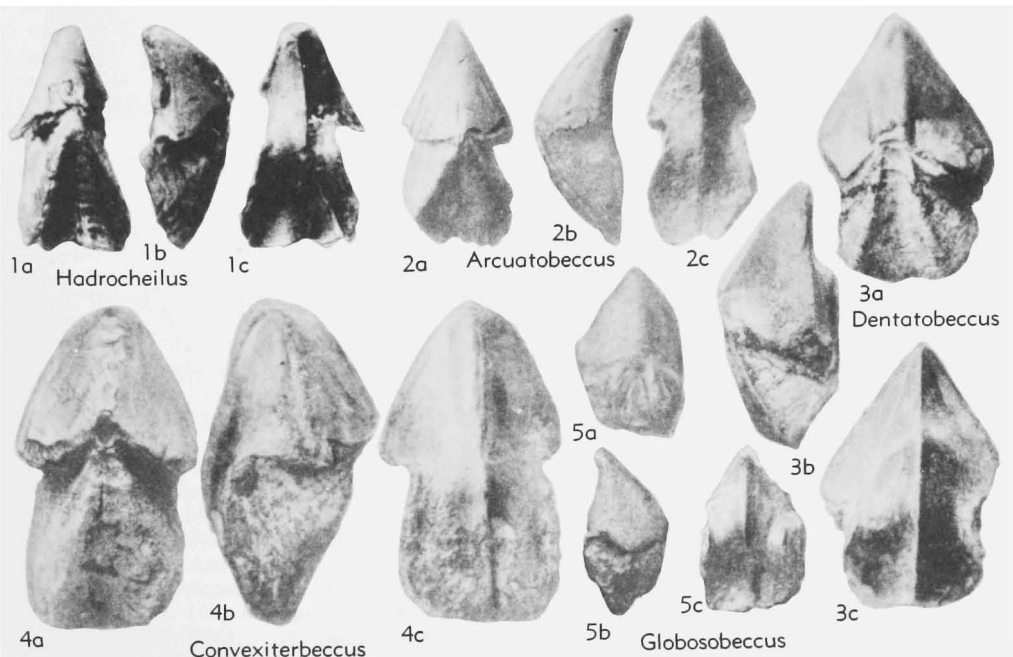


FIG. 345,1-5. Rhyncholites,  $\times 1.5$  (48, 49) (p. K479-K480).

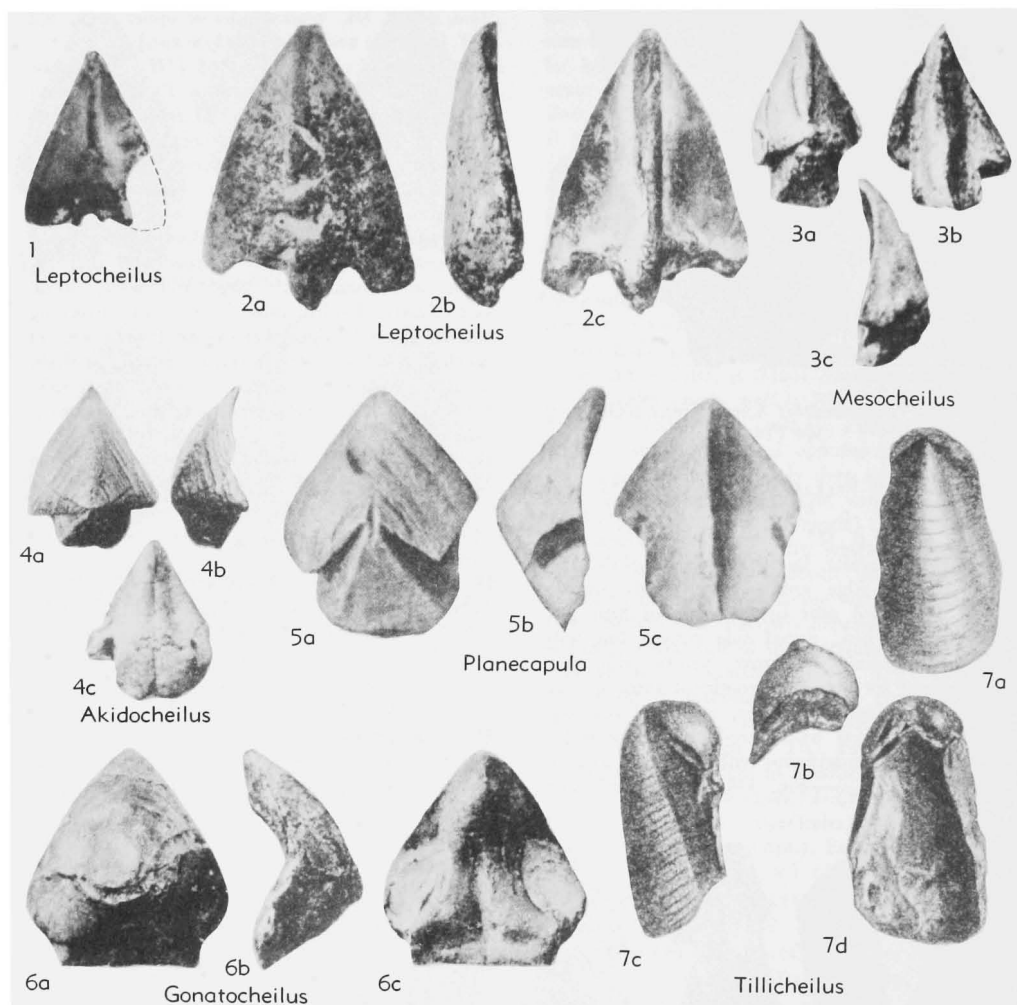


FIG. 346, 1-6. Rhyncholites,  $\times 1.5$  (44, 48, 49) (p. K480-K481).

ventral side. *L.Cret.(Neocom.)*, Eu.(Fr.-USSR).  
—FIG. 345, 4. \**H. (C.) convexus* TILL, Fr.;  
4a-c, dorsal, lat., ventral sides,  $\times 2$  (48).

**H. (Dentatocheilus)** SHIMANSKIY, 1947, p. 1476  
[\**Hadrocheilus gibber* TILL, 1907, p. 590; OD].  
Ventral side with strong, sharp, generally wide  
toothlike outgrowth beneath middle of hood or  
its apex. *M.Jur.-L.Cret.*, Eu.(Fr.-USSR). —FIG.  
345, 3. \**H. (D.) gibber* TILL, *L.Cret.(Neocom.)*,  
Fr.; 3a-c, dorsal, lat., ventral sides,  $\times 2$  (48).

**H. (Globosobecus)** SHIMANSKIY, 1947, p. 1476  
[\**Hadrocheilus globosus* TILL, 1909, p. 585;  
OD]. Both dorsal and ventral sides strongly  
convex, whole upper beak subspheroid. *L.Jur.-*  
*M.Jur.*, Eu.(Fr.-USSR). —FIG. 345, 5. \**H. (G.)*  
*globosus* TILL, *L.Jur.*, Fr.; 5a-c, dorsal, lat.,  
ventral sides,  $\times 2$  (49).

**Leptocheilus** TILL, 1907, p. 617 [\**L. Geyeri*; SD  
SHIMANSKIY, 1947, p. 1477]. Thin, with arrow-  
head-like hood bearing well-defined longitudinal  
median rib on dorsal side, shallowly concave  
ventral side also with longitudinal keel; shaft small,  
sulcate in transverse section. *M.Jur.-L.Cret.*, Eu.  
(Fr.-Aus.-USSR).

**L. (Leptocheilus)**. Shaft very diminutive, less  
than half length of hood and much narrower.  
*M.Jur. - L. Cret.*, Eu.(Fr.-Aus.-USSR). — FIG.  
346, 1. \**L. (L.) geyeri*, U.Jur., Austria; dorsal  
side,  $\times 2$  (48). — FIG. 346, 2. *L. (L.) excavatus*  
TILL, U.Jur., Fr.; 2a-c, dorsal, lat., ventral sides,  
 $\times 2$  (48).

**L. (Mesocheilus)** TILL, 1909, p. 601 [\**Meso-*  
*cheilus proceroides*; SD SHIMANSKIY, 1947, p.  
1477]. Shaft nearly equal to hood in length.

*M. Jur.*, Eu.(Fr.-USSR).—FIG. 346,3. \**L. (M.) proceroides* (TILL), Fr.; 3a-c, dorsal, ventral, and lat. sides,  $\times 2$  (49).

**Akidocheilus** TILL, 1907, p. 629 [*\*A. ambiguus*; OD]. Like *Leptocheilus* but dorsal side of hood smooth and shaft, though short, notably wider, ventral side concave, with low median keel on hood and with or without narrow furrow on shaft. *M. Jur.-L. Cret.*, Eu.(Fr.-USSR).

**A. (Akidocheilus)**. Shaft with furrow. *M. Jur.-L. Cret.*, Eu.(Fr.-USSR).—FIG. 346,4. *A. (A.) tauricus* TILL, U. Jur., USSR (Crimea); 4a-c, dorsal, lat., ventral sides,  $\times 2$  (48).

**A. (Planecapula)** SHIMANSKIY, 1947, p. 1477 [*\*A. (P.) infirus*; OD]. Shaft without furrow, its dorsal side flat. *L. Cret.*, Eu.—FIG. 346,5. \**A. (P.) infirus*, Apt., USSR (Crimea); 5a-c, dorsal, lat., ventral sides,  $\times 1.3$  (44).

**Gonatocheilus** TILL, 1907, p. 641 [*\*Rhynchoteuthis Brunneri* OOSTER, 1857, p. 6; OD]. Hood thin, sharp-pointed, heart- to arrowhead-shaped, dorsal side smooth, ventral side concave, with strong tooth near anterior extremity; shaft thin, moderately broad, nearly concealed by hood in dorsal view, ventral side with narrow fissure-like groove. *M. Jur.-L. Cret. (Apt.)*, Eu. (Ger.-Fr.)-USSR (Crimea).—FIG. 346,6. \**G. brunneri* (OOSTER), U. Jur., Fr.; 6a-c, dorsal, lat., ventral sides,  $\times 2$  (48).

**Tillicheilus** SHIMANSKIY, 1947, p. 1477 [*\*Rhyncholithes obtusus* TILL, 1906, p. 121; OD] [= *T. (Unguibeccus)* SHIMANSKIY, 1949, pl., p. 201 (nom. nud.)]. Hood diminutive, subglobular, smooth, prominent in front view but barely visible in dorsal view, marked off from shaft by suture-like furrow; shaft large, width slightly greater than hood but length at least 3 times greater, dorsal side strongly convex, sides flattened or slightly concave, ventral side distinctly concave both transversely and longitudinally, smooth. *Carb.-L. Cret.*, Eu.—FIG. 346,7. \**T. obtusus* (TILL), L. Cret., Ger.; 7a-d, dorsal, ant., lat., ventral views,  $\times 2$  (47).

**Erlangericheilus** SHIMANSKIY, 1947, p. 1477 [*\*E. insignis*; OD (M)]. Hood short, conical, tooth-like, distinct from well-defined shaft which on dorsal side bears longitudinal furrow bordered by ridges, ventral side slightly convex. *L. Cret. (Apt.)*, USSR (Crimea).—FIG. 347,1. \**E. insignis*; 1a-c, dorsal, lat., ventral sides,  $\times 1.3$  (44).

## GENERA ORIGINALLY CLASSED AS NAUTILOID MANDIBLES BUT LATER AS GASTROPOD OPERCULA

**Cyclidia** ROLLE, 1862, p. 121, 122 [*\*C. valida*; OD (M)] [*non Cyclidia* GUENÉE, 1857]. Believed by author to be cephalopod beak; according to ZITTEL (54) and TILL (47) is a gastropod operculum. *Tert. (Mio.)*, Eu.(Ger.).

**Peltarion** EUDES-DESLONGCHAMPS & EUDES-DESLONGCHAMPS, 1858, p. 153 [*\*P. unilobatum*; SD

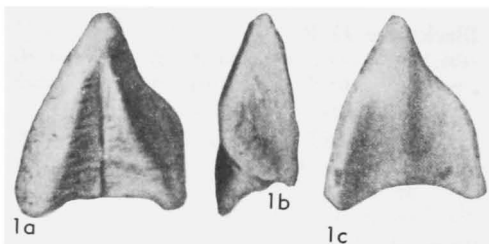


FIG. 347. \**Erlangericheilus insignis* SHIMANSKIY,  $\times 1.3$  (44) (p. K481).

TEICHERT, MOORE & ZELLER, herein] [*non Peltarion* JACQUINOT & LUCAS, 1853 (1847?). *Lias?* (*L. Jur.*), Eu.(Fr.-Ger.).

**Rhynchidia** LAUBE, 1870, p. 54, 56 [*\*R. cassiana*; OD (M)] [= *Rhynchidia* LAUBE, 1868, p. 538 (nom. nud.)]. Originally thought to be cephalopod beak, but ZITTEL (54, p. 387) described it as gastropod operculum. *Trias.*, Eu.(Austria).

**Scaphanidia** ROLLE, 1862, p. 127 [*\*Rhyncholithus Buchi* MÜLLER, 1851; OD] [= *Peltarion* EUDES-DESLONGCHAMPS & EUDES-DESLONGCHAMPS, 1858, according to ZITTEL (54, p. 387)]? *Jur.*, Eu.(Fr.-Eng.); *Cret.*, Eu.(Ger.).

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## DOUBTFUL TAXA

By CURT TEICHERT

[United States Geological Survey]

### ORDER UNCERTAIN

#### Family NEPTUNOCERATIDAE

Shimanskiy, 1956

Weakly cyrtconic conchs, slightly expanding, with subquadrangular cross section; surface ornamented by fine, transverse ribs. [Assigned to Nautilida, superfamily Rutocerataceae, by SHIMANSKIY, but lack of knowledge of siphuncle structure makes this placement doubtful. May be intermediate between Oncocerida and Nautilida. According to FURNISH, GLENISTER & HANSMAN (1962) the specimens on which the two genera of this family are based may well represent growth stages of *Brachycycloceras*, a genus of deciduous Pennsylvanian orthocerids.] *U.Carb.*

*Neptunoceras* SHIMANSKIY, 1949 [\**N. sakmarensis*; OD]. Cyrtconic conchs with quadrangular cross section; weakly annulate; sutures slightly wavy; siphuncle unknown. *U.Carb.*, S.USSR.—FIG.

348,2. \**N. sakmarensis*; 2a, convex side, 2b, lat., ×3 (11).

*Tetrapleuroceras* SHIMANSKIY, 1949 [\**T. karpinskiyi*; OD]. Weakly cyrtconic conchs with subquadrangular cross section; surface weakly annulate; sutures almost straight; siphuncle near convex side. *U.Carb.*, S.USSR.—FIG. 348,1. \**T. karpinskiyi*; 1a, concave side, 1b, lat., 1c, adapical, ×2 (11).

### Order & Family UNCERTAIN

*Dartoceras* FOERSTE, 1936 [\**D. nodosum*; OD]. Weakly cyrtconic, rapidly expanding conch with weak transverse annulations and single row of widely spaced nodes along each ventrolateral side; siphuncle unknown. [Possibly a barrandocerid.] *M.Sil.*, E.Can.—FIG. 349. \**D. nodosum*, Gaspé Penin.; ×1 (4).

*Hedstroemoceras* FOERSTE, 1930, p. 126 [\**H. hael-luddense*; OD (M)]. Conch small, erect, dorsal outline faintly convex, ventral outline more distinctly convex; cross section nearly circular,

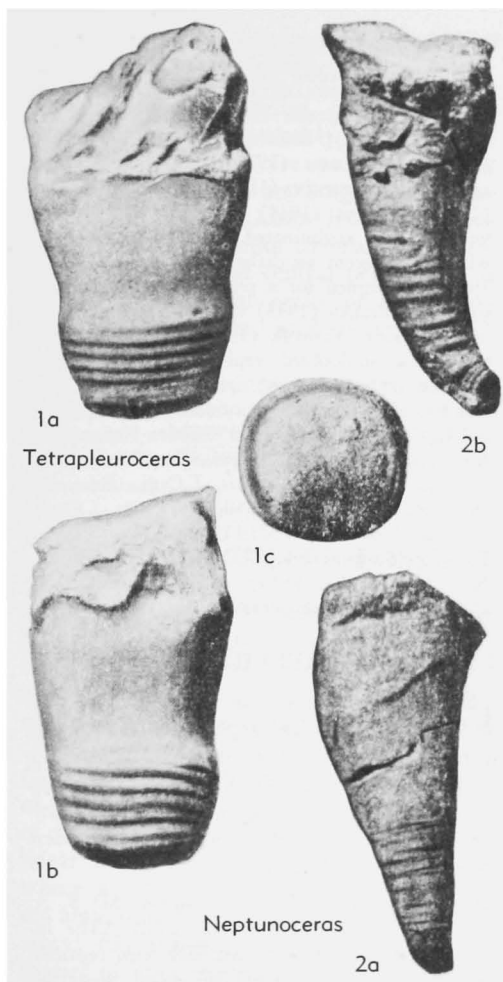


FIG. 348. Order Uncertain, Family Neptunoceratidae (p. K484).

slightly compressed laterally; living chamber enlarging but slightly; siphuncle located near ventral side of conch, but not in contact with it, its segments fusiform in outline. *L.Ord.* (*Vaginatium* *Ls.*), Eu. (Sweden, Öland Is.).

## TAXA DOUBTFULLY CLASSIFIABLE AS NAUTILOIDS

This section is set apart for treatment of some puzzling fossils which have been considered by various authors to be primitive representatives of the class Cephalopoda, and if so, most closely related to one or more of the nautiloid orders. On the other hand, there is ample room for doubt that they are cephalopods at all. [Some notes by



FIG. 349. \**Dartoceras nodosum* FOERSTE, Order and Family Uncertain (p. K484).

D. W. Fisher have been incorporated into this section.]

## Order VOLBORTHELLIDA Kobayashi, 1937

[*nom. correct* ZHURAVLEVA, 1955, ex Volborthellidea KOBAYASHI, 1937] [=Protochoanites GRABAU & SHIMER, 1910 (order); Volborthellacea KUHN, 1949 (order)]

Small, orthoconic, or slightly cyrtconic shells of circular cross section, having closely spaced septa with central perforations that may indicate presence of a siphuncle. *L.Cam.-M.Cam.*

## Family VOLBORTHELLIDAE Kiaer, 1916

[=Paleonavtili VOLBORTH (1869, MS.) in GEKKER, 1928]

Minute longiconic shells of circular cross section, divided internally by very closely spaced conical partitions having narrow perforations at their tips so as to form central tube interpreted by some authors as analogous to siphuncle of cephalopods, conical partitions about 6 to 8 in 1 mm., spaces between them filled with quartz and dark minerals. [The nature of the central tube is problematical, since no outer wall has been observed with certainty. Also the character of the shell material is doubtful; it may have consisted of some organic substance or possibly it was calcareous with organic admixtures. Originally included in the order was *Volborthella* alone, believed to be a cephalopod. Probably the assemblage should be more widely construed to include representatives of short-lived abortive groups of Early Cambrian animals that competed unsuccessfully with trilobites, gastropods, and hyolithids.] *L.Cam.-M.Cam.*



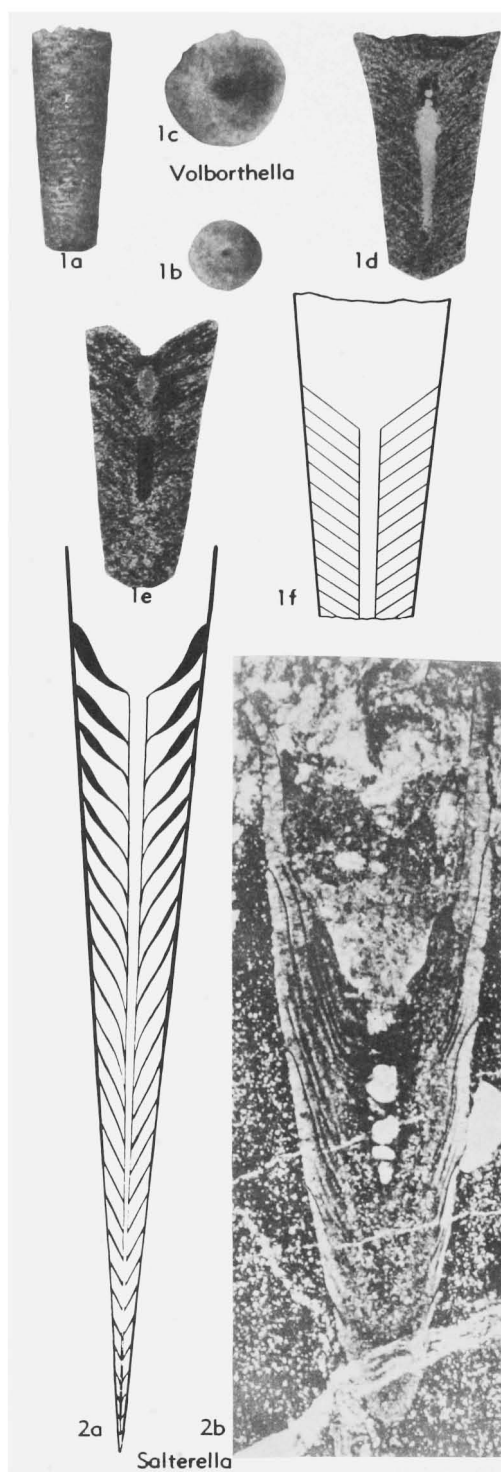


FIG. 350. Volborthellidae (p. K486); Salterellidae (p. K486).

**Volborthella** SCHMIDT, 1888 [*\*V. tenuis*; M] [= *Volborthella* DAVITASHVILI, 1958 (nom. null.)]. Characters of family. [External characters of this genus have been described by SCHMIDT (1888), KARPINSKY (1903), BRAASTED (1915), and KIAER (1916), and internal characters by KARPINSKY (1903) and SCHINDEWOLF (1928). GÜRICH (1934) compared *Volborthella* with certain agglutinated protozoans and also with some Recent ascidians. SCHINDEWOLF (1928, 1934) has argued for a primitive cephalopod assignment. MILLER (1943) was convinced that they are pteropods. FLOWER (1954) pointed out that the oldest undoubted cephalopods (Cambrian) possessed cyrtconic, not orthoconic conchs. The affinities of *Volborthella* continue to be controversial.] *L.Cam.*, Eu. (USSR-Est.-Sweden-Norway)-N. Am. (Can.)-Australia; *M.Cam.*, Eu. (Czech.-Pol.). —FIG. 350,1a. *\*V. tenuis*, *L.Cam.*, Est.; side view,  $\times 10$  (9). —FIG. 350,1b,c. *V. sp.*, *L.Cam.*, Est.; apical, oral views,  $\times 10$  (9). —FIG. 350,1d,e. *V. conica* SCHINDEWOLF, *L.Cam.*, Est.; long. secs.,  $\times 13$  (9). —FIG. 350,1f. *V. sp.*, diagram. sec. as interpreted by Schindewolf (9).

#### Family SALTERELLIDAE Poulsen, 1932

Small, slender, conical calcareous conchs with strongly conical septa; shell long and straight or gently curved, with encircling striae on exterior; thick, slightly sinuate septa resembling invaginated cones; foramen at apex of conch may be surrounded by elongated collar. *L.Cam.*

**Salterella** BILLINGS, 1861 [*\*S. rugosa*; SD S. A. MILLER, 1889]. Characters of family. [The internal structures of this fossil have been regarded by some authors as septa and septal necks, respectively. Similarly, a central tube has been considered to be a siphuncle. CLARK (1925) and POULSEN (1932) regarded *Salterella* as a primitive cephalopod. TEICHERT (1935) and FLOWER (1943, 1954) interpreted it as an invertebrate of uncertain affinities. BILLINGS, COBBOLD, and WILCOTT considered *Salterella* to be a pteropod. KOBAYASHI (1937) thought that *Salterella* and *Volborthella* were allied, forming a "solid group of fossils intermediate between the hyolithids and nautiloids, but closer to the latter." A. K. MILLER (1943) regarded these two genera as pteropods, but such an assignment is quite unsubstantiated. It seems probable that *Salterella* is molluscan in nature but having very slight affinities with any modern representative of the Mollusca.] *L.Cam.*, N. Am. (Mex.-USA-Can.-Greenl.)-Eu. (Eng.)-Asia. —FIG. 350,2a. *S. conulata* CLARK, Can.; diagram. sec.,  $\times 4$  (1). —FIG. 350,2b. *\*S. rugosa*, Greenl., transv. sec.,  $\times 10$  (7).



## Family VOLOGDINELLIDAE

Balashov, 1962

Very small cylindrical conchs of depressed cross section; weakly concave transverse partitions that are as thick as the spaces between them are long, having central perforation. [BALASHOV interprets transverse partitions as septa covered with cameral deposits and the central perforation as siphuncle. No septal necks or connecting rings have, however, been observed.] *M. Cam.*

*Vologdinella* BALASHOV, 1962, p. 72 [*\*Orthoceras? antiquus* VOLOGDIN, 1930] [= *Vologdinella* SHIMANSKIY, 1956 (*nom. nud.*)]. Characters of family. Very poorly known. *M. Cam.*, USSR (Kazakhstan).

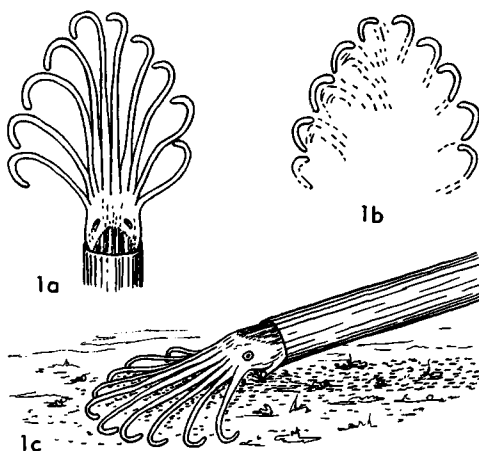


FIG. 351. 1a-c. Possible reconstruction of orthocerid with tentacles in position in which they may have made impressions; 1b. Impressions interpreted as those of an orthocerid (adapted from 3).

## NAUTILOID TRACE FOSSILS

The most authentic record of impressions and trails made by nautiloid cephalopods is from the Upper Ordovician of Ohio, USA (3). The following types, all ascribed to action of individuals belonging to the genus *Orthonyboceras*, have been distinguished: (1) orthoconic cephalopod shells at the end of linear trails, made by forward movement of the animal shortly before death; (2) short linear trails, rounded at both ends, made where a cephalopod came to rest on the sea bottom, moved forward, and then swam away; (3) similar trails clustered around masses of organic debris, indicating a feeding place; and (4) crescentic impressions arranged more or less in a semicircle in groups of ten, believed to be left by distal ends of tentacles seeking a hold on the bottom (Fig. 351). According to FLOWER (1942), "Similar markings are associated with *Petryoceras* in the Sherburne member [Upper Devonian], and with various smooth-shelled *Pseudorthoceratidae* and with *Bactrites* in higher beds."

Although the evidence is admittedly tenuous, it suggests that the *Orthocerida* and *Actinocerida* might have possessed ten arms, rather than a much larger number of tentacles, as in living *Nautilus*. This suggestion is interesting in view of the fact that, from altogether different lines of evidence, it is concluded that the *Orthocerida* are ancestral to the belemnites and to modern *Dibranchiata*, including the *Decapoda*.

The following trace fossils have been formally named and believed by the authors to be due to the action of cephalopods.

*Petalichnus* S. A. MILLER, 1880 [*\*P. multipartitus*; M]. *U. Ord.*, N. Am. (Ohio). [See p. W208; interpreted as trilobite track.]

*Saerichnites* BILLINGS, 1866 [*\*S. abruptus*; M]. *Ord.*, Can. (Anticosti). [See p. W215.]

*Teratichnus* S. A. MILLER, 1880 [*\*T. confertus*; M]. *U. Ord.*, N. Am. (Ohio). [See p. W218; interpreted as probable trilobite track.]

*Trachomatichnus* S. A. MILLER, 1880 [*\*T. numerosus*; SD S. A. MILLER, 1889]. *U. Ord.*, N. Am. (Ohio). [See p. W219; interpreted as probable trilobite track.]

These trace fossils (all included by HÄNTZSCHEL in *Treatise* Part W) are in need of restudy and modern analysis before their cephalopodous origin can be accepted.

## DOUBTFUL AND REJECTED GENERA

BARRANDE (1867) divided breviconic and short cyrtoconic shells with lobate apertures into groups according to the number of apertural lobes. These conchs now are distributed among the *Oncocerida* and *Discosorida*. In tables (p. 203, 265) he attached names to these groups, but did not italicize

the names nor did he introduce or discuss them in the text. Seemingly these names published without description or discussion should be regarded as formulae which have no standing in zoological nomenclature (ICZN, Opinion 2).

**Dimeres** BARRANDE, 1867. Species group of *Phragmoceras*, characterized by 2 apertural lobes. *M.Sil.*

**Dimorion** BARRANDE, 1867. Species group of *Gomphoceras*, characterized by 2 apertural lobes. *M.Sil.*

**Hexameres** BARRANDE, 1867. Species group of *Phragmoceras*, characterized by 6 apertural lobes. *M.Sil.*

**Hexamorion** BARRANDE, 1867. Species group of *Gomphoceras*, characterized by 6 apertural lobes. *M.Sil.*

**Octameres** BARRANDE, 1867. Species group of *Phragmoceras*, characterized by 8 apertural lobes. *M.Sil.*

**Pentamorion** BARRANDE, 1867. Species group of *Gomphoceras*, characterized by 5 apertural lobes. *M.Sil.*

**Tetrameres** BARRANDE, 1867. Species group of *Phragmoceras*, characterized by 4 apertural lobes. *M.Sil.*

**Tetramorion** BARRANDE, 1867. Species group of *Gomphoceras*, characterized by 4 apertural lobes. *M.Sil.*

**Trimorion** BARRANDE, 1867. Species group of *Gomphoceras*, characterized by 3 apertural lobes. *M.Sil.*

## UNRECOGNIZABLE SUPPOSED NAUTILOID GENERA

**Achelois** DEMONTFORT, 1808 [*\*A. pyramidatum*; M]. Described as straight, chambered, conical shell with central siphuncle, from Altdorf, Switz., hence probably Mesozoic belemnite phragmocone and rostrum. [FOORD (1888, p. 1) listed name in synonymy of *Orthoceras*.]

**Amblyceras** GLOCKNER, 1842 [*\*A. riitbergense*; M]. Gyroconic conch. *Paleoz.*, Czech.

**Amimopus** DEMONTFORT, 1808 [*\*A. elephantinus*; M]. Described as straight-chambered, curved shell with central siphuncle and entire aperture. Boetstein, Altdorf, Switz., hence probably Mesozoic. [Possibly a crinoid stem. FOORD (1888, p. 262) listed name in synonymy of *Cyrtoceras*.]

**Bisiphites** DEMONTFORT, 1808.

**Curvites** PETTER, 1959 [cited by SHIMANSKIY, 1962, p. 118].

**Deltoceras** HYATT, 1894, p. 449 [*\*D. planum*; OD]. Compressed, inconspicuously ornamented sub-discoidal serpenticones, rapidly expanded dorso-ventrally, not impressed dorsally; at maturity,

adapical part of conch not in contact with adjacent volution. Sutures with slight lateral lobes. Siphuncle subventral, interior unknown. *L.Ord.* (?*U.Canad.*), Can., ?Eu. [Type-specimen never illustrated.] [W. C. SWEET.]

**Diadiploceras** HYATT, 1884.

**Gyrocerus** KING, 1844 [no assigned species]. "Tendrill-shaped or open-coiled" shells. Horizon and locality unknown.

**Hortulus** DEMONTFORT, 1808 [*\*H. convolvans*; M]. Described as being similar to *Lituites*. From dark limestone near Namur, Belg., hence probably *Carb.*

**Koleoceras** PORTLOCK, 1843 [no type-species] [= *Coleoceras* M'COY, 1846 (*nom. null.*)]. Flattened fossils that may be either orthocerid conchs or endocerid siphuncles. Several species described from "*Sil.*," Ire.

**Nautilites** PALLAS, 1771 [*\*N. complanatus*; M]. Hand-sized smooth shell with depressed, evenly convex cross section, sharp keel, and undulating sutures. Age unknown, Volga region, USSR.

**Oceanus** DEMONTFORT, 1808 [*\*O. flammeus*; M]. Name given to rather widely varied fossil and Recent involute nautilids. [Possibly includes *Nautilus umbilicatus* LAMARCK (1808) and could thus be a junior synonym of *Nautilus* LINNÉ (1758).]

**Parksoceras** FOERSTE & SAVAGE, 1927 [*\*Orthoceras (Thoracoceras) lepidodendroides* PARKS, 1915; OD]. Large orthoconic conch preserved as internal mold with tuberculate elevations arranged in diagonally intersecting rows. Siphuncle unknown. [May be orthocerid or oncocerid.] *U.Ord.*, N.Am.(Can.).

**Pteronautilus** MEEK in MEEK & HAYDEN, 1865 [*\*Nautilus seebachianus* GEINITZ, 1861; OD]. Strongly involute conch, outer (?body) chamber very large, its inner (?dorsal) side wide open and its lateral margins expanded to form large wing-like flanges. [Cephalopod affinities uncertain; might be a bellerophonitid gastropod.] *U.Perm.*, Ger.

**Remeleceras** HYATT, 1894 [*\*R. depressum*; M] [= *Remeleoceras* HYATT in ZITTEL, 1900 (*nom. null.*)]. Based on whorl fragments; whorl section with slightly impressed dorsal zone and sutures with broad dorsal lobes. Age and locality of type material unknown. [See B. KUMMEL, 1963, p. 326.]

**Schoulogoceras** SHIMANSKIY, 1951 [cited by SHIMANSKIY, 1962, p. 154, as invalid name].

**Ungerceras** STURGEON & MILLER, 1948 [*\*U. ungeri*; OD]. Cyrtoceraconic conch with compressed cross section; surface with fine longitudinal and coarse, sinuous, transverse ribs; sutures with broad, shallow lateral lobes and dorsal and ventral saddles; siphuncle unknown. (Could be either a nautilid (?*Rutoceratidae*) or an orthocerid (?*Kionoceratinae*)). *M.Penn.*, USA (Ohio).

## NAMES FOR HYPOTHETICAL NAUTILOID GENERA

The following names proposed for nautiloid cephalopods are invalid because not based on actual specimens, living or fossil.

**Lituunculus** BARRANDE, 1867. Proposed for forms resembling *Lituites*, but with simple apertures; no such specimens known.

**Metorthoceras** NAEF, 1921. Proposed for hypothetical cephalopods transitional between Tetrabranchiata and Dibranchiata.

**Proteropiloceras** RUEDEMANN, 1905. Proposed for forms like *Piloceras*, but noncamerate in apical part; no such specimens known.

**Protorthoceras** NAEF, 1921. Hypothetical ancestor ("Ur-form") of all cephalopods.

**Prorovaginoceras** RUEDEMANN, 1905. Hypothetical ancestor of *Proterovaginoceras* RUEDEMANN, 1905 (endoceratid).

**Teihardoceras** GRABAU, 1929. "... primitive ancestral form of the Holochoanites which ... has not yet been discovered with certainty. ... ." [Name was validated by TEILHARD DE CHARDIN, 1931, by being made an objective synonym of *Biconulites* TEILHARD DE CHARDIN, 1931; taxonomic position uncertain; see p. W138.]

## NAUTILOID NOMINA NUDA

**Arctinoceras** FLOWER & KUMMEL, 1950 [*non* DE CASTELNAU, 1843, *nom. null. pro Actinoceras* BRONN, 1832]. Listed with family Brevioceratidae; no species assigned. [See p. K204, *Actinoceras*.]

**Bisonoceras** KOTTLOWSKI, FLOWER, THOMPSON, & FOSTER, 1956, and FLOWER, 1958 (*nom. nud.*). Undescribed piloceratid, *L.Ord.(up.Mid.Canad.)*, USA(W.Tex.-N.Mex.).

**Conorthoceras** TROEDSSON, 1931. Intended for *Orthoceratites conicus* HISINGER, but not formally established. *Ord.*, Sweden. (See also JAANUSSON & MUTVEI, 1953, p. 19.)

**Cyrtacleistoceras** FLOWER, 1943.

**Diphragmoceras** HYATT in ZITTEL, 1900. [See SCHUCHERT & DUNBAR, 1934, p. 47.] *Ord.*, Can. (Newf.).

**Endogomphus** FLOWER, 1938. Possibly *nom. null. pro Endoplanoceras*.

**Engorthoceras** FLOWER, 1962, p. 34 ["*Orthoceras wortheni* MEEK & WORTHEN"; OD]. Cited type-species seemingly nonexistent. Reported to occur in M. Dev. of Ohio. Genus designated as type of Engorthoceratidae FLOWER, 1962. [W. C. SWEET.]

**Eosactoceras** SHIMIZU & OBATA, 1935 [*\*E. minimum* (= *Armenoceras nanum* ENDO, 1932; *non* GRABAU, 1922)]. Published without diagnosis or description. *M.Ord.*, Manchuria.

**Exosiphonites** SALTER, 1865 (*fide* BLAKE, 1882). [See also ETHERIDGE, 1888, p. 122.] *Sil.*,? Eng.

**Kolyoceras** TEICHERT, 1929. Intended to be established as subgenus of *Spyroceras* HYATT but not done.

**Kutorgoceras** BALASHOV, 1961. Listed with *Clitendoceras*, *Cotteroceras*; no species assigned.

**Mistioceras** BALASHOV, 1961. Listed with *Proterocameroceras* and *Penhsioceras*; no species assigned.

**Northoceras** MEEK & HAYDEN, 1864. Included in a list of genera of Nautilidae (*s.l.*).

**Orchadoceras** FOERSTE, 1928. A single species (*O. incertum*, *Sil.*, Anticosti Is.) described under this name was only tentatively assigned to the genus, which was never formally described.

**Proterokaipingoceras** OBATA, 1940. Mentioned in comparison with *Neokaipingoceras* OBATA (*gen. dub.*).

**Ptenacleistoceras** FLOWER & KUMMEL, 1950. Listed with family Acleistoceratidae; no species assigned.

## SUPPOSED NAUTILOIDS, REJECTED FROM NAUTILOID ORDERS

**Aganides** DEMONTFORT, 1808 [*\*A. capucinus* SCHLOTHEIM, 1820; SM]. Originally described without assigned nominal species. Frequently cited as possible senior synonym of *Aturia* BRONN, 1838 (see *Treatise*, p. L75), because of action taken by D'ORBIGNY (1826, p. 161) who assigned *Nautilus aturi* BASTEROT (type-species of *Aturia*) and *N. zigzag* SOWERBY to this genus, overlooking the fact that VON SCHLOTHEIM had formally named the species described (but not named) by DEMONTFORT. Since the fossil on which DEMONTFORT based his generic description was reported to come from black, fetid limestone in the vicinity of Namur, Belgium, it is almost certainly a goniatite of Carboniferous age and possibly senior synonym of *Imitoceras* SCHINDEWOLF, 1923, an ammonoid. *L.Carb.*, Belg. (See J. S. TURNER, 1962, p. 183.)

**Brittoceras** MILLER, DOWNS & YOUNGQUIST, 1949 [*\*B. ornatissimum*; OD] [= *Porcellia* LEVEILLE, 1835 (gastropod) (see MILLER, 1950, p. 506)]. *Miss.*, USA(Mo.).

?**Coeloceratoides** DERVILLE, 1931 [*\*C. fragilis*; M] [= *Koninckopora* LEE, 1912 (calcareous alga) (see JOHNSON & KONISHI, 1956, p. 48-122)]. *Carb.*, Fr.

**Coelonautilus** FOORD in FOORD & CRICK, 1889 [*nom. subst. pro Trematodiscus* MEEK & WORTHEN, 1861 (*non* HAECKEL, 1860)] [= *Discus* KING, 1844 (obj.); *Trematoceras* HYATT, 1884 (*non* EICHWALD, 1860) (obj.); *Streptodiscus* MILLER, 1889 (obj.); *Collonautilus* TILL, 1907 (*nom. null.*)]. Long regarded as synonym of *Vestinautilus* RYCKHOLT, 1852, but technically synonymous with *Ammonellipsites* PARKINSON, 1822 (ammonoid) (see TURNER, 1954).

**Elkoceras** LINTZ & LOHR, 1958 [*\*E. volborthi*; OD]. Originally believed to be member of family Ruto-

- ceratidae, subsequently recognized as synonym of gastropod *Straparollus* (*Euomphalus*) (LINTZ, 1962). *Miss.*, Nev.
- Gyroceras** DEKONINCK, 1844. Originally used for Carboniferous nautiloids as *nom. van. pro Gyroceratites* MEYER, 1831 (ammonoid) (see MILLER, DUNBAR, CONDRA, 1933).
- Pichyceras** RUSCONI, 1955 [*\*P. jorusconii*; M]. Probably stem fragment of pelmatozoan echinoderm (?eocrinid, ?paracrinoid). *M.Cam.*, S.Am.(Arg.).
- ?**Shelbyoceras** ULRICH & FOERSTE, 1930 [*\*S. robustum* ULRICH & FOERSTE, 1936; SD ULRICH & FOERSTE, 1936]. Small, weakly cyrtconic conchs with compressed cross section, surface with annulations that slope adapically from concave to convex side of shells. Siphuncles not discovered and no comparable Cambrian cephalopods known. [Originally described as cephalopod, without any named species; the genus cannot be assigned with certainty to any class or phylum until internal structure becomes known (2).] *U.Cam.*, USA (Mo.-Texas).
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## BACTRITOIDEA

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## INTRODUCTION

The bactritoids are cephalopods that have long been interpreted as the most primitive representatives of the Ammonoidea, but also by some authors as belonging to one of the nautiloid orders, or with about equal justification assignable to either nautiloids or ammonoids. Also, they have been classified noncommittally as external-shelled (ectocochleate) cephalopods of uncertain affinities.

## GENERAL SHELL FEATURES

The shell of the Bactritoidea [and of its single contained order, the Bactritida]<sup>1</sup> is relatively uniform in shape. It consists of a small protoconch and a much larger conch which includes the camerate phragmocone and a rather large body chamber. Aptychi or anaptychi and jaw structures are not known.

The protoconch is globular to egg-shaped with circular cross section, generally with a slightly to strongly constricted aperture. The caecum has been observed, but a prosiphon and a cicatrix are still not known in the Bactritida.

The conch is orthoconic or slightly cyrtoconic. The surface generally is smooth, sculptured forms being exceptions. Color markings have not been observed. Apertural constrictions of adult stages are not known. The ontogenetic development and shape of the peristome are considered to be reflected by the development and shape of the growth lines (Fig. 352). These are generally simple. In the Bactritidae they always contain at least a ventral (hyponomic)

sinus, to which, in most forms, a dorsal saddle is added. Other elements (lateral sinus, and even ventrolateral and dorso-lateral saddles, or dorsal sinus) appear only in two exceptional genera. On the flanks, the growth lines typically are rursiradial, rectiradial lirae being restricted to a very few forms. The growth lines of the Parabactritidae are known only in *Parabactrites*. Here they are straight and rectiradial, lacking the hyponomic sinus.

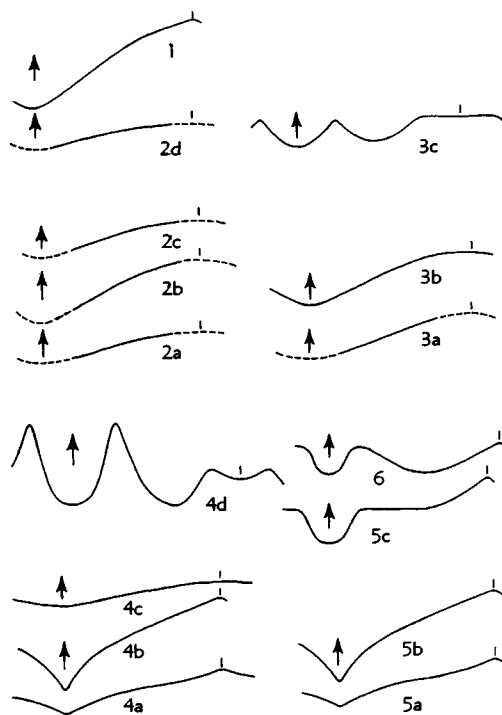


FIG. 352. Diagrams illustrating development of growth lines in some Bactritida (7, 8).—1. *Lobobactrites ellipticus* (FRECH), adult stage.—2. *Bactrites gracilior* CLARKE; 2a, from early, 2b, from middle, 2c, from final part of the second ontogenetic phase; 2d, adult stage.—3. *Pseudobactrites peneau* ERBEN; 3a, from early, 3b, from middle stage of second ontogenetic phase; 3c, from adult stage.—4. *Pseudobactrites bicarinatus* FERRONNIÈRE; 4a, from early, 4b, from middle, 4c, from final part of second ontogenetic phase; 4d, from adult stage.—5. *Cyrtobactrites asinuatus* ERBEN; 5a, from early, 5b, from middle part of second ontogenetic phase; 5c, from adult stage.—6. *Cyrtobactrites sinuatus* ERBEN, adult stage.

<sup>1</sup> The group of fossils included in this section of Part K is considered by Dr. ERBEN to be best classified as a sub-order (Bactritina) placed in the order Ammonoidea. Under urging of Dr. TEICHERT, who thinks that these cephalopods should be ranked at least on a level with the several nautiloid orders and considered to belong in intermediate position between Orthocerida and Ammonoidea, use of the ordinal name Bactritida was agreed to by Dr. ERBEN. Subsequently, as outlined in a foregoing discussion of "Main Divisions of Cephalopoda," decision has been made to recognize six subclasses of cephalopods one of which, named Bactritoidea, contains a single order, the Bactritida.—R. C. Moore.

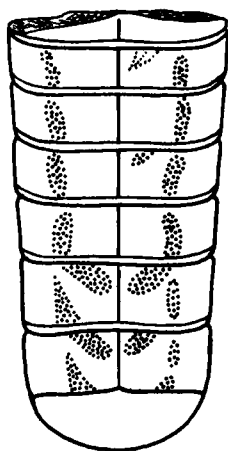


FIG. 353. *Bactrites ausauensis* STEININGER, U.Dev., Ger.,  $\times 12$ . Dorsal view showing septal furrow and lateral to dorsolateral depressed "annular elevations" (7).

On the dorsum of well-preserved internal casts a septal furrow (*Normallinie*, *ligne normale*) appears. Series of horseshoe-shaped annular elevations (Fig. 353), which have been found by ERBEN (7) on the dorsal and dorsolateral zone of exceptionally well-preserved internal casts, represent contact areas of the retractor muscles (in the sense of MUTVEI, 1957).

In all Bactritida the septa are concave adorally. Prosepta have not yet been observed. The septal necks are invariably retrosiphonate. They are orthochoanitic in primitive forms and suborthochoanitic to cyrtochoanitic in advanced genera (Fig. 354). Straight connecting rings have been observed in some specimens in connection with orthochoanitic necks. With cyrtochoanitic septal necks they have been reported to be inflated. Siphuncular and cameral deposits are unknown. In adult stages, the siphuncle has a ventral position. In the earliest ontogenetic stages it is subventral and may be subventral in the latest stage also.

The sutures are always simple, the adult stage having at least one small, shallow, V-shaped ventral lobe. In more advanced genera a dorsal saddle and lateral lobes may be added.

The test seems to consist of three main layers, as in other cephalopods. In *Bactrites*

and *Lobobactrites* the "wrinkled layer" (*Runzelschicht*) has been observed by ERBEN (7). *Parabactrites* has been claimed by SHIMANSKIY (24) to have a test consisting of numerous lamellae similar to an initial belemnoid rostrum. The illustration, however, shows no more than what could be expected from an ordinary cephalopod test, the few layers of which were split during diagenesis or weathering, as may be observed not infrequently in similarly preserved tests of nautiloids, ammonoids, and also in conothecas of belemnoid phragmocones.

## ONTOGENY

The ontogeny of *Bactrites*, *Lobobactrites*, *Pseudobactrites*, and *Cyrtobactrites* is known, but that of *Ctenobactrites* remains doubtful. In several genera three phases have been observed, and in all genera at least the first one seems to be present. They become evident by shell constrictions and changes of the configuration of growth lines (8). The first phase comprises the formation of the protoconch from its apex to its invariably constricted peristome (first shell constriction). The second phase includes the "nepionic stage" of HYATT and reaches from the first shell constriction to a rather ill-defined second shell constriction (in ammonoids often wrongly called "first constriction") where a sudden change in the configuration of growth lines may occur. The third phase includes the "neanic stage" of HYATT and all later developments. It extends from the change of growth lines and, if present, the second constriction to the latest part of the conch.

## FIRST PHASE

Although the protoconch is commonly globular to ovoid, its shape may even show variations within a species. Its axis generally coincides with the axis of the following conch, but in some it may be slightly inclined (Fig. 355, 1d, 1f, 3b, 2, 3a). The growth lines are imperfectly known, but the peristome commonly is straight and rectiradiate, except in the above-mentioned example of an inclined protoconch.

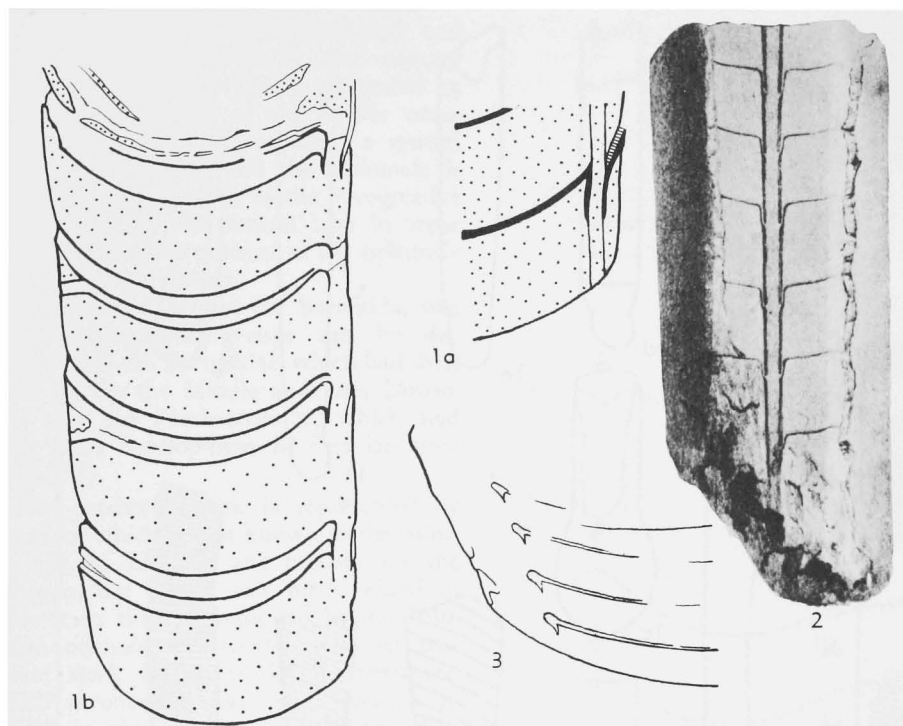


FIG. 354. Diagrams illustrating septal necks in the Bactritida.—1. *Bactrites*; 1a, *B. büdesheimensis* ROEMER, orthochoanitic, with connecting rings, U.Dev., Ger.,  $\times 8$ ; 1b, *B. schlotheimi* (QUENSTEDT), orthochoanitic, M.Dev., Ger.,  $\times 3$  (8).—2. *Lobobactrites timanicus* SCHINDEWOLF, orthochoanitic, with connecting rings, U.Dev., USSR, enlarged (12).—3. *Belemnitomimus palaeozoicus* SHIMANSKIY, cyrtchoanitic, L.Perm., USSR,  $\times 8.5$  (24).

## SECOND PHASE

In the second ontogenetic phase, after the first shell constriction, the cross section may (Fig. 355, 1a,b,g) or may not (Fig. 355, 1c,i,4) regain the size of the largest cross section of the protoconch, and it may become even larger.

The growth lines always have a ventral sinus; also, in most specimens a dorsal saddle appears and the position of the growth lines is strongly rursiradiate. In *Pseudobactrites* it has been observed that near the end of this phase a secondary, almost rectiradiate, position is suddenly regained, the ventral sinus and dorsal saddle becoming abruptly reduced (Fig. 352, 4a-c; 355, 3b). In *Bactrites* (Fig. 352, 2a-d; 355, 1a), the change to a less rursiradiate position of the growth lines is not so abrupt. The end of this second phase may (Fig. 355, 1b,g,h,3b) or may not (Fig. 355, 1a,d,f,i,4) be characterized by a minor reduction in cross section, called the second constriction.

## THIRD PHASE

In this phase after the weak constriction and the secondary simplification of growth lines, the final development starts. A ventral sinus and dorsal saddle develop again and are retained; additional elements appear (lateral sinus, and others) and the mature cross section develops.

The first ontogenetic phase probably represents the embryonic stage, while the second phase may be correlated with the larval and the third one with the postlarval development.

The different stages of development of the suture cannot be exactly correlated with the above-mentioned phases, for each septum is formed at a later stage than the corresponding part of the conch in which it appears, each part representing the former living chamber before origin of the corresponding septum. It is evident from observation of some exceptional individuals (Fig. 355, 1d,g) and of a specimen that

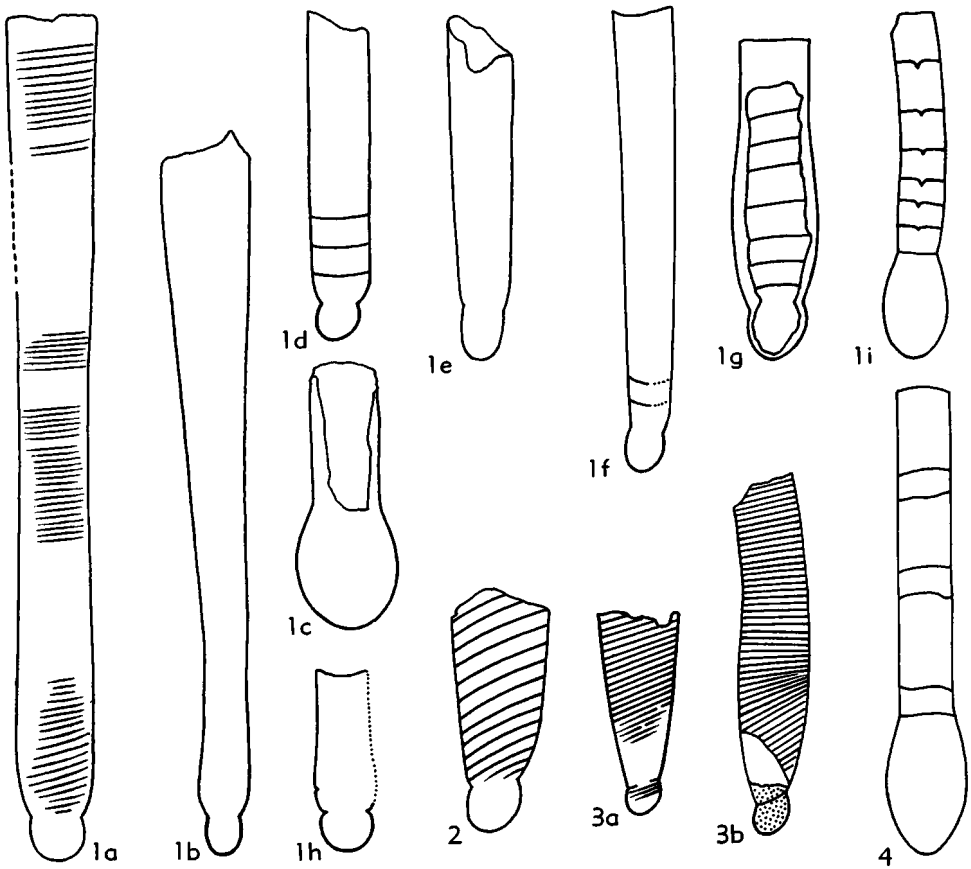


FIG. 355. Diagrams illustrating types of protoconchs of the Bactritida.—1. *Bactrites*; 1a, *B. gracilior* CLARKE, U.Dev., USA,  $\times 22.5$  (15); 1b, *B.? aciculum* (HALL), U.Dev., USA,  $\times 19$  (15); 1c, *B.? sp.*, L.Dev., Fr.,  $\times 15$  (7); 1d, *B. gracilior* CLARKE, U.Dev., USA,  $\times 13.5$  (7, 15); 1e, *B.? aciculum* (HALL), U. Dev., USA,  $\times 11$  (15); 1f, *B.? aciculum* (HALL), U.Dev., USA,  $\times 19$  (15); 1g, *B. gracilior* CLARKE, U. Dev., USA,  $\times 13.5$  (7, 15); 1h, *B. primus* (SHIMANSKIY), L.Perm., USSR,  $\times 11$  (25); 1i, *B. schlotheimi* (QUENSTEDT), M.Dev., Ger.,  $\times 17$  (21).—2. *Cyrtobactrites asinuatus* ERBEN, L.Dev., Ger.,  $\times 7.5$  (7).—3. *Pseudobactrites*; 3a, *P. peneau* ERBEN, L.Dev., Fr.,  $\times 7.5$  (8); 3b, *P. bicarinatus* FERRONNIÈRE, L. Dev., Fr.,  $\times 7.5$  (8).—4. *Lobobactrites ellipticus* (FRECH), M.Dev., Ger.,  $\times 11$  (21). (Where orientation was possible, the venter is on the left.)

seems to be the internal cast of a not-yet camerate larva (Fig. 355, 1c), that the first septum probably appeared in the late stages or at the end of the second ontogenetic phase.

At least the first septum lacks the ventral lobe (Fig. 356, 1a) that develops in the following stages. In this septum, the siphuncle lies on the ventral side of the center (8). It acquires its ventral position in subsequent stages.

During later ontogenetic stages the ventral lobe may become obsolete and the

siphuncle may shift secondarily from a ventral to subventral position (7). Such regressive development occurs, however, only in rare individuals, excepting *Kokenia*, where it is the rule in the late ontogenetic stages (Fig. 356, 3b).

## PHYLOGENY AND EVOLUTION

The Bactritida are thought to have evolved, probably in Ordovician time, from orthoconic and longiconic orthochoanitic



nautiloids with a globular protoconch and eccentric siphuncle (probably some member of the Orthocerida). This is suggested by the primitive shape of the earlier ontogenetic stages of *Bactrites* where a ventral lobe is still lacking and the siphuncle is still eccentric, as well as by the retrogressive development of the ventral lobe in some specimens and the position of the siphuncle in gerontic individuals.

It seems that within the Bactritida, two main phylogenetic groups can be distinguished—the Bactritidae, which had their acme during the Middle and Late Devonian, and the Parabactritidae, which had their main development in Permian time (Fig. 357).

The persistent stock is represented by *Bactrites*, which is first known in the Silurian (33, pl. 136-137) and persists into the Permian, but which may have existed in Ordovician time, as indicated by its Ordovician offshoot, *Eobactrites*. Another persistent stock is formed by *Lobobactrites*, which erroneously has been reported to appear in the Silurian (Ludlovian) (7), whereas the oldest known true representatives actually come from the Early Devonian (late Siegenian, Emsian). It is known, therefore, from Early to Late Devonian.

Since *Eobactrites* is stratigraphically isolated from other bactritids, some authors have suggested that it should be excluded from the Bactritida. However, the fact that *Bactrites* now is known from the Silurian makes the stratigraphic interval separating *Eobactrites* from later bactritids seem less significant.

It is believed that a trend toward decrease in size of the protoconch can be discerned in the evolution of the Bactritida (25) and that possibly the larval phase became generally prolonged, as has been demonstrated in *Cyrtobactrites* and *Pseudobactrites* (8). The available evidence, however, is as yet incomplete.

Iterative evolution is evident in the formation of a lateral lobe and lateral sinus which were acquired independently in different lines, as indicated by the pattern of sutures (e.g., *Lobobactrites*, *Koķenia*, *Aktastioceras*, *Tabantaloceras*) or growth lines (e.g., *Cyrtobactrites*, *Pseudobactrites*). Homeomorphy occurs in *Pseudobactrites*,

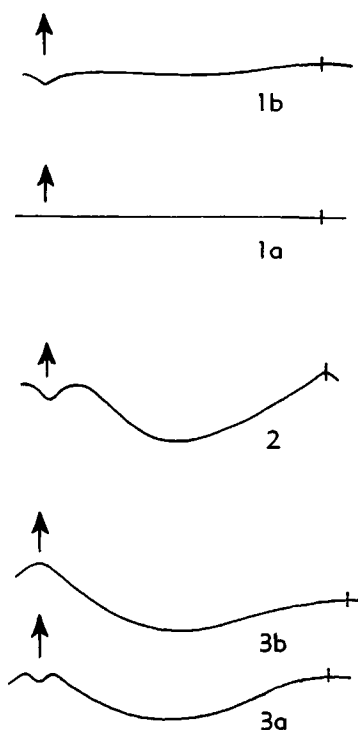


FIG. 356. Diagrams illustrating the development of the suture in some Bactritida.—1. *Bactrites schlotheimi* (QUENSTEDT); 1a, earliest suture; 1b, adult suture (8, 21).—2. *Lobobactrites*; adult suture (21).—3. *Koķenia obliquecostata* HOLZAPFEL; 3a, early suture; 3b, late suture (7).

in which the biconvex, rectiradiate growth lines and peristome resemble those of the Agoniatitidae and Anarcestidae. Furthermore, the ventrolateral ridges of *Pseudobactrites bicarinatus* strikingly resemble analogous ridges of certain representatives of the ammonoid *Gyroceratites*.

The Bactritidae seem to have given rise to the Parabactritidae, as suggested by intermediate features (septal necks, apical angle, length of camerae) of the primitive genus *Parabactrites*.

Some authors, especially SCHINDEWOLF, have regarded the Bactritidae as ancestors of the coiled ammonoids (17, 21), whereas others, especially SPATH (28), believed that the ammonoids were derived from coiled nautiloids of the type of *Barrandeoceras*. The latter postulate is based on the similarity in shape of the conchs of these genera and those of early coiled ammonoids. Fundamental differences, however, are seen

in the shape of the protoconch and in absence of a ventral lobe in the above-mentioned nautiloids. In my opinion (6,8), evolution of early ammonoids probably took place in the very early Devonian (probably Siegenian) via *Bactrites*→*Lobobactrites*→*Cyrtobactrites*→*Anetoceras*→*Teichertoceras*→(?*Convoluticeras*)→*Mimagoniites*→Anarcestidae. The evidence consists of (1) the combination of a ventral siphuncle and ventral lobe, which is common to both Bactritidae and early coiled Ammonoidea; (2) the morphological identity (primitive species of *Anetoceras*), or at least similarity, of early ontogenetic stages in both; (3) the *Lobobactrites*-like growth lines, peristome, sutures, and whorl section of the most primitive Anarcestaceae; (4) the similarity of annular elevations in both groups; and (5) the gradual increase of coiling and involution, which, among other features, characterizes the above-mentioned sequence of genera.

The Bactritida have been regarded as the ancestors of the Belemnoidea (*sensu lato*), first by HYATT & SMITH (1905, p. 204), later by GRABAU (11), and finally by SHIMANSKIY (24), whereas other authors look for ancestors of the belemnoids in orthoconic nautiloids. The first-stated opinion, however, is supported by the invariable ventral position of the siphuncle, as well as by the identical shape of the protoconchs (and their inclination in some specimens) in both Bactritida and Belemnoidea. Recently, ERBEN (6) has suggested a diphyletic origin of the Belemnoidea from different groups of the Bactritida. He considered the Bactritidae as ancestors of the Protobelemnoidea and the Parabactritidae as those of the Belemnoidea *s.s.* The first suggestion is supported by the small apical angles and longiconic shapes of the conchs, by the orthochoanitic septal necks with cylindrical connecting rings, and by the relatively high camerae in the phragmocones of both Bactritidae and early Protobelemnoidea. The evidence supporting the second suggestion consists of the large apical angles and breviconic shapes of the conchs, the tendency to develop cyrtchoanitic septal necks with inflated connecting rings, and the invariably short camerae of the phragmocones in the Parabactritidae and the Belemnoidea *s.s.*<sup>1</sup>

## DISTRIBUTION

The oldest known bactritids have been found in Morocco, Czechoslovakia (Bohemia), and Germany (Hunsrück, Harz and Kellerwald Mountains). Thus, they come from regions which once were part of the Mediterranean Tethyan sea, or at least marginal extensions of it. This accords with the fact that in Early Devonian time bactritids apparently are restricted to the Hercynian-Bohemian magnafacies where they are found to be common in Middle Devonian beds, and that they have never been found in the typical Rhenish magnafacies. The persistent stocks of *Bactrites* and *Lobobactrites* were world-wide in distribution during Middle and Late Devonian, as well as in Carboniferous and Permian times. The short-range offshoots, however, always seem to have a more restricted geological distribution.

The oldest known species ("*Orthoceras*" *pygmaeum* DEKONINCK) tentatively referred to the Parabactritidae comes from the Lower Carboniferous of Belgium, whereas the Mississippian *Bactrites nevadensis* YOUNGQUIST from Nevada (USA) is considered to be close to their direct ancestor (24). On the other hand, the same species was cited by FLOWER & GORDON (10) as possibly related to the Carboniferous belemnites. The main development of this group, however, apparently occurred in the Uralian geosyncline in Permian time.

<sup>1</sup> It should be noted that FLOWER & GORDON (10) deny any difference between Protobelemnoidea ("*aulacoceratids*") and Belemnoidea *s.s.* The same view was expressed by FLOWER (1944) in pointing out that intermediate forms serve to connect the two groups. This view, however, is based on errors of earlier authors (MOJSISOVICS, GEMMELLARO, and others) who wrongly included some Triassic phragmocones (e.g., "*Aracites*" *convergens* HAUER, 1847; "*A.*" *conicus* and "*A.*" *ellipticus* MOJSISOVICS, 1871; "*A.*" *meneghinii* SALOMON, 1895; "*A.*" *giganteus* GEMMELLARO, 1904; "*A.?*" *breviconus* REIS, 1907 [= "*A.*" sp., MOJSISOVICS, 1886, pl. 16, fig. 4], and *Zugmuntites mojsisovici* REIS, 1907) in the Protobelemnoidea (former "*Aulacoceratidae*"), perhaps influenced by the idea, commonly held in earlier times, that true Belemnoidea first occur in the Lower Jurassic and that all earlier dibranchiats must have been aulacoceratids. That the above-mentioned species are not representatives of the Protobelemnoidea, however, is demonstrated by their cyrtchoanitic septal necks with inflated connecting rings and their short camerae, as well as by the breviconic shape and large apical angle of their phragmocones. In these features, they differ strongly from all protobelemnoids and resemble the Belemnoidea *s.s.*; they must, therefore, be included in the latter. Thus, no intermediate forms between Protobelemnoidea and Belemnoidea exist. On the contrary, a strong morphological difference between both groups, as expressed in the above-mentioned characters, is evident.

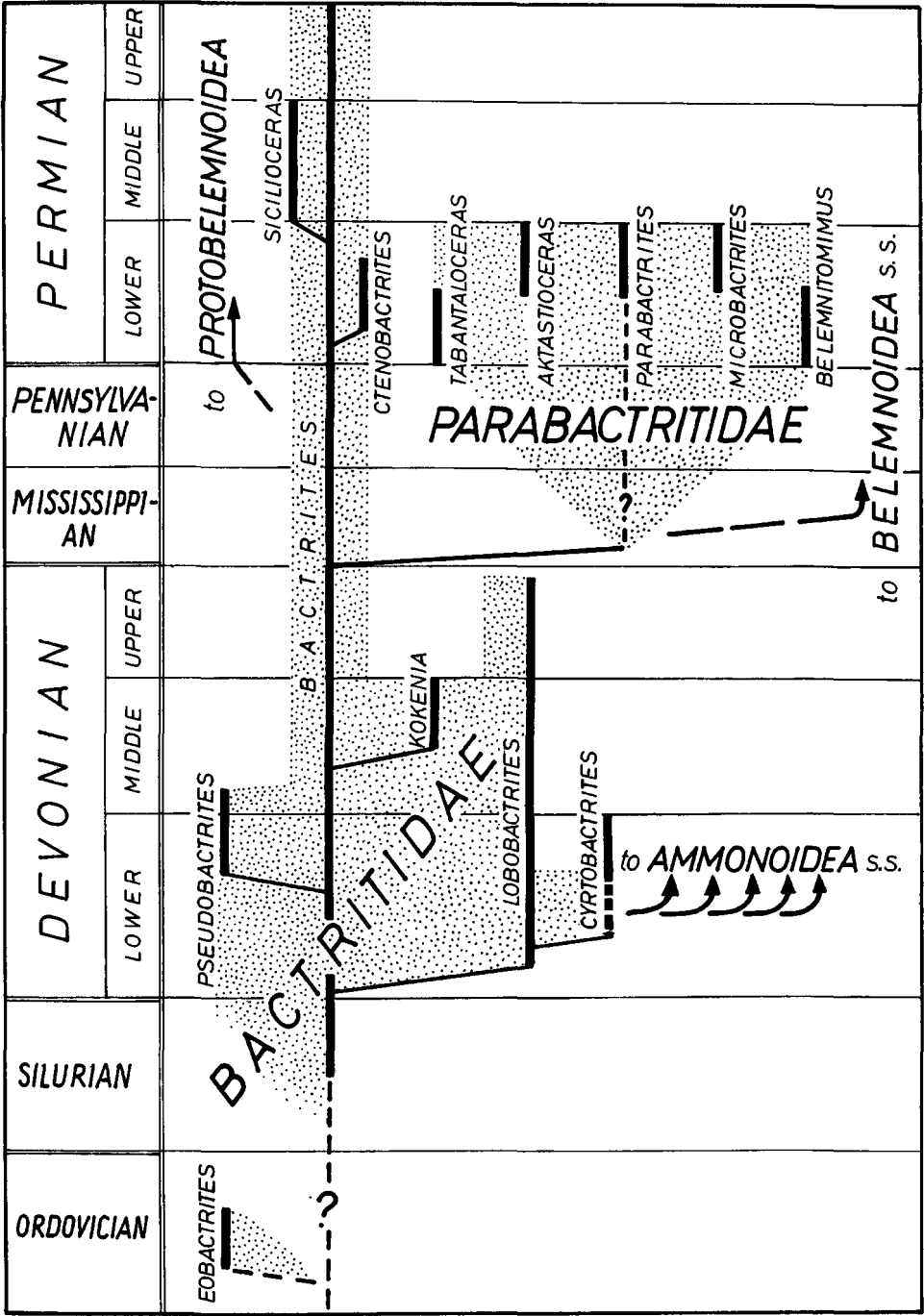


Fig. 357. Suggested phylogeny of the Bactritida (8).

## TAXONOMIC POSITION

Differing opinions concerning affinities of the bacritids have been noted in the introduction. The Bacritida are morphologically intermediate between the nautiloid orders and coiled Ammonoidea, showing generally the orthoconic conch of the former and the combination of marginal siphuncle and siphonal lobe of the latter. The cyrtconic *Cyrtobacrites* shows that this intermediate position is also expressed in the shape of the shell. This morphologically intermediate position, in the opinion of certain authors, including myself, seems to imply an intermediate position in phylogeny. Under these circumstances, it would seem that the Bacritida, from the point of view of morphology, as well as of phylogeny, could be included with equal justification in either of the two groups, i.e., their ancestors or their descendants, if questions of diagnosis were not involved.

It has been claimed (21) that the basic and only fundamental difference between nautiloids and ammonoids is the simultaneous presence of a marginal siphuncle and a siphonal lobe in the latter. If this is upheld, the Bacritida *per definitionem* would have to be assigned to the Ammonoidea. Although the taxonomic value of siphuncle position and suture shape has been questioned (28,29), the objections have been rejected (2,17,22). In the meantime, however, at least five undoubted nautiloid genera (*Lobendoceras*, *Cyrtendoceras*, *Ventroloboceras*, *Thylacoceras*, *Catoraphiceras*) have been described (31,32) with some species showing a marginal (ventral) siphuncle and at the same time a siphonal (ventral) lobe that in shape and position strongly resembles the corresponding lobe of the Bacritida and primitive coiled ammonoids. However, width of the siphuncle, presence of endocones, or shape of the septal necks suggests that these are examples of homeomorphy. Since in other groups of animals the occurrence of homeomorphic forms neither alters nor affects the basic structure of natural groups, the features mentioned should be regarded as general diagnostic characters of the Ammonoidea. For this reason, I am inclined to include the bacritids in this order.

Recently, some authors (17,24) have regarded the bacritids as an independent order, or even superorder, on the same level with the Nautiloidea and the Ammonoidea. In view of their obvious phylogenetical significance, in a way this may seem to be justified. However, the diagnostic differences between bacritids and ammonoids (i.e., the former never being perfectly coiled and their ventral lobe being less developed) are judged by me to have comparatively low taxonomic value and do not seem to support this suggestion.

## CLASSIFICATION

As emphasized by SHIMANSKIY (24), the characters of highest taxonomic value in the Bacritida evidently are the apical angle (i.e., the longiconic or breviconic shape of the conch), and the relative height of camerae. Furthermore, the shape of the septal necks has been shown to be of equal importance (7). It must be noted, however, that the relative height of the camerae is rather variable in longiconic bacritids; only in breviconic forms does it become somewhat stabilized. The cited features have been used to distinguish two phylogenetic groups as families, namely, the Bacritidae and the Parabacritidae.

Shells of the Parabacritidae closely resemble exfoliated phragmocones of the Belemnoidea s.s., a feature that has led to the suggestion by FLOWER & GORDON (10) that they may not belong to the Bacritida but to the Coleoidea. These authors have pointed out two features which seem to support this interpretation—(1) the shell surfaces of the Parabacritidae, being smooth or having only a very faint relief, could be interpreted, in the opinion of the authors, as one of the two inner layers of a conotheca, and (2) no living chamber had been found in the Parabacritidae. However, more recently a living chamber of *Parabacrites ruzhencevi* has been figured by SHIMANSKIY (26, pl. 12, fig. 4) (see Fig. 360,1). As far as FLOWER & GORDON's first argument is concerned, I cannot share their view, because smooth or only very faintly sculptured surfaces are by no means restricted to the inner layers of the belemnoid phragmocone. They are, however, very

common in the outer layer of the bactritids, particularly in less advanced forms, and only in some advanced forms does the sculpture become more prominent.

Also the question has been discussed whether the Parabactritidae could be phragmocones of belemnites which had chitinous rostra, not preserved in fossils (10). Such an assumption would support J. ROGER's (1952) opinion that the chitinous rostra of the Lower Jurassic Chitinodeuthidae may represent an archaic condition. This was not accepted by FLOWER & GORDON and both concepts seem very improbable indeed.

The problem of the morphological differences between belemnite phragmocones and the conchs of the Parabactritidae is still under discussion. FLOWER & GORDON (10) quoted SHIMANSKIY (24) as suggesting that the relatively long septal necks of the bactritids differed from the short ones of atractid belemnites, and they denied this difference. SHIMANSKIY (26), however, pointed out that he had been misunderstood, apparently on account of an incorrect translation of his paper, and that he had stated, on the contrary, that the short septal necks of the Parabactritidae are in contrast to long ones of the belemnite *Atractites*. FLOWER & GORDON (10) also denied that an important difference in size distinguishes genera of the Parabactritidae from fossils classed as belemnites, because some species of *Atractites* are very small.

This discussion seems to afford little help, because *Atractites* (= *Ausseites* of FLOWER) is referred to as an example of the belemnites. However, this genus does not belong to the Belemnoida s.s. but to the Proto-belemnoida (= "aulacoceratids"), which strongly differ in the nature of their phragmocones from both the Parabactritidae and Belemnoida. On the other hand, the species "*A. convergens*", with which this discussion is concerned, does not belong to *Atractites* but to a new genus of Triassic Belemnoida s.s. In this species the exact length of the septal necks is not well known and from the figures given by MOJSISOVICS distinction between septal necks and connecting rings cannot be made. Generally, septal necks of the Belemnoida s.s. are relatively short, particularly in Jurassic and Cretaceous genera. Thus, no significant dif-

ference from the bactritids seems to be observable in this respect. In some Proto-belemnoida the septal necks are considerably longer (e.g., *Choanoteuthis*). In most genera (e.g., *Aulacoceras*, *Atractites*=*Ausseites*) they are about the same in length or only slightly shorter than in the Bactritida. In general, it seems that the length of the septal necks is no criterion for distinguishing phragmocones of the Coleoidea and conchs of the Parabactritidae.

Solution of these problems depends on whether the Parabactritidae were ectocochleate or endocochleate cephalopods. It is true that the absence of rostra in fossils belonging to the Parabactritidae could be explained by conditions of preservation. Thus, no conclusive evidence seems to favor an assumption that this group was not endocochleate. On the other hand, ectocochleate cephalopod shells generally are characterized by the presence of a living chamber. Furthermore, the ectocochleate position of the shell can be indicated by the presence of a hyponomic sinus. Although the latter has not yet been described from the Parabactritidae and has been found lacking in the one example of figured growth lines (*Parabactrites*; 26, pl. 12, fig. 3a), this group has been found to possess true living chambers, as previously mentioned. Therefore, and in agreement with SHIMANSKIY (24, 26), they are placed here in the Bactritida.

On the basis of presence of ribs, a family named Ctenobactritidae has been established (24), which, however, has been shown not to represent a natural unit (7), because the principal characters of its genera coincide with those of the Bactritidae. Furthermore, because of the striking configuration of growth lines and peristome of the fossils, a separate family (Bojobactritidae) has been proposed for *Bojobactrites* (13), a junior synonym of *Pseudobactrites*. However, the growth lines and peristome of bactritids are generally to be considered as characters of subordinate taxonomic value, and similar trends are indicated among some Bactritidae. For these reasons, the family Bojobactritidae is rejected (7).

In the Bactritida the most important features for differentiation of genera are judged to be (1) general shape of the suture, (2) nature of the growth lines, (3)

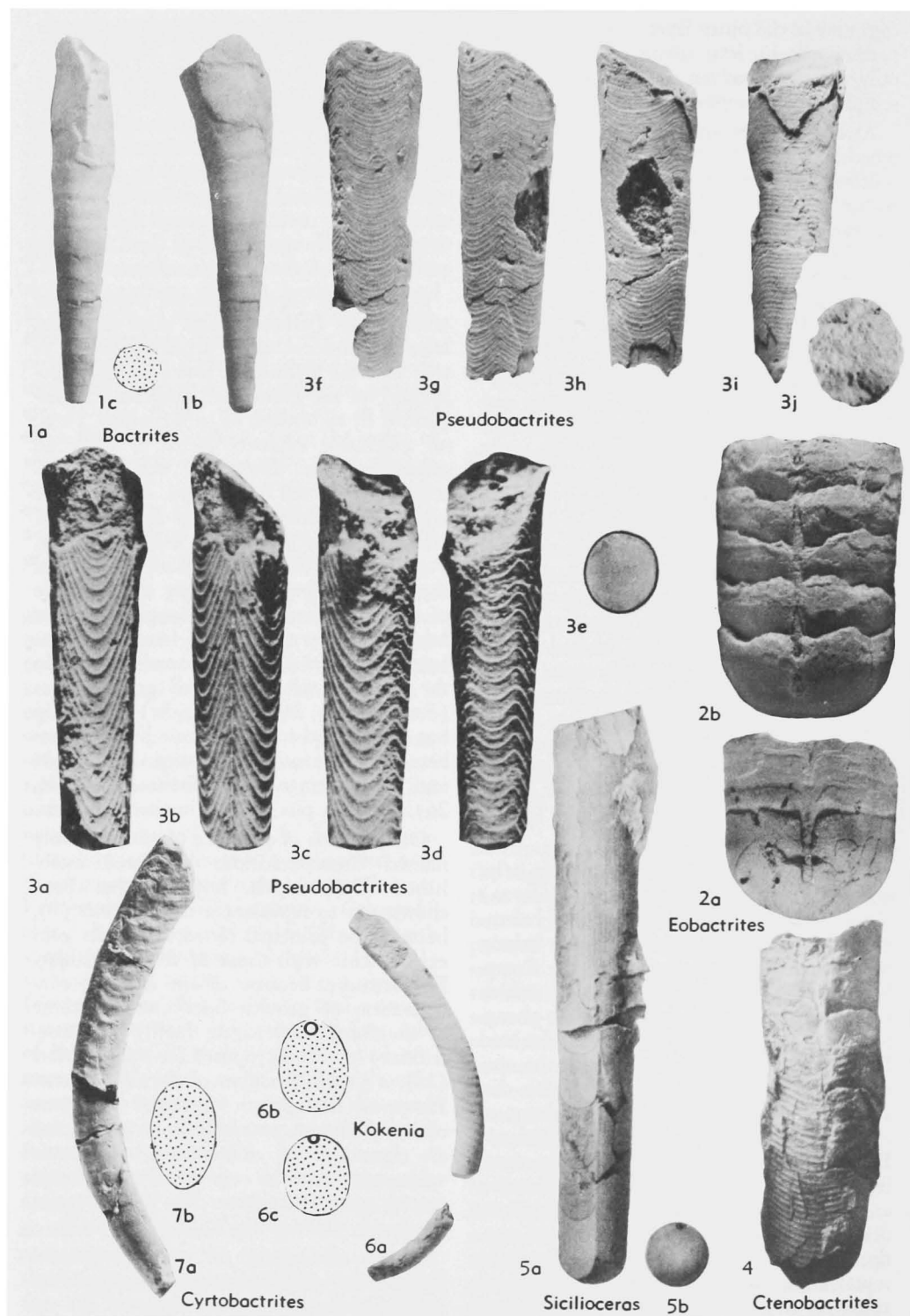


FIG. 358. Bactritidae (p. K501-K502).

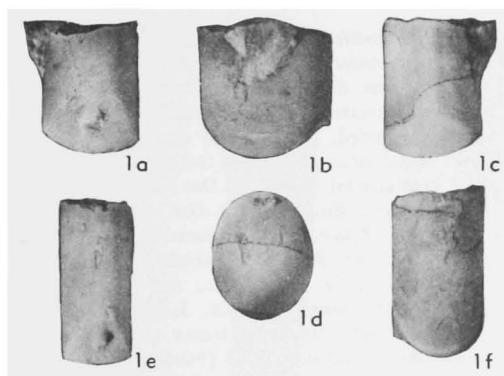


FIG. 359. \**Lobobacrites ellipticus* (FRECH)  
(Bacritidae) (p. K501-K502).

characters of the peristome, and (4) shape of the conch, including its cross section. Variations of these features are regarded as secondary in importance and are used for distinction of species.

## SYSTEMATIC DESCRIPTIONS

### Subclass BACTRITOIDEA Shimanskiy, 1951

[*nom. transl.* MOORE, herein (*ex order* Bacritioidea SHIMANSKIY, 1951)] [=Bacritioidea RUZHENTSEV, 1957 (*superorder*)]

Conch orthoconic to cyrtoconic, longiconic or breviconic, with small or large apical angle. Siphuncle narrow, invariably in contact with ventral wall; septal necks orthochoanitic to cyrtochoanitic. Suture uniformly with V-shaped ventral lobe. Protoconch globular to egg-shaped (7,17,21,24). *Ord.-Perm.*

### Order BACTRITIDA Shimanskiy, 1951

[*nom. correct.* SHIMANSKIY, 1954 (*pro order* Bacritioidea SHIMANSKIY, 1951)] [=Bacritina MILLER & FURNISH, 1954 (*suborder*)]

Characters of the subclass. *Ord.-Perm.*

### Family BACTRITIDAE Hyatt, 1884

[=Bacritaceae KINDLE & MILLER, 1939 (*superfam.*); incl. Ctenobacritidae SHIMANSKIY, 1951; Bojobacritidae HORNÝ, 1957; Lobobacritidae SHIMANSKIY, 1962; Bacritaceae SHIMANSKIY, 1962]

Conch orthoconic to cyrtoconic, longiconic, with small apical angle (less than about 10 degrees). Septal necks orthochoanitic. Height of camerae variable (7,21, 24). *Ord.-Perm.*

**Bacrites** SANDBERGER, 1843 [\**B. subconicus*; OD] [=? *Stenoceras* D'ORBIGNY, 1849; *Hemibacrites* SHIMANSKIY, 1954]. Conch orthoconic, cross section nearly circular to broadly oval. Sutures almost straight, with small ventral lobe only, on flanks rectiradiate or prorsiradiate. Growth lines rursiradiate, with broad shallow ventral sinus and low dorsal saddle (15,18,21,24). ?*Sil.*, *L.Dev.* (*U. Siegen.*)-*U. Perm.*, Eu.(Ger.-Fr.-Urals-Sicily)-N. Afr.(Morocco)-Australia-N. Am.(USA-Mex.)-S. Am.(Peru).—FIG. 358,1. \**B. subconicus*, M. Dev., Ger.; 1a-c, holotype, vent., lat., transv. sec.,  $\times 3$  (Erben, n).

?**Ctenobacrites** SHIMANSKIY, 1951 [\**C. costatus*; OD]. Like *Bacrites* but with rursiradiate ribs forming broadly rounded ventral sinus and broad dorsal saddle (23-25). [If the isolated conical protoconch figured by SHIMANSKIY (25) really belongs to *Ctenobacrites*, this genus should be excluded from the Bacritida.] *L.Perm.*, USSR.

**C. (Ctenobacrites)**. Ribs rounded and intercostal space relatively broad (27). *L.Perm.*, USSR.—FIG. 358,4. \**C. costatus*, Urals; vent.,  $\times 0.75$  (24).

**C. (Mirites)** SHIMANSKIY, 1962 [\**C. mirus* SHIMANSKIY, 1954; OD]. Ribs flattened and intercostal space narrow (27). *L.Perm.*, USSR.

**Cyrtobacrites** ERBEN, 1960 [\**C. sinuatus*; OD]. Conch exogastrically cyrtoconic, with narrow oval cross section. Growth lines with linguiform ventral sinus; ventrolateral saddles, lateral sinuses, and dorsal saddle lacking or slightly developed (7, 8). *L.Dev.*(*Ems.*), Eu.(N.Fr.-Ger.).—FIG. 358,7. \**C. sinuatus*, Ger.; 7a, lat.,  $\times 2$ ; 7b, transv. sec.,  $\times 5$  (7).

**Eobacrites** SCHINDEWOLF, 1932 [\**Bacrites sandbergeri* BARRANDE, 1867; OD]. Like *Bacrites* but cross section circular, ventral lobe narrower and deeper, and growth lines rectiradiate without dorsal saddle (1,20,22). *L.Ord.*(*Llandeil.*), Eu.(Czech.-Norway).—FIG. 358,2. \**E. sandbergeri* (BARRANDE), Czech.; 2a,b, vent. views,  $\times 1$  (Erben, n).

**Kokenia** HOLZAPFEL, 1895 [\**K. obliquecostata*; OD]. Conch exogastrically cyrtoconic to almost gyroconic, with oval cross section and with fold-like sigmoidal rursiradiate ribs which are faint dorsally and ventrally. Sutures of juvenile stages with small ventral lobe, deeply rounded lateral lobes and prominent dorsal saddle. In late ontogenetic stage place of ventral lobe is taken by secondary ventral saddle and siphuncle shifts from ventral to subventral position (7). *M.Dev.* (*Givet.*), Eu.(Ger.-Fr.-Czech.).—FIG. 358,6. \**K. obliquecostata*, Ger.; 6a, lat. (venter right),  $\times 1.5$ ; 6b, transv. sec. adult shell,  $\times 5$ ; 6c, transv. sec. juv. shell,  $\times 5.4$  (7).

**Lobobacrites** SCHINDEWOLF, 1932 [\**Bacrites ellipticus* FRECH, 1897 (= *Bacrites carinatus* SAND-

BERGER & SANDBERGER, 1852 (*partim*), non *Orthoceras* *carinatus* MÜNSTER, 1840; OD]. Like *Bactrites* but cross section more narrowly oval, some forms with flattened flanks and rarely with dorsal carina. Sutures with small ventral lobe, well-developed lateral lobes and dorsal saddle. Growth lines as in *Bactrites* but more strongly rursiradial, dorsal saddle more prominent and commonly pointed (20,21,30). *L.Dev.*(?*U.Siegen.*)-*U.Dev.*, Eu.(N.Fr.-S.Fr.-Ger.-Pol.-Czech.-USSR)-N. Afr. (Morocco)-Asia (China)-Australia-N. Am. —FIG. 359,1. \**L. ellipticus* (FRECH), M.Dev., Ger.; 1a-d, lectotype (SANDBERGER & SANDBERGER, 1852, pl. 17, fig. 3, *partim*), vent., dors., lat. (venter at right), adapical,  $\times 2$ ; 1e,f, another of the SANDBERGERS' specimens, vent., lat. (venter at left),  $\times 2$  (Erben, n).

*Pseudobactrites* FERRONNIÈRE, 1921 [\**P. bicarinatus*

(=*Bojobactrites ammonitans* HORNÝ, 1957); OD] [= *Bojobactrites* HORNÝ, 1957]. Like *Bactrites* but growth lines differentiated; ventral sinus linguiform, ventrolateral saddle prominent, lateral sinus deeply rounded, and likewise dorsolateral saddle and dorsal sinus (7,9,13). [Only the type-species has ventrolateral ridges.] *L.Dev.*(*U.Ems.*)-*M.Dev.* (*basal Eifel.*), Eu.(Fr.-Czech.-Ger.)-Asia(Turkey). —FIG. 358,3a-e. \**P. bicarinatus*, L.Dev., Czech. (3a-d)-Fr.(3e); 3a-d, vent., ventrolat., lat., dors.,  $\times 2.25$  (13); 3e, transv. sec.,  $\times 3$  (7). —FIG. 358,3f-j. *P. péneaui* ERBEN, L.Dev., Fr.; 3f-j, vent., ventrolat., lat., dors., transv. sec.,  $\times 1.5$  (7). *Sicilioceras* SHIMANSKIY, 1954 [\**Orthoceras paterno* GEMMELLARO, 1887; OD]. Like *Bactrites* but with straight longitudinal ribs (24). *M.Perm.*, Eu. —FIG. 358,5. \**S. paterno* (GEMMELLARO), Sicily; 5a,b, vent., transv. sec.,  $\times 0.5$  (34).

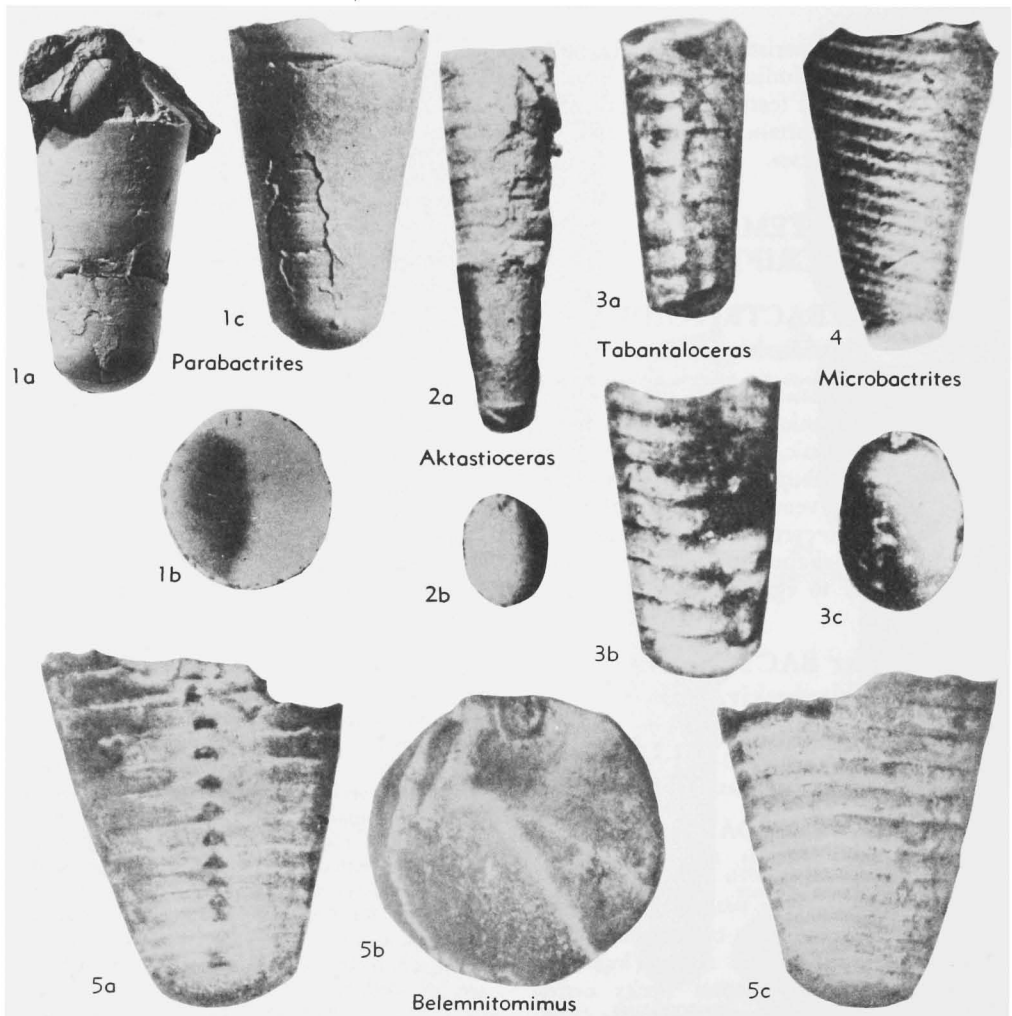


FIG. 360. *Parabactritidae* (p. K503).



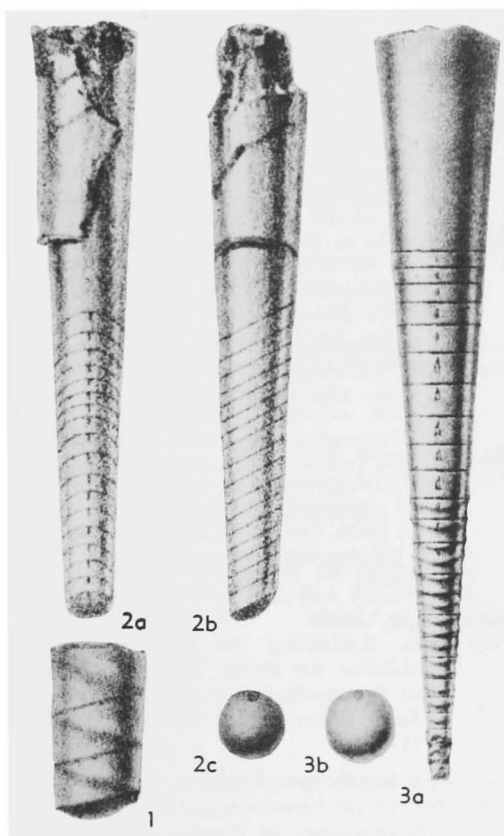


FIG. 361. Doubtful Genera; 1, *Cyclobactrites*; 2, *Devonobactrites*; 3, *Cochleiferoceras* (p. K503).

### Family PARABACTRITIDAE Shimanskiy, 1951

[=Parabactritaceae SHIMANSKIY, 1962]

Conch orthoconic and breviconic, with large apical angle (more than about 10 degrees). Septal necks ?orthochoanitic or suborthochoanitic to cyrtchoanitic. Length of camerae equal to, or less than, 0.3 of conch diameter (7,24). ?*Carb.*, *Perm.*

**Parabactrites** SHIMANSKIY, 1948 [*\*P. ruzhencevi*; OD]. Conch slightly breviconic (apical angle 12 to 18 degrees); cross section almost circular to broadly oval. Septal necks ?orthochoanitic or ?suborthochoanitic. Sutures rectilinear except for ventral lobe (23,24). ?*Carb.*, *L.Perm.*, USSR.—FIG. 360,1. *\*P. ruzhencevi*, Urals; 1a, vent., with body chamber,  $\times 1.36$  (SHIMANSKIY, 1960); 1b,c, oral, vent.,  $\times 2$  (24).

**Aktastioceras** SHIMANSKIY, 1948 [*\*A. kruglovi*; OD]. Conch slightly breviconic; cross section broadly to narrowly oval. Siphuncle with septal

necks ?suborthochoanitic. Suture with small ventral lobe, rounded lateral lobes and dorsal saddle (23). *L.Perm.*, USSR.—FIG. 360,2. *\*A. kruglovi*, Urals; 2a,b, vent., transv. sec.,  $\times 3$  (24).

**Belemnitomimus** SHIMANSKIY, 1954 [*\*B. palaeozoicus*; OD]. Like *Microbactrites* but conch much more strongly breviconic (apical angle about 30 degrees), camerae shorter, shell smooth, and sutures with weak dorsal saddle and some specimens without ventral lobe (24). *L.Perm.*, USSR.—FIG. 360,5. *\*B. palaeozoicus*, Urals; 5a-c, vent., adoral, lat.,  $\times 2.5$  (24).

**Microbactrites** SHIMANSKIY, 1954 [*\*M. scorobogatovae*; OD]. Conch strongly breviconic (apical angle about 20 degrees); camerae very short; cross section almost circular to broadly oval. Siphuncle with cyrtchoanitic septal necks. Sutures with small ventral lobe only. Surface of shell bearing oblique folds (24). *L.Perm.*, USSR.—FIG. 360,4. *\*M. scorobogatovae*, Urals; lat.,  $\times 9$  (24).

**Tabantaloceras** SHIMANSKIY, 1954 [*\*T. planum*; OD]. Like *Aktastioceras* but cross section more narrowly oval, with flattened flanks and cyrtchoanitic septal necks (24). *L.Perm.*, USSR.—FIG. 360,3. *\*T. planum*, Urals; 3a-c, vent., lat., transv. sec.,  $\times 2.5$  (24).

### DOUBTFUL GENERA

**Cochleiferoceras** SHIMANSKIY, 1962 [*\*Orthoceras cochleiferum* SANDBERGER & SANDBERGER, 1852; OD]. Similar to *Bactrites*, but apical angle larger, camerae less high, ventral lobe and dorsal saddle absent and sculpture consisting of strong oblique foldlike ribs (27). [May not belong to Bactritida.] *M.Dev.*, Eu.(Ger.).—FIG. 361,3. *\*C. cochleiferum* (SANDBERGER & SANDBERGER); 3a,b, vent., adoral;  $\times 2$  (19).

**Cyclobactrites** SHIMANSKIY, 1955 [*\*C. erbeni* (= *Bactrites carinatus* SANDBERGER & SANDBERGER, 1852, pl. 17, fig. 3e, non cetera); OD]. Like *Bactrites*. Sculpture consisting of oblique foldlike ribs (27). [Generic independence doubtful because of occurrence of same sculpture in adult stages of *Bactrites* and *Lobobactrites*.] *M.Dev.*, Eu.(Ger.).—FIG. 361,1. *\*C. erbeni*; venter on right;  $\times 4$  (19).

**Devonobactrites** SHIMANSKIY, 1962 [*\*Orthoceratites obliqueseptatum* SANDBERGER & SANDBERGER, 1852; OD]. Like *Bactrites*. Sutures dorsally inclined and camerae relatively low (27). [Generic independence doubtful because of highly variable orientation of sutures within single individuals of certain representatives of *Bactrites*. Lowness of camerae in this case appears not to be a diagnostic criterion, being caused here by normal crowding of sutures in late ontogenetic stages, which occurs in all ectocochleate cephalopods. *M.Dev.*, Eu.(Ger.).—FIG. 361,2. *\*D. obliqueseptatus* (SANDBERGER & SANDBERGER); 2a,b, vent., lat. with venter on right;  $\times 2$ ; 2c, adoral; all  $\times 1$  (19).

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## INDEX

Italicized names in the following index are considered to be invalid; those printed in roman type, including morphological terms, are accepted as valid. Suprafamilial names are distinguished by the use of full capitals and authors' names are set in small capitals with an initial large capital. Page references having chief importance are in boldface type (as K332).

- Acanthonautilus, **K441**  
*ACETABULIFERA*, K10  
*ACETABULIFÈRES*, K10  
 Achelois, **K488**  
 achoanitic, K39, **K54**  
 Acleistoceras, **K308**  
 Acleistoceratidae, K100, K277, K279, K281, **K308**, K489  
*ACTINOCERACEA*, K203  
 Actinoceras, K94, K95, K190, K191, K193, K194, K196, K197, K199, **K204**, K489  
*Actinocerataceae*, K102  
*ACTINOCERATIDA*, K96, K102, K203  
 Actinoceratidae, K94, K100, K102, **K204**  
*ACTINOCERATINA*, K203  
*Actinoceratites*, K204  
*ACTINOCERATOIDEA*, K3, K12, K94, K96, K97, K98, K100, K102, K104, K109, K110, K127, K128, K129, **K190**, K202, **K203**  
*ACTINOCERIDA*, K12, K26, K30, K34, K36, K39, K40, K41, K45, K46, K49, K50, K95, K96, K97, K100, K109, K117, K121, K125, K129, K132, K190, **K203**, K216, K218, K221  
*ACTINOCEROIDEA*, K95, K129, K203  
 Actinomorpha, K43, K279, **K291**  
*ACTINOSIPHITAE*, K94, K203  
*ACTINOSIPHONATA*, K95, K220, K279, K281, K282  
 actinosiphonate, K40, **K54**  
 actinosiphonate deposits, Onco-  
 cerida, K279  
*Actubonautilidae*, K103, K386, K394  
*Actubonautilus*, K394  
*Adamsoceras*, K199, K211  
 Adelphoceras, K95, **K416**  
*Adelphoceras*, K416  
*Adelphoceratidae*, K416  
*Adnathoceras*, K246  
 adnation area, K40, **K54**  
 adnation surfaces, K190  
 Adnatoceras, **K246**  
*Aegoceras*, K359  
 Aethoceras, K22, K50, K344, **K358**  
*Aetoceras*, K358  
*Avanides*, K489  
 AGASSIZ, K95  
 Agoniatitidae, K495  
 Aipoceras, K123, K397, **K440**  
 Aipocerataceae, K96, K102, K103, K112, K113, K384, K388, K397, K402, K406, K410, K412, **K440**  
 Aipoceratidae, K102, K103, **K440**  
 air chamber, **K54**  
 Akidocheilus, K468, **K481**  
 Aktastioceras, K495, **K503**  
*Aktubonautilidae*, K424  
*Aktubonautilus*, K424  
 alae, K66  
 Alaskoceras, **K358**  
 Albertoceras, **K134**  
 Aletoeras, **K300**  
 Alexandronautilus, **K446**  
 alimentary canal, K7  
 Allanoceras, **K246**  
 Allocotoceras, **K178**  
 Allopiloceras, **K172**  
 Allotrioceras, **K184**  
 Allotrioceratidae, K43, K100, K102, K161, K162, K165, **K184**  
 Allumettoceras, **K290**  
*Allumettoceratidae*, K103, K290  
 Alpenoceras, K322, K324, **K336**  
*Alpheiceras*, K416  
*Aluveroeras*, K211  
 Amblyceras, **K488**  
 Amimomus, **K488**  
 Ammonellipsites, K229, K489  
 AMMONITIDA, K12  
 AMMONOIDEA, K11, K12, K95, K109, K111, K127, K491, K496, K498  
 amorphous band, **K54**, K321  
*Amphereopsis*, K314  
 Amphicyrtoceras, K280, K281, **K308**  
*Amphereopsis*, K314  
*Amphoroceras*, K140  
 Anarcestaceae, K496  
 Anarcestida, K12  
 Anarcestidae, K495, K496  
 Anaspyroceras, **K230**  
 Anastomoceras, **K246**  
 anatomy, Nautilus, K60  
 Ancistroceras, K346, **K366**  
*Ancistroceras*, K366  
*Andoceras*, K173  
 Anetoceras, K496  
 aneuchoanitic, **K54**  
*Angaroceras*, K147  
 ANGELIN, K343  
 Angelinoceras, K118, **K366**  
 Anglicornus, **K300**  
 Anglonautilus, K404, **K453**  
*Angulites*, K456  
*Angulithes*, K456  
 Anguloceras, **K148**  
 anneaux obstructeurs, K193  
 annular elevation, **K54**  
 annular lobe, K31, **K54**  
 annular ridges, K27  
 annulate, **K54**  
 annulation, K21, **K54**  
*ANNULOSIPHONATA*, K95, K198, K203, K220, K369  
 annulosiphonate, **K54**  
 annulosiphonate deposits, K41  
 annulus, K44, **K54**  
 Anomaloceras, K388, K394, **K416**  
 Anomeioceras, **K308**  
 Anoploceras, K392, **K413**  
 anteroventral aponeurosis, K70  
 Anthoceras, K160, **K166**  
 Antiphragmoceras, K50, **K332**  
 Antiptectoceras, **K372**  
 Antonoceras, **K318**  
*Antonoceratidae*, K103  
 apertural flanges, K22  
 apertural ridge, **K54**  
 aperture, K25, K26, **K54**  
 Aphelaecceras, K400, K406, K410, **K428**  
*Aphelaecceratinae*, K103, K427  
*Aphelaecceras*, K428  
 Aphetoceras, **K358**, K370  
 Aphragmites, **K273**  
 apical camera, K45, **K54**  
 Apioceras, **K318**  
 Aploceras, **K215**  
*Apocrinoceratidae*, K152  
 Apogonoceras, K400, **K428**  
 aponeuroses, K27, K69  
 aponeurotic bands, **K54**  
 APPELLÖF, K36, K77, K78  
 Apsidoceras, K369, **K382**  
 Apsidoceratidae, K101, K103, K368, K369, K370, K371, **K380**  
 Aptychus, K476  
 Archiacoceras, K42, K278, K279, **K312**  
 Archiacoceratidae, K100, K103, K279, K281, **K312**  
 Architeuthis, K5  
*Arcoceras*, K360  
*Arctinoceras*, K204, K489  
 Arcuatobeccus, **K479**  
*Arogoceras*, K314

- Argocheilus, **K314**  
 Argonauta, **K8**  
 ARISTOTLE, **K94**  
 Arkoceras, **K360**  
 Arkonoceras, **K217, K226**  
 Armenoceras, **K49, K192, K193, K194, K196, K199, K206**  
 Armenoceratidae, **K50, K94, K100, K102, K190, K202, K206**  
 ARMSTRONG, **K14**  
 Arpaoceras, **K251**  
 Arthrophyllum, **K220, K234**  
*Arthuroceras*, **K448**  
*Articheilus*, **K390, K427**  
 Asaphiceras, **K284**  
 ASCOCERACEA, **K96, K269**  
 Ascoceras, **K95, K263, K265, K266, K267, K273**  
 ASCOCERATIDA, **K96, K102, K269, K271**  
 Ascoceratidae, **K100, K103, K264, K269, K271**  
*Ascoceratides*, **K271**  
 ASCOCERATINA, **K269**  
 Ascoceratinae, **K100, K263, K264, K271**  
 Ascocerida, **K12, K26, K28, K40, K48, K49, K51, K95, K96, K98, K100, K105, K110, K112, K117, K118, K121, K128, K132, K219, K261, K263, K269**  
 ascoceroid conch, **K54, K263**  
 ascoceroid septum, **K54**  
*Asoceras*, **K273**  
 Asymptoceras, **K397, K441**  
 Atractites, **K499**  
 Aturia, **K13, K25, K39, K49, K98, K113, K125, K126, K128, K388, K404, K457, K472, K489**  
*Aturiaceae*, **K104, K457**  
*Aturidae*, **K386, K457**  
 Aturiidae, **K31, K102, K104, K383, K404, K457**  
 Aturoidea, **K397, K403, K404, K456**  
 Augustoceras, **K279, K291**  
 Aulacoceras, **K499**  
*Aulacoceratidae*, **K496**  
 aulacoceratids, **K496, K499**  
 Aulaconautilus, **K404, K410, K452**  
 Aulametacoceras, **K390, K404, K410, K413**  
 Ausfüllungsmasse, **K36**  
 Ausseites, **K499**  
 Austinoceras, **K308**  
 Avaoceras, **K148**  
 Avilonella, **K373**
- Bactritacea*, **K501**  
*Bactritaceae*, **K501**  
 Bactrites, **K487, K492, K493, K495, K496, K501**  
 BACTRITIDA, **K12, K102, K110, K132, K491, K495, K499, K501**  
 Bactritidae, **K95, K102, K491, K495, K496, K501**  
 BACTRITINA, **K491, K501**  
 BACTRITOIDEA, **K3, K12, K96, K102, K127, K491, K501**  
 BACTRITOIDEA, **K501**  
 Bactrocera, **K155**  
 Baeopleuroceras, **K370, K380**  
*Baepleuroceras*, **K380**  
 Bajkaloceras, **K187**  
 Bajkaloceratidae, **K100, K187**  
 BALASHOV, **K127, K130, K133, K163, K343**  
 Balticoceras, **K226**  
*Baltoceras*, **K154, K217**  
 Baltoceratidae, **K34, K100, K102, K108, K110, K112, K131, K132, K154, K164, K219, K220**  
 BARRANDE, **K15, K30, K35, K47, K48, K51, K52, K94, K126, K133, K193, K261, K343, K487**  
 Barrandeoceras, **K369, K370, K372, K495**  
 BARRANDEOCERATIDA, **K96, K105, K369, K372, K383**  
 Barrandeoceratidae, **K100, K103, K348, K369, K370, K371, K372**  
 BARRANDEOCERATINA, **K103, K372**  
 BARRANDEOCERIDA, **K12, K28, K34, K39, K40, K45, K46, K50, K96, K98, K100, K105, K109, K110, K112, K116, K123, K125, K128, K348, K368, K369, K370, K372, K383, K384, K394**  
*Barrandioceras*, **K372**  
*Barrandoceras*, **K372**  
 basal septum, **K54**  
 basal zone, **K54**  
*Basleonautilus*, **K414**  
 Basse, **K11**  
 Bassleroceras, **K148**  
*Basslerocerataceae*, **K102**  
 BASSLEROCERATIDA, **K96**  
 Bassleroceratidae, **K100, K102, K109, K112, K131, K148, K280, K348**  
 Bathmoceras, **K40, K95, K110, K129, K130, K132, K156, K199**  
*Bathmoceras*, **K156**  
*Bathmocerataceae*, **K102**  
 Bathmoceratidae, **K100, K102, K108, K132, K156**  
 Beckmanoceras, **K360**  
*Beckmanoceratidae*, **K103, K359**  
 Belemnitimimus, **K503**  
 BELEMNOIDEA, **K95**  
 BELEMNITIDA, **K12**  
 Beloitoceras, **K278, K284**  
 Bergoceras, **K44, K252**  
*Besseloceras*, **K210**  
*Besseloceratinae*, **K210**  
 BESSLER, **K468**
- Bickmorites, **K370, K373**  
*Bickmoritidae*, **K103, K372**  
 Biconulites, **K489**  
 BIDDER, **K9, K59**  
 Bifoveoceras, **K26, K217, K224**  
 BIGUET, **K467, K468, K471, K473**  
*Billingoceras*, **K273**  
 BILLINGS, **K129, K262**  
 Billingsites, **K264, K266, K273**  
 biology, *Nautilus*, **K87**  
 biostratonomy, **K124, K476**  
 Bisiphites, **K488**  
 Bisiphytes, **K404**  
*Bisonoceras*, **K489**  
 Bistrialites, **K394, K446**  
 Bitauinioceras, **K226**  
 black layers, *Nautilus*, **K72**  
 blade, **K54**  
 BLAINVILLE, DE, **K2, K468, K471, K473**  
 Blakeoceras, **K280, K305**  
*Blastoceras*, **K300**  
 Blastocerina, **K300**  
 BLUMENBACH, **K468, K471, K473**  
 body, **K60, K66**  
 body chamber, **K13, K25, K54**  
 Bøggild, **K14, K15**  
 Bohemites, **K230**  
 BÖHM, **K468, K472**  
 BÖHMERS, **K84**  
*Bojobactrites*, **K499, K502**  
*Bojobactritidae*, **K499, K501**  
*Bolboceras*, **K318**  
 Bolloceras, **K50**  
*Bolloceratidae*, **K103, K305**  
 Boreoceras, **K182, K305**  
*Bothmoceras*, **K156**  
 Brachycycloceras, **K48, K50, K51, K217, K232, K484**  
 Brachycycloceratidae, **K48, K100, K110, K112, K217, K232**  
 Brachydomoceras, **K316**  
 Bradfordoceras, **K251**  
 BRADY, **K468, K476**  
 branchiae, *Nautilus*, **K66**  
*Brazaturia*, **K457**  
 Brevioceras, **K49, K279, K300**  
 Brevioceratidae, **K100, K103, K277, K279, K280, K299**  
 brevicone, **K54**  
 breviconic cyrtocones, **K16**  
*Breynioceras*, **K260**  
 BREYNIUS, **K94**  
 Bridgeoceras, **K134**  
 brim, **K54**  
*Brittsoceras*, **K489**  
 BRODERIP, **K338**  
 Broeggeroceras, **K333**  
 BROILI, **K95**  
 BRONN, **K94, K262**  
 buccal mass, **K60**  
 Buchanoceras, **K44, K217, K251**  
 BUCKLAND, **K338, K477**  
 Buehleroceras, **K134**  
 bullette, **K44, K54, K322**

- bundled, **K54**  
 Burenoceras, **K50, K134**  
 Butsoceras, **K44, K50, K218, K235**  
*Butsoceratidae*, **K102**  
 Byronoceras, **K308**  
  
 cadicone, **K54**  
 caecum, **K46, K54**  
*Calchasiceras*, **K314**  
 Calhounoceras, **K216**  
 Calliaonutilus, **K396, K442**  
 Calocyrtoceras, **K242**  
*Camaroceras*, **K174**  
 camera, **K13, K54, K71**  
 cameral deposits, **K16, K31, K54**  
 cameral deposits, episeptal, **K32**  
 cameral deposits, hyposeptal, **K32**  
 cameral mantle, **K35**  
 Cameroceras, **K5, K38, K163, K165, K174**  
 Campbelloceras, **K346, K355**  
 Campendoceras, **K166**  
*Campulites*, **K312**  
 Campyloceras, **K254**  
 capuchon céphalique, **K63**  
 Carbactinoceras, **K46, K193, K197, K215**  
*Carbactinoceratidae*, **K50, K100, K202, K203, K215**  
 Carinonutilus, **K404, K449**  
 Carloceras, **K398, K432**  
*Carloceras*, **K432**  
 Casoceras, **K134**  
 Cassinoceras, **K172**  
 Casteroceras, **K388, K416**  
 Catoraphiceras, **K132, K152, K498**  
 Catyrepnoceras, **K368, K376**  
 Cayugoceras, **K340**  
 Cayutoceras, **K251**  
*Cayutoceratinae*, **K100, K218, K221, K251**  
 CECIONI, **K130**  
*Cedarvilleoceras*, **K238**  
 Cenoceras, **K113, K391, K397, K398, K403, K404, K408, K410, K449, K472**  
 central canal, **K54, K192**  
 central tube, **K323**  
 centrifugal deposits, **K54**  
 Centroceras, **K383, K432**  
*Centrocerataceae*, **K103, K386, K398, K427**  
*CENTROCERATIDA*, **K96, K383, K412, K427**  
*Centroceratidae*, **K102, K103, K113, K383, K386, K388, K398, K400, K406, K432**  
*CENTROCERATINA*, **K103, K393, K412, K427**  
*Centrocyrtoceras*, **K370, K373**  
*Centrocyrtoceratidae*, **K372**  
 Centrolitoceras, **K416**  
 Centroonoceras, **K221, K233**  
 Centrorizoceras, **K284**  
*CENTROSIPHONATA*, **K96**  
 Centrotarphyceras, **K346, K355**  
  
 cephalic cartilage, **K60**  
 CEPHALOPODA, **K4, K12, K96, K127**  
*CEPHALOPODES ACÉTABULIFÈRES*, **K474**  
*CEPHALOPODES, LES*, **K4**  
 cephalopodium, **K60**  
 CERITITIDA, **K12**  
*Certoceras*, **K380**  
 Chadwickoceras, **K308**  
 chambers, **K13, K54, K75**  
 chambre d'habitation, **K75**  
 Changkiuoceras, **K187**  
 Charactoceras, **K371, K382**  
 Charactocerina, **K382**  
 Chazyoceras, **K174**  
 chemical composition, Nautilus shell, **K71**  
 CHENOWETH, **K126**  
 CHENU, **K472**  
 Chepuloceras, **K134**  
 Chicagoceras, **K216, K259**  
 Chidleyenoceras, **K382**  
 Chihlioceras, **K179**  
*Chihlioceratidae*, **K43, K100, K102, K161, K163, K165, K179**  
*Chihlioceras*, **K179**  
*Chilioceras*, **K179**  
*Chilosceras*, **K175**  
 Chitinoteuthidae, **K475, K499**  
 chitinous zone, **K54**  
*Choanicerias*, **K276**  
 Choanoceras, **K276**  
*Choanoceratidae*, **K100, K103, K262, K267, K269, K276**  
 Choanoteuthis, **K499**  
*Choniceras*, **K276**  
 Chouteauoceras, **K400, K428**  
 cicatrix, **K47, K54, K82**  
 Cimomia, **K13, K397, K404, K405, K456**  
*Cimonia*, **K456**  
 Cinctoceras, **K340**  
 circulatory system, **K8**  
 circulatory system, Nautilus, **K68**  
 circulus, **K54, K190**  
 circumspuncular ridge, **K55, K190**  
*Cirthoceratites*, **K312**  
 CLARKE, **K140, K266**  
*Clarkeoceras*, **K135**  
 Clarkesvillia, **K333**  
 Clarkoceras, **K130, K135**  
 classification, **K12, K94, K130, K163, K198, K220, K261, K281, K323, K346, K368, K383, K472, K498**  
 Clathroceras, **K298**  
 Clelandoceras, **K140**  
 Cliftonoceras, **K374**  
 Clinoceras, **K28, K216, K220, K240**  
*Clinoceratidae*, **K100, K102, K217, K219, K221, K238**  
 Clonyssiceras, **K308**  
 Clitendoceras, **K166, K489**  
 cloisons, **K71**  
*Clostomiceras*, **K140**  
  
 Clydonautilaceae, **K102, K103, K112, K384, K386, K388, K394, K396, K397, K398, K402, K406, K408, K410, K412, K442**  
*Clydonautilidae*, **K102, K103, K383, K386, K396, K403, K410, K442**  
*Clydonautilus*, **K396, K408, K410, K442**  
 CLYMENIIDA, **K12**  
*Clymenionautilus*, **K439**  
*Clymenonautilinae*, **K103, K437**  
*Clymenonautilus*, **K403, K439**  
*Clynoceras*, **K240**  
 Clytoceras, **K358**  
*Coanoceras*, **K276**  
 COCHLEATI, **K94, K198, K203**  
 Cochleiferoceras, **K503**  
 Cochlioceras, **K28, K39, K130, K154**  
*Cochlioceratidae*, **K154**  
 Codoceras, **K280, K316**  
*Coeloceratoides*, **K489**  
 Coelocyrtoceras, **K316**  
 Coelogasteroceras, **K395, K446**  
 coelom, Nautilus, **K68**  
*Coelonautilus*, **K489**  
 COELOSPHITAE, **K94**  
 COLEOCERAS, **K488**  
 Coleoidea, **K3, K11, K12, K106, K127, K467, K498, K499**  
 COLLINSON, **K394**  
*Collonautilus*, **K489**  
 collum, **K55**  
*Coloceras*, **K445**  
*Coloceratidae*, **K444**  
 coloration, Nautilus, **K71**  
 Colpoceras, **K188**  
 Columenoceras, **K237**  
 compressed, **K18, K55**  
 concavosiphonate, **K40, K55**  
*Concerina*, **K140**  
 conch, **K13, K55, K102**  
 conch, ascoceroïd, **K263**  
 conch, color markings, **K16, K24**  
 conch shape, **K16**  
 conch surface, **K20**  
 conchal furrow, **K16, K26, K29, K55**  
 conchal zone, **K55**  
 conchial zone, **K55**  
 conchiolinous zone, **K55**  
*Conchorhynchus*, **K478**  
 conchorhynchus, **K471**  
*Conchorhynchus*, **K468, K471, K472, K474, K476, K477, K478**  
 Condraoceras, **K395, K447**  
 conellae, **K15**  
 connecting rings, **K13, K38**  
 Conoceras, **K188**  
*Conoceratites*, **K188**  
 Conocerina, **K140**  
*Conoclarites*, **K188**  
*Conorthoceras*, **K489**  
 Conostichoceras, **K42, K305**  
*Conotabularia*, **K204**

- conotheca, K13, **K55**  
*Conotubularia*, K204  
 CONRAD, K380  
*Conradiceras*, K447  
*Conradoceras*, **K295**  
*Conradoceras*, K295, K333  
 constricted, **K55**  
 constriction, **K55**  
 contact layer, **K55**  
 contracted, **K55**  
*Convexiterbeccus*, **K479**  
 convolute, K18  
*Convoluticeras*, K496  
*Cooperoceras*, K118, K391,  
     K410, **K413**  
*Cophiceras*, K140  
*Cophinaceras*, K416  
*Cophinoceras*, K416  
*Copiceras*, K130, **K140**  
*Coralloceras*, K234  
*Coreanoceras*, **K180**  
 coronate, **K55**  
*Cosmonautilus*, K396, K408,  
     **K442**  
 costae, K20, **K55**  
*Cotteroceras*, **K166**, K489  
 Cox, K222  
*Cranoceras*, K305  
*Cranoceratidae*, K305  
*Crateroceras*, **K308**  
 crura, K66  
*Cryptoceras*, K273, K441  
*Cryptorhoceras*, K216, **K248**  
*Ctenobactrites*, K492, **K501**  
*Ctenobactritidae*, K499, K501  
*Ctenoceras*, K26, **K225**  
*Cumberloceras*, K130, **K140**  
*Cumingsoceras*, **K374**  
*Curtoceras*, K346, **K360**  
*Curvites*, **K488**  
*Cyclendoceras*, K173  
*Cyclendoceratidae*, K172  
*Cyclidia*, K470, **K481**  
*Cyclobactrites*, **K503**  
*Cycloceras*, **K259**  
*Cycloceratinae*, K102  
*Cyclocyrtendoceras*, **K182**  
*Cyclolituites*, **K366**  
*Cyclonautilus*, K447  
*Cycloplites*, **K316**  
*Cycloplectoceras*, **K355**  
*Cyclorizoceras*, K288  
*Cyclostomiceras*, K130, **K140**  
*Cyclostomiceratidae*, K102,  
     K108, K134  
*Cycoceras*, K259  
*Cymatoceras*, K403, K404, **K453**  
*Cymatoceratidae*, K102, K104,  
     K383, K397, K403, K404,  
     K406, K408, K410, **K452**  
*Cymatoceratinae*, K104  
*Cymatonautilus*, K404, **K453**  
*Cymmomea*, K456  
*Cymomia*, K456  
*Cyrtendoceras*, **K166**, K498  
*Cyrtendocerina*, K166  
*Cyrtacteistoceras*, K489  
*Cyrtactinoceras*, K218, **K256**  
*Cyrtendoceras*, **K182**  
*Cyrtendoceratidae*, K100, K102,  
     K165, **K181**  
*Cyrtoceratites*, **K305**  
*Cyrtocerus*, K312  
*Cyrtactinoceras*, K256  
*Cyrtobactrites*, K492, K495,  
     K496, K498, **K501**  
*Cyrtocera*, K312  
*CYRTOCERACEA*, K282  
*Cyrtoceras*, K50, K94, K95,  
     K284, K288, K305, K333,  
     K376, K380, K488  
*Cyrtocerataceae*, K103  
*Cyrtoceratidae*, K103, K281,  
     K305  
*Cyrtoceratites*, **K312**  
*Cyrtocerina*, K40, K130, **K159**  
*Cyrtocerinidae*, K100, K132,  
     **K158**  
*CYRTOCEROIDEA*, K95, K281,  
     K282  
*Cyrtocerus*, K380  
*Cyrtocheilus*, **K316**  
*CYRTOCHOANITES*, K95,  
     K198, K220, K279, K281,  
     K369  
*CYRTOCHOANITES ACTINO-*  
*SPIHONATA*, K282  
 cyrtchoanitic, K39, **K55**  
 cyrtcone, K16, **K55**  
*Cyrtocycloceras*, **K242**  
*Cyrtogomphoceras*, K322, **K328**  
*Cyrtogomphoceratidae*, K100,  
     K103, K323, K324, **K328**  
*Cyrtogomphus*, **K314**  
*Cyrtonbyoceras*, K49, K192,  
     K198, K199, **K208**  
*Cyrtoönoceras*, K233  
*Cyrtorhizoceras*, K284  
*Cyrtorizoceras*, **K284**  
*Cyrtospyroceras*, **K248**  
*Cyrtothoracoceras*, **K249**  
*Cyrtovaginoceras*, **K182**  
*Cyrtovaginoceratidae*, K102,  
     K181  
*Dakeoceras*, **K140**  
*Damesites*, K174  
*Danaoceras*, K279, K280, **K293**,  
     K316  
*Dartoceras*, **K484**  
 DAVITASHVILI, K96  
*Dawsonoceras*, K14, **K238**  
*Dawsonoceratidae*, K100, **K238**  
*Dawsonocerina*, **K238**  
 DEAN, K48, K49, K59  
 DECAPODA, K12  
 deciduous conch, **K55**, K263  
*Deckeroceras*, **K382**  
 decollation, K47, **K55**  
 DEECKE, K29  
*Deiroceras*, K193, **K212**  
*Dieroceratidae*, K102, K210  
*Deltoceras*, **K488**  
*Deltoceratidae*, K357  
*Deltocymatoceras*, K404, K408,  
     K410, **K454**  
*Deltoidonautilus*, K404, K410,  
     **K456**  
*Dentatobeccus*, **K480**  
*Dentoceras*, **K442**  
*Dentoceras*, K442  
*Dentoceratidae*, K103, K386,  
     K398, K442  
 depressed, K18, **K55**  
*Desioceras*, K130, **K140**  
*Devonobactrites*, **K503**  
*Devonocheilus*, **K312**  
 DEWITZ, K33, K35  
*Diademoceras*, **K418**  
*Diadioloceras*, **K488**  
*Diagoceras*, **K249**  
*Diaphoroceras*, **K148**  
 diaphragm, **K55**  
*Diastoloceras*, K22, **K152**  
 DIBRANCHIATA, K10, K11,  
     K60, K89, K109  
*Dictyoceras*, **K259**  
*Dideroceras*, K175  
*Diestoceras*, K44, K50, K278,  
     K279, **K293**  
*Diestoceratidae*, K100, K103,  
     K279, K280, K281, **K293**  
*Digenucoceras*, K284  
 digestion, K8  
 digestive system, Nautilus, K68  
*Digonioceras*, K404, K449  
*DIGONIOCERATIDA*, K221,  
     K448  
 Diluvialgeschichte, K343  
*Dimeres*, **K488**  
 Dimorion, **K488**  
 dimorphism, K48, K472  
*Diodoceras*, K400, **K429**  
*Diorugoceras*, K398, **K432**  
*Diphragmoceras*, K489  
*Diploceras*, **K188**  
*Diploceras*, K188, K260  
*Discites*, K429  
*Discitoceras*, K400, **K429**  
*Discoactinoceras*, **K210**  
*Discoactionoceras*, K210  
*Discoceras*, K14, **K360**  
*Discoceras*, K360  
 DISCOSORIDA, K12, K26,  
     K28, K34, K36, K39, K40,  
     K41, K45, K49, K50, K96,  
     K98, K100, K103, K105,  
     K109, K110, K117, K118,  
     K122, K128, K131, K198,  
     K220, K221, **K320**, **K324**,  
     K487  
*Discosoridae*, K45, K50, K100,  
     K103, K324, **K335**  
*Discosoridae*, K335  
*Discosoridae*, K324  
*DISCOSOROIDEA*, K96, K324  
*Discosorus*, K198, K323, **K336**  
*Discus*, K489  
 disease, K51  
 distal deposits, **K55**  
 distal division of siphonal fun-  
     nel, **K55**  
 distribution, K88, **K94**, K132,  
     K165, K203, K219, K267,  
     K280, K324, K369, K476,  
     K496  
*Dnestroceras*, **K251**  
*Dolorthoceras*, K2, K15, K217,  
     **K249**

- Dolorthoceratinae*, K221, K246  
*Domatoceras*, K113, K390, K398, K400, K401, K402, K403, K406, K408, K410, **K433**  
*Domatoceratidae*, K103, K386, K432  
domiciliary division, **K55**  
*Donacoceras*, **K259**  
dorsal aponeurosis, K69  
dorsal area, **K55**  
dorsal furrow, K16, K30, **K55**  
dorsal hiatus, **K55**  
dorsal lobe, **K55**  
dorsolateral bands, **K55**  
dorsomyarian, K27, K28, K55  
dorsoventral section, **K55**  
dorsum, **K55**  
*Dowlingoceras*, **K295**  
*Dresseroceras*, K152  
*Duerleyoceras*, **K418**  
*Dunleithoceras*, **K284**  
*Dunleitoceras*, K284  
duplication, K66  
*Dwightoceras*, **K148**  
*Dyscritoceras*, **K148**
- Ecdyceras*, **K277**  
*ECDYCERATIDA*, K269  
*Ectenoceras*, K140  
*Ectenolites*, K140  
*ECTOCOCHLIA*, K3, K10, K11  
*Ectocycloceras*, **K152**  
*Ectocyrtoceras*, **K308**  
ectosiphon, **K55**  
ectosiphuncle, K13, K38, **K55**, K70, K75  
ectosiphuncular suture, K38, **K55**  
*Edaphoceras*, K392, **K424**  
eggs, K9, K80  
*Ehlersoceras*, **K284**  
EHRENBERG, K110  
EICHWALD, K15  
*Eichwaldoceras*, **K359**  
*Eifeloceras*, **K244**  
EKSTRAND, K15  
*Ekwanoceras*, **K284**  
*Eleusoceras*, K279, **K301**  
*Elkoceras*, K489  
*Ellesemroceras*, K134  
*Ellesmereoceras*, K134  
*Ellesmereoceratidae*, K134  
*Ellesmeroceras*, K129, **K134**  
*ELLESMEROCERATIDA*, K96, K102, K134  
*Ellesmeroceratidae*, K100, K107, K108, K131, K133, **K134**  
*ELLESMEROCERIDA*, K3, K12, K26, K34, K36, K39, K40, K41, K50, K96, K97, K100, K104, K105, K108, K110, K111, K112, K121, K128, K129, K131, K132, K133, **K134**, K219, K220, K280, K346, K348  
*Ellinoceras*, **K205**  
*Ellinocerataceae*, K102, K204  
*Ellinoceratidae*, K102, K204  
ellipchoanitic, K39, **K55**  
*ELLIPOCHOANOIDA*, K95  
ellipticone, **K55**  
*Elrododoceras*, K193, K199, **K208**  
embryo, Nautilus, K80  
*Emmonsoceras*, K43, **K182**  
*Emmonsoceratidae*, K100, K102, K165, **K182**  
*Enclimatoceras*, K456  
*Encoilceras*, K389, K392, **K413**  
*Encoilcerataceae*, K103, K386, **K413**  
*Encoilceratidae*, K103, K386, K413  
*ENDOCERACEA*, K165  
*Endoceras*, K94, K95, K126, K160, K163, **K173**, K174  
*ENDOCERATIDA*, K96, K102, K165  
*Endoceratidae*, K95, K100, K102, K108, K163, K165, **K172**  
*ENDOCERATINA*, K102, K163, K165  
*Endoceratinae*, K172  
*ENDOCERATOIDEA*, K3, K12, K50, K96, K98, K100, K102, K104, K108, K127, K128, K129, **K160**, **K165**  
*ENDOCERIDA*, K12, K26, K34, K36, K39, K40, K41, K42, K46, K50, K94, K96, K97, K100, K108, K109, K117, K120, K125, K131, K132, **K165**, K216, K220  
*ENDOCEROIDEA*, K95, K128, K165  
*ENDOCOCHLIA*, K3, K10, K11, K12  
endocone, K43, **K55**, K161, K322  
*Endocycloceras*, **K154**  
*Endocycloceratidae*, K152  
*Endodiscosorus*, **K338**  
endogastric, K18, **K55**  
*Endogomphus*, K489  
*Endolobus*, K392, K394, **K424**  
*Endoplanoceras*, K370, **K380**, K489  
*Endoplectoceras*, **K338**  
endosiphoblade, **K55**  
endosiphocoleon, **K55**, K162  
endosiphocone, **K55**, K161  
endosiphofuncles, K162  
endosiphonling, **K55**  
endosiphon, **K55**  
endosiphotube, **K55**  
endosiphowedge, **K55**  
endosiphuncle, K38, K40, **K56**  
endosiphuncular blade, **K56**, K162  
endosiphuncular canal, K16, K41, K43, K192, K322  
endosiphuncular deposits, K40  
endosiphuncular lining, **K56**  
endosiphuncular structures, K38  
endosiphuncular tube, **K56**, K161  
endosiphuncular vascular system, K192  
endosiphuncular wedge, **K56**, K161  
*Endostokesoceras*, K336  
*Engorthoceras*, K489  
*Enoploceras*, K392, **K413**  
entonnoir, K65  
*Eobactrites*, K132, K495, **K501**  
*Eorizoceras*, **K283**  
*Eosactoceras*, K489  
*Eospyroceras*, K231  
*Eothinoceras*, K40, K130, K133, **K156**  
*Eothinoceratidae*, K102, K156  
*Eotrimoceras*, **K298**  
*Eotripteroceras*, **K226**  
*Ephippioceras*, K395, **K448**  
*Ephippioceratidae*, K102, K103, K113, K383, K386, K395, **K448**  
*Ephippiorthoceras*, **K256**  
*Epicymatoceras*, K404, **K454**  
épidermides, K15  
*Epidomatoceras*, K400, K410, **K433**  
episeptal deposits, **K56**  
episeptal tubercle, **K56**  
*Epistroboceras*, K400, K406, K410, **K429**  
*Ephippioceratidae*, K448  
ERBEN, K491, K492, K496  
*Eremoceras*, **K140**  
*Eridites*, **K249**  
*Erlangericheilus*, **K481**  
*Escharendoceras*, **K170**  
*Eskimoceras*, **K212**  
*Eskimoceratidae*, K102, K210  
*Estonioceras*, **K357**  
*Estonioceratidae*, K100, K343, K344, K346, K348, **K357**  
*Eucymatoceras*, K404, **K454**  
*EUDES-DESLONGCHAMPS*, K470  
*Eudoceras*, **K318**  
*Euhuronina*, K214  
*Euloxoceras*, **K249**  
*Euomphalus*, K490  
*Euophioceras*, K367  
*Euormoceras*, K214  
*Euorthoceras*, K214  
*Eurasiaticoceras*, K360  
*Euryrizoceras*, **K310**  
*EURYSIPHONATA*, K96  
euryisiphonate, K36, **K56**  
*Eurystomites*, **K355**  
*Eushantungoceras*, K206  
*Eusthenoceras*, K220, K221, **K254**  
*Eutrepoceras*, K13, K14, K15, K29, K397, K403, K404, **K449**  
*Eutrepoceratidae*, K448  
*Evencoceras*, **K187**  
*Evlanoceras*, **K316**  
evolute, K18, **K56**  
evolution, **K106**, K130, K164, K198, K323, K405, K494  
excretory system, Nautilus, K67  
*Exocyrtoceras*, **K301**



- exogastric, K18, **K56**  
*Exomegoceras*, K288  
*Exosiphonites*, K489  
 external lobe, **K56**  
 external suture, K31, **K56**  
 eyelet, **K56**
- Faberoceras, K324, **K333**  
 falcate, **K56**  
*Falcilituites*, K357  
 falcoid, **K56**  
 false contact, **K56**  
 fasciculate, **K56**  
 Fayettoceras, **K293**  
*Featherstonhaughoceras*, K178  
 FÉRUSSAC, K10  
 first lateral lobe, **K56**  
 FISCHER, K34, K485  
 flanks, K18, **K56**  
 flared, **K56**
- FLOWER, K2, K12, K15, K35,  
 K36, K49, K96, K110, K114,  
 K119, K126, K129, K163,  
 K192, K193, K198, K199,  
 K221, K222, K265, K266,  
 K268, K282, K348, K369,  
 K370, K380, K383, K388,  
 K394, K398, K399, K481,  
 K496, K498, K499  
 Floweroceras, **K205**  
*Floweroceratidae*, K204  
 FOERSTE, K24, K49, K120, K129,  
 K193, K198, K262, K279,  
 K281, K343, K369  
*Foerstella*, K178  
 Foerstellites, **K178**  
 Foerstoceras, K279, **K301**  
*Foersteoceras*, K226, K301  
 food, Nautilus, K88  
 FOORD, K262, K474, K477  
 Foordiceras, K393, **K425**  
*Foordoceras*, K425  
 foramen, **K56**  
 Franklinoceras, K324, **K328**  
 free part, K191  
 free part of connecting ring,  
**K56**  
 free part of septum, **K56**  
 Fremontoceras, **K382**  
 function of shell, Nautilus, K90  
 FUNNAPERTA, K10  
 funnel, **K56**  
 funnel emargination, **K56**  
 FUNNOCLAUSA, K10  
 FURNISH, K4, K47, K111,  
 K114, K343, K484  
 Fusicoceras, **K249**
- GAILLARDOT, K468, K474  
 Galtoceras, **K310**  
*GAMOCHONIA*, K10  
 GARNER, K399  
 Garryoceras, **K259**  
 gas chamber, **K56**  
 Gasconsoceras, **K373**  
 GASIOROWSKI, K476  
 Gaspocytoceras, **K242**  
 GEISLER, K124, K126  
 Geisonoceras, K28, K217, **K236**  
 Geisonoceratidae, K100, K102,  
 K218, K219, K220, **K236**  
 Geisonocerina, **K237**  
 Geisonoceroidea, **K250**  
 GEMMELLARO, K496  
 Germanonautilus, K50, K391,  
 K414, K468, K472  
 Gigantei, K94, K198, K203,  
 K210  
 Gigantoceras, K369, K380  
 gills, K11  
 gills, Nautilus, K66  
 Girtyoceras, K416  
 GLENISTER, K47, K130, K343,  
 K484  
 Glenisteroceras, **K235**  
 Globosobeccus, **K480**  
 Glossoceras, K95, K264, K266,  
**K273**  
*Glyptoceras*, K333  
 Glyptodendron, K323, **K333**  
 GOLDRING, K126  
 Goldringia, K418  
 GOMPHOCERACEA, K282  
 Gomphoceras, K94, K95, **K318**  
*Gomphoceratidae*, K103  
*Gomphoceratites*, K318  
 GOMPHOCEROIDEA, K95,  
 K281, K282  
 Gonatocheilus, K468, **K481**  
 Gonatocytoceras, **K310**  
 GONIATITIDA, K12  
 Gonioceras, K94, K121, K197,  
 K208  
 Gonioceratidae, K100, K102,  
 K190, K202, **K208**  
 Gonionaedyceras, **K301**  
 Gonionautilidae, K102, K103,  
 K386, K396, K410, **K448**  
 Gonionautilus, K128, K397,  
 K408, K410, **K448**  
*Goniotrochoceras*, K373  
 gonocoele, K69  
 Gorbyoceras, K218, **K256**  
 GORDON, K496, K498, K499  
 Gordonoceras, **K250**  
 Gorgonoceras, **K235**  
 goulot siphonal, K75  
 GRABAU, K35, K496  
*Grabauoceras*, K179  
 Graciloceras, K102, K132, **K283**  
 Graciloceratidae, K100, K280,  
**K283**  
 Graftonoceras, K344, **K360**  
 granular zone, **K56**, K321  
 Greenlandoceras, **K342**  
 Greenlandoceratidae, K100,  
 K103, **K342**  
 GRÉGOIRE, K34, K36  
 GRIFFIN, K59, K71, K73  
 GRIMPE, K10  
 Grimsbyoceras, **K310**  
 growth lines, K20, **K56**  
 growth lines, Nautilus, K74  
 growth of septa, Nautilus, K86  
 Grypoceras, K113, K390, K400,  
 K406, K408, **K432**  
 Grypoceratidae, K102, K103,  
 K113, K386, K390, K400,  
 K402, K406, K410, **K432**  
*Grypoceratinae*, K103, K432  
*Gryponautilidae*, K432  
 Gryponautilus, K401, K406,  
 K408, K410, **K435**  
*Gyroceras*, K301, K490  
*Gyroceratinae*, K413  
 Gyroceratites, K490, K495  
 Gyrocerus, **K488**  
 gyrocone, K18, **K56**  
 Gyronaedyceras, **K301**  
 Gzheloceras, K392, **K414**  
*Gzheloceratidae*, K103, K386,  
 K389, K394, K413
- Hadeoceras*, K290  
 Hadoceras, **K290**  
 Hadrocheilus, K468, K472,  
 K474, K475, K476, **K479**  
 HAECKEL, K10  
 HAGENOW, K468  
 HALL, K94  
 Hallocceras, **K418**  
*Halloceratidae*, K416  
*Hammellocceras*, K256  
*Hammelloceratidae*, K255  
 HANSMAN, K47, K484  
 HÄNTZSCHEL, K487  
*Haploceras*, K215  
 Hardmanoceras, K123, K344,  
**K361**  
 Harrisoceras, K44, K50, **K237**  
 Haydenoceras, **K373**  
 head-foot, K60  
 Hebetoceras, K262, **K277**  
*Hebetoceratidae*, K100, K103,  
 K262, K266, K268, K269,  
**K277**  
 Hecatoceras, **K333**  
 Hedstroemoceras, K25, **K484**  
*Helenites*, K206  
 Heloceras, **K260**  
*Hemibactrites*, K501  
*Hemiceras*, K188  
 Hemiceratites, **K188**  
 Hemichoanella, **K140**  
 hemichoanitic, K39, **K56**  
 Hemilirocceras, K394, **K447**  
*Heminautilinae*, K104, K452  
 Heminautilus, K397, K404,  
 K408, K410, **K454**  
 Hemiphragmoceras, **K295**  
*Hemiphragmoceratidae*, K50,  
 K100, K103, K279, K280,  
**K295**  
*Hemiphraygmoceras*, K295  
 Hemipiloceras, **K188**  
*Hemipiloceratidae*, K172  
*Hemipoloceras*, K188  
 hemocoelic membrane, K68  
*Hendersonia*, K178  
 Heptameroceras, K295  
 Heracloceras, **K380**  
*Hercoceracea*, K413  
 Hercoceras, K95, K388, K413,  
**K418**  
*HERCOCERATIDA*, K221  
*Hercoceratidae*, K416

- Hercocyrtoceras, **K310**  
 Hercoglossa, K388, K397, K404, **K456**, K472  
 Hercoglossidae, K31, K102, K104, K383, K386, K397, K403, K404, K410, **K455**  
 Hercoglossoceras, K397, K451  
 Herkimercoceras, **K302**  
 Hermiceratites, K188  
 Hesperoceras, **K226**  
 Heurekoceras, K394, K424  
 Hexagonites, K392, **K414**  
 Hexameres, **K488**  
 Hexameroceras, K25, **K295**  
 Hexamoceras, K295  
 Hexamorion, **K488**  
 Hindeoceras, **K418**  
 Hipparionoceras, **K316**  
 Hoeloceras, K210  
 Holconautilus, K392, **K414**  
 HÖLDER, K52  
 HOLM, K33, K35, K36, K129  
 Holmiceras, **K366**  
 Holmoceras, K366  
 HOLOCHOANITES, K95, K165, K489  
 holochoanitic, K39, **K56**  
 HOLOCHOANOIDA, K95  
 Homaloceras, K398, **K432**  
 homeomorphy, K50  
 Homoadelphoceras, **K418**  
 hood, K62, K471  
 Hopeioceras, **K216**  
 Hormoceras, K211  
 Hortolus, **K488**  
 Hortolus, K364  
 Huanghoceras, K392, K414  
 Hudsonoceras, K182  
 Humeoceras, K165, **K184**  
 Humeoceratidae, K100, **K184**  
 Hunanoceras, K392, **K414**  
 Huronia, K94, **K210**  
 Huroniella, **K210**  
 Huroniidae, K100, K102, K190, K202, **K210**  
 HUTCHINSON, K107  
 HYATT, K41, K47, K82, K95, K96, K163, K198, K220, K221, K262, K264, K265, K266, K279, K281, K282, K343, K383, K394, K399, K496  
 Hyatticeras, K416  
 Hyperoceras, K293  
 hyponome, K25, **K56**, K65  
 hyponomic sinus, K16  
 hyposeptal deposits, **K56**  
 hyposeptal fossa, **K56**  
 Hypospyrocera, K231  
 Imitoceras, **K489**  
 impressed area, K18, **K56**  
 impressed zone, K18, **K56**  
 Indonautilus, K395, **K447**  
 initial camera, K45  
 initial chamber, **K56**  
 injuries, K51  
 ink sac, K8  
 inner ostracum, Nautilus, K78  
 Intejoceras, **K186**  
 INTEJOCERATIDA, K102, K184  
 Intejoceratidae, K100, K102, **K186**  
 INTEJOCERATINA, K163, K184  
 INTEJOCERIDA, K12, K42, K50, K96, K97, K100, K120, K162, **K184**  
 INTEJOCORATIDA, K184  
 intercameral deposits, **K56**  
 intercostae, **K56**  
 INTERJECTOCERATINA, K184  
 intermediate area, **K56**  
 internal lobe, **K56**  
 internal suture, **K56**  
 interseptal lining, **K56**  
 interspaces, **K56**  
 Inversoceras, K49, **K298**  
 involute, K18, **K56**  
 IREDALE, K87  
 Isorthoceras, **K256**  
 Jasperoceras, **K361**  
 Javanoceras, K456  
 Jecholoceras, K208  
 JELETZKY, K467  
 Joachimoceras, **K237**  
 Jolietoceras, **K374**  
 Jonesoceras, **K237**  
 Jovellania, K42, **K302**  
 Jovellaniidae, K98, K100, K103, K279, K281, **K302**  
 Jovelliania, K302  
 Juvavionautilus, K403, K408, **K439**  
 Kailuanoceras, **K189**  
 Kaipingoceras, **K189**  
 Kammern, K71  
 Karoceras, **K314**  
 Karoceratidae, K100, K103, K279, K281, **K312**  
 Kawasakiceras, **K174**  
 KAY, K126  
 Kayoceras, **K338**  
 keel, **K56**  
 Kentlandoceras, **K284**  
 KERR, K65  
 KESLING, K263  
 KESSLER, K52  
 Kiaeroceras, **K328**  
 KIESLINGER, K125  
 Kindleoceras, **K293**  
 KING, K222  
 Kionoceras, K28, **K229**  
 Kionoceratidae, K229, K489  
 Kionoceratinae, K100, K102, **K229**, K489  
 Kirkoceras, **K170**  
 Knightoceras, K393, **K426**  
 Knightoceratidae, K103  
 Knightoceratinae, K424  
 KOBAYASHI, K49, K96, K125, K133, K221  
 Kochooceras, K38, K46, K49, K193, K196, **K206**, K305  
 Kogenoceras, K259  
 Kokenia, K494, K495, **K501**  
 Kokujoceras, K206  
 KOLB, K111, K126  
 Koleoceras, **K488**  
 Kolyoceras, K489  
 KOMÁRKOVÁ, K125  
 Konglungenoceras, **K329**  
 KONINCK, DE, K198  
 Koninckioceracea, K424  
 Koninckioceras, K393, K424  
 KONINCKIOCERATIDA, K413  
 Koninckioceratidae, K102, K103, K113, K383, K386, K389, K392, K393, **K424**  
 Koninckioceras, K424  
 KONINCKIOCERATIDA, K221  
 Koninckioceratidae, K424  
 Koninckopora, K489  
 Kopffuss, K60  
 Kopfkappe, K63  
 Kophinoceras, K416  
 Kotoceras, **K174**  
 KRINSLEY, K126  
 KUHN, K95, K96, K222  
 KUMMEL, K12, K96, K119, K221, K369, K383, K388, K394, K398, K406  
 Kutorgoceras, **K174**  
 Kutorgoceras, K174, K489  
 Kyminoceras, K154  
 lacuna, **K56**  
 LAMARCK, K222  
 Lambeoceras, K121, K193, K197, **K209**  
 Lambeoceratidae, K208  
 lamelles rayonnantes, K278  
 Lamelloceras, K234  
 Lamellorthoceras, **K234**  
 Lamellorthoceratidae, K100, K102, K125, K219, K220, **K233**  
 Lamottoceras, **K174**  
 lanceolate, **K57**  
 Landeroceras, **K329**  
 LANKESTER, K10  
 Laphamoceras, K290  
 lateral angle, **K57**  
 lateral areas, K18, **K57**  
 lateral lobe, **K57**  
 lateral saddle, **K57**  
 lateral sinus, **K57**  
 LAUBE, K470  
 Laumontoceras, **K302**  
 Laureloceras, **K374**  
 Lavaloceras, **K333**  
 Lawrenceoceras, **K148**  
 Lawrensoceras, K148  
 Lebetoceras, K130, **K140**  
 Lechritrochoceras, **K376**  
 Lechritrochoceratidae, K101, K103, K368, K369, K370, **K376**  
 Leonardocheilus, K390, K427  
 Lepadites, K468, K473  
 Leptocheilus, K468, K473, **K480**  
 Leptocyrtoceras, K148

- Leuroceras*, K400, K406, K410, **K429**  
*Leurocycloceras*, K33, K217, **K230**  
*Leurocycloceratinae*, K100, **K230**  
*Leuromotoceras*, K373  
*Leurorthoceras*, K191, **K206**  
*Leurotrochoceras*, **K376**  
*Levisoceras*, **K140**  
*Liaotungoceras*, K179  
*Librovitschiceras*, K393, **K441**  
*Librovitschiceras*, K426  
 ligne normale, K30, K492  
 ligne sutural, K75  
*Linchengoceras*, **K189**  
*Lindstroemoceras*, K264, **K273**  
*LINDSTRÖM*, K261, K262, K265, K266, K268, K343  
 lineation, **K57**  
*Lingchengoceras*, K189  
*LINNÉ*, K94  
*Linormoceras*, K206  
 lirae, K20, **K57**  
 lirate, **K57**  
*Liroceras*, K113, K393, K394, K403, K408, **K445**  
*Lirocerataceae*, K103, K386, K395, K396, K442  
*Liroceratidae*, K102, K103, K113, K383, K384, K386, K393, K394, K396, K406, K408, **K444**  
*LIROCERATINA*, K103, K386, K412, K442  
*Liskeardia*, **K178**  
*Lispoceras*, K400, **K429**  
*Lissoniceras*, K456  
*Lithuites*, K366  
*Litoceras*, **K361**  
*Litoceras*, K361  
*Litoceres*, K361  
*Litogyroceras*, K393, **K418**  
*Litogyroceratidae*, K103, K386, K393, K394, K416  
 lituicone, K18, **K57**  
*Lituidae*, K362  
*Lituites*, K25, K94, K343, K346, **K364**, K489  
*Lituites*, K364  
 lituiticone, **K57**  
*Lituitidae*, K28, K34, K98, K100, K103, K105, K109, K122, K123, K343, K344, K345, K346, K348, **K362**, K369  
*Lituitus*, K366  
*Litulies*, K366  
*Lituunculus*, K489  
 living chamber, **K57**  
*LLOYD*, K119, K406  
 lobe, K31, **K57**, K75  
 Loben, K75  
*Lobendoceras*, **K166**, K498  
*Lobobactrites*, K492, K495, K496, **K501**  
*Lobobactritidae*, K501  
*Lobosiphon*, **K170**  
 locomotion, *Nautilus*, K89  
 loculi, K71  
*LOESCH*, K51  
*Loganoceras*, **K284**  
 loges, K71  
 longiconic cyrticone, K16  
*Longocapuchones*, K478  
*Lophoceras*, K392, K393, **K427**  
*Lophoceras*, K427  
*Lopingoceras*, **K250**  
*Lorieroceras*, **K305**  
*LOWENSTAM*, K34  
 lower annular ridge, **K57**  
*Lowoceras*, **K334**  
*Lowoceratidae*, K100, K103, K324, **K334**  
*Loxoceras*, **K260**  
*Loxoceratidae*, K102, K210  
*Loxochoanella*, K130, **K144**  
 loxochoanitic, K39, **K57**  
 Luftkammern, K75  
 lunette, **K57**  
*Lyckholmoceras*, **K295**  
*Lycoceras*, K217, **K242**  
*Lyrioceras*, **K380**  
*Lysagoroceras*, **K314**  
*LYTOCERATIDA*, K12  
*Maccocyoceras*, K400, **K429**  
*MACROCHOANITES*, K95  
 macrochoanitic, K39, **K57**  
*Macrodomoceras*, **K316**  
*Macroloxoceras*, K217, **K254**  
*Macroloxoceratinae*, K252  
*Madiganella*, K44, K50, K323, **K328**  
*Maelonoceras*, **K284**  
*Maelonoceratidae*, K103, K283  
*Manchuriceras*, K179  
*Manchuroceras*, K161, **K179**  
*Manchuroceratidae*, K100, K102, K120, K148, K163, K165, **K179**  
*Manchurocerus*, K179  
*Mandaloceras*, **K340**  
*Mandaloceratidae*, K50, K100, K103, K280, K324, **K340**  
*Manitoulinoceras*, **K293**  
*Manitoulinoceratidae*, K290  
*Manitouoceras*, **K170**  
*Mannoceras*, K178  
 mantle, *Nautilus*, K66  
 Maquoketa coquina, K2  
 marginal attachment band, **K57**  
 marginal siphuncle, K16  
*Mariceras*, **K442**  
*Maruyamaceras*, K203  
*Maruyamacerina*, K203  
 mature part of conch, **K57**  
 maturity, *Nautilus*, K87  
*M'Coy*, K94  
*Mcqueenoceras*, **K166**  
*Mecynoceras*, **K314**  
*Megadisocosorus*, **K208**  
*Megaglossoceras*, K395, K396, **K448**  
*Mecasiphonia*, K457  
*Meia*, K230  
*Mellia*, K230  
*Meloceras*, K284, K288  
*Melonoceratidae*, K283  
*MELVILLE*, K222  
*Menasquaceras*, **K237**  
*Menisoceras*, K43, **K166**  
*Menuthionautilus*, K400, **K435**  
*MERIAN*, K468  
*Mesoceras*, K95, K264, **K341**  
*Mesoceratidae*, K100, K103, K324, **K341**  
*Mesochasmoceras*, K400, **K429**  
*Mesocheilus*, K468, **K480**  
*METACEPHALOPODA*, K10  
*METACHOANITES*, K95, K165  
*Metacoceras*, K113, K390, K400, K406, **K414**  
*Metactinoceras*, K204  
*Metaellesmeroceras*, K134  
*Metaphragmoceras*, **K305**  
*Metaplectoceras*, K374  
*Metarizoceras*, **K288**  
*Metarmenoceras*, K192, K193, **K214**  
*Metaspyroceras*, **K231**  
*Metastromatoceras*, **K251**  
*Metephippiorthoceras*, **K256**  
*Metorthoceras*, K489  
*Miamoceras*, **K288**  
*Michelinoceras*, K110, **K225**  
*MICHELINOCERATIDA*, K96, K221, K222, K224, K369  
*Michelinoceratidae*, K221, K222  
*MICHELINOCERATINA*, K224  
*Michelinoceratinae*, K48, K100, **K225**  
*MICHELINOCEROIDA*, K224  
*Michelinocerotidae*, K224  
*Microbactrites*, **K503**  
*MICROCHOANITES*, K95  
*Micronoceras*, **K301**  
*MILLER*, K2, K4, K111, K114, K120, K129, K262, K266, K343, K394, K399  
*Millkoninckioceras*, K392, **K424**  
*Mimagoniatites*, K496  
*Minganoceras*, K279, **K293**  
*Mirabiloceras*, K184  
*Mirites*, **K501**  
*Mistioceras*, K489  
*Mitorthoceras*, **K250**  
*Mitroceras*, K50, K279, **K301**, **K422**  
*Mitroceratinae*, K103, K299  
*MIXOCHOANITES*, K95, K265, K269  
*Mixosiphonoceras*, **K302**  
*Mojsisoceras*, K414  
*Mojsisovics*, K472, K496, K499  
*Mojsvaroceras*, K113, K390, K400, K406, **K414**  
*Molossus*, K220, K221, **K260**  
*Monilifer*, K414  
*Monocyrtoceras*, **K208**  
*Monogonoceras*, **K149**  
*Monomuchites*, **K257**  
*MONTFORT*, DE, K94  
*Montyoceras*, **K277**  
*Mooreoceras*, **K244**

- Mooreoceratidae*, K242  
 Moos, K468, K474  
*Moreauoceras*, K343, K344, K355  
 morphology, K13, K130, K160, K190, K216, K262, K277, K320, K343, K368, K470  
*Mosquoceras*, K390, K414  
*Mosquoceratidae*, K103, K386, K389, K390, K413  
*Mstikhinoceras*, K214  
 MUGGLIN, K59  
*Muirocera*, K418  
 MÜLLER, K468, K470  
*Multicameroceras*, K130, K131, K146  
 MÜNSTER, K468, K472  
 mural deposits, K32, K57  
 mural part of septum, K59  
 mural ridge, K57  
*Murayamaceras*, K203  
 MURCHISON, K338  
*Murrayoceras*, K155  
 muscles, *Nautilus*, K69  
 MUTVEI, K5, K27, K54, K193  
*Mysterioceras*, K254  
*Mysterioceratidae*, K100, K219, K222, K254  
*Mysticoceras*, K170  
  
 nacreous layer, K13  
*Naedyceras*, K301  
*Naedyceratidae*, K103, K299  
*Naedyceratinae*, K103  
 NAEF, K4, K78, K82, K84, K95  
 Nanno, K162, K178  
*Nannoceras*, K447  
*Narheoceras*, K183  
*Narthecoceras*, K183  
*Narthecoceratidae*, K100, K102, K165, K183  
*Nassauoceras*, K423  
*Nautilacea*, K412, K448  
*Nautilaceae*, K102, K103, K113, K384, K386, K388, K398, K403, K406, K410, K448  
*Nautilacées*, K448  
 nautilicone, K57  
*Nautilida*, K11, K12, K30, K34, K39, K40, K46, K47, K49, K50, K96, K98, K101, K103, K104, K116, K118, K123, K125, K127, K128, K197, K383, K384, K386, K393, K397, K405, K410, K412, K472, K484  
*Nautilidae*, K94, K102, K103, K126, K383, K386, K388, K398, K403, K404, K412, K448, K474  
*NAUTILINA*, K103, K386, K412  
*Nautilinae*, K104  
*Nautilites*, K488  
*Nautilites*, K449  
*Nautiloceras*, K428  
*NAUTILOIDEA*, K2, K3, K12, K95, K96, K97, K98, K100, K102, K106, K109, K127, K128, K129, K133, K383, K410, K498  
*NAUTILOIDEA*, K412  
*Nautilopsis*, K457  
*Nautilorhynchus*, K478  
*Nautilus*, K7, K13, K15, K16, K25, K27, K29, K30, K36, K39, K46, K47, K48, K50, K51, K59, K65, K80, K84, K92, K94, K95, K106, K113, K114, K115, K123, K126, K127, K383, K388, K390, K404, K405, K448, K456, K467, K468, K470, K471, K472, K474, K477, K487, K488  
*Nautilus pompilius*, K18, K94, K124  
*Nautilus-Schnäbel*, K474  
 NEAVE, K244  
 neck, K26, K57  
*Nelimenia*, K319  
*Neocycloceras*, K244  
*Neocymatoceras*, K453  
*Neodiscosorus*, K336  
*Neodomatoceras*, K436  
*Neokaipingoceras*, K189, K489  
*Neorthoceras*, K260  
*Neothrincoceras*, K431  
*Neothrincoceratidae*, K103, K427  
*Neowutinoceras*, K206  
 nephridia, K8  
*Nephriticeras*, K369, K370, K376, K380  
*Nephriticeratidae*, K50, K101, K369, K370, K376  
*Nephriticerina*, K380  
*Nephritidae*, K376  
 nepionic bulb, K57  
 nepionic flange, K57  
 nepionic line, K57  
*Neptunoceras*, K484  
*Neptunoceratidae*, K48, K102, K103, K386, K484  
 nervous system, K8, K66  
*Neumatoceras*, K288  
*Nicht-Nautilus-Rhyncholithen*, K474  
*Nicht-Nautilus-Schnäbel*, K474  
 NICOL, K476  
*Nilaturia*, K457  
*Nodosaria*, K222  
 NOETLING, K33, K36, K343  
*Nolimenia*, K319  
 Normallinie, K30, K75, K492  
*Northoceras*, K489  
*Nothoceras*, K50, K95, K305  
*Nothoceras*, K206, K305  
*Nothoceratidae*, K98, K100, K103, K279, K281, K305  
*Nothoceratidae*, K305  
*Notocycloceras*, K154  
*NUMMULARIA*, K198, K203  
 nummulis, K57  
 nummuloidal, K40  
*Nybyoceras*, K190, K208  
*Nybyoceratinae*, K206  
  
*Obinautilus*, K113, K404, K449  
*Oceanus*, K488  
*Octamerella*, K295  
*Octameres*, K488  
*Octameroceras*, K295  
*OCTOPODIDA*, K4, K12  
*Octopus*, K7  
 ocular emargination, K57  
 ocular sinus, K57  
*Oderoceras*, K170  
*Oelandoceras*, K144  
*Offleyoceras*, K242  
*Offleyoceratidae*, K100, K242  
*Ogygoceras*, K155  
*Ohioceras*, K229  
*Ohioceratidae*, K229  
*Onchorhynchus*, K478  
*Oncoceras*, K49, K278, K280, K284  
*ONCOCERATIDA*, K96, K102, K282, K283  
*Oncoceratidae*, K100, K112, K279, K280, K283  
*ONCOCERATINA*, K282  
*ONCOCERIDA*, K11, K12, K26, K28, K34, K36, K39, K40, K41, K43, K45, K49, K50, K94, K95, K96, K98, K100, K104, K105, K109, K112, K117, K118, K122, K128, K132, K221, K277, K278, K279, K280, K281, K282, K370, K383, K384, K388, K412, K484, K487  
*ONCOCEROIDA*, K282  
*ONCOCEROIDEA*, K282  
*ONCODOCERAS*, K397, K441  
*Oneotoceras*, K144  
*Onoceras*, K284  
 ontogeny, K45, K80, K162, K193, K262, K323, K472, K492  
*Onychoceras*, K148  
*Oocenia*, K288  
*Ooceras*, K288  
*Ooceratidae*, K103, K288  
*Oocerina*, K288  
*Oocerinidae*, K103, K281, K283  
*Oonoceras*, K280, K288, K316  
*Oonoceratidae*, K283  
 OOSTER, K468  
*Ophidioceras*, K367  
*Ophidioceratidae*, K100, K109, K343, K344, K345, K346, K348, K352, K367  
*Ophioceras*, K123, K367  
*Ophioceras*, K367  
*Ophioceratidae*, K367  
*Ophionautilus*, K404, K449  
 ORBIGNY, d', K10, K424, K468  
*Orchadoceras*, K489  
*Ordosoceras*, K203  
 orientation, K16  
 orientation of conch, K15  
*Ormoceras*, K94, K191, K198, K199, K211  
*Ormoceratidae*, K100, K190, K202, K210  
*Ormoceratites*, K211

- Orotocycloceras*, K152  
*Ortaoceras*, K224  
*Orthocera*, K94, K222  
**ORTHOCERACEA**, K95, K96, K222, K223  
*Orthoceras*, K26, K28, K48, K50, K94, K95, K97, K217, K220, K222, **K224**, K496  
*Orthoceras truncatum*, K47  
*Orthocerataceae*, K39, K50, K97, K100, K110, K112, K125, K217, K218, K219, K220, K222, **K224**  
**ORTHOCERATIDA**, K102, K220, K223, K224  
*Orthoceratidae*, K48, K100, K102, K219, K220, K222, **K224**  
*Orthoceratinae*, K100, K102, **K224**  
*Orthoceratites*, K94, K202, K489  
**ORTHOCERIDA**, K12, K26, K30, K33, K34, K36, K39, K40, K41, K48, K50, K51, K94, K96, K97, K100, K104, K105, K109, K110, K111, K112, K117, K121, K128, K132, K197, **K216**, K219, K220, K222, **K223**, K369, K487, K491, K495  
*orthocerids*, K25  
*Orthochoea*, K224  
*Orthoceros*, K222  
**ORTHOCEROTIDA**, K224  
*Orthocerotidae*, K134, K224  
*Orthocerotoidea*, K224  
*Orthocerus*, K222  
**ORTHOCHOANITES**, K95, K220, K221, K369  
*orthochoanitic*, K39, **K57**  
*orthocones*, K16, **K57**  
*orthocones, breviconic*, K16  
*orthocones, longiconic*, K16  
*Orthonybyoceras*, **K214**, K487  
*Orygoceras*, K154  
*Osbornoceras*, **K314**  
*Osnovv Paleontologii*, K102  
*osphradium*, K6  
*ostracum*, Nautilus, K77  
*otocones*, K66  
*outer ostracum*, Nautilus, K78  
*Ovoceras*, K49, **K301**  
*Ovocerina*, **K340**  
*OWEN*, K10, K11, K71, K474  
*Owen's organ*, K64  
*Oxfordoceras*, **K235**  
*Oxfordoceras*, K235  
*oxycone*, **K57**  
*oxyconic*, K18  
*Oxygonioceras*, K280, **K301**  
*Oxynautilus*, K403, K406, K408, K410, **K440**  
  
*Pachecdyoceras*, K277  
*Pachendoceras*, K107, K130, **K155**  
*Pachtoceras*, **K318**  
  
*Pachydiscus*, K5  
*Padunoceras*, **K187**  
*Padunoceratidae*, K100, K102, **K187**  
*Palaeoceras*, K106, K107, K130, K131, K132, **K146**  
*Palaeoclymenia*, K360  
*Palaeocycloceras*, K225  
*Palaeonautilus*, K359  
*Palaeoteuthidae*, K472  
*Palaeoteuthis*, K468, K474, **K478**  
*Palaeoteuthis*, K478  
*Palaeotheutis*, K478  
*Palelialia*, K404, K451  
*paleoecology*, **K114**, K268, K476  
*Paleonavtili*, K485  
*pallial cavity*, K66  
*pallial fold*, K66  
*pallium*, K66  
*Palmeroceras*, **K250**  
*Paquettoceras*, K370, **K374**  
*Parabactritaceae*, K503  
*Parabactrites*, K491, K492, K495, K499, **K503**  
*Parabactritidae*, K102, K491, K495, K496, K498, K499, **K503**  
*Paracenoceras*, K404, **K451**  
*Paracenoceratidae*, K102, K383, K397, K403, K404, K410, **K451**  
*Paracleistoceras*, **K310**  
*Paracodoceras*, K316  
*Paraconradoceras*, **K305**  
*Paractinoceras*, K191, **K206**  
*Paracyclostomiceras*, K130, **K144**  
*Paracymatoceras*, K397, K400, K410, **K455**  
*Paracymatoceras*, K451  
*Paradomatoceras*, K410, **K436**  
*Paraendoceras*, **K170**  
*Parakionoceras*, **K229**  
*Paraloxoceras*, **K254**  
*Parametacoceras*, **K414**  
*Paranautilidae*, K103, K383, K384, K386, K444  
*Paranautilus*, K113, K394, K395, K396, K403, K408, **K447**  
*Parapenascoceras*, K436  
*Paraphragmites*, K216, **K242**  
*Paraphragmitidae*, K50, K100, K102, K220, K221, **K241**  
*Parapiloceras*, **K172**  
*Pararhiphaeoceras*, **K424**  
*Pararinceras*, K400, **K429**  
*Pararmenoceras*, K208  
*Parascoceras*, K263, K265, K266, K268, **K273**  
*Parastenopoceras*, K400, K401, **K436**  
*Paraturia*, K456  
*Paravaginoceras*, **K189**  
*Parendoceras*, K170  
*parietal deposits*, **K57**, K322  
*Parksoceras*, **K488**  
*Paroocerina*, K288  
*Parormoceras*, **K214**  
  
*Parryoceras*, **K329**  
*pearls*, K15  
*Pectinoceras*, K43, **K316**  
*Peismoceras*, K369, **K376**  
*Pelagus*, K457  
*Peltarion*, K470, **K481**  
*Peltarion*, K481  
*Penascoceras*, K433  
*Penchioceras*, K189  
*pendent deposits*, **K57**  
*Penhioceras*, **K189**, K489  
*Pentameroceras*, **K299**  
*Pentamorian*, **K488**  
*Perigrammoceras*, K259  
*Perimecoceras*, K280, **K308**  
*Periodanoceras*, **K310**  
*Peripetoceras*, K395, **K447**, K472  
*periphraet*, **K57**  
*Periptoceras*, K447  
*perispatial deposits*, **K57**, K192  
*perispantium*, K45, **K57**, K192  
*peristome*, K25, **K57**  
*Permoceras*, K397, K410, **K437**  
*Permoceratidae*, K102, K103, K386, K397, **K436**  
*Permodomatoceras*, K433  
*Permonautilus*, K15, K394, **K447**  
*Petalichnus*, **K487**  
*Petránek*, K125  
*Petryoceras*, **K250**, K487  
*Phaceras*, K432  
*Phacoceras*, K398, K406, K408, K410, **K432**  
*Phacoceratidae*, K103, K432  
*Phaedrysmocheilus*, K392, **K414**  
*Phloioceras*, K392, **K414**  
*Phragmocera*, K338  
*Phragmoceras*, K50, K94, K95, K323, **K338**  
*Phragmoceratidae*, K50, K98, K100, K103, K281, K323, K324, **K338**  
*Phragmoceratidae*, K338  
*Phragmoceratites*, K338  
*Phragmocerina*, K338  
*Phragmocerus*, K338  
*phragmocone*, K13, K29, **K57**  
*Phragmosiphon*, **K170**  
**PHRAGMOTEUThIDIDA**, K12  
*Phragmoteuthis*, K9  
**PHYLLOCERATIDA**, K12  
*phylogeny*, **K106**, K219, K266, K280, K346, K369, K388, K494  
*Pichyceras*, K490  
*Pictetoceras*, **K319**  
*Piersaloceras*, K283  
*Piloceras*, **K171**, K489  
*Piloceratidae*, K100, K102, K108, K120, K164, K165, **K171**  
*Pilotoceras*, K344, **K355**  
*Pionoceras*, **K355**  
*Plagiostomoceras*, K29, K51, K217, **K226**  
*Planctoceras*, K359  
*Planecapula*, **K481**

- Planetoceras, K392, K393, **K427**  
 planulate, **K57**  
 platycone, **K57**  
*Platynautilus*, K454  
 Platsiphon, **K170**  
 Plectoceras, K369, K371, **K374**  
**PLECTOCERATIDA**, K221, K369  
 Plectoceratidae, K101, K103, K107, K369, K371, **K374**  
 Plectronoceras, K106, **K146**  
 Plectronoceratidae, K100, K102, K108, K110, K130, K131, **K146**  
 pleuromyarian, K27, **K57**  
**PLEURONAUTILIDA**, K221  
*Pleuromytilidae*, K386, K392, K413  
*Pleuromytilinae*, K103  
*Pleuromytilus*, K15, K50, K389, K390, K391, K392, K410, **K414**  
*Pleuromytilus*, K419  
*Pleurorhynchoceras*, **K226**  
**PLEUROSIPHONIDES**, K165  
 plicate, **K57**  
 Pliendoceras, K170  
 Plummeroceras, K400, K410, **K436**  
*Polycrinites*, K418  
 Polydesmia, K132, K190, K192, K198, K199, **K203**  
*Polydesmidae*, K203  
*Polydesmidae*, K100, K102, K132, K202, **K203**  
*Polyelasmoceras*, K42, K279, **K136**  
*Polyelasmoceratidae*, K100, K103, K277, K279, **K316**  
*Polygrammoceras*, **K230**  
 porcelainous ostracum, K13  
 Porcellia, **K489**  
 Poterioceras, K48, K278, **K314**  
 Poterioceratidae, K100, K103, K281, **K314**  
 Poteriocerina, **K310**  
*Porteroceras*, K256  
 Potoceras, K393, K394, **K447**  
 Pradoceras, **K189**  
 prebasal segment, **K57**  
 Pristeroceras, **K338**  
 Probillingsites, K49, K265, **K266**, **K276**  
 Probillingsitinae, K100, K264, **K276**  
**PROTOCHONITES**, K95  
*Procladonauutilus*, K442  
*Procladonauutilus*, K50, K396, K397, K404, K408, K410, **K442**  
 procoelous, K71  
 Procymatoceras, K404, **K455**  
 Proendoceras, **K170**  
 Projovellania, **K302**  
**PROLECANITIDA**, K12  
 Proteoceras, **K256**  
 Proteoceratidae, K100, K219, **K255**  
 Proterocameroceras, K160, **K166**, K489  
 Proterocameroceratidae, K39, K100, K102, K131, K132, K160, K163, K164, K165, **K166**, K218  
**PROTEROCAMEROCERATINA**, K102, K163, K165  
*Proterocameroceratinae*, K166  
*Proterokaipingoceras*, K489  
*Proteropiloceras*, K489  
*Proterovaginoceras*, K160, K163, **K175**, K489  
*Protobactolites*, K260  
 Protobactrites, **K260**  
 Protobaltoceras, K154  
**PROTOBELEMNOIDEA**, K496, K499  
**PROTOCEPHALOPODA**, K10  
**PROTOCHONITES**, K485  
 protoconch, K45, **K57**  
 protoconch, Nautilus, K82  
 Protocycloceras, **K152**  
 Protocycloceratidae, K34, K100, K102, K107, K108, K130, K132, **K152**  
 Protokionoceras, **K237**  
 Protophragmoceras, **K339**  
*Protorthoceras*, K489  
*Protovaginoceras*, K489  
 proximal deposits, **K57**  
 proximal division of siphonal funnel, **K57**  
 PRUVOT-FOL, K74  
 Pselioceras, K401, K402, **K436**  
 Pseudactinoceras, **K252**  
*Pseudactinoceratidae*, K102, K252  
*Pseudactinoceratinae*, K50, K100, K219, **K252**  
 Pseudaganides, K397, K404, K408, K410, **K451**  
*Pseudaganidinae*, K104, K451  
*Pseudascoceras*, K273  
*Pseudeskimoceras*, K259  
 Pseudobactrites, K492, K493, K495, K499, **K502**  
 Pseudoceneroceras, K404, **K450**  
 Pseudocycloceras, **K250**  
 Pseudocyrtocheras, **K244**  
*Pseudofoordiceras*, K392, K414  
 Pseudogomphoceras, K323, **K340**  
*Pseudometacoceras*, K433  
*Pseudonauutilus*, K102, K103, K386, K397, K403, K408, K410, **K451**  
*Pseudonauutilus*, K397, K410, K472, **K451**  
*Pseudorthoceras*, K2, K14, K15, K34, K36, K217, **K244**  
*Pseudorthocerataceae*, K34, K39, K41, K45, K50, K97, K100, K110, K125, K217, K218, K219, K222, **K242**  
*Pseudorthoceratidae*, K100, K102, K218, K219, K221, K222, **K242**, K487  
*Pseudorthoceratinae*, K100, K218, **K242**  
*Pseudoscoceras*, K273  
 pseudoseptum, **K58**  
*Pseudotemnnocheilus*, K427  
 Psiaoceras, **K302**  
*Ptenacleistoceras*, K489  
 Ptenoceras, K14, **K420**  
**PTENOCERATACEAE**, K103  
*Ptenoceratidae*, K103, K281, K416  
*Pteronauutilus*, **K488**  
 Ptyssoceras, **K421**  
 Pycnoceras, **K359**  
*Pyrenoceras*, K359  
 Quebecoceras, **K145**  
 QUENSTEDT, K15, K94, K126, K198, K468  
 radial canals, **K58**, K192  
 Rasmussenoceras, **K290**  
 Rayonnoceras, K190, K199, K202, **K215**  
 recumbent brim, **K58**  
 Reedsoceras, K295, **K333**  
**REGULARES**, K94  
 REMELÉ, K33, K343  
 Remeleceras, **K488**  
 Remeleceras, K354  
 Remeleceras, K354, K488  
 reproductive system, Nautilus, K68  
 Reticyclocheras, **K250**, K259  
 retrochoanitic, K39, **K58**  
 Retroclitendoceras, **K170**  
 retrosiphonate, **K58**  
 REYMENT, K2, K15, K119, K124, K125, K126  
*Rhadinocerataceae*, K376  
 Rhadinoceras, K369, K370, **K380**  
**RHADINOCERATIDA**, K221, K369  
*Rhadinoceratidae*, K103, K369, K376  
*Rhineceras*, K429  
*Rhineceratidae*, K427  
 Rhiphaeoceras, **K423**  
*Rhiphaeocerataceae*, K103, K386  
*Rhiphaeoceratidae*, K102, K103, K386, K392, **K423**  
 Rhiphaeonautilus, **K424**  
 Rhomboceras, **K310**  
*Rhombocheilus*, K478  
 Rhynchidia, K470, **K481**  
*Rhynchidia*, K481  
*Rhynchoceras*, K366  
 rhyncholites, K61, K102, **K467**, K471, K474  
*Rhyncholites*, K468, K478  
*Rhyncholithes*, K467, K468, K477  
*Rhyncholithus*, K467, K478  
*Rhyncholithus*, K478  
*Rhyncholythes*, K478  
 Rhynchorthoceras, K344, K346, **K366**

- Rhynchotenthis*, K478  
*Rhynchoteuthis*, K468, K474, K476, K477, **K478**  
*Rhynchotheutis*, K478  
*Rhyncolite*, K467, K468, K472, **K477**  
*Rhyncolites*, les, K467  
*Rhyncolites*, K468, K474, K477  
*Rhyncolyte*, K467  
*Rhyncorthoceras*, K366  
*RHYTICERATIDA*, K413  
 ribs, K58  
*Richardsonoceras*, **K288**  
*Rineceras*, K400, **K429**  
*Rineceratidae*, K399, K400, K427  
*Ringoceras*, **K283**  
*Rhiphaocerataceae*, K413  
*Rizoceras*, K288  
*Rizoceratidae*, K283  
*Rizosceras*, K25, **K288**  
*Robsonoceras*, **K145**  
*Robsonoceratidae*, K134  
 ROEMER, K468  
 ROGER, K499  
 ROLLE, K470  
*Romingoceras*, K288  
*Romingoceras*, **K288**  
*Rossicoceras*, K174  
*Roussanoffoceras*, **K421**  
*Roussanofoceras*, K421  
*Rudolfoceras*, **K154**  
*Rudolfoceratidae*, K152  
 RUEDEMANN, K49, K129, K140, K161, K343  
*Ruedemannoceras*, K320, K322, K323, K324, **K326**  
*Ruedemannoceratidae*, K100, K103, **K324**  
 RÜGER, 468, K474  
 Runzelschicht, K15, K492  
*Ruthenoceras*, K106, K131, **K147**  
*Ruthenoceratidae*, K146  
*Rutoceras*, **K416**  
*Rutocerataceae*, K103, K386, K398, K413, K484  
*RUTOCERATIDA*, K96, K383, K412, K413  
*Rutoceratidae*, K43, K101, K103, K112, K369, K383, K384, K386, K388, K392, K393, K412, **K416**, K489, K490  
*RUTOCERATINA*, K103, K386, K393, K412, K413  
 RUTTE, K468, K477  
 RUZHENTSEV, K11, K102, K388, K389, K390, K392, K397  
*Ryticeracea*, K413  
*Ryticeras*, K416  
*RYTICERATIDA*, K221  
*Ryticeratidae*, K416  
*Sactoceras*, K211  
*Sactoceratidae*, K102, K210  
*Sactocerina*, K342  
*Sactorthoceras*, K221, **K233**  
*Sactorthoceratidae*, K100, K102, K219, K221, **K233**  
 saddles, K31, **K58**  
 SAEMANN, K94, K193, K198  
*Saerichnites*, **K487**  
*Saffordoceras*, **K206**  
*Saffordoceras*, K170  
*Salterella*, K107, **K486**  
*Salterellidae*, K127, **K486**  
 SANDBERGER, K15  
*Sannionites*, K220, K221, **K260**  
*Savageoceras*, **K374**  
*Scaphanidia*, K470, **K481**  
*Scaptorhynchus*, K479  
*Scaptorrhynchus*, K468, **K479**, K498  
*Sceptrites*, **K250**  
 Scheidewände, K71  
 SCHINDEWOLF, K47, K95, K96, K111, K193, K348, K495  
*SCHISTOCHOANITES*, K95  
*SCHIZOSIPHONA*, K10  
*SCHIZOCHOANITES*, K95  
 SCHLOTHEIM, VON, K468, K473  
 SCHNEIDER, K4  
*Schofieldoceras*, K288  
*Schoulgoceras*, **K488**  
 SCHRÖDER, K33, K36, K343  
*Schroederoceras*, K360  
*Schuchertoceras*, K49, K265, K266, **K275**  
*Schuchertoceratidae*, K262, K271  
 SCHWARZ, K3, K10  
*Scofieldoceras*, **K288**  
*Scyphoceras*, **K442**  
*Scyphoceratidae*, K102, K103, K386, K398, **K442**  
*Seelyoceras*, **K357**  
 segment of siphuncle, **K58**  
*Selkirkoceras*, K46, K49, K193, K197, **K208**  
 selles, K75  
*Sepia*, K7, K9, K84, K468, K474  
*SEPIIDA*, K4, K12  
 septa, K13, K265  
 septa, *Nautilus*, K75, K86  
 septal angle, **K58**  
 septal elements, **K58**  
 septal foramen, K13, K30, **K58**  
 septal funnel, **K58**  
 septal furrow, K30, **K58**  
 septal neck, K13, K30, K38, K39, **K58**  
*Septameroceras*, K295  
 septate division, **K58**  
 septum, K30, **K58**  
 septum of truncation, K47, **K58**  
 serpenticone, **K58**  
 sexes, K8  
 sexual dimorphism, K48, K74  
 shaft, K471  
*Shamattawaceras*, **K276**  
*Shansinautilus*, K392, K414  
*Shantungoceras*, K106, **K145**  
*Shantungoceras*, K206  
*Shelbyoceras*, K132, K490  
 shell, **K58**  
 shell attachments, *Nautilus*, K69  
 shell function, *Nautilus*, K90  
 shell, *Nautilus*, K71  
 shell structure, *Nautilus*, K77  
 shell truncation, K47  
 shell wall, K13, **K58**  
*Shideleroceras*, **K159**  
*Shideleroceratidae*, K100, K102, K130, **K159**  
*Shikhanoceras*, **K250**  
*Shikhanoceratidae*, K242  
 SHIMANSKIY, K3, K12, K47, K96, K102, K127, K153, K384, K386, K388, K389, K390, K392, K393, K394, K396, K397, K399, K403, K404, K473, K492, K495, K496, K498, K499  
*Shimizuoceras*, K226  
*Sholakoceras*, **K424**  
*Shumardoceras*, **K359**  
*Shuranoceras*, **K314**  
*Siberioceras*, K214  
*Siberionautilidae*, K31, K102, K386, K396, **K448**  
*Siberionautilus*, K31, K98, K128, K397, **K448**  
*Sibyllonautilus*, K395, **K449**  
*Sicilioceras*, **K502**  
*Sidemina*, **K189**  
*Sigmocycloceras*, **K233**  
 sigmoid suture, **K58**  
*Sigmorthoceras*, K221, K233  
*Simardoceras*, **K334**  
*Simorthoceras*, **K244**  
*Sinclairioceras*, **K334**  
*Sinoceras*, **K227**  
*SINOCERATIDA*, K224  
*Sinoceratidae*, K224  
*Sinoceremoceras*, K147  
*Sinoeremoceras*, K131, **K147**  
 sinus, **K58**  
 siphon, K13  
 siphon, **K58**, K70  
 siphonal caecum, **K58**  
 Siphonaldüte, K75  
 siphonal funnel, **K58**  
 siphonal lobe, **K58**  
 siphonal tube, **K58**  
 siphonopodium, K65  
 siphuncle, K36, **K58**, K192  
 siphuncular cord, **K58**, K60  
 siphuncular cord, *Nautilus*, K70  
 siphuncular segment, **K58**  
*Slocmoceras*, **K310**  
*Slokomoceras*, K310  
 SMITH, K496  
*Smithvilloceras*, **K145**  
*Solenoceras*, K447  
*Solenocheilidae*, K440, K441  
*Solenocheilus*, K441  
*Solenochilaceae*, K386, K440  
*SOLENOCHILIDA*, K96, K383, K412, K440  
*Solenochilidae*, K102, K386, K398, **K441**  
*Solenochilidae*, K440  
*Solenochilus*, K397, **K441**  
*Somaliceras*, K452  
*Somalinautilus*, K404, **K452**, K472, K477  
 SORNAY, K51

- SOWERBY, K94, K199, K338, K456, K457  
 SPATH, K82, K110, K456, K495  
 sphaerocone, **K58**  
*Sphaeronautilus*, K404, K449  
*Sphenaturia*, K457  
 Sphooceras, K47, K48, K117, **K232**  
 Sphooceratidae, K100, K112, **K231**  
 Sphyradoceras, K369, K370, **K380**  
*Sphyradoceratidae*, K376  
 spiculum, K161  
 spiess, K161  
*Spiroceras*, K246  
 Spirula, K9  
*Spirulites*, K364, K419  
 Spyroceras, **K246**, K489  
*Spyroceratidae*, K246  
 Spyroceratinae, K100, K218, K219, K221, **K246**  
 Staufferoceras, **K293**  
 Stearoceras, K402, K403, **K436**  
 STEININGER, K338  
 Stemtonoceras, **K146**  
*Stemtonoceratidae*, K134  
*Stenoceras*, K501  
*Stenodomatoceras*, K433  
 Stenogomphoceras, **K299**  
 Stenopoceras, K25, K398, K400, K401, K403, K406, K408, K410, **K436**  
 Stenosiphon, **K170**  
*STENOSIPHONATA*, K96  
 stenosphonate, K36, **K58**  
 STENZEL, K2, K49, K125, K399, K470  
 Stereoplasmodoceras, **K255**  
 Stereoplasmodoceratidae, K100, K218, K219, K221, K222, **K255**  
*Stereoplasmodocera*, K255  
 Stereospyroceras, K218, **K259**  
 Stereotoceras, **K302**  
 Sthenoceras, **K340**  
 STOKES, K94  
 Stokesoceras, **K338**  
 Stolbovoceras, **K208**  
 STRAND, K343  
 Strandoceras, **K329**  
 Straparollus, K490  
 Streptoceras, **K310**  
*Streptodiscus*, K489  
 Striacoceras, K29, **K237**  
 striae, K20, **K58**  
*Striatoceras*, K342  
*Striatoceratidae*, K342  
 Strionautilus, K404, **K450**  
 Stroboceras, K400, **K431**  
 Stromatoceras, **K252**  
*Strombolituites*, K366  
*Stromotoceras*, K252  
 Strophiceras, K398, **K432**  
*Strophioceras*, K432  
 STUMBUR, K51  
 Stützring, K58  
*Stylocyrtoceras*, K148  
 Styronautilus, K396, K408, K410, **K443**  
 Subclymenia, K400, **K431**  
*Subclymeniidae*, K103, K427  
 subholochoanitic, K39, **K58**  
 submicroscopic shell structure, Nautilus, K78  
 suborthochoanitic, K38, **K58**  
 Subpenhioceras, **K189**  
 Subspyroceras, **K260**  
 Subtofangoceras, **K216**  
*Subvaginoceras*, K174  
 Subvestinautilus, **K393**, **K427**  
*Succoceras*, K178  
*Sueoceras*, K178  
*Sueoceras*, K178  
*Sueoceratidae*, K172  
 supporting ring, **K58**  
*Surreghmatoceras*, K422  
 Suttonoceras, **K295**  
 Suture, K75  
 sutural elements, K31, **K58**  
 suture, K20, K31, **K58**, K75  
 Suturlinie, K75  
 SWEET, K343, K348, K352, K369  
 Sycoceras, **K318**  
*Syrroceras*, K318  
*Syrinautilus*, K455  
 Syringoceras, K403, **K440**  
 Syringonautilidae, K31, K102, K383, K386, K398, K402, K403, K406, K408, K410, K412, **K437**  
*Syringonautilinae*, K103, K437  
 Syringonautilus, K403, K404, **K439**, K455  
 Syronautilus, **K455**  
 Syrrhgmatoceas, K394, **K422**  
 systegnosis, **K58**  
 Systrophoceras, K369, **K376**  
 Tabantaloceras, K495, **K503**  
 tabulate, **K58**  
*Tachoceras*, K301  
 Tainionautilus, K392, **K414**  
 Tainoceras, K390, **K413**  
 Tainocerataceae, K50, K101, K103, K112, K383, K384, K388, K390, K397, K398, K402, K406, K410, K412, **K413**  
*Tainocerataceae*, K413  
 Tainoceratidae, K101, K103, K113, K386, K388, K389, K390, K392, K397, K406, **K413**  
*TAINOCERATINA*, K103, K386, K412, K413  
*Tainoceratinae*, K103, K413  
 Talassoceras, **K166**  
 Tallinnoceras, K183  
 Tanchiashanites, K392, **K415**  
 Tarphophioceracone, **K58**  
 tarphyceracone, **K58**  
 Tarphyceras, K369, **K354**  
*TARPHYCERATIDA*, K96, K103, K352  
 Tarphyceratidae, K100, K103, K109, K343, K344, K346, K348, **K352**, K369  
*TARPHYCERATINA*, K103, K352  
 TARPHYCERIDA, K11, K12, K28, K34, K39, K40, K45, K46, K50, K96, K98, K100, K105, K108, K109, K110, K112, K116, K118, K122, K123, K125, K128, K132, K197, **K343**, K344, K346, K348, **K352**, K369, K370  
 Tasmanoceras, K43, K161, **K179**  
 TASNÁDI-KUBACSKA, K48  
 TEICHERT, K34, K35, K49, K95, K96, K125, K126, K130, K163, K193, K198, K281, K343, K398  
*Teichertia*, K456  
 Teichertoceras, **K334**, K496  
*Teihardoceras*, K489  
*Temnocheilaceae*, K103, K386, K394, K424  
*Temnocheilidae*, K103, K386, K413, K424  
 Temnocheilus, K390, K392, **K427**, K468, K472  
 Temperoceras, **K237**  
 tentacles, K62  
*TENTACULIFERA*, K10  
 Teratichnus, **K487**  
 test, **K58**  
 TETRABRANCHIATA, K10, K11, K59, K89  
 Tetragnoceras, **K423**  
 Tetragnoceratidae, K102, K103, K113, K383, K384, K386, K388, K398, **K422**  
 Tetrameres, K488  
 Tetrameroceras, **K295**  
 Tetramorion, **K488**  
 Tetranooceras, **K422**  
 Tetrapleuroceras, **K484**  
 TEUTHIDIDA, K4, K12  
 THIELE, K78  
 Thoracoceras, **K230**  
*Thoracoceras*, K230  
 Threoroceras, **K422**  
 Thrincoceras, K400, **K431**  
*Thrinoceratidae*, K386, K427  
*Thrinoceratinae*, K103  
*Thuleoceras*, K331  
 Thuringionautilus, K391, **K416**  
 Thylacoceras, K131, K132, **K163**, K498  
 Thylacoceratidae, K100, K102, K131, K160, K164, **K165**  
 Tienoceras, **K260**  
 TILL, K468, K470, K471, K472, K474, K476, K477  
 Tillicheilus, K476, **K481**  
 Tirolonautilus, K391, **K416**  
 Titanoceras, K98, **K436**  
 Tithonoceras, K404, **K452**  
 Tofangoceras, **K259**  
*Tofangocera*, K259  
*TOMOCHONIA*, K10  
 torticone, K18, **K58**  
*Toufangocera*, K259  
 tooth, K71  
 trace fossils, **K487**  
*Trachinautilus*, K416



- Trachomaticnus*, **K487**  
*Trachynautilus*, K392, **K416**  
*Tragoceras*, K28, **K359**  
*Trematoceras*, K220, **K229**  
*Trematoceras*, K229, K422, K489  
*Trematodiscus*, K489  
*Treptoceras*, K214  
*Tretoceras*, K188, **K260**  
*Triboloceras*, K400, K431  
*Tribolocerataceae*, K386, K427  
*Triboloceratidae*, K386, K393, K399, K427  
*Trichter-rohr*, K65  
*Triendoceras*, **K176**  
*Trifurcatoceras*, **K189**  
*Trigonoceras*, **K428**  
*Trigonocerataceae*, K102, K103, K112, K384, K388, K393, K397, K398, K406, K408, K410, K412, **K427**  
*Trigonoceratidae*, K102, K103, K113, K393, K398, K400, K406, **K427**  
*Trigonoceratinae*, K103  
*Trigonodema*, **K319**  
*Trigonodema*, K302  
*Trilacinoceras*, **K367**  
*Trimeroceras*, **K298**  
*Trimeroceratidae*, K100, K103, K280, **K298**  
*Trimorion*, **K488**  
*Tripleuroceras*, **K302**  
*Tripleuroceratidae*, K100, K103, K281, **K302**  
*Triplooceras*, K369, **K380**  
*Tripteroceras*, **K290**  
*Tripteroceratidae*, K100, K280, **K290**  
*Tripterocerina*, **K290**  
*Tripteroceroides*, **K251**  
*Tritoceras*, K260  
*Trochoceras*, K25, K95, K388, K416, **K422**  
*Trochoceras*, K299, K301, K422  
*Trochoceratidae*, K299, K416  
*trochoceroïd*, K18, **K58**  
*Trochodictyoceras*, **K376**  
*Trocholites*, K51, **K359**  
*Trocholithes*, K360  
*Trocholithidae*, K359  
*Trocholitidae*, K100, K103, K109, K343, K344, K345, K346, K348, K352, **K359**, **K369**  
*Trocholitoceras*, **K361**  
*TROEDSSON*, K193  
*Troedssonella*, K218, **K235**  
*Troedssonellidae*, K50, K100, K132, K218, K220, **K235**  
*Troedssonoceras*, **K214**  
*Troedssonoceratidae*, K210  
*Troedssonoceras*, K214  
*Troostoceras*, **K206**  
*truncation*, **K58**  
*Trundleoceras*, K172  
*Trypteroceras*, K290  
*Tubiferoceras*, **K340**  
*Tumidoceras*, **K310**  
*Tumidonautilus*, K447  
*Tungkanoceras*, K392, K414  
*Tunguskoceras*, K206  
*TUREKIAN*, K14  
*Turnoceras*, **K308**  
*Turoceras*, **K318**  
*Tuyloceras*, **K334**  
*Tylodiscoceras*, K392, K394, **K427**  
*Tylonautilus*, K391, **K416**  
*Tylrothoceras*, K229, K388, **K422**  
*Tyrioceras*, **K367**  
*Tyrrelloceras*, K373  
  
*ULRICH*, K129, K133, K266, K343  
*Ulrichoceras*, **K329**  
*Umbeloceras*, **K340**  
*umbilical angle*, K20, **K58**  
*umbilical areas*, **K58**  
*umbilical perforation*, **K58**  
*umbilical seam*, K20, **K58**  
*umbilical shoulder*, K20, **K59**  
*umbilical slope*, K20, **K59**  
*umbilical suture*, **K59**  
*umbilical wall*, K20, **K59**  
*umbilicus*, K18, **K59**  
*Ungeroceras*, **K488**  
*Unguibeccus*, K481  
*upper annular ridge*, **K59**  
*Uralorthoceras*, **K244**  
*Uranoceras*, K369, **K374**  
*Uranoceratidae*, K101, K103, K369, K370, **K374**  
*Utoceras*, **K172**  
  
*vacuosiphonate*, **K59**  
*VAGINATI*, K94, K165  
*Vaginatum Limestone*, K2  
*Vaginoceras*, K163, **K176**  
*Vaginoceras*, K175  
*Valcouroceras*, K279, **K291**  
*Valcouroceratidae*, K100, K279, K280, K281, **K290**  
*Valenciennes' organ*, K64  
*Vallhällites*, K392, **K427**  
*Van der Hoeven's organ*, K64  
*Vaningenoceras*, **K179**  
*Vassaroceras*, **K154**  
*Vaupelia*, **K288**  
*Venatoroceras*, **K442**  
*venter*, **K59**  
*ventral lobe*, **K59**  
*ventral sinus*, K20, **K59**  
*ventrolateral angle*, **K59**  
*ventrolateral furrows*, K29  
*ventrolateral masses*, K34, **K59**  
*ventrolateral shoulder*, **K59**  
*Ventroloboceras*, K130, **K146**, K498  
*ventromyarian*, K27, K28, **K59**  
*VENTROSIPHONATA*, K96  
*Verkalkungstreifen*, K77, K78  
*Verticoceras*, K49, **K302**  
*Vesporoceras*, **K340**  
*Vestinautilus*, K25, K400, **K431**, K489  
*VINCENT*, K470  
*viniculum*, **K59**, K321  
*Virgaloceras*, K402, **K436**  
  
*Virgoceras*, K218, K219, **K238**  
*Vitreledonellidae*, K5  
*Volborthelia*, K486  
*Volborthella*, K107, **K486**  
*VOLBORTHELLACEA*, K485  
*Volborthellida*, K127, **K485**  
*Volborthellidae*, K127, **K485**  
*VOLBORTHELLIDEA*, K485  
*Vologdinella*, K107, **K487**  
*Vologdinella*, K487  
*Vologdinellidae*, K127, **K487**  
*volution*, K16, **K59**  
*Vorticoceras*, K454  
  
*Wadeoceras*, K49, **K318**  
*Waderoceras*, K318  
*Walcottoceras*, **K154**  
*Wanwanoceras*, K131, **K147**  
*Wellerooceras*, **K315**  
*Wellsooceras*, **K423**  
*WELTER*, K125  
*Westenoceras*, K331  
*Westonoceras*, K125, K198, K322, K323, **K331**  
*Westonoceratidae*, K100, K322, K323, **K331**  
*Wetherbyoceras*, **K319**  
*WETHERELL*, K456, K457  
*Whiteavesites*, K216, **K240**  
*WHITFIELD*, K129  
*Whitfieldoceras*, K216, **K240**  
*whorl*, K16, **K59**  
*whorl sections*, K18, **K59**  
*whorl sides*, K18, **K59**  
*Wichitoceras*, K344, **K361**  
*WIEDEMANN*, K387  
*WILLEY*, K48, K51, K59, K65, K66, K71, K80, K84, K91, K388  
*Wilsonoceras*, **K382**  
*Windung*, K71  
*Winnipegoceras*, K324, **K334**  
*Wissenbachia*, K302  
*Wohnkammer*, K75  
*Wolungoceras*, **K236**  
*Woodringia*, K456  
*WOODWARD*, K338  
*Woosteroceras*, **K146**  
*Worthenoceras*, **K310**  
*wrinkled layers*, K15  
*Wutinoceras*, K208  
*Wutinoceratidae*, K198, K199, K206  
  
*Xenoceras*, K279, **K316**  
*Xenocheilus*, K397, **K451**  
  
*Yabeites*, K206  
*Yehlioceras*, **K189**  
*YONGE*, K4, K106  
*YOUNGQUIST*, K2  
  
*ZHURAVLEVA*, K3, K12, K96, K102, K277  
*ZIETEN*, K468, K474  
*ZITTEL*, K95, K470  
*ZITTEL-EASTMAN*, K369  
*Zittelloceras*, K22, **K288**  
*Zitteloceras*, K290  
*Zugmontites*, K496