

TREATISE ON INVERTEBRATE PALEONTOLOGY

*Prepared under the Guidance of the
Joint Committee on Invertebrate Paleontology*

*Paleontological
Society*

*Society of Economic
Paleontologists and
Mineralogists*

*Palaeontographical
Society*

Directed and Edited by

RAYMOND C. MOORE

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CEPHALOPODA
AMMONOIDEA

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EDITORIAL PREFACE

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

The *Treatise* is divided into parts which bear index letters, each except the initial and concluding ones being defined to include designated groups of invertebrates. The chief purpose of this arrangement is to provide for independence of the several parts as regards date of publication, because it is judged desirable to print and distribute

each segment as soon as possible after it is ready for press. Pages in each part will bear the assigned index letter joined with numbers beginning with 1 and running consecutively to the end of the part. When the parts ultimately are assembled into volumes, no renumbering of pages and figures is required.

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

Features of style in the taxonomic portions of this work have been fixed by the Editor with aid furnished by advice from the Joint Committee on Invertebrate Paleontology representing the societies which have undertaken to sponsor the *Treatise*. It is the Editor's responsibility to consult with authors and co-ordinate their work, seeing that manuscript properly incorporates features of adopted style. Especially he has been called on to formulate policies in respect to many questions of nomenclature and procedure.

The subject of family and subfamily names is reviewed briefly in a following section of this preface, and features of *Treatise* style in generic descriptions are explained.

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

FORM OF ZOOLOGICAL NAMES

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

CLASSIFICATION OF ZOOLOGICAL NAMES

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

CO-ORDINATE NAMES OF TAXA GROUPS

Five groups of different-rank taxonomic units (termed *taxa*, sing., *taxon*) are discriminated, within each of which names are treated as co-ordinate, being transferrable from one category to another without

change of authorship or date. These are: (1) Species Group (subspecies, species); (2) Genus Group (subgenus, genus); (3) Family Group (tribe, subfamily, family, superfamily); (4) Order/Class Group (suborder, order, subclass, class); and (5) Phylum Group (subphylum, phylum). In the first 3 of these groups, but not others, the author of the first-published valid name for any taxon is held to be the author of all other taxa in the group which are based on the same nominate type and the date of publication for purposes of priority is that of the first-published name. Thus, if author A in 1800 introduces the family name X-idae to include 3 genera, one of which is X-us; and if author B in 1850 divides the 20 genera then included in X-idae into subfamilies called X-inae and Y-inae; and if author C in 1950 combines X-idae with other later-formed families to make a superfamily X-acea (or X-oidea, X-icae, etc.); the author of X-inae, X-idae and X-acea is A, 1800, under the Rules. Because taxonomic concepts introduced by authors B and C along with appropriate names surely are not attributable to author A, some means of recording responsibility of B and C are needed. This is discussed later in explaining proposed use of "*nom. transl.*"

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

ORIGINAL AND SUBSEQUENT FORMS OF NAMES

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

acceptable and some quite unacceptable under the Rules.

VALID AND INVALID NAMES

Valid names. A valid zoological name is one that conforms to all mandatory provisions of the Rules (Copenhagen Decisions, p. 43-57) but names of this group are divisible into subgroups as follows: (1) "*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 published class/order-group name); (3) "*imperfect names*," which as originally published and with or without subsequent duplication meet mandatory requirements but contain defects such as incorrect gender of an adjectival specific name (for example, *Spironema recta* instead of *Spironema rectum*) or incorrect stem or form of ending of a family-group name (for example, Spironemidae instead of Spironematidae); (4) "*transferred names*," which are derived by valid emendation from either of the 2nd or 3rd subgroups or from a pre-existing transferred name (as illustrated by change of a family-group name from -inae to -idae or making of a superfamily name); (5) "*improved names*," which include necessary as well as somewhat arbitrarily made emendations allowable under the Rules for taxonomic categories not now covered by regulations as to name form and alterations that are distinct from changes that distinguish the 4th subgroup (including names derived from the 2nd and 3rd subgroups and possibly some alterations of 4th subgroup names). In addition, some zoological names included among those recognized as valid are classifiable in special categories, while at the same time belonging to one or more of the above-listed subgroups. These chiefly include (7) "*substitute names*," introduced to replace invalid names such as junior homonyms; and (8) "*conserved names*," which are names that would have to be re-

jected by application of the Rules except for saving them in their original or an altered spelling by action of the International Commission on Zoological Nomenclature in exercising its plenary powers to this end. Whenever a name requires replacement, any individual may publish a "new name" for it and the first one so introduced has priority over any others; since newness is temporary and relative, the replacement designation is better called substitute name rather than new name. Whenever it is considered desirable to save for usage an otherwise necessarily rejectable name, an individual cannot by himself accomplish the preservation, except by unchallenged action taken in accordance with certain provisions of the Copenhagen Decisions; otherwise he must seek validation through ICZN.

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

valid emendations of previously published valid or invalid names. Void names do have status in nomenclature, being classified as junior synonyms of valid names.

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

SUMMARY OF NAME CLASSES

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

Definitions of Name Classes

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

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

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

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

nomen negatum (*nom. neg.*). Name that as originally published (with or without subsequent identical spelling) constitutes invalid original spelling and although possibly meeting all other mandatory requirements of the Rules, is not correctable to establish original authorship and date ("denied name"). (See Copenhagen Decisions, paragraph 71-1-b-iii.)

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

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

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

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

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

nomen vanum (*nom. van.*). Name consisting of an invalid intentional change in form (spelling) from a previously published name, such invalid emendations having status in nomenclature as junior objective synonyms ("vain or void name"). (See Copenhagen Decisions, paragraphs 71-2-a-ii, 73-3.)

Except as specified otherwise, zoological names accepted in the *Treatise* may be understood to be classifiable either as *nomina inviolata* or *nomina perfecta* (omitting from notice *nomina correctata* among specific names) and these are not discriminated. Names which are not accepted for one reason or another include junior homonyms, a few senior synonyms classifiable as *nomina negata* or *nomina nuda*, and numerous junior synonyms which include both objective (*nomina vana*) and subjective (all classes of valid names) types; effort to classify the invalid names as completely as possible is intended.

NAME CHANGES IN RELATION TO GROUP CATEGORIES

SPECIFIC AND SUBSPECIFIC NAMES

Detailed consideration of valid emendation of specific and subspecific names is unnecessary here because it is well understood and relatively inconsequential. When the form of adjectival specific names is changed to obtain agreement with the gender of a generic name in transferring a species from one genus to another, it is never needful to label the changed name as a *nom. transl.* Likewise, transliteration of a letter accompanied by a diacritical mark in manner now called for by the Rules (as in changing originally published *bröggeri* to *broeggeri*) or elimination of a hyphen (as in changing originally published *cornuoryx* to *cornuoryx* does not require "*nom. correct.*" with it. Revised provisions for emending specific and subspecific names are stated in the report on Copenhagen Decisions (p. 43-46, 51-57).

GENERIC AND SUBGENERIC NAMES

So rare are conditions warranting change of the originally published valid form of generic and subgeneric names that lengthy discussion may be omitted. Only elimination of diacritical marks of some names in this category seems to furnish basis for valid emendation. It is true that many changes of generic and subgeneric names have been published, but virtually all of these are either *nomina vana* or *nomina nulla*. Various names which formerly were classed as homonyms are not now, for two names that differ only by a single letter (or in original publication by presence or absence of a diacritical mark) are construed to be entirely distinct. Revised provisions for emendation of generic and subgeneric names also are given in the report on Copenhagen Decisions (p. 43-47).

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

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

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

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

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

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

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

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

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

nominate genus of the superfamily. The publication of the author containing introduction of the superfamily *nomen translatum* is likely to furnish the information on taxonomic considerations that support definition of the unit.

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

Subfamily STYLININAE d'Orbigny, 1851

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

**Superfamily ARCHAEOCTONOIDEA
Petrunkevitch, 1949**

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

Superfamily CRIOCERATITACEAE Hyatt, 1900

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

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

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

Family STREPTELASMATIDAE Nicholson, 1889

[*nom. correct.* WEDEKIND, 1927 (ex Streptelasmidae NICHOLSON, 1889, *nom. imperf.*)]

Family PALAEOSCORPIIDAE Lehmann, 1944

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

Family AGLASPIDIDAE Miller, 1877

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

Superfamily AGARICIICAE Gray, 1847

[*nom. correct.* WELLS, herein (ex Agaricioidea 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 ARIETTIDAE Hyatt, 1874

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

**Family STEPHANOCERATIDAE
Neumayr, 1875**

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

FAMILY-GROUP NAMES; REPLACEMENTS

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

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

family-group name based on a junior objective synonym because the latter happens to have priority of publication is unsettling. Conversely, a long-used family-group name founded on a junior objective synonym and having priority of publication is better continued in nomenclature than a replacement name based on the senior objective synonym. The Copenhagen Decisions (paragraph 45) take account of these considerations by providing a relatively simple procedure for fixing the desired choice in stabilizing family-group names. In conformance with this, the *Treatise* assigns to contributing authors responsibility for adopting provisions of the Copenhagen Decisions.

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

FAMILY-GROUP NAMES; AUTHORSHIP AND DATE

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

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

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

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

Order DISPARIDA Moore & Laudon, 1943

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

Suborder FAVIINA Vaughan & Wells, 1943

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

Suborder FUNGIINA Verrill, 1865

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

TAXONOMIC EMENDATION

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

Most zoologists, including paleozoologists, who have signified emendation of zoological names refer to what they consider a material change in application of the name such as may be expressed by an importantly altered diagnosis of the assemblage covered by the name. The abbreviation "*emend.*" then may accompany the name, with statement of the author and date of the emendation. On the other hand, a multitude of workers concerned with systematic zoology think that publication of "*emend.*" with a zoological name is valueless because more or less alteration of taxonomic sort is introduced whenever a subspecies, species, genus,

or other assemblage of animals is incorporated under or removed from the coverage of a given zoological name. Inevitably associated with such classificatory expansions and restrictions is some degree of emendation affecting diagnosis. Granting this, still it is true that now and then somewhat radical revisions are put forward, generally with published statement of reasons for changing the application of a name. To erect a signpost at such points of most significant change is worth while, both as aid to subsequent workers in taking account of the altered nomenclatural usage and as indication that not-to-be-overlooked discussion may be found at a particular place in the literature. Authors of contributions to the *Treatise* are encouraged to include records of all specially noteworthy emendations of this nature, using the abbreviation "emend." with the name to which it refers and citing the author and date of the emendation.

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

STYLE IN GENERIC DESCRIPTIONS

DEFINITION OF NAMES

Most generic names are distinct from all others and are indicated without ambiguity by citing their originally published spelling accompanied by name of the author and date of first publication. If the same generic name has been applied to 2 or more distinct taxonomic units, however, it is necessary to differentiate such homonyms, and this calls for distinction between junior homonyms and senior homonyms. Because a junior homonym is invalid, it must be replaced by

some other name. For example, *Callopora* HALL, 1851, introduced for Paleozoic trepostome bryozoans, is invalid because GRAY in 1848 published the same name for Cretaceous-to-Recent cheilostome bryozoans, and BASSLER in 1911 introduced the new name *Hallopora* to replace HALL's homonym. The *Treatise* style of entry is:

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

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

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

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

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

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

CITATION OF TYPE SPECIES

The name of the type species of each genus and subgenus is given next following the generic name with its accompanying author and date, or after entries needed for definition of the name if it is involved in homonymy. The originally published combination of generic and trivial names for this species is cited, accompanied by an asterisk (*), with notation of the author and date of original publication. An exception in this procedure is made, however, if the species was first published in the same

paper and by the same author as that containing definition of the genus which it serves as type; in such case, the initial letter of the generic name followed by the trivial name is given without repeating the name of the author and date, for this saves needed space. Examples of these 2 sorts of citations are as follows:

Diplotrypa NICHOLSON, 1879 [**Favosites petropoli-tanus* 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:

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

It is judged desirable to record the manner of establishing the type species, whether by original designation or by subsequent designation, but various modes of original designation are not distinguished.

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

Subsequent designation of type species; use of “SD” and “SM.” The type species of many genera are not determinable from the publication in which the generic name was introduced and therefore such genera can acquire a type species only by some manner of subsequent designation. Most commonly this is established by publishing a statement naming as type species one of the species originally included in the genus, and in the *Treatise* fixation of the type species in this manner is indicated by the letters “SD” accompanied by the name of the subsequent author (who may be the same person as the original author) and the

date of publishing the subsequent designation. Some genera, as first described and named, included no mentioned species and these necessarily lack a type species until a date subsequent to that of the original publication when one or more species are assigned to such a genus. If only a single species is thus assigned, it automatically becomes the type species and in the *Treatise* this subsequent monotypy is indicated by the letters “SM.” Of course, the first publication containing assignment of species to the genus which originally lacked any included species is the one concerned in fixation of the type species, and if this named 2 or more species as belonging to the genus but did not designate a type species, then a later “SD” designation is necessary. Examples of the use of “SD” and “SM” as employed in the *Treatise* follow.

Hexagonaria GÜRICH, 1896 [**Cyathophyllum hexagonum* GOLDFUSS, 1826; SD LANG, SMITH & THOMAS, 1940].

Muriceides STUDER, 1887 [**M. fragilis* WRIGHT & STUDER, 1889; SM WRIGHT & STUDER, 1889].

SYNONYMS

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

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

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

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

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

Some junior synonyms of either objective or subjective sort may take precedence desirably over senior synonyms wherever uniformity and continuity of nomenclature are served by retaining a widely used but technically rejectable name for a generic assemblage. This requires action of ICZN using

its plenary powers to set aside the unwanted name and validate the wanted one, with placement of the concerned names on appropriate official lists. In the *Treatise* citation of such a conserved generic name is given in the manner shown by the following example.

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

ABBREVIATIONS

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

Abbreviations

Abh., Abhandl., Abhandlungen
Abt., Abteilung, -en
Abys., Abyssinia
Acad., Academia, Académie, Academy
Accad., Accademia
Act., Acta, -as, -es, -os
Afghan., Afghanistan
Afr., Africa, -an
Akad., Akademie
Alb., Albian
Alba., Alberta
Alg., Algeria
Am., America, -n
Anis., Anisian
Ann., Analen, Annals, Annual
Apt., Aptian
Arch., Archiv, -es
Arg., Argentina
Ariz., Arizona
Ark., Arkansas
Arth., ARTHABER
AsiaM., Asia Minor
Assoc., Association
Aus., Austria
Austral., Australia
Baj., Bajocian
Baluch., Baluchistan
Barr., BARRANDE
Barrem., Barremian
Bath., Bathonian
Baug.-S., BAUGIER & SAUZÉ
Bayer., Bayerischen
B.C., British Columbia
Behr., BEHRENDSEN
Beil., Beilage
Beitr., Beitrag, Beiträge
Belg., Belgique, Belgium
Ben., BENECKE
Berrias., Berriasian
Beyr., VON BEYRICH
Biol., Biological, Biology
Blainv., DE BLAINVILLE
Blake-H., BLAKE & HUDLESTON
Blanf., BLANFORD
Bol., Boletín, ín
Bol., Bolivia
Bon., BONARELLI
Bor., BORISSJAK

Boule-L.-T., BOULE, LEMOINE & THEVENIN
Braz., Brazil
Breistr., BREISTROFFER
Brit., Britain, British
Brongn., BRONGNIART
Brug., BRUGUIÈRE
Buch., VON BUCH
Buck., BUCKMAN
Bull., Bulletin
Bundesanst., Bundesanstalt
Bur., Bureau
Burck., BURCKHARDT
C., Central
Calif., California
Callov., Callovian
C.Am., Central America
Camp., Campanian
Can., Canada
Carb., Carboniferous
Carn., Carnian
Cauc., Caucasus Mountains
Cenom., Cenomanian
Centralbl., Centralblatt
Cienc., Ciencias
Cl., Classe
Coah., Coahuila
Cock., COCKERELL
Coll., Collection, -s; College
Colo., Colorado
Colom., Colombia
Com., Comité
Comm., Committee
Comp., Comparative
Congr., Congrès, Congreso, Congress
Coni., Coniacian
Connaiss., Connaissance
Contr., Contribution, -s
Coq., COQUAND
cosmop., cosmopolitan
Court., COURTILLER
Cret., Cretaceous
Czech., Czechoslovakia
d., das, der, die
Dec., December
Defr., DEFRANCE
Del., Delaware
Denck., DENCKMANN

Denkschr., Denkschriften
Dept., Department, Departments
Dépt., Département
dét., détaillée
deutsch., deutschen
Dev., Devonian
Dissert., Dissertation
Douv., DOUVILLÉ
Ditt., DITTMAR
Duft., DUFTSCHMID
Dum., DUMORTIER
E., East
Econ., Economie
Edws., EDWARDS, F. E.
Eichw., EICHWALD
Eng., England
Eth., ETHERIDGE, RORERT, JR.
Eu., Europe
Exped., Expedition
f., für, für
Fac., Facultad, Faculté, Faculty
fasc., fascicle
Festschr., Festschrift
fig., figure, -s
Font., FONTANNES
Forsch., Forschung
Fr., France, Française, -e, French
Freb., FREBOLD
Frech-A., FRECH & ARTHABER
Ga., Georgia
Gemm., GEMMELLARO
Gén., Général
Geog., Geography
Geogn., Geognostische
Geol., Geología, Geological, Geológico, Geologie, Geologisch, Geologiska, Geology
Géol., Géologie, Géologique
Ger., Germany
Gesell., Gesellschaft
Gior., Giornale
Greenl., Greenland
Griep., GRIEPENKERL
Gries., GRIESBACH
Gross., DE GROSSOUVE
Gümb., GÜMBEL
Gug., GUGENBERGER

Haan, DE HAAN
Hauteriv., Hauterivian
H.Douv., DOUVILLÉ, H.
Helvet., Helvetiae
Hemis., Hemisphere
Herb., HERBICH
Hett., Hettangian
Himal., Himalaya Mountains
Hist., Histoire, -ia, Historia,
 History
Hofmus., Hofmuseums
Hohen., HOHENEGGER
Holl., Holland
Hond., Honduras
Hung., Hungarica, Hungary
Hyatt-S., HYATT & SMITH
I., Island, -s
ICZN, International Commis-
 sion on Zoological Nomen-
 clature
Ida., Idaho
Ill., Illinois
illus., illustration, -s
Imp., Imperial
incl., includes
Ind., Indiana
Ind.O., Indian Ocean
Indon., Indonesia
IndoPac., Indo-Pacific
Infravalang., Infravalangian
Inst., Institut, Institute, Insti-
 tutet, Institution, Instituto,
 Instituut
Internat., International, -en
Ire., Ireland
Ital., Italiana
Jaarb., Jaarboek
Jahrb., Jahrbuch
Jahresber., Jahresbericht
Jahresh., Jahreshefte
Jahrg., Jahrgang
Jan., January
J.Buck., BUCKMAN, J.
J.deC.Sow., SOWERBY, J. DEC.
Johns., JOHNSTON
Jour., Journal
J.Sow., SOWERBY, J.
Jur., Jurassic
K., Kaiserlich
K.K., Kaiserlich Königlich
Kak., KAKHADZÉ
Kans., Kansas
Karp., KARPINSKY
Keys., KEYSERLING
Kimm., Kimmeridgian
Kl., Klasse
Klip., KLIPSTEIN
Koenen, VON KOENEN
Kon., DE KONINCK
Kongr., Kongress
Krafft-D., KRAFFT & DIENER
Krum., KRUMBECK
Kut., KUTASSY
Ky., Kentucky
L., Lower; Land
Lab., Laboratoire, Laboratory,
 Laboratories
Ladin., Ladinian
Lah., LAHUSEN
Lam., LAMARCK
Landesanst., Landesanstalt
Leck., LECKENBY
Lias., Liassic
Lief., Lieferung, -en
Linn., Linnean
livr., livraison
Loriol, DE LORIOLE
Low., Lower
M., Middle
Maastr., Maastrichtian
McL., McLEARN
Madag., Madagascar
Mag., Magazine
Math., Mathematische
Math., MATHEWS
Mart., MARTELLI
Mayer-E., MAYER-EYMAR
Meddel., Meddelelser
Medit., Mediterranean
Meek-W., MEEK & WORTHEN
Mem., Memoir, -ia, -s
Mém., Mémoire, -s
Men., MENEGHINI
Merid., Meridionale
Mex., Mexico
Mich., Michigan
Mijnw., Mijnwezen
Miller-F., MILLER & FURNISH
Miller-O., MILLER & OWEN
Min., see Mineral
Mineral., Mineralogical, Min-
 eralogie, Mineralogisch, -e
Minéral., Minéralogique
Miss., Mississippi, Mississippian
Mitt., Mitteilungen
Mo., Missouri
Mojs., MOJSISOVICS
Mon., Monograph
Monatsber., Monatsbericht
Mont., Montana
Moore-S.B., MOORE & SYLVES-
 TER-BRADLEY
Moroc., Morocco
Münst., MÜNSTER
Mus., Musée, Museo, Museum
N., North
N.Am., North America
Nat., Natural; Naturale, -s;
 Naturali; Naturelle, -s
Natl., National
Nat.-Med., Naturwissenschaft-
 lichen-Medizinischen
Naturf., Naturforschende
Naturh., Naturhistorie, -ischen
Naturk., Naturkunde
Naturwiss., Naturwissenschaft-
 lich
N.Caled., New Caledonia
N.Dak., North Dakota
Nederl., Nederlandsch, -e
Neocom., Neocomian
Neum., NEUMAYR
Neum.-U., NEUMAYR & UHLIG
Neuv., Nevada
N.Guinea, New Guinea
Nic., NICOLESCO
N.J., New Jersey
N.Mex., New Mexico
no., number, -s; numéro, -s;
 número, -s
Noetl., NOETLING
Nomencl., Nomenclature
Nor., Norian
nouv., nouveaux, nouvelle
 n.s., new series
N.S.W., New South Wales
N.Y., New York
N.Z., New Zealand
N.Zem., Novaya Zemlya
obj., objective
Oct., October
OD, original designation
Öster., Österreich
Okla., Oklahoma
Orb., d'ORBIGNY
Ore., Oregon
Oxf., Oxfordian
p., page, -s
Pa., Pennsylvania
Pak., Pakistan
Pak., PAKUCKAS
Paläont., Paläontologie, Pal-
 äontologisch
Palaeont., Palaeontologia
Palaeontogr., Palaeontographia,
 Palaeontographica, Palaeonto-
 graphical
Paleont., Paleontologia, Pale-
 ontologia, Paleontological,
 Paleontologiese, Paleontology
Paléont., Paléontologie
Parona-B., PARONA & BONARELLI
Patag., Patagonia
pend., pending
Penn., Pennsylvania
Perm., Permian
Perv., PERVINQUIÈRE
Petitcl., PETITCLERC
Petrol., Petrology
Phil., PHILIPPI
Philip., Philippines
Phill., PHILLIPS
Philos., Philosophical
Phys., Physique, Physikalische
Pictet-C., PICTET & CAMPICHE
pl., plates, -s
Pliensb., Pliensbachian
Plummer-S., PLUMMER & SCOTT
Pol., Poland
Pomp., POMPECK J
Port., Portugal, Portuguese
Portl., Portlandian
Portl., PORTLOCK
Preuss., Preussische
Prob., Problème, -s; Problem, -s
Proc., Proceedings
Prof., Professional
Protect., Protectorat
pt., part, -s
Pub., Publication
Quart., Quarterly
Queensl., Queensland
Quenst., QUENSTEDT

R. Douv., DOUVILLE, R.
reconstr., reconstructed, -ion
Redt., REDTENBACHER
Reichsanst., Reichsanstalt
Rein., REINECKE
Renz-R., RENZ & RENZ
Rept., Report, -s
Rev., Review
Rhaet., Rhaetian
Riv., RIVISTA
Roll., ROLLIER
Roy., ROYAL, -e
Russ., Russia, Russisch
Ruzh., RUZHENEV
S., South; Sea
Sal., SALOPEK
SaltR., Salt Range
S.Am., South America
Sandb.-S., SANDBERGER &
 SANDBERGER
Santon., Santonian
Sard., Sardinia
Sask., Saskatchewan
S.Buck., BUCKMAN, S.
Schind., SCHINDEWOLF
Schloen., SCHLOENBACH
Schloth., SCHLOTHEIM
Schram., SCHRAMMEN
Schweiz., Schweizerische
Sci., Sciences, Scientifique
Scot., Scotland
Scyth., Scythian
SD, subsequent designation
SE., Southeast
sec., section, -s
Sed., Sedimentary
Senckenberg., Senckenber-
 gischen
Senon., Senonian
ser., series, serial
Serv., Serviço, Service
sh., shale
Sib., Siberia

Siem., SIEMIRADZKI
Simon., SIMIONESCU
Simp., SIMPSON
Sinem., Sinemurian
Sitzungsber., Sitzungsbericht
sl., slate
SM, subsequent monotypy
Soc., Sociedad, Società,
 Société, Society
Somali., Somaliland
Sow., SOWERBY, J. or J.DEC.
Sp., Spain
Spec., Special
Spitz., Spitzbergen
ss., sandstone
Staatsinst., Staatsinstitut
Stchir., STCHIROWSKY
Stef., DI STEFANO
Stol., STOLICZKA
Stoy., STOYANOW
Stratig., Stratigraphy
subgen., subgenera, subgenus
subj., subjective
Suppl., Supplement
SW., Southwest
Swin., SWINNERTON
Switz., Switzerland
Tangan., Tanganyika
Teiss., TEISSEYRE
Terr., Territory
Tex., Texas
Thev., THEVENIN
Thioll., THIOILLIER
Tithon., Tithonian
Toarc., Toarcian
Tornq., TORNQUIST
Tosc., Toscana
Toum., TOUMANSKY
Trans., Transactions
Traut., TRAUTSCHOLD
Trav., Travaux
Trias., Triassic

Truc.-W., TRUEMAN &
 WILLIAMS
Turk., Turkey
Turon., Turonian
u., und
U., Upper
Univ., Universidad, Università,
 Université, Universitets,
 University
Up., Upper
U.S., United States
USA, United States (America)
USSR, Union of Soviet Socialist
 Republics
v., volume, -s
Valang., Valanginian
vaterl., vaterländische
Venez., Venezuela
Ver., Verein, -s
Verh., Verhandlung, -en;
 Verhandlungen
Vern., DE VERNEUIL
Visch., VISCHNIAKOFF
Volg., Volgian
W., West
Waag., WAAGEN
Wdkd., WEDEKIND
Whit., WHITEAVES
Whitf., WHITEFIELD
Wiss., Wissenschaften, Wis-
 senschaftliche, -en
Woodw., WOODWARD
Wyo., Wyoming
Yorks., Yorkshire
Yugo., Yugoslavia
Young-B., YOUNG & BIRD
z., zone
Zeitschr., Zeitschrift
Zentralbl., Zentralblatt
Ziet., ZIETEN
Zimm., ZIMMERMANN
Zool., Zoologi, Zoologia,
 Zoological, Zoologie, Zoolo-
 gisch, Zoologiska

REFERENCES TO LITERATURE

Each part of the *Treatise* is accompanied by a selected list of references to paleontological literature consisting primarily of recent and comprehensive monographs available but also including some older works recognized as outstanding in importance. The purpose of giving these references is to aid users of the *Treatise* in finding detailed descriptions and illustrations of morphological features of fossil groups, discussions of classifications and distribution, and especially citations of more or less voluminous literature. Generally speaking, publications listed in the *Treatise* are not original sources of inform-

ation concerning taxonomic units of various rank but they tell the student where he may find them; otherwise it is necessary to turn to such aids as the *Zoological Record* or NEAVE'S *Nomenclator Zoologicus*. References given in the *Treatise* are arranged alphabetically by authors and accompanied by index numbers which serve the purpose of permitting citation most concisely in various parts of the text; these citations of listed papers are inclosed invariably in parentheses and are distinguishable from dates because the index numbers comprise no more than 3 digits. Ordinarily, index numbers for literature references are given at the end of generic or family diagnoses.

SOURCES OF ILLUSTRATIONS

At the end of figure captions an index number is given to supply record of the author of illustrations used in the *Treatise*, reference being made to an alphabetically arranged list of authors' names which follows. The names of authors, but generally not individual publications, are cited. Illustrations consisting of exact copies of previously published figures (except for possible

change of scale) are distinguished by the use of an asterisk (*) with the index number, and previously unpublished illustrations are marked by the letter "n" (signifying "new") with the index number; all other indications of the sources of illustrations are construed to mean "after" the cited author or authors, that is, embodying some degree of change. Addition of the abbreviation "mod." denotes appreciable alteration of the source figure. RAYMOND C. MOORE

INTRODUCTION TO CEPHALOPODA¹

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

Class CEPHALOPODA Leach, 1817

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

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

the application to these animals of such terms as anterior, posterior, dorsal, and ventral, with what appears to be their customary meaning, but it can be justified on the basis of usage.

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

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

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

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

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

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

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

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

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

There are several fundamental differ-

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

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

Provisionally, at any rate, it seems best to regard cephalopods as falling into 2 cate-

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

The stratigraphic distribution of Cephalopoda is from Cambrian to Recent.