

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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PARTS

The indicated Parts (excepting the first and last) are to be published at whatever time each is ready. All may be assembled ultimately in bound volumes. The list of contributing authors is subject to change.

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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 formu-

lated 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 investi-

gations 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 Paleon-

tology 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 zoological 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 \$25,000 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.

FAMILY AND SUBFAMILY NAMES

Rules adopted as guides in preparing taxonomic parts of *Treatise* text include the following provisions with respect to family and subfamily names.

(1) Family and subfamily names are formed by adding the prescribed endings *-idae* and *-inae*, respectively, to the stem of the generic name chosen as nomenclatorial type of the assemblage. This accords with stipulations given in Article 4 of the International Rules of Zoological Nomenclature. No restriction is imposed on an author in choosing the type genus of a new family or subfamily, but a subfamily that includes the type genus of the family to which it belongs (nominotypical subfamily) must be named after such genus. The type genus of a family or subfamily need not be the first-published among those included, but once fixed by publication, it cannot be replaced by another genus in the assemblage unless the type genus in question is transferred to a family or subfamily having an earlier chosen different type genus.

(2) Family and subfamily names are co-ordinate, which signifies that a name published with the ending *-idae* may be changed to *-inae* or vice versa without change in citation of author and date from those of the original publication.

(3) The first-published name of a family or subfamily assemblage shall be accepted unless it is unavailable, as in case of names based on junior homonyms or synonyms or on invalid emendations of generic names, and unless the name conflicts with requirements stated in paragraph 4.

(4) If a family is divided into subfamilies, the name of no such subfamily can antedate the family name. Every family divided into subfamilies must have a nominotypical (*sensu stricto*) subfamily, which has as its type genus the same one which serves as type of the family, and because the name of the family is based on the generic name which (among all included in the assemblage) was first published as type of a familial category, this applies also to the nominotypical subfamily. The author and date of the nominotypical subfamily invariably are identical with those of the family, without reference to whether the author of the family or some subsequent author introduced subfamily divisions. Thus, the family Astrocoeniidae Koby, 1890, contains the subfamilies Astrocoeniinae Koby, 1890 (not Astrocoeniinae Felix, 1898), and Pinacophyllinae Vaughan & Wells, 1943; Koby did not subdivide the family. Just as the nominotypical subgenus of a genus must be ascribed to the author who erected the genus and must bear the same date, so a nominotypical subfamily cannot be attributed to an author other than the one who first selected the genus that serves the family and nominotypical subfamily as type and it cannot bear a date subsequent to that of erecting the family.

(5) Change from the originally published form of family and subfamily names is required (a) if the taxonomic rank assigned to the assemblage is altered, (b) if the stem of the nominotypical generic name is incorrectly distinguished, or (c) if the name of the type genus is changed.

(6) Changes of the sort specified in 5a and 5b do not call for change in citing author and date of family or subfamily assemblages, for these remain as in the original publication. Style of such citations employed in the *Treatise* is illustrated by the examples "Family Exochellidae Bassler, 1935 [as Exochellinae]" and "Family

Rhabdomesidae Vine, 1883 [as Rhabdomesontidae]." The name enclosed in parentheses indicates the originally published form.

(7) If the name of the type genus of a family or subfamily is changed, the familial name must be altered accordingly and not replaced by a name based on a different genus. For example, the family name Electrinidae d'Orbigny, 1851, based on *Electrina* d'Orbigny, 1851 (*non* Baird, 1850) is altered to Electridae Lagaij, 1952, based on *Electra* Lamoureaux, 1816 (senior synonym of *Electrina*) and the *Treatise* style of citation is "Family Electridae Lagaij, 1952 [=emend. Electrinidae d'Orb., 1851]."

(8) Names not available for family or subfamily assemblages include (a) vernacular designations, such as membranipores (English), Pisokrinoiden (German), and Aulacocératidés or Syringoporiens (French); (b) terms not founded on generic names, as for example "Hastatidae Stolley, 1919," for which no corresponding generic name exists (derivation presumably based on the "section" of the broad genus *Belemnites* called Hastati, after the species *Hibolites hastatus*); (c) names not originally of suprageneric rank, as terms derived from trivial names of species; (d) names formed from the stem of generic or subgeneric names which are junior homonyms or synonyms; (e) names based on a type other than that having priority of designation among all genera and subgenera included in the assemblage; and (f) names based on invalid emendations of generic or subgeneric names, as for example "Family Zitteloceratidae," based on invalid emendation of *Zitteloceras* Hyatt to *Zitteloceras* (even though this genus patently was named for Zittel). Present International Rules do not contain some of these stipulations.

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)]." 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]", but in the latter 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 petropopolitanus* PANDER, 1830]" and "*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 "*Acervularia* SCHWEIGGER, 1819 [**A. baltica* (= **Madrepora ananas* LINNÉ, 1758)]."

It is judged desirable to record the man-

ner of establishing the type species, whether by original designation or by subsequent designation, but various modes of original designation are not distinguished. According to convention adopted in the *Treatise*, absence of any indication as to manner of fixing the type species is to be understood as signifying original designation. If the type species has been fixed by subsequent designation, this is indicated by the letters "SD" followed by the name of the author and date of such subsequent designation; for example, "*Hexagonaria* GÜRICH, 1896 [**Cyathophyllum hexagonum* GOLDFUSS, 1826; SD LANG, SMITH, & THOMAS, 1940]."

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 be subjective. An example showing *Treatise* style in listing of synonyms is offered by the following entry: "*Calapoecia* BILLINGS, 1865 [**C. anticostiensis*; SD LINDSTRÖM, 1883] [= *Columnopora* NICHOLSON, 1874; *Houghtonia* ROMINGER, 1876]." A synonym which is also a homonym is recorded in the following: "*Lyopora* NICHOLSON & ETHERIDGE, 1878 [**Palaeopora? javosa* M'COY, 1850] [= *Liopora* LANG, SMITH, & THOMAS, 1940 (*non* GIRTY, 1915)]."

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 lists.

Abbreviations of Stratigraphic and Place Names, Morphological Terms, and Words Used in Bibliographic Citations

Abh., Abhandlung
 Acad., Academia, Académie,
 Academy
 Accad., Accademia

Adv., Advancement
afd., afdeeling, afdeling
Afr., Africa
Akad., Akademie
Ala., Alabama
Alb., Albian
Alba., Alberta
Am., America, American
Ann., Annual
antarct., Antarctic
Antarct., Antarctica
Appalach., Appalachian
Apt., Aptian
Aquit., Aquitanian
Arc., Arctic
Arenig., Arenigian
Arg., Argentina
Ariz., Arizona
Ark., Arkansas
Årssk., Årsskrift
art., article, -s
Assoc. Association
Atl., Atlantic
Aus., Austria
Austral., Australia
Auver., Auversian
Baj., Bajocian
Balt., Baltic
Barton., Bartonian
Bath., Bathonian
B.C., British Columbia
Bd., Band, Bände
Belg., Belgium, Belgique
Blk., Black
Blkriv., Blackriveran
Bol., Bolivia
Boll., Bollettino
Br., British
Braz., Brazil
Brux., Bruxellian
Bull., Bulletin, -s
Bur., Bureau
Burdig., Burdigalian
C., Central
Calif., California
Cam., Cambrian
Camp., Campanian
Can., Canada
CanaryI., Canary Islands
Caradoc., Caradocian
Carb., Carboniferous
Cenom., Cenomanian
Chaz., Chazyan
cheil., cheilostome
Chemung., Chemungian
Chest., Chesteran
Claib., Claibornian
Clift., Cliftonian
Clint., Clintonian
Colo., Colorado
Colom., Colombia
Coni., Coniacian
Contr., Contribution, -s
Cret., Cretaceous
crypt., cryptostome
cten., ctenostome
cycl., cyclostome
C.Z., Canal Zone
Czech., Czechoslovakia
Dan., Danian
Deerpark., Deerparkian
Denkschr., Denkschriften
Denm., Denmark
Dept., Department
Desmoine., Desmoinesian
Dev., Devonian
E., East
econ., economische
Eden., Edenian
Ellesm., Ellesmereland
Eng., England
Eoc., Eocene
Est., Estonia
Eur., Europe
Exped., Expedition
fig., figure, -s
Fla., Florida
Fr., France
Ga., Georgia
G.Brit., Great Britain
geol., geologischen
Geol., Geological, Geology
géol., géologique
Ger., Germany
Gesell., Gesellschaft
Gior., Giornale
Gotl., Gotland
Greenl., Greenland
Held., Helderbergian
Helv., Helvetian
hist., histoire
Hist., Historia, History
Holl., Holland
Hung., Hungary
hydrol., hydrologie
I., Island, -s
Ill., Illinois
Ind., Indiana
Inst., Institut, Institute,
 Institution, Instituto,
 Institutió, Instituut
Ire., Ireland
ital., italiana
Jackson., Jacksonian
Jahrg., Jahrgang
Jour., Journal
Jur., Jurassic
K., Kaiserlich
Kans., Kansas
Keys., Keyseran
Kind., Kinderhookian
Kl., Klasse
Ky., Kentucky
La., Louisiana
Lab., Laboratories, Laboratory
Latt., Lattorfian
Led., Ledian
Lias., Liassic
Lief., Lieferung, -en
Lockport., Lockportian
long., longitudinal
Lut., Lutetian
Maastr., Maastrichtian
Madag., Madagascar
Mal., Malaya
Man., Manitoba
math., mathematische
Maysv., Maysvillian
Md., Maryland
Medin., Medianan
Medit., Mediterranean
Mem., Memoir
Mém., Mémoire
Meramec., Meramecian
Mex., Mexico
Mich., Michigan
Micros., Microscopical
Midway., Midwayan
mineralog., mineralogisch
Mineralog., Mineralogical
Minn., Minnesota
Mio., Miocene
Misc., Miscellaneous
Miss., Mississippi, -an
Missour., Missourian
Mitt., Mitteilungen
Mo., Missouri
Mon., Monograph
Mongol., Mongolia
Mont., Montana
Morrow., Morrowan
mtg., meeting
Mus., Musée, Museo, Museum
N., North
nac., nacional
N.Am., North America
nat., natural, naturali,
 naturelle, -s
Natl., National
Naturgesch., Naturgeschichte
N.Car., North Carolina
NE. Northeast
Nebr., Nebraska
Neocom., Neocomian
Niag., Niagaran
N.J., New Jersey
N.Mex., New Mexico
no., number, -s, número, -s
 número, -s
n.s., new series
N.Scot., Nova Scotia
N.S.W., New South Wales
NW. Northwest
N.Y., New York
N.Z., New Zealand
N.Zem., Nova Zembla
obj., objective
océanogr., océanographique
Okla., Oklahoma
Oligo., Oligocene
Onesqueth., Onesquethawan
Onond., Onondagan
Ont., Ontario
Ord., Ordovician
Osag., Osagian
Oxf., Oxfordian
p., page, -s
Pac., Pacific
Palaeontogr., Palaeontographica,
 Palaeontographical
paläont., paläontologische
Paläont., Paläontologia,
 Paläontologie
Paleoc., Paleocene

Paleont., Paleontologic, -al,
 Paleontology
paléont., paléontologie
Patag., Patagonian
Penn., Pennsylvanian
Perm., Permian
 pl., plate, -s
Pleisto., Pleistocene
Plio., Pliocene
Pol., Poland
Portl., Portlandian
Priabon., Priabonian
Proc., Proceedings
 pt., part, -s
Pub., Publication
Quart., Quarterly
Quat., Quaternary
Que., Quebec
Queensl., Queensland
Rec., Recent
Rept., Report, -s
Richmond., Richmondian
Roy., Royal, Royale
Rupel., Rupelian
Russ., Russia, Russisch
S., Sea, South
SaltR., Salt Range
S.Am., South America
Santon., Santonian
S.Car., South Carolina
 sci., science, -s, scientific,
 scientifique, -s, scienza,
 scienze
Scot., Scotland
SE., Southeast
 sec., -s section, -s
Selsk., Selskabs
Senon., Senonian
 ser., serial, series
Shrops., Shropshire
Sib., Siberia
Sil., Silurian
Skr., Skrifter
Soc., Société, Society
Sp., Spain
Spitz., Spitzbergen
Sta., Station
Staatsinst., Staatsinstitut
suppl., supplement
SW., Southwest
Swed., Sweden, Swedish
Switz., Switzerland
t., tome, tomo, tomos
tang., tangential
Tasm., Tasmania
Tenn., Tennessee
Tert., Tertiary
Tex., Texas
Tongr., Tongrian
Tonol., Tonolowayan
Tort., Tortonian
Trans., Transactions
transv., transverse
Trav., Travaux
Tremad., Tremadocian
Trenton., Trentonian
trep., trepostome
Trias., Triassic
Turk., Turkey
Turon., Turonian
Undiff., Undifferentiated
Univ., Universidad, Université,
 Universitets, University
U.S., United States
V., Valley
Va., Virginia
Valang., Valanginian
Verh., Verhandlung, -en
Vicksb., Vicksburgian
Vidensk., Videnskabernes
 vol., volume, -s
Vt., Vermont
W., West
Wenlock., Wenlockian
Wilcox., Wilcoxian
Wis., Wisconsin
Wiss., Wissenschaften
Yorks., Yorkshire
Ypres., Ypresian
Yugo., Yugoslavia
Zeitschr., Zeitschrift
zool., zoologisch, -e, -er, -es
Zool., Zoologi, -a, Zoological,
 Zoologiska, Zoology

*Abbreviations of Authors'
Names*

Bill., Billings, Elkanah
Blainv., Blainville, H. M. D. de
Canu-B., Canu, Ferdinand, &
 Bassler, R. S.
Canu-L., ——— & Lecointre,
 Georges
Condra-E., Condra, G. E., &
 Elias, M. K.
Cumings-G., Cumings, E. R.,
 & Galloway, J. J.
DeKon., DeKoninck, L. G.
Duv., Duvergier, J.
Ehr., Ehrenberg, C. G.
Eichw., Eichwald, Edouard von
Ellis-S., Ellis, John, &
 Solander, Daniel

Eth., Etheridge, Robert, Jr.
Eth.-F., ——— & Foord, A. H.
Fenton-F., Fenton, C. L., &
 Fenton, M. A.
Gabb-H., Gabb, W. M., &
 Horn, G. H.
Goldf., Goldfuss, August
Hag., Hagenow, Friederich von
Hall-S., Hall, James, &
 Simpson, G. B.
Hall-W., ——— & Whitfield,
 R. P.
ICZN, International Commission
 on Zoological Nomenclature
Lamx., Lamouroux, J. V. F.
Lev., Levensen, G. M. R.
Lonsd., Lonsdale, William
MacGill., MacGillivray, P. H.
Maple., Maplestone, C. M.
Meek-W., Meek, F. B., &
 Worthen, A. H.
Mich., Michelin, J. L. H.
M.Edw., Milne-Edwards, Henri
M.Edw.-H., ——— & Haime,
 Jules
Moore-D., Moore, R. C., &
 Dudley, R. M.
Nekh., Nekhoroshev, A.
Nich., Nicholson, H. A.
Nich.-E., ——— & Etheridge,
 Robert, Jr.
Nich.-F., ——— & Foord, A. H.
Nickles-B., Nickles, J. M., &
 Bassler, R. S.
Nikif., Nikiforova, A. J.
Ok., Okulitch, V. J.
d'Orb., d'Orbigny, A. D.
Quenst., Quenstedt, F. A.
Raf., Rafinesque, C. S.
Schloth., Schlotheim, E. F.
Rom., Rominger, Carl
Shulga., Shulga Nesterenko,
 M. J.
Stuck., Stuckenburg, A.
T.Woods., Tenison Woods, J. E.
Ulr., Ulrich, E. O.
Ulr.-B., ——— & Bassler, R. S.
Vig., Vigneaux, M.
Vinassa., Vinassa de Regny, P. E.
Waag.-W., Waagen, William,
 & Wentzel, Joseph
Whitf., Whitfield, R. P.
Y.-Y., Young, John, & Young,
 John
Yabe-H., Yabe, H., & Hayasaka,
 I.
Yabe-S., ——— & Sugiyama,
 T.

REFERENCES TO LITERATURE

Each part of the *Treatise* is accompanied by a selected list of references to paleontological literature consisting primarily of most 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 classification 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 are distinguishable from dates because the index numbers comprise no more than 3 digits. Ordinarily, the index numbers for literature references are given at the end of generic or family diagnoses.

The selected references pertaining to Bryozoa and index numbers used in this part of the *Treatise* are given at the end of the text (p. G236).

SOURCES OF ILLUSTRATIONS

At the end of figure captions an index number commonly 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 list of References to Literature. Index numbers printed in lightface roman type denote reproduction of original illustrations in modified form, as in redrawing (in the manner commonly recorded by the example "after SCHUCHERT"),

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AID FROM THE INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE

In the course of formulating policies for guidance of *Treatise* authors in dealing with many sorts of problems in zoological nomenclature, the Editor conducted a rather extensive correspondence with American and European specialists, including the Secretary of the International Commission on Zoological Nomenclature, MR. FRANCIS HEMMING, as well as other present and former members of this Commission. In addition, a number of personal conferences were held in London, Paris, Frankfurt-a.-M., Washington, and elsewhere. It is appropriate to express great appreciation on behalf of the *Treatise* project to individuals who thus contributed to the shaping of decisions. MR. HEMMING has aided especially by expediting as much as possible action by the International Commission on questions referred to it for decision, several of these calling for use of the Commission's plenary powers. Without prejudice to any decisions ultimately made, MR. HEMMING has acquiesced to a proposal that recommended nomenclatural dispositions submitted to the Commission but not yet decided when *Treatise* manuscript is ready for the press may be published with the accompanying notation "ICZN pend.", which signifies that action of the International Commission on Zoological Nomenclature is pending.

RAYMOND C. MOORE