

TREATISE ON INVERTEBRATE PALEONTOLOGY

Part O

ARTHROPODA 1

Trilobita, Revised

Volume 1: Introduction,
Order Agnostida, Order Redlichiida

H. B. WHITTINGTON, B. D. E. CHATTERTON, S. E. SPEYER, R. A. FORTEY,
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Introduction, Order Agnostina, Order Redlichiida

VOLUME 1

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INFORMATION ON TREATISE VOLUMES

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 is made ready for the press. Copies can be obtained from the Publication Sales Department, The Geological Society of America, 3300 Penrose Place, P.O. Box 9140, Boulder, Colorado 80301.

VOLUMES ALREADY PUBLISHED

- Part A. INTRODUCTION, xxiii + 569 p., 371 fig., 1979.
- Part C. PROTISTA 2 (Sarcodina, Chiefly "Thecamoebians" and Foraminiferida), xxxi + 900 p., 5,311 fig., 1964.
- Part D. PROTISTA 3 (Chiefly Radiolaria, Tintinnina), xii + 195 p., 1,050 fig., 1954.
- Part E. ARCHAEOCYATHA, PORIFERA, xviii + 122 p., 728 fig., 1955.
- Part E, Revised. ARCHAEOCYATHA, Volume 1, xxx + 158 p., 871 fig., 1972.
- Part F. COELENTERATA, xvii + 498 p., 2,700 fig., 1956.
- Part F. COELENTERATA, Supplement 1 (Rugosa and Tabulata), xl + 762 p., 3,317 fig., 1981.
- Part G. BRYOZOA, xii + 253 p., 2,000 fig., 1953.
- Part G, Revised. BRYOZOA, Volume 1 (Introduction, Order Cystoporata, Order Cryptostomata), xxvi + 626 p., 1,595 fig., 1983.
- Part H. BRACHIOPODA, xxxii + 927 p., 5,198 fig., 1965.
- Part H, Revised. BRACHIOPODA (Introduction), xx + 539 p., 417 fig., 40 tables, 1997.
- Part I. MOLLUSCA 1 (Mollusca General Features, Scaphopoda, Amphineura, Monoplacophora, Gastropoda General Features, Archaeogastropoda, Mainly Paleozoic Caenogastropoda and Opisthobranchia), xxiii + 351 p., 1,732 fig., 1960.
- Part K. MOLLUSCA 3 (Cephalopoda General Features, Endoceratoidea, Actinoceratoidea, Nautiloidea, Bactritoidea), xxviii + 519 p., 2,382 fig., 1964.
- Part L. MOLLUSCA 4 (Ammonoidea), xxii + 490 p., 3,800 fig., 1957.
- Part L, Revised. MOLLUSCA 4, Volume 4 (Cretaceous Ammonoidea), xx + 362 p., 2,070 illus. on 216 fig., 1996.
- Part N. MOLLUSCA 6 (Bivalvia), Volumes 1 and 2 (of 3), xxxvii + 952 p., 6,198 fig., 1969; Volume 3, iv + 272 p., 742 fig., 1971.
- Part O. ARTHROPODA 1 (Arthropoda General Features, Protarthropoda, Euarthropoda General Features, Trilobitomorpha), xix + 560 p., 2,880 fig., 1959.
- Part P. ARTHROPODA 2 (Chelicerata, Pycnogonida, Palaeoisopus), xvii + 181 p., 565 fig., 1955.
- Part Q. ARTHROPODA 3 (Crustacea, Ostracoda), xxiii + 442 p., 3,476 fig., 1961.
- Part R. ARTHROPODA 4, Volumes 1 and 2 (Crustacea Exclusive of Ostracoda, Myriapoda, Hexapoda), xxxvi + 651 p., 1,762 fig., 1969.
- Part R. ARTHROPODA 4, Volumes 3 and 4 (Hexapoda), xxii + 655 p., 1,489 fig., 1992.
- Part S. ECHINODERMATA 1 (Echinodermata General Features, Homalozoa, Crinozoa, exclusive of Crinoidea), xxx + 650 p., 2,868 fig., 1967 [1968].
- Part T. ECHINODERMATA 2 (Crinoidea), Volumes 1–3, xxxviii + 1,027 p., 4,833 fig., 1978.
- Part U. ECHINODERMATA 3 (Asterozoans, Echinozoans), xxx + 695 p., 3,485 fig., 1966.
- Part V. GRAPTOLITHINA, xvii + 101 p., 358 fig., 1955.
- Part V, Revised. GRAPTOLITHINA, xxxii + 163 p., 507 fig., 1970.
- Part W. MISCELLANEA (Conodonts, Conoidal Shells of Uncertain Affinities, Worms, Trace Fossils, Problematica), xxv + 259 p., 1,058 fig., 1962.

- Part W, Revised. MISCELLANEA, Supplement 1 (Trace Fossils and Problematica), xxi + 269 p., 912 fig., 1975.
Part W, Revised. MISCELLANEA, Supplement 2 (Conodonts), xxviii + 202 p., frontis., 858 fig., 1981.

THIS VOLUME

- Part O, Revised. ARTHROPODA 1, TRILOBITA 1 (Introduction, Order Agnostida, Order Redlichiida), xxiv + 530 p., 309 fig., 1997.

VOLUMES IN PREPARATION

- Part B. PROTISTA 1 (Chrysoomonadida, Coccolithophorida, Charophyta, Diatomacea, etc.).
Part E, Revised. PORIFERA. Volume 2.
Part G, Revised. BRYOZOA (additional volumes).
Part H, Revised. BRACHIOPODA (additional volumes).
Part I. Introduction to MOLLUSCA (part).
Part J. MOLLUSCA 2 (Caenogastropoda, Streptoneura exclusive of Archaeogastropoda, Euthyneura).
Part L, Revised. MOLLUSCA 4 (Ammonoidea) (additional volumes).
Part M. MOLLUSCA 5 (Coleoidea).
Part O, Revised. ARTHROPODA 1 (Trilobita) (additional volumes).
Part Q, Revised. ARTHROPODA 3 (Ostracoda).

EDITORIAL PREFACE

From the outset the aim of the *Treatise on Invertebrate Paleontology* has been to present a comprehensive and authoritative yet compact statement of knowledge concerning groups of invertebrate fossils. Typically, preparation of early *Treatise* volumes was undertaken by a small group with a synoptic view of the taxa being monographed. Two or perhaps three specialists worked together, sometimes co-opting others for coverage of highly specialized taxa. Recently, however, both new *Treatise* volumes and revisions of existing ones have been undertaken increasingly by teams of specialists led by a coordinating author. This volume, Part O, Arthropoda 1, Revised, the first of a series of volumes on the trilobites, has been prepared by such a team of specialists whose work was coordinated by Professor H. B. Whittington. Editorial matters specific to this volume are

discussed near the end of this editorial preface.

ZOOLOGICAL NAMES

Questions about the proper use of zoological names arise continually, especially questions regarding both the acceptability of names and alterations of names that are allowed or even required. Regulations prepared by the International Commission on Zoological Nomenclature (ICZN) and published in 1985 in the *International Code of Zoological Nomenclature*, hereinafter referred to as the *Code*, provide procedures for answering such questions. The prime objective of the *Code* is to promote stability and universality in the use of the scientific names of animals, ensuring also that each generic name is distinct and unique, while avoiding

unwarranted restrictions on freedom of thought and action of systematists. Priority of names is a basic principle of the *Code*, but under specified conditions and by following prescribed procedures, priority may be set aside by the Commission. These procedures apply especially where slavish adherence to the principle of priority would hamper or even disrupt zoological nomenclature and the information it conveys.

The Commission, ever aware of the changing needs of systematists, is undertaking a revision of the *Code* that will further enhance nomenclatorial stability. Nevertheless, the nomenclatorial tasks that confront zoological taxonomists are formidable and have often justified the complaint that the study of zoology and paleontology is too often merely the study of names rather than the study of animals. It is incumbent upon all systematists, therefore, at the outset of their work to pay careful attention to the *Code* to enhance stability by minimizing the number of subsequent changes of names, too many of which are necessitated by insufficient attention to detail. To that end, several pages here are devoted to aspects of zoological nomenclature that are judged to have chief importance in relation to procedures adopted in the *Treatise*, especially in this volume. Terminology is explained, and examples are given of the style employed in the nomenclatorial parts of the systematic descriptions.

GROUPS OF TAXONOMIC CATEGORIES

Each taxon belongs to a category in the Linnaean, hierarchical classification. The *Code* recognizes three groups of categories, a species-group, a genus-group, and a family-group. Taxa of lower rank than subspecies are excluded from the rules of zoological nomenclature, and those of higher rank than superfamily are not regulated by the *Code*. It is both natural and convenient to discuss nomenclatorial matters in general terms first

and then to consider each of these three, recognized groups separately. Especially important is the provision that within each group the categories are coordinate, that is, equal in rank, whereas categories of different groups are not coordinate.

FORMS OF NAMES

All zoological names can be considered on the basis of their spelling. The first form of a name to be published is defined as the original spelling (*Code*, Article 32), and any form of the same name that is published later and is different from the original spelling is designated a subsequent spelling (*Code*, Article 33). Not every original or subsequent spelling is correct.

ORIGINAL SPELLINGS

If the first form of a name to be published is consistent and unambiguous, the original is defined as correct unless it contravenes some stipulation of the *Code* (Articles 11, 27 to 31, and 34) or unless the original publication contains clear evidence of an inadvertent error in the sense of the *Code*, or, among names belonging to the family-group, unless correction of the termination or the stem of the type genus is required. An original spelling that fails to meet these requirements is defined as incorrect.

If a name is spelled in more than one way in the original publication, the form adopted by the first reviser is accepted as the correct original spelling, provided that it complies with mandatory stipulations of the *Code* (Articles 11 and 24 to 34).

Incorrect original spellings are any that fail to satisfy requirements of the *Code*, represent an inadvertent error, or are one of multiple original spellings not adopted by a first reviser. These have no separate status in zoological nomenclature and, therefore, cannot enter into homonymy or be used as replacement names; and they call for correction. For example, a name originally published with a

diacritical mark, apostrophe, dieresis, or hyphen requires correction by deleting such features and uniting parts of the name originally separated by them, except that deletion of an umlaut from a vowel in a name derived from a German word or personal name unfortunately requires the insertion of *e* after the vowel. Where original spelling is judged to be incorrect solely because of inadequacies of the Greek or Latin scholarship of the author, nomenclatorial changes conflict with the primary propose of zoological nomenclature as an information retrieval system. One looks forward with hope to a revised *Code* wherein rules are emplaced that enhance stability rather than classical scholarship, thereby facilitating access to information.

SUBSEQUENT SPELLINGS

If a subsequent spelling differs from an original spelling in any way, even by the omission, addition, or alteration of a single letter, the subsequent spelling must be defined as a different name. Exceptions include such changes as an altered termination of adjectival specific names to agree in gender with associated generic names; changes of family-group names to denote assigned taxonomic rank; and corrections that eliminate originally used diacritical marks, hyphens, and the like. Such changes are not regarded as spelling changes conceived to produce a different name. In some instances, however, species-group names having variable spellings are regarded as homonyms as specified in the *Code* (Article 58).

Altered subsequent spellings other than the exceptions noted may be either intentional or unintentional. If “demonstrably intentional” (*Code*, Article 33, p. 73), the change is designated as an emendation. Emendations may be either justifiable or unjustifiable. Justifiable emendations are corrections of incorrect original spellings, and these take the authorship and date of the original spellings. Unjustifiable emendations are names having their own status in nomen-

clature, with author and date of their publication. They are junior, objective synonyms of the name in its original form.

Subsequent spellings, if unintentional, are defined as incorrect subsequent spellings. They have no status in nomenclature, do not enter into homonymy, and cannot be used as replacement names.

AVAILABLE AND UNAVAILABLE NAMES

Editorial prefaces of some previous volumes of the *Treatise* have discussed in appreciable detail the availability of the many kinds of zoological names that have been proposed under a variety of circumstances. Much of that information, while important, does not pertain to the present volume, in which authors have used fewer terms for such names. The reader is referred to the *Code* (Articles 10 to 20) for further details on availability of names. Here, suffice it to say that an available zoological name is any that conforms to all mandatory provisions of the *Code*. All zoological names that fail to comply with mandatory provisions of the *Code* are unavailable and have no status in zoological nomenclature. Both available and unavailable names are classifiable into groups that have been recognized in previous volumes of the *Treatise*, although not explicitly differentiated in the *Code*. Among names that are available, these groups include inviolate names, perfect names, imperfect names, vain names, transferred names, improved or corrected names, substitute names, and conserved names. Kinds of unavailable names include naked names (see *nomina nuda* below), denied names, impermissible names, null names, and forgotten names.

Nomina nuda include all names that fail to satisfy provisions stipulated in Article 11 of the *Code*, which states general requirements of availability. In addition, they include names published before 1931 that were unaccompanied by a description, definition, or indication (*Code*, Article 12) and names

published after 1930 that (1) lacked an accompanying statement of characters that differentiate the taxon, (2) were without a definite bibliographic reference to such a statement, (3) were not proposed expressly as a replacement (*nomen novum*) of a preexisting available name (*Code*, Article 13a), or (4) for genus-group names, were unaccompanied by definite fixation of a type species by original designation or indication (*Code*, Article 13b). *Nomina nuda* have no status in nomenclature, and they are not correctable to establish original authorship and date.

VALID AND INVALID NAMES

Important considerations distinguish valid from available names on the one hand and invalid from unavailable names on the other. Whereas determination of availability is based entirely on objective considerations guided by articles of the *Code*, conclusions as to validity of zoological names may be partly subjective. A valid name is the correct one for a given taxon, which may have two or more available names but only a single correct, hence valid, name, which is also generally the oldest name that it has been given. Obviously, no valid name can also be an unavailable name, but invalid names may be either available or unavailable. It follows that any name for a given taxon other than the valid name, whether available or unavailable, is an invalid name.

One encounters a sort of nomenclatorial no-man's land in considering the status of such zoological names as *nomina dubia* (doubtful names), which may include both available and unavailable names. The unavailable ones can well be ignored, but names considered to be available contribute to uncertainty and instability in the systematic literature. These can ordinarily be removed only by appeal to the ICZN for special action. Because few systematists care to seek such remedy, such invalid but available names persist in the literature.

NAME CHANGES IN RELATION TO GROUPS OF TAXONOMIC CATEGORIES

SPECIES-GROUP NAMES

Detailed consideration of valid emendation of specific and subspecific names is unnecessary here, both because the topic is well understood and relatively inconsequential and because the *Treatise* deals with genus-group names and higher categories. When the form of adjectival specific names is changed to agree with the gender of a generic name in transferring a species from one genus to another, one need never label the changed name as *nomen correctum*. Similarly, transliteration of a letter accompanied by a diacritical mark in the manner now called for by the *Code*, as in changing originally *bröggeri* to *broeggeri*, or eliminating a hyphen, as in changing originally published *cornu-oryx* to *cornuoryx*, does not require the designation *nomen correctum*. Of course, in this age of computers and electronic databases, such changes of name, which are perfectly valid for the purposes of scholarship, run counter to the requirements of nomenclatorial stability upon which the preparation of massive, electronic databases is predicated.

GENUS-GROUP NAMES

Conditions warranting change of the originally published, valid form of generic and subgeneric names are sufficiently rare that lengthy discussion is unnecessary. Only elimination of diacritical marks and hyphens in some names in this category and replacement of homonyms seem to furnish basis for valid emendation. Many names that formerly were regarded as homonyms are no longer so regarded, because two names that differ only by a single letter or in original publication by the presence of a diacritical mark in one are now construed to be entirely distinct.

As has been pointed out above, difficulty typically arises when one tries to decide whether a change of spelling of a name by a subsequent author was intentional or unintentional, and the decision has often to be made arbitrarily.

FAMILY-GROUP NAMES

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 of any of these groups, 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. Moreover, every family containing differentiated subfamilies must have a nominate subfamily (*sensu stricto*), which is based on the same type genus as the family. Finally, the author and date set down for the nominate subfamily invariably are identical with those of the family, irrespective of whether the author of the family or some subsequent author introduced subdivisions.

Corrections in the form of family-group names do not affect authorship and date of the taxon concerned, but in the *Treatise* recording the authorship and date of the correction is desirable because it provides a pathway to follow the thinking of the systematists involved.

Family-Group Names: Use of *nomen translatum*

The *Code* specifies the endings only for subfamily (-inae) and family (-idae) names, but all family-group taxa are defined as coordinate (*Code*, Article 36, p. 77): "A name established for a taxon at any rank in the family group is deemed to be simultaneously established with the same author and date for taxa based upon the same name-bearing

type (type genus) at other ranks in the family group, with appropriate mandatory change of suffix [Art. 34a]." Such changes of rank and concomitant changes of endings as elevation of a tribe to subfamily rank or of a subfamily to family rank, if introduced subsequent to designation of a subfamily or family based on the same nominotypical genus, are *nomina translata*. In the *Treatise* it is desirable to distinguish the valid alteration in the changed ending of each transferred family-group name by the term *nomen translatum*, abbreviated to *nom. transl.* Similarly for clarity, authors should record the author, date, and page of the alteration.

Family HEXAGENITIDAE Lameere, 1917

[*nom. transl.* DEMOULIN, 1954, p. 566, ex Hexagenitinae LAMEERE, 1917, p. 74]

This is especially important for superfamilies, for the information of interest is the author who initially introduced a taxon rather than the author of the superfamily as defined by the *Code*. The latter is merely the individual who first defined some lower-ranked, family-group taxon that contains the nominotypical genus of the superfamily. On the other hand, the publication that introduces the superfamily by *nomen translatum* is likely to furnish the information on taxonomic considerations that support definition of the taxon.

Superfamily AGNOSTOIDEA M'COY, 1849

[*nom. transl.* SHERGOLD, LAURIE, & SUN, 1990, p. 32, ex Agnostinae M'COY, 1849, p. 402]

Family-group Names: Use of *nomen correctum*

Valid name changes classed as *nomina correctae* do not depend on transfer from one category of the family group to another but most commonly involve correction of the stem of the nominotypical genus. In addi-

tion, they include somewhat arbitrarily chosen modifications of endings for names of tribes or superfamilies. Examples of the use of *nomen correctum* are the following.

**Family STREPTELASMATIDAE
Nicholson, 1889**

[*nom. correct.* WEDEKIND, 1927, p. 7, *pro* Streptelasmidae NICHOLSON in NICHOLSON & LYDEKKER, 1889, p. 297]

**Family PALAEOSCORPIDAE
Lehmann, 1944**

[*nom. correct.* PETRUNKEVITCH, 1955, p. 73, *pro* Palaeoscorpionidae LEHMANN, 1944, p. 177]

**FAMILY-GROUP NAMES:
REPLACEMENTS**

Family-group names are formed by adding combinations of letters, which are prescribed for family and subfamily, to the stem of the name belonging to the nominotypical genus first chosen as type of the assemblage. The type genus need not be the first genus in the family to have been named and defined, but among all those included it must be the first published as name giver to a family-group taxon. Once fixed, the family-group name remains tied to the nominotypical genus even if the generic name is changed by reason of status as a junior homonym or junior synonym, either objective or subjective. Seemingly, the *Code* requires replacement of a family-group name only if the nominotypical genus is found to have been a junior homonym when it was proposed (*Code*, Article 39, p. 79), in which case “. . . it must be replaced either by the next oldest available name from among its synonyms, including those of its subordinate taxa, or, if there is no such name, by a new replacement name based on the valid name of the former type genus.” Authorship and date attributed to the replacement family-group name are determined by first publication of the changed family-group name. Recommendation 40A of the *Code* (p. 81), however, specifies that for subsequent application of the rule of priority, the family-group name “. . . should be

cited with its own author and date, followed by the date of the replaced name in parentheses.” Many family-group names that have been in use for a long time are *nomina nuda*, since they fail to satisfy criteria of availability (*Code*, Article 11f). These demand replacement by valid names.

The aim of family-group nomenclature is to yield the greatest possible stability and uniformity, just as in other zoological names. Both taxonomic experience and the *Code* (Article 40) indicate the wisdom of sustaining family-group names based on junior subjective synonyms if they have priority of publication, for opinions of the same worker may change from time to time. The retention of first-published, family-group names that are found to be based on junior objective synonyms, however, is less clearly desirable, especially if a replacement name derived from the senior objective synonym has been recognized very long and widely. Moreover, to displace a widely 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.

A family-group name may need to be replaced if the nominotypical genus is transferred to another family-group. If so, the first-published of the generic names remaining in the family-group taxon is to be recognized in forming a replacement name.

**Suprafamilial Taxa: Taxa above Family-
Group**

International rules of zoological nomenclature as given in the *Code* affect only lower-rank categories: subspecies to superfamily. Suprafamilial categories (suborder to phylum) are either not mentioned or explicitly placed outside of the application of zoological rules. The *Copenhagen Decisions on Zoological Nomenclature* (1953, Articles 59 to 69) proposed adopting rules for naming suborders and higher taxa up to and including

phylum, with provision for designating a type genus for each, in such manner as not to interfere with the taxonomic freedom of workers. Procedures were outlined for applying the rule of priority and rule of homonymy to suprafamilial taxa and for dealing with the names of such taxa and their authorship, with assigned dates, if they should be transferred on taxonomic grounds from one rank to another. The adoption of terminations of names, different for each category but uniform within each, was recommended.

The Colloquium on Zoological Nomenclature, which met in London during the week just before the 15th 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 that 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, a class or order defined by an author at a given date, using chosen morphologic characters (e.g., gills of bivalves), should not be allowed to freeze nomenclature, taking precedence over another class or order that is proposed later and distinguished by different characters (e.g., hinge teeth of bivalves). Even the fixing of type genera for suprafamilial taxa would have little, if any, value, hindering taxonomic work rather than aiding it. No basis for establishing such types and for naming these taxa has yet been provided.

The considerations just stated do not prevent the editors of the *Treatise* from making rules for dealing with suprafamilial groups of animals described and illustrated in this publication. Some uniformity is needed, especially for the guidance of *Treatise* authors. This policy should accord with recognized general practice among zoologists; but where general practice is indeterminate or nonexistent, our own procedure in suprafamilial no-

menclature 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 that, on taxonomic grounds, are changed from their originally assigned rank. Accordingly, a few rules expressing *Treatise* policy are given here, some with examples of their application.

1. The name of any suprafamilial taxon must be a Latin or Latinized, uninominal noun of plural form, or treated as such, with a capital initial letter and without diacritical mark, apostrophe, diaeresis, or hyphen. If a component consists of a numeral, numerical adjective, or adverb, this must be written in full.

2. Names of suprafamilial taxa may be constructed in almost any manner. A name may indicate morphological attributes (e.g., Lamellibranchiata, Cyclostomata, Toxoglossa) or be based on the stem of an included genus (e.g., Bellerophontina, Nautilida, Fungiina) or on arbitrary combinations of letters (e.g., Yuania); none of these, however, can end in *-idae* or *-inae*, which terminations are reserved for family-group taxa. No suprafamilial name identical in form to that of a genus or to another published suprafamilial name should be employed (e.g., order Decapoda LATREILLE, 1803, crustaceans, and order Decapoda LEACH, 1818, cephalopods; suborder Chonetoidea MUIRWOOD, 1955, and genus *Chonetoidea* JONES, 1928). Worthy of notice is the classificatory and nomenclatorial distinction between suprafamilial and family-group taxa that, 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 is not coordinate with superfamily Bellerophontacea MCCOY, 1851 or family Bellerophontidae MCCOY, 1851).

3. The rules of priority and homonymy lack any force of international agreement as applied to suprafamilial names, yet in the interest of nomenclatorial stability and to avoid confusion these rules are widely

applied by zoologists to taxa 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 changes cannot rationally be judged to alter the authorship and date of the taxon as published originally. A name revised from its previously published rank is a transferred name (*nomen translatum*), as illustrated in the following.

Order CORYNEXOCHIDA Kobayashi, 1935

[*nom. transl.* MOORE, 1959, p. 217, *ex* suborder *Corynexochida* KOBAYASHI, 1935, p. 81]

A name revised from its previously published form merely by adoption of a different termination without changing taxonomic rank is a *nomen correctum*.

Order DISPARIDA Moore & Laudon, 1943

[*nom. correct.* MOORE in MOORE, LALICKER, & FISCHER, 1952, p. 613, *pro* order *Disparata* MOORE & LAUDON, 1943, p. 24]

A suprafamilial name revised from its previously published rank with accompanying change of termination, which signals the change of rank, is recorded as a *nomen translatum et correctum*.

Order HYBOCRINIDA Jaekel, 1918

[*nom. transl. et correct.* MOORE in MOORE, LALICKER, & FISCHER, 1952, p. 613, *ex* suborder *Hybocrinites* JAEKEL, 1918, p. 90]

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

Subclass ENDOCERATOIDEA Teichert, 1933

[*nom. transl.* TEICHERT in TEICHERT & others, 1964, p. 128, *ex* order *Endoceroidea* TEICHERT, 1933, p. 214]

Order ENDOCERIDA Teichert, 1933

[*nom. correct.* TEICHERT in TEICHERT & others, 1964, p. 165, *pro* order *Endoceroidea* TEICHERT, 1933, p. 214]

TAXONOMIC EMENDATION

Emendation has two distinct meanings as regards zoological nomenclature. These are alteration of a name itself in various ways for various reasons, as has been reviewed, and alteration of the taxonomic scope or concept for which a name is used. The *Code* (Article 33a and Glossary, p. 254) concerns itself only with the first type of emendation, applying the term to intentional, either justified or unjustified changes of the original spelling of a name. The second type of emendation primarily concerns classification and inherently is not associated with change of name. Little attention generally has been paid to this distinction in spite of its significance.

Most zoologists, including paleontologists, who have emended 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 must accompany the name with statement of the author and date of the emendation. On the other hand, many systematists think that publication of *emend.* with a zoological name is valueless because alteration of a taxonomic concept is introduced whenever a subspecies, species, genus, or other taxon is incorporated into or removed from a higher zoological taxon. 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 more extensive revisions are put forward, generally with a published statement of the reasons for changing the application of a name. To erect a signpost at such points of most significant change is worthwhile, both as an aid to subsequent workers in taking account of the altered no-

menclatorial usage and to indicate where in the literature cogent discussion may be found. Authors of contributions to the *Treatise* are encouraged to include records of all especially noteworthy emendations of this nature, using the abbreviation *emend.* with the name to which it refers and citing the author, date, and page of the emendation. Examples from *Treatise* volumes follow.

Order ORTHIDA Schuchert & Cooper, 1932

[*nom. transl. et correct.* MOORE in MOORE, LALICKER, & FISCHER, 1952, p. 220, *ex suborder* Orthoidea SCHUCHERT & COOPER, 1932, p. 43; *emend.*, WILLIAMS & WRIGHT, 1965, p. 299]

Subfamily ROVEACRININAE Peck, 1943

[Roveacrininae PECK, 1943, p. 465; *emend.*, PECK in MOORE & TEICHERT, 1978, p. 921]

STYLE IN GENERIC DESCRIPTIONS

CITATION OF TYPE SPECIES

In the *Treatise* the name of the type species of each genus and subgenus is given immediately following the generic name with its accompanying author, date, and page reference or after entries needed for definition of the name if it is involved in homonymy. The originally published combination of generic and trivial names of this species is cited, accompanied by an asterisk (*), with notation of the author, date, and page of original publication, except if the species was first published in the same paper and by the same author as that containing definition of the genus of which it is the type. In this instance, the initial letter of the generic name followed by the trivial name is given without repeating the name of the author and date. Examples of these two sorts of citations follow.

Orionastraea SMITH, 1917, p. 294 [**Sarcinula phillipsi* MCCOY, 1849, p. 125; OD].

Schoenophyllum SIMPSON, 1900, p. 214 [**S. aggregatum*; OD].

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

Actinocyathus D'ORBIGNY, 1849, p. 12 [**Cyathophyllum crenulate* PHILLIPS, 1836, p. 202; M; =*Lonsdaleia floriformis* (MARTIN), 1809, pl. 43; validated by ICZN Opinion 419].

In some instances the type species is a junior homonym. If so, it is cited as shown in the following example.

Prionocyclus MEEK, 1871b, p. 298 [**Ammonites serratocarينات* MEEK, 1871a, p. 429, *non* STOLICZKA, 1964, p. 57; =*Prionocyclus wyomingensis* MEEK, 1876, p. 452].

In the *Treatise* the name of the type species is always given in the exact form it had in the original publication except that diacritical marks have been removed. Where other mandatory changes are required, these are introduced later in the text, typically in a figure caption.

Fixation of Type Species Originally

It is desirable to record the manner of establishing the type species, whether by original designation (OD) or by subsequent designation (SD). The type species of a genus or subgenus, according to provisions of the *Code*, may be fixed in various ways in the original publication; or it may be fixed subsequently in ways specified by the *Code* (Article 68) and described in the next section. Type species fixed in the original publication include (1) *original designation* (in the *Treatise* indicated by OD) when the type species is explicitly stated or (before 1931) indicated by n. gen., n. sp. (or its equivalent) applied to a single species included in a new genus, (2) defined by use of *typus* or *typicus* for one of the species included in a new genus (adequately indicated in the *Treatise* by the specific name), (3) established by *monotypy* if a new genus or subgenus has only one originally included species (in the *Treatise* indicated as M), and (4) fixed by *tautonymy* if the genus-group name is identical to an included species name not indicated as the type.

Fixation of Type Species Subsequently

The type species of many genera are not determinable from the publication in which the generic name was introduced. 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. In the *Treatise* such fixation of the type species by subsequent designation 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 publication date and page number of the subsequent designation. Some genera, as first described and named, included no mentioned species (for such genera established after 1930, see below); these necessarily lack a type species until a date subsequent to that of the original publication when one or more species is assigned to such a genus. If only a single species is thus assigned, it automatically becomes the type species. Of course, the first publication containing assignment of species to the genus that originally lacked any included species is the one concerned in fixation of the type species, and if this publication names two or more species as belonging to the genus but did not designate a type species, then a later SD designation is necessary. Examples of the use of SD as employed in the *Treatise* follow.

Hexagonaria GURICH, 1896, p. 171 [**Cyathophyllum hexagonum* GOLDFUSS, 1826, p. 61; SD LANG, SMITH, & THOMAS, 1940, p. 69].
Mesephemera HANDLIRSCH, 1906, p. 600 [**Tineites lithophilus* GERMAR, 1842, p. 88; SD CARPENTER, herein].

Another mode of fixing the type species of a genus is action of the International Commission of Zoological Nomenclature using its plenary powers. Definition in this way may set aside application of the *Code* so as to arrive at a decision considered to be in the best interest of continuity and stability of zoological nomenclature. When made, it is binding and commonly is cited in the *Treatise* by the letters ICZN, accompanied by the date of announced decision and reference to the appropriate numbered opinion.

Subsequent designation of a type species is admissible only for genera established prior

to 1931. A new genus-group name established after 1930 and not accompanied by fixation of a type species through original designation or original indication is invalid (*Code*, Article 13b). Effort of a subsequent author to validate such a name by subsequent designation of a type species constitutes an original publication making the name available under authorship and date of the subsequent author.

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 two or more distinct taxonomic units, however, it is necessary to differentiate such homonyms. 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, *Callophora* HALL, 1852, introduced for Paleozoic trepostomate bryozoans, is invalid because Gray in 1848 published the same name for Cretaceous-to-Holocene cheilostomate bryozoans. Bassler in 1911 introduced the new name *Hallophora* to replace Hall's homonym. The *Treatise* style of entry is given below.

Hallophora BASSLER, 1911, p. 325, *nom. nov. pro Callophora* HALL, 1852, p. 144, *non* GRAY, 1848.

In like manner, a replacement generic name that is needed may be introduced in the *Treatise* (even though first publication of generic names otherwise in this work is generally avoided). An exact bibliographic reference must be given for the replaced name as in the following example.

Mysterium DE LAUBENFELS, herein, *nom. nov. pro Mysterium* SCHRAMMEN, 1936, p. 183, *non* ROGER, 1862 [**Mysterium porosum* SCHRAMMEN, 1936, p. 183; OD].

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

Synonymous 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 that 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 synonymous homonyms. In the *Treatise* the junior of one of these is indicated by the abbreviation *jr. syn. hom.*

Not infrequently, identical family-group names are published as new names by different authors, the author of the name that was introduced last 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, being based on the same type genus, are nomenclatorial homonyms. They are also synonyms. Wherever encountered, such synonymous homonyms are distinguished in the *Treatise* as in dealing with generic names.

A rare but special case of homonymy exists when identical family names are formed from generic names having the same stem but differing in their endings. An example is the family name Scutellidae RICHTER & RICHTER, 1925, based on *Scutellum* PUSCH, 1833, a trilobite. This name is a junior homonym of Scutellidae GRAY, 1825, based on the echinoid genus *Scutella* LAMARCK, 1816. The name of the trilobite family was later changed to Scutelluidae (ICZN, Opinion 1004, 1974).

SYNONYMS

In the *Treatise*, citation of synonyms is given immediately after the record of the type species. If two or more synonyms of differing date are recognized, these are ar-

ranged in chronological order. Objective synonyms are indicated by accompanying designation obj., others being understood to constitute subjective synonyms, of which the types are also indicated. Examples showing *Treatise* style in listing synonyms follow.

Mackenziophyllum PEDDER, 1971, p. 48 [**M. insolitum*; OD] [= *Zonastraea* TSYGANKO in SPASSKIY, KRAVTSOV, & TSYGANKO, 1971, p. 85, *nom. nud.*; *Zonastraea* TSYGANKO, 1972, p. 21 (type, *Z. graciosa*, OD)].

Kodonophyllum WEDEKIND, 1927, p. 34 [**Streptelasma Milne-Edwardsi* DYBOWSKI, 1873, p. 409; OD; = *Madrepora truncata* LINNE, 1758, p. 795, see SMITH & TREMBERTH, 1929, p. 368] [= *Patrophontes* LANG & SMITH, 1927, p. 456 (type, *Madrepora truncata* LINNE, 1758, p. 795, OD); *Codonophyllum* LANG, SMITH, & THOMAS, 1940, p. 39, obj.].

Some junior synonyms of either the objective or the subjective sort may be preferred over senior synonyms whenever uniformity and continuity of nomenclature are served by retaining a widely used but technically rejectable name for a genus. This requires action of the ICZN, which may use its plenary powers to set aside the unwanted name, validate the wanted one, and place the concerned names on appropriate official lists.

OTHER EDITORIAL MATTERS

BIOGEOGRAPHY

Purists, *Treatise* editors among them, would like nothing better than a stable world with a stable geography that makes possible a stable biogeographical classification. Global events of the past few years have shown how rapidly geography can change, and in all likelihood we have not seen the last of such change as new, so-called republics continue to spring up all over the globe. One expects confusion among readers in the future as they try to decipher such geographical terms as U.S.S.R., Yugoslavia, or Ceylon. Such confusion is unavoidable, as books must be completed and published at some real time. Libraries would be limited indeed if publication were always to be delayed until the political world had settled down.

Insofar as possible, trilobite genera from the former Soviet Union are referred to the

republics in which they are found, but in some instances other kinds of information may be given instead. In addition, such terms as central Europe and western Europe are likely to mean different things to different people. Some imprecision is introduced by the use of all such terms, of course, but it is probably no greater than the imprecision that stems from the fact that the work of paleontology is not yet finished, and the geographical ranges of many genera are imperfectly known.

NAMES OF AUTHORS: TRANSLATION AND TRANSLITERATION

Chinese scientists have become increasingly active in systematic paleontology in the past two decades. Chinese names cause anguish among English-language bibliographers for two reasons. First, no scheme exists for one-to-one transliteration of Chinese characters into roman letters. Thus, a Chinese author may change the roman-letter spelling of his name from one publication to another. For example, the name Chang, the most common family name in the world reportedly held by some one billion people, might also be spelled Zhang. The principal purpose of a bibliography is to provide the reader with entry into the literature. Quite arbitrarily, therefore, in the interest of information retrieval, the *Treatise* editorial staff has decided to retain the roman spelling that a Chinese author has used in each of his publications rather than attempting to adopt a common spelling of an author's name to be used in all citations of his work. It is entirely possible, therefore, that the publications of a Chinese author may be listed in more than one place under more than one name in the bibliography.

Second, most but by no means all Chinese list their family name first followed by given names. People with Chinese names who study in the West, however, often reverse the order, putting the family name last as is the Western custom. Thus, for example, Dr. Yi-Maw Chang, recently of the staff of the Pa-

leontological Institute, was Chang Yi-Maw when he lived in Taiwan. When he came to America, he became Yi-Maw Chang, and his subsequent bibliographic citations are listed as Chang, Yi-Maw. The *Treatise* staff has adopted the convention of listing family names first, inserting a comma, and following this with given names or initials. We do this even for Chinese authors who have not reversed their names in the Western fashion.

Several systems exist for transliterating the Cyrillic alphabet into the roman alphabet. We have adopted the American Library Association/Library of Congress romanization table for Russian and other languages using the Cyrillic alphabet.

MATTERS SPECIFIC TO THIS VOLUME

This volume departs from previous volumes of the *Treatise* in several important respects. Stratigraphical ranges of genera are typically given as zones rather than exclusively as universal stage names. In order to represent these zones clearly, we have used *or* in place of the solidus (/) and *to* in place of the en-dash (-). Replacing the dash with *to* eliminates ambiguity in zones with hyphenated names. This use of refined stratigraphy has obviated the traditional *Treatise* range charts of genera and higher taxa. In its place is presented a detailed chart of Cambrian stratigraphy that correlates stage names and zones in numerous geological regions. Finally, unlike previous volumes of the *Treatise*, the classification of the trilobites is presented here in preliminary form. Publication of a final classification must await the completion of the research that is underway for preparation of future volumes on the trilobites.

ACKNOWLEDGMENTS

The Paleontological Institute's Assistant Editor for Text, Elizabeth Brosius, and the Assistant Editor for Illustrations, Jane Kerns, have faced admirably the formidable task of moving the volume through the various

stages of editing and into production. In this they have been ably assisted by members of the other editorial team, Jill Hardesty and Karen Renteria; by Jack Keim with photography; and by Jean Burgess with word processing. Jill Krebs, the remaining member of the Paleontological Institute staff, is involved with preparation of PaleoBank, the paleontological database for future *Treatise* volumes, and has not been closely involved with the trilobite *Treatise*.

This editorial preface and other, recent ones are extensive revisions of the prefaces prepared for previous *Treatise* volumes by former editors, including the late Raymond C. Moore, the late Curt Teichert, and Richard A. Robison. I am indebted to them for preparing earlier prefaces and for the leadership they have provided in bringing the *Treatise* project to its present status.

Finally, I am pleased to extend on behalf of the members of the staff of the Paleontological Institute, both past and present, our most sincere thanks to Professor H. B. Whittington for the unwavering scholarship, dedication to the task, and scrupulous attention to detail that have marked his involvement with the project from the outset and, indeed, his entire career as a specialist on the Trilobita.

REFERENCES

- Ride, W. D. L., C. W. Sabrosky, G. Bernardi, and R. V. Melville, eds. 1985. International Code of Zoological Nomenclature. International Trust for Zoological Nomenclature. University of California Press. Berkeley & Los Angeles. xx + 338 p.

Roger L. Kaesler
Lawrence, Kansas
July 15, 1997

STRATIGRAPHIC DIVISIONS

The major divisions of the geological time scale are reasonably well established throughout the world, but minor divisions (e.g., substages, stages, and subseries) are more likely to be provincial in application. The stratigraphical units listed here represent an authoritative version of the stratigraphic column for all taxonomic work relating to revision of Part O. They are adapted from the International Union of Geological Sciences 1989 Global Stratigraphic Chart, compiled by J. W. Cowie and M. G. Bassett.

Paleozoic Erathem

Permian System

- Upper Permian Series
- Lower Permian Series

Carboniferous System

- Upper Carboniferous Subsystem
 - Stephanian Series
 - Westphalian Series
 - Namurian Series (part)
- Lower Carboniferous Subsystem
 - Namurian Series (part)
 - Visean Series
 - Tournaisian Series

Devonian System

- Upper Devonian Series
- Middle Devonian Series
- Lower Devonian Series

Silurian System

- Pridoli Series
- Ludlow Series
- Wenlock Series
- Llandovery Series

Ordovician System

- Upper Ordovician Subsystem
 - Cincinnatian Series
 - Champlainian Series (part)
- Lower Ordovician Subsystem
 - Champlainian Series (part)
 - Canadian Series

Cambrian System

- Lower Cambrian Series
- Middle Cambrian Series
- Upper Cambrian Series

AUTHOR'S PREFACE

The introduction is intended to correct and amplify the general description given by Harrington in the first edition of *Treatise*, Part O (in Moore, 1959, p. 38–117), in the light of research published by the end of 1993. Historical matters such as early studies and the development of ideas on classification are omitted. Particularly the discovery and description of new silicified material have greatly added to knowledge of exoskeletal morphology, as the section on this subject shows. In the following section new and earlier information on the limbs is summarized, before considering possible musculature, mode of walking, and sensory devices. The publication of Memoir 67 on paleoecology by the Geological Society of America in 1957 and the publication in 1955 of Professor A. Seilacher's studies on trace fossils attributed to trilobites stimulated work in these fields. In conjunction with the increasing knowledge of sedimentary rocks and diagenetic processes, much research has been published on matters unrepresented in the 1959 edition. Other new studies have resulted in plausible reconstructions of Paleozoic world geography and enabled fresh thinking on faunal realms. The sections on mode of life, habits, occurrence, and use of numerical and cladistic methods are no more than an introduction to these subjects by reference to examples in which additional works are listed.

I am indebted to Dr. Euan N. K. Clarkson, Edinburgh University, for kindly contributing the account of the trilobite eye and for his collaboration in describing coaptative structures. Professor Brian D. E. Chatterton, University of Alberta, and Dr. Stephen E. Speyer have provided an entirely new account of ontogeny; Dr. Richard A. Fortey, Natural History Museum, London, has provided the classification to be used in this revision and in collaboration with Dr. R. M. Owens, National Museum of Wales, an account of evolution. Dr. Nadine V. Wilmot collaborated in describing the microstructure

of the exoskeleton and provided the originals of Figures 70 and 71.

Throughout the text, when considering a specific exoskeletal structure, reference is made to structures found in related taxa or the affinities of a particular genus are indicated. As Fortey points out in his discussion of classification, many family-group names are long established, widely understood, and accepted. Such familiar names are used here to indicate relationship, either formally or informally. For example, *Cheirurus* and related genera may be referred to as Cheiruroidea (the superfamily), Cheiruridae (the family), or Cheirurinae (the subfamily). Informally, a superfamily group may be referred to as cheiruroids or a family group as cheirurids. Such informal terms as cheirurine or cheiruride lack precise meaning and will not be used. At a higher taxonomic level there is little or no agreement on natural groups, and a new, as yet incomplete, grouping into orders and suborders is outlined below by Fortey. In the text, names of these ordinal and subordinal taxa are used formally to indicate that it is the group defined in this new arrangement that is being referred to—i.e., as Olenellina (the suborder) or Proetida (the order). This procedure means that a suborder composed of a single superfamily, for example Eodiscina or Calymenina, may be referred to also as eodiscoids or calymenoids, but this is not the case with suborders that include more than one superfamily. For example, the suborder Agnostina is not embraced by the informal term agnostoid, which refers only to the superfamily Agnostoidea.

In the preparation of this introduction I have benefited from discussions and correspondence with Drs. W. T. Dean, R. A. Fortey, C. P. Hughes, P. D. Lane, R. M. Owens, A. W. A. Rushton, J. H. Shergold, D. J. Siveter, and A. T. Thomas, but responsibility for its content remains with me. I express my gratitude to the Leverhulme Trust for their support of my research and the

Department of Earth Sciences, University of Cambridge, for the provision of facilities in the preparation of this account, including all the new figures. Mrs. Sandra J. Last has put much skill and effort into the preparation of the text.

Authorship of the systematic sections is indicated, the diagnoses of the class Trilobita, orders, and suborders being by R. A. Fortey and me. I am indebted to these authors for their willingness to contribute and for their patience and promptness in answering queries and giving additional information at the editorial stage. A grant from *Treatise* funds enabled Professor W. T. Chang to substitute

photographs for drawings of Redlichiina. Most helpful has been Dr. J. H. Shergold's willingness to provide the section on Cambrian correlation. Work began on this revision in 1980, and two further volumes on systematics are proposed. I am happy, now that Volume 1 is completed, to pass the reins of coordinating authorship into the hands of Dr. R. A. Fortey and to wish him well in a daunting task.

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England

REPOSITORIES AND THEIR ABBREVIATIONS

Abbreviations and locations for museums and institutions holding type material, which are used throughout the systematic sections of this volume, are listed below.

AGSO: Australian Geological Survey Organisation (formerly Bureau of Mineral Resources, BMR), Canberra, Australia

AMF: Australian Museum, Sydney, Australia

AMNH: American Museum of Natural History, New York, USA

ANU: Australian National University, Canberra, Australia

AUGD: South Australian Museum, Adelaide, Australia

BAF CB: Universidad de Buenos Aires, Departamento de Biología, Buenos Aires, Argentina

BGS: British Geological Survey (formerly the Geological Survey and Museum, GSM), London, U.K.

BGU: Geological Museum, Buryat Geological Board, Ulan-Ude, Russia

BMNH: British Museum (Natural History), London, U.K. (now Natural History Museum, London, NHM)

BU: Department of Geology, Birmingham University, Birmingham, U.K.

CAGC: Chinese Academy of Geological Sciences, Beijing, China

CIGMR: Chengdu Institute of Geology and Mineral Resources, Chengdu, Sichuan, China

CNIGR: Central Scientific Research Geological Exploration Museum (Chernyshev Museum), St. Petersburg, Russia

CSGM: Central Siberian Geological Museum, United Institute of Geology, Geophysics and Mineralogy, Siberian Branch of the Russian Academy of Sciences, Novosibirsk, Russia

CU: Cornell University, Ithaca, New York

CUGB: China University of Geosciences, Beijing, China

GGU: Grønlands Geologiske Undersøgelse (Geological Survey of Greenland), Copenhagen, Denmark

GIN: Geological Institute, Academy of Sciences, Moscow, Russia

GIT: Geological Institute of Tallinn, Estonia

GMAN: Geological Museum, Geological Institute, Kazakhstan Academy of Sciences, Alma Ata, Kazakhstan

GMU: Geological Museum, Ukrainian Academy of Sciences, Kiev, Russia

GPCN: Paleontological Division, Museum of West Siberian Geological Production Company, Novosibirsk, Russia

GSC: Geological Survey of Canada, Ottawa, Ontario, Canada

GSE: Institute of Geological Sciences, Edinburgh, Scotland

GSI: Geological Survey of India, Calcutta, India

HBG: Hunan Provincial Bureau of Geology, Changsha, Hunan, China

HMB: Museum for Natural Science, Humboldt-University, Berlin, Germany

ICS: Institute for Cambrian Studies, Boulder, Colorado, USA

IGGN: see CSGM

IGiG: Institute of Geology and Geophysics, Uzbekistan Academy of Sciences, Tashkent, Uzbekistan

IGR: Institut of Geology, University of Rennes, France

IGUW: Institute of Geology, University of Warsaw, Warsaw, Poland

IPM: Institut de Paléontologie, Museum National d'Histoire Naturelle, Paris, France

IRScNB: Institut Royal des Sciences Naturelle de Belgique, Brussels, Belgium

KazIMS: Kazakhstan Scientific Research Institute of Mineral Resources, Alma Ata, Kazakhstan

- KUMIP:** Museum of Natural History, University of Kansas, Division of Invertebrate Paleontology, Lawrence, Kansas, USA
- KGC:** Kunming Geological School, Kunming, China
- LACMIP:** Los Angeles County Museum, Los Angeles, California, USA
- LGSB:** Laboratory of Geology, Sorbonne, Paris, France
- LO:** Geological Institute Museum, Department of Historical Geology, University of Lund, Lund, Sweden
- LU:** Department of Geology and Mineralogy, Laval University, Montreal, Quebec, Canada
- MCZ:** Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA
- MGUH:** Geological Museum, Copenhagen University, Copenhagen, Denmark
- MHN:** Museo de Historia Natural de Argentina, Mendoza, Argentina
- MLU:** Museum für Mitteldeutsche Erdgeschichte, Martin-Luther Universität, Halle, Germany
- MMG:** Museum of the Ministry of Geology, Tashkent, Uzbekistan
- MMK:** Geological Museum, Copenhagen University, Copenhagen, Denmark
- MNHN:** Institut de Paléontologie, Museum National d'Histoire Naturelle, Paris, France
- MWSGPC:** Paleontological Division, Museum of West Siberian Geological Production Company, Novokuznetsk, Russia
- NIGMR:** Nanjing Institute of Geology and Mineral Resources, Nanjing, China
- NIGP:** Nanjing Institute of Geology and Palaeontology, Academia Sinica, Nanjing, China
- NMING:** National Museum of Ireland, Dublin, Ireland
- NMP:** Národní Muzeum of Natural History, Prague, Czech Republic
- NMVP:** National Museum of Victoria, Melbourne, Australia
- NMW:** National Museum of Wales, Cardiff, U.K.
- NYSM:** New York State Museum, Albany, New York, U.S.A.
- OMR:** Regional Museum of B. Horák, Rokycany, Czech Republic
- OUM:** Oxford University Museum, Oxford, U.K.
- PIN:** Paleontological Institute, Russian Academy of Sciences, Moscow, Russia
- PIW:** Paleontological Institute, Würzburg University, Würzburg, Germany
- PM:** Palaeontological Museum, Uppsala University, Uppsala, Sweden
- PMO:** Palaeontological Museum, University of Oslo, Oslo, Norway
- PU:** Department of Geology, Princeton University, Princeton, New Jersey
- RM:** Swedish Museum of Natural History, Stockholm, Sweden
- SAMA:** South Australian Museum, Adelaide, Australia
- SG:** Museo di Paleontologia, Servizio Geologico d'Italia, Rome, Italy
- SGM:** Geological Survey of Morocco (Service Geologique du Maroc), Rabat, Morocco
- SGU:** Swedish Geological Survey, Uppsala, Sweden
- SM:** Sedgwick Museum, Department of Earth Sciences, University of Cambridge, Cambridge, U.K.
- SMF:** Senckenberg Museum, Frankfurt am Main, Germany
- SMNH:** Shanghai Museum of Natural History, Shanghai, China
- SNIIGGIMS:** see CSGM
- TsGM:** Central Scientific and Geological Museum, St. Petersburg, Russia
- UBA:** Department of Geology, University of Buenos Aires, Buenos Aires, Argentina
- UBC:** Department of Geology, University of British Columbia, Vancouver, British Columbia, Canada
- UCR:** Department of Earth Sciences, University of California, Riverside, California, U.S.A.
- UM:** Department of Geology, University of Montpellier, Montpellier, France
- UMC:** Department of Geology, University of Missouri-Columbia, Columbia, Missouri, USA
- UMU:** Geological-Paleontological Museum, Münster University, Münster, Germany
- UMUT:** University Museum, University of Tokyo, Tokyo, Japan
- UP:** Museum of Paleontology, University of Pisa, Pisa, Italy
- UQF:** Department of Geology, University of Queensland, Brisbane, Australia
- USNM:** U.S. National Museum, Washington, D.C., USA
- UTGD:** Department of Geology, University of Tasmania, Hobart, Tasmania
- VNIGNI:** All Union Scientific Institute of Oil Prospecting, Moscow, Russia
- XIGMR:** Museum of the Xinjiang Institute of Geology and Mineral Resources, Geological Bureau of Xinjiang Uygur Autonomous Region, Urumqi, China
- YIGS:** Yunnan Institute of Geological Sciences, Kunming, Yunnan, China
- YPM:** Yale University, Peabody Museum of Natural History, New Haven, Connecticut, USA
- YPM(PU):** Yale University (Princeton University specimens), Peabody Museum of Natural History, New Haven, Connecticut, USA
- ZSGU:** West Siberian Research Institute for Geology, Geography and Mineral Resources, Novokuznetsk, Russia