



This volume is dedicated to
Raymond Cecil Moore

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Founder of the Treatise on Invertebrate Paleontology

TREATISE ON INVERTEBRATE PALEONTOLOGY

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Part A

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EDITORIAL PREFACE

Preparation of this volume was postponed until most volumes in the series were either published or well on their way toward completion. Initial organization and assignment of authors for Part A began about 1968 under the direction of CURT TEICHERT. Some authors soon submitted manuscripts, but for a variety of reasons, preparation of other manuscripts was delayed. With the death of R. C. MOORE in 1974, other *Treatise* responsibilities required TEICHERT's attention, and major responsibility for the Part A project was transferred to R. A. ROBISON for completion.

As originally conceived, this volume was intended to include three major parts: 1) a general chapter on fossilization, 2) discussions of the evolution and geographic distribution of invertebrate faunas, and 3) stratigraphic distribution charts compiled for all invertebrate groups covered by the *Treatise*. The first part was assigned to Prof. A. H. MÜLLER, the second part was

subdivided with each Phanerozoic system and the Precambrian being assigned to either one or two authors, and work on the third part was begun by *Treatise* staff members.

Because some authors, again for a variety of reasons, were unable to complete original assignments, a few replacements were made during 1974 and 1975. At the same time it was decided that publication of the stratigraphic range charts had become impractical, partly because delays had made compilations from the earliest *Treatise* volumes out-of-date, and partly because of lack of information for some invertebrates covered in a few first-edition volumes still in preparation. Therefore, all authors dealing with evolution and biogeography were asked to add a discussion of biostratigraphy to their respective chapters, a request was made for updating of those manuscripts already received, and the stratigraphic range charts were abandoned for Part A. Response was

positive, and for this the editors express appreciation, particularly to those authors who completed their assignments promptly and were patient and cooperative when subsequent revisions were solicited.

The chapter on the Precambrian differs from other chapters in this volume by the addition of a section with systematic descriptions of metazoans as well as comprehensive generic lists of other fossils. Some Ediacaran taxa were assigned to the Lower Cambrian in previous *Treatise* volumes, but an assignment to the Upper Precambrian is now generally accepted. Other recently described taxa are unrecorded in the *Treatise*. Therefore, the updating and assembly of these descriptions and lists should be of value to many readers. Features of style in zoological nomenclature that apply to these Precambrian taxa have been discussed in the prefaces of other published *Treatise* parts.

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 year of publication of each individual part. Such work has value in providing a most useful summary of the collective results of multitudinous investigations and thus constitutes 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 is yielding needed foundation for future research.

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 was judged desirable to print and distribute each segment as soon as possible after it is ready for press. Pages in each part bear the assigned index letter joined with numbers beginning with 1 and running consecutively to the end of the part. In numerous cases materials for individual parts were so voluminous that these parts had to be published in two or even three volumes. In such cases, pagination is continuous through successive volumes.

A generous grant of \$35,000 was made in 1948 by the Geological Society of America for initial work in preparing *Treatise* illustrations. Additional grants were made by The Geological Society of America in 1971 (\$6,200), 1972 (\$6,000), \$7,000 each year for 1973 and 1974, and \$20,000 each for 1975-1978. Administration of expenditures has been in charge of the editors and most of the work by photographers and artists has been done under their direction at the University of Kansas, but sizable parts of this program have also been carried forward in Washington, London, Ottawa, and many other places.

In December, 1959, the National Science Foundation of the United States, through its Division of Biological and Medical Sciences and the Program Director for Systematic Biology, made a grant in the amount of \$210,000 for the purpose of aiding the completion of yet-unpublished volumes of the *Treatise*. Payment of this sum was provided to be made in installments distributed over a five-year period, with administration of disbursements handled by the University of Kansas. An additional grant (No. GB 4544) of \$102,800 was made by the National Science Foundation in January, 1966, for the two-year period 1966-1967, and this was extended for the calendar year 1968 by payment of \$25,700 in October, 1967. This grant was extended further by payments of \$57,800 in 1968 for calendar year 1969, and \$66,000 each for calendar years 1970-1972. For the years 1973-1977 grants totaled \$197,400. These funds were used primarily to maintain editorial operations at the University of Kansas and to provide assistance to authors needed in preparation of manuscripts and illustrations. Grateful acknowledgement to the Foundation is expressed on

behalf of the societies sponsoring the *Treatise*, the University of Kansas, and innumer-

able individuals benefited by the *Treatise* project.

ABBREVIATIONS

Abbreviations used in this division of the *Treatise*, except for those in the references or peculiar to specific figures, are explained in the following alphabetically arranged list.

aff. , <i>affinis</i> (related to)	IGC , International Geological Congress	OD , original designation
Afr. , Africa, -an	indet. , <i>indeterminata</i> (indeterminate)	Ord. , Ordovician
Am. , America, -an	INQUA , International Union for Quaternary Research	p. , page(s)
approx. , approximately	int. , internal	Penn. , Pennsylvania
Arg. , Argentina	Internat. , International	Perm. , Permian
auctt. , <i>auctorum</i> (of authors)	I.U.G.S. , International Union of Geological Sciences	pers. commun. , personal communication
B.P. , before present	Jour. , Journal	pl. , plate
by , billion years	K. , kaiserlich, königlich	Precam. , Precambrian
C , centigrade	kg , kilogram(s)	R. , river
C. , Central	km , kilometer(s)	reconstr. , reconstruction
ca. , <i>circa</i> (about)	L. , Lower	reg. , region
Can. , Canada	Loc. , locality	Repts. , Reports
CCD , carbonate compensation depth	low. , lower	S. , South, southern
cf. , <i>confer</i> (compare)	M , monotypy, monotype	SE , southeast
Charn. , Charnian	M. , Middle	ser. , series
cm , centimeter(s); cm³ , cubic centimeter(s)	m , meter(s)	Sib. , Siberia
Co. , Company	Ma , mega-annum, unit of years multiplied by 10 ⁶ , measured from 1950 A.D. pastward	Sil. , Silurian
Coll. , Collection	Miss. , Mississippian	s.l. , <i>sensu lato</i> (in the wide sense, broadly defined)
Congr. , Congress	mm , millimeters(s); mm² , square millimeter(s)	sp. , species
Dept. , Department	Mt. , Mount	Spec. , Special
Dev. , Devonian	Mus. , Museum	sp. nov. , new species
diagramm. , diagrammatic	my , million years	sq km , square kilometer(s)
DSDP , Deep Sea Drilling Project	mya , million years ago	s.s. , <i>sensu stricto</i> (in the strict sense, narrowly defined)
E. , East, eastern	MYBP , million years before present	SSR , Soviet Socialist Republic
ed. , editor	N. , North, northern	SW , southwest
e.g. , <i>exempli gratia</i> (for example)	n(.) , new	Swed. , Sweden
emend. , <i>emendatus</i> (-a) (emended, emendation)	N.Car. , North Carolina	Trias. , Triassic
Eng. , England	no. , number	U. , Upper
et al. , <i>et alii</i> (and others, persons)	nom. nud. , <i>nomen nudum</i> (naked name)	Univ. , University
etc. , <i>et cetera</i> (and others, objects)	nom. transl. , <i>nomen translatus</i> (transferred name)	unpub. , unpublished
et seq. , <i>et sequens</i> (-tes) (and those that follow)	nom. van. , <i>nomen vanum</i> (vain, void name)	up. , upper
fig. , figure(s)	nr. , near	USA , United States of America
gen. , genus	NW , northwest	U.S.S.R. , USSR , Union of Soviet Socialist Republics
Geol. , Geology, Geological	obj. syn. , objective synonym	v. , volume
gm , gram		Vend. , Vendian
Gr. , Group		vs. , versus
i.e. , <i>id est</i> (that is)		W. , West, western
		Yudom. , Yudomian

REFERENCES TO LITERATURE

Each part of the *Treatise* is accompanied by a list, or lists, of references to the paleontological literature. In *Treatise* parts published in the 1950's and early 1960's, these lists were highly selective, consisting primarily of recent and comprehensive monographs, but also including some important older works. In time, however, *Treatise* authors and readers pressed for more exhaustive documentation, and for volumes published from about 1965 the aim has been to provide documentation, complete with author, publication year, and page number, for all publications to which reference is made anywhere in the text.

The following is a statement of the full names of serial publications which are cited in abbreviated form in the lists of references in the present volume. The information thus provided should be useful in library research work. The list is alphabetized according to the serial titles which were employed at the time of original publication. Those following in parentheses are those under

which the publication may be found currently in the *Union List of Serials*, the United States Library of Congress listing, and most library card catalogues. The names of serials published in Cyrillic are transliterated; in the reference lists these titles, which may be abbreviated, are accompanied by transliterated authors' names and titles, with English translation of the title. The place of publication is added (if not included in the serial title).

The method of transliterating Cyrillic letters that is adopted as "official" in the *Treatise* is that suggested by the Geographical Society of London and the U.S. Board on Geographic Names. It follows that names of some Russian authors in transliterated form derived in this way differ from other forms, possibly including one used by the author himself. In *Treatise* reference lists the alternative (unaccepted) form is given enclosed by square brackets (e.g., Chernyshev [Tschernyschew], T.N.).

List of Serial Publications

- Académie Impériale des Sciences, St. Pétersbourg (Akademiya Nauk, SSSR, Leningrad), Mémoires.
 Académie Polonaise des Sciences (Polska Akademia Umiejętności), Bulletin. Warsaw.
 Académie Royale de Belgique, Classe des Sciences, Bulletins; Mémoires. Brussels.
 Académie des Sciences, Agriculture, Commerce, Belles-lettres et Arts du Département de la Somme (Académie des Sciences, des Lettres, et des Arts d'Amiens), Mémoires.
 Académie des Sciences de Paris, Comptes-rendus.
 Acta Geologica Polonica. Warsaw.
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 Acta Palaeontologica Sinica (Ku Sheng Wu Hsüeh Pao). Peking.
 Acta Universitatis Stockholmiensis (Stockholm Contributions in Geology).
 Akademie der Wissenschaften in Göttingen, mathematisch-physikalische Klasse, Nachrichten.
 Akademie der Wissenschaften und der Literatur zu Mainz, mathematisch-naturwissenschaftliche Klasse, Abhandlungen. Wiesbaden.
 [K.] Akademie der Wissenschaften zu Wien, mathematisch-naturwissenschaftliche Klasse, Anzeiger; Denkschriften; Sitzungsberichte. Vienna.
 Akademiya Nauk Gruzinskoi SSR, Soobshcheniya. Tiflis.
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SOURCES OF ILLUSTRATIONS

At the end of each figure caption, the name of the author of the illustration and the date of publication are given, reference being made to publications cited in the reference lists. Although original sources do not always produce the best illustrations, they are, historically speaking, definitive and are commonly selected by *Treatise* authors. Previously unpublished illustrations are indicated by the name of the author and the letter n ("new"). Repository and museum catalogue numbers are given where appropriate.

STRATIGRAPHIC DIVISIONS

As commonly cited in the *Treatise*, classification of rocks forming the geologic column is reasonably uniform and firm throughout most of the world as regards major divisions (e.g., series, systems, and rocks representing eras), but it may be variable and unfirm as regards minor divisions (e.g., substages, stages, and subseries), which tend to be provincial in application. Users of the *Treatise* have suggested the desirability of publishing reference lists showing the stratigraphic arrangement of at least the most commonly cited divisions. Accordingly, a tabulation of European and North American units, which generally follows usage by authors of this volume, is given here. Some of the minor divisions are applicable also to other continents.

Generally Recognized Divisions of Geologic Column

EUROPE	NORTH AMERICA
CENOZOIC ERATHEM	CENOZOIC ERATHEM
QUATERNARY SYSTEM	QUATERNARY SYSTEM
Holocene Series (Recent)	Holocene Series (Recent)
Pleistocene Series	Pleistocene Series
TERTIARY SYSTEM¹	TERTIARY SYSTEM^{1, 2}
Pliocene Series	Pliocene Series
Astian-Piacenzian Stage	Upper Pliocene Stage
Tabanian-Zanklian Stage	Middle Pliocene Stage
Miocene Series	Lower Pliocene Stage
Messinian Stage	Miocene Series
Tortonian Stage	Clovellian Stage
Serravallian Stage	Ducklakean Stage
Langhian Stage	Napoleonvillean Stage
Burdigalian Stage	Anahaucan Stage
Aquitanian Stage	Oligocene Series
Oligocene Series	Chackasawayan Stage
Chattian Stage	Vicksburgian Stage
Rupelian Stage	Eocene Series
Lattorfian Stage	Jacksonian Stage
Eocene Series	Claibornian Stage
Wemmelian Stage	Sabinian Stage
Lutetian Stage	Paleocene Series
Cuisian Stage	Midwayan Stage
Paleocene Series	
Ilerdian Stage	
Thanetian Stage + Montian	
Danian Stage	
MESOZOIC ERATHEM	MESOZOIC ERATHEM
CRETACEOUS SYSTEM	CRETACEOUS SYSTEM
Upper Cretaceous Series	Upper Cretaceous Series
Maastrichtian Stage	Maastrichtian Stage
Campanian Stage	Campanian Stage
Santonian Stage	Santonian Stage
Coniacian Stage	Coniacian Stage
Turonian Stage	Turonian Stage
Cenomanian Stage	Cenomanian Stage
Lower Cretaceous Series	Lower Cretaceous Series
Albian Stage	Albian Stage
Aptian Stage	Aptian Stage
Barremian Stage	Barremian Stage

Hauterivian Stage
Valanginian Stage
Berriasian Stage

JURASSIC SYSTEM

Upper Jurassic Series
Tithonian Stage
Kimmeridgian Stage
Oxfordian Stage
Middle Jurassic Series
Callovian Stage³
Bathonian Stage
Bajocian Stage⁴
Lower Jurassic Series (Liassic)
Toarcian Stage
Pliensbachian Stage
Sinemurian Stage
Hettangian Stage

TRIASSIC SYSTEM

Upper Triassic Series
Rhaetian Stage
Norian Stage
Carnian Stage
Middle Triassic Series
Ladinian Stage
Anisian Stage
Lower Triassic Series

Scythian Stage

PALEOZOIC ERATHEM

PERMIAN SYSTEM

Upper Permian Series
Tatarian Stage
Kazanian Stage⁵
Lower Permian Series
Artinskian Stage⁵
Sakmarian Stage
Asselian Stage

CARBONIFEROUS SYSTEM

Silesian Subsystem
Stephanian Series³
Westphalian Series⁶
Namurian Series⁶
Dinantian Subsystem
Viscan Series⁶
Tournaisian Series⁶

Hauterivian Stage
Valanginian Stage
Berriasian Stage

JURASSIC SYSTEM

Upper Jurassic Series
Portlandian Stage
Kimmeridgian Stage
Oxfordian Stage
Middle Jurassic Series
Callovian Stage³
Bathonian Stage
Bajocian Stage⁴
Lower Jurassic Series (Liassic)
Toarcian Stage
Pliensbachian Stage
Sinemurian Stage
Hettangian Stage

TRIASSIC SYSTEM

Upper Triassic Series
Rhaetian Stage
Norian Stage
Carnian Stage
Middle Triassic Series
Ladinian Stage
Anisian Stage
Lower Triassic Series (Scythian)
Spathian Stage
Smithian Stage
Dienerian Stage
Griesbachian Stage

PALEOZOIC ERATHEM

PERMIAN SYSTEM

Upper Permian Series
Ochoan Stage
Guadalupian Stage
Lower Permian Series
Leonardian Stage
Wolfcampian Stage

PENNSYLVANIAN SYSTEM

Virgilian Series⁶
Missourian Series⁶
Desmoinesian Series⁶
Atokan Series⁶
Morrowan Series⁶
MISSISSIPPIAN SYSTEM
Chesterian Series⁶
Meramecian Series⁶
Osagian Series⁶
Kinderhookian Series⁶

DEVONIAN SYSTEM

Upper Devonian Series

Famennian Stage

Frasnian Stage

Middle Devonian Series

Givetian Stage

Eifelian Stage

Lower Devonian Series

Emsian Stage

Siegenian Stage

Gedinnian Stage

SILURIAN SYSTEM

Pridolian Series

Ludlovian Series

Wenlockian Series

Llandoveryian Series

ORDOVICIAN SYSTEM

Ashgillian Series

Caradocian Series

Llandeilian Series

Llanvirnian Series

Arenigian Series

Tremadocian Series⁸

CAMBRIAN SYSTEM

Upper Cambrian Series (Merioneth)

Middle Cambrian Series (St. David's)

Lower Cambrian Series (Comley)

ROCKS OF PRECAMBRIAN ERAS

PROTEROZOIC ERATHEM

Dalradian, Eocambrian,

Vendian, Riphean,

and equivalents

DEVONIAN SYSTEM

Chautauquan Series⁷

Bradfordian Stage⁷

Cassadagan Stage⁷

Senecan Series⁷

Cohocton Stage⁷

Fingerlakesian Stage⁷

Erian Series⁷

Taghanican Stage⁷

Tioughniogan Stage⁷

Cazenovian Stage⁷

Ulsterian Series

Onesquethawan Stage⁷

Deerparkian Stage⁷

Helderbergian Stage⁷

SILURIAN SYSTEM

Pridolian Series

Ludlovian Series

Wenlockian Series

Llandoveryian Series

ORDOVICIAN SYSTEM

Cincinnatian Series (Upper Ordovician)

Richmondian Stage

Maysvillian Stage

Edenian Stage

Champlainian Series

(Middle Ordovician)

Mohawkian Stage

Chazyian Stage

Whiterockian Stage

Canadian Series (Lower Ordovician)

CAMBRIAN SYSTEM

Upper Cambrian Series (Croixian)

Trempealeauan Stage

Franconian Stage

Dresbachian Stage

Middle Cambrian Series (Albertan)

Lower Cambrian Series (Waucoban)

ROCKS OF PRECAMBRIAN ERAS

PROTEROZOIC ERATHEM

Algonkian, Beltian,

Hadrynian, Helikian,

Aphebian, and equivalents

RICHARD A. ROBISON and CURT TEICHERT

¹ For convenience Miocene and Pliocene are often assigned to the Neogene Subsystem, and Paleocene, Eocene, and Oligocene are assigned to the Paleogene Subsystem.

² Follows essentially Gulf Coast usage.

³ Included in Upper Jurassic by some authors.

⁴ Lower part includes Alenian of some authors.

⁵ The Kungurian Stage of some authors is a probable

facies of the upper Artinskian and lower Kazanian stages.

⁶ These units have been designated as stages in previous *Treatise* volumes.

⁷ Applies essentially to eastern United States; in western North America, European stage terminology is used.

⁸ Tremadocian is placed in Cambrian by some authors.

PART A

INTRODUCTION

FOSSILIZATION (TAPHONOMY)

BIOGEOGRAPHY AND BIOSTRATIGRAPHY

By W. A. BERGGREN, A. J. BOUCOT, M. F. GLAESSNER, HELMUT HÖLDER,
M. R. HOUSE, VALDAR JAANUSSON, E. G. KAUFFMAN, BERNHARD KUMMEL,
A. H. MÜLLER, A. W. NORRIS, A. R. PALMER, ADOLF PAPP, C. A. ROSS,
J. R. P. ROSS, and J. A. VAN COUVERING

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