Treatise on Invertebrate Paleontology

Part B

Protoctista 1

Volume 1:

Charophyta

Monique Feist, Coordinating Author

by Monique Feist, Nicole Grambast-Fessard, Micheline Guerlesquin, Kenneth Karol, Lu Huinan, Richard M. McCourt, Wang Qifei, and Zang Shenzen

Prepared under Sponsorship of
The Geological Society of America, Inc.

The Paleontological Society | *SEPM (Society for Sedimentary Geology)*
The Palaeontographical Society | *The Palaeontological Association*

Raymond C. Moore
Founder

Roger L. Kaesler
Editor

Jean Burgess, Jill Hardesty, Jane Kerns
Michael Cormack, Denise Mayse
Assistant Editors and Editorial Staff

The Geological Society of America, Inc.
and
The University of Kansas
Boulder, Colorado, and Lawrence, Kansas
2005

Library of Congress Catalogue Card Number 53–12913
ISBN 0–8137–3002–3

Distributed by the Geological Society of America, Inc., P.O. Box 9140, Boulder, Colorado 80301, www.geosociety.org, from which current price lists of parts in print may be obtained and to which all orders and related correspondence should be directed. Editorial office of the *Treatise:* Paleontological Institute, The University of Kansas, 1475 Jayhawk Blvd., Room 121, Lawrence, Kansas 66045-7613, www.ku.edu/~paleo.

Citation information: Kaesler, R. L., ed. 2005. Treatise on Invertebrate Paleontology, Part B, Protoctista (Charophyta), vol. 1. The Geological Society of America & The University of Kansas. Boulder & Lawrence. xvi + 170 p., 79 fig., 9 tables.

The *Treatise on Invertebrate Paleontology* has been made possible by (1) funding principally from the National Science Foundation of the United States in its early stages, from The Geological Society of America through the bequest of Richard Alexander Fullerton Penrose, Jr., from the Paleontological Society, and from The Kansas University Endowment Association through the bequest of Raymond C. and Lillian B. Moore; (2) contribution of the knowledge and labor of specialists throughout the world, working in cooperation under sponsorship of The Geological Society of America, the Paleontological Society, the SEPM (Society for Sedimentary Geology), the Palaeontographical Society, and the Palaeontological Association; (3) acceptance by The University of Kansas of publication without any financial gain to the University; and (4) generous contributions by our individual and corporate sponsors.

PART B

PROTOCTISTA 1

VOLUME 1: CHAROPHYTA
(Moellerinales, Sycidiales, Charales)

Monique Feist, Nicole Grambast-Fessard, Micheline Guerlesquin, Kenneth Karol, Lu Huinan, Richard M. McCourt, Wang Qifei, and Zang Shenzen

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, www.geosociety.org.

PUBLISHED VOLUMES

Part A. Introduction: Fossilization (Taphonomy), Biogeography, and Biostratigraphy, xxiii + 569 p., 169 fig., 1979.

Part C. Protista 2 (Sarcodina, Chiefly "Thecamoebians" and Foraminiferida), Volumes 1 and 2, xxxi + 900 p., 653 fig., 1964.

Part D. Protista 3 (Protozoa: Chiefly Radiolaria, Tintinnina), xii + 195 p., 92 fig., 1954.

Part E. Archaeocyatha and Porifera, xviii + 122 p., 89 fig., 1955.

Part E, Revised. Archaeocyatha, Volume 1, xxx + 158 p., 107 fig., 1972.

Part E, Revised. Porifera, Volume 2 (Introduction to the Porifera), xxvii + 349 p., 135 fig., 10 tables, 2003.

Part E, Revised. Porifera, Volume 3 (Demospongea, Hexactinellida, Heteractinida, Calcarea), xxxi + 872 p., 506 fig., 1 table, 2004.

Part F. Coelenterata, xx + 498 p., 358 fig., 1956.

Part F. Coelenterata, Supplement 1 (Rugosa and Tabulata), Volumes 1 and 2, xl + 762 p., 462 fig., 1981.

Part G. Bryozoa, xiii + 253 p., 175 fig., 1953.

Part G, Revised. Bryozoa, Volume 1 (Introduction, Order Cystoporata, Order Cryptostomata), xxvi + 625 p., 295 fig., 1983.

Part H. Brachiopoda, Volumes 1 and 2, xxxii + 927 p., 746 fig., 1965.

Part H, Revised. Brachiopoda, Volume 1 (Introduction), xx + 539 p., 417 fig., 40 tables, 1997.

Part H, Revised. Brachiopoda, Volumes 2 and 3 (Linguliformea, Craniiformea, Rhynchonelliformea [part]), xxx + 919 p., 616 fig., 17 tables, 2000.

Part H, Revised. Brachiopoda, Volume 4 (Rhynchonelliformea [part]), xxxix + 768 p., 484 fig., 3 tables, 2002.

Part I. Mollusca 1 (Mollusca General Features, Scaphopoda, Amphineura, Monoplacophora, Gastropoda General Features, Archaeogastropoda, Mainly Paleozoic Caenogastropoda and Opisthobranchia), xxiii + 351 p., 216 fig., 1960.

Part K. Mollusca 3 (Cephalopoda General Features, Endoceratoidea, Actinoceratoidea, Nautiloidea, Bactritoidea), xxviii + 519 p., 361 fig., 1964.

Part L. Mollusca 4 (Cephalopoda: Ammonoidea), xxii + 490 p., 558 fig., 1957.

Part L, Revised. Mollusca 4, Volume 4 (Cretaceous Ammonoidea), xx + 362 p., 216 fig., 1996.

Part N. Mollusca 6 (Bivalvia), Volumes 1 and 2 (of 3), xxxvii + 952 p., 613 fig., 1969.

Part N. Mollusca 6 (Bivalvia), Volume 3, iv + 272 p., 153 fig., 1971.

Part O. Arthropoda 1 (Arthropoda General Features, Protarthropoda, Euarthropoda General Features, Trilobitomorpha), xix + 560 p., 415 fig., 1959.
Part O, Revised. Arthropoda 1 (Trilobita: Introduction, Order Agnostida, Order Redlichiida), xxiv + 530 p., 309 fig., 1997.
Part P. Arthropoda 2 (Chelicerata, Pycnogonida, Palaeoisopus), xvii + 181 p., 123 fig., 1955 [1956].
Part Q. Arthropoda 3 (Crustacea, Ostracoda), xxiii + 442 p., 334 fig., 1961.
Part R. Arthropoda 4, Volumes 1 and 2 (Crustacea Exclusive of Ostracoda, Myriapoda, Hexapoda), xxxvi + 651 p., 397 fig., 1969.
Part R. Arthropoda 4, Volumes 3 and 4 (Hexapoda), xxii + 655 p., 265 fig., 1992.
Part S. Echinodermata 1 (Echinodermata General Features, Homalozoa, Crinozoa, exclusive of Crinoidea), Volumes 1 and 2, xxx + 650 p., 400 fig., 1968 [1967].
Part T. Echinodermata 2 (Crinoidea), Volumes 1–3, xxxviii + 1,027 p., 619 fig., 1978.
Part U. Echinodermata 3 (Asterozoans, Echinozoans), xxx + 695 p., 534 fig., 1966.
Part V. Graptolithina, xvii + 101 p., 72 fig., 1955.
Part V, Revised. Graptolithina, xxxii + 163 p., 109 fig., 1970.
Part W. Miscellanea (Conodonts, Conoidal Shells of Uncertain Affinities, Worms, Trace Fossils, Problematica), xxv + 259 p., 153 fig., 1962.
Part W, Revised. Miscellanea, Supplement 1 (Trace Fossils and Problematica), xxi + 269 p., 110 fig., 1975.
Part W, Revised. Miscellanea, Supplement 2 (Conodonta), xxviii + 202 p., frontis., 122 fig., 1981.

THIS VOLUME

Part B, Part B. Protoctista 1 (Charophyta), xvi + 170 p., 79 fig., 9 tables, 2005.

VOLUMES IN PREPARATION

Part B. Protoctista 1 (Chrysomonadida, Coccolithophorida, Diatomacea, Pyrrhophyta, etc.).
Part E, Revised. Porifera (additional volumes).
Part F, Revised. Cnidaria (Scleractinia).
Part G, Revised. Bryozoa (additional volumes).
Part H, Revised. Brachiopoda (additional volumes).
Part K, Revised. Mollusca 3 (Nautiloidea).
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).
Part R, Revised. Arthropoda 4 (Crustacea Exclusive of Ostracoda).
Part T, Revised. Echinodermata 2 (Crinoidea).
Part V, Revised. Graptolithina.
Part W, Revised. Trace Fossils.

EDITORIAL PREFACE

ROGER L. KAESLER
[The University of Kansas]

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 has been prepared by such a team.

Given the aim of the *Treatise*, one might be excused for wondering about our decision, following the earlier lead of Raymond C. Moore when he first organized the project, to include in the *Treatise on Invertebrate Paleontology* the phylum Charophyta. Invertebrates, after all, are defined as animals without backbones. Of all the kinds of organisms that are likely to make it into the *Treatise*, the charophytes are perhaps the least animal-like. On the contrary, they are among the most plantlike of the algae, and indeed some authors have regarded the charophytes as the basal group of kingdom Plantae.

The present arrangement, of course, stems from Moore's sense of practicality and his interest in completeness. From the outset his plan was to include a number of taxa of protists in the *Treatise*. Some of the groups that are related to the charophytes—in the same kingdom at least—are among the most useful and intensively studied kinds of fossils. To have omitted the order Foraminiferida from the *Treatise*, for example, would have done a great disservice to paleontology as a whole.

Part C of the *Treatise* covers the order Foraminiferida, now regarded by MARGULIS and SCHWARTZ (1998) as class Foraminifera of the phylum Granuloreticulosa. Part D, a rather slim volume, details the radiolarians, which comprise two classes of the phylum Actinopoda (MARGULIS & SCHWARTZ, 1998). Part B, of which this is the first volume, is intended to deal with all the plantlike protists: calcareous nannoplankton, benthic calcareous algae, dinoflagellates, silicoflagellates and ebridians, diatoms, and, herein, the charophytes.

We have departed from Moore's original plan in one major way that may disturb some systematists. The part of the *Treatise* that deals with foraminifera (in two volumes) is labeled formally as C Protista $2^{(1)}$ and C Protista $2^{(2)}$. The radiolarian *Treatise* is D Protista 3. Clearly Moore intended the present volume and others that deal with the plantlike protists to be formally B Protista 1. We have, instead, labeled this volume B Protoctista 1, following MARGULIS and others (1990), MARGULIS, MCKHANN, & OLENDZENSKI (1992), MARGULIS & SCHWARTZ (1998), and L. MARGULIS (personal communication, 2004). BROWN (1993, p. 2,389), in a widely used dictionary defined protist as follows: "A member of the kingdom Protista of simple organisms regarded as intermediate between or distinct from animals and plants, including protozoans, algae and (now less commonly) bacteria and fungi; *esp.* a unicellular eukaryote, a protozoan or single-celled alga."

MARGULIS and SCHWARTZ (1998, p. 112) pointed out that for more than one hundred years the term protist has connoted a single-celled organism. The basis for grouping single-celled organisms separately from multicellular forms is no longer tenable for at least two reasons. First, the single-celled

prokaryotes and the single-celled eukaryotes are organized biologically in fundamentally different ways and ought not to be classified together in the kingdom Protista. Second, many of the predominantly single-celled eukaryote phyla have multicellular members that have evolved independently of each other. MARGULIS and SCHWARTZ (1998, p. 112) capped their argument by pointing out that COPELAND (1956) along with numerous 19th-century biologists recognized "the absurdity of referring to giant kelp by the word 'protist,' a term that had come to imply unicellularity and, thus, smallness." Use of the kingdom Protoctista obviates this absurdity, and we have adopted herein the term for that reason.

Users of previous volumes of the *Treatise* have found in the Editorial Preface details pertaining to use of the *International Code of Zoological Nomenclature* (RIDE & others, eds., 1999; please refer to the most recent *Treatise* volume, Part E(R), vol. 3, 2004, for guidance about preparation of manuscript according to zoological nomenclature). The charophytes, of course, are governed by the *International Code of Botanical Nomenclature* (GREUTER & others, 2000), the provisions of which are in many instances quite unlike those of the *ICZN*. In delving into the use of the botanical code, we on the *Treatise* editorial staff have been assisted by E. L. Taylor, C. H. Haufler, both of The University of Kansas, and M. Feist, the coordinating author of this volume. Nomenclatorial codes tend to be rather legalistic and difficult to navigate. Fortunately, a number of sources are available that guide the interested invertebrate paleontologist who is dealing with the *ICBN* for the first time. One source that we found to be most useful is the set of notes by FENSOME and WILLIAMS (2004).

The charophyte *Treatise* has had a rather interesting history. R. E. Peck was the original author of the volume. He worked with both R. C. Moore and Curt Teichert. In 1983 Peck turned over his manuscript and responsibility for the volume to R. M. Forester, who enlisted the help of M. Feist and N. Grambast-Fessard. Dr. Peck died in 1984, and in 1991 pressure from his other work necessitated that Dr. Forester resign his *Treatise* responsibilities. In 1995 J. A. Eyer offered to assist with the project but given the active work of Drs. Feist and Grambast-Fessard did not get involved further. Dr. Feist, as coordinating author, and her team made steady progress. They were assisted by the preliminary editorial work of R. M. McCourt.

Some languages, most notably the Polish and Czech languages, are enriched with the use of diacritical marks that provide enhanced alphabetical diversity. While celebrating diversity, we have nevertheless elected to omit such marks from Polish and Czech geographical terms used in the *Treatise*. We continue to insert diacritical marks into authors' names. Two factors have led us to this editorial decision. First, we in the *Treatise* editorial office typeset electronically all the pages, and such diacritical marks must be inserted by hand into the final computer-prepared pages. This is a costly and time-consuming operation that is fraught with the possibility of introducing errors. Second, in the burgeoning information age of the new millennium, databases and schemes for information retrieval will be of critical importance in managing paleontological information. Stability and uniformity of terminology are requisites of database-management systems, and the use of diacritical marks and computer technology are likely to remain incompatible for some time to come. We hope that linguistic purists will be tolerant of this transgression, which we have undertaken solely in the interest of expediency, consistency, and information retrieval.

In this volume we have taken special pains to acknowledge authorship of chapters and subsections. Readers citing the volume are encouraged to pay close attention to the actual authorship of a chapter or subsection.

Stratigraphic ranges of taxa have been compiled from the ranges of lower taxa. In all instances, we have used the *range-through* method of describing ranges. In instances,

therefore, where the work of paleontology is not yet finished, some ranges of higher taxa will not show gaps between the ranges of their subtaxa and may seem to be more complete than the data warrant.

While editor of the *Treatise*, the late Professor Curt Teichert once remarked that a published *Treatise* volume is a progress report and should by no means be regarded as the last word on the systematics and paleontology of the organisms discussed. All of us associated with publishing this volume hope that it will stimulate a burst of activity of research on the charophytes.

ACKNOWLEDGMENTS

The Paleontological Institute's Assistant Editors for Text, Jean Burgess and Jill Hardesty, and the Assistant Editor for Illustrations, Jane Kerns, have faced admirably the formidable task of moving this volume through the various stages of editing and into production. In this they have been assisted ably by other members of the editorial team including Mike Cormack with his outstanding computer skills, Chasity Gaultney with her work on illustrations, and Denise Mayse with general support. Jill Krebs, the remaining member of the Paleontological Institute editorial staff, is involved with preparation of PaleoBank, the paleontological database for future *Treatise* volumes, and has not been closely involved with this volume.

It is quite unlikely that this volume would have been published without the efforts of Monique Feist. She was the driving force behind the volume and has been a paragon as a coordinating author. Her synoptic view of the charophytes, her skill in bringing together an international team of specialists, and her careful attention to detail have made the work of the editors much easier. We are grateful to her for her dedication.

Roger L. Kaesler
Lawrence, Kansas
May 3, 2005

REFERENCES

Brown, L. 1993. The New Shorter Oxford English dictionary, vol. 2. Clarendon Press. Oxford. p. i–viii, 1,877–3,801.

Copeland, H. F. 1956. The Classification of Lower Organisms. Pacific Books. Palo Alto, California. 302 p.

Fensome, R. A., & G. L. Williams. 2004. The Lentin and Williams Index of Fossil Dinoflagellates, 2004 edition. American Association of Stratigraphic Palynologists Contributions Series 42:909 p.

Greuter, W., J. McNeill, F. R. Barrie, H. M. Burdet, V. Demoulin, T. S. Filgueiras, D. H. Nicholson, P. C. Silva, J. E. Skog, P. Trehane, N. J. Turland, & D. L. Hawksworth. 2000. International Code of Botanical Nomenclature (Saint Louis Code). Koeltz Scientific Books. Königstein, Germany. 474 p.

Margulis, L, J. O. Corliss, M. Melkonian, & D. J. Chapman. 1990. Handbook of Protoctista. Jones and Bartlett Publishers. Boston. 914 p.

Margulis, L., H. I. McKhann, & L. Olendzenski. 1993. Illustrated Glossary of Protoctista. Jones and Bartlett Publishers. Boston. 288 p.

Margulis, L., & K. V. Schwartz. 1998. Five Kingdoms. An Illustrated Guide to the Phyla of Life on Earth, 3rd ed. W. H. Freeman and Company. New York. 520 p.

Ride, W. D. L., H. G. Cogger, C. Dupuis, O. Kraus, A. Minelli, F. C. Thompson, & P. K. Tubbs, eds. 1999. International Code of Zoological Nomenclature, 4th ed. International Trust for Zoological Nomenclature. London. 306 p.

STRATIGRAPHIC DIVISIONS

The major divisions of the geological time scale are reasonably well-established throughout the world, but minor divisions (e.g., subseries, stages, and substages) are more likely to be provincial in application. The stratigraphic units listed here represent an authoritative version of the stratigraphic column for all taxonomic work relating to this volume. They are adapted from the International Stratigraphic Chart, and units are approved by the International Commission on Stratigraphy (ICS) and ratified by the International Union of Geological Sciences (IUGS). A copy of the comple chart can be obtained at the following website: http://www.iugs.org/iugs/pubs/intstratchart.htm.

Cenozoic Erathem
- **Neogene System**
  - Holocene Series
  - Pleistocene Series
  - Pliocene Series
  - Miocene Series
- **Paleogene System**
  - Oligocene Series
  - Eocene Series
  - Paleocene Series

Mesozoic Erathem
- **Cretaceous System**
  - Upper Cretaceous Series
  - Lower Cretaceous Series
- **Jurassic System**
  - Upper Jurassic Series
  - Middle Jurassic Series
  - Lower Jurassic Series
- **Triassic System**
  - Upper Triassic Series
  - Middle Triassic Series
  - Lower Triassic Series

Paleozoic Erathem
- **Permian System**
  - Lopingian Series
  - Guadalupian Series
  - Cisuralian Series
- **Carboniferous System**
  - Pennsylvanian Subsystem
  - Mississippian Subsystem
- **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 Series
  - Middle Ordovician Series
  - Lower Ordovician Series
- **Cambrian System**
  - Furongian Series
  - Middle Cambrian Series
  - Lower Cambrian Series

COORDINATING AUTHOR'S PREFACE

MONIQUE FEIST

[Université Montpellier II, France]

The Charophyta, commonly called charophytes or stoneworts, are green algae that occur worldwide, sometimes abundantly, in fresh and brackish water. Long considered a distinctive group, recent morphological and molecular studies have shown conclusively that charophytes are members of the evolutionary lineage of green algae that gave rise to land plants. Their importance is enhanced by a fossil record more complete and well studied than nearly any other calcareous algae, with the exception of the Dasycladales.

Extant charophytes are of little commercial importance; however, they are of great scientific value. Their primary importance is as model organisms in studies of membrane electrophysiology and cell physiology; and ecological studies are often in relation to recent problems of water management (see chapter on Ecology, p. 29).

Although fossil charophytes were reported as early as the 18th century (SCHREBER, 1759), most charophyte research has been performed within the last century. After the first attempts to establish a coherent classification of the group (see chapter on Classification, p. 83) authors paid attention to the description of assemblages, first in the Paleozoic of Russia (KARPINSKY, 1906) and in the Paleozoic and Mesozoic of North America (PECK, 1934a, 1934b, 1938). Studies of Tertiary charophyte floras started in England (REID & GROVES, 1921); then they were developed in Germany (MÄDLER, 1955), Sweden (HORN AF RANTZIEN, 1959b), France, England, Belgium (GRAMBAST, 1958, 1959b, 1962), and in the former USSR (MASLOV, 1966a).

At the same time, new observations of particular characters of the gyrogonite (basal plate, apical aperture, and ornamentation) facilitated the distinction of genera and species (GRAMBAST, 1956a, 1956c, 1957). GRAMBAST (1964) also revealed the existence of phylogenetic relationships within the charophytes and especially within the family Clavatoraceae, whose lineage to the plant kingdom is quite remarkable (see chapter on Evolutionary History, p. 60).

Charophytes are represented in the fossil record mainly by the calcified female fructifications, consisting of the gyrogonite and utricle. These fructifications are broadly spherical bodies, ranging from 200 to 3,500 µm. Fossil charophytes provide an excellent source of stratigraphic data, which have numerous applications in paleontology. Their distribution in space and time has provided the basis for establishing biozonal scales (see chapter on Stratigraphic Distribution, p. 39).

Research developed in the last twenty years has been concerned primarily with the application of cladistic analyses and molecular biology to infer phylogenetic relationships both within the Charophyta and the plant kingdom (see chapters on Evolutionary History and Molecular Phylogeny, p. 60 and p. 77, respectively).

Fossil and extant charophytes are often studied independently by different groups of researchers. The present volume brings together knowledge of fossil and extant forms; it is thus intended to be a synthesis that is useful to a wide variety of scientists who study charophytes. The group comprises 86 genera, 12 families, and 3 orders, which are described in this volume, the first edition of the *Treatise* to include coverage of this important group.

We wish to thank the following colleagues who have given permission to reproduce illustrations and in many cases have provided original artwork: Dr. Jean-Pierre Berger, Institut de Geologie, Fribourg, Switzerland; M. Hagen Has and Dr. Hans Kerp, Forschungsstelle für Paläobotanik, West-

fälische Wilhelms-Universität, Münster, Germany; Dr. Dieter Korn, Department of Invertebrate Palaeontology, Humboldt Museum, Berlin, Germany; Dr. Lu Huinan and the late Dr. Wang Zhen, Nanjing Institute of Geology and Palaeontology, Nanjing, China; Dr. Carles Martin-Closas, Facultat de Geología; University of Barcelona, Spain; Dr. Eduardo Musacchio, Universidad Nacional de la Patagonia San Juan Bosco, Comodoro Rivadaria, Argentina; Dr. Michael Schudack, Institut für Paläontologie, Freie Universität Berlin, Germany; Dr. Ingeborg Soulié-Märsche, Laboratoire de Paléontologie, Université Montpellier II, Montpellier, France; Dr. Gajendra Pratap Srivastava, Birbal Sahni Institute of Palaeobotany, Lucknow, India; Dr. Yang Guodong, North-West China Bureau of Petroleum Geology, Ulumqi, China; and Dr. Zhang Zerun, Petroleum Geology, Ministry of Geology and Mineral Resources, Zhengzhou, China.

We are grateful to Dr. Gilbert Klapper, Department of Geology, University of Iowa, Iowa City, USA, and to Dr. Richard McCourt, Academy of Natural Sciences, Philadelphia, USA, for reviewing portions of the manuscript. We thank M. Michel Pons who assisted with photography, and Jacqueline Courbet and Laurence Meslin for preparing original drawings, all from the Laboratoire de Paléontologie, Université Montpellier II, Montpellier, France.

REPOSITORIES AND THEIR ABBREVIATIONS

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

AGE: Archiv für Geschiebekunde, Geologisch-Paläontologisches Institut, Hamburg, Germany
AI: Institute of Geological Sciences, Polish Academy of Sciences, Kraków, Poland
AMNH: American Museum of Natural History, New York City, New York, USA
AM or AMu: Australian Museum, Sydney, Australia
BGMRH: Bureau of Geology and Mineral Resources of Henan, Henan, China
BGR: Bundesanstalt für Geowissenschaften und Rohstoffe, Hannover, Germany
BGS: British Geological Survey, MPK collection, Nottingham, United Kingdom
BIG: Beijing Institute of Geology, Beijing, China
BM: Berlin Museum, Berlin, Germany
BMNH: British Museum (Natural History), London, United Kingdom
BMS: Buffalo Museum of Science, Buffalo, New York, USA
BPGNC: Bureau of Petroleum Geology of North China, Zhengzhou, Henan, China
BPNWC: Bureau of Petroleum of North West China, Wulumuqi, Xinjiang, China
BSPGM: Bayerische Staatssammlung für Paläontologie und historische Geologie, München, Germany
BYU: Geology Department, Brigham Young University, Provo, Utah, USA
CCG: Chengdu College of Geology (now Chengdu University of Technology), Chengdu, Sichuan, China
CEGH-UNC: Cátedra de Estratigrafía y Geología Histórica, Universidad Nacional de Córdoba, Córdoba, Argentina
CSGM: Central Siberian Geological Museum, United Institute of Geology, Geophysics, & Mineralogy, Siberian Branch of the Russian Academy of Sciences, Novosibirsk, Russia
CU: University of Cincinnati, Cincinnati, Ohio, USA
CUG: Colgate University, Geology Department Collections, Hamilton, New York, USA
CPC: Bureau of Mineral Resources, Canberra, Australia
CRICYT: Centro Regional de Investigaciones Científicas y Tecnológicas, Mendoza, Argentina
DNPM: Departamento Nacional da Produçao Mineral, Rio de Janeiro, Brazil
FEGI: Far East Geological Institute, Russian Academy of Sciences, Vladivostok, Russia
FM: Field Museum (Natural History), Chicago, Illinois, USA
FUB: Freie Universität Berlin, Institut für Geologische Wissenschaften, Fachrichtung Paläontologie, Berlin, Germany
GII: Institut für Geologie und Paläontologie der Universität Innsbruck, Innsbruck, Austria
GIK: Geologisch-Paläontologisches Institut, Universität zu Köln, Köln, Germany
GISO: Geological Institute of Shengli Oil Field, Dongying, Shandong, China.
GMU: Geological Museum, Ukrainian Academy of Sciences, Kiev, Ukraine
GPIMH: Geologisch-Paläontologisches Institut und Museum der Universität Hamburg, Hamburg, Germany
GSC: Geological Survey of Canada, Ottawa, Canada
GSM: British Geological Survey (formerly Geological Survey Museum; Institute of Geological Sciences, London), Keyworth, Nottinghamshire, United Kingdom
GSS: Geological Survey of Scotland, Edinburgh, United Kingdom
GSWA: Geological Survey of Western Australia, East Perth, Australia
HM: Hunterian Museum, University of Glasgow, Glasgow, United Kingdom
IGASB: Institute of Geology, Academia Sinica, Beijing, China
IGPTU: Institut und Museum für Geologie und Paläontologie, Tübingen Universität, Tübingen, Germany
IPFUB: Institut für Paläontologie, Freie Universität, Berlin, Germany
IPPAS: Institute of Palaeobiology, Polish Academy of Sciences, Warsaw, Poland
IPM: Institut de Paléontologie du Muséum national d'Histoire naturelle de Paris, Paris, France
IPUB: Institüt für Paläontologie, Universität Bonn, Bonn, Germany
IPUM: Instituto di Paleontologia, Università di Modena, Modena, Italy
IRSNB: Institut Royal des Sciences naturelles de Belgique, Brussels, Belgium
ISM: Illinois State Geological Survey, Urbana, Illinois, USA, formerly at Illinois State Museum, Springfield, Illinois, USA
IU: Indiana University, Bloomington, Indiana, USA
JPI: Jianghan Petroleum Institute, Jingsha, Hubei, China
KIGM: Institute of Geology and Mineral Deposits, Kraków, Poland
KUMIP: University of Kansas, Lawrence, Kansas, USA
LGI: Leningrad Mining Institute, Leningrad, Russia
MCCA: Museo Comunale in Cortina d'Ampezzo, Cortina d'Ampezzo, Italy

MCZ: Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA
MFGI: Museum Far Eastern Geological Institute, Vladivostok, Russia
MGSB: Museo Geologico, Seminari Conciliar, Barcelona, Spain
MHGI: Museum of the Hungarian Geologic Institute, Budapest, Hungary
MIGT: Museum, Institute of Geology, Dushambe, Tajikistan
MLGIN: Micropalaeontological Laboratory, Geological Institute, Academy of Sciences, Moscow, Russia.
MLP: Collection Paleobotanica, Museo de la Plata, La Plata, Argentina
MMMN: Manitoba Museum of Man and Nature, Winnipeg, Canada
MMF: Geological and Mining Museum, Sydney, Australia
MNCN: Museo Nacional de Ciencias Naturales, Madrid, Spain
MNHN: Muséum National d'Histoire Naturelle de Paris, Paris, France
MNMPB: Magyar Nemzeti Museum, Budapest, Hungary
MNS: Museum für Naturkunde, Stuttgart, Germany
MUZ IG: Museum of the State Geological Institute, Warsaw, Poland
NHM: Natural History Museum, London, United Kingdom
NIGP: Nanjing Institute of Geology and Palaeontology, Nanjing, China
NIGPAS: Nanjing Institute of Geology and Paleontology, Academia Sinica, Nanjing, China
NIUPGAS: Nanjing Institute of Geology and Paleontology, Academia Sinica, Nanjing, China
NMV: National Museum of Victoria, Melbourne, Australia
NRM: Naturhistoriska Riksmuseet (Swedish Museum of N atural History), Stockholm, Sweden
NYSM: New York State Museum, Albany, New York, USA
ODM: Old Dominion College, Norfolk, Virginia, USA
OSU: Ohio State University, Department of Geology, Columbus, Ohio, USA
OUZC: Ohio University Zoological Collections, Athens, Ohio, USA
PDMNH-P: Paleontological Department of the National Museum, Museum of Natural History, Prague, Czech Republic
PIUB: Paleontological Institute of the University of Bonn, Bonn, Germany
PIUFB: Paläontologisches Institut, Freie Universität Berlin, Berlin, Germany
PIUW: Paläontologichen Instituts, Universität Wien, Vienna, Austria
PIUZ: Paleontological Institute, University of Zürich, Zürich, Switzerland
PIW: Institut für Paläontologie der Universität Würzburg, Würzburg, Germany
P-MD: Provincial Museum of Danzig, Danzig, Germany
PMUK: Palaeontological Museum, University of Kiev, Ukraine
PRM: Peter Redpath Museum, Montreal, Canada
PU: Princeton University, Princeton, New Jersey, USA
ROM: Royal Ontario Museum, Toronto, Canada
RMS: Palaeobotanical Department, Riksmuseum, Stockholm, Sweden
SAM: South Australian Museum, Adelaide, Australia
SGIP: Sammlung des Geologisch-Paläontologichen Institutes der Universität Palermo, Palermo, Italy
SGS: Geological Collection, Swedish Geological Survey, Uppsala, Sweden
SMF: Natur-Museum und Forschungs-Institut, Senckenberg, Germany
SPIE: Sammlung des Institut für Paläontologie, Universität Erlangen-Nürnberg, Erlangen, Germany
SPIML: Sammlung des Paläontologischen Institutes der Universität Marburg, Lahn, Germany
SPIT: Sammlung des Paläontologischen Institutes der Universität Tübingen, Tübingen, Germany
SSPHG: Staatliches Sammlung für Paläontologie und historische Geologie, München, Germany
SSSBGF: Stratigraphische Sammlung der Sektion Geowissenschaften der Bergakademia Freiberg, Freiberg, Germany
SUP: Sydney University, Department of Geology, Sydney, Australia
TMM: Texas Memorial Museum, University of Texas, Austin, Texas, USA
TsNIGER: Ts NIGER Museum, Russia
UA: University of Alberta, Edmonton, Alberta, Canada
UAF: University of Alaska, Fairbanks, Alaska, USA
UC: University of Cincinnati, Cincinnati, Ohio, USA
UCC: Chicago Natural History Museum, formerly in Walker Museum, Chicago, Illinois (see also FM), USA
UCM: Universidad Complutense de Madrid, Madrid, Spain
UG: University of Göttingen, Göttingen, Germany
UL: Lodz University, Institute of Geography, Lodz, Poland
UM: University of Minnesota, Minneapolis, Minnesota, USA
UMC: University of Missouri-Colombia, Colombia, Missouri, USA
UMG: University of Montana, Department of Geology, Missoula, Montana, USA
UMP: University Montpellier II , Department of Paleontology, Montpellier, France. C, L. Grambast Collection; CF, M. Feist Collection; CM, M. Massieux Collection; CSM, I. Soulié-Märsche Collection
UNE: University of New England, Armidale, New South Wales, Australia
UPLGS: Université de Paris, Laboratoire de Géologie de la Sorbonne, Paris, France

USGS: U.S. Geological Survey, Type algae collection, Denver, Colorado, USA
USNM: U.S. National Museum, Washington, D.C., USA
U-SK: Universitäts-Sammlung zu Kiel, Germany
UTBEG: University of Texas, Bureau of Economic Geology, Austin, Texas, USA
VK: Theo Van Kemper Collection, Amsterdam, The Netherlands
WAGS: Western Australia Geological Survey, Perth, Australia
WAM: Western Australia Museum, Perth, Australia
WIF: Wadi Institute of Himalayan Geology, Dehra Dun, India
WMC: Woodwardian Museum, University of Cambridge, Cambridge, United Kingdom
WMNM: Wesfälisches Museum für Naturkunde, Münster, Germany
YaFAN: Institute of Geology, Yakut Branch, Siberian Division AN SSR, Yakutsk, Russia
YPM: Yale Peabody Museum, New Haven, Connecticut, USA
ZPAL: Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland