Fossil Crinoids

Crinoids have graced the oceans for more than 500 million years. Brightly coloured feather stars fascinate divers in coral reefs, and stalked sea lilies are among the most attractive fossils. Crinoids had a key role in the ecology of marine communities through much of the fossil record, and their remains are prominent rock-forming constituents of many limestones.

This is the first comprehensive volume on crinoids to bring together information on their form and function, classification, evolutionary history, occurrence, preservation and ecology. The main part of the book is devoted to assemblages of intact fossil crinoids, which are described in their geological setting, ranging from the Ordovician to the Tertiary. The final chapter deals with living sea lilies and feather stars. The volume is exquisitely illustrated with abundant photographs and line drawings of crinoids from sites around the world.

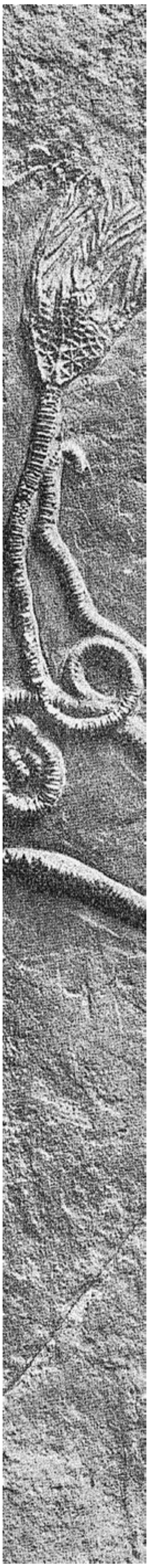
This authoritative account re-creates a fascinating picture of fossil crinoids for palaeontologists, geologists, evolutionary and marine biologists, ecologists and amateur fossil collectors.

Hans Hess is affiliated with the Basel Natural History Museum.

William I. Ausich is chairman of and professor in the Department of Geological Sciences, The Ohio State University.

Carlton E. Brett is a professor of Geology at the University of Cincinnati, Ohio.

Michael J. Simms is curator of palaeontology at the Ulster Museum, Belfast.



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HANS HESS

WILLIAM I. AUSICH

CARLTON E. BRETT

MICHAEL J. SIMMS

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Contributors

William I. Ausich (Introduction; Chapters 1, 3, 4, 5, 8 and 16–19; review of manuscript) was born in 1952 and raised in Galva, Illinois. He earned a bachelor of science degree in geology from the University of Illinois, and master's and doctoral degrees from Indiana University. At Indiana University, he studied under the guidance of Professor N. Gary Lane. His research interests have included Mississippian, Silurian, and Ordovician crinoids and the topics of palaeoecology, constructional morphology, systematics and evolutionary history. He has held faculty positions at Wright State University, Dayton, Ohio, and The Ohio State University, Columbus, where he is presently Professor and Chair.

Carlton E. Brett (Chapters 1, 4, 6, 7, 10, 12, 14, and 15) was born in 1951. He received his doctoral degree in 1978 from the University of Michigan for research on Silurian pelmatozoan echinoderms and their palaeoecology. He taught at the University of Rochester from 1978 to 1998 and is now Professor of Geology at the University of Cincinnati, Ohio. He has authored numerous papers and edited four volumes on various subjects, including Palaeozoic echinoderms, modern and ancient taphonomy, sequence stratigraphy, regional geology of the Ordovician–Devonian rocks in the Appalachian Basin, ancient organism interaction and evolutionary ecology of Palaeozoic marine faunas. He was co-recipient (with William I. Ausich) of the Palaeontological Society's Schuchert Medal in 1990 and is a Fellow of the Geological Society of America.

Stephen K. Donovan (Chapter 3; review of manuscript) was born in 1954 and raised in London. After leaving school he spent five years working in telecommunications before entering the University of Manchester, where he was awarded his bachelor of science degree in 1980. His doctoral degree supervised by Professor Christopher R. C. Paul at the University of Liverpool, was awarded in 1983. From 1986 to 1998 he taught at the University of the West Indies in Kingston, Jamaica, as Professor of Palaeozoology. He is now Keeper of Palaeontology at The Natural History Museum, London. In 1994 he was awarded a bachelor of science degree by the University of Liverpool. His principal research interests centre on the palaeozoology of the Caribbean region.

Hans Hagdorn (Chapter 21) was born in 1949 in Schwäbisch-Hall, Baden-Württemberg. He studied Germanic languages and geography at the University of Tübingen and currently teaches at the Künzelsau Commercial School. Since his school days, he has accumulated a fine collection of Triassic fossils, which is exhibited at the Muschelkalkmuseum in Ingelfingen. His research concentrates on the stratigraphy and palaeoecology of the Germanic Triassic, including the systematics and evolutionary biology of crinoids. He is a member of two commissions on Triassic stratigraphy. In 1988 he received an honorary degree from Tübingen University and in 1995 the Zittel Medal from the Paläontologische Gesellschaft.

Hans Hess (originator and main editor; Introduction and Chapters 1, 3, 4, 9, 11, 13, 20, 23, 25–29; Appendix I and II; Bibliography; Indices) was born in 1930 and raised in Basel, Switzerland, where he studied pharmacy, leading to a career in the chemical industry. He retired in 1991 as the head of Pharmacy Research and Development of Ciba-Geigy Corporation. From his school days he was interested in fossils and specialized in Jurassic echinoderms, an area well suited to a hobby palaeontologist. His work, mainly on asteroids, ophiuroids and crinoids, earned him an honorary degree from Basel University in 1989. He now works part time for the Basel Natural History Museum.

René Kindlimann (all line drawings, redrawn from sources as indicated or new) was born in 1950 and raised in Zürich, where he attended the Industrial School of Art. He works as an independent graphic artist for fairs and exhibitions, more recently also for museums and special exhibitions. As a hobby palaeontologist, he has accumulated an important collection of remains of fossil sharks, on which he has also published.

D. Bradford Macurda, Jr. (Prelude) was born in 1936 and raised in Westchester County, New York. He earned bachelor's and doctoral degrees from the University of Wisconsin, where he studied blastoids under the guidance of Professor L. M. Cline. Subsequently, as a faculty member at the University of Michigan, he focused on Palaeozoic blastoids and living crinoids. He also held positions at Exxon Production Research and with the Energists, in Houston, Texas.

Michael J. Simms (Chapters 1–3, 5, 22, 24) was born in 1960. He first developed an interest in fossils at the age of 6 and by the age of 14 had come to specialize in the Lower Jurassic, in particular its echinoderm fauna. He obtained a first class honours degree in geology with zoology from Bristol University in 1983 and in 1986 completed a doctorate at Birmingham University on Lower Jurassic crinoids. Since then he has held a succession of research fellowships and short-term posts in higher education and in national museums. He has worked on phylogenetic relationships among crinoids. Other research interests include evidence for climate change in the Triassic and karst geomorphology and hydrology. Currently he is serving a two-year appointment as Curator of Palaeontology at the Ulster Museum, Belfast.

Wendy L. Taylor (Chapters 7 and 10) was born in 1962 in Erie, Pennsylvania. She graduated with a bachelor's degree in geosciences and biology from the State University of New York College at Fredonia in 1989. She obtained a master's degree in geology in 1993 at the University of Rochester and completed her doctorate in 1996. She was hired as the Paleontological Research Institute's first collections manager in 1995. Ms. Taylor's master's research describes the taphonomy and palaeoecology of extraordinary fossil assemblages from the Rochester Shale. Her doctoral research is a comparative study of the Palaeozoic echinoderm fossil assemblages in western New York, southern Ontario and selected parts of eastern North America. Her other research interests include problematic animals known as machaeridians and Palaeozoic trace fossils.

Photographs: Source indicated in figure captions.

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Prelude

D. BRADFORD MACURDA, JR.

When we stand on a wave-swept shore, the physical force of the waves is the dominant stimulus to our imagination. The surface of the ocean is grey and blue, stretching as far as the eye can see, frosted by waves curling and breaking under the wind. The sea appears to be lifeless and empty. No hint of the life teeming within it is evident, except in tide pools along the shore or in the bounty offered by fishermen who have just landed their catch.

During the 1800s, we began to probe the sea in a scientific manner. Our sampling was remote – we used dredges and nets. We were surprised at some of the animals we recovered. Among these were great masses of stalked crinoids, which looked like living fossils. The advent of scuba diving and deep-diving submersibles finally opened the door to direct observation and study. Crinoids were described as being virtually extinct. But dive the Great Barrier Reef in Australia: more than 50 species live there. Free-living crinoids festoon the reef, arms spread in broad fans to filter the water, or they are tucked into crevices, hidden from predators. Dive reefs throughout the western Pacific – in Indonesia, Malaysia, Papua New Guinea and Fiji, and the vertical underwater cliffs at Palau; free-moving crinoids are abundant and numerous. Cross the Indian Ocean to Mauritius, the Seychelles, Tanzania, and the fabled spice island of Zanzibar, and there they are again. Dive the Red Sea at night. By day, the white plates of coralline animals are barren of apparent life. At night they are covered with masses of red crinoids that have come out to feed.

Sail the glittering waters of the Bahamas. Wherever you dive on the reefs, crinoids are to be found. Follow the Antilles south, cross northern South America in Venezuela and Colombia, dive the San Blas Islands of Panama and the islands off Nicaragua, Honduras and Belize. Crinoids are there to greet you. In the shallow waters of the tropics, we have come to learn they are alive, diverse and doing well.

For those who have collected fossil crinoids from Palaeozoic rocks and those of the Triassic and Jurassic, the ultimate time machine is a submersible. Fasten down the hatch, descend below 100 m into the world where the sunlight doesn't shine, and you will find living stalked crinoids, some with stems a metre long. Crinoids with great parabolic fans recurved into the currents have shown their life habits to be different from many reconstructions and have enabled us to better understand their ancestors. Small five-armed crinoids come into view, revealing a set of different strategies as to how high to live above the bottom. In the Straits of Florida,

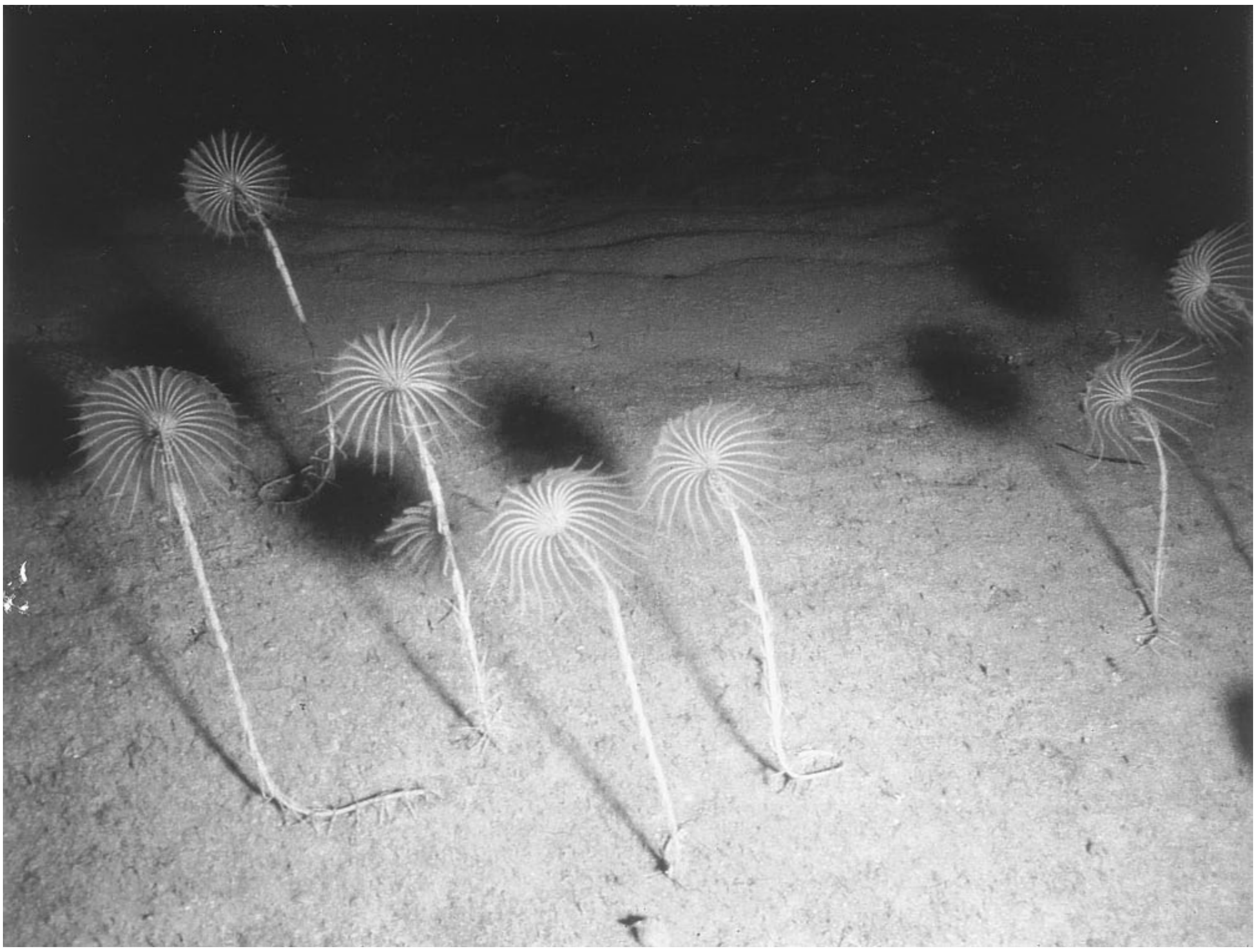

Fig. 1. Group of living *Neocrinus decorus* on carbonate hard bottom, with crowns forming parabolic filtration fan. The current runs from the foreground to the background, and the oral surfaces of the crowns face away from the viewer (i.e., downcurrent). Stems are bent proximally at nearly a right angle, orienting the crowns perpendicular to the current. A comatulid (*Stylometra spinifera*) clings to the stem of the specimen third from left. Northeastern Straits of Florida, south of the west end of Grand Bahama Island, at 420 m. (Photograph from the Johnson Sea Link submersible; courtesy C. G. Messing.)

crinoids anchor on the bare rock of the sea floor looking like ghostly sentinels in the light or like a field of sunflowers turned toward the sun (Fig. 1).

We are fortunate indeed to live at a time when we can compare the modern and the ancient first-hand. It is these insights that enable us to better understand the fossil remains of crinoids, to reconstruct their life habits and to learn how they have changed and evolved.

Introduction

HANS HESS AND WILLIAM I. AUSICH

Brightly coloured feather stars fascinate divers in tropical coral reefs, and stalked sea lilies are among the most attractive fossils. Both belong to the class of crinoids, suspension feeders that have graced the oceans for more than 500 million years. Crinoids are common fossils, had a key role in the ecological structuring of marine communities through much of the fossil record and played an important role in rock-building. Crinoids are the topic of this book, which brings together for the first time the essentials of crinoid morphology, preservation, systematics, phylogeny and mode of life in the context of the most important and interesting crinoid fossil assemblages. The book attempts to re-create a picture of fossil crinoids alive in their natural habitats. We hope that some of our enthusiasm for these living and fossil animals will be conveyed to our readers, professionals and amateurs alike.

Crinoids are a class of echinoderms (phylum Echinodermata). These marine animals are characterized by a calcareous endoskeleton of distinct plates or ossicles, radial symmetry[1] and an internal water-vascular system. The echinoderm skeleton is highly porous in a living animal but is easily transformed into solid calcite during fossilization, which explains the richness of crinoidal remains throughout geological history. Crinoids differ from other classes of living echinoderms, such as starfish (Asteroidea), brittle stars (Ophiuroidea), sea urchins (Echinoidea) and sea cucumbers (Holothuroidea), by their morphological organization and their way of feeding. These other echinoderms seek food mostly on the sea floor, so their mouths are directed downward, whereas crinoids filter the water for plankton and direct their mouths upward. Crinoids are placed in the subphylum Pelmatozoa along with other, extinct classes, commonly grouped in the blastozoans.

Crinoids differ fundamentally from other pelmatozoans in the development of true arms. Arms are extensions of the body wall that contain the food-collecting grooves and also the extensions of the haemal, nervous, water-vascular and reproductive systems. Crinoid arms are supported by plates directly continuous with the highest plates of the cup. In contrast, blastozoans had simple armlets or brachioles attached to their cups or thecae that also contained specialized respiratory pores. Like crinoids, blastozoans lived mostly upright. Their oral side was directed upward, and their appendages must have served as food-gathering organs, so that their ambulacra were developed into food grooves. The Lower to Middle Cambrian genus *Gogia* (Fig. 2) provides an example of primitive blastozoans. The oldest known pelmatozoans are from the Lower Cambrian, whereas the first true crinoids did not appear until the Lower Ordovician. Blastozoans lived exclusively during the Palaeozoic Era.

Crinoids flourished during the Palaeozoic Era, when they reached their peak numbers during the Early Carboniferous (Fig. 3). They almost became extinct at the end of the Permian, but recovered to flourish again

Fig. 2. *Gogia spiralis*. Two individuals of an early pelmatozoan. Wheeler Shale, Middle Cambrian, Antelope Spring, House Range, Utah. The specimens are on the bedding plane of a highly argillaceous, micritic limestone. See Robison (1965) for further details. (Hess Collection; photograph S. Dahint.) ×1. To view this figure in colour, see the colour plate section following page xv.

during the Mesozoic. More than 6,000 fossil species, belonging to more than 800 genera, have been described. Today, approximately 600 living species are known; most are free-living feather stars or comatulids living in the shallow seas. Approximately 80 species of stalked sea lilies are restricted to the deeper water of today's oceans.

Like other echinoderms, crinoids are exclusively marine. Nevertheless, during their long history, they adapted to almost all marine habitats and developed an incredible array of morphologies. Crinoids have populated reefs and hardgrounds as well as muddy bottoms. Many were anchored with a holdfast and others moved sluggishly. The great majority of crinoids were stalked (stemmed). In some, notably the post-Palaeozoic comatulids, the stem was greatly reduced or is absent, but this conferred other advantages, such as the ability to hide from predators, to attain various feeding positions or even to swim. A number of forms became free-floating, including very small, pelagic crinoids; large, free-floating forms; and the largest stalked sea lilies ever found, which were anchored to floating logs.

Crinoids are efficient food collectors, and much of the skeleton is devoted to this purpose. A central cup of calcareous plates contains most of the soft parts, such as the mouth, gut and anus. The stem is composed of disc-shaped columnals, and for most crinoids the stem elevates the animals into a favourable feeding position up in the water column. The cup bears the food-gathering arms with the tube feet, extensions of the water-vascular system. Suspended food is trapped on the tube feet and passed along the food groove to the mouth by tube foot

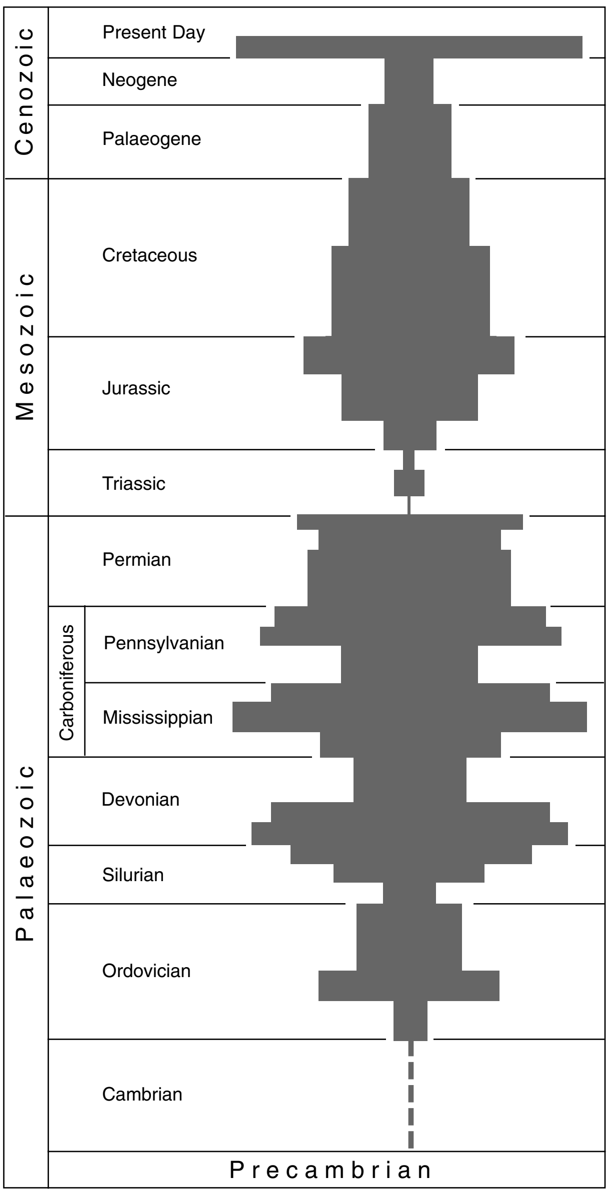

Fig. 3. Evolutionary history of crinoids based on number of genera. (Redrawn from Broadhead & Waters 1980.)

and ciliary action. In living crinoids the arms also contain the gonads, which release a large number of eggs and sperm into the surrounding water during spawning.

The Palaeozoic Era produced the majority of described crinoid species, which are traditionally classified into three subclasses – the Camerata, Flexibilia and Inadunata (Moore & Teichert 1978). During the Mesozoic the subclass Articulata diversified from survivors of the end-Permian extinction. This subclass, which includes all the living crinoids, is named for the development of muscular articulations in the arms, which increases the mobility between ossicles.

Most crinoid ossicles, other than those in the arms, were bound together in life by ligaments. Both ligamentary and muscular articulations produced characteristic patterns that are important not only for classification but also for understanding crinoid function. However, upon death these connective tissues quickly decay, and the great majority of fossil crinoidal remains are disarticulated. The study of disarticulated crinoid ossicles is an essential task in crinoid palaeontology, and characteristics of isolated ossicles are described in the first part of this book.

The introductory chapters discuss the form and function of crinoid morphology, classification, evolutionary history, occurrence, preservation and ecology. In view of the vast fossil record of crinoids, which contains so many unique and extraordinary forms, these chapters cannot be exhaustive. Rather, they prepare the scene for understanding the fossil assemblages. For more detailed information, readers are directed to Part T of the *Treatise on Invertebrate Paleontology* (Moore & Teichert 1978). The primary focus of this book is the complete crinoid organism and assemblages of intact crinoids. Complete specimens occur only rarely but are found repeatedly on bedding planes throughout geological history. Such *Lagerstätten*, treasuries of unique information, are described in their geological setting in the second, and main, part of this book, where we also try to reconstruct the fossils' mode of life. In view of the widespread occurrence of crinoid assemblages, and the corresponding difficulties of gaining access to material and information, this task has been divided among the authors. Even so, the advice of other specialists was essential, and our sincere thanks are expressed to all of these who share our fascination with the crinoids.

NOTE

1. Radial, typically pentameral symmetry is superimposed on basically bilateral symmetry.