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THE STUDY OF CRINOIDS DURING THE 20TH CENTURY AND THE CHALLENGES OF THE 21ST CENTURY

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ABSTRACT—Development of a phylogenetic classification has been a primary pursuit of crinoid paleontologists during the 20th century. Wachsmuth and Springer and Bather vigorously debated crinoid classification during the waning years of the 19th century, and although tremendous progress has been made a comprehensive phylogenetic classification is still the primary objective for crinoid research during the early 21st century. Twentieth century crinoid studies are divisible into four periods. The direct influence of Frank Springer and Francis Bather continued until approximately 1925. Descriptive studies dominated the period of 1926–1943 and culminated in a comprehensive classification of Paleozoic crinoids that was a combination of the ideas of Wachsmuth and Springer and Bather. The end of the third period, 1944–1978, was marked by publication of the *Treatise on Invertebrate Paleontology*. The *Treatise* compilation brought together classification ideas for the entire class into a truly comprehensive classification, although problems remained with the phylogenetic underpinnings of the *Treatise* classification. During the third period, pioneering work on crinoid paleobiology laid the foundation for significant paleobiology advances for the fourth, 1979–1999, period. This last period also witnessed significant advances in the taxonomy of crinoid faunas at critical intervals, the taxonomy of crinoids from new geographic areas, and working toward the solution to the origin and early evolution of the Crinoidea.

Continued work on crinoids in the 21st century promises to provide significant advances both for understanding the evolutionary history of crinoids and for understanding the history of epifaunal benthic communities through time. Immediate challenges include completion of a comprehensive phylogenetic classification, which will open the door for evolutionary paleoecologic and paleobiologic studies; utilization of computerized morphometric techniques in the analysis of functional morphology; systematic studies of new faunas in critical intervals; discovery of faunas in new geographic areas to better constrain knowledge of crinoid biogeography; and modern systematic revision of classic North American and European faunas.

INTRODUCTION

A CONTINUING THEME in crinoid systematics has been the struggle to create classification schemes based on presumed phylogenetic criteria as opposed to those merely phenetic. At the turn of the last century the phylogenetic content of classification schemes was being debated, as it is when we enter the 21st century.

The two great crinoid paleontologists of the late nineteenth century and first quarter of the twentieth century, Frank Springer (1848–1927) and Francis A. Bather (1863–1934), neared completion of their scientific study of crinoids by 1925. Despite the disagreements and unresolved debate (sometimes with considerable vigor, see below) on super-familial classification, when their careers were complete, the study of crinoids was in a remarkably robust state. The principal unfinished business in 1925 was settling the Springer-Bather debate on crinoid classification.

Twentieth century work on crinoids is readily divisible into four periods. As mentioned above, 1925 is a convenient break that approximately corresponds with the completion of the work of Springer and Bather, and 1925 was also within the publication renewal following World War I. The second period, 1926–1943, had a slightly increased level of work compared to 1900–1925. The publication of two benchmark studies in 1943, Moore and Laudon's, *Evolution and Classification of Paleozoic Crinoids* and Bassler and Moodey's, *Bibliographic and Faunal Index of Paleozoic Pelmatozoan Echinoderms* brought the second period of study to a close. The third period, 1944–1978, was characterized by the advent of paleobiologic approaches, such as functional morphology and paleoecology. It was completed by publication of the *Treatise on Invertebrate Paleontology, Part T* (Moore and Teichert, 1978). The fourth period includes from 1979 to the end of the century.

CRINOID STUDIES 1900 TO 1925

In order to understand the evolution of crinoid classification schemes during the early part of the 20th century, it is necessary to briefly review the state of the art at the end of the 19th century. Charles Wachsmuth and Frank Springer had established their authority as crinoid experts with their series on ''Revision of the Palaeocrinoidea'' (1880, 1881, 1885, 1886). At that time all Paleozoic crinoids were thought to have a covered mouth and were grouped in the subclass Palaeocrinoidea, whereas Mesozoic and Cenozoic crinoids had an exposed mouth and were grouped in the subclass Neocrinoidea. Discovery of Paleozoic crinoids with exposed mouths (cyathocrine cladids and flexibles; note: all taxonomic names in parentheses follow Moore and Teichert, 1978) required abandonment of the Palaeocrinoidea-Neocrinoidea dichotomy, and in its place they proposed the subclasses Inadunata, Camerata, and Articulata (flexibles and articulates) (Wachsmuth and Springer, 1891, 1897) (Table 1). Also in their 1891 paper they spent 12 pages challenging Bather's (1890b) extensive revisions of their earlier classification of the Fistulata (disparids and cladids with an anal sac or tube). Thus began an acrimonious exchange of papers that lasted more than a decade and helped lay the foundation for 20th century crinoid taxonomy (Bather, 1890a, 1890b, 1891, 1898, 1898–1899, 1899, 1900a, 1900b; Wachsmuth and Springer, 1891, 1897; Springer, 1900). Bather's (1898–1899) six-part review of Wachsmuth and Springer's (1897) *The North American Crinoidea Camerata* was hypercritical, and he used it as a means to promote his own ideas on morphology and classification.

Their critiques were strident as they referred to each other's ideas as ''faulty'' or ''ridiculous'' (Wachsmuth and Springer, 1891; Bather, 1891). Bather claimed that the accusations of ''my very friendly antagonists'' would ''damage my scientific reputation'' and that they were ''learned rather than lucid writers.'' Bather (1898–1899, p. 526) even went so far as to state that Wachsmuth and Springer (1897) had told one of their illustrators to put in structures the illustrator ''really had a difficulty in seeing.'' This led Springer (1900) to vigorously protest Bather's ''accusation of misrepresentation of facts.'' Bather (1900b) subsequently apologized for this remark but stated that his ''oft-repeated criticism of the assertions of Wachsmuth and Springer'' caused ''a definite advance in science.'' These exchanges were

TABLE *1*—Early classifications of the Crinoidea.

Wachsmuth and Springer (1891, 1897)	Bather (1899)	Moore and Laudon (1943)
Class CRINOIDEA	Class CRINOIDEA	Class CRINOIDEA
Order INADUNATA	Subclass MONOCYCLICA	Subclass INADUNATA
Suborder LARVIFORMIA	Order INADUNATA	Order DISPARATA
Suborder FISTULATA	Order ADUNATA	Order CLADOIDEA
Order CAMERATA	Order CAMERATA	Subclass FLEXIBILIA
Order ARTICULATA	Subclass DICYCLICA	Order TAXOCRINOIDEA
Suborder IMPINNATA	Order INADUNATA	Order SAGENOCRINOIDEA
Suborder PINNATA	Order FLEXIBILIA	Subclass CAMERATA
	Grade IMPINNATA	Order DIPLOBATHRA
	Grade PINNATA	Order MONOBATHRA
	Order CAMERATA	

not of the caliber of the Marsh-Cope rivalry in paleontology, but the degree of acrimony is remarkable nonetheless.

The details of their arguments usually concerned the morphology of the anal and tegminal plates in the Fistulata and the phylogenetic significance of inferred homologies among these plates. But their arguments extended to higher level classification with Bather (1898) suggesting that Wachsmuth and Springer's (1897) crinoid classification was ''a key to structure rather than an epitome of genetic affinity.'' Ultimately such harsh exchanges probably did help advance the field, as Bather (1900b) asserted.

Bather's (1890b, 1893, 1898) focus on analysis of the Fistulata of Wachsmuth and Springer, (1885; see Springer, 1913) led him to infer that the Larviformia (disparids mostly, lacking an anal sac or tube) and Fistulata (Table 1) were evolutionary grades, a viewpoint never accepted by Springer (Bassler and Moodey, 1943). Subsequently, Bather (1899) created the Monocyclica Inadunata (disparids mostly) and the Dicyclica Inadunata, which was further divided into the Cyathocrinoidea (Cyathocrinina) and the Dendrocrinoidea (Dendrocrinina and Poteriocrinina), divisions later retained by Moore and Laudon (1943) and revised in Moore et al. (1978) (Table 1). Bather (1890b, 1893) had previously accepted Wachsmuth and Springer's (1885) Inadunata, but later took the very unusual step of creating two crinoid subclasses on the basis of the number of plate circlets below the radials, thus the Monocyclica and Dicyclica (Bather, 1899), where monocyclic crinoids have one circlet beneath the radial plates and dicyclic crinoids have two. He believed these two groupings to be monophyletic as he could not bridge the evolutionary gap between their cup types. Peculiarly, both subclasses included the orders Inadunata and Camerata, which he recognized were polyphyletic, but he retained them stating it is ''well to accept existing terms so far as possible.'' Wachsmuth and Springer (1897) had not separated camerates on the basis of plate circlets, but Bather's (1899) Monocyclica Camerata and Dicyclica Camerata anticipated Moore and Laudon's (1943) Monobathra and Diplobathra. Bather (1899) also created the Monocyclica Adunata for camerates lacking fixed brachials in the cup. The one area of agreement was that both sides grouped the flexibles and articulates together with each recognizing the Impinnata (flexibles) and the Pinnata (articulates) in the Flexibilia (Bather, 1899) or Articulata (Wachsmuth and Springer, 1897). Springer (1920) later accepted the term Flexibilia, but there is little evidence he accepted Bather's higher-level taxonomy as indicated in Bassler and Moodey (1943), who basically followed Springer's ideas on higher-level classification. The Bather-Wachsmuth and Springer exchanges brought attention to major taxonomic divisions that only later were recognized in Moore and Laudon (1943) and Moore and Teichert (1978), although it took these later studies to sort it all out (see below).

Jaekel (1918) published an extensive classification introducing several new subclasses, orders and suborders, few of which were incorporated in later classifications, these being the suborders Hybocrinina and Poteriocrinina in Moore and Teichert (1978). He recognized three subclasses: Eocrinoidea (now their own class), Cladocrinoidea (basically camerates), and Pentacrinoidea (disparids, cladids, flexibles, and articulates). Jaekel's efforts apparently had little impact on later classification schemes (Lane, 1978).

Between 1900 and 1925, study of modern crinoids was largely confined to descriptive studies and dominated by the results of oceanographic expeditions, such as, among others, the voyages of the Albatross (A. H. Clark, 1908, 1911) and the Endeavor (H. L. Clark, 1916), the Siboga Expedition (Döderlein, 1907), and Bock's Expedition (Gislén, 1922). These systematic treatments expanded both the taxonomic diversity of living crinoids as well as expanding the documented geographic distribution of living crinoids. Systematic work on living crinoids culminated during this period with the beginning of the publication of A. H. Clark's Monograph on the Existing Crinoidea (Clark, 1915, 1931), although publication of the parts of this significant contribution was not completed until 1967 (Clark and Clark, 1967).

Similarly, systematic work dominated post-Paleozoic fossil crinoid studies during this interval, but, as mentioned above, agreement did not exist on the phylogenetic and systematic relationships between Paleozoic and post-Paleozoic crinoids. The orders Comatulida and Uintacrinida were defined by A. H. Clark (1908) and Broili (1921), respectively; and division of the comatulids into currently used superfamilies was completed by 1925, with the exception of the superfamily Paracomatulacea (Hess, 1951).

CRINOID STUDIES 1926 TO 1943

Several workers, including Goldring, Schmidt, Wright, Kirk, Laudon, Moore, and Wanner, made significant contributions to the study of fossil crinoids during this period. Winifred Goldring became the first woman State Paleontologist of New York in 1934 and later the first woman president of the Paleontological Society in 1949. She wrote extensively on Devonian crinoids from 1923 to 1951, with her first publication the massive *Devonian Crinoids of the State of New York* (1923). Her body of work is still important to students of Devonian crinoids. W. Erich Schmidt (1934, 1942, and others) wrote from 1906 to 1952, mostly on European Devonian crinoids. James Wright wrote numerous papers from 1911–1960 on British and Irish Carboniferous crinoids. His first major monograph *The Scottish Carboniferous Crinoidea* (1939) appeared just before WWII. After the war the synthesis of his life's work, *A Monograph of the British Carboniferous Crinoidea,* was published in 10 installments (Wright, 1950–1960). Wright's body of work is still an authoritative source on British Carboniferous crinoids. Edwin Kirk produced a substantial body of work from 1929 to 1948, mostly on Carboniferous cladids (e.g., Kirk, 1938). Lowell Laudon is best known for his work on Kinderhookian crinoids (e.g., Laudon and Beane, 1937). Raymond C. Moore began an extensive study of upper Paleozoic crinoids (e.g., Moore and Plummer, 1940). Johannes Wanner wrote extensively on Permian crinoids from Timor (e.g., Wanner, 1931).

In 1943 Moore and Laudon's *Evolution and Classification of*

TABLE 2—Examples of faunal studies of crinoids during the 1944–1978 interval that were responsible for expanding the systematic data base during this interval. Many others could also be cited.

Time	North America	Europe, Australia, Timor
Cenozoic	Oregon (Moore & Vokes, 1953)	Europe (Rasmussen, 1972)
Cretaceous	Mississippi (Moore, 1967) Texas (Peck, 1943; Peck & Watkins, 1972)	Bohemia (Nekvasilova & Prokop, 1963) England (Peck, 1955) Europe (Rasmussen, 1961, and others)
Jurassic	Wyoming (Koch, 1962)	Switzerland (Hess, 1972, and others) Europe (Sieverts-Doreck, 1951, and others)
Triassic	Mexico (Peck, 1948)	Poland (Lefeld, 1958)
Permian	Nevada (Lane & Webster, 1966)	Australia (Teichert, 1949; Willink, 1978) Timor (Wanner, 1949, and others)
Pennsylvanian (Upper Carboniferous)	Appalachian Basin (Burke, 1968, 1973, and others) Arkansas, Oklahoma, and Texas, (Moore & Strimple, 1973 and others) Illinois (Strimple & Moore, 1971)	United Kingdom (Wright, 1950 to 1960)
Mississippian (Lower Carboniferous)	Alberta (Laudon et al., 1952) Indiana (Van Sant & Lane, 1964) Mississippi River Valley (Laudon, 1973)	
Devonian	Ohio (Kesling & Mintz, 1963; Kesling, 1965, and others)	Czech Republic (Prokop, 1970 and others) Spain (Breimer, 1962)
Silurian	Oklahoma (Strimple, 1963)	Sweden (Ubaghs, 1956, and others)
Upper and Middle Ordovician	Illinois and Wisconsin (Kolata, 1975) Minnesota (Brower & Veinus, 1978) Missouri (Brower, 1973; Strimple & Watkins, 1955) Tennessee and Virginia (Brower & Veinus, 1974)	United Kingdom (Ramsbottom, 1961)
Early Ordovician	California (Strimple & McGinnis, 1972) Utah (Lane, 1970)	France (Ubaghs, 1969, 1972) United Kingdom (Bates, 1968)

Paleozoic Crinoids was published. This seminal work was greatly influenced by Wachsmuth and Springer's and Bather's ideas on classification. Moore and Laudon's classification of Paleozoic crinoids encompassed three subclasses, including the Inadunata and Camerata of Wachsmuth and Springer (1885) and Zittel's (1895) Flexibilia (Table 1). Bather's emphasis on monocyclic and dicyclic cups led to Moore and Laudon's Disparata and Cladoidea within the Inadunata, and their Monobathra and Diplobathra within the Camerata. Moore and Laudon also incorporated Bather's (1899) Cyathocrinoidea and Dendrocrinoidea as the two primary divisions of their Cladoidea. Thus, Wachsmuth and Springer's ideas regarding subclasses prevailed, whereas Bather's ideas regarding orders and suborders prevailed. Moore and Laudon created the Disparata, Cladoidea, Monobathra, and Diplobathra because of the obvious unacceptability of Bather's (1899) Monocyclica Inadunata, Dicyclica Inadunata, Monocyclica Camerata, and Dicyclica Camerata, respectively. They also placed Bather's (1899) Monocyclica Adunata in the Monobathra because these crinoids with superficially simple calyces were a polyphyletic grouping with origins among different monocyclic camerates. Prior to Moore and Laudon (1943), North American workers had followed Wachsmuth and Springer's (1897) classification, whereas European workers had followed Bather (1899, 1900a).

Another key publication in 1943 was Bassler and Moodey's (1943) *Bibliographic and Faunal Index of Paleozoic Pelmatozoan Echinoderms.* This was based on Springer's card files that still remain in the Smithsonian. This card file was completed, with the help of Springer's daughter Ada, through 1915, with updates by Moodey (Bassler and Moodey, 1943, p. 1). This comprehensive compilation of literature and faunal lists greatly helped to facilitate a rapid increase in crinoid studies following WWII.

Study of post-Paleozoic crinoids continued with further monographs by A. H. Clark, plus numerous systematic studies. Key during this period was the publication of *Fossilium Catalogous* volumes on post-Paleozoic crinoids (Biese, 1934, 1935–1937; Biese and Sieverts-Doreck, 1937, 1939a, 1939b; Sieverts-Doreck and Biese, 1939).

CRINOID STUDIES 1944 TO 1978

1944–1978 systematic studies.—1943 marked the close of the influence of Frank Springer, but it began the dominant influence of Raymond C. Moore on the study of the Crinoidea. In North America, Moore, his students, and his colleagues made substantial strides describing new Paleozoic faunas and beginning paleobiologic studies of crinoids, ultimately leading to publication of the crinoid *Treatise on Invertebrate Paleontology* (Moore and Teichert, 1978).

In Europe, two Treatises were also published during this interval: *Treaté de Paléontologie, Tome III* (Ubaghs, 1953) and *Klass Crinoidea. Morskie lilii. Sistematicheskaia chasti* (Class Crinoidea. Crinoids. Systematic part) (Arendt and Hecker, 1964). Both were important syntheses, but Ubaghs (1953) had a broader, more significant impact, both in itself and because it was a basis from which Ubaghs prepared major portions of the *Treatise* (Moore and Teichert, 1978).

During this interval, which included both the post-World War II revitalization of academic science and the expansion of North American colleges and universities to accommodate the ''baby-boom'' generation, an increase in studies significantly broadened the crinoid data base, both through refinement of known faunas and by discovery of new faunas (especially in North America and Europe). A comprehensive listing is not possible, but examples are cited in Table 2. Most significant among these were description of Early and Middle Ordovician faunas that began to shape the understanding of the initial two radiations of crinoids. The ''Age of Crinoids,'' the Mississippian, received considerable study in North America, the United Kingdom, and Ireland. Knowledge of Pennsylvanian and Permian crinoids, previously known from relatively few faunas and largely from poorly preserved material, was expanded considerably.

Independent classifications of crinoid columnals and pluricolumnals were proposed by Stukalina (1966) and Moore and Miller (1968), and this approach was developed extensively by several additional workers. A principal aim in columnal and pluricolumnal studies has been to develop a means by which to capitalize

TABLE 3—Crinoid classification by Moore and Teichert (1978).

- Class CRINOIDEA Miller, 1821
  - Subclass ECHMATOCRINEA Sprinkle and Moore, 1978
    - Order ECHMATOCRINIDA Sprinkle and Moore, 1978
  - Subclass CAMERATA Wachsmuth and Springer, 1885
    - Order DIPLOBATHRIDA Moore and Laudon, 1943
    - Order MONOBATHRIDA Moore and Laudon, 1943
  - Subclass INADUNATA Wachsmuth and Springer, 1885
    - Order DISPARIDA Moore and Laudon, 1943
    - Order HYBOCRINIDA Jaekel, 1918
    - Order CORONATA Jaekel, 1918
    - Order CLADIDA Moore and Laudon, 1943
  - Subclass FLEXIBILIA Zittel, 1895
    - Order TAXOCRINIDA Springer, 1913
    - Order SAGENOCRINIDA Springer, 1913
  - Subclass ARTICULATA Zittel, 1879
    - Order MILLERICRINIDA Sieverts-Doreck, 1952
    - Order CYRTOCRINIDA Sieverts-Doreck, 1952
    - Order BOURGUETICRINIDA Sieverts-Doreck, 1952
    - Order ISOCRINIDA Sieverts-Doreck, 1952
    - Order COMATULIDA A. H. Clark, 1908
    - Order UINTACRINIDA Broili, 1921
    - Order ROVEACRINIDA Sieverts-Doreck, 1952
- *Class HEMISTREPTOCRINOIDEA Arendt, 1976
    - Order HEMISTREPTOCRINIDA Arendt, 1976

* New Class of Crinoidea proposed by Arendt (1976).

on the abundance of columnal fragments for biostratigraphic purposes. Although, it has had some success, it also has yielded a sometimes confusing parataxonomy for crinoids. A later exception discussed below was the Ordovician-Silurian boundary study by Donovan (1986, 1989, 1994).

Post-Paleozoic crinoid systematics were stabilized by the works of Sieverts-Doreck (1952, 1953). Of the seven orders recognized in Rasmussen (1978), only two had been recognized prior to 1950 (see Table 3). Sieverts-Doreck (1952, 1953) named the orders Millericrinida, Cyrtocrinida, Bourgueticrinida, Isocrinida, and Roveacrinida (Table 3). These seminal studies established the Articulata subdivisions into orders that have since remained in place with only the recent addition of the Encrinida (Hagdorn, 1988) and the Ampelocrinida for stem articulates (Webster and Jell, 1999) (see below).

With the exception of Rasmussen, Peck, and Hess, relatively little work was completed on post-Paleozoic fossil crinoids during this interval (Table 2), however this time witnessed the completion of systematic studies of living crinoids by A. H. Clark and T. Gislén, and A. M. Clark.

The systematic treatment of the Articulata in the *Treatise* was a much needed complete compilation, as discussed in Rasmussen (1978, p. T813). Rasmussen (1978) brought together largely the work of H. Sieverts-Doreck, A. H. Clark, and his own (in addition to contributions by H. A. Lowenstam and R. E. Peck). This synthesis added only a few new suprageneric categories, and this comprehensive consideration was invaluable.

The work by systematists on Paleozoic crinoids was significantly advanced by the *Bibliography and Index of Paleozoic Crinoids* by Webster (1973, 1977). These and subsequent compilations are a continuation of Bassler and Moodey (1943) and provide ready access to both the history of names and the history of taxonomic concepts for Paleozoic crinoids.

1944 to 1978 paleobiology.—The beginnings of modern ecologic and paleobiologic studies occurred during this interval. However, relatively little of this work was incorporated into the *Treatise*, and certainly, the impact of this early work for paleobiologic and paleoecologic studies for the remainder of the century was not anticipated in the *Treatise*.

Pioneering ecologic work was completed on both unstalked and stalked crinoids through in vivo observation and study. Unstalked crinoids were studied in the Red Sea (Magnus, 1963, 1967; Rutman and Fishelson, 1969) and in the Caribbean Sea (Meyer, 1973a, 1973b; Macurda, 1973). Scientific study from submersibles opened access to deep sea, stalked crinoids, with studies largely in the depths of the Caribbean Sea (Macurda and Meyer, 1974, 1976). These ecologic studies significantly changed our understanding of crinoids—crinoids should not be viewed as rheophobic (current avoiding) but as rheophilic (current seeking) organisms. Crinoids rely on ambient currents for feeding, and they actively orient their arms into a filtration fan when currents are present. Shallow-water unstalked crinoids most commonly develop planar filtration fans when exposed to unidirectional currents, and deep-water stalked isocrinids position their arms into a parabolic fan. When currents are slack, feeding is much reduced or absent.

Actualistic taphonomy studies were also initiated during this interval (Blyth Cain, 1968; Meyer, 1971; Liddell, 1975). These and later studies provided an explanation as to why complete crinoid fossils are relatively rare, i.e., a dead, unstalked crinoid lying on the sea floor completely disarticulated into isolated ossicles in only a few days. Thus, very rapid burial is required for complete preservation of fossil crinoids. Crinoid lagerstätten are now known to be obrution deposits, the result of rapid burial of live crinoids.

These early ecologic and taphonomic studies were quickly adapted to the interpretation of fossil crinoids, resulting in a number of pioneering paleobiologic studies. Important examples among these are the paleoecology of stalked crinoids (Lane, 1963, 1973), paleoecology of epiplanktonic crinoids (Seilacher et al., 1968), paleocommunity analysis (Lane, 1972, 1973), taphonomic studies (Lane, 1973), and biometric studies and ontogeny (Brower, 1973, 1974). Innovative paleobiologic studies by Haugh (1973, 1975a, 1975b) used chertified molds and casts of crinoid to reconstruct the details of soft-part, internal anatomy of Lower Mississippian camerates.

Application of scanning electron microscopy to paleontology opened a new field of inquiry on the morphology of crinoid articular facets. The work of Macurda and Meyer (1975, 1981) delineated microstructure patterns on facets; however, few studies have attempted to carry this work further and to apply it to paleobiologic questions because of the apparent paucity of unaltered stereom.

The 1978 Treatise.—The *Treatise* (Moore and Teichert, 1978) was an extraordinary compilation that consolidated what was known about crinoids and forced decisions on issues less well known. Like any treatise that comprehensively summarizes a topic, publication immediately exposed gaps in knowledge and established an agenda for continued work. Some of the problems could only be recognized in the context of this new comprehensive treatment. Some problems were created by the mere act of compilation, such as in the following anecdote related by H. L. Strimple. After being enthusiastically criticized by a colleague about the familial placement of a specific genus in the *Treatise*, Strimple was reported to have replied ''We had to put it somewhere!'' (personal commun., A. S. Horowitz, 1978).

The basic classification of Moore and Laudon (1943) was adopted in the *Treatise* (Moore and Teichert, 1978), with all but one of the post-Paleozoic crinoids placed in the subclass Articulata, addition of the Cambrian subclass Echmatocrinea, elevation of the hybocrinids and coronoids to orders within the Inadunata, and mention of the hemistreptocrinids (Table 3). Thus, Frank Springer and Francis Bather continued to influence thinking on the Crinoidea. As argued by Ausich (1998a, 1998c), the structure of this classification was based largely on knowledge of the morphology of Silurian to Mississippian crinoids. Thus, the phylogenetic relationships of this classification were derived largely by

TABLE 4—Crinoid classification by Simms and Sevastopulo (1993).

- Class CRINOIDEA
  - Subclass CAMERATA
    - Order DIPLOBATHRIDA
    - Order MONOBATHRIDA
  - Subclass DISPARIDA
  - Subclass CLADIDA
    - ‘‘STEM-GROUP CLADIDS’’
    - Infraclass CYATHOCRININA
    - Infraclass FLEXIBILIA
    - Infraclass ARTICULATA
  - Incertae Sedis (‘Subclass’) HYBOCRINIDA

inferring lineages from these middle Paleozoic crinoids back into the lower Paleozoic.

CRINOID STUDIES 1979 TO 2001

Crinoid systematic study since 1978.—The *Treatise* classification left those expecting a phylogenetic classification puzzled in many instances. Four examples illustrate this point. First, two diplobathrid camerate genera (one Ordovician and one Devonian) were grouped into the suborder Zygodiplobathrida, separate from all other diplobathrids. These two crinoids share an unusual calyx construction with radial and basal plates in a single circlet, but does this make sense phylogenetically? Second, all post-Paleozoic crinoids were placed in the Articulata, except *Encrinus* (Middle Triassic), which was placed in the Cladida. What was the origin and early evolution of the Articulata with this sort of temporal classification? The third and fourth issues concern the integrity of the Inadunata (sensu Moore and Teichert, 1978). Third, the monophyly of the Inadunata was questioned by Kelly (1982, 1986), Donovan (1988), Sevastopulo and Lane (1988), Simms and Sevastopulo (1993), and Simms (1994), who regarded the cladids as not closely related to the disparids. Ultimately, Simms and Sevastopulo (1993) eliminated the Inadunata and elevated the Cladida and Disparida to subclass level. Fourth, higher-level taxa within the Cladida lacked diagnostic definitions, which raised serious questions about the monophyly of cladid suborders (McIntosh, 1979, 1986; Kammer and Ausich, 1992), particularly the placement of all pinnulate cladids in the Poteriocrinina, which may have been derived from different lineages in the Dendrocrinina. Further work is needed on this problem.

Simms and Sevastopulo (1993) concluded that the Articulata was monophyletic and that the Disparida and Cladida were subclasses based on a strict monophyletic analysis. These decisions are uniformly accepted. However, other results from this strict monophyletic approach have been questioned. Rather than including the Flexibilia and Articulata in the Cladida, Ausich (1998a, 1998c) (Tables 4 and 5) recognized these all as subclass in rank. Also, Simms and Sevastopulo (1993) recognized ‘‘stem-group articulates’’ among Paleozoic cladids, whereas Webster and Jell (1999) recognized these advanced forms as articulates. Simms and Sevastopulo (1993) defined the Articulata on the basis of three characters: 1, dicyclic or cryptodicyclic aboral cup; 2, no anal plates in the aboral cup; and 3, the entoneural system enclosed within brachials and radial plates. Thus, articulates are monophyletic and post-Paleozoic. Alternatively, Webster and Jell (1999) did not regard the absence of anal plates in the aboral cup to be a synapomorphy for the Articulata. They defined the Articulata as crinoids with ‘‘brachial pairs with alternating muscular and cryptosyzygial articulations.’’ In this view Paleozoic crinoids as old as *Corythocrinus* Kirk (late Osagean, Tournaisian) are articulates and are assigned to the articulate order Ampelocrinida (Webster and Jell, 1999) (Table 6). These primitive articulates are characterized by the following: 1) dicyclic or cryptodicylic aboral cup; 2) one to three anal plates in the aboral cup; 3) entoneural system enclosed within brachials and radial plates; 4) first arm division on the second to fourth primibrachial; 5) cuneate uniserial arms; 6) syzygial brachial pairs with muscular articulations alternating with a cryptosyzgial ligamentary articulation; 7) pinnulate arms; 8) brachial articular facets with well-defined muscular and ligamentary fossae; and 9) cirri with multiradiate articular facets distally and articular facets with a transverse ridge throughout (Webster and Jell, 1999). Webster and Jell’s hypothesis regarding the recognition of Paleozoic articulates from among the cladids has yet to be evaluated by other crinoid workers.

TABLE 5—Crinoid subclass classification in Ausich (1998c).

- Class CRINOIDEA
  - Subclass AETHOCRINEA
  - Subclass CLADIDA
  - Subclass CAMERATA
  - Subclass FLEXIBILIA
  - Subclass ARTICULATA
  - Subclass DISPARIDA

This addition to the orders of the Articulata (sensu Rasmussen, 1978) was added to a previous one by Hagdorn (1988). Hagdorn (1988) elevated Encrinacea Matsumoto (1929) to the Order Encrinida.

Important taxa removed from the Crinoidea since 1978 include the coronate echinoderms (Brett et al., 1983); the Hemistreptocrinoidea (Arendt and Rozhnov, 1995), and *Echmatocrinus* (Conway Morris, 1993; Simms et al., 1993; and Ausich and Babcock, 1998, 2000; but see Sprinkle and Collins, 1998).

Crinoid classification and phylogeny is based on an understanding of the basic homologies of aboral cup plates among the Crinoidea, and even this basic tenet was brought under discussion during the last decade. Simms (1994) concluded that plate homologies between the two basic types of aboral cup construction, monocyclic and dicyclic, were not always as had traditionally been assumed. Alternatively, Ausich (1996) countered the arguments of Simms (1994) and proposed other deviations from the strict homologies of Moore and Teichert (1978). Ausich (1996) proposed that the most primitive crinoid had a four-circlet (tricyclic) aboral cup composed of, from top to bottom, radials, basals, infrabasals, and lintels (three circlets beneath the radials). In the Ausich (1996) scheme, only disparids depart from Moore and Teichert (1978) homologies, by having a calyx constructed of either radials, infrabasals, and lintels or only infrabasals and lintels.

The Crinoidea as a whole is regarded as monophyletic, but from whence this clade was derived and where it fits within the Echinodermata are matters of debate. A multiple, irregular plated ancestor has been the traditional expectation for the crinoid ancestor, and *Echmatocrinus* seemed like a possible ancestor for nearly two decades (Sprinkle and Moore, 1978; Ubaghs, 1978). However, the affinities of *Echmatocrinus* were questioned by several authors (Conway Morris, 1993; Signor and Vermeij, 1994;

TABLE 6—Classification of the suborder Articulata from Webster and Jell (1999).

- Subclass ARTICULATA Zittel, 1879
  - Order AMPELOCRINIDA Webster and Jell, 1999
  - Order ENCRINIDA Matsumoto, 1929
  - Order MILLERICRINIDA Sieverts-Doreck, 1952
  - Order CYRTOCRINIDA Sievents-Doreck, 1952
  - Order BOURGUETICRINIDA Sieverts-Dork, 1952
  - Order ISOCRINIDA Sieverts-Doreck, 1952
  - Order COMATULIDA A.H. Clark, 1908
  - Order UINTACRINIDA Broili, 1921
  - Order ROVEACRINIDA Sieverts-Doreck, 1952

Donovan, 1995), and in 1998 Ausich and Babcock (see also Ausich and Babcock, 2000) concluded that *Echmatocrinus* was an octocoral. Reconsideration of crinoid origins where *Echmatocrinus* is not an echinoderm led Ausich (1998a, 1998b, 1999) to conclude that crinoids were derived from primitive rhombiferans and that the first crinoids had tricyclic aboral cups. The notion that crinoids evolved from *Echmatocrinus* is maintained by Sprinkle and Guensburg (1997), Guensburg and Sprinkle (1997, 1998), and Sprinkle and Collins (1998); and they have also argued that the multiple, irregular plated ancestor was ultimately derived from edrioasteroids (Guensburg and Sprinkle, 1997, 2001). Ultimately, the interpretation of important, new Early Ordovician echinoderms (Guensburg and Sprinkle, 2001) may lead to a better understanding of the crinoid clade origins. Also, this new material may help resolve echinoderm plylogenetic questions raised by David et al. (2000), who place the stylophorans as a sister group of crownward crinoids.

Systematic studies have largely been faunistic in nature, with the exception of the revision of the Dichocrinidae (Broadhead, 1981). Significant systematic contributions from this interval include thorough systematic revisions of entire faunas and description of new faunas either in new geographic areas or in critical stratigraphic intervals. Revisions of faunas at critical intervals, such as the late Osagean-early Meramecian of the midcontinental United States (Ausich and Kammer, 1990; Kammer and Ausich, 1992; and others), is prerequisite to evolutionary paleoecologic studies (Ausich et al., 1994; Kammer et al., 1997, 1998). Key stratigraphic intervals where important new faunas filled gaps in the understanding of crinoids includes the Early Ordovician, Early Silurian, and Permian (Table 7). Especially significant new findings among Permian crinoids is that the majority of crinoids from Timor are actually Early Permian rather than Late Permian, thus moving the principal biotic crisis for crinoids from the end-Permian to the end-Early Permian (Webster, 1990; Webster and Jell, 1992).

Descriptive studies of faunas from new geographic regions are key as evolutionary paleoecologic questions become more global in scope. Examples of this ‘‘frontier crinoid paleontology’’ include the Devonian of China (Lane et al., 1997), Mississippian of China (Chen and Yao, 1993), Permian of Australia (Willink, 1979; Webster and Jell, 1992, 1999), Permian of Thailand (Webster and Jell, 1993), Eocene of Antarctica (Meyer and Oji, 1993; Baumiller and Gaździcki, 1996), and living, deep-water faunas from New Caledonia (Roux, 1994) (see Table 7).

Lane and Sevastopulo (1982) and Sevastopulo and Lane (1988) are examples of a series of studies on Paleozoic microcrinoids. These are adult, undoubtedly paedomorphic, crinoids with an aboral cup height generally less than one millimeter. This work has resulted in a more robust taxonomy of these very small crinoids, and more important, it has led to a more complete understanding of early ontogeny, especially among disparids.

Substantial systematic revisions among living crinoids were few, with the exception of the comasterids. Rowe et al. (1986) revised the comasterids (Order Comatulida) by recognizing the type and arrangement of pinnule combs as key diagnostic features for genera, thus differing from Clark (1931).

The Webster (1986, 1988, 1993) *Bibliography and Index of Paleozoic Crinoids* continued to be published and a comprehensive volume that includes the entire history of Paleozoic crinoid study is anticipated. These nomenclatoral works have incalculable value for furthering the study of Paleozoic crinoids. Publication of *Fossil Crinoids* (Hess et al., 1999) should also promote future study of crinoids, generating both interest and understanding in this the most diverse and abundant group of pelmatozoan echinoderms.

1979 to 1999 paleobiology.—Ecologic and paleoecologic studies of crinoids flourished during the final quarter of the twentieth century. A very productive synergism developed among crinoid biologists, crinoid paleontologists, and those who worked in both fields. Some of the more important ecologic and biologic findings include 1) feeding mechanisms of crinoids (Meyer, 1979; Baumiller and Woodley, 1991); 2) ecology of living crinoids (Meyer and Macurda, 1980; Messing et al., 1990); 3) stalked crinoids can detach their holdfasts and move to more favorable sites (Messing et al., 1988); 4) a crownless crinoid may remain erect and alive for more than one year (Conan et al., 1981; Fujita et al., 1987; Messing et al., 1988; and Oji and Amemiya, 1998); 5) even pluricolumnal segments on the sea floor may remain alive for a long period of time (Oji and Amemiya, 1998); 6) delineation of connective tissue types among living crinoids (Holland and Grimmer, 1981; Grimmer et al., 1985; and others); and 7) regeneration capabilities of crinoids (Amemiya and Oji, 1992; Candia Carnevalli et al., 1993; and others).

Parallel to these are the following important paleoecologic/paleobiologic advances: 1) niche differentiation, feeding mechanisms, and community structure in fossil faunas (Ausich, 1980; Ausich and Bottjer, 1982; Kammer, 1985), which delineated the paleoecologic structure of the majority of benthic crinoids; 2) reexamination of the paleoecology of unusual fossil crinoids, such as uintacrinids (Milsom et al., 1994; Meyer et al., 1999), marsupiocrinds and antedonids (Milsom, 1994; Milsom et al., 1994), calceocrinids (Ausich, 1986a), myelodactylids (Donovan and Franzén-Bengtson, 1988), pseudoplanktonic crinoids (Haude, 1980; Simms, 1986; Hess et al., 1999), among others; 3) differentiation of crinoid paleocommunities (Ausich et al., 1979; Brett, 1985; Kammer and Ausich, 1987; Chesnut and Ettensohn, 1988; Holterhoff, 1996).

Early actualist taphonomic studies were developed further both for shallow- and deep-water crinoids (Meyer and Meyer, 1986; Lewis et al., 1990; Baumiller et al., 1995). These studies were applied in many ways to establish preservational constraints and to expand extractable information from the fossil record: 1) to delineate burial conditions for complete crinoid preservation and to recognize that tempestites are one of the most common agents of crinoid preservation (Lewis, 1980; Taylor and Brett, 1996; and many others); 2) definition of preservational expectations among major clades and taphonomic facies that follow (Meyer et al., 1989; Ausich and Sevastopulo, 1994); 3) delineation of crinoid deposit types (Ausich, 1997; Brett et al., 1997); and 4) determination of soft-tissue types and characteristics in Mesozoic and Paleozoic crinoids (Baumiller and Ausich, 1992; Ausich and Baumiller, 1993; and others).

Macroevolutionary advances include 1) those delineating the morphological disparity of crinoids through the Phanerozoic (Foote, 1995, 2000); 2) recognition of three macroevolutionary faunas during the Paleozoic (Baumiller, 1993; Ausich et al., 1994); 3) consideration of the patterns and processes bounding these faunas, such as the origin of crinoids (Ausich, 1998a, 1998b, 1998c, 1999; Sprinkle and Collins, 1998), the Early Ordovician radiation of epifaunal suspension feeders (Guensburg and Sprinkle, 1992), the end-Ordovician extinction and Early Silurian recovery of crinoids (Eckert, 1988; Donovan, 1988, 1989, 1994), the end-Osagean rapid faunal turnover (Ausich et al., 1994; Kammer et al., 1997, 1998), and 4) the demise of shallow-water stalked crinoids (Meyer and Macurda, 1977).

CHALLENGES FOR THE TWENTY-FIRST CENTURY

The close of the 20th century saw a decline in the rate of crinoid publications, which reflects retirements among the post-WWII generation of academic paleontologists rather than a diminishing interest in crinoid paleontology. Many significant ques-

TABLE *7*—Examples of faunal studies of crinoids during the 1979–99 interval. Many more of these important studies are from outside North America and Europe than during previous intervals. Many more studies could also be cited.

Time	North America	Europe	Elsewhere
Modern			Indonesia (Améziane, 1997) Philippines (Bourseau & Roux, 1989) Japan (Fujita, et al., 1987) New Caledonia (Roux, 1994) Spain (Roux, 1977; Conan et al., 1981)
Cenozoic		Belgium and Netherlands (Jagt, 1995, 1999)	Antarctica (Meyer & Oji, 1993; Baumiller & Gaździcki, 1996)
Cretaceous		Czech Republic (Zitt, 1979, 1980, and others) Crimea (Klikushin, 1987)	Japan (Oji, 1985)
Jurassic		Crimea (Klikushin, 1996) Europe (Sieverts-Doreck, 1981, and others) France (Manni et al., 1985) Poland (Pisera & Dzik, 1979) Switzerland (Hess, 1983, and others) Turkey (Nicosia, 1991) United Kingdom (Simms, 1989)	
Triassic		Austria, Turkey, Indonesia (Kristan-Tollman, 1990) Germany (Hagdorn, 1993) Worldwide (Hagdorn, 1995)	
Permian			Australia (Webster, 1990; Willink; 1979, and others; Webster and Jell, 1992) Oman (Jell & Willink, 1993) Thailand (Webster & Jell, 1993) Tunisia (Lane, 1979)
Pennsylvanian (Upper Carboniferous)	Nebraska, Kansas, and Iowa (Pabian & Strimple, 1985, and others)		
Mississippian (Lower Carboniferous)	Alabama (Burdick & Strimple, 1982) Indiana, Iowa, Illinois (Ausich & Kammer, 1990; Kammer & Ausich, 1992, and others) Kentucky (Chesnut & Etlensohn, 1988; Meyer & Ausich, 1997, and others) Nevada (Webster & Lane 1987) Utah and Wyoming (Webster, 1997)		China (Chen & Yao, 1993)
Devonian	United States (McIntosh, 1984, and others)	Czech Republic (Prokop & Petr, 1997, and others) France (LeMenn, 1985) Germany (Hauser, 1997) Worldwide (Haude, 1992)	Australia (Jell et al., 1988; Jell, 1999) China (Lane et al., 1997) South Africa (Jell & Theron, 1999)
Silurian	Iowa (Witzke & Strimple, 1981) New York (Brett, 1981; Eckert, 1984, and others) Ohio (Ausich, 1984, 1986a, and others) Iowa, Minnesota (Brower, 1996, and others)	Europe (Rozhnov, 1981)	
Middle Ordovician	Oklahoma (Sprinkle, 1982) Newfoundland (Ausich et al., 1998) Tennesse (Guensburg, 1984)		
Early Ordovician	California (Ausich, 1986b)	Russia (Rozhmov, 1989, 1998)	

tions are still in need of study. The immediate challenge for the study of crinoids is to establish a phylogenetic classification for the entire class. Homeomorphy is rampant among the Crinoidea with much of it still unrecognized, and disagreements are present about crinoid origination and early evolution. Both discovery of new faunas in critical intervals and uniform application of various phylogenetic techniques will be needed to sort out the pressing issues and to develop a working consensus. Especially important concerns are homology of aboral cup plates, origination of the Crinoidea, early morphologic diversification, phylogeny of the cladids, and definition and early phylogeny of the Articulata. Molecular techniques should be able to help resolve phylogenetic questions within the articulates, but most major phylogenetic questions are among various Paleozoic groups for which little help can be expected from molecular information.

Alpha taxonomy must still play a vital role in the crinoid research agenda. The current taxonomy of many faunas does not comply with modern species concepts, and a suspicion exists that many genera and species may be incorrectly defined on the basis of geography. Both of these factors preclude asking 21st century questions of these data. Description of new faunas at critical intervals is essential to learn more about the patterns and processes at macroevolutionary junctures in crinoid history, and new faunas from continents exclusive of North America and Europe will further our global perspective on the evolution of the Crinoidea.

The next generation of advances in macroevolution and evolutionary paleoecology will not occur until a well-tested phylogenetic classification is established. However, with a well-constrained phylogenetic classification, the significance of future crinoid studies is considerable, both for understanding the evolutionary history of crinoids and for understanding Phanerozoic benthic communities in general. This promise is a function of the fact that the crinoid data set is unique in many respects as compared to other invertebrates. First, because of the rapid disarticulation of dead crinoids, faunas with complete or nearly complete specimens are typically preserved on smothered sea bottoms, so taphonomic problems, time-averaging concerns, etc. are manageable. The record of crinoid crowns is a series of these data-rich occurrences. Second, unlike most invertebrate fossils, a major part of the food-gathering apparatus, the arms, is commonly preserved on crinoids. Thus, crinoid paleontologists can make direct inferences on the feeding ecology of ancient crinoids. The trophic history of the Crinoidea is well preserved in the fossil record. Third, crinoids typically occupy the highest tier in epifaunal communities, thus the overall tiering structure (Ausich and Bottjer, 2001) of epifaunal suspension-feeding communities can be delineated using crinoids. Finally, despite the strict preservational requirements for complete crinoid preservation, well-preserved crinoid faunas are relatively common through the Phanerozoic. These unique aspects of the crinoid fossil record insure that crinoid paleontology is not insular. Understanding the evolutionary patterns and interpreting the processes responsible for these patterns will lead to fundamental advances that will help delineate the evolutionary history of shallow-water, epifaunal, suspension-feeding communities from the Early Ordovician through at least the Early Cretaceous. It is also a window into understanding the micro- and macroevolutionary importance of trophic evolution that is typically unavailable among benthic invertebrates.

Within the context of evolutionary paleoecology, will it be possible to better identify factors responsible for the turnover of crinoid evolutionary faunas? Will collaboration with other geologists, such as sedimentary isotope geochemists or paleoceanographers, provide the necessary insight and data? Will improved classification schemes allow better understanding of extinction and radiation events?

Will we make strides in analysis of functional morphology by creating virtual crinoids rather than analog models in flumes? For example, current morphometric techniques have been used to create computer animations of the skeleton of *Triceratops*, and even flesh out the bones with muscle and integument to show their function while walking (Chapman et al., 1999; Perkins, 2000; Walters et al., 2000). Might it be possible with current or future computer hardware and software to recreate crinoid assemblages on a virtual sea floor to test the fluid dynamics and feeding efficiencies of Paleozoic crinoids? Might we be able to model the preferred conditions of different types of calyx and arm structures and learn more about niche differentiation of long extinct animals? For example, could we determine why both the robust-plated camerates and the gracile cladids were so diverse during the Mississippian?

We need a better understanding of crinoid biogeography. Certainly crinoids lived on a worldwide basis during the Phanerozoic, yet Paleozoic crinoids are best known from North America and Europe, whereas Mesozoic crinoids are best known in Europe. How much of this is real and how much is a function of where we have looked? In recent years this picture has begun to change with the various frontier work discussed above, but much of Asia, Africa, and South America have yet to be carefully searched for crinoids. This is an important agenda for the 21st century as we attempt to fill both the temporal and spatial gaps in our knowledge of the fossil record of crinoids.

Our understanding of crinoids increased exponentially during the 20th century. Will it do so again in the 21st? There are many interesting and important questions yet to be adequately addressed.

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