# BIOSTRATIGRAPHY AND PALEOBIOGEOGRAPHY OF EOCENE COMATULID CRINOIDS FROM FLORIDA

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## I. ABSTRACT

Fossil comatulid crinoids are reported herein from two localities and stratigraphic units in Florida. This paper is an interpretation of their paleobiogeographic implications and a description of their biostratigraphic distribution. The crinoid *Himerometra bassleri* Gislén is present in the Lower Ocala Limestone (Eocene) in west central Florida and a second, unidentified species has been found in the Upper Ocala Limestone (Eocene) of northwestern Florida. The specimens of *H. bassleri* represent an addition to the geographic distribution of this genus already known from the Eocene of Louisiana and South Carolina in the Gulf and Atlantic Coastal Plains of the United States. Skeletal elements of *H. bassleri* examined for this study consist of centrodorsals and their associated basal rays and radial plates. The unidentified comatulid specimens from the Upper Ocala Limestone are limited to a single centrodorsal and several brachial plates. *Himerometra bassleri* occurs with other fossils known to have Tethyan affinities, such as the mollusks *Velates* and *Nayadina*. This association, as well as the geographic locations of other fossil and modern species of *Himerometra*, supports an interpretation that the distribution of the crinoids is related to circulation patterns of the Tethys Seaway. A paleobiogeographic shift westward, enabled by the circum-equatorial circulation, resulted in fossil taxa preserved in Atlantic margin areas during the Paleogene; modern taxa, in contrast, have been isolated to the west in the Indo-Pacific region after closure of the Tethys Seaway.

## II. INTRODUCTION

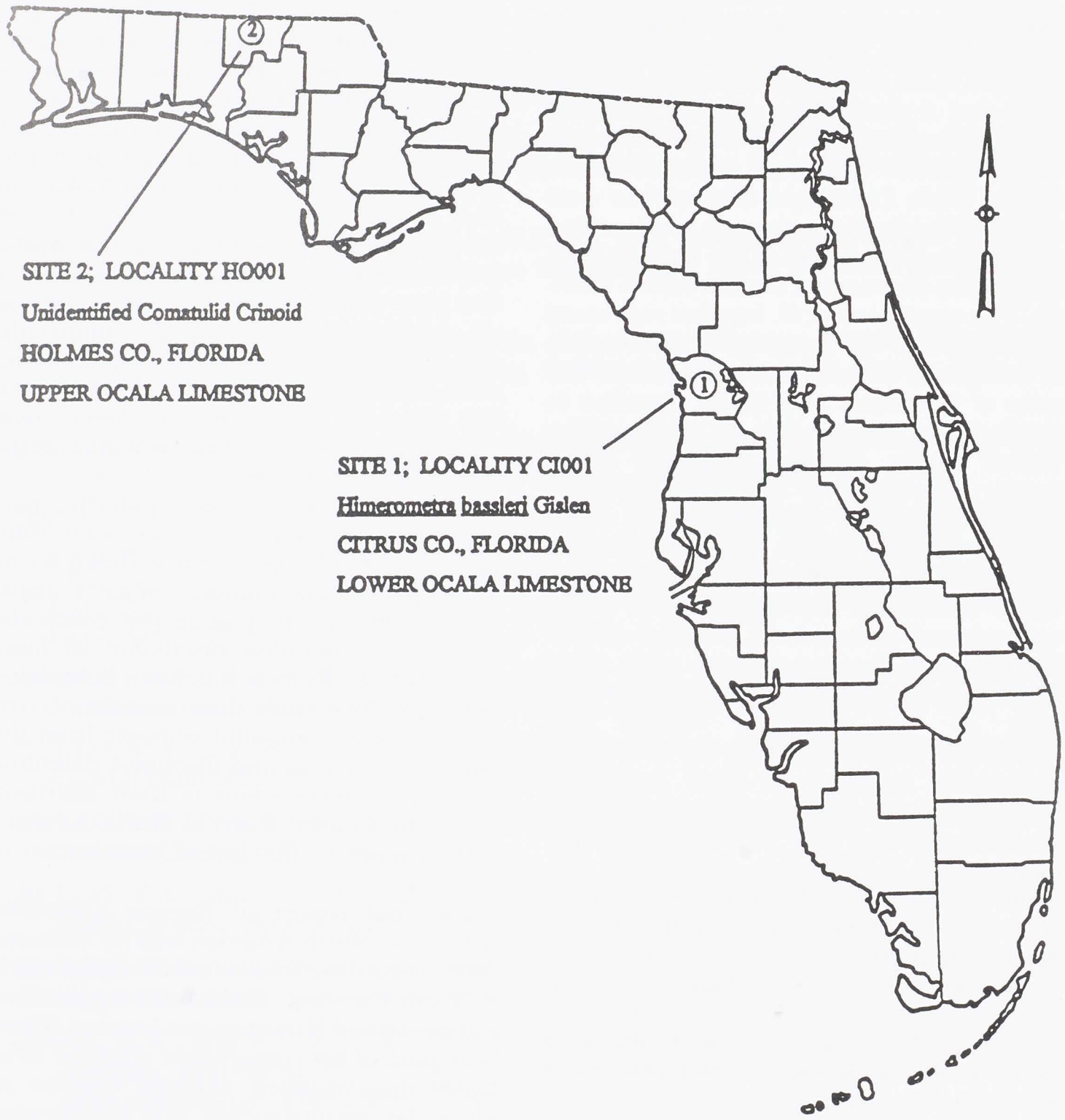
The Cenozoic invertebrate fossil record of Florida consists of both macro- and micro-fossils, which have been studied intensely for more than a century. Echinoderms often have been discussed and described in paleontologic literature regarding Florida. However, most studies have focused on echinoids (*e.g.*, Carter and McKinney, 1992 and references therein), and not the other classes of echinoderms that also have a fossil record. Howe (1942) published a discussion of Tertiary fossils that had been overlooked by Gulf Coast paleontologists, even though the fossils may be abundant. At the time of publication he noted that he was unable to find prior references to four classes of fossil echinoderms, including ophiuroids, comatulid crinoids, asteroids, and holothurians, from these sediments. He attributed the absence of studies on these fossil echinoderms to neglect by paleontologists, not a poor fossil record.

Much work on fossil echinoderms, particularly fossil echinoids, has been completed in the fifty years since Howe wrote his paper. Unfortunately, neglect apparently continues to plague the comatulid crinoids; no detailed discussion of fossil crinoids from Florida has been completed until now. This study describes the occurrence of fossil comatulid crinoids from the Eocene of Florida and discusses paleobiogeographic implications of their distribution in the Coastal Plain of North America with respect to the global distribution of the taxa.

The first report of Eocene comatulid crinoids in North America was by Emmons (1858) regarding fossils from Eocene marls in North Carolina. Gislén (1934) identified and described *Himerometra bassleri* (Plate 1) as part of his remarkable study of over 23,000 disarticulated skeletal ossicles in which he reconstructed and interpreted comatulid arm branching patterns. These ossicles were collected from Eocene (Middle Jacksonian) sediments near Baldock, Barnwell County, South Carolina by R. Bassler as part of an unrelated bryozoan study and then given to Gislén for his

study. Howe (1942) discussed *H. bassleri* with reference to Gislén's (1934) work but did not offer specific taxonomic identifications for comatulid specimens figured in his manuscript. Howe reported comatulid ossicles to be common in Eocene sediments from near Jackson, Alabama, and included at least one figured specimen (Figure 20, *in* Howe, 1942) that may indeed represent an occurrence of *H. bassleri* in Alabama.

Zullo and Kite (1985) reported the presence of *H. bassleri* from the Late Eocene (Jacksonian) Griffins Landing Member of the Dry Branch Formation, Aiken County, South Carolina. This represents a second location in South Carolina from which *H. bassleri* has been collected in addition to the Barnwell County site from which Gislén's original fossil material was collected. Zullo and Kite found fossil comatulid ossicles second in abundance only to barnacles




Text-figure 1. State of Florida map showing known UF localities for comatulid crinoids. Site 1 (UF Locality CI001) represents the collection site for *Himerometra bassleri* Gislén in Citrus County, and site 2 (UF Locality HO001) shows the collection site for the unidentified crinoid in Holmes County.

in their Aiken County samples; thus, both South Carolina localities, as well as Howe's Alabama locality, have been reported to contain significant numbers of comatulid ossicles.

The previous references were the only papers discussing specific stratigraphic distribution of *H. bassleri* until Oyen (1992a, 1992b) reported the occurrence of this species in Florida. Many papers have been published concerning other taxa of modern and fossil comatulids, and several that discuss related taxa will be noted here. Austin Hobart Clark has published a monograph of more than 4300 pages on modern crinoids (Clark 1915, 1921, 1931, 1941, 1947, 1950; Clark and Clark, 1967). This exhaustive study included a taxonomic discussion and description of living species of *Himerometra* (Clark, 1941) that is invaluable for species locations globally. Rasmussen (1978) provided general stratigraphic and geographic information for *Himerometra* and listed the distribution of the Eocene fossils in North America from South Carolina to Louisiana. Unfortunately, Rasmussen did not provide references for locality information; therefore, verification of any reported occurrences other than South Carolina (Gislén, 1934) is not possible. Strimple and Mapes (1984) described two new species of fossil comatulids, *H. caldwellensis* and *H. louisianensis*, from Louisiana. These descriptions were based on a single centrodorsal for each species collected from the Eocene (Jacksonian) Moodys Branch Formation. Rasmussen (1978, p. T890) referred to these Eocene crinoids from Louisiana under the *Heterometra* genus description, not *Himerometra*.

The occurrence of potential comatulid crinoid ossicles in Eocene rocks of Florida was noted by Vernon (1951) but no further identification was given in his paper. His identification seems uncertain given his statement that ". . . small plates believed to be Comatulid brachials are common" (Vernon, 1951, p. 142), in his description of the sediments containing the fossils. This description is for the Eocene (lower Jacksonian) Williston Member of the Moodys Branch Formation in Citrus and Levy Counties, Florida. Vernon also included occurrences of what he calls "brachials" or "comatulid brachials" as part of sediment descriptions from surface outcrops and cores from Orange, Osceola, and Marion Counties in Florida. No plates illustrating these fossils are present in Vernon's paper and the invertebrate paleontology collection of the Florida Geological Survey (now in the Florida Museum of Natural History) does not contain his samples. Therefore, verification of what Vernon was describing as potential comatulid ossicles is not possible. Finally, Oyen (1992a, 1992b) first reported the occurrence of *H. bassleri* in Florida from the Lower Ocala Limestone (formerly Inglis Formation; Jacksonian).

The fossil crinoids examined for this study consist of several different skeletal components from two species of comatulids. Specimens of *H. bassleri* were collected from an outcrop of the Lower Ocala Limestone in northwestern Citrus County, Florida, and another species (not yet identified) of comatulid crinoid was collected from the Upper Ocala Limestone in Holmes County, Florida (Figure 1).

## III. ACKNOWLEDGMENTS

I thank Dr. Douglas Jones (FLMNH) for suggesting I examine these fossils and for supporting this research with constructive comments and financial support as a Research Assistant in the FLMNH (National Science Foundation Grant BSR-9002689). I am grateful to Roger Portell (FLMNH) for his helpful suggestions and discussions regarding the fossil comatulids, for his aid in procuring reference materials that were not readily available in the U.F. libraries, and for a review of this paper with constructive criticisms. I would like to thank Dr. Larry McEdward (Dept. of Zoology, U.F.) for discussions about comatulid crinoid larval dispersal and helpful literature references regarding this topic, and Dr. David Dilcher (FLMNH) for allowing my use of his binocular microscope and camera for photomicrographs of the specimens. I thank Dr. Michael McKinney (Dept. of Geological Sciences, University of Tennessee) for taking time to provide a review of this paper with several suggestions and comments for improving its content. Finally, I thank Dr. Warren Allmon for careful editorial review of my paper and for inviting me to participate in this volume. This is University of Florida Contribution to Paleontology number 427.

## IV. STRATIGRAPHY AND GEOLOGIC SETTING

The stratigraphic nomenclature regarding the Eocene limestones in Florida has yet to be uniformly agreed upon. A brief synopsis of the stratigraphic nomenclature is provided here to illustrate the relationship of terminology used in literature discussing the Late Eocene of Florida. Stratigraphic terminology used in this paper will follow the current usage of Ocala Limestone as a formation unit with the exception of the historical review or when citing previous articles. Previous nomenclature updated to current stratigraphic nomenclature will cite older formation names in parentheses following Ocala Limestone to allow readers unfamiliar with the stratigraphic terminology used in Florida to understand the relationship between units. Problems with the Eocene stratigraphic nomenclature involve determining the stratigraphic status of the Ocala (*i.e.*, should it be a formation or a group?), the status of its subdivisions (*i.e.*, formations or members?), and the relationship of stratigraphic interpretations to the *North American Stratigraphic Code* (North American Commission on Stratigraphic Nomenclature, 1983).

Dall (*in* Dall and Harris, 1892) first used the term "Ocala limestone" for all Jackson age limestones in central Florida. Cooke (1915) continued this formation status, but more importantly, recognized conclusively that the Ocala Limestone was Late Eocene in age because it is found underlying the Marianna Limestone, which is of Oligocene age. Applin and Applin (1944) divided the Ocala Limestone into two units, a Lower and an Upper Member, based on both paleontologic (primarily foraminifera taxa) and lithologic characteristics. Vernon (1951) modified the Applins' nomenclature by elevating their members to formation status, calling the Upper Member the Ocala Limestone (restricted) and the Lower Member the Moodys Branch Formation. Vernon subdivided his Moodys Branch into two members with the upper unit called the Williston Member and the lower unit called the Inglis Member (Figure 2). Puri noted that Vernon used the term "Ocala group" without formally defining the unit and he defined the Ocala Group to include ". . . all calcareous sediments of the Jackson stage in Florida" (Puri, 1957, p. 22). He also re-stated his proposal (1953) to subdivide the Ocala Group into three formations by elevating the members in Vernon's (1951) Moodys Branch to formation status and eliminating the Moodys Branch name. This revision resulted in the Late Eocene Ocala Group being composed of the Inglis Formation, Williston Formation, and a newly defined unit Puri called the Crystal River Formation (in order from lower to upper; see Figure 2). The Crystal River Formation, therefore, is considered synonymous with the "Ocala limestone (restricted)" of Vernon (Puri, 1957, p. 31).

Most workers studying the Late Eocene limestones in Florida since 1957 have followed the stratigraphic nomenclature of either Applin and Applin (1944) or Puri (1957). One of the reasons for the split in

<table>
<tr><td colspan="3">UPPER EOCENE</td><td>SERIES</td></tr>
<tr><td colspan="3">JACKSONIAN</td><td>STAGE</td></tr>
<tr><td colspan="3">Ocala Limestone</td><td rowspan="3">Applin & Applin, 1944</td></tr>
<tr><td colspan="2">Lower Member</td><td>Upper Member</td></tr>
<tr><td colspan="2">Moodys Branch Formation</td><td rowspan="2">Ocala Limestone (restricted)</td></tr>
<tr><td>Inglis Member</td><td>Williston Member</td><td rowspan="2">Vernon, 1951</td></tr>
<tr><td colspan="3">Ocala Group</td><td rowspan="2">Puri, 1957</td></tr>
<tr><td>Inglis Formation</td><td>Williston Formation</td><td>Crystal River Formation</td></tr>
</table>

Text-figure 2. Stratigraphic nomenclature comparison diagram for the Upper Eocene in Florida. Note the status of the Ocala as applied by the three authors and the potential for confusion regarding the stratigraphic hierarchy.

acceptance of these stratigraphic interpretations follows the use by the United States Geological Survey (USGS) and the Florida Geological Survey (FGS). The USGS has chosen to follow the Applin and Applin nomenclature and interpretation while the FGS followed Puri's nomenclature in their publications. In 1991, the FGS returned to using the Applin and Applin stratigraphic terminology for the Late Eocene (Scott *et al.*, 1991). A major reason for the disagreement in stratigraphic nomenclature for the Eocene of Florida is the use of fossils to determine formation boundaries, particularly by Puri. He established several faunizones for the Ocala Group and subsequently divided the Ocala into three formations based principally on the faunizones, not lithologic characteristics. This is not in accordance with the definition of a formation as found in Article 24(c) of the *North American Stratigraphic Code* (NACSN, 1983, p. 858). Such use of fossils defines a biostratigraphic unit rather than a lithostratigraphic unit, such as a formation. It should be noted, however, that all of the stratigraphic interpretations presented here for the Eocene were made prior to the establishment of some of the "rule books" for stratigraphic nomenclature including the *Code of Stratigraphic Nomenclature* (ACSN, 1961), the *International Stratigraphic Guide* (ISSC, 1976), and the *North American Stratigraphic Code* (NACSN, 1983).

An additional area of debate among stratigraphers is the age of the Lower Ocala Limestone. Many invertebrate paleontologists still refer to the Lower Ocala as a lower Jackson Stage equivalent, but vertebrate faunas associated with the formation are considered to be upper Middle Eocene (Upper Claibornian Stage) by some vertebrate paleontologists (*e.g.*, Domning *et al.*, 1982). In addition to fossil sirenians, other fossil vertebrates collected from the Lower Ocala Limestone in Citrus County also support a Middle Eocene age determination (Gary Morgan, personal comm., 1993). The stratigraphic position of the Lower Ocala is not critical for this study since Tethyan associated invertebrates are found in Middle Eocene as well as Upper Eocene deposits (see Palmer, 1967). Implications of the stratigraphic and geographic distribution of the comatulids is discussed more thoroughly in the paleobiogeography section of this paper.

Although it is beyond the scope of this discussion to describe in detail the specific problems with the previous stratigraphic interpretations, readers who are not familiar with Florida geology must be aware that recent publications regarding the Upper Eocene may use either system of nomenclature for these Eocene rocks. In this paper, the formation names of Applin and Applin (1944) are used in accordance with the USGS and, more recently, the FGS. More detailed reviews of Eocene stratigraphic nomenclature can be found in most of the previously cited references, as well as in Hunter (1976) and Jones (1982). In addition, Randazzo (1976) illustrates several specific problems with the Florida stratigraphic nomenclature as related to the *North American Stratigraphic Code*.

The geologic setting and depositional environments of the Late Eocene in Florida have been interpreted and discussed by many workers doing paleontologic, stratigraphic, or sedimentologic research. Lithologic descriptions of the Ocala Limestone (or its stratigraphic equivalents) may be found in numerous publications, including several of the previously cited references such as Applin and Applin (1944), Vernon (1951), Puri (1957), Randazzo (1976), and Hunter (1976). The general lithology of the Lower Ocala (Inglis Formation) consists of a light cream to tan colored, chalky, porous, soft to densely crystalline, fossiliferous packstone or grainstone. Randazzo and Saroop (1976, p. 280) reported an average fossil content of 33.7% by volume with up to 60% fossil grains in some facies. Miliolid foraminifera dominate the fossil grain components and significant numbers of additional fossils such as mollusks, crustose algae, ostracodes, echinoids, and bryozoans are preserved, in addition to the forams. Finely crystalline dolomite is present as a limited lithologic component (Chen, 1965), but only minor (usually less than 10%) non-carbonate grains such as quartz are present in the limestones of the Lower Ocala (Inglis Formation). The general lithology of the Upper Ocala Limestone is more variable than the Lower Ocala and is dependent on the facies examined. It is a cream to white

colored, chalky, porous, soft and granular to dense and crystalline, fossiliferous wackestone to grainstone. Fenk (1979) noted a trend toward muddier lithologies in the Upper Eocene, with micrite-rich wackestones and packstones more common than in the Lower Eocene stratigraphic units. The limestone has abundant foraminifera, mollusks, echinoids, bryozoans, ostracodes, and smaller percentages of coralline algae, crustaceans, and corals. Puri (1957) describes portions of the Upper Ocala (Crystal River Formation) as a soft coquina because of the high abundance of fossil material, and the faunal diversity as a whole is greater in the Upper Ocala than in the lower units of the Eocene, including the Lower Ocala (Inglis Formation). Although the lithology is more mud-rich in the Upper Eocene, the volume of non-carbonate grains is still very low, with generally less than 5% insoluble residue present (Oyen, unpublished data).

Late Eocene sediments of the Florida Platform have been interpreted to represent warm, shallow marine environments on a relatively flat, carbonate shelf similar to those found on the modern Great Bahama Bank (Chen, 1965). Several lithofacies (or subfacies) have been identified in the Ocala Limestone, and these facies show changes between high and low energy conditions associated with transgressive and regressive sequences on the Florida Platform. A general transgressive sequence has been interpreted for the limestones found during the time between deposition of the Lower Ocala (Inglis Formation) and deposition of the Upper Ocala (Crystal River Formation) (Fenk, 1979). The Lower Ocala (Inglis Formation) is interpreted to represent higher energy, shallow subtidal environmental conditions that predominated during the Early Jacksonian (Randazzo and Saroop, 1976; Fenk, 1979). Cleanly washed packstone and grainstone lithologies seem to support the higher energy interpretation, since winnowing of carbonate mud has occurred to produce these lithologies. The Upper Ocala (Crystal River Formation) fauna and lithologies of muddy packstones and wackestones are interpreted to represent relatively lower energy, deeper subtidal conditions during the Late Jacksonian (Fenk, 1979). Carbonate mud-rich packstones and wackestones that dominate the lithologies of the Upper Ocala (Crystal River Formation) support this interpretation of deposition in deeper water, below the effective wave base, where intense winnowing occurs.

Cheetham (1963) made paleobathymetric and paleoecologic interpretations for these stratigraphic units using fossil cheilostome bryozoans, and his interpretations are similar to those of Fenk and of Randazzo and Saroop, with only minor differences regarding the water depth during the Early Jacksonian. Cheetham's work is important for understanding the ecologic conditions during the Eocene in the Florida Platform environment. Since cheilostome bryozoans as a group can be considered stenohaline and various species are stenothermal, he concluded that during most of the Eocene the platform was characterized by normal, open marine salinities and temperatures ranging from 19-26° C (Cheetham, 1963, p. 32). Open marine circulation and salinity are important for the paleobiogeographic interpretations of the comatulid crinoids presented below, because echinoderms are also stenohaline organisms requiring open marine salinities. Therefore, the environmental setting in Florida during the Jacksonian

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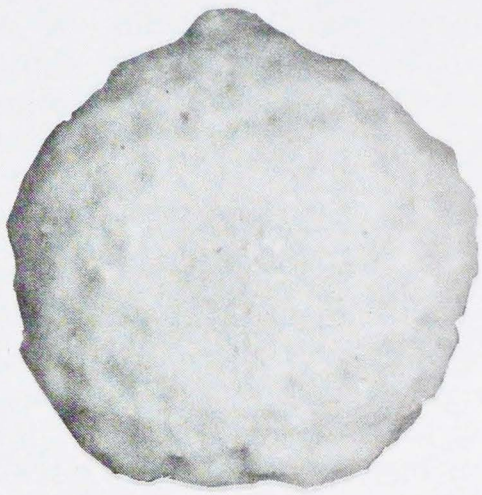
PLATE 1

Figures

1. *Himerometra bassleri* Gislén, 1934. Locality: UF C1001.
   1a. UF 39067; dorsal view of centrodorsal element (X5).
   1b. UF 39067; ventral view of centrodorsal, with attached radial plates (X5).
   1c. UF 39088; ventral view of centrodorsal, with radial plates absent, which allows distinctive rod-shaped basal rays to be observed (X5).
2. Unidentified comatulid crinoid. Locality: UFG HO001.2a. 126; dorsal view of centrodorsal element; diameter 2.0 mm (X10).
   2b. UF 48126; ventral view of centrodorsal element; diameter 2.0 mm (X10).
   2c,d. UF 48125; brachial plates; lengths approximately 1.5 mm (X10)



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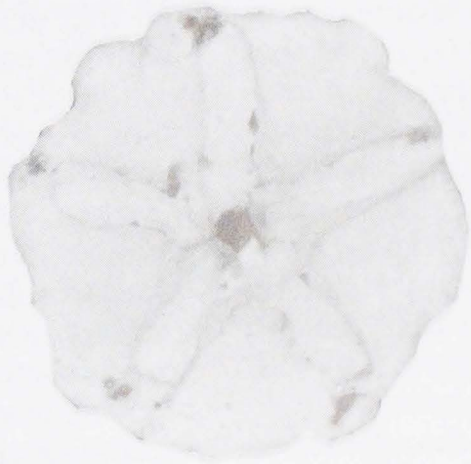

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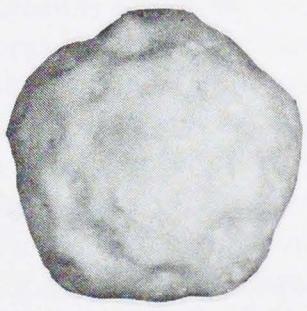


2a

2b

2c

2d

PLATE 1

was suitable for inhabitation by the crinoids, and analogous to that which exists in the Bahamas Bank today.

## V. MATERIALS STUDIED

Fossil crinoid specimens discussed in this study were collected from two localities in Florida (Figure 1). These fossils are disarticulated skeletal ossicles from two species of comatulid crinoids, *Himerometra bassleri* Gislén and a second, as yet unidentified species. Specimens of *H. bassleri* were collected in 1974 by FLMNH researchers during bulk sampling of Early Pleistocene sediments (which contained weathered out remains of thousands of Lower Ocala Limestone invertebrates from surrounding limestones) for fossil vertebrate material. Upon sieving, the comatulid fossils were separated from matrix material and placed, unidentified, in the Invertebrate Paleontology Collection of the museum. (This example seems to correlate well with Howe's [1942] belief that comatulids are probably more common in Coastal Plain strata than previously known simply because they were neglected by researchers, whether intentionally or unintentionally.) The collection of *H. bassleri* consists of skeletal components including 50 centrodorsals, 53 radial plates, and 20 basal rays found at UF locality CI001 (UF 39054 - UF 39090). Specimens are small, with most centrodorsals less than 10 mm in diameter, and the effects of sedimentary diagenesis (including recrystallized ossicles and epitaxial cements) are visible in many of the fossils. Plate 1 shows representative views of the dorsal and ventral surfaces of the centrodorsal, included radial plates, and basal rays for this species, as well as the imperfect preservation state of the crinoid components.

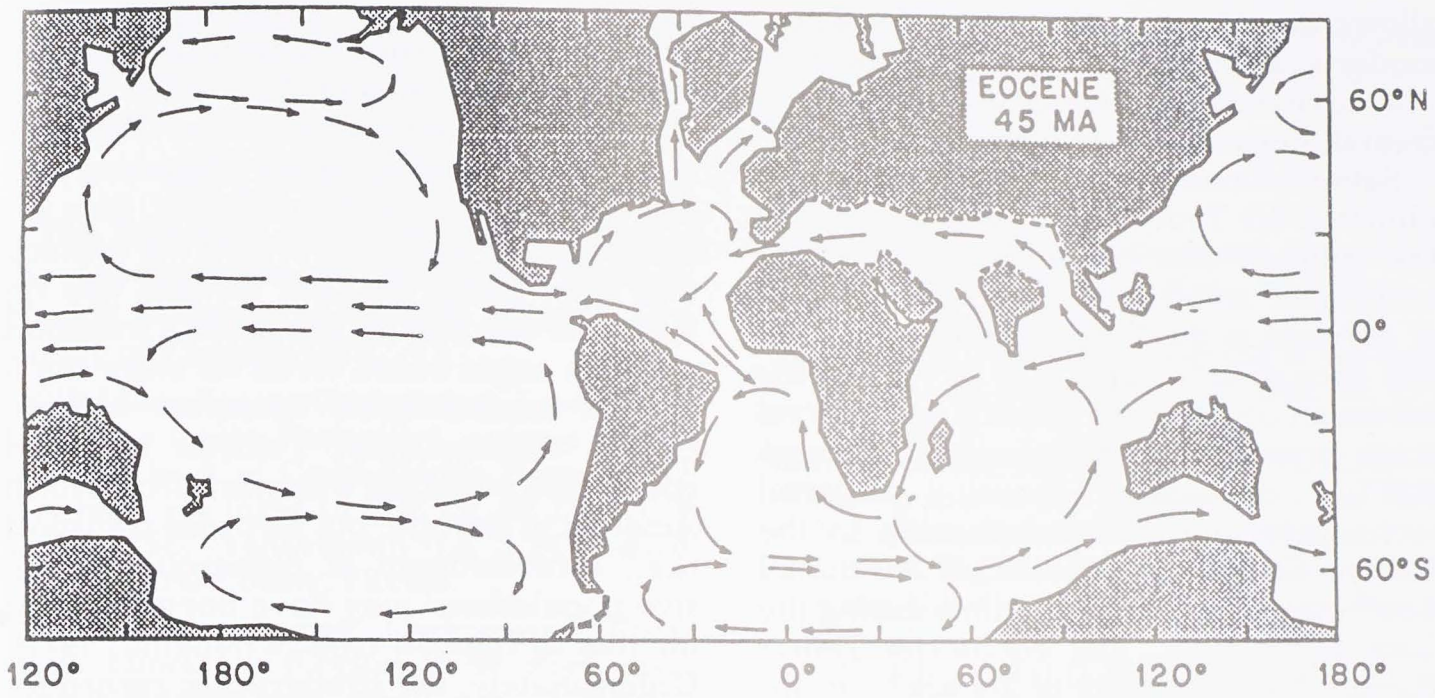
A second species of comatulid crinoid was discovered in 1992 while picking through the fine-fraction matrix of a bulk sample collected in 1977 from the Upper Ocala Limestone (Crystal River Formation). The number of skeletal components found consists of five brachial plates and only one centrodorsal from UF locality HO001 (UF 48125 and UF 48126). Plate 1 shows dorsal and ventral views of the centrodorsal and two of the five brachial plates. These specimens are distinctly smaller than those of *H. bassleri*, with the centrodorsal measuring approximately 2.0 mm in diameter and the brachials averaging 1.0-1.5 mm in length. The taxonomic status of these specimens is still uncertain and more work is currently being done to determine which species of comatulid crinoid is present in the Upper Ocala Limestone (Crystal River Formation) of Florida.

## VI. PALEOBIOGEOGRAPHIC CONSIDERATIONS

Examination of the paleobiogeographic and stratigraphic distribution for species of *Himerometra* shows an interesting pattern during the geologic history of the genus. Ten species of *Himerometra* have been described in the literature, with six extant species and four fossil species from the Eocene (three species) and Oligocene (one species). In order to understand better how the biogeographic distribution pattern for this genus may have been produced, we must consider the life histories of these crinoids.

Three general patterns of development exist for marine invertebrate organisms (Barnes, 1980). These include: 1) direct development – having no larval stage; 2) planktotrophic development – having feeding larvae with a relatively long larval life; and 3) lecithotrophic development – having non-feeding larvae dependent on nutrition from yolk sacs during their relatively short larval life. Larvae also may vary between active, free-swimming varieties or passive, non-swimming forms. The phylum Echinodermata is diverse and development styles are consistent only at lower taxonomic levels. Modern crinoids are the only living class of echinoderm in which the entire larval development stage is lecithotrophic and which, therefore, lack the ability to feed (McEdward *et al.*, 1988). A consequence of a lecithotrophic larval stage is its reduced larval stage duration as compared to typical planktotrophic larval stage durations; the larval dispersal range is limited by a finite energy source available in its yolk.

The relationship between larval dispersal ability and paleobiogeographic distribution for the species of *Himerometra* is yet uncertain because of limited data regarding specific larval stage duration for these taxa. Breimer (1978, p. T53) pro-




Text-figure 3. Inferred global surface circulation patterns during the Middle Eocene. The circum-equatorial Tethys Seaway would provide a path for global distribution of species of *Himerometra* as noted in the fossil record from sites in the southeastern United States, Germany, and modern faunas in the Indian-Pacific Oceans regions (figure from Haq, 1981).

vided a general time range of 5 to 108 hours for the swimming larval stage of modern crinoids. McEdward *et al.* (1988) assembled development times for ten species of modern crinoids, including at least one genus (*Heterometra*) in the family Himerometridae. The development times range from one to six days (see McEdward *et al.*, Table I, for details) for those species for which data are available. The key point to note is that all larval stage durations listed are relatively short (less than six days) and the dispersal range achieved in the larval stage only is likely to be small. This presents a problem for reconstructing the dispersal methods that have allowed the paleobiogeographic distribution for *Himerometra* species to become established as known from the fossil record. Further, the stratigraphic occurrences of these species are apparently anomalous since fossil species are known from the Eocene and Oligocene, and Recent species are found in the Indian and Pacific Oceans, but no fossil reports are known from the Miocene through the Pleistocene.

A common link among the geographic occurrences of the fossil and modern species is their location in an approximate circum-equatorial belt that generally corresponds to the position of the Tethys Seaway (Figure 3). Eocene species *H. caldwellensis*, *H. louisianensis*, and *H. bassleri* are found in the Coastal Plain of the southeastern United States, and the Oligocene species *H. grippae* is found in Europe (Germany). The six modern species (*H. bartochi*, *H. magnipinna*, *H. martensi*, *H. persica*, *H. robustipinna*, and *H. sol*) are distributed in the southwestern Pacific Ocean to the Indian Ocean, with one of the species also known from the Persian Gulf (Clark, 1941). Dispersal of the crinoids may have been aided by the ocean currents of the Tethys Seaway during both the larval and adult stages of their lifespan. The *H. bassleri* specimens from Florida can be considered part of the Tethyan fauna due to their stratigraphic and faunal relationship with previously established Tethyan faunal assemblages. Mollusks are the dominant Tethyan faunal members associated with the crinoids found in the Lower Ocala Limestone. Descriptions of these mollusks and their stratigraphic distribution include papers by Richards and Palmer (1953), Palmer (1967), Givens (1989), and Nicol (1991), among others. The association of *H. bassleri* with the Tethyan mollusks leaves little question that the comatulids in Florida were influenced by circulation of the Tethys Seaway, and this

allows an inference that other fossil and modern *Himerometra* occurrences may also have resulted (at least to some degree) from this circulation influence.

Several lines of reasoning support the idea that the Tethys Seaway contributed to the crinoids' distribution, but was not the only factor involved. First, the rate of flow of currents in the Tethys probably was not fast enough to transport the larval crinoids across an ocean basin within a single larval stage prior to metamorphosis. Scheltema (1977) discussed larval dispersal techniques and their relationship to the Tethys Seaway and provided calculated flow rates as well as travel time during the Late Cretaceous. The equatorial Tethys current had a velocity of 2-4 knots at this time, and taking into account the size of the Late Cretaceous Atlantic Ocean, it is estimated the passive travel time across the Atlantic was 28-56 days. Assuming a similar current velocity for the Eocene and Oligocene, the travel time would be significantly longer due to the continual tectonic spreading along the Mid-Atlantic Ridge system, resulting in a greater distance to travel in periods younger than the Cretaceous.

Using information regarding larval stage durations discussed earlier (all less than seven days), it is unlikely that transport across the entire ocean basin occurred within a single lifespan of these comatulids, if we assume transport is limited to the larval stage only. Current knowledge regarding crinoid development rates and styles of development (lecithotrophic *versus* planktotrophic) however, is quite limited, and information regarding fossil crinoids is unknown or uncertain, so the possibility exists that different development rates or styles existed earlier in the evolutionary history of crinoids, which may have allowed greater dispersal distances to occur through several different methods than presently known from modern crinoids (Larry McEdward, personal comm., 1992).

A second problem exists in defining the Tethys as the primary paleobiogeographic control over the distribution of *Himerometra* species. This is due to the poor biostratigraphic record of the genus and its geographic distribution with respect to the Tethys Seaway. The genus evolved in the Eocene, according to the known stratigraphic record, and three species are known from the southeastern Gulf and Atlantic Coastal Plains of the United States. The sole reported species in the Oligocene is found in Germany. If the Oligocene species did not evolve independently, then it is less likely the Tethys provided the contact, and more likely the Gulf Stream was responsible (see Figure 3). Again, a transport problem exists based on larval stage durations if trans-Atlantic transport was required. Alternatively, Tethyan transport could have occurred westward from North America to Europe, but stepwise transport (*i.e.*, establishment of numerous successive populations) may have been required for this to happen (see Scheltema, 1977). Unfortunately, the stratigraphic record for *Himerometra* species is very limited and they are known only from the United States and Germany. The geographic ranges on modern *Himerometra* species in the Indo-Pacific region, however, would support this idea; no species are known in the fossil record from the Miocene through the Pleistocene.

Perhaps the most difficult aspect of interpreting paleobiogeographic and evolutionary patterns of the genus *Himerometra* is the poor fossil record. This is a problem common to most fossil taxa, but it seems to be somewhat more pronounced in the comatulid crinoids (as the paucity of references on these fossils would support) than in other taxonomic groups. As Howe (1942) noted, this is likely due to neglect and lack of recognition of skeletal fragments by paleontologists rather than rarity of fossil materials. The preservation potential for these crinoids is good (at least for individual skeletal plates) because of their high-Mg calcite composition. Furthermore, the comatulid skeleton normally disarticulates quickly and individual plates are quite small and may be overlooked in the field. Finally, comatulid crinoids seem to be poorly recognized by many workers and likely overlooked unintentionally even when present in the strata. It is hoped that this report will help bring attention to fossil comatulids and aid other paleontologists in recognizing these fossils when examining samples and outcrops. As work continues on fossil comatulids such as *Himerometra*, our ability to refine what is known about the biostratigraphic and paleobiogeo-

graphic distribution of these fossils will only improve.

## VII. LOCALITY DATA

The following are collecting localities of the Invertebrate Paleontology Division, Florida Museum of Natural History, University of Florida (UF):

CI001 Late Eocene (Jacksonian), Lower Ocala Limestone (Inglis Formation), outcrop located on north bank of Cross Florida Barge Canal, vertebrate site Inglis 1A, (SE 1/4, SE 1/4, sec. 9, T17S, R16E, Yankeetown 7.5' USGS quadrangle), Citrus County, Florida.

HO001 Late Eocene (Jacksonian), Upper Ocala Limestone (Crystal River Formation), natural outcrop in a spring run on Wright's Creek, approximately 4-5 mi (6.4-8.1 km) north of Bonifay, (SW1/4, SE1/4, sec. 2, T5N, R15W, Bonifay 7.5' USGS quadrangle), Holmes County, Florida.

## VIII. LITERATURE CITED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