NEW CRINOIDS FROM THE EOCENE LA MESETA FORMATION OF SEYMOUR ISLAND, ANTARCTIC PENINSULA

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The excellent record of marine invertebrates from the Eocene La Meseta Formation of Seymour Island (Antarctic Peninsula) includes several well-preserved crinoids. Two crinoid species have been previously reported from the upper part of the La Meseta Formation; here we describe three additional taxa from the lower units (Telm1–2) of this formation: an isocrinid, *Eometacrinus australis* gen. et sp. n., a comatulid, *Notocrinus seymourensis* sp. n., and a cyrtocrinid, *Cyathidium holopus* Steenstrup, 1847. These data are important in providing new information for the time-environment distribution of crinoids and for constraining phylogenetic hypotheses and evolutionary scenarios. The co-occurrence of these three taxa is unusual because sedimentological, stratigraphic, and paleoecological evidence suggests that the lower part of the La Meseta Formation was deposited in a shallow-marine setting whereas today, isocrinids, cyrtocrinids, and comatulids co-occur only in deep water. Also, the morphology of *E. australis* indicates that the syzygial articulation between the first and second primibrachials, thought to represent a character of primary phylogenetic importance among the Isocrinidae, may have evolved more than once.

Key words: Crinoidea, taphonomy, taxonomy, paleoecology, Eocene, Antarctica.

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INTRODUCTION

The fossil record of articulate crinoids, a group which includes all post-Paleozoic crinoids, extends back to the Triassic, an interval during which, or shortly before which, they originated (SIMMS and SEVASTOPULO 1993). Today articulates can be subdivided into three functional groups: those bearing stalks throughout ontogeny, the isocrinids, bourgueticrinids, and millericrinids, those which lose the stalk as juveniles and live as stalkless, relatively motile adults, the comatulids, and those which cement the cup directly to the substrate, the cyrtocrinids. In modern oceans representatives of these three functional groups co-occur only in deep water since the cyrtocrinids and the stalked crinoids are restricted to depths greater than 100 m. The three crinoids described in this study, the comatulid *Notocrinus seymourensis* sp. n., the isocrinid *Eometacrinus australis* gen. et sp. n., and the cyrtocrinid *Cyathidium holopus*, all occur in the lower part of the La Meseta Formation which, based on sedimentologic and paleontologic criteria, has been interpreted as representing shallow-marine or even estuarine settings. Thus in addition to providing new taxonomic data relevant to our understanding of the evolutionary history of crinoids, this study also helps constrain the timing of the previously documented offshore shift of some crinoid lineages since the late Mesozoic/early Cenozoic (*e.g.* BOTTJER and JABLONSKI 1988).

The investigated crinoid collection is kept in the Institute of Paleobiology of the Polish Academy of Sciences, Warszawa under the catalogue number ZPAL Ca.V.

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GEOLOGY AND STRATIGRAPHY

The La Meseta Formation, which crops out in the northeastern portion of Seymour (Marambio) Island is a sequence of richly fossiliferous, shallow-marine–estuarine, poorly consolidated sandstones and siltstones, approximately 800 m thick (Text-fig. 1). The sedimentological and stratigraphic framework of the La Meseta Formation has been described by RINALDI *et al.* (1978), ELLIOT and TRAUTMAN (1982), SADLER (1988), STILWELL and ZINSMEISTER 1992, and POREBSKI (1995).



Fig. 1

Crinoid locality index map of the La Meseta Formation on Seymour Island. ZPAL 1 — *Eometacrinus australis* and *Cyathidium holopus* site, ZPAL 3 — *Metacrinus fossilis* site, ZPAL 6 — *Notocrinus seymourensis* site.

ELLIOT and TRAUTMAN (1982) initially subdivided the La Meseta Formation into three informal members (Units I, II, and III). SADLER (1988, fig. 1) mapped the La Meseta Formation and identified seven numbered lithological units (Telm1 through Telm7), which demonstrate the lateral variability of the formation. SADLER's units are correlatable with the ones recognized earlier by ELLIOT and TRAUTMAN (1982) [see SADLER (1988, fig. 3); STILWELL and ZINSMEISTER (1992, fig. 4)].

The La Meseta Formation has been dated as Eocene to possibly early Oligocene on the basis of fossil penguins (SIMPSON 1971), molluscs (ZINSMEISTER and CAMACHO 1980, 1982), polydolopid marsupials (WOODBURNE and ZINSMEISTER 1982, 1984), and cetaceans (FORDYCE 1989). MARENSSI *et al.* (1994) determined that the middle part of the La Meseta Formation (Telm4–5) is middle Eocene based on correlation of terrestrial mammals found in these units with those from South America (Patagonia). Recent studies of marine palynomorphs (mostly dinoflagellate cysts) by ASKIN *et al.* (1991), COCOZZA and CLARKE (1992), and BARNES and RIDING (1994) support an Early Eocene age for the lower part of the La Meseta Formation (Telm1–2); a result that is consistent with ages obtained previously by HARWOOD (1986, 1988) and WRENN and HART (1988).

Crinoids which have been previously described from the upper part of the La Meseta Formation (Telm6-7) include the isocrinid *Metacrinus fossilis* (RASMUSSEN 1979; MEYER and OJI 1993) and the



Fig. 2

Composite stratigraphic column of the La Meseta Formation on Seymour Island (South Section) showing the distribution of main lithofacies and location of crinoid sites. Section adapted from SADLER (1988).

comatulid *Notocrinus rasmusseni* (MEYER and OJI 1993). We report here three additional taxa from the lower part of the La Meseta Formation (Telm1-2) which crops out southwest of Cross Valley near the López de Bertodano Bay (Text-figs 1-2) [see also Geological Map of Seymour Island in FELDMANN and WOODBURNE (1988)]. The isocrinid *Eometacrinus australis* gen. et sp. n. and the cyrtocrinid *Cyathidium holopus* were collected at *Bill Hill*. locality ZPAL 1 [Text-fig. 1 see also Gaździcki and Tatur (1994, pl. 2: 2)]. The comatulid *Notocrinus seymourensis* sp. n. was found at the locality ZPAL 6 (Text-fig. 1).

The Telm1 crinoids, *Eometacrinus australis* and *Cyathidium holopus*, occur within an up to 2 m thick interval of basal, transgressive facies represented in this area by grey to red-brown limonitic, sandy siltstones, sandstones, and pebble conglomerates with intercalations of shelly hash. Crinoids represent

only a small portion of the total biota recognized in Telm1 lithofacies *sensu* STILWELL and ZINSMEISTER (1992). They are associated with abundant cyclostome and cheilostome bryozoans which form multilamellar spheroidal colonies up to 12 cm in diameter (GAźDZICKI and HARA 1994; HARA 1995), numerous brachiopods (BITNER 1996 this volume), stylasterids (STOLARSKI in preparation), solitary and colonial minitrabecular corals (STOLARSKI 1996 this volume), gastropods, polychaete worms, asteroids, cidaroid echinoids (RADWAŃSKA 1996 this volume), gadiform fish remains, shark teeth, and characteristically large *Ostrea* and *Pecten* shells and shell fragments. Microfossils are represented by benthic foraminifera and ostracods.

The comatulid, *Notocrinus seymourensis*, occurs in unit Telm2 which in the Cross Valley area is characterized by laminated fine-grained sands, silty sands, calcareous siltstones, and clay beds up to 250 m thick (STILWELL and ZINSMEISTER 1992). The two specimens of *N. seymourensis* were collected at locality ZPAL 6 (Text-fig. 1) in the lower part of unit Telm2 (Text-fig. 2) from a calcareous sandstone lithofacies which also contained molluscs, echinoids, and bryozoans.

In addition to the faunal assemblage, the presence of sedimentary structures such as flaser and wavy bedding and climbing-ripple laminations indicate that the Telm1 and the lowermost Telm2 lithofacies represent a nearshore, shallow-marine environment with normal salinity.

TAPHONOMY

One of the more unusual aspects of the crinoids from the La Meseta Formation is their mode of preservation. For example, the comatulids have well-preserved, articulated arms and pinnules but the centrodorsal and cirri are poorly preserved or missing (MEYER and OJI 1993; this study). This is unusual because normally the centrodorsal is the only element that is fossilized and recovered. Experiments on extant comatulids have revealed that the crown normally disarticulates quickly and that in the process of post-mortem disarticulation a characteristic sequence is followed: the pinnules disarticulate first, followed by the cirri, the distal arms, and finally the proximal arms (LIDDELL 1975; D.L. MEYER and K.B. MEYER 1986; BAUMILLER 1994). This suggests that when arms and pinnules are found intact, they ought to be attached to the centrodorsal. The mode of comatulid preservation in the La Meseta Formation is not consistent with this prediction. It is likely that these comatulids were buried quickly, possibly when still alive. They remained intact during the process of burial, compaction, and fossilization; the loss of the centrodorsal and cirri occurred after the specimens were exposed on the outcrop.

The mode of preservation of isocrinids in the La Meseta Formation also differs from that of other fossil isocrinids and from what would be expected based on results of taphonomic experiments (BAUMILLER 1994, in preparation). Isocrinids possess articulations specialized for autotomy in the stalk, the synostoses/cryptosymplexies, and in the arms, the syzygies. The animal can actively shed parts of the skeleton at these articulations; this happens when it is physically stressed by temperature or salinity changes (BAUMILLER 1994, in preparation) and by mechanical stimulation (OJI and OKAMOTO 1994). Furthermore, these articulations represent planes of weakness during post-mortem transport or decay, *i.e.*, carcasses disarticulate first along autotomy planes, and only later along other articulations. As in comatulids, there is a characteristic disarticulation sequence (BAUMILLER 1994, in preparation); failure occurs in the following order from first to last: distal-most syzygies, pinnules, medial syzygies, proximal syzygies, stalk synostoses, cirri, proximal columnals, radials, and basals. The reason that proximal columnals remain attached to the basals and radials longer than other skeletal elements is that the proximal stalk lacks synostoses — these develop between nodals and infranodals several centimeters below the base of the cup (LLEWELLYN and BAUMILLER 1993; BAUMILLER 1994, in preparation). The preservation of *Eometa*crinus australis (this study) and Metacrinus fossilis (MEYER and OJI 1993; this study) with articulated crowns, articulated pinnules but lacking attached stalks is highly unusual. MEYER and OJI (1993) noted this peculiarity in M. fossilis from Telm6-7 and suggested that it indicates shedding of the stalk by juveniles, and a free-living, comatulid-like adult existence. A similar inference could be made about E. australis since it is also preserved without stalks attached. However, the presence of adult-sized pluricolumnals in proximity of the crowns, argues against such an interpretation and suggests that E. australis retained its stalk through adulthood but that its loss preceded burial.

TAXONOMIC METHODOLOGY AND TERMINOLOGY

The taxonomy of crinoids is complicated by the fact that these animals possess multiplated skeletons which disarticulate readily after death; what we recover as fossils are typically the animals' fragmentary remains. The definition of species based on fragments can lead to a proliferation of taxa as different fragments of a single animal may be used for designating new species. This is especially problematic when stalk elements (columnals) are used to define taxa because columnal morphologies vary greatly within individuals and between individuals of the same species. In our treatment, we have tried to avoid using fragments for erecting new taxa.

Another problem posed by the low preservation potential of complete crinoids is the incompatibility of species and generic definitions of Recent and fossil organisms. The monumental effort of A.H. CLARK (1908, 1923) during the first half of this century resulted in the publication of his multi-volume work on extant comatulids in which he described over 100 genera basing his definitions on minute differences, such as in the morphology of pinnules and cirri. Since neither pinnules nor cirri are commonly fossilized, the criteria used for distinguishing Recent taxa are largely inapplicable to fossils. In fact, most of the comatulid fossil record is represented by centrodorsals only and differences in centrodorsal morphology are used to differentiate among fossil comatulids. The contrasting criteria have hindered a uniform taxonomic treatment of comatulids. The comatulids of the La Meseta Formation represent unusual fossils: the arms and pinnules are in a better state of preservation than the centrodorsal. This mode of preservation allows some comparisons of comatulids from the La Meseta Formation to other fossil taxa based on the centrodorsal and also provides some means, based on the morphology of the arms, for comparing them to Recent taxa.

In the taxonomic treatment of crinoids from the La Meseta Formation we use differences in discrete character states for discriminating crinoid genera. We define a crinoid genus as consisting of individuals sharing a unique combination of discrete, rather than continuous, characters; differences in discrete characters reflect large morphological discontinuities and minimize the potential for error in identification. Using the above definition, the genus *Eometacrinus*, for example, includes those isocrinids possessing a synarthry between the first and second primibrachial and a muscular articulation between the first and second secundibrachial. Our treatment of species allows for the use of objective definitions based on differences in continuous characters.

In terminology, we follow the Treatise on Invertebrate Paleontology (BREIMER 1978).

TAXONOMIC DESCRIPTIONS

Class Crinoidea MILLER, 1821 Subclass Articulata ZITTEL, 1879 Order Isocrinida SIEVERTS-DORECK, 1953 Family Isocrinidae GISLÉN, 1924 Genus Eometacrinus gen. n.

Type species: Eometacrinus australis gen. et sp. n.

Derivation of the name: From the Greek eo - dawn, earliest, oldest.

Diagnosis. — Isocrinidae with a synarthrial IBr₁₋₂, muscular IIBr₁₋₂, and typically 5 primibrachials. **Remarks.** — This genus possesses an unusual combination of proximal brachial articulations: a synarthry at IBr₁₋₂ and a muscular articulation at IIBr₁₋₂. These characters are thought to be of primary phylogenetic importance and have been used to subdivide the Isocrinidae (OJI 1985; SIMMS 1988). OJI (1985) included all isocrinids with a synarthry at IBr₁₋₂ in his "old group" and all those with a syzygy at IBr₁₋₂ in his "new group". SIMMS (1988) used the IIBr₁₋₂ articulation to further subdivide OJI's "new group": he placed taxa with syzygies at IBr₁₋₂ and synarthries at IIBr₁₋₂ in one group and those with syzygies at IBr₁₋₂ is syzygial and IIBr₁₋₂ muscular. *Eometacrinus* in another. In *Metacrinus* and *Saracrinus*, however, IBr₁₋₂ is syzygial and IIBr₁₋₂ muscular articulation at IIBr₁₋₂; *Eometacrinus* is therefore assumed to have close affinity to these two extant taxa. In possessing a synarthry at IBr_{1-2} , however, *Eometacrinus* resembles members of OJI's "old group". Given the above, it is likely that the *Eometacrinus-Metacrinus-Saracrinus* lineage and the "new group" represent independent offshoots from the "old group".

Eometacrinus australis sp. n. (Pl. 27: 3-8; Text-fig. 3-6)

1994. Metacrinus sp.; BAUMILLER and GAŹDZICKI, fig. 2A.

Holotype: ZPAL Ca.V/1.

Type horizon: Telm1, La Meseta Formation (Eocene). Type locality: ZPAL 1 (*Bill Hill*), Seymour Island, Antarctic Peninsula. Derivation of the name: From the Latin *australis* — southern.

Diagnosis. — As for the genus.

Material. — Three crowns: one with radials and brachials through pentibrachs, the second with radials, basals, and brachials through tetribrachs, and the third with the most proximal columnal, basals, radials, and brachials through tetribrachs. Thirty four pluricolumnals, 2 to 22 columnals long.

Description. — Dorsal cup bowl-shaped and low with a nearly flat base. Basals small, rhombic, 1 mm high and 1 mm wide, tumid, and with lower edges distinctly downward protruding over the uppermost columnals; separated from each other on dorsal surface by a gap exceeding their width. Radials very low, approximately 2–3 times wider than high; width 4–5 mm (Text-fig. 3). Five primibrachials. Suture between the radial and the first primibrachial strongly concave down. First primibrachial low, 4–5 times wider than high. IBr_{1–2} synarthrial. Synarthry with a well-developed central ridge (4 mm in length and 0.3 mm wide)

with a large central canal, 0.4 mm in diameter; ligament fossae deep and symmetrical around the ridge. Second and third primibrachials 2-3 times wider than high. IBr₂₋₃ and IBr₃₋₄ oblique muscular. Fourth primibrachial low, 4-5 times wider than high. IBr₄₋₅ cryptosyzygial or synostosial, tightly fused and showing nearly straight suture on dorsal surface. The arms are divided isotomously as many as 4 times; arms more slender towards distal ends, but almost uniform within each brachitaxis. Axillaries nearly triangular; their distal articular faces form an angle of approximately 60° with the axis of the arm; 1.5 times wider than high. Between 7 and 9 secundibrachials. Syzygial or cryptosyzygial articulations: IIBr₃₋₄, IIIBr₃₋₄, IVBr₃₋₄, and VBr_{3-4} . Brachials smooth, 2–3 times wider than high proximally but becoming higher than wide distally; quartibrachials 1.2–1.5 times higher than wide. First pinnules on IBr₂. First pinnular as wide as high, slightly flared at both ends. Pinnular facet with a central, narrow fulcral ridge.

Only single columnal found attached to one of the specimens; pentastellate; length from margin of radius to margin of opposite interradius, 4.0 mm. Lumen circular, 0.4 mm in diameter.

Pluricolumnals numerous, from 2 to 22 columnals long. Nodals and internodals of subequal dimensions. Internodals pentagonal to rounded subpentagonal in outline; nodals more pentalobate. Internodals average 4.6 mm in diameter (range: 3.9–5.4 mm) and 1.3 mm in height (range: 1.1–1.5 mm). Nodals slightly greater in height, but not significantly different in diameter. Two complete noditaxes with 11 columnals per noditaxis; two pluricolumnals lacking nodals with 12 internodals. Cirrus scars always five in number, directed outward and slightly upward; of moderate



Fig. 3

Camera lucida drawing of cup plates and proximal brachials of *Eometacrinus australis* gen. et sp. n. b — basal; R — radial; 1-5 — first through fifth primibrachials; single arrow — syzygy; double arrow — synarthry; all other articulations — muscular (ZPAL Ca.V/3).



Fig. 4 The synarthrial articulation at IBr_{1-2} in *Eometacrinus australis* gen. et sp. n. Arrows point to synarthrial ridge. a — ZPAL Ca.V/2, × 10; b — ZPAL Ca.V/3, × 10.

size (34–44% of nodal diameter), occupying the entire height of the nodal but not impinging on infra- or supra-nodals; weakly depressed and elliptical in outline. Articular ridge of cirrus socket straight with the long axis perpendicular to columnal axis; closer to the supra-nodal than the infra-nodal margin of the socket. Ends of ridge slightly raised; canal subcircular. Proximal cirrals (only two present) low and disc shaped; circular to slightly oval in outline with a raised outer rim. Articular ridge also raised and displaced upwards. Articulation between nodal and infranodal synostosial or cryptosymplectial; nodal articulum slightly concave and faintly petaloid. All other articular facets symplectial. Elliptical areola surrounded by moderate sized culmina reaching their maximum length a third of the distance between the margin and the lumen and oriented at a slight angle to each other. No radial space but a radial groove may be developed. Number of culmina per petal fairly constant: 3–4 adradially and 4–6 marginally. Lumen small (0.3 mm in diameter on a columnal of 4.3 mm diameter) and round. On cryptosymplectial articulations lumen generally occluded (on 8 of 8 nodals and 8 of 9 infranodals). Latera straight but may be slightly inflated into rounded, faint epifacets.

Remarks. — The specimens of isocrinids found in Telm1 of the La Meseta Formation are excellently preserved and, based on the characters of the crown and stalk, belong to a single species. The presence of 5 primibrachials in all specimens distinguishes them from the vast majority of known isocrinids which possess only 2 primibrachials; only *Metacrinus* and *Saracrinus* have 4 or more primibrachials. According to CLARK (1923) specimens with 4 primibrachials are assignable to *Saracrinus* while those with more than 4, typically 7, to *Metacrinus*. Although OJI (1986) has shown that the number of primibrachials in extant members of these two genera can be variable, he retained CLARK's scheme. The 5 primibrachials of the Telm1 isocrinids fall within the range encountered in *Metacrinus* but because of the presence of synarthries rather than syzygies at IBr_{1-2} , they are assigned to *Eometacrinus*.

In 1979 RASMUSSEN described a new isocrinid species, *Metacrinus fossilis*, from the Telm6–7 of the La Meseta Formation and more recently MEYER and OJI (1993) reported numerous well-preserved crowns of *M. fossilis* from the same locality. A re-examination of some specimens described by MEYER and OJI and of additional crowns collected by one of us (AG) from Telm6–7 revealed striking similarities between



Fig. 5 The number of secundibrachials in *Eometacrinus australis* gen. et sp. n. (Telm1; solid bars) and *Metacrinus fossilis* (Telm6–7; open bars).



Fig. 6 Shape of axillaries in *Eometacrinus australis* gen. et sp. n. (Telm1; solid squares) and *Metacrinus fossilis* (Telm6-7; open squares).

Metacrinus fossilis and Eometacrinus australis. In the shape of the crown, shape and size of basals and radials, and number of primibrachials the two species are very similar to each other, in fact the specimens of *E. australis* were referred to Metacrinus sp. (BAUMILLER and GAźDZICKI 1994) before additional preparation exposed the distal facet of IBr₁ (Text-fig. 4). This facet in *E. australis* is a synarthry whereas in *M. fossilis* it has been described by RASMUSSEN (1979) and MEYER and OJI (1993) as a synostosis. As

the latter two authors noted however, the IBr_{1-2} "suture has small ridge-like projections, similar to synarthrial articulations" (MEYER and OJI 1993, p. 253). Indeed, a re-examination of IBr_{1-2} sutures in *M*. *fossilis* confirmed their enigmatic nature: they are slightly concave distally and a ridge-like projection is visible in some specimens. In the one specimen with the distal facet of IBr_1 exposed, however, there is no sign of a dorso-ventral ridge; this may be a preservational artifact, however, as the articulation is poorly preserved.

Another important difference between *M. fossilis* and *E. australis* relates to the stalk. No pluricolumnals have been found associated with *M. fossilis* and the stalk segments attached to the crowns are typically very short (the longest segment reported is 31 mm long) and distally tapering while 34 pluricolumnals were collected with the three crowns of *E. australis*. Although the stalk material is isolated and all *E. australis* crowns generally lack columnals, our designation of the pluricolumnals as *E. australis* is based on (1) the co-occurrence of pluricolumnals and crowns and the fact that *E. australis* is the only isocrinid recovered from the Telm1 localities, (2) the morphology of the cirrals: cirrals found with the crowns match closely the two pluricolumnal cirrals in general outline, size and shape of the fulcrum, and the position and size of the central canal.

Although the single columnal attached to the crown of *E. australis* is smaller in diameter, more pentastellate than those in the isolated material, and has a slightly larger lumen, this is consistent with the differences between proximal and distal columnals in other isocrinid species.

There are other, minor, differences between the Telm1 and Telm6–7 isocrinids. For example, the number of secundibrachials is generally lower in *E. australis* than in *M. fossilis* (Text-fig. 5) and its axillaries have a greater height-to-width ratio (Text-fig. 6). However, both characters can vary within individuals and within species and their taxonomic value is uncertain.

Given the level of morphological similarity, and geographic and temporal proximity between *E*. *australis* and *M*. *fossilis*, there can be little doubt that they are closely related. In fact, it is only the apparent difference in IBr_{1-2} that justifies assigning them to separate genera; until appropriate material becomes available to conclusively determine the nature of IBr_{1-2} in the Telm6–7 isocrinids, we favor retaining them within *M*. *fossilis*.

Occurrence. — Seymour Island, La Meseta Formation: ZPAL 1 (Bill Hill), Telm1 (Eocene).

Order **Comatulida** A.H. CLARK, 1908 Family **Notocrinidae** MORTENSEN, 1920

Genus Notocrinus MORTENSEN, 1920

Type species: Notocrinus virilis MORTENSEN, 1917, p. 206.

Notocrinus seymourensis sp. n. (Pl. 27: 1; Text-figs 7–8)

1994. Notocrinus sp.: BAUMILLER and GAZDZICKI, fig. 2C.

Holotype: ZPAL Ca.V/5. Paratype: ZPAL Ca.V/6. Type horizon: Telm2, La Meseta Formation (Eocene). Type locality: ZPAL 6, Seymour Island, Antarctic Peninsula. Derivation of the name: From Seymour Island, where the specimens were found.

Diagnosis. — A small *Notocrinus* with radial having small or no free dorsal surface and radial edge projecting downward in midradial area between the uppermost cirrus sockets.

Material. — Two crowns on a single block of sandstone. The holotype with only a portion of centrodorsal and articulated arm segments 1-1.5 cm long; the paratype with a centrodorsal distorted by compression, several cirri, and only the most proximal brachials.

Description. — Centrodorsal conical to subconical; sides straight to gently convex. Dorsal end not exposed. Dimensions of exposed part of centrodorsal: maximum width about 2.6 mm at the level of radials, height about 2.4 mm. Cavity exposed at level of radials in abraded specimen; 0.6 mm in diameter. Sides of centrodorsal covered by fairly large cirrus sockets; on the single, clearly exposed radial area of centrodorsal, sockets not arranged in distinct columns or rows, closely spaced. Sockets circular, smooth, no articular ridge, no crenellae, relatively shallow, with a small axial pore.

Cirri more than XXV, short, stout, and strongly curved; longest, incomplete cirrus 8.5 mm. Cirrals smooth, cylindrical, varying in shape: several proximal ones shorter than wide (diameter 0.5 mm, length 0.3 mm) medial slightly longer than wide (diameter 0.5 mm, length 0.7); distal cirrals and terminal claw unknown. Basals not visible on free surface. Radials as high as wide (1.5 mm) with no distinct free surface. Ventral edge of radial not straight but projects downward in the mid-radial area between the uppermost cirrus sockets. Articular facet almost flat, very steep, but this may be in part due to distortion of specimen. Dorsal ligament fossa large with a distinct ligament pit. Central canal large and subcircular in outline. Articular ridge reaches the interradial areas just above the centrodorsal. Ridge well-developed and nearly straight with the distal ends curving slightly dorsally.

Brachials with smooth free surface. IBr_1 rectangular and low; width 1.5–1.8 mm, height 0.4–0.6 mm (Text-fig. 7). IBr_{1-2} synarthrial. IBr_2 axillary, nearly triangular; proximal edge concave with central region slightly protruding down to synarthrial node; distal articular faces slightly concave, form an angle of about 60°; height 1.1–1.3 mm, width 1.6–2.1 mm.

First secundibrachial lower than the second: IIBr₁ width 1.1–1.3 mm, height of abradial sides 0.4–0.5 mm; IIBr₂ width 1.2–1.4 mm, abradial height 0.6–0.7 mm. Proximal articulation of IIBr₁ muscular, distal articulation synarthrial with node on IIBr₂ well developed. IIBr_{2–3} muscular. Syzygies at IIBr_{3–4} and IIBr_{9–10}; brachials of syzygial pairs approximately equidimensional.

First pinnule on $IIBr_2$, abradial. Only few proximal portions of pinnules preserved; segments smooth, rounded, and stout. First two pinnulars: width 0.3–0.4 mm,

height 0.3–0.4 mm. More distal pinnulars not preserved. Arm length indeterminate; distance between IBr_{1-2} and $IIBr_{13-14}$, about 10.5 mm.

Remarks. — The taxonomic assignment of the Telm2 comatulids is difficult because of their poor preservation: the indeterminate nature of the dorsal and ventral sides of the centrodorsal hinders comparison to fossil comatulids while lack of complete pinnules and cirri inhibits assignment to Recent taxa. Nevertheless, there are enough characters present on the two specimens to conclude that these comatulids are assignable to the genus *Notocrinus*; these characters include the conical centrodorsal, sockets lacking ornamentation, stout cirri and arms, steep and flat radial facets (Text-fig. 8).

A recently described comatulid from Telm6-7 of the La Meseta Formation, Notocrinus rasmusseni MEYER et OJI, 1993, differs significantly from the Telm2 comatulids described herein. The most obvious difference is its size: N. rasmusseni is much larger than N. seymourensis such that in the former the distance between IBr_{1-2} and $IIBr_{3-4}$ is 5.0 mm, while in the latter it is 2.5 mm. In addition to the size difference, the two differ in the shape of brachials. Whereas in N. rasmusseni the first primibrachial (IBr_1) is trapezoidal and the second primibrachial (IBr₂) pentagonal, in N. seymourensis the former is rectangular while the latter more triangular than pentagonal. The shapes of distal brachials also differ being more wedge-shaped in N. rasmusseni. Given these differences, the assignment of the Telm2 and Telm6-7 comatulids to a separate taxon seems justified. In fact, the morphology of *N. seymourensis* is more like that of the extant species Notocrinus mortenseni JOHN, 1938 than that of N. rasmusseni. The small, conical centrodorsal, the short, curved cirri with rounded segments, the robust arms with syzygies at $IIBr_{3-4}$ and $IIBr_{9-10}$, and the stout, rounded pinnules are characters shared by N. seymourensis and N. mortenseni. N. seymourensis, however, possesses a unique suite of characters distinguishing it from N. mortenseni and other Notocrinus, including a concealed free surface of the radial, a near-vertical radial



Fig. 7

Camera lucida drawing of proximal arms of *Notocrinus seymourensis* sp. n. 1 — first primibrachial; 2 — second primibrachial; all other brachials — secundibrachials; dotted lines — inferred plate edge; stippled plates — pinnulars; single arrow — syzygy; double arrow — synarthry; all other brachial articulations — muscular (ZPAL Ca.V/5).



Fig. 8 Notocrinus seymourensis sp. n. Side view of crown with centrodorsal and exposed radial facet. Paratype ZPAL Ca.V/6, \times 6.

facet, and a downward projecting ventral edge of the centrodorsal separating the uppermost cirrus sockets; in fact, these characters are reminiscent of Paleogene Conometridae such as *Bruennichometra* and *Cypelometra*, especially the Patagonian, Miocene comatulid, *Cypelometra iheringi* DE LORIOL, 1902. Only the centrodorsal of this genus has been described and in its shape and size it is not unlike *N. seymourensis*. Unlike *N. seymourensis*, however, the cirrus sockets in *C. iheringi* form 10 columns which are separated by a socket-free, vermiculate radial area.

RASMUSSEN (1978) placed *C. iheringi* and other members of the Conometridae within the Tropiometracea because of the resemblance of their centrodorsals and radials. The prismatic, carinate pinnules, exposed basals, and generally more than 10 arms of the Tropiometracea do not support a close relationship between this family and the Telm2 comatulids. It is probable that *C. iheringi*, and possibly the rest of the Conometridae, are more closely related to the Telm2 comatulids and are thus members of the Notocriniacea and not the Tropiometracea; the lack of information on cirri and arms in *C. iheringi* and the Conometridae hinders a definite resolution of this issue.

Occurrence. — Seymour Island, La Meseta Formation: ZPAL 6, Telm2 (Eocene).

Order Cyrtocrinida Sieverts-Doreck, 1953 Family Holopodidae Zittel, 1879 Genus Cyathidium Steenstrup in Michaelis and Scherk 1847

Type species: Cyathidium holopus STEENSTRUP in MICHAELIS and SCHERK 1847.

Cyathidium holopus STEENSTRUP in MICHAELIS and SCHERK 1847 (Pl. 27: 2)

1847. Cyathidium holopus; STEENSTRUP in MICHAELIS and SCHERK, pp. 119, 150.

- 1853. Microporocrinus Gastaldii; MICHELIN, p. 93.
- 1884. Cyathidium; CARPENTER, pp. 143, 202, 211-216.
- 1899. Cyathidium holopus; HENNIG, p. 116, fig. 21.

- 1913. Cyathidium holopus; NIELSEN, pp. 19, 27, 39, 56; pl. 4: 1-20; pl. 5: 1-43; text-figs 17-20, 31, 33-34.
- 1930. Cyathidium sp.; KUHN, p. 548.
- 1930. Cyathidium holopus; RICHTER, p. 64.
- 1961. Cyathidium holopus; RASMUSSEN, p. 242; pl. 35: 1-10.
- 1994. Cyathidium; BAUMILLER and GAŹDZICKI, p. 10, fig. 2B.

Description. - Rigid theca, presumably composed only of radials, with no apparent sutures. Cup irregular conical, tapering towards base. Wide articulations for arms separated by small triangular projections at interradii. The 5 primibrachials and 10 secundibrachials form a solid dome over the theca. Surface of plates unornamented and smooth. Each ray with single axillary primibrachial; primibrachial wide and pentagonal in outline (6.2 mm high and 11 mm wide at its base). Primibrachial may be composed of two fused primibrachials, but no evidence of this can be seen. Distal end of each primibrachial consists of two articulations for the secundibrachials oriented at an obtuse angle to each other. Length of articulations between primibrachials and secundibrachials averages 6 mm; width averages 1.7 mm. Proximal articular facet between primibrachial and secundibrachial muscular, sloping gently inward with faint, long, narrow fulcral ridge positioned closer to adoral than aboral surface of primibrachial. Small circular lumen of the axial canal situated just adoral to fulcral ridge; aboral side with elongated, elliptical ligament pit. Secundibrachials triangular; rather large, 6.0 mm average width and 8.8 mm average height. Surface finely granulate. Joint faces between adjacent secundibrachials covered by crenellae. Specimen strongly compressed laterally. Total height, 35.3 mm, maximum width at level of primibrachials, 24.1 mm, minimum width, 10.83 mm; difference in width due to distortion caused by compression. Shape of upper edge of cup highly distorted due to compression. Articular facets not observed.

Remarks. — Like all holopodid cyrtocrinids, which are adapted for cementation on hard substrates, the specimen from the La Meseta Formation lacks a stalk: its dorsal cup consists of fused radials attached directly to the substrate. Unlike the only other holopodid, *Holopus*, the La Meseta Formation specimen has only 15 exposed brachials (5 primibrachials and 10 secundibrachials) forming a complete covering over the ventral side of the theca. Its rounded, thin-walled theca distinguish it from the Cretaceous holopodid *Cyathidium senessei*, and its large size, smooth plates, and narrow base from *Cyathidium depressus*.

Occurrence. — Seymour Island, La Meseta Formation: ZPAL 1 (*Bill Hill*), Telm1 (Eocene). Danian of Denmark, Sweden and ?Austria; Maastrichtian of the Netherlands.

CONCLUDING REMARKS

The crinoids from the La Meseta Formation described above provide information relevant to several paleontological problems. For example, today comatulids are diverse and common in shallow-water, reef settings while all other groups have low diversities and are restricted to water deeper than 100 m. This pattern of distribution and diversity is not mirrored by the fossil record however: in the fossil record comatulids are sparse and their diversities low, and throughout most of the Mesozoic stalked articulates are often associated with shallow-water deposits. Since these patterns can be susceptible to certain biases, one goal of crinoid research has been to determine whether they are accurate. If the patterns are accurate, additional questions arise: When did changes leading to the differences in diversity and distribution between Recent and fossil articulates occur? What caused these changes?

The diversity of comatulids in modern oceans is well documented (RASMUSSEN 1978) but given their preference for reef environments, which are poorly sampled in the post-Paleozoic fossil record, their low resistance to transport and post-mortem disarticulation, and a difference in the taxonomic criteria used for recognition of living and fossil taxa the comatulid fossil record is likely to be very incomplete. Thus we can have little confidence in direct comparisons of diversity between the neontological and paleontological records. This limitation can be overcome only by quantitatively evaluating the taphonomic biases, expanding the fossil data base, and establishing uniform taxonomic criteria for fossil and Recent forms. The La Meseta Formation crinoid, *Notocrinus seymourensis* sp. n., described in this study, augments the extremely depauperate Cenozoic record of comatulids and, in having pinnules, brachials, and cirri preserved together

with the centrodorsal, possesses characters that are taxonomically useful for both Recent and fossil comatulids.

The shift of stalked crinoids into deep water during the post-Paleozoic is a pattern that is not subject to the same biases as comatulid diversity and one that has been much better established. The presence of stalked crinoids in shallow-water settings in ancient rocks and their absence from shallow depths today indicates that their distribution must have changed through time; this interpretation could be in error only if the environments of deposition of fossils had been misinterpreted or the carcasses had been transported into shallow water settings, both unlikely scenarios. A question that remains relates to the timing of the shift of stalked crinoids into deeper waters. Work by BOTTJER and JABLONSKI (1988) demonstrates that for isocrinids in the Euramerican Region the shift started by the Early Cretaceous and was essentially complete by the Eocene, but whether the timing of the shift was synchronous globally is still uncertain.

In spite of the much greater robustness of the isocrinid pattern of distribution, new data on fossil occurrences, especially outside the Euramerican Region, help constrain the timing of the environmental shift and narrow the range of hypotheses about causes for the shift. The presence of *Eometacrinus australis* gen. et sp. n. in the lower part of the La Meseta Formation provides new information on the temporal-environmental distribution of isocrinids, and demonstrates that outside the Euramerican Region isocrinids were still found in shallow-water settings during the Eocene (see also MEYER and OJI 1993). Also, data on the morphology of *E. australis* is relevant to the evolution of synarthrial and syzygial articulations between the first and second primibrachial, a character thought to be of primary phylogenetic importance (OJI 1985; SIMMS 1988) and used to subdivide the isocrinids into two major subgroups.

Finally, this study provides additional information on the stratigraphic and geographic distribution of the cyrtocrinid, *Cyathidium holopus* heretofore known only from the Cretaceous: the La Meseta Formation specimen represents its southernmost occurrence and extends its range into the Tertiary.

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PLATE 27

Notocrinus seymourensis sp. n.
Fig. 1. Side view of crown with abraded centrodorsal, holotype ZPAL Ca.V/5, ZPAL 6, Telm2, \times 3.0.
Cyathidium holopus STEENSTRUP, 1847
Fig. 2a. Side view of crown, ZPAL Ca.V/4, ZPAL 1, Telm $1, \times 1.8$.
Fig. 2b. Oral view of crown, ZPAL Ca.V/4, ZPAL 1, Telm1, \times 1.7.
Eometacrinus australis gen. et sp. n
Fig. 3a. Side view of crown, ZPAL Ca.V/2, ZPAL 1, Telm1, \times 1.1.
Fig. 3b. Side view of crown, ZPAL Ca.V/2, ZPAL 1, Telm1, \times 1.2.
Fig. 3c. Synarthry at IBr ₁₋₂ , arrow points to synarthrial ridge of IBr ₁ , ZPAL Ca.V/2, ZPAL 1, Telm1, × 3.3.
Fig. 4a. Side view of crown, ZPAL Ca.V/3, ZPAL 1, Telm1, \times 1.2.
Fig. 4b. Side view of crown, ZPAL Ca.V/3, ZPAL 1, Telm1, \times 1.3.
Fig. 4c. View of cup with basals and most proximal columnal, ZPAL Ca.V/3, ZPAL 1, Telm1, × 2.8.
Fig. 5a. Side view of crown, holotype ZPAL Ca.V/1, ZPAL 1, Telm1, × 1.1.
Fig. 5b. Aboral view of abraded cup with basals missing, ZPAL Ca.V/1, ZPAL 1, Telm1, \times 3.0.
Fig. 6. Symplectial facet of an internodal columnal, ZPAL Ca.V/8, ZPAL 1, Telm1, × 6.5.
Fig. 7. Synostosial (cryptosymplectial) facet of an infranodal columnal, ZPAL Ca.V/9, ZPAL 1, Telm1, × 7.

Fig. 8. Side view of pluricolumnal, ZPAL Ca. V/7, ZPAL 1, Telm1, $\times 2.0$.



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