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## ABSTRACT

*Rheocrinus aduncus*, new genus, and new species, subclass Camerata, and *Parisocrinus mulletensis*, new species, subclass Inadunata, occur in a Late Ordovician (Richmondian) submarine channel fill in the Georgian Bay Formation. This occurrence greatly extends the stratigraphic ranges of the respective families, Anthracocrinidae and Ampheristocrinidae, thereby providing morphologic and temporal support to proposed evolutionary relationships of the foregoing families with the Rhodocrinitidae and Cyathocrinitidae, respectively.

Unusual morphological features of *R. aduncus* indicate that it could form an inclined, parabolic filtration baffle, as do certain living stalked crinoids. A vertically held, planar baffle is suggested for *P. mulletensis*. These species are believed to have occupied two distinctive microhabitats defined by feeding level, current energy, and feeding mode. They are presently the oldest, known channel-dwelling crinoids, and contain among the oldest three dimensional preserved internal organs.

## INTRODUCTION

In the Toronto area, extensive fossil collections from a number of localities have been made over the years (Fritz, 1925; Dyer, 1925a, 1925b; Parks, 1925), most notably from the exposures along Don Valley in eastern Toronto and from the banks of the Credit River and its tributaries approximately 12 miles southwest of downtown Toronto. Dyer (1925a, p. 50) reported "101 species or varieties" of fossils from the upper part of the "Dundas Formation" and overlying "Richmond Formation" (= Meaford Formation of Foerste, 1924) of which "at least three-quarters of the total fauna is from the Richmond." Parks (1925, p. 100) reported 150

species (which excludes 37 species of "vermes") from the underlying "DunJas Formation." Thus, the total reported faunal diversity from the Lower Georgian Bay Member is relatively great—on the order of 225 species of skeletonized invertebrates. Of this number, bryozoans, pelecypods, and brachiopods constitute approximately three-quarters of the faunal diversity, and are by far the most numerically abundant individuals in the fauna.

Echinoderms are exceedingly rare in this fauna. Fritz (1925) reported fragments of one species of asteroid, three species of inadunate crinoids, known only from a few incomplete

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crowns and fragments of stems and arms, and one species of camerate crinoid, *"Glyptocrinus dedactylus,"* whose presence was inferred on the basis of large stems; no crowns are known. The three small inadunates, and the large camerate (whatever it may be?) all occur in what appears to have been a typical, muddy, level-bottom milieu. No echinoderms are known to be associated with carbonate bioherms. The unexpected discovery of abundant, well-preserved crinoids in otherwise crinoid-impoverished strata is, therefore, paleoecologically interesting. Furthermore, both new species of this crinoid faunule are significant phyletically and temporally with respect to well-known Middle Ordovician and Middle Silurian taxa. The family Anthracocrinidae, to which *Rheocrinus aduncus* belongs, was previously known only from Middle Ordovician strata, and the family Ampheristocrinidae, to which *Parisocrinus mulletensis* belongs, was not known to occur in pre-Middle Silurian strata. Both new species serve to emphasize our temporally incomplete knowledge of biozones.

## OCCURRENCE OF THE CRINOID FAUNULE

Specimens of both new species of crinoids occur in the "zone of *Strophomena varsensis*" of Dyer (1925b, p. 121). This local range zone encompasses approximately 18 ft. of shale marked by sandy limestone and calcareous sandstone "hardband" interbeds. This sequence of strata is well exposed along a portion of Mullet Creek between the bridge on Mississauga Road and the Credit River (fig. 4). A single, very distinctive, fossilferous bioclastic limestone and siltstone horizon also occurs in this shale-hardband sequence. The bioclastic limestone and siltstone typically ranges from 6 inches to 18 inches thick along several hundred yards of discontinuous lateral exposure, but at two localities it thickens abruptly to form pod-shaped bodies up to 8 ft. thick and 60 ft. in lateral extent. Dyer (1925b, p. 121) termed one of these bodies "the bryozoan reef." Examination of this so-called reef revealed a number of significant lithologic features: (1) the lateral and lower contacts sharply truncate the adjacent shale and hardband strata that characterize the

Lower Georgian Bay Member throughout the Toronto area (fig. 1); (2) the lower border of the pod-shaped body has an undulatory, fluted cross-sectional profile (fig. 1) and several minor sandstone lenses within the body have fluted lower surfaces; (3) fragments of the surrounding shale-hardband lithology are included in the body, but the converse is not the case, and (4) the upper surface of the body has an even, comformable, horizontal contact with the overlying shale-hardband sequence (fig. 1). These features suggest that the so-called bryozoan reef is actually a submarine channel fill—a view also taken by Burke, Kidd and Walker (MS).

The lithology of the pod-shaped mass is best described as mixed and chaotic. The dominant lithology is brownish gray, bryozoan, echinoderm, brachiopod biorudite, which is unbedded and occurs as a melange of irregular, packed masses set in a shale-siltstone matrix. The irregularity and angularity of the packed limestone masses suggested to Burke, Kidd and Walker (MS) that the limestone masses were lithified prior to being transported into the channel; however, I dispute this point because a number of delicate, well-preserved camerates (complete with arms, pinnules, long attached stems, and associated holdfasts) are found lithified to the limestone surfaces in contact with the shale and siltstone matrix. Most of the fossil debris is fragmental, indicating some degree of transport, but I believe that it accumulated as unconsolidated mounds on the floor of the channel, along with an admixture of mud and silt. Subsequent differential compaction and lithification of the lime-patches relative to the mud and silt may have accentuated the limestone masses, thereby creating a post-depositional "melange effect." Angular fragments of calcareous sandstone, almost certainly derived from the hardbands outside the channel, appear to constitute good evidence for erosional scour of adjacent Georgian Bay strata. The mud, silt, and minor sand of the channel fill were probably derived from both the adjacent level-bottom sediment and a nearby interdistributary shoal, or subaerial feature, and carried in suspension or by bottom traction along the channel. The occurrence of a thin discontinuous, lateral limestone band of channel lithology is interpreted as a possible submarine
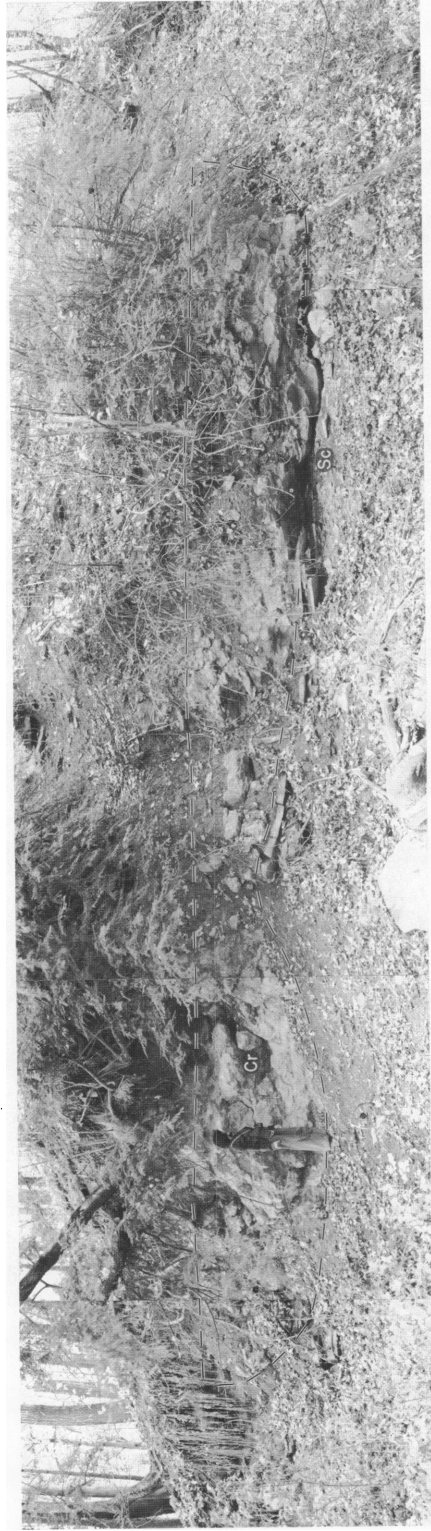
Fig. 1. Photomosaic of the channel fill exposed on the south bank of Mullet Creek. The channel boundary is outlined by dashes, width approximately 60 ft., maximum thickness approximately 8 ft. Crinoids were found at location Cr. Well-developed scour flutes at the base of the channel fill and truncation of underlying strata are exposed at Sc. Note the uneven erosional topography of the floor of the channel.

FIG. 2. Typical lithology of the Georgian Bay Formation is well exposed in Mullet Creek. Resistant "hardbands" of sandstone, Ss, alternate with softer shales, Sh. Approximately 25 ft. of stratigraphic section is exposed in the photo.

"spillover feature" that may represent "fingers" of the main submarine channel. "Spillover fingers" have been documented for the 170-mile-long Mississippian Bethal Sandstone submarine channel fill of western Kentucky and south-central Indiana (Hagan, et al., 1969).

Specimens of the large camerate, *Rheocrinus aduncus*, and the small inadunate, *Parisocrinus mulletensis*, were all collected from a single "colony" in a siltstone lens and from limestone contact surfaces in the main channel fill (fig. 1). The remarkable completeness of these fragile crinoids indicates that they lived in the channel. The well-preserved holdfasts, bearing numerous appendages (=radicles; figs. 7F, 8D, E,G,J), and belonging to *Rheocrinus aduncus*, clearly indicate that this crinoid was adapted for sedentary attachment in the soft sediment of

the channel floor. The inadunate, *Parisocrinus mulletensis*, is intimately associated with *Rheocrinus aduncus* in the colony and would otherwise have gone unnoticed because of its small size. No holdfasts of *Parisocrinus mulletensis* have been collected; individuals of this species may have anchored by wrapping the distal segment of their stem around a stationary object such as a trepostome bryozoan. All evidence indicates that the crinoid faunule lived in the submarine channel at the site were they were recovered. No specimens have ever been found in adjacent, typical, hardband strata outside the channel fill.

The channel-dwelling crinoid faunule is, therefore, unusual in comparison with the more common level-bottom or reef associations reported for most Paleozoic crinoids. Channel-dwelling blastoids from the Mississippian Sap-

pington Formation, Montana, (Sprinkle and Gutschick, 1967) represent a similar environmental situation, and recently, Ausich (1977b, pp. 884-885) has reported crinoids in "submarine distributary sandstone channels" in the Lower Mississippian Edwardsville Formation—a part of the ancient Borden Delta.

## PRESERVATION

The crinoid faunule is unusually well preserved, both in terms of structural detail and completeness of individuals. Most of the camerate specimens were collected with the proximal portion of the stem still attached, and two specimens of the small inadunate also have an attached stem segment. None of the specimens were recovered with a complete stem, but this is due primarily to the difficulties encountered in quarrying the specimens from the vertical

face of the channel fill. The numerous club-shaped holdfasts recovered from the colony indicate that entire individuals likely existed at the site of collection. A state of such complete preservation is commonly taken as evidence for a sudden influx of sediment that overwhelmed an entire life assemblage. The current-dominated environment normally disaggregated the crinoids and other invertebrate skeletons, producing the bioclastic carbonate channel fill.

The calyx of many of the camerates has a slightly collapsed and perforated side (figs. 5A,C,E,G, 6E). This side was situated upward in reference to the floor of the channel. I believe that this orientation indicates that the viscera decayed in such a way that the upward side of the calyx was weakened differentially by entrapped gaseous and fluid by-products of decay. Subsequent compaction of the sediment



FIG. 3. Flute casts, arrows, on the base of sandstone "hardbands" indicate episodes of submarine erosion of the underlying mud prior to deposition of the sand layer. Upper surfaces of the sandstone are commonly ripple marked, as on the small displaced slab to the upper left of the center arrow.

crushed the upper side. Many of the specimens also remained hollow and geode-like, with internal calcite ($CaCO_3$) and celestite ($SrSO_4$) crystal development. Despite this great degree of secondary mineralization, both hollow, and infilled specimens have preserved perivisceral coelomic organs (=PvC; figs. 5I, 6E, 8A, C, 13A). These are among the oldest known three-dimensional preserved internal organs in camerate crinoids (also see Brower, 1973, pl. 70, fig. 2). This fact is of considerable biological significance because it demonstrates a remarkable consistent visceral organization whithin the subclass Camerata from the Late Ordovician through the Mississippian (and likely throughout their range: Early Ordovician–Late Permian).

Many of the camerates were recovered in groups of from two to three individuals, fused together with arms intertwined and conforming to the contours of contiguous crowns (fig. 5A,C,D,E). Individuals are also closely associated on small slabs. All the small inadunates were found either cemented to or immediately adjacent to a larger camerate. Some of the camerate holdfasts also occur in groups of two or three individuals whose radicles are intertwined—presumably their original life association (fig. 8E). These findings indicate that the channel-dwelling colony consisted of groupings, or "stands," of several neighboring long-stemmed camerates and allied short-stemmed inadunates. Lane (1963, 1973) has reported similar groupings and "stratification" of Mississippian crinoids from the Borden Delta fauna at Crawfordsville, Indiana. Individuals of *Rheocrinus aduncus* had a generally consistent axial alignment, presumably due to the prevailing current at the time of death. If the crinoids died exactly at the collecting site with their holdfasts still effectively anchored, the crown, which has great hydrodynamic drag, would have been swept down current. The current direction indicated by this observed alignment is south to north. The arm posture of nearly all specimens is an up-folded "tear-shaped survival posture" that has been inferred to represent a response to dangerously strong currents (Haugh, 1978).

## SYSTEMATIC PALEONTOLOGY

### CLASS CRINOIDEA MILLER, 1821

### SUBCLASS CAMERATA WACHSMUTH AND SPRINGER, 1885

### ORDER DIPLOBATHRIDA MOORE AND LAUDON, 1943

### SUPERFAMILY RHODOCRINITACEA ROEMER, 1885

### FAMILY ANTHRACOCRINIDAE STRIMPLE AND WATKINS, 1955

#### *RHEOCRINUS*, NEW GENUS

TYPE SPECIES: *Rheocrinus aduncus*, new species, by monotypy.

DEFINITION: The genus is presently congruent with its only known species, so the definition is deferred to the diagnosis of the type species, below.
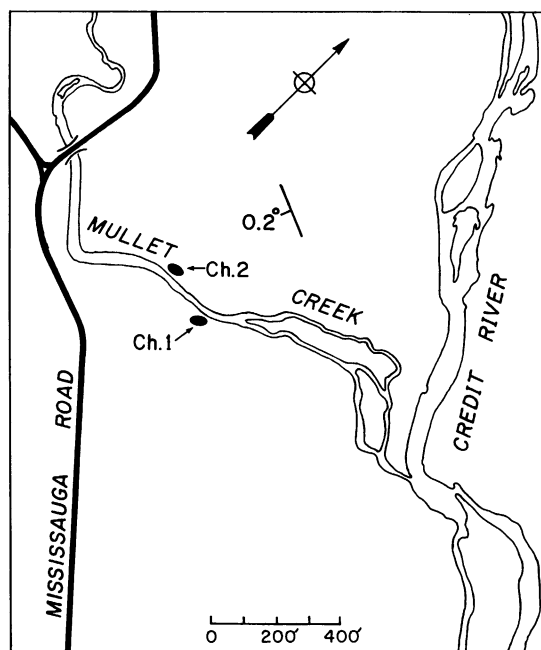
KNOWN RANGE AND DISTRIBUTION: Late



FIG. 4. Detailed locality map of the exposures of the Georgian Bay Formation along Mullet Creek at Erindale, Ontario. The locations of the crinoid-bearing channel fill, Ch. 1, as well as a second channel fill, Ch. 2, are indicated.

Ordovician, Richmondian (Ashgillian), southern Ontario, Canada.

ETYMOLOGY: From the Greek *Rheos* stream, current; in reference to its inferred topographic and ecological occurrence in an ancient submarine channel; the Greek *Krinon* lily [neuter].

## Rheocrinus aduncus, new species
Figures 5A-I; 6E; G-J; 7A-F; 8A-E; G-J; 9A,B; 10A-C; 11A-C; 13A-F

DIAGNOSIS: An "anthracocrinid" with a low subconical dorsal cup. Median ray ridges very faintly developed on slightly elevated ray taxis. No median interray ridges in any of the interrays. Sutures distinct and moderately depressed, especially near the plate corners. Plate surfaces smooth, unornamented. Lower dorsal cup border distinctively crenulate due to dorsally projecting, spade-shaped radials alternating with withdrawn trapezoidal basals intercalated in the same lowest plate "bicirclet." Infrabasals completely hidden in a basal invagination. Interrays all of equal width. Posterior interray distinguished by a single large primanal followed by a single large interbrachial (anal) plate; remaining higher order posterior interbrachial plates small, irregular polygonal, and variable in number from specimen to specimen. Lateral interrays consisting of a large first interbrachial whose lower corners only, contact the radials, followed by two subequal medium-sized interbrachials, the latter followed by several smaller interbrachials, variable in number among interrays, and not continuing onto the tegmen. All upper interradial spaces filled by fixed pinnules that "bridge" the lower interbrachials. Free arms proximally cuneate uniserial, distally biserial, unbranched, densely pinnulate, four arms per ray. Tegmen highly doomed, plate pattern and precise position of anal vent unknown. Stem large and pentameral proximally, tapering to a smaller diameter with round cross section medially, distal region expanded into a club-shaped, radicle-bearing radix with pentagonal cross section.

DESCRIPTION: Shape of dorsal cup of adults variable in form from subglobular to subconical through juvenile to full adult stages, respectively. Dorsal cup much wider than high, asymmetrical in profile view, with one side having a greater surface length and convexity that the other; stem subcentral, commonly inserted at an angle to the dorsoventral cup axis, and slightly displaced toward the shorter, less convex side. This asymmetry and stem offset discernible in both profile and dorsal view even though the types are slightly laterally compressed and eroded. Base of calyx distinctly crenulate in profile view; no broad, external, basal surface concavity, rather, a deep invagination into the base of the dorsal cup. Infrabasals five, apparently equal, precise shape unknown, forming the top of an "intracalical cylinder" around the proximal inserted section of the proxistele and completely hidden from external view. Lowest visible plates in the cup consisting of a basal-radial "bicirclet" of 10 alternating plates forming the bottom of the intracalical cylinder. Basals five, equal, trapezoidal in external view, higher than wide, distinctly smaller than, and depressed relative to adjacent radials in the bicirclet. Lower externally visible basal margin straight and withdrawn ventrally, forming the "crenels" of the lower crenulate border profile. Upper basal margin straight, contacting the first interbrachial or primanal. Radials five, equal, spade-shaped, higher than wide in external view, larger than the basals and elevated relative to the basals. Radial surface obtusely arched, bearing a faint median ridge that continues to the fixed brachials. Lower externally visible radial border rounded, projecting dorsally well below the basals, thus forming the "merlons" of the lower crenulate border profile. Upper radial margin straight to slightly curved, projecting slightly higher than the upper margin of the basals. Ventrolateral corners of the radials barely in contact with, and slightly truncated by the first interbrachials. Dorsal bicirclet flaired outward in subconical adults, but more prominently so in juvenile subglobular forms. Both basals and radials reflexed inward (aduncate) to form the dorsal part of the intracalical cylinder. Lateral interrays narrow, filled by a lower group of true interbrachials and an upper group of fixed pinnular
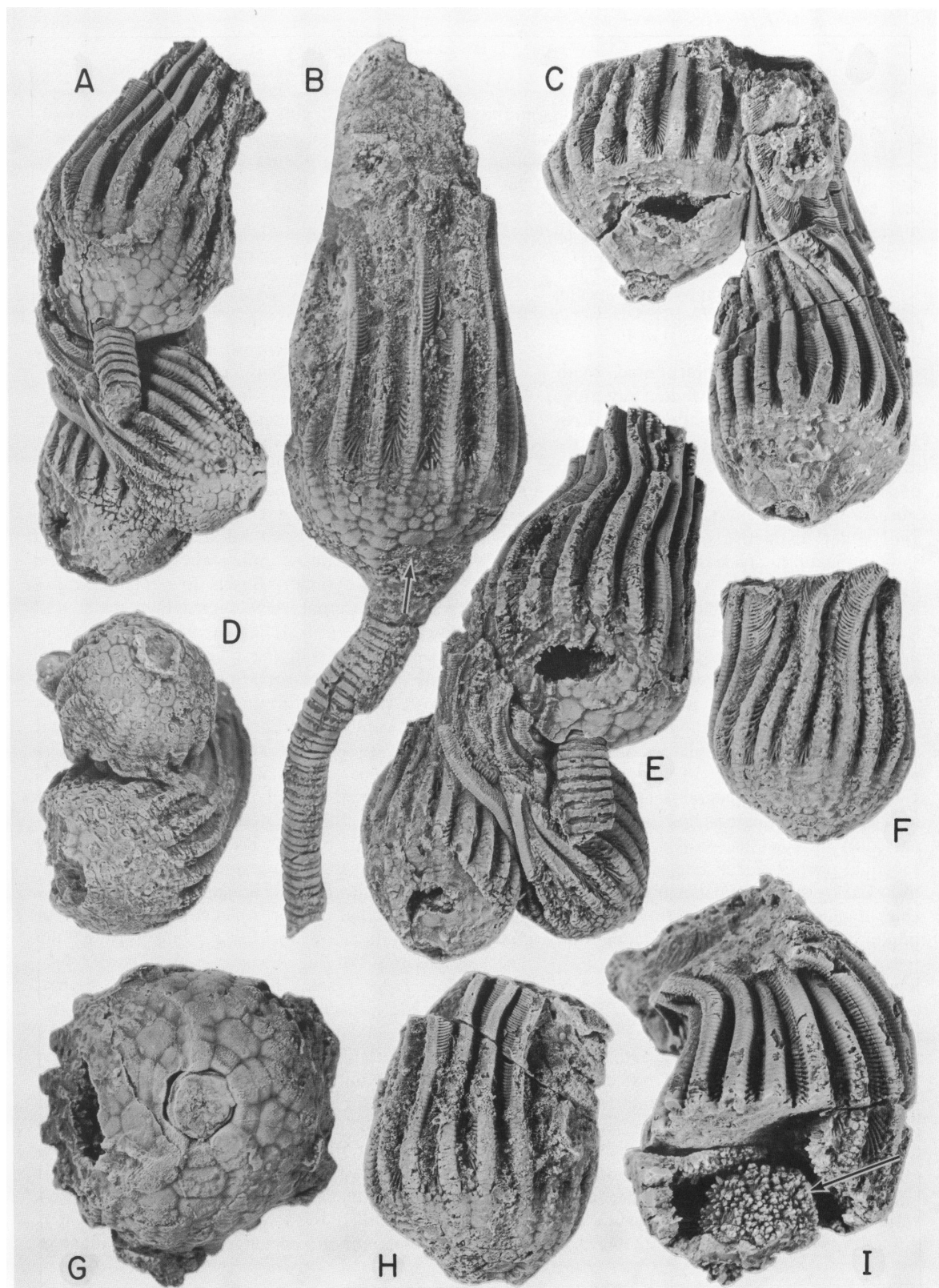
plates. First interbrachials the largest plates in the dorsal cup, one per interray, bordering laterally: first primibrachials, second primibrachials (axil), and first secundibrachials. First interbrachials approximately equidimensional, octagonal or nonagonal irregular polygons. Second interbrachials of moderate size, two per interray, subequal in size, bordering laterally: first secundibrachials, second secundibrachials (axil), and first tertibrachials. Higher orders of interradial plates variable among rays of an individual. Inter-half-ray plates forming a short taxis of two or three small plates in lateral contact with the first secundibrachials through the second tertibrachials. Inter-half-ray plates rarely not developed between one or more rays of an individual. Posterior interray of width equal to the lateral interrays. Primanal octagonal, large, size equal to the other first interbrachials, but invariably succeeded by a single large anal plate. Succeeding posterior interray plates unordered and variable in number from two through seven. Interray ridges absent. Ventral interray spaces of the dorsal cup filled (bridged) with hypertrophied fixed pinnules, most commonly two per interray. Fixed pinnule size decreases from interray to inter-half-ray to inter-quarter-ray as follows: interray fixed pinnules composed of three to four pinnulars arising from the second tertibrachials; inter-half-ray fixed pinnules composed of two to three pinnulars arising from the second tertibrachials; and inter-quarter-ray fixed pinnules of one or two pinnulars arising from the forth tertibrachials. Very small fixed pinnules arising sporadically from fifth tertibrachials. Distal segments of

fixed pinnules becoming abruptly slender and free between the arm bases. All interradial areas becoming less depressed at the top of the cup. Plate sutures of two types: below the primaxils a close straight suture, above the primaxils a close crenulate suture (symplexy), the latter including the fixed pinnulars and the lower ten to fifteen free brachials.

Fixed brachials branching isotomously within the calyx producing four arms per ray. First primibrachial quadrangular, much wider than high. Second primibrachials (axil) pentagonal, height and width about equal. First secundibrachials hexagonal, wider than high, in lateral contact with one another and with an intersecundibrachial (except in rare instances). Second secundibrachials (axil) pentagonal, height and width about equal, but smaller than the second primibrachials (axil). Tertibrachials two through six in fixed brachitaxis, all wider than high, giving rise to fixed pinnules as noted above. Arms free by seventh tertibrachials, becoming cuneate through 11 or 12, biserial thereafter to arm tips, approximately 125-130 tertibrachials. Free arms unbranched, densely pinnulate, uniformly tapering to tips. Total adult free arm length averages approximately 55 mm. on nearly complete arms of the holotype and several paratypes. Aboral sides of arms evenly rounded, and laterally delimited by a prominent pinnular articulation joint ligament notch.

Pinnules lath-shaped with flat aboral surface and lateral sides, densely packed, almost in lateral contact. Each pinnule consisting of about 12 pinnulars. Proximal pinnulars of the

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Fig. 5. All specimens are *Rheocrinus aduncus*. A. Three fused adults at slightly different stages of development. Compare the more immature arms of the central individual with the arms of the top individual. X1.2. ROM 36380a, b, c. B. A large adult with preserved proxistele and an unusually large number of plates in the CD-interray, arrow. X1.2. ROM 36376. C. Two fused large adults illustrating exceptionally long, densly pinnulate arms. X1.2. ROM 36381a, b. D. The upper individual illustrates the difference of plating of the CD-interray, upper left, compared to the DE-interray, lower center. X1.2. ROM 36380b, c. E. The same three individuals as in figure 5A, which may have lived together as a "stand" and fell to the seafloor with arms and stems intertwined. Note the crenulate dorsal cup border and relatively large stem of the upper individual. X1.2. ROM 36380a, b, c. F. A young adult whose pinnular spacing has not achieved maximum density. X1.2. ROM 36377. G. Basal view of an adult illustrating the "bicirclet" of 10 alternating basal and radial plates. Note the pentagonal nature of the stem and intracalical cylinder. The CD-interray is oriented down. X1.7. ROM 36380a. H. Lateral profile of an adult illustrating the asymmetry of the dorsal cup and lateral offset of the stem. X1.2. ROM 36381b. I. A hollow specimen with a three dimensional perigastric coelmic organ, arrow. X1.7. ROM 36379.
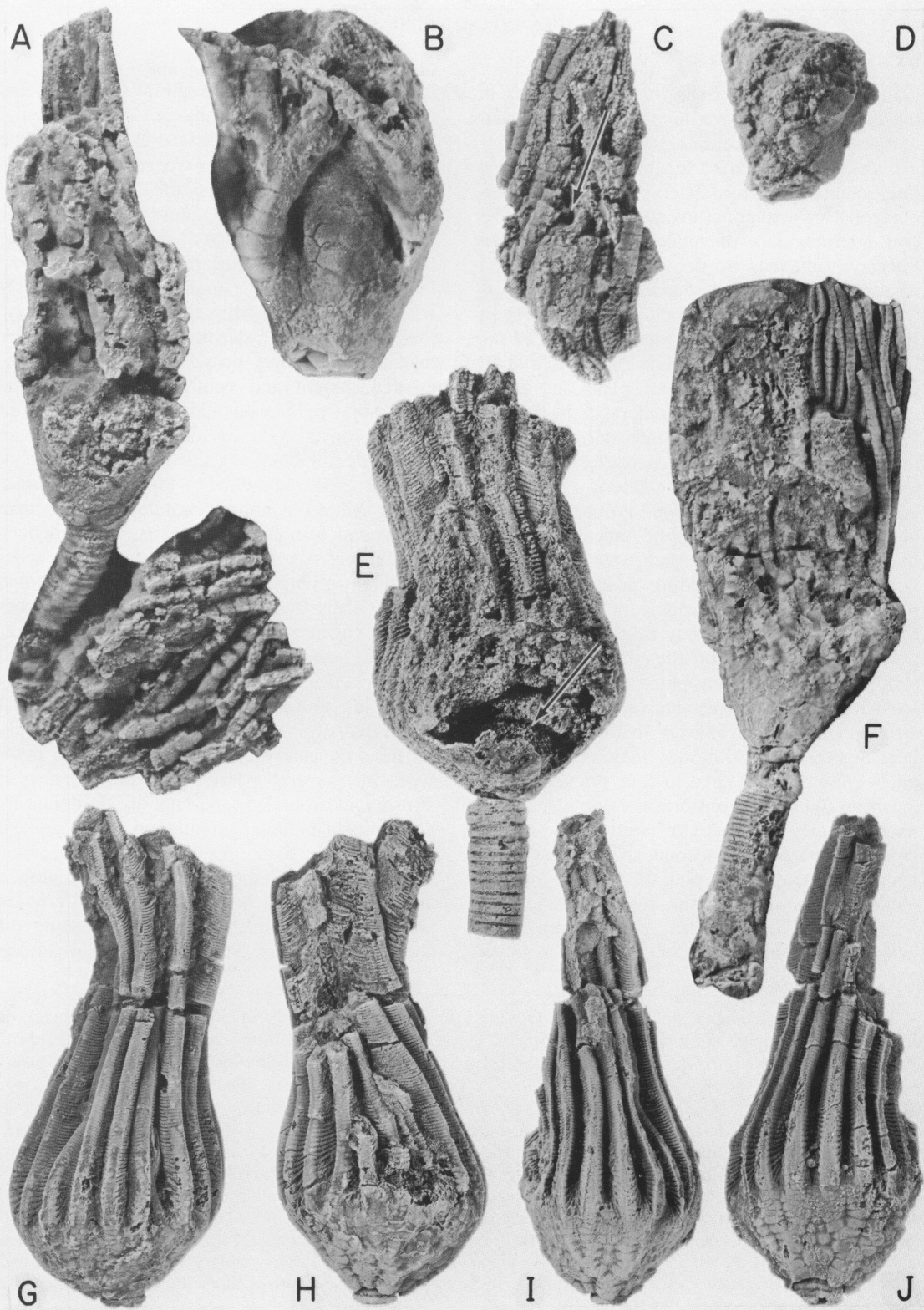
following average dimensions: 1.0 mm. length, 0.3 mm. width, and 0.5 mm. oral-aboral thickness. Distal pinnulars becoming shorter, less thick, but of uniform width nearly to the tip.

Tegminal surface obscured by the arms on all specimens, but broken and sawed specimens indicate a high convex structure. Anal vent probably central, at the summit.

Stem large for the size of the crown, deeply inserted into the basal invagination. Heteromorphic as follows: proxistele pentagonal, of large diameter proximally, tapering down distally, consisting of a simple noditraxis $(N1)_n$, nodals with gently rounded epifacets, weak narrow symplexial crenularium, large pentalobate concave areolae, and pentalobate lumen; internodals much reduced in diameter relative to the nodals, lens-shaped, "nested" within the concave areolae of the nodals, and with narrow peripheral crenularia in weak symplexial articulation, internodal areolae gently convex with curvature matching that of the nodals, lumen pentalobate, about 15 internodals present; mesistele gradually becoming circular, consisting of a simple noditaxis $(N1)_n$, nodals with gently rounded epifacets, articula same as in proxistele, internodals of larger relative diameter and greater height than in proxistele, epifacets with central encircling ridge; dististele tapering to an enlarged diameter, becoming pentagonal and terminating in a club-shaped radix bearing radicles along the angles. Dististele becoming homeomorphic, composed of very "thin" columnals with strong symplexial union, but with a surficial rugose ornamentation. Rugose surface lineation may be inclined slightly to the true columnal articulations—a divericate ornamentation.

DISCUSSION: *Rheocrinus aduncus*, new genus and species is characterized by a bicirclet of 10 basal and radial plates (fig. 9). The presence of a dorsal cup bicirclet of alternating radials and basals with the infrabasals in radial contact has been interpreted by Ubaghs (1953) as a character of high-level taxonomic importance, and presumably of fundamental unifying phylogenetic significance. His suborder Zygodiplobathrina embodies the bicirclet as the defining character (synapomorphy) of the group. *Cleiocrinus, Spyridiocrinus, Paulocrinus, Dimerocrinites, Rhipidiocrinus, Simplococrinus,* and now *Rheocrinus* all feature one or more species with a bicirclet construction; yet on other systematic grounds the foregoing genera are taxonomically distributed among several families that are nominally regarded as being within the suborder Eudiplobathrina (=dicyclic camerates with separate infrabasal, basal, and radial plate circlets). Furthermore, some species of a genus (e.g., *Rhipidiocrinus* and *Dimerocrinites*) have a bicirclet, whereas other species of the same genus do not. Therefore, it seems prudent to remove these two suborders from the taxonomic scheme (also see Brower, 1975, pp. 643-644). *Rheocrinus aduncus* is the most extreme example of bicyclical development known to me, and represents a clear case of independent derivation of the "zygodiplobathrinid condition."

*Rheocrinus aduncus* possesses characters of both the long-established family Rhodocrinitidae Bassler, 1938; family Archae-

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FIG. 6. Specimens A-D, F are *Parisocrinus mulletensis*; specimens E, G-J are *Rheocrinus aduncus*. A. The holotype viewed from the CD-interray. The end of the anal sac has been broken off; the arms, below, appear to belong to this crown. See figure 12A for a camera lucida drawing of this specimen. X4.7. ROM 36401. B. A specimen viewed from the CD-interray illustrating the well-preserved proximal section of the anal sac. See figure 12B for a camera lucida drawing of this specimen. X4.7. ROM 36402. C and D. The distal section of the arms and anal sac, C, and dorsal cup, D, belong to the same individual. The proximal arms and anal sac are not preserved. Note the distal position of the anal vent, arrow. Also see figure 8F for an enlargement. X4.7. ROM 36404. E. A hollow specimen of *R. aduncus* with a three-dimensional perigastric coelomic organ, arrow. Note the relatively large proxistele. X1.7. ROM 36378. F. A nearly complete specimen of *P. mulletensis* viewed from the A-ray. The dorsal cup is slightly crushed in the plane of the photo. See figure 12C for a camera lucida drawing of this specimen. X2.7. ROM 36403. G-J. Four views of the holotype of *R. aduncus* as follows: C-ray, E-ray, D-ray, AB-interray. Note the asymmetry of the dorsal cup and the elevation of the surfaces of the rays relative to the interrays. A few millimeters of even the longest arms is missing. All X1.2. ROM 36375.
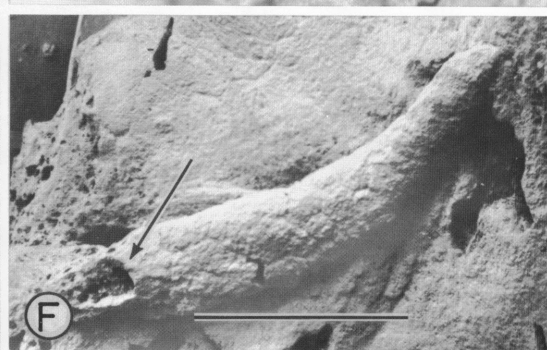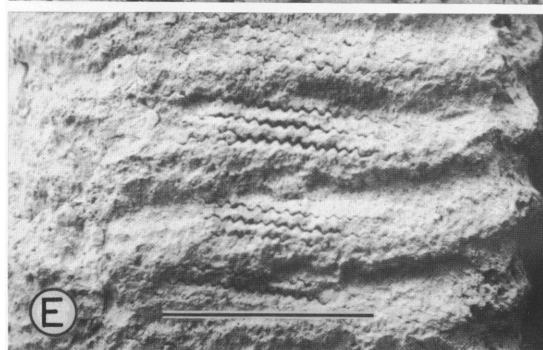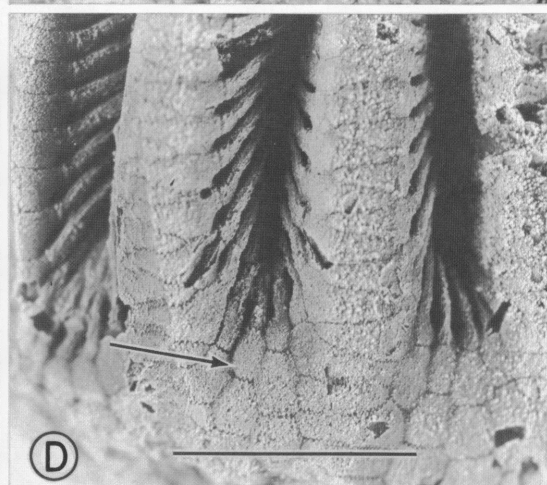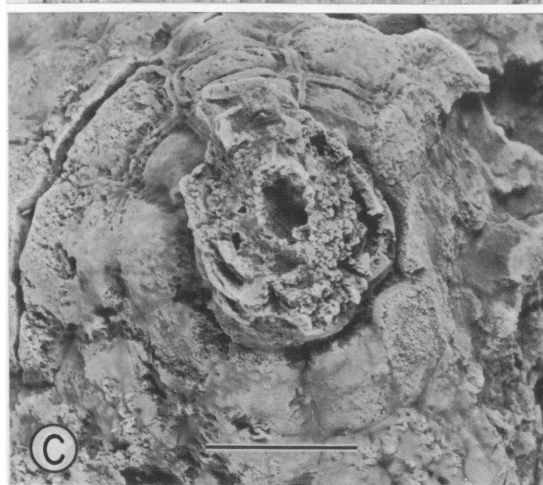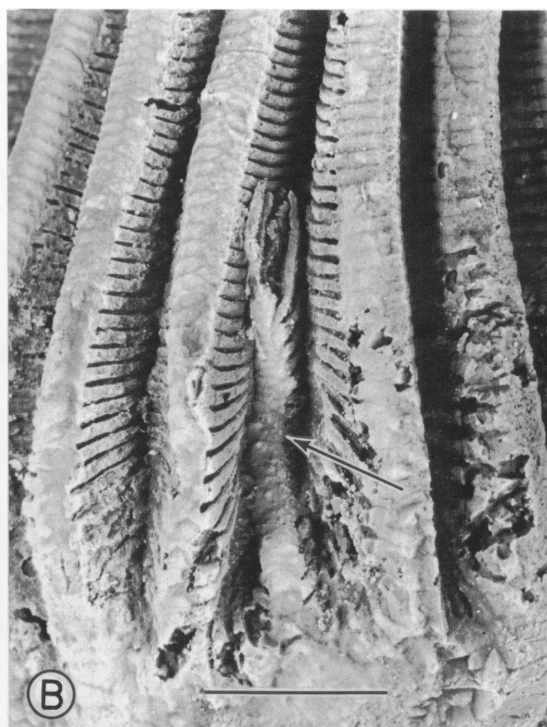
ocrinidae Moore and Laudon, 1943; and the taxonomically impoverished family Anthracocrinidae Strimple and Watkins, 1955. The deeply invaginated infrabasal cylinder (figs. 8A, 13A), narrow interrays with few large plates, and interradial fixed pinnules which "bridge" the top of the dorsal cup (figs. 10, 11) are features distinctive of the Anthracocrinidae. Conversely, the near congruence of the plate patterns among the interrays (including the CD-interray), very faintly developed median ray ridges, and the presence of long, tapering, densely pinnulate, wide biserial arms ally *Rheocrinus* with the Rhodocrinitidae, such as the Late Ordovician genera *Maquoketacrinus* and *Atactocrinus*, and the Silurian genus *Lyriocrinus*. The arms of *Rheocrinus* differ from *Anthracocrinus* which has 15 (three per ray) uniserial, unbranched arms; *Lyriocrinus* has only 10 wide, gently tapering, biserial arms; the arms of *Maquoketacrinus* and *Atactocrinus* are unknown. The arm branching pattern of *Simplococrinus*, with 40 unbranched biserial arms, is similar to *Rheocrinus*, but the former has ramules separated laterally by small interbrachials, and has a distinctly elevated, narrow, fixed brachial taxis.

To my knowledge, the anal plate pattern in the lower CD-interray (fig. 10) of *Rheocrinus* is a unique and primary defining character of the genus: an octagonal primanal in full horizontal straight-sutural contact with a single, large, succeeding anal plate. *Lyriocrinus* has an octagonal primanal in arched contact with three succeeding large interbrachials (anals); *Maquoketacrinus* and *Atactocrinus* have heptagonal primanals succeeded by two equal, pentagonal interbrachials (anals); *Anthracocrinus* has an irregular hexagonal primanal succeeded by two irregular interbrachials (anals); and *Simplococrinus* has an irregular hexagonal primanal succeeded by three irregular interbrachials (anals).

Perhaps the most fundamental distinguishing feature of *Rheocrinus* is its crenulate, lower cup border as viewed in profile (figs. 5E, 6H, 8H). This feature, seemingly, is the result of enlargement of the stem, with a consequent upward displacement of the basals. The pentagonal nature of the stem also produces an internal crenulation of the invaginated infrabasal cylinder, as viewed in cross section (figs. 8C, 13B). The latter character is also present in *Anthracocrinus*, according to Strimple and Watkins (1955).

The lateral interrays of *Rheocrinus* illustrate a comparatively advanced structural condition for Ordovician camerate crinoids. The lateral interrays are relatively narrow and have a plate pattern similar to that of the CD-interray. The relative narrowness of the interrays is partly a consequence of the great width of the fixed brachials. The latter feature is judged to be an advanced character state that first appears in rhodocrinitids, such as *Wilsonicrinus culmensinuosis* Brower (1974), in the Middle Ordovician, and *Rheocrinus aduncus* in the Late Ordovician, but is uncommon until the Middle Silurian, for example: *Wilsonicrinus* Springer (1926) and *Lyriocrinus* Hall (1852). The interbrachials of *Rheocrinus* are not continuous onto the tegmen; rather, they are "bridged" by the fixed pinnules (figs. 7D, 10, 11), a condition shared with *Deocrinus*, *Hercocrinus*, and *Anthracocrinus*. The bridged character state appears to be advanced relative to the situation in which numerous small interbrachials (with, or without ramules) continue onto the tegmen as found in *Simplococrinus*, *Archaeocrinus*, *Pararchaeocrinus*, and *Neoarchaeocrinus*. Seemingly more advanced forms, such as *Maquoketracinus* and *Atactocrinus* illustrate further

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FIG. 7. All specimens are *Rheocrinus aduncus*. A. Arm and pinnule detail. Note the cuneate proximal arms, left arrow, and the closely spaced lath-shaped pinnules, upper arrow. Scale 1 cm. ROM 36381b. B. A regenerated arm with pinnules, arrow. Scale 5 mm. ROM 36375. C. A dorsal cup "bicirclet" and proxistele. Scale 5 mm. ROM 36381a. D. Fixed pinnules, arrow, and proximal sections of arms. Note the symplexial (zigzag) sutures. Scale 5 mm. ROM 35652. E. The divaricate pattern of the columnals and surface rugae on one of the radices. Scale 2 mm. S.E.M., ROM 36387. F. A broken radicle composed of small polygonal plates. Arrow indicates the axial canal. Scale 2 mm. S.E.M., ROM 36390.
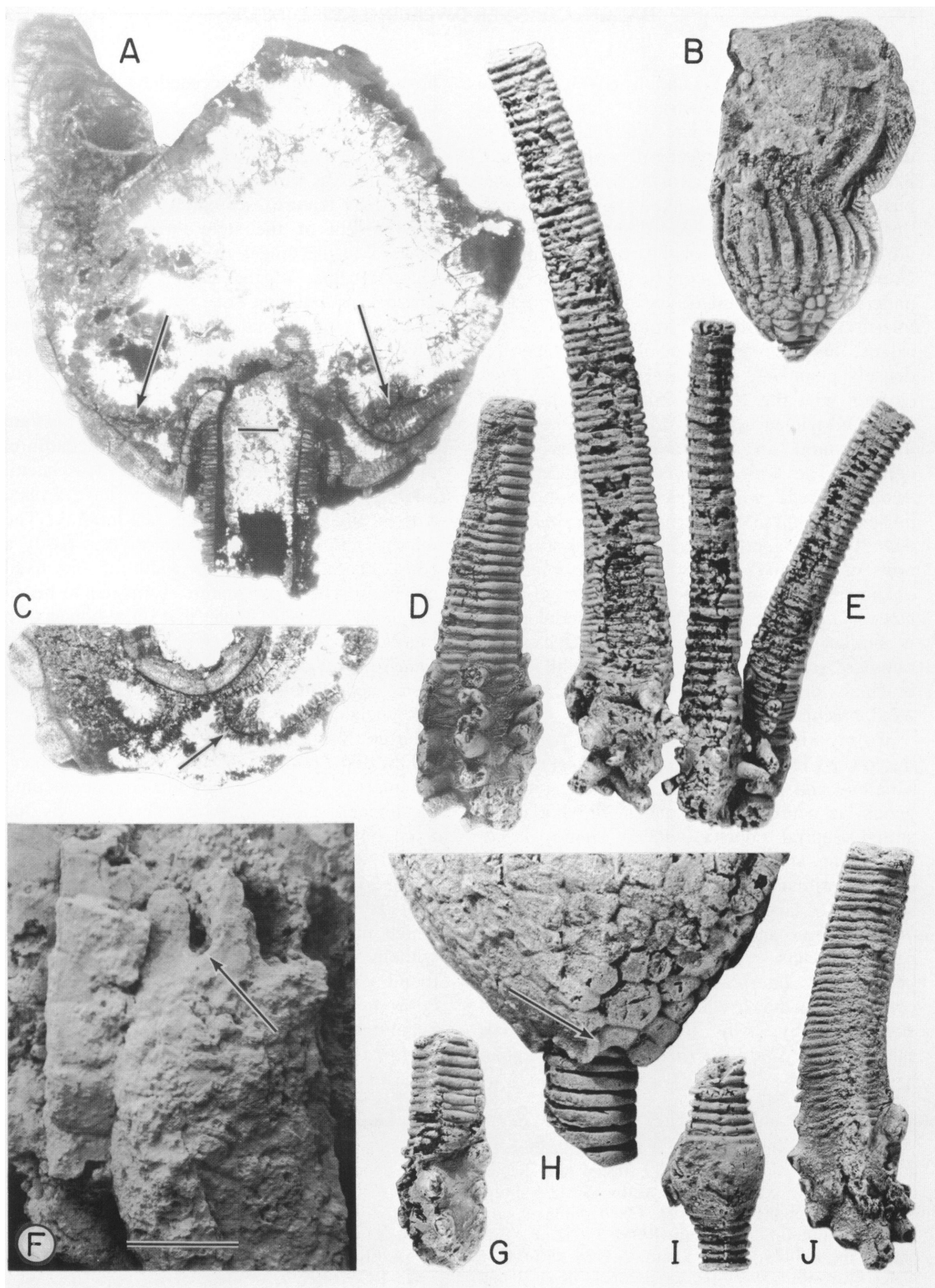
reduction of interbrachial plates, elimination of fixed pinnules and attainment of even pentameral symmetry.

The "disposition" and "attitude" of arms among the archaeocrinids, rhodocrinitids and anthracocrinids appear to fall into two categories: (1) strongly grouped arms that protrude laterally outward (=grouped-lobate), and (2) relatively evenly disposed arms that project ventrally upward as an even continuation of the cup's marginal profile (=ungrouped-marginate). The former group is represented by *Diabo-* *locrinus* and *Paradiabolocrinus*, and the latter group is apparently represented by all other known genera in the archaeocrinids, rhodocrinitids, and anthracocrinids. The grouped lobate condition is, therefore, uncommon and may represent a distinct adaptation for physical–paleoecological conditions and feeding dynamics.

CHARACTER RELATIONSHIPS AND PHYLOGENY: Despite the rather great and recent proliferation of Ordovician archaeocrinid, rhodocrinitid, and anthracocrinid genera (Strimple
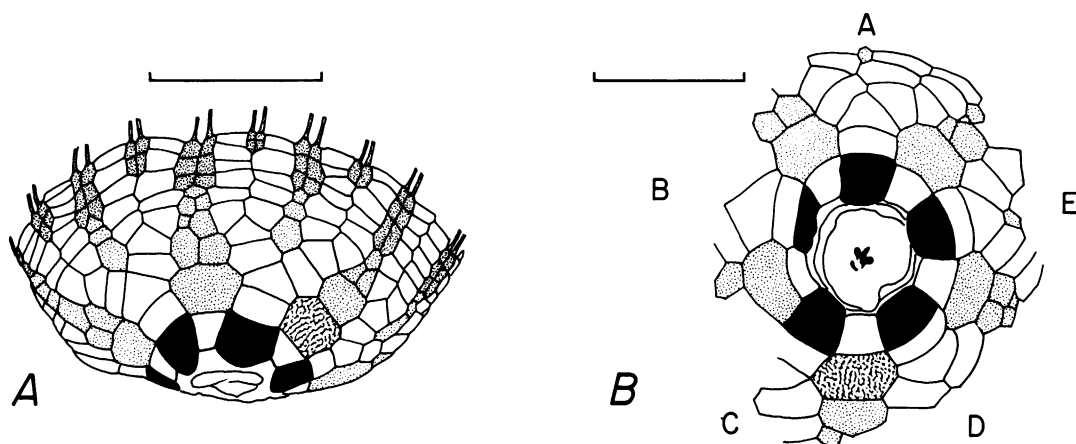


FIG. 9. *Rheocrinus aduncus* plate patterns. A. Oblique view of dorsal cup. ROM 26377. B. Basal view of dorsal cup; specimen crushed on left side. ROM 36380a. Radials, black; interbrachials, dot stipple; fixed pinnules, line stipple; primanal, wrinkle stipple. Both scales 1 cm.

FIG. 8. Specimen 8F is *Parisocrinus mulletensis*; all others are *Rheocrinus aduncus*. A and C. Vertical and horizontal thin sections, respectively, through the crown. The horizontal line in A indicates the line of section of C. Arrows indicate collapsed perivisceral coelom. Note the deeply invaginated intracalical cylinder, aduncate (hook-shaped) radial plate, and the large scalloped stem lumen. The anal vent may be at the summit of the tegmen. See figures 13A, B for diagrams of the thin sections. X4.0. ROM 36382b, c. B. A juvenile individual with uniserial cuneate pattern extending about one-half the length of the arms. The crenulate lower border of the dorsal cup, and characteristic interray plate pattern are like those of an adult. X1.6. ROM 36383. D. An attachment radix with five vertical rows of radicles along the angles of pentagonal section. X1.6. ROM 36386. E. A group of three intertwined attachment radices, which indicates that individuals lived together in small "stands" of several individuals. X1.6. ROM 36385. F. Terminal end of the anal sac of *P. mulletensis*. The anal vent, arrow, is terminal. The extreme end and upper right side of the sac are missing. The arm fragment to the left reveals its wedge-shaped cross section. scale 1 mm. S.E.M., ROM 36404. G. An attachment radix with pronounced angularity and radicular scars along the angles. X1.6. ROM 36388. H. The dorsal cup and proxistele of a large adult whose basals have become "notched," arrow, presumably in order to maintain (during ontogeny) a given degree of tilt of the crown relative to the proxistele. X2.4. ROM 36384. I. A stem-swelling which may have been induced by the ectoparasite, *Phosphannulus*. X1.6. ROM 36389. J. An attachment radix with broken, hollow radicles. X1.6. ROM 36387.
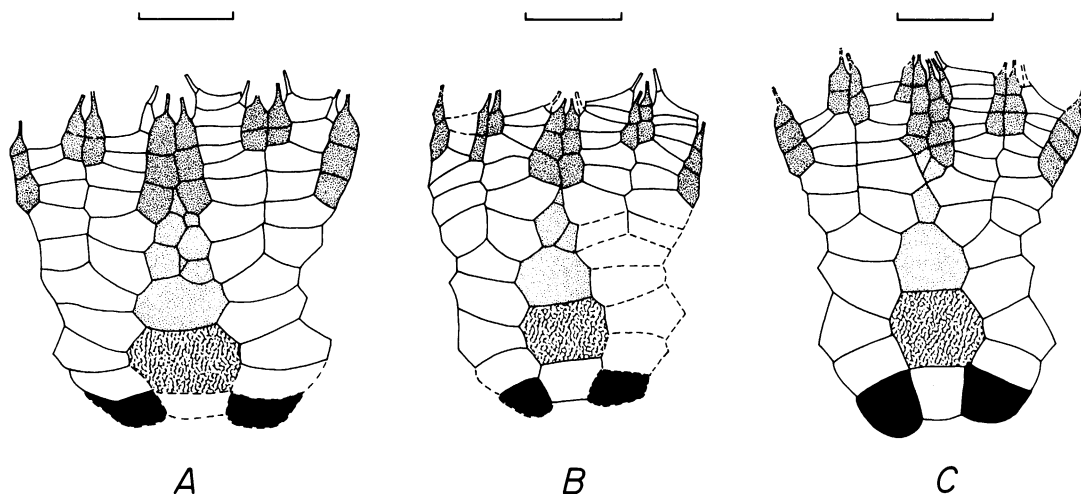
FIG. 10. Plate variation among three specimens of *Rheocrinus aduncus*, CD-interray view. A. ROM 36376. B. ROM 363816. C. ROM 36381a. Plate symbols are the same as in figure 9. All scales 5 mm.
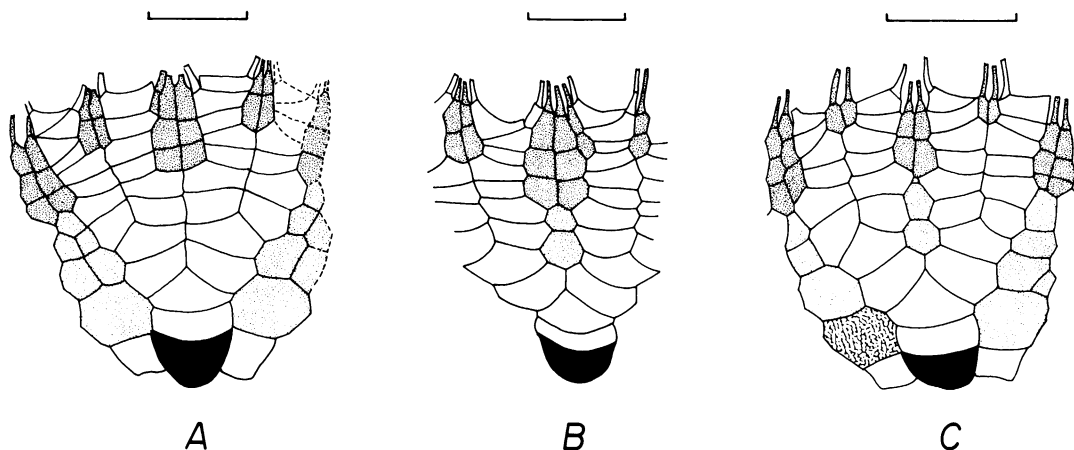


FIG. 11. Plate variation among three specimens of *Rheocrinus aduncus*. A. Holotype, A-ray. ROM 36375. B. Holotype, D-ray. ROM 36375. C. C-ray. ROM 36380b. Plate symbols are the same as in figure 9. All scales 5 mm.

and Watkins, 1955; Frest, Strimple and Kelley, 1976; Brower and Veinus, 1974; Haugh, this paper) evolutionary interrelationships remain obscure. Brower and Veinus (1974, p. 66) concluded that "the Rhodocrinitidae and Archaeocrinidae are a highly diverse group with little distinction between the two families." I agree with their assessment in terms of our present understanding of these families, but I have followed Ubaghs' (in press) practice of using Anthracocrinidae at the familial level.

The family Anthracocrinidae features the following synapomorphies: (1) interbrachials between all fixed brachial series low in the dorsal cup, followed by fixed pinnules (i.e., true brachial plates) that bridge (fill) the spaces between the arms high in the dorsal cup; hence, true interbrachials do not "continue onto the

tegmen" as in the Archaeocrinidae and Rho-docrinitidae; (2) unbranched uniserial-cuneate, or biserial arms, and (3) all interrays of about the same width, containing one very large in-terbrachial (largest plate in the cup) that fills most or all the space from the radials up through the level of the second secun-dibrachials. These character states are judged to be "phyletically advanced" and perhaps evolved from comparable, yet more primitive character states within the Archaeocrinidae such as Rhaphanocrinus, Parachaeocrinus, Archae-ocrinus, and Simplococrinus. In species of the latter genera the following character states are synapomorphies: (1) interbrachials present be-tween all fixed brachial series, and these inter-brachials "continue onto the tegmen," with or without incorporation of ramules into the top of the dorsal cup; (2) branched uniserial to biserial free arms; (3) lateral interrays narrower than

the CD-interray, and containing one dorsal, small or medium-sized interbrachial plate that fills part or all of the space from the radials up through the level of the first primibrachials. I would (cautiously) infer that these latter three character states may have been ancestral to the former three character states, typical of Rheo-crinus. Proceeding to an even more speculative "phyletic scenario," it may be that a species with Pararchaeocrinus-like characters evolved into a species with Anthracocrinus-like char-acters, which in turn evolved into a species with Rheocrinus-like characters.

TYPES: The type specimens are deposited in the Department of Invertebrate Palaeontology Collections of the Royal Ontario Museum, Toronto, Ontario, and bear the following ROM numbers: holotype=ROM 36375, and 17 para-types=ROM 36376 through ROM 36391 and ROM 35652.



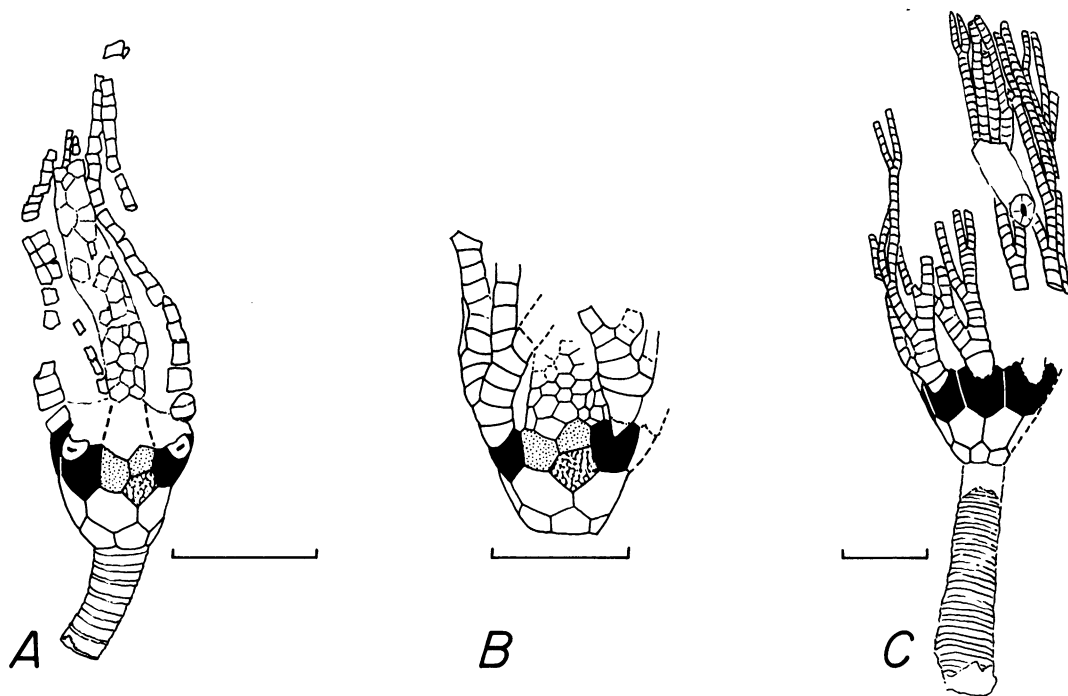FIG. 12. *Parisocrinus mulletensis*. A. Holotype, CD-interray view. The middle portion of the anal sac and several arms are poorly preserved. ROM 36401. B. CD-interray view. The RA, X, RT and proximal anal sac are well preserved. ROM 36402. C. Anterior view of a specimen with well-preserved arms. ROM 36403. Radials, black; radianal, wrinkle stipple; anal X and right tube plate, dot stipple. All scales 5 mm.

MATERIAL: A total of 30 nearly complete crowns, holdfasts, and numerous associated stem segments were collected from a single "colony" within a channel fill in the Georgian Bay Formation exposed in the south bank of Mullet Creek, between Mississauga Road and the Credit River at Erindale, Ontario (fig. 4).

DIMENSIONS: Measurements of several of the types are given in table 1.

ETYMOLOGY: The specific name is from the Latin *aduncus* bent, hooked; in reference to the upward bending of the basal and radial plates that form the aperture of the deep basal invagination.

SUBCLASS INADUNATA WACHSMUTH AND SPRINGER, 1897

ORDER CLADIDA MOORE AND LAUDON, 1943

SUBORDER CYATHOCRININA BATHER, 1899

FAMILY AMPHERISTOCRINIDAE MILLER, 1889

GENUS *PARISOCRINUS* WACHSMUTH AND SPRINGER, 1880

TYPE SPECIES: By subsequent designation by Wachsmuth and Springer, 1879 [1880], p. 115, *Poteriocrinites perplexus* (Meek and Worthen), 1869, p. 138.

DIAGNOSIS: The genus resembles both *Cyathocrinites* with which it is closely allied and *Poteriocrinites* with which it has been confused because of a similar three-element anal plate series. The dorsal cup low and conical, with a wide CD-interray occupied by three anal series plates: a large radianal (RA), succeeded by an anal X (X) to the upper left, and a right tube plate (RT) immediately above. Infrabasals five, equal, pentagonal. Basals five, three being equal, hexagonal, and two azygous heptagonal in the CD-interray. Radials five, bearing narrow, horseshoe-shaped articular facets that are inclined upward as in *Cyathocrinites*. Arms uniserial, apinnulate, branching isotomously several times. Ventral sac long, slender, cylindrical, bearing a terminal vent; sac not crenulate as in *Poteriocrinites*.

REMARKS: According to Moore and Laudon (1943, p. 51) the Ampheristocrinidae "form a somewhat dubious family assemblage" because of poor preservation for some of the included genera. Furthermore, a wide structural latitude is encompassed; some genera have three infrabasals (e.g., *Ampheristocrinus*), whereas others have five infrabasals (e.g., *Parisocrinus*). *Parisocrinus* is most abundant in the Lower Mississippian, but is also reported (Springer, 1926) to occur in the Middle Silurian

TABLE 1
Measurements (in Millimeters) of *Rheocrinus aduncus* types

| | ROM 36375 | ROM 36376 | ROM 36377 | ROM 36380a | ROM 36380b |
|---|---|---|---|---|---|
| Dor cup height | 13.2 | 15.5 | 12.0 | 14.1 | 9.0 |
| Dor. cup dia. | 28.3 | 28.5 | — | 29.7 | 18.7 |
| R-IAx height | 7.7 | — | 6.2 | 7.1 | 5.2 |
| Bicirc. dia. | 11.5 | — | 8.8 | 12.5 | 8.8 |
| Arm length[a] | 57.0 | 53.0 | — | — | — |
| Stem dia. | 6.0 | 8.0 | 4.9 | 6.1 | 5.0 |
| | ROM 36383 | ROM 36384 | ROM 36391a | ROM 36391b | ROM 36391c |
| | 7.2 | 15.9 | 13.7 | 12.0 | 12.2 |
| | 13.4 | 25.6 | 32.0 | 27.5 | 23.2 |
| | 4.7 | 7.1 | 8.3 | 6.7 | 5.0 |
| | 7.5 | 10.7 | 13.1 | 10.0 | 9.1 |
| | 23.0 | — | — | 55.0 | — |
| | 3.5 | 6.4 | 7.0 | 6.0 | 4.8 |

[a]Measured lengths are short by about 3 to 5 millimeters due to loss of arm tips.

(Niagaran) of North America. With the discovery of *Parisocrinus mulletensis*, new species, in the Late Ordovician (Richmondian) temporal support is given to the theory that an ampheristocrinid was the possible ancestor of the first cyathocrinids in the Ordovician (Moore and Laudon, 1943, p. 38).

KNOWN RANGE AND DISTRIBUTION: The chronological range is extended back to the Late Ordovician, Richmondian (Ashgillian) of North America, and continues to the Mississippian of North America, and Lower Carboniferous of Great Britain and Europe.

### Parisocrinus mulletensis, new species
Figures 6A-D, F; 8F; 12A-C

DIAGNOSIS: An ampheristocrinid having a low, conical dorsal cup with five equal, infrabasals. Arms very robust proximally, branching isotomously three to four times, distally composed of wedge-shaped brachials. Anal sac slender, cylindrical, composed of many irregular, subequal, polygonal plates that apparently lack sutural pores. Tegmen low, with concave lateral "slopes," reaching a central "summit" at the height of the first primibrachials. Proximal stem relatively large, occupying the full diameter of the lower border of the infrabasal circlet, homeomorphic, composed of very thin columnals.

DESCRIPTION: Dorsal cup conical, height slightly less than diameter. Cup plate surfaces smooth with plate borders slightly depressed so as to produce distinct plate sutures. Infrabasals five, equal, regularly pentagonal, yielding a faintly scalloped lower border, and a zigzag upper border. Basals five: three equal, regularly hexagonal, and two azygous, unequal, irregularly heptagonal, slightly wider than high, occupying the CD-interray area. Radials five: four equal, with regular "hexaform" dorsolateral border and a horseshoe-shaped ventral articular border, height approximately equal to width, and one azygous, irregular hexaform in the C-ray. Radial articular facets small, horseshoe-shaped, about two-thirds the width of the radials, with steep upward inclination; ventral border notched by an ambulacral groove. Facet surface concave, bearing an aboral nerve foramen, and lacking an articular ridge. CD-interray conspicuously wide, composed of three

anal plate elements: a large, irregularly pentagonal radianal (RA) that extends dorsally well into the basal circlet; the RA bounded to the upper left by a smaller, irregularly heptagonal anal X (X), having a single, vertical sutural contact with the D-radial and an inclined contact with two overlying sac plates; and to the upper right, an irregularly heptagonal right tube plate (RT), in wide horizontal contact with the RA below, the C-radial to the right, and the X to the left. The X and RT of about equal size. Ventral sac long, cylindrical, slender, composed of a large number of unequally-sized, irregular polygonal plates. Sutural pores apparently lacking, at least in the proximal portion of the sac. Length of ventral sac less than that of the arms. Anal vent terminal.

Arms robust, branching isotomously three to four times, uniserial, apinnulate. Primibrachials two, the second being axillary; secundibrachials three or four per taxis, the final one being axillary. Primibrachials wider than high, with evenly rounded aboral surfaces; tertibrachials and succeeding higher ordinal brachials about equidimensional, developing an aboral angular "keel" resulting in a wedge-shaped appearance for the individual brachials.

Proximal stem round, of relatively large, uniform diameter, occluding the full lower infrabasal diameter. Columnals homeomorphic, with straight latera, yielding a smooth-sided cylindrical column. Individual columnals very thin, giving a height:diameter ratio of approximately 1:5, sutures symplexial. Mesistele and dististele unknown.

REMARKS: *Parisocrinus mulletensis*, new species is distinguishable from *P. siluricus* by its relatively higher basal and radial plates, its relatively narrower radial articular facets (see Springer, 1926: pl. 31, figs. 8, 8a), its longer ventral sac, its wedge-shaped distal brachials, and its more robust homeomorphic proxistele. It differs from *P. crawfordsvillensis* by its apparent lack of sutural pores on the ventral sac, shorter sac length, and irregularity of sac plating. Both *P. siluricus* and *P. crawfordsvillensis* appear to have more arched cup plate surfaces, resulting in greater depression of the plate sutures. In *P. crawfordsvillensis* the arm length relative to cup height is greater than in *P. mulletensis*.

TYPES: The types are deposited in the Department of Invertebrate Palaeontology Collections of the Royal Ontario Museum, Toronto, Ontario, and bear the following ROM numbers: holotype=ROM 36401, and three paratypes=ROM 36402 through ROM 36404.

MATERIAL: Only five crowns, of varying degrees of completeness, two with a section of the column, were recovered from the crinoid colony in the channel fill containing *Rheocrinus aduncus*, in the Georgian Bay Formation exposed on the south bank of Mullet Creek, between Mississauga Road and the Credit River at Erindale, Ontario (fig. 4).

DIMENSIONS: Measurements of the types are given in table 2.

ETYMOLOGY: The specific name is derived from the type locality, Mullet Creek.

## PALEOECOLOGY AND FUNCTIONAL MORPHOLOGY

The Lower Georgian Bay Member apparently represents a regressive marine clastic facies associated with the Taconic Orogeny. These gray shales and sandstones intergrade with the overlying redbeds of the Queenston Formation (=Queenston Delta) approximately 100 feet stratigraphically above the channel horizon. The presence of (1) the major submarine channel fills; (2) abundant minor scour flutes on the base of sandy hardbands; (3)

### TABLE 2
### Measurements (in Millimeters) of *Parisocrinue mulletensis* types

|  | ROM 36401 | ROM 36402 | ROM 36403 | ROM 36404 |
|---|---|---|---|---|
| Dor. cup height | 4.1 | 4.0 | 6.0 | — |
| Dor. cup dia. | 5.7 | 7.0 | 8.0[a] | 6.0 |
| Basal height | 2.2 | 2.3 | 2.7 | 2.1 |
| Basal width | 2.0 | 2.8 | 2.6 | 2.3 |
| Radial height | 2.4 | 2.3 | 3.1 | 2.5 |
| Radial width | 2.1 | 2.9 | 3.3 | 2.6 |
| Arm fac. width | 1.2 | 2.0 | — | 1.2 |
| Stem dia. | 1.5 | — | 3.2 | — |
| Arm length | — | — | 23.0 | — |

[a]This specimen is crushed; measurement given is greater than natural.

abundant ripple marks on the top of sandy hardbands, and (4) the facies gradation with the overlying strata of the Queenston Delta all suggest a shallow-water, current-dominated, deltaic milieu. The exposed channel fills are postulated to be part of the Queenston submarine deltaic distributary system or a local tidal flow feature. *Heterotrypa definata*, *Strophomena planumbona* and *Byssonychia* sp. occur with the crinoids in the channel fill. Organisms living in the channels would have been emphatically rheophilic—taking advantage of down-channel drainage currents, and depending on water depth and tidal intensity, tidal ebb current and tidal bore current. It may be stated with confidence that stalked crinoids began to exploit a rheophilic life-mode at least by the Late Ordovician. Stalked crinoids, especially camerates, are commonly associated with turbulent reef environments by the Middle Silurian (Lowenstam, 1957; Lane, 1969; and Manten, 1971); and unstalked crinoids flourish in turbulent reef environments today (Macurda and Meyer, 1977). A close modern ecologic analogue has been reported by Macurda (1975, pp. 13-14) on Great Bahama Bank, adjacent to Andros Island. Here, the comatulid, *Analcidometra armata*, specifically concentrates in tidal exchange channels (bights) where it perches on gorgonians, high above the channel floor. Macurda (1975, p. 14) suggested that "prolific development there is attributed to currents induced by tidal reversals through the Bights of Andros, resulting in predictable current flow apparently necessary for the growth of *Analcidometra*."

*Rheocrinus aduncus* exhibits a number of morphologic features that appear to represent adaptations for moderate to strong currents:

(1) The proxistele is exceptionally enlarged relative to the size of the calyx as compared to many other camerates (figs. 8A,H, 13A,C). The adaptive advantage of this enlargement could have been to provide a large ligamental area between each columnal. This would increase the strength of the stem—an advantage in moderate to strong currents.

(2) The base of the dorsal cup is deeply invaginated, forming the "intracalical cylinder." The intracalical cylinder is composed of a bicirclet of 10 alternating basal and radial

plates, and five infrabasals. This construction is judged to be an adaptation to increase the diameter and surface area of the intracalical cylinder. The advantages of these increases are twofold: a larger stem diameter may be accommodated, and potential ligamental area is increased. I suggest that ligaments may have spanned the space between the intracalical cylinder and the adjacent surface of the proxistele (figs. 8A, 13A, B). If such a ligamental arrangement existed, it may have provided a controllable gimbals-mechanism for orienting the crown in a current, and also provided a shock-absorber feature for dealing with current surges and eddies in the channel.

(3) The pentagonal intracalical cylinder and the proxistele form a loosely interlocking, spined couple that limits axial rotation of the crown relative to the proxistele (figs. 7C, 13B); this may have damped axial twisting caused by current eddies. The intracalical cylinder also limits the tilt of the calyx relative to the proxistele; the crenulate lower border of the bicirclet acts as a "tilt stop" against the pentagonal proxistele (figs. 5A,G, 6H). Significantly, several large specimens have basal plates whose lower border has become notched (fig. 8H), thereby maintaining a full degree of tilt as the diameter of the adult stem increased allometrically. I submit that the ontogenetic development of the latter feature, notching of the basals, represents compelling morphological evidence that the crown of *Rheocrinus aduncus* could become greatly inclined—perhaps horizontal—during feeding. Thus, *Rheocrinus aduncus* probably formed a parabolic filtration baffle, held transverse to the channel current (see Haugh, 1978, fig. 9). Analogous parabolic filtration baffles are utilized by living stalked crinoids (e.g., *Cenocrinus asterius*, Macurda and Meyer, 1974) *Endoxocrinus* sp. and *Isocrinus* sp., Macurda and Meyer, 1977). A reconstruction of *Rheocrinus aduncus* (fig. 13C) depicts this inclined, transverse, parabolic feeding baffle, with reflexed arm tips as in living stalked crinoids.

(4) The attachment radix is an expanded, club-shaped, rhizoidal affair with five longitudinal rows of spikelike radicles (figs. 7F, 8D, E, G, J, 13C, F). This construction afforded firm anchoring in the muddy substrate. Franzen

(1977: 221) has described similar "cirriferous holdfasts" (her type 2c) with a network of "pseudocirri" (i.e., radicles with an axial canal but composed of irregular plates, not discoidal cirrals; see Moore, Jeffords and Miller, 1968, p. 29) from what appears to have been soft substrates on the Silurian reefs of Gotland. The rhizoidal radices of *Rheocrinus aduncus* are typically intertwined, forming a "mangrove-like" network (fig. 8E) that must have improved the stability of all crinoid individuals concerned. As the individuals of a stand grew larger with ever increasing hydrodynamic drag, and as stand baffles developed, the mangrove-like network apparently became an effective group adaptation that allowed these rheophilic crinoids to colonize their soft-bottom channel niche.

(5) Finally, *Rheocrinus aduncus* has 20 biserial, unbranched, pinnulate arms. The pinnules are long and closely spaced (figs. 7A, B, 13C) resulting in a durable, fine-mesh baffle, for full mucus-net feeding.

It has been suggested that the observed, patchy geographic distribution of living comatulids is attributable in large measure to localized, high primary productivity (Clark, A.H., 1908; Clark, H.L., 1915) that is stimulated by continental run-off of nutrients. For example, nutritional enrichment, directly offshore from major river deltas (Curl, 1960), has been postulated to account for distinctively greater population densities and biological diversity in nearshore Columbian and Panamanian crinoid faunas (Meyer, 1973, pp. 126-127). Knowledge of both type and quantity of phytoplankton and zooplankton, in conjunction with knowledge of specific current regimes, may be the key to understanding subtile, specific, distributional patterns of living crinoids. The foregoing principles also seem to be generally applicable to occurrences of fossil crinoids. The diverse and prolific fossil crinoid faunas of the Mississippian Borden Delta, Edwardsville Formation, of central and southern Indiana (e.g., the Crawfordsville fauna) appear to mirror certain modern ecologic examples, with the exception that the Borden crinoids are stalked forms (Lane, 1973; Ausich, 1977b). I suggest further, that the analogy can be extended temporally to the channel-dwelling crinoids, *Rheo-*

A

Pp

Av

T

Pgc

IBB

R L B

B

C

L

IB

C

D

L

E

L

F
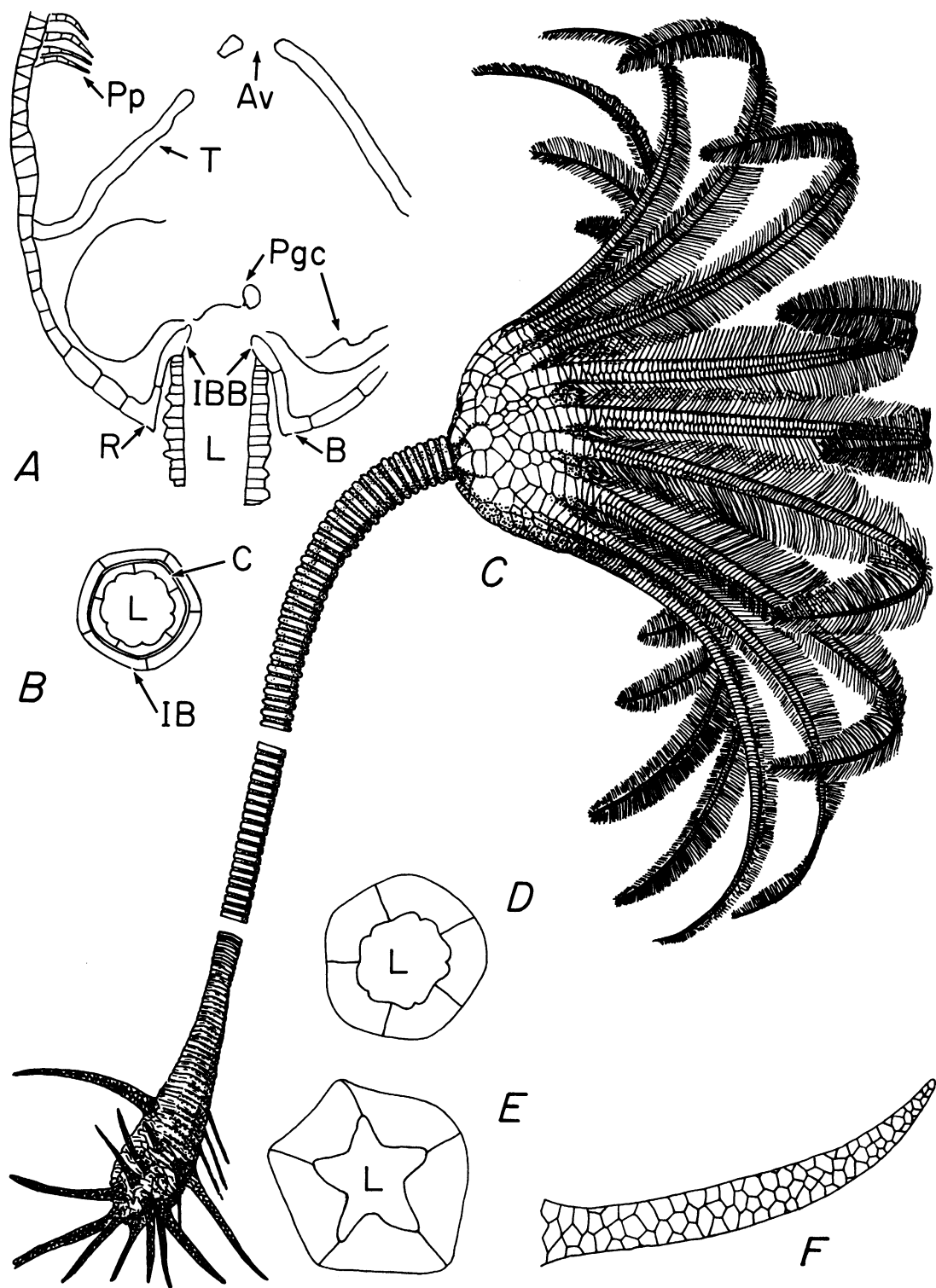
*crinus aduncus* and *Parisocrinus mulletensis.* By Late Ordovician time the Queenston Delta reached its farthest westward extent, including southern Ontario (Sloss, Dapples and Krumbein, 1960, Map 17). This places the Lower Georgian Bay crinoid faunule in a generally similar ecologic setting. It seems reasonable to infer that by Late Ordovician time the distribution of some crinoids was explicitly determined by (1) current regime (in this case, channelized) and (2) nutrient concentration that, in turn, stimulated high primary productivity (a planktic food source). I wish to emphasize, however, that diverse crinoid assemblages, whether living or fossil, are not restricted to actual or inferred deltaic marine settings. The greatest known diversity for an extant crinoid fauna occurs at Lizard Island, Great Barrier Reef, where over 30 species co-exist (Macurda, personal commun.). In the fossil record the greatest known diversity, approximately 150 species of stalked crinoids, (through an average stratigraphic thickness of 75 ft.) occurs in the Mississippian Age Burlington Limestone. It seems reasonable to infer that a typical level-bottom Burlington crinoid fauna might include individuals from as many as 60 co-existing species, dispersed in densely populated stands on the seafloor. There is no evidence of a deltaic influence that would contribute to nutrient enrichment or provide a current source for either the Lizard Island or Burlington crinoid faunas. Clearly, inference of the paleoecology of fossil crinoid faunas should include local physical sedimentological data as well as regional paleogeographic data.

The occurrence of *Parisocrinus mulletensis* in the channel fill is also functionally and paleoecologically interesting. Specimens (figs. 6A-D, F, 12A-C) reveal that it too has a relatively large proxistele, and rather stout, branched

arms—presumably adaptations for moderate currents. Unfortunately, an entire stem was not recovered; however, it is likely that these small cyathocrinid inadunates were low-level feeders. They probably fed within, or just above the branched trepostome bryozoans that lived on the floor of the channel. Thus, the bilevel stratification of the crinoid faunule could have allowed *Rheocrinus aduncus* to feed from the full force of the channel currents, and allowed *Parisocrinus mulletensis* to feed from slower, bottom currents that were damped by the bryozoan community baffle.

The isotomously branched arms of *Parisocrinus mulletensis* lack the finer subdivisions termed ramules or pinnules. By analogy with similar structures and the ecologic setting of living crinoids and basketstars (Briemer, 1969; Lane and Briemer, 1974; and Meyer and Lane, 1976) the feeding mode and current regime of fossil crinoids has been inferred. Such comparisons indicate that *Parisocrinus mulletensis* probably utilized "tube feet and ciliary feeding"; individuals probably could not have formed an effective mucus net which spanned the arms. Traditionally, fossil crinoids with unbranched, or sparsely branched, non-ramulate or non-pinnulate arms have also been regarded as rheophobic (current avoiders) and unable to form a "filtration fan." They were thought to feed by gravitational settling of particulate food by means of a vertically held "collecting bowl." Clearly, the occurrence of *Parisocrinus mulletensis* contradicts these previous interpretations; hence, the degree of arm branching does not rigorously indicate whether a crinoid was rheophobic or rheophilic. *Parisocrinus mulletensis*, despite its sparsely branched arms, must be considered a moderate-energy rheophile. Its channel-dwelling life-mode indicates

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FIG. 13. *Rheocrinus aduncus*, structural detail and reconstruction of life-mode. A. Vertical section through crown and proxistele. B. Cross section through top of intracalical cylinder. C. Reconstruction of the life-mode of *R. aduncus* forming a parabolic filtration baffle with reflexed arm tips. D. Cross section of the dististele, just above the radix, illustrating the pentagonal external shape and scalloped lumen. E. Cross section through the radix illustrating the pentagonal external shape and star-shaped lumen. F. Exterior detail of a single radicle with irregular polygonal plating. Anal vent, Av; basal, B; columnal, C; infrabasal(s), IB (IBB); lumen, L; perigastric coelomic organ, Pgc; pinnules, Pp; radial, R; tegmen, T.

that it may have formed a vertical, open-mesh, planar filtration baffle held transverse to the current. A similar interpretation has been applied to individuals of several of the species of the Silurian crinoid genus, *Pisocrinus* (Ausich, 1977a) which occupied various level-bottom or reefoid niches. The likelihood of full mucus net feeding in *Rheocrinus aduncus*, as opposed to tube feet and ciliary feeding in *Parisocrinus mulletensis* suggests the possibility of two distinct microhabitats for these Late Ordovician, channel-dwelling, rheophilic crinoids.

## ACKNOWLEDGMENTS

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