Bulletins of American Paleontology

Begun in 1895

NUMBER 360 **MARCH 1, 2001**

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James D. Eckert

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Carlton Brett

Paleontological Research Institution
1259 Trumansburg Road
Ithaca, New York, 14850 U.S.A.

PALEONTOLOGICAL RESEARCH INSTITUTION

BULLETINS OF AMERICAN PALEONTOLOGY
and
PALAEONTOGRAPHICA AMERICANA

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Subscriptions to *Bulletins of American Paleontology* are available for US $150 per year (individual or institution) plus postage. Issues are available and priced individually. Numbers of *Palaeontographica Americana* are priced individually.

for additional information, write or call:

Paleontological Research Institution
1259 Trumansburg Road
Ithaca, NY 14850 USA
(607) 273-6623
FAX (607) 273-6620
www.priweb.org

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ISSN 0007-5779
ISBN 0-87710-452-2
Library of Congress Control Number: 00-134801

Note: Beginning with issue number 356, *Bulletins of American Paleontology* is no longer designating volumes. The journal will continue to publish approximately 2–4 issues per year, each of which will continue to be individually numbered.

Printed in the United States of America
Allen Press, Inc.
Lawrence, KS 66044 U.S.A.

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EARLY SILURIAN (LLANDOVERY) CRINOIDS FROM THE LOWER CLINTON GROUP, WESTERN NEW YORK STATE

JAMES D. ECKERT

P.O. Box 168
Cobalt, Ontario P0J 1C0
CANADA

AND

CARLTON E. BRETT

Department of Geology
University of Cincinnati
Cincinnati, Ohio 45221-0013, U. S. A.

ABSTRACT

Early Silurian (Llandovery) crinoids have been poorly known. The present paper describes 26 species and six unassigned columnal taxa of Early Silurian crinoids on the basis of new and well preserved fossils from the lower Clinton Group of western New York. The new material, comprising eighteen genera, and unclassified skeletal material, spans the late middle Llandovery to the latest Llandovery and has been derived from several lithostratigraphic units. The Reynales Formation (Aeronian) contains the following new genera: *Dynamocrinus*, *Thaerocrinus*, *Haptocrinus*, and *Prolixocrinus*; new species include *Dynamocrinus robustus*, *Thaerocrinus crenatus*, *Haptocrinus calvatus*, *Prolixocrinus nodocaudis* and *Macrostylocrinus* sp. Two species of disparid *Eomyelodactylus*, *E. sparteus* Eckert and *E. uniformis* Eckert, and one unusual camerate *Stipatocrinus hulveri* Eckert and Brett, have been previously described from the Reynales Limestone. *Compsocrinus relictus*, *Dendrocrinus ursae*, and an unidentified camerate occur in the laterally equivalent Bear Creek Shale. New taxa from the Wolcott Limestone (lower Telychian) include the Atalocrinacea, new superfamily; Atalocrinidae, Callistocrinidae, and Anisocrinidae, new families; *Callistocrinus*, *Tormosocrinus*, *Atalocrinus*, *Aclistocrinus*, *Kyphosocrinus*, and *Scapanocrinus*, all new genera; and the species *Callistocrinus tesselatus*, *Tormosocrinus furberi*, *Atalocrinus arctus*, *Aclistocrinus capistratus*, *Kyphosocrinus tetreaulti*, *Scapanocrinus muricatus*, *Myelodactylus linae*, *Euspirocrinus wolcottense*, *Dendrocrinus aphelos*, *D. bactronodosus*, *Haptocrinus* sp., ?anisocrinid sp., and an unidentified flexible crinoid. *Protaxocrinus anellus* n. sp. and five unidentified columnal types occur in the upper Telychian Willowvale Shale. Taxonomic revisions also necessitate reassignments of three previously described taxa. The disparid *Macnamaratylus* Bolton is synonymized with *Eomyelodactylus*, the flexible crinoid *Clidochirus americanus* Springer is reassigned to *Prolixocrinus* n. gen. and the cladid genus *Quinquecaudex* Brower and Veinus, 1981, is synonymized with *Dendrocrinus*. The erroneous species *Glyptocrinus plumosus* Hall is reviewed; the cotype specimens in part represent the cirral column of a myelodactylid disparid crinoid, here tentatively assigned to *Eomyelodatylus* (*E. ? plumosus* (Hall)); the remaining material consists of columnals and pluricolumnals probably belonging to *Haptocrinus*.

Physically stressed, uncrowded environments of the Early Silurian in western New York were characterized by low diversity crinoid assemblages and provided a refuge for relictual Ordovician taxa that became extinct in the late Llandovery. Diverse assemblages of crinoids dominated by Wenlock precursors inhabited mixed carbonate-siliciclastic regimes distal to shoals.

Early Silurian crinoids of the Clinton Group are highly endemic in marked contrast to the generally low provincialism of other taxa (*e.g.*, brachiopods) during this interval.

ACKNOWLEDGMENTS

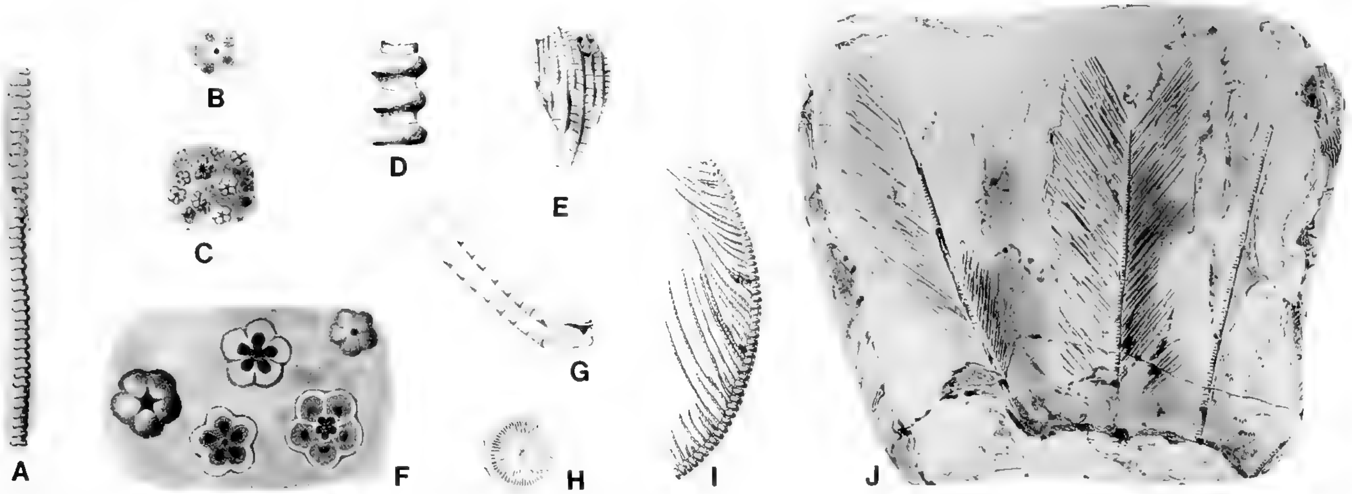
This study is based on part of a Ph. D. dissertation completed at the University of Rochester by the senior author. This monograph benefited from critical reviews by William Ausich, Judy Massare, George C. McIntosh, and Curt Teichert. We also thank Warren Allmon for his assistance in preparation of this manuscript for publication.

We are grateful to R. Sheldon Furber who kindly permitted Eckert to collect and excavate on his property. Bea-Yeh Lin Eckert discovered many good specimens and additional material was found by Denis Tetreault.

Financial support for this study was provided by Bea-Yeh Lin, NSF Grant EAR 9219807 (to CB), the Geological Society of America, and Roy and Enid Eckert.

INTRODUCTION

The Early Silurian was a critical interval in the evolutionary history of the marine biosphere during which



Text-figure 1.—"Crinoidea of the Clinton Group", refigured from Hall (1852, pl. A 41) with original descriptions. Original plate figure numbers and modern interpretation of figures indicated by square brackets

Glyptocrinus plumosus

A. [3c]. A fragment of the column, probably of the same species [partial column of *Haptocrinus* n. gen.]. B. [3e]. The end of the same column enlarged. C. [3f]. A fragment of the rock, with the surface nearly covered with the joints [columnals] of this crinoid. D. [3d]. A few joints of the same enlarged, showing the longitudinal line of separation between the five parts of the plate [*Haptocrinus* pluricolumnal illustrating pentamere suture]. F. [3g]. Several of these joints enlarged, showing their variable character. G. [3b]. Two joints of the finger enlarged, with several of the tentacular joints attached [detail of *Eomyleodactylus* cirri]. H. [4]. *Glyptocrinus* sp. [columnal of unknown crinoid]. I. [3a]. A portion of a single finger, with the tentacula attached. [supposed crinoid arm, actually a partial column of *Eomyelodactylus* (herein tentatively designated *Eomyelodactylus*? *plumosus* (Hall)), figured upside down]

Ichthyocrinus? clintonensis

E. [5]. Partial arms of a flexible crinoid, possibly *Prolixocrinus* n. gen. Undetermined species J. [6a]. The specimen of the pinnulate arms of an undetermined camerate crinoid; natural size.

major restructuring of ecosystems occurred following Late Ordovician extinctions (Sheehan, 1975, 1982; Brenchley, 1989; Boucot, 1990). Crinoids rebounded from this crisis and underwent a dramatic evolutionary radiation in the Early Silurian; subsequently, they became conspicuous and important elements of Wenlock marine communities (Frest *et al.,* 1999). Early Silurian crinoids have traditionally been represented by a conspicuous paleontologic gap that has inhibited investigations of the origin and paleoecology of their diverse Late Silurian descendants. In less than a decade, this situation changed dramatically. Early Silurian material described from the Hopkinton Dolomite of Iowa (Witzke and Strimple, 1981), Power Glen Formation of New York (Brett, 1978) and Ontario (Eckert, 1984), Brassfield Formation of Ohio (Ausich, 1984a, b; 1985, 1986a, c, d; 1987, Ausich and Dravage, 1988), and the lower Clinton Group of New York (this study) comprise about 70 crinoid genera represented by at least 100 species. This stands in stark contrast to only 15 species of crinoids, many of them poorly known, listed from the Lower Silurian of North America by Bassler and Moodey (1943). Subsequently, Donovan *et al.* (1992) and Donovan (1993) have also described six new Llandovery crinoids from the British Isles.

Previous work on crinoids of the lower Clinton Group of New York has been extremely limited. Hall (1852) figured fragmentary remains from these strata and erected two new species, *Glyptocrinus plumosus* and *Icthyocrinus? clintonensis,* both from the Reynales Limestone (Text-fig. 1). *Glyptocrinus plumosus* is a composite of two disparid genera, consisting of a partial cirri-bearing column of *Eomyelodactylus* and columnals and an incomplete column probably belonging to *Haptocrinus calvatus* n. gen. and sp. *G. plumosus* is herein tentatively reasigned to *Eomyelodactylus* on the basis of the cirriferous column. *Ichthyocrinus? clintonensis* is represented by arms of an indeterminable flexible crinoid.

Gillette (1947), in his detailed lithostratigraphic and faunal study of the Clinton Group of New York, listed *Dimerocrinus brachiatus* Hall from the Reynales Limestone at Mink Creek, near Williamson, and *Dendrocrinus longidactylus* Hall from the Lower Sodus Shale in a tributary of Sterling Creek near Martville. Unfortunately, these specimens were not described or figured and their whereabouts are now unknown. However, it is very probable that they were misidentified. *Dimerocrinites* (*Dimerocrinus*) *brachiatus* is known only from the Upper Silurian Rochester Shale; Gillette's material was probably *Stipatocrinus hulveri,* described by Eckert and Brett (1987) from the Reynales Limestone at Rochester, New York. *Dendrocrinus longidactylus* Hall is known only from the Rochester Shale.

Thus, in an interval spanning nearly 150 years since the pioneering studies of Hall (1852) on Silurian faunas of New York, not a single crinoid species has been formally described from the Lower Silurian portion of the Clinton Group. Yet, the Wenlock age Rochester Shale overlying these strata has yielded at least 28 crinozoan and blastozoan genera represented by more than 30 species.

The primary explanation as to why lower Clinton echinoderms have remained poorly known for so long is simply that these strata have never been carefully investigated for echinoderm remains. Instead, attention has been focused on the Rochester Shale, justly famous for its abundant, well preserved fossils (see Taylor and Brett, 1996). Most of the present study material was obtained east of Rochester, New York (Text-fig. 2). Here, the Clinton outcrop belt occurs in relatively flat-lying terrrain extensively mantled by glacial deposits. Consequently, exposures tend to be small, patchy, and easily overlooked or discounted (Pl. 11, figs. 1–4). In addition, except for hematites, formerly excavated for paint oxides in now defunct, small-scale mines, the lower portion of the Clinton Group has had little economic value. It lacks thick carbonate sequences suitable for aggregate and manufacture of concrete, such as those that have been quarried in the Brassfield Limestone and Hopkinton Dolomite. Therefore, except for a few roadcuts and railroad embankments, artifical exposures of the lower Clinton Group are also limited. These factors, together with the tendency of well preserved echinoderms to occur in thin, easily overlooked horizons, explains why investigation of Early Silurian echinoderms in New York has been sporadic and desultory.

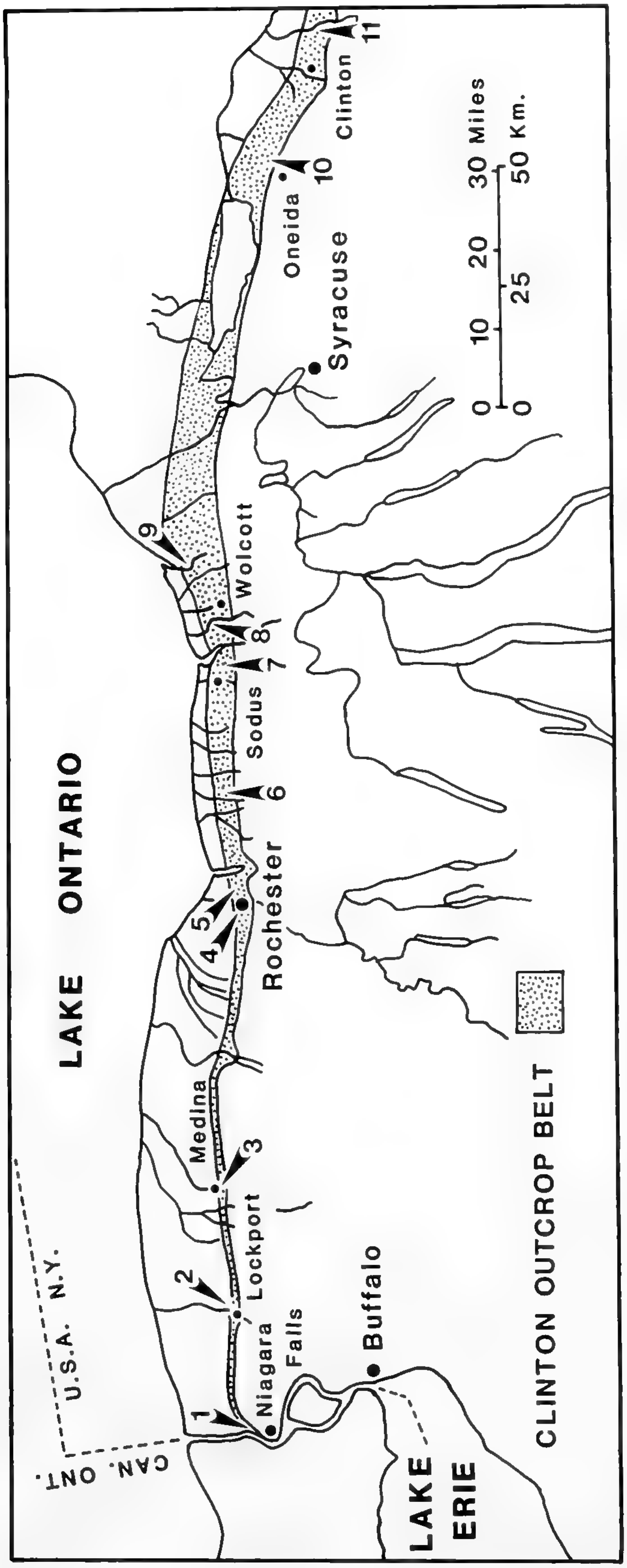
STRATIGRAPHY OF THE CLINTON GROUP IN NEW YORK

Only a brief summary of the stratigraphy of the Clinton Group is presented here; for detailed review see Gillette (1940, 1947), Kilgour (1963), Hunter (1970), and Muskatt (1972). This summary is derived from stratigraphic revisions of Lin and Brett (1988), Brett *et al.* (1990, 1995), and LoDuca and Brett (1994). The Clinton Group, named for exposures in the vicinity of Clinton, New York (Vanuxem, 1842), consists of approximately 30–107 m (100–350 feet) of varied siliciclastic and carbonate strata that have been subdivided into about sixteen formations. Sea level oscillation in the Early Silurian, coupled with isostatically induced, progressive eastward migration of the Appalachian Basin axis (Goodman and Brett, 1994) created a complex sequence of lithostratigraphic units whose interrelationships are still not thoroughly understood. In its thickest succession in central New York, the Clinton Group consists of dominantly siliciclastic rocks deposited in the eastern fringe of the Appalachian Basin. To the west, these strata grade into a thinner sequence of shelf carbonates interrupted by unconformities (Brett *et al.*, 1990, 1998).

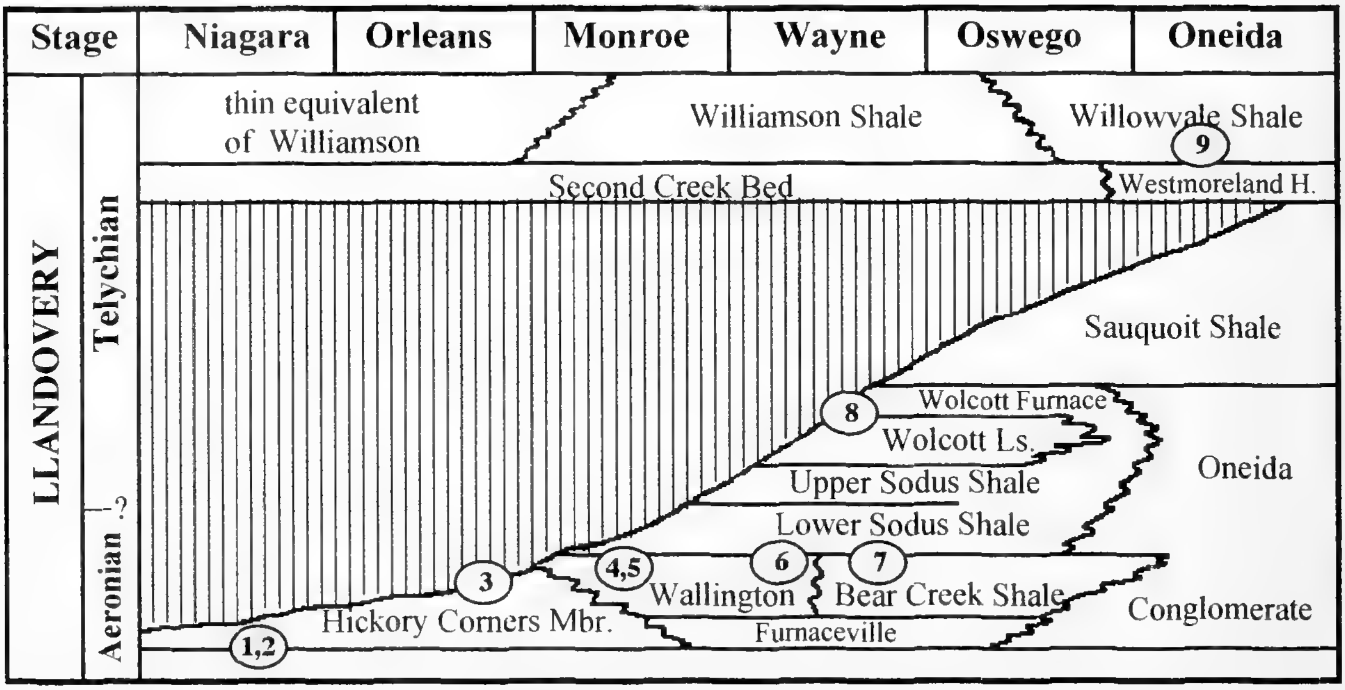
Gillette (1947) subdivided the Clinton Group into lower, middle, and upper intervals. Stratigraphy of the lower part of the Clinton Group was subsequently revised by LoDuca and Brett (1994). In western New York, the lower and middle Clinton are respectively represented by the Neahga-Maplewood Formation through Wolcott Furnace Iron Ore interval, and the Sauquoit Shale (LoDuca and Brett, 1994; Text-fig. 3). These have been interpreted as third order depositional sequences S-II and S-III by Brett *et al.* (1990, 1998). In western New York, the upper Clinton is represented by the Williamson Shale, Rockway Formation, Irondequoit Limestone, and Rochester Shale (Brett *et al.*, 1990, 1995); in central New York it consists of the Westmoreland Iron Ore, Willowvale Shale, Dawes Formation, Kirkland Iron Ore, and Herkimer Sandstone interval. The upper Clinton strata above the Williamson Shale and laterally equivalent Willowvale Shale, is Wenlock in age and is not considered further here.

LoDuca and Brett (1994) revised the stratigraphy of the lower portion of the Clinton Group. The Clinton unconformably overlies the upper Medina Group (Thorold and Kodak sandstones). The basal contact of the Clinton Group, a sequence bounding unconformity, is marked by a thin (1–20 cm), but widespread phosphatic pebble bed, the Densmore Creek phosphate bed, at the base of the Maplewood-Neahga shales in western New York (Brett *et al.*, 1990, 1995; LoDuca and Brett, 1994).

The unconformable contact is locally succeeded by the Neahga Shale in extreme western New York (Niagara County) and by equivalent Maplewood Shale in the Rochester area (Monroe County). The Neahga Shale consists of up to 2.2 m (7 feet) of greenish-gray, poorly fossiliferous, *Eocoelia*-bearing shale. At Rochester, the Maplewood Shale consists of 6.5 m (21 feet) of green, fissile, dominantly barren shale. Samuel J. Ciurca of Rochester (pers. comm., 1988) collected small, undescribed camerate crinoids associated with orthoconic nautiloids from this unit. Both the Neahga and Maplewood shales represent quiet water conditions in localized embayments or lagoons. East of Rochester, near Webster, New York, the Maplewood thins abruptly and its position is taken by a thin (20–



Text-figure 2.—Map of study area in western New York indicating localities where Early Silurian crinoids were collected. A brief description of each locality is given in the Appendix.



Text-figure 3.—Lithostratigraphic and chronostratigraphic relationships of Lower Silurian strata of western New York, modified from Lin and Brett (1988). Numbered circles show the approximate stratigraphic level and geographic position of numbered localities identified in Appendix 1.

30 cm), hematitic, phosphate bearing conglomerate, termed the Webster bed (LoDuca and Brett, 1994).

In Niagara and Orleans counties, the Reynales Formation comprises argillaceous wackestones, packstones, and crinoidal grainstones of the Hickory Corners Member (Pl. 10, figs. 1, 2). The top of this fossiliferous unit has been beveled by an extensive regional unconformity (see below). In Monroe County, the Reynales Formation consists of the Brewer Dock, Seneca Park hematite bed (of the Furnaceville Iron Ore), and Wallington members (LoDuca and Brett, 1994). The 1 m (3 feet) thick Brewer Dock Member is lithologically and faunally equivalent to most of the Hickory Corners Member. The Furnaceville is a thin, variably hematitic limestone consisting largely of fossil fragments partly or wholly replaced by hematite. The succeeding Wallington Member consists of calcisiltites and *Pentamerus*-bearing packstones with thin shale partings. Eastward, the Wallington becomes increasingly shaly and passes into the Bear Creek Shale (Gillette, 1947). The Sterling Station Iron Ore is situated above the Bear Creek Shale.

The Lower Sodus Shale and Upper Sodus Shale, named for type exposures in the vicinity of Sodus Bay, collectively consist of about 14 m (45 feet) of distinctive, purplish-brown and greenish gray clay shales, with interbedded, thin laminated sandstones and *Eocoelia*-bearing packstones (Pl. 10, fig. 6). At Rochester, only the Lower Sodus Shale is present; the Upper Sodus Shale is truncated by the same unconformity that bevels the Hickory Corners Member to the west.

The Wolcott Limestone, represents a shoal facies, equivalent, in part, to the Upper Sodus Shale. The Wolcott consists of *Pentamerus*-bearing packstones and crinoidal grainstones, which pass upward from a 1 m (3 feet) thick basal unit of calcareous shale bearing locally abundant, well preserved bryozoans and crinoids. The contact between the Upper Sodus Shale and the overlying Wolcott Limestone is transitional and, for the purposes of this study, is defined by the appearance of *Pentamerus*. The Wolcott Limestone is 7 m (22 feet) thick at the type locality at Wolcott; to the west it pinches out between Fruitland and Rochester. The Wolcott Furnace Iron Ore, a thin bed of fossiliferous, hematitic limestone, locally caps the Wolcott Limestone.

At Second Creek near Alton, New York, a distinctive 3–6 cm thick bed of pyritic, phosphatic limestone with quartz pebble and limestone clasts occurs at the base of the Williamson Shale. This unit, designated the Second Creek Bed by Lin and Brett (1988), represents a transgressive lag deposit and records a major, westward-overstepping unconformity within the Clinton Group. This unit is gradational into the Westmoreland Iron Ore in central New York and probably persists as a lag at the top of the Merritton Limestone in southern

Ontario, Canada (Eckert and Brett, 1988; Brett *et al.*, 1995; Text-fig. 3). The succeeding dark gray and green, *Monograptus*-bearing Williamson Shale and its shallower water equivalent, the Willowvale shale, record a major late Llandovery transgressive event (Eckert and Brett, 1988; Brett *et al.*, 1990, 1998).

AGE AND CORRELATION

The Lower Silurian, Llandovery Series is presently subdivided into the Rhuddanian, Aeronian, and Telychian stages. Crinoids described herein come from Aeronian to late Telychian strata. In this paper we also retain the use of lettered designations for subdivisions of the Llandovery following Berry and Boucot (1970), together with the currently used stage names, for historic reasons and because, in some cases, these lettered divisions are somewhat more precise than the stages.

The Clinton Group has been dated principally by conodonts (Rexroad and Rickard, 1965; Nicoll and Rexroad, 1968; Rexroad and Nicoll, 1971), brachiopods (Berry and Boucot, 1970; Ziegler *in* Rickard, 1975), and graptolites. Berry and Boucot (1970) considered the entire lower Clinton Group to span a narrow interval (Aeronian to Telychian; Llandovery C4 to C6 of Berry and Boucot) within the late Llandovery. However, detailed brachiopod zonation based on *Eocoelia* lineages (Ziegler *in* Rickard, 1975) suggests that a considerably longer interval is represented. The crinoids *Dynamocrinus robustus* n. gen. and sp., *Thaerocrinus crenatus* n. gen. and sp., *Eomyelodactylus sparteus* Eckert, *Haptocrinus calvatus* n. gen. and sp., and *Prolixocrinus nodocaudis* n. gen. and sp. from the basal portion of the Hickory Corners Member of the Reynales Formation are considered to be of latest middle Llandovery (B3) to earliest late Llandovery (Aeronian; C1) age and constitute the oldest material described herein. *Eocoelia hemisphaerica* in the Wallington Member places *Stipatocrinus hulveri, Macrostylocrinus* sp., *Haptocrinus calvatus* n. gen. and sp., *Eomyelodactylus uniformis* Eckert, *Compsocrinus relictus* n. sp., and *Dendrocrinus ursae* n. sp. within the lower Aeronian Stage (C1–C2). The lower portion of the Lower Sodus Shale contains *Eocoelia hemisphaerica*? and is assigned to the lower-middle Aeronian (?C2). *Eocoelia intermedia* in the remaining Sodus shales and Wolcott Limestone places these strata in the late Llandovery (upper Aeronian to lower Telychian; C3–C5). Based on occurrence of *Eocoelia curtisi,* the Sauquoit Shale is of early Telychian (C4–C5) age. The diagnostic graptolite *Monograptus clintonensis* and conodonts of the uppermost *P. celloni* and *Pterospathodus amorphognathoides* Zones (M. Kleffner, personal comm., 2000) places the Williamson Shale and Willowvale Shale, the latter unit with *Protaxocrinus anellus* n. sp, in the upper Telychian Stage (Llandovery C6).

Recent detailed conodont biostratigraphy may modify dating of the Clinton Group somewhat. According to M. A. Kleffner (1988, personal communication), the Wallington Member of the Reynales Formation and the Lower Sodus Shale contains conodonts diagnostic of the *P. celloni* Zone, suggesting an early Telychian (C4–C5) age for these strata. This suggests that an unconformity representing most or all of C2–C4 time exists between the Brewer Dock Member and Furnaceville Iron Ore. Further work is needed to resolve this problem, but the Wolcott Limestone is still narrowly bracketed within the early to middle Telychian (C4–C5). Accordingly, most of the crinoids described herein, including *Tormosocrinus furberi* n. gen. and sp., *Callistocrinus tesselatus* n. gen. and sp., *Atalocrinus arctus* n. gen. and sp., *Aclistocrinus capistratus* n. gen. and sp., *Euspirocrinus wolcottense* n. sp., *Dendrocrinus aphelos* n. sp., *D. bactronodus* n. sp., *Myelodactylus linae* n. sp., *Haptocrinus* sp., *Kyphosocrinus tetreaulti* n. gen. and sp., and *Scapanocrinus muricatus* n. gen. and sp. are of late Llandovery (Telychian; C4–C5 age).

Early Silurian crinoids are highly endemic (Frest *et al.*, 1999), making correlation of various occurrences difficult even within the North American craton. The Brassfield Formation with its abundant and diverse crinoids (Ausich, 1984 a,b; 1986 a,c,d; Ausich and Dravage, 1988) has been variously dated from early Llandovery to late Llandovery by Rexroad (1967), Berry and Boucot (1970), and McDowell (1986). These discrepancies are perhaps explained by the time-transgressive nature of this complex unit (Nelson and Coogan, 1984; Gordon and Ettensohn, 1984). Most Brassfield crinoids have been obtained from the uppermost portion of the formation, an interval considered by Berry and Boucot (1970) to be of early late Llandovery C1–C2 age based on occurrence of the brachiopods *Microcardinalia* and *Triplesia.* On the basis of conodonts, the Brassfield has been assigned to the early to middle Llandovery (Rhudannian-early Telychian; Rexroad, 1967; Nicol and Rexroad, 1968; Cooper, 1967; Kleffner, 1985). The crinoids are probably all of Aeronian age (Ausich and Dravage, 1988). This suggests that the upper Brassfield is approximately coeval with the lower Reynales Formation and occurrence of *Prolixocrinus* n. gen. and *Eomyelodactlyus* in both of these formations supports this interpretation.

The *Cyclocrinites* beds of the Hopkinton Dolostone of Iowa are of late Llandovery (Telychian; C4) age and equivalent in age to the Wolcott Limestone (Johnson and Campbell, 1980; Johnson *et al.*, 1985; Frest *et al.*, 1999). However, these strata share only *Mye-*

lodactylus. The *Cyrtia* beds of the Hopkinton Dolomite (late Telychian C6) do not contain any echinoderms in common with the Williamson Shale and Willowvale Shale with which they are correlated.

The lower Clinton of New York is actually a rather thin and condensed sequence in comparison to about 540 m (1770 feet) of strata representing this interval on Anticosti Island, Quebec. Anticostian crinoids, reported by Bolton (1981), exhibit little in common with lower Clinton material of New York (A. I. Ausich, pers. comm., 2000). The early to middle Llandovery (A4–B2) Gun River Formation contains *Dendrocrinus, Herpetocrinus,* and *Alisocrinus* in its upper portion. The middle to late Llandovery (B3–C4) Jupiter Formation (Barnes and McCracken, 1981) has *Dimerocrinites, Caryocrinites, Eucalyptocrinites,* and *Sagenocrinites.* The latest Llandovery (C6) Chicotte Formation contains *Pycnosaccus, Periechocrinites,* and *Eucalyptocrinites.*

TAPHONOMY AND PALEOECOLOGY

INTRODUCTION

Taphonomy encompasses biostratinomic and diagenetic processes of fossilization and strongly influences the study of fossil echinoderms by controlling quality and completeness of preservation (see summaries of Brett *et al.*, 1997; Martin, 1999). Biostratinomy comprises the study of reorientation, disarticulation, fragmentation, reworking and other processes that occur between death of organisms and their final interment within the sediment. Preservation of articulated crinoids is uncommon because their multi-element skeletons are highly sensitive to biostratinomic processes. Post-mortem disarticulation typically occurs within a few hours or days in absence of rapid burial (Meyer 1971; Liddell, 1975; Meyer and Meyer, 1986; Meyer *et al.*, 1989; Brett *et al.*, 1997). From the viewpoint of the taxonomist, taphonomic bias is generally a nuisance that reduces the amount of data that can be retrieved from the fossil record. However, as Brett and Baird (1986) and others have indicated, taphonomy can also be viewed in a more positive light, providing important insights into paleoenvironments and paleoecology (see Martin, 1999, for summary).

The several occurrences of middle to late Llandovery crinoids described herein, like those discussed in Eckert (1984) from the early Llandovery, generally exhibit very good preservation, as compared to other Early Silurian crinoids from the midwestern United States. Crinoids from the Brassfield Formation discussed by Ausich (1984a,b, 1985, 1986a,c, d, 1987; Ausich and Dravage, 1988) are articulated cups and crowns that have undergone a rather high degree of alteration due to dolomitization. This recrystallization may obscure plate sutures. Llandovery crinoids from the Hopkinton Dolomite of Iowa (Witzke and Strimple, 1981) are strictly internal and external molds in dolostone and few specimens retain arms. Conversely, echinoderms from the lower Clinton beds of New York occur as parts of obrution deposits in which rapid burial has led to preservation of arms and columns in many instances. With few exceptions, these specimens have not been strongly dolomitized or otherwise recrystallized. This has permitted relatively unambiguous identification of plate sutures and other details. In most cases, the Clinton Group crinoids are preserved on the upper surfaces of limestone slabs. Ironically, this means that while the complete column and even holdfast are describable in several species, parts of the calyx may be embedded in matrix and inaccessible for study (*e.g.*, in *Callistocrinus* n. gen. and *Atalocrinus* n. gen.).

In the following sections, the taphonomy of several echinoderm assemblages discovered in this study is evaluated, together with paleoecology in order to understand these occurrences and depositional environments that influenced their preservation.

REYNALES FORMATION

Description

The Hickory Corners Member of the Reynales Formation is abundantly fossiliferous, but articulated crinoids are largely restricted to interbedded wackestone and shale near the base of this member. Excavation of an interval 20–25 cm above the base of the Hickory Corners Member in the Niagara Gorge near Lewiston, New York (locality 1), yielded the new camerate crinoid *Dynamocrinus,* new disparids, *Haptocrinus* and *Thaerocrinus,* and the new flexible crinoid *Prolixocrinus.* Calices and crowns, commonly with attached partial columns, occur on the upper surfaces of wackestone beds and, to a lesser extent, on their lower surfaces. The crinoids are associated with a diverse biota including abundant fragments of ramose bryozoan zoaria up to 15 cm long, the brachiopods *Hyattidina, Platystrophia, Eocoelia,* and *Coolinia,* the rugose coral *Enterolasma,* and rare dorsal exoskeletons of the trilobites *Encrinurus* and *Liocalymene* (Pl. 10, fig. 1). The wackestone beds tend to be lens-shaped in cross section and are rarely traceable laterally for more than a few tens of meters before they pinch out or break up into a series of thinner beds interbedded with shale. The best fossil preservation is typically encountered near the lateral margins of the wackestone beds. The interbedded shales are typically devoid of fossils beyond a few millimeters above or below the wackestones.

Interpretation

The concept of proximality trends (see Aigner and Reineck, 1982; Aigner, 1985; Brett *et al.*, 1986, 1993) provides a conceptual framework for interpreting taphonomic processes in context of a bathymetric gradient. In this scheme, the basal portion of the Hickory Corners Member represents a moderate energy, offshore regime between normal and maximum storm wave base (BA-3; 20–50 m, according to Liebau, 1980; Brett *et al.*, 1993). The seafloor consisted of a carbonate substrate broken up into a mosaic or patchwork by intervening muds. Benthic organisms preferentially colonized the carbonate areas; the muds apparently did not provide a firm enough substrate. Encrusting pelmatozoan holdfasts attached to bryozoan zoaria indicate that crinoids selectively inhabited bryozoan "thickets". Variably preserved skeletal material in the wackestones reflects relatively long periods of time during which multiple generations of crinoids and other organisms lived and died. A slow net rate of carbonate sedimentation, together with reworking, allowed the bulk of this skeletal material to become thoroughly disarticulated and fragmented. In some instances, corals were exposed long enough on the seafloor to become corroded (Pl. 10, fig. 1). Articulated crinoids on the lower surfaces of wackestone beds were buried by rapid, episodic lateral migration of resuspended carbonate sediment and skeletal material from storm-generated currents. Occasionally, carbonate sedimentation was temporarily terminated by mud tempestites that rapidly blanketed the seafloor and resulted in localized occurrences of well preserved crinoids on the upper surfaces of wackestone beds. The storm deposits were relatively thin and subject to reworking and redistribution, accounting for the rarity of articulated crinoids in these strata. As indicated previously, the best material tends to occur in the more argillaceous, distal lateral margins of the wackestone beds; these areas may represent slight depressions on the seafloor that were unaffected by sediment reworking.

Crinoidal grainstones capping the Hickory Corners Member consist almost entirely of the distinctive pentameric columnals of *Haptocrinus* n. gen. (Pl. 10, fig. 2). Few other fossils, including rare columnals of the new genera *Dynamocrinus* and *Prolixocrinus,* together with the brachiopods *Hyattidina* and *Coolinia,* occur in these beds. Bryozoans are essentially absent. The grainstones locally exhibit small scale cross stratification and contain rip up clasts derived from interbedded calcisiltites. These features, together with development of a major unconformity at the upper contact of these beds, indicate that they accumulated in a very shallow water setting within normal storm wave base (15 m or less; Liebau, 1980; Brett *et al.,* 1993) before emergence. The thoroughly disarticulated condition of the bulk of the fossils in the grainstones indicates that net sedimentation rate was low. Locally, storm-generated currents resuspended skeletal sediment and rapidly buried clusters of articulated *Hyattidina* in life position and entombed calices and crowns of *Haptocrinus calvatus* n. sp.

In outcrop, gradual upward transition from the high diversity bryozoan-brachiopod-crinoid assemblages characteristic of the lower portion of the Hickory Corners Member to low diversity, *Haptocrinus*-dominated assemblages at the top of this member reflects increased ecosystem stress in a shoaling-upward sequence. Few taxa could adapt to the shallow, agitated environment and episodically reworked, shifting substrates characteristic of the closing phase of deposition of the Hickory Corners Member. The extraordinary abundance of *Haptocrinus* in the grainstone beds is intriguing; this crinoid is an otherwise minor constituent of lower Clinton faunas. This disparid was apparently an opportunistic species that could tolerate a stressful environment, and flourished to the virtual exclusion of other benthos. In fact, stressful environments such as existed in the Early Silurian of western New York seem to have provided refuges for relict Ordovician lineages represented by *Haptocrinus, Stipatocrinus,* and *Compsocrinus. Haptocrinus* was far and away the most abundant of these crinoids. Adaptions that may have contributed to its success are discussed in the systematic section.

Taphonomy and paleoecology of the type occurrence of *Stipatocrinus hulveri* in the Wallington Member has been discussed previously (Eckert and Brett, 1987). Taphonomy of crinoids in this unit is difficult to evaluate because very little material has been recovered *in situ.* Partly articulated specimens of *Haptocrinus* occur in the Wallington associated with thin encrinites or below shale partings on the upper surfaces of packstone beds rich in *Pentamerus.* The shale partings represent tempestites that fortuitously escaped reworking in a dominantly high energy regime.

Boucot (1975) subdivided Silurian brachiopod assembages into five benthic assemblages (BA-1 through BA-5). The Reynales Formation contains BA-2 and BA-3 elements. The BA-2 brachiopod *Eocoelia* occurs rarely in the lower portion of the Hickory Corners Member and abundantly in the uppermost portion of the Wallington Member. The characteristic BA-3 brachiopod *Pentamerus* is common throughout most of the Wallington Member but it is absent from the Hickory Corners Member.

BEAR CREEK SHALE

Description

The camerate crinoids *Compsocrinus relictus* n. sp. and an unidentified taxon, cladid *Dendrocrinus ursae* n. sp., and rare columnals of *Haptocrinus* are the only echinoderms known from the Bear Creek Shale. *C. relictus* is by far the most common of these crinoids; columnals of this species occur throughout the Bear Creek Shale. Excavation of a 3 cm thick interval of silty shale near the top of this unit at Bear Creek yielded 14 nearly complete specimens of *C. relictus* from an area of about 0.5 m^2, together with a single specimen of an unidentified camerate crinoid, a few disarticulated valves of *Eocoelia,* and rare *Tentaculites* individuals. In this occurrence, *C. relictus* is represented by nearly complete crowns and attached, distally incomplete columns up to 30 cm long. Commonly, the arms are complete on the lower surfaces of the crowns but the center arms on the upper surfaces are represented by only their proximal portions (Pl. 3, fig. 1). Calices tend to be somewhat crushed and flattened. A gastropod tentatively identified as *Naticonema* is commonly attached to the tegmen of these crinoids.

Interpretation

The Bear Creek Shale represents a near shore, siliciclastic facies of the Wallington Member of the Reynales Formation (see also Frest *et al.,* 1999, pp. 665–666). The faunas of these formations are remarkably dissimilar. Moderate diversity *Pentamerus*-coral-bryozoan assemblages characterize the Wallington Member; the Bear Creek Shale contains a low diversity *Eocoelia* and bivalve-dominated fauna (bivalves include *Ctenodonta, Cyrtodonta, Modiolopsis,* and *Pyrenomoeus*). The low faunal diversity of the Bear Creek Shale reflects high ecosystem stress and dominance by opportunistic BA-2 organisms that could tolerate a muddy environment and soft substrate. Locally, *C. relictus* existed as small populations or stands on an otherwise sparsely populated seafloor. Coprophagous gastropods were attracted to the crinoids. The occurrence excavated at Bear Creek represents a stand that was torn away from its original location, transported a short distance, and rapidly buried by an influx of muddy sediment. This burial layer may have been originally too thin to completely cover the prone crinoid crowns, thereby exposing elevated arms to disarticulation. Alternatively, these individuals may have been covered completely, but were subsequently partially exhumed by winnowing.

WOLCOTT LIMESTONE

Description

The Wolcott Limestone contains diverse assemblages of crinoids varying in preservation from disarticulated, abraded columnals to extraordinarily well preserved entire crinoids with holdfasts. The lowest meter of these strata consists of calcareous shale and several thin beds of crinoidal grainstone. The grainstone beds exhibit sharp upper and lower contacts; upper surfaces are typically planar to wavy, lower contacts commonly display scour and fill structures. Shale pebbles are incorporated into the bases of these beds. The fossil content of the grainstones consists almost entirely of abraded columnals and pluricolumnals of a variety of crinoids, together with disarticulated valves of *Pentamerus.* Barren calcisiltites with *Chondrites* also occur in this interval. Passing upward, the crinoidal grainstones become successively thicker and coarser grained with pelmatozoan ossicles showing little or no abrasion and a tendency to occur as increasingly longer pluricolumnals. Interbedded shales in the lowest portion of the Wolcott Limestone are mostly barren but contain certain horizons with generally disarticulated brachiopods. These include *Eocoelia, Atrypa, Coolinia,* and *Leptaena* representing assemblages transitional between BA-2 and BA-3 (see Frest *et al.,* 1999; pp. 707–708).

The bulk of the articulated crinoid material in the Wolcott Limestone was collected from a narrow stratigraphic interval 1.0–1.1 m above the base of this formation at Mudge Creek (locality 8). This interval begins with a distinctive, 1 cm thick bed of silty, bluish gray calcareous shale abruptly overlying fissile barren shale. The silt-sized material is not distributed homogeneously through this bed, rather, it is concentrated in the basal several millimeters in thin laminae merging into calcareous shale above in a fining upward sequence. The laminae are locally disrupted by vertical burrows. The sharp lower contact of this bed is marked by disarticulated valves up to 1 cm long of juvenile individuals of *Pentamerus,* up to 1 cm long, together with crinoid ossicles. The non-laminated upper portion contains broken fronds of the bryozoan *Fenestella* and occasional specimens of the new flexible crinoid *Kyphosocrinus tetreaulti* and new camerate *Tormosocrinus furberi* preserved as crowns commonly with attached partial columns up to 10 cm long. This horizon is succeeded by 2 to 8 cm of very fossiliferous calcareous shale notable for exceptional preservation of fossils. This shale is packed with nearly complete fronds of the bryozoans *Fenestella tenuis* and *Semicoscinium tenuiceps,* and the coral *Striatopora flexuosa* (Pl. 10, fig. 3). Ramose bryozoans occur as large, isolated colonies up to 30 cm in diameter. Camerate, cladid, and flexible crinoids represented by the new taxa *Tormosocrinus furberi, Euspirocrinus wolcottense,* and *Kyphosocrinus tetreaulti* are the most abundant pelmatozoans in this interval. Less common forms include the new camerates *Aclistocrinus capistratus* and *Atalocrinus arctus,* the disparids *Myelodactylus linae* n. sp. and *Haptocrinus* sp., new cladids *Dendrocrinus aphelos* and *D. bactronodosus,* the flexible crinoids *Scapanocrinus muricatus* n. gen. and sp. and an unidentified taxon. A single specimen of an unidentified asterozoan was the only other echinoderm found associated with the crinoids. In fact, the bryozoans and crinoids are accompanied by very few other fossils; careful collecting in this interval yielded only scattered, disarticulated valves of *Pentamerus,* trilobite fragments, and a complete dorsal shield of the trilobite *Acernaspis.*

Unlike the clustering observed in the Bear Creek Shale, these crinoids occur as mostly solitary individuals. They are commonly exceptionally well preserved; many specimens of *Euspirocrinus wolcottense* are crowns retaining the entire column and holdfast and *Myelodactylus linae, Tormosocrinus furberi, Kyphosocrinus tetreaulti, Scapanocrinus muricatus,* and *Aclistocrinus capistratus* are also represented by complete or nearly complete individuals, in many instances attached to fenestrate bryozoans. Slight to severe disarticulation, when it occurs, is generally restricted to one side of calices or crowns (Pl. 8, figs. 11, 15). However, in an otherwise complete specimen of *Euspirocrinus,* the arms are completely missing (Pl. 6, fig. 9). Some cirri are incomplete on both sides of the column of the holotype specimen of *M. linae* (Pl. 6, fig. 3).

The fossiliferous interval discussed above passes upward into 10 cm of fissile shale packed with fenestrate bryozoans to the virtual exclusion of all other fossils. Interbedded thin, lenticular beds of limestone are variable in lithology and fossil content; some are *Haptocrinus*-dominated grainstones, others are packstones bearing *Fenestella* or *Pentamerus.* The bryozoan-rich limestones contain *Euspirocrinus, Kyphosocrinus, Aclistocrinus,* and the camerate crinoid *Callistocrinus tesselatus* n. gen. and sp. Preservation of echinoderms in the limestones is typically not as good as in the shaley interval below; most specimens consist of partly disarticulated crowns. However, the upper surface of one bed yielded a specimen of *Aclistocrinus capistratus* possessing a complete column and holdfast (Pl. 4, fig. 9).

The bryozoan-rich shales are in turn succeeded by medium to thick-bedded, coarse-grained crinoidal grainstones and *Pentamerus* packstones. The grainstones are dominated by robust columnals and pluricolumnals up to 1.5 cm in diameter of an unknown crinoid and sections of its column up to 30 cm long occur in thin shale partings between these beds (Pl. 9. figs. 10, 20). In the packstones, *Pentamerus* occurs as large robust valves, some still articulated, together with *Haptocrinus* columnals.

Interpretation

The Wolcott Limestone represents an offshore shoal complex that prograded shoreward during a rise in sea level, encroaching upon an inner muddy shelf, lagoonal environment (see Frest *et al.,* 1999, p. 707, for discussion of *Tormosocrinus-Kyphosocrinus* Association and its paleoenvironment). Gradual replacement of the low diversity *Eocoelia* biofacies of the Upper Sodus Shale by the higher diversity *Pentamerus* biofacies of the Wolcott Limestone reflects decreased ecosystem stress probably resulting from improved water circulation. As the *Pentamerus* shoals neared the Wolcott area, they were repeatedly swept by storms that transported winnowed skeletal material shoreward. Thin beds of crinoidal grainstone in the lower Wolcott Limestone are tempestites recording this storm activity (Pl. 10, fig. 5). The laminated bed at the base of the productive crinoid horizon is also a tempestite derived from disturbance of "thickets" of fenestrate bryozoans that inhabited sheltered margins of shoals. The bryozoans were fragmented by storm activity and buried with crinoids torn away from their holdfasts. Subsequently, dead zoaria and other skeletal material provided a firm substrate for colonization by new generations of bryozoans and crinoids. In fact, such "facilitative taphonomic feedback" (Kidwell and Jablonski, 1983) was a critical precursor for colonization by crinoids because nearly all crinoids known from this interval required hard substrates for initial attachment. *Tormosocrinus* is a possible exception to this generalization as it apparently possessed a recumbent stem anchored to the substrate by cirri at irregular intervals. The crinoids are inferred to have been attached to dead rather than living zoaria for two reasons. First, the holdfasts are invariably attached to small zoarium fragments rather than the large, nearly complete fronds that are abundant in this interval. Secondly, the holdfasts of large individuals contain rootlets that could only have been functional if they were inserted in the substrate (Pl. 6, fig. 7).

The preservation of crinoids in the calcareous shales above the tempestite is typically remarkably good. Entirely articulated individuals of *Euspirocrinus wolcottense* are common in this interval. Burial of these specimens must have been essentially instantaneous and coincident with their death. However, missing arms in one *Euspirocrinus* individual (Pl. 6, fig. 9) and distally incomplete cirri in the holotype specimen of *Myelodactylus linae* (Pl. 6, fig. 3) indicate that death of these crinoids preceeded entombment by perhaps several hours, just long enough for decay and disarticulation to begin. Evidence of an upright, posthumous pre-burial orientation is also provided by the "telescoped" condition in the *Euspirocrinus* individual just discussed and also in a specimen of *Scapanocrinus muricatus* (Pl. 8, fig. 1). In these specimens, the base of the calyx is partially concealed, apparently resulting from gravitational collapse of a decaying crown downward onto the column. The most probable cause of death was an influx of turbid, possibly anoxic water arising from storm disturbance of the seafloor.

The complete or nearly complete crinoids that occur throughout the 10 cm thick interval of calcareous shale succeeding the basal tempestite reflect multiple burial events. Current activity accompanying burial must have been relatively weak, but just sufficient to topple crinoids and fenestrate bryozoans onto the substrate. The fact that large colonies of ramose bryozoans with relatively narrow branches, averaging 0.5 cm in diameter, could exist in this environment points to a generally low energy regime. Furthermore, these colonies were preserved essentially *in situ* without fragmentation, indicating that even the burial events were relatively low energy phenomena. The mud tempestites responsible for preservation of complete crinoids must have been up to several centimeters thick. However, occurrence of specimens displaying disarticulation on one side only indicates that they either were not completely buried or that they were subsequently partly exhumed by winnowing, allowing the exposed upper surfaces to disarticulate. Many of the complete or nearly complete crinoids were draped over by fenestrate bryozoans that may have acted as mats inhibiting disarticulation. Abundance of these bryozoans may also have enhanced preservability of articulated echinoderms by inhibiting reworking of the substrate by infaunal organisms; burrows are virtually absent in the fenestrate-rich shales but they are common in barren shales below this interval. Presumably, the zoaria acted as physical barriers impeding burrowing.

Thin, laterally discontinuous beds of carbonate wackestone and crinoidal grainstone interbedded with the fenestrate-rich shales are also tempestites dominated by *Pentamerus* and *Haptocrinus*. Preservation of echinoderm material in these beds is typically fragmentary, but specimens of *Callistocrinus tesselatus, Aclistocrinus capistratus,* and large crowns of *Scapanocrinus muricatus* on both upper and lower surfaces of these beds represent species absent or rarely seen in the calcareous shales below. These specimens provide a rare glimpse into echinoderm assemblages that inhabited shoals where preservation potential of multielement skeletons was minimal. The dominant crinoid in the shoals, so abundant as to have been a major contributor of skeletal carbonate in the Wolcott Limestone, was a large robust form, which is unfortunately represented only by columnals and partial columns (Pl. 9, figs. 10, 20).

The shales immediately succeeding the productive crinoid interval are packed with *Fenestella tenuis.* Zoaria of this bryozoan are so abundant in this interval as to confer a high degree of fissility to the shales, which split along bedding planes covered with bryozoan fronds. The abundance of bryozoans suggests that these shales should be a good source of echinoderm material but this is not the case. In fact, crinoids are completely absent here and fossils of any sort other than *Fenestella* are extremely rare. Argillaceous limestones at the top of the Wolcott Limestone at Second Creek contain abundant zoaria of *Fenestella* and rare specimens of the brachiopods *Stricklandia, Eoplectodonta,* and *Dolerorthis.* Possibly, the bryozoans became so abundant that they largely crowded out other filter feeders including crinoids. Ausich (1986b) suggested that fenestrate bryozoans competed with calceocrinids and contributed to their decline and eventual extinction. Apparently, calceocrinids were adversely affected because their recumbent living position placed them within the same tier occupied by the bryozoans, forcing them to compete for food. It is interesting to note that calceocrinids are unknown from the Wolcott Limestone, yet they occur in the Hickory Corners Member of the Reynales Limestone in which fenestrate bryozoans are a minor component.

In theory, crinoids other than calceocrinids should have been able to exist in dense thickets of bryozoans providing their columns were long enough to elevate the crowns above the *Fenestella* tier. However, many Wolcott crinoids possessed relatively short stems that would not have elevated the crowns above the bryozoans, thus forcing them to compete for food. Short-stemmed individuals, such as some specimens of *Euspirocrinus* (Pl. 6, fig. 6), should have been able to exist if they had perched on living bryozoan fronds at the top of this tier. However, as indicated above, crinoids in the lower Wolcott Limestone are attached to small fragments of zoaria that are inferred to have been dead when the crinoid larvae settled on them. The living bryozoans probably possessed chemical or other mechanisms that prevented settling of epibionts, as is known to occur in many modern colonial organisms. The bryozoans may have even eaten crinoid larvae. If this scenario is correct, surviving crinoid larvae would have had to settle on zoaria fragments directly on the seafloor in the midst of a dense overstory of bryozoan fronds that effectively baffled and thoroughly exploited nutrient-laden currents. The survival potential of juvenile crinoids, brachiopods, and other benthic organisms may have been been poor under such conditions.

In a vertical sense, the sequence of echinoderm assemblages and other fossils observed in the Upper Sodus Shale and Wolcott Limestone exhibit profound changes in abundance and diversity correlated with an increasingly higher energy regime. Generally restricted, quiet water conditions prevailing during deposition of the Upper Sodus Shale were dominated by the *Eocoelia* assemblage of BA-2. This environment was marginal for echinoderms and tolerated only by certain small disparids and a single camerate species. As circulation improved during deposition of the lower Wolcott Limestone, these low diversity assemblages were replaced by fenestellid bryozoans and diverse, locally abundant crinoids in BA-3 and BA-4. These echinoderms were eventually crowded out by bryozoans. As shoals encroached still further, energy levels became too high for most bryozoans. They may have been supplanted by *Pentamerus* banks and stands of large, robust crinoids that were able to withstand, and may have required, strongly agitated conditions for their growth. The general trend toward increasing size of crinoids in the Upper Sodus Shale through Wolcott Limestone interval supports observations by Lane (1971) that the size of fossil crinoids is correlated with paleoenvironmental energy levels. Small crinoids typified quiet water conditions, whereas reef-dwelling crinoids were generally larger and more robust.

WILLOWVALE SHALE

Description

The Willowvale Shale was not as thoroughly investigated as other formations in this study, but occurrences of articulated echinoderms in these strata are apparently rare. A horizon 2 m above the base of the Willowvale Shale in a tributary of Sauquoit Creek at New Hartford, formerly Willowvale (locality 11), yielded seven specimens of *Protaxocrinus anellus* n. sp. preserved as crowns in some instances with attached partial columns. The crinoids were found on the upper surface of a 1 cm thick bed of shale approximately 2 m in lateral extent. This bed is packed with peculiar, branching pseudocirri (Pl. 9, figs. 18, 25) representing holdfasts of an unknown crinoid, together with columnals and pluricolumnals of several other unknown taxa. One grotesquely swollen pluricolumnal is extensively pitted by *Tremichnus* (Eckert, 1988), see Pl. 9, figs. 14–17. Other fossils in this occurrence, generally represented by disarticulated or fragmented remains, include the brachiopods *Leptaena, Coolinia, Eoplectodonta, Atrypa,* and *Eospirifer,* bivalves *Pyrenomoeus* and *Ctenodonta,* the trilobites *Liocalymene* and *Dalmanites,* and occasional specimens of the "button" coral *Palaeocyclus.* Bryozoans are relatively rare; only a few fragments of ramose and encrusting forms were found.

A single crown of *Protaxocrinus anellus* was discovered in the Willowvale Shale in a drainage ditch at Exit 33 of the New York State Thruway near Verona (locality 10). The specimen was embedded in fissile, gray shale abounding in *Fenestella* and gently curved, stoloniferous pluricolumnals (recumbent columns) of a large, unknown crinoid species (Pl. 9, figs. 21, 24). Thin beds of coquinite limestone in this section contain abundant, typically disarticulated specimens of *Atrypa* and *Eoplectodonta,* and loose slabs with *Costistricklandia* are the only occurrence of this large brachiopod known from the Willowvale Shale. *Palaeocyclus* is fairly common in this exposure.

Interpretation

Analysis of facies geometry provides insight into taphonomy and paleoecology of the fauna of the Willowvale Shale. The relative abundance of coquinoid limestones in the northernmost exposures of this formation indicate deposition in relatively shallow, moderately agitated conditions favorable for a fairly diverse fauna including *Protaxocrinus* and an unknown species of a robust, partly recumbent crinoid. To the south and east, coquinites become less common and, at New Hartford, the Willowvale Shale is almost entirely shale (Eckert and Brett, 1988; O'Brien *et al.,* 1998). In the Sauquoit Valley, the Willowvale Shale represents an offshore, muddy regime between deeper, graptolitic facies of the Williamson Shale to the west, and sandy, nearshore deposits to the east (Eckert and Brett, 1988; O'Brien *et al.,* 1998).

In the New Hartford occurrence of *Protaxocrinus,* the seafloor was initially colonized by large unknown crinoids. Several explanations are possible as to why these individuals are represented by pseudocirri only. The crinoids may have been torn away from their holdfasts by a strong storm disturbance. Alternatively, they may have lived and died while sedimentation rates were slow so that they became disarticulated after death. Perhaps they were buried as complete individuals only to be exhumed and disarticulated by winnowing. Whatever the reason for their destruction, these crinoids generated skeletal substrates that were subsequently colonized by *Protaxocrinus.* The small size of these individuals relative to other species of *Protaxocrinus* suggests that their lives were prematurely ended by tempestite burial.

DIAGENESIS

Diagenetic processes, including recrystallization and dissolution, can adversely affect preservation of fossils. Extensive recrystallization obliterated plate sutures in certain camerate crinoids from the Lower Silurian Cabot Head Formation of southern Ontario, rendering their identity uncertain (Eckert, 1984). Fortunately, plate outlines are readily discerned in the majority of specimens discussed herein. Exceptions occur in calceocrinids from the Reynales Formation in which sutures are faint but still visible, especially when immersed in water. Details of the distal portions of interrays of *Compsocrinus relictus* n. sp. from the Bear Creek Shale are typically not apparent but outlines of plates in the critical proximal portions of calices are preserved.

Partial or complete dissolution of echinoderms is common in dolostone and siltstone. Crinoids and other echinoderms in the Lower Silurian Hopkinton Dolomite of Iowa are commonly preserved as molds. The Upper Devonian of western New York comprises dominantly clastic facies in which calcareous fossils are typically preserved as molds. In some instances, this mode of preservation is not a major hindrance to the paleontologist because detailed artificial casts can be manufactured. Unfortunately, diagenetic history of some of the material in this study was characterized by substantial dissolution before the enclosing sediments were lithified; detailed natural molds are therefore absent or poorly preserved. In the Willowvale Shale, distal portions of the arms of *Protaxocrinus anellus* n. sp. have been completely dissolved away without leaving molds that would indicate their former existence (Pl. 9, fig. 7). The columns of *P. anellus* and other unknown crinoids in the Willowvale Shale commonly exhibit partial or complete dissolution. Their former existence is recorded by limonitic traces superficially resembling horizontal burrows of trace fossils or by poorly preserved, flattened molds and casts lacking fine structural details. Brachiopods and trilobites associated with these crinoids are also commonly decalcified.

More than twenty crinoids represented by crowns and attached long columns were discovered in the Upper Sodus Shale at Second Creek, near Alton, New York (locality 7). Unfortunately, these specimens were completely decalcified early in diagenesis; thin crusts of pyrite and indistinct impressions preserve only their overall outlines. Twenty-armed camerate crinoids and small cladids with heterotomous arms are represented by this material, but more detailed identification is not possible.

Acidic solutions responsible for destruction of calcareous fossils in the Upper Sodus and Williamson shales probably originated from early diagenetic oxidation of pyrite. In modern muddy marine environments, the bacterium *Desulphovibrio* reduces sulfate in an anoxic zone extending from near the sediment-water interface to a maximum depth of about 10 m (Curtis, 1980; Canfield and Raiswell, 1991). Metabolic products of this process include include hydrogen sulfide which combines with iron in the sediment to form pyrite. Episodic oxygenation of this zone by storms and bioturbation oxidizes the newly formed pyrite, forming sulfuric acid that dissolves calcite (Aller, 1982; Reaves, 1984; Canfield and Raiswell, 1991). An abundance of organic matter in the sediment protects pyrite by promoting anoxia. Significantly, dissolution of calcareous fossils in the Upper Sodus and Willowvale shales is most extensive in greenish, sparsely fossiliferous shales. Furthermore, the varicolored gray, green, red, and purple shales of the Upper Sodus Shale demonstrate that fluctuating oxidation states condusive to oxidation of pyrite or iron monosulfide existed during deposition of these strata.

Early diagenetic dissolution of fossils also occurred in sparsely fossiliferous, greenish, bioturbated shales in the lower portion of the Wolcott Limestone. *Pentamerus* occurs as calcified valves in packstone and grainstone beds within the Wolcott Limestone, yet this robust brachiopod, with a shell as much as 5 mm thick near the umbo, is commonly completely decalcified in the greenish shales. Crinoids in the greenish shales are decalcified to the extent that they are of little taxonomic value. However, most crinoids in the lower Wolcott Formation occur in calcareous shale associated with abundant fenestellid bryozoans that commonly exhibit partial dissolution. These bryozoans, easily dissolved during diagnesis by virtue of their large surface/volume ratios, may have protected the crinoids from dissolution by acting as carbonate donors that buffered acidic pore waters. Similarly, dissolution of carbonate mud in thin *Eocoelia*-bearing packstone beds of the Lower and Upper Sodus Shales accounts for the excellent preservation of brachiopods in these "pearly layers".

Pyrite is abundant in disseminated grains in the Bear Creek Shale. These dark gray silty shales originated as organic rich muds. The abundance of organic matter, coupled with general absence of bioturbation, promoted formation and persistence of pyrite in the sediment. Pyrite is especially common in specimens of *Compsocrinus relictus* n. sp. where it infills the calyx and lumen and coats or replaces plates. Unfortunately, the soft enclosing shales weather rapidly, exposing the crinoids to the elements where oxidation of pyrite destroys them.

Finally, dewatering and compaction of muddy sediments tended to crush echinoderms and other fossils preserved in poorly calcareous shales such as the Willowvale Shale. Specimens preserved in limestones and calcareous shales, as in the Wolcott Limestone, tend to retain their approximate original shapes because these strata lithified early in diagenesis.

SYSTEMATIC PALEONTOLOGY

INTRODUCTION AND PHILOSOPHY OF CLASSIFICATION

Classification and terminology used in this study are adopted from part T of the *Treatise on Invertebrate Paleontology* (Moore and Teichert, 1978) with some modifcations. In particular, Simms and Sevastopolo (1993) and Ausich (1998) recognized that the taxon "Inadunata" constitutes an artificial and possibly polyphyletic group. As such, Ausich abandoned Subclass Inadunata and elevated the taxa Disparida and Cladida from ordinal to subclass rank and raised their component suborders to orders. We follow Ausich (1998) in recognizing the subclasses Disparida and Cladida, but also retaining Flexibilia as a subclass.

We utilize a morphospecies approach with explicit recognition that biological species are impossible to define with fossils. Also, many morphospecies recognized by paleontologists, on the basis of specimens distributed through both time and space, may well represent groups of closely related species.

Many crinoid genera and families need to be more rigorously defined and higher classification, particularly at the level of family and superfamily, requires revision. Revision of these groups will require a thorough cladistic analysis of many taxa. These tasks are formidable and beyond the scope of the present study; only a few of the more pertinent problems are addressed here.

Homologies of cup plates in certain primitive disparid crinoids are a difficult problem (Moore, 1962; Ubaghs, 1978; Guensburg, 1984). We are skeptical of the taxonomic value of the so-called compound radial or biradial used in classifying certain disparid crinoids. The implication that a radial can be divided into an inferradial and superradial is misleading because these plates are discrete entities and only one plate in each ray can directly support a brachitaxis. Problems arise when a plate identified as an inferradial is nearly as large as undivided radials, when all lateral rays are similar, or when the cup is not clearly demarcated from the arms. Designation of inferradials and superradials then becomes subjective and taxonomic assignment arbitrary. *Tornatilicrinus* Guensburg provides an excellent example. Based on minor differences in proportions of ray plates, Guensburg (1984) interpreted *Tornatilicrinus* to possess five compound rays, or possibly one, and assigned it to the Tornatilicrinidae. However, *Tornatilicrinus* resembles *Ibexocrinus* Lane, 1976 of the Homocrinidae Kirk, 1974, a family characterized by three compound rays. Furthermore, *Tornatilicrinus* also resembles *Pariocrinus,* a genus considered by Eckert (1984) to have only one compound ray. Thus, small differences in proportions of plates result in assignment of closely related genera to different families. The result is an artificial system of classification that does not accurately reflect phylogeny. We consider that the putative superradials of the Tornatilicrinidae are actually fixed brachial plates. The familiy is allied to the Myelodactylidae Miller, 1883 rather than Homocrinidae on the basis of symmetry.

Also, the terminology of interradial plates of camerate crinoids is inconsistent (W. I. Ausich, personal comm., 1990). The lowest plates can be called interprimibrachials; above this level, however, the plates can be referred to as second range, third range interbrachials, etc. This avoids confusion of fixed non-brachials *within* a ray, which can be termed intersecundibrachials, intertertibrachials, etc.

The Flexibilia need a thorough taxonomic revision. Divergent genera lumped together indicate that certain families are clearly artificial in concept. The Homalocrinidae, as previously defined, provide an excellent example. *Anisocrinus* and *Asaphocrinus* are apparently distantly related to each other. Consequently, we have proposed the new family Anisocrinidae (replacing Subfamily Anisocrininae, in part) to accommodate *Anisocrinus* and related forms.

REPOSITORIES

BMS: Buffalo Museum of Science, Buffalo, New York
ROM: Royal Ontario Museum, Toronto, Ontario, Canada

SYSTEMATICS

Subphylum **CRINOZOA** Matsumoto, 1929

Class **CRINOIDEA** Miller, 1821

Subclass **CAMERATA** Wachsmuth and Springer, 1885

Order **DIPLOBATHRIDA** Moore and Laudon, 1943

Suborder **EUDIPLOBATHRINA** Ubaghs, 1953

Superfamily **RHODOCRINITACEA** Roemer, 1855

Family **CALLISTOCRINIDAE** new family

Diagnosis.—Rhodocrinitaceans with obconical cup shape, lacking infrabasals (pseudomonocyclic); ray ridges indistinct or absent. Radial circlet divided by both the basals and proximal parts of interprimibrachials (interradials). Interrays containing ten or more interbrachials; interradials followed by a tier of two plates. CD interray presently unknown. Arms uniserial.

Remarks.—The proposed family Callistocrinidae is closely allied to the family Rhodocrinitidae Roemer, 1855. However, *Callistocrinus* differs from all rhodocrinitids in being pseudomonocyclic, in having radial circlet divided by both basals and interprimibrachials and possessing radicular cirri.

As presently defined, the Rhodocrinitidae constitute a heterogeneous group of 34 genera. Silurian genera presently assigned to the Rhodocrinitidae include *Kyreocrinus* Ausich, 1986, L. Sil. (middle or late Llandovery); *Luxocrinus* Witzke and Strimple, 1981, L. Sil. (late Llandovery); *Lyriocrinus* Hall, 1852, U. Sil. (Wenlock); *Paragazacrinus* Springer, 1926, U. Sil. (Wenlock); *Stereoaster* Foerste, 1919, L. Sil. (middle or late Llandovery); and *Xysmacrinus* Ausich, 1986, L. Sil. (middle or late Llandovery). Ausich (1986a) informally sudivided this family into two groups; he assigned most Silurian forms to Group I. Group I is characterized by biserial arms, variable, but typically obconical cup shape, and a tier of two plates above each interradial. Group II embraces forms with bowl-shaped calices with median ridges on rays, interradials generally succeeded by a tier of three plates, and primitively uniserial arms (biserial in some advanced forms). *Callistocrinus* is most similar to Group I rhodocrinitids in cup shape and in configuration of interbrachials plates, but differs in having uniserial arms. However, none of the rhodocrinitid material described by Ausich (1986a) from the Lower Silurian Brassfield Formation of Ohio is allied with *Callistocrinus*, nor is *Luxocrinus* Witzke and Strimple from the Hopkinton Dolomite. No known Ordovician rhodocrinitacean, with the possible exception of *Rhaphanocrinus* Wachsmuth and Springer, 1885, is a plausible ancestor of *Callistocrinus*. Callistocrinidae is presently monotypic, based on characters of the highly distinctive genus *Callistocrinus*. Several characters of *Callistocrinus*, including its obconical cup with inflated interrays and numerous interbrachials, separation of radials by basals and lowest interprimibrachials, and absence of prominent median ridges on rays, all indicate affinities with the diplobathran family Rhodocrinitidae. However, as presently known, none of the Rhodocrinitidae, with the possible exception of *Diamenocrinus* Oehlert, 1891, are pseudomonocyclic, and none possess radicular cirri (Brett, 1981). Infrabasals within the Rhodocrinitidae are small and commonly confined to basal concavity. It would have been a relatively simple step to evolve from this condition to the pseudomonocylism seen in the Callistocrinidae. It might be argued that the definition of Rhodocrinitidae should simply be expanded to accomodate *Callistocrinus*, particularly because the latter is based on a single specimen. However, as noted, the Rhodocrinitidae is already a heterogenous catch-all and features of *Callistocrinus* are quite distinctive.

Genus **CALLISTOCRINUS**, new genus

Type species.—*Callistocrinus tesselatus* n. sp.

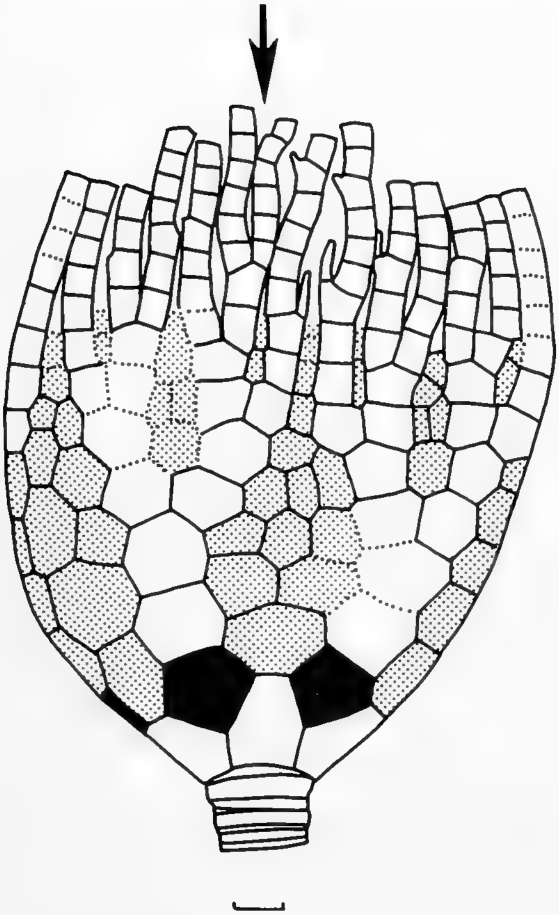
Diagnosis.—A pseudomonocyclic crinoid with obconical cup and inflated interrays. Radial circlet divided by basals and proximal interprimibrachials (interradials). Second tier interbrachials two, third tier interbrachials three, fourth tier interbrachials (outer quarter-ray) three; intersecundibrachials (inner or adaxial quarter-ray) numerous. Arms thirty, six per ray, uniserial, may divide above cup. Column round, xenomorphic; distal terminus bearing small, short, radicular cirri.

Remarks.—The monotypic genus *Callistocrinus* n. gen. is founded on a single individual of *C. tesselatus* n. sp. described below. The holotype specimen is remarkably complete and well preserved, yet it is puzzling in some ways. Preliminary observation suggested that infrabasals are absent in *C. tesselatus* and this was confirmed by temporarily detaching the cup from the column to check for concealed infrabasals; none were present. If *Callistocrinus* were to be made to "fit" the classification scheme adopted in the *Treatise*, it would be assigned to the Monobathrida although it does not appear to be related to any crinoid in this suborder. Instead, if classification is to reflect phylogeny, it is best to assign *Callistocrinus* to the Diplobathrida. We infer that it is a pseudomonocyclic crinoid and tentatively assign it to the superfamily Rhodocrinitacea, Such an interpretation is not without precedent; infrabasals are apparently absent in the Lower Devonian crinoid *Diamenocrinus* Oehlert, yet it is placed in the Rhodocrinitidae in the *Treatise*.

Pseudomonocyclism has been inferred to occur in several lineages of crinoids. Most modern comatulid crinoids are pseudomonocyclic; larval infrabasals are resorbed or fused to the centrodorsal during ontogeny (Bury, 1888; Warn, 1975). The monocyclic family Hybocrinidae Zittel, 1879 possesses cladid-like characters and is inferred to be pseudomonocyclic (Sprinkle, 1981). Broadhead (1984) suggested that monocyclic camerate crinoids arose from dicyclic ancestors through paedomorphic (heterochronic) loss of infrabasals.

The origin of *Callistocrinus* is unknown. It was probably derived from a rhodocriniticean ancestor with 20 uniserial arms.

Etymology of name.—*callistos* (Gr.) = most beau-



Text-figure 4.—*Callistocrinus tesselatus* n. gen. and sp., plate diagram of holotype BMS E26335 in lateral view. Arrow indicates arm dividing immediately above cup. Radials black, interbrachials stippled. Scale is 1 mm

tiful (refers to the appearance of the type specimen) + *krinon* (Gr.) = lily.

Callistocrinus tesselatus, new species
Plate 5, figures 2, 10; Text-figure 4

Diagnosis.—As for the genus. Cup plates smooth, unornamented

Description.—Cup obconical, height equal to width, interrays inflated, plates smooth, unornamented. CD interray not observable. Basal and radial circlets each comprising approximately 15% of cup height. Observed basals hexagonal, higher than wide (h/w = 1.1–1.2). Observed radials pentagonal, slightly wider than high (h/w = 0.9), separated from each other by basals and proximal primibrachials. Each first primibrachial hexagonal, wider than high (h/w = 0.6–0.8), succeeded by heptagonal, axillary second primibrachial (h/w = 0.7–0.8). Secundibrachials two in each half-ray, tertibrachials two in each inner (adaxial) quarter-ray and three in each outer quarter-ray. One entire interprimibrachial interray observed, consisting of a hexagonal (interradial) plate (h/w = 0.8) succeeded by one tier of two plates, two tiers of three plates each, and a narrow row of several additional interbrachials connected to tegmen. Intersecundibrachial interrays each consisting of a heptagonal or octagonal proximal intersecundibrachial, a tier of two plates, and several additional plates. Intertertibrachials indistinct, apparently at least two plates incorporated into each interray.

Arms thirty, six per ray, three in each half-ray, uniserial, pinnulate. Arms typically atomous; one arm dividing isotomously immediately above cup on second quartibrachial and lower portions of other arms bearing stout pinnules apparently representing incipient divisions of other arms (Text-fig. 4). Free brachial height equal to or slightly exceeding width. Distal brachials somewhat cuneate.

Column xenomorphic, round, diameter tapering gradually distally (Pl. 5, fig. 2). Proximal noditaxis formula N, IN. Medial noditaxis formula N, 2IN, 1IN, 2IN. Distal terminus of column bearing small radicular cirri, spaced at intervals of several columnals.

Remarks.—Description of *Callistocrinus tesselatus* n. sp. is based on one small specimen. Relatively wide spacing of pinnules and incipient, undeveloped branches of arms suggest that it is not a fully adult individual. Revised description, including morphology of the CD interray, must await discovery of additional specimens. Unfortunately, *C. tesselatus* is apparently a rare species.

Type and occurrence.—The holotype, BMS E26335, was obtained 1.1 m above the base of the Wolcott Limestone on the upper surface of a thin bed of limestone rich in fenestellid bryozoans; Mudge Creek (locality 8).

Measurements (in mm).—Orientation of specimen is unknown; plates are measured from right to left beginning with ray at right in Pl. 5, fig. 10.

Crown height = 25.3; cup height = 8.6, width (crushed) = 10.9; B height = 1.7, width = 1.4; R height = 1.4, width = 1.6; IBr1 height = 1.3, width = 1.7; 1Br2 height = 1.4, 1.8; B height = 1.6, width = 1.5; iIBr1 height = 1.5, width = 1.8; R height = 1.4, width = 1.7; 1Br1 height = 1.3, width = 2.0, 1Br2 height = 1.3, width = 1.9; Column length = 80, proximal diameter = 2.2, distal diameter = 1.9.

Etymology of name.—*tesselatus* (L.) = mosaic-inlaid; the trivial name refers to the numerous plates in the cup of this species.

Family **EMPEROCRINIDAE,** Frest and Strimple, 1981

Emended diagnosis.—Rhodocrinitaceans with bowl-shaped to pentagonal cup, bases of arms lobed in some genera. Infrabasals five, small, situated in basal concavity. Radial circlet divided by basals, proximal interprimibrachials, and primanal. Interbrachials and anal plates few. Tegminal plates large, polygonal. Anal tube present. Arms ten, generally poorly known, includes biserial forms.

Included genera.—*Emperocrinus* Miller and Gurley, 1895, L. Sil. (Wenlock); *Peremocrinus* Frest and Strimple, 1981, U. Sil. (Ludlow); *Tormosocrinus* n. gen., L. Sil. (late Llandovery).

Remarks.—As originally conceived by Frest and Strimple (1981), depressed interrays and equal width of all interrays were diagnostic characters of the Emperocrinidae. The emended diagnosis herein permits *Tormosocrinus* n. gen. to be accomodated in the Emperocrinidae; this is justified because *Tormosocrinus* closely resembles *Emperocrinus* except that the former has inflated interrays and an extra anal plate. Also, equal width of all interrays is not a distinguishing characteristic of this family because the CD interray of *Peremocrinus depressus* (Weller, 1900) is approximately 40% greater in width than the remaining interrays.

Frest and Strimple (1981) and Ausich (1986a) have commented on the unsatisfactory suprageneric classification of rhodocrinitaceans. A fundamental problem in this state of affairs is that rhodocrinitaceans encompass a large, heterogenous group of crinoids generally without clear demarcation between included families. For example, the Emperocrinidae and Rhodocrinitidae are transitional into each other; emperocrinids are basically rhodocrinitids with few interbrachials or anal plates.

Genus **TORMOSOCRINUS,** new genus

Diagnosis.—A genus of Emperocrinidae with bowl-shaped cup and inflated interrays. Infrabasals and lower portions of basals situated within intracalical cylinder. Radial circlet divided by basals, interbrachials and primanal. Primibrachials typically two, fixed secundibrachials two. Single interprimibrachial in each lateral interray, primanal followed by secundanal only. Tegminal plates large, polygonal. Anal tube large. Arms ten, biserial, atomous. Column round, xenomorphic, partly recumbent

Remarks.—*Tormosocrinus* bears a considerable resemblance to *Emperocrinus,* but the former possesses inflated rather than depressed interrays, a more prominent intracalical cylinder, and two anal plates instead of primanal only. *Peremocrinus,* the only other member of the Emperocrinidae, has a wide CD interray with many plates.

A remarkable characteristic of *Tormosocrinus* is the deep invagination in the base of its cup. Upturned lower portions of basals form a deep "intracalical cylinder" (*sensu* Haugh, 1979) that extends approximately one-half the height of the cup. The infrabasals and lower portions of basals are concealed within this concavity by the proximal column. Haugh (1979) suggested that the intracalical cylinder of the Late Ordovician channel-dwelling anthracocrinid *Rheocrinus aduncus* from the Georgian Bay Formation of Ontario strengthened the junction between the proxistele and cup to better resist disarticulation by currents. This can be interpreted as an aptation; occurrence of similar bases in many rhodocrinitaceans that were not restricted to channel deposits or environments characterized by strong current activity argues that invaginated bases served another, unknown function. Alternatively, *Tormosocrinus* may have evolved from another group of crinoids that inhabited high energy environments in which this structure was adaptive.

Rhodocrinitaceans have a sporadic fossil record, rendering interpretation of their phylogeny difficult (Frest and Strimple, 1981). Ancestry of *Tormosocrinus* is very problematical. It may have been derived from an unknown rhodocrinitid genus with few interbrachials. However, most Ordovician rhodocrinitids possess large numbers of interbrachials and are rather divergent compared to *Tormosocrinus.* Rhodocrinitids with few interbrachials appeared in the Late Ordovician (*Maquoketacrinus* Slocum, 1924, *Atactocrinus* Weller, 1916) but these genera do not resemble *Tormosocrinus.* Furthermore, none of the rhodocrinitaceans described from the Lower Silurian (Llandovery) Brassfield Formation of Ohio by Ausich (1986a) resembles *Tormosocrinus.* As in patelliocrinid camerates, heterochrony (progenesis) may have been instrumental in evolution of simplified rhodocrinitids, including *Tormosocrinus.*

The close resemblance of *Tormosocrinus* to *Emperocrinus* has been noted previously. *Tormosocrinus* (Silurian, late Llandovery) is slightly older than *Emperocrinus* (Wenlock) and probably gave rise to the latter by development of raised rays, a deeper basal concavity, and deletion of the secundanal.

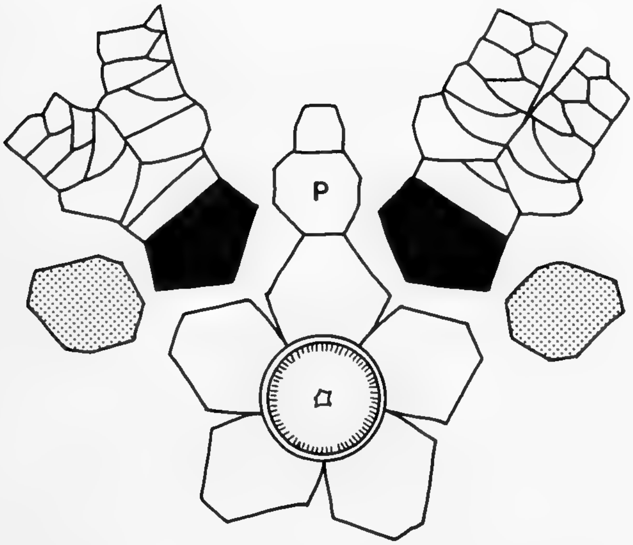
Etymology of name.—*tormos* (Gr.) = hole or socket (refers to the deeply excavated base) + *krinon* (Gr.) = lily. Type species.—*Tormosocrinus furberi* n. sp.

Tormosocrinus furberi, new species

Plate 4, figures 1–14; Text-figures 5, 6A–D

Diagnosis.—As for the genus.

Description.—Cup bowl-shaped, wider than high (h/w = 0.6–0.7, see Table 1). Cup plates generally smooth, lower margins of basals and lateral margins of ray series possessing slightly thickened rims in some instances. Infrabasals apparently five, small, sit-



Text-figure 5.—*Tormosocrinus furberi* n. gen. and sp., expanded plate diagram. Radials black, interbrachials stippled. *D-57*

uated at top of deep intracalical cylinder; diameter of infrabasal circlet slightly exceeding diameter of proximal column (Pl. 4, fig. 7). Basal circlet comprising approximately 40% of cup height. Basals five, upturned lower margins forming deep intracalical cylinder. In side view, basals six-sided, wider than high (h/w = 0.6–0.9), lower margins concave. Radials pentagonal, wider than high (h/w = 0.6–0.8), separated from each other by basals, first interprimibrachials (interradials), and primanal. First primibrachial in each ray wider than high (h/w = 0.3–0.5), rectangular or nearly so (upper corners slightly truncated in some instances; Text-figs. 5, 6D). Second primibrachials typically axillary, wider than high (h/w = 0.3–0.5), exceptionally variable in size and shape; largest examples pentagonal, in lateral contact with two interrays; smaller second primibrachials four-sided, in lateral contact with one interray only (Text-fig. 6A); smallest examples triangular with margins completely enclosed by first primibrachial and first secundibrachials (Text-fig. 6D). Second primibrachial absent in C ray of BMS E26344 (Pl. 4, fig. 1). Secundibrachials wider than high; proximal two secundibrachials in each half-ray incorporated into cup. First secundibrachial five-sided, interray side bearing a fixed pinnule in all but the smallest examples of this species. Second and third secundibrachials wedge-shaped. First and second secundibrachials of each pair of half-rays adjoining each other laterally. All interrays similar in width, consisting of few plates. First interprimibrachial large, elongate (h/w = 1.1–1.7), eight- to twelve-sided. Sutures between first interprimibrachial and ray series commonly strongly depressed. First interprimibrachial extending almost to tegmen, succeeded by proximal fixed pinnulars in largest individuals. Primanal smaller (height less) than first interprimibrachials, eight- to ten-sided (h/w = 0.9–1.4), extending up to first secundibrachials; followed by one or more small interbrachial plates. Secundanal roughly hexagonal, height about equal to or greater than width (h/w = 1.1–1.4).

Tegmen conical, sloping upward toward anal tube (Pl. 4, fig. 6). Margin of tegmen consisting of pairs of elongate plates above each lateral interray. Each pair of plates succeeded by a large, subequal, domed plate adjoining anal tube. Ambulacral grooves of each pair of half-ray separated from each other by an elongate plate succeeded by a wider, polygonal plate attached to the upper surfaces of a pair of large, domed plates (Text-fig. 6B).

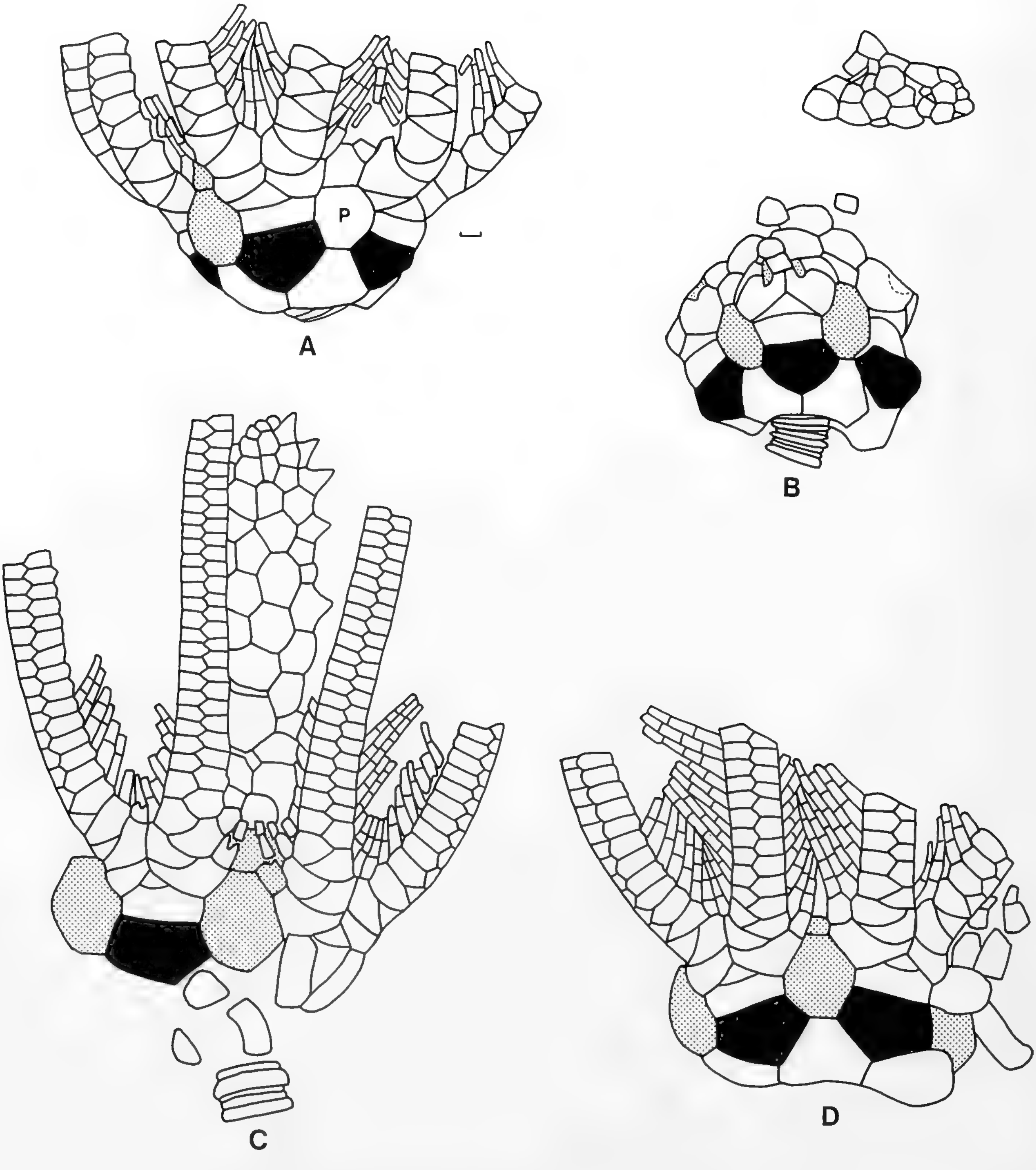
Anal tube large, length twice cup height, excentrically situated on tegmen directly above CD interray (Pl. 4, fig. 2). Anal tube consisting of polygonal (five- to seven-sided), subequal plates arranged in vertical rows proximally. Distal plates spinose.

Arms ten, biserial, atomous, length three and one-half times height of cup. Pinnules narrow (diameter 0.3–0.4 mm), pinnulars typically slightly elongate.

Column round, xenomorphic, tapering gradually in diameter distally. Proximal-most portion of column concealed within intracalical cylinder. Proximal and medial sections of column heteromorphic, noditaxes complex; formulas include N, 2IN, 2IN, 2IN, 1IN, 2IN, 2IN, 2IN and N, 2IN, 1IN, 2IN in proximal section and N, 1IN in medial section. Nodals up to 130% of internodal diameter, bearing thick, gently rounded epifacets. Distal portion of column isomorphic, consisting of columnals with rounded latera. Abruptly curved section of distal column consisting of wedge-shaped columnals situated above pseudocirri borne at intervals of several columnals (Pl. 4, fig. 3). Proximal columnal height 0.1–0.9 mm, distal columnal height 0.5–0.8 mm. Lumen pentastellate in proximal column, diameter one-quarter of nodal width.

Remarks.—Two specimens of *Tormosocrinus furberi* (BMS E26341, E26342a) have nearly complete columns with abruptly curved distal sections containing wedge-shaped columnals below which stout pseudocirri were apparently given off at irregular intervals. This indicates that the distal section of the column was recumbent on the substrate, as is known to have occurred in several lineages of camerate crinoids (Brett, 1981).

Types and occurrence.—Seventeen specimens of *Tormosocrinus furberi* (BMS E26336a, E26337–E26347c, E26348, E26349) were obtained from a thin interval 1.0–1.1 m above the base of the Wolcott



Text-figures 6A–D.—*Tormosocrinus furberi* n. gen. and sp., plate diagrams. A. CD interray of BMS E26343. B. Anterior view of cup of BMS E26345. The arms are missing, exposing tegmen and displaced anal tube. C. Lower portion of crown of BMS E26342a preserving complete, distally spinose anal tube. D. Cup of BMS E26341 centered on DE interray. Radials black, interbrachials and ambulacral areas stippled. Scale for all figures is 1 mm.

Table 1.—Measurements (in mm) of five specimens of *Tormosocrinus furberi* n. gen. and sp.

	BMS E26336a (holotype)	BMS E26338	BMS E26341	BMS E26343	BMS E26344
Crown height	—	—	—	25.7	21.2
Cup height	9.7	7.3	7.3	6.9	6.0
Cup width	8.0*	12.4	14.2*	11.5*	4.2*
AB B height	—	2.7	3.4	2.3	2.1
AB B width	—	4.0	4.0	3.1	3.2
BC B height	3.4	2.7	2.8	2.5	2.1
BC B width	5.0	4.4	3.9	3.1	2.7
CD B height	3.1	2.6	2.7	2.6	2.2
CD B width	5.0	4.7	4.0	3.5	2.5
DE B height	3.5	2.9	2.9	2.7	2.5
DE B width	5.1	4.7	3.8	3.3	2.9
EA B height	3.4	2.8	2.8	2.4	2.5
EA B width	4.8	4.4	3.7	3.3	2.9
A R height	—	2.6	3.0	2.1	2.1
A R width	—	4.3	4.1	3.3	—
B R height	—	2.9	—	2.1	2.2
B R width	—	4.3	—	3.2	3.4
C R height	3.1	2.7	—	2.2	1.9
C R width	4.0	4.3	—	3.1	2.9
D R height	—	3.4	2.8	2.4	1.6
D R width	—	5.0	4.1	3.5	3.1
E R height	3.6	3.1	2.6	2.2	2.2
E R width	4.6	4.5	4.2	3.4	3.1
A IBr1 height	—	1.2	1.3	1.0	0.9
A IBr1 width	—	3.2	3.3	2.8	2.7
B IBr1 height	—	1.3	—	0.9	1.2
B IBr1 width	—	3.6	—	2.7	2.7
C IBr1 height	1.7	1.3	—	0.9	1.1
C IBr1 width	—	4.0	—	2.6	2.7
D IBr1 height	2.2	1.4	1.0	1.0	1.0
D IBr1 width	4.2	3.8	3.5	3.1	2.6
E IBr1 height	1.9	1.3	1.2	0.9	0.9
E IBr1 width	3.9	3.9	3.5	2.9	2.6
A IBr2 height	—	—	1.0	1.0	0.8
A IBr2 width	—	—	2.1	3.1	3.0
B IBr2 height	—	1.1	—	0.9	0.7
B IBr2 width	—	4.0	—	2.9	1.4
C IBr2 height	1.2	1.2	—	0.9	—
C IBr2 width	2.9	3.4	—	2.5	—
D IBr2 height	1.4	—	0.7	1.0	0.9
D IBr2 width	2.9	—	1.4	2.4	3.0
E IBr2 height	1.5	—	0.7	0.9	0.8
E IBr2 width	3.2	—	1.6	3.1	2.8
AB iIBr1 height	—	—	—	3.3	2.5
AB iIBr1 width	—	3.4	—	2.0	1.9
BC iIBr1 height	—	4.0	—	3.0	2.5
BC iIBr1 width	—	3.5	—	2.2	1.9
DE iIBr1 height	5.7	3.9	3.6	3.3	2.9
DE iIBr1 width	4.2	3.5	2.8	2.5	2.0
EA iIBr1 height	—	—	3.5	3.2	—
EA iIBr1 width	—	3.4	2.7	2.2	—
Primanal height	3.5	3.6	2.4	2.9	1.4
Secundanal height	2.8	—	—	2.0	1.2
Secundanal width	2.7	—	—	1.4	0.9
Column length	—	—	90**	—	—

* Crushed cup (width greater than diameter).

** Nearly complete column.

Limestone, Mudge Creek (locality 8). The holotype specimen is BMS E26336a.

Etymology of name.—The species is named in honour of Sheldon Furber, to who kindly granted permission to excavate crinoids on his property adjoining Mudge Creek, where this species was obtained.

Order **MONOBATHRIDA** Moore and Laudon, 1943

Suborder **COMPSOCRININA** Ubaghs, 1978

Superfamily **XENOCRINACEA** S. A. Miller, 1890

Family **TANAOCRINIDAE** Bather, 1899

Diagnosis.—Xenocrinaceans with conical to obconical cup and prominent median ridges on rays and anitaxis. Basals four, radial circlet divided by CD interray basal and primanal. Interbrachials regular, numerous. Arms two to four per ray, uniserial.

Included genera.—*Canistrocrinus* Wachsmuth and Springer, 1885, U. Ord. (late Ashgillian); *Compsocrinus* S. A. Miller, 1883, U. Ord. (late Ashgillian)—L. Sil. (late Llandovery).

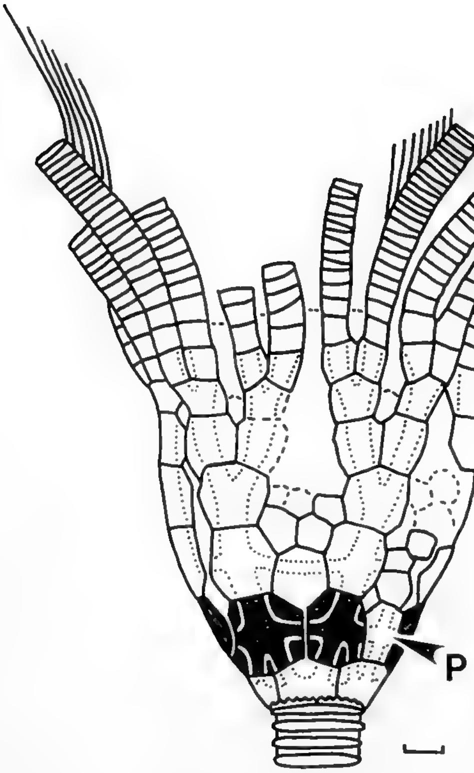
Remarks.—*Proxenocrinus inyoensis* Strimple and McGinnis, 1972, previously assigned to the Tanaocrinidae, is a diplobathrid rhodocrinitid camerate (Ausich, 1986a). The remaining two genera *Canistrocrinus* and *Compsocrinus* were previously known only from Upper Ordovician deposits; the present description extends the range of the family to the Lower Silurian.

Genus **COMPSOCRINUS** S. A. Miller, 1883

Type species.—*Compsocrinus harrisi* S. A. Miller, 1881, p. 74, pl. 1, figs. 4, 4a.

Diagnosis.—A genus of Tanaocrinidae with high, obconical cup and median ridges on rays and anitaxis. Basals four, radial circlet divided by CD interray basal and primanal. Primibrachials two, fixed secundibrachials two or three. Interbrachials numerous, regular polygons, similar in size to adjoining ray plates. CD interray wider than other interrays, bearing median anitaxis. Arms uniserial, ten to twenty. Column quadrangular or round.

Remarks.—*Compsocrinus* is dominantly an Upper Ordovician crinoid. *C. harrisi* S. A. Miller, 1881 and *C. miamiensis* S. A. Miller, 1883 occur in the Waynesville Member of the Bull Fork Formation (Richmondian) in southeastern Indiana. *C. harrisi* has also been reported from the Georgian Bay Formation (Richmondian) of Manitoulin Island, Ontario (Foerste, 1924). *C. nodosus* Brower, 1973, the youngest Ordovician representative of *Compsocrinus,* occurs in the Girardeau Limestone (Gamachian) of Missouri (Brower, 1973). Discovery of *C. relictus* n. sp. extends the



Text-figure 7.—*Compsocrinus relictus* n. sp., plate diagram of holotype BMS E26294a. Dotted lines outline ridges on rays and proximal interbrachials. Radials black. Scale is 2 mm.

range of *Compsocrinus* into the Early Silurian (late Llandovery).

Compsocrinus relictus, new species
Plate 3, figures 1–4, 8, 10–13, Text-figure 7

Diagnosis.—A large species of *Compsocrinus* characterized by weakly ornamented interrays, two or three fixed tertibrachials, twenty arms, and a round, heteromorphic column.

Description.—Cup obconical, higher than wide (h/w = 1.3–1.4), median ridges on rays and anitaxis. Ray ridges rounded, narrow, average width 40% of respective ray plates, dividing aborally near centers of radials, branches proceeding onto basals below, forming borders of triangular depressed areas (Pl. 4, fig. 8). Aboral division of B ray median ridge absent in small individuals, poorly developed in large specimens. Proximal ray plates and interbrachials ornamented with weakly developed ridges radiating from plate centers, distal interbrachials smooth (Pl. 4, fig. 1). Basal and radial circlets comprising approximately 10% and 15% of cup height, respectively. Basals four, wider than high (h/w = 0.5–0.8), separated from each other by sutures in B, C, D, and E rays. BC and DE interray basals pentagonal, CD and EB interray six-sided, EB interray basal wider than other basals. Radial circlet divided by CD interray basal and primanal. Radials higher than wide (h/w = 1.1–1.5), A and E ray radials hexagonal, other radials heptagonal. First primibrachial in each ray hexagonal, height equal to or exceeding width. Second primibrachials roughly pentagonal, upper corners slightly truncated in some instances. Two secundibrachials in each half-ray, succeeded by two or three fixed tertibrachials in each quarter-ray. First interprimibrachial hexagonal, elongate (h/w = 1.2), succeeded by tier of two plates extending to distal margins of first primibrachials. Distal interbrachials numerous but plate outlines generally obscured by pyrite in type material. First intersecundibrachial in each half-ray small, hexagonal, succeeded by several additional plates. Intertertibrachials present except in small individuals (cup height less than 10 mm). CD interray wider than other interrays. Primanal hexagonal, higher than wide, supporting median anitaxis consisting of at least nine plates flanked by interbrachials.

Arms twenty, atomous, four per ray, uniserial, length four and one-half times height of cup in a large individual (BMS E26294b). Proximal free brachials rectangular, remaining brachials cuneate (Text-fig. 7). Pinnules narrow, average width 0.2 mm, pinnulars elongate.

Column round, heteromorphic, long (incomplete column 27 cm long in BMS E26294b, proximal and distal diameters 5.9 mm and 2.8 mm, respectively). Simple noditaxis in medial portion of column N, 2IN, 1IN, 2IN, but commonly more complex. Noditaxes appearing deceptively simple from exterior of column; thick epifacets concealing adjacent columnals. Largest nodals twice internodal diameter.

Remarks.—In spite of a gap of at least 10 million years between their respective occurrences, *Compsocrinus relictus* n. sp. is quite similar to the type species *C. harrisi,* from which it may be distinguished by weakly developed plate ornamentation, fewer fixed tertibrachials, and a round rather than quadrangular column. *C. relictus* is a large species of *Compsocrinus*; the cups of adult specimens are about twice the height of those of *C. harrisi. C. miamiensis* is characterized by spines or nodes on interbrachials and only two or three arms in each ray. *C. nodosus* is unique among species assigned to *Compsocrinus* in possessing rather small and irregular interbrachials similar to those of *Xenocrinus.*

Many specimens of *C. relictus* have a gastropod tentatively identified as *Naticonema* attached to the tegmen. *Ptychocrinus medinensis* Brett from the Power Glen Formation (Rhuddanian) of western New York and southern Ontario provides the only other example of an inferred coprophagous gastropod/crinoid association known from the Lower Silurian (Brett, 1978a; Eckert, 1984).

Types and occurrence.—Compsocrinus relictus is locally abundant in the Bear Creek Shale at locality 9. The holotype, BMS E26294a and paratypes BMSE26294b–d and E26295–E26302 are from a horizon 25 cm below the Sterling Station Iron Ore.

Measurements (in mm) of BMS E26296.—Cup height = 21.3, crushed width = 16.8; CD B height = 2.0; DE B height = 2.4, width = 3.0; D R height = 3.8, E R height = 4.2, width = 3.8; D IBr1 height = 3.7, width = 3.5; E IBR1 height = 3.9, width 3.4; D IBr2 height = 3.6, width = 3.3; DE iIBr1 height = 3.4, width = 2.8; primanal height = 3.0; incomplete column length = 48.8; proximal diameter of column 5.0.

Etymology of name.—relictus (L.) = surviving, remaining; emphasizing this unique occurrence of *Compsocrinus* in the Silurian.

Suborder Uncertain

Superfamily **ATALOCRINACEA,** new superfamily

Diagnosis.—Basals five, radial circlet divided by CD interray basal and primanal. Interbrachials few.

Remarks.—In view of its unique morphology, suprageneric classification of *Atalocrinus* n. gen., described below, is uncertain. The divided radial circlet and absence of infrabasals seemingly indicates compsocrinine affinities. However, no other compsocrinines, including at least 93 genera distributed among the Xenocrinacea, Periechocrinacea, Carpocrinacea, and Hexacrinitacea are known to possess five basals. This remarkable fact suggests that *Atalocrinus* n. gen., discussed below, may actually represent an unusual glyptocrinid completely unrelated to compsocrinines. However, diagnosis of the entire suborder Glyptocrinina would have to be substantially emended in order to accommodate a single crinoid specimen if *Atalocrinus* were assigned to this suborder. Furthermore, if this was attempted, the fundamental distinction between the Compsocrinina and Glyptocrinina, that is, divided radial circlet in the former but not in the latter, would cease to exist.

McIntosh (1987) pointed out that a monobathrid archetype should have possessed five basals and a radial circlet interrupted by a primanal plate. From such a hypothetical ancestor the earliest members of the Compsocrinina could have evolved by the loss (by fusion) of a basal. Conversely, the Glyptocrinina could have arisen from this ancestor by ejecting the primanal from the radial circlet. *Atalocrinus,* although somewhat more advanced, resembles the hypothetical ancestral condition, as does a poorly preserved but as yet unnamed species illustrated by Ausich (1987). In view of these considerations, it is simpler to erect a new superfamily and a new family and to leave the subordinal classification uncertain, rather than to attempt revision and evaluation of the validity of entire suborders. *Atalocrinus* and the Atalocrinacea should perhaps be assigned to an unique suborder, but we are hesitant to do so on the basis of a single specimen.

Family **ATALOCRINIDAE,** new family

Diagnosis.—Atalocrinaceans with conical cup and narrow interrays. Basals five, radial circlet divided by CD interray basal and primanal. Primibrachials two, fixed secundibrachials two. Interbrachials and anal plates few. Arms ten, biserial.

Included genus.—Atalocrinus n. gen.

Remarks.—The Atalocrinidae is presently a monotypic family; emendation with respect to numbers of arms or other characters may be necessary should additional representatives of this family be discovered.

Genus **ATALOCRINUS,** new genus

Type species.—Atalocrinus arctus n. sp.

Diagnosis.—Cup conical, without median ridges on rays or anitaxis. Basals five, CD interray basal and octagonal primanal dividing radial circlet. Primibrachials two, fixed secundibrachials two. Interrays narrow, interprimibrachials few. Secundanal and tertanal occupying nearly entire CD interray. Arms ten, uniserial proximally, biserial distally.

Remarks.—The subordinal classification of *Atalocrinus* is deliberately left uncertain because of its discordant characteristics. If it were to be included within the Compsocrinina it would be unique in possessing five basals. All presently recognized members of this suborder have four or fewer basals. Indeed, compsocrinines exhibited an evolutionary trend toward reduction in numbers of basals. All known Ordovician compsocrinines including the Xenocrinidae and Tanaocrinidae have four basals. This presumably primitive character persisted into the Silurian in the Abacocrinidae, but Silurian compsocrinines were dominated by periechocrinids and carpocrinids with three basals. This trend culminated in the Hexacrinitacea and in certain Carboniferous families with two basals (Acrocrinidae, Dichocrinidae). The Lower Devonian Parahexacrinidae is an extreme example in which basals may be fused into a single plate (*Amonohexacrinus* Shevchenko, 1967, *Parahexacrinus* Shevchenko, 1967).

Alternatively, *Atalocrinus* may not be a compsocrinine. Assuming this to be correct, *Atalocrinus* could have originated from glyptocrinine stock by migration of the primanal downward into the radial circlet. This is known to have occurred in some individuals of "*Melocrinites*" *gracilis* (McIntosh, 1987).

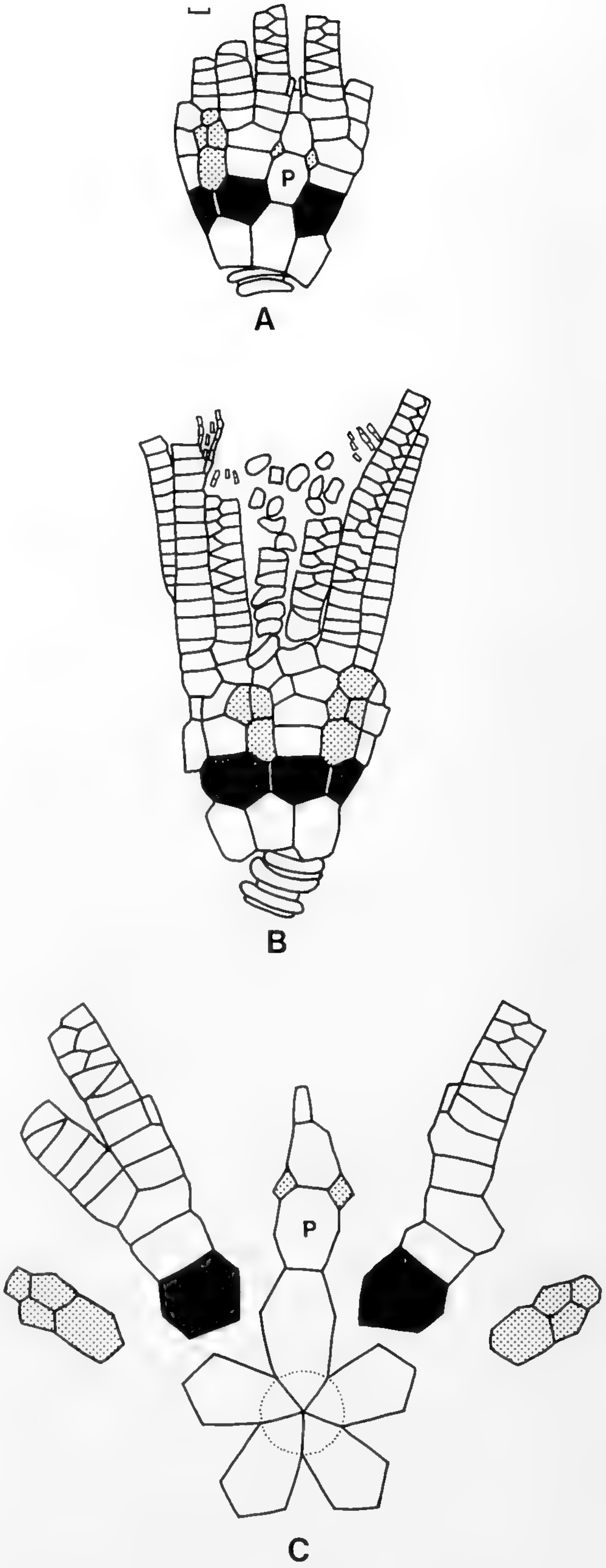
Another possibility is that *Atalocrinus* may have been derived from diplobathran stock by loss of infrabasals. This would imply that *Atalocrinus* was pseudomonocyclic. Several instances of probable pseudomonocyclism in fossil crinoids are known (Moore and Laudon, 1943; Sprinkle, 1981; see also above under discussion of Callistocrinidae). The infrabasals of many diplobathrans are small and inconspicuous. It may have been a small step to lose this circlet entirely, as occurs during ontogeny of species of *Antedon* (Warn, 1975). It this interpretation is correct, *Atalocrinus* may have evolved from a ten-armed dimerocrinitid, such as *Dimerocrinites* Phillips, 1839. In any case, the genus is unique enough to warrant a distinct family and superfamily.

Etymology of name.—atalos (Gr.) = distinct + *krinon* (Gr.) = lily; the generic name emphasizes the uncertain phylogenetic affinities of this crinoid.

Atalocrinus arctus, new species
Plate 5, figures 8, 13; Text-figures 8A–C

Diagnosis.—As for the genus. Cup plates smooth, unornamented. Proximal column heteromorphic, epifacets prominent.

Description.—Cup conical, higher than wide (h/w = 1.2), interrays narrow, depressed distally. Cup plates smooth, unornamented. Basal circlet comprising approximately 30% of cup height. CD interray basal hexagonal, slightly higher than wide (h/w = 1.1), extending upward into radial circlet; remaining four basals smaller, pentagonal, higher than wide (h/w = 1.2). Radial circlet divided by CD interray basal and primanal, comprising approximately 25% of cup height. Radials wider than high (h/w = 0.6–0.8), C and D ray radials hexagonal, remaining radials seven-sided. Each first primibrachial wider than high (typical h/w = 0.5–0.6), rectangular in A and E rays, six-sided in C and D rays. Second primibrachial in each ray six- or seven-sided, wider than high (h/w = 0.4–0.7), axillary. Fixed secundibrachials three in each half-ray, quadrangular, wider than high, adjoining fixed secundibrachials of adjacent half-ray. Second and third secundibrachials flanking CD interray bear fixed pinnules. First interprimibrachial in each interray six or seven-sided, elongate (h/w = 1.3), succeeded by a tier of two smaller, five-sided plates and one additional interbrachial. Primanal octagonal, slightly higher than wide (h/w = 1.1), shoulders supporting two small quadrangular interbrachials (Pl. 5, fig. 8; Text-fig. 8B). Secundanal irregular nine-sided polygon (h/w = 1.1), tapering in width distally. Tertanal narrow, wedge-shaped, extending to tegmen.



Text-figures 8A–C.—*Atalocrinus arctus* n. gen and sp. plate diagrams. A. CD interray of holotype BMS E26351. B. Anterior view of same, B ray at left. C. Expanded plate diagram. Radials black, interbrachials stippled. Scale for figures A and B is 1 mm.

Arms ten, atomous, pinnulate, biserial above fourth to sixth secundibrachial. Pinnules narrow (diameter 0.1–0.2 mm), pinnulars slightly elongate.

Proximal 6.5 cm of column heteromorphic, round, uniform in diameter (Pl. 5, fig. 13). Noditaxes complex; typical formulas N, 3IN, 2IN, 3IN, 1IN, 3IN, 2IN, 3IN at proximal end and N, 2IN, 1IN, 2IN at opposite end of preserved column. Nodals and larger internodals bearing prominent, wide epifacets. Epifacets thick, about equal to columnal height, latera rounded. Nodal h/w = 0.2–0.3, internodal h/w = 0.2–0.4.

Remarks.—*Atalocrinus arctus* n. sp. is known only from a single specimen. The anterior side of the cup is crushed and some of the plates are slightly ajar. Fortunately, the posterior side of the cup including the critical anal series is well preserved and undistorted.

Type and occurrence.—Holotype BMS E26351 was collected from bryozoan-rich shale 1.1 m above the base of the Wolcott Limestone: Mudge Creek (locality 8).

Measurements (in mm).—Crown height = 29.4; cup height = 9.1, crushed width = 8.6; BC B height = 2.6, width = 2.1; CD B height = 2.8, width = 2.6; DE B height = 2.2; EA B height = 2.2, width = 1.8; A R height = 1.9, width = 2.6, B R height = 2.0, width = 2.8; C R height = 2.0, width = 2.4; D R height = 1.8, width = 2.7; E R height = 2.0; A IBr1 height = 1.3, width = 2.0; B IBr1 height = 1.7, width = 1.9; C IBr1 height = 1.0, width = 2.0; D IBr1 height = 1.1, width = 2.2; E IBr1 height = 1.3; A IBr2 height = 1.1, width = 2.5; C IBr2 height = 1.6, width = 2.3; D IBr2 height = 1.2, width = 2.5; E IBr2 height = 1.1; DE iIBr1 height = 2.1; EA iIBr1 height = 2.2, width = 1.7; primanal height = 2.2, width = 2.0; secundanal height = 1.7, width = 1.6.

Etymology of name.—*arctus* (L.) = close, pressed together; the trivial name refers to the lateral joining together of fixed secundibrachials.

Suborder GLYPTOCRININA Moore, 1952

Superfamily MELOCRINITACEA d'Orbigny, 1852

Family PARAMELOCRINIDAE Ubaghs, 1958

Diagnosis.—Melocrinitaceans with bowl-shaped to high conical cup and few interbrachials. Posterior interray differentiated from lateral interrrays. Proximal secundibrachials incorporated into cup. Arms biserial, simple or dividing isotomously.

Included genera.—*Closterocrinus* Hall, 1852, L. Sil. (early Wenlock); *Dynamocrinus* n. gen., L. Sil. (Llandovery B3–C1), *Paramelocrinus* Ubaghs, 1958, U. Sil. (late Wenlock–late Ludlow).

Remarks.—*Closterocrinus* was assigned to the Paramelocrinidae by emending the diagnosis of this previously monotypic family (McIntosh, 1987). This broadened diagnosis permits *Dynamocrinus* n. gen. to be readily accomodated within the Paramelocrinidae although, as discussed below, this genus apparently combines characteristics typical of both *Closterocrinus* Hall 1852 with those typical of *Paramelocrinus* Ubaghs 1858.

Genus **DYNAMOCRINUS,** new genus

Type species.—*Dynamocrinus robustus* n. sp.

Diagnosis.—A genus of Paramelocrinidae characterized by a bowl-shaped cup with flat base circumscribed by a ridge on basal circlet. Cup ornamented with low ridges radiating from plate centers. Lateral interrays narrow, interprimibrachials three, in vertical row. Hexagonal primanal supporting tier of two plates succeeded by vertical row of two plates. Arms ten, biserial, atomous. Column heteromorphic, epifacets prominent.

Remarks.—*Dynamocrinus* appears to represent a link between the Paramelocrinidae, as presently understood, and the Clonocrinidae Bather, 1899. Paramelocrinid characters in *Dynamocrinus* and *Closterocrinus* include ten biserial arms and lateral interrays each consisting of a vertical row of interprimibrachials. However, the posterior interray of *Dynamocrinus* is apparently highly simplified for a melocrinitacean; it apparently contains seven plates, two of which are fixed pinnulars, in contrast to an estimated nine or ten plates in the posterior interray of *Closterocrinus.* Moreover, the cup of *Closterocrinus* is high conical, whereas *Dynamocrinus* has a bowl-shaped cup.

Phylogeny of *Dynamocrinus* is unknown. The biserial arms of *Dynamocrinus* preclude it from being in the lineage ancestral to melocrinitids. Rather, it was presumably derived from a melocrinitid stock, but it is highly derived relative to all known melocrinitids, including *Alisocrinus tetrarmatus* Brower, 1973 from the Upper Ordovician (Gamachian) Girardeau Limestone of Missouri, the only melocriniticean older than *Dynamocrinus.* Simplification of the interrays of *Dynamocrinus* and *Closterocrinus* suggests that heterochrony (progenesis) played a part in their evolution from a common ancestor. *Dynamocrinus* appears to be advanced in cup shape and the nature of the CD interray with respect to both *Closterocrinus* and *Paramelocrinus.* Each of these latter two taxa apparently represent separate offshoots that became extinct without leaving descendants. Conversely, *Dynamocrinus* may be closely related to the Clonocrinidae. It would only require elimination of one or more anal plates and acquisition of 20 arms to convert *Dynamocrinus* into a clonocrinid not far removed from *Clonocrinus* Quensted, 1876.

Etymology of name.—dynamo = an electric generator; the namesake of this genus refers to discovery of the holotype specimen near large hydroelectric installations + *krinon* (Gr.) = lily

Dynamocrinus robustus, new species
Text-figures 7.1–7.2; Plate 1, figures 3, 4, 13–15, 26, 27

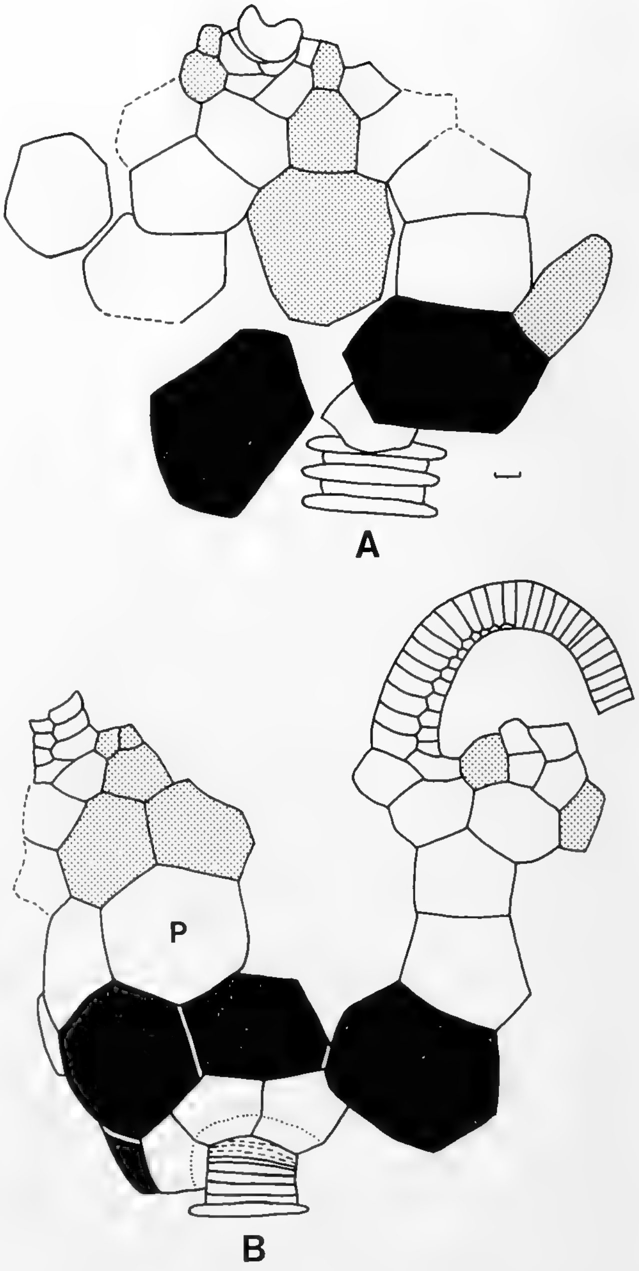
Diagnosis.—As for the genus.

Description.—Cup bowl-shaped, wider than high (height approximately two-thirds width). Basals bisected by lateral ridge, lower portions forming flat base of cup approximately twice the diameter of proximal column (Pl. 1, fig. 27). Proximal cup plates above basals ornamented with distinctive pattern of low, straight to slightly wavy ridges (Pl. 1, fig. 3). Longest ridges radiating from center of each plate to plate corners, enclosing subtriangular areas containing additional ridges with short branches. Basals four; basal circlet low, comprising about 10% of cup height. Radial circlet uninterrupted by primanal. Radials largest plates in cup, hexagonal, wider than high (height/width = 0.6–0.7). Primibrachials two, first primibrachials rectangular or pentagonal, second primibrachials pentagonal. First secundibrachial in each half-ray hexagonal, followed by one or two pairs of plates before free arms (Pl. 1, fig. 27). Interrays narrow, simple; lateral interrays each consisting of a single vertical row of three interprimibrachials (Text-fig. 9A). First interbrachial large, nine-sided, height approximately equal to width, succeeding tier a single interbrachial, much smaller, elongate. One or two intersecundibrachials present above and between the proximal secundibrachials of adjoining half-rays. CD interray wider than other interrays. Primanal hexagonal, subequal, supporting tier of two plates, in turn succeeded by a vertical row of at least two additional plates flanked distally by fixed pinnulars (Text-fig. 9B).

Arms ten, two per ray, stout, biserial, atomous. Pinnules not observed.

Column strongly heteromorphic; epifacets prominent (Pl. 1, figs. 13–15). Epifacets thin (0.3–0.4 mm thick), wide (nodals up to 2½ times diameter of internodals), becoming more widely spaced and less prominent in distal region of column where they extend only slightly beyond internodal diameter. Internodals extremely thin throughout known column (h/w = 0.03–0.05). Holdfast unknown.

Remarks.—Description of the cup of *Dynamocrinus robustus* is based on a single, crushed, partly disarticulated crown preserving two interrays (BMS E26304). Some doubt exists as to the orientation of these interrays. The wider interray with more plates is believed to be the CD interrray; the other interray is narrower, contains fewer plates, and is inferred to be a lateral interray. If so, the first primibrachials bordering the large first interbrachials should be quadrangular in all rays except the C and D rays. However, this plate is pentagonal in the inferred B ray, suggesting that the AB interray, not preserved, contained more plates than



Text-figures 9A, B.—*Dynamocrinus robustus* n. gen. and sp. plate diagrams. A. Holotype BMS E26304 centered on EA interray. B. CD interray view of same. Radials black, interbrachials stippled. Ridge on basals indicated by dotted line. Scale for both figures is 1 mm.

in the preserved lateral interray. Two possibilities exist; the lateral interrays could be somewhat variable in construction, or the CD interray is incorrectly identified. Discovery of specimens with better preservation is needed to resolve this issue.

Measurements of BMS E26304 (in mm).—Cup height = 16, width (crushed) = 23; CD interray B height = 2.0, width = 3.8; B ray R height = 4.9, width = 6.7; D ray R height = 4.6, width = 6.5, E ray R height = 5.0, width = 7.2; B ray IBr1 height = 3.9, width = 5.1; E ray IBr1 height = 3.3, width = 4.9; B ray IBr2 height = 3.1, width = 3.9; E ray IBr2 height = 3.0, width = 4.4; EA interray iIBr1 height = 5.4, width = 5.4, iIBr2 height = 3.0, width = 2.4, iIBr3 height = 1.4, width = 1.0; primanal height = 5.3, width = 5.2.

Types and occurrence.—The holotype specimen, represented by a partial crown (BMS E26304) and sections of column consisting of paratypes BMS E26402 and BMS E26403 were collected 20 cm above the base of the Hickory Corners Member of the Reynales Formation, locality 1. A radial plate (paratype BMS E26400) and distal column (paratype BMS E26401) were obtained in talus from the Hickory Corners Member at locality 2.

Etymology of name.—The species namesake refers to the robust, thick plates of the cup.

Superfamily **EUCALYPTOCRINITACEA** Roemer, 1855

Family **EUCALYPTOCRINITIDAE** Roemer, 1855

Diagnosis.—Eucalyptocrinitaceans with four basals confined to basal concavity or partly to completely exsert. Primibrachials one or two, secundibrachials two, fixed tertibrachials few. First interprimibrachial large, succeeded by pair of smaller plates. Tegminal partition plates variably developed, partly or wholly separating 20 biserial arms into 10 pairs.

Included genera.—*Eucalyptocrinites* Goldfuss, 1831, L. Sil. (late Llandovery)—M. Dev. (Eifelian); *Aclistocrinus* n. gen., L. Sil. (late Llandovery); *Archaeocalyptocrinus* Witzke and Strimple, 1981, L. Sil. (late Llandovery)—?U. Sil. (Wenlock); *Calliocrinus* d'Orbigny, 1849, (late Llandovery)—U. Sil. (Wenlock); *Chicagocrinus* Weller, 1900, U. Sil. (Wenlock).

Remarks.—The Eucalyptocrinitidae are morphologically far removed from all Ordovician crinoids and even the most general details of the origin of this specialized group are speculative. They are postulated to have evolved from a clonocrinid-like ancestor (Moore and Laudon, 1943) or from a patelliocrinid stock (Witzke and Strimple, 1981), but corroborative evidence is absent.

Genus **ACLISTOCRINUS**, new genus

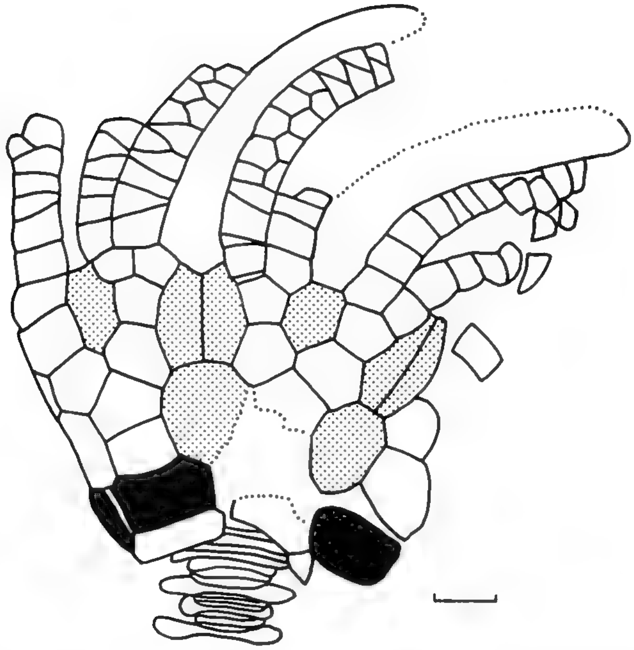
Type species.—*Aclistocrinus capistratus* n. sp.

Diagnosis.—A genus of Eucalyptocrinitidae with conical cup and partly exsert basals. Cup plates slightly granulose Primibrachials two, secundibrachials two. All interrays similar, each first interprimibrachial succeeded by tier of two elongate plates. Tegminal partitions extending full height of twenty biserial arms. Anal tube extending above arms, distally expanded, spinose. Column round, xenomorphic, with prominent epifacets.

Remarks.—The monotypic genus *Aclistocrinus* n. gen. is intermediate in morphology between *Archaeocalyptocrinus* and *Eucalyptocrinites.* Detailed comparison of these genera is difficult because *Archaeocalyptocrinus* and *Eucalyptocrinites* are presently broadly defined. One of the characteristics of *Archaeocalyptocrinus* is the ten small vertical partitions dividing the tegmen (Witzke and Strimple, 1981, p. 126). However, these partitions have been observed only in the type species *A. nodosus* from the Hopkinton Dolomite (Silurian, late Llandovery) of Iowa. *Eucalyptocrinites obconicus* (Hall 1865) and *E. slocomi* Foerste 1920 were reassigned to *Archaeocalyptocrinus* by Witzke and Strimple (1981), although the tegmen of these species is unknown. Accordingly, diagnosis of *Archaeocalyptocrinus* is based mainly on *A. nodosus,* a species characterized by a small basal concavity concealing lower portions of basals, tegminal partitions apparently much shorter than the arms, and strongly lobed arm bases. Following this more rigorous diagnosis, *Aclistocrinus* may be distinguished from *Archaeocalyptocrinus* by tegminal partitions extending to distal tips of the arms and absence of lobed arm bases.

Aclistocrinus is closely allied with *Eucalyptocrinites,* also a broadly defined genus in need of revision. The type species, *E. rosaceus* Goldfuss, 1831 from the Middle Devonian of Germany, is divergent when compared to Silurian species assigned to this genus. It has a wide, bowl-shaped cup, large spinose projections on radials, generally one primibrachial per ray, and wide, rather than elongate first interprimibrachials. These differences are sufficient to justify future revision of *Eucalyptocrinites. Aclistocrinus* differs from the majority of Silurian species presently assigned to *Eucalyptocrinites* in that the concavity in the base of the cup of the former genus is smaller and the basals are reflexed and not confined to it. *Aclistocrinus* probably evolved from *Archaeocalyptocrinus* and was direct ancestor of *Eucalyptocrinites.*

Etymology of name.—*aclistos* (Gr.) = hidden, sheltered; the generic epithet refers to partial concealment



Text-figure 10.—*Aclistocrinus capistratus* n. gen. and sp., plate diagram of lateral view of cup of BMS E26354b. Radials black, interbrachials stippled. Scale is 1 mm.

Table 2.—Measurements (in mm) of holotype specimen (BMS E26352) of *Aclistocrinus capistratus* n. gen. and sp.

Crushed crown height	10.5	1Br1 height	0.8
Actual height of crown	18.8	1Br1 width	1.5
Cup height	5.5	1Br1 height	0.8
Cup width	8.5	1Br1 width	1.5
B height	—	1Br1 height	0.7
B width	2.1	1Br1 width	1.6
B height	0.8	1Br2 height	1.0
B width	2.6	1Br2 width	1.8
B height	1.0	1Br2 height	1.1
B width	2.4	1Br2 width	1.8
B height	—	1Br2 height	0.8
B width	2.5	1Br2 width	1.9
R height	1.1	1Br2 height	1.2
R width	2.5	1Br2 width	1.8
R height	1.0	1Br2 height	1.0
R width	2.5	1Br2 width	1.9
R height	1.0	iIBr1 height	2.0
R width	2.5	iIBr1 width	2.0
R height	1.2	iIBr1 height	2.0
R width	2.5	iIBr1 width	1.9
R height	1.0	iIBr1 height	1.9
R width	2.6	iIBr1 width	2.0
IBr1 height	0.8	iIBr1 height	1.9
IBr1 width	1.5	iIBr1 width	1.9
IBr1 height	0.8	iIBr1 height	1.9
IBr1 width	1.4	iIBr1 width	2.0

* Rays measured in a clockwise direction viewed from tegmen beginning with ray at left on Plate 5, figure 4.

of basals by basal concavity in cup + *krinon* (Gr.) = lily.

Aclistocrinus capistratus, new species
Plate 5, figures 1, 3–7, 9, 11, 12; Text-figure 10

Diagnosis.—As for the genus.

Description.—Cup low conical (h/w = 0.6–0.7) with basal concavity and inflated interrays (Table 2). Cup plates plates smooth or slightly granulose, sutures impressed. Basal and radial circlets comprising approximately 15% and 20% of cup height, respectively. Basals four; upturned lower margins forming slightly flaring basal concavity (Pl. 5, fig. 12). In side view of cup, basals much wider than high (h/w = 0.3–0.4); two quadrangular basals visible as low pentagons and two five-sided basals resemble low hexagons. Remainder of cup displaying perfect pentamerous symmetry. Radials six- or seven-sided, wider than high (h/w = 0.4–0.5), distal margins adjacent to first primibrachials straight in small individuals, arcuate in larger specimens. First primibrachial in each ray smaller than radial, low rectangular (h/w = 0.4–0.6). Second primibrachial pentagonal, wider than high (h/w = 0.4–0.7), axillary. First secundibrachial low, hexagonal; second secundibrachial pentagonal, axillary. Fixed portion of each quarter-ray consisting of pair of quadrangular tertibrachials. Interprimibrachial interrays each consisting of a large ten-sided interbrachial (h/w = 1.0–1.1) in lateral contact with primibrachials and first secundibrachials, followed by a pair of elongate, pentagonal plates (Text-fig. 10). A single intersecundibrachial is incorporated into cup between each pair of half rays.

Arms twenty, biserial, relatively short (length approximately two and one-half times height of cup), enclosed between ten elongate partitions extending to arm tips. Each partition plate situated above paired distal interprimibrachials; each pair of partition plates enclosing two arms. Anal tube extending to summit of crown, distally expanded, cogwheel-like, spinose, apparently without terminal anal vent (Pl. 5, fig. 6).

Column xenomorphic, relatively short (length approximately twice crown height in BMS E26354a), tapering rapidly distally. Typical noditaxis formula in proximal and medial sections N, 2IN, 2IN, 1IN, 2IN, 2IN. Nodals and first order internodals bearing wide epifacets. Epifacets triangular in cross section, tapering uniformly abaxially to sharp-edged margins. Distal portion of column isomorphic, without epifacets. Holdfast bearing numerous branching pseudocirri (Pl. 5, fig. 9).

Types and occurrence.—The six known specimens of *Aclistocrinus capistratus*, represented by BMS E26352–E26355, and BMS E26410 are from the Wolcott Limestone, 1.0–1.1 m above the base of this formation, locality 8. The holotype is BMS E26352.

Etymology of name.—*capistratus* (L.) = masked, hooded; the specific epithet refers to concealment of the distal tips of the arms and tegminal partition plates by the flattened terminus of the anal tube.

Superfamily **PATELLIOCRINACEA** Angelin, 1878
Family **PATELLIOCRINIDAE** Angelin, 1878

Diagnosis.—Patelliocrinaceans characterized by three basals, exceptionally fused together, in cup of variable shape. Interprimibrachials consisting of a single plate or several plates arranged in brachitaxes or tiers. Arms two or four per ray, uniserial, biserial, or consisting of compound brachials.

Included genera.—*Patelliocrinus* Angelin, 1878, L. Sil. (Llandovery)—U. Sil. (Wenlock); *Allocrinus* Wachsmuth and Springer *in* Miller, 1889, L. Sil. (late Llandovery)—U. Sil. (Ludlow); *Bolicrinus* Witzke and Strimple, 1981, L. Sil. (late Llandovery); *Boliviacrinus* McIntosh, 1988, L. Dev. (Emsian); *Briarocrinus* Angelin, 1878, U. Sil. (Wenlock); *Centriocrinus* Bather, 1899, M. Dev. (Eifelian); *Eopatelliocrinus* Brower, 1973, U. Ord. (Hirnantian); *Krinocrinus* Witzke and Strimple, 1981, L. Sil. (late Llandovery); *Kylixocrinus* Eckert, 1984, L. Sil. (early Llandovery); *Laurelocrinus* Springer, 1926, U. Sil. (Wenlock); *Macrostylocrinus* Hall, 1852, U. Ord. (Richmondian)—U. Sil. (Ludlow); *Thomasocrinus* Witzke and Strimple, 1981, L. Sil. (late Llandovery).

Remarks.—Statistical analysis suggests that the Patelliocrinidae originated from the Middle Ordovician crinoid *Pycnocrinus* (*Glyptocrinus*) *ornatus* (Brower, 1973). According to Brower, the first step in the glyptocrinid-patelliocrinid transition involved reduction in the number of basals from five to three. No documentation of this trend is known from the fossil record. Fewer basals may have been of adaptive advantage by strengthening the base of the cup against lateral shear (Brower, 1973).

Patelliocrinids underwent a dramatic evolutionary radiation in the Early Silurian. Witzke and Strimple (1981) considered this family to have given rise to the Prokopicrinidae, Hirneacrinidae, Hapalocrinidae, Platycrinitidae, Stelidiocrinidae, Clonocrinidae, Dolatocrinidae, Polypeltidae, Eucalyptocrinitidae, and Marsupiocrinidae. If true, *Pycnocrinus* would have indirectly given rise to more than 50 genera of camerate crinoids. However, the phylogenetic scheme presented by Witzke and Strimple (1981, p. 105) is almost certainly incorrect in part, because, as pointed out by Ausich (1985) and McIntosh (1988), it would involve fusion of five basals into three followed by reacquisition of five basals in the Stelidiocrinidae, and possibly others. Detailed phylogeny of these groups will remain a mattter of guesswork until intermediate taxa to substantiate linkage of families are found.

Another evolutionary trend in patelliocrinids was the adoption of biserial instead of uniserial arms. This improved food-gathering ability. The most striking trend in patelliocrinid evolution was reduction in numbers of plates in the cup. This was taken to an extreme in *Patelliocrinus* and *Centriocrinus,* genera that contain only one or two interprimibrachials in each interray. The functional significance of cup simplification in patelliocrinids and other camerate groups in the Early Silurian is unknown. It may have decreased problems of integration and coordination of ontogeny, partly through simplification of the aboral nerve network (Brower, 1973), but there is no evidence that crinoids had such "problems". Instead, heterochrony, specifically progenesis, may have been involved. Progenesis is typically associated with early maturation and reproduction (Gould, 1977). Rapid maturation and early reproduction may have aided survival of crinoids in stressed environments in the Late Ordovician and Early Silurian.

Genus **MACROSTYLOCRINUS** Hall, 1852

Type species.—*Macrostylocrinus ornatus* Hall, 1852, p. 204, pl. 46, figs. 4a–4g.

Diagnosis.—A patelliocrinid with conical to bowl-shaped cup and depressed to inflated interrays. Basals three, radials uninterrupted by primanal. Interrays consisting of several tiers of plates. CD interray wider than remaining interrays; median anitaxis poorly developed or absent. Primanal heptagonal or octagonal, followed by three to five plates in next tier. Column round, cirriferous in some species.

Macrostylocrinus sp.
Plate 1, figure 24

Description.—Crown small, height approximately 35 mm. Cup obconical, interrays inflated. Basals not observed, radials apparently largest plates in cup. Primanal large, heptagonal, supporting tier of three plates. Column short, slightly longer than crown, round, heteromorphic, cirriferous throughout, bearing cirri on expanded nodals at irregular intervals of 15 to 23 columnals. Thick epifacets, triangular in cross section, borne by priminternodals of proximal column. Holdfast small, discoidal.

Remarks.—The illustrated specimen possibly represents a new species, but the available material is too badly weathered to permit formal description.

Material and occurrence.—This species is represented by BMS E26329a and paratypes E26330a and E26330b from spoil heaps of the Wallington Member of the Reynales Formation, locality 6.

Superfamily **STIPATOCRINACEA** Eckert and Brett, 1987

Diagnosis.—Cup narrow, conical. Basal circlet consisting of pair of large basals and pair of smaller basals. Rays very narrow, elevated. Interrays undifferentiated, consisting of hundreds of small, irregular ossicles extended into narrow anal sac above CD interray. Arms ten, uniserial, pinnulate.

Family **STIPATOCRINIDAE** Eckert and Brett, 1987

Diagnosis.—Monotypic, as for superfamily.

Genus **STIPATOCRINUS** Eckert and Brett, 1987
Text-figure 11

Type species.—Stipatocrinus hulveri Eckert and Brett, 1987, p. 3, text-figures 3–8; pl. 1, figs. 1–21; pl. 2, figs. 1–12.

Diagnosis.—A genus of Stipatocrinidae with narrow, conical crown and depressed interrays. Ray series extremely narrow; T-shaped lateral projections of radials bridging proximal interrays. Primibrachials two, fixed secundibrachials four to six. Interrays undifferentiated, filled with hundreds of exceptionally small, irregular ossicles. Tegmen and narrow, excentrically situated anal sac consisting of small, irregular plates. Arms ten, uniserial, atomous. Column round, heteromorphic, tapering distally nearly to a point.

Remarks.—This remarkable species was thoroughly described and illustrated by Eckert and Brett (1987). It apparently represents an archaic lineage that persisted into the Early Silurian.

Types and occurrence.—Holotype specimen ROM 44310a and paratypes ROM 44309 and 44310b–44323 were collected from talus derived from the lowest meter of the Wallington Member of the Reynales Formation at locality 4. Recently, this interval has yielded additional specimens at locality 5 associated with *Pentamerus, Favosites,* and columnals of the new disparid crinoid genus *Haptocrinus.*

Order unknown

Camerate crinoid species A
Plate 3, figure 9

Description.—Cup conical with prominent, narrow median ridges on rays and anitaxis. Ray ridges dividing aborally near centers of radials, branches continuing to centers of basals, forming borders of triangular depressed areas. Junctions of ray ridges on basals and radials each with a prominent node. Interbrachials ornamented with short, irregular ridges and nodes. Cup apparently monocyclic in side view. Number of basals unknown. Radial circlet divided by CD interray basal and primanal. Primibrachials two in each ray, secundibrachials four in each half-ray, succeeded by two or three fixed tertibrachials. Large abaxial fixed pinnule borne by each second secundibrachial. Interbrachials difficult to discern; each interray containing several tiers of interprimibrachials. Intersecundibrachials and a few intertertibrachials also present. CD interray wider than other interrays. Primanal supporting median anitaxis flanked by interbrachials.

Arms twenty, four per ray. Proximal 3 mm of each arm uniserial, pinnulate. Remainder of arms unknown.

Column incomplete, round, heteromorphic, coiled distally, bearing thin, downcurved epifacets.

Remarks.—Without sectioning the base of the cup to see whether it is monocyclic or dicyclic this crinoid cannot be identified and, as only one specimen is known, this procedure was not attempted. A peculiarity of this crinoid is the presence of four fixed secundibrachials in each ray; this precludes assignment to *Compsocrinus* or *Ptychocrinus* Wachsmuth and Springer, 1885, crinoids it superficially resembles.

Occurrence.—BMS E26394e was collected from the Bear Creek Shale associated with *Compsocrinus relictus,* 25 cm below the Sterling Station Iron Ore, locality 9.

Measurements (in mm) of BMS E26394e.—Cup height = 10.1, crushed width = 14.5; incomplete column length = 75 mm, proximal diameter = 3.3, distal diameter = 3.3.

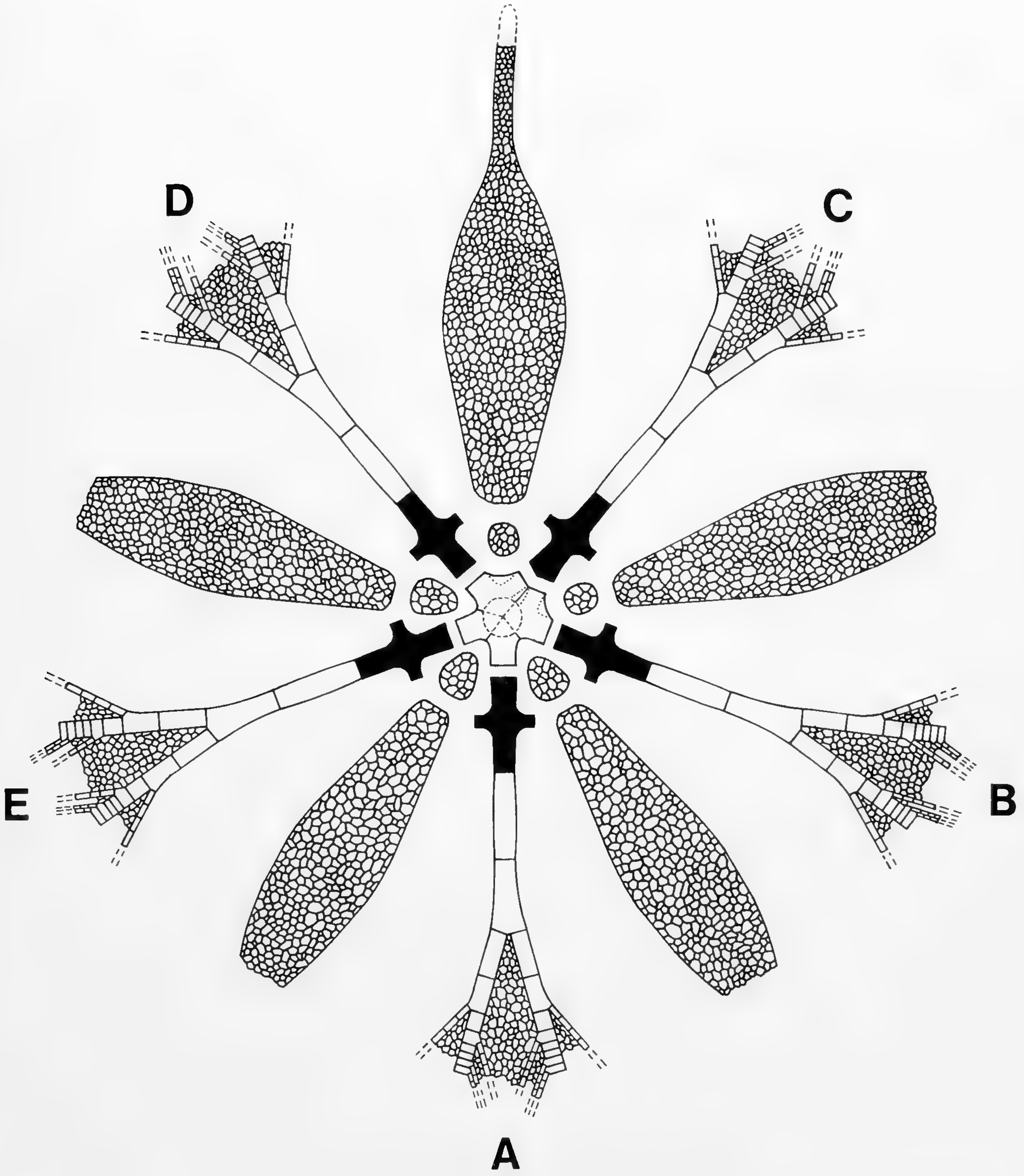
Subclass **DISPARIDA** Moore and Laudon, 1943

Superfamily **CALCEOCRINACEA** Meek and Worthen, 1869

Family **CALCEOCRINIDAE** Meek and Worthen, 1869

Diagnosis.—Crown recumbent, flattened and tending toward perfect bilateral symmetry in E ray through BC interray plane, articulating with column on subtriangular hinge consisting of one to four basals. B, C, and E ray radials compound, B and C ray superradials fused together in some instances. Axil arms ramulate or exceptionally pinnulate.

Included genera.—Calceocrinus Hall, 1852, M. Ord. (Blackriveran)—U. Sil. (Ludlow); *Anulocrinus* Ramsbottom, 1961, U. Ord. (Ashgillian); *Catatonocrinus* Brett, 1981, U. Sil. (Wenlock); *Charactocrinus* Brett, 1981, U. Sil. (Wenlock); *Chirocrinus* Angelin, 1878, U. Sil. (Wenlock); *Chiropinna* Moore, 1962, U. Sil. (Wenlock, Ludlow); *Cremacrinus* Ulrich, 1886, M. Ord. (Blackriveran)—U. Sil. (Ludlow); *Cunctocrinus* Kesling and Sigler, 1969, M. Dev. (Givetian); *Darraghcrinus* Jell, 1999, U. Sil. (Ludlow); *Deltacrinus* Ulrich, 1886, M. Dev. (Givetian); *Diaphorocrinus*



Text-figure 11.—*Stipatocrinus hulveri* Eckert and Brett. Expanded plate diagram taken from Eckert and Brett (1987). Radials black.

Eckert, 1984, L. Sil. (Llandovery); *Eohalysiocrinus* Prokop, 1970, L. Dev.; *Epihalysiocrinus* Arendt, 1965, L. Permian (Artinskian); *Espanocrinus* Webster, 1976, L. Dev. (Emsian); *Grypocrinus* Strimple, 1963, U. Sil. (Ludlow); *Halysiocrinus* Ulrich, 1886, M. Dev. (Givetian)—L. Miss. (Osagean); *Minicrinus* Prokop, 1970, L. Dev. (Emsian)—M. Dev. (Givetian); *Senariocrinus* Schmidt, 1934, L. Dev. (Emsian); *Stibarocrinus* Ausich, 1984, L. Sil. (Llandovery); *Thaerocrinus* n. gen., L. Sil. (Llandovery); *Trypherocrinus* Ausich, 1984, L. Sil. (Llandovery).

Remarks.—The family Calceocrinidae is among the most distinctive and specialized groups of disparid crinoids. Calceocrinids are presumed to have originated from a homocrinid ancestor (Moore, 1962), probably before the Middle Ordovician. They were apparently little affected by Late Ordovician extinction perhaps because of their unique lifestyle and eurytopic habit. Occurrence of *Diaphorocrinus* and at least two species of *Calceocrinus* in the Lower Silurian of Ontario (Eckert, 1984) suggests that renewed evolutionary radiation of calceocrinids began in the Early Llandovery (Rhuddanian), preceding diversification of many other groups of Silurian crinoids.

Genus **THAEROCRINUS,** new genus

Type species.—*Thaerocrinus crenatus* n. sp.

Diagnosis.—A genus of Calceocrinidae with three basals all taking part in column facet. E ray inferradial expanded and forked proximally, occupying most of hinge line, typically in narrow contact with E ray superradial. Subanal (fused B and C ray superradials) situated between trapezoidal B and C ray inferradials and A and D ray superradials. Arms dividing repeatedly with tendency toward isotomy. Column xenomorphic.

Remarks.—*Thaerocrinus* n. gen. appears to be closely related to the monotypic genus *Diaphorocrinus* Eckert, 1984 from the Lower Silurian Cabot Head Formation of southern Ontario. In *Diaphorocrinus,* however, only the two lateral basals take part in the stem facet and the main axil series is intercalated with non-axillary plates. *Diaphorocrinus* apparently evolved from *Calceocrinus* Hall, 1852 by fusion of the DE and EA interray basals and repeated division of ramules. *Thaerocrinus* may have evolved from *Diaphorocrinus* by bringing all basals into contact with the column facet, elimination of non-axillary plates in the main axil series, and broadening and shortening of the anal tube. Alternatively, *Thaerocrinus* could represent an independent offshoot of *Calceocrinus. Trypherocrinus* Ausich, 1984a from the Lower Silurian Brassfield Formation of Ohio is also characterized by a deviant style of repeatedly branching ramules, but this genus has discrete B and C ray superradials.

Moore (1962) emphasized what he considered to be a consistent arrangement of ramules in the Calceocrinidae. "The pattern of branching is remarkably constant, alpha-ramules being given off invariably on the abanal side of the arm, beta-ramules on the adanal side, and so on" (Moore, 1962, p. 36). This pattern can still be detected in *Diaphorocrinus* and *Trypherocrinus,* although it is modified by repeatedly branching ramules. *Thaerocrinus,* however, deviates significantly in that axil arms may display endotomy, in effect reversing the typical pattern in calceocrinids because distal ramules (gamma-ramules, delta-ramules, etc.) may face in either abanal or adanal directions. Apparently, unlike all other calceocrinids, bilateral endotomy was not restricted to the E ray of *Thaerocrinus.*

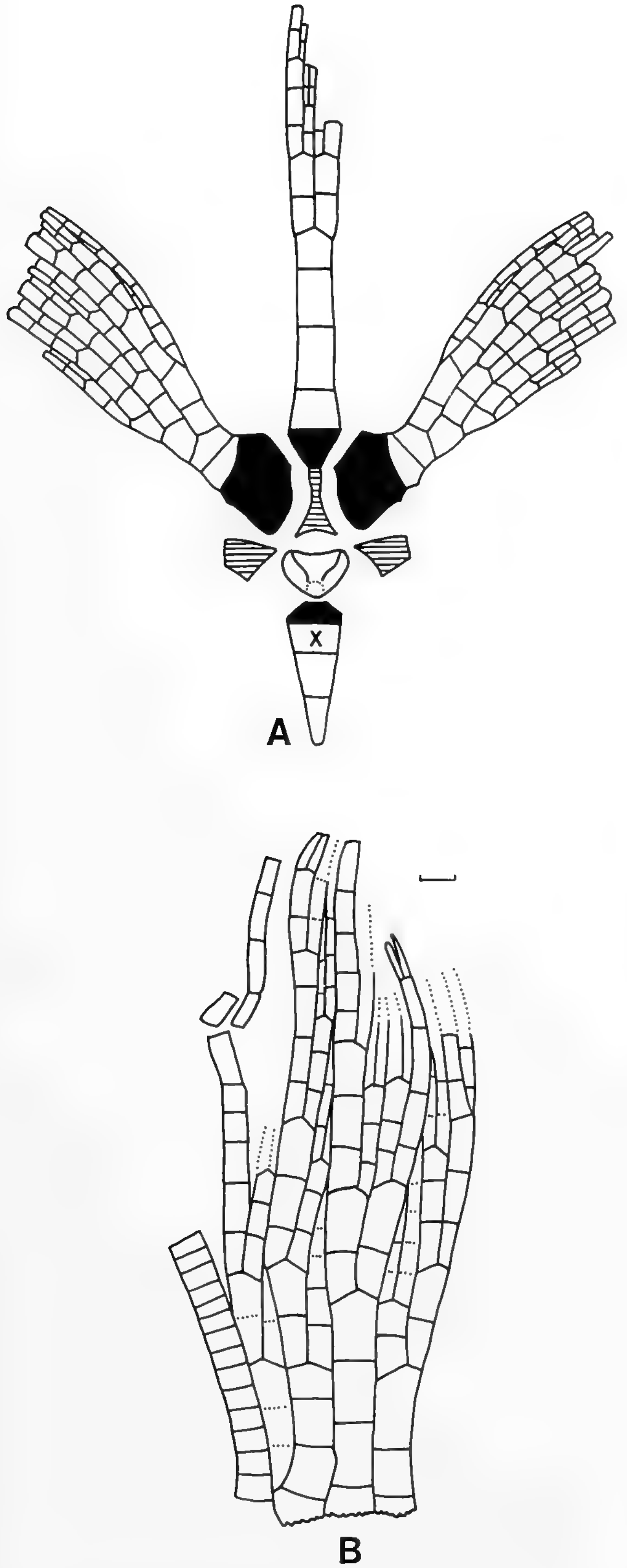
Throughout their evolutionary history, calceocrinids displayed a trend toward proliferation of axil arms and ramules. *Diaphorocrinus, Thaerocrinus,* and *Trypherocrinus* were unusual in that they had relatively few axil arms and repeatedly dividing ramules. *Trypherocrinus* is not closely related to *Diaphorocrinus* and *Thaerocrinus,* indicating that iterative evolution played a part in development of an arm branching style unique to these genera. This trend toward increased complexity of arms increased food-gathering efficiency and also may reflect niche partitioning.

Etymology of name.—*thaeros* Gr.) = hinge (refers to the basal hinge) + *krinon* (Gr.) = lily.

Thaerocrinus crenatus, new species
Plate 1, figures 5–8, 16–18, 21, 23;
Text-figures 12A, B

Diagnosis.—As for the genus.

Description.—Crown small to moderate in size (Table 3). Cup small, laterally compressed, plates smooth. Basal circlet subtriangular, wider than high (h/w = 0.4). Basals three, all taking part in stem facet. Median basal (fused DE and EA basals) triangular, wider than high (h/w = 0.5), occupying most of hinge line, sutures with AB and CD basals sinuous (Pl. 1, fig. 7). Lateral basals strongly rounded, with curved sides bordering inferradials. B and C ray inferradials trapezoidal, of similar size, separated medially by subanal. E ray inferradial variable in shape, expanded and forked proximally, occupying about 60% width of hinge, typically in narrow contact with neary triangular E ray superradial (Pl. 1, fig. 5). A and D ray radials approximately quadrangular with arcuate distal margins below axil series. Subanal six-sided, distal margin arcuate, wider than high (h/w = 0.5), situated immediately above basal circlet between B and C ray inferradials



Text-figures 12A, B.—*Thaerocrinus crenatus* n. gen. and sp., plate diagrams. A. Expanded plate diagram (radials and superradials black, inferradials horizontally ruled). B. Arms of BMS E26307. Note repeatedly dividing ramules and endotomy in second axil arm from right. Scale is 1 mm.

Table 3.—Measurements (in mm) of three specimens of *Thaerocrinus crenatus* n. gen. and sp.

	BMS E26305 (holotype)	BMS E26306a	BMS E26308x
Crown height	17.8	—	—
Cup height	4.1	4.9	4.1
Cup width	3.7	4.5	3.6
Bi R height	—	—	1.9
Bi R width	—	—	1.6
Ci R height	2.1	2.3	2.4
Ci R width	1.2	1.3	1.5
Ei R height	2.1	3.0	2.3
Ei R width	1.0	1.6	1.5
Es R height	0.9	1.2	1.1
Es R width	1.7	2.3	2.1
As R height	—	—	3.7
As R width	—	—	1.9
Ds R height	3.7	4.0	3.6
Ds R width	2.3	2.6	2.3
Subanal height	0.9	1.2	0.9
Subanal	—	—	2.2
Anal X height	0.5	1.2	1.3
Anal X width	—	—	2.2
X1 height	1.3	1.9	1.6
X1 width	—	—	1.6

and A and D ray superradials. Anal tube tapering rapidly distally, extending beyond main axil series, distal portion concealed by lateral arms. Anal X trapezoidal, distal width approximately one-half proximal width. X1 trapezoidal, subequal, succeeding anal plates elongate.

Axil arms four, distal arm represented by branched omega ramule. Main axil series borne by non-axillary, wide, quadrangular brachial. Proximal divisions of axil arms strongly heterotomous, distal divisions isotomous or heterotomous (Pl. 1, fig. 18; Text-fig. 12B). Axillary brachials include second alphabrachial, second betabrachial, second or third gammabrachial, and second to fourth deltabrachial. Structure of proximal ramules concealed by abutting axil arms; distal ramules dividing repeatedly on every third or fourth brachial. E ray arm dividing isotomously on fourth or fifth brachial and heterotomously on second secundibrachial and third tertibrachial.

Column xenomorphic, relatively long, exceeding three times height of crown (Pl. 1, fig. 17). Proximal column heteromorphic, nodals with gently rounded latera alternate with internodals. Medial and presumably distal column isomorphic. Columnals successively more elongate distally; h/w ratios ranging from 0.2 proximally to 0.6 distally. Holdfast unknown.

Types and occurrence.—*Thaerocrinus crenatus* is represented by six specimens; holotype BMS E26305, paratypes BMS E26306a–d, BMS E26307, and BMS

E26308 from the basal 25 cm of the Hickory Corners Member, Reynales Formation, localities 1 and 2.

Etymology of name.—*crenatus* (L.) = notched (refers to the notched base of the E ray inferradial).

Superfamily **MYELODACTYLACEA** Miller, 1883

Family **MYELODACTYLIDAE** Miller, 1883

Diagnosis.—Disparids with distinctive coiled and recurved column bearing two rows of cirri. Crown small, commonly concealed within coil. Compound ray, if present, in C ray only. Anal tube long, narrow. Arms isotomous or heterotomous, dividing several times.

Included genera.—*Myelodactylus* Hall, 1852, L. Sil. (Wenlock)—L. Dev. (Lochkovian); *Brachiocrinus* Hall, 1858, L. Dev. (Lochkovian); *Crinobrachiatus* Moore, 1962, L. Sil. (Wenlock); *Eomyelodactylus* Foerste, 1919, L. Sil. Llandovery); *Herpetocrinus* Salter, 1873, U. Sil. (Wenlock).

Genus **EOMYELODACTYLUS** Foerste, 1919

Macnamaratylus Bolton, 1970, p. 64.

Type species.—*Eomyelodactylus rotundatus* Foerste, 1919, p. 19, pl. 1, fig. 8; pl. 2, fig. 3.

Diagnosis.—A myelodactylid with pentameric, elliptical to subrectangular column. Three pentameres situated on outer margin of coil, two larger pentameres on inner side. Medial and distal sections of column bearing two rows of undivided cirri originating on A and C ray pentameres. Proximal cirrals fused laterally to column, projecting obliquely toward plane of coiling. Cup small, compound radial in C ray only. Higher divisions of arms heterotomous. Anal sac long, narrow, bearing median anitaxis.

Remarks.—*Eomyelodactylus* has been thoroughly reviewed and redescribed (Eckert, 1990). The pentameric, elliptical to subrectangular column and lateral fusion of proximal cirrals to cirrinodals are primitive myelodactylid characters. *Eomyelodactylus* gave rise to *Herpetocrinus* by partial fusion of pentameres and migration of cirral sockets into the plane of coiling.

For a review of the paleoecology of myelodactylids, see discussion of *Myelodactylus* in this report.

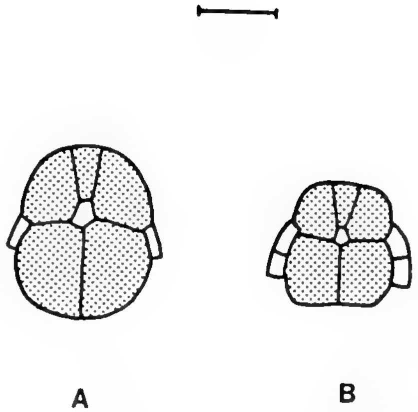
Eomyelodactylus sparteus Eckert, 1990

Plate 2, figures 1–5, 15, 22; Text-figure 13A

Eomyelodactylus sparteus Eckert, 1990, pp. 137–138, figs. 1.1, 2.2–2.4, 5.3–5.5, 5.8, 5.16, 5.19.

Diagnosis.—A large species of *Eomyelodactylus* characterized by an elliptical column and alternating, irregular placement of large and small cirri. Cirrals barrel-shaped with circular axial canal.

Types and occurrence.—The holotype (BMS E26309) is from the Reynales Formation, 35 cm above the base of the Hickory Corners Member at locality 1. Paratypes (columnals) E26405a–e, E26406, and E26407a–d are from 1.4 m above the base of this member, locality 2. Paratypes BMS E26310–E26314 and E26404 (columnals) are from the basal 30 cm of the Hickory Corners Member at locality.



Text-figure 13A, B.—*Eomyelodactylus*, diagrams of columnals. A. *E. sparteus*, BMS E26407a. B. *E. uniformis*, BMS E26409. Scale is 1 mm.

Eomyelodactylus uniformis Eckert, 1990

Plate 2, figures 18, 20; Text-figure 13B

Eomyelodactylus uniformis Eckert, 1990, pp. 138–140, figs. 2.6, 5.6, 5.15, 5.17, 5.18.

Diagnosis.—A species of *Eomyelodactylus* with rather uniform, closely spaced cirri (no nudinodals) in portions of medial column. Medial columnals roughly rectangular in cross section with rounded corners and flat inner surfaces. Columnals of proximal coil rounded on outer side, flat to slightly concave on inner margin.

Remarks.—*E. uniformis* is distinguished from *E. sparteus* by closely spaced, relatively uniform cirri and flat to concave rather than rounded inner margins of columnals (Text-fig. 13).

Types and occurrence.—The holotype, BMS E26409, is a section of medial column from talus of the Wallington Member of the Reynales Formation, locality 6. Paratype BMS E26315 is a small proximal coil from 1.4 m above the base of the Hickory Corners Member at locality 2.

Eomyelodactylus ?plumosus (Hall, 1852), new comb.

Glyptocrinus plumosus Hall 1852, p., pl. A41, figs. 3a, 3b; Text-fig. 1, herein

Diagnosis.—A species of *Eomyelodactylus* of small size, with rounded medial columnals bearing uniform, short cirri.

Remarks.—James Hall (1852, pl. A41) illustrated a series of crinoid remains to which he assigned the name *Glypocrinus plumosus.* No holotype was designated and it is clear from the illustration that this material actually constitutes portions of two unrelated taxa of crinoids, neither of which is related to *Glyptocrinus.* As was common practice in Hall's time, no holotype was designated and it is implicit that the specimens represent subequal co-types. Moreover, the original materal is apparently lost. A portion of Hall's figured material (pl. A41, figs. 3c–g) consists of roundly pentameric columnals and pluricolumnals. The distinctive morphology of these crinoids columns appears to match that of columns in *Haptocrinus calvatus* n. sp., illustrated herein, but we do not feel that Hall's species should be recognized on the basis of these columnals. The other two illustrations (Pl. A41 3a–b) clearly represent a portion of a cirral column of a myelodactylid crinoid. Hall mistakenly identified this pluricolumnal as a pinnulate crinoid arm. The feathery appearance of the specimen undoubtedly led to the species epithet "*plumosus*" and Hall's identification of the form as a camerate crinoid. Hence, this specimen most closely fits Hall's concept of "*Glyptocrinus plumosus*".

As noted above, myelodactylids are among the only crinoid genera diagnosed on the basis of the column alone. While it is clear from Hall's illustration that this specimen represents a myelodactylid (illustrated in inverted orientation), it is not definite that it falls in *Eomyelodactylus.* No pentameric portion of the column is visible. Its provenance, from Reynales Basin and its association with probable *Haptocrinus* columnals leaves little doubt that the specimen was derived from the Reynales Limestone. Thus, based on age and general appearance we tentatively assign the species to *Eomyelodactylus.* Its general appearance is similar to that of *E. uniformis* Eckert, differs in its small size and more rounded medial columnals. If the type material were found and prepared it might prove this specimen to be a juvenile of *E. uniformis.* In such case, the name *Eomyelodactylus plumosus* (Hall) would be a senior synonym of *E. uniformis* Eckert. At present, we choose to leave this form as a separate species, tentatively assigned to *Eomyelodactlus.*

Genus **MYELODACTYLUS** Hall, 1852

Type species.—*Myelodactylus convolutus* Hall, 1852, p. 192, p. 42, figs. 5a, b; 6a–h.

Diagnosis.—Column bilaterally symmetrical, bimeric, coiled and recurved proximally, exhibiting substantial variation in diameter. Proximal columnals round to elliptical in cross section, medial columnals typically crescentic, distal columnals round or pentagonal. Cirri in two rows, one on each side of coil, consisting of elongate, cylindrical cirrals. Crown five-rayed, compound radial in C ray only, superradial supporting narrow anitaxis on upper left shoulder and arm to right. Radial facets occupying entire width of radials. Arms isotomous or weakly heterotomous.

Remarks.—*M. linae* n. sp., described below, is the oldest known species referrable to *Myelodactylus* with confidence, extending range of this genus into the Early Silurian (late Llandovery). Ausich (1986c) described a columnal possibly belonging to *Myelodactylus* from the Brassfield Formation (middle or early late Llandovery).

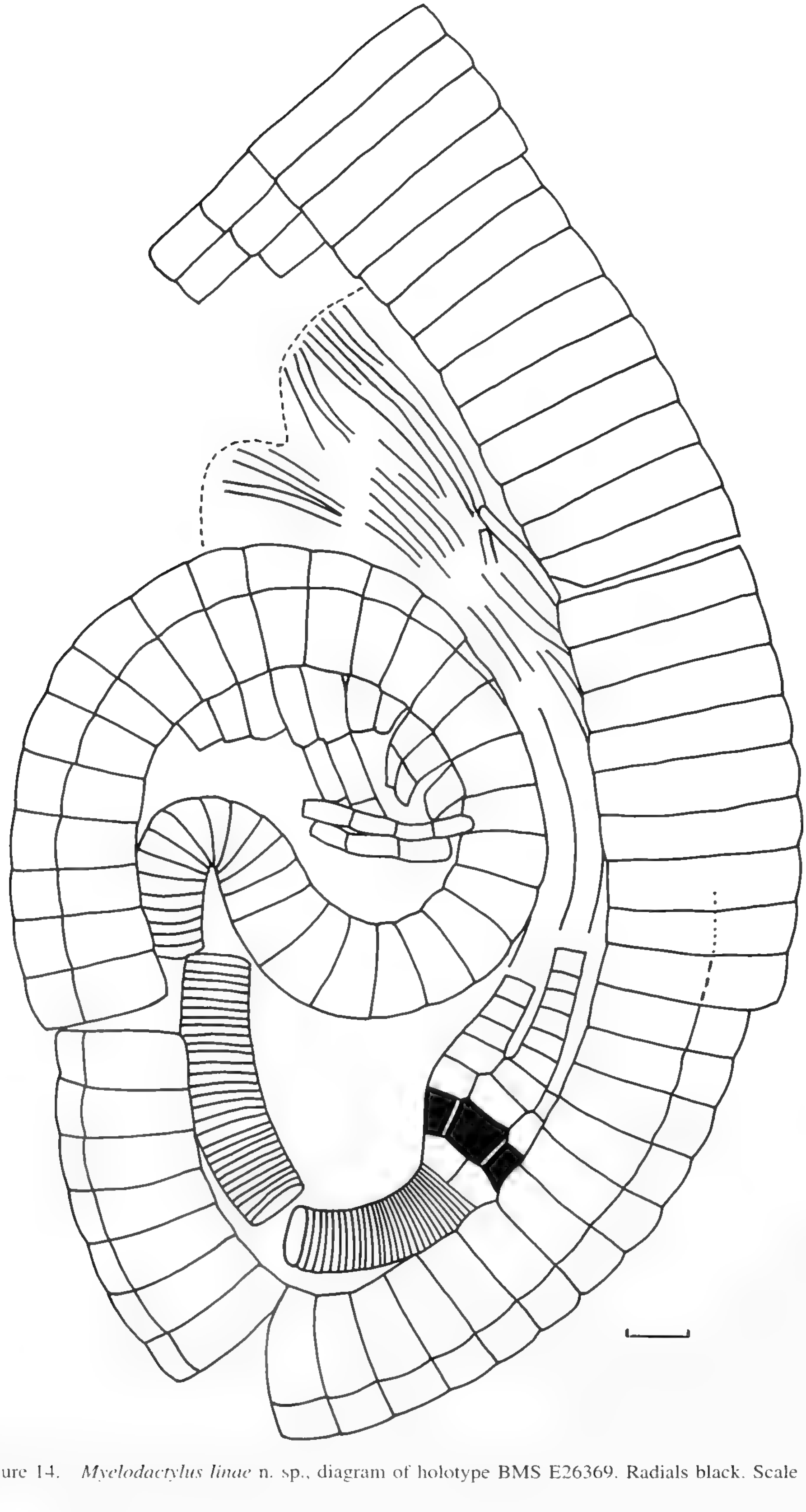
The functional morphology and paleoecology of myelodactylids has been extensively discussed. Bather (1893) believed that myelodactylid cirri were used for temporary attachment to the substrate and that these crinoids were able to move or swim. A pelagic mode of life has also been suggested (Kirk, 1911; Ehrenberg, 1923; Springer, 1926a; Moore, 1962). Brett (1984) and Eckert and Brett (1985) believed that that the stout, branching cirri of *Crinobrachiatus* Moore, 1962 were embedded in the substrate and served to prop up the column and crown in a semi-recumbent orientation. Donovan and Franzén-Bengtson (1988) postulated that an upright orientation for myelodactylids was impossible because cuneiform columnals indicated that the coil was permanent. Instead, they believed that *Myelodactylus* and *Herpetocrinus* Salter, 1873 were unattached, with the coiled column resting flat on its side on the substrate. This interpretation is unlikely; both *M. linae* n. sp. and *M. convolutus* had radix-type holdfasts with radially disposed rootlets that could only have been functional if the holdfast was embedded in the substrate in a conventional, upright orientation. *Herpetocrinus* and *Eomyelodactylus* do not differ greatly from *Myelodactylus,* suggesting that these crinoids also had a conventional upright orientation.

Myelodactylus linae, new species

Plate 6, figures 1–3, 5, Text-figure 14

Diagnosis.—A species of *Myelodactylus* characterized by small crown with two fixed primibrachials in lateral rays. Column exhibiting exceptional variation in diameter, longitudinal sutures poorly developed. Arms dividing isotomously several times.

Description.—Column xenomorphic, displaying exceptional variation in shape and diameter. Viewed perpendicular to plane of coiling, faint longitudinal suture visible on each side of column. Proximal column recurved, S-shaped, surrounded by one turn outer coil enclosing crown (Pl. 6, fig. 2). Section of column between cup and recurved junction elliptical in cross section, flattened in plane of coiling, consisting of short



Text-figure 14. *Myelodactylus linae* n. sp., diagram of holotype BMS E26369. Radials black. Scale is 1 mm.

columnals (maximum height 0.15 mm). Recurved, U-shaped junction and inner coil consisting of wedge-shaped columnals (height 0.4–0.6 mm). Width of column, viewed perpendicular to plane of coiling, increasing rapidly from 0.9 mm at recurved junction to 2 mm in outer coil. Columnals elliptical in cross section in inner portion of coil, rectangular with rounded corners in outer coil, and crescentic in medial section of column. Columnals from outer portion of coil bimeric with narrow, crescentic lumen; articular surfaces bearing coarse culminae on inner side of coil. Column between outer portion of coil and holdfast bearing two rows of cirri. Cirrinodals each possessing two cirri, cirral sockets situated in plane of coiling. Cirri essentially uniform, closely abutting laterally (Pl. 6, fig. 5). A complete or nearly complete cirrus from the outer coil of BMS E26369 is 10.2 mm long with a proximal width of 0.6 mm and a distal width of 0.2 mm. In coiled section of column, each cirrus elliptical in cross section proximally, cylindrical distally. Cirri in medial and distal sections of column tending to be cylindrical throughout. Cirrals elongate (length 0.5–1 mm, h/w = 2.5–3.3), straight-sided. Proximal cirrals tapering in width distally, distal cirrals uniform in width. Distal columnals near holdfast non-cirriferous, roughly cylindrical in cross section, concave inner margins absent. Holdfast consisting of approximately twelve columnals bearing short, unbranched cirri (Pl. 6, fig. 3). Distal ends of cirri expanded, cemented to fenestellid bryozoan zoarium.

Crown small, situated within proximal coil and completely concealed by cirri. Crown resting against concave inner margin of outer coil in downward, reversed orientation. Cup conical with slightly elliptical base (minor axis in plane of coiling), plates smooth, unornamented. Morphology of C ray unknown. Basal and radial circlets comprising approximately 23% and 27% of cup height, respectively. Basals five, pentagonal, wider than high. A, B, and E ray radials wider than high (h/w = 0.7), each with five major sides and one or two truncated upper corners. First two primibrachials in each lateral ray rectangular with one or more slightly truncated corners, wider than high (h/w = 0.6), incorporated into cup (Text-fig. 14). At least eight primibrachials apparently present in one ray. Arms dividing isotomously several times.

Types and occurrence.—Myelodactylus linae is represented by two specimens, holotype BMS E26369 and paratype BMS E26370, from shale bearing abundant bryozoans 1.1 m above the base of the Wolcott Formation, locality 8.

Remarks.—The holotype specimen of *Myelodactylus linae* n. sp. is a remarkably well preserved individual retaining the crown, most of the column, and holdfast. The crown of myelodactylids is commonly missing or is obscured by the cirri (see Eckert and Brett, 1985) and the crown is unknown in the type species of *Myelodactylus, M. convolutus* Hall, 1852. However, in the *M. linae* holotype specimen, distal portions of the arms could be seen protruding beyond the coiled section of the column. The specimen was then partially dissected by removing cirri on one side of the coil, revealing the crown.

Myelodactylus linae is similar to the younger type species *M. convolutus* Hall from the Rochester Shale (Silurian, Wenlock). The column of *M. convolutus* exhibits well developed longitudinal sutures only faintly developed in *M. linae,* and the distal-most portion of the column is pentameric with rootlets developed at pentamere junctions. More detailed comparison of these species must await description of the crown of *M. convolutus. M. keyserensis* Springer from the Keyser Formation (U. Silurian; Pridoli) has a rather narrow column with only moderate change in diameter and a large crown causing the cirri to bulge out to either side of the coil (see Springer, 1926a, pl. 6, fig. 3). Furthermore, the arms of *M. keyserensis* are slightly heterotomous and the proximal primibrachials are low and rectangular in contrast to the isotomous arms and elongate brachials of *M. linae. M. ammonis* Bather and *M. extensus* Springer, both from the Beech River Member of the Brownsport Formation (Silurian, Ludlow) of Tennessee, are peculiar species with cuneate columnals giving off cirri on alternate sides in an arrangement analogous to pinnules borne by uniserial brachials. This contrasts with the columnals of *M. linae* and *M. convolutus* which each give off paired cirri (two cirri borne by each columnal).

Measurements (in mm) of BMS E26369.—Crown height = 15.2; cup height = 2.2, width = 2.0; B height = 0.5, width = 0.7; R height = 0.6, width = 0.8; IBr1 height = 0.5, width = 0.8; IBr2 height = 0.5, width = 0.8; column length (uncoiled) = 115, length of coiled and recurved section = 55.

Etymology of name.—The species is named in honour of Bea-Yeh Lin, who discovered the remarkable holotype specimen.

Family **TORNATILICRINIDAE** Guensburg, 1984

Emended diagnosis.—Disparids with compound ray in C ray of narrow cup. Fixed primibrachials incorporated into lateral rays in some genera; minor differences may exist in relative proportions of radials. Arms dividing isotomously once above cup, branches bearing numerous endotomous ramules. Anal sac long, narrow, supported by median anitaxis. Column round to pentalobate, pentameric.

Included genera.—Tornatilicrinus Guensburg, 1984, M. Ord. (Blackriveran); *Pariocrinus* Eckert, 1984, L. Sil. (early Llandovery); *Haptocrinus* n. gen., L. Sil. (late middle Llandovery—late Llandovery).

Remarks.—Diagnosis of the Tornatilicrinidae is emended in order to accomodate *Haptocrinus* n. gen. and *Pariocrinus,* crinoids that closely resemble *Tornatilicrinus,* within this family. These three genera are each monotypic as presently understood. Guensburg (1984) considered *Tornatilicrinus* to possess biradials in all rays. However, he also acknowledged the possibility that only the C ray is biradial, noting that, in the lateral rays, the putative superradials could alternatively be considered to represent fixed brachials. *Tornatilicrinus* is herein interpreted to possess a single compound ray (C ray) and one fixed primibrachial in each lateral ray. This reinterpretation eliminates the subjectivity inherent in attempting to determine numbers of compound rays in crinoids with little difference in plate proportions between rays. If the *Treatise* system of classification were to be followed, *Tornatilicrinus, Pariocrinus,* and *Haptocrinus* n. gen would be subdivided among two or more families depending on how many lateral rays were interpreted to be compound in each of these genera. This system does not reflect phylogeny and is clearly artificial. Instead, recognition that variable numbers of primibrachials can be incorporated into the cups of primitive disparid crinoids provides a more natural, objective approach to classification, at least in the Tornatilicrinidae.

Pariocrinus was initially assigned to the Iocrinidae (Eckert, 1984a) in a monograph published about ten months earlier than that of Guensburg (1984). Therefore, the writer was initially unaware of *Tornatilicrinus.* With the advantage of hindsight, it is now apparent that *Pariocrinus* is at best distantly related to the Iocrinidae Moore and Laudon, 1943. The generic epithet of *Pariocrinus* is therefore misleading, implying a link to *Iocrinus,* but it will have to stand according to the rules of nomenclature.

The Tornatilicrinidae represent a lineage of low diversity but exceptional longevity, that persisted for at least 45 million years from the Middle Ordovician (early Blackriveran) to the Early Silurian (late Llandovery).

The revised diagnosis of this family places Tornatilicrinidae close to the Myelodactylidae. Members of the latter group also possess compound ray C ray radials, simple radials in the remaining rays, the X_1 plate supported on the left shoulder of the C ray superradial, and a pentameric column. The myelodactylids differ in their much more specialized, coiled and cirriferous columns, and in details of arm branching. Tornatilicrinids are both more ancient and less specialized members of the Myelodactylacea and may lie close to the ancestral stock of the myelodactylids.

Reinterpretation of plate homologies in Tornatilicrinidae suggests a more distant relationship of tornatilicrinids to homocrinaceans, such as *Ibexocrinus* Lane, 1970 than that inferred by Guensburg (1984). Despite superficial similarities, homocrinaceans possess divided radials in the B and E rays, as well as the C ray, and a different plane of bilateral symmetry than myelodactylaceans.

Genus **HAPTOCRINUS,** new genus

Type species.—*Haptocrinus calvatus* n. sp.

Diagnosis.—A genus of Tornatilicrinidae with small lekythosiform, cylindrical, or slightly barrel-shaped cup. Two primibrachials in each lateral ray fixed into cup. Arms dividing isotomously once, branches bearing endotomous ramules on every second or third brachial. Anal sac narrow, supported by median row of subequal to elongate plates. Column pentameric, dominantly pentalobate.

Remarks.—Hall's *Glyptocrinus plumosus* was based partly on columnals and an incomplete column of *Haptocrinus* (Text-fig. 1). However, as discussed above, *G. plumosus* was also based on columns of a myelodactylid and the species is tentatively reassigned to *Eomyelodactylus.*

Haptocrinus n. gen. differs from *Pariocrinus* only in having two fixed primibrachials in each lateral ray; *Pariocrinus* has none. *Haptocrinus* also resembles *Tornatilicrinus* but the left shoulder of the superradial of former genus is straight rather than deeply concave and an additional primibrachial is fixed in each lateral ray. Furthermore, *Tornatilicrinus* is peculiar in that intercalated short plates give the medial portion of the anal sac the appearance of a heteromorphic crinoid column.

Heterochrony probably played a key role in the evolution of *Pariocrinus* and *Haptocrinus.* Several features of *Pariocrinus,* including its very small cup, absence of fixed primibrachials, and isomorphic column are typically juvenile crinozoan features, suggesting that this genus was a progenetic derivative of a *Tornatilicrinus*-like ancestor. Small size, a trait commonly accompanying progenesis, allowed *Pariocrinus* to quickly achieve sexual maturity and thus survive in the stressful, siliciclastic-dominated paleoenvironment represented by the Power Glen Formation (Rhuddanian; Eckert, 1984). In contrast, *Haptocrinus calvatus* n. sp. was apparently a neotenic descendant of *Pariocrinus* that flourished in less stressful paleoenvironments represented by crinoidal grainstones and brachiopod packstones of the Reynales Formation. *Hap-*

tocrinus became much larger than *Pariocrinus* and sexual maturity probably occurred later in life.

Etymology of name.—*hapto* (Gr.) = to fasten or bind; a reference to the fixed primibrachials of this genus + *krinon* (Gr.) = lily.

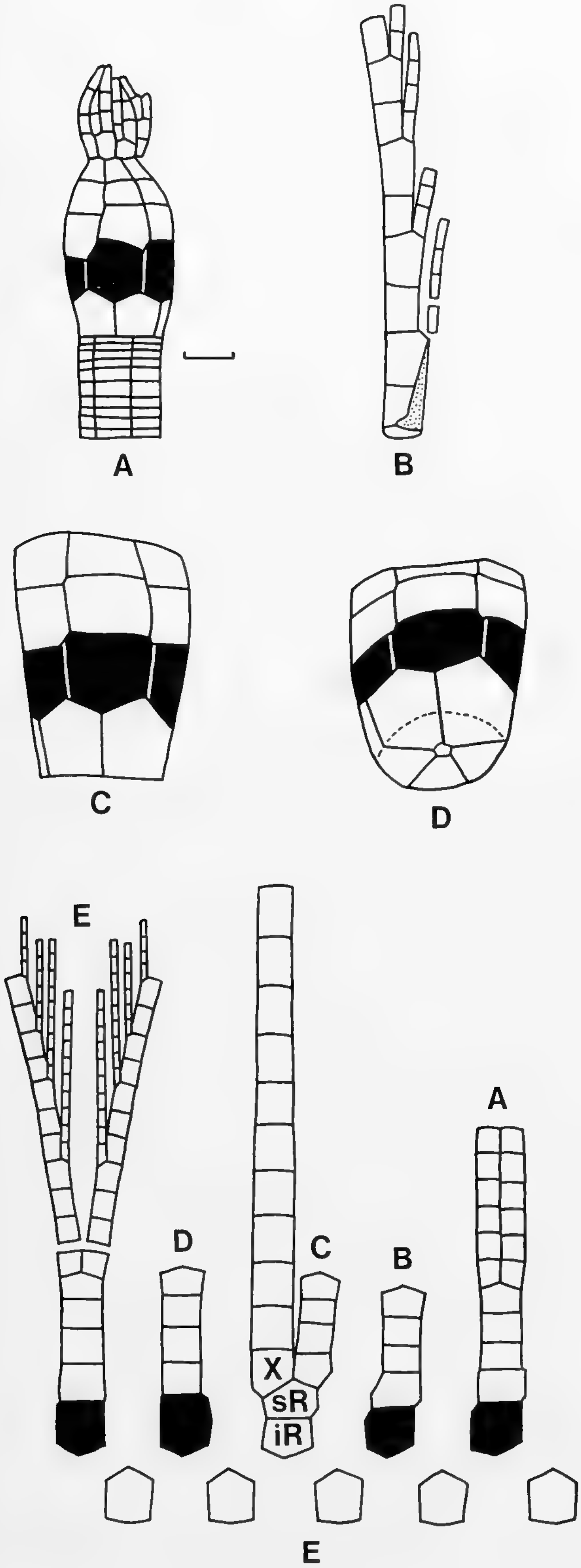
Haptocrinus calvatus, new species

Plate 1, figures 1, 2, 9–12, 19, 20, 22, 25; Plate 2, figures 10–14
Text-figures 15A–D

Glyptocrinus plumosus Hall, 1852, p. 180, pl. A 41, figs. 3a–g (partim).

Diagnosis.—As for the genus. Cup plates smooth, unornamented. Column long, xenomorphic, pentameric, strongly pentalobate throughout most of its length, tapering almost to a point distally.

Description.—Cup lekythosiform (high conical), cylindrical, or slightly barrel-shaped, higher than wide (h/w = 1.3–1.6), diameter equal to or slightly exceeding that of proximal column. Cup consisting of four circlets of smooth, unornamented plates (basals, radials, first and second primibrachials). Basal, radial, and combined primibrachial circlets each comprising approximatelyone-third of cup height (Table 4). Basals approximately pentagonal, h/w ratios variable (0.8–1.2), lower margins extending obliquely downward toward pentamere junctions. Basals greatly thickened proximally; diameter of cicatrix approximately 15% that of base of cup (Text-fig. 15D). C ray radial compound, remaining radials undivided. A, B, and E ray radials approximately pentagonal, wider than high to slightly higher than wide (h/w = 0.8–1.1); height to distal margins not varying more than 10% between rays, corners higher than distal margins of adjoining radials truncated. B and D ray radials six-sided, subequal (h/w = 0.8–1.1), constricting slightly next to C ray superradial. C ray radial divided equally into inferradial and superradial. Inferradial situated below truncated distal corners of B and D ray radials. Inferradial five-sided, wider than high (h/w = 0.8–0.9), contracting slightly in width distally. Superradial six-sided, wider than inferradial (h/w = 0.6–0.7), expand-



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Text-figures 15A–E.—*Haptocrinus calvatus* n. gen. and sp. diagrams. A. Crown of BMS E26332a with regenerated arms. B. Partial arm with incomplete ramules on every other brachial, BMS E26436a. C. Cup of BMS E26331 centered on A ray. D. Oblique view of above illustrating the remarkably thick basal plates. E. Expanded plate diagram. A ray arm is depicted in natural configuration, concealing ramules. Left and right branches of E ray arm are rotated 90 degrees counterclockwise and clockwise, respectively, in order to illustrate ramules. Undivided radials black, ramule groove stippled. Scale for figures A–D is 1 mm.

Table 4.—Measurements (in mm) of five specimens of *Haptocrinus calvatus* n. gen. and sp.

	BMS E26339 (holotype)	BMS E26317	BMS E26318	BMS E26323	BMS E26331
Cup height	5.0	3.0	3.6	4.6	5.6
Cup width	3.9	2.1	2.3	3.1	4.2
AB B height	1.6	0.7	1.2	—	1.6
AB B width	—	—	—	—	1.4
BC B height	—	—	1.1	1.3	1.4
BC B width	—	—	1.2	1.4	—
CD B height	1.7	—	1.1	1.5	—
CD B width	—	—	—	1.3	—
DE B height	1.7	0.0	—	-	—
DE B width	1.6	—	—	—	—
EA B height	1.7	0.9	—	—	1.6
EA B width	1.4	1.1	—	—	1.6
A R height	1.9	0.8	—	—	1.6
A R width	1.9	1.1	—	—	1.7
B R height	—	0.8	1.3	1.5	1.7
B R width	—	—	1.2	—	—
C iR height	—	—	0.9	1.3	—
C iR width	—	—	1.2	1.5	—
C sR height	—	—	1.7	2.0	—
D R height	1.8	0.9	1.3	1.6	—
D R width	2.0	—	—	—	
E R height	1.6	0.9	—	—	1.7
E R width	1.5	1.1	—	—	—
A IBr1 height	1.4	0.7	—	—	1.2
A IBr1 width	—	1.0	—	—	1.7
B IBr1 height	—	0.6	0.8	1.1	1.4
B IBr1 width	—	—	1.0	—	1.2
C IBr1 height	—	—	1.1	0.7	—
C IBr1 width	—	—	1.0	1.1	—
D IBr1 height	1.2	0.6	0.7	0.6	—
D IBr1 width	1.5			–	—
E IBr1 height	1.1	0.7	—	—	1.1
E IBr1 width	1.5	1.0	—	—	—
A IBr2 height	1.3	0.7	—	—	1.5
A IBr2 width	—	0.9	—	—	1.5
B IBr2 height	—	0.7	0.9	0.9	1.7
B IBr2 width	—	—	0.8	—	1.4
D IBr2 height	1.0	—	0.7	—	—
D IBr2 width	1.3	–			—
E IBr2 height	1.0	0.8	—	—	1.6
E IBr2 width	1.5	0.9	—		—
Anal X height	—	—	1.5	1.2	—
Anal X width	—		1.2	1.1	

ing distally, extending upward into first primibrachial circlet. Superradial shoulders asymmetric; left shoulder longer, more acutely sloping than right shoulder. First primibrachial of C ray pentagonal, remaining fixed primibrachials approximately rectangular, wider than high to slightly elongate (h/w = 0.6–1.2); B and C ray fixed primibrachials narrower than those of other rays. Fixed primibrachial circlets slightly constricted, leaving narrow opening for tegmen. Second primibrachials rounded in transverse cross section, top of cup slightly pentalobate in adoral view.

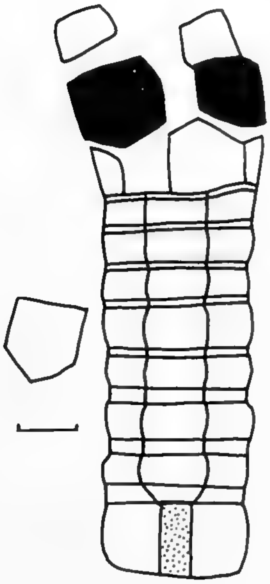
Arms five, apparently long, dividing isotomously on fourth or fifth primibrachial, giving rise to ramulate branches (Pl. 1, fig. 25). Axillary primibrachials pentagonal, expanding slightly in width distally, remaining primibrachials rectangular, wider than high (h/w = 1.3–2.2). Proximal secundibrachials subequal, higher secundibrachials elongate (h/w = 1.2–1.5). Endotomous ramules borne by every third secundibrachial proximally, every other secundibrachial distally. Ramules incompletely known, narrow (proximal width averaging 0.5 mm), consisting of elongate brachials (h/w = 1.2–1.4). Proximal portions of ramules impressed into grooves on ventral sides of arms.

Anal sac long, narrow, represented by anitaxis of subequal to moderately elongate plates (h/w = 0.9–1.4) with wide ventral groove (Pl. 1, fig. 22).

Column pentameric, xenomorphic, long, substantially exceeding 22 cm in length (Pl. 1, fig. 1). Proximal section heteromorphic, round, consisting of alternating thick and thin columnals of equal diameter. Maximum observed diameter of column 3.6 mm in heteromorphic, pentalobate medial section; each noditaxis consisting of a relatively thick (height 1.2–1.9 mm) biconcave nodal with rounded latera and a thin internodal. Distal section of column round, isomorphic, tapering nearly to a point (diameter at incomplete distal end 0.7 mm in BMS E26334), columnals becoming successively more elongate distally. Lumen small, pentagonal, angles of axial canal alternating with pentameres.

Remarks.—Crowns of *Haptocrinus calvatus* are apparently quite rare; not a single complete example is known despite careful search. Partial arms are preserved in 3 of 14 specimens (BMS E26320, E26329a, E26332a). The remainder consist of cups commonly with attached partial columns. In specimens without arms the cup tends to be constricted distally, as if to protect the tegmen. The typical absence of preserved arms suggests that they may have been autotomized during periods of stress that commonly preceeded death and burial. If the situation was not lethal the arms could be regenerated (BMS E26332a, Pl. 1, fig. 11; Text-fig. 15A).

The paleoecology of *H. calvatus* is partly discussed earlier in this study. Several aspects of the functional morphology of this crinoid allowed it to thrive in environments marginal for other crinoids. *Haptocrinus* was not a particularly robust crinoid but it possessed the ability to tightly close the arms into a narrow cylinder that protected the delicate ramules, much as in the Ordovician crinoid *Ectenocrinus* S. A. Miller, 1889. This was possible in *Haptocrinus* because the proximal ramules fit into deep slots in the arms. Even if the arms were torn off or autotomized, they could



Text-figure 16.—*Haptocrinus* sp., plate diagram of fragmentary individual (BMS E26371). Radials black. Scale is 1 mm.

be regenerated. During the regenerative phase, *Haptocrinus* may have perhaps been able to absorb nutrients directly through its long column.

The shoals that were favored by *Haptocrinus* were probably characterized by shifting, unstable substrates consisting mostly of *Haptocrinus* columnals. Crinoids with primary, rhizoid holdfasts were generally rare in such conditions (Brett, 1984). The column of *Haptocrinus calvatus* tapers distally to less than 1 mm in diameter; a rhizoid or encrusting holdfast is apparently absent but the actual mode of attachment is unknown (Pl. 1, fig. 20).

Types and occurrence.—The holotype, BMS E26329b, and paratypes BMSE26331–E26334, and E26346 are from the Wallington Member of the Reynales Formation, locality 6. Paratype BMS E26316 was collected 30 cm above the base of the Hickory Corners Member at locality 1. Paratype BMS E26319 is from 42 cm above the base of the Hickory Corners Member at locality 2 and paratypes BMS E26317, E26318, E26320, and E26321 are from talus of this member at locality. Paratypes BMS E26322–26324 are from the Hickory Corners Member, locality 3.

Etymology.—*calvatus* (L.) = bald; referring to the fact that arms are rarely preserved in this species.

Haptocrinus sp.

Text-figure 16; Plate 6, figure 18

Description.—The only specimen, BMS E26371, consists of a fragmentary cup and short section of the column. Basals five, pentagonal, wider than high. Two radials visible, pentagonal, wider than high, facets occupying full width of radials. First primibrachials trapezoidal, tapering slightly in width distally. Proximal 7 mm of column slightly pentalobate in cross section, heteromorphic, pentameric.

Remarks.—The Wolcott Limestone abounds in columnals and incomplete columns resembling those of *Haptocrinus calvatus* from the Reynales Limestone except that they are typically larger and more robust. Unfortunately, only a single incomplete cup of the Wolcott form was discovered, indicating persistence of the *Haptocrinus* lineage into the late Landovery.

Occurrence.—Wolcott Limestone, 1.2 m above base, locality 8.

Subclass **CLADIDA** Moore and Laudon, 1943

Order **CYATHOCRINIDA** Bather, 1899

Superfamily **CYATHOCRINITACEA** Bassler, 1938

Family **EUSPIROCRINIDAE** Bather, 1890

Emended diagnosis.—Cyathocrinitaceans with large conical to bowl-shaped cup and five basals. Radial facets wide, declivate, horseshoe-shaped with deeply notched, V-shaped ventral groove; transverse ridge absent or weakly developed. Three to six anal plates in cup. Radianal pentagonal, situated obliquely below C ray radial. Anal sac large, without pores. Orals commonly large. Arms isotomous or weakly heterotomous, outstretched or coiled distally.

Included genera.—*Euspirocrinus* Angelin, 1878, L. Sil. (Llandovery)—U. Sil. (Wenlock); *Eoparisocrinus* Ausich, 1986, M. Ord. (Caradocian)—U. Sil. (Wenlock); *Monaldicrinus* Jell, 1999, U. Sil. (Ludlow); *Vasocrinus* Lyon, 1857, L. Dev. (Emsian)—M. Dev. (Givetian).

Remarks.—The Euspirocrinidae is a broadly defined, synthetic family in need of revision. The emended diagnosis herein reflects removal of three genera assigned to Euspirocrinidae in the *Treatise*, in accordance with information provided by George C. McIntosh (personal communication, 1988). *Ampheristocrinus* Hall, 1879 is a dendrocrinid with three infrabasals. *Caelocrinus* Xu, 1962, is poorly known genus of uncertain affinities. The anal sac of *Parisocrinus* Wachsmuth and Springer, 1880 is perforated with pores.

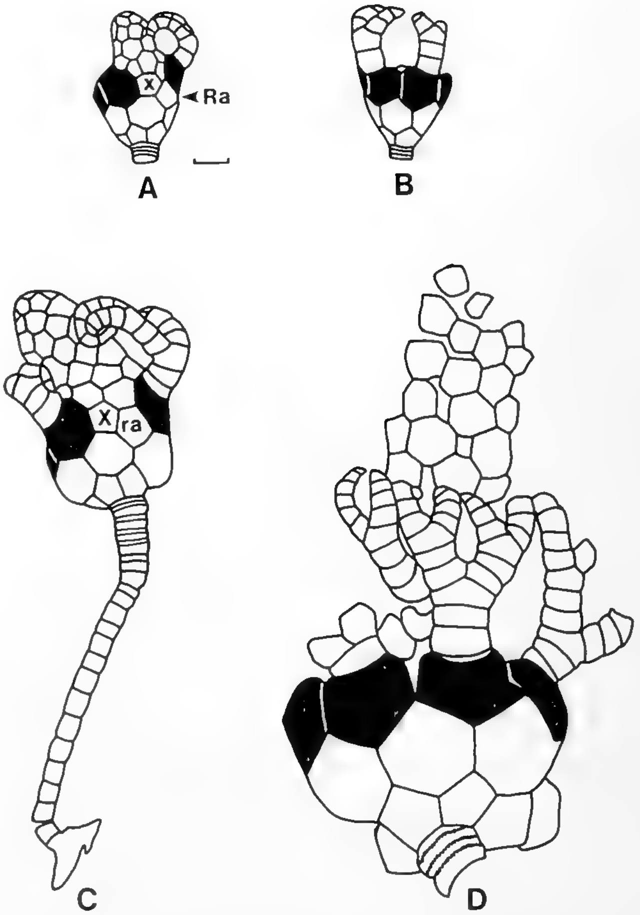
Genus **EUSPIROCRINUS** Angelin, 1878

Type species.—*Euspirocrinus spiralis* Angelin, 1878, p. 24, pl. 4, figs. 7 a–e.

Diagnosis.—A genus of Euspirocrinidae with medium conical to obconical cup. Radial facets wide, declivate, without transverse ridge. Three or four anal plates in cup. Radianal pentagonal, situated obliquely below C ray radial. Arms isotomous to slightly heterotomous, commonly coiled distally. Orals five, large. Anal sac plates subequal polygons. Column round, in part pentameric.

Remarks.—*Euspirocrinus* is closely related to *Eoparisocrinus.* According to Ausich (1986c), *Euspirocrinus* is distinguished from *Eoparisocrinus* by a low to medium bowl-shaped cup, a CD interray with fewer plates, and slender, incurved arms. However, some specimens of *Euspirocrinus wolcottense* n. sp. have a conical cup as in *Eoparisocrinus.* Furthermore, the CD interray of *Eoparisocrinus mulletensis* (Haugh, 1979) from the Upper Ordovician Georgian Bay Formation of Ontario has three anal plates in the cup as in *E. spiralis* and most specimens of *E. wolcottense* n. sp. These similarities indicate that only differences in radial facets and the arms distinguish *Euspirocrinus* from *Eoparisocrinus.* The radial facets and brachials of *Euspirocrinus* are wider than those of *Eoparisocrinus,* fewer brachials occur per taxis, and the arms are commonly coiled distally rather than stretched out.

The ability of *Euspirocrinus* to tightly coil the arms was unique among Silurian cladids and is reminiscent of the distally coiled arms commonly seen in flexible crinoids. Acquisition of this characteristic suggests a shift in utilization of trophic resources from passive capture of small food particles in *Eoparisocrinus* to active, raptorial entrapment of larger prey within a chamber created by coiling of arms. Then the prey could be gradually broken down and digested, as is postulated to have occurred in many lineages of flexible crinoids (McIntosh, 1982). In *Euspirocrinus,* this specialization was associated with invasion of higher energy environments.



Text-figures 17A–D.—*Euspirocrinus wolcottense* n. sp., diagrams of partial growth series. A. CD interray of BMS E26364. B. Anterior view of same with B ray arm to left. C. CD interray of BMS E26361 with complete column and holdfast. D. Anterior view of BMS E26362. Radials black. Scale for all figures is 2 mm.

Euspirocrinus wolcottense, new species
Plate 6, figures 4, 6–17, 19, 20, Plate 7, figure 17
Text-figures 17A–D

Diagnosis.—A species of *Euspirocrinus* with three or rarely four plates in CD interray and two or three primibrachials. Cup ornamented with ridges and pustules. Distal arms commonly slightly heterotomous with weakly developed endotomy. Anal sac nodose distally. Column pentameric distally.

Description.—Cup conical to obconical, height and width about equal (Table 5). Small cups smooth; low ridges radiating from smooth centers of plates to plate corners and margins in larger individuals (Pl. 6, fig. 7). Ridges straight, irregular, or broken up into a series of coarse pustules. Lower portions of infrabasals in some instances possessing a series of fine longitudinal ridges extending onto proximal column (Pl. 6, fig. 20). Infrabasal, basal, and radial circlets comprising approximately 25%, 40%, and 35% of cup height, respectively. Infrabasals five, pentagonal, subequal (h/w = 0.9–1.1). Basals five, slightly wider than high to higher than wide (h/w = 0.9–1.2). C and D ray basals heptagonal, remaining basals hexagonal. Radianal pentagonal, height equal to or slightly exceeding width (h/w = 1.0–1.1), situated obliquely below and to the left of C ray radial. Radials roughly pentagonal, subequal (h/w = 0.9–1.1), upper corners truncated for reception of large orals. Radial facets crescentic, wide, averaging 75% of radial width, strongly declivate, slightly excavated. Transverse ridge absent, crenulae situated adjacent to lower margin of each facet. Anal X pentagonal or hexagonal, height greater than width (h/w = 1.1–1.4), supporting two or three anal plates in cup.

Orals five, large, occupying most of tegmen (Pl. 6, fig. 16). Ambulacrals small, irregular polygons.

Arms typically tightly coiled distally, causing them to appear deceptively short (equal to cup height); actual length of fully extended arms approximately three times height of cup. Brachials less than 3.2 times wider

Table 5.—Measurements (in mm) of five specimens of *Euspirocrinus wolcottense* n. sp.

	BMS E26362 (holotype)	BMS E26360	BMS E26361	BMS E26363	BMS E26365
Crown height	28.0	23.7	11.7	—	51.2
Cup height	8.6	11.5	6.0	10.6	17.0
Cup width	8.4*	14.1*	6.4*	11.0*	17.0*
A IB height	3.1	—	—	2.9	4.0
A IB width	3.2	—	—	2.8	—
B IB height	—	—	—	3.0	—
B IB width	—	—	—	3.0	—
C IB height	—	—	1.5	2.5	—
C IB width	—	—	1.4	2.6	—
D IB height	3.1	2.4	1.5	2.5	4.1
D IB width	—	2.2	—	2.4	4.8
E IB height	3.0	—	—	2.7	4.1
E IB width	3.1	—	—	4.6	—
AB B width	4.6	—	—	4.3	—
BC B height	—	—	2.5	4.5	—
BC B width	—	—	2.5	5.0	—
CD B height	—	3.7	2.2	4.5	6.0
CD B width	—	—	2.5	4.7	—
DE B height	4.6	4.4	2.3	4.7	6.9
DE B width	4.5	4.4	—	3.8	7.3
EA B height	4.6	—	—	4.5	6.1
EA B width	5.0	3.4	—	4.8	—
A R height	4.5	4.6	—	4.4	—
A R width	4.6	—	—	4.5	—
B R height	4.1	—	2.9	5.0	—
B R width	—	—	2.6	4.5	—
C R height	—	—	3.1	4.2	—
C R width	—	—	—	4.2	—
D R height	—	4.7	3.0	4.8	7.6
D R width	—	5.3	3.0	4.8	7.5
E R height	4.3	4.7	—	4.7	7.3
E R width	4.8	4.9	—	4.8	7.0
RA height	—	—	2.0	3.5	4.8
RA width	—	—	1.8	3.4	—
Anal X height	—	3.1	1.5	3.5	3.8
Anal X width	—	3.0	1.6	2.5	3.7
Column length	—	40.0	18.3	—	110.0
Proximal diameter	—	2.9	1.6	—	3.9
Distal diameter	—	2.5	0.9	—	2.8

* Cup crushed (width greater than diameter).

than high, smooth or ornamented with slight median keel and fine longitudinal ridges. Arms dividing isotomously on second or third primibrachials. Higher divisions commonly slightly heterotomous with weakly developed endotomy; outer main branches forming ill-defined rami with successive divisions typically on every third brachial. Inner branches dividing less frequently, typically at intervals of four to fifteen or more brachials.

Anal sac slender, distally nodose, height equal to height of cup in small specimens, up to two and one-half times height of cup in large individuals (Pl. 6, fig. 17). Anal sac comprised of polygonal, subequal plates arranged in ill-defined spiral rows, proximal plates arcuate in cross section with depressed sutures.

Column round, xenomorphic, length exceedingly variable (one-half to two and one-quarter times crown height). Proximal and medial noditaxes complex, typical proximal formula N, 3IN, 2IN, 3IN, 1IN, 3IN, 2IN, 3IN. Latera of nodals and larger internodals rounded. Distal section of column pentameric, isomorphic or heteromorphic (noditaxis formula N, IN or more complex). Holdfast discoidal, supplemented by stout, branched radicles in large individuals. Columnals wider than high (h/w = 0.1–0.4) except in the smallest individuals, where they are commonly elongate. Lumen circular.

Remarks.—In addition to *E. wolcottense* n. sp., *Euspirocrinus* is represented by the type species *E. spiralis* Angelin, 1878 from the Wenlock of Gotland, *E. heliktos* Ausich, 1986c from the Lower Silurian Brassfield Formation of Ohio, and *E. cirratus* Strimple, 1963 from the Henryhouse Formation (Silurian, Ludlow) of Oklahoma. Of these species, *E. wolcottense* is most closely allied with *E. heliktos,* from which it is distinguished by three anal plates fully incorporated into the cup (X1 and right tube plate of *E. heliktos* extend above radial facets), absence of brachial keels or nodes, third primibrachial commonly axillary (rare in *E. heliktos*), and a more strongly heteromorphic column with well-defined nodals. The cup of *E. spiralis* has smooth rather than sculptured plates, the anal sac is more slender and contains fewer plates around its circumference, and the column is pentameric throughout most of its length. *E. cirratus* is inferred to possess three infrabasals, according to Strimple (1963), suggesting that the single known specimen of this species is abnormal or does not belong in *Euspirocrinus. E. cirratus* is also characterized by unornamented cup plates and lobed arm bases.

Types and occurrence.—Thirteen specimens of *Euspirocrinus wolcottense* n. sp. are represented by holotype BMS E26356a and paratypes BMS E26336b, E26347, and E26357–E26365. They are all from 1.0–1.1 m above the base of the Wolcott Formation, locality 8.

Etymology of name.—The species is named after its occurrence in the Wolcott Limestone.

Order **DENDROCRININA** Bather, 1899

Superfamily **DENDROCRINACEA** Wachsmuth and Springer, 1886

Family **DENDROCRINIDAE** Wachsmuth and Springer, 1886

Diagnosis.—Dendrocrinaceans with high conical, cup lacking radial ridges on plates, and large exsert infrabasals. Radial facets variable in width, declivate, arcuate, transverse ridge weakly developed or absent. Two to several anal plates in cup. Radianal pentagonal or exceptionally quadrangular, situated directly below C ray radial or obliquely to its left. Anal sac commonly large. Arms isotomous or heterotomous.

Included genera.—Dendrocrinus Hall, 1852, M. Ord. (Caradocian)—U. Sil. (Ludlow); *Grenprisia* Moore, 1962, M. Ord. (Caradocian).

Remarks.—George C. McIntosh (personal communication, 1988) is thoroughly reviewing the Dendrocrinidae and the entire order Dendrocrinida. Several genera were incorrectly assigned to the Dendrocrinidae in the Treatise, including *Atractocrinus* Kirk, 1948 and *Esthonocrinus* Jaekel, 1918. *Alsopocrinus* Tansey, 1924 is actually the flexible crinoid *Lecanocrinus* (McIntosh, 1981). *Bactrocrinites* Schnur, 1849 is a thalamocrinid (McIntosh and Brett, 1988). The taxonomic affinities of *Parisangulocrinus* Schmidt, 1934 are uncertain because sutures are obscured in the pyritized type material.

Recently, Jell (1999), following the lead of McIntosh, modified the definition of Dendrocrinidae by excluding certain forms with cup plates ornamented by low radiating ridges and inflated anal sacs of small, plicate plates. The latter were assigned to the new family Plicodendrocrinidae and include forms, such as "*Dendrocrinus*" *casei* Meek, 1871, which was reassigned to *Plicodendrocrinus* by Brower (1995), and two new genera from the Ludlow Series of Central Victoria, Australia. However, the species described below clearly belong to *Dendrocrinus* and Dendrocrinidae *sensu stricto.*

Genus **DENDROCRINUS** Hall, 1852

Quinquecaudex Brower and Veinus, 1982

Type species.—Dendrocrinus longidactylus Hall, 1852, p. 193, pl. 43, figs. 1a-k.

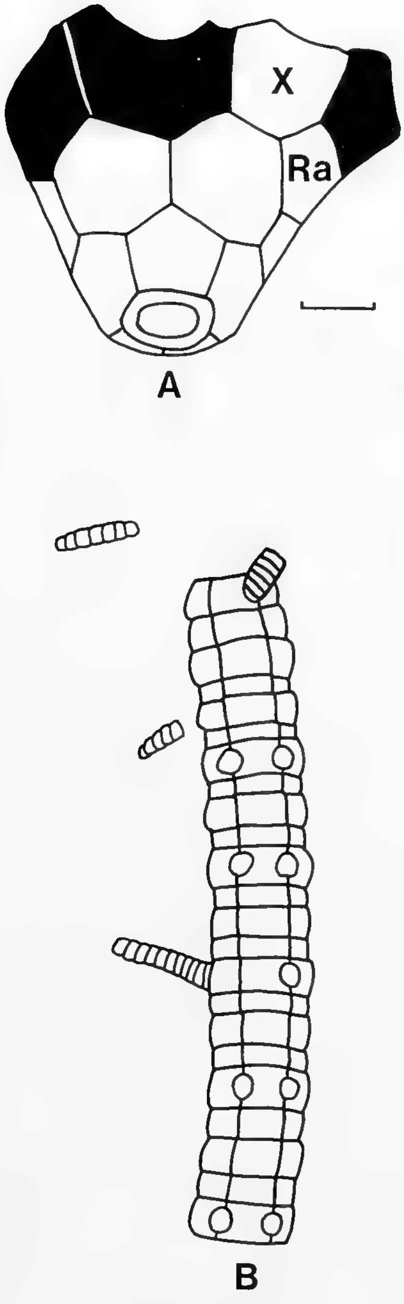
Diagnosis.—A genus of Dendrocrinidae with high conical cup and five large infrabasals. Radial facets narrow to medium width, arcuate, declivate, with transverse ridge absent or weakly deined. Radianal typically pentagonal, situated directly below C ray radial or in inferradial position. Anal sac large, composed of vertical rows of plicate plates. Arms isotomous or weakly heterotomous. Column round or pentagonal, may be cirriferous.

Remarks.—The type species of *Dendrocrinus, D. longidactylus* is closely similar to the putative genus *Quinquecaudex* Brower and Veinus; the crowns of these genera are indistinguishable from each other. "*Quinquecaudex*" is merely a *Dendrocrinus* with an exclusively pentameric column. This single criterion is not really a good basis for distinguishing these genera because of its transitional nature. For example, the column of *D. celsus* Ringueberg, 1888 is undivided proximally, pentameric distally. There are also dendrocrinids such as *D. aphelos* n. sp. in which pentameres are faint because of partial fusion. For these reasons, and to better classify dendrocrinids in which complete columns are unknown, *Quinquecaudex* is here considered to be a junior synonym of *Dendrocrinus.*

Dendrocrinus is a rather widespread Ordovician and Silurian crinoid known from more than a dozen species. It was eurytopic with respect to energy levels and substrate and is found in a wide variety of lithotopes ranging from coarse-grained skeletal carbonates deposited in agitated environments to lower energy, deeper water environments represented by fine-grained terrigenous clastics deposited near the limit of storm wavebase. However, *Dendrocrinus* was typically a minor component of most echinoderm assemblages, except in environments marginally favorable to most crinoids such as occurred during deposition of portions of the Rochester Shale. In these conditions, characterized by episodic, generally high rates of terrigenous sedimentation, *Dendrocrinus* was locally abundant. Evidently, it was an opportunistic crinoid (see Frest *et al.,* 1999, pp. 663–665; Jell, 1999).

The crown of *Dendrocrinus,* with its simple radial facets and typically isotomous arms, is generalized with respect to most dendrocrinids. However, *Dendrocrinus* exhibits great variation in morphology of the column and holdfast. Cirri are absent on the columns of many species of *Dendrocrinus,* but *D. ursae* n. sp., described below, bears whorls of stout cirri and the column of *D. longidactylus* is partly covered with abundant hirsute cirri. Furthermore, the column of *Dendrocrinus* may taper almost to a point distally or terminate in stout radicles. The ability of *Dendrocrinus* to colonize a wide variety of substrates was facilitated by its flexible attachment strategies.

Brower (1973, p. 452) believed *Dendrocrinus* to be among the most important cladid stem groups in the Ordovician. It was probably the rootstock from which many other cladids evolved. For example, *Mastigocrinus* Bather, 1892 the type genus of the Mastigocrinidae Jaekel, 1918 and of the superfamily Mastigocrinacea, from the Wenlock of Great Britain is basically comparable to *Dendrocrinus* without a radianal. Heterochrony was instrumental in evolution of heterotomous ramulate or pinnulate arms characteristic of advanced dendrocrinids. Curiously, dendrocrinids only began to diversify in the Late Silurian, with a major phase of taxonomic radiation occurring in the Devonian. This radiation postdates the first known appearance of *Dendrocrinus, D. villosus* Brower and Veinus, 1982 in the



Text-figures 18A, B.—*Dendrocrinus ursae* n. sp., diagrams of holotype BMS E26303. A. Cup centered on D ray. B. Pentameric column with incomplete cirri. Radials black. Scale for both figures is 1 mm.

Bromide Formation of Oklahoma, by at least 45 million years.

Dendrocrinus ursae, new species

Plate 3, figures 5–7; Text-figures 18A, B

Diagnosis.—A species of *Dendrocrinus* characterized by a smooth, unornamented cup, low infrabasal circlet, and pentameric column bearing whorls of lateral cirri.

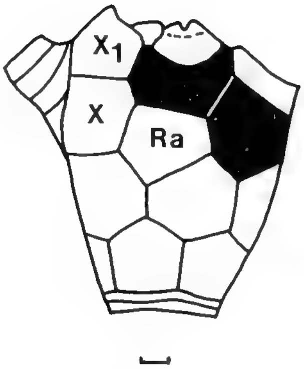
Description.—Cup small, conical, height and width about equal, plates unornamented. Infrabasal, basal, and radial circlets respectively comprising approximately 25%, 40%, and 35 % of cup height. Infrabasals five, pentagonal, typically wider than high (h/w = 0.6–1.0). Basals five, height and width similar (h/w = 1.0–1.1), relatively thick at base of cup (0.6 mm). CD interray basal heptagonal, remaining basals hexagonal. Radianal pentagonal, wider than high (h/w = 0.8), smaller than C ray radial situated directly above. Radials five-sided, wider than high (h/w = 0.8). Radial facets gently arcuate, wide, occupying 70% width of radials. Anal X large, heptagonal, wider than high (h/w = 0.8), distal margin level with radial facets. Anal sac and arms not preserved.

Proximal 5.5 cm of column heteromorphic, uniform in diameter (1.2 mm), slightly pentalobate with prominent pentameres (Pl. 3, fig. 7). Noditaxis formula N, IN. Maximum thickness of nodals and internodals 0.5 mm and 0.3 mm, respectively. Proximal nodals each bearing up to five cirri, cirral scars straddling pentamere sutures (Text-fig. 18B). Cirri incompletely known, slender (proximal diameter 0.2–0.3 mm), consisting of short, beaded cirrals.

Remarks.—The cup of the holotype and only known specimen of *D. ursae* n. sp. is separated from a cirriferous column by 1.5 cm. This column is inferred to belong to the cup for several reasons. First, both cup and column were recovered from a sparsely fossiliferous horizon devoid of other crinoids. Secondly, with the exception of *Eomyelodactylus,* pentameric, cirriferous columns are known to occur only in cladid crinoids. Finally, cirriferous distal columns have already been documented in *Dendrocrinus longidactylus* (see Brett, 1981, fig. 1g). However, *D. longidactylus* differs from *D. ursae* in possessing a proximally round column with abundant, very fine, hair-like cirri restricted to medial and upper distal portions of the column. *D. ursae* is incompletely known but differs from all other known species of *Dendrocrinus* (and nearly all other Silurian crinoids) in having whorled cirri on the proximal column.

Type and occurrence.—The single known specimen, BMS E26303, is from the upper portion of the Bear Creek Shale, 35 cm below the Sterling Station Iron Ore, locality 9.

Measurements of BMS E26303 (in mm).—Cup height = 3.5, crushed width = 5.3; C IB height = 0.9, width = 1.0; D IB height = 1.0, width = 1.0; E IB height = 0.8, width = 1.3; CD B height = 1.7, width = 1.5; DE B height = 1.7, width = 1.6; C R height = 1.3, width = 1.7; D R height = 1.6, width = 2.0;



Text-figure 19.—*Dendrocrinus aphelos* n. sp., plate diagram of cup of BMS E26367. Radials black. Scale is 1 mm.

E R height = 1.4; RA height = 1.1, width = 1.3; anal X height = 1.4, width = 1.7.

Etymology of name.—ursa (L.) = bear; the specific epithet refers to the name of the type locality, Bear Creek.

Dendrocrinus aphelos, new species

Plate 7, figures 1, 13; Text-figure 19

Diagnosis.—A large, robust species of *Dendrocrinus* characterized by smooth, unornamented cup, elevated radial facets, arms branching on the seventh to ninth primibrachial, plicate anal sac, and transversely round, xenomorphic column composed of thin columnals with partly fused pentameres.

Description.—Cup conical, height equal to width, cicatrix wide. Cup plates smooth, unornamented. Infrabasal, basal, and radial circlets comprising, respectively, approximately 25%, 35%, and 40% of cup height. Infrabasals five, pentagonal, typically wider than high (h/w = 0.6–1.0). Basals five, height and width similar (h/w = 1.0–1.1). CD interray basal heptagonal, remaining basals hexagonal. Radianal situated directly under C ray radial, pentagonal, wider than high (h/w = 0.8). Radials five-sided, C ray radial smaller than radianal and other radials, wider than high (h/w = 0.6), remaining radials higher than wide (h/w = 1.1–1.2). Radial facets U-shaped, narrow, occupying not more than 45% width of radials. Each radial facet has a narrow, deep, V-shaped ventral groove (Pl. 7, fig. 13). Anal X large, six-sided, slightly wider than high, supporting a small anal plate to upper left and larger, pentagonal X_1 directly above. X_1 incorporated into cup, distal margin slightly above adjoining radial facets. Anal sac large, consisting of six rows of plicate, wedge-shaped to roughly rectangular plates each with three to five laterally directed ridges. Distal portion of anal tube unknown.

Arms five, robust, isotomous, successive divisions occurring on seventh to ninth primibrachial, ninth or tenth secundibrachial, and thirteenth to eighteenth tertibrachial. Higher divisions probably present but not preserved. Brachials less than 2½ times wider than high, U-shaped in articular view with deep, narrow, V-shaped ventral groove.

Column incompletely known; proximal 5.3 cm preserved in the holotype specimen (BMS E26366). Column nearly round but subpentagonal outline apparent on close examination. Columnals thin (0.05–0.5 mm), thinner columnals alternate with thicker columnals. Lumen pentastellate, corners alternating with indistinct, partly fused pentameres. Pentamere sutures not apparent on exterior surface of column; junctions between pentameres marked by shallow, longitudinal furrows.

Remarks.—Dendrocrinus aphelos n. sp. is not compared with all known species of *Dendrocrinus*; only Silurian forms are considered here. The narrow, elevated radials facets of *D. aphelos* are a specialized character that contrasts with gently arcuate radial facets without elevated rims typical of the Early Silurian species *D. parvus* Eckert, 1984, *D. bactronodosus* n. sp., *D. ursae* n. sp., and the Wenlock species *D. longidactylus* Hall, 1852 and *D. celsus* Ringueberg, 1888. *Dendrocrinus arrugius,* recently described from the Ludlow of Victoria, Australia (Jell, 1999), is distinctive in having very broad, circular radial facets with weakly defined transverse ridges.

Dendrocrinus daytonensis Ausich, 1986c from the Brassfield Formation of Ohio has elevated radial facets as in *D. aphelos* n. sp., but its round column is distinctly pentameric. The columns of other *Dendrocrinus* species are also distinct from that of *D. aphelos*; *D. parvus* possesses a pentalobate column, *D. celsus* and *D. bactronodosus* have at least partly pentameric columns, and *D. longidactylus* Hall, 1852 and *D. ursae* possess cirriferous columns. The column is not known in *D. ?gasworksensis* Donovan, 1993, but this form has more robust arms that branch on the second primibrachial (Donovan, 1993), as compared to the seventh to ninth primibrachial in *D. aphelos.*

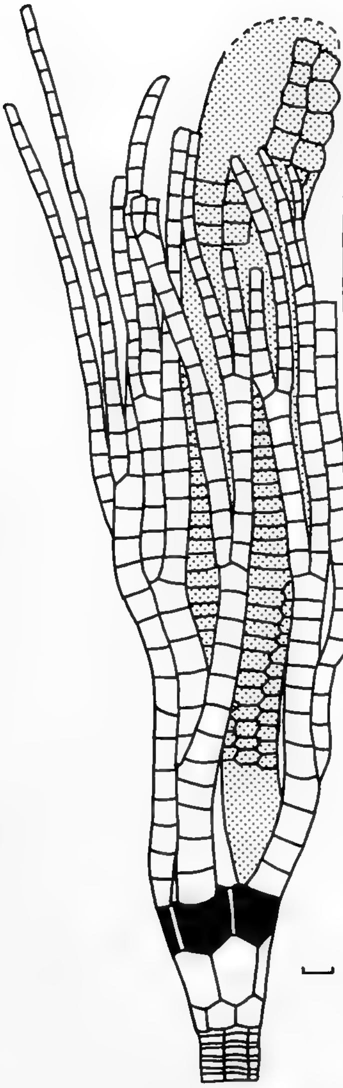
Types and occurrence.—Dendrocrinus aphelos n. sp. is known from two specimens, holotype BMS E26366 and paratype BMS E26367. The type material was collected from a thin stratum of calcareous shale and limestone 1.0–1.1 m above the base of the Wolcott Limestone at locality 8.

Etymology of name.—aphelos (Gr.) = even, smooth; the specific epithet refers to the smooth, unornamented surfaces of the cup and stem.

Dendrocrinus bactronodosus, new species

Plate 7, figure 21; Text-figure 20

Diagnosis.—A species of *Dendrocrinus* characterized by a smooth, unornamented cup, pentastellate



Text-figure 20.—*Dendrocrinus bactronodosus* n. sp., diagram of crown of BMS E26368. Radials black, anal tube stippled. Scale is 1 mm.

Table 6.—Measurements (in mm) of two specimens of *Dendrocrinus aphelos* n. sp.

	BMS E26366 (holotype)	BMS E26367
Cup height	11.9	8.5
Cup width*	13.6	8.6
Cicatrix width	5.3	3.1
A IB height	—	2.0
A IB width	—	2.5
B IB height	—	2.1
B IB width	—	2.3
C IB height	—	1.9
C IB width	—	2.2
D IB height	2.5	2.3
D IB width	4.0	2.3
E IB height	2.6	2.1
E IB width	3.5	2.9
AB B height	4.2	3.0
AB B width	4.2	3.1
BC B height	—	3.2
BC B width	—	2.9
CD B height	—	3.1
CD B width	—	2.9
DE B height	4.3	3.4
DE B width	3.8	3.1
EA B height	4.2	3.1
EA B width	4.4	2.8
A R height	6.0	3.4
A R width	5.0	3.2
B R height	—	3.4
C R height	—	1.9
C R width	—	3.1
D R height	4.4	3.6
D R width	—	2.9
E R height	5.8	4.4
E R width	4.9	3.6
RA height	—	2.3
RA width	—	2.8
Anal X height	—	2.5
Anal X width	—	2.7
X1 height	—	1.8
X 1 width	—	2.4

* Crushed cup (width greater than diameter).

proximal column with pentameres, and distally nodose anal sac.

Description.—Cup small, conical, height equal to width, consisting of smooth, unornamented plates. Infrabasal, basal, and radial circlets comprising 25%, 45%, and 30% of cup height, respectively. Infrabasals five, pentagonal, height equal to or slightly greater than width (h/w = 1.0–1.1). Basals five, height equal to width. CD interray basal heptagonal, remaining basals hexagonal. Radials five-sided, wider than high (h/w = 0.7–0.9). Radial facets declivate, U-shaped, relatively wide, occupying 59%–65% width of radials. Anal X large, six-sided, height approximately equal to width, distal margin level with D ray radial facet but below C ray radial facet. X1 pentagonal, situated above D ray radial, lower portion extending below distal margin of C ray radial.

Anal sac long, consisting of vertical rows of plates. Proximal plates wider than high, plicate; distal plates subequal (height approximately equal to width), each with a large, centrally located node (Pl. 7, fig. 21; Text-fig. 20).

Arms five, long; dividing isotomously on fourth to seventh primibrachial, sixth to eighth secundibrachial, and seventh to twelfth tertibrachial. Distal portions of arms not preserved, at least nineteen tertibrachials present in two rays. Brachials strongly rounded dorsally, less than 1.7 times wider than high.

Proximal 2 mm of column strongly pentastellate. Columnals thin (height 0.02–0.1 mm), distinctly pentameric on articular surfaces but pentameres not visible from exterior of column. Lumen small, pentagonal, corners alternating with pentameres.

Remarks.—*D. bactronodosus* n. sp. is the only species of *Dendrocrinus* known to possess a nodose anal sac. The pentameric, pentastellate column also differentiates *D. bactronodosus* from all other species of *Dendrocrinus,* including *D. aphelos* n. sp., with which this species is associated.

Type and occurrence.—*D. bactronodosus* is known only from holotype specimen BMS E26368. It was collected from the upper surface of a 3 cm thick bed of limestone 1.1 m above the base of the Wolcott Limestone, locality 8.

Measurements (in mm).—Crown height = 31 (distal tips of arms not preserved); cup height = 3.8, width = 3.7; A IB height = 0.8; D IB height = 1.0, width = 0.9; E IB height = 0.8, width = 0.8; CD B height = 1.7; DE height = 1.8, width = 1.3; EA B height = 1.7, width = 1.2; D R height = 1.2, width = 1.7; E R height = 1.5, width = 1.7; Anal X height = 1.2; X1 height = 1.0.

Etymology of name.—*bactros* (Gr.) = staff, *nodosus* (L.) = knotty, full of knots or nodes; the specific epithet refers to the nodose distal portion of the anal sac.

Subclass **FLEXIBILIA** Zittel, 1895

Order **TAXOCRINIDA** Springer, 1913

Superfamily **TAXOCRINACEA** Angelin, 1878

Family **TAXOCRINIDAE** Angelin, 1878

Diagnosis.—Taxocrinaceans with conical cup and elongate, ovoid crown. One or two anal plates in cup. Radianal, if present, situated directly below C ray radial. Anal X supporting anal sac or tube. Interbrachials few or absent. Arms isotomous or heterotomous.

Included genera.—*Taxocrinus* Phillips *in* Morris, 1843, M. Dev. (Givetian)—U. Miss. (Chesterian); *Eutaxocrinus* Springer, 1906, U. Sil. (Wenlock)—L. Miss. (Tournaisian); *Gnorimocrinus* Wachsmuth and Springer, 1880, Sil. (Wenlock–Ludlow); *Haereticotaxocrinus* Franzén, 1982, U. Sil. (Wenlock–Ludlow); *Meristocrinus* Springer, 1906, U. Sil. (Wenlock); *Parichthyocrinus* Springer, 1902, L. Miss. (Osagean); *Protaxocrinus* Springer, 1906, M. Ord. (Caradocian)—L. Dev. (Lochkovian).

Genus **PROTAXOCRINUS** Springer, 1906

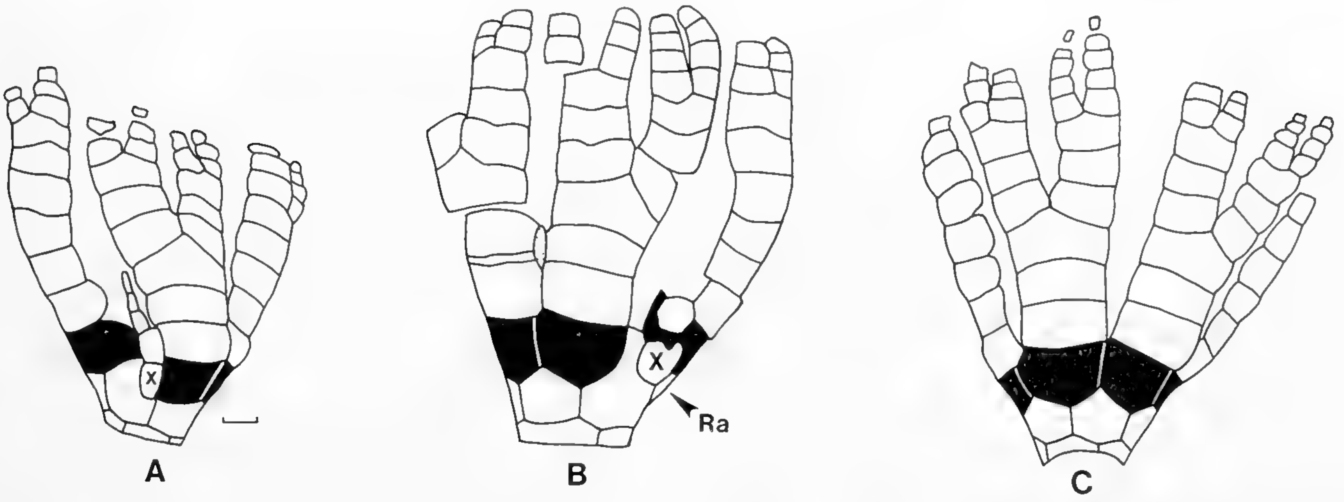
Type species.—*Taxocrinus ovalis* Angelin, 1878, by designation of Springer, 1906 p. 515.

Diagnosis.—A genus of Taxocrinidae with small, high conical cup. Radianal pentagonal, situated directly below C ray radial. Anal sac large in primitive species, proximally sutured to C ray; reduced to small tube with median anitaxis in advanced forms. Primibrachials two or three. Interbrachials few or absent. Arms isotomous, patelloid processes absent or weakly developed.

Remarks.—Most species of *Protaxocrinus* have two primibrachials in each ray. Eckert (1984) emended diagnosis of *Protaxocrinus* to accomodate the Early Silurian species *P. cataractensis,* which has two or three primibrachials in each ray. *P. anellus* new species, has three primibrachials in all rays.

Evolutionary trends in *Protaxocrinus* included reduction in size of infrabasals and changes in the CD interray. Primitive forms, including the Ordovician species *P. elegans* (Billings, 1857), *P. laevis* (Billings, 1857), *P. girardeau* Springer, 1920 and the Early Silurian species *P. cataractensis* Eckert 1984, are characterized by large infrabasals that, measured to their distal tips, comprise approximately 27%–33% of cup height. However, the infrabasal circlet of *P. amii* Bolton, 1970 (late Llandovery, Telychian), is considerably lower, comprising about 20% of cup height. Low infrabasal circlets, 10%–15% of cup height, are typical of *P. interbrachiatus* (Angelin, 1878), *P. ovalis* (Angelin, 1878), and *P. salteri* (Angelin, 1878) from the Silurian (Wenlock) of Gotland.

Protaxocrinus in the Ordovician is also characterized by a large, robust anal sac sutured to the proximal portion of the C ray to the level of X3 or higher and X1 is situated directly above the CD interray basal. In contrast, more advanced Silurian forms, including P. anellus, have a relatively small anal sac or tube free of connection with the C ray beyond X1 or X2. Also, X1 is smaller and situated lower in the cup on the right shoulder of the CD interray basal. Similar construction of the CD interray also occurs in *P. interbrachiatus, P. ovalis,* and *P. salteri* and this is interpreted to be an advanced characteristic. Placement of X1 lower in the cup, and suture of this plate along an arcuate, rather than straight-edged margin of the CD interray basal, probably strengthened attachment of the anal sac to the cup and compensated reduced lateral suture of the sac to the C ray. Springer (1911, 1920) believed that *Protaxocrinus* was closely related to the Ordovician cladid *Cupulocrinus* d'Orbigny, 1850. However, he did not go so far as to state that it was definitely derived from *Cupulocrinus,* only that these genera show a "fairly close approach to the point of divergence of the Flexibilia from the Inadunates" and that they probably shared a common ancestor (Springer, 1920, p. 345). The earliest known species of *Protaxocrinus, P. elegans* (Billings, 1857) and *P. laevis,* (Billings, 1857) are Middle Ordovician (Mohawkian; Shermanian) in age, but *Cupulocrinus* extends back into the Blackriveran Lebanon Limestone of Tennessee (Guensberg,



Text-figures 21A–C.—*Protaxocrinus anellus* n. sp. plate diagrams. A. CD interray of BMS E26392, an individual in which the radianal is apparently absent. B. Crown of BMS E26393 centered on D ray. C. Anterior view of BMS E26392 with A ray to left. Radials black, interbrachial stippled. Scale for all figures is 1 mm.

1984). If *Protaxocrinus* and *Cupulocrinus* did share a common ancestor, origin of the Flexibilia and divergence of the *Protaxocrinus* lineage may have occurred in the Llandeilian or earlier. In this respect, occurrence of the flexible-like cladid *Archaetaxocrinus* Lewis 1981 in the Middle Ordovician (Llanvirnian) Kanosh Shale and Oil Creek Formation is noteworthy, although large interbrachials in this genus suggests that it represents a separate lineage.

Protaxocrinus was probably an important root-stock in evolution of the Taxocrinidae. *Taxocrinus* probably evolved from *Protaxocrinus* by incorporating more interbrachials into the cup, reducing the size of the anal sac and freeing it of lateral attachment to the C ray.

Protaxocrinus anellus, new species

Plate 9, figures 2–5, 7–9; Text-figures 21A–C

Diagnosis.—A small species of *Protaxocrinus* characterized by low infrabasals and symplectial sutures between cup plates. CD interray basal distally arcuate, three primibrachials in each ray, anal tube small.

Description.—Crown pyriform, small (Table 6), plates smooth, unornamented. Margins of cup plates and proximal brachials crenulate, sutures symplectial (Pl. 9, fig. 4). Cup conical, wider than high (h/w = 0.6). Infrabasal circlet averaging 15% of cup height. Infrabasals three, separated from each other by sutures in BC, CD, and EA interrays. AB and DE infrabasals six-sided with broad, arcuate distal margins. C ray infrabasal smaller, five-sided. Basals five, height and width similar (h/w = 0.9–1.1) except CD interray basal, which is elongate (h/w = 1.3). AB and DE interray basals pentagonal, BC and EA interray basals hexagonal. CD interray basal extending to distal margins of radials, modified heptagonal with deeply arcuate, concave shoulders (Pl. 9, fig. 4). Radials wider than high (h/w = 0.5–0.7) with arcuate, concave distal margins. BC ray radial six-sided, other radials five-sided. Radianal small, pentagonal, slightly wider than high (h/w = 0.9), situated directly below C ray radial. Radianal absent in one specimen (BMS E26392). Anal X pentagonal, height equal to or greater than width (h/w = 1.0–1.2), situated in deeply notched right shoulder of CD interray basal. Right side of anal X sutured to radianal and C ray radial. X_1 typically quadrangular, slightly elongate (h/w = 1.1), loosely sutured to C ray radial and first primibrachial. Anal sac free above, extending at least to distal margin of third primibrachial. X_2 rectangular, narrow (h/w = 1.8) supporting at least two additional, progressively narrower plates (Pl. 9, fig. 7; Text-fig. 21A).

Arms free above radials, dividing isotomously on third primibrachial and the third or fourth secundibrachial. Higher divisions probably present but not preserved. Brachials less than two times wider than high, rounded dorsally, distal margins concave.

Column round, xenomorphic, tapering gradually below short enlarged section adjacent to cup. Proximal section heteromorphic, consisting of irregularly alternating, straight-sided columnals with symplectial sutures. Proximal columnal height 0.2–0.7 mm. Columnals more uniform in size with rounded latera in medial section of column. Presumed distal section of column isomorphic, consisting of elongate (maximum h/w = 2.0), cylindrical to barrel-shaped columnals (Pl. 9, fig. 2).

Remarks.—*Protaxocrinus anellus* is the only species of *Protaxocrinus* with three primibrachials in each ray. Exceptionally, *P. cataractensis* Eckert 1984 has three primibrachials in one or more rays, but it has a longer, much more robust anal sac and anal X is situated directly above the CD interray basal rather than on its shoulder (Eckert, 1984, p. 36, text-fig. 16c).

One specimen of *P. anellus* (BMS E26392) is considered to be an abnormal individual without a radianal (Text-fig. 21A; Pl. 9, fig. 7).

Types and occurrence.—Eight specimens including holotype BMS E26393 and paratypes BMS E26392, E26394–E26397, E26399 are from 2 m above the base of the Willowvale Shale, locality 11. BMS E26398 is from the lower portion of the Willowvale Shale at locality 10.

Etymology of name.—*anellus* (L.) = little ring, referring to the low infrabasal circlet of this species.

Order **SAGENOCRINIDA** Springer, 1913

Remarks.—In contrast to their rarity in Lower Silurian deposits, Wenlock Sagenocrinida constitute a diverse group of crinoids with at least 15 genera distributed among 6 families. Phylogenetic relationships among these crinoids are very poorly known. However, recent study of the lower Clinton crinoids has begun to fill this gap; in the present report we describe new genera and species of sagenocrinids from the Llandovery of New York.

Superfamily **ICTHYOCRINACEA** Angelin, 1878

Family **ICTHYOCRINIDAE** Angelin, 1878

Diagnosis.—Icthyocrinaceans with ovoid to pyriform crown without demarcation between cup and arms in lateral view. Infrabasals typically small, visible in side view or concealed. Radianal situated directly below C ray radial. Anal X, if present, in some instances succeeded by additional plates. Anal sac and interbrachials absent. Arms isotomous, proximal brachials sutured laterally.

Included genera.—*Icthyocrinus* Conrad, 1842, U. Sil. (Wenlock)—L. Dev. (Lochkovian); *Cleistocrinus* Springer, 1920, L. Sil. (Wenlock); *Clidochirus* Angelin, 1878, L. Sil. (Llandovery)—L. Dev. (Lochkovian); *Metichthyocrinus* Springer, 1920, L. Miss.; *Paraclidochirus* Webster and Fox, 1986, L. Dev. (early Lochkovian)—U. Dev. (Famennian); *Prolixocrinus* n. gen., L. Sil. (Llandovery); *Synaptocrinus* Springer, 1920, M. Dev. (Givetian) U. Dev. (Famennian).

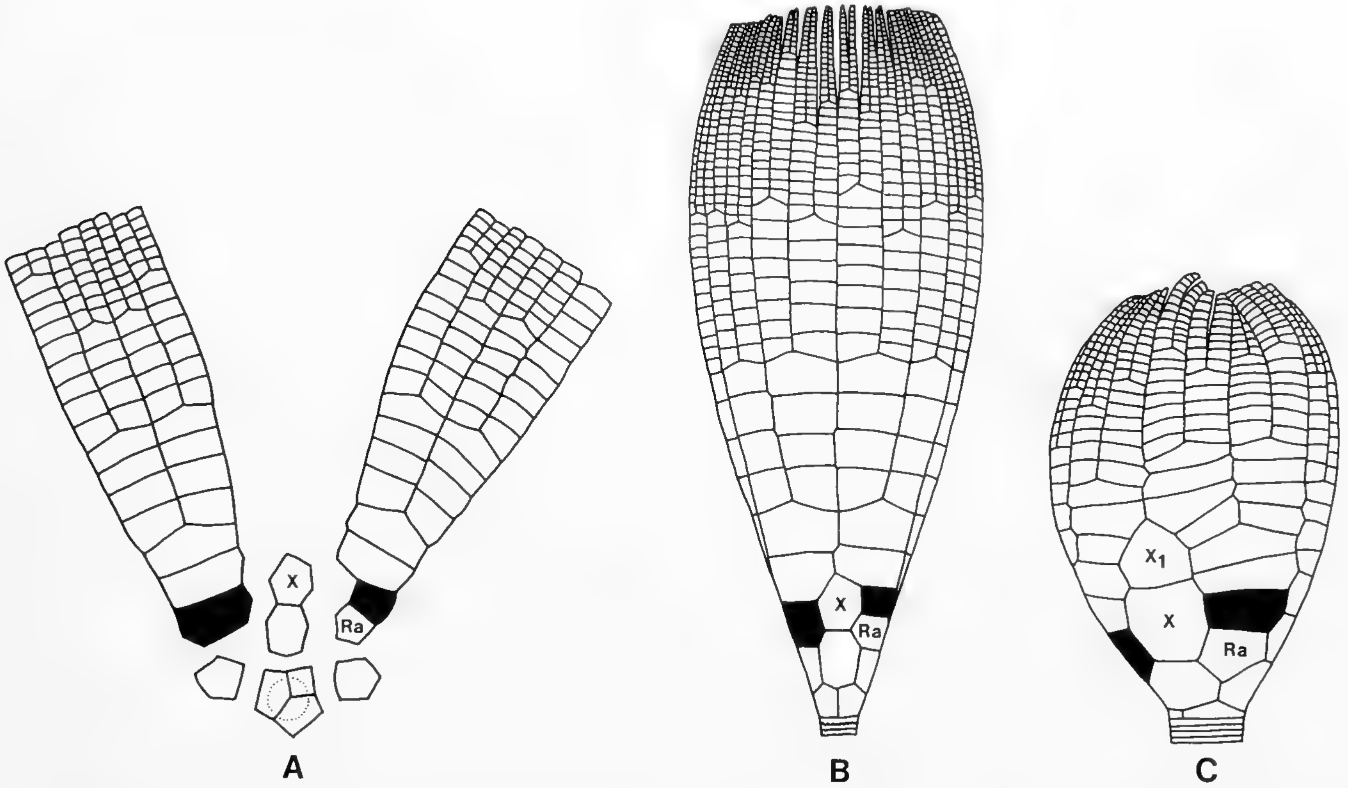
Genus **PROLIXOCRINUS,** new genus

Type species.—*Prolixocrinus nodocaudis* n. sp.

Diagnosis.—A genus of Icthyocrinidae with narrow pyriform crown and large infrabasals. C ray radial much narrower than other radials. Two anal plates in cup. Radianal situated below C ray radial. Arms isotomous, primibrachials two, proximal brachials sutured laterally. Column round.

Remarks.—*Prolixocrinus* is closely related to *Clidochirus* and in fact could be accomodated in that genus, but diagnosis of *Clidochirus* has been emended to the point where it has little taxonomic value. A preliminary step in rectifying this situation has been taken by Webster and Fox (1986), who assigned *C. keyserensis* Springer, 1920 and *C. gratiosus* Strimple, 1963 to their new genus *Paraclidochirus.* The latter is distinguished from *Clidochirus* by its concealed infrabasals and absence of a radianal in some species. Additional subdivision is undoubtedly warranted. For example, although exact affinities of *C. springeri* Ausich 1984b from the Brassfield Formation of Ohio are uncertain, this crinoid closely resembles primitive Ordovician species of *Protaxocrinus* including *P. elegans* (Billings, 1857), *P. laevis* (Billings, 1857), and the Early Silurian species *P. cataractensis* Eckert 1984. However, the proximal portion of the anitaxis of *C. springeri* is apparently sutured to both the C and D rays and interbrachials are absent. It seems best to regard *C. springeri* as a transitional form more closely related to *Protaxocrinus* than to *Clidochirus,* but a thorough review of *Clidochirus* is beyond the scope of this study. The concept of *Clidochirus* should probably not stray far the type species *C. pyrum* Angelin, 1878 from the Wenlock of Gotland. *C. pyrum* is characterized by a pyriform crown, low and wide infrabasals, laterally abutting and interlocking proximal arms, and two or three large anal plates (Springer, 1920, Pl. 37, figs. 1, 3b, 5b). Accordingly, *Prolixocrinus* is differentiated from *Clidochirus* by its elongate crown with high conical cup, larger infrabasals, narrow radianal and C ray radial, and posterior interray with small anal X only. Furthermore, the anitaxis of *Clidochirus* may extend to the level of proximal secundibrachials, but in *Prolixocrinus* the anal X does not extend beyond the first primibrachial. Additionally, the arms of *Prolixocrinus* are more elongate than those of *Clidochirus* and consist of narrower brachials. Following this diagnosis, *C. americanus* Springer, 1920 from the Brassfield Formation of Ohio is reassigned to *Prolixocrinus* (*P. americanus* (Springer)).

Late Ordovician and Early Silurian flexible crinoids are too poorly known to permit ancestry of *Prolixocrinus* to be inferred. *C. serrulatus* Brower, 1973, based on its stratigraphic position (Upper Ordovician Girardeau Formation), is a potential progenitor of *Prolixocrinus.* However, morphological divergence between these genera appears to rule out any close relationship. *Prolixocrinus* does bear a considerable resemblance to the Late Silurian (Wenlock) crinoid *Ic-*



Text-figures 22A–C.—Flexible crinoid plate diagrams. A. Expanded plate diagram of *Prolixocrinus nodocaudis* n. gen. and sp. B. Restoration of uncrushed crown of *P. nodocaudis*. C. Restoration of uncrushed crown of *Clidochirus pyrum*, modified from Springer

thyocrinus and may have given rise to this genus by reduction in size of infrabasals and elimination of anal X.

Etymology of name.—*prolixus* (L.) = stretched out, long (refers to the elongate crown) + *krinon* (Gr.) = lily.

Prolixocrinus nodocaudis, new species
Plate 2, figures 7–9, 19, 21; Text-figures 22A, B

Diagnosis.—As for the genus. Cup plates smooth, unornamented. Column xenomorphic, medial and presumed distal portions isomorphic, nodose.

Description.—Cup high conical, merging smoothly upward into narrow pyriform crown (Text-fig. 22B). Crown height/width = 2.5 (Table 7). Demarcation between cup and arms not evident. Plates smooth, unornamented. Infrabasal, basal, and radial circlets respectively comprising approximately 25%, 35%, and 40% of cup height measured to distal margin of radials. Infrabasals three, relatively large, erect, wider than high (h/w = 0.5–0.8); circlet divided by sutures in BC, CD, and EA interrays. Azygous (C ray) infrabasal pentagonal, bordered laterally by sutures in BC and CD interrays, remaining infrabasals six-sided. Basals five, higher than wide (h/w = 1.1–1.5). CD interray basal heptagonal, larger (higher) than lateral basals, extending upward into next circlet. AB and DE interray basals pentagonal; BC and EA interray basals hexagonal. Radials wider than high (h/w = 0.6–0.8). Radianal situated directly under C ray radial, small, pentagonal, wider than high (h/w = 0.8–0.9). Radials wider than high (h/w = 0.6–0.8). C ray radial five-sided, much smaller than other radials, narrow in comparison with proximal ray series above (width 54%–67% of first primibrachial of C ray). B ray radial six-sided; A, D, and E radials five-sided. Distal margins of radials straight to slightly arcuate, corners slightly truncated in some instances. Anal X small, hexagonal, higher than wide (h/w = 1.2), extending upward into first primibrachial circlet but not dividing it (Pl. 2, fig. 6). No additional anal plates.

Rays dividing isotomously three or four times, successive divisions on second primibrachial, third to fifth secundibrachial, fifth to ninth tertibrachial, and eleventh to fifthteenth quartibrachial. Proximal portions of rays sutured together at least to level of lower secundibrachials. Axillary brachials low pentagonal, remaining brachials rectangular, not exceeding 2.3 times wider than high. Patelloid processes absent.

Column incompletely known, exceeding 11 cm in length, xenomorphic, round. Column enlarged immediately below cup, known remainder uniform in diameter. Columnals thin (h/w = 0.02–0.2) with straight latera. Thickest columnals commonly possessing a row of twelve or more nodes on latera (Pl. 2, fig. 8).

Remarks.—*Prolixocrinus nodocaudis* n. sp. is differentiated from *P. americanus* (Springer, 1920) n. comb. by its higher infrabasals and nodose rather than smooth column.

Available specimens of *Prolixocrinus nodocaudis* comprise a partial growth series with crown height ranging from approximately 20 mm to 47 mm. Only primibrachials are sutured together laterally in the smallest specimen (BMS E26327). However, in the largest specimen (ROM 43634), the rays are laterally united to the level of highest secundibrachials, indicating that progressively more brachials became fixed into the cup as this species grew.

Types and occurrence.—The holotype specimen (ROM 43634) was discovered more than three decades ago by Beverly Seyler in talus on the east side of the gorge of the Niagara River, locality 1. Attempts to discover more specimens at this locality proved fruitless for many years, but eventually *P. nodocaudis* was traced to its source in the basal 25 cm of the Hickory Corners Member of the Reynales Formation. Excavation in this interval produced paratype specimens BMS E26325–E26327, all of which are figured.

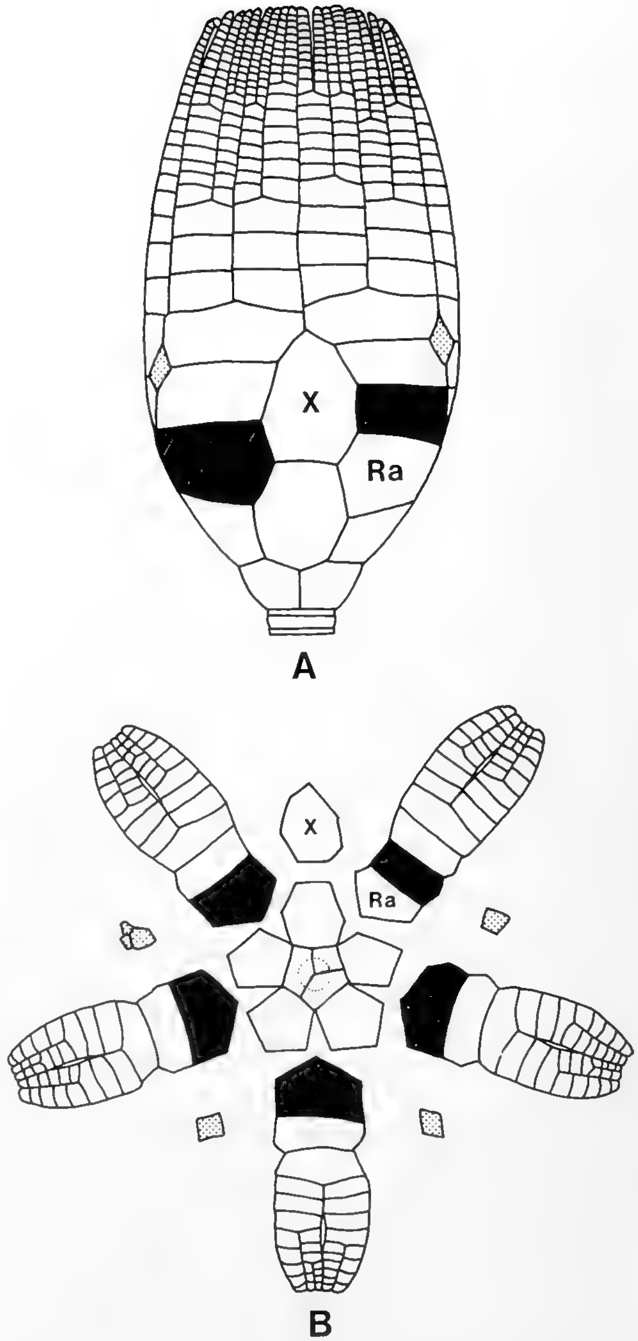
Etymology of name.—*nodos* (Gr.) = knotty, node + *caudis* (L.) = stem (refers to the nodose column of this species).

Superfamily **SAGENOCRINITACEA** Roemer, 1854

Family **ANISOCRINIDAE,** new family

Diagnosis.—Sagenocrinitaceans with short ovoid crown. Infrabasals visible in lateral view. Radianal typically present, pentagonal, situated directly below C ray radial. Anal X succeeded by additional plates in some instances. Distal arms isotomous to slightly heterotomous in some instances. Interbrachials absent or consisting of one to several plates in each interray.

Included genera.—*Anisocrinus* Angelin, 1878, Sil. (Wenlock–Ludlow); *Cryptanisocrinus* Donovan, Doyle, and Harper, 1992, L. Silurian (late Llandovery) *Kyphosocrinus* n. gen., L. Sil. (late Llandovery); *Paranisocrinus* Frest and Strimple, 1978, U. Sil. (Ludlow); *Proanisocrinus* Frest and Strimple, 1978, U. Ord. (Richmondian).



Text-figures 23A, B.—*Kyphosocrinus tetreaulti* n. gen. and sp. A. Restoration of uncrushed crown. B. Expanded plate diagram. Radials black, interbrachials stippled.

Remarks.—The new family Anisocrinidae partly replaces the subfamily Anisocrininae Frest and Strimple. As defined by Frest and Strimple (1978) the Anisocrininae included *Anisocrinus, Asaphocrinus* Springer, 1920, *Paranisocrinus, Proanisocrinus,* and *Cryptanisocrinus. Asaphocrinus* is markedly divergent compared to other members of this group, as it possesses an anal tube or sac and a quadrangular radianal situated obliquely below the C ray radial. Frest and Strimple (1978) considered the Anisocrininae to be a subfamily of the Homalocrinidae Angelin, 1878, to which were assigned *Homalocrinus* and *Calpiocrinus* Angelin, 1878. Both of these taxa are peculiar; in *Homalocrinus* the radianal is small and situated in the basal

Table 7.—Measurements (in mm) of three specimens of *Protaxocrinus anellus* n. sp.

	BMS E26383 (holotype)	BMS E26392	BMS E26399
Crown height	13.0*	18.0*	10.8*
Cup height	3.6	3.3	3.5
Cup width	6.0**	5.1**	5.7**
AB IB height	0.7	0.6	0.6
AB IB width	2.5	—	—
CIB height	0.8	—	
CIB width	2.1	—	—
DE IB height	0.7	0.5	0.6
DE IB width	2.6		—
AB B height	1.8	1.7	1.7
AB B width	2.0	—	1.6
BC B height	1.7	—	—
BC B width	2.0		—
CD B height	3.1	—	—
CD B width	2.4	—	—
DE B height	1.8	1.4	1.6
DE B width	2.1		—
EA B height	1.7	1.7	1.8
EA B width	1.7	1.7	1.9
AR height	1.8	1.6	1.8
AR width	2.7	2.6	2.5
BR height	1.8		1.7
BR width	2.8	—	—
CR height	1.7	1.2	—
CR width	2.5	2.2	—
DR height	1.8	—	
DR width	2.6		—
ER height	1.7	1.8	1.7
ER width	2.1	2.6	2.5
AI Br1 height	1.5	1.5	1.2
AI Br1 width	3.0	2.7	2.6
BI Br1 height	1.5	—	1.3
BI Br1 width	3.0	—	—
CI Br 1 height	1.3	1.0	—
CI Br1 width	2.6	2.4	—
DI Br1 height	1.4	—	
DI Br1 width	2.7	—	—
EI Br1 height	1.5	1.4	1.4
EI Br1 width	2.6	2.6	2.7
AI Br2 height	1.3	1.2	1.0
AI Br2 width	2.7	2.6	2.4
BI Br2 height	1.4	—	1.1
BI Br2 width	2.8		—
CI Br2 height	1.3	1.1	—
CI Br2 width	2.6	2.6	—
DI Br2 height	1.3	—	—
DI Br2 width	2.7		—
EI Br2 height	1.3	1.2	1.1
EI Br2 width	2.5	2.6	2.5
RA height	1.7	+	—
RA width	1.9	+	—
Anal X height	1.4	0.7	
Anal X width	1.2	0.7	—
X1 height	1.2	0.8	—
X1 width	1.1	0.7	—
X2 height	—	0.9	—
X2 width	—	0.5	—
Column length	—	—	58.0++
Proximal diameter	—	—	2.5
Distal diameter	—	—	1.0

* Distal portions of arms not preserved.
** Crushed cup (width greater than diameter).
\+ Radianal absent.
\+\+ Incomplete column.

circlet and in *Calpiocrinus* the infrabasals envelop the basals. For these reasons, we consider anisocrinids to comprise a family of their own. As discussed below, they are related to the Icthyocrinidae.

Genus **KYPHOSOCRINUS,** new genus

Type species.—Kyphosocrinus tetreaulti n. sp.

Diagnosis.—A genus of Anisocrinidae with large, slightly bulging infrabasal circlet and relatively large pentagonal basals. Radianal pentagonal, situated directly below C ray radial. Anal X large, succeeded by regular polygonal X1 or smaller, irregularly arranged plates. Interbrachials absent or few in number, small. Arms isotomous proximally, commonly heterotomous distally with weakly developed endotomy. Column round, xenomorphic. Plates smooth, unornamented.

Remarks.—Kyphosocrinus n. gen. Differs from the other Llandovery anisocrinid, *Cryptanisocrinus* Donovan, Doyle, and Harper, in possessing relatively large pentagonal basals, as opposed to low triangular ones, and small interprimibrachials, unlike the prominent, large plates in *Cryptanisocrinus* (see Donovan *et al.*, 1992). *Kyphosocrinus* is closely related to *Proanisocrinus* Frest and Strimple 1978, from the Upper Ordovician (Richmondian) Maquoketa Formation of Illinois. Both genera are monotypic. The CD interray of the single known specimen of *P. oswegoensis* consists of numerous, irregularly arranged plates (Frest and Strimple, 1978, text-fig. 2B). Anal X is small, occupying less than one-third of the CD interray and extending only to the top of the radial circlet. In contrast, the CD interray of *Kyphosocrinus tetreaulti* is completely filled or nearly so by a large, polygonal anal X extending into the first or second primibrachial circlet. Accessory anal plates, infrequently present, are few in number and much smaller than anal X (Text-fig. 24A). Furthermore, the two known lateral interrays of *P. oswegoensis* are larger than those of *Kyphosocrinus* and contain at least four irregularly arranged plates each. Most specimens of *K. tetreaulti* have a single small quadrangular plate in each interray or no interbrachials and the distal arms are commonly heterotomous rather than isotomous.

Etymology.—kyphosos (Gr.) = hunchback + *krinon* (Gr.) = lily (refers to the rounded contours of the crown).

Kyphosocrinus tetreaulti, new species

Plate 7, figures 2–12, 14–16, 18–20; Plate 8, figures 2–6, 8, 9
Text-figures 23A, B, 24A–F

Diagnosis.—As for the genus.

Description.—Crown ovoid, small (Table 8). Arms free above first or second primibrachial. Cup obconical, height equal to or slightly exceeding width (h/w = 1.0–1.2), consisting of smooth, unornamented plates. Infrabasal, basal, and radial circlets comprising approximately 15%, 45%, and 40% of cup height, respectively. Infrabasals three, wider than high (h/w = 0.5–0.7), separated from each other by sutures in BC, CD, and EA interrays. AB and DE ray infrabasals six-sided, each with broad, concave distal margin. C ray infrabasal smaller (azygous), pentagonal. Infrabasal circlet bulging outward in profile, forming a break in otherwise smooth contours of cup (Pl. 7, fig. 20). Cicatrix slightly concave, lower margins of infrabasals concealing latera of first columnal. Basals five, height equal to or exceeding width (h/w = 1.0–1.3). CD interray basal large, heptagonal, AB and DE interray basals pentagonal, BC and EA interray basals pentagonal with convex lower margins. Radial circlet divided by CD interray basal and anal X. Radials wider than high (h/w = 0.6–0.8), roughly pentagonal, upper corners commonly slightly truncated. C ray radial narrower and shorter than other radials. Radianal pentagonal, wider than high (h/w = 0.7–0.8), situated directly below C ray radial. First primibrachials wider than high (h/w = 0.3–0.5), roughly rectangular, upper and lower corners commonly slightly truncated. Lateral interrays each commonly consisting of a small quadrangular or irregular polygonal interbrachial situated between truncated corners of first and second primibrachials (Pl. 7, fig. 18). Exceptionally, as many as four small interbrachials may occupy a single interray, or they are absent altogether (Text-figs. 24A–C). Anal X large, typically occupying entire CD interray, alate (h/w = 1.3–1.6), seven- to nine-sided, roughly almond-shaped, extending to second primibrachials. Small, irregularly arranged, accessory anal plates present in some instances. Exceptionally, anal X relatively short (extending into first primibrachial circlet), truncated distally, supporting regular hexagonal X1 extending to secundibrachials (Pl. 7, fig. 12).

Arms dividing isotomously on second primibrachials. Endotomy with heterotomous divisions commonly developed in higher arms (Pl. 7, fig. 3). Outer arm branches forming ill-defined rami with successive divisions on second to fourth secundibrachial and sixth to eighth tertibrachial; higher divisions concealed by coiled arms. Inner branches dividing on the third to sixth tertibrachial; higher divisions concealed by coiled arms. Brachials less than three times wider than high, patelloid processes absent.

Column round, xenomorphic, relatively long, length of complete column 16.5 cm in BMS E26372. Column tapering little distally. Proximal and medial sections of column heteromorphic with complex noditaxes, typical formula N, 3IN, 2IN, 3IN, 1IN, 3IN, 2IN, 3IN. Latera of nodals and larger internodals rounded. Columnals wider than high (height 0.2–1.3 mm, h/w = 0.1–0.5). Distal section of column isomorphic, terminating in radicular holdfast. Lumen round.

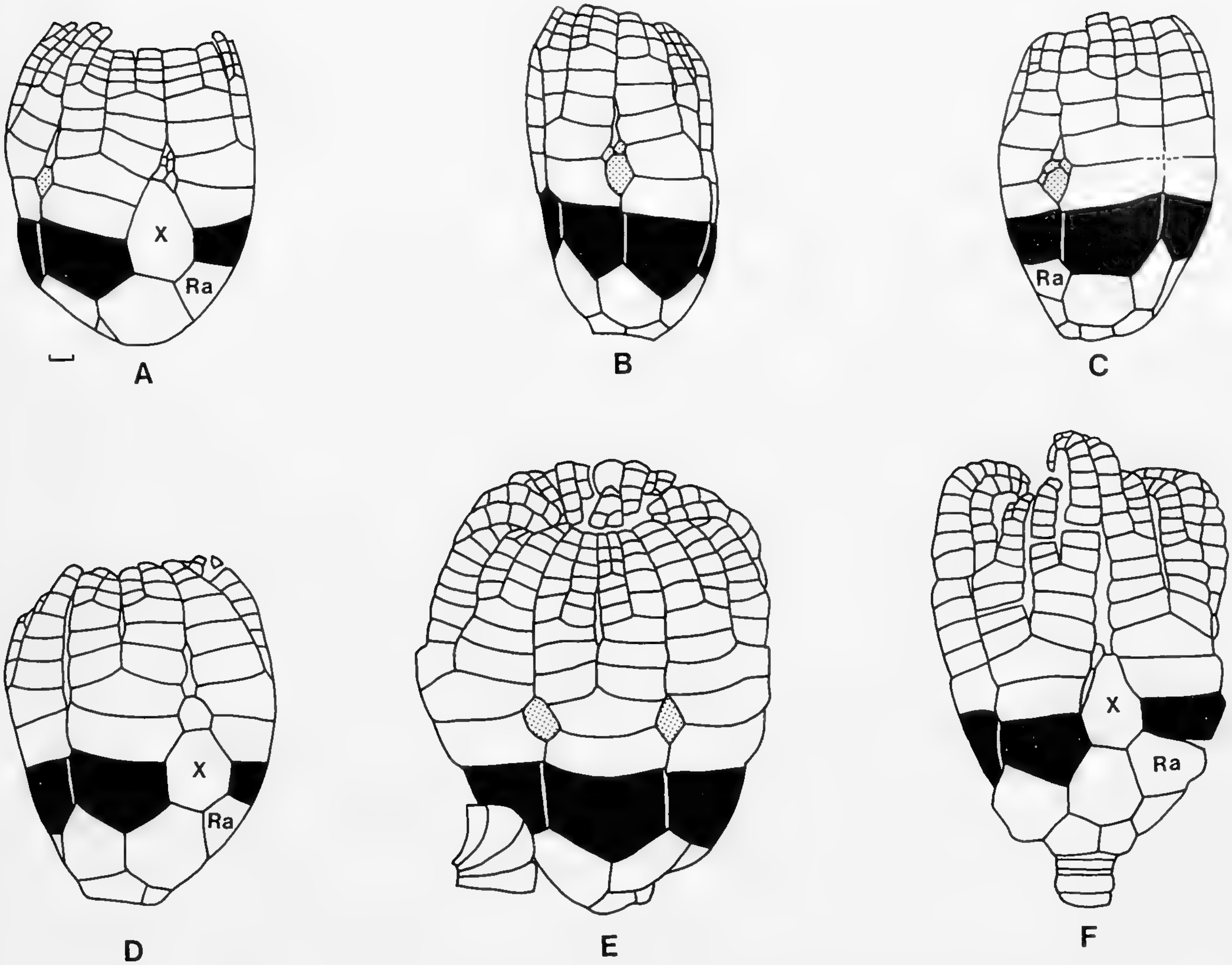
Table 8.—Measurements (in mm) of three specimens of *Prolixocrinus nodocaudis* n. gen. and sp.

	ROM 43634 (holotype)	BMS E26325	BMS E26326
Crown height	4	8.0	29.0
Crown width	32.0	14.0	—
Cicatrix width	3.3	3.4	—
AB IB height	2.0	2.0	—
AB IB width	—	3.5	—
CI B height	2.0	1.9	—
CI B width	2.5	2.9	—
DE IB height	—	1.7	—
DE IB width	4.0	3.4	
AB B height	3.4	3.4	3.7
AB B width	2.6	2.7	3.0
BC B height	—	3.4	3.6
BC B width	2.4	2.8	3.2
CD B height	4.4	4.0	4.3
CD B width	3.0	3.2	3.6
DE B height	3.8	—	3.6
DE B width	3.4	—	3.0
EA B height	3.5	3.7	4.0
EA B width	—	3.0	3.3
Ar height	—	2.8	3.4
Ar width	—	3.7	4.5
Br height	3.4	2.8	3.2
Br width	4.7	3.8	4.1
Cr height	2.7	1.9	2.5
Cr width	3.8	3.3	3.9
Dr height	3.4	—	3.0
Dr width	4.0	—	4.0
Er height	3.1	2.8	3.0
Er width	3.9	—	2.4
Ra width	2.9	2.5	3.2
Anal X height	4.4	—	3.3
Anal X width	3.6	—	2.8

* Crushed cup (width greater than diameter).

Remarks.—*Kyphosocrinus tetreaulti* n. sp. is a somewhat variable species. In some individuals, the arms exhibit only very slight heterotomy, in others the rays are strongly heterotomous and endotomous. Even in a single individual, the degree of heterotomy may vary between rays. Morphology of the interrays is also quite variable. Out of a total of 28 observed interrays in 11 individuals, 17 interrays had only one interbrachial, one interray had two plates, one interray had four plates, and 9 interrays had no interbrachials. Most specimens have two or more rays with interbrachials, and some are characterized by interbrachials in all lateral interrays (BMS E26382).

One specimen assigned to *K. tetreaulti* is especially interesting. This individual (BMS E26372) has only one interbrachial in the BC interray; interbrachials are



Text-figures 24A–F.—*Kyphosocrinus tetreaulti* n. gen. and sp., diagrams of interray variation. A–C. Three lateral views of BMS E26383. A. CD interray with extra anal plates. B. EA interray with three interbrachials. C. Crown centered on B ray. AB interray has no interbrachials; BC interray has four small interbrachials. D. BMS E26375 centered on D ray. CD interray has extra anal plate. E. Anterior view of BMS E26356b. F. CD interray with anal **X** flanked by two smaller plates, BMS E26378. Radials black, interbrachials stippled. Scale for all figures is 1 mm.

absent in the remaining interrays (Pl. 7, figs. 4, 5). It would only require the elimination of this single plate, addition of one or more regular polygonal anal plates, and less marked heterotomy to create a form indistinguishable from *Clidochirus*. Evidently, the Anisocrinidae is the ancestral stock of the Icthyocrinidae.

Types and occurrence.—The 15 known specimens of *K. tetreaulti* n. sp. (holotype BMS E26377, paratypes BMS E26347d–e, BMS E26356b, BMS E26373–E26376, BMS E26378–E26385) are all from the Wolcott Limestone, locality 8.

Etymology of name.—The species is named for Denis Tetreault, a former graduate student at the University of Rochester, who discovered the first specimen of this species.

?Anisocrinid species A
Plate 8, figure 6; Text-figure 25

Description.—This species is represented by a single damaged crown 16.3 mm high with attached partial column 35 mm long. Cup smooth, unornamented, arms free above primibrachials. Infrabasal circlet comprising 15% of cup height, infrabasals mostly missing. CD interray basal heptagonal, elongate (h/w = 1.5). Radial circlet divided by CD interray basal and anal X. Radials pentagonal, wider than high (h/w = 0.7–0.8). Radianal small, pentagonal, situated directly below C ray radial. Primibrachials two, wider than high (h/w = 0.4–0.6), truncated shoulders supporting small, quadrangular interbrachial in DE interray. Anal X hep-

Table 9.—Measurements (in mm) of six specimens of *Kyphosocrinus tetreaulti* n. sp.

	BMS E26377 (holotype)	BMS E26372	BMS E26375	BMS E26380	BMS E26382	BMS E26383
Crown height*	28.0	22.7	14.0	13.8	14.0	16.6
Cup width**	17.0	15.8	11.0	10.5	8.7	10.9
AB IB height	1.5	2.3	—	1.6	1.3	1.7
AB IB width	—	3.8	—	2.9	2.5	2.3
C IB height	1.6	1.8	1.3	1.3	—	1.9
C IB width	2.7	3.0	2.2	2.4	1.9	2.3
DE IB height	—	2.3	1.6	1.5	1.3	1.8
DE IB width	—	4.2	—	2.8	2.9	3.6
AB B height	4.2	5.0	—	3.2	2.9	3.6
AB B width	—	4.2	—	3.3	2.8	3.4
BC B height	3.6	4.1	3.4	3.5	3.0	3.5
BC B width	3.6	3.8	3.0	3.3	2.8	3.4
CD B height	4.4	4.9	3.7	3.7	3.4	4.5
CD B width	4.1	4.7	3.6	3.6	3.9	4.7
DE B height	—	4.9	3.2	3.1	4.2	4.9
DE B width	—	4.4	3.0	3.0	3.0	3.8
EA B height	—	5.3	—	3.5	3.0	3.8
A R height	—	4.1	—	3.2	3.2	3.5
A R width	—	6.4	—	4.5	4.1	5.0
B R height	3.9	4.0	—	3.2	2.8	3.3
B R width	5.2	6.0	—	4.9	3.9	4.5
C R height	—	3.2	2.1	2.2	2.1	2.3
C R width	4.0	4.7	3.6	3.8	3.5	4.0
D R height	3.5	3.9	3.2	3.0	3.0	3.2
D R width	—	5.5	4.0	4.1	3.5	4.0
E R height	—	4.1	3.0	3.2	3.0	3.5
E R width	—	5.7	3.9	4.6	4.2	5.5
A IBr1 height	—	2.5	—	2.0	1.6	1.9
A IBr1 width	—	6.9	—	4.8	3.9	5.2
B IBr1 height	2.1	2.3	—	1.8	1.7	2.1
B IBr1 width	5.5	6.5	—	4.8	4.2	5.1
C IBr1 height	1.9	2.5	1.8	1.7	1.7	1.8
C IBr1 width	4.3	4.9	4.2	4.5	3.8	4.8
D IBr1 height	2.1	2.3	1.9	1.6	1.7	1.8
D IBr1 width	—	5.8	4.7	4.3	3.8	4.9
E IBr1 height	—	3.2	2.1	1.8	1.8	1.7
E IBr1 width	—	6.8	4.2	4.6	4.2	5.3
A IBr2 height	—	2.5	—	1.7	1.6	2.0
A IBr2 width	—	6.1	—	4.0	3.4	4.5
B IBr2 height	2.0	2.3	—	1.7	1.6	2.1
B IBr2 width	5.1	6.2	—	4.1	3.6	4.4
C IBr2 height	2.1	2.3	2.0	2.0	1.7	2.0
C IBr2 width	5.0	6.0	4.5	4.3	3.5	5.1
D IBr2 height	2.1	2.6	2.0	1.7	1.7	1.9
D IBr2 width	—	6.3	4.6	4.3	3.0	5.0
E IBr2 height	—	2.5	1.8	2.0	1.7	1.7
E IBr2 width	—	6.3	3.9	4.0	3.7	3.8
AB iIBr1 height	1.4	+	—	+	1.1	1.0
AB iIBr1 width	—	+	—	+	0.8	0.5
BC iIBr1 height	1.9	2.2	—	1.1	1.0	1.0
BC iIBr1 width	1.5	1.3	—	1.1	0.8	0.6
DE iIBr1 height	—	+	+	1.4	1.2	1.1
DE iIBr1 width	—	+	+	1.0	0.8	0.9
EA iIBr1 height	—	+	—	1.7	1.2	+
EA iIBr1 width	—	+	—	1.1	0.9	+
RA height	2.7	3.5	2.6	2.5	2.2	2.7
RA width	3.9	4.4	3.3	3.7	2.9	3.7
Anal X height	4.3	6.3	3.4	4.0	3.7	4.5
Anal X width	3.3	4.2	2.6	2.5	2.5	3.1

Table 9.—Continued.

	BMS E26377 (holotype)	BMS E26372	BMS E26375	BMS E26380	BMS E26382	BMS E26383
X1 height	+	+	1.4	0.9	1.0	+
X1 width	+	+	1.3	0.6	0.7	+
Column length	—	165	—	—	—	—
Proximal diameter	—	2.0	—	—	—	—
Distal diameter	—	1.8	—	—	—	—

* Distal arms coiled.

** Crushed cup (width greater than diameter).

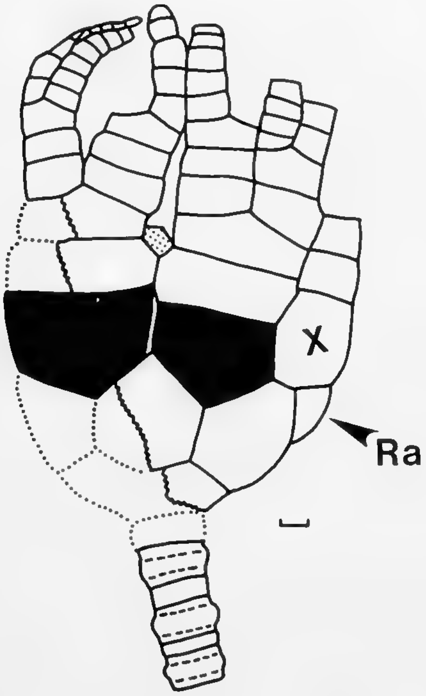
\+ This plate absent.

tagonal, higher than wide (h/w = 1.2). X_1 and X_2 trapezoidal, wider than high, sutured to C ray only. X_3, now missing, originally sutured to C ray. Distal anitaxis missing, originally consisting of several additional plates extending at least to tertibrachials.

Arms free above first primibrachials, dividing isotomously on second primibrachials. Higher divisions on second or third secundibrachials and second to fifth tertibrachials slightly heterotomous with weakly developed endotomy. Distal portions of arms unknown.

Proximal section of column round, heteromorphic, consisting of alternating nodals and internodals.

Remarks.—The resemblance of this specimen to *Kyphosocrinus tetreaulti* is obvious; perhaps it is just a mutation of this species. However, the anitaxis of this specimen, distally sutured to the C ray only, precludes assignment to *Kyphosocrinus* as presently defined and it seems unwise to emend an already somewhat broadly defined genus. The significance of this individual, if it is indeed a mutant *Kyphosocrinus,* is that it demonstrates the ease with which rapid evolutionary change (cladogenesis) could occur in the Flexibilia. The absence of a radianal in *Paranisocrinus* and a specimen of *Protaxocrinus anellus* n. sp. are also excellent examples of mutations leading to rapid and important changes in morphology.



Text-figure 25.—?Anisocrinid species A, plate diagram of BMS E26390. Radials black, interbrachial stippled. Scale is 1 mm.

Material and occurrence.—Figured specimen BMS E26390 is from calcareous shale 1.0 m above the base of the Wolcott Limestone, locality 8.

Family SAGENOCRINITIDAE Roemer, 1854

Emended diagnosis.—Sagenocrinitaceans with large, ovoid to pyriform crown. Infrabasals visible in side view or concealed. Radianal situated directly below C ray radial, exceptionally dividing basal circlet. Anal tube absent. Fixed brachials and interbrachials numerous. Arms isotomous or heterotomous with variably developed endotomy.

Included genera.—*Sagenocrinites* Austin and Austin, 1842, Sil. (Wenlock-Ludlow); *Forbesiocrinus* De Koninck and Le Hon, 1854, L. Miss. (Tournaisian)—U. Miss. (Chesterian); *Scapanocrinus* n. gen., L. Sil. (late Llandovery); *Trampidocrinus* Lane and Webster, 1966, L. Perm.

Remarks.—Diagnosis of the Sagenocrinitidae is herein emended in order to accommodate forms with heterotomous arms. The origin of this group, discussed below, is obscure.

Genus SCAPANOCRINUS, new genus

Type species.—*Scapanocrinus muricatus* n. sp.

Diagnosis.—A genus of Sagenocrinitidae with ovoid crown and nearly cylindrical infrabasal circlet. Basal circlet undivided. Radianal pentagonal, situated directly below C ray radial, supporting anal X in radial circlet. Rays dividing two or three times in cup. Interrays wide, similar in width, interbrachials numerous.

Arms heterotomous, endotomous. Column round, dominantly heteromorphic.

Remarks.—The monotypic genus *Scapanocrinus* n. gen. is the earliest described representative of the Sagenocrinitidae. *Sagenocrinites* is said to occur in the late Llandovery Jupiter Formation of Anticosti Island, but the material is undescribed (Bolton, 1981). *Scapanocrinus* is apparently closely related to *Sagenocrinites,* but exact ancestor-descendant relationships of these genera are unknown. *Scapanocrinus* differs from *Sagenocrinites* in possessing a cup with a constricted base, heterotomous rather than isotomous arms, and a radianal situated above rather than in the basal circlet. The single known specimen of *Sagenocrinites americanus* Springer, 1902 from the Beech River Member of the Brownsport Formation (Silurian, Ludlow) of Tennessee should be removed from this genus. It is anomalous in possessing an uninterrupted basal circlet and a quadrangular radianal situated obliquely below the C ray radial (see Springer, 1926b, p. 216, pl. 22, fig. 5). Although it is older, *Scapanocrinus* was probably not ancestral to *Sagenocrinites* because the heterotomous arms of *Scapanocrinus* are an advanced character in contrast to the isotomous arms of *Sagenocrinites* and *Temnocrinus* Springer, 1902. On the other hand, placement of the radianal within the basal circlet of *Sagenocrinites* is clearly a derived, advanced character in comparison to *Scapanocrinus,* which retains the radianal in a primitive position directly below the C ray radial. It seems probable that these taxa are separate offshoots of an unknown ancestral stock like *Scapanocrinus* but with isotomous arms. In turn, the Sagenocrinitidae gave rise to the Dactylocrinidae Bather, 1899 through simplification of the cup (fewer interbrachials) and development of more marked heterotomy.

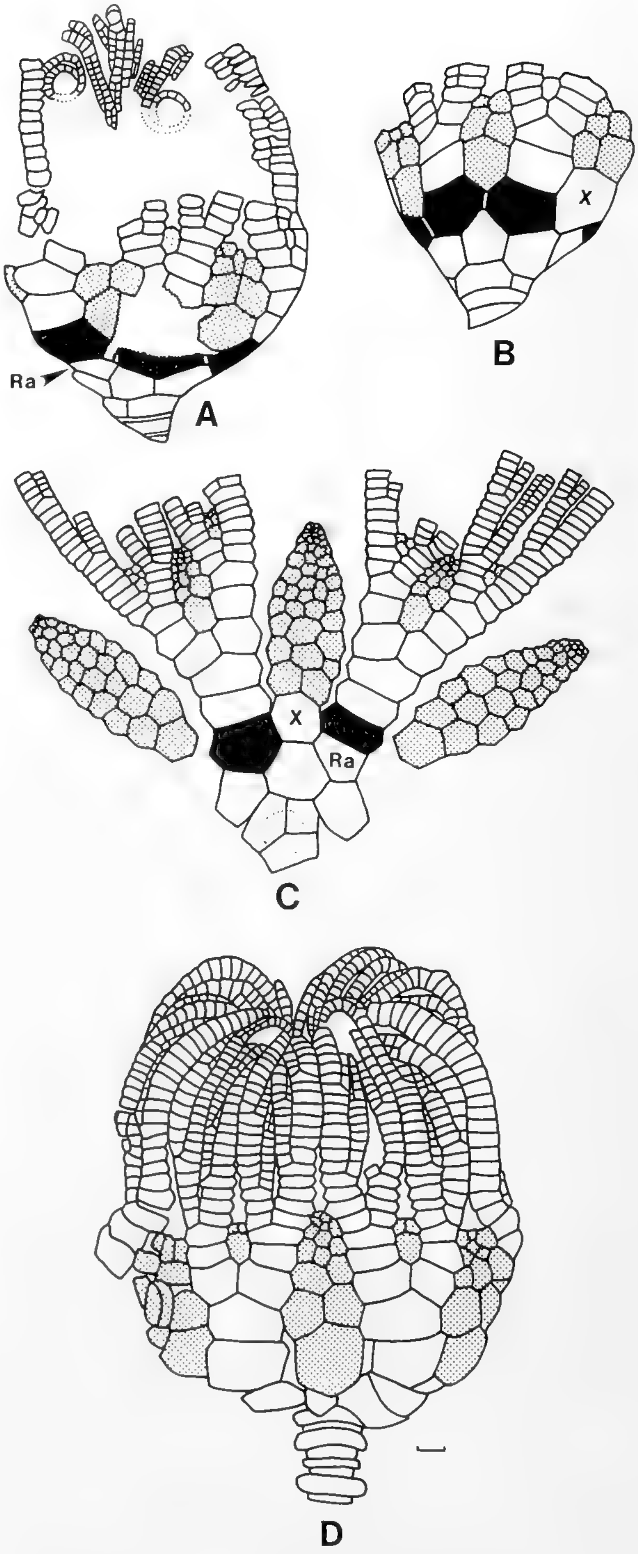
Etymology of name.—*scapanos* (Gr.) = spade, digging tool (pick and shovel work resulted in discovery of this genus) + *krinon* (Gr.) = lily.

Scapanocrinus muricatus, new species

Plate 8, figures 1, 7, 12–14, 16–18; Text-figures 26A–D

Diagnosis.—A species of *Scapanocrinus* characterized by median keels on rays, angular brachials in proximal arms, and dominantly heteromorphic column.

Description.—Crown ovoid, exceptionally large (adult height estimated to be at least 100 mm). Cup bowl-shaped, wider than high (h/w = 0.8), expanding rapidly above constricted base formed by nearly cylindrical infrabasal circlet (Pl. 8, fig. 18). Arms free above secundibrachials in small individuals (cup height 14–20 mm), free above tertibrachials in larger individuals.



Text-figures 26A–D.—*Scapanocrinus muricatus* n. gen. and sp. A. Plate diagram of incomplete crown centered on B ray, holotype BMS E26385. B. Same specimen centered on DE interray. C. Expanded plate diagram. D. Lateral view of crown displaced downward onto column, BMS E26386. Radials black, interbrachials stippled. Scale for figures A, B, and D is 2 mm.

Radials and fixed brachials V-shaped in transverse cross section, forming median keels on rays (Pl. 8, fig. 16). Remaining cup plates smooth, unornamented. Infrabasal circlet comprising approximately 15% of cup height. Infrabasals three, wider than high (h/w = 0.4), separated from each other by sutures in BC, CD, and EA interrays. C ray infrabasal pentagonal, AB and DE infrabasals six-sided. Basal circlet uninterrupted, basals five, height equal to or slightly exceeding width (h/w = 1.0–1.1). CD interray basal heptagonal, AB and DE interray basals pentagonal, BC and EA interray basals hexagonal. Radials wider than high; AB and D ray radials seven-sided, D ray radial six-sided, C ray radial five-sided, smaller than other radials. Radial circlet divided by CD interray basal and anal X. Radianal pentagonal, wider than high (h/w = 0.6), situated directly below C ray radial. First primibrachials roughly rectangular, wider than high (h/w = 0.3–0.6), upper corners commonly slightly truncated. Second primibrachials pentagonal, wider than high (h/w = 0.4–0.6), lower corners commonly truncated. Secundibrachials wider than high, two or three in each half-ray. Anal X heptagonal, subequal, situated between C and D ray radials directly above CD interray basal. CD interray above anal X not differentiated from lateral interrays (Text-fig. 26B). Interrays wide, interbrachials numerous. First interprimibrachial in each interray hexagonal, slightly wider than high (h/w = 1.1), succeeded by tier of two plates and at least 15 more interbrachials in an individual of moderate size (BMS E26386), additional interbrachials present in large specimens. Each pair of half-rays separated by several intersecundibrachials. Intertertibrachials present in the largest individuals (Pl. 8, fig. 17).

Free arms strongly heterotomous with well developed endotomy. In two observed rays of BMS E26386, outer rami of each quarter-ray divide on fourth to sixth tertibrachial and eighth or ninth quartibrachial, higher divisions concealed by distally coiled arms (Pl. 8, fig. 16; Text-fig. 26D). Inner (adaxial) arms of each quarter-ray narrower than outer arms, dividing on third or fourth tertibrachial, seventh to at least eleventh quartibrachial, and ninth quintibrachial. Median ray keels merging with dorsally rounded arms. Proximal free brachials angular-sided (V-shaped), distal brachials smooth-sided. Brachials less than three times wider than high.

Column round, relatively short (65 mm in BMS E26386), length not exceeding height of outstretched crown. Proximal diameter of column 4.8 mm in BMS E26386, diameter tapering gradually to 2.6 mm near distal end. Proximal and medial sections of column heteromorphic. Typical proximal noditaxis formula N, 3IN, 2IN, 3IN, 1IN, 3IN, 2IN, 3IN. Noditaxes becoming simpler distally; typical medial formula N, 2IN, 1IN, 2IN, and N, IN near distal end. Epifacets of nodals and larger internodals thick, rounded. Largest nodals up to 160% diameter of adjacent internodals. Columnal height 0.2–1.4 mm in BMS E26386. Holdfast radicular, bearing numerous stout, branching radicles cemented to bryozoan zoarium (Pl. 8, fig. 7).

Remarks.—Shale rich in fenestellid bryozoans yielded only a single small specimen of this taxon (BMS E26386). Larger, incomplete individuals are restricted to limestone beds representing tempestites derived from nearby shoals. Apparently, *Scapanocrinus* was largely restricted to higher energy conditions than existed during deposition of the shale. It therefore may have been more abundant than presently indicated.

Types and occurrence.—*Scapanocrinus muricatus* n. sp. is represented by specimens, holotype BMS E26385 and paratypes BMS E26386–E26387 and 4485BMS E26389 from an interval of shale and limestone 1.1–1.2 m above the base of the Wolcott Limestone, locality 8.

Measurements (in mm) of BMS E26385.—Crown height (distal arms coiled) = 28.1, actual height estimated to be approximately 37); cup height = 14.0; crushed cup width = 21.2, original diameter 17.5; AB IB height = 1.9, width = 4.3; C IB height = 1.5, width = 3.7; DE IB height = 2.0, width = 4.7; AB B height = 4.1, width = 4.0, BC B height = 3.4, width = 3.5; CD B height = 4.0, width = 3.8; DE B height = 4.0, width = 4.0; EA B height = 4.4, width = 4.0; A R height = 4.5, width = 5.3; C R height = 2.8, width = 4.0; D R height = 3.8, width = 5.3, E R height = 4.2, width = 6.3; A IBr_1 height = 2.7, width = 4.3; C IBr1 height = 2.3, width = 3.9; D IBr_1 height = 2.4, width = 4.8; E IBr1 height = 2.6, width = 4.6; A IBr2 height = 2.8, width = 4.4; C IBr_2 height = 2.1, width = 4.2; D IBr_2 height = 2.4, width = 5.8; E IBr2 height = 2.5, width = 4.5; AB iIBr1 width = 3.8; DE $iIBr_1$ height = 4.0, width = 3.6; EA iIBr1 height = 4.4, width = 3.9; RA height = 2.7, width = 4.5; anal X height = 4.6, width = 4.4.

Etymology of name.—*muricatus* (L.) = full of sharp points, pointed; the specific epithet refers to the angular brachials of the proximal free arms.

Family unknown

Flexible crinoid species A

Plate 8, figures 11, 15

Description.—This species is represented by a single crown with an almost entirely disarticulated cup (BMS E26391). Nothing is known about the structure of the infrabasals, basals, radials, and anal plates. Number of primibrachials in each ray unknown. Distal interray areas each containing a large, polygonal interbrachial between axillary primibrachials.

Arms free above primibrachials, first observed division of each isotomous. Arms strongly heterotomous distally with well developed endotomy. Stout inner and outer rami dividing on third secundibrachials, fifth to seventh tertibrachial, and at least once more on sixth or higher quartibrachials. Adaxial branches dividing on second or third tertibrachials, higher divisions concealed. Brachials thick (maximum thickness 2.2 mm), rounded dorsally, less than two times wider than high.

Remarks.—Incomplete material precludes identification of this species. The single small interbrachial in each ray suggests *Kyphosocrinus* but the strongly heterotomous arms are like *Scapanocrinus.* However, the thick robust plates are unlike either of these genera.

Material and occurrence.—Figured specimen BMS E26391 is from a horizon with abundant bryozoans 1.1 m above the base of the Wolcott Limestone, locality 8.

Subclass unknown

Crinoid species B

Plate 2, figures 16, 17

Description.—Encrusting, five-lobed holdfasts up to 12 mm in diameter with five narrow slits alternating with lobes. Lobes of large examples may have smaller, subsidiary lobes (Pl. 2, fig. 17). Holdfasts attached to skeletal material including zoaria of bryozoans and fragments of trilobite exoskeletons.

Remarks.—The illustrated examples are attached to the inner surface of a pygidium of a large illaenid trilobite, possibly *Bumastus ioxus.*

Material and occurrence.—Figured pygidium BMS E26408 is from an unknown horizon in the Hickory Corners Member of the Reynales Formation, locality 2.

Crinoid species C

Plate 9, figures 10, 20

Description.—Column round, xenomorphic, robust and long (up to 13 mm in diameter, substantially exceeding 29 cm in length), gradually tapering distally. Proximal section consisting of nodals with rounded, slightly nodose latera and straight-sided internodals, typical noditaxis formula N, 1IN, 1IN, 1IN. Columnals in medial section of column straight-sided, noditaxes more complex, consisting of a nodal, two or three second order internodals, a first order internodal, and two or three second order internodals. Nodals in distal section of column possessing large nodes on latera, noditaxes similar to those of medial section. Lumen round, occupying 60% diameter of proximal column, 25% diameter of medial column. Remainder of each columnal occupied by narrow areola and broad crenularium. Columnals low, wide (height 0.4–2.8 mm, h/w = 0.03–0.23), sutures sympectial.

Remarks.—Many packstone and grainstone beds within the Wolcott Limestone consist almost entirely of columnals and pluricolumnals of this species. Similar pluricolumnals are also encountered in the argillaceous facies of the lower portion of the Wolcott Limestone. However, they are never more than a few cm long in contrast to sections of column more than 30 cm long in the upper beds. These fossils represent large, robust, stenotopic crinoids that inhabited carbonate shoals where they must have formed immense stands. Unfortunately, the agitated conditions preferred by these crinoids were not condusive to their preservation as articulated individuals. Thin beds of crinoidal limestone in the dominantly clastic facies of the lower portion of the Wolcott Limestone represent distal tempestites of powerful storms that swept these shoals.

Material and occurrence.—Figured specimens BMS E26416 and E26417 are from crinoidal grainstones 1.5 m above the base of the Wolcott Limestone, locality 8.

Crinoid species D

Plate 9, figures 1, 6, 11–13

Description.—Column long (incomplete examples exceeding 20 cm in length), xenomorphic, pentameric, with distinct longitudinal sutures. Column diameter 6–10 mm, approximately constant within individuals. Columnals thin (height 0.5–1.4 mm, h/w = 0.08–0.2), becoming progressively thinner distally. Inferred proximal portion of column obscurely pentagonal, grading into round medial section. Distal section pentagonal, distal-most several centimeters giving off rootlets at junctions of pentameres. Proximal lumen round, diameter 50% of column; lumen in medial section of column pentastellate, angles alternating with pentameres, diameter approximately 15% of column. Areola narrow, depressed, crenularium broad. Culminae fine, numerous, typically 15 to 25 on articular surface of each pentamere.

Remarks.—Columnals and pluricolumnals of this unknown crinoid are among the most distinctive echinoderm fossils of the Willowvale Shale. Unfortunately, its identity remains unknown in absence of preserved crowns or calices. The pentameric structure of the column suggests cladid affinities.

Material and occurrence.—A nearly complete column (BMS E26411a–c) and pluricolumnals BMS E26412 and E26413 are from the Willowvale Shale, 2 m above the base of this formation, locality 11.

Crinoid species E
Plate 9, figures 21, 24

Description.—Known from partial holdfasts only, consisting of gently curved pluricolumnal segments up to 11 cm in length. Segments oval in cross section, flattened in inferred dorsal-ventral plane, bearing numerous abortive cirri and attachment scars of rootlets on lower surfaces. Columnals commonly wedge-shaped, thin (height 0.6–1.6 mm, h/w = 0.06–0.2), with symplectial sutures tending toward partial fusion. Lumen large, round or slightly oval, average diameter 50% that of column.

Remarks.—These holdfasts closely resemble creeping stems or stolons (Franzén, 1977, p. 222, fig. 2F; Brett, 1978a, p. 351, fig. 4H) and the form genus *Eurax eugenes* Moore and Jeffords, 1968 (see Ubaghs, 1978, T75, fig. 54, no. 10). They represent sections of columns that, in life, were recumbent on the seafloor, to which they were attached by radicles and digitate extensions of stereom.

Material and occurrence.—Figured specimens BMS E26437 and BMS E26438 are from the Willowvale Shale, locality 10.

Crinoid species F
Plate 9, figures 22, 23

Description.—Columnal doughnut-shaped, 13.6 mm in diameter with a central opening 6.1 mm in diameter. Maximum thickness 3.3 mm adjacent to central opening, tapering abaxially. Columnal smooth, articular surfaces worn away.

Remarks.—This fossil closely resembles specimens described by Hall (1852, p. 182, pl. 41, figs. 7a–e). This material is believed to be of crinozoan origin because blastozoans are extremely rare in the lower Clinton Group. These columals are commonly associated with hematite-rich, oolitic limestones that originated as regressive lag deposits in shallow, high energy regimes characterized by low net rates of sedimentation. These environments were evidently ideal for growth of certain crinoid taxa but not for their preservation. After death, the crinoids were thoroughly disarticulated and their ossicles became extensively abraded as they were washed about by wave and current activity on an abrasive substrate.

Material and occurrence.—Figured specimen BMS E26439 is from the Kirkland Iron Ore, locality 11. Similar material occurs in the Willowvale Shale at this locality.

Crinoid species G
Plate 9, figures 18, 25

Description.—This species is represented by partial holdfasts consisting of incomplete, branching pseudocirri more than 10 cm in length. Pseudocirri each consisting of a gently arcuate main branch up to 5 mm in diameter with smaller branches given off on one side at regular intervals, diverging from the main branch at angles of 45 to 55 degrees. Smaller branches subparallel to each other, dividing at least once. Pseudocirrals short, cylindrical segments (height 1.1–2 mm, h/w = 0.2–0.8) with smooth articular surfaces and small, round lumen.

Remarks.—These distinctive fossils are locally abundant in the Willowvale Shale and rare examples also occur in the upper portion of the Williamson Shale. In the Willowvale Shale they are associated with stout, heteromorphic pluricolumnals that may belong to this species (Pl. 9, fig. 19). The pseudocirri probably represent large, radial props that supported the column of a large, robust species of crinoid. Probably only the subsidiary branches and distal end of the main branch were actually inserted in the substrate.

Material and occurrence.—Figured specimens BMS E26414 and BMS E26415 are from a thin, fossiliferous horizon 2 m above the base of the Willowvale Shale, locality 11.

Ichnogenus *Tremichnus* Brett, 1985
Ichnospecies *Tremichnus cysticus* Brett, 1985
Plate 9, figures 14–17

Description.—The specimen consists of a grotesquely deformed pluricolumnal 39 mm long and 11–14 mm in diameter. The columnals are fused together by excess stereom covered with more than 220 pits of the ichnospecies *Tremichnus cysticus* Brett, 1985.

Remarks.—Eckert (1988) described and illustrated the remarkable example of *T. cysticus* refigured herein. It is the only example of *T. cysticus* known from the Early Silurian. *Tremichnus* probably represents embedment sites of unknown, host-specific epizoans (Franzén, 1974; Brett, 1978b, 1985).

Type and occurrence.—Hypotype ROM 44359 is from the Willowvale Shale, locality 11.

APPENDIX

LOCALITY REGISTER

Crinoids were collected from the following 11 localities (see Text-figure 2). A topographic map reference is given for each locality.

Loc. 1. Hickory Corners Member of Reynales Formation; east side of Niagara River Gorge opposite Sir Adam Beck No. 1 hydroelectric station, 1.8 km (1.1 miles) south of Artpark, Lewiston, Niagara Co., New York. United States Geological Survey Lewiston 7.5′ Quadrangle.

2. Hickory Corners Member of Reynales Formation;

embankments of Somerset Railroad 0.7 km (0.43 miles) northeast of Niagara Street, Lockport, Niagara Co., New York. USGS Lockport 7.5′ Quadrangle.

3. Hickory Corners Member of Reynales Formation; bed and east bank of Oak Orchard Creek, John E. Butts Memorial Park, Medina, Orleans Co., New York. USGS Medina 7.5′ Quadrangle.

4. Wallington Member of Reynales Formation; Genesee River Gorge 0.3 km (0.2 miles) north of lower falls, talus slope east of Rochester Gas and Electric access road, Rochester, Monroe Co., New York. USGS Rochester West 7.5′ Quadrangle.

5. Wallington Member of Reynales Formation, Densmore Creek, 100 m (330 feet) east of Densmore Road, Rochester, Monroe Co., New York. USGS Rochester East 7.5′ Quadrangle.

6. Wallington Member of Reynales Formation; spoil heaps on north side of abandoned strip mine west of Knickerbocker Road, Ontario Center, Monroe Co., New York. USGS Ontario 7.5′ Quad.

7. Upper Sodus Shale; bed of Second Creek 20 m (65 feet) downstream (north) of dam on north side of Red Mill Road, Wayne Co., New York. USGS Rose 7.5′ Quadrangle.

8. Wolcott Formation; east bank of Mudge Creek 55 m (180 feet) north of Chapin Road bridge, Wayne Co., New York. USGS North Wolcott 7.5′ Quad.

9. Bear Creek Shale; bank exposures in waterfall of Bear Creek 180 m (590 feet) south of Caywood Road, Wayne Co., New York. USGS Fair Haven 7.5′ Quadrangle.

10. Willowvale Shale; exposures in drainage ditch on north side of exit ramp of Interchange 33, New York State Thruway, 0.5 km (0.3 miles) east of Route 365, Oneida Co., New York. USGS Vernon 7.5′ Quadrangle.

11. Willowvale Shale; tributary of Sauquoit Creek 2.5 km (1.5 miles) west of Bridgewater Street, New Hartford (Willowvale), Oneida Co., New York. USGS Utica West 7.5′ Quadrangle.

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PLATES

EXPLANATION OF PLATE 1

Figure — Page

1, 2, 9–12, 19–20, 25. ***Haptocrinus calvatus*** new genus and species. All specimens are from the Reynales Formation, Hickory Corners and Wallington members. 42

- 1–2. 1. Large individual with cup and long, incomplete, pentameric column. Weathering has exposed lumen in proximal column, ×1; 2. Anterior view of cup. Note two fixed primibrachials in each ray, ×2. Paratype BMS E26331.
- 9–10. 9. Anterior view of partial crown. Arms divide isotomously on fourth primibrachial and branches abut each other closely, concealing ramules. Arrow indicates axillary secundibrachial with missing ramule. Pentameres of column are visible below cup, ×3; 10. Overall view, column incomplete, ×1.5. Holotype BMS E26329a.
- 11. Anterior view of crown with small, regenerated arms, ×4. Paratype BMS E26332a.
- 12. Articular surface of proximal columnal, ×4.5. Paratype BMS E26324a.
- 19. Articular surface of medial columnal, ×4. Paratype BMS E26324b.
- 20. Distal column, ×2.5. Paratype BMS E26334.
- 22. Anterior view of small crown preserved in hard crinoidal grainstone. Anitaxis, indicated by upper arrow, is grooved ventrally. Note ramule (lower arrow) in left arm, ×2.5. Paratype BMS E26320.
- 25. Partial arm. Incomplete ramules are borne by every other secundibrachial, ×4.5. Paratype BMS E26436a.

3, 4, 13–15, 26, 27. ***Dynamocrinus robustus*** new genus and species. Reynales Formation, Hickory Corners Member. 30

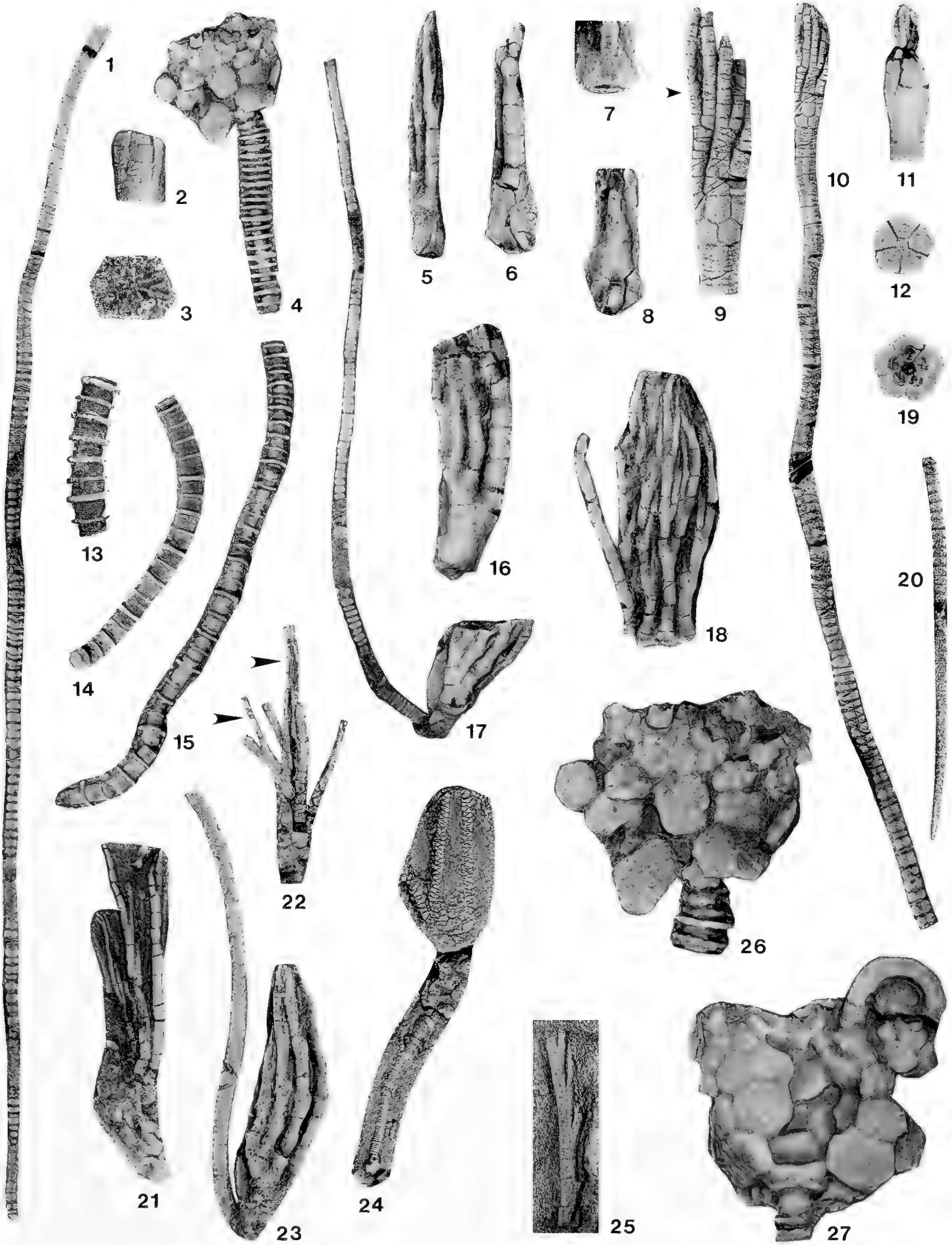
- 3. Isolated radial plate with ridges radiating from plate center, ×2. Paratype BMS E26400.
- 4, 26, 27. 4. Inferred anterior view of crushed calyx and proximal column. Interray (center) consists of single row of interbrachials successively narrower distally. Heteromorphic column has wide, narrow epifacets, ×1; 26. Inferred anterior view, ×2; 27. Inferred posterior view. Primanal is bounded above by two plates before CD interray constricts to a single row of plates distally. Flat base of cup is circumscribed by ridge on basal circlet, ×2. Holotype BMS E26304.
- 13. Medial section of column, ×2. Paratype BMS E26401.
- 14. Medial section of column, ×1.2. Paratype BMS E26402.
- 15. Medial and incomplete distal sections of column, ×1. Paratype BMS E26403.

5–8, 16–18, 21, 23. ***Thaerocrinus crenatus*** new genus and species. Reynales Formation, Hickory Corners Member. 36

- 5, 7, 23. 5. Oblique E ray view of crown. Expanded and forked base of E ray inferradial is in narrow contact with triangular E ray superradial. First division of E ray arm is isotomous, higher divisions are heterotomous, ×2.5; 7. Basal view. All three basals are in contact with column facet, ×5; 23. A ray view of crown and column, ×3. Holotype BMS E26305.
- 6, 8, 16. 6. E ray view of crown. E ray inferradial constricts rapidly distally and does not appear to be in contact with superradial, ×2.5; 8. CD interray view of lower portion of crown. Note stout, rapidly tapering anal tube, ×3; 16. A ray view of crown, ×3. Paratype BMS E26308.
- 17. A ray view of incomplete crown and column, ×2. Paratype BMS E26306a.
- 18. A ray view of large crown with missing base. Arms are spread out, revealing heterotomous ramules and endotomy in secundaxil arm, ×2.3. Paratype BMS E26307.
- 21. A ray view of crown with damaged cup, ×2. Paratype BMS E26306c.

24. ***Macrostylocrinus*** sp. Reynales Formation, Wallington Member. 33

- 24. CD interray view of deeply weathered crown, column and holdfast. Large primanal supports secundanal flanked by smaller plates. Incomplete cirri are borne by swollen nodals. Note small discoidal holdfast, ×2. Figured specimen BMS E26329b.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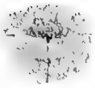
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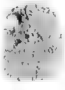
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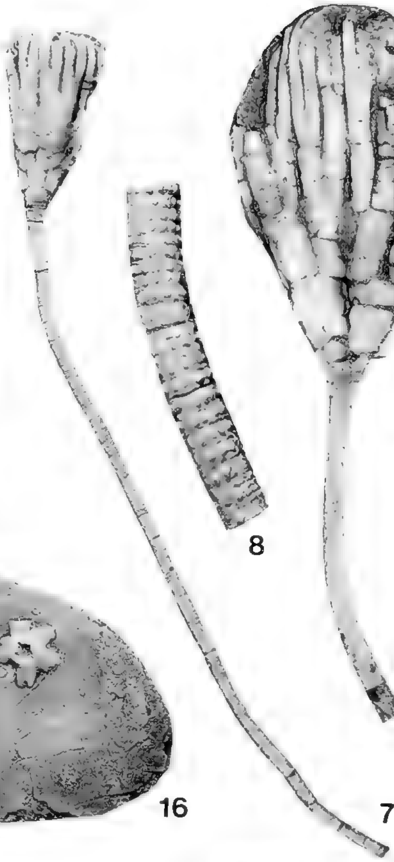
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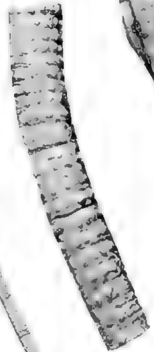
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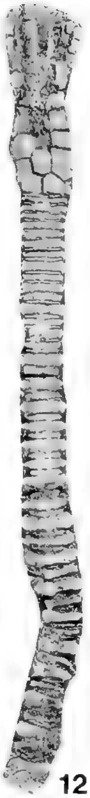
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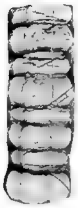
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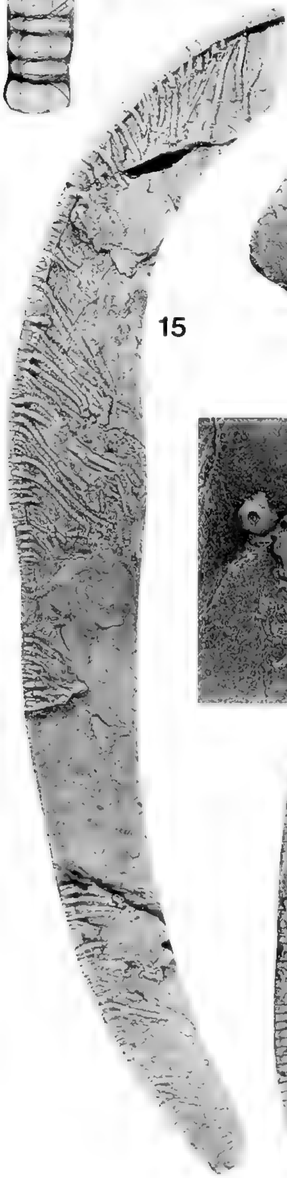
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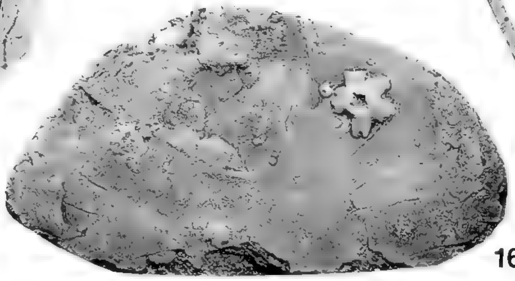
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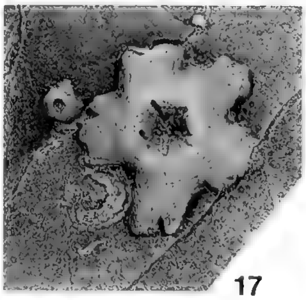
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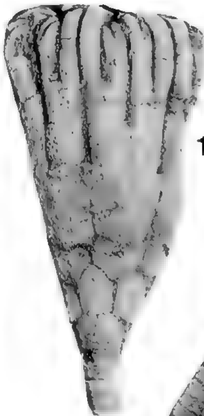
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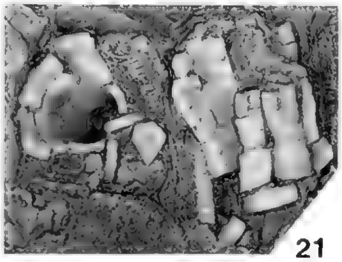
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EXPLANATION OF PLATE 2

Figure Page

2, 4, 15, 22. ***Eomyelodactylus sparteus*** Eckert. Reynales Formation, Hickory Corners Member. 38

1. Weathered columnal from coiled portion of column. Note obscurely pentagonal outline of columnal and distinct pentameres. Large, lenticular lumen is excentrically situated near convex, outer side of columnal, ×5. Paratype BMS E26404.
2. Columnal from cirriferous section of column. Columnal is elliptical with long axis in plane of coiling. Two rows of cirri are each represented by a single cirral projecting obliquely toward plane of coiling. Cirrals are fused longitudinally to adjacent pentameres on inner side of columnal. Small, bell-shaped lumen is excentrically situated near outer side, ×5. Paratype BMS E26405a.
4. Columnal from inner portion of coil near recurved junction. Columnal is elliptical with long axis perpendicular to plane of coiling. Large, lens-shaped lumen is situated near outer margin of columnal, ×5. Paratype BMS E26407a.

15, 22. 15. Cirriferous medial and distal sections of column of large individual. Cirri become progressive smaller and more closely spaced distally, ×0.9; 22. Detail of medial section of cirriferous column. Cirri, initially projecting obliquely from column, are brought into plane of coiling by curved cirrals fused to columnals. Note irregular arrangement of small and large cirri. Barrel-shaped cirrals have expanded distal margins and deeply impressed sutures, ×3. Holotype BMS E26309.

3, 5, 18, 20. ***Eomyelodactylus uniformis.*** Eckert Reynales Formation, Hickory Corners and Wallington members. 38

3. Nudinodal probably from distal region of column, ×5. Paratype BMS E26406.
5. Proximal coiled column of a small individual, ×4. ParatypeBMS E26315.

18, 20. Overall view of incomplete, cirriferous column, ×2; 20. Detail of cirri, ×4. Holotype BMS E26409a.

6–9, 19, 21. ***Prolixocrinus nodocaudis*** new genus and species. Reynales Formation, Hickory Corners Member. 54

6. CD interray view of partial crown with missing infrabasals. Anal **X** is situated above hexagonal CD interray basal. BC interray basal, situated directly below radianal, is smaller than remaining basals, ×1.5. Paratype BMS E26326.

7, 8, 19. 7. Nearly complete young individual centered on A ray, ×1; 54

8. Detail of nodose proximal column, ×3; 19. Detail of crown illustrating high, conical shape and large infrabasals, ×2. Paratype BMS E26325.
9. Crushed crown of large individual. C ray is to left. Radianal is situated directly below narrow C ray radial and anal X is visible on the extreme left, ×1. Holotype ROM 43634.
21. Small, disarticulated crown divided into lower and upper portions on opposite sides of pinnulate arm of unknown camerate crinoid, ×2. Paratype BMS E26327.

10–14. ***Haptocrinus calvatus*** new genus and species. Reynales Formation, Hickory Corners Member. 42

10. Cup and proximal column of very small individual. C ray is to left, ×5. Paratype BMS E26324.
11. Cup and proximal column, ×3. Paratype BMS E26332b.
12. Weathered crown and partial column of an immature individual centered on B ray, ×4. Paratype BMS E26322.
13. Anterior view of narrow, cylindrical cup and partial column, ×2. Paratype BMS E26317.
14. Detail of pentameric, pentalobate section of medial column, ×2.5. Paratype BMS E26331.

16, 17. Indeterminate holdfasts, crinoid species B 64

16. Holdfasts of unknown crinoids and bryozoans attached to concave, inner side of large illaenid trilobite pygidium, ×1.
17. Detail of largest holdfast, ×2.7. BMS E26408.

EXPLANATION OF PLATE 3

Figure Page

1–4, 8, 10–13. ***Compsocrinus relictus*** new species. Bear Creek Shale. 26

1. Anterior view of crown and incomplete, heteromorphic column of a large individual. Stellate ornament consisting of ridges radiating from centers of plates is visible on lower portion of cup, ×0.6. Paratype BMS E26294b.

2. Anterior view of immature individual with large gastropod attached to tegmen, ×1.5. Paratype BMS E26294d.

3, 4. 3. Small cup and partial column centered on D ray, ×1; 4. Detail of cup. Radial circlet is divided by CD interray basal and primanal. Wide posterior interray has median anitaxial ridge, ×2.5. Paratype BMS E26295.

8. Crown and column of large specimen centered on DE interray. Crushed CD interray is visible on extreme right. Note crenulate lower margins of basals. Lower portion of cup has weakly developed stellate ornament. Free brachials become successively more cuneate distally but remain uniserial, ×1.2. Holotype BMS E26294a.

10. Anterior view of partial crown and column, ×1.5. Paratype BMS E26296.

11, 12. 11. Sectioned base of cup with four basals, ×3; 12. Partial crown centered on E ray. Incomplete gastropod is attached to tegmen, ×2.2. Paratype BMS 26302.

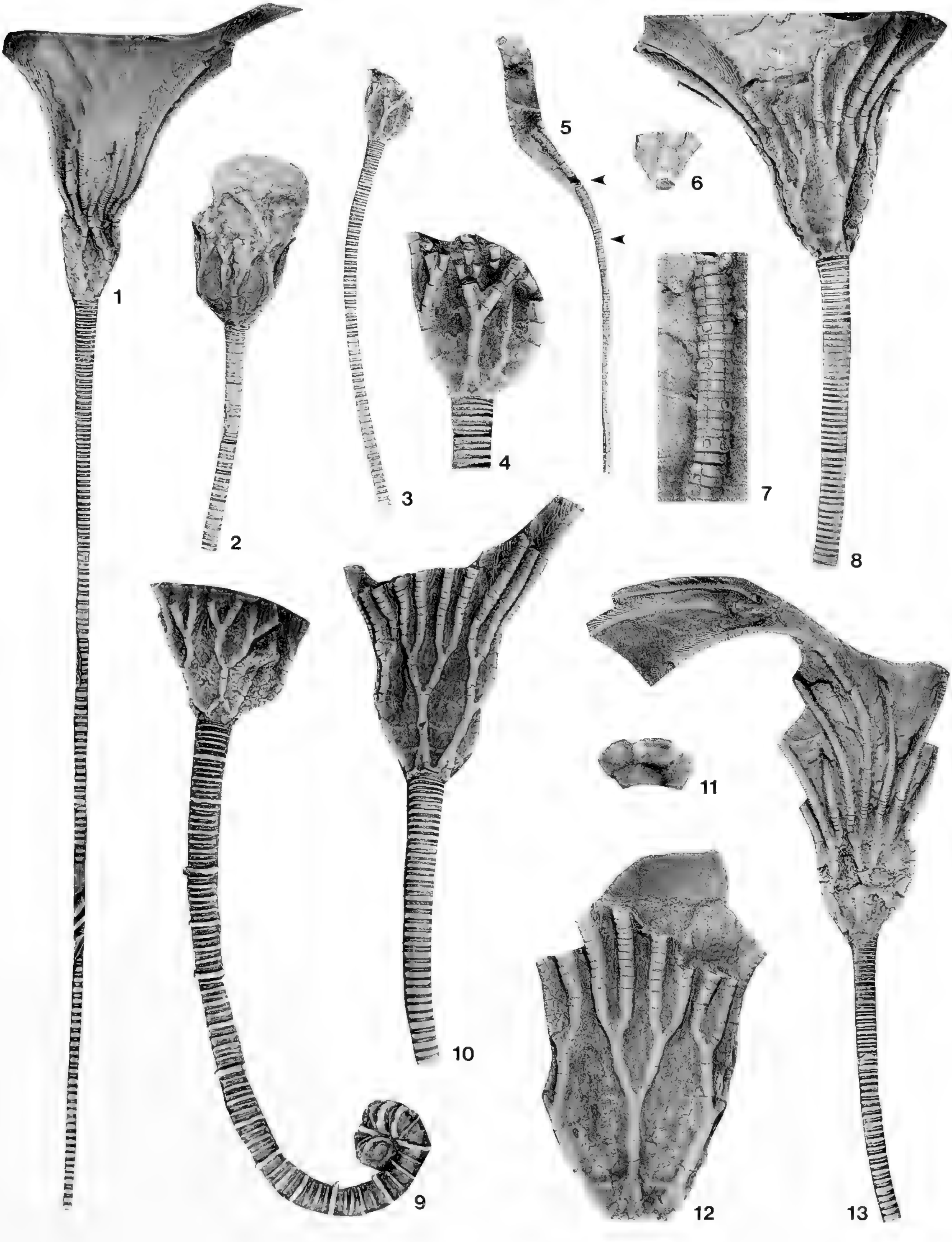
13. Large, nearly complete pyritized crown and partial column centered on E ray. Decomposition of pyrite has largely destroyed cup plates, ×1. Paratype BMS E26301.

5–7. ***Dendrocrinus ursae*** new species. Bear Creek Shale. 48

5–7. 5. Cup and detached column, ×1.2; 6. Detail of cup centered on CD interray, ×2; 7. Detail of section of column indicated by arrows on Figure 5. Incompletely preserved cirri are borne at junctions of pentameres, ×5. Holotype BMS E26303.

9. Unidentified camerate crinoid. Bear Creek Shale.

9. Nearly complete individual centered on D ray. Figured specimen BMS E26303.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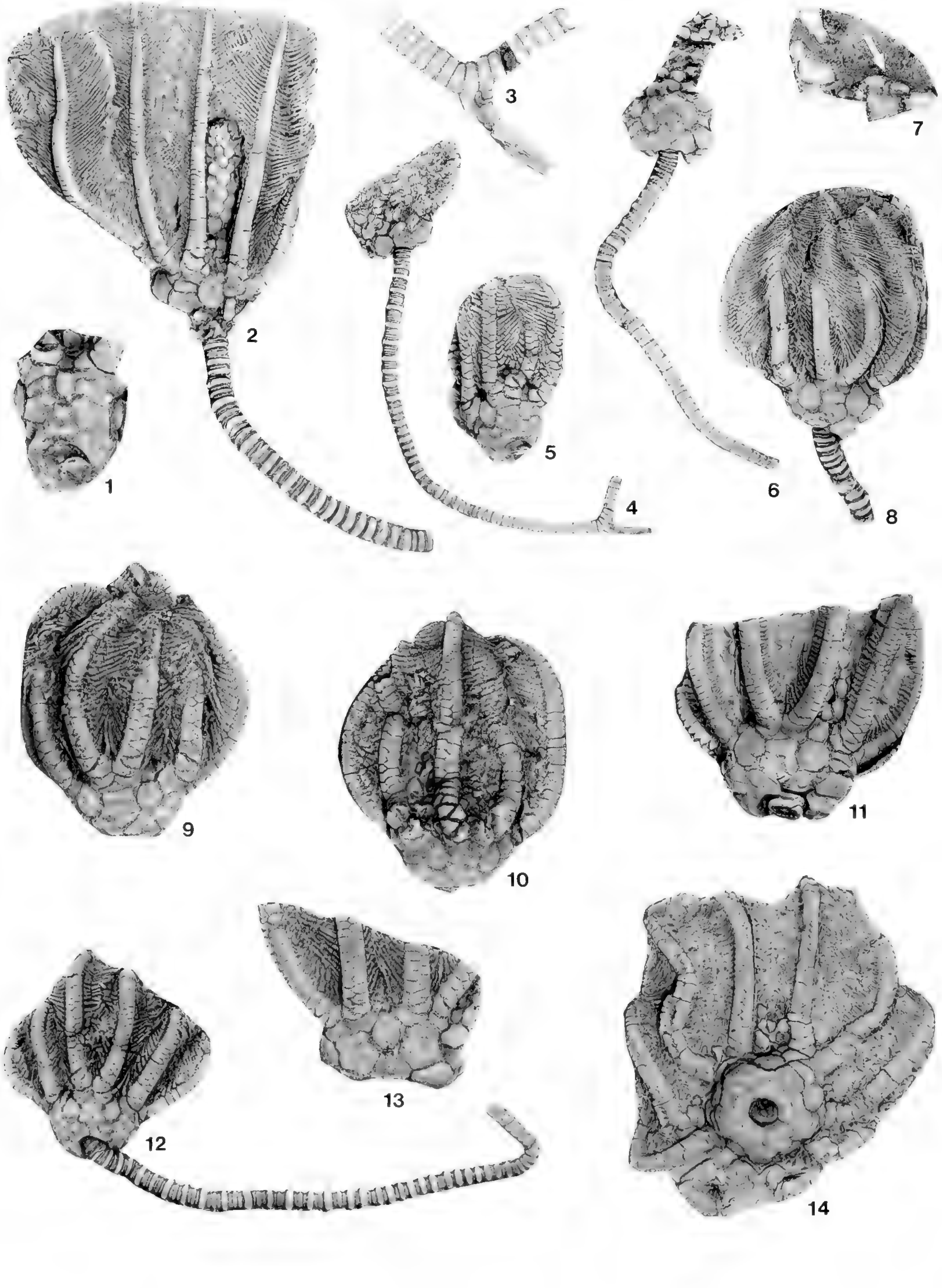
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Explanation of Plate 4

Figure Page

1–14. ***Tormosocrinus furberi*** new genus and species. Wolcott Limestone. 22

1, 5. 1. CD interray view of small cup. C ray is abnormal; second primibrachial is missing and secundibrachials are directly supported by the first primibrachial, ×3; 5. Crown centered on D ray, ×1.5. Paratype BMS E26344.

2. Anterior view of large crown and partial column. Base of cup is disarticulated but remainder of crown is remarkably well preserved. Pinnules were selectively removed during preparation, exposing prominent, distally spinose anal tube. Fixed pinnules are visible in center interray, ×1.3. Paratype BMS E26342a.

3, 4, 13. 3. Detail of distal column. Two pseudocirri borne on adjoining columnals are fused together longitudinally, ×2.5; 4. Partial crown and nearly complete column. A ray is at extreme right. Column displays transition from heteromorphic proximal and medial sections to isomorphic distal region, ×1; 13. Opposite side of crown centered on DE interray. Axillary primibrachials are reduced in size, allowing lower corners of first secundibrachials in each ray to touch first primibrachial below. Proximal portion of crushed anal tube is visible at extreme right, ×2. Paratype BMS E26341.

6. Cup and partial column of a small specimen. Arms are entirely missing, exposing tegmen and partly disarticulated anal tube, ×1. Paratype BMS E26345.

7. Partly disarticulated cup sectioned longitudinally. Infrabasal circlet, indicated by arrow, is situated at top of intracalical cylinder, ×3. Paratype BMS E26349.

8. Anterior view of well preserved crown and proximal column, ×1.3. Paratype BMS E26342b.

9–10. 9. Crown centered on D ray. Primanal and secundanal are visible below pinnules concealing anal tube. Primanal is smaller than DE interray interbrachial, ×2; 10. Oppposite side of crown. B ray is to left, ×2. Paratype BMS E26343.

11. Large, incomplete crown centered on D ray. Upturned lower margins of basals in intracalical cylinder surround proximal column. Anal tube is partly visible, ×1.5. Holotype BMS E26336a.

12. Anterior view of crown with nearly complete column, ×1.3. Paratype BMS E26337.

14. Aboral view of crown. Column has been removed, exposing intracalical cylinder. CD interray is at top center, ×1.5. Paratype BMS E26338.

EXPLANATION OF PLATE 5

Figure Page

1, 3–7, 9, 11, 12. ***Aclistocrinus capistratus*** new genus and species. Wolcott Limestone. 31

1, 3–5. 1. Lateral view of distorted but otherwise well preserved specimen, ×2.5; 3. Lateral view of same rotated to right approximately 180 degrees, ×2.5; 4. Lateral view with additional 90 degrees rotation to right. Arms and partition plates are obliquely crushed downward, largely concealing them from view in this photograph, ×3; 5. Oblique adoral view. Note long partitions dividing biserial arms. Several distal plates of anal tube are visible at upper left, ×2.5. Holotype BMS E26352.

6, 7. 6. Adoral view of small, well preserved crown. Expanded, cogwheel-like terminus of anal tube apparently gave rise to at least three spines represented by elevated attachment scars near center of summit, ×4; 7. Oblique adoral view of crown, ×4. Paratype BMS E26355.

9. Lateral view of essentially complete crinoid. Dominantly heteromorphic column with wide epifacets is displaced slightly from holdfast (columnal facet indicated by arrow). Some pseudocirri are attached to cirriferous pluricolumnal of unknown crinoid, ×3. Paratype BMS E26354a.

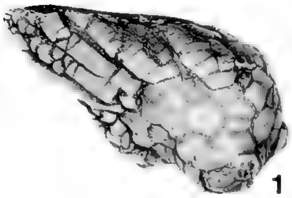
11. Incomplete crown, ×3.5. Paratype BMS E26354b.

12. Large, disarticulated specimen. Cup is disarticulated above radials. Only lower portions of basals are confined to concavity in base of cup. Wide ventral groove is visible in arm to left and a partition plate is situated to lower right. Cup is bounded on left and right by first interprimibrachials, ×1.8. Paratype BMS E26410.

2, 10. ***Callistocrinus tesselatus*** new genus and species. Wolcott Limestone. 2, 10. 2. Lateral view of crown and nearly complete column, ×1.6; 10. Detail of crown. Two rays are visible, each giving rise to five arms. One arm divides again above the cup and incipient divisions of at least two other arms are represented by large proximal pinnules. Basal at lower center is in contact with interbrachial above, separating radials of left and right rays. Interrays consist of numerous plates, ×2.8. Holotype BMS E26335. 21

8, 13. ***Atalocrinus arctus*** new genus and species. Wolcott Limestone. 28

8, 13. 8. A ray view of crown with crushed cup and incomplete column, ×1.7; 13. Opposite side of crown centered on narrow CD interray. Large, hexagonal CD interray basal and primanal divide radial circlet, ×2.5. Holotype BMS E26351.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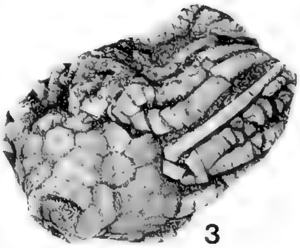
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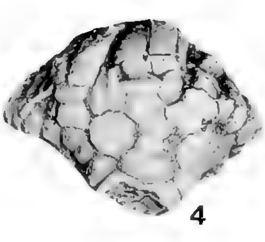
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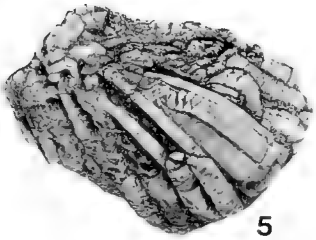
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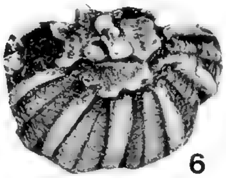
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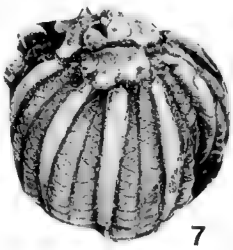
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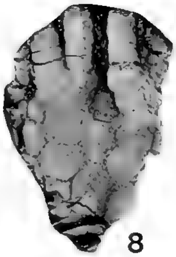
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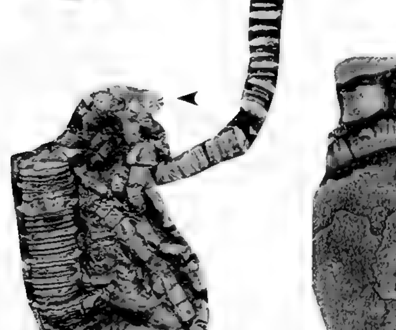
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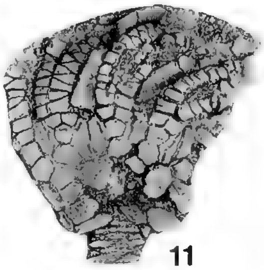
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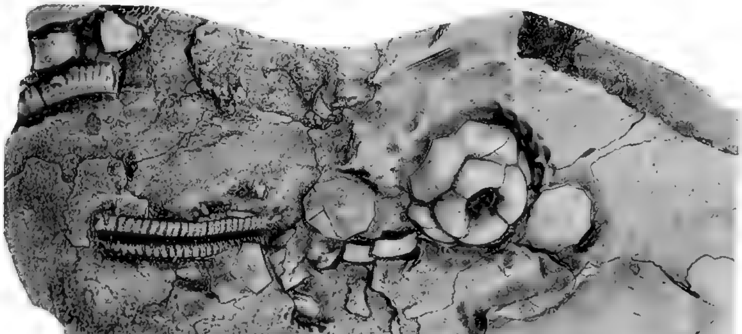
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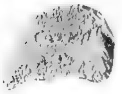
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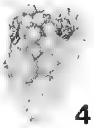
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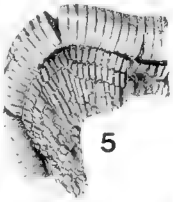
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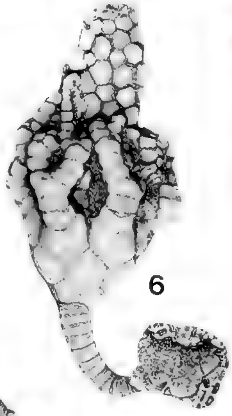
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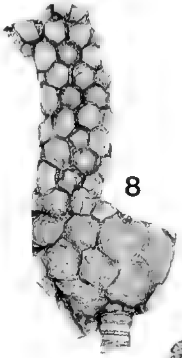
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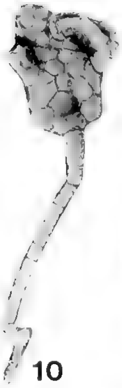
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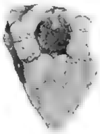
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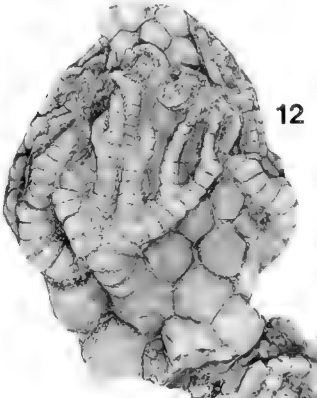
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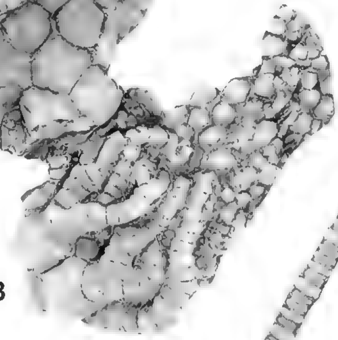
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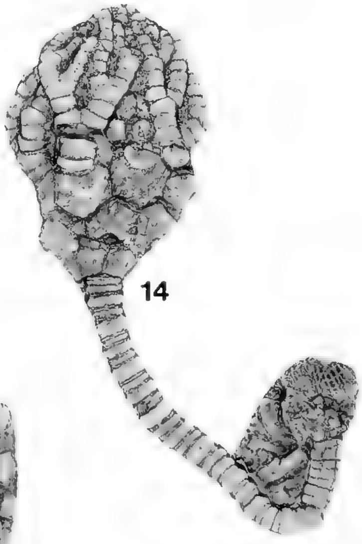
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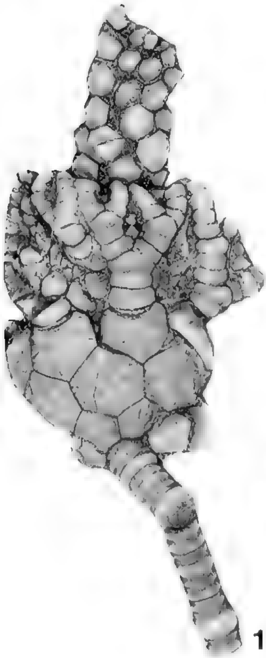
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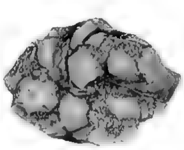
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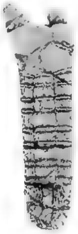
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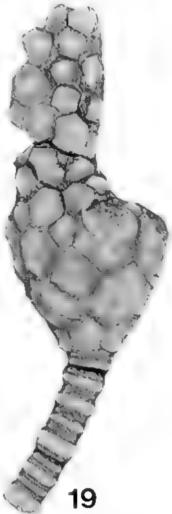
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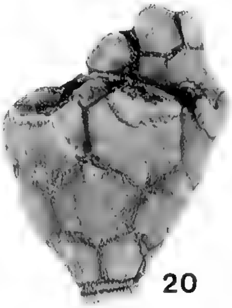
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EXPLANATION OF PLATE 6

Figure Page

1–3, 5. ***Myelodactylus linae*** new species. Wolcott Limestone. 39

1, 5. 1. Articular surface of columnal, ×3; 5. Portion of cirriferous column, ×1.5. Paratype BMS E26370.

2, 3. 2. Anterior view of crown tightly enrolled within proximal coil. Cirri were removed in order to expose crown, ×2; 3. Lateral view of complete individual. Crown is concealed by cirri. Holdfast bears short radicles attached to fragmentary zoarium of *Fenestella*, ×1.5. Holotype BMS E26369.

4, 6–17, 19, 20. ***Euspirocrinus wolcottense*** new species. Wolcott Limestone. 46

4, 11. 4. CD interray view of very small crown. Short anal sac does not extend beyond arms, ×2; 11. Anterior view of crown. Short, complete arms are preserved in A and B rays, ×2. Paratype BMS E26361.

6. Anterior view of complete individual. Unusually short column with discoidal holdfast is attached to fenestellid bryozoan, ×2. Paratype BMS E26357.

7. Anterior view of complete specimen. Holdfast bears stout radicles attached to fenestellid bryozoan. Low ridges radiate from centers of cup plates. Arms are coiled distally, ×1.5. Paratype BMS E26358.

8, 9. 8. Detail of cup and anal sac. Base of cup has been pushed upward, partly concealing infrabasals, ×1.5; 9. CD interray view of nearly complete crinoid. Pentameres are visible in distal column. Holdfast is attached to bryozoan, ×0.9. Paratype BMS E26359.

10. Complete juvenile individual centered on CD interray, ×1.5. Paratype BMS E26361.

12. CD interray view of incomplete crown. Note slightly heterotomous arms and weakly developed endotomy, ×2. Holotype BMS E26347a.

13. Anterior view of incomplete crown. A large oral plate is situated above interradial notch, ×2. Paratype BMS 26347b.

14. Complete crinoid. CD interray is partly visible at extreme right of crown. D and E ray arms are displaced slightly from cup, exposing radial facets. Base of anal sac is visible between arms. Pentameric distal column is attached to fenestellid bryozoan, ×1. Paratype BMS E26360.

15. Anterior view of crown, ×2. Paratype BMS E26362.

16, 19, 20. 16. Tegmen. Note large orals. Base of anal sac is at upper right, ×2; 19. Cup, anal sac, and proximal column. B ray is at extreme right, ×2; 20. Cup centered on E ray. Proximal columnals and lower portions of infrabasals have fine longitudinal ridges, ×2.5. Paratype BMS E26363.

17. Exceptionally large, complete crinoid tentatively assigned to this species. CD interray is partly visible at extreme right. Arms are tightly coiled distally, exposing most of long anal sac. Numerous pustules and short, undulating ridges on cup an atypical ornamentation for this species, ×1. Paratype BMS E26365.

18. ***Haptocrinus*** sp. Wolcott Limestone. 45

18. Partial cup and proximal, pentameric column, ×3. Figured specimen BMS E26363.

EXPLANATION OF PLATE 7

Figure Page

1, 13. ***Dendrocrinus aphelos*** new species. Wolcott Limestone. 49

1. Anterior view of large, partial crown and column. B ray is at extreme left, ×1. Holotype BMS E26366.

13. Incomplete, small individual centered on A ray, ×1.5. Paratype BMS E26367.

2–12, 14–16, 18–20. ***Kyphosocrinus tetreaulti*** new genus and species. Wolcott Limestone. 57

2, 9, 10, 14. 2. Crown centered on E ray. Note quadrangular interbrachial in DE and EA interrays, ×2; 9. B ray view, ×2; 10. Adoral view illustrating distally coiled arms, ×2.5; 14. CD interray view, ×2. Paratype BMS E26382.

3. CD interray view of crushed crown and partial column. Endotomy is evident in slightly heterotomous distal divisions of arms, ×1.5. Paratype BMS E26378.

4, 5. 4. CD interray view of crown. Note large anal X and heterotomous arm in C ray, ×1.2; 5. Anterior view of entire individual. A small interbrachial is visible at left in BC interray above first primibrachials, ×1. Paratype BMS E26372.

6, 7. 6. CD interray view of small, crushed crown, ×2; 7. Anterior view. B ray is to left, ×2. Paratype BMS E26381.

8. CD interray view of crown and partial column, ×1.5. Paratype BMS E26347e.

11. Small crown. CD interray is at extreme right, ×1.3. Paratype BMS E26347d.

12. CD interray view of crown with distally coiled arms. Anal X, truncated distally, is succeeded by X_1, ×2. Paratype BMS E26375.

15. Crown and proximal column centered on B ray, ×1.5. Paratype BMS E26379.

16. Incomplete crown centered on CD interray, ×2.5. Paratype BMS E26376.

18. Anterior view of crown. Single quadrangular interbrachial in each interray is situated above upper corners of first primibrachials, ×2. Paratype BMS E26356b.

19, 20. 19. Crown and curved column centered on C ray, ×1.5; 20. Detail of crown. BC interray contains quadrangular interbrachial. Note bulging profile of infrabasal circlet, ×2. Holotype BMS E26377.

17. ***Euspirocrinus wolcottense*** new species. Wolcott Limestone. 46

17. CD interray view of partial crown with distally coiled arms, ×2. Paratype BMS E26356a.

21. ***Dendrocrinus bactronodosus*** new species. Wolcott Limestone. 50

21. Anterior view of crown. D ray is at extreme right. Plicate proximal plates of anal sac are visible between D and E ray arms. Anal sac is nodose distally. Proximal, pentameric column is pentastellate, ×2.5. Holotype BMS E26368.


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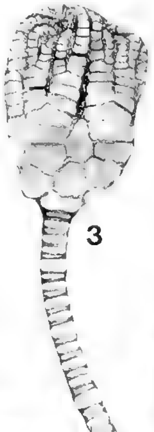
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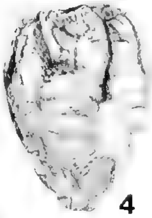
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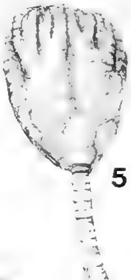
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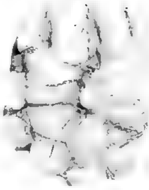
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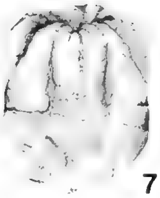
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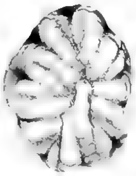
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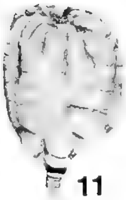
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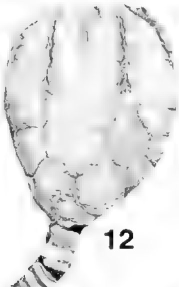
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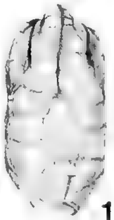
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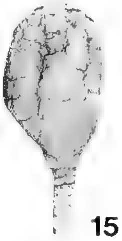
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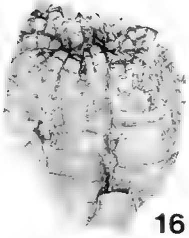
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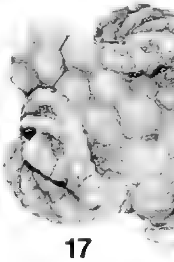
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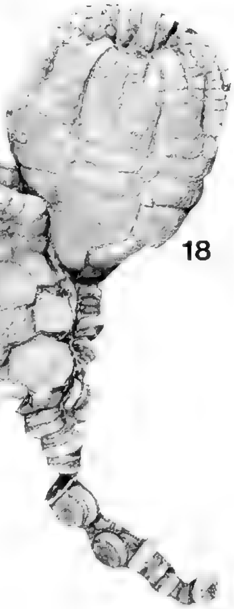
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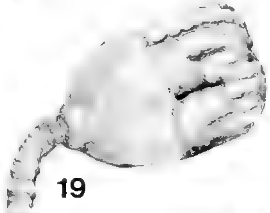
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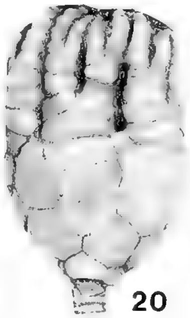
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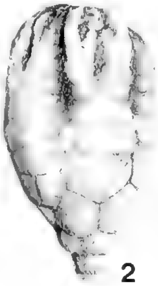
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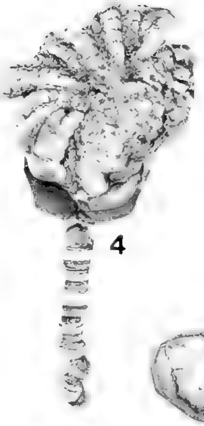
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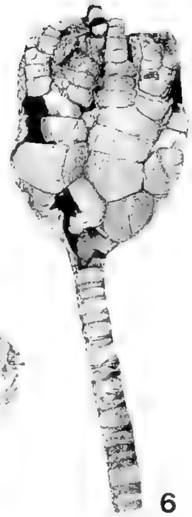
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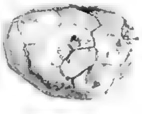
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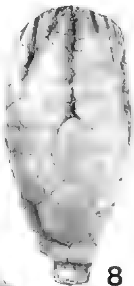
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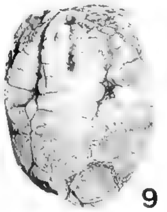
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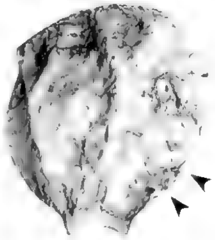
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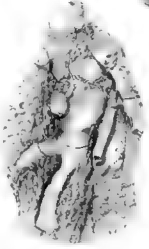
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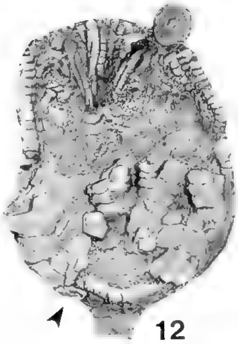
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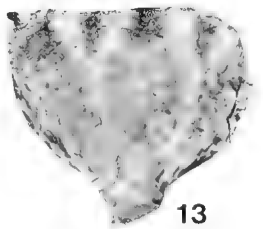
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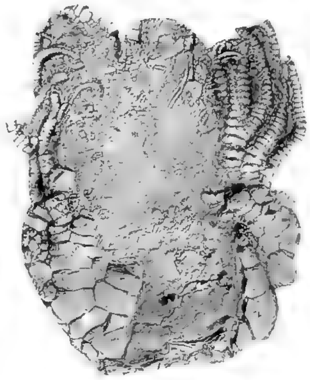
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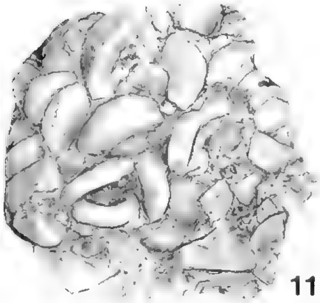
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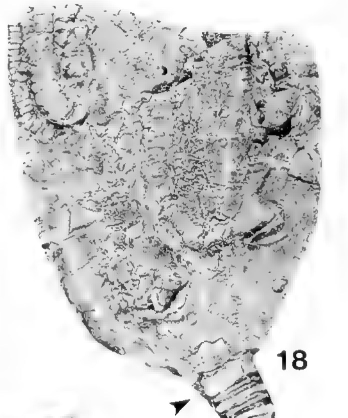
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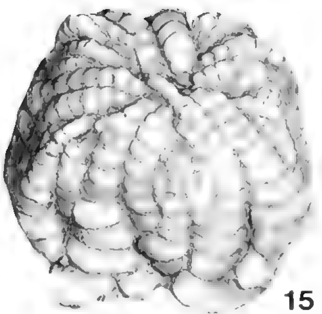
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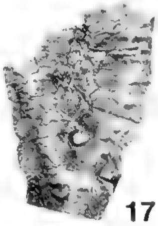
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EXPLANATION OF PLATE 8

Figure Page

1, 7, 10, 12–14, 16–18. ***Scapanocrinus muricatus*** new genus and species. Wolcott Limestone. 62

1, 7, 16. 1. Anterior view of nearly complete individual attached to fenestellid bryozoans. Base of crown and column are pushed together, concealing basal and infrabasal circlets, ×1; 7. Detail of holdfast, ×1.9; 16. Detail of crown. Note large numbers of interbrachials incorporated into cup and angular-sided proximal free brachials. Heterotomous arms are strongly endotomous, ×2. Holotype BMS E26386.

10, 12, 13. 10. Oblique view of cup. Crushed CD interray is at right. Hexagonal CD interray basal and anal X divide radial circlet. Upper and lower arrows indicate C ray radial and radianal, respectively. Note nearly cylindrical infrabasal circlet, ×1.7; 12. Opposite side of crown centered on damaged B ray. Arrow indicates radianal, ×1.5; 13. Cup centered on DE interray, ×1.5. Paratype BMS E26385.

14. Incomplete crown, ×1. Paratype BMS 26389.

17, 18. 17. Detail of intertertibrachials, ×2; 18. Large, incomplete crown and proximal column. Infrabasal circlet is indicated by arrow, ×1. Paratype BMS E26387.

2–5, 8, 9. ***Kyphosocrinus tetreaulti*** new genus and species. Wolcott Limestone. 57

2, 3, 8. 2. Crown centered on B ray, ×2; 3. D ray view, ×2; 8. CD interray view, ×2. Paratype BMS 26383.

4. Crown in adoral view, ×2. Paratype BMS E26384.

5, 9. 5. Aboral view of crown, ×2.5; 9. CD interray, ×2. Paratype BMS 26380.

6. ?Anisocrinid species A. Wolcott Limestone. 58

6. Damaged crown and partial column. CD interray is at right. Anal X was originally succeeded by a single row of plates extending almost to top of crown but the distal anitaxis was lost during preparation, ×2. Figured specimen BMS E26390.

11, 15. Flexible crinoid species B. Wolcott Limestone. 63

11. Crown viewed from disarticulated base, ×2; 15. Lateral view illustrating strongly heterotomous arms and endotomy, ×2. BMS E26391.

EXPLANATION OF PLATE 9

Figure Page

1, 6, 11–13. Unknown crinoid species D. Willowvale Shale. 64

- 1, 6, 11. Proximal, medial, and distal sections, respectively, of nearly complete column. Pentameric column is round proximally, pentagonal distally, ×1.2. BMS E26411a–c.
- 12. Articular surface of medial columnal with large lumen and distinct pentameres, ×2. BMS E26412.
- 13. Articular surface of distal columnal, ×2. BMS E26413.

2–5, 7–9. ***Protaxocrinus anellus*** new species. Willowvale Shale. 52

- 2. Anterior view of crown and long, incomplete column. Distal columnals are barrel-shaped, ×2. Paratype BMS E26399.
- 3. Anterior view of small crown. Distal tips of arms were dissolved in early diagnesis, ×2.5. Paratype BMS E26394b.
- 4, 5. 4. Crown centered on D ray. Anal sac is represented by anal X and X1 only, ×2.5; 5. B ray view, ×2.5. Paratype BMS E26393.
- 7, 8. 7. C ray view of crown that suffered complete dissolution of distal arms and most of column in early diagenesis. Note narrow anitaxis attached to concave right shoulder of CD interray basal, ×3; 8. Opposite side of crown. A ray is at extreme left, ×2.5. Holotype BMS E26392.
- 9. Anterior view of crown. Distal arms have been dissolved, ×2.5. Paratype BMS E26394a.

10, 20. Unknown crinoid species C. Wolcott Limestone 64

- 10. Proximal column, ×1. BMS E26416.
- 20. Distal column, ×1. BMS E26417.

14–17. *Tremichnus cysticus* Brett Willowvale Shale. 65

- 14. Lateral view of pluricolumnal engulfed by excess stereom covered with pits of *T. cysticus*, ×1.5; 15. Inferred distal end. Excess stereom has tripled diameter of column, ×2; 16. Inferred proximal end, ×2; 17. Lateral view of opposite side, ×1.5. Hypotype ROM 44359.

18, 19, 25. Unknown crinoid species G. Willowvale Shale. 65

- 18. Large, branched pseudocirrus comprising part of holdfast, ×1. BMS E26414.
- 19. Slightly curved pluricolumnal probably of this species, ×1.2. BMS E26418.
- 25. Two partial holdfasts. Example at right is encrusted by bryozoans, ×1.5. BMS E26415.

21, 24. Unknown crinoid species E. Willowvale Shale. 64

- 21. Section of recumbent column. Rootlets are represented by elevated attachment scars, ×1. BMS E26437.
- 24. Pluricolumnal with encrusting bryozoans, ×1. BMS E26438.

22, 23. Unknown crinoid species F. Kirkland Iron Ore. 65

- 22. Axial view of large columnal extensively abraded before final burial. Articular surface has been completely obliterated, ×1.3; 23. Side view, ×1.3. BMS E26439.


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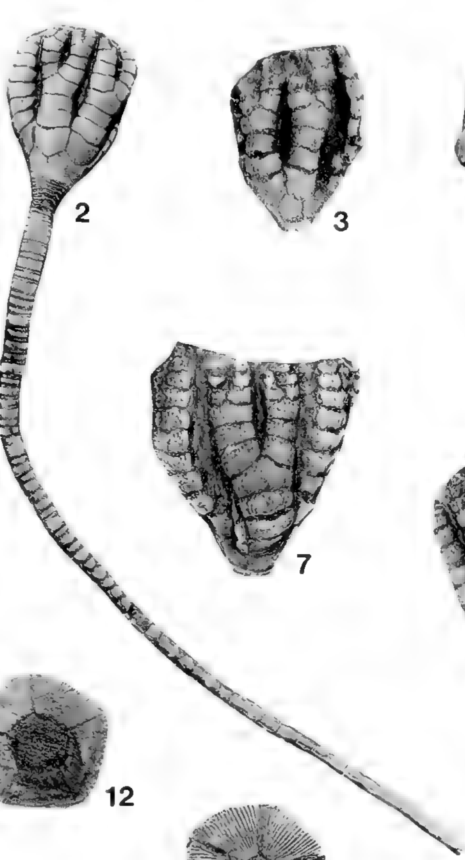
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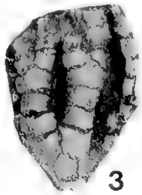
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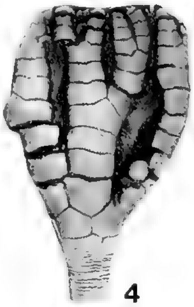
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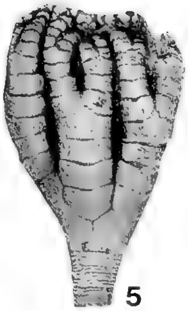
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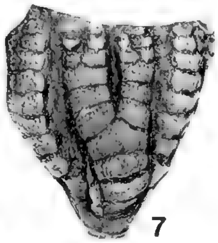
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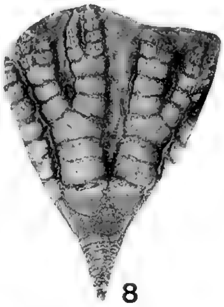
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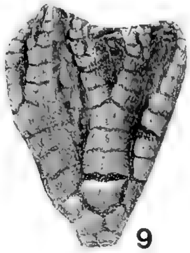
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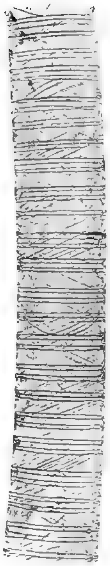
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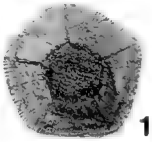
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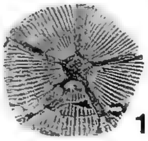
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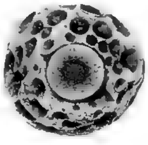
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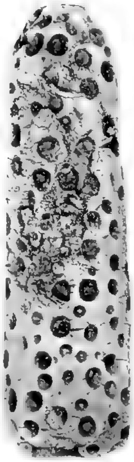
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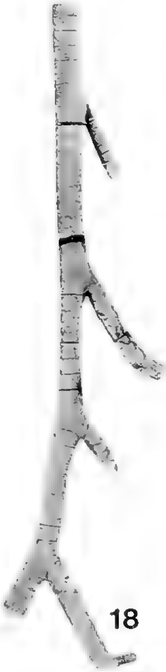
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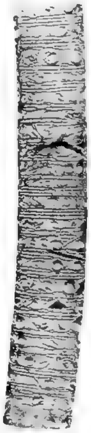
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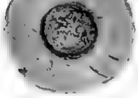
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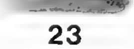
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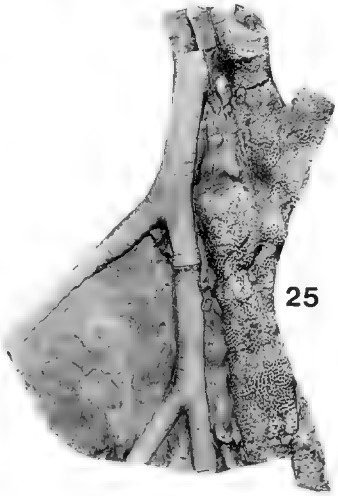
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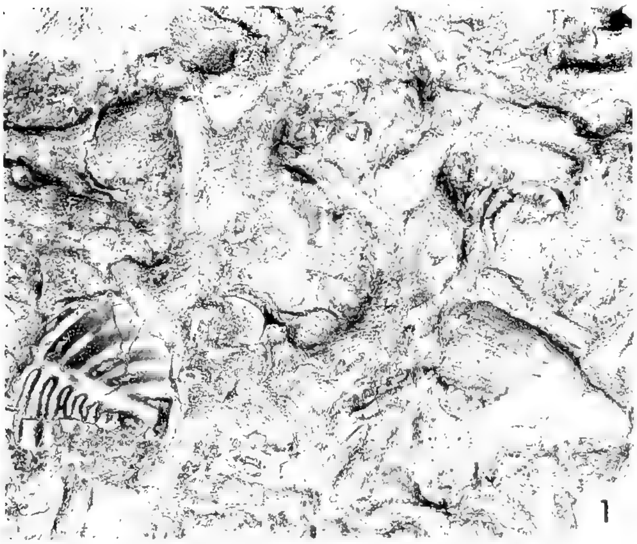
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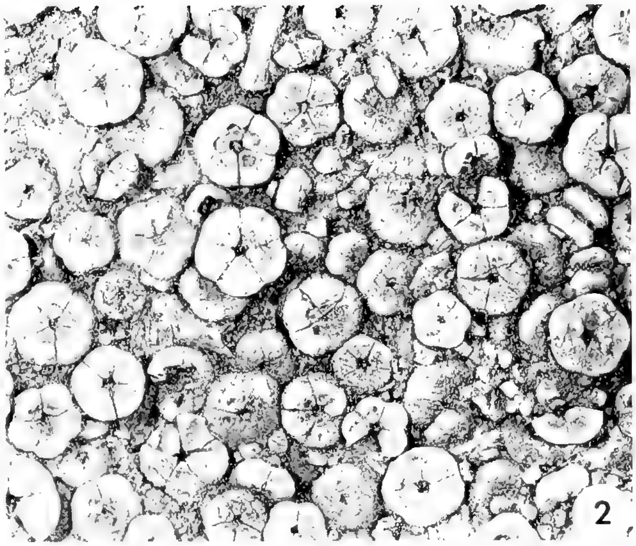
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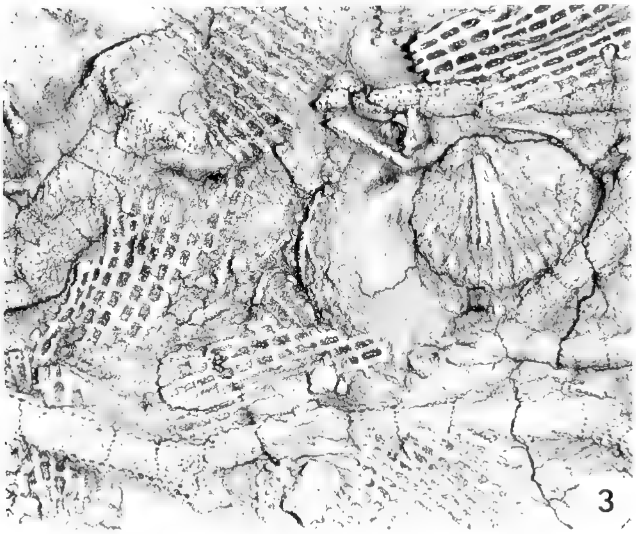
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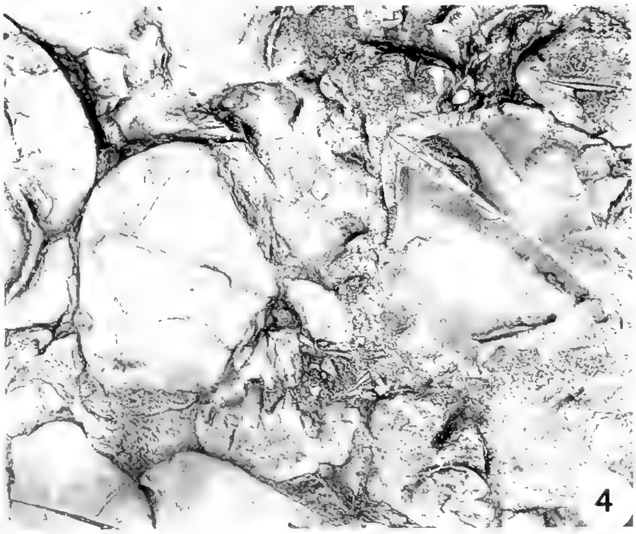
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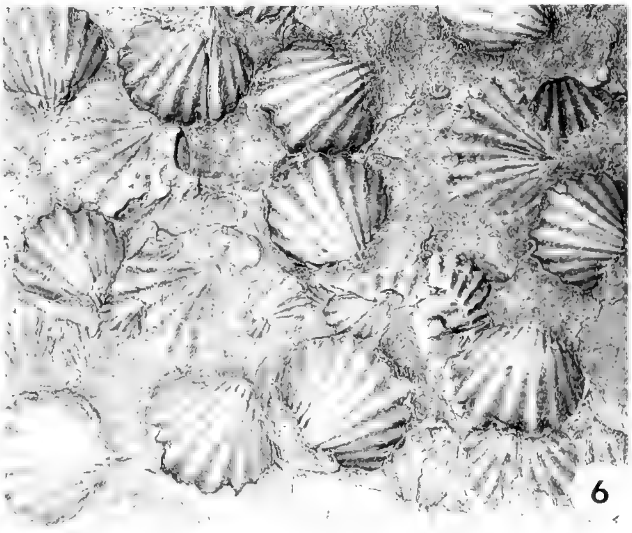
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Explanation of Plate 10

Figure Page

1–6. Fossil assemblages of lower Clinton Group. 12–15

1. Packstone bearing ramose bryozoans, calymenid trilobite pygidium (lower left), and corroded rugose coral (lower right), ×2.2. Reynales Formation near base of Hickory Corners Member, locality 2.
2. Crinoidal grainstone consisting almost entirely of columnals of *Haptocrinus* n. gen., ×3.8. Reynales Formation near top of Hickory Corners Member, locality 2.
3. Bryozoan assemblage dominated by ***Fenestella tenuis*** (example in upper right) and ***Striatopora flexuosa*** (narrow branch crossing photograph near bottom). A small, articulated specimen of ***Atrypa*** is also visible, ×3.4. Lower Wolcott Limestone, locality 8.
4. Brachiopod wackestone containing disarticulated and fragmented valves of ***Pentamerus*****,** ×1. Wolcott Limestone, locality 8.
5. Grainstone consisting of fragmented and abraded ramose bryozoans, crinoid columnals, and small brachiopods, ×2. Upper Sodus Shale, locality 7.
6. Shale bedding plane covered with the brachiopod ***Eocoelia hemisphaerica*****,** represented by internal molds of mostly disarticulated valves, ×3. Upper Sodus Shale, locality 7.

EXPLANATION OF PLATE 11

Figure		Page
1–4.	Lower Clinton Group exposures.	8

1. Crinoidal grainstone beds near top of Hickory Corners Member, Reynales Formation, locality 3.
2. Thin-bedded wackestones of basal Hickory Corners Member overlying Neahga Shale (contact at top of lens cover), locality 1.
3. Exposure on bank of Bear Creek. Sterling Station Iron Ore, between arrows, is situated above Bear Creek Shale and below Lower Sodus Shale, locality 9.
4. Excavation in bank of Mudge Creek. Tools rest on poorly exposed shales and limestones of the lower portion of the Wolcott Limestone, locality 8.


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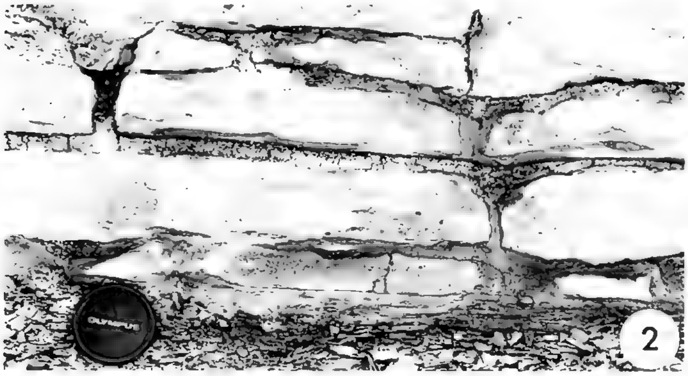

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Note: Page numbers for descriptions of genera and species are shown in **bold type**.