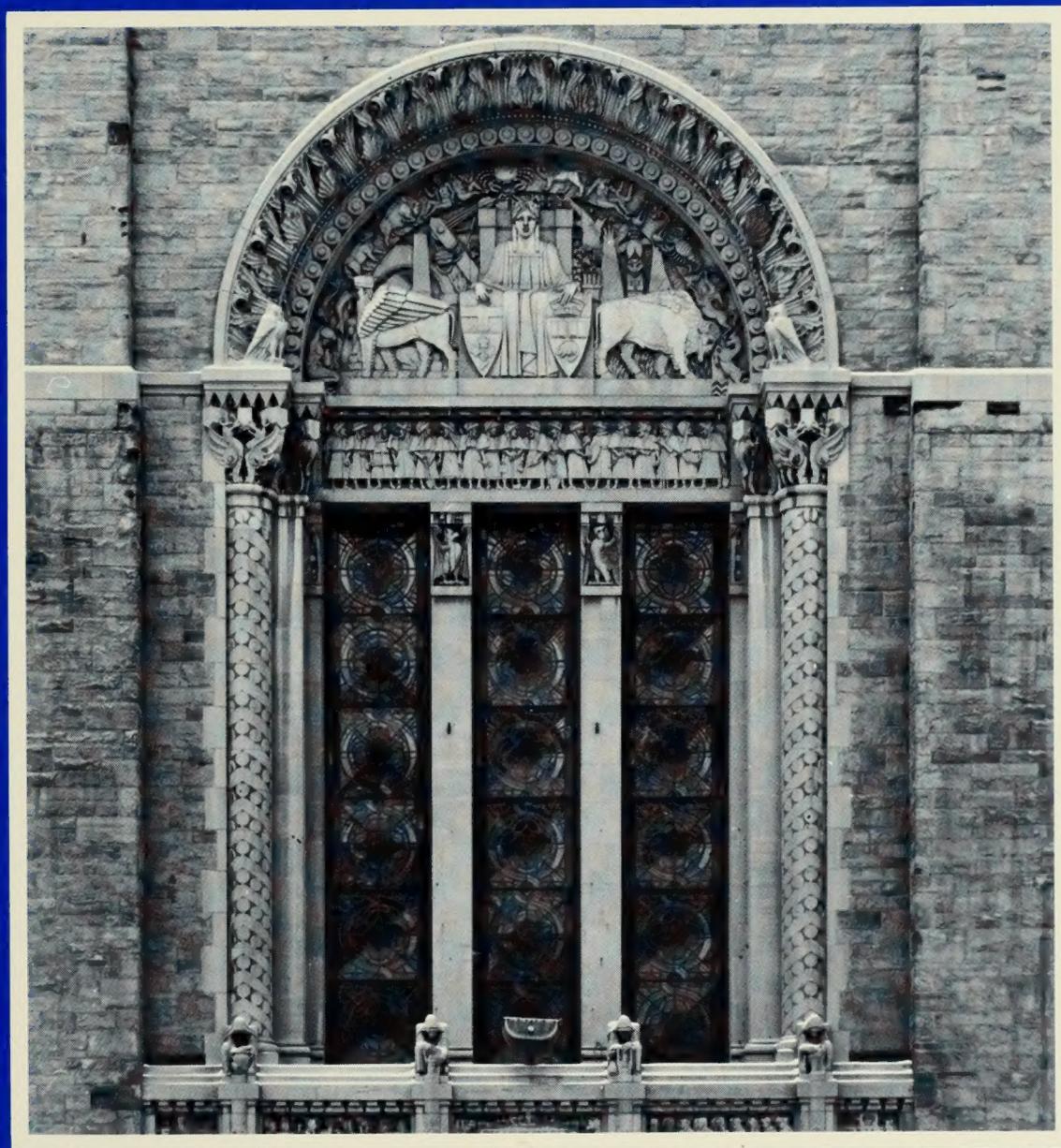


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*Stipatocrinus*, a New and Unusual  
Camerate Crinoid from the  
Lower Silurian of Western New York

James D. Eckert and Carlton E. Brett

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# *Stipatocrinus*, a New and Unusual Camerate Crinoid from the Lower Silurian of Western New York

## Abstract

*Stipatocrinus hulveri* gen. et sp. nov. is described from the Upper Llandoveryan Reynales Formation of western New York. Diagnostic characters of this unusual camerate crinoid include a peculiar cup in which the lowest circlet, consisting of two large and two small plates designated as basals divided by sutures passing through the AE-interray and C-ray, possesses a combination of infrabasal, basal, and radial features. Unique t-shaped radials bridge interrays consisting of numerous small interbrachials irregular in shape and arrangement. *Stipatocrinus* probably represents an archaic, previously unrecognized lineage of camerate crinoids that persisted into the Silurian but became extinct in the late Llandoveryan. Thinly plated, flexible interrays of *Stipatocrinus* reduced metabolic cost of skeletal growth and possibly aided in respiration.

## Introduction

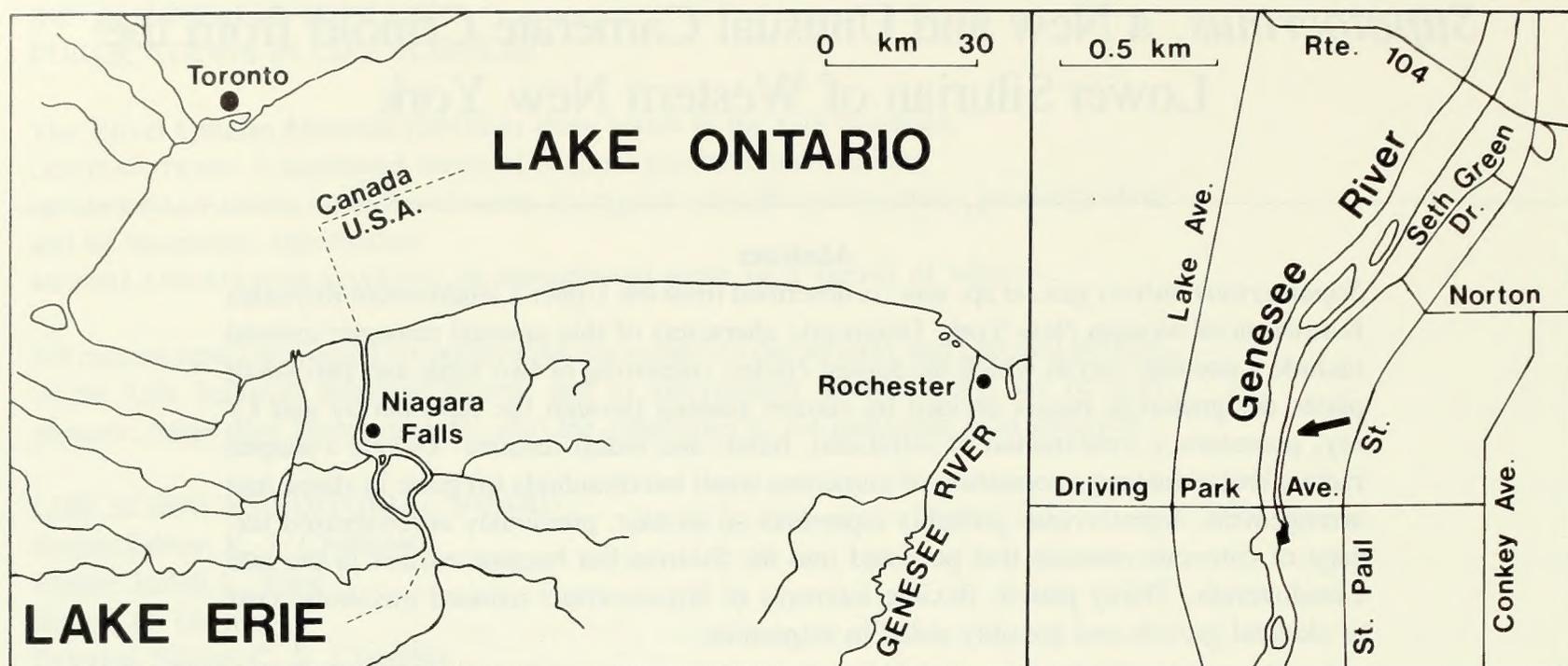
Crinoids are poorly represented in Lower Silurian (Llandoveryan) strata of eastern North America. This interval is critical to understanding the evolution of the class, for it followed major Late Ordovician extinctions that decimated crinoids and other groups of marine invertebrates and preceded major taxonomic radiation and restructuring of crinoid assemblages in the Late Silurian (Wenlockian). One might predict, therefore, that Llandoveryan crinoid assemblages would comprise transitional forms, including ancestral stocks of certain of the major Wenlockian clades. Indeed, such precursor taxa have been reported from the Hopkinton Dolomite (late Llandoveryan, C<sub>3</sub>-C<sub>6</sub>) in Iowa (Witzke, Frest, and Strimple, 1979; Witzke and Strimple, 1981), and a slightly older fauna is known from the Brassfield Formation of Ohio (Ausich, 1985, 1986a, 1986b) in strata considered to be of late Llandoveryan (C<sub>1</sub>-C<sub>2</sub>) age (Berry and Boucot, 1970). Potential ancestors of Wenlockian crinoids also occur in the Cataract Group of Ontario (Eckert, 1984) and in the lower Clinton Group (middle to late Llandoveryan, B<sub>3</sub>-C<sub>4</sub>) of the northern Appalachian Basin in New York State (Eckert, in prep.). However, Early Silurian crinoid assemblages of Ontario and New York State are also distinctly Ordovician in aspect and

characterized by persistence of primitive lineages. For example, *Ptychocrinus medinensis*, a species closely related to the Late Ordovician crinoid *P. splendens*, is locally abundant in the Power Glen Formation (early Llandoveryan, A<sub>2</sub>-A<sub>3</sub>) of New York and the Cabot Head Formation of Ontario (Brett, 1978; Eckert, 1984). The Reynales Formation contains undescribed crinoids very similar to the Middle Ordovician crinoid *Tornatiliocrinus* from the Lebanon Limestone of Tennessee. *Stipatocrinus hulveri* gen. et sp. nov. is also inferred to represent a primitive but persistent Ordovician lineage. These taxa appear to represent relict lineages that escaped Ashgillian extinction. *Stipatocrinus hulveri* formed monotypic, high-density assemblages, suggesting that it may have acted as an opportunistic species that thrived in physically stressed, uncrowded environments such as existed in the Early Silurian of the northern Appalachian Basin. These environments may have provided a refuge for primitive holdover taxa that became extinct or were displaced coincidentally with an invasion of diverse Wenlockian echinoderm associations that may have evolved in the North American midcontinent (Witzke, Frest, and Strimple, 1979) or in presently unknown areas.

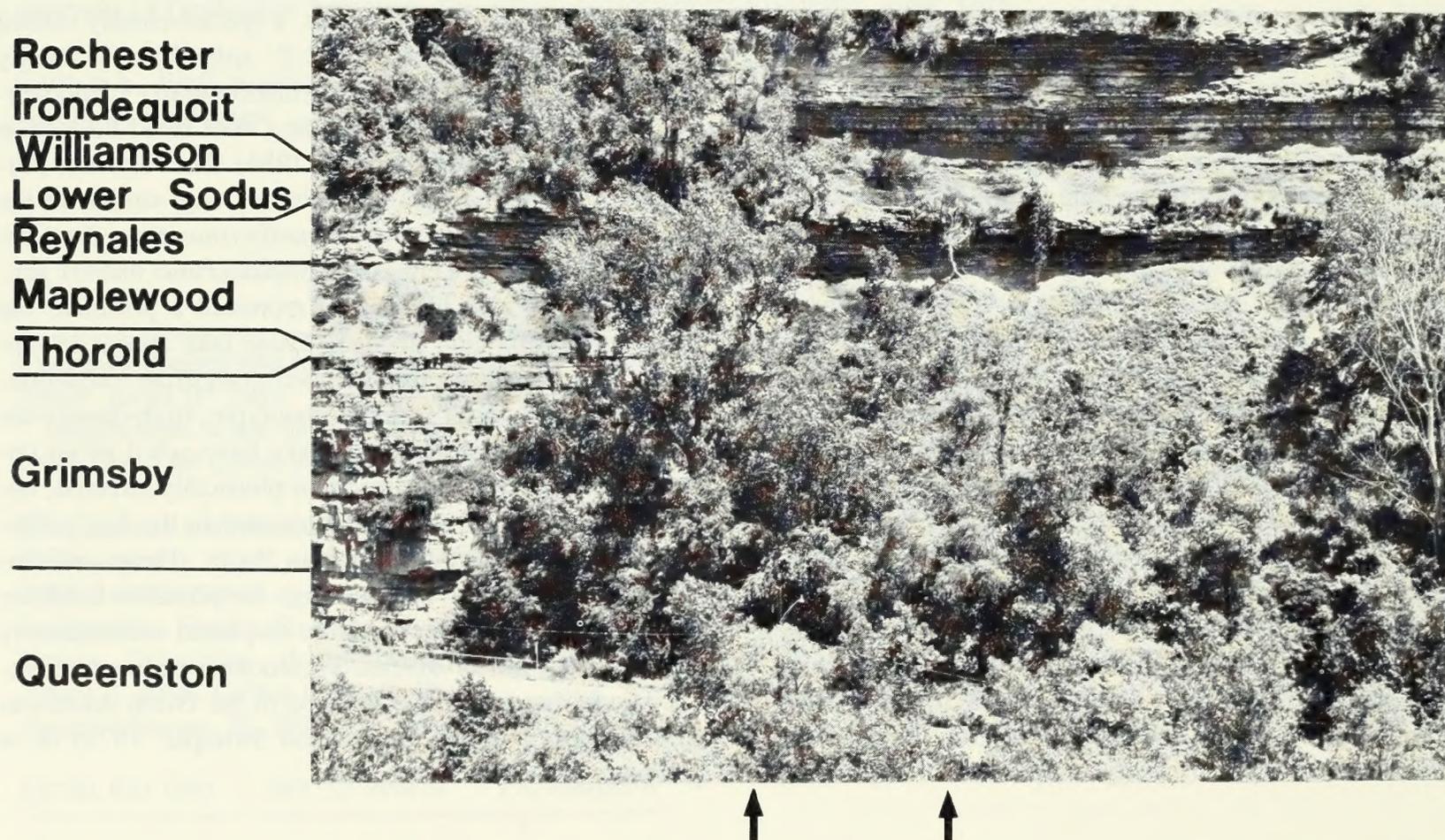
## Occurrence and Stratigraphy

In 1983, while studying Early Silurian brachiopod communities in western New York, Michael Hulver of the University of Chicago discovered dolostone slabs covered with long crinoid stems from talus in the eastern side of the gorge of the Genesee River at Rochester, New York

(Text-Figs. 1, 2). Subsequent investigation by Brett resulted in discovery of numerous nearly complete individuals of *Stipatocrinus hulveri* gen. et sp. nov. at this site, 0.3 km north of the lower falls of the Genesee River and 10 to 40 m east of the Rochester Gas and Electric access



TEXT-FIG. 1. Locality map of southwestern Ontario and western New York State. Arrow in inset at right indicates occurrence of *Stipatocrinus hulveri* gen. et sp. nov.



TEXT-FIG. 2. Upper Ordovician Queenston Formation and Silurian formations exposed in eastern side of gorge of Genesee River at Rochester, New York. Vertical section is approximately 50 m. Slabs bearing *Stipatocrinus hulveri* gen. et sp. nov. were found on talus slope between access road and Reynales Formation exposed in cliff. Arrows indicate lateral extent of occurrence.

road south of Seth Green Drive, Rochester, Monroe County, New York (United States Geological Survey, Rochester West 7.5' Quadrangle).

Crinoid-bearing slabs appear to comprise parts of a large rockfall from the Wallington Member of the Reynales Formation, exposed in the cliff above the talus (Text-Fig. 2). Laminated calcisiltite containing crinoids closely resembles that found interbedded with green shales near the base of the Wallington Member. Crinoid columns and distinctive t-shaped radials were obtained *in situ* from the lowest metre of this member, which probably represents the horizon from which the study material was eroded.

The Reynales Formation, also known as the Reynales Limestone, consists of complex, time-transgressive, dominantly carbonate strata extending from the Niagara area eastwards to near Wolcott, New York, where it grades

laterally into the Bear Creek Shale. The Wallington Member (Fisher, 1960) is the uppermost unit of the Reynales Formation in the Rochester area. Approximately 4 m thick in the Genesee Gorge, the Wallington consists of thin- to medium-bedded, light grey, cherty, dolomitic limestone and dolostone with greenish-grey shale partings. Cross-lamination with a maximum amplitude of 2 cm occurs in calcisiltite (pelletal grainstone beds). Several horizons of fossiliferous packstone and grainstone within the Wallington contain abundant specimens of the brachiopods *Pentamerus oblongus* and *Eocoelia hemispherica*. On the basis of these brachiopods, the Wallington was considered to be of late Llandoveryan (C<sub>4</sub>) age (Berry and Boucot, 1970). However, further consideration of brachiopod and conodont biostratigraphy led Rickard (1975) to propose an earlier (C<sub>2</sub>) age.

## Materials and Methods

Most specimens of *Stipatocrinus hulveri* gen. et sp. nov. are embedded in a hard, dolomitic calcisiltite and proved difficult to prepare. Attempts to remove matrix, using sodium bicarbonate in an airbrasive machine, were not successful. Dolomite powder proved to be an effective abrasive but readily damaged the thin plates of these crinoids. Fortunately a few specimens, including the holotype, are embedded in a softer, slightly argillaceous matrix and were prepared using needles and airabrasion with little damage.

Immersion of specimens in ethanol facilitated morphologic study. Text-Figures 5, 6, and 7 were prepared by tracing over photographs. Plate dimensions were measured using vernier calipers; orientations of these plates are given in Table 1.

All study material is deposited in the collections of the Department of Invertebrate Palaeontology, Royal Ontario Museum (ROM) in Toronto, Ontario, Canada.

## Systematic Palaeontology

Class Crinoidea Miller, 1821

Subclass Camerata Wachsmuth and Springer, 1885

?Order Monobathrida Moore and Laudon, 1943

Superfamily Stipatocrinacea superfam. nov.

### DIAGNOSIS

Lowest circlet in cup consisting of four plates (basals?); two large plates adjacent to one another along C-ray suture and two small plates directly in line with A- and E-ray radials. This circlet divided by sutures in AB-, DE-, and EA-interrays. Radials and fixed brachials narrow, elongate, raised. Primanal and anitaxis absent. Interbrachials small, exceptionally numerous, irregular in shape and arrangement.

### Family Stipatocrinidae fam. nov.

### DIAGNOSIS

Characters of superfamily.

### *Stipatocrinus* gen. nov.

### TYPE SPECIES

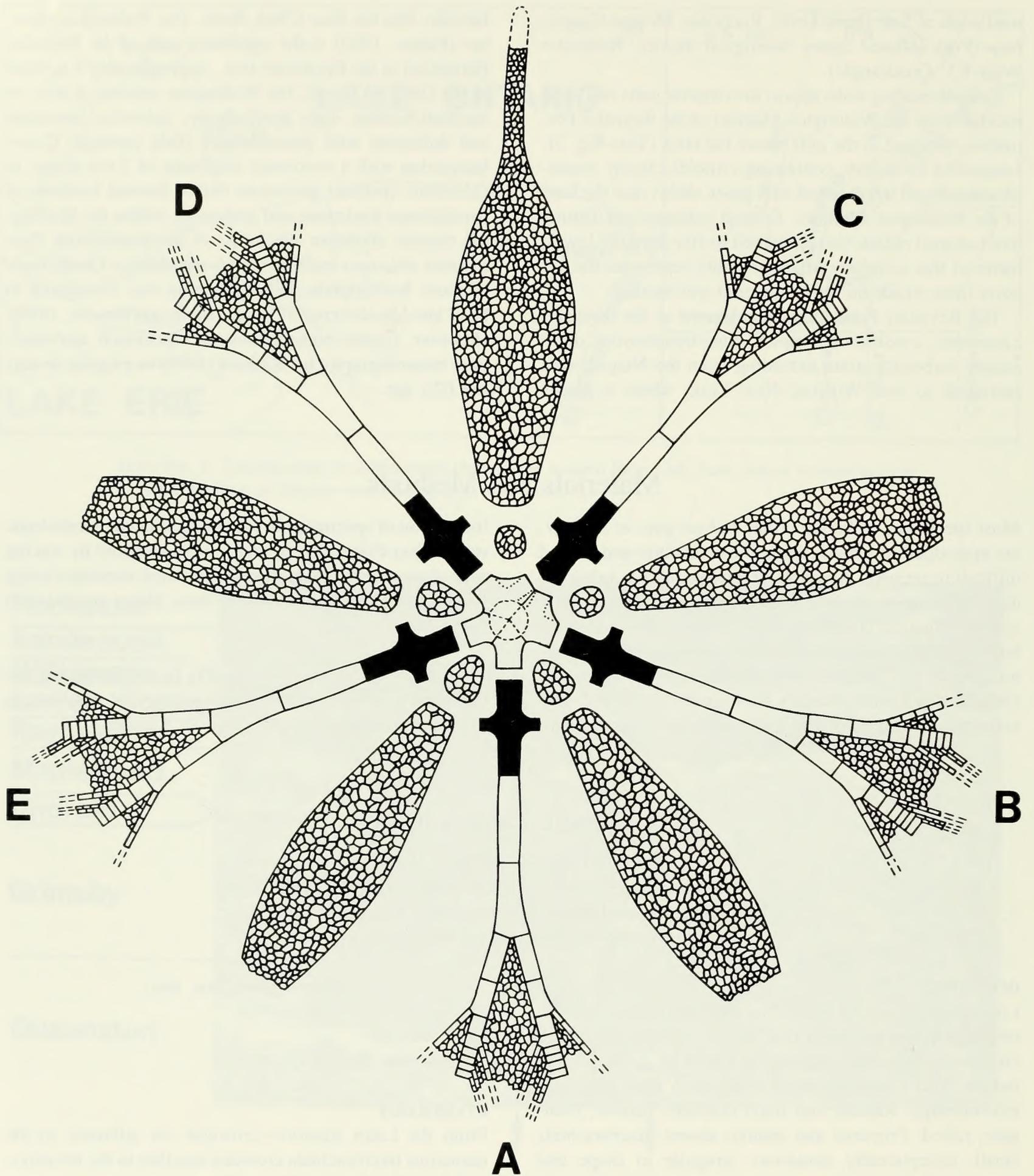
*Stipatocrinus hulveri* sp. nov.

### ETYMOLOGY

From the Latin *stipatus*—crowded—in reference to the numerous interbrachials crowded together in the interrays, and from the Greek *krinon*—lily.

### DIAGNOSIS

Monotypic genus of Stipatocrinidae with narrow conical cup and depressed interrays. Radials t-shaped, bridging interrays. Primibrachials two in each ray, elongate, straight sided, grooved ventrally. Fixed secundibrachials four to



TEXT-FIG. 3. Plate diagram of *Stipatocrinus hulveri* gen. et sp. nov. Note peculiar configuration of proximal circle, divided into bilaterally symmetrical halves by sutures in AE-interray and C-ray. The t-shaped radials (black) enclose suboval interbrachial areas and are smaller in BC- and CD-interrays than in remaining interrays.

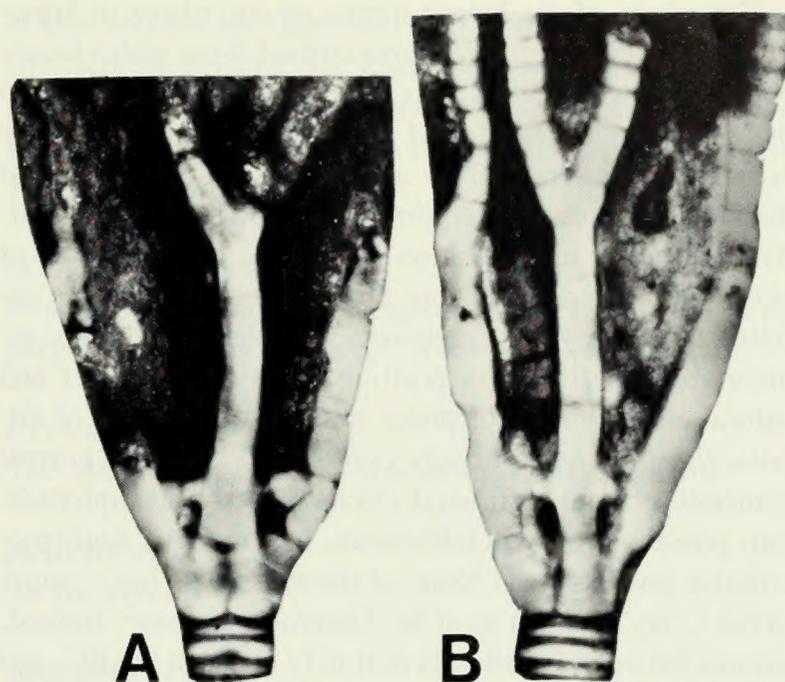
six in each ray branch. Fixed pinnule borne by second secundibrachial. Interbrachials smooth, without ornamentation. Narrow cylindrical anal tube eccentrically located on tegmen. Arms ten, pinnulate; brachials in immature biserial arrangement. Column transversely circular.

#### DISCUSSION

There is little doubt that *Stipatocrinus* gen. nov. belongs to the subclass Camerata in view of its densely pinnulate arms, fixed ray series, fixed pinnules, and numerous interbrachials. However, below this level, classification becomes difficult. It is not clear whether *Stipatocrinus* should be classified among the Monobathrida or the Diplobathrida, or in a separate order altogether, because the peculiar plate configuration of the base of the cup in this crinoid renders plate homologies obscure. The problem is compounded, for the column of *Stipatocrinus* is neither pentameric nor pentagonal, but cylindrical with a round lumen. Hence, this column does not provide any indication of orientation of thecal plates relative to the entoneural system, as suggested by the "Law of Wachsmuth and Springer" (Warn, 1975).

Even the location of radials in *Stipatocrinus* is somewhat problematic. The A- and E-rays are each supported by a single uninterrupted row of plates beginning in the lowest circling of the cup (Text-Fig. 3). Thus, plates of this circling in the A- and E-rays could be considered to be radials. However, if this interpretation is followed, the radials of these rays would lie immediately above the stem facet, a feature unknown in all other crinoids. In the B-, C-, and D-rays the lowest plates of the rays are t-shaped and situated within the second circling of plates (Text-Fig. 3). These t-shaped plates are relatively narrow, as in fixed brachials, and are even grooved ventrally (Pl. 1, figs. 16,20). However, they are differentiated from all other cup plates by their lateral processes, and they form a distinctive circling. We feel fairly confident in designating plates of the second circling as radials because a t-shaped plate of the C-ray overlies a suture between plates of the lowest circling. This plate is therefore in typical radial position. Furthermore, the strong differentiation of these plates is also suggestive of radials. In other primitive camerate crinoids, including reteocrinids and xenocrinids, the radials are always markedly separate from other adjacent plates (Brower, pers. comm., 1986).

Configuration of the lowest circling of cup plates in *Stipatocrinus* is unique among camerate crinoids, both in terms of the shapes and relative sizes of these plates and, most notably, in their orientation with respect to the radials. The lowest circling combines features of infrabasals, basals, and radials. Three of four sutures dividing this circling are interrarial (AB-, DE-, and EA-interrays), a characteristic of infrabasals; the fourth suture is directly below the C-ray radial as it would be in a normal basal



TEXT-FIG. 4. *Stipatocrinus hulveri* gen. et sp. nov. Specimens immersed in ethanol.

A. Individual centred on C-ray. Proximal circling is divided by suture in C-ray but not in BC- or CD-interrays. Aborally directed bifurcation of C-ray ridge continues on basals. Small suboval interbrachial areas in BC- and CD-interrays, bounded above by t-shaped radials, are of similar size. Interbrachials, underlain by black integument, are poorly preserved. Paratype ROM 44309a,  $\times 4.0$ .

B. Individual centred on D-ray. Proximal circling is divided by suture in C-ray and DE-interray but not in CD-interray. Suboval interbrachial area in DE-interray, bounded above by t-shaped radials, is smaller than adjacent area in CD-interray. Interbrachials are well preserved in this specimen, and proximal portion of anal tube is visible. Paratype ROM 44309b,  $\times 4.0$ .

circling (Text-Figs. 3, 4A,B). Furthermore, two plates in the lowest circling resemble radials because they are directly in line with and support the A- and E-rays.

An unusual and interesting feature of *Stipatocrinus* is that the plates of the lowest circling are dissimilar in size and shape with respect to each other. Two plates of this circling, directly in line with the A- and E-rays, are five-sided and considerably smaller (narrower) than the larger six-sided plates that they adjoin laterally (Text-Fig. 3). Pairing of each larger plate with a smaller one divides the lowest circling into bilaterally symmetrical halves, each with two plates, about a sutural plane passing through the AE-interray and C-ray. To our knowledge, no other camerate crinoids, including xenocrinids, possess a basal circling with this symmetry.

We emphasize that the peculiar configuration of the lowest circling of cup plates in *Stipatocrinus* is not an abnormality. Consistent orientations have been observed in all seven specimens that have been adequately prepared. Furthermore, plate organization appears well coordinated with ray ridge configuration.

Homology of the lowest circlet of cup plates in *Stipatocrinus* is a problem. We have termed these plates basals because they comprise the only circlet of plates between the stem facet and inferred radial circlet. However, the proximal circlet resembles a typical basal circlet only at the C-ray suture, situated directly below the C-ray radial. An alternative interpretation is that the lowest circlet of plates in *Stipatocrinus* may be homologous with the infrabasals of dicyclic camerates, in which the sutures are invariably interradsial in position. However, number and sutural configuration of plates in the lowest circlet of *Stipatocrinus* do not precisely conform to that of a normal camerate crinoid infrabasal circlet. Nearly all diplobathrans possess five equal infrabasals, although the Anthemocrinidae possess four. None of these crinoids has a suture in the C-ray position as in the *Stipatocrinus* base. Instead, sutures between infrabasals normally occur in the BC- and CD-interrays; such sutures are absent in *Stipatocrinus* (Text-Figs. 3, 4A).

The origin of the unequal basals in *Stipatocrinus* is unclear. The infrabasal circlet of anthemocrinids, a family unrelated to *Stipatocrinus*, possesses a large plate presumably derived from fusion of two smaller plates. In contrast, *Stipatocrinus* possesses two large and two small plates in the lowest circlet. The two large plates could have developed by lateral fusion of two pairs of plates in an infrabasal circlet that originally possessed six plates. However, this seems unlikely, for crinoids with six infrabasals are unknown. A more plausible explanation is that the two larger plates of *Stipatocrinus* were derived in two different ways: one by fusion of two plates, the other by enlargement of a single plate, so that the sutural position migrated from an interradsial to a radial position. This would imply an ancestral condition with five plates in the lowest circlet, for which no evidence exists.

If the lowest cup plates of *Stipatocrinus* are homologous with infrabasals, we are faced with the obvious problem of absence of a basal circlet. Most researchers have implied that a pseudomonocyclic condition results from loss of infrabasals (Warn, 1975; Ubaghs, 1978). For example, the inadunate genus *Iocrinus* could have evolved from *Merocrinus* by loss of infrabasals. Alternatively, certain monocyclic inadunates including *Belemnocrinus* may have evolved from dicyclic forms by loss of the basal circlet (McIntosh, 1979). The latter process may also have occurred in *Stipatocrinus*.

The interrays of *Stipatocrinus* are peculiar in several respects. Most notably, they are filled with an exceptional number of small ossicles, more than 400 plates in the CD-interray of the holotype specimen (ROM 44310a, Pl. 1, figs. 1,3). Moreover, these plates are irregular in size, shape, and arrangement and are unusually thin. Unlike the majority of camerate crinoids, *Stipatocrinus* has interrays without a well-developed gradient of progressively smaller

plates distally. Finally, *Stipatocrinus* lacks a primanal and anitaxis but possesses a cylindrical anal tube composed of plates resembling interbrachials.

Moore and Laudon (1943) considered small, irregular, and numerous interbrachials to be a primitive character. Brower (1974a) believed this characteristic to be advanced in xenocrinids, crinoids with interrays plating similar to *Stipatocrinus* and occurring stratigraphically above supposedly related camerates with fewer and larger interbrachials. However, this conclusion was based, in part, on a misinterpretation of the phylogeny of xenocrinids (Brower, pers. comm., 1986). Poorly known phylogenies of camerate crinoids do not prove that either of these conflicting theories is correct. However, we believe that ontogenetic patterns of growth in primitive pelmatozoans and biostratigraphic evidence lend support to the Moore and Laudon hypothesis.

Ontogeny of interbrachials in most camerate crinoids was closely integrated and coordinated with increase in size of the cup (Brower, 1974b). Originating near the periphery of the tegmen, interbrachials were derived from tegmen interambulacrals that were modified in size and shape, becoming regular polygons as they were gradually incorporated into interrays. Consequently, interrays of most camerate crinoids typically show a well-developed gradient of progressively smaller and more irregular interbrachials towards the tegmen. This gradient apparently evolved early in the history of camerates, first appearing in the Lower Ordovician crinoid *Proxenocrinus*.

Unlike that of most crinoids, ontogeny of interbrachials in *Stipatocrinus* and the Late Ordovician crinoid *Xenocrinus* was poorly coordinated and poorly integrated with overall growth of the cup. In these crinoids, interbrachials grew more slowly than other calyx plates, necessitating an intercalatory mode of growth (Brower, 1974a). As a consequence of this mode of growth, interbrachials in *Stipatocrinus* and *Xenocrinus* are irregular in shape and arrangement. Interbrachials could have been added anywhere within interrays of these crinoids. This pattern is especially well developed in *Stipatocrinus*, in which small interbrachials adjacent to larger interbrachials are scattered throughout interrays. Intercalation increased the number of interbrachials at a given level within the cup as this crinoid grew. New interbrachials were also added by incorporation of interambulacrals. Interbrachials in *Stipatocrinus* merge smoothly into the tegmen, indicating that tegmen plates were incorporated into interrays, unaccompanied by substantial modification in size or shape of these ossicles. Because of an intercalatory mode of growth, interrays of *Stipatocrinus* and *Xenocrinus* display a poorly developed gradient of progressively smaller plates distally.

The origin of camerate crinoids and their relationships to other groups of pelmatozoans is poorly known. However, biostratigraphic evidence indicates that primitive

Cambrian pelmatozoans, including the probable crinoid *Echmatocrinus*, are characterized by thecae possessing a large number of plates irregular in shape and arrangement. Moreover, thecae of these echinoderms typically show a poorly developed gradient of progressively smaller plates distally, and these plates commonly merge into the tegmen with little differentiation. We suggest that similar features in *Stipatocrinus* represent primitive characters.

The calyces of *Stipatocrinus* and *Xenocrinus* are similar in that both possess large numbers of small irregular interbranchials. However, *Xenocrinus* has a well-developed anitaxial ridge, and configuration of the lowest circlet of plates in *Stipatocrinus* is unlike that of *Xenocrinus*. We conclude that similar morphology of interrays suggests simply that these crinoids belong to archaic lineages probably not closely related to each other. In fact, superficial similarity of these genera could be an example of convergent evolution, although this possibility seems doubtful. It implies repeated development of large numbers of small interbranchials from ancestors with larger regular interbranchials, which is contrary to evolutionary trends in camerate lineages of simplifying cup structure by reducing numbers of interbranchials or eliminating them altogether.

Even the assumption that *Stipatocrinus* is related to diplobathran camerates does not provide insight into the evolution of this genus. *Gaurocrinus* and *Reteocrinus*, both members of the Reteocrinidae, possess large numbers of irregular interbranchials as in *Stipatocrinus*. However, these crinoids have a primanal within the radial circlet and also possess a prominent, ridged anitaxis. Furthermore, *Reteocrinus* has divergent characters, including interinfrabasal gaps, spiculelike interbranchials, and apinnulate, branching arms. None of the more advanced diplobathrans is at all similar to *Stipatocrinus*. Thus, *Stipatocrinus* presently stands by itself. We follow convention in tentatively assigning this genus to the Monobathrida because only a single circlet of plates is situated below the radials. However, we also emphasize that the present monocyclic-dicyclic schism in classification of crinoids, discussed by Warn (1975), may obscure phylogenetic relationships. In fact, *Stipatocrinus* may belong to a sister group of the Diplobathrida. Discovery of additional genera related to *Stipatocrinus* may readily justify erection of a new order to encompass these unusual crinoids. We conclude that the several seemingly primitive features of *Stipatocrinus* suggest that it may have been a "living fossil" in late Llandoveryan seas.

#### *Stipatocrinus hulveri* sp. nov.

Text-Figs. 1–8; Pl. 1, figs. 1–21; Pl. 2, figs. 1–12

#### TYPE MATERIAL

Numbered slabs containing approximately 75 calyces and crowns associated with numerous columnals and columns

of this species are deposited in the collections of the Department of Invertebrate Palaeontology at the Royal Ontario Museum, catalogue numbers ROM 44309–44344. Figured specimens: holotype ROM 44310a; paratypes ROM 44309a,b,d; 44310b–44323.

#### OCCURRENCE

Reynales Formation, Wallington Member, exposed in the gorge of the Genesee River, Rochester, New York.

#### ETYMOLOGY

The species is named in honour of Michael Hulver.

#### DIAGNOSIS

As for genus.

#### DESCRIPTION

Calyx steeply conical (height/width = 1.5–1.7), with highly elevated ray ridges and depressed interrays. CD-interray about 20 per cent wider than other interrays.

Four plates in lowest cup circlet, here designated as basals, possibly representing infrabasals. Proximal circlet comprising approximately 15 per cent of calyx height, divided by sutures in AB-, DE-, and EA-interrays and in C-ray, undivided in BC- and CD-interrays (Text-Figs. 3, 4A,B; Pl. 1, figs. 1,5,6,13–15). Basals two large and two small (Pl. 1, fig. 13). Basals directly underlying A- and E-ray radials five-sided, smaller (narrower) than larger six-sided basals occupying AB- through DE-interrays (Text-Figs. 3, 4A,B, 7; Pl. 1, figs. 5,6). Smaller basals elongate, widest just above stem facet (Pl. 1, fig. 5). Larger basals expanding in width distally. Sutures passing through AE-interray and C-ray divide basal circlet into bilaterally symmetrical halves (Text-Fig. 3). In AB-, DE-, and EA-interrays basals meeting along straight suture for about one-third to one-half of basal height, diverging above forming concave margins of proximal interrays (Text-Fig. 3; Pl. 1, fig. 5). In BC- and CD-interrays these concave margins less pronounced, not extending as close to stem facet (Text-Figs. 3, 4A). Basals in A- and E-rays each with ridge continuing onto A- and E-ray radials, respectively. Larger basals meeting directly below C-ray along straight suture for about 80 per cent of basal height, each possessing two adradially directed ridges. Pair of ridges divided by suture separating these basals merging upwards, forming single ridge on C-ray radial (Text-Figs. 3, 4A).

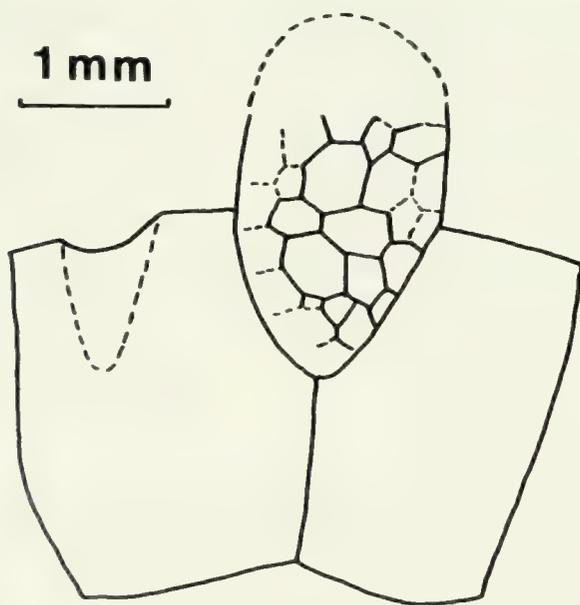
Radials and higher fixed brachials grooved ventrally (Pl. 1, figs. 16,17,20,21), extremely narrow, forming highly elevated ray ridges extending full width of brachials (Text-Figs. 3, 4A,B, 8; Pl. 2, figs. 1–5). Radials t-shaped (height/maximum width = 1.6–1.8). Each radial bisected near midpoint by pair of short, narrow, laterally directed projections (Text-Figs. 3, 4A,B; Pl. 1, figs. 5,20). Projections

forming ridges lower in height than ray ridges, crossing proximal interray areas, narrowly joining radials together.

First primibrachials rectangular, highly elongate (height/width = 3.0–5.0), straight-sided. Second primibrachials Y-shaped (height/width = 1.4–1.6), axillary (Pl. 1, fig. 10). Each ray bifurcating near centre of second primibrachial, forming two straight ray ridge segments continuing upwards towards arms. First secundibrachials rectangular (height/width = 1.5–1.9), each bearing a stout fixed pinule bounded by interprimibrachials (Pl. 1, figs. 1,4). Second secundibrachials equidimensional (height/width = 1.0). Succeeding fixed secundibrachials rectangular, wider than high (height/width = 0.6–0.8). Arms free beyond third to seventh secundibrachial.

Interrays filled with exceptionally numerous interbrachials (more than 400 ossicles in CD-interray of holotype specimen, ROM 44310a; Pl. 1, fig. 1). Interrays of smaller individuals with fewer plates (Pl. 2, figs. 10,11). Interbrachials immediately above basals enclosed in suboval to subtriangular depressed areas bounded above by lateral projections of radials (Text-Figs. 3, 4B, 5; Pl. 1, fig. 19). These enclosed areas smaller in BC- and CD-interrays than in remaining interrays (Text-Figs. 3, 4A,B; Pl. 1, fig. 6). Interbrachials irregular polygons, typically five- or six-sided, varying from four- to seven-sided. Largest interbrachials commonly with rounded corners. Interrays displaying poorly developed gradient of progressively smaller plates distally; smaller plates occurring between larger plates throughout interrays (Pl. 1, fig. 3). Interbrachials smooth, without ornamentation, very thin (approximately 0.03 mm thick), resting on black layer representing degraded organic matter (Text-Figs. 3, 4A; Pl. 1, fig. 5). Interray areas loosely sutured to straight-sided ray series.

Primanal and anitaxis absent. Narrow cylindrical anal

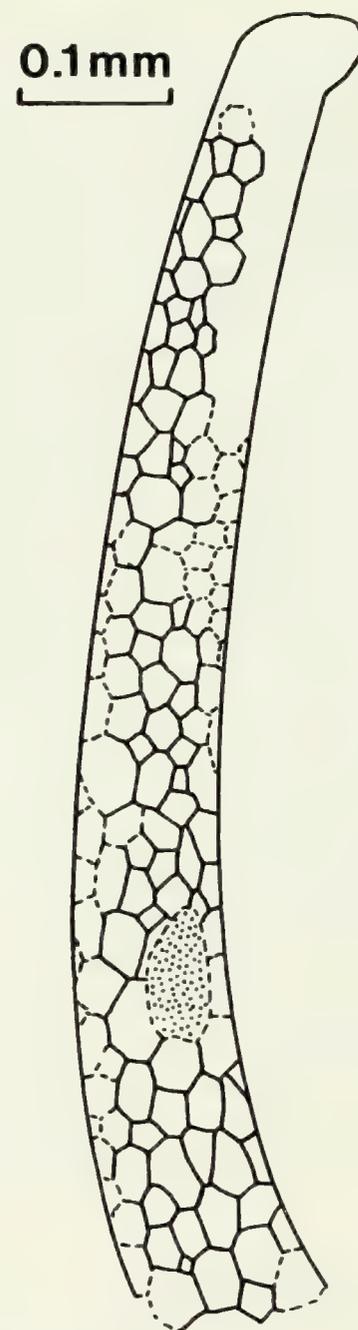


TEXT-FIG. 5. Plate diagram of basals and proximal interbrachials in AB-interray of *Stipatocrinus hulveri* gen. et sp. nov. Paratype ROM 44310b, Pl. 2, fig. 19.

tube developed in CD-interray, eccentrically situated near edge of tegmen (Pl. 1, figs. 1,11; Pl. 2, figs. 1,9). Anal tube incompletely preserved in available specimens, composed of smooth polygonal plates resembling interbrachials (Text-Fig. 6; Pl. 1, figs. 2,4).

Tegmen seen only in cross-section, forming shallow dome consisting of polygonal plates resembling interbrachials in size and shape. Some tegmental plates nodose, commonly bearing short spines (Pl. 1, fig. 12).

Arms ten, pinnulate, relatively long (Table 1). Proximal brachials in uniserial arrangement (Pl. 1, fig. 5), rectangular, wider than high (height/width = 0.4–0.6). Succeeding brachials cuneate, in immature biserial arrangement in distal portions of arms (Pl. 1, fig. 8). Pinnules incompletely known. Pinnulars attached directly to free brachi-



TEXT-FIG. 6. Plate diagram of anal tube of *Stipatocrinus hulveri* gen. et sp. nov. Anal plates resemble interbrachials. Dotted area represents area damaged during preparation. Holotype ROM 44310a, Pl. 1, fig. 2.

als, short, quadrangular, tapering distally (Pl. 1, fig. 7). Succeeding pinnules lath-shaped (height/width = 2.2–2.7).

Column transversely circular, heteromorphic, tapering uniformly almost to a point distally (Pl. 2, figs. 4,5,8,10). Proximal nodals biconcave in longitudinal cross-section with thickened, rounded epifacets concealing adjacent internodals (Text-Fig. 7A,B; Pl. 1, fig. 18). Internodals rectangular or slightly biconvex in longitudinal cross-section.

Proximal columnals thin (nodal height/width = 0.25–0.33, internodal height/width = 0.06–0.13). Columnals becoming successively thicker in distal portion of column (nodal height/width = 0.28–0.36, internodal height/width = 0.17–0.22). Noditaxis typically consisting of one nodal, two or three second-order internodals, a first-order internodal, and two or three second-order internodals (Text-Fig. 7A–D). Lumen small, round (Pl. 2, figs. 6,7).

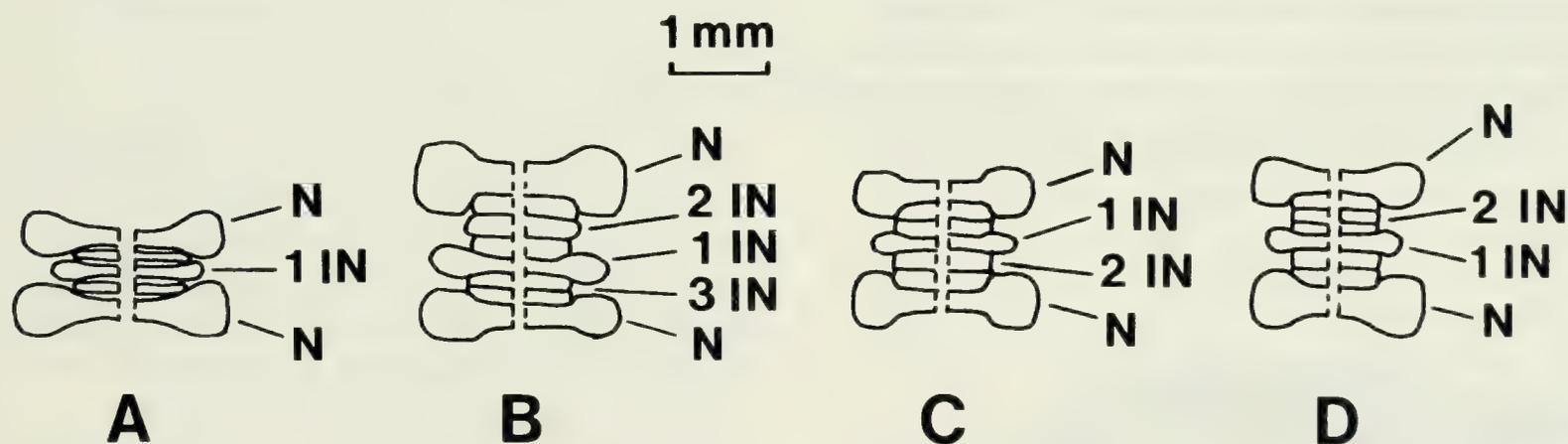
TABLE 1. Measurements (in mm) of types of *Stipatocrinus hulveri* gen. et sp. nov.

Orientation of plate measurements as follows: ROM 44309a—below B- and C-rays (basal), C-ray (radial–secundibrachial); ROM 44309b and 44310a—below C- and D-rays (basal), D-ray (radial–secundibrachial); ROM 44310b—below B- and C-rays (basal), B-ray (radial–secundibrachial).

Measurements	Paratype ROM 44309a	Paratype ROM 44309b	Holotype ROM 44310a	Paratype ROM 44310b
Calyx height	13.7	14.1	18.4	13.2
Calyx width	9.1*	9.2*	10.5*	—
Arm length	33.0†	—	—	18.0†
Proximal stem diameter	2.5	2.8	3.1	2.5
Basal height	2.1	1.9	2.2	2.5
Basal width	2.1	1.9	2.5	2.5
Radial height	3.2	3.6	3.8	3.5
Radial width	2.1	2.1	2.0	2.0
First primibrachial height	2.8	3.6	3.8	3.2
First primibrachial width	1.0	1.2	1.2	0.89
Second primibrachial height	2.4	2.7	2.9	2.5
Second primibrachial width	1.8	1.9	2.0	1.5
Second secundibrachial height	1.4	1.6	2.0	1.4
Second secundibrachial width	1.0	0.97	1.0	0.81

\*Specimen crushed. Actual width less than indicated.

†Distal portions of arms not preserved.



TEXT-FIG. 7. Diagrams of longitudinal cross-sections through pluricolumnals of *Stipatocrinus hulveri* gen. et sp. nov. Nodals and internodals are indicated, respectively, as follows: N, 1 IN, 2 IN, 3 IN.

A. Pluricolumnal between 9 and 10 mm below cup of paratype ROM 44319, indicated by upper pair of arrows on Pl. 1, fig. 18. Very thin second-order internodals are not visible from exterior of proximal column.

B. Pluricolumnal between 26 and 28 mm below cup of paratype ROM 44319, indicated by lower pair of arrows on Pl. 1, fig. 18. Second-order internodal is incipient nodal. Note prominent, thickened epifacets of nodals, which partly enclose adjacent third-order internodals.

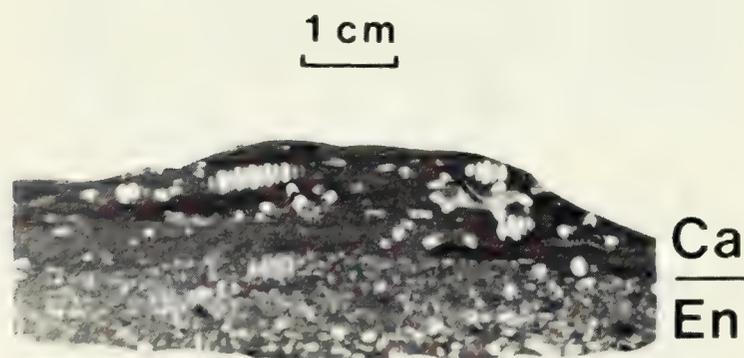
C. Distal pluricolumnal of paratype ROM 44320, indicated by upper pair of arrows on Pl. 1, fig. 9.

D. Distal pluricolumnal of paratype ROM 44320, indicated by lower pair of arrows on Pl. 1, fig. 9.

## Palaeoecology

Limited lateral extent of slabs bearing *Stipatocrinus hulveri* on a talus slope in the gorge of the Genesee River and apparent absence of similar slabs in the cliff wall above indicate that these crinoids comprised a highly localized stand, or "garden," on the seafloor. The area of seafloor occupied by this stand, assuming that the majority of specimens have been discovered, did not exceed 0.2 m<sup>2</sup>. This occurrence represents a high-density stand (*sensu* Brower, 1973) with about 400 crinoids per square metre. Few fossils, including poorly preserved specimens of the brachiopod *Coolinia?* and encrusting bryozoans are associated with these crinoids (Pl. 2, fig. 10). The horizon from which the *Stipatocrinus* material was apparently derived is nearly devoid of fossils, indicating that the seafloor surrounding this stand was sparsely populated by skeletonized benthic organisms. Stands of Early Silurian crinoids described by Brett (1978) and Eckert (1984) also occur in poorly fossiliferous strata. Clustering of conspecific crinoids in these environments may have conferred adaptive advantage by providing viable breeding populations (Brower, 1973).

Polished slabs obtained by sectioning perpendicular to bedding planes reveal that well-preserved *Stipatocrinus* individuals consisting of nearly complete crowns with long stems occur in calcisiltite adjacent to a thin encrinite (Text-Fig. 8). Although it is not possible to demonstrate conclusively the sequence of deposition of these layers because the slabs were not recovered *in situ*, comparison with stands of Early Silurian crinoids excavated *in situ* (Eckert, 1984) and personal observations of occurrences of well-preserved crinoids in the Middle Devonian Hamilton Group of western New York and Ontario strongly suggest that well-preserved *Stipatocrinus* individuals are situated immediately above the encrinite. Consisting almost entirely of *Stipatocrinus* columnals, cup plates, and arm fragments, the encrinite rests with a sharp lower contact on plane-laminated, unfossiliferous calcisiltite. Com-



TEXT-FIG. 8. Vertical section through slab containing *Stipatocrinus hulveri* gen. et sp. nov. Basal encrinite (En) is inferred to represent lower surface of slab. Calcisiltite layer (Ca) above encrinite shows well-preserved, sectioned cups and pluricolumnals of *S. hulveri*. Paratype ROM 44322.

plete calyces, typically lacking arms and columns, are embedded in the lower surface of this encrinite.

In reconstructing the palaeoecology of this occurrence, we infer that the *Stipatocrinus hulveri* stand originated from a chance spatfall on a sparsely populated seafloor. Most of these pioneer individuals attained maturity, as indicated by the large size of radials in the encrinite (Pl. 1, fig. 20). Death, decay, and subsequent disarticulation of these crinoids under conditions of generally slow sedimentation gradually formed a carpet of ossicles, represented by encrinite, below the stand. Resuspension of ossicles by currents buried decaying, partly articulated, individuals relatively quickly. Small crinoids, evidently juveniles, associated with larger individuals indicate that the stand survived for more than one generation. Eventually the stand was completely extirpated by rapid burial, indicated by excellent preservation of articulated crinoids in calcisiltite, displaying undulatory laminations. Burial must have been rapid because modern crinoids exposed on the seafloor typically decay and disarticulate quickly after death (Meyer, 1971; Liddell, 1975; Meyer and Meyer, 1986).

In the Reynales Formation at Rochester, beds of *Pentamerus*, a brachiopod that inhabited relatively shallow, rough-water environments (Boucot, 1975; McKerrow, 1978) alternate with sparsely fossiliferous strata deposited in relatively quiescent, probably deeper water conditions. Thus, occurrence of well-preserved *Stipatocrinus* specimens in sparsely fossiliferous strata lacking *Pentamerus* is consistent with a previous interpretation (Brett and Eckert, 1982) that occurrences of well-preserved crinoids are typically associated with quiet-water palaeoenvironments near the limit of normal wave base but within reach of storm-generated waves and currents. Several slabs bearing *S. hulveri* show prominent, subparallel orientation of crowns and columns suggestive of storm-generated currents during or immediately preceding burial (Pl. 2, figs. 10, 12). After burial the crinoids rapidly decayed, but disarticulation was prevented by overlying sediment and absence of bioturbation. Internal organs were not preserved in any specimens of *Stipatocrinus*. However, a black carbonaceous film representing degraded organic matter commonly covers inner surfaces of interbranchials (Text-Figs. 3, 4A; Pl. 1, figs. 5, 11). A reducing, acidic environment was apparently generated within the calyces as decay proceeded, inducing formation of syngenetic pyrite on some specimens. Acidic conditions caused dissolution of interbranchials in some individuals (Text-Figs. 3, 4A; Pl. 1, figs. 5, 11). Dissolution probably occurred before lithification because the crinoids are not preserved as steinkerns.

Many *Stipatocrinus* calyces are filled with sparry calcite. These specimens are typically less crushed or flat-

tened than individuals filled with calcisiltite. Precipitation of calcite within hollow calyces early in diagenesis may have allowed the crinoids to resist compaction (see Sprinkle and Longman, 1982:69). However, it is also possible that calcite was precipitated late in diagenesis after lithification. When calcite was absent, thinly plated interrays of *Stipatocrinus* made these crinoids susceptible to compaction, distorting and flattening them.

Densely pinnulate arms and the flexibility of the proximal portion of the column suggest that *Stipatocrinus* was a rheophilic filter feeder. The t-shaped radials that bridge proximal interray areas helped to strengthen the base of the calyx. However, narrow brachials and unusually thin interbrachials that do not interlock with the ray series made the *Stipatocrinus* calyx relatively fragile in construction when compared to most other camerates, perhaps restricting this crinoid to relatively low-energy environments. Apparent absence of *Stipatocrinus* in the *Pentamerus* community is consistent with this interpretation.

Extremely narrow fixed brachials and t-shaped radials made possible incorporation of more interbrachials in *Stipatocrinus* than any other described crinoid of similar size. Functional morphology of this interray plating is conjectural. The ease with which *Stipatocrinus* calyces were flattened during compaction of the sediment, without breakage of plates, demonstrates that the interrays were flexible in life. Brower (1974a) postulated that large numbers of interbrachials in *Xenocrinus* aided respiration by diffusion of oxygen through plate sutures, enhanced by pumping action of flexible interrays. Perhaps oxygen could diffuse directly through the unusually thin (0.03 mm thick) interbrachials of *Stipatocrinus*. We note, however, that unlike certain Ordovician crinoids with pore-bearing calyces, there

is no evidence of auxiliary respiratory structures in Early Silurian crinoids. Numerous interbrachials in *Stipatocrinus* may simply be a scaling phenomenon involving thickness/width ratios of plates: reduction in plate thickness necessitated smaller plate size in order to retain resistance to breakage.

Unusually thin interray plating and a thick but very narrow fixed ray series of the calyx of *Stipatocrinus* incorporated the smallest amount of calcite possible consistent with requirements for sufficient strength and rigidity. Thus, metabolic cost of calcite secretion in *Stipatocrinus* was minimal compared to most other thicker-plated crinoids. By reducing metabolic cost, overall growth of *Stipatocrinus* may well have been rapid, perhaps allowing early reproduction. If *Stipatocrinus* is assumed to have colonized environments generally unfavourable to most crinoids, as occurred during deposition of the lower Wallington Limestone, an r-selective strategy of early reproduction may have ensured survival.

The column of *Stipatocrinus* is relatively short, not exceeding 10 cm in length, and tapers gradually almost to a point distally. Curvature of the distal portion in paratype ROM 44314 (Pl. 2, fig. 8) and in other specimens suggests that the column of *Stipatocrinus* was coiled distally around other objects for anchorage. This mode of attachment is characteristic of many camerates with gradually tapering, heteromorphic columns, including *Alisocrinus*, *Glyptocrinus*, *Xenocrinus*, and most diplobathrids (Brett, 1981). Possession of a distally coiled column permitted attachment to a wide variety of substrates (Brett, 1985) and was probably a contributing factor in the survival of melocrinidids, glyptocrinids, dimerocrinitids, rhodocrinitids, and the lineage leading to *Stipatocrinus* into the Silurian.

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Diligent field work by Michael Hulver resulted in discovery of the study material, and we are indebted to him for making us aware of this occurrence. Additional specimens were collected by Gordon Baird and Karla Parsons. George C. McIntosh, James Brower, and James Sprinkle critically reviewed the manuscript. Janet Waddington of the De-

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PLATE 1, figs. 1–21.

*Stipatocrinus hulveri* gen. et sp. nov. Reynales Formation, Rochester, New York. Specimens immersed in ethanol.

1. CD-interray of well-preserved individual. Note absence of primanal and anitaxis. Proximal cirlet is divided by suture in DE-interray but not in CD-interray; t-shaped radials bridge proximal interray areas, enclosing interbrachials between basals and lateral projections of radials. Narrow, highly raised brachials enclose thinly plated interrays consisting of numerous, polygonal interbrachials. Distal interbrachials merge with plates of anal tube and tegmen without differentiation. See also Text-Fig. 6; Pl. 1, figs. 2–4, 10; Pl. 2, fig. 1. Holotype ROM 44310a,  $\times$  3.5.

2. Cylindrical anal tube of above individual showing arrangement of irregular polygonal plates. Distal portion of tube is missing. See Text-Fig. 6 for a diagram of this specimen. Holotype ROM 44310a,  $\times$  8.0.

3. CD-interray detail between first primibrachial and second secundibrachial. Interray, slightly separated from C-ray in this individual, is composed of numerous polygonal interbrachials irregular in shape and arrangement. Holotype ROM 44310a,  $\times$  7.0.

4. C-ray and adjoining interbrachials showing proximal portion of anal tube and first pinnular of fixed pinnule borne by second secundibrachial. Holotype ROM 44310a,  $\times$  7.0.

5. Anterior view of nearly complete crown. Orientation of rays unknown. Interbrachials, apparently dissolved during diagenesis, are absent in most of interray area, revealing underlying black layer representing degraded organic matter. Interray areas below lateral projections of radials are subtriangular in this specimen. Proximal free brachials are uniserial. See also Pl. 2, fig. 12. Paratype ROM 44311f,  $\times$  3.0.

6. Specimen centred on B-ray. Numerous irregular polygonal interbrachials are visible in BC-interray. Basal cirlet is divided by suture in AB-interray but not in BC-interray. See also Text-Fig. 5; Pl. 1, fig. 19; Pl. 2, fig. 3. Paratype ROM 44310b,  $\times$  4.0.

7. Proximal arm detail. Note short pinnules. Paratype ROM 44321,  $\times$  5.0.

8. Distal portion of arm with cuneate brachials. Paratype ROM 44309d,  $\times$  5.0.

9. Longitudinal cross-section through distal column. Nodals have prominent, thickened epifacets. Typical noditaxis consists, sequentially, of a nodal, two or three second-order internodals, a first-order internodal, and two or three second-order internodals. See Text-Fig. 7C,D for diagrams of two noditaxes indicated here by pairs of arrows. Paratype ROM 44320,  $\times$  4.0.

10. Intersecundibrachial detail between bifurcation of D-ray. Holotype ROM 44310a,  $\times$  6.0.

11. CD-interray of crown. Incomplete anal tube is outlined by black integument. Most interbrachials are missing. See also Pl. 2, fig. 12. Paratype ROM 44311a,  $\times$  2.0.

12. Longitudinal cross-section through distal fixed secundibrachials and tegmen. Many tegmental plates possess nodes or short spines. Paratype ROM 44315,  $\times$  6.0.

Figs. 13–16. Sequential series of cross-sections through lower portion of cup destroyed by progressive grinding. C-ray is at upper left of each section.

13. Basals just above stem. Note small opening for lumen. Basal suture at upper left is directly below C-ray. Two basals below B-, C-, and D-rays are larger than remaining basals.

14. Slightly higher section through basals showing initial development of ridges on rays.

15. Basals sectioned near top of cup with prominent ridges on rays.

16. Section through proximal portions of radials and interrays. Each radial has prominent ventral groove.

17. Cup transversely sectioned just below bifurcation of rays. Cup has been strongly compressed, demonstrating flexibility of thinly plated interrays. Paratype ROM 44316,  $\times$  3.0.

18. Longitudinal cross-section through column and proximal portion of cup. One basal and part of adjoining radial are visible. Proximal nodals are transversely biconcave with slightly thickened epifacets. Internodals are typically transversely biconvex. See Text-Fig. 7A,B for diagrams of two noditaxes indicated here by pairs of arrows. Paratype ROM 44319,  $\times$  3.0.

19. Proximal AB-interray area enclosed by basals and lateral projections of t-shaped radials. Numerous irregular, polygonal interbrachials are visible. See Text-Fig. 5 for a diagram of this specimen. Paratype ROM 44310b,  $\times$  10.0.

20. Isolated radial showing characteristic lateral projections and deep ventral groove. Left projection is incomplete. Paratype ROM 44323,  $\times$  5.0.

21. Transverse cross-section through three calyces, each sectioned near bifurcation of rays. Fixed brachials contain prominent ventral groove. Paratype ROM 44313,  $\times$  3.0.



1



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4



6



7



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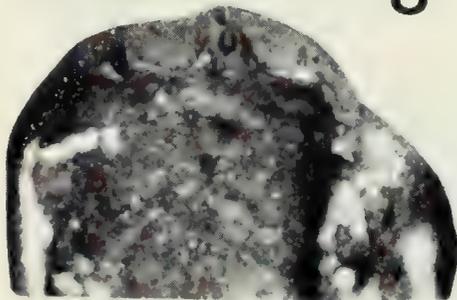
9



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PLATE 2, figs. 1–12.

*Stipatocrinus hulveri* gen. et sp. nov. Reynales Formation, Rochester, New York. Blackened specimens whitened with ammonium chloride.

1. CD-interray of holotype specimen. Suboval interbrachial area in CD-interray, bounded by a single basal and t-shaped radials of C- and D-rays, is smaller than adjacent area in DE-interray, bounded below by two basals. See also Text-Fig. 6; Pl. 1, figs. 1–4,10. ROM 44310a,  $\times 3.5$ .

2. Lateral view of nearly complete crown centred on B-ray. See also Pl. 2, fig. 12. Paratype ROM 44311d,  $\times 1.5$ .

3. Crown centred on B-ray. Suboval interbrachial area of proximal AB-interray is larger than adjacent suboval area in BC-interray. See also Text-Fig. 5; Pl. 1, figs. 6,19. Paratype ROM 44310b,  $\times 2.8$ .

4. Partial crown centred on C-ray. Proximal bifurcation of C-ray ridge continues on basals. See also Pl. 2, fig. 12. Paratype ROM 44311b,  $\times 2.8$ .

5. CD-interray view of crown with most of column. See also Pl. 2, fig. 12. Paratype ROM 44311e,  $\times 2.0$ .

6. Pluricolumnal. Two internodals are attached to nodal with prominent epifacet. Paratype ROM 44318b,  $\times 7.0$ .

7. Pluricolumnal. Internodal is attached to nodal displaying broad epifacet. Note small lumen. Paratype ROM 44317a,  $\times 7.0$ .

8. Incomplete column coiled distally. Paratype ROM 44314,  $\times 2.0$ .

9. CD-interray of individual with proximal portion of anal tube. See also Pl. 2, fig. 12. Paratype ROM 44311a,  $\times 3.0$ .

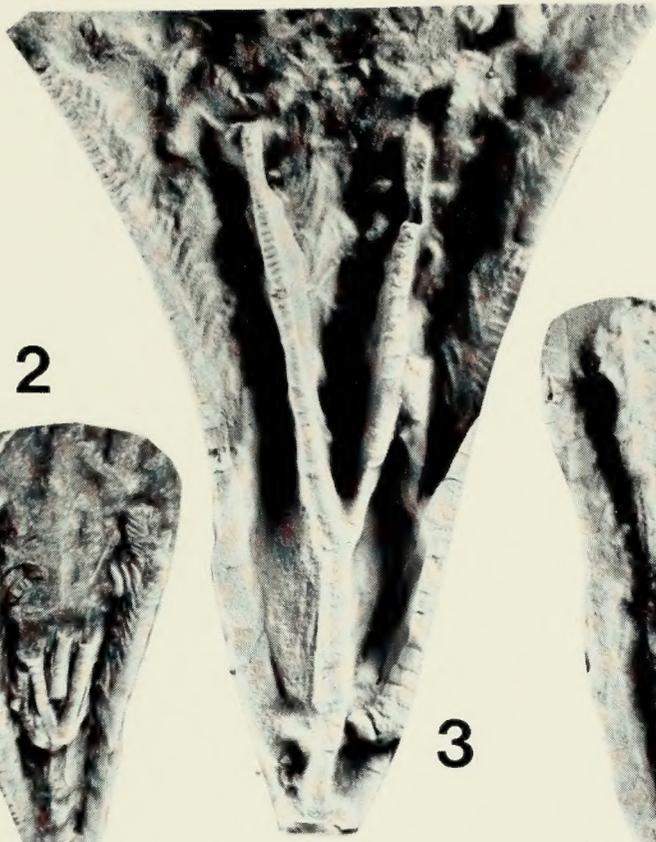
10. Small slab with nearly complete crown and column near centre of photograph, two additional partial crowns and numerous pluricolumnals. These small specimens represent juvenile crinoids. Paratypes ROM 44312a–c,  $\times 0.8$ .

11. Detail of above slab. Lower crown possesses two essentially complete arms. Paratypes ROM 44312a–c,  $\times 1.6$ .

12. Well-preserved crinoids on small slab. Specimens are oriented subparallel to each other, suggesting unidirectional current at time of burial. Paratypes ROM 44311a–i,  $\times 0.8$ .



1



2



3



4



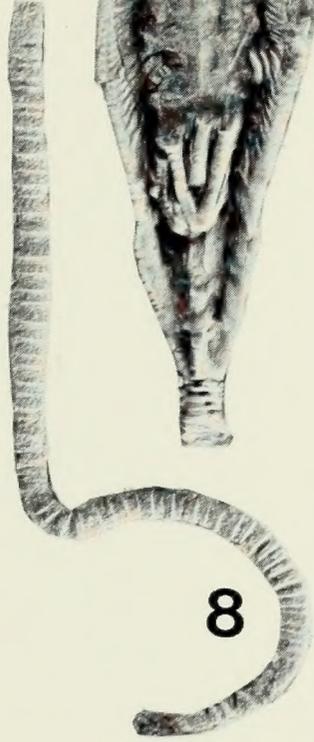
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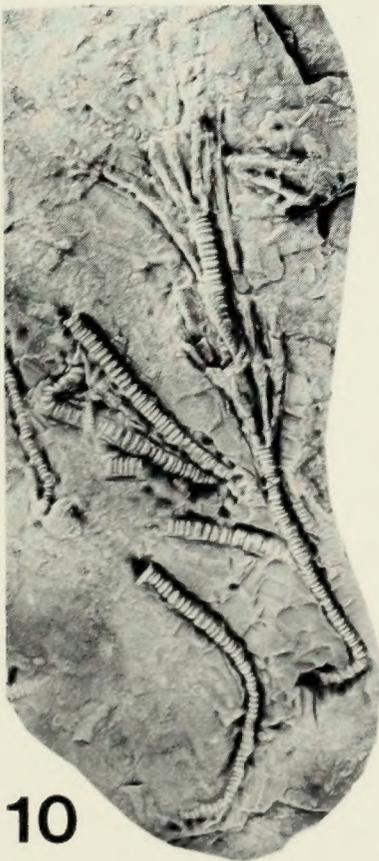
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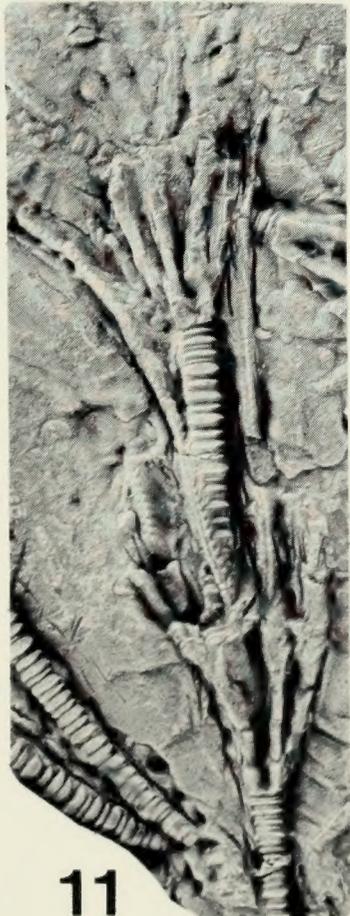
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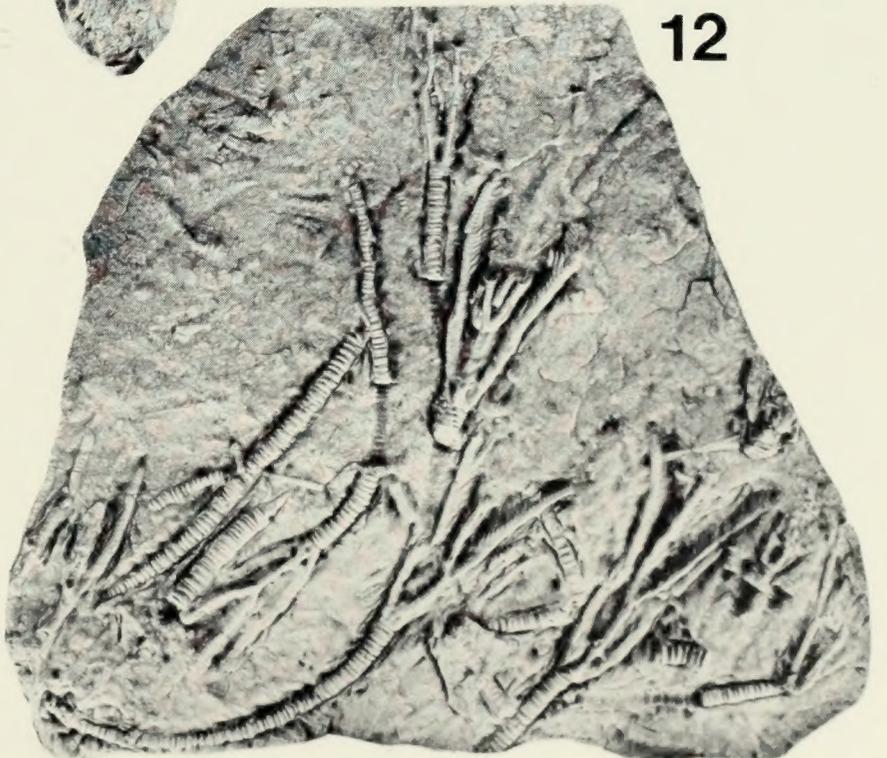
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