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**Notes**

# A field guide to the Silurian Echinodermata of the British Isles: Part 2 – Crinoidea, minor groups and discussion

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**SUMMARY:** Crinoids are the most common and diverse group of echinoderms in the Silurian of the British Isles. This guide describes examples of all nominal crinoid groups recognized from this interval and region (48 genera, about 100 species). In contrast, coronate, edrioasteroid, mitrate and cyclocystoid echinoderms are rare, the first three higher taxonomic groups being represented by a single species each, and the last by two species. Of 145 species of echinoderms in the Silurian of the British Isles, 74 are known from the Much Wenlock Limestone Formation of Wenlock age at Dudley in the West Midlands. For comparison, the most diverse faunas from the Llandovery Series (North Esk Inlier, Pentland Hills, Scotland) and Ludlow Series (Lower Leintwardine Formation, Leintwardine, Herefordshire) consist of only 16 and 17 species, respectively. If the echinoderm-rich succession at Dudley was unknown, the three older series of the Silurian, the Llandovery, Wenlock and Ludlow, would each include about 30 known species of echinoderm. It is the extreme diversity of the Much Wenlock Limestone Formation at Dudley that makes the echinoderm diversities of the Llandovery and Ludlow appear depauperate.

This paper forms the second and final part of a field guide to the Silurian Echinodermata of the British Isles, illustrating and describing all genera of Crinoidea known from this interval and region, plus certain poorly represented groups. ('Minor groups' in the title refers to their limited diversity in the British Silurian, not necessarily their whole fossil record.) The first part of the guide (Lewis *et al.* 2007) considered the more diverse, non-crinoid groups of echinoderms of the British Isles, namely echinoids, ophiuroids, asteroids, ophiocistioids and rhombiferans. Of the 35 genera discussed therein, most only include one nominal species from the British Silurian. In contrast, many genera of crinoids in the Silurian of the British Isles include two or more nominal species (Table 1). More species of crinoids are known from the Silurian of the British Isles than the combined total of all other echinoderm groups. It is therefore unexpected that no monograph of British Silurian crinoids has been published, although two unpublished Ph.D. theses consider those of the Lower Palaeozoic (Ramsbottom 1954) and Wenlock (Widdison 2001a). This guide therefore goes some way towards filling an appreciable gap in the literature. As with the companion guide, we hope to encourage collectors to slip a copy of the guide into their pocket for reference during field work; we encourage laminating the pages, or at least the figures, in plastic to protect them from the elements.

The stratigraphical and geographical distributions of the crinoid taxa considered herein are summarized in Table 1. Of the 98 species of crinoids listed in Table 1, nearly two-thirds (62%) are known from the Much Wenlock Limestone Formation (Wenlock Series, Homerian Stage) at Dudley in the West Midlands, and half are known only from the Much Wenlock Limestone Formation at that locality. Many, perhaps most specimens were probably from the Wren's Nest at Dudley (Hardie 1971; Siveter 2000). Most of the localities and horizons listed herein were discussed in detail by Aldridge

*et al.* (2000). For further explanation of the litho-, bio- and chronostratigraphical terminology used, see Cocks *et al.* (1992). Localities yielding the species discussed herein outside the British Isles are not mentioned; data on these are available from Webster (2003) and references therein.

## 1. SYSTEMATIC PALAEOONTOLOGY

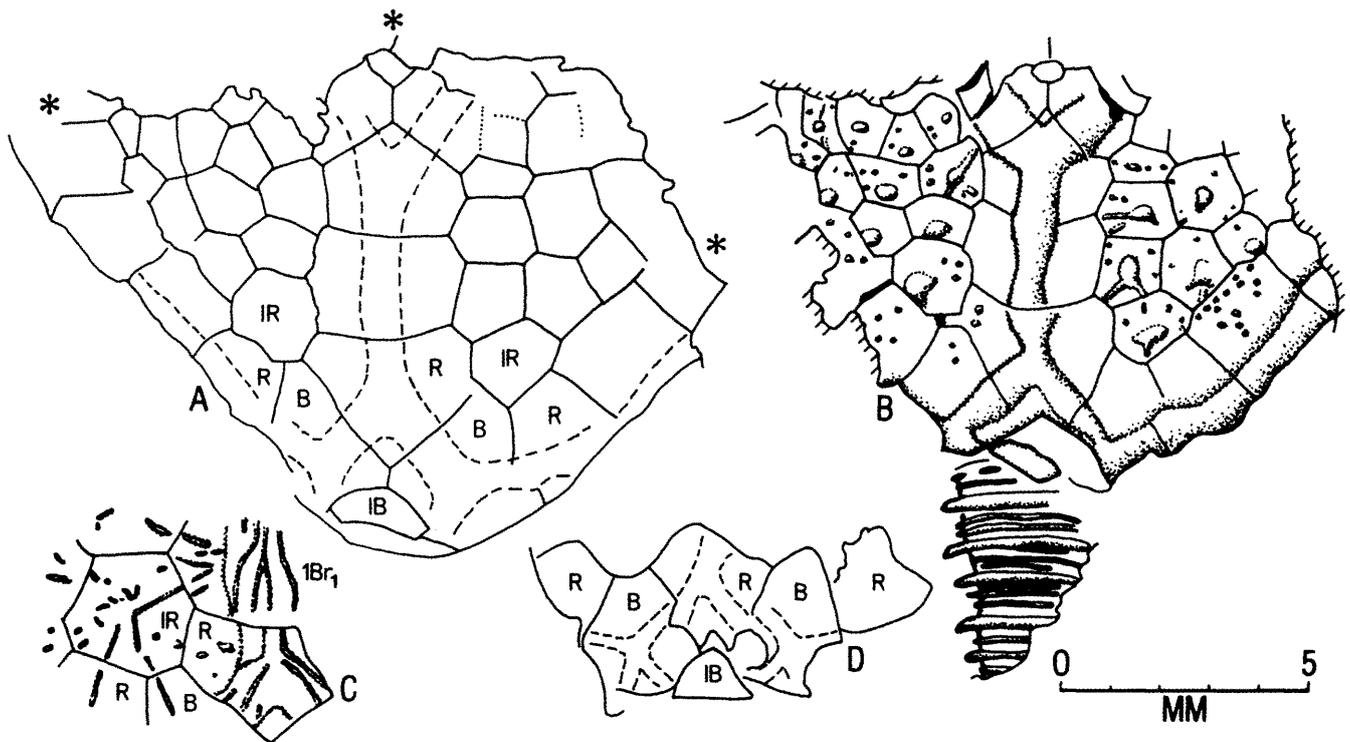
Terminology of the echinoderm endoskeleton is explained in the Appendix; see also Ubaghs (1978a) and Moore *et al.* (1978a) for crinoids. The notation for heteromorphic columns follows Webster (1974). Illustrated specimens are principally in the collections of the Natural History Museum, London (BMNH), but also in those of the British Geological Survey, Keyworth (BGS GSM), the James Mitchell Museum, University College Galway (JMM), the Geological Museum, University of Copenhagen (MGUH), the National Museum of Wales, Cardiff (NMW), and the Sedgwick Museum, Cambridge (SM). Individual taxa are illustrated in Figures 1–15.

In order to keep the survey of crinoids to a manageable length, systematic descriptions are mainly at the hierarchical level of genus. This entails examination of 48 genera, including about 100 species (Donovan *et al.* 2008, tables 16.1–16.3). Where a taxon is monospecific in the study area, it is referred to under the specific epithet. Taxa are listed within the major groups of Palaeozoic crinoids (Simms & Sevastopulo 1993), that is, diplobathrid and monobathrid camerates, cladids, sagenocrinid and taxocrinid flexibles, and disparids. The descriptions are based on the personal observations of the authors, supported by Ramsbottom (1954), Moore & Teichert (1978), Widdison (2001a) and other references as indicated. Unless stated otherwise, columns are assumed to be holomeric.



**Table 1**  
Continued

	Llandovery						Wenlock			Ludlow		Přídolí	
	Rh	Ae	Telychian			Lland	Much Wenlock Lst Fm	Wen	Ludf	Lud			
	A	B	C	D	E	F		G	H	I	J		K
<i>Dictenocrinus decadactylus</i> (Salter)							+						
<i>Dictenocrinus pinnulatus</i> (Bather)							+						
<i>Enallocrinus scriptus</i> (Hisinger)							+						
<i>Gissocrinus arthriticus</i> (Phillips)							+						
<i>Gissocrinus capillaris</i> (Phillips)							+						
<i>Gissocrinus cyrili</i> Bouska									+				
* <i>Gissocrinus goniodactylus</i> (Phillips)							+		+				
<i>Gissocrinus scoparius</i> (Salter)							+						
<i>Gissocrinus squamiferus</i> (Salter)							+						
<i>Mastigocrinus bravoniensis</i> Ramsbottom										+			
<i>Mastigocrinus loreus</i> Bather							+						
<i>Petalocrinus bifidus</i> Donovan & Fearnhead						+							
<i>Petalocrinus</i> cf. <i>visbyensis</i> Bather						+							
<i>Segmentocolumnus</i> (col.) <i>clarksoni</i> Donovan & Harper				+									
<i>Thenarocrinus callipygus</i> Bather							+						
<i>Thenarocrinus gracilis</i> Bather							+						
<b>Sagenocrinida</b>													
<i>Calpiocrinus intermedius</i> Springer							+						
<i>Clidochinus?</i> sp.					+								
<i>Cryptanisocrinus kilbridensis</i> Donovan <i>et al.</i>				+									
<i>Homalocrinus nanus</i> (Salter)							+						
<i>Hormocrinus anglicus</i> Springer							+						
<i>Icthyocrinus intermedius</i> Angelin							+						
<i>Icthyocrinus phillipsianus</i> Springer							+						
* <i>Icthyocrinus pyriformis</i> (Phillips)							+		+				
<i>Lecanocrinus bacchus</i> (Salter)							+						
<i>Pycnosaccus bucephalus</i> (Bather)							+						
<i>Sagenocrinites expansus</i> (Phillips)							+						
* <i>Temnocrinus tuberculatus</i> (J. S. Miller)							+		+				
<b>Taxocrinida</b>													
<i>Eutaxocrinus maccoyanus</i> (Salter)											+		
<i>Gnorimocrinus</i> sp. nov.									+				
<i>Meristocrinus minor</i> Springer									+				
<i>Meristocrinus orbigny</i> (M'Coy)												+	
<i>Meristocrinus</i> sp. nov.							+						
<b>Disparida</b>													
<i>Calceocrinus anglicus</i> (Springer)							+						
<i>Calceocrinus turnbulli</i> Donovan		+											
<i>Calceocrinus?</i> sp.		+											
<i>Chirocrinus fletcheri</i> (Salter)							+						
<i>Cicerocrinus elegans</i> Sollas												+	
* <i>Myelodactylus ammonis</i> (Bather)							+	+	+				
<i>Myelodactylus convolutus</i> Hall					+								
* <i>Myelodactylus fletcheri</i> (Salter)							+		+				
<i>Myelodactylus hibernicus</i> Donovan & Sevastopulo				+									
<i>Myelodactylus parvispinifer</i> (Brower)			+										
<i>Myelodactylus penkillensis</i> Donovan & Sevastopulo						+							
<i>Parapisocrinus</i> cf. <i>sphaericus</i> (Rowley)											+		
<i>Pisocrinus campana</i> S.A. Miller				cf.									
* <i>Pisocrinus pilula</i> de Koninck							+		+				
<i>Synchirocrinus gradatus</i> (Salter)							+						
<i>Synchirocrinus inclinus</i> (Ramsbottom)							+						
<i>Synchirocrinus nitidus</i> (Bather)							+						
<i>Synchirocrinus pugil</i> (Bather)							+						
<i>Synchirocrinus serialis</i> (Austin)							+						
<b>Number of species</b>	6	2	6	3	2	4	62	6	15	4	3	1	



**Fig. 1.** *Chaosoocrinus ornatus* Donovan (after Donovan 1993, fig. 10). (A, B, D) Holotype. (A) SM A32803b, flattened theca with dorsal cup, fixed arms and interradial plates. Sculpture of ray ridges dashed. Interradial plates between arms; (B) SM A32803a, with dorsal cup in same orientation as A; (C) paratype, SM A32093c, detail of part of theca to show sculpture (contrast with B); (D) SM A32803c, dorsal cup. Key: IB = infrabasal; B = basal; R = radial; IR = proximal interradial; 1Br<sub>1</sub> = first primibrachial; \* = positions of arms. All camera lucida drawings of internal mould (A) and latex casts (B–D).

Class **CRINOIDEA** J. S. Miller, 1821

Subclass **CAMERATA** Wachsmuth & Springer, 1885

Order **DIPLOBATHRIDA** Moore & Laudon, 1943

**Remarks.** The diplobathrids are the dicyclic camerate crinoids, with a rigidly sutured calyx including an armoured tegmen, proximal arms typically fixed and uniserial, and free arms pinnulate and commonly biserial.

*Chaosoocrinus ornatus* Donovan, 1993 (Fig. 1)

**Description.** Proxistele circular in section, heteromorphic N3231323, composed of low columnals of differing diameters. Dorsal cup medium bowl shaped. Five low, unsculptured infrabasals. Five octagonal basals in contact at short suture and with prominent Y-shaped ridges. Five large, heptagonal radials with both tubercles and ridges in inverted Y-shape. Radials separated by single small, hexagonal interradial plates. Median ray ridges on arms. Arms fixed to second or third secundibrachial, uniserial, branching at second primibrachial. Free arms pinnulate, branching heterotomously once. Interradial and interbrachial plates with a sculpture of tubercles or radiating ridges.

**Locality and horizon.** Haverford Mudstone Formation (= Gasworks Mudstones), Rhuddanian (lower Llandovery), Haverfordwest, Pembrokeshire, SW Wales.

**Remarks.** Interpretation of the thecal plating of the camerate crinoids can be problematic for the uninitiated, particularly differentiating between plates of the cup, the fixed arms, and the interradial and interbrachial plates. As the first of the camerate crinoids discussed herein and in order to demystify this group, *C. ornatus* is illustrated by camera lucida drawings

with features such as the different plate circlets of the dorsal cup labelled (Fig. 1); also, Carpenter rays (see Appendix) and other features are labelled on diagrams of a flexible and a disparid crinoid (Figs 12, 14).

*Lyriocrinus britannicus* Ramsbottom, 1950 (Fig. 2A)

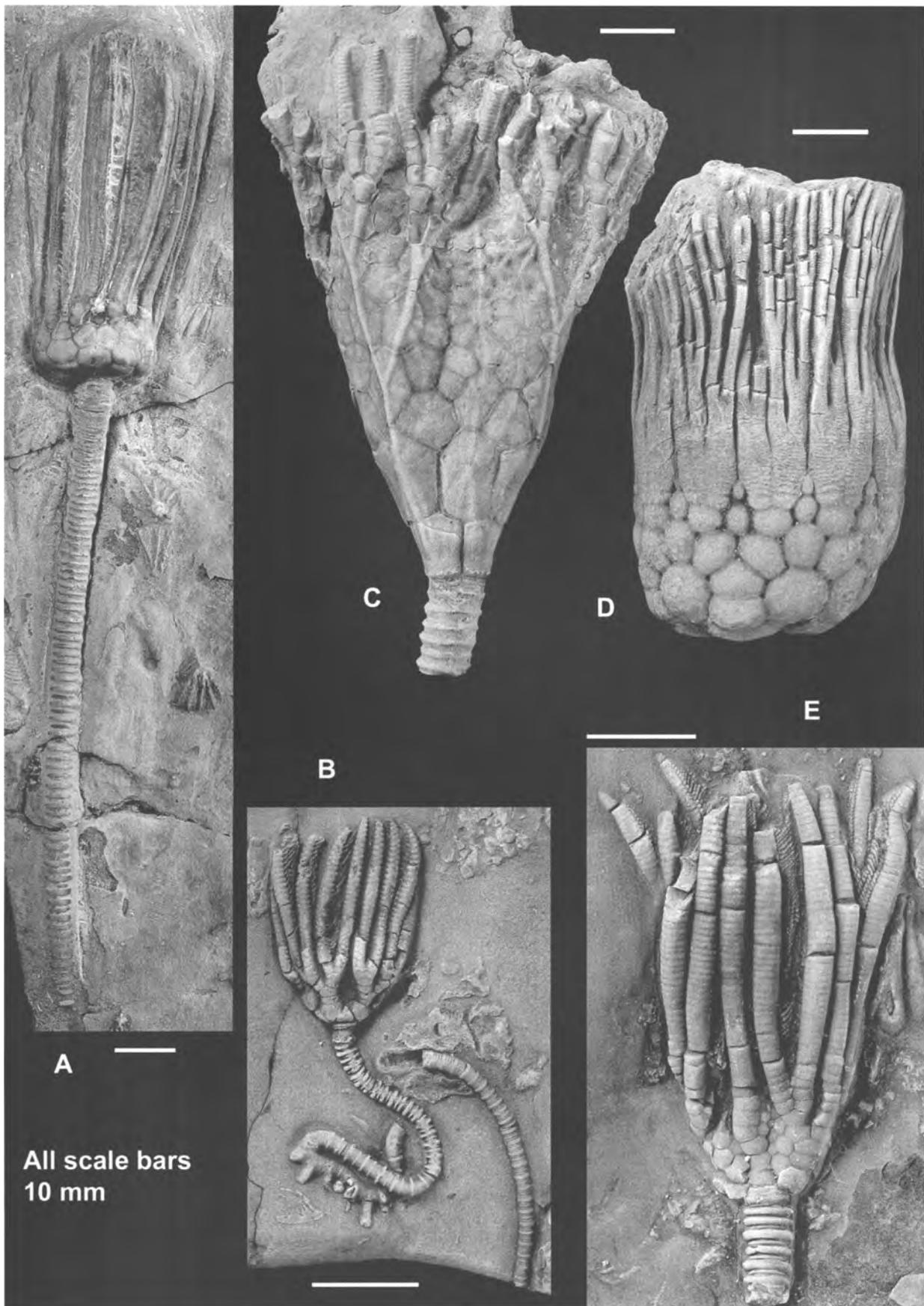
**Description.** Column round in section, heteromorphic, nodals with convex latera. Bowl-shaped dorsal cup with smooth plates, wider than high with flat base. Infrabasals concealed in basal concavity by proxistele. Five equal hexagonal basals on base of cup and extending into concavity. Five equal hexagonal to heptagonal radials, poorly seen in lateral view, separated by interradial plates. Tegmen composed of numerous small plates; anal tube central and shorter than arms. Arms branch once isotomously. Two primibrachials and two most proximal secundibrachials uniserial, fixed, supporting ten biserial, pinnulate free arms. Interradial plates few and large.

**Locality and horizon.** Much Wenlock Limestone Formation, Wenlock, Dudley, West Midlands; also from the same formation at Tividale, Dudley, and Benthall Edge, 5 km NE of Much Wenlock, Shropshire (Ramsbottom 1950; Widdison 2001a, p. 41).

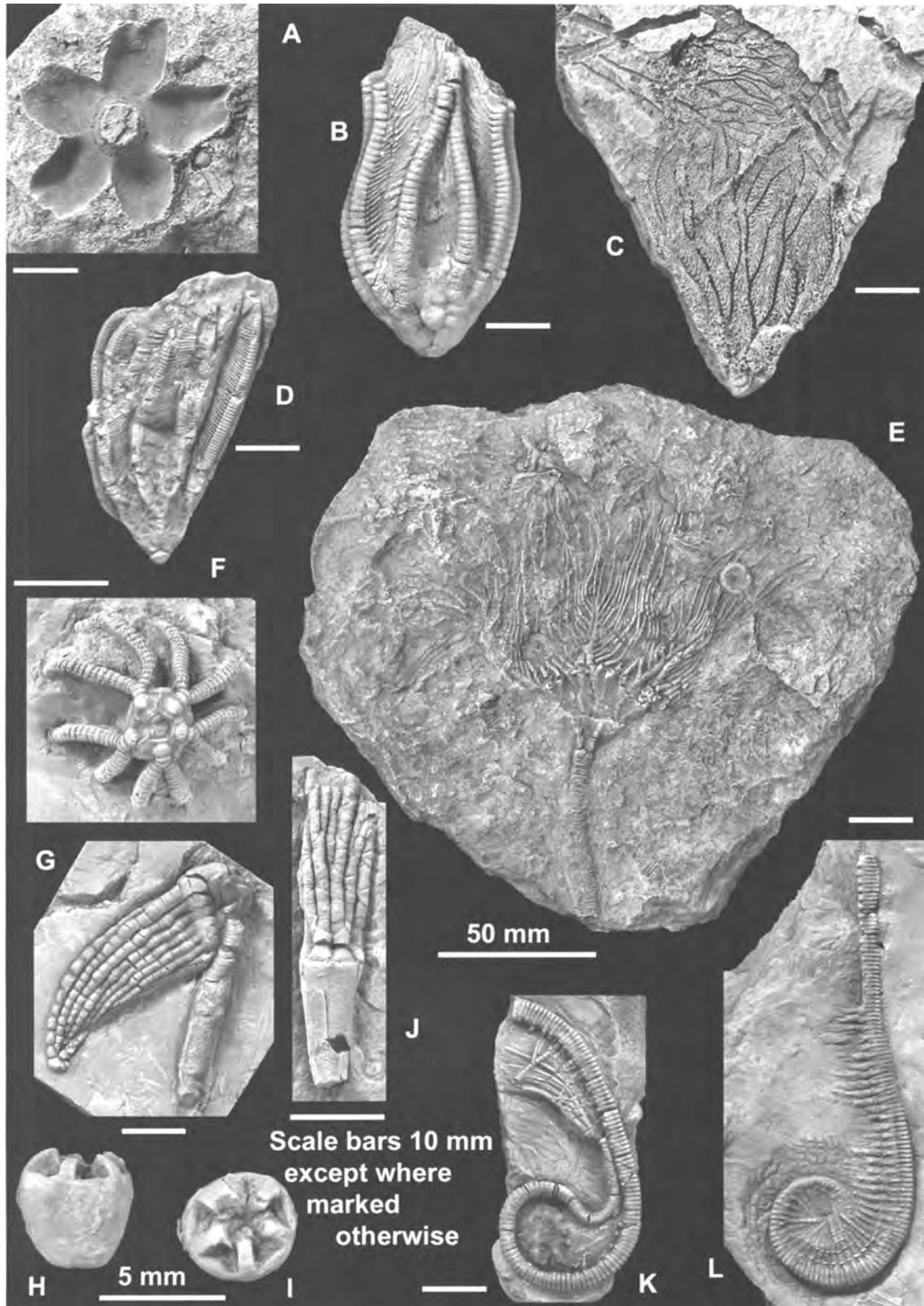
**Remarks.** This is one of the relatively few species of Wenlock crinoid recognized from the Much Wenlock Limestone Formation in Shropshire (Table 1).

*Dimerocrinites* spp. (Figs 2B, 3D)

**Description.** Calyx small, low or moderately high, conical to bowl-shaped. Five infrabasals, five basals and five radials. All



**Fig. 2.** Diplobathrid (A, B) and monobathrid (C–E) camerate crinoids from the Wenlock, Much Wenlock Limestone Formation, Dudley, West Midlands, of the British Isles. (A) *Lyriocrinus britannicus* Ramsbottom, BMNH 40259; (B) *Dimerocrinites speciosus* (Angelin), BMNH E1446; (C) *Periechocrinus costatus* Austin & Austin, BMNH 57249; (D) *Clonocrinus polydactylus* (M'Coy), BMNH 40257, holotype. (E) *Desmidocrinus macrodactylus* Angelin ex. gr., BMNH E45597.



**Fig. 3.** Crinoids from the Silurian of the British Isles. Unless stated otherwise, specimens are from the Wenlock, Much Wenlock Limestone Formation, Dudley, West Midlands. (A) Diplobathrid(?) *Floricolumnus* (col.) *girvanensis* Donovan & Clark, BMNH E49739b, paratype, middle Llandoverly Newlands Formation, Girvan, Ayrshire; (B) Monobathrid *Carpocrinus simplex* (Phillips), BMNH E45600; (C) Monobathrid '*Scyphocrinites*' *pulcher* (M'Coy), BMNH 42905, Coniston Grits, Lower Ludlow, Benson Knot, Kendal, Cumbria; (D) Diplobathrid *Dimerocrinites decadactylus* Phillips, BMNH 57106; (E) Monobathrid *Promelocrinus anglicus* Jaekel, BMNH 40328; (F) Monobathrid *Cordylocrinus* sp. nov., BMNH E418; (G) Disparid *Synchirocrinus serialis* (Austin), BMNH E57427; (H, I) Disparid *Pisocrinus pilula* de Koninck, BMNH 57261. Wenlock, Wenlock Shale (probably Coalbrookdale Formation), Malvern; (H, I) Lateral view; (I) Oral view; (J) Disparid *Cicerocrinus elegans* Sollas, BMNH E26071. Upper Ludlow, Whitcliffe Flags, Whitcliffe Hill, Ludlow, Shropshire; (K) Disparid *Myelodactylus fletcheri* (Salter), BMNH 47859; (L) Disparid *Myelodactylus ammonis* (Bather), BMNH E6336.



**Fig. 4.** *Ptychocrinus mullochillensis* Fearnhead & Donovan, BGS GSM 92136, holotype (after Fearnhead & Donovan 2007a, text-fig. 2). Latex cast of crown about 12 mm in height.

radials in contact except CD interray. Rays of calyx pronounced, with or without median ray ridges, interray areas depressed (except *D. uniformis*). Anal plates of calyx joined to tegmen. Ten to 20 free arms, biserial and pinnulate. Proxistele slender, heteromorphic. Columnals circular in section with a pentastellate lumen.

*Locality and horizon.* All but one of the British species are from the Much Wenlock Limestone Formation, Wenlock, at Dudley. The exception is *Dimerocrinites pentlandicus* Brower, 1975, from the Telychian (upper Llandovery) of the North Esk Inlier, Pentland Hills, Scotland (Table 1).

*Remarks.* Widdison (2001a, pp. 43–53) recognized four species of *Dimerocrinites* from the Much Wenlock Limestone Formation of Dudley. *Dimerocrinites decadactylus* Phillips, 1839 (Figs 2B, 3D) and *D. uniformis* Salter, 1873, have ten arms; *D. speciosus* (Angelin, 1878) has 20 arms; and *D. icosidactylus* Phillips, 1839, has two to four, typically three, arms per ray, that is, about 15 arms. *Dimerocrinites uniformis* is distinguished from *D. decadactylus* by not having depressed interray areas and in possessing a flattened base to the dorsal cup. *Dimerocrinites pentlandicus* had at least 20 arms and is distinguished from *D. speciosus* by its small basals that are not in lateral contact, more numerous interradial plates and more polygonal primibrachials (Brower 1975, p. 641).

*Ptychocrinus* spp. (Fig. 4)

*Description.* Proxistele round or rounded pentagonal in section. Dorsal cup dicyclic, small, conical, medium bowl-shaped. Infrabasal circling may be obscured by proximal columnals. Five basals, with a high basal in the CD interray that supports a primanal. Radials pentagonal, separate. Fixed arms uniserial, pinnulate, branching isotomously once (*Ptychocrinus longibrachialis* Brower, 1975) or twice (*Ptychocrinus mullochillensis* Fearnhead & Donovan, 2007a). All fixed brachials broad, brachial plates tall. Free arms long and slender. Pinnules short. Interbrachial plates polygonal.

*Locality and horizon.* *Ptychocrinus longibrachialis* is from the Telychian (upper Llandovery) of the North Esk Inlier, Pentland Hills, Scotland. *Ptychocrinus mullochillensis* is from the Aeronian (middle Llandovery) Newlands Formation, Mulloch Hill, near Girvan, Ayrshire, Scotland.

*Remarks.* This genus is rare in the Silurian of the British Isles. The two species of *Ptychocrinus*, both from the Llandovery of Scotland, are each based on single specimens.

*Floricolumnus* (col.) *girvanensis* Donovan & Clark, 1992 (Fig. 3A)

*Description.* Heteromorphic crinoid columns with strongly pentastellate to rounded crenulate nodal columnals. Nodal

epifacet unsculptured and inflated, with articular facet lying in a depression. 'Rays' of epifacet highly variable between columnals. Articulation symplectial, narrow circular or pentagonal articular facet with narrow crenularium. No areola. Conical claustrum sloping into lumen of pentagonal to rounded outline. Up to five orders of internodals developed, priminternodals highest *et seq.*, with decreasingly convex latera.

*Locality and horizon.* Common in the Newlands Formation (Aeronian, middle Llandovery), of the Girvan district, Ayrshire, SW Scotland. *Floricolumnus* (col.) sp. cf. *girvanensis* is rare in the Haverford Mudstone Formation (= Gasworks Mudstones), Rhuddanian (lower Llandovery), Haverford-west, Pembrokeshire, SW Wales (Donovan 1993).

*Remarks.* Based only on very distinctive columnals, which Donovan & Clark (1992) thought were most probably derived from a diplobathrid.

#### Order MONOBATHRIDA Moore & Laudon, 1943

*Remarks.* The monobathrids are the monocyclic camerate crinoids, with a rigidly sutured calyx including an armoured tegmen, proximal arms typically fixed and uniserial, and free arms pinnulate and commonly biserial.

*Promelocrinus anglicus* Jaekel, 1902 (Fig. 3E)

*Description.* Crowns large and with numerous arms. Four basals, one large and three small. Five radials large, hexagonal, in lateral contact. Median ray ridges weakly to strongly developed; plate sculpture smooth to finely granulose, other sculptures less common. Primibrachials two, secundibrachials two, fixed arms uniserial and attached by interradians and interbrachials up to low level in the tertibrachials. Free arms of outer branches of each ray biserial, unbranched and pinnulate; inner pair of branches uniserial, but bearing multiple (12–15) biserial, pinnulate ramules. Column round in section, heteromorphic with four orders of internodals, lumen pentalobate.

*Locality and horizon.* Much Wenlock Limestone Formation, Wenlock, Dudley, West Midlands.

*Remarks.* Brower (1976, p. 663) noted a second, albeit indeterminate taxon, *Promelocrinus* sp., from the Much Wenlock Limestone Formation at Dudley. The functional morphology of the distinctive arms of *Promelocrinus* was discussed by Cowen (1981).

*Scyphocrinites* spp. (Figs 3C, 5)

*Description.* Distal 'attachment' large, bulbous and chambered, formed from numerous branching radices and termed loboliths. Column heteromorphic, circular in transverse outline, articulating symplectially and with a pentastellate lumen. Dorsal cup monocyclic, five pentagonal basals and five larger, polygonal radials. Theca large, incorporating primaxillaries and secundaxillaries of arms, the latter with fixed pinnules. Interradians and interbrachials large proximally, smaller more distally. Robust anal tube. Fixed arms uniserial, free arms uniserial or biserial. Arms branching isotomously, pinnulate.

*Locality and horizon.* Loboliths of *Scyphocrinites* sp. are from Catasuent Cove, Porthluney, south Cornwall, and are presumed to be from the Přídolí Series. '*Scyphocrinites pulcher*' (M'Coy, 1851) is known from a number of Ludlow

localities in Cumbria, including Knott Hollow Quarry, Ulverston; Osmotherley Common, Ulverston; and Benson Knott and Shepherd's Quarry, Kendal. Specimens from Osmotherley Common are from the Coniston Grits (Coniston Group, Windermere Supergroup), which are of early Ludlow age. Specimens from Knott Hollow Quarry are probably from the underlying Wray Castle Formation, also of early Ludlow age. Welsh specimens are from the Lower Ludlow Beds, Nant Gwrhyd (Uchaf), south of Llangollen, Denbighshire (Ramsbottom 1954, p. 197). Specimens from Ireland are currently being studied by G. D. Sevastopulo and co-workers.

*Remarks.* There are two occurrences of *Scyphocrinites sensu lato* in the British and Irish Silurian. Loboliths from SW England are undoubtedly *Scyphocrinites sensu stricto* (Bather 1907; Fig. 5). The widespread '*Scyphocrinites pulcher*' (Fig. 3C) represents a new genus close to *Scyphocrinites* on which loboliths are not developed (Donovan and co-workers research in progress).

*Periechocrinus* spp. (Fig. 2C)

*Description.* Calyx monocyclic, conical, high. Three tall basals. Five radials, equal, in contact except in the CD interray, where a primanal of equal size is intercalated. Median ray ridges commonly present. Radials and primibrachials high. Ten to 50 free arms, biserial (except *Periechocrinus* sp. nov.), only branching uncommonly. Interradians and interbrachials numerous. Tegmen composed of numerous small plates, forming a long anal tube. Column xenomorphic, heteromorphic proximally and homeomorphic more distally. Column circular in section with a small circular or pentagonal lumen.

*Locality and horizon.* The four British species are all known from the Much Wenlock Limestone Formation (Wenlock), Dudley. *Periechocrinus limonium* is also known from Cefn Ila, Usk (Widdison 2001a, p. 83), also from the Wenlock Series.

*Remarks.* Three nominal species of *Periechocrinus* have been recognized in the British Wenlock (Ramsbottom 1954, pp. 176–186; Widdison 2001a, pp. 78–84), *P. costatus* Austin & Austin, 1843 (Fig. 2C), *P. limonium* Salter, 1873, and *P. simplex* Salter, 1873. The large *P. costatus* has seven to ten arms, commonly eight, per ray; *P. limonium* has six arms per ray; and *P. simplex* has four arms per ray. Ramsbottom (1954, pp. 185–186, pl. 26, figs 4, 5) also described *Periechocrinus* sp. nov., but this taxon remains unpublished. *Periechocrinus* sp. nov. has four arms per ray, as does *P. simplex*, but unlike other British species, it has uniserial free arms; it may thus not be a true *Periechocrinus*.

*Carpocrinus simplex* (Phillips, 1839) (Fig. 3B)

*Description.* Calyx monocyclic, conical, about as wide as high, with a faint granular sculpture. Three basals, low, unequal in size. Radials five, hexagonal to heptagonal, almost twice as high as basals, as wide as or wider than high. Radials in contact except in CD interray, where the heptagonal primanal is in the radial circlet. Tegmen unknown. Interradians large and depressed. Ten arms, uniserial throughout, arms branch at the second primibrachial. First secundibrachials in contact. Free arms bipinnulate to hyperpinnulate. Proxistele heteromorphic and strongly nodose, becoming homeomorphic more distally. Columnals circular in section with a pentalobate lumen.

*Locality and horizon.* Much Wenlock Limestone Formation, Wenlock, Dudley, West Midlands.

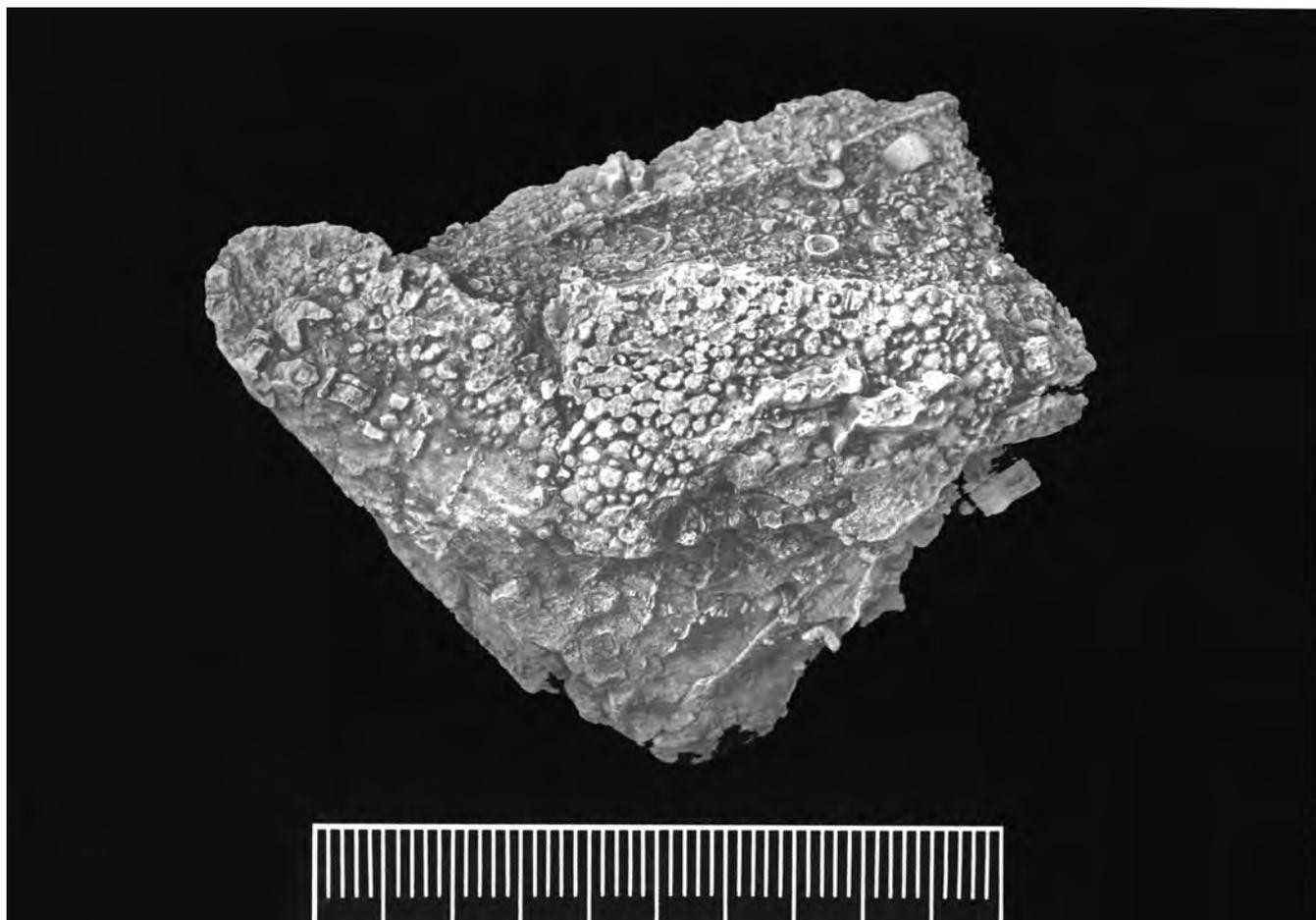


Fig. 5. *Scyphocrinites* sp., BGS GSM 85522, plating of lobolith. Entire scale bar = 50 mm.

**Remarks.** Both Ramsbottom (1954, p. 194) and Widdison (2001a, pp. 88–92) recognized that there were further species of *Carpocrinus* from the Much Wenlock Limestone Formation at Dudley. However, these await publication.

*Desmidocrinus* spp. (Fig. 2E)

**Description.** Calyx monocyclic, conical to bowl shaped, about as wide as high, sculpture smooth to finely granular. Three unequal basals, not as high as radials. Five radials, in contact except in the wide CD interray where the circlet is interrupted by the primanal. Tegmen not seen. Fixed arms branch isotomously or heterotomously more than once; fixed tertribrachials in both species. Free arms uniserial, alternate brachials supporting pinnules, three to four (*D. macrodactylus* ex. gr.) or ten arms per ray (*D. pentadactylus*). Few interradial plates. Column round and nodose.

**Locality and horizon.** Much Wenlock Limestone Formation, Wenlock, Dudley, West Midlands.

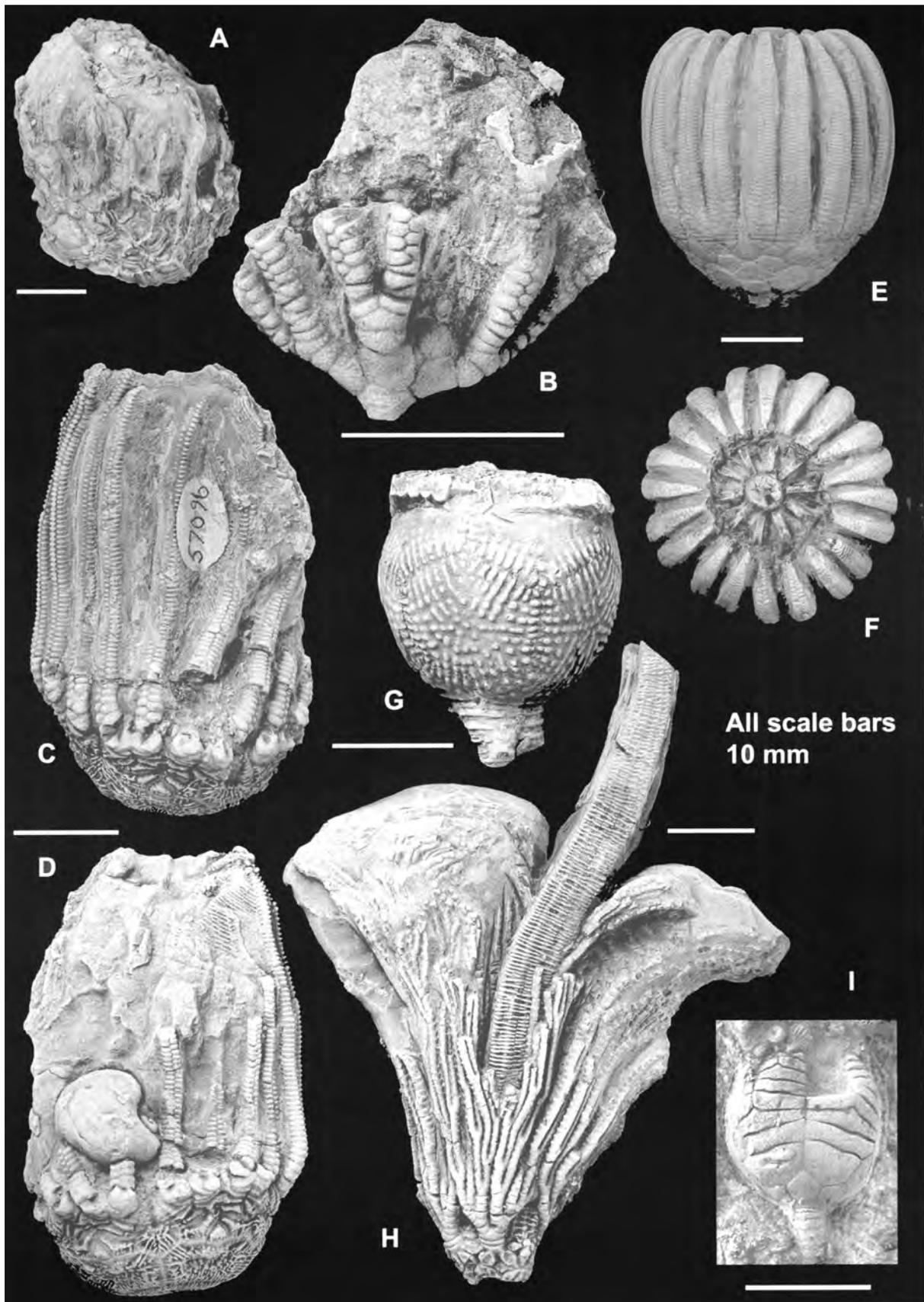
**Remarks.** There is some uncertainty concerning which and how many species of *Desmidocrinus* occur in the Wenlock Series at Dudley. Ramsbottom (1954, pp. 188–190) recognized *D. macrodactylus* Angelin, 1878, which he synonymized with *D. heterodactylus* Angelin, 1878, and *D. tridactylus* Angelin, 1878; Angelin (1878, p. 5) noted that these species had “*Brachia tridactyla*” (*D. macrodactylus*) or “*Brachia tridigitata*”. Widdison (2001a, pp. 53–56) identified *D. pentadactylus* Angelin, 1878, with ten arms per ray, but agreed with Ramsbottom’s synonymy (2001a, p. 53, ‘other species’). Webster

(2003) only listed *D. heterodactylus* from England, but considered *D. heterodactylus*, *D. macrodactylus* and *D. tridactylus* to be valid. Herein, and until the British material is critically compared with the type specimens of these species from Gotland, it is considered conservative to regard the Dudley specimens as representing *D. pentadactylus* and *D. macrodactylus* ex. gr. (Fig. 2E).

*Eucalyptocrinites* spp. (Fig. 6E, F)

**Description.** Column rounded pentagonal in section, robust, heteromorphic, perhaps N1. Crown large, robust, shaped like a papaya fruit. Dorsal cup small, bowl-shaped, base concave. Basals three to four, in basal concavity. Radials five, hexagonal, in contact with CD interray (=posterior), not differentiated. Fixed arms branching at second primibrachial and second secundibrachial. Free arms biserial, elongate, pinnulate. Large interradian plate between primibrachials, supporting a smaller plate; interbrachials also developed after primaxillary. Ten prominent, elongate interradians (5) and interbrachials (5), otherwise known as partition plates, extending length of free arms, which are thus grouped in pairs. Interradians and interbrachials surrounding anal series, which may be developed as a pronounced multiplated cone apically.

**Locality and horizon.** *Eucalyptocrinites decorus* (Phillips, 1839) is known from the Much Wenlock Limestone Formation at Dudley, West Midlands, and possibly also from the same formation at Hurst Hill, Sedgley, West Midlands (Widdison 2001a, p. 66). *Eucalyptocrinites granulatus* (Lewis, 1847) is



**Fig. 6.** Monobathrid (A–F), cladid (G, H) and sagenocrinid flexible crinoids from the Wenlock, Much Wenlock Limestone Formation, Dudley, West Midlands, of the British Isles. (A) *Calliocrinus* cf. *beyrichianus* (Angelin), BMNH 57457; (B) *Macrostylocrinus anglicus* Jaekel, BMNH E45553; (C, D) *Marsupiocrinites coelatus* Phillips, BMNH 57096. Both lateral views; (E, F) *Eucalyptocrinites* sp. nov., BMNH E1456; (E) Lateral view; (F) Apical view; (G) *Crotalocrinites verucosus* (Schlotheim), BMNH 40204; (H) *Gissocrinus capillaris* (Phillips), BMNH E22602; (I) *Lecanocrinus bacchus* Salter, BMNH 57469.

from the Coalbrookdale Formation at Walsall, West Midlands (Widdison 2001a, p. 71). *Eucalyptocrinites* sp. nov. (Ramsbottom 1954, p. 216; Widdison 2001a, pp. 69–71, pl. 9, fig. 7) is from the Much Wenlock Limestone Formation at Dudley. All are from the Wenlock Series.

*Remarks.* Of the three British members of this distinctive genus, *Eucalyptocrinites* sp. nov. is globular and lacks a basal concavity, whereas *E. decorus* is distinctly elongate with partition plates that are swollen distally. The rare *Eucalyptocrinites granulatus* has a granular sculpture to the arms and partition plates.

*Calliocrinus* cf. *beyrichianus* (Angelin, 1878) (Fig. 6A)

*Description.* Robust calyx with strong sculpture of concentric and radiating ridges, and a particularly deep basal concavity with a marked pentagonal rim. Dorsal cup low and bowl-shaped. Basals within basal concavity. Five radials, in contact, low in lateral view; difficult to discern these and other plates due to sculpture. Fixed arms branching twice, presumably at second primibrachial and second secundibrachial (Ubaghs 1978b, fig. 299.2b), free arms not preserved. Partition plates above fixed arms extending only a short distance, laterally in contact to form anal tube.

*Locality and horizon.* Much Wenlock Limestone Formation, Wenlock, Dudley, West Midlands.

*Remarks.* Both Ramsbottom (1954, pp. 218–220, pl. 31, figs 3–4) and Widdison (2001a, pp. 62–64, pl. 1, figs 1–2) described a new species of *Calliocrinus*, as yet unpublished, from the Much Wenlock Limestone Formation at Dudley. This genus is similar to *Eucalyptocrinites*, but partition plates only extend a short distance above the fixed arms.

*Clonocrinus polydactylus* (M'Coy, 1849) (Fig. 2D)

*Description.* Proxistele homeomorphic, circular in section, broad, with a central, circular(?) lumen and symplectial articulation. Crown with bowl-shaped calyx, basal concavity and numerous slender arms. Surface smooth, calyx plates convex. Basals not seen, concealed in basal concavity by proxistele. Five radials, low in lateral view and curving into basal concavity. Fixed arms broad, uniserial, branching isotomously at second primibrachial and second secundibrachial. Arms free from low tertibrachials. Free arms pinnulate, biserial, composed of low brachials and branching at least three further times near-isotomously. Large, rounded interradial plate just above radials, supporting column of three more plates of decreasing size to about the level of the fifth tertibrachial. Interbrachials between second secundibrachials, supporting one smaller plate. Most distal interbrachials and interradials teardrop shaped, tapering distally. Anal series not discerned.

*Locality and horizon.* Much Wenlock Limestone Formation, Wenlock, Dudley, West Midlands.

*Remarks.* Rare. Distinguished by the distinct pattern of arm branching and low brachials.

*Macrostylocrinus* spp. (Fig. 6B)

*Description.* Articular facet at base of dorsal cup circular with a small, rounded, central lumen. Column circular in outline. Calyx conical. Basals three, polygonal, moderately high in lateral view. Radials five, hexagonal, in contact, larger than basals. Fixed arms uniserial, branching isotomously at the second primibrachial. Free arms commonly ten, but may be

more, biserial, pinnulate and unbranched. Lowermost interradial large, heptagonal(?), supporting few plates. Interradial areas slightly sunken. Arms widely separated at CD interray, primanal large, supported by C and D radials.

*Locality and horizon.* *Macrostylocrinus silurocirrifer* Brower, 1975, is from the Telychian (upper Llandovery) of the North Esk Inlier, Pentland Hills, Scotland. *Macrostylocrinus anglicus* Jaekel, 1918, is from the Much Wenlock Limestone Formation (Wenlock) at Dudley, West Midlands, and *Macrostylocrinus? jefferiesi* Donovan & Lewis, 2008, is from the same formation in Coalbrookdale, Shropshire. *Macrostylocrinus?* sp. is from the Rhuddanian (lower Llandovery) of the Haverford Mudstone Formation, Haverfordwest, Pembrokeshire, SW Wales.

*Remarks.* The calyx of *M. anglicus* has a sculpture of fine, densely packed, intermittent to continuous ridges, arrayed longitudinally on arms, and radially and either concentrically or granularly on others. *Macrostylocrinus?* sp. has a sculpture of low radial ridges on radial plates that extend onto the arms as ray ridges. The crown of *M. silurocirrifer* bears a sculpture of small nodes or granules. *Macrostylocrinus? jefferiesi* has a moderately large dorsal cup, a granular surface sculpture, and at least 20 arms branching at the second primibrachial and second secundibrachial, and broad primibrachials; ray ridges are absent.

*Marsupiocrinites coelatus* Phillips, 1839 (Fig. 6C, D)

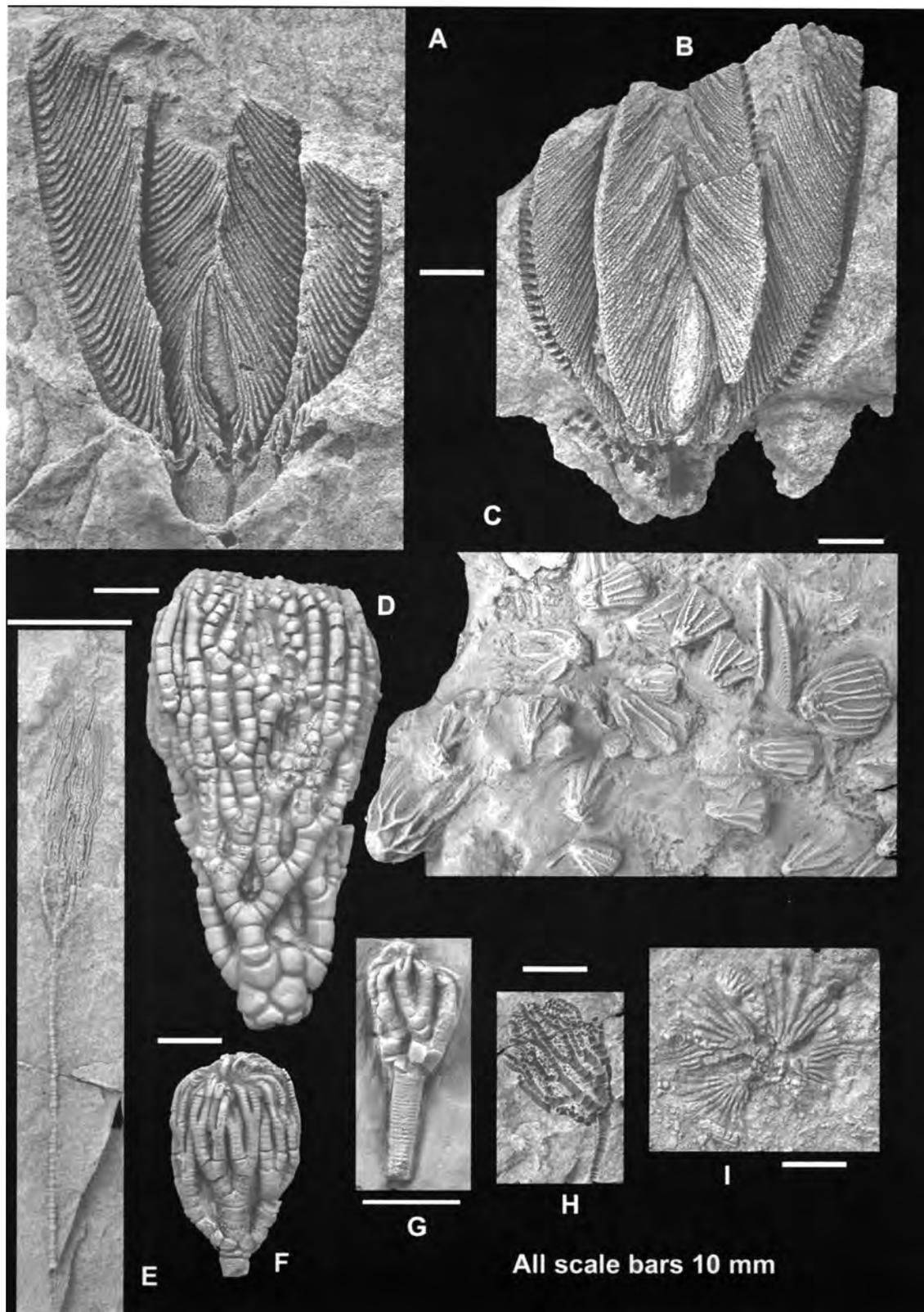
*Description.* Proxistele circular in section, heteromorphic, N434243414342434, nodals largest *et seq.*, all columnals with flanged epifacets except quartinternodals, articulation symplectial. Calyx low bowl-shaped with flattened base, plates with a sculpture of moderately fine radial ridges. Basals (three) and part of the radial cirlet (five) hidden on base of dorsal cup, and not apparent laterally. Radials large, in contact. Fixed arms uniserial, branching isotomously at the first primibrachial and second secundibrachial. The first secundibrachial large, asymmetrical, resting on both short, triangular primaxillary and radial. Arms free above about the fourth tertibrachial. Free arms biserial, pinnulate, large, 20 in number and slightly tapered. Large, teardrop-shaped interradial supported by shoulders of adjacent radials. Tegmen composed of numerous small plates, anal opening eccentric.

*Locality and horizon.* Much Wenlock Limestone Formation, Wenlock, at Dudley, West Midlands, including Tividale, and at Gleedon Hill, Wenlock Edge, Shropshire (Ramsbottom 1954, p. 223).

*Remarks.* *Marsupiocrinites coelatus* is the type species of *Marsupiocrinites*. Although the genus *Marsupiocrinus* was erected by Morris in 1843 (Ubaghs 1978b, p. T509), this appears to be a junior synonym of *Marsupiocrinites* Phillips, 1839 (p. 672).

*Clematocrinus* spp. (Fig. 7A-C)

*Description.* Column heteromorphic, slender, circular in transverse section, articulation symplectial, with or without whorls of radices. Crown high, conical, slender and elongate. Dorsal cup low, broad, bowl shaped. Basals three, basal cirlet smaller than radial cirlet. Radials five, in contact, moderately large. Two primibrachials incorporated into calyx, branching isotomously at the second primibrachial, arms free just above primaxillary. Free arms uniserial or biserial, pinnulate, long, may branch once more. First interradial large, in contact



**Fig. 7.** Crinoids from the Silurian of the British Isles. Unless stated otherwise, specimens are from the Wenlock, Much Wenlock Limestone Formation, Dudley, West Midlands. (A, B) Monobathrid *Clematocrinus ramsbottomi* Fearnhead in Fearnhead & Donovan, 2007, holotype, upper Llandovery, Damery Beds, Damery Bridge, Tortworth Inlier, Gloucestershire. (A) BMNH E51660b, external mould of crown; (B) BMNH E51660a, internal mould of crown; (C) Monobathrid *Clematocrinus retarius* (Phillips), BMNH E5615; (D) Cladid *Cyathocrinites monile* Salter, BMNH E1450; (E) Cladid *Dendrocrinus* sp. nov., BMNH E26574. Lower Ludlow, Church Hill, Leintwardine, Herefordshire; (F) Sagenocrinid flexible *Temnocrinus tuberculatus* (J. S. Miller), BMNH 57466; (G) Taxocrinid flexible *Meristocrinus minor* Springer, BMNH E5721; (H) Taxocrinid flexible *Eutaxocrinus maccoyanus* (Salter), BMNH E26578. Lower Ludlow, Church Hill, Leintwardine, Herefordshire; (I) Cladid *Petalocrinus bifidus* Donovan & Fearnhead, BMNH E70060. Upper Llandovery, *Petalocrinus* Limestone, Woolhope Inlier, Herefordshire.

laterally with primibrachials. Tegmen with several small plates.

*Locality and horizon.* *Clematocrinus ramsbottomi* Fearnhead in Fearnhead & Donovan, 2007a, is from the Damery Beds (Telychian, upper Llandovery) of the Tortworth Inlier, Gloucestershire. *Clematocrinus retiarius* (Phillips, 1839) is only known from the Much Wenlock Limestone Formation (Wenlock) at Wren's Nest, Dudley, West Midlands. *Clematocrinus quinquepennis* (Ramsbottom, 1958) is from the Lower Leintwardine Formation (Ludfordian, upper Ludlow) of Church Hill Quarry, Leintwardine, Herefordshire.

*Remarks.* The British species of *Clematocrinus* can be differentiated by the features of the column. *Clematocrinus ramsbottomi* developed radices in the dististele that are directed distally (it is uncertain whether they also occurred in the proxistele); elongate radices occur in the proxistele of *C. retiarius* and are angled up towards the crown; and radices are absent in *C. quinquepennis*.

*Cordylocrinus* sp. nov. 1 (Fig. 3F)

*Description.* Column poorly seen, but proxistele bears whorls of radices. Facet at base of dorsal cup rounded with a small, central lumen. Dorsal cup low and bowl-shaped. Basals three, in pentagonal circlet on the base of the cup, wider than the column facet, but not apparent in lateral view. Radials five, in contact, geniculated and forming part of base of cup. Raised, tuberculated knob in centre of radial bears arm facet. Arms uniserial, pinnulate, brachials bearing aboral sculpture of tooth-like longitudinal ridges. Arms branch isotomously at the second primibrachial, free above the first secundibrachial, arms long. One large interradial plate. Anal series not recognized.

*Locality and horizon.* Wenlock Shale (now the Coalbrookdale Formation; Aldridge *et al.* 2000), Wenlock, Wren's Nest, Dudley, West Midlands.

*Remarks.* Ramsbottom (1954, pp. 225–230, pl. 15, figs 4–6, pl. 32, fig. 1) described two new species of *Cordylocrinus*, both unpublished more than 50 years later. The second taxon, designated *Cordylocrinus* sp. nov. 2 herein (Table 1), was diagnosed as having an inverted pear-shaped ('obpyriform') dorsal cup, basals apparent in lateral view and low brachials (Ramsbottom 1954, p. 228). *Cordylocrinus* sp. nov. 2 is known only from the Much Wenlock Limestone Formation at Dudley.

#### Subclass CLADIDA Moore & Laudon, 1943

*Remarks.* Gracile to robust, apinnulate (Devonian and younger cladids may be pinnulate), dicyclic crinoids with none, one or more anal plates incorporated into the dorsal cup and a commonly prominent anal sac (Moore *et al.* 1978c, p. T578). Arms commonly branched.

*Cyathocrinites* spp. (Fig. 7D)

*Description.* Attachment structure distal. Column round to pentagonal in section, heteromorphic proximally, but homeomorphic more distally. Articulation symplectial. Crown elongate and conical. Dorsal cup conical, bowl-shaped or globular, dicyclic, with five low infrabasals, five polygonal basals and five radials with narrow to moderately broad arm facets. Anal X supported by CD basal and incorporated in radial circlet, anal tube narrow. Robust tegmen with five orals. Arms uniserial, apinnulate, narrow, branching isotomously at

least twice; at least five times in *Cyathocrinites monile* Salter, 1873. Ambulacral cover plates particularly robust.

*Locality and horizon.* *Cyathocrinites monile* Salter, 1873, *C. vallatus* Bather, 1892b, and *Cyathocrinites* sp. nov. of both Ramsbottom (1954) and Widdison (2001a) are all known from the Much Wenlock Limestone Formation (Wenlock) at Dudley, West Midlands. *Cyathocrinites monile* is also known from other Wenlock localities, including Wenlock Edge (Ramsbottom 1954, p. 103); it is the commonest species of *Cyathocrinites* at Dudley.

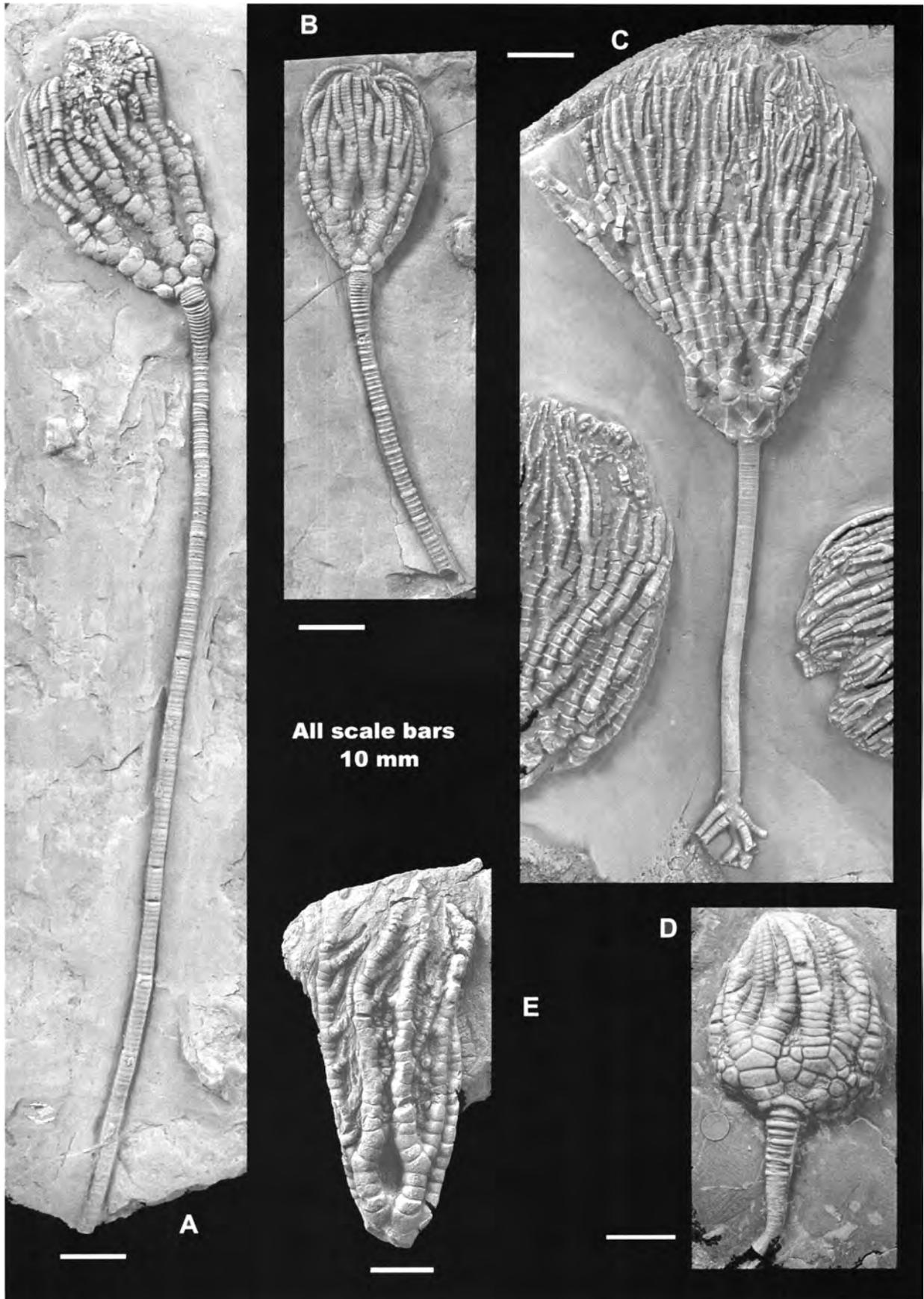
*Remarks.* *Cyathocrinites monile* has a conical dorsal cup with concavo-convex sides (plate sutures depressed), and cup plates that are smooth and swollen, whereas *Cyathocrinites vallatus* Bather, 1892b, has a slightly ovoid dorsal cup with rounded sides, particularly clear plate margins, and flat cup plates that are smooth or have a concentric sculpture. The unpublished *Cyathocrinites* sp. nov. of both Ramsbottom and Widdison differs in its pustulose sculpture, more reminiscent of *Crotalocrinites* spp. (see below), and the bowl-shaped dorsal cup (Ramsbottom 1954, pp. 102–105, pl. 17, figs 3–6; Widdison 2001a, pp. 110–114, pl. 6, figs 3–6, pl. 7, fig. 1).

*Gissocrinus* spp. (Figs 6H, 8C)

*Description.* Attachment by distal dendritic radice. Column circular in section, heteromorphic proximally (perhaps N1), homeomorphic more distally. Crown large, elongate and vase-shaped. Dorsal cup broad, bowl shaped with sharp ridges. Infrabasals low, three or five. Basals five, pentagonal, with a raised central boss and a ridge confluent with ridges on each adjacent radial. Radials five, large, octagonal(?), in contact with adjacent radials by moderately long sutures, arm facet rounded and angled away from oral surface. Radial circlet interrupted by anal X supported by CD basal. Anal sac robust. Arms uniserial, apinnulate, branching isotomously several times and producing a dense group of arms.

*Locality and horizon.* Most of the species listed below are known from the Much Wenlock Limestone Formation (Wenlock) at Dudley. The exception is *G. cyrili* Bouska, 1944, known from the Wenlock Shale of the Malvern district (probably the Coalbrookdale Formation) and the Wenlock(?) Shale at Sedgley, West Midlands. *Gissocrinus goniodactylus* (Phillips, 1839) is also known from the Much Wenlock Limestone Formation of Malvern. The distinctive brachials of *Gissocrinus* spp. are locally common in the Much Wenlock Limestone Formation on Wenlock Edge at Farley, near Much Wenlock, Shropshire (S.K.D. and co-workers, research in progress).

*Remarks.* There are six nominal species of *Gissocrinus* from the Wenlock of the British Isles: common to very common *G. arthriticus* (Phillips, 1839), *G. capillaris* (Phillips, 1839), *G. goniodactylus* and *G. squamiferus* (Salter, 1873), and rare *G. cyrili* and *G. scoparius* (Salter, 1873). *Gissocrinus luculentus* Ramsbottom, 1951, is a junior synonym of *G. goniodactylus* (Widdison 2001a, p. 121). Of the common species, *G. arthriticus* has a rounded dorsal cup, strong granular sculpture on the crown, brachials with a strongly marked distal expansion aborally and laterally, and the proximal arms and anal tube oriented horizontally, that is, in the same plane as the oral surface; *G. capillaris* has a low, conical dorsal cup with strong, rounded rugose ridges, arms slender, long and branching five to six times proximally only, and small brachials with a ridge along the lateral edge of the distal margin;



**Fig. 8.** Crinoids from the Wenlock, Much Wenlock Limestone Formation, Dudley, West Midlands. (A, B) Sagenocrinid flexible *Temnocrinus tuberculatus* (J. S. Miller) (A) BMNH E1418, (B) (Miller), BMNH 57468; (C) Cladid *Gissocrinus goniodactylus* (Phillips), BMNH E45528; (D) Sagenocrinid flexible *Calpiocrinus intermedius* Springer, BMNH 57470, syntype; (E) Cladid *Bathericrinus ramosus* (Bather), BMNH 57217, holotype.

*G. goniodactylus* has strong axial ridges, arms branching six times and expansions at the distal ends of brachials; and *G. squamiferus* has a low, conical dorsal cup, moderate axial ridge system, arms bifurcating four times (horizontal proximally) and brachials with flat, broad aboral surfaces (Ramsbottom 1954, pp. 106–123, pls 14, 18–20, pl. 36, figs 1–2; Widdison 2001a, pp. 114–124, pl. 10, pl. 11, figs 1–5).

*Crotalocrinites* spp. (Fig. 6G)

**Description.** Large crinoids. Attachment by large, dendritic, anastomosing pseudoradices(?); slightly more proximal stem warty. Column circular to irregular in section, more distal part with multiple radiating canaliculae in nodals. Columnals low, column heteromorphic N1. Articulation symplectial, lumen central. Crown conical vase-shaped, high. Dorsal cup rounded bowl shaped. Articular facet for column large, rounded and conical. Infrabasals five, forming a pentagonal cirlet at base of cup, visible in lateral view. Sculpture on cup plates of multiple radiating ridges arrayed perpendicular to sides of plates. Basals five, large and pentagonal, except in the CD interray where a hexagonal plate supports the small, square anal X. Radials five, low, pentagonal, in lateral contact except in CD interray. Radials bear numerous (up to about 12) narrow articular facets in close association and directed laterally. Arms fan-like, reticulate, brachials joined laterally.

**Locality and horizon.** All three species discussed below are known from the Much Wenlock Limestone Formation (Wenlock) at Dudley, West Midlands. *Crotalocrinites verucosus* (Schlotheim, 1820) is also known from the same formation on Wenlock Edge, Shropshire. Disarticulated basal plates are particularly large and distinctive.

**Remarks.** The two nominal species of *Crotalocrinites* reported from the Much Wenlock Limestone Formation, *C. verucosus* and *C. pulcher* (Hisinger, 1840), are distinguished by the pattern in which their brachials are linked laterally. Arms of *C. pulcher* are discrete, whereas those of *C. verucosus* link laterally to form a crown shaped like a funnel. However, the presence of *C. pulcher* in the Much Wenlock Limestone Formation at Dudley is unconfirmed. A third species, awaiting publication (R.E.W. research in progress), has a conical rather than globular dorsal cup and smooth calyx plates (Ramsbottom 1954, pp. 124–133, pl. 21, figs 1–11; Widdison 2001a, pp. 127–132, pl. 5, figs 7–8, pl. 6, figs 1–2).

*Petalocrinus bifidus* Donovan & Fearnhead in Fearnhead & Donovan, 2007a (Fig. 7I)

**Description.** Dorsal cup small and conical. Three small infrabasals. Five much larger basals, folded outwards. Five radials, arm facets in centre of proximal edge. Arms separated and splayed. One(?) low primibrachial. Articular facet at base of fused brachial semicircular, slightly incurved adorally. Fused brachials irregularly triangular, approximately symmetrical, strongly bifid. Fused brachials divided by a distal central notch and an associated proximal, longitudinal adoral ridge. Distal notch varies from elongate and narrow, over half the length of the plate, to more square. Adoral grooves trough-like, grooves branching two to three times. Ambulacral cover plates small, bead-like, in biserial columns. Aboral surface unsculptured.

**Locality and horizon.** *Petalocrinus* Limestone (Pocock, 1930), Haugh Wood Formation (Upper Haugh Wood Beds); upper

Telychian (upper Llandovery), Woolhope Inlier, Herefordshire.

**Remarks.** The fused, fan-shaped arms of *Petalocrinus* are highly distinctive and quite unlike those of any other crinoid, either extinct or living. *Petalocrinus bifidus* is distinctive in having the arms divided by a distal notch (Fearnhead & Donovan 2007a). A second, rarer species, *Petalocrinus* sp. cf. *P. visbyensis* Bather, 1898, is known from the Mulloch Hill Formation (upper Rhuddanian, lower Llandovery) of the Girvan district, Ayrshire (Ward 1989, pl. 7.7, fig. 1; Fearnhead & Harper 2007).

*Enallocrinus scriptus* (Hisinger, 1828) (Fig. 9A)

**Description.** Distal, dendritic, radicular attachment structure. Column circular in section, broad with a broad axial canal, heteromorphic, N3231323(?). Crown high, vase-like. Dorsal cup with distinct and complex reticulate sculpture, comparatively low, bowl shaped with a broad base and only slightly wider oral surface. Infrabasals five(?), low, pentagonal, but near-triangular, just in contact laterally. Basals five, low hexagonal, weakly in contact laterally. Radials five, inverted pentagons, in contact. Arms very numerous, uniserial, apinnulate. Arms branch isotomously at small, triangular first primibrachial, narrower than radial. Second secundibrachial resting on radial. Second secundibrachial and second tertibrachial axillary, isotomously branched. More distal branches either isotomous or producing elongate ramules. Adjacent arm branches stabilized by slightly serrated edges.

**Locality and horizon.** Much Wenlock Limestone Formation, Wenlock, Dudley, West Midlands.

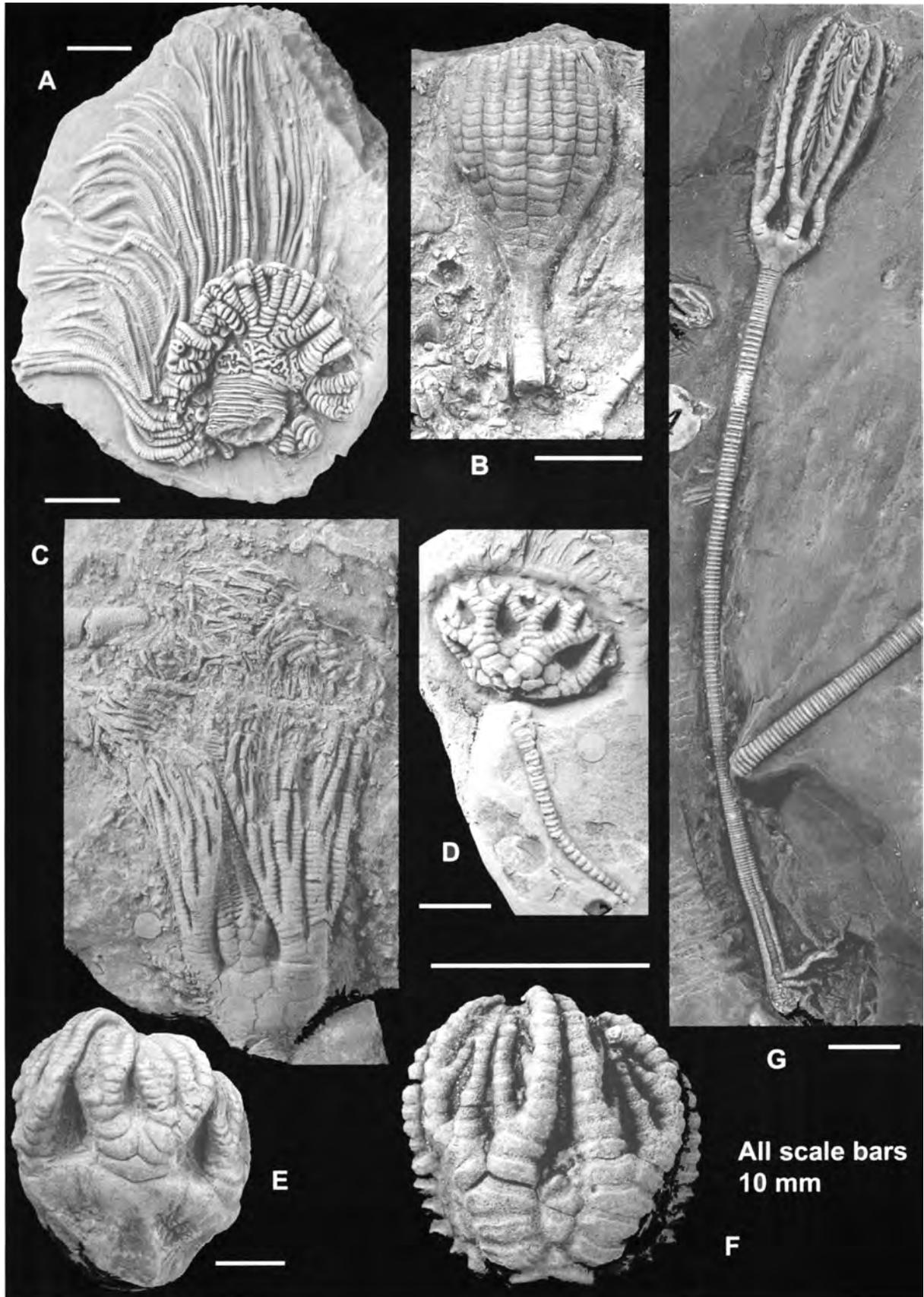
**Remarks.** Widdison (2001a, pp. 124–127, pl. 16, figs 4–6) suggested that this taxon is sufficiently distinct from *Enallocrinus sensu stricto* to warrant erection of a new genus.

*Mastigocrinus* spp. (Fig. 10B)

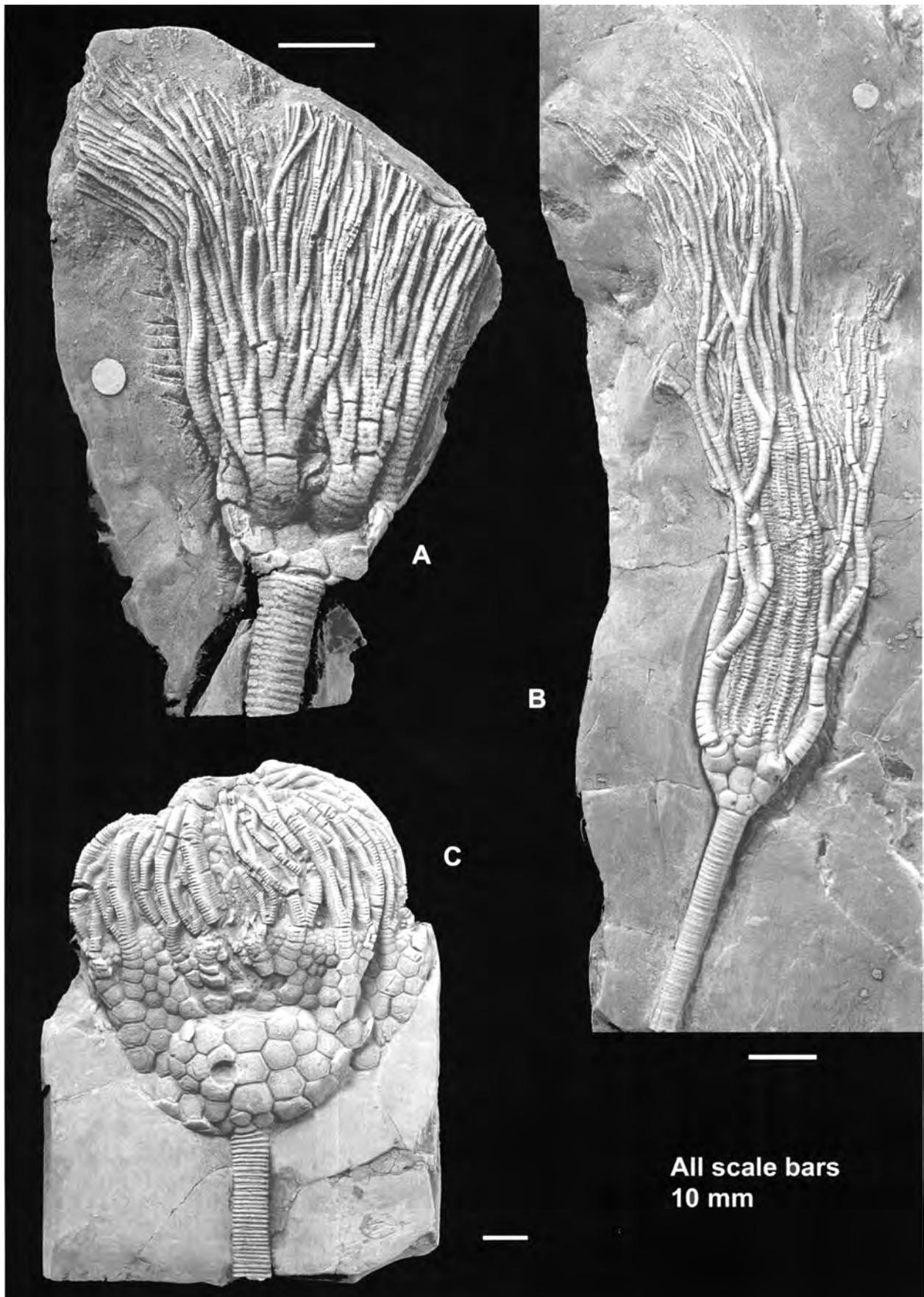
**Description.** Column pentameric, heteromorphic, circular to subpentagonal in section. Articulation symplectial, lumen small and pentagonal. Crown high, elongate vase-shaped. Dorsal cup conical; smooth or slightly granular sculpture. Infrabasals five, pentagonal, tall, about a quarter height of cup. Basals five, hexagonal, about as wide as high. Radials five, slightly wider than high, arm facets broad and almost as wide as plate. Radial absent. Anal X large, hexagonal, wider than high, between and in line with posterior radials, supporting three plates. Anal sac large, elongate, consisting of low, broad plates with a strongly folded sculpture. Tegmen of numerous small ossicles. Arms uniserial, apinnulate, long and slender, branching isotomously on the fourth or fifth primibrachial and three to four (*M. bravoniensis*) or at least eight times more (*M. loreus*).

**Locality and horizon.** *Mastigocrinus loreus* Bather, 1892a, is from the Much Wenlock Limestone Formation (Wenlock) of Dudley, West Midlands. *Mastigocrinus bravoniensis* Ramsbottom, 1958, is from the Lower Leintwardine Formation (Ludfordian, upper Ludlow) of Church Hill Quarry, Leintwardine, Herefordshire.

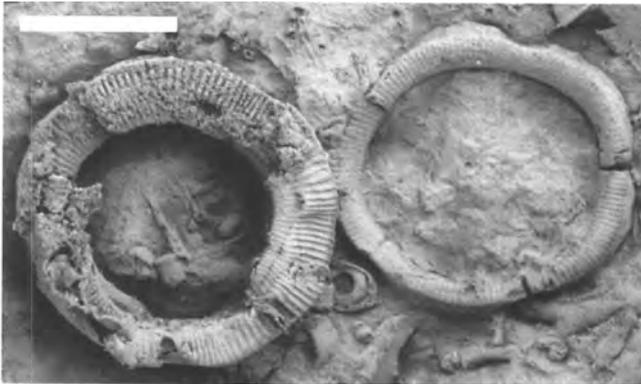
**Remarks.** These are the only two members of the genus; *M. loreus* is the type species (Webster 2003). *Mastigocrinus bravoniensis* “. . . is easily distinguished from *M. loreus* . . . by the length of the brachials and the small size” (Ramsbottom



**Fig. 9.** Cladid (A, C, G) and sagenocrinid flexible (B, D–F) crinoids from the Wenlock, Much Wenlock Limestone Formation, Dudley, West Midlands. (A) *Enallocrinus scriptus* Hisinger, BMNH 57479; (B) *Ichthyocrinus pyriformis* (Phillips), BMNH E5598; (C) *Thenarocrinus callipygus* Bather, BMNH E6388, posterior view with CD interray central (see also Fig. 10A); (D) *Hormocrinus anglicus* Springer, BMNH E1426, syntype; (E) *Pycnosaccus bucephalus* (Bather), BMNH E5625; (F) *Homalocrinus nanus* (Salter), BMNH E1422; (G) *Dictenocrinus decadactylus* (Bather), BMNH E1412, syntype.



**Fig. 10.** Cladid (A, B) and sagenocrinid flexible (C) crinoids from the Wenlock. Much Wenlock Limestone Formation, Dudley, West Midlands. (A) *Thenarocrinus callipygus* Bather, BMNH 57478a (see also Fig. 9C); (B) *Mastigocrinus loreus* Bather, BMNH 57048; (C) *Sagenocrinites expansus* (Phillips), BMNH 57458.



**Fig. 11.** *Segmentocolumnus* (col.) *clarksoni* Donovan & Harper, MGUH 26679, latex casts of paratype columnals (after Donovan & Harper 2003, fig. 2H), from the Kilbride Formation (Telychian), west of Ireland. Scale bar represents 5 mm.

1958, p. 111). Brachials are higher than wide in larger *M. bravoniensis*, wider than high in smaller *M. loreus*.

*Bathericrinus ramosus* (Bather, 1891b) (Fig. 11)

**Description.** Stem unknown. Crown elongate vase-shaped. Dorsal cup small and low, conical, sculpture smooth. Infrabasals five, pentagonal. Basals five, hexagonal, slightly higher than wide. Radials five, in contact except in CD interray, arm facets almost as wide as plates, separated by interradial notches. Radianal small, quadrangular. Anal X large, projects above C and D radials. Anal sac unknown. Arms uniserial, apinnulate, branching isotomously at the fourth primibrachial. Arm branches bear large ramules about every second secundibrachial and on alternate sides. Axillaries slightly nodose, brachials bearing ramules wedge-shaped, other brachials quadrangular. Arms long, about six times height of dorsal cup.

**Locality and horizon.** Much Wenlock Limestone Formation, Wenlock, Dudley, West Midlands.

**Remarks.** *Bathericrinus* Jaekel is monospecific (Webster 2003). Although the unique holotype has a damaged base, Jaekel (1918) considered the distinctive structure of the arms sufficient to enable definition of a new genus.

*Dictenocrinus* spp. (Fig. 9G)

**Description.** Attachment by distal dendritic radice. Column xenomorphic, with pentameric dististele, possibly holomeric proximally. Column subpentagonal, slender, articulation symplectial, lumen pentagonal. Crown elongate, slender, vase-like. Dorsal cup high, steeply conical, plates gently convex. Plates smooth or with minor longitudinal folds on basals. Infrabasals five, pentagonal. Basals five (three hexagonal and two heptagonal), smooth or with faint axial folds. Radials five, projecting outwards, may have faint axial folds, arm facet narrow. Radianal small, quadrangular. Anal X smaller than radials, supporting three plates. Anal sac elongate and narrow, formed by rows of low and broad, strongly plicate plates, with opening just beneath summit. Arms uniserial, apinnulate, long, branching isotomously at primibrachials three to five and with one or two further branches. Ramules on alternate sides of successive brachial.

**Locality and horizon.** Much Wenlock Limestone Formation, Wenlock, Dudley, West Midlands.

**Remarks.** *Dictenocrinus decadactylus* (Salter, 1873), the type species, has ten arms with robust ramules and an anal tube with coarse ridging. The second and rarer British species, *Dictenocrinus pinnulatus* (Bather, 1891a), has up to 20 arms bearing elongate, slender ramules and an anal tube lacking distinctive ridging (Widdison 2001a, pp. 139–140).

*Dendrocrinus* spp. (Fig. 7E)

**Description.** Column long, slender, pentagonal or circular in section and heteromorphic. Articulation symplectial. Crown conical, elongate, with or without sculpture of ridges. Dorsal cup dicyclic, conical. Infrabasals five, small to moderately high, polygonal. Basals five, large, pentagonal to hexagonal. Radials five, prominent, pentagonal to hexagonal, arm facets broad. Radianal in C ray and CD basal supporting anal X, the latter in the radial cirlet. Anal series forming a large, multi-plated tube. Arms slender, uniserial, apinnulate, branching isotomously several times.

**Locality and horizon.** *Dendrocrinus? gasworksensis* Donovan, 1993, is from the Rhuddanian (lower Llandovery) upper part of the Haverford Mudstone Formation (formerly the Gasworks Mudstones), Haverfordwest, Pembrokeshire, SW Wales. *Dendrocrinus extensidiscus* Brower, 1975, is from the Telychian (upper Llandovery) of the North Esk Inlier, Pentland Hills, Scotland. *Dendrocrinus* sp. nov. (*in* Ramsbottom, 1954, pp. 153–155, pl. 15, fig. 3) is from the Wenlock? Shale of Sedgley, West Midlands.

**Remarks.** *Dendrocrinus? gasworksensis* has a small, unsculptured dorsal cup, a low radianal, small anal X, broad radial facets supporting robust arms and broad brachials. *Dendrocrinus extensidiscus* has a similar dorsal cup, but arms are slender and brachial ossicles high. *Dendrocrinus* sp. nov. has a dorsal cup with strongly developed axial ridges, a particularly well developed anal series and relatively short arms with sharp aboral ridges; it may more correctly belong to *Plicodendrocrinus* Brower, 1995.

At least three further species of *Dendrocrinus sensu lato* await formal description. These are from the Rhuddanian (lower Llandovery) Mulloch Hill Formation, Girvan, Ayrshire; the Ludfordian (upper Ludlow) Lower Leintwardine Formation of Church Hill Quarry, Leintwardine, Herefordshire (Fig. 7E) (specimens of both in the BMNH); and the Telychian (upper Llandovery) Hughley Shales of Devil's Dingle, Buildwas, Shropshire (specimen in the collections of British Geological Survey, Keyworth) (Donovan and co-workers, research in progress).

*Thenarocrinus* spp. (Figs 9C, 10A)

**Description.** Column pentameric. Proxistele broad, circular in section, columnals low. Mesistele heteromorphic N1, proxistele possibly homeomorphic. Articulation symplectial, lumen circular or rounded pentagonal, moderately broad. Crown tall, vase-shaped, with many distal arm branches. Dorsal cup conical with steep, straight sides. Infrabasals five, pentagonal or hexagonal, apparent in lateral view and moderately high. Basals five, hexagonal, higher than infrabasals. Radials five, with broad arm facets, larger than basals, pentagonal (=truncated hexagonal). Radianal large, in basal cirlet, resting on C ray infrabasal and below C radial, irregular pentagonal (*T. callipygus*) to hexagonal in shape (*T. gracilis*)

and supporting anal X equally with CD basal. Anal X reaching top of radial circlet. Anal sac large, composed of vertical rows of plicate plates. Tegmen flexible, consisting of numerous small ossicles. Arms uniserial, apinnulate, long, branching isotomously about five (*T. gracilis*) to at least eight times (*T. callipygus*), the latter resulting in over a thousand branches with about 50,000 brachial ossicles (Bather 1890b, p. 227).

*Locality and horizon.* Much Wenlock Limestone Formation, Wenlock, Dudley, West Midlands.

*Remarks.* The type species, *Thenarocrinus callipygus* Bather, 1890b, has a pentagonal radianal, very numerous slender and elongate distal arms, and steeply conical calyx. The rare *Thenarocrinus gracilis* Bather, 1891a, has a pentagonal radianal, fewer distal arms and a less steeply conical dorsal cup (Widdison 2001a, p. 103).

*Segmentocolumnus* (col.) *clarksoni* Donovan & Harper, 2003 (Fig. 11)

*Description.* Mesistele of robust pentameric columns pentagonal in section with rounded angles. Lumen central, broad, pentagonal in section with rounded angles, coincident with columnal outline. Claustrum narrow. Areola absent. Articulation symplectial. Crenulae numerous, unbranched, arrayed perpendicular to circumference of articular facet and extending into claustrum. Latera unsculptured and gently concave. Column of mesistele heteromorphic, N212 to N3231323. Nodals tallest *et seq.* Meric sutures straight, apparent in centres of sides in pentagonal columnals, showing no rotational or longitudinal displacement. Pluricolumnals straight or gently curved, disarticulated between columnals before meres, but may show post-mortem collapse along meric sutures.

*Locality and horizon.* Upper part of the (informally named) Finny School member (or beds), Kilbride Formation, Telychian (upper Llandoverly), Kilbride Peninsula, Co. Galway/Co. Mayo border, western Ireland.

*Remarks.* Only known from large and distinctive pluricolumnals, which are tentatively interpreted as being derived from a cladid crinoid. This species is common at the type locality (Donovan & Harper 2003). Other columnal morphotaxa from the Finny School member await description (Fearnhead & Harper, research in progress).

Infraclass **FLEXIBILIA** von Zittel, 1895  
Order **SAGENOCRINIDA** Springer, 1913

*Remarks.* 'Infrabasals abutting on dorsal side of basals, more or less erect, and taking part in the calyx wall. Crown usually small, short, rotund, with arms abutting, frequently interlocking, and closely infolding at the distal ends' (Springer 1913, p. 203). Dicyclic.

*Sagenocrinites expansus* (Phillips, 1839) (Fig. 10C)

*Description.* Distal radicular holdfast. Column moderately long in mature specimens, heteromorphic, circular in section with pentapetaloid axial canal. Crown large, theca medium globose (*sensu* Ubaghs 1978a, fig. 72), thecal plates quite thick. Infrabasals three, low and slightly depressed, just visible in lateral view. Basals five, small, pentagonal, in contact along shortest sides. Radials five, large, inverted heptagonal, commonly just touching laterally. Hexagonal radianal interrupts basal circlet below C radial; anal X interrupts radial circlet in CD interray. Arms uniserial, apinnulate, branching isotomously at the second primibrachial and secundibrachials

three or four, fixed to about level of tertibrachials three or four. Free arms branch heterotomously numerous times, distal tips curving adorally. Interbrachial and interradianal plates mainly hexagonal.

*Locality and horizon.* Much Wenlock Limestone Formation, Wenlock, Dudley, West Midlands.

*Remarks.* The figured specimen has a shallow circular pit (the ichnospecies *Oichnus paraboloides* Bromley, 1981) centred at a plate triple junction between the first primibrachial and two adjacent interradianal plates, presumably a weak point for a boring or imbedding organism (Donovan 1991). Similar pits are known in at least ten other species from the Much Wenlock Limestone Formation at Dudley (Widdison 2001b).

*Homalocrinus nanus* (Salter, 1873) (Fig. 9F)

*Description.* Column circular in section, heteromorphic. Infrabasals three, small, forming a ring-like circlet. Theca small, low to medium bowl. Basals five, separated, triangular extensions interradianally, with a low radianal in this circlet below the C radial. Radials five, about twice as wide as high and angular kidney-shaped, in contact except where separated by basal and lozenge-shaped anal X in CD interray. Arms uniserial, apinnulate. Fixed arms branch isotomously at the second primibrachial; fixed to secundibrachials two or three. Free arms branching heterotomously a few times, curving adorally. Few interradianal plates. Anal series short, uniserial.

*Locality and horizon.* Much Wenlock Limestone Formation, Wenlock, Dudley, West Midlands.

*Remarks.* This is the type species of *Homalocrinus*, being a senior synonym of the type species by monotypy, *Homalocrinus parabasalis* Angelin, 1878 (Widdison 2001a, p. 147).

*Cryptanisocrinus kilbridensis* Donovan, Doyle & Harper, 1992 (Fig. 12)

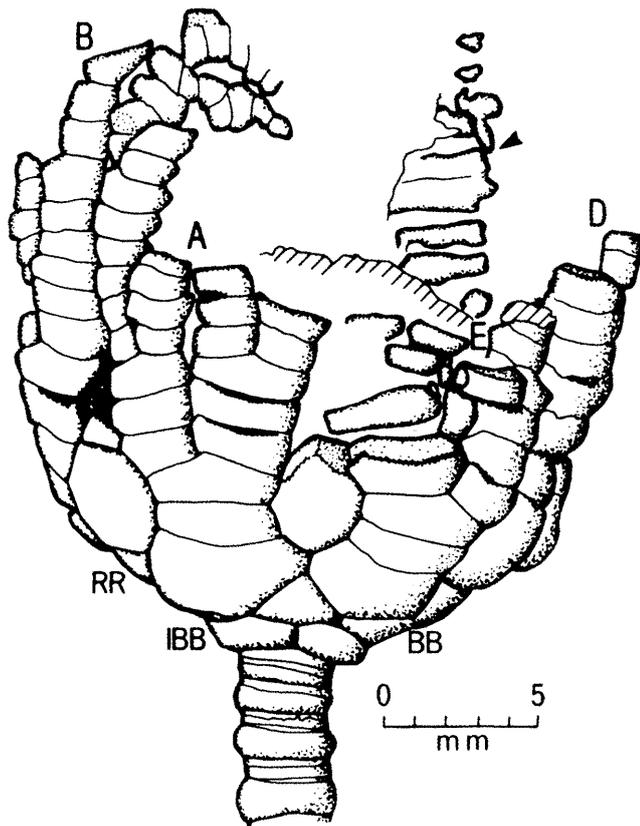
*Description.* (Abridged from Donovan *et al.* 1992, pp. 263–264.) Attachment structure unknown. Proxistele circular in section, heteromorphic N212, nodals highest with convex latera. Dorsal cup broad, low, bowl-shaped with a small infrabasal concavity. Infrabasal circlet low, presumed three infrabasals. Presumed five basals, low, wider than high, triangular, but slightly flattened at contact with adjacent basals. Radials presumed five, large, heptagonal, laterally in contact at short sutures and with broad radial facet. Five uniserial, apinnulate arms, branching isotomously at least three times, including at the second primibrachial and third secundibrachial. Arms closely abutting, fixed below the second secundibrachial. Brachials broad proximally. At least two interradianals in each interray, the lowest a large, octagonal ossicle. Anal series unknown.

*Locality and horizon.* Upper part of the Finny School member, Kilbride Formation, Telychian (upper Llandoverly), Kilbride Peninsula, Co. Galway/Co. Mayo border, western Ireland.

*Remarks.* Known only from the incomplete holotype, an external mould of one side of the crown.

*Calpiocrinus intermedius* Springer, 1920 (Fig. 8D)

*Description.* Column heteromorphic, circular in section, tapering distally where it is less nodose. Cup low bowl-shaped. Infrabasals three, large, concealing five basals. Radials five, broad, heptagonal, in contact except where separated by anal



**Fig. 12.** *Cryptanisocrinus kilbridensis* Donovan, Doyle & Harper, holotype, JMM. CR.100 (after Donovan *et al.* 1992, fig. 4), from the Kilbride Formation (Telychian), west of Ireland. Camera lucida drawing of crown and proximal column taken from a latex cast. Arrow indicates probable C-ray arm. Key: A, B, D, E = Carpenter rays; IBB = infrabasal circllet; BB = basal circllet; RR = radial circllet.

X. Arms uniserial, apinnulate, branching isotomously at the second primibrachial. Prim- and secundibrachials broad. Secundibrachials one and two in contact, arms free above this level. Few interradians, lowest plate large. Free arms branching heterotomously, bi-endotomously. Distal arms closely clustered. Anal series short and uniserial.

*Locality and horizon.* Much Wenlock Limestone Formation, Wenlock, Dudley, West Midlands.

*Temnocrinus tuberculatus* (J. S. Miller, 1821) (Figs 7F, 8A, B)

*Description.* Column long, tapered gently proximally, mesistele heteromorphic with four to five orders of regularly intercalated internodals (Fig. 8B). Column circular in section, axial canal narrow and central. Crown with tubercular sculpture. Infrabasals three, low, mainly concealed by proxistele. Basals five, pentagonal, in lateral contact. C radial supported by radianal. Radials five, heptagonal, in contact except in CD interray where separated by small anal X plate. Arms uniserial, apinnulate, branching isotomously at the second primibrachial and third secundibrachial, free above this level. Free arms branch increasingly heterotomously more distally, curving adorally at distal extremities. A few interradians support numerous granular plates.

*Locality and horizon.* Much Wenlock Limestone Formation, Wenlock, Dudley, West Midlands; basal Woolhope Limestone, Sheinwoodian (lower Wenlock), quarries at Clencher Mill Lane, Ledbury, Herefordshire.

*Remarks.* The type species of *Temnocrinus*.

*Ichthyocrinus* spp. (Fig. 9B)

*Description.* Column circular in section and tapering away from the base of the crown, composed of low columnals with a small, central lumen. Crown elongate, oval to conical or pear-shaped, expanding away from the base, largely consisting of interlocking, firmly sutured rays. Infrabasals three, small, concealed by proxistele. Basals five, small, equal, concealed or apparent laterally. Radials five, equal, broad and low. Low, smaller radianal below C radial, but no anal X in CD interray. No interradianal plates. Arms uniserial, apinnulate, branching isotomously at the second primibrachial, secundibrachials three to four and at least twice more. Arms interlock to at least secundaxillary and closely abutting thereafter; fixed and free brachials of similar morphology.

*Locality and horizon.* All species are known from the Much Wenlock Limestone Formation of Dudley, West Midlands. *Ichthyocrinus pyriformis* (Phillips, 1839) is also known from the Wenlock of Hurst Hill, near Sedgley, West Midlands (Ramsbottom 1954, p. 167).

*Remarks.* Springer (1920, p. 264) considered *Ichthyocrinus* to be a 'typical and perhaps the most characteristic representative of the Crinoidea Flexibilia.' There are three nominal species of this genus from the Wenlock of the British Isles, *I. intermedius* Angelin, 1878, *I. phillipsianus* Springer, 1920, and *I. pyriformis* (Ramsbottom 1954, pp. 166–167; Widdison 2001a, pp. 105–110). The smooth, conical, but angular crown of *I. intermedius* has large basals visible as pentagons, strong radial ridges, a rounded base and secundibrachials one to four; this is the most common *Ichthyocrinus* at Dudley (Widdison 2001a, p. 108). The crown of *I. pyriformis* is pear-shaped, has a granular to wrinkled sculpture while lacking radial ridges, well-developed basals and commonly secundibrachials one to four. *Ichthyocrinus phillipsianus* has an ovoid, angular crown with radial ridges and small basals concealed by the column, and secundibrachials one to three (Springer 1920, p. 272).

*Clidochirus?* sp. (Fig. 13)

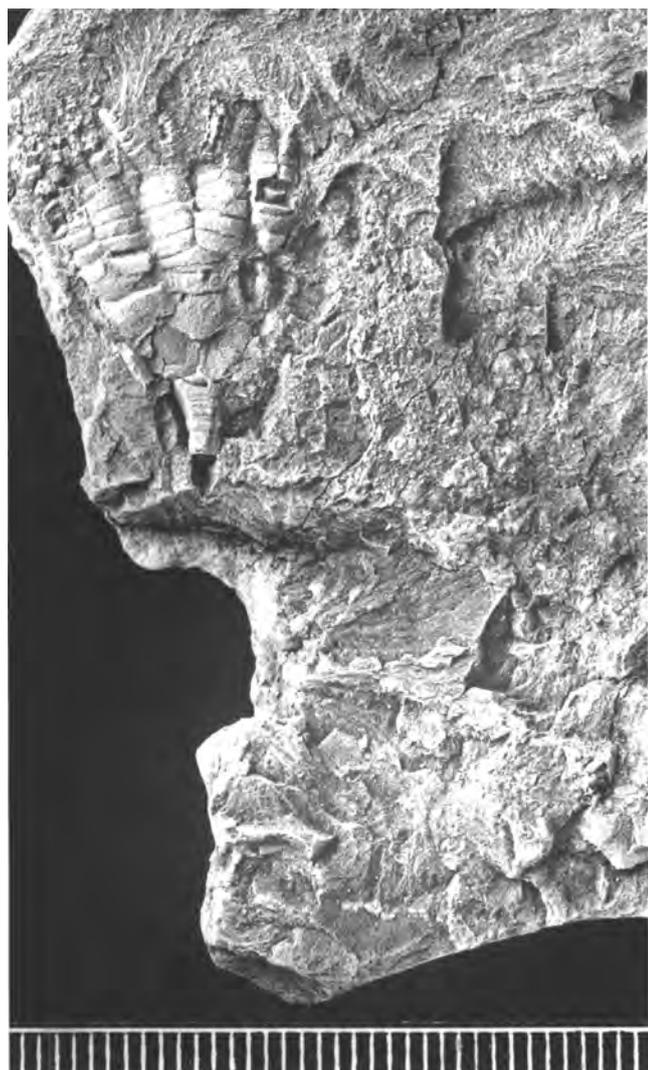
*Description.* (Abridged after Donovan & Lewis 2005, pp. 348–349.) Attachment distal, terminal, comprised of dendritic radices that bifurcate at least once near their distal extremity. Column about 25 mm in length, about half as long again as the height of the crown. Column xenomorphic. Dorsal cup dicyclic, medium conical, unsculptured. Infrabasals moderately high, pentagonal in outline, as wide as column at base. Basals tall, broad, hexagonal in outline. Radials broad, tall, not as high as basals, with a broad articular facet the width of plate. Arms uniserial, short, broad, robust, branching isotomously twice. Primibrachials broad, two; secundibrachials broad, four; tertibrachials tapering distally, about seven to nine.

*Locality and horizon.* Hughley Shales, Telychian (upper Llandovery), Devil's Dingle, Buildwas, Shropshire.

*Remarks.* Known only from a single specimen.

*Lecanocrinus bacchus* (Salter, 1873) (Fig. 6I)

*Description.* Column circular in section, heteromorphic, long. Crown globular, dorsal cup medium bowl-shaped. Three low infrabasals. Basals five, pentagonal except in CD interray which is shared with a radianal and supports the anal X. Radials five, large, inverted pentagonal, in lateral contact



**Fig. 13.** *Clidochirus?* sp., NMW 00.22G.324a, crown and proxistele, orientation uncertain. From the Hughley Shales (Telychian), Devil's Dingle, Shropshire. Scale in mm.

except where separated by X in CD interray. Arms broad, uniserial, apinnulate, abutting, branching isotomously at the second primibrachial and heterotomously at least once thereafter. No interradial plates.

*Locality and horizon.* Much Wenlock Limestone Formation, Wenlock, Dudley, West Midlands.

*Hormocrinus anglicus* Springer, 1920 (Fig. 9D)

*Description.* Column circular in section, columnals nodose with longitudinal ribs. Dorsal cup broad and low bowl shaped. Cup plates and interradials with finely granulose sculpture, arms more ridged. Infrabasals three, low, with fine median ray ridges extending obliquely onto basals. Basals five, pentagonal, in contact. Radials five, large, heptagonal, in contact except in CD interray where there is a large hexagonal(?) anal X. Arms uniserial, apinnulate, branching isotomously at the second primibrachial, secundibrachials three to four and about the third tertibrachial. Free arms widely separated. Proximal interradial plates few, large, to about height of the second primibrachial.

*Locality and horizon.* Much Wenlock Limestone Formation, Wenlock, Dudley, West Midlands.

*Remarks.* Moore (1978, fig. 519.3) illustrated numerous small interradial plates extending to the low tertibrachials in the type species, *H. tennesseensis* (Worthen). No such plates are apparent in the sole BMNH specimen (Fig. 9D), but they may have been removed when the specimen was prepared, possibly before it was purchased in 1886. Springer (1920, pl. 14, fig. 6) illustrated the same specimen in the same state of preservation.

*Pycnosaccus bucephalus* (Bather, 1890a) (Fig. 9E)

*Description.* Column circular in section with small, central axial canal. Proxistele heteromorphic. Medium bowl-shaped dorsal cup, all plates large and robust. Infrabasals three, low. Basals five, large, hexagonal(?), with Y-shaped folding. Square radial supports pentagonal anal X and C radial. Radials five, large, pentagonal, in contact laterally except in CD interray. First primibrachial axillary, not quite as broad as a radial. Arms uniserial, apinnulate, branching at least four times. Branching isotomously at the first primibrachial and secundibrachials one to three, heterotomously more distally. Arms curve adorally more distally.

*Locality and horizon.* Much Wenlock Limestone Formation, Wenlock, Dudley, West Midlands, including Tividale.

*Remarks.* The arms of the BMNH specimens are apparently free above the radials. Moore (1978, fig. 519.1) illustrated this genus with numerous small interradial plates to above the level of the primaxillary. These may have been removed in preparation of the BMNH specimens.

#### Order TAXOCRINIDA Springer, 1913

*Remarks.* 'Infrabasals usually abutting on dorsal side of basals, but low, taking little part in the calyx wall. Crown usually elongate, with arms divergent, and not abutting above interbrachial areas. Interbrachials present all round' (Springer 1913, p. 205). Dicyclic.

*Eutaxocrinus maccoyanus* (Salter, 1873) (Fig. 7H)

*Description.* Column circular in section, articulation symplectial. Proxistele homeomorphic, composed of low columnals gently tapering away from the base of the dorsal cup. Proximal mesistele heteromorphic, N3231323. Dorsal cup small, wider than high, unsculptured. Infrabasals three, cirlet low, broad pentagonal in lateral view. Basals five, a little higher than infrabasals, pentagonal. Radials five, largest, inverted pentagonal with broad arm facets, in contact except in CD interray where the basal supports the short, uniserial anal series. Arms uniserial, apinnulate, branching isotomously at the second primibrachial, third secundibrachial and at least once thereafter. Arms curved adorally. Numerous granular interradial plates to at least the second secundibrachial.

*Locality and horizon.* Lower Leintwardine Formation, Ludfordian (upper Ludlow), Church Hill Quarry, Leintwardine, Herefordshire.

*Remarks.* The two specimens in the collection of the BMNH, both external moulds without counterpart, have dorsal cups that are slightly disarticulated.

*Gnorimocrinus* sp. nov. (not illustrated)

*Description.* (Generic description after Moore 1978, pp. T771-T772.) 'Crown low, rotund; infrabasals usually extending slightly beyond stem impression; rhombic radial obliquely at left below C radial. Rays as in *Eutaxocrinus* with 2

primibrachs followed by divergent arm branches which bifurcate isotomously; interprimibrachs [=proximal interrads] few or lacking. Stem short, not enlarging near calyx, terminating distally in branched root.'

*Locality and horizon.* Wenlock Shale(?), Sedgley, West Midlands.

*Remarks.* Ramsbottom (1954, pp. 172–173, pl. 15, fig. 2) described a new species of *Gnorimocrinus* Wachsmuth & Springer, based on a single specimen. This species remains unpublished and will form the subject of a future research paper.

*Meristocrinus* spp. (Fig. 7G)

*Description.* (Based mainly on the syntype of *Meristocrinus minor* Springer, 1920, BMNH E5721.) Proxistele homeomorphic, circular in section, cylindrical or tapering gently away from base of dorsal cup, composed of low columnals, articulation symplectial. Crown elongate, high vase-shaped. Dorsal cup unsculptured or granular. Infrabasals probably three, apparent in lateral view, but low. Basals five, a little higher than infrabasals, hexagonal(?). CD basal large, supporting large anal X; anal tube simple. Radials five, large, heptagonal, in contact except in CD interray. Radial beneath C radial. Interradials few or absent. Arms uniserial, apinnulate, curved adorally, branching isotomously only twice at the third primibrachial and secundibrachials four to five.

*Locality and horizon.* The only specimen of *Meristocrinus orbignyi* (M'Coy, 1850) is from the Ludfordian (upper Ludlow) Bannisdale Slates, *leintwardinensis* Biozone, 'Asterias Bed,' Underbarrow, Kendal, Cumbria (Ramsbottom 1958, p. 107). *Meristocrinus minor* Springer, 1920, is from the Wenlock Shale at Dudley, West Midlands. *Meristocrinus* sp. nov. (in Ramsbottom 1954, p. 164) is from the Much Wenlock Limestone Formation at Dudley.

*Remarks.* The proxistele of *M. orbignyi* is cylindrical and brachials slightly expand distally, whereas the proxistele of *M. minor* tapers distally and the arms have no distal expansion. Unlike these species, the unpublished *Meristocrinus* sp. nov. has a granular sculpture.

#### Subclass **DISPARIDA** Moore & Laudon, 1943

*Remarks.* Small, monocyclic, gracile, apinnulate crinoids. The plane of bilateral symmetry, if developed, is acquired in different planes in different groups (Moore *et al.* 1978b, p. T520).

*Myelodactylus* spp. (Fig. 3K, L)

*Description.* Crinoids with a dististele that commonly curves or coils around the crown. Dististele consists of broadly U-shaped columnals, holomeric or bimeric. The proxistele is doubly recurved in an S-shape. Crown gracile and occurring adjacent to the inner surface of the coiled dististele. Numerous unbranched radices arising from the closely spaced nodals of the proximal portion of the dististele commonly conceal the crown.

*Locality and horizon.* *Myelodactylus hibernicus* Donovan & Sevastopulo, 1989, is from the Kilbride Formation (Telychian, upper Llandovery), Kilbride Peninsula, Co. Galway, western Ireland. *Myelodactylus parvispinifer* (Brower, 1975) is from the Telychian of the North Esk Inlier, Pentland Hills, Scotland. *Myelodactylus penkillensis* Donovan & Sevastopulo,

1989, is from the Penkill Formation (Telychian) of the Girvan district, SW Scotland. *Myelodactylus convolutus* Hall, 1852, is from the Hughley Shales (Telychian) of Devil's Dingle, Buildwas, Shropshire (Donovan & Lewis 2005). *Myelodactylus ammonis* (Bather, 1893) and *M. fletcheri* (Salter, 1873) are best known from the Much Wenlock Limestone Formation (Wenlock) of the Dudley area, West Midlands, but also occur elsewhere in the Wenlock (Donovan & Sevastopulo 1989, pp. 698, 701), *M. ammonis* being known from the same formation on Wenlock Edge.

*Remarks.* Perhaps the most peculiar and distinctive of all Palaeozoic crinoids, bearing more similarity to a catherine wheel firework than most crinoids. Unusually, the column is much more diagnostic than the crown. The peculiar features of *Myelodactylus* have led to a number of interpretations of its functional morphology (Donovan 2006). Most probably, it was recumbent, lying on its 'side' on the sea floor.

There are six nominal species of *Myelodactylus* in the British Silurian (Donovan & Sevastopulo 1989; Donovan & Lewis 2005). The commonest species are both from the Wenlock, *M. ammonis* and *M. fletcheri*. Radice morphology is an important character in differentiating between species of *Myelodactylus*, as follows: *M. fletcheri*, bead-like; *M. hibernicus* and *M. parvispinifer*, truncate conical; *M. convolutus* and *M. ammonis*, elongate. *Myelodactylus parvispinifer* has relatively few radices compared to the stem of *M. hibernicus*. *Myelodactylus convolutus* and *M. ammonis* are separated by the former having a homeomorphic dististele, each columnal (nodal) bearing a pair of radice scars. In contrast, *M. ammonis* varies between heteromorphic, N1, each nodal bearing two radice scars, and 'homeomorphic,' each wedge-shaped nodal bearing one radice scar on alternating sides. *Myelodactylus penkillensis* differs from all of the above in having a dististele with a section reminiscent of a Gothic arch; crown and radices are unknown.

*Pisocrinus* spp. (Fig. 3H, I)

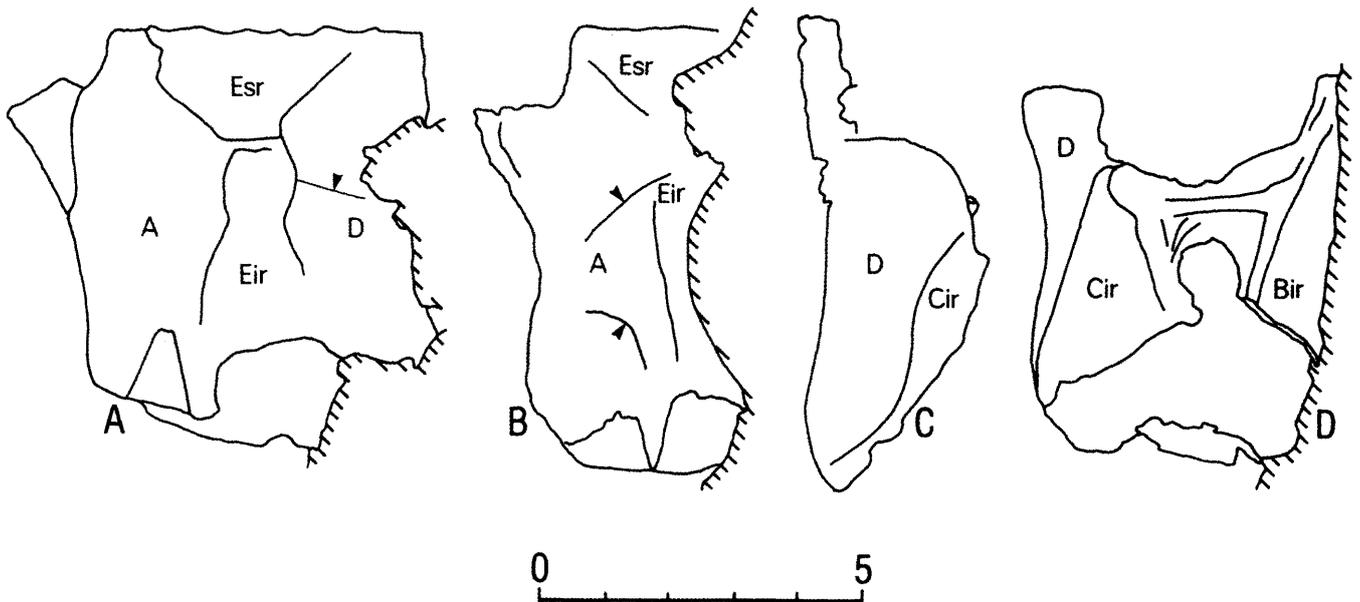
*Description.* Minute, gracile, monocyclic crinoids. Column string-like and homeomorphic, rounded in section. Dorsal cup small, bead-like (*P. pilula* de Koninck, 1858) to more conical (*P. cf. campana* S. A. Miller, 1891) and smooth. Five slender, long, uniserial, unbranched arms of triangular section.

*Locality and horizon.* *Pisocrinus pilula* is a widespread species in the Coalbrookdale Formation of the Malvern district and Shropshire, and also occurs in the Much Wenlock Limestone Formation of Dudley (all Wenlock). *Pisocrinus cf. campana* is from the Telychian (upper Llandovery) of the North Esk Inlier, Pentland Hills, Scotland (Brower 1975; Fearnhead 2008).

*Remarks.* The pisocrinids are particularly gracile disparids, with small cups, slender arms and string-like columns. *Pisocrinus* differs from *Ciceroocrinus* in having unbranched arms.

*Parapisocrinus cf. sphaericus* (Rowley, 1904) (not illustrated)

*Description.* Column slender, mesistele homeomorphic(?). Columnals of proxistele very low in basal concavity of dorsal cup, low thereafter, moderately high in mesistele, but with slight, apparently irregular variation in height. Latera convex with a tuberculated ridge at mid-height. Dorsal cup rounded bowl-shaped, with a concave base much broader than the proxistele, concealing basals. Sculpture pustulose, extending onto interradsial processes. Plating poorly apparent, but, of the



**Fig. 14.** *Calceocrinus turnbulli* Donovan (after Donovan 1993, fig. 4), from the Haverford Mudstone Formation (Rhuddanian), Haverfordwest, SW Wales. (A) Paratype, SM A32143b, E ray view; (B–D) Holotype, SM A32134a (B, C), A32134b (D). (B) E ray view; (C) Lateral view, CD interray towards right; (D) BC interray view; BC superradial top centre (unlabelled). Key: A to E = Carpenter rays; ir = inferradial; sr = superradial; arrows = cracks in dorsal cup. All camera lucida drawings from latex casts. Scale in mm.

two radials at the front, that on the right appears triangular (E?); radial on left apparently large (A?). Interradial processes high, elongate pentagonal and lanceolate. Arms elongate, slender, unbranched, uniserial, apinnulate, unsculptured except the first primibrachial. More distal primibrachials tall to very tall. Aboral surface of arms convex, lateral surface flattened. Anal series not seen.

**Locality and horizon.** Lower Leintwardine Formation, Ludfordian (upper Ludlow), Church Hill Quarry, Leintwardine, Herefordshire.

**Remarks.** This identification is based on a solitary specimen, an external mould without counterpart, now in the collection of the Oxford University Museum of Natural History.

*Cicerocrinus elegans* Sollas, 1900 (Fig. 3J)

**Description.** Proxistele circular in section, slightly tapered below cup, composed of low columnals, possibly homeomorphic, later planar. Dorsal cup monocyclic, unsculptured, tall, slender, conical and vase-like. Widest at oral surface, about half the height. Basals five, elongate pentagonal (three) or tetragonal (two), higher than wide, but forming less than a third of the height of cup. Pentagonal basals larger; tetragonal basals beneath B inferradial (positioned more in BC interray) and D radial. Radial circlet tall, composed of six plates. Radials are tall (A, D rays), small (C, E rays) or split with a small superradial (B ray). Radial facets broad, adjacent first primibrachials touching. Arms uniserial, moderately slender and elongate, tapering distally, ramulate, branching isotomously only once, at the second primibrachial, or twice, the second time at secundibrachials 18 or 19. Arms about three times longer than the height of the dorsal cup. Anal series a simple tube.

**Locality and horizon.** Known from a number of localities, all in the Ludlow Series (Ramsbottom 1954, pp. 95–96), including Whitcliffe, near Ludlow, Shropshire; quarry near the old

bridge at Ludlow; and Stapleton Castle, near Presteigne, and near Knighton, both in Powys.

**Remarks.** *Cicerocrinus elegans* is the type species. The holotype and only known example of a second British species, *Cicerocrinus anglicus* (Jaekel, 1900), was never illustrated and is lost (Ramsbottom 1954, pp. 98–99). It probably came from the Ludlow at Presteigne.

*Calceocrinus* spp. (Fig. 14)

**Description.** Column circular in section, homeomorphic, composed of low columnals. Crown recumbent on column, bilaterally symmetrical in the plane BC-E. Basals four, in a trapezoid circlet, all forming part of facet of column. The broadest edge of the basal circlet acted as a hinge and articulated with the A radial, E inferradial and D radial. Super- and inferradials in the E ray. B and C inferradials small, separated by basals, and sharing a fused superradial in the BC interray that supports the anal series, but no arm. E ray arm unbranched or branched isotomously, commonly broader than branches of other arms. E ray arm flanked symmetrically by A and D arms, branching heterotomously two to three times. Anal series simple.

**Locality and horizon.** *Calceocrinus turnbulli* Donovan, 1993, and *Calceocrinus*(?) sp. are from the Haverford Mudstone Formation (Rhuddanian, lower Llandovery), Haverfordwest, Pembrokeshire, SW Wales. *Calceocrinus anglicus* (Springer, 1926) is from the Much Wenlock Limestone Formation (Wenlock), Dudley, West Midlands.

**Remarks.** The calceocrinids are a peculiar group of crinoids in which the dorsal cup is hinged and the symmetry is approximately bilateral, with the arms on either side of the symmetry axis showing multiple episodes of branching in their lower part. The E ray arm, in the plane of symmetry, is branched symmetrically or unbranched, and flanked by the A and D radials and arms. The fused superradial in the B and C rays is

in the plane of symmetry and supports the anal series, but it bears no arm. Calceocrinids probably lived recumbent on the sea floor (Brower 1985). British Silurian calceocrinids include *Calceocrinus* Hall (two nominal species), *Chirocrinus fletcheri* (Salter) and *Synchirocrinus* Jaekel (five nominal species). These genera are differentiated by their progressive increase in number of arm branches from *Calceocrinus* (least; Fig. 3G) to *Synchirocrinus* (most; Fig. 17).

*Calceocrinus turnbulli* has a dorsal cup that is highly compressed BC-E, a trapezoid pattern of ridges on the BC superradial, a pustular sculpture on the dorsal cup and proximal arms, and an unbranched E ray arm; the pattern of arm branching is not known. *Calceocrinus anglicus* has a quadrangular dorsal cup, and an E ray arm that branches isotomously at the first primibrachial and heterotomously thereafter; it is known only from the holotype. *Calceocrinus?* sp. differs from *C. turnbulli* in having a more robust dorsal cup with a rounded transverse section that is not so compressed BC-E. It lacks large ligament fossae at the base of the dorsal cup

*Chirocrinus fletcheri* (Salter, 1873) (not illustrated)

*Description.* (Based on Ramsbottom 1952, pp. 36–37; Moore et al. 1978b, pp. T527–T529.) Column slender, circular in section. Crown bilaterally symmetrical. Dorsal cup quadrangular and funnel-shaped. Basals three. B and C inferradials spear-shaped, separated by basals and supporting fused super-radial which, in turn, supports anal X. E ray inferradials quadrangular, small, but elongate, narrowly in contact with the broad, low superradial. E ray arm unbranched. Large, heptagonal radials in A and D rays. A and D arms branch unevenly at the first primibrachial, narrower branch adjacent to E ray, broader branch bearing secundaxillary, similar branching pattern repeated at secund- and tertaxillaries. Tertaxillary supports quartaxillary, the narrower, unbranched ramule of which is adjacent to the anal tube. More distal arms branch heterotomously, with elongate ramules developed on E ray side of arms. Anal tube simple.

*Locality and horizon.* Much Wenlock Limestone Formation, Wenlock, Dudley, West Midlands.

*Remarks.* *Chirocrinus fletcheri* is distinguished from *Calceocrinus* by the more complex branching pattern of the A and D arms.

*Synchirocrinus* spp. (Fig. 3G)

*Description.* Crown perfectly bilaterally symmetrical. Basals three, articular facet of proxistele shared by posterior pair. E ray infer- and superradials in contact or separated. E ray arm commonly unbranched. A and D radials large with broad articular facets; these arms branch several times immediately above radials. More distally, arms in strongly parallel array, with elongate ramules parallel to branched arms. B and C inferradials separated by basals, supporting fused superradial that, in turn, supports X and the anal series.

*Locality and horizon.* Much Wenlock Limestone Formation, Wenlock, Dudley, West Midlands.

*Remarks.* Five species of *Synchirocrinus* have been identified from the Much Wenlock Limestone Formation of Dudley; *S. serialis* (Austin M. S. in Salter, 1873), *S. pugil* (Bather, 1893), *S. inclinus* (Ramsbottom, 1952), *S. gradatus* (Salter, 1873) and *S. nitidus* (Bather, 1893), the type species. Rams-

bottom (1952) used the following criteria to differentiate between these species, with terminology of the dorsal cup as revised by Moore (1962). *Synchirocrinus serialis* has a low, quadrangular dorsal cup that contracts upward, E ray infer- and superradials separate and one narrow, stout primibrachial in the A and D rays. *Synchirocrinus pugil* has a quadrangular dorsal cup without lateral constriction; the E ray infer- and superradials are separated; and the A and D rays each with two primibrachials, the second in contact with the radial. *Synchirocrinus inclinus* has a dorsal cup that is flared aborally and markedly constricted; the E ray infer- and superradials are commonly in contact; the A and D rays each have two primibrachials; the fused superradial of the B+C rays is broad; and axillaries are nodose. *Synchirocrinus gradatus* has a quadrate dorsal cup with lateral constriction; the E ray superradial is long and in contact with the inferradial; the E ray arm is not much larger than A and D ray branches; and one wide primibrachial in each of the A and D rays. *Synchirocrinus nitidus* has a quadrangular dorsal cup without lateral constriction; the E ray infer- and superradials are not in contact, the latter supporting a large arm; one wide primibrachial in each of the A and D rays; and the B and C inferradials not thinning posteriorly, supporting a small fused superradial.

Class **BLASTOIDEA** Say, 1825

Subclass **CORONATA** Jaekel, 1918

Family **STEPHANOCRINIDAE** Wachsmuth & Springer, 1886

*Remarks.* 'Coronates are a small but distinctive group of Lower Palaeozoic pelmatozoans with a functional stem, a small theca with five interradial coronal processes ventrally and a fixed arrangement of thecal plates very similar to that of blastoids, and erect, biserial, pinnate arms' (Donovan & Paul 1985, p. 527).

*Cupulocorona salopiae* Donovan & Paul, 1985 (Fig. 15F)

*Description.* (Adapted from Donovan & Paul 1985, p. 538.) Stem unknown. Theca pear-shaped. Base triangular with rounded corners, articular facet for column round and depressed. Thecal cross-section changes from triangular to rounded pentagonal just above base. Coronal processes large and triangular with blunt angles. Sutures between adjacent plates bear broad ridges. Aboral surface of theca with sculpture of fine ridges in rhombic patterns. Ambulacra five, bearing paired food grooves, concealed by paired ambulacral plates, which slope gently away from the mouth and extend about 65 % of the way to the periphery of the oral surface. Five oral cover plates lie interradially over the mouth.

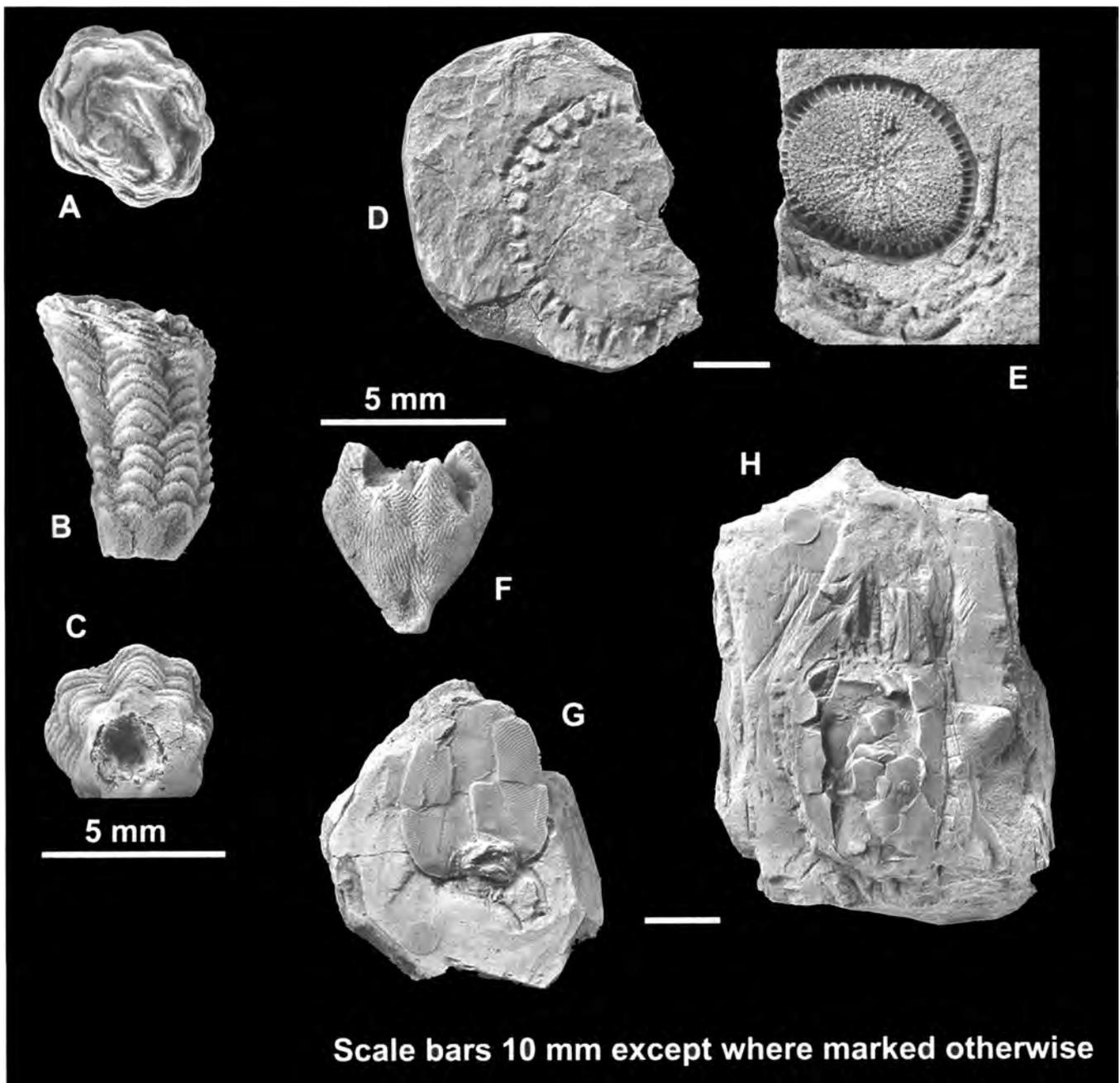
*Locality and horizon.* Buildwas Formation (originally Buildwas Beds), Wenlock Series, east bank of the River Severn, a short distance above Buildwas Bridge, Shropshire.

*Remarks.* A further species, *Stephanocrinus ramsbottomi* Donovan & Paul, 1985 (p. 536), may come from the Rhuddanian (lower Llandovery) of Keisley, Westmorland. However, this species is otherwise limited to the Ashgill, particularly the Hirnantian, and the Silurian occurrence is regarded as uncertain.

Class **EDRIOASTEROIDEA** Billings, 1858

Order **ISOROPHIDA** Bell, 1976

*Remarks.* 'Edrioasteroids are an extinct group of eleutherozoic echinoderms that occur only rarely in the Lower



**Fig. 15.** Minor echinoderm groups. (A–C) Edrioasteroid *Pyrogocystis ansticei* Bather, BMNH E16235, holotype, from the Coalbrookdale Formation (Wenlock), near Coalbrookdale, Shropshire. (A) Oral view; (B) Lateral view; (C) Basal view; (D, E) Cyclocystoids, (D) *Diastocycloides?* sp., BMNH E29551, from Wenlock Shale, Dudley, (E) *Polytryphocycloides davisi* (Salter), BMNH E29056, neotype, from the Mulloch Hill Formation (Rhuddanian), SW Scotland; (F) Coronate *Cupulocorona salopiae* Donovan & Paul, BMNH E45532, paratype; (G, H) Mitrata *Placocystites forbesianus* de Koninck, from the Hughley Shales (Telychian), Devil's Dingle, Shropshire, (G) BMNH E7540, dorsal view, (H) BMNH E7544, ventral view.

Palaeozoic of the British Isles and which were attached in life by the aboral surface' (Donovan *et al.* 1996, p. 263).

*Pyrogocystis ansticei* Bather, 1915 (Fig. 15A–C)

**Description.** (Adapted from Bather 1915.) Peduncle subcylindrical, tapering distally, composed of about 50 tiers of imbricated thin, wide plates, commonly organized into about eight columns separated by grooves. Adoral surface about a half to two thirds height. Five broad, straight rays on the oral surface of other species of *Pyrogocystis*, but poorly known in *P. ansticei*.

**Locality and horizon.** Wenlock Shale (undifferentiated = Buildwas and Coalbrookdale formations), Wenlock Series, Jig House (Jiggers) Bank, right hand side of Lloyd Brook dingle, near Coalbrookdale, Shropshire.

**Remarks.** Although known from the Upper Ordovician to the Mississippian of the British Isles (Smith 1983; Donovan *et al.* 1996), edrioasteroids are rare and only locally common. Bather (1915, p. 51) had 14 specimens available of *P. ansticei*, but it is known only from the type locality.

### Class **CYCLOCYSTOIDA** Miller & Gurley, 1895

*Remarks.* Cyclocystoids are a group of rounded eleutherozoic echinoderms with a near-flat test bordered by a ring of robust marginal ossicles and enclosing numerous smaller plates. The ventral surface is distinguished by its radial structure and central opening; the dorsal surface consists of polygonal plates surrounding a central dorsal cone. Notes on British Silurian cyclocystoids are based on Smith & Paul (1982).

*Polytriphocycloides davisii* (Salter in Salter & Billings, 1858) (Fig. 15E)

*Description.* Test ovoid, bilaterally symmetrical, marginal frame of 48–52 ossicles. Interrays on ventral surface narrow. Four primary rays bifurcate three or four times; flat, angular cover plates largely cover rays. Dorsal surface with four large plates at centre surrounded by smaller plates.

*Locality and horizon.* Mulloch Hill Formation, Rhuddanian (lower Llandovery), Ayrshire, SW Scotland; and May Hill Sandstone Group, Telychian (upper Llandovery), May Hill Inlier, Gloucestershire.

*Remarks.* The holotype from May Hill is lost, but Smith & Paul (1982, p. 638) nominated a neotype from Mulloch Hill.

*Diastocycloides?* sp. (Fig. 15D)

*Description.* Known only from a partial, sub-circular marginal frame.

*Locality and horizon.* Wenlock Shales, Wenlock, Dudley, West Midlands.

*Remarks.* Known from a single, distinctive, but poorly preserved specimen.

### 'CARPOIDS'

#### Order **MITRATA** Jaekel, 1918

*Remarks.* (Adapted from Donovan 1999, pp. 592–593.) Carpoids, otherwise known as calcichordates, are an enigmatic Palaeozoic group interpreted as either aberrant, asymmetric echinoderms or echinoderm-like, invertebrate chordates. The skeleton possesses stereom microstructure otherwise typical of echinoderms. Mitrates consist of a flattened, asymmetrical, multi-plated box, the head or theca, to which is attached an elongate, serially-plated, flexible tail or stele.

*Placocystites forbesianus* de Koninck, 1869 (Fig. 15G, H)

*Description.* Tail multi-plated, dorsal surface bladed. Proximal tail short, robust, tapering distally and flexible, with numerous small ossicles dorsally. Attached to the short, tapered mid tail, which in turn supports the elongate, slender, flexible distal tail. Theca elongate, rectangular, asymmetric, but approaching bilateral symmetry, particularly ventrally, formed from relatively few (27), thin, rigidly sutured calcareous plates. Transverse, cuesta-shaped ridges on dorsal and ventral surfaces, steep faces directed away from the tail. Oral plates at anterior surface. Elongate left and right oral appendages unjointed, but articulate at base, flanking the oral region.

*Locality and horizon.* Hughley Shales (Telychian, upper Llandovery), Devil's Dingle, Buildwas, Shropshire; Much Wenlock Limestone Formation (Wenlock), Dudley, West Midlands (Jefferies & Lewis 1978).

*Remarks.* The known Silurian carpoids are rare and limited to the mitrates. *Placocystites forbesianus* is the only mitrate of

this age from western Europe, and one of only two species of Silurian mitrate known outside Australasia (Domínguez Alonso *et al.* 2002). The oral appendages would have acted to give *P. forbesianus* greater stability on the sea floor by increasing its virtual area, while being able to wave from side-to-side to stir up sediment for feeding. The cuesta-shaped ribs indicate that the animal moved rearwards, pulled by the tail.

## 2. DISCUSSION

“... with its long and finely ringed column, its well-proportioned cup, the delicacy of its ventral sac, and its more than myriad arms, the living *Thenarocrinus* must have been one of the most beautiful and wonderful forms in that paradise of lovely marvels, the Wenlock Sea” (Bather 1890b, p. 235).

This guide (including Lewis *et al.* 2007) recognizes 145 species of echinoderms from the Silurian of the British Isles (Table 2). Of these, there are 98 crinoid species, eleven other pelmatozoans and 34 eleutherozoans (echinoids, ophiuroids, asteroids, ophiocistioids, edrioasteroids and cyclocystoids). The greater diversity of pelmatozoans, particularly crinoids, is a well-known feature of the Palaeozoic fossil record (Paul & Smith 1984, fig. 14). It is expected that this diversity of Silurian crinoids will be increased further when their isolated columnals have been described; these ossicles represent an abundant component of many horizons that do not produce complete fossil echinoderms (Fearnhead 2006; Fearnhead & Donovan 2007b). The list herein includes certain new taxa that are well documented in theses (Ramsbottom 1954; Widdison 2001a); further taxa await discovery, not just in the field, but also in museum collections (for example, see *Dendrocrinus*, above).

Similarly, it is unsurprising that the greatest diversity of echinoderms from this interval and area should come from the Much Wenlock Limestone Formation at Dudley (Table 2). Crinoids are particularly diverse (Table 1). It is unusual for a major natural history museum not to have a collection of crinoids from Dudley, bought from dealers in the late 19<sup>th</sup> or early 20<sup>th</sup> centuries when the quarries were active. In comparison, the best known echinoderm faunas from the Llandovery and Ludlow have only about 20% of the diversity of the Much Wenlock Limestone Formation at Dudley (note that Table 2 includes echinoderms from the Wenlock Shale at Dudley in the category 'other Wenlock').

Whether the chosen *Echinodermen Lagerstätten* (i.e., exceptional echinoderm-rich deposits) are typical of their interval is debatable. Despite the great diversity of echinoderms listed from Dudley, some groups are only known from other localities, horizons or both; perhaps most unexpectedly, ophiuroids remain poorly known from the Wenlock. British Silurian ophiuroids are best known from siliciclastic units, so their absence from the Much Wenlock Limestone Formation may be related to lithofacies.

The greatest contrast is in the Llandovery. All British Llandovery echinoids, ophiuroids and asteroids, ten species in total, are known from the Telychian of the North Esk Inlier. The only examples of British Llandovery rhombiferans, coronates and mitrates, one species of each, are also Telychian, and all come from the Buildwas and Devil's Dingle area of Shropshire. Now that crinoids are being described from Devil's Dingle from museum collections (Donovan &

**Table 2**

Echinoderms of the Silurian of the British Isles. The North Esk Inlier (Telychian, upper Llandovery), Dudley (Much Wenlock Limestone Formation, Homerian, upper Wenlock); and Church Hill Quarry (Lower Leintwardine Formation, Ludfordian, lower Ludlow) are the most echinoderm-rich localities in each of the three Silurian series that yield common echinoderms. The total number of known species in each major group is given in brackets. The order of taxa follows the arrangement in this guide; eleutherozoan groups are indicated thus\*

	North Esk Inlier	Other Llandovery	Dudley	Other Wenlock	Church Hill Quarry	Other Ludlow
* Echinoids (5)	1	–	1	–	2	1
* Ophiuroids (10)	3	–	–	1	7	4
* Asteroids (16)	6	–	5	4	3	2
Rhombiferans (9)	–	1	6	3	–	1
* Ophiocistioids (3)	–	–	–	1	1	1
Diplobathrids (10)	2	3	5	1	–	–
Monobathrids (25)	1	2	17	6	1	2
Cladids (26)	1	4	18	5	1	–
Sagenocrinids (12)	–	2	10	2	–	–
Taxocrinids (5)	–	–	1	2	1	1
Disparids (18)	2	4	10	3	1	2
Coronates (1)	–	1	–	–	–	–
* Edrioasteroids (1)	–	–	–	1	–	–
* Cyclocystoids (2)	–	1	–	1	–	–
Mitrates (1)	–	1	1	–	–	–
<b>Totals spp. (145)</b>	<b>16</b>	<b>19</b>	<b>74</b>	<b>30</b>	<b>17</b>	<b>14</b>

Lewis 2005), it must be suspected that we have been remiss in not collecting this site more thoroughly before it was landscaped and lost to collectors.

An interesting pattern emerges if we imagine that the Much Wenlock Limestone Formation at Dudley and its rich diversity of echinoderms had remained undiscovered. In short, what would be the 'shape' of the British Silurian echinoderm fauna in the absence of its richest locality? Ignoring these data, there are 35 species of echinoderm known from the Llandovery, 30 from the 'other' Wenlock and 28 from the Ludlow, that is, all are of a similar order of magnitude. Following the end of the Ordovician and the effects of the late Ordovician mass extinction, the British Llandovery echinoderms, particularly crinoids, have been perceived as being of only limited diversity (Donovan 1994); echinoderm re-diversification was considered to be a mainly Wenlock phenomenon. This may be true, but it is surely significant that, without the influence of the most diverse Silurian echinoderm locality in the British Isles, the Wenlock has a diversity comparable to that of the Llandovery and Ludlow. The British Llandovery echinoderms only appear depauperate when compared to a truly exceptional Silurian fauna, such as that of Dudley, perhaps suggesting that this pattern is more strongly influenced by the taphonomic signal than has been appreciated hitherto.

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## APPENDIX: GLOSSARY OF MORPHOLOGICAL TERMS

### Crinoidea

*A, A ray* – see rays.

*adoral groove* – a longitudinal groove on the adoral surface of an arm or brachial, connecting it to the mouth.

*ambulacral cover plates* – small, moveable plates adjacent to the adoral groove which can be opened when feeding and closed for protection.

*ambulacrum* – radial covered groove of echinoderms, associated with feeding. In crinoids, the ambulacra radiate from the mouth, extend across the tegmen and along the arms (=adoral groove).

*anal X* – found in disparid, cladid and flexible crinoids. A plate located in the CD interray, the lowest of the anal series, situated within or above the radial circlet.

*anal sac* – a multiplated, elongate, commonly ornate, bag-like structure in cladids, flexibles and disparids that elevates the opening of the anus (at or near the end of the sac) above the oral surface. Anal sacs may be shorter than, as long as or longer than the arms.

*anal series* – the plates between the anus and the most proximal plate of the posterior interray.

*anal tube* – a tube in camerates that elevates the opening of the anus above the oral surface.

*apinnulate* – arm lacks pinnules.

*areola* – planar to gently concave feature of the articular facet of a columnal, situated between the symplectial articulation and the lumen, and, in life, being associated with the dense ligamentation that maintains columnals in close proximity.

*arm facet* – articular facet on a radial plate on which the arm articulates.

*arms* – serial, elongate, upright and commonly branched structures, elevated above the oral surface of the calyx and adapted for capturing plankton for food using the tube feet.

*articular facets* – the adjacent faces of columnals, cirral ossicles, radicular ossicles, brachials or pinnules at which ligamentary or muscular articulations permit or induce relative movement (except at cryptosymplectial and synostiosal articulations, where relative movement is not possible, although such facets, if present, are regularly spaced through a structure).

*attachment structure* – see holdfasts.

*axial canal* – the canal that follows the long axis of the column and, in life, includes certain soft tissues, particularly nervous tissues. Commonly central and apparent as an opening on each articular facet of a columnal. Commonly circular or pentagonal in outline. The opening of the axial canal on an articular facet is termed the lumen.

*axillary* – a brachial plate that supports two more distal branches of an arm.

*B, B ray* – see rays.

*basal concavity* – depression in the basal circlet of a monocyclic crinoid. The proxistele attaches to the articular facet in the centre of the depression.

*basals* – the crinoid dorsal cup is composed of two or three (rarely four) circlets of plates, exclusive of the tegmen. Each circlet is commonly formed of five plates, although these show considerable variation between genera. In a dicyclic cup, the lowest plate circlet, the infrabasals, support the basals, which support the radials. In a monocyclic cup the

basals are the lower circlet. Basals are offset from infrabasals and radials.

*BC interray* – see rays.

*bipinnulate* – two pinnules developed on a single brachial.

*biserial* – a sequence of two parallel columns of alternating plates. The arms of many species of Palaeozoic crinoids are typically biserial, at least in part.

*brachials* – ossicles of the arms, generally with a U-shaped section, the groove being adoral in position.

*C, C ray* – see rays.

*calyx* – the part of the crown below the free arms, formed from the dorsal cup, fixed arms, interradials and (if present) interbrachials, but not the tegmen (compare with theca).

*camerate* – robust monocyclic (monobathrids) and dicyclic crinoids (diplobathrids) that are commonly pinnulate with fixed proximal arms and an armoured tegmen.

*canaliculae* – radial canals within nodals, connecting the lumen and latus.

*Carpenter rays* – see rays.

*CD interray* – see rays.

*claustrum* – a constriction of the axial canal produced by an inward growth of the columnal calcite. The outline defined by the claustrum of a columnal may or may not be the same as that of the axial canal.

*column* – the part of the stem between the attachment structure and dorsal cup. In most crinoids the column elevates the crown above the sea floor.

*columnals* – the uniserial, disc-like ossicles (holomeric) or circlets of ossicles (pentameric) that form the column.

*crenulae* – ridge and adjacent furrow of the articular facet of a columnal with symplectial articulation.

*crenularium* – the pattern of ridges and grooves that interlock between adjacent articular facets that articulate symplectially or are apposed in a syzygial brachial articulation. Symplectial articulations of the column and radices are commonly radial, but the crenularium may be arranged perpendicular to the circumference of the articular facet or, as in isocrinids, may have a petaloid arrangement.

*crown* – the part of the crinoid above the stem, consisting of the calyx and free arms.

*D, D ray* – see rays.

*dendritic radice* – attachment structure with numerous radices with morphology like a 'tree stump.'

*dicyclic* – a dorsal cup comprised of two basal circlets, the lower infrabasals supporting the basals. The basals, in turn, support the radial circlet.

*dististele* – the most distal part of the column, commonly grading in morphology into the attachment structure.

*dorsal cup* – lowest part of the calyx/crown, consisting of two (monocyclic) or three circlets of plates (dicyclic). The arms form a continuous series of plates articulating with the topmost plates of the dorsal cup (radials).

*E, E ray* – see rays.

*endotomous* – bifurcating arms which branch further only on their inner (=adradial) sides.

*epifacet* – a columnal latus that is extended to form a flange-like structure.

*fixed arms* – proximal, inflexible series of brachials at base of arms that are rigidly sutured into the calyx. Most typical of camerates, but also found in other groups.

*free arms* – the flexible parts of the arms above the calyx.

*fused brachials* – triangular, fan-like arms found in the cladid *Petalocrinus*.

*geniculated* – bent like a knee.

- heteromorphic* – a heteromorphic column is composed of columnals which differ in size (height and/or diameter) and/or shape and sculpture from adjacent columnals. It is thus distinguished from a homeomorphic column, which is composed of columnals which have identical morphologies.
- heterotomous* – unequal branching of arms.
- holdfast* – see attachment structure.
- holomeric* – a columnal formed from a single calcite plate, which is true for the majority of pelmatozoan columnals.
- homeomorphic* – a column or part of a column composed of identical columnals (nodals).
- hyperpinnulate* – more than two pinnules developed on a single brachial.
- inferradial* – the lower plate of a biradial or split radial, that is, a radial that comprises two separate plates, one supporting the other. The upper plate is a superradial.
- infrabasal concavity* – depression in the infrabasal cirlet of a dicyclic crinoid. The proxistele attaches to the articular facet in the centre of the depression.
- infrabasals* – the lowest plate cirlet in a dicyclic crinoid cup.
- interbrachials* – plates that occur between branches of an arm.
- internodal* – columnals intercalated between nodals in a heteromorphic column. Internodals are commonly lower or narrower or lower and narrower than nodals, and do not support radices or other attachment structures.
- interradials* – plates above the dorsal cup and between the rays.
- interray* – see rays.
- isotomously* – equal branching of arms.
- laus* (*plural, latera*) – the part of a columnal that lies outside the areas of the two articular facets; that is, the part of a columnal that is exposed when an articulated column is examined.
- lobolith* – the globular, distal, multiplated flotation structure of *Scyphocrinites*.
- lumen* – an opening in the centre of a columnal articular facet formed by the intersection of the axial canal and the articular facet.
- meric sutures* – straight or zigzag suture apparent on the latera of pentameric pluricolumnals. Five radial sutures are apparent on the articular facet of columnals.
- mesistele* – the middle part of a xenomorphic pelmatozoan column.
- monocyclic* – a dorsal cup comprising one basal cirlet supporting the radial cirlet (that is, an infrabasal cirlet is absent).
- nodals* – all the columnals of a homeomorphic column and the largest plates of a heteromorphic column, the latter commonly regularly inserted. Radices or pseudoradices or other attachment structures articulate with or are otherwise attached to nodals.
- orals* – five articulated, tegmental plates in interradian positions and protecting the mouth.
- ossicles* – calcareous plates of the echinoderm endoskeleton.
- partition plates* – greatly extended interbrachial plates of *Eucalyptocrinites* and related genera.
- pentameric* – columns in which each columnal is formed from a cirlet of (most commonly) five wedge-shaped ossicles (pentameres) of equal size.
- pinnulate* – possessing pinnules.
- pinnule* – a slender, unbranched, minor branch arising from an arm. Where present, pinnules commonly arise alternately from either side of the oral groove on successive brachial plates.
- primanal* – the lowermost plate of the anal series in camerate crinoids.
- primaxillary* – the highest primibrachial plate of any branched crinoid arm. The primaxillary is the point of branching, supporting two more distal branches (=secundibrachials).
- primibrachials* – the most proximal series of arm plates, supported by the radials. The highest primibrachial in branched arms is the primaxillary; in unbranched arms, all brachials are primibrachials.
- priminternodals* – the largest and first formed of the internodal columnals.
- proxistele* – the proximal part of a xenomorphic crinoid column.
- pseudoradices* – solid calcite extensions from nodals of the attachment structure, superficially similar to radices, but unjointed.
- quartaxillary* – the highest quartibrachial (that is, fourth order brachial) of a crinoid arm branching four or more times. The quartaxillary supports two more distal branches.
- quartinternodals* – fourth order internodals.
- radials* – the highest cirlet of plates of the dorsal cup, supported by the basals and supporting the arms.
- radial* – an inferradial in the C ray that supports the anal X plate of the anal opening.
- radice* – a branched or unbranched, root-like structure composed of radice ossicles which articulate symplectially or synostosially.
- radicular* – bearing root-like extensions, branched or unbranched, either as the distal termination of the column or arising from one side of the dististele. Radicles/radices may be unbranched or branched.
- ramules* – major branches of crinoid arms that do not branch further; the other branch from the same axillary does branch again.
- rays* – the five rays of a crinoid, each including a radial plate of the dorsal cup that supports an arm, are named A, B, C, D and E. These are separated by interrays AB, BC, CD, DE and EA. The CD interray is identified as the position of the anal series and is regarded as posterior. On the opposite side of the dorsal cup is the A ray (anterior).
- secundaxillary* – the highest secundibrachial plate of any crinoid arm that branches at least twice. The secundaxillary is the point of branching, supporting two more distal branches (=tertibrachials).
- secundibrachials* – the two arm branches supported by the primaxillary. The highest secundibrachial in arms that branch more than twice is the secundaxillary.
- stem* – the attachment structure plus column, that is, the part of a crinoid below the crown.
- subapical* – close to, but not at, the apex. May refer to, for example, the position of the anus in camerate crinoids with a well-plated tegmen.
- superradial* – the upper plate of a biradial or split radial, that is, a radial that comprises two separate plates, one supporting the other. The lower plate is an inferradial.
- symplectial* – the commonest mode of articulation between pelmatozoan columnals. Adjacent articular facets are comprised of interlocking crenellated faces held in place by collagenous ligaments. A symplexy allows some slight flexure of the stem, but prevents twisting movements which could break ligament fibres.

*tegmen* – the adoral part of the theca, situated above the free arms. The tegmen may be calcified and multiplated, particularly in camerates, and bears the anal opening and associated structures (such as an anal tube or sac).

*tertibrachials* – the arm branches supported by secundaxillaries. In the isotomously branching arms of a crinoid with five rays, there will be five series of primibrachials, ten series of secundibrachials and twenty series of tertibrachials.

*tertaxillary* – the highest tertibrachial plate of any crinoid arm that branches at least thrice. The tertaxillary is the point of branching, supporting two more distal branches (=quartibrachials).

*theca* – the ‘box-like’ part of a crinoid, that region above the stem and below the free arms, composed of the calyx and tegmen.

*uniserial* – a linear sequence of plates. For example, the arms of many species of crinoids are typically uniserial, at least in part.

*xenomorph* – a xenomorphic column is divided into a number of morphologically distinct zones. These different morphologies reflect functional differences between distinct regions of the column.

### Coronata

*coronal processes* – distinct, raised, triangular processes at the top of the theca and interradial in position; thus, there are five per theca.

*oral cover plates* – group of five plates covering the mouth.

*pinnate (arms)* – bearing pinnules.

### Edrioasteroidea

*eleutherozoic* – free-living animals, generally applied to echinoderm groups apart from the Crinoidea and Blastoidea, that is, apart from those that commonly have a true stem. Unusually among the eleutherozoans, edrioasteroids were attached by a peduncle.

*peduncle* – a flexible, stalk-like process; in edrioasteroids, commonly composed of imbricated plates.

### Cyclocystoidea

Adapted from Smith & Paul (1982, pp. 597–599).

*central opening* – opening in centre of ventral surface that may represent the peristome (‘mouth’).

*dorsal cone* – group of protruding plates in centre of dorsal surface that may represent the periproct (‘anus’).

*marginal frame* – the ring that borders the disc and is composed of marginal ossicles.

*marginal ossicles* – large, distinctive ossicles that articulate laterally to form the marginal frame or ring.

### Mitrata

*oral appendages* – paired, elongate, unjointed appendages, articulated at base and flanking the oral region.

*stereom* – three-dimensional framework of calcite rods that form all echinoderm plates, defining interconnecting pore spaces that may be filled with unmineralized tissues.

*tail (=stete)* – elongate, flexible, multiplated structure divided into three regions and defining the posterior of the animal. Widest proximally, with a short, conical mid-stete and an elongate, slender distal stete.

*theca* – flattened, more or less asymmetric, ‘body’ formed of calcite plates.

### NOTE ADDED IN PROOF

Since the publication of the first part of this guide (Lewis *et al.* 2007), two important papers on the asteroids of the Much Wenlock Limestone Formation have been published, respectively examining the functional morphology of multi-armed *Lepidaster grayi* Forbes (Herringshaw *et al.* 2007a) and the diversity of the fauna (Herringshaw *et al.* 2007b). The latter includes descriptions of three new species. These data have been added to Table 2 herein.

HERRINGSHAW, L. G., SMITH, M. P. & THOMAS, A. T. 2007a. Evolutionary and ecological significance of *Lepidaster grayi*, the earliest multiradiate starfish. *Zoological Journal of the Linnean Society*, **150**, 743–754.

HERRINGSHAW, L. G., THOMAS, A. T. & SMITH, M. P. 2007b. Starfish diversity in the Wenlock of England. *Palaeontology*, **50**, 1211–1229.

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