

A field guide to the Silurian Echinodermata of the British Isles: Part 1 - Eleutherozoa and Rhombifera

D.N. Lewis, S.K. Donovan, P. Crabb & D.J. Gladwell

Lewis, D.N., Donovan, S.K., Crabb, P. & Gladwell, D.J. A field guide to the Silurian Echinodermata of the British Isles: Part 1 - Eleutherozoa and Rhombifera. *Scripta Geologica*, **134**: 27-59, 4 pls., 6 figs., 1 table, Leiden, March 2007.

David N. Lewis, Department of Palaeontology, The Natural History Museum, Cromwell Road, London, SW7 5BD, England (dnl@nhm.ac.uk); Stephen K. Donovan, Department of Geology, Nationaal Natuurhistorisch Museum, Postbus 9517, NL-2300 RA Leiden, The Netherlands (donovan@naturalis.nnm.nl); Philip Crabb, Photographic Unit, The Natural History Museum, Cromwell Road, London, SW7 5BD, England (P.Crabb@nhm.ac.uk); David J. Gladwell, Department of Geology, University of Leicester, Leicester, LE1 7RH, England (djg15@leicester.ac.uk).

Key words – Echinoderms, Silurian, British Isles, echinoids, asteroids, ophiuroids, cystoids, ophiocystioids.

The Palaeozoic echinoderms of the British Isles are most diverse in the Silurian and Lower Carboniferous. This guide discusses and illustrates members of all major groups of echinoderms, apart from the crinoids, from the Silurian of these islands. Groups considered include the echinoids (five taxa), ophiuroids (ten taxa) and asteroids (thirteen taxa), and the extinct ophiocystioids (three species) and rhombiferan cystoids (nine species).

Contents

Introduction	27
Systematic palaeontology	28
Acknowledgements	46
References	46
Appendix	48

Introduction

In the Palaeozoic of the British Isles, echinoderms are most diverse in the Silurian and Lower Carboniferous. Silurian echinoderms from these islands are best known from the Much Wenlock Limestone Formation (Wenlock), but well-preserved specimens are also locally common in the Lower (Llandovery) and Upper Silurian (Ludlow). These echinoderms have never been documented together and hence remain known only to the few conversant with a widely disseminated literature. This is the first of two guides to the Silurian echinoderms of the British Isles, in which we aim to produce a usable document for field identification and illustrating most genera. By publishing in this format, we hope to encourage collectors to slip a copy of the guide into their pocket whenever they visit the field; we encourage laminating the pages, or at least plates, in plastic to protect them from the elements.

Crinoids are particularly diverse and will form the subject of the second guide. Herein, we consider all other echinoderm groups, mainly free-living (eleutherozoans), including familiar taxa such as echinoids, asteroids and ophiuroids, but also those extinct

oddities the ophiocistioids, and one non-crinoid pelmatozoan (stalked) group, the rhombiferan cystoids. Despite the geographical focus for the figured specimens, many of the genera considered herein have a wide distribution in Europe, North America and elsewhere. Use of this guide requires a basic knowledge of echinoderm morphology, which is available from most undergraduate textbooks and the references listed herein. A glossary of some of the specialist terms is appended (see Appendix). We have also minimised overlap with the forthcoming guide to the Upper Llandovery stelleroids of the Pentland Hills (Gladwell, in press), which considers the taxa from this site in considerably more detail.

Echinoderms are considered in the order shown on the four plates. Unless stated otherwise, taxa are from the Middle Silurian (Wenlock), Much Wenlock Limestone Formation at Dudley, West Midlands (Worcestershire). Localities and horizons listed herein were discussed in detail in Aldridge *et al.* (2000). All illustrated specimens are in the collections of The Natural History Museum, London (BMNH). Many of the species considered in this guide belong to monospecific genera. Table 1 summarises the stratigraphic distribution of the taxa considered herein.

Systematic palaeontology

Echinoids

Remarks – Silurian echinoids are rare globally, but are best known from the British Isles (Kier, 1973). Palaeozoic echinoids are invariably ‘regular’ (Pl. 1, figs. 1, 2; Fig. 1) and were epifaunal in habit. The ambulacra can range up to about 20 columns per ray and the interambulacra have up to 32 columns of polygonal plates per ray. Lanterns of Silurian and later Palaeozoic echinoids are well-developed (Pl. 1, fig. 3), and in general resemble those of post-Palaeozoic echinoids, though they are low angled in comparison with later examples (Smith, 1984). This would have enabled the echinoid to use the lantern as a scoop, in addition to grazing or biting. Perignathic girdles are absent in Lower Palaeozoic echinoids. The tests of many Palaeozoic echinoids had imbricate plating and consequently were flexible. However, as they were held together solely by soft tissues, they tended to fall apart soon after death. Specimens which are more complete probably underwent rapid burial, and commonly are preserved crushed and flattened. Unlike the ophiocistioids (see below), echinoids lack podial appendages, but bear robust spines. See also Jackson (1912) and Kier (1973).

Aptilechinus caledonensis Kier

Fig. 1.

Description – Test ooidal, with narrow ambulacra composed of two columns, each plate bearing a primary tubercle. Pore pairs uniserial, close to perradial suture, piercing ambulacral plates. Interambulacra about twice the width of ambulacra, with four columns of large, thin, strongly imbricated plates. Radioles of ambulacra short, but robust; radioles almost absent from interambulacra. Lantern well developed.

Locality and horizon – Upper Llandovery, Gutterford Burn Starfish Bed, North Esk Inlier, Pentland Hills, Scotland.

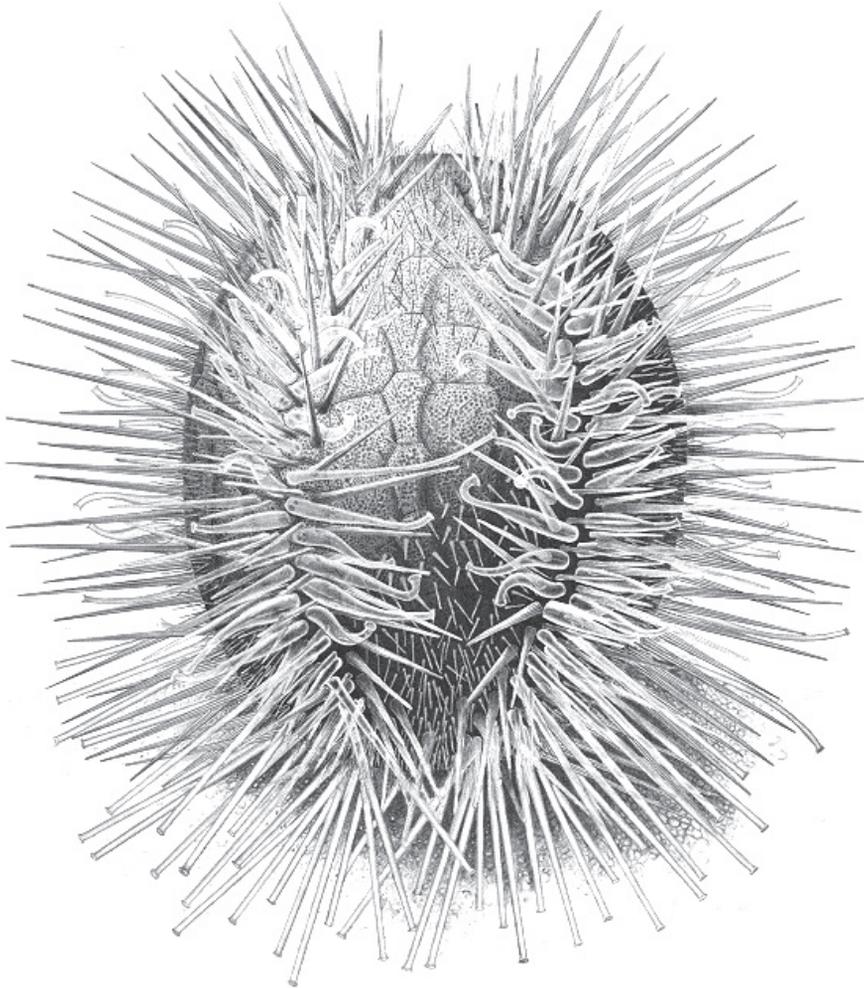


Fig. 1. *Aptilechinus caledonensis* Kier, reconstruction in lateral view (after Kier, 1973, text-fig. 4). Height of test approximately 20 mm.

Remarks – Type species of *Aptilechinus*.

***Echinocystites pomum* Wyville Thomson**

Pl. 1, fig. 1.

Description – Test subspherical, with narrow ambulacra in four columns composed of primary plates, demiplates and occluded plates which alternate with the primary plates. Pore pairs biserial and approximately central. Interambulacra wide, with about eight columns of very irregular, thin plates bearing small perforate primary tubercles and secondary tubercles. Radioles small. Lantern well developed.

Locality and horizon – Upper Ludlow, Lower Leintwardine Formation of Church Hill Quarry, Leintwardine, Herefordshire.

Remarks – Type species of *Echinocystites*.

***Myriastiches gigas* Sollas**

Description – Test large, sac-like, with narrow ambulacra in two(?) columns of small plates. Pore pairs uniserial, close to perradial suture. Interambulacra very broad, with more than 32 columns of small, scale-like, imbricate plates in regular columns. Radioles short, tubercles not apparent. Lantern apparently well-developed.

Locality and horizon – Probably Lower Ludlow (Lister & Downie, 1967), locality unknown.

Remarks – Type species of *Myriastiches*. Sollas (1899, p. 700) noted that the scale-like nature of the interambulacral plating gave the crushed and flattened test a ‘fish-like’ quality.

***Palaeodiscus ferox* Salter**

Pl. 1, fig. 2.

Description – A subspherical, flexible echinoid composed of thin, imbricating plates; the apical disc has five ocular plates and five genital plates. Ambulacra each have two columns of polygonal plates with flanges that almost enclose the radial water vessel; plating simple, with undifferentiated uniserial pore pairs. Interambulacra have many columns of small plates with sparse, irregularly spaced tubercles which have fine, hair-like radioles. Peristome small with ambulacral plates extending over it.

Locality and horizon – Upper Ludlow, Lower Leintwardine Formation of Church Hill Quarry, Leintwardine, Herefordshire.

Remarks – Type species of *Palaeodiscus*.

***Lepidocentrus?* sp.**

Pl. 1, fig. 3.

Description – A large, low lantern with shallow angled pyramids, shallow foramen magnum and short, stout rotulae. Epiphyseal suture with an irregular, but unpitted surface. Epiphyses slender.

Remarks – Jackson (1912) assigned this specimen to *Lepidocentrus* or a closely related taxon in spite of there being no associated test material.

Ophiuroids

Remarks – Modern asterozoans can be conveniently divided into the asteroids (sea

stars or starfishes) and the ophiuroids (brittle stars). The most obvious distinctions between extant members of these groups are that the ophiuroids have a circular, central disc and thin flexible arms arising from it, whereas asteroids have thicker arms which appear to abut their neighbours directly and which do not arise individually from a central disc. However, in the Lower Palaeozoic the distinction between the gross morphology of the two groups is commonly less clear, particularly where some characters normally associated with asteroids are present in specimens together with features normally found in ophiuroids (e.g., compare Fig. 2A and B). Additional features which are of more use in characterising Palaeozoic ophiuroids include having muscular arms which are supported mainly by four ambulacral ossicles per 'segment', and internal radial water vessels and podia which are not equipped with suction cups. See also Spencer (1914-1940), Owen (1965), Spencer & Wright (1966), Dean (1999) and Gladwell (2005, in press).

Stuertzaster marstoni (Salter)

Pl. 1, fig. 4; Fig. 2B.

Description – Arms petaloid with rounded tips, composed of stout plates, biserial, with the two columns of ambulacral ossicles alternating. Ambulacral ossicles with T-shaped adoral (=ventral) ridges. Lateral arm plates elongated and flattened, with marginal, saddle-shaped extensions. There are slender spines on the arms which are longer

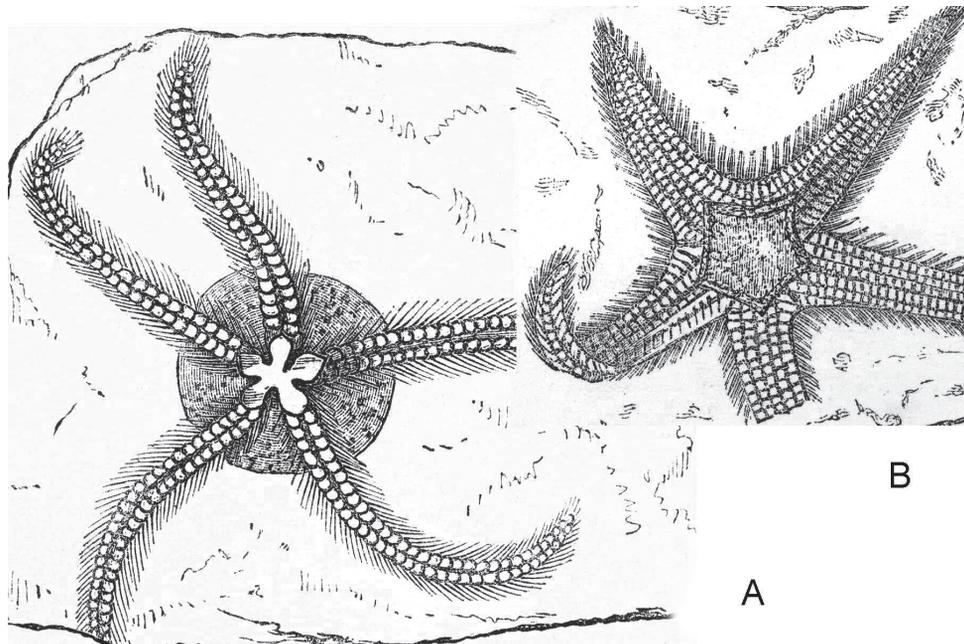


Fig. 2. Contrasting British Silurian ophiuroids. (A) *Lapworthura miltoni* (Salter) (after Taylor, 1885, fig. 111). (B) *Stuertzaster marstoni* (Salter) (after Taylor, 1885, fig. 114).

than a lateral arm plate. Radial water vessel within an open perradial groove. Disc large, swollen and forms a wide U-shape between the arms, reaching tips of arms on aboral surface. Madreporite not known (but large in related *Stuertzaster colvini* (Salter)). Disc composed of a very loose meshwork of triradiate ossicles with intervening space presumably occupied by soft tissue. Mouth angle plates short.

Locality and horizon – Upper Ludlow, Lower Leintwardine Formation of Church Hill Quarry, Leintwardine, Herefordshire.

Remarks – Type species of *Stuertzaster*. A second species from the same locality, *S. colvini*, has relatively narrower arms with a distally closed ambulacral channel, a more spinose disc and a narrower mouth.

***Rhopalocoma pyrotechnica* Salter**

Pl. 1, fig. 5.

Description – Body flat with pentagonal outline and short, blunt arms. Ambulacral ossicles alternating with adoral (ventral) L-shaped ridge. Lateral plates sub-ventral with a row of spines along oral margin and with adoral T-shaped ridge; sub-lateral plates well exposed and wide, articulating with laterals by ball and socket joints. Podial basins wide and shallow, shared between successive ambulacrals. Ambulacral grooves wide. Disc has large oral interrays with cylindrical marginals bearing large club-shaped spines. Mouth angle plates elongate. Madreporite large and circular; marginal and interradial in position.

Locality and horizon – Upper Ludlow, Lower Leintwardine Formation of Church Hill Quarry, Leintwardine, Herefordshire; Ludlow(?), Lake District, Westmorland.

Remarks – Type species of *Rhopalocoma*.

***Bdellacoma vermiformis* Salter**

Description – An ophiuroid with very long, separated arms and a disc so small that the arms appear to be joined at the proximal ends. Arms have long, thin spines which are grooved and expand slightly distally. There are also thick, squat pedicellariae irregularly spaced along the radius and each side of it. Pedicellariae bivalved, rounded subtriangular with process on either disto-lateral corner. Ambulacral ossicles alternating and with adoral T-shaped ridge. Podial basins large and shallow, shared between successive ambulacrals. Inner lateral plates narrow and almost hidden by outer lateral plates. Mouth angle plates prominent with narrow ridges along the interradial edges; spines also present along ridges. Madreporite large.

Locality and horizon – Upper Ludlow, Lower Leintwardine Formation of Church Hill Quarry, Leintwardine, Herefordshire.

Remarks – Type species of *Bdellacoma*.

Crepidosomea wenlocki Spencer

Fig. 3.

Description – Disc large, almost circular, bordered by three prominent marginal ossicles in each interradius. In aboral view, the central ossicle is shaped like an hourglass, flanked by two ossicles with a S and Z shape. Arms long and slender, finely drawn out towards tip. Ambulacral ossicles alternating, cylindrical and long aborally (= dorsally), with perradial triangular ridge adorally (ventrally). Lateral arm plates large and wide dorsally; boot-shaped ventrally. Mouth frame petaloid. Mouth angle plates small.

Locality and horizon – Upper Llandovery, Gutterford Burn Starfish Bed, North Esk Inlier, Pentland Hills, Scotland.

Remarks – Type species of *Crepidosomea*.

Urosoma hirudo (Forbes)

Description – Similar to *C. wenlocki*, but lacking a marginal frame to the weakly calcified disc. Disc extending to about the eighth segment of the arms and with con-

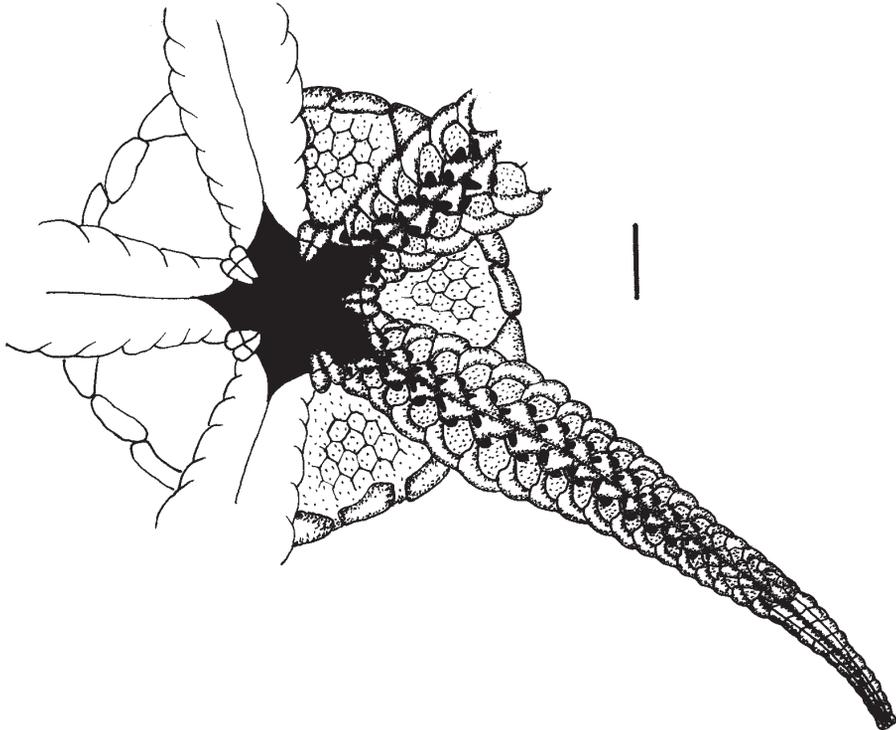


Fig. 3. *Crepidosomea wenlocki* Spencer; partial restoration of oral surface based on Spencer (1930, text-fig. 277). Scale bar represents 1 mm.

cave margins. Mouth frame strong. Arms petaloid, widest proximally, tapering in the more distal half, up to 10 mm long in largest specimens. Ambulacral ossicles alternating and with ventral perradial triangular ridge. Lateral arm plates ventrally boot-shaped.

Locality and horizon – Ludlow, Bannisdale Slates, Potters Fell and High Thorns, near Kendal, Westmorland.

Remarks – Type species of *Urosoma*.

Loriolaster sp. nov.

Pl. 1, fig. 7.

Description – Slender arms tapering to whip-like extremities. Biserial, with two columns of ambulacral ossicles alternating. Ambulacral ossicles boot-shaped ventrally, cylindrical dorsally. Well-developed gaps for the inter-ossicle muscles. Lateral arm plates very elongate and L-shaped. Radial water vessel enclosed by ambulacral plates, but there are no dorsal or ventral arm plates. Disc very large, forming a wide U-shaped area between the arms and almost reaching their tips. There are no large plates visible. Jaw frame is V-shaped.

Locality and horizon – Upper Ludlow, Lower Leintwardine Formation of Church Hill Quarry, Leintwardine, Herefordshire. Tentatively also known from the Upper Llandovery, Gutterford Burn Starfish Bed, North Esk Inlier, Pentland Hills, Scotland.

Remarks – *Loriolaster sp. nov.* (formerly classified, erroneously, within *Loriolaster gracilis* (Ruedeman)) is distinguished from other (albeit non-British) members of this genus by the L-shaped lateral arm plates (Gladwell, 2005).

***Lapworthura miltoni* (Salter)**

Pl. 1, fig. 8; Pl. 2, fig. 1; Fig. 2A.

Description – A large ophiuroid with arms up to 100 mm long. Arms tapering gradually to fine thin tips and comprised of biserial ambulacra, with plates opposing. Ambulacral ossicles boot-shaped ventrally and hourglass-shaped to subquadrate dorsally. Lateral arm plates are boot-shaped ventrally and subtriangular dorsally, and have spines which are rather longer than the plates themselves. Radial water vessel enclosed by ambulacral plates. There are no dorsal or ventral plates present. Disc large and weakly calcified, resulting in fossils which have a disc impression rather than the plates of the disc itself. Madreporite large and crenulated. Jaw frame V-shaped and prominent. Mouth frame dorsally petaloid.

Locality and horizon – Upper Ludlow, Lower Leintwardine Formation of Church Hill Quarry, Leintwardine, Herefordshire.

Remarks – Type species of *Lapworthura*.

Protaster sedgwickii Forbes

Fig. 4.

Description – Disc rounded, lacking a marginal frame, plated by numerous small, regular, scale-like, polygonal plates of approximately equal size. Surface of disc granular. Arms long (incomplete in figure), with a comparatively narrow ambulacral groove, side shields on arms formed by lateral arm plates ‘wrapping around’. Ambulacral ossicles alternating; boot-shaped ventrally and subquadrate dorsally. Lateral arm plates boot-shaped. Spination weak, perhaps absent. Mouth angle plates elongate. Mouth frame dorsally petaloid.

Locality and horizon – Wenlock, ‘Wenlock Shales’ (Pen-y-Glog Group?), Castell-Dinas-Bran, near Llangollen, Wales; Ludlow, Kirkby Moore Formation, Docker Park, The Lake District, Westmorland; Silurian of Scotland (precise locality and horizon unknown).

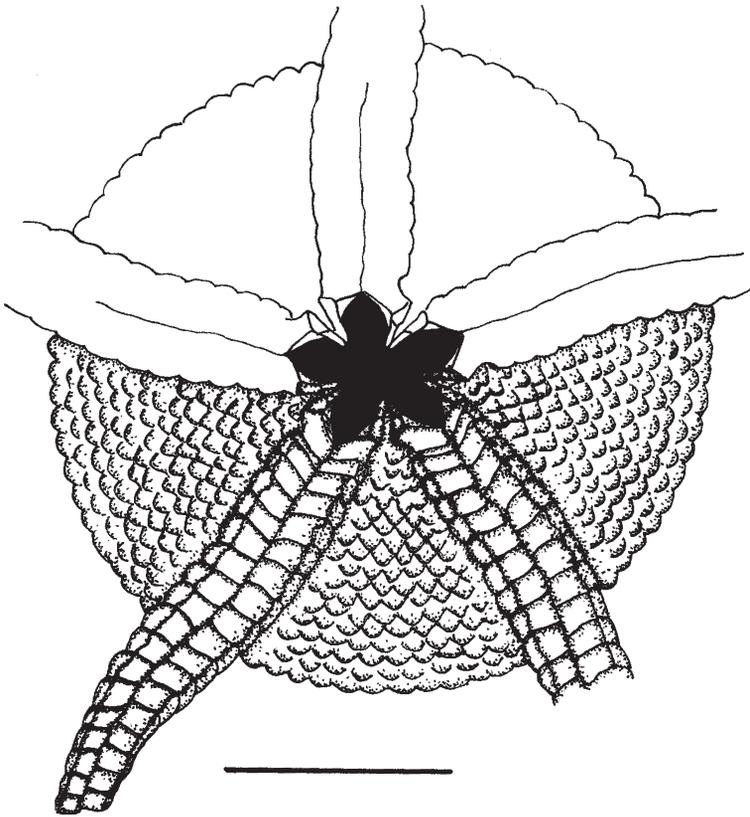


Fig. 4. *Protaster sedgwickii* Forbes, partial reconstruction of aboral surface based on Spencer (1934, text-fig. 298). Scale bar represents 5 mm.

Remarks – Type species of *Protaster*.

***Furcaster leptosoma* (Salter)**

Pl. 1, fig. 6; Pl. 2, fig. 2.

Description – Arms robust with needle-shaped spines along the sides that are parallel with the long axis of the arm. Arms tapering to whip-like extremities. Ambulacral ossicles with perradial ridge and groove dorsally; each ambulacral pair thus has a pronounced median oval ridge. Proximal-most ambulacrals may also have a transverse bifurcating ridge (in dorsal view). Ambulacral ossicles boot-shaped ventrally. Interior of lateral plates have long vertical ridges at right angles to the adoral edge. Lateral plates form prominent margin to arm ventrally. Mouth frame petaloid. Mouth angle plates elongate and rod-like.

Locality and horizon – Upper Llandovery, Gutterford Burn Starfish Bed, North Esk Inlier, Pentland Hills, Scotland; Upper Ludlow, Lower Leintwardine Formation of Church Hill Quarry, Leintwardine, Herefordshire; Ludlow, Kirkby Moor Formation, Benson Knot, Westmorland.

Remarks – Type species of *Furcaster*.

Asteroids

Remarks – Asteroids generally have relatively broad arms composed of ossicles of variable size, configuration and number, usually with some kind of marginal frame. They have an internal space to carry the water vascular system which is equipped with ampullae connected to tube feet. The tube feet are found in open ambulacral grooves on the oral side. The arms do not arise separately from a distinct central disc. See also Spencer (1914-1940), Owen (1965), Spencer & Wright (1966) and Gladwell (2005, in press).

***Eoactis simplex* Spencer**

Pl. 2, fig. 3.

Description – A small stellate starfish whose marginal frame does not reach to the end of the arms. In the axils there is a large, stout odontophore, each side of which is a flat inferomarginal in the inter-radial angles. Adambulacral plates broad and swollen, bordering a wide ambulacral groove. Ambulacral plates exposed and opposing. Mouth angle plates rounded and overlain by paired adambulacral plates. Apical surface has a covering of small plates.

Locality and horizon – Upper Wenlock or Lower Ludlow, Hafod, near Llandovery, Wales.

Remarks – Type species of *Eoactis*.

***Palasterina antiqua* (Hisinger)**

Pl. 2, fig. 4.

Description – A medium sized, pentastellate starfish with a large, strongly calcified disc separating the bases of cylindrical arms with open ambulacral groove. Ambulacral ossicles wide and with ventral L-shaped ridge; opposing proximally to alternating distally. Adambulacral plates stout, without a ridge, but with long robust spines and accessory plates alongside. Inferomarginal plates swollen and stout. Numerous irregular interradial infilling plates present. Mouth angle plates elongated, swollen and with rounded sides; odontophore appears to be absent. Madreporite large and thin. Discrete columns of plates along dorsal length of arms, including relatively prominent superomarginals.

Locality and horizon – Upper Llandovery, Gutterford Burn Starfish Bed, North Esk Inlier, Pentland Hills, Scotland; Wenlock, Much Wenlock Limestone Formation, Dudley, Worcestershire; Upper Ludlow, Lower Leintwardine Formation of Church Hill Quarry, Leintwardine, Herefordshire.

Remarks – A second species, *P. primaeva* (Forbes) from the Ludlow of the Lake District, Westmorland, has a relatively small number of plates in the interradia.

***Protactis wenlockensis* (Spencer)**

Description – A small, robust and pentastellate starfish, closely similar to *Palasterina*, best known from the oral surface. Disc composed of three radiating columns of plates, the central regular, composed of bead-like plates and tapering towards the margin, flanked by two less regular columns. Arms up to 20 mm long, with a narrow ambulacral groove, flanked by columns of robust ambulacral and adambulacral plates. Ambulacral ossicles opposing to slightly alternating and with ventral T-shaped ridge. Lateral surfaces steep. Mouth angle plates narrow and elongate, first pair of ambulacral plates forming distinct Y. Spines and madreporite not known.

Locality and horizon – Upper Llandovery, Gutterford Burn Starfish Bed, North Esk Inlier, Pentland Hills, Scotland.

Remarks – Type species of *Protactis*. The Gutterford Burn Starfish Bed was formerly considered to be Wenlock in age, but this does not explain why Spencer named this specimen *wenlockensis*, implying it came from Much Wenlock in Shropshire.

***Lepidaster grayi* Forbes**

Pl. 2, fig. 5.

Description – A starfish with up to 13 arms of semicircular section. Adambulacral plates occupy most of the oral surface and arm margins distally. The plates of the disc form a framework of closely set, wide, oblong polygonal ossicles with prominent transverse ridges proximally, on which there are spines. Proximal ambulacral plates

flat with projecting pegs which fit into sockets on preceding plates. Projecting knob articulates with adjacent ventrolateral plate. Low thin ridge for separation of tube feet is present. Articulation between plates very loose. Inferomarginals in axils of arms long and flat, becoming globular and rounded on arms. Interradial area filled with flat ventrolateral plates. Madreporite large and present in arm axil exterior to the inferomarginal plates. Mouth angle plates large, triangular, fitted with very stout torus with spine pits.

Remarks – Type species of *Lepidaster*.

***Lepidactis wenlocki* Spencer**

Pl. 2, fig. 6.

Description – A fairly small pentastellate starfish. Proximal inferomarginal plates prominent, not uniformly swollen, and ornamented by large irregular bulges. Other inferomarginal plates well developed, swollen, with pustular ornament and form a slight margin to the oral surface. Most of the oral surface formed by oblong and very convex adambulacral plates, which become smaller and more regular in shape distally. Odontophore flat, shield-shaped, with five spine-bearing ridges fanning out from the pointed proximal end. Madreporite very large, swollen, with raised markings and located entirely on the oral surface. Supero- and inferomarginal plates almost opposite. Superomarginal plates not symmetrical; those on one side being stout and robust, whereas on the other they are smaller. Ornament of radial and superomarginal plates pustular.

***Urasterella ruthveni* (Forbes)**

Pl. 2, fig. 7.

Description – A medium sized starfish with long arms of rounded cross section, parallel sided proximally, tapering gradually towards the tips. Arms rarely preserved complete. Disc small. Oral surface composed of block-like ambulacral and adambulacral plates. Ambulacrals opposing, subrectangular and wide, with no sutural gaps. Adambulacrals border a deep ambulacral groove, and each have a prominent transverse ridge and a row of spines. Dorsally along the length of the arm, there are well-defined, nodose, polygonal plates with smaller marginal plates either side. Perradial column of plates prominent (the carinals). Aboral surface has a distinct central plate which is surrounded by polygonal plates, forming the calycinal system. Mouth small. Madreporite small, oval, dorsal and interradian in position.

Locality and horizon – Upper Ludlow, Lower Leintwardine Formation of Church Hill Quarry, Leintwardine, Herefordshire; Ludlow, Kirkby Moor Formation, Lake District, Westmorland.

Remarks – Type species of *Urasterella*. A second British Silurian species, *U. gutterfordensis* Spencer from the Upper Llandovery, Gutterford Burn Starfish Bed, North Esk Inlier, Pentland Hills, Scotland, is of broadly similar morphology.

***Cocaster bulbiferus* Spencer**

Pl. 2, fig. 8.

Description – A small pentastellate starfish with a disc consisting of a centrale surrounded by five intermediate plates and ten large primary radial plates and interradial plates. Primary radial plates very swollen. Perradial column composed of the carinals, which are rounded and dorsally convex. Superomarginal plates finger-like and swollen. Inferomarginal plates less numerous than adambulacral plates, there being two inferomarginals to three adambulacrals. Adambulacrals border a deep ambulacral groove. Ambulacral plates possess a strong ridge and appear to touch over their entire length. Superomarginal plates and inferomarginal plates alternate when seen in lateral view. Slender spines present on small tubercles on a ridge on face of inferomarginal plates. Odontophore almost pentagonal, swollen, with a re-entrant angle at its base. Its sides are slightly concave where it touches the ambulacral plates. Mouth angle plates large and triangular.

Locality and horizon – Upper Ludlow, Lower Leintwardine Formation of Church Hill Quarry, Leintwardine, Herefordshire.

Remarks – Type species of *Cocaster*.

***Arisaigaster* sp.**

Pl. 2, fig. 9; Pl. 3, fig. 1.

Description – A small pentastellate starfish with a broad disc and fairly short, wide arms. Marginal plates large and blocky. Superomarginals and inferomarginals alternate along the arm length. Small intermediate ossicles separate carinal ossicles from superomarginal ossicles on the aboral surface.

Locality and horizon – Middle Silurian (Wenlock), Much Wenlock Limestone Formation, Wenlock Edge, near Much Wenlock, Shropshire, and Dudley, Worcestershire.

***Schuchertia wenlocki* Spencer**

Pl. 3, fig. 2.

Description – A small, pentastellate starfish. Apical surface covered by many small, undifferentiated paxillose plates arranged in rows. On the adoral surface the odontophore is very prominent and flat, with a curved proximal edge and the two distal edges slightly concave, coming together in a point. Proximal edge has a mouth angle plate and two adjacent ambulacral plates. Mouth angle plates high, narrow, projecting into the buccal cavity. Spines on these plates also project into the buccal cavity. The proximal two pairs of ambulacral plates are smaller than succeeding ones; none meet across the perradius. Ambulacral ossicles opposing and with ventral L-shaped ridge. Adambulacrals ventrally subtriangular, bordering a shallow ambulacral groove. Proximal inferomarginal plates large, broader than long and gently convex, becoming longer than broad and rather bulbous from about midway along the arm to the tip, swelling over to

the adapical surface. Inferomarginal plates alternate with adambulacral plates. Inter-radial disc plates polygonal and variable in number. Large, oval madreporite.

Locality and horizon – Lower Silurian (Llandovery), Gutterford Burn Starfish Bed, North Esk Inlier, Pentland Hills, Scotland.

***Taeniactis wenlocki* Spencer**

Fig. 5.

Description – Starfish with five long, spinose arms and an aboral skeleton of a disc and the bases of arms only. Apical skeleton robust, comprised of a prominent centrale surrounded by two circlets of primary plates, bearing raised pits for articulation of large spines, intercalated with numerous smaller plates. Distinct column of dorsally convex carinals along length of arm. Few irregular plates in interradial of oral surface. Ambulacral plates proximally opposing to distally alternating; near-square with a T-shaped ridge, the top adjacent to the ambulacrum and the long stem articulating with the stem of a shorter T-shaped ridge on the adambulacra, together forming a broad H. Mouth angle plates elongate and narrow, distinctly ridged where they are in contact.

Locality and horizon – Lower Silurian (Llandovery), Gutterford Burn Starfish Bed, North Esk Inlier, Pentland Hills, Scotland.

Remarks – Type species of *Taeniactis*.

***Lepyriactis nudus* Spencer**

Description – Aboral skeleton reduced and not seen. Disc pentagonal. Arms five, long, with narrow adambulacrals and an arrangement on T-shaped ridges on adjacent ambulacrals-adambulacrals reminiscent of *Taeniactis*. Ambulacral ossicles with wide ambulacral channel. Ambulacral groove wide and shallow. Mouth angle plates elongate, narrow; proximal ambulacrals with a deep radial V.

Locality and horizon – Lower Silurian (Llandovery), Gutterford Burn Starfish Bed, North Esk Inlier, Pentland Hills, Scotland.

Remarks – Type species of *Lepyriactis*.

Rhombiferan cystoids

Remarks – All specimens are glyptocystitid rhombiferans. Rhombiferans have rhombic sets of respiratory canals (= rhombs), with half of each set occurring on two adjacent plates (Kesling, 1967). The column is xenomorphic and holomeric. The proxistele is almost as wide as the theca, but conical, tapering rapidly distally with flanged, annular columnals; the long dististele is homeomorphic and consists of cylindrical columnals. Rhombiferans are differentiated from crinoids by the distinctive structure of the column, the respiratory structures of the pill-like theca and the lack of true (and branched) arms. See also Paul (1967a, b, 1971).

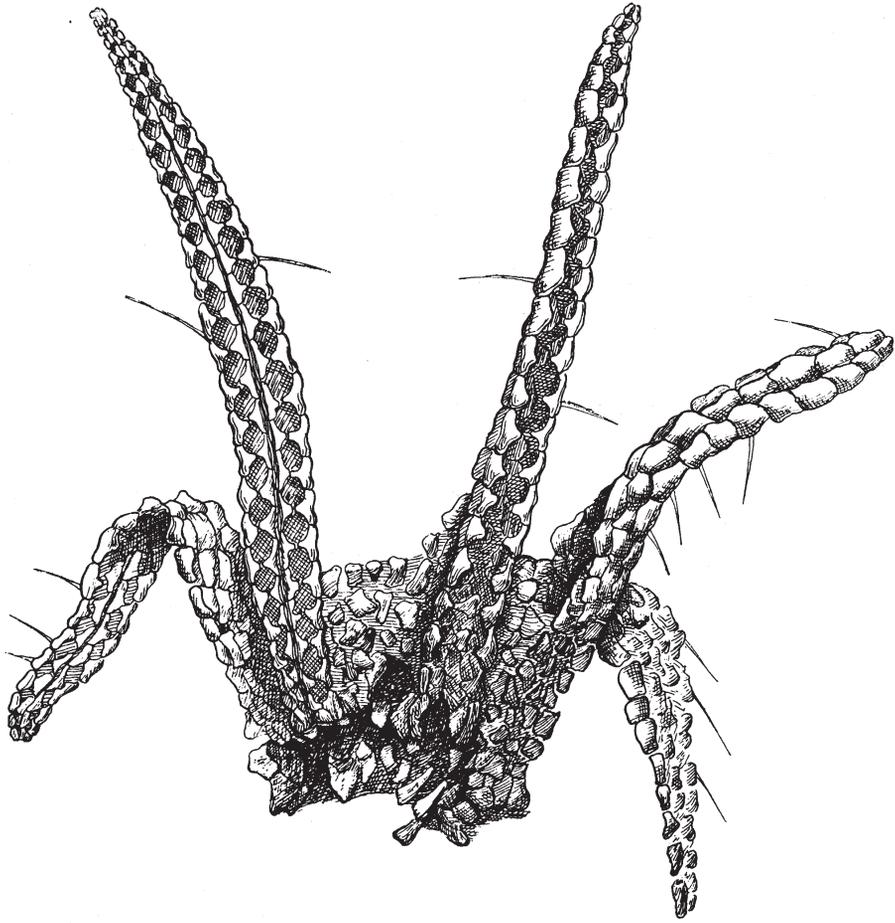


Fig. 5. *Taeniactis wenlocki* Spencer, specimen with arms flexed ventrally to the disc; arms about 15 mm long (after Spencer, 1927, text-fig. 245).

***Prunocystites fletcheri* Forbes**

Pl. 3, fig. 3.

Description – Theca small and ovate, composed of four basal, five infra-lateral, five lateral, five radial and an unknown number of oral plates, bearing two disjunct pectinirhombs. Radial circlet broken by lateral L5 extended orally. Four(?) short ambulacra confined to apex. Periproct bordered by four plates, bearing anal pyramid. Brachioles long, five to ten in number. Mouth presumed apical, gonopore and hydropore unknown. All known specimens are small and imperfectly preserved.

Remarks – Type species of *Prunocystites*.

***Schizocystis armata* (Forbes)**

Pl. 3, figs. 4, 5.

Description – Theca sac-like, ovate aborally, somewhat laterally compressed adorally, composed of four basal, five infra-lateral, five lateral, five radial and seven oral plates, bearing two or three disjunct pectinirhombs. Two short ambulacral grooves extend from summit (Pl. 3, fig. 5b, d, e), irregularly branched and with five brachiole facets in total. Periproct strongly protruding, bordered by four plates, bearing anal pyramid. Hydropore a curved slit, adjacent gonopore a circular hole. The type species, *S. armata*, seems to show two distinct forms, with either two or three pectinirhombs, although they probably are not sexual dimorphs.

Locality and horizon – *Schizocystis armata* occurs at a number of sites in the Middle Silurian Wenlock shales in the Lower Palaeozoic inliers of the Welsh borderlands.

Remarks – Type species of *Schizocystis*. The closely related *Glansicystis baccata* (Forbes), from the Middle Silurian Much Wenlock Limestone Formation of Dudley and Walsall, has the radial circlet interrupted by L5, three pectinirhombs and a more pyriform theca.

***Osculocystis monobrachiolata* Paul**

Pl. 3, figs. 6, 7.

Description – Theca small, oval, composed of four basal, five infra-lateral, five lateral, five radial and an uncertain number of very reduced oral plates, with three disjunct pectinirhombs. The single brachiole is long and slender. Periproct lateral, surrounded by four plates. The mouth and gonopore are small and apical, separated by the prominent, nearly dumb-bell shaped hydropore.

Locality and horizon – Upper Llandovery (Telychian) Hughley Shales at Devil's Dingle, Buildwas, Shropshire.

Remarks – Type species of *Osculocystis*.

***Apiocystites pentrematoides* Forbes**

Pl. 3, figs. 8, 9.

Description – Theca ovate and 'plum-shaped', rounded in section, composed of four basal, five infra-lateral, five lateral, five radial and seven oral plates, with three small pectinirhombs. Four long ambulcra, extending over theca to column. Periproct small, surrounded by three or four plates. Mouth elongate and gently curved. Hydropore semi-circular, slit-like, close to circular gonopore, both close to mouth.

Remarks – Type species of *Apiocystites*.

***Tetracystis oblongus* (Forbes)**

Pl. 3, figs. 10, 11.

Description – Theca elongate, subquadrate, composed of four basals, five infra-laterals, five laterals and four radials, with three disjunct pectinirhombs. Radial circlet broken by lateral L5 extended orally. Four broad, prominent ambulacra with wide main food grooves extending to column. Brachioles relatively widely spaced. Periproct lateral, depressed, surrounded by four plates. The inconspicuous gonopore and hydropore, and the slit-like mouth are all apical in position.

***Staurocystis quadrifasciata* (Pearce)**

Pl. 3, fig. 12; Pl. 4, figs. 1, 2.

Description – Theca ovate to subovate, with a sub-octagonal outline in oral view produced by protuberant ambulacra. Theca composed of four basal, five infra-lateral, five lateral, five radial and seven oral plates, bearing three disjunct pectinirhombs. Theca bearing four long unbranched ambulacra extending to the column. Brachioles closely spaced. Mouth not seen, presumed oral. Hydropore dumb-bell shaped, hard against small circular gonopore, both oral. Periproct small, bearing an anal pyramid, bordered by three plates and the corner of a fourth.

Locality and horizon – Middle Silurian (Wenlock), Much Wenlock Limestone Formation at Dudley, West Midlands (Worcestershire) and Walsall (Staffordshire). The commonest cystoid in this unit.

Remarks – Type species of *Staurocystis*.

***Pseudocrinites bifasciatus* Pearce**

Pl. 4, figs. 3, 4.

Description – Theca lensoid, biconvex, rounded in outline, composed of four basals, five infra-laterals, five laterals and five radials, bearing three disjunct pectinirhombs. Two ambulacra at periphery of theca, commonly extending to the column. Brachiole facets closely spaced. Hydropore, gonopore, and narrow, curved mouth all oral. Periproct lateral, surrounded by four plates.

Remarks – Type species of *Pseudocrinites*. A second British species, *P. pyriformis* Paul, differs from *P. bifasciatus* in having shorter ambulacra that do not reach the column and having a pyriform (pear-like) outline with a narrow base. *Pseudocrinites pyriformis* is only known in the Upper Silurian (Ludlow) Sedgley Limestone of Sedgley, Staffordshire.

Ophiocistioidea

Remarks – Ophiocistioids are an extinct group of free-moving, five-rayed, dome-shaped echinoderms which have a plated box-like structure, probably with large tube-

feet, but without arms or brachioles. The body may be completely enclosed by plates or it may have plates on one side only and an integument which may or may not be armoured with thin calcite. The oral and aboral surfaces are very different in appearance, with variations in the plating of the aboral surface being either irregular or approximately radial in organisation. The symmetry in most known genera is pentaradiate, with five radial ambulacral areas of three columns of plates which terminate at the margin, five narrow interradial interambulacral areas and five groups of tube feet. There is a buccal armature forming jaws in the centre of the oral surface, composed of five pairs of interradial plates. The anus is present either on the aboral surface or at the margin. See also Ubaghs (1967).

Eucladia johnsoni Woodward

Pl. 4, fig. 5.

Description – The test is weakly five-lobed and has a flat or gently convex oral surface grading into an arched aboral surface, though the aboral surface itself is not known. Peristome central and circular; madreporite and probable gonopores on the oral surface in the interray position. Opposing ambulacral pores alternating very slightly in position around the peristome. Plated podial appendages cylindrical and hollow, directly homologous with tube feet, but very much larger. The first pair are smaller than the five succeeding pairs, which slightly alternate. Jaws well-developed.

Locality and horizon – Upper Silurian (Lower Ludlow) Limestone of Sedgley, Staffordshire.

Remarks – Type species of *Eucladia*.

Sollasina woodwardi (Sollas)

Pl. 4, fig. 6.

Description – Test elliptical, low domed. Elliptical peristome central with strong jaws. Aboral surface composed of many thin, irregularly polygonal or circular plates which are smooth or have tiny scattered granules. Periproct present on aboral border. Radial areas of oral surface perforated by double rows of circular holes which are probably ambulacral pores; additionally, an unpaired pore is located at the aboral-most end of the ambulacrum. Peristome has a circlet of five perradial plates, ten interradial plates, and an additional plate with a conical tubercle containing the madreporite and probably a single gonopore. There are also single pores which correspond to the position of the buccal tentacles or tube feet. Three pairs of slightly opposed tube feet along each ambulacrum and one single, perradial tube foot at the extreme aboral end of the ambulacrum, close to the margin.

Locality and horizon – Upper Silurian (Upper Ludlow), Church Hill, Leintwardine, Herefordshire.

Remarks – Type species of *Sollasina*.

Euthemon ignera Sollas

Fig. 6.

Description – Test pentagonal with a central, circular peristome with five strong jaws. Aboral surface composed of few large plates. Buccal apparatus robust, buccal armature consisting of five large, triangular, interradial plates. Peristome surrounded by a circlet of at least fifteen plates, five single perradial and ten, paired interradial plates. Each ambulacrum comprised of three perradial and perhaps three lateral adradial plates, supporting the appendages. Two pairs of podial appendages symmetrically arrayed along each ambulacrum, a longer pair flanked by two shorter individuals.

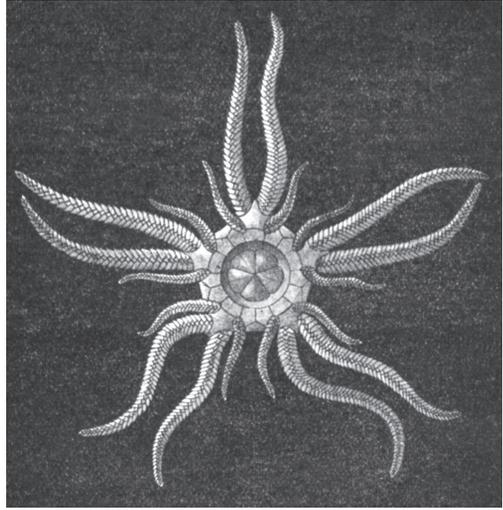


Fig. 6. *Euthemon ignera* Sollas, reconstruction of oral surface (after Sollas, 1899, fig. 4). Diameter over podia about 38 mm.

Locality and horizon – Wenlock, Much Wenlock Limestone Formation, Croft Farm, Malvern district, Herefordshire.

Remarks – Type species of *Euthemon*.

Acknowledgements

The copyright of this publication is retained by the parent institutions of the authors. We thank the Palaeontological Association for permission to reproduce Figure 1. Paul Jeffery (Oxford University Museum of Natural History) gave invaluable assistance in ascertaining the antiquity of *Myriastiches gigas*. Reviews of an earlier incarnation of this paper by Chris Paul and Charlotte Jeffery (both University of Liverpool) are gratefully acknowledged. Incisive reviews by Professors Johnny A. Waters (Appalachian State University, Boone, North Carolina) and Colin D. Sumrall (University of Tennessee, Knoxville) are gratefully acknowledged.

References

- Aldridge, R.J., Siveter, David J., Siveter, Derek J., Lane, P.D., Palmer, D. & Woodcock, N.H. 2000. *British Silurian Stratigraphy*. Joint Nature Conservation Committee, Peterborough: xviii+542 pp.
- Dean, J. 1999. What makes an ophiuroid? A morphological study of the problematic Ordovician stelleroid *Stenaster* and the palaeobiology of the earliest asteroids and ophiuroids. *Zoological Journal of the Linnean Society*, **126**: 225-250.
- Gladwell, D.J. 2005. *The Biota of Upper Silurian Submarine Channel Deposits, Welsh Borderland*. Unpublished Ph.D. thesis, University of Leicester: 189 pp.
- Gladwell, D.J. (in press). Stelleroids. In: Clarkson, E.N.K., Harper, D.A.T., Anderson, L. & Taylor, C. (eds), *Fossils of the Pentland Hills*. Palaeontological Association Field Guides to Fossils.

- Jackson, R.T. 1912. Phylogeny of the Echini, with a revision of the Paleozoic species. *Memoirs of the Boston Society for Natural History*, **7**: 490 pp.
- Kesling, R.V. 1967. Cystoids. In: Moore, R.C. (ed.), *Treatise on Invertebrate Paleontology, Part 5, Echinodermata* **1** (1): S85-S267. Geological Society of America & University of Kansas Press, New York & Lawrence.
- Kier, P.M. 1973. A new Silurian echinoid genus from Scotland. *Palaeontology*, **16**: 651-663.
- Lister, T.R. & Downie, C. 1967. New evidence for the age of the primitive echinoid *Myriastiches gigas*. *Palaeontology*, **10**: 171-174.
- Owen, H.G. 1965. The British Palaeozoic Asterozoa. Table of contents, supplement and index. *Monograph of the Palaeontographical Society, London*, **118** (505): xii+541-583.
- Paul, C.R.C. 1967a. The British Silurian cystoids. *Bulletin of the British Museum (Natural History)*, Geology, **13**: 299-355.
- Paul, C.R.C. 1967b. *Osculocystis*, a new British Silurian cystoid. *Geological Magazine*, **104**: 449-454.
- Paul, C.R.C. 1971. A second specimen of *Osculocystis* Paul 1967. *Geological Magazine*, **107**: 383-387.
- Smith, A.B. 1984. *Echinoid Palaeobiology*. George Allen & Unwin, London: xii+191 pp.
- Sollas, W.J. 1899. Fossils in the University Museum, Oxford: I. On Silurian Echinoidea and Ophiuroidea. *Quarterly Journal of the Geological Society, London*, **55**: 692-715.
- Spencer, W.K. 1914-1940. A monograph of the British Palaeozoic Asterozoa. *Monograph of the Palaeontographical Society, London*, (1) 1914, **67** (328 for 1913): 1-56; (2) 1916, **69** (335 for 1915): 57-108; (3) 1918, **70** (338 for 1916): 109-168; (4) 1919, **71** (342 for 1917): 169-196; (5) 1922, **74** (349 for 1920): 197-236; (6) 1925, **76** (356 for 1922): 237-324; (7) 1927, **79** (366 for 1925): 325-388; (8) 1930, **82** (376 for 1928): 389-436; (9) 1934, **87** (394 for 1933): 437-494; (10) 1940, **94** (420): 495-540.
- Spencer, W.K. & Wright, C.W. 1966. Asterozoans. In: Moore, R.C. (ed.), *Treatise on Invertebrate Paleontology, Part 4, Echinodermata* **3** (1): U4-U107. Geological Society of America & University of Kansas Press, New York & Lawrence.
- Taylor, J. E. 1885. *Our Common British Fossils and Where to Find Them. A Handbook for Students*. Chatto & Windus, London: xii+331 pp.
- Ubaghs, G. 1967. Ophiocistioids. In: Moore, R.C. (ed.), *Treatise on Invertebrate Paleontology, Part 5, Echinodermata* **1** (1): S174-S188. Geological Society of America & University of Kansas Press, New York & Lawrence.

Appendix: Glossary of morphological terms

Echinoidea

- ambulacra* – five rays of the test, radial in position, formed of pored plates which support the radial water vessel and associated tube feet.
- apical disc* – a group of plates at the apex of the test, divided into five ocular plates at the top of each ambulacral zone, and up to five genital plates, interradial in position, and through which the gonads open via genital pores. The disc may also include additional plates.
- biserial* – two columns of plates or two apparent columns of pores.
- column* – a series of plates in a vertical sequence.
- demiplate* – an ambulacral plate that is in contact with the adradial suture, but not the perradial suture.
- epiphyseal suture* – the suture between the epiphysis and the demipyramid of a lantern.
- epiphysis* – the component more or less fused on the proximal end of a demipyramid.
- foramen magnum* – the ‘U’-shape formed between the two demipyramids of a lantern.
- genital plate* – plate of the apical disc which has one or more pores for the discharge of genital products.
- imbricate plating* – overlapping plates that are able to move over one another.
- interambulacra* – five areas of the test that lie between the five ambulacra.
- lantern* – the jaw mechanism of an echinoid made of about 40 components.
- occluded plate* – an ambulacral plate that is in contact with the perradial suture, but not the adradial suture.
- ocular plate* – one of the five radial plates of the apical disc.
- perforate* – the hole in a tubercle and a radiole. The hole has a supporting rod inserted into it in life.
- perignathic girdle* – the attachment structure for the muscles of the lantern. This may be continuous or discontinuous.
- peristome* – the aperture in the test which surrounds the mouth and which is covered in life by a membrane.
- perradial suture* – plate suture at centre of a biserial ambulacrum.
- pore pairs* – the holes in ambulacral plates through which pass the tube feet.
- primary plate* – an ambulacral plate that extends from the perradial to the adradial suture.
- primary tubercle* – the main tubercle of an ambulacral or interambulacral plate which articulates with a primary radiole.
- pyramid* – a component of the lantern (or jaws), composed of two demipyramids.
- radial water vessel* – the internal water tubes that are radial in position and which supply the ampullae and hence the tube feet.
- radiole* – a spine.
- regular* – a test that has the appearance of radial symmetry, with the mouth on the lower surface and the anus within the apical disc.
- rotula* – a component of the lantern that is ambulacral in position and serves as a brace. There are five of these.

secondary tubercles – tubercles that surround a primary tubercle or which are situated elsewhere on the test.

test – the ‘shell’ of an echinoid.

uniserial – a single column of plates or pore pairs.

Ophiuroidea

aboral surface – the surface opposite the mouth and ambulacral grooves; also dorsal.

adoral surface – the surface with the mouth.

ambulacral channel – perradial channel between ambulacral ossicles (also seen in asteroids).

ambulacral ossicles – the ossicles that make up the axial skeleton.

biserial – two columns of ambulacral ossicles, sometimes alternating.

disc – central part of the ophiuroid distinctly separate from the arms.

inner lateral plates – inner series of plates along the sides of an arm.

inter-ossicle muscles – muscles between the ossicles that control the flexing of an arm.

interradial – the position between two radial areas.

lateral arm plates – plates along the sides of an arm.

madreporite – a multi-perforate plate which serves as an inlet for water to the water vascular system.

marginals – ossicles along the margins of the body; may be infero- (lower surface) or supero- (upper surface).

mouth angle plates – prominent ossicles that project into the mouth and form as a pair.

oral inter-rays – the area between two rays on the oral surface.

outer lateral plates – outer series of plates along the sides of an arm.

perradial groove – groove on the oral side of an arm (=ambulacral channel).

petaloid – shaped like a petal.

podia – tube feet.

radial, radius – ambulacral in position. This can refer to various ossicles and organs.

sub-lateral plates – plates in primitive ophiuroids which lie between an ambulacral and lateral plate.

Asterozoa

accessory plate – an ossicle that is not part of the primary structure.

adambulacral – an ossicle that is adjacent to an ambulacral ossicle.

adoral – towards the oral surface or mouth.

ambulacral plate – an ossicle of the axial skeleton.

ambulacral groove – a groove along the oral surface of an arm.

ampulla – the dorsal internal part of a tube foot that when contracted by muscles causes the tube foot to extend. It is linked to the radial water vessel.

apical surface – the surface opposite the mouth.

axil – the angle formed at the junction of straight-sided arms. There are no inter-brachial areas.

buccal cavity – the internal cavity that forms part of the mouth.

- carinal* – ossicle in series along dorsal surface of arm in perradial position. In line with the primary radius.
- centrale* – a prominent plate in the centre of the aboral surface of the starfish.
- inferomarginal plate* – the larger series of marginal plates along the oral surface of the arms and the disc.
- interradial* – the position between two radial areas.
- madreporite* – a multi-perforate plate which serves as an inlet for water to the water vascular system.
- marginal frame* – the main ossicles forming the framework of the starfish.
- mouth angle plates* – prominent ossicles that project into the mouth and form as a pair.
- odontophore* – a single axillary plate found at the distal end of two mouth angle plates.
- oral* – the surface that contains the mouth.
- ossicles* – individual component plates of the body.
- pentastellate* – five-rayed; shaped like a star.
- perradial* – next to the radius.
- spine pits* – depressions in an ossicle which bore spines.
- stellate* – star-like or star-shaped.
- superomarginal plates* – the upper series of marginal plates.
- sutural gaps* – wider than normal gaps between plates for the passage of tube-feet.
- torus* – a flat ossicle that projects into the mouth from the mouth angle plate. It may carry a spine.
- tube feet* – the external extensions of the ampullae which are protruded when the ampullae are contracted.
- water vascular system* – water-filled canals that are linked together, and which include the calcified stone-canal, the ring canal, the radial canals, ampullae and tube feet.

Cystoids

- ambulacrum* – radial area of the theca extending down (=aborally) from the mouth. It has a narrow food groove along the mid-line, joined by side food grooves.
- basals* – lowermost plate circlet of the theca, where column attached, supporting the infra-laterals.
- brachiole* – erect, unbranched feeding structure, arising from an ambulacrum.
- column* – elongate, jointed structure that supports the theca.
- dististele* – distal column.
- gonopore* – opening through which eggs and sperm are released.
- holomeric* – column in which the constituent columnals are each composed of a single calcite plate.
- hydropore* – external opening of the water vascular system in the theca.
- homeomorphic* – a column composed of columnals of identical morphology.
- infra-lateral* – second plate circlet above the base of theca, supported by basals and supporting laterals.
- lateral* – third plate circlet above the base of theca, supported by infra-laterals and supporting radials.
- monospecific* – a genus comprised of a single known species.
- oral* – topmost plate circlet of theca, encircling the mouth.

pectinirhomb – rhombic sets of respiratory canals (=rhombs), with half of each set occurring on two adjacent plates.

periproct – opening in the theca for the anus.

proxistele – proximal column.

radial – fourth plate circlet above the base of theca, supported by laterals and supporting orals.

theca – capsule, supported by the column and in turn supporting the brachioles, enclosing the visceral mass and composed of up to five circlets of plates (which may include basals, infra-laterals, laterals, radials and orals).

xenomorph – column which is divided into two or more morphologically distinct regions.

Ophiocistioidea

adradial plates – plates on the oral surface, flanking the perradial plates of the ambulacrum.

ambulacral pores – perforations for the tube feet in radial area of oral surface.

buccal armature – part of the jaw mechanism, having five pairs of interradial plates, somewhat like the demipyramids of echinoid lanterns.

buccal tentacles – podial appendages associated with the jaw plates.

gonopore – pore for the passage of reproductive products.

integument – a plated membrane.

interradial plates – plates between the radii or ambulacral areas.

pentaradiate – five-rayed.

peristome – position of the mouth.

perradial plates – plates along the radius or ambulacral areas.

podial appendages – large structures which are probably homologous to the tube feet of other echinoderms.

Plate 1

Echinoids (Figs. 1-3) and ophiuroids from the Silurian of the British Isles.

Fig. 1. *Echinocystites pomum* Wyville Thomson, BMNH E34352.

Fig. 2. *Palaeodiscus ferox* Salter, BMNH 40307.

Fig. 3. *Lepidocentrus?* sp., BMNH E12206, Aristotle's lantern.

Fig. 4. *Stuertzaster marstoni* Salter, BMNH E2590.

Fig. 5. *Rhopalocoma pyrotechnica* Salter, BMNH 40293.

Fig. 6. *Furcaster leptosoma* (Salter), BMNH E20243.

Fig. 7. *Loriolaster* sp. nov., BMNH 38527.

Fig. 8. *Lapworthura miltoni* (Salter), BMNH E20232.

All specimens coated with ammonium chloride for photography. All natural moulds except Figure 3. Scale bars represent 10 mm.

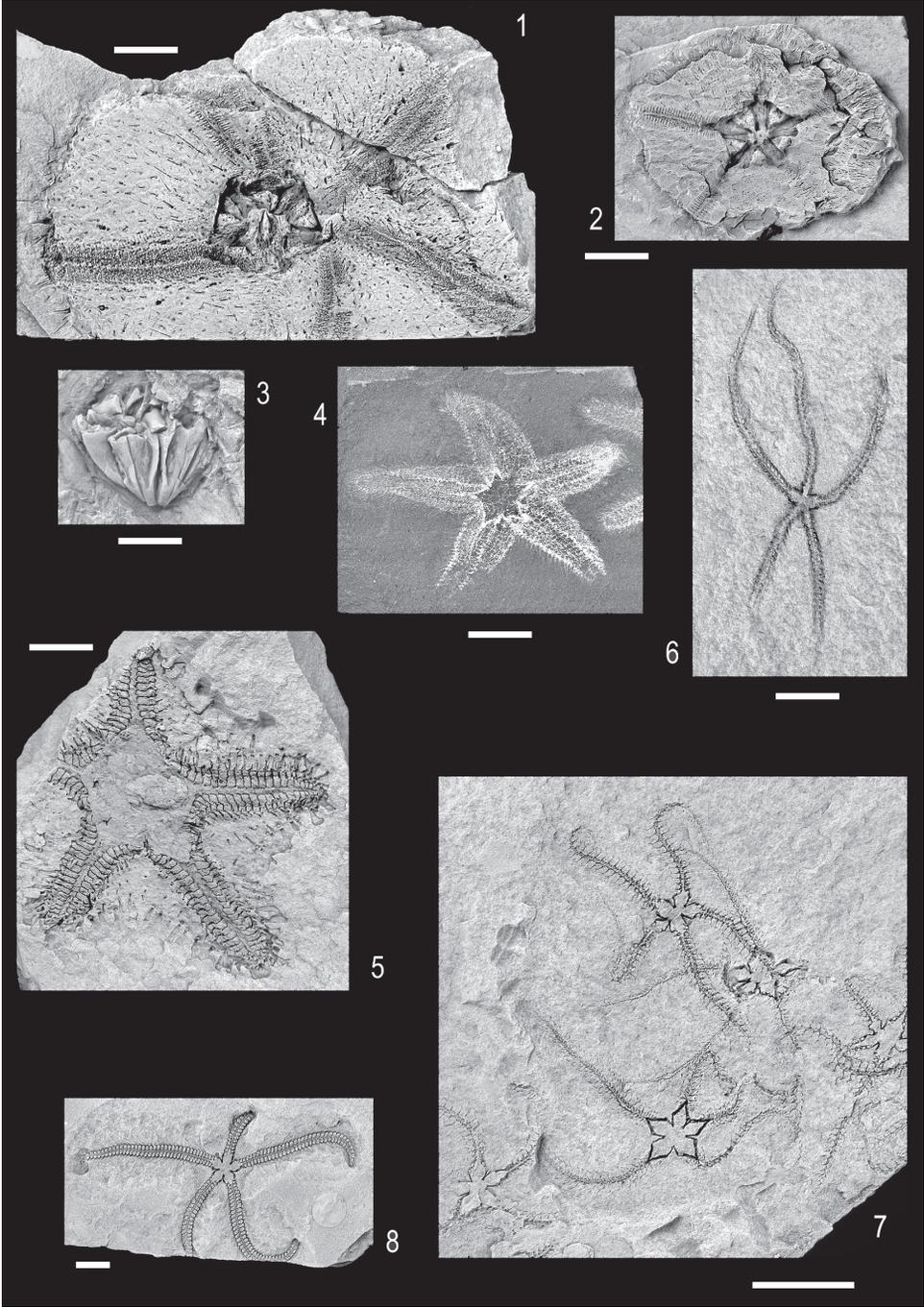


Plate 2

Ophiuroids (Figs. 1, 2) and asteroids from the Silurian of the British Isles.

Fig. 1. *Lapworthura miltoni* (Salter), BMNH E20231.

Fig. 2. *Furcaster leptosoma* (Salter), BMNH E20260.

Fig. 3. *Eoactis simplex* Spencer, BMNH E13154.

Fig. 4a, b. *Palasterina antiqua* (Hisinger), BMNH 40299a, b, respectively (part and counterpart external moulds).

Fig. 5. *Lepidaster grayi* Forbes, BMNH 40215.

Fig. 6. *Lepidactis wenlocki* Spencer, BMNH 57426.

Fig. 7. *Urasterella ruthveni* Forbes, BMNH E13952.

Fig. 8. *Cocaster bulbiferus* Spencer, BMNH E13956.

Fig. 9. *Arisaigaster* sp., BMNH E53614.

All specimens coated with ammonium chloride for photography. All natural moulds except Figures 5, 6 and 9. Scale bars represent 10 mm.

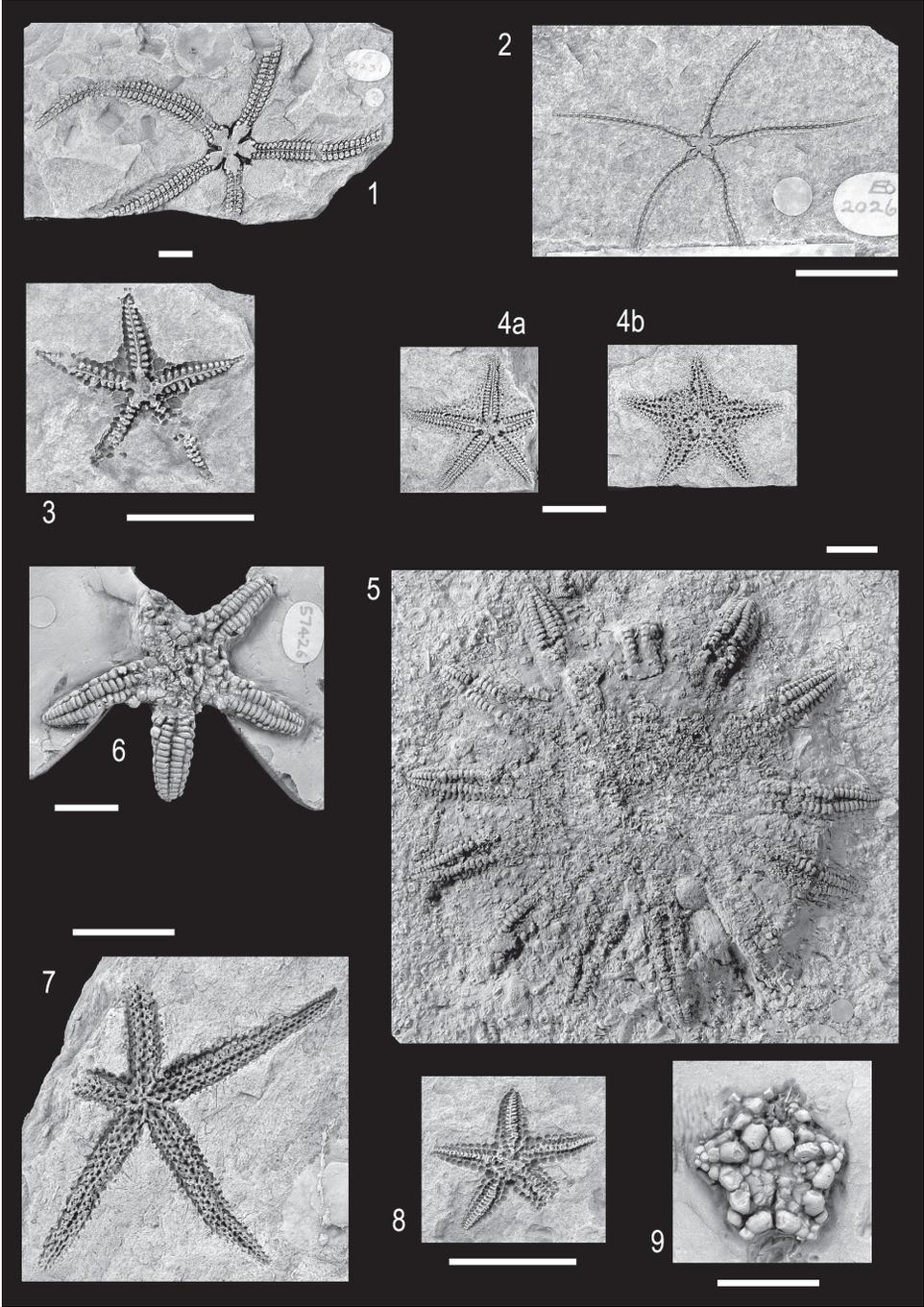


Plate 3

Asteroids (Figs. 1, 2) and rhombiferan cyctoids from the Silurian of the British Isles.

Fig. 1. *Arisaigaster* sp., BMNH 13572, artificial cast.

Fig. 2. *Schuchertia wenlocki* Spencer, BMNH E13585.

Fig. 3. *Prunocystites fletcheri* Forbes, BMNH 57395, theca and column.

Figs. 4, 5. *Schizocystis armata* (Forbes). (4) BMNH 57442, theca and column. (5) BMNH E7590, theca and proxistele in lateral (a-d) and oral views (e).

Figs. 6, 7. *Osculocystis monobrachiolata* Paul. (6) BMNH E29328, theca and proxistele in lateral (a-d) and oral views (e). (7) BMNH E29281, theca and column.

Figs. 8, 9. *Apiocystites pentremoides* Forbes. (8) BMNH 47830, theca and column. (9) BMNH E29074, theca and proxistele in lateral (a-d) and oral views (e).

Figs. 10, 11. *Tetracystis oblongus* (Forbes). (10) BMNH 57437, theca and column. (11) BMNH 57379, theca and proxistele in lateral (a-d) and oral views (e).

Fig. 12. *Staurocystis quadrifasciata* (Pearce), BMNH 48197, theca and proxistele in lateral (a-d) and oral views (e).

All specimens coated with ammonium chloride for photography. Scale bars represent 10 mm.

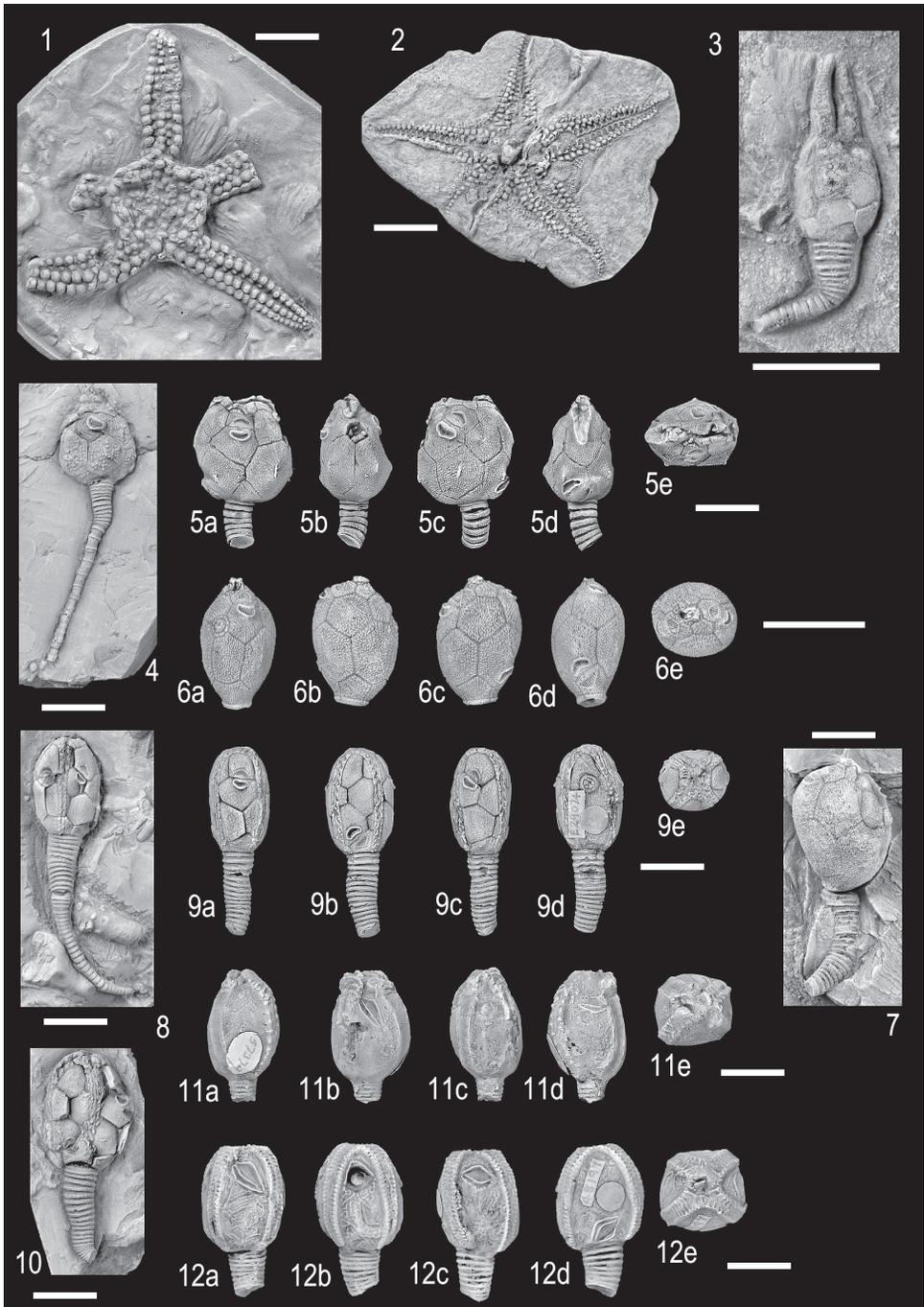


Plate 4

Rhombiferan cystoids (Figs. 1-4) and ophiocistioids from the Silurian of the British Isles.

Figs. 1, 2. *Staurocystis quadrifasciata* (Pearce). (1) BMNH E7512, theca retaining brachioles. (2) BMNH 46745, theca and column.

Figs. 3, 4. *Pseudocrinites bifasciatus* Pearce. (3) BMNH 40193, theca and proxistele in lateral (a-d) and oral views (e). (4) BMNH E1460, theca and column.

Fig. 5. *Eucladia johnsoni* Woodward, BMNH E1444, oral surface.

Fig. 6. *Sollasina woodwardi* (Sollas), BMNH E27030a, b, aboral surface, natural mould.

All specimens coated with ammonium chloride for photography. Scale bars represent 10 mm.

