RARE AND PROBLEMATICAL TAXA FROM THE MUCH WENLOCK LIMESTONE FORMATION

by

LIAM GEORGE HERRINGSHAW

Thesis submitted to
The University of Birmingham
for the degree of
DOCTOR OF PHILOSOPHY

School of Geography, Earth and Environmental Sciences
University of Birmingham
September 2003

Pages 0 to 60
Title page, introductory matter, Chapters 1-4

Chapters 5-8, References and Appendix are in two additional files

ABSTRACT

The Much Wenlock Limestone Formation (Silurian: Wenlock, Homerian) of England and Wales contains a diverse invertebrate fauna including many rare and problematical taxa. This study investigates the palaeobiology and palaeoecology of five such groups: asteroids (starfish), the crinoid *Calyptocymba mariae* gen. et sp. nov., rostroconch molluscs, machaeridians and cornulitids. Six species of asteroids are recognized, including three new forms (*Palasterina orchilocalia* sp. nov., *Hudsonaster? carectum* sp. nov., and *Doliaster brachyactis* gen. et sp. nov.), that show a diverse range of morphologies. Most distinctive is the 13-rayed *Lepidaster grayi* Forbes, 1850, the oldest known multiradiate starfish. The variety of asteroid body shapes indicates a diversification of behaviour, particularly feeding strategies. By functional convergence, *L. grayi* is interpreted as an active predator. *C. mariae* is an unusual species of camerate crinoid, with a small, thinly plated calyx. This, combined with its slender body morphology, is interpreted as an adaptation to life in a low energy environment. Four rostroconch taxa [*Mulceodens aedicula* sp. nov., *M? aequicostatus* (Phillips, 1848), *M. latus* sp. nov., and *Redstonia sima* sp. nov.] occur, and are interpreted as mobile, semi-infaunal, deposit feeders. Differences between *Mulceodens* and *Redstonia* probably reflect adaptations by closely related taxa to specific environments, with *Mulceodens* living in higher energy conditions, rather than indicating that they belong to separate families as has been suggested previously. Machaeridians are problematical taxa having elongate bodies covered with serially repeated calcitic sclerites, and three species – *Turrilepas wrightiana* (de Koninck, 1857), *Lepidocoleus ketleyanus* (Reed, 1901) and *L? extraplax* sp. nov. – are recognized in the Much Wenlock Limestone Formation. By analysis of their body morphology, skeletal structure and growth pattern, machaeridians are interpreted here as molluscs, probably the sister group of Polyplacophora + Conchifera. Using a similar approach, *Cornulites* is interpreted as a stem group anthozoan. *Cornulites* species show various life positions: *C. scalariformis* Vine, 1882, attached itself to live brachiopods, with its aperture positioned close to the host's feeding currents, *C. gremialis* formed clusters growing upon one another, and *C. cellulosus* was solitary and unattached.

APOLOGIES

I have encountered so many splendid people during my stint in Britain's second city that I cannot even begin to try and acknowledge them all. So, instead, I wish to apologize to those whom I have caused particular trouble.

First and foremost I apologize to my family, particularly Mum and Dad, for being 26, unemployable, and still living at home. One day I shall be able to repay all I owe you.

Secondly, I apologize to my supervisors, Alan Thomas and Paul Smith, for being virtually unsupervisable and taking so long to write a few thousand words about a load of fossil oddballs. I now realize that organization is nothing without a bit of self-discipline.

I apologize to my sub-Great Hall cellmates, Paul, Gareth and Sandy, for my incessant playing of strange compilation tapes, although the full 10 minutes 43 seconds of Bob Dylan's 'Sad Eyed Lady Of The Lowlands' is an education in itself. I would apologize to those in office 116 too, but Julian's predilection for The Carpenters is far, far worse than anything of mine.

I apologize to Banksy, Mike, Toby, Gerwyn, Cath, Lauren, Paul and Carl for never doing any cleaning or washing up. Similarly, I apologize to Alan, Louise, Ivan, Bill and Phil, who had to put up with similar in Pembrokeshire. Talking of which, I apologize to all those undergrads whose burgeoning geological careers were derailed by my erratic demonstrating. There probably are whirlpool structures in the rock record somewhere, just not Wiseman's Bridge.

I apologize to Jemma, Lucy, Dan, Marguerite, Alice and the rest of the LapSoc posse for never getting round to doing the Christmas/Easter/Summer show I so regularly promised. The world shall now never see 'Ken Thomson's School Days' or hear the palaeontological version of 'I Will Survive'. I also apologize to Alexia, Pete, T-Bray, Ger and the late* Philip Edward Hall for involving them in so many hare-brained schemes for taking over the media world. [*- not dead, just always late]

I apologize to Messrs Clatworthy, Mullen, Clarke, Sumner, Blum, Bunch, Wilson, Walker, Rees and Haacke for all the footballing debacles (but not the cricketing successes). Now, if only we could get Mr. Holford to play…

I apologize to all the museum curators (including Jon) whose fossils I kidnapped. You can have them back now.

And last, but certainly not least, I apologize to all the palaeo [and honorary palaeo] girls, especially Kate, Jo, Eithne, Aruna, Rosie, Laura, Jane, and Miss Tucker (again), for being so much better than they at gossip and idle chatter. It won't be the same without you all to distract, disturb and annoy.

I do not apologize to Neil, as it was all his own fault.

A COLLECTOR

My finds,
But they will scatter them again
To the four winds
As soon as I am dead.

Old gadgets,
Fossilized plants and shells,
Coloured postcards, books,
Broken dolls.

And all the words
That I have found.
My incomplete,
My unsatisfied words.

(Erich Fried, 1921-1988, Translated from the German)

Ein Sammler

Meine Funde
Aber sie werden sie wieder
Zerstreuen in alle vier Winde
Wenn ich erst tot bin.

Alte Geräte
Versteinerte Pflanzen und Tiere
Bunte Postkarten Bücher
Zerbrochene Puppen

Auch alle Worte
Die ich gefunden habe
Meine unvollständigen
Meine ungesättigten Worte

CONTENTS LIST

CHAPTER ONE

INTRODUCTION

THE Much Wenlock Limestone Formation (Silurian: Wenlock) of the English Midlands and Welsh Borderlands is among the most celebrated of palaeontological horizons, with specimens of its diverse fauna found in almost every geological collection worldwide. More than 600 species of invertebrates have been described, with much of the finest material coming from the inliers in and around the town of Dudley (Text-fig. 1.1). However, despite two centuries of study, the fauna includes many taxa that are poorly described and little understood. Given the quality and quantity of fossils present, the Much Wenlock Limestone Formation provides a unique opportunity to examine Silurian marine ecosystems, but this can only be achieved by including the rare and problematical species in the unit, as well as the well-understood taxa, such as brachiopods (see e.g. Bassett 1972; Ratcliffe 1991) bryozoans (Snell 2002), crinoids (Widdison 2002) and trilobites (Thomas 1978, 1981; Siveter 1996). Furthermore, the high quality preservation of the fauna enables the skeletal structure and growth of the problematical taxa to be studied in detail, and thus their zoological affinities to be reassessed. Given the significance of stem-group taxa to our understanding of early metazoan evolution and diversification of body plans, such opportunities are of major palaeobiological significance.

The fossils dealt with here include both rare and problematical taxa from the Much Wenlock Limestone Formation. They were selected on the grounds of having been very rarely or never previously described (Asteroidea, chapters 2 and 3; Rostroconchia, chapter 5), being particularly unusual forms of well-known groups (Crinoidea, chapter 4), or being of particularly problematical affinities (Machaeridia, chapter 6; *Cornulites*, chapter 7). A number of other problematical taxa occur in the formation, most notably carpoids, conulariids, receptaculitids and tentaculitids, but these are not considered in detail here. Carpoids have been the subject of much recent discussion, with the one species from the Much Wenlock Limestone Formation – *Placocystites forbesianus* de Koninck – examined by both Jefferies and Lewis (1978) and Ruta (1998). Conulariids, receptaculitids and tentaculitids from the formation have not been reviewed in recent years, but the groups as a whole have. Conulariids are now regarded as cnidarians most closely related to scyphozoans (Van Iten 1991; Jerre 1993, 1994*a*, 1994*b*; but see Babcock and Feldmann 1986; Babcock 1991 for alternative interpretation), whilst receptaculitids, of which one key taxon (*Ischadites*
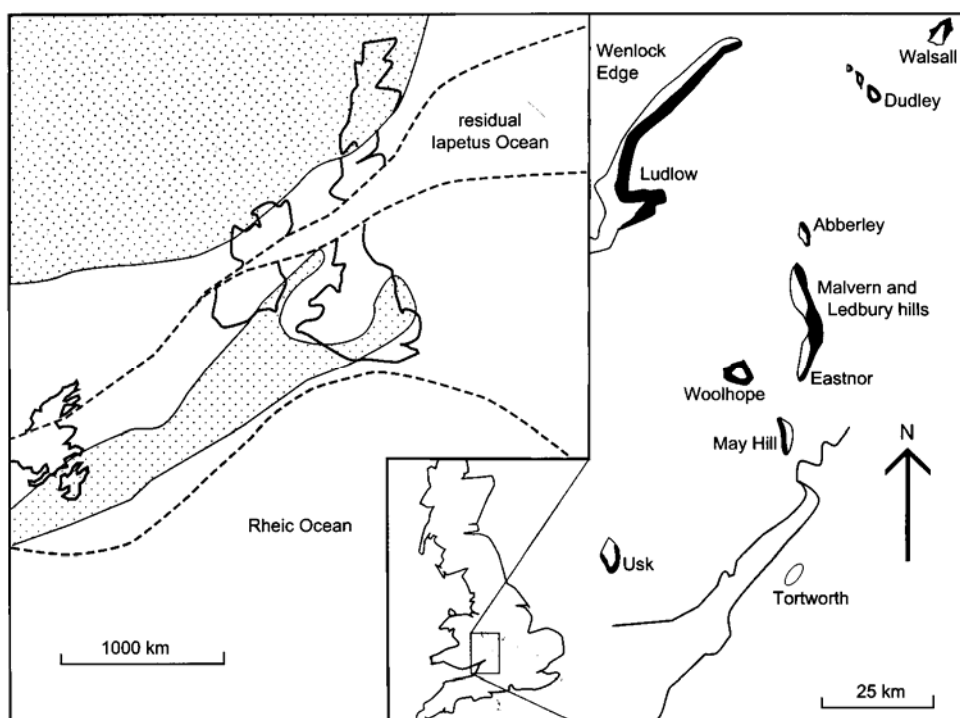
TEXT-FIG. 1.1. Palaeogeography of UK during the Wenlock (stippled areas indicate land), with map of outcrops of Much Wenlock Limestone Formation (from Ratcliffe and Thomas 1999).

koenigii Murchison) is present in the formation, are generally interpreted as dasycladacean algae (Nitecki *et al*. 1999). The affinities of tentaculitids are uncertain (see discussion in chapter 7), but Larsson (1979*a*) provided a comprehensive review of the group's diversity, ontogeny and ecology based on material from the Silurian of Gotland.

1.1 GEOLOGICAL SETTING

Surface outcrops of the Much Wenlock Limestone Formation occur in a number of places across the English Midlands and Welsh Borderlands (Text-fig. 1.1). The most significant areas are the extensive outcrops on Wenlock Edge and the Ludlow Anticline, where the top of the formation coincides with the Wenlock-Ludlow boundary (Lawson and White 1989), and Dudley, where three inliers (Text-fig.) have yielded many of the finest palaeontological specimens. The term 'Wenlock Limestone' was first used in print by Murchison (1833), who noted the faunal and lithological similarities between the limestones of Wenlock Edge and those of Dudley. It is now apparent that the limestones were laid down diachronously, with deposition beginning in the West Midlands before it did on Wenlock Edge (Bassett 1974, 1976; Dorning 1983; Ratcliffe and Thomas 1999), but all recent workers have regarded the

limestones of Dudley and Wenlock as part of the same unit, the Much Wenlock Limestone Formation, rather than as separate stratigraphical units.

At the time of deposition, the English Midlands and Welsh Borderlands were around 15º south of the Equator, part of the microcontinent of Eastern Avalonia, which lay on the southern margin of the closing Iapetus Ocean (Woodcock 2000). The Much Wenlock Limestone Formation was laid down in shallow marine conditions on the Midland Platform, with deeper water out in the Welsh Basin. Water depth was not constant during limestone deposition, and this is reflected in the number of lithofacies seen in the formation. In the Much Wenlock area, Bassett (1989) recognized reef and off-reef tracts, with four lithofacies in the former and three in the latter. The three off-reef lithofacies – tabular limestone, nodular limestone, and pelmatozoan limestone (see Bassett 1989, fig. 36) – correspond broadly with the lithofacies in the West Midlands described by Ratcliffe and Thomas (1999). There, the formation is divided into three members (Lower Quarried Limestone, Nodular Beds, and Upper Quarried Limestone), within which there are four laterally persistent lithofacies. In stratigraphical order, they are: thick bedded oncolite-rich lithofacies, nodular limestone lithofacies, interbedded limestone and silty mudstone lithofacies, and crinoidal grainstone lithofacies (Ratcliffe and Thomas 1999). The environments of deposition were interpreted by Ratcliffe and Thomas (1999) and are discussed in greater detail in the appendix, but the overall pattern is one of shelf sedimentation between storm and fair weather wave-base to begin with, a slight deepening prior to deposition of the nodular limestone lithofacies, followed by a regression that led ultimately to shallow-water (above fair weather wave-base), high energy conditions of the crinoidal grainstone lithofacies.

1.2 PROVENANCE AND PRESERVATION OF FOSSILS

All specimens examined in this study are from museum collections, and very few have detailed information concerning horizon and exact locality. For palaeoecological purposes, it is important to be able to combine the functional morphology of the organism with lithological data, so thin sections of the matrix from a variety of specimens were made and examined petrographically. This enabled direct comparison with the lithologies described in previous studies of the Much Wenlock Limestone Formation (e.g. Butler 1939; Bassett 1989; Ratcliffe and Thomas 1999). The results are described in the Appendix.

Similarly, relatively little is known about the taphonomy of the fauna. No examples of soft-tissue preservation are known, but many organisms with skeletons formed of individual plates (e.g. asteroids, crinoids and machaeridians) are found partly or wholly articulated, indicating that they were rapidly buried whilst alive or soon after death. Horizons

containing such specimens are generally interpreted as storm-generated obrution deposits (Thomas and Smith 1998), but the concentration and preservation of fossils varies between lithofacies and the precise burial mechanisms have never been examined in detail. The topic is discussed in chapter 8 (see also Appendix), but further taphonomic studies are required.

1.3 AIMS AND OBJECTIVES

The overall objective of the project is to provide new palaeobiological and palaeoecological information on various rare and problematical taxa from the Much Wenlock Limestone Formation, using the following methods:

- Investigation of the diversity of asteroids in the unit;
- Examination of the likely origin and ecological significance of supernumerary rays in *Lepidaster grayi* Forbes, 1850, the first multiradiate starfish;
- Morphological and palaeoecological study of aberrant crinoids;
- Assessment of the diversity and functional morphology of Wenlock rostroconchs;
- Ascertaining the likely systematic position of machaeridians via examination of skeletal microstructures and growth patterns;
- Examining the diversity and autecology of Silurian cornulitids;
- Comparative investigation of the shell structures of cornulitids.

CHAPTER TWO

ASTEROIDS FROM THE SILURIAN OF ENGLAND

ABSTRACT. Although their record extends back to the early Ordovician, the occurrence of fossil starfish (Echinodermata: Asteroidea) is dependent almost exclusively upon horizons of exceptional preservation. Thus, asteroids found in Silurian obrution deposits of the English Midlands and Welsh Borderlands are particularly significant to an understanding of the early diversity of the group. Six species are described here: *Lepidaster grayi* Forbes, 1850, *Lepidactis wenlocki* Spencer, 1918, *Siluraster*? *ketleyi* (Spencer, 1916), *Palasterina orchilocalia* sp. nov and *Doliaster brachyactis* gen. et sp. nov, from the Much Wenlock Limestone Formation, and *Hudsonaster*? *carectum* sp. nov., from the Lower Elton Formation. *L. grayi* is the earliest multiradiate taxon known, whilst *D. brachyactis* is the first asteroid to show the short-rayed body form of extant cushion stars. Combined with the extremely long rays seen in *L. wenlocki*, this indicates that, by the early Silurian, starfish were exploiting a similar variety of feeding habits and ecological niches to living taxa.

Abundant in modern seas, starfish have an extremely uneven distribution in the geological record. From the first unequivocal examples in the Tremadoc (495 Ma), fossil asteroids are limited almost exclusively to event beds. This is true of many echinoderms, as their bodies are composed of individual calcite plates (ossicles) held together by soft tissue that rapidly decays after death, causing the ossicles to separate and disperse on the sea floor. In the case of vagile epifaunal echinoderms such as starfish, a sudden and quite substantial influx of sediment is thus required to bury the animal whilst it is still alive or very recently deceased, in order for complete preservation to occur (see Goldring and Stephenson 1972). Additionally, there is considerable variation in the preservation potential of different species of asteroid, demonstrated by LeClair (1993) as being primarily dependent on two factors – the arrangement of soft tissues holding the ossicles together, and the environment in which the starfish lived.

Obrution horizons in the Much Wenlock Limestone Formation of the English Midlands and Welsh Borderlands, particularly those of Wren's Nest and Castle Hill, Dudley, have yielded numerous species of echinoderms. Crinoids are the most varied and abundant, with 56 species known (Widdison 2002). Thirteen fossil asteroids have been found, belonging to five species, listed alphabetically as follows: *Doliaster brachyactis* gen. et sp. nov., *Lepidactis wenlocki* Spencer, 1918, *Lepidaster grayi* Forbes, 1850, *Palasterina orchilocalia* sp. nov. and *Siluraster*? *ketleyi* (Spencer, 1916). Additionally, a species -

Hudsonaster? *carectum* sp. nov. – is described that is of uncertain provenance, possibly the Much Wenlock Limestone Formation, but more probably the overlying Lower Elton Formation (see below, and Appendix for further discussion). These make up the total asteroid fauna from the British Wenlock, although a small number of specimens of the ophiuroid *Lapworthura* sp. (J. Dean, pers. comm. 1999) have been found in the Nantglyn Flags Group (Upper Sheinwoodian-Homerian) of Llanrwst, North Wales, and there are two further asterozoans – *Eoactis simplex* Spencer, 1916 and *Urosoma hirudo* (Forbes, 1848) – with specimens of possible Wenlock age.

This scarcity of material is prevalent throughout the British Silurian – the Llandovery has only one locality, Gutterford Burn in the Pentland Hills near Edinburgh, from which more than a single starfish has been found, and the Ludlow only two, the Upper Leintwardine Formation of Church Hill, Leintwardine, Herefordshire, and the Bannisdale Slates around Kendal, Cumbria. The specimens from Gutterford Burn were originally described as being of Wenlock age (Peach and Horne 1899; Spencer 1916, 1919, 1922, 1927) and new species such as *Taeniactis wenlocki* Spencer, 1922 and *Protactis wenlockensis* Spencer, 1922 were named on that basis, but subsequent work (Lamont 1947, Robertson 1989) has shown the rocks to be of Upper Llandovery (Telychian) age.

Forbes (1848) produced the first work on asteroids from the British Silurian, which also constituted the first publication on asterozoans from the Palaeozoic of the UK, the specimens coming from the Ludlow rocks of Cumbria. Silurian starfish were well documented during this early period, with Forbes (1848, 1849*a*, 1849*b*, 1850) and Salter (1857) naming fifteen species. Forbes concentrated his efforts primarily on material from the Lake District and Salter on Leintwardine specimens; the erection of *Lepidaster grayi* by Forbes (1850) was the first description of an asteroid from the Much Wenlock Limestone Formation. However, in the century and a half that has followed, virtually nothing has been published on starfish from the Wenlock, and relatively little on Silurian asterozoans in general. Indeed, until Spencer's monograph (1914-40), only two specimens had been described from the Much Wenlock Limestone Formation, one being Forbes' holotype of *Lepidaster grayi*, the other *Trichotaster plumiformis* Wright, 1873. The latter fossil, despite being the only example, was not figured by Wright in either 1873 or 1880 and had vanished by the time of Spencer (1918). Salter (1873, p. 129) recorded 'two fine large specimens' of *Lepidaster grayi* from the Fletcher Collection of the Geological Museum, Cambridge University, but neither was described or figured.

Seven new Wenlock asteroid specimens were described by Spencer (1916, 1918, 1922), consisting of four additional examples of *Lepidaster grayi*, the first British Wenlock
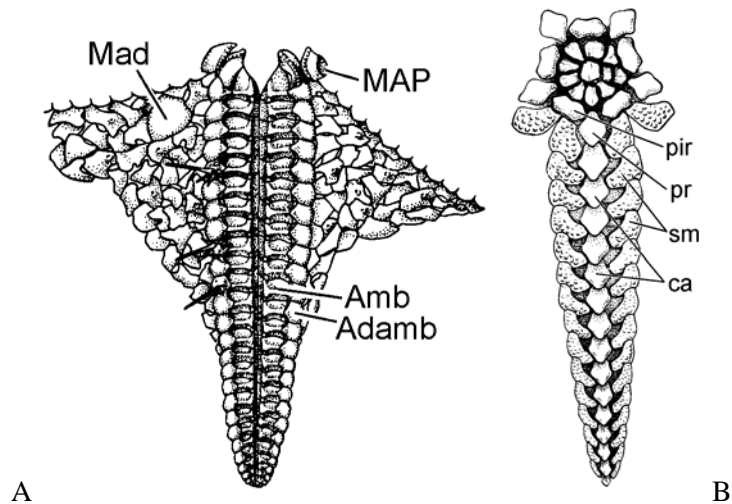
TEXT-FIG. 2.1. General asteroid terminology, from Spencer and Wright (1966). A, oral surface, showing ambulacral (Amb) and adambulacral (Adamb) ossicles, madreporite (Mad), and mouth-angle plates (MAP); B, aboral surface, showing carinal (ca), primary inter-radial (pir), primary radial (pr) and supero-marginal ossicles (sm).

specimen of *Palasterina antiqua* (Hisinger, 1837) and one each of two new species, *Mesopalaeaster? ketleyi* Spencer, 1916 and *Lepidactis wenlocki* Spencer, 1918. Subsequently, there have been no further descriptions of Wenlock starfish from the UK.

Since Spencer's death in 1954 a number of new asteroid specimens from the Much Wenlock Limestone Formation have come to light, including the first from Wenlock Edge. In order to compare these finds with previously known material, it has proved necessary to review Spencer's monograph and re-examine his interpretations and conclusions.

2.1 SYSTEMATIC PALAEONTOLOGY

Institutional abbreviations. The specimens listed below come from the collections of the Lapworth Museum, University of Birmingham (specimen numbers prefixed with BU); the Sedgwick Museum, Cambridge (SM); Geologisk Museum, Copenhagen (GMK); Dudley Museum & Art Gallery (DUDMG); British Geological Survey, Keyworth (BGS); The Natural History Museum, London (NHM); Wollaton Hall Natural History Museum, Nottingham (NOTNH) and Oxford University Museum of Natural History (OUM).

Terminology. The R:r ratio refers to the difference in length between the two major radial axes in starfish, with R representing the distance from the centre of the disc to the tip of the ray, and r representing the distance from the centre of the disc to the interradius.

7

In the following descriptions and diagnoses, the term 'ray' is used to denote the radial projections of the asteroid body wall in preference to 'arm', since the latter implies a function comparable with the arm of vertebrates, an analogy that is best avoided. All other terms are as outlined by Spencer and Wright (1966; see Text-fig. 2.1), except the designation of letters A-E to each of the five primary rays in asteroids, which is as defined by Moore and Fell (1966, p. U129).

Class ASTEROIDEA de Blainville, 1830

Family LEPIDASTERIDAE Gregory, 1899

Remarks. Gregory (1899) erected Lepidasteridae with two genera, *Lepidaster* Forbes, 1850 and *Etheridgaster* gen. nov. Schuchert (1915) emended Lepidasteridae to include two other genera, *Helianthaster* Römer, 1863 and *Lepidasterella* Schuchert, 1915, whilst deciding that *Etheridgaster* was synonymous with *Monaster* Etheridge, 1892 and removing it to that genus. Spencer (1918) made comprehensive revisions and removed Lepidasteridae entirely, placing *Lepidaster* and *Lepidactis* Spencer, 1918, in a new family Lepidactinidae on the basis that *Lepidactis* is more primitive than *Lepidaster*, but Owen (1965) stated that Lepidactinidae is a subjective junior synonym of Lepidasteridae and reverted to the latter, again containing *Lepidactis* and *Lepidaster*. Spencer and Wright (1966) kept *Lepidaster* in the Family Lepidasteridae but removed *Lepidactis* to Mesopalaeasteridae, Subfamily Lepidactininae, thus placing the two genera in different orders – *Lepidaster* in Paxillosida and *Lepidactis* in Valvatida – which seems wholly inappropriate given the number of similarities between them. Characters shared by *Lepidaster* and *Lepidactis* are the size, shape and arrangement of the adambulacrals and inferomarginals within the ray, the oral-interradial position of the madreporite, the shape of the mouth-angle plates, the small, irregular ossicles making up the central disc, and the proximal modification of the adambulacrals.

Genus LEPIDASTER Forbes, 1850

Type species. *Lepidaster grayi* Forbes, 1850, by original designation.

Diagnosis. Multi-rayed lepidasterids with large central disc. Large oval madreporite with radial striae. Oral interradial areas occupied by fan-shaped array of triangulate to dentiform plates formed by conjunction of inferomarginals of adjacent rays. Aboral surface of rays without clear arrangement of ossicles.

Horizon and localities. Known only from the Much Wenlock Limestone Formation (Homerian) of Dudley, England.

Remarks. *Lepidaster* is monospecific. *Hudsonaster australis* Withers and Keble, 1934, a five-rayed starfish from the Ludlow of Victoria, Australia, was described by Spencer (1950, p. 406) as showing 'a resemblance to the Wenlock genus *Lepidaster*', leading Pickett *et al*. (2000, p. 147) to list '*Lepidaster australis* (Withers and Keble, 1934)' as one of fifteen species of Silurian starfish from Australia. However, comparison of the oral surface of *H. australis* (Withers and Keble 1934, text fig. 3.) with that of *L. grayi* shows that the asteroids do not belong in the same genus. The inferomarginals of *H. australis* are larger than the adambulacrals proximally, but rapidly decrease in size distally, whilst the adambulacrals also decrease in size distally. In contrast, the inferomarginals of *L. grayi* are an almost constant size along the entire length of the ray, and smaller than the adambulacrals, except at the very proximal part of the ray, where the adambulacrals decrease rapidly in size. Also, the axillary plate of *H. australis* is a single, large, rounded ossicle, rather than the distinctive fan-shaped array of ossicles seen in *L. grayi*.

Lepidaster is the earliest known example of a multiradiate asteroid – all Ordovician species are five-rayed, with rare six-rayed specimens thought to be the result of problems during development (J. Dean, pers. comm. 2000) – and represents a significant development in the evolutionary history of starfish (see Chapter 3). Recent studies on modern multiradiate asteroids (e.g. Lawrence 1988, Hotchkiss 1998*a*, 1998*b*, 2000) have shown ray number to be variable at ordinal, familial, generic and specific level. With few specimens known, it is unclear to what level the multiradiate state of *Lepidaster* can be termed diagnostic, but without five-rayed specimens which can be unequivocally attributed to *Lepidaster*, it is regarded here as generically characteristic.

Lepidaster grayi Forbes, 1850

Text-figs 2.2-2.6

v*   1850   *Lepidaster Grayi* Forbes, p. 1, pl. 1, figs 1-3.

      1859   *Lepidaster Grayii* Forbes; Murchison, p. 249.

      1863   *Lepidaster Grayi* Forbes; Wright, p. 35 [reiterates Forbes 1850].

      1869   *Lepidaster Grayi* Forbes; Woodward, p. 244 [list of all Silurian species of starfish then known].

vp	*1873*	*Lepidaster Grayii* Forbes; Salter, p. 117 [catalogues two specimens in Sedgwick Museum, but neither figures nor describes them].
?	1873	*Trichotaster plumiformis* Wright, p. 421.
?	*1874*	*Trochitaster* [sic] *plumiformis* Wright; Woodward, p. 7 [included in revised list of Silurian starfish from Woodward 1869].
	1874	*Lepidaster Grayi* Forbes; Woodward, p. 8 [discusses fossil sun-stars].
	1879	*Lepidaster Grayi* Forbes; Zittel, p. 454.
?	1880	*Trichotaster plumiformis* Wright; Wright, p. 169 [expands on Wright 1873].
	1890	*Lepidaster Grayi* Forbes; Stürtz, p. 222, pl. xxviii, figs 19, 20.
	1893	*Lepidaster Grayi* Forbes; Stürtz, p. 52.
	1899	*Lepidaster Grayi* Forbes; Gregory, p. 353 [erection of Lepidasteridae without description of *Lepidaster*].
	1914	*Lepidaster grayi* Forbes; Spencer, p. 40 [review of previous work on Palaeozoic starfish].
	1915	*Lepidaster grayi* Forbes; Schuchert, p. 38.
v	1918	*Lepidaster grayi* Forbes; Spencer, p. 112 (text figs. 71-78), pl. vi, fig. 6; pl. vii, figs 1-6 [first description of material other than holotype].
?	*1918*	*Trichotaster plumiformis* Wright; Spencer, p. 116.
	1947	*Lepidaster grayi* Forbes; Lamont, p. 203.
	1965	*Lepidaster grayi* Forbes; Owen, p. 564 [lists all known specimens].
	1966	*Lepidaster grayi* Forbes; Spencer and Wright (*in* Moore), p. U44, fig. 43,6.
	1989	*Lepidaster grayi* Forbes; Blake and Guensburg, p. 362 [discussion of multiradiate Palaeozoic asteroids].
	2000	*Lepidaster grayi* Forbes; Hotchkiss, p. 342.

Holotype. NHM 40215, from Upper Quarried Limestone Member of Much Wenlock Limestone Formation (Homerian), Castle Hill, Dudley, England.

Other material. BGS 27515 (with separately mounted ray, BGS 28826), SM A5496, NOTNH FS03795, NOTNH FS03800, DUDMG 606 (whereabouts of specimen presently unknown), OUM C00515, and BU 673, all from Much Wenlock Limestone Formation, Dudley. NOTNH FS03795 and NOTNH FS03800 are from the Nodular Beds Member.

Diagnosis. As for genus.
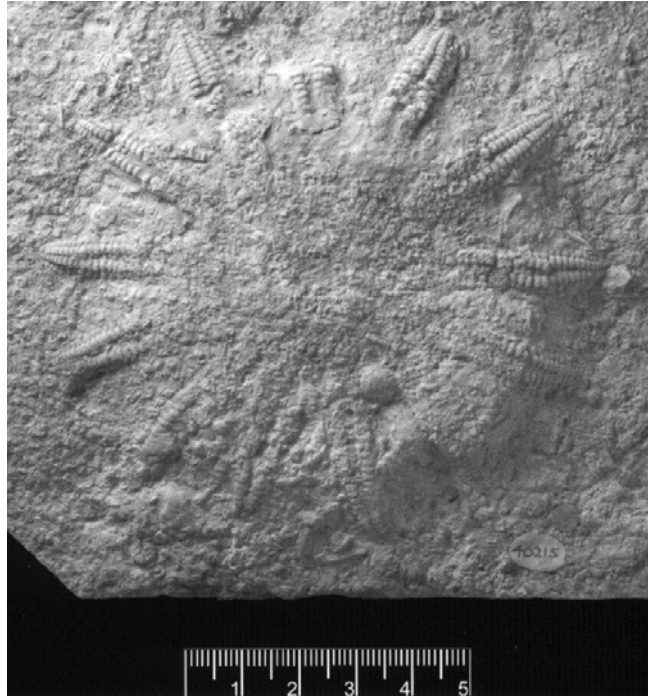
TEXT-FIG. 2.2. *Lepidaster grayi* Forbes, 1850. Oral surface of holotype NHM 40215, showing thirteen rays and large, round madreporite. Major scale bar increments in cm (photograph courtesy of NHM).

Description. Multiradiate asteroids, with maximum 13 rays. Madreporite positioned in oral interradius. Oral surface of ray made up solely of ambulacrals, adambulacrals and inferomarginals. Ambulacrals flat, in opposite pairs; adambulacrals also oppose one another, alternating with ambulacral pairs; inferomarginals alternate with adambulacrals. Distally, adambulacrals convex, of rounded oblong shape, with small, incurved projection on ambulacral side; proximally, this projection becomes bar-shaped and adambulacrals narrow considerably. Inferomarginals squamose, globular distally, becoming flattened and elongate proximally, forming fan-shaped array of dentiform or triangular plates in interradius. Oral surface of central disc composed of numerous small ossicles with no obvious organisation; mouth region with elongate, blade-like mouth-angle plates, abutted proximally by large, rounded tori. Aboral surface of central disc not known.

Specimen size. NHM 40215 is the largest specimen; BU 673 the smallest (see table 2.1 for R:r measurements). General pattern is of R:r ratio decreasing as specimens get larger – central disc size increases in relation to rays as starfish become mature.

Remarks. Until the work of Spencer (1918), the holotype (Text-fig. 2.2), which has thirteen rays, was the only specimen of *Lepidaster grayi* to have been described and figured.
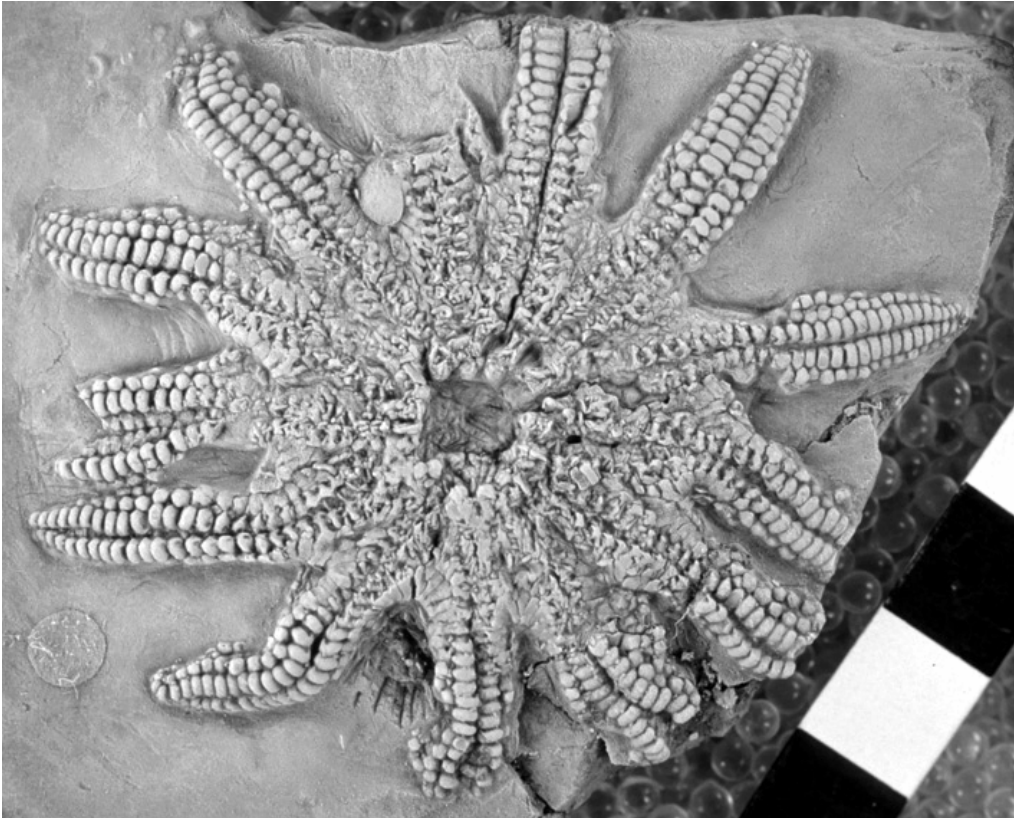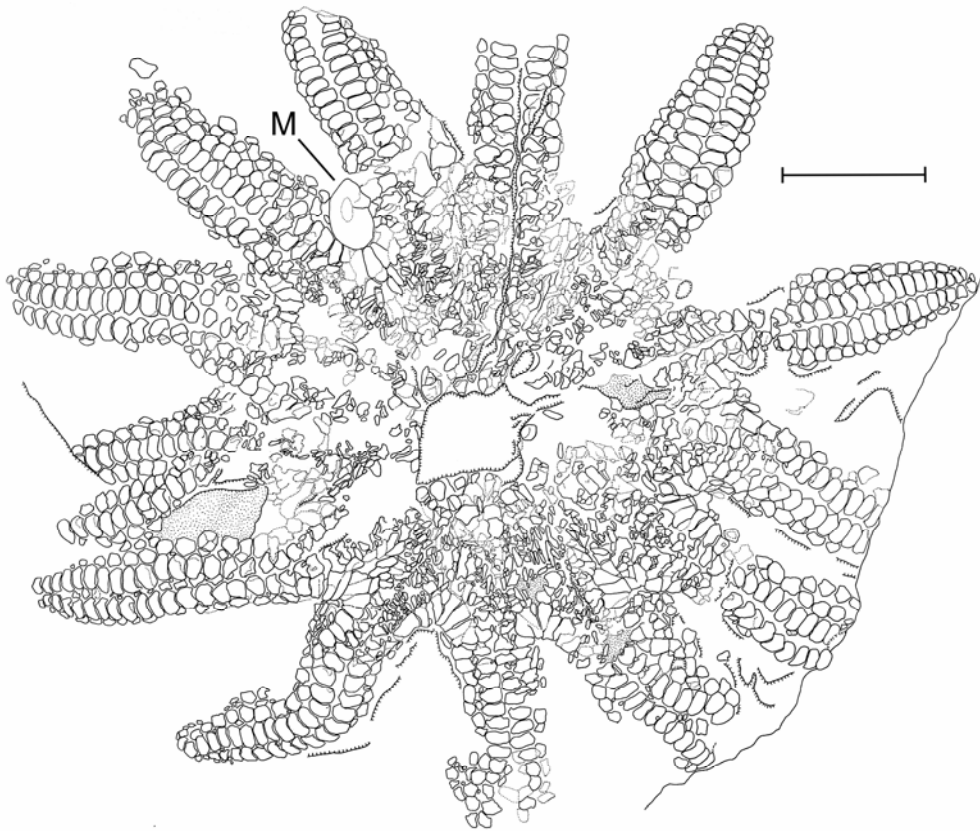
TEXT-FIG. 2.3. *Lepidaster grayi* Forbes, 1850. A, oral surface of BGS 27515, showing 12 preserved rays; B, explanatory c*amera lucida* drawing of same, with madreporite (M) marked; ray to right of madreporite is mounted separately as BGS 28826 and has been superimposed. Scale bar = 10 mm.

TABLE 2.1. R:r measurements, in mm, for specimens of *Lepidaster grayi*, with Spencer's (1918) figures in brackets. Measurements for NOTNH FS03795 are approximate; OUM C00515 too poorly preserved to measure; DUDMG 606 not seen.

Specimen	R	r	R:r
NHM 40215	54 [51]	24 [22]	2.3 [2.3]
NOTNH FS03800	44 [-]	18 [-]	2.4 [-]
NOTNH FS03795	~37 [-]	~16 [-]	~2.3 [-]
BGS 27515	34 [34]	15 [14]	2.3 [2.4]
SM A5496	24 [23.2]	8 [9.3]	3 [2.5]
BU 673	13 [14.5]	5 [5.5]	2.6 [2.6]

Only the oral surface is visible, with the madreporite present but poorly preserved, and the ossicles of the central disc cannot be made out with certainty. Forbes (1850, pl. 1, fig. 2) figured the aboral surface of one excavated ray, which has not been located, showing a disorganized array of polygonal ossicles.

The best-preserved specimen is BGS 27515 (Text-fig. 2.3), again displaying the oral surface and thirteen rays. The rays are more completely preserved, showing the proximal modification of the adambulacrals and the progression of inferomarginals from distal tip to interradii; the ambulacrals are also exposed in the distal portion of one ray. Additionally, the madreporite is more complete than that of the holotype, although no ornament remains, and the central disc is almost entire, being composed of numerous small ossicles. The mouth region can be clearly defined, with some mouth-angle plates and tori *in situ*. BGS 28826 is a single ray of BGS 27515, amputated by Spencer (1918) in order to obtain comparison with Forbes' (1850) figure of the aboral surface of a ray. Spencer (1918, p. 122) described having 'obtained exactly the same [aboral] arrangement as in Forbes' figure', but this is difficult to confirm as that surface of the ray has been glued to a glass slide, through which the layout of the ossicles cannot be clearly made out.

Of the other specimens, NOTNH FS03800 also has thirteen rays, and further elucidates the arrangement of the oral surface of the central disc, showing the complete progression of adambulacrals from ray tip to mouth-parts (Text-fig. 2.4b) and an almost entire assemblage of mouth-angle plates and tori (Text-fig. 2.5). NOTNH FS03795 shows the aboral surface, but is poorly preserved and little of the original plate arrangement can be made out. However, one ray (Text-fig. 2.4a) appears to confirm the observations of Forbes (1850) and Spencer (1918) that the aboral ossicles are not aligned in clear rows.
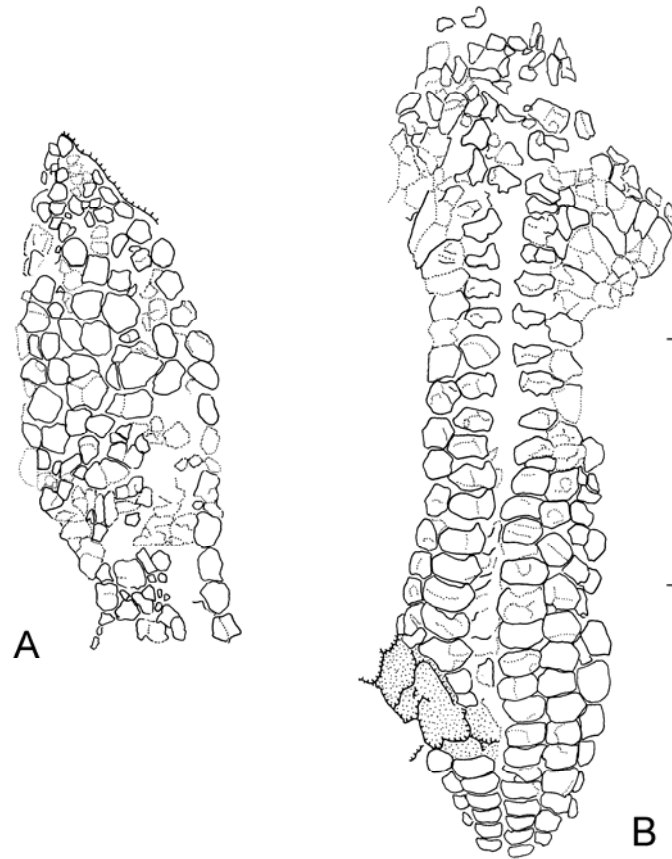
TEXT-FIG. 2.4. *Camera lucida* drawings of *Lepidaster grayi* Forbes, 1850, to illustrate arrangement of ray ossicles. A, NOTNH FS03795, aboral surface, showing the irregular layout of ossicles; B, NOTNH FS03800, oral surface, showing the full distal-proximal sequence of adambulacral and inferomarginal ossicles. Scale bar = 10 mm.

BU 673 (Text-fig. 2.6) is the smallest example of *L. grayi* and may have been a juvenile, a suggestion made by Spencer (1918) on the basis of its size, the smaller number of rays and reduced interradial plates. The specimen is distorted, but certainly seems to have fewer than thirteen rays, whilst the adambulacrals are narrower in relation to the inferomarginals than in other specimens, although of the same shape and arrangement. Likewise, the fan-shaped array of inferomarginals in the interradius is made of fewer plates and, based on comparisons with extant starfish, these features indicate that Spencer's (1918) hypothesis of BU 673 being immature is probably correct. SM A5496 is incomplete, and OUM C00515 even more so, such that neither offers further information on the structure of *Lepidaster grayi*.

DUDMG 606 was described and figured by Spencer in 1918, but the specimen has subsequently been lost, and it has thus not been possible to compare it directly with other
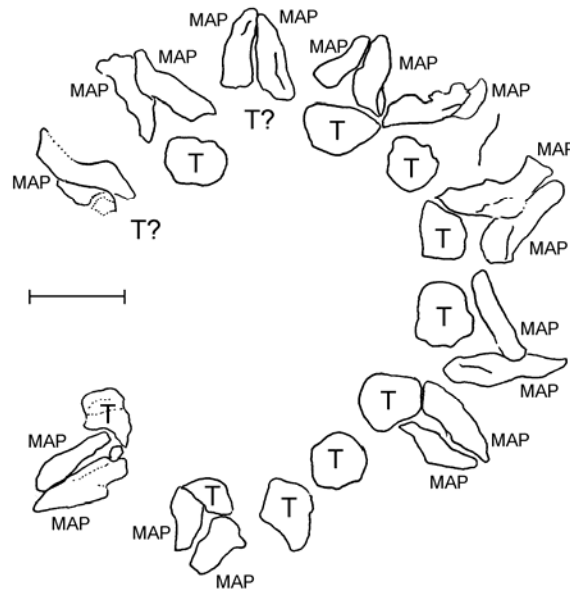
TEXT-FIG. 2.5. *Lepidaster grayi* Forbes, 1850, NOTNH FS03800. Simplified *camera lucida* drawing of mouth region, showing pairs of mouth-angle plates (MAP) and tori (T). Scale bar = 2 mm.

material. Spencer (1918, p. 120) stated that it is 'almost exactly the same size as the holotype' and mentioned thirteen rays, with eight showing the oral surface and five the aboral, due to the central disc being folded. The layout of ossicles on the oral surface of the rays was described by Spencer (1918) as identical to that of BGS 27515 and his illustration of the madreporite of DUDMG 606 (Spencer 1918, fig. 74) indicates that it is the best preserved in all examples of *L. grayi*. The figure shows a surface covered with striae radiating from a centre line that divides the madreporite into approximately symmetrical halves. Additionally, the aboral surface of one ray showed no organisation of plates distally, 'but a more proximal portion of the same arm showed a distinctly regular structure…proving that *Lepidaster* is descended from a form with regularly arranged apical plates' (Spencer 1918, p. 122, text fig. 77 [wrongly captioned as 'from the Birmingham University Museum']).

　　　Lepidaster grayi may not have been the only multiradiate asteroid in the Much Wenlock Limestone Formation. In 1873, Wright described a small echinoderm from Dudley, which he interpreted as a new species of asteroid, *Trichotaster plumiformis*, with a large central disc and ten short rays, but no figure was included and it is clear from his description that the only specimen was very poorly preserved. Wright (1873) listed it as being in the Grindrod Collection, now housed in the Oxford University Museum of Natural History, but it had been lost before Spencer published his monograph, and he suggested (Spencer 1918, p. 123) that it was another juvenile example of *Lepidaster grayi*. Wright's (1873, p. 421) description of each ray being 'terminated by a stem-like multiarticulate process as long as the
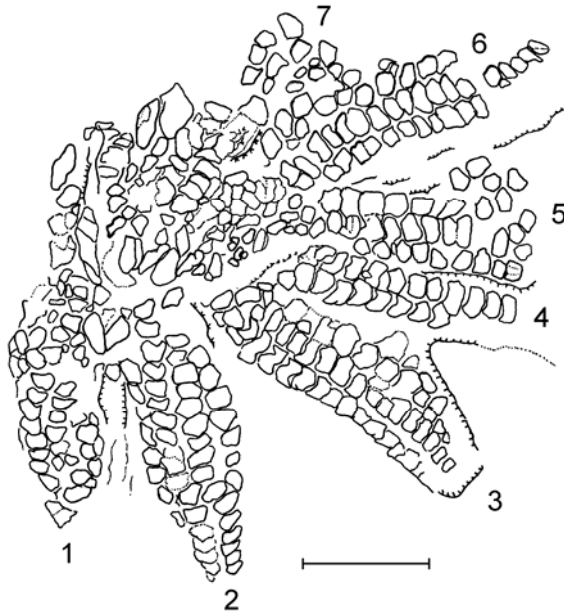
TEXT-FIG. 2.6. *Camera lucida* drawing of BU 673, a small specimen of *Lepidaster grayi* Forbes, 1850, showing the oral surface and at least seven rays (numbered arbitrarily). Scale bar = 4 mm.

ray, from towards the extremity of which spring slender lateral processes, giving it a tufted appearance' suggests an echinoderm quite unlike *L. grayi*, but as the specimen of *T. plumiformis* is still missing, this cannot be confirmed.

Genus LEPIDACTIS Spencer, 1918

Type species. *Lepidactis wenlocki* Spencer, 1918, by original designation.

Diagnosis. Five-rayed lepidasterids with small central disc. Madreporite of curved oblong shape with anastomosing ornament. Proximal inferomarginals bulbous; interradius with large rhomboid axillary almost enclosed by square inferomarginals. Aboral surface of rays with single row of widened hexagonal carinals bordered by square to hexagonal superomarginals; proximally, small adradials separate carinals and superomarginals.

Remarks. *Lepidactis* is monospecific.

Lepidactis wenlocki Spencer, 1918
Text-figs 2.7, 2.8

16
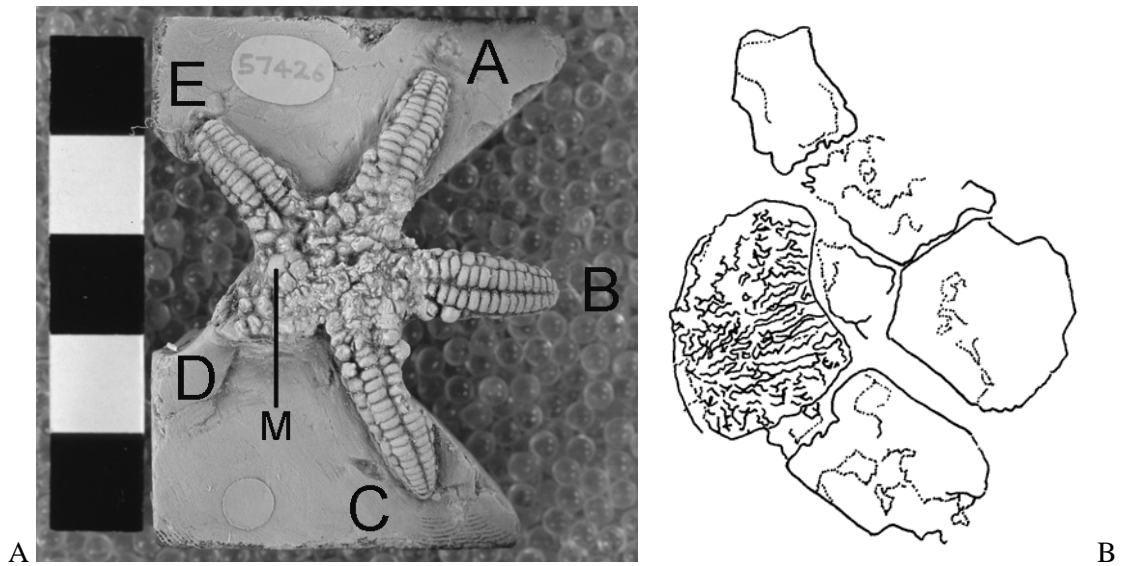
TEXT-FIG. 2.7. *Lepidactis wenlocki* Spencer, 1918, NHM 57426. A, Oral surface of holotype, showing five rays (A-E) and madreporite (M), scale bar = 50 mm; B, *camera lucida* drawing of madreporite, showing anastomosing ornamentation, x 8.

vp	*1873*	*Lepidaster Grayii* Forbes; Salter, p. 117 [lists two specimens of '*Lepidaster Grayii*' without description or illustration].
v*	1918	*Lepidactis wenlocki* Spencer, p. 112 (text figs 68-70), pl. vi, fig. 5.
	1947	*Lepidactis wenlocki* Spencer; Lamont, p. 203.
	1965	*Lepidactis wenlocki* Spencer; Owen, p. 564.
	1966	*Lepidactis wenlocki* Spencer; Spencer and Wright (*in* Moore), p. U51, figs 49,1a-b.

Holotype. NHM 57426, from Much Wenlock Limestone Formation (Homerian) of Dudley, England.

Other material. One specimen, SM A12568, from same locality as holotype.

Diagnosis. As for genus.

Description. Lepidasterid with long, tapering rays. Holotype (Text-fig. 2.7) has large madreporite with anastomosing ornamentation in oral interradius. Oral surface of ray very similar to *Lepidaster*, formed only of ambulacrals, adambulacrals and inferomarginals, though ambulacrals not exposed. Adambulacrals rounded oblongs of consistent size along most of

17
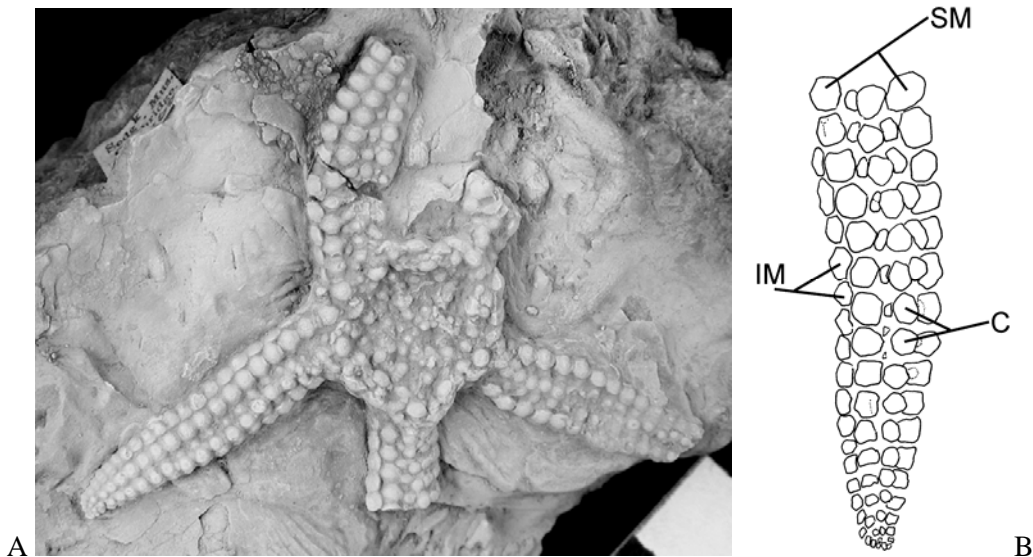
TEXT-FIG. 2.8. *Lepidactis wenlocki* Spencer, 1916, SM A12568. A, Aboral surface of specimen, showing three complete rays and central disc, scale bar = 10 mm; B, *camera lucida* drawing of best-preserved ray, showing superomarginals (SM), inferomarginals (IM) and carinals (C), x 5.

ray, becoming markedly reduced in size towards mouth region; in opposing pairs along ray, two pairs to each pair of inferomarginals. Inferomarginals square or sub-hexagonal, projecting out beyond ray perimeter. Interradius occupied by large rhomboid axillary, possibly odontophore, distal edge almost enclosed by inferomarginals. Oral surface of central disc without clear arrangement of plates; mouth region not preserved; single elongate mouth-angle plate displaced near madreporite on holotype. Aboral surface of central disc similar to oral surface, with many small ossicles; rays with superomarginals in alternation with inferomarginals, of identical shape and size; single row of carinal plates separated from superomarginals by small adradials proximally, in contact with superomarginals distally.

Remarks. SM A12568 (Text-fig. 2.8) was originally identified as an example of *Lepidaster grayi* by Salter (1873, p. 117), but was neither figured nor described, and was not discussed by Spencer (1918). The specimen is larger than the holotype of *Lepidactis wenlocki*, but in possessing five rays and a clear aboral arrangement of carinals, superomarginals and proximal adradials, it shows far stronger affinity with that species than with *Lepidaster grayi*. The main objection to placing SM A12568 in *Lepidactis* is the relative sizes of the ossicles on the aboral surface of the ray. Spencer (1918, text fig. 70) depicted the aboral surface of one ray of NHM 57426, showing the carinals to be larger and more oblong than the superomarginals. SM A12568 has carinals that are smaller than the superomarginals, and rounded, and the rays taper more gradually than in the holotype. Further specimens may show SM A12568 to be

18

conclusively separable from either *Lepidaster grayi* or *Lepidactis wenlocki*, or both, but at present it is placed in the latter species.

Family HUDSONASTERIDAE Schuchert, 1914

Remarks.   Schuchert erected the Hudsonasteridae in 1914, but did not list the familial characters until the following year. He described the hudsonasterids (1915, p. 53) as the 'most primitive known Phanerozonia' and diagnosed the family as comprising small, five-rayed asteroids with spines restricted to adambulacrals and inferomarginals, single axillaries, five rows of aboral ray ossicles (carinals, superomarginals and inferomarginals, but no accessory plates), and a prominent centrale separated from primary circlet of five large primary radials and five large interradials by small accessory plates. Two genera were included – *Hudsonaster* Stürtz, 1900, and *Siluraster* Jaekel, 1903.

Spencer (1916, pp. 68, 69) revised the family, adding three new genera – *Girvanaster*, *Belaster*, and *Coccaster*. He argued that spines were present on both infero- and superomarginals, but otherwise concurred with Schuchert (1915). Subsequently, Spencer (1950) noted (*after* Raymond 1921) that the shape of the axillary plate was important in differentiating the various forms of the Hudsonasteridae, and split the family into three groups. The first group was defined on the basis of the axillary inferomarginals being very similar to the remaining inferomarginals, the second group with axillaries distinctly larger than inferomarginals, longer than broad, and the third group with axillaries as of group two, but broader than long. It is not clear whether Spencer (1950) intended the three groups as generic or subfamilial: Group 1 was unnamed; Group 2 was described as of 'one lineage, and therefore grouped under *Protopalaeaster* Hudson (1912, p. 25), since this generic name holds priority' (Spencer 1950, p. 405); and Group 3 included only the genus *Coccaster* Spencer, 1916. Nonetheless, his classification was problematic, since the type species *Hudsonaster rugosus* (Billings, 1857) could not be placed in any of the groups, as nothing is known of its axillaries or inferomarginals.

Spencer and Wright (1966) listed the characteristics of the Hudsonasteridae as single axillaries with free distal edge, superomarginals within frame of inferomarginals, aboral surface of rays normally with carinals and superomarginals only, and central disc with centrale and primary circlet. The family was divided into three subfamilies – Hudsonasterinae with the aboral ray surface composed of carinals and superomarginals only and a protrusible cap on the central disc, Coccasterinae without a protrusible cap, and Silurasterinae with adradials separating carinals and superomarginals. Both Coccasterinae

and Silurasterinae contained a single genus, and the former subfamily was based on a species – *Coccaster bulbiferus* Spencer, 1916 – of which only one specimen is known.

Hudsonasteridae has been excessively subdivided, and Spencer and Wright's (1966) erection of new subfamilies on very limited material has complicated matters. Dean (1999*b*) stated that for Palaeozoic asterozoans, the most accurate classification is at generic level, and reviewed the genera that had been previously placed in Hudsonasteridae. Her cladistic analysis defined the diagnostic characters for the Hudsonasteridae as the presence of both inferomarginals and superomarginals, the primary radials and interradials being larger than the remaining radials and forming a primary circlet, the axillary being larger than adjacent inferomarginals, and the circumoral plates meeting the mouth-angle plates at an obtuse angle. The genera she included were *Tabellaster* Dean, 1999*b*, *Niphadosaster* Dean, 1999*b*, *Girvanaster* Spencer, 1916, *Hudsonaster* Stürtz, 1900, and *Siluraster* Jaekel, 1903.

Genus SILURASTER Jaekel, 1903

Type species. *Siluraster perfectus* Jaekel, 1903, by original designation.

Siluraster? *ketleyi* (Spencer, 1916)
Text-fig. 2.9

v*   1916   *Mesopalaeaster*? *ketleyi* Spencer, p. 64, (text fig. 59).
        1918   *Mesopalaeaster*? *ketleyi* Spencer; Spencer, p. 122.
        1947   *Mesopalaeaster*? *ketleyi* Spencer; Lamont, p. 203.
        1965   *Mesopalaeaster*? *ketleyi* Spencer; Owen, p. 569.

Holotype. BU 674, the only specimen, from the Much Wenlock Limestone Formation (Homerian) of Dudley, England.

Diagnosis. Hudsonasterid with primary circlet of large, irregular primary radials and interradials, abutting directly against proximal superomarginals and carinals. Small, circular, radially grooved madreporite in aboral interradius. Aboral surface of ray with large superomarginals, small carinals and numerous tiny adradials.

Description. Five-rayed asteroid with small central disc and slender rays. Aboral surface of
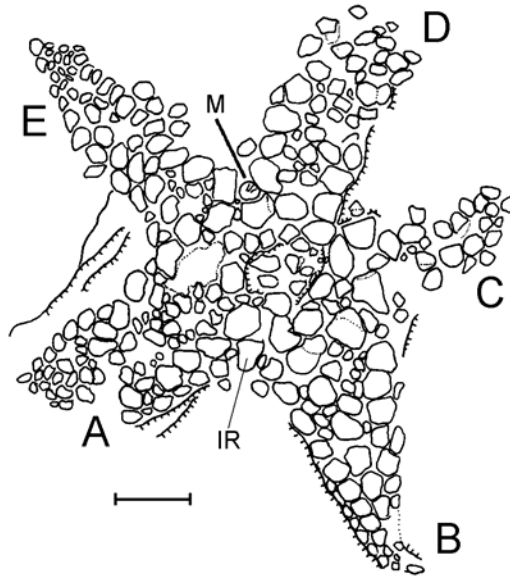
TEXT-FIG. 2.9. *Siluraster*? *ketleyi* (Spencer, 1916), BU 674. *Camera lucida* drawing of aboral surface, showing five rays (A-E), large inter-radial ossicle (IR) and madreporite (M). Scale bar = 2 mm.

central disc with primary circlet of large, irregular radials and primary interradials; small accessory plates within circlet. Ossicular arrangement of aboral surface of rays variable, but superomarginals generally large, irregular, often wedge-shaped; carinals are smaller, rhomboid, sometimes separated from superomarginals by tiny adradials. Inferomarginals in alternation with superomarginals, but smaller, more rounded; intermarginal ossicles occasionally present between infero- and superomarginals. Terminal ossicle preserved on ray E. Oral surface not seen.

Remarks. BU 674 (Text-fig. 2.9) was first described by Spencer (1916) and placed provisionally in the genus *Mesopalaeaster* Schuchert, 1914. Spencer noted (1916, p. 101) that it showed 'general resemblances to both "*Hudsonaster*" and "*Mesopalaeaster*" stock' but, as the oral surface was unexposed, could not verify with certainty whether the axillary plate was enclosed by inferomarginals as in mesopalaeasterids, or had a free distal edge as in hudsonasterids. However, he suggested that the large ossicle in the interradius between rays A and B – labelled 'IR' on Text-fig. 2.9 – was an intermarginal rather than an inferomarginal, on the grounds that it did not show 'articulation, on its apical surface, for the fitting of the covering supero-marginalia' (Spencer 1916, p. 101). This placed BU 674 in the Mesopalaeasteridae, but Spencer (1916) did not claim the interpretation to be definitive and, for the reasons outlined below, it is not followed here. The axillary ossicle discussed is many times larger than any other preserved intermarginal on BU 674, fits the space between the two primary superomarginals rather better than Spencer (1916) described, slots uniformly into the

sequence of inferomarginal ossicles running away along the margin of both adjacent rays (being of roughly the same size) and is of a similar shape to the axillaries of other members of the Hudsonasteridae (see e.g. Dean 1999*b*). It is therefore more appropriate to place BU 674 in that family.

At generic level, the presence of carinals and adradials along the centre line of the aboral ray surface indicates that BU 674 is most closely related to *Siluraster* Jaekel, 1903. *Siluraster* and *Mesopalaeaster* were placed together in the Mesopalaeasterinae, subfamily of the Promopalaeasteridae, by Owen (1965), who suggested that their similarities were numerous (see Owen 1965, p. 568). However, Spencer and Wright (1966, p. U51) placed *Siluraster* in the Hudsonasteridae and *Mesopalaeaster* in the Mesopalaeasteridae.

Dean (1999*b*) left *Siluraster* in the Hudsonasteridae, but considered the two confirmed species of *Mesopalaeaster* (*M. shafferi* (Hall, 1868) and *M. primus* (Spencer, 1916)) to be insufficiently distinct as to warrant a separate genus and transferred both to *Hudsonaster*. Neither of Dean's generic diagnoses for *Hudsonaster* and *Siluraster* can be applied unequivocally to BU 674, but the specimen shows greater affinity with the latter and is tentatively placed in that genus. The variation of ossicle arrangement seen in the rays of *S*.? *ketleyi* makes accurate specific and generic identification difficult, and unless other specimens are discovered, its true systematic position is likely to remain unresolved.

Genus HUDSONASTER Stürtz, 1900

Type species. *Palasterina rugosa* Billings, 1857. By original designation.

Hudsonaster? *carectum* sp. nov.
Text-fig. 2.10

Derivation of name. From the Latin '*carectum*', a sedgy place, in reference to Sedgley, near Dudley, England, where the holotype was found. Erected as a noun in apposition.

Holotype. BU 4350, the only specimen, from the Lower Elton Formation (?Wenlock-Ludlow) of Sedgley, near Dudley, England.

Diagnosis. Hudsonasterid with large, hexagonal axillary plates. Adambulacrals small, square, of consistent size along ray. Inferomarginals square, large along greater length of ray; distally of same size as adambulacrals.
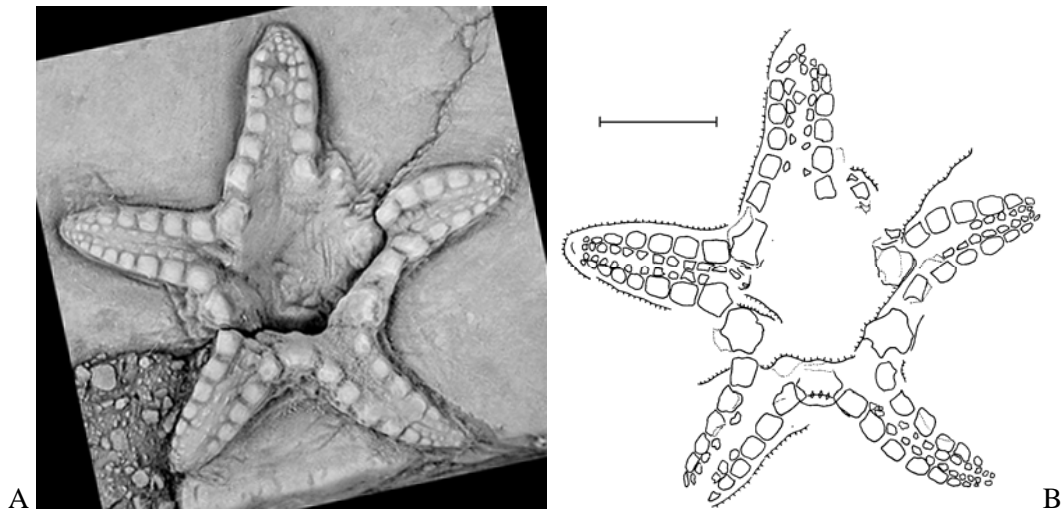
TEXT-FIG. 2.10. *Hudsonaster*? *carectum* sp. nov., BU 4350. A, photograph, and B, c*amera lucida* drawing of holotype, showing oral surface. Scale bar = 6 mm.

Description. Central disc small, rays relatively short (R:r value = 11 mm:4 mm). Axillary plate with free distal edge joins strong frame of inferomarginals, which are much larger than small, square adambulacrals for greater length of ray, two distal-most pairs of inferomarginals are much reduced and similar to adambulacrals. Ambulacrals not seen. Central disc and mouth region not preserved. Aboral surface not seen.

Remarks. The holotype (Text-fig. 2.10) has never been described previously, but was listed as '*Coccaster bulbiferus*' in the catalogue of the Holcroft Collection of the Lapworth Museum, University of Birmingham. However, BU 4350 can be distinguished from *Coccaster bulbiferus* Spencer, 1916, on a number of criteria, most notably the marked size difference between the inferomarginals and adambulacrals, the hexagonal axillaries and the fact that the inferomarginals remain large until almost the tip of the ray. *Hudsonaster*? *carectum* bears closer similarity to *Hudsonaster narrawayi* (Hudson, 1912) from the Lower Ordovician of the USA, as figured by Spencer and Wright (1966, fig. 47,3c), and is questionably referred to the same genus, although the inferomarginal plates of *H*. *narrawayi* are smaller and show a gradual decrease in size along the length of the ray, and the axillary plates are pentagonal.

Genus DOLIASTER gen. nov.

Type species. *Doliaster brachyactis* gen. et sp. nov., the only known species.

23

Derivation of name. From the Latin words '*dolium*', a barrel or cask, and '*aster*', star, in reference to the barrel-shaped first pair of superomarginal ossicles. Gender masculine.

Diagnosis. Small pentagonal asteroids, with rays barely projecting beyond central disc. Marginal plates extremely large, only three pairs to each ray. First pair of superomarginals dolioform, becoming squarer distally; separated by small, elongate, sub-triangular carinals. Inferomarginals positioned outside superomarginals within frame of, and in phase with inferomarginals of same length, though reduced width.

Horizon and localities. Known only from the Much Wenlock Limestone Formation (Silurian: Wenlock: Homerian) of Wenlock Edge, Shropshire, England.

Remarks. There are broad morphological similarities between *Doliaster* and the modern cushion- and biscuit-stars (e.g. *Asterina phylactica* Emson and Crump, 1979; members of the genus *Culcita*) but the plates on the aboral surface of *Doliaster brachyactis* are proportionally much larger, and it seems unlikely that any close relationship exists. Amongst Palaeozoic forms, no asteroids have the near-pentagonal shape and large, blocky superomarginal plates seen in *Doliaster*. There are some similarities to *Arisaigaster leintwardensis* (Spencer, 1916) but insufficient to consider the two congeneric (see specific remarks for *D. brachyactis*, below). It may be that *Doliaster* is a juvenile form of another genus and would have developed more pronounced rays at a more mature stage, but this cannot be verified without further specimens. The highly distinctive basic morphology of *Doliaster* suggests, however, that this is not the case.

In terms of familial classification, *Doliaster* is difficult to assign, since one of the main characters for identification at family level is the arrangement of the axillary plates in relation to the inferomarginals. No axillary ossicles are visible on *D. brachyactis*, suggesting that they were either wholly enclosed by inferomarginals, or absent. Coupled with the generic characteristics, this means that *Doliaster* does not fit unequivocally into any of the five families that Spencer and Wright (1966) placed in the Superfamily Palaeasteraceae Miller, 1889. Of the five – Palaeasteridae Miller, 1889, Hudsonasteridae Schuchert, 1914, Neopalaeasteridae Schuchert, 1915, Mesopalaeasteridae Schuchert, 1914, and Xenasteridae Gregory, 1899 – *Doliaster* displays a greater number of features diagnostic of the Hudsonasteridae, but most hudsonasterids have axillaries with a free distal edge.

Doliaster brachyactis sp. nov.

Text-fig. 2.11

Derivation of name. From the Greek words '*brachys*', short, and '*aktis*', ray, in reference to the almost pentagonal body shape.

Holotype. NHM E53614, the only specimen, from the Much Wenlock Limestone Formation (Homerian), Coates Quarry, Wenlock Edge, near Much Wenlock, Shropshire, England.

Diagnosis. As for genus.

Description. Specimen measures 8 mm from centre of disc to tip of ray. Aboral surface of rays composed of three pairs of large, blocky superomarginals separated by small, elongate carinals, with rhomboid terminal plate. Oral surface of rays not seen, but inferomarginals thrust upwards in two interradii shown to be positioned directly below superomarginals, of same length, but reduced width; no axillary plate visible. Aboral surface of central disc with primary circlet formed of five radials and five primary interradials, with former pushed distally relative to latter; second circlet of five, larger, interradials and first five carinals lies beyond primary circlet, with distal edge of the second interradials abutting primary superomarginals. Possible madreporite in notch between superomarginals and interradial.

Remarks. The type specimen of *D. brachyactis* (Text-fig. 2.11) was found in 1970 by H. M. Pedley, an undergraduate from the University of Leicester, but it has never been described. It was tentatively identified by staff in the NHM as belonging to the genus *Arisaigaster*, which Spencer and Wright (1966, p. U51) listed as having been erected by Spencer in 1953. However, no record exists of any publication by Spencer in 1953, and no mention of *Arisaigaster* has been found in any other of that author's works. The first published reference to *Arisaigaster* is that of Spencer and Wright (1966), printed 12 years after Spencer's death, and thus the genus should be ascribed to *Arisaigaster* Spencer and Wright, 1966. Their generic diagnosis was brief and rather inconclusive – 'Disc large; arms short and broad' – with the type species *A. parviusculus* (Billings, 1860) from the Silurian of Arisaig, Nova Scotia. The figure of *A. parviusculus* (Spencer and Wright 1966, p. U52, fig. 49, 3a) shows a row of adradial plates between the carinals and superomarginals, a feature absent from NHM E53614. Also figured was *A. leintwardinensis* [sic – should be *A. leintwardensis* as the species was originally described as *Mesopalaeaster? leintwardensis* by Spencer in 1916 (p. 89)] (Spencer, 1916) from the Ludlow of Herefordshire. Again the figured specimen is markedly different from NHM E53614. It is thus clear that, although the generic diagnosis of *Arisaigaster* is ambiguous, NHM E53614 does not belong to that genus.
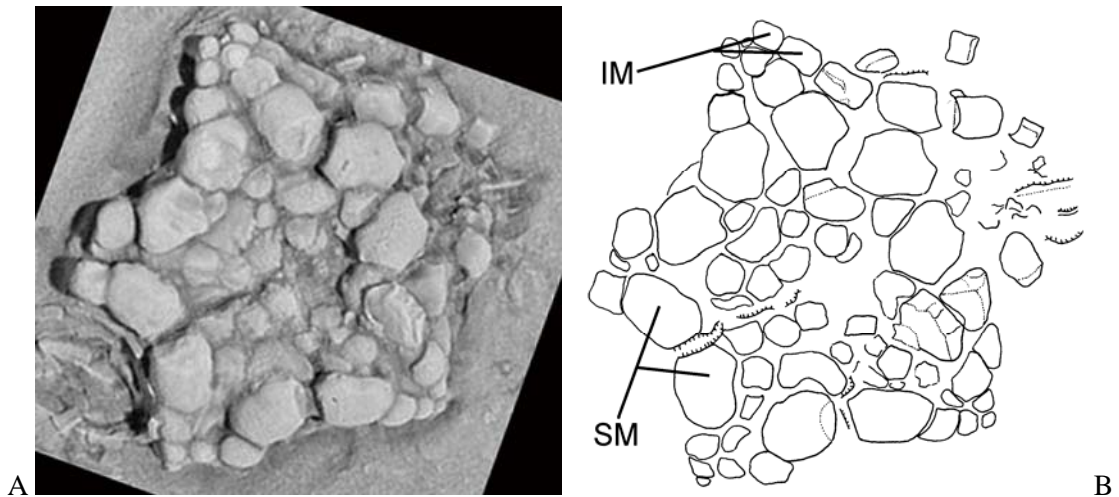
TEXT-FIG. 2.11. *Doliaster brachyactis* gen. et sp. nov., NHM E53614. A, photograph, and B, *camera lucida* drawing of aboral surface, showing superomarginals (SM) and inferomarginals (IM), x 4.

Spencer and Wright (1966) placed *Arisaigaster* in the Family Mesopalaeasteridae and Subfamily Mesopalaeasterinae, and it is on the grounds of their familial and sub-familial diagnoses that *Doliaster* can be unequivocally separated from *Arisaigaster*. *D. brachyactis* does not possess either the familial characteristic of aboral intermediate ossicles, or the sub-familial characteristic of papular areas either side of the primary radials.

Family PALASTERINIDAE Gregory, 1899

Genus PALASTERINA M'Coy, 1851

Type species. *Uraster primaevus* Forbes, 1848, by original designation.

Diagnosis. See Spencer and Wright (1966, p. U45).

Remarks. In terms of consistent and accurate generic diagnoses, *Palasterina* has been extremely poorly defined. M'Coy (1851) erected the genus on the basis that *Uraster primaevus* Forbes, 1848, from the Ludlow rocks of the Lake District, was distinct from other forms of *Uraster* 'as the rays were not contracted at base, etc.,' (M'Coy 1851, p. 59) but he did not list the generic characters. Salter (1857, p. 327) remedied this, with a comprehensive diagnosis, based on *Palasterina primaeva* (Forbes, 1848), and described a second species, *P. antiqua* (Hisinger, 1837) from the Silurian of Gotland, Sweden. It is unclear, however,
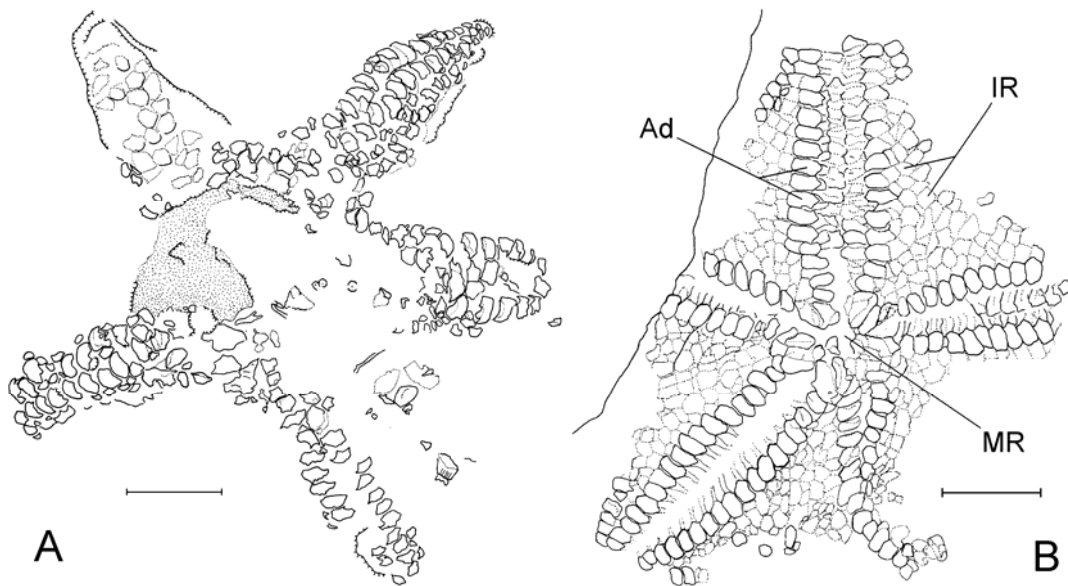
TEXT-FIG. 2.12. *Camera lucida* drawings of two species of *Palasterina* M'Coy 1851. A, *Palasterina orchilocalia* sp. nov., BU 675, oral surface, showing five imperfectly preserved rays; scale bar = 5 mm. B, *Palasterina antiqua* (Hisinger, 1837), GMK 606, oral surface of holotype, showing mouth region (MR), adambulacrals (Ad) and inter-radial ossicles (IR); scale bar = 5 mm.

whether Salter's generic diagnosis was based on the holotype of *P. primaeva*, since he listed the localities of occurrence of the species as 'Underbarrow, Westmoreland [and] Leintwardine, Shropshire' but only figured a specimen from Leintwardine (NHM 40299a/b). Wright (1863) reiterated much of Salter's (1857) work, but in describing *P. primaeva* as being solely found in the Lake District, he illustrated the species with the Leintwardine specimen NHM 40299a/b.

Gregory (1899) misread the previous work and described the genus as *Palaeasterina* [sic] rather than *Palasterina*. He did, however, make a comprehensive generic revision, removing *P. antiqua* to a new genus *Lindstromaster* whilst adding a new species *Palaeasterina bonneyi*, with holotype NHM 40299a/b. Gregory's generic diagnosis (p. 349) is detailed, but it is not certain that the characters are based on *P. primaeva*, since he included no figures of the type species and described *P. bonneyi* as better displaying the generic characters.

Schuchert (1915, p. 150) noted that, in erecting *Palasterina*, M'Coy (1851) 'did not point out a single generic character of present value' and emended the diagnosis, but used *P. bonneyi* rather than *P. primaeva* as typical of the genus because the type specimens of the latter were 'not complete enough to work out the generic characters' (Schuchert 1915, p. 151). Spencer (1922) appears to have been the first author to define the genus using *P. primaeva*; his diagnosis was revised by Spencer and Wright (1966).

Most recently, Dean (1999*b*) undertook a cladistic analysis of Ordovician asterozoans and included three Silurian genera: *Palasterina*, *Rhopalocoma* Salter, 1857, and *Sturtzaster* Etheridge, 1899. Her emended generic diagnosis of *Palasterina* was based not on the type species *P. primaeva* but on *P. antiqua*, and the holotype of *P. antiqua* was not used. Instead, the generic characters were collated from a re-description of the Leintwardine specimen NHM 40299a/b figured by Salter (1857) as *P. primaeva*, Gregory (1899) as *P. bonneyi* and Spencer (1922) as *P. antiqua*. This casts doubt on the validity of the assertion (Dean 1999*b*) that *Palasterina*, along with *Rhopalocoma* and *Sturtzaster*, belongs in a new Order Eopentaroida, showing some characters of, but separate from, both asteroids and ophiuroids. Pending further analysis, *Palasterina* is here retained within the Asteroidea.

Palasterina orchilocalia sp. nov.

Text-fig. 2.12A

1922   *Palasterina antiqua* (Hisinger); Spencer, p. 228, 231, 232 (text fig. 167).

1925   *Palasterina antiqua* (Hisinger); Spencer, pl. XVIII, fig. 1 [plate to accompany description in Spencer 1922].

1965   Palasterina antiqua (Hisinger); Owen, p. 562.

Derivation of name. From the Greek '*orchilos*', wren, and '*kalia*', bird's nest, in reference to Wren's Nest National Nature Reserve, Dudley, England, where many of the finest Much Wenlock Limestone Formation fossils were found.

Holotype. BU 675, the only specimen, from the Much Wenlock Limestone Formation (Homerian) of Dudley, England.

Diagnosis. *Palasterina* with rays projecting distinctly beyond central disc; interradii and oral ray margins with small, irregular accessory ossicles; inferomarginals indistinguishable from accessory ossicles. Adambulacrals strongly convex, with incurved projection towards ambulacral groove. Ambulacrals broad and flat.

Description. Five-rayed species of *Palasterina* almost identical in size (R:r approx. 17 mm:6 mm) to largest specimen of *Palasterina primaeva* and holotype of *P. antiqua*. Interradii with more accessory ossicles than in *P. primaeva* but distinctly fewer than *P. antiqua*. Adambulacrals asymmetrical and pronouncedly convex, with projection which incurves

proximally on ambulacral side of ossicle. Ambulacrals flatter than in *P. antiqua*. Inferomarginals, if present, very similar to accessory ossicles on oral margin of ray. Central disc not preserved. Aboral surface not seen.

Remarks. The holotype (Text-fig. 2.12a) was originally described as a new specimen of *Palasterina antiqua* (Hisinger, 1837) by Spencer in 1922. It has only four rays preserved, but when photographed by Spencer (1925, pl. 18, fig. 1) all five rays were present. Why one ray has since been removed is not clear, but, from Spencer's photograph, the missing ray was well-preserved and may have shed further light on the ossicle arrangements. The remainder of the specimen is quite poorly preserved, making specific and generic assignation difficult, but it is quite different from the holotype of *P. antiqua* (GMK 606, Text-fig. 2.12b) and the specimen of *P. antiqua* figured by Dean (1999*b*, pl. 12, fig. a). The adambulacrals of *Palasterina antiqua* are more symmetrical, without incurving projections, the ambulacral groove is deeper, with ambulacral plates that have a distinct transverse ridge, and the inter-radial areas are occupied by a far greater number of ossicles. Spencer (1922, p. 232) noted that BU 675 showed clear differences from the holotype of *P. antiqua* in terms of the shape of the adambulacrals and the arrangement of interradial plates, but with only a single specimen known, felt it unnecessary to erect a new species. Undoubtedly, further material would be of great assistance, but the differences between BU 675 and GMK 606 are so marked that they cannot belong to the same species. On first examination, there was some doubt as to whether BU 675 even belonged to the same genus as GMK 606, but, following the generic diagnosis of *Palasterina* (Spencer and Wright 1966), and on the basis of the very limited material, it seems injudicious to remove BU 675 to a new genus.

2.2 DISCUSSION

Although the total number of specimens is small, the asteroid fauna of the Much Wenlock Limestone Formation is a remarkable one, as it includes the earliest known multiradiate species, *Lepidaster grayi*, and the first starfish with a cushion-star body morphology, *Doliaster brachyactis*. Additionally, a third, distinctive body shape is seen in the extremely long-rayed form of *Lepidactis wenlocki* (specimen SM A12568). This wide morphological variation between taxa is in sharp contrast to the relatively conservative morphologies seen in Ordovician taxa, and indicates that a diversification of asteroid body plans had occurred by the Wenlock.

As noted above, there are very few horizons at very few localities in which Silurian starfish are preserved, primarily as a function of the asteroid skeleton being formed of

separate ossicles connected by soft tissue that decays rapidly after death. However, even despite the scarcity of horizons, it is notable that the taxa present in the Much Wenlock Limestone Formation do not show close morphological similarities to many of the other species described from Silurian rocks in other areas: *Lepidaster*, *Lepidactis* and *Doliaster* are all monospecific genera found only in the formation. The small number of starfish present in the Wenlock rocks of Gotland have never been formally described, but examination indicates that none of the material is conspecific with that from the Much Wenlock Limestone Formation, whilst the same is true of the faunas from the Llandovery of the Pentland Hills, Scotland, and the Ludlow of Leintwardine. With only six species present in the Much Wenlock Limestone Formation, four of which are known only from one surface (oral or aboral) and thus cannot be directly compared with other taxa, a cladistic analysis of the asteroids has not been attempted. A comprehensive phylogenetic analysis of all Silurian starfish would be far more informative, but such an approach was not possible within the scope and time constraints of this project.

The apparent morphological diversity of asteroids both within the Much Wenlock Limestone Formation and between Silurian faunas may be an artefact of the scarcity of material, and may also reflect preservation of taxa adapted to different ecological niches. However, it may also be the result of behavioural diversification. Some authors (e.g. Gale 1987; Donovan and Gale 1990; Gale and Donovan 1992) have interpreted Palaeozoic asteroids as having been capable only of feeding on detritus or small, immobile benthos, with asteroids not beginning to occupy the wide range of environmental and behavioural niches seen in extant forms until the Mesozoic. However, it might be expected that, if they utilized only a very limited number of feeding methods, Palaeozoic starfish would show a relatively limited range of body shapes. This may be true of Ordovician taxa (see e.g. Dean 1999*a*, *b*), but the morphological diversity seen in asteroids from the Much Wenlock Limestone Formation suggests that, at least by the Wenlock, starfish had begun to utilize a wider range of feeding techniques or occupy a wider variety of ecological niches than has been previously appreciated. This topic is discussed further in Chapter Three.

CHAPTER THREE

BIOLOGICAL AND ECOLOGICAL SIGNIFICANCE OF *LEPIDASTER GRAYI*, THE FIRST MULTIRADIATE STARFISH

ABSTRACT. *Lepidaster grayi* Forbes, 1850, from the Much Wenlock Limestone Formation (Silurian: Wenlock) of England, is the first species of starfish (Echinodermata: Asteroidea) to deviate from pentaradial symmetry, having thirteen rather than five rays. Based on supernumerary ray development in extant multiradiate asteroids, two models are proposed for the addition of eight rays seen in *L. grayi*. In the 'all-in-one' hypothesis, all rays were added in the same interradius, whereas in the 'quadrants' hypothesis generations of rays were added in each of four interradii. A small specimen, apparently having only nine rays, suggests that the latter hypothesis might apply to *L. grayi*. The presence of supernumerary rays in Silurian starfish, combined with the numerous other Palaeozoic multiradiate taxa, shows that asteroids have been able to deviate from pentamerism for much, if not all, of their evolutionary history, although the different methods of supernumerary ray addition reveal that the multiradiate condition is not homologous in all taxa. The ecological significance of Silurian starfish having supernumerary rays is discussed: by functional convergence with morphologically similar extant forms *L. grayi* is interpreted as an active predator.

The five classes of the Phylum Echinodermata display a wide array of unusual and unique features, from the ability of sea cucumbers to eviscerate themselves then regenerate the lost internal organs, to the elaborate jaw structure (Aristotle's Lantern) found in echinoids. Perhaps the most striking characteristic of the phylum, though, is the five-fold body symmetry of most adult echinoderms.

The origins and nature of echinoderm pentamerism are well debated (e.g. Nichols 1967*a*, 1967*b*; Stephenson 1967, 1974, 1979; Lawrence 1988; Lawrence and Komatsu 1990; Hotchkiss 1998*a*, 1998*b*, 2000) but remain contentious, particularly because a number of early taxa (e.g. helicoplacoids) are not pentaradial. Almost all extant echinoderms, however, show five-fold symmetry. Echinoids and holothurians are the most consistent, always having five ambulacral grooves, although holothurians and some echinoids have a superimposed bilateral symmetry. Crinoids may have supernumerary arms, but these normally occur in pentamerous multiples, due to bifurcation of the five primary brachia.

Asteroids, and to a lesser extent ophiuroids, are the exception, for although most species are five-rayed, deviations from pentamery are encountered on numerous occasions, across both time and taxa. Of 34 extant asteroid families, 20 include only five-rayed forms,

nine have both five-rayed and multiradiate species, and five families are solely multiradiate (Hotchkiss 2000). As most of these multiradiate forms have ray numbers that are indivisible by five, questions are raised about the nature of pentamerism, both in starfish and across the phylum as a whole.

3.1 ASTEROID PENTAMERISM

Most species of starfish are five-rayed and this is tightly regulated developmentally, such that deviation from pentamerism in five-rayed species is rare (Lawrence and Komatsu 1990). However, the presence of both non-pentameral species and of non-pentameral individuals in otherwise five-rayed species shows that there is a degree of variability not seen in other echinoderms. A number of hypotheses have been proposed to explain this variability (see Hotchkiss 1998*a* for summary) but two broad schools of thought prevail (Hotchkiss 2000). The first states that the number of rays is naturally variable, but that five has, for reasons unspecified, been naturally selected in most echinoderms (see e.g. Dawkins 1996). The second argues that pentamerism is fixed and that it is the deviations that need explanation (Hotchkiss 1998*a*, 1998*b*, 2000). Given that most asteroids are pentaradial and that the symmetry is present in all other crown-group echinoderms, the latter hypothesis appears to be the more plausible, but until the recent work of Hotchkiss, outlined below, there had not been a comprehensive examination of the phenomenon.

On the basis of the suggestion by Lawrence (1987, p. 7) that five-part symmetry is 'rigidly programmed into the developmental process [of echinoderms]' Hotchkiss (1998*a*, 2000) examined the ontogeny of starfish, both pentameral and non-pentameral, to try to establish the underlying pattern. This followed his earlier research into echinoderm pentamerism (Hotchkiss 1995, 1998*b*) and the proposal of a 'rays-as-appendages' model (Hotchkiss 1998*b*) for its origin. One of the predictions of that model was that asterozoans with a non-pentaradial number of rays as adults actually begin with five rays, adding the supernumerary rays later in embryological development. This was supported by studies of the metamorphosis of extant multiradiate asteroids (summarized by Hotchkiss 2000): *Acanthaster planci* is five-rayed at metamorphosis before adding up to 16 extra rays; the six-rayed species *Leptasterias polaris* and *Leptasterias hexactis* show a distinct time separation between developing the first five rays and the one supernumerary ray; *Stichaster australis* (9-12 rays) and *Pycnopodia helianthoides* (up to 24 rays) both metamorphose with five rays, as does the nine-rayed *Luidia senegalensis*. Hence, Hotchkiss (1998*a*, 2000) proposed the 'FIVE-PLUS' hypothesis, that five primary rays are generated synchronously as a developmentally constrained unit and that separate, independent pathways produce supernumerary rays. The

nature of these pathways is not clear, but Hotchkiss (2000) suggested post-generation of rays in the incompletely developed starfish or intercalated regeneration of rays in the imago as two possibilities.

Most extant echinoderms have the ability to regenerate lost body parts and there is evidence that at least some Palaeozoic forms were able to do the same (see e.g. Ausich and Baumiller 1993; Bartels *et al*. 1998; Donovan and Schmidt 2001). Crinoids can grow new arms, pinnules, cirri and even regenerate the calyx (I. C. Wilkie, pers. comm. 2001); ophiuroids are capable of re-growing their rays and central disc; echinoids can regenerate spines and pedicellariae; holothurians, as noted earlier, can eject their internal organs, creating replacements within five weeks (Garcia-Arraras *et al*. 1999) and asteroids can re-acquire rays lost to predation or autotomy. Some starfish, such as the Pacific genus *Linckia*, are even capable of growing new bodies from a single autotomized ray (Rideout 1978).

The presence of five primary rays in multiradiate starfish indicates that an underlying pentameral symmetry is as persistent in asteroids as it is in other crown-group echinoderms, with deviations being the result of secondary modifications of the primitive five-part subdivision of the body. The presence of supernumerary rays is a derived character, superimposed onto an originally pentaradial animal, in the same way that the derived asymmetry of irregular echinoids obscures the original pentamerism. The earliest, Ordovician starfish species are all five-rayed, with very rare six-rayed individuals probably the result of developmental irregularities (J. Dean, pers. comm. 2000). There are no four-rayed asteroid species, living or fossil, most extant taxa are five-rayed, and five primary rays are present in multiradiate forms. Thus, Dawkins' (1996) argument that the existence of multiradiate starfish disproves the hypothesis that echinoderms are fundamentally pentaradial is difficult to uphold. Furthermore, his assertion that the occurrence of 'mutant [asteroid] *individuals* with three, four or six-way symmetry' (Dawkins 1996, p. 216) supports the argument is to imply that organisms must never deviate from a paradigm in order for it to hold true. Unquestionably, the existence of asteroid species with more than five rays requires a plausible explanation, but the 'FIVE-PLUS' hypothesis provides this. Using teratological specimens to refute echinoderm pentamerism is as logical as arguing that humans are not ten-fingered because occasional polydactylous individuals occur.

Additionally, the variety of body plans seen in extant echinoderms means that the potential for deviation from pentamerism is not constant across the phylum. In order to subdivide their bodies into six portions, rather than five, echinoids and holothurians would have to go undergo a major anatomical rearrangement that 'would certainly be disadvantageous' (Stephenson 1967, p. 994), and the effect would be similar for crinoids adding a sixth radial plate and brachium. Even ophiuroids, with a body layout superficially resembling that of asteroids, are rarely non-pentameral. The physical demarcation of the

central disk from the rays in brittle stars may make the acquisition of additional rays more difficult than in starfish, but the limited number of multiradiate ophiuroids is probably the result of functional constraints associated with their mode of locomotion (J. M. Lawrence, pers. comm. 2001). Unlike asteroids, which use tube feet to pull themselves forward, ophiuroids move by snaking their rays from side to side across the sea floor and additional rays would interfere with the motion of the primary rays. As starfish have a body unconstrained by skeletal rigidity (as compared to an echinoid test, for example), and with the functional ability of the five primary rays not inhibited by the acquisition of supernumerary rays, their potential for being non-pentaradial is much greater than other echinoderm classes. It is not surprising, therefore, that forms with more than five rays are known from as far back as the Wenlock, nor that unrelated multiradiate starfish have occurred on numerous occasions across the last 425 million years.

3.2. DEVIATION FROM PENTAMERISM IN PALAEOZOIC ASTEROIDS

From their first appearance in the Tremadoc, and throughout the Ordovician, all species of asteroid are pentaradial (Dean 1999*b*). As noted above, very occasional six-rayed individuals are known, but it is not until the Silurian that consistently multiradiate species are recorded. *Lepidaster grayi* Forbes, 1850 from the Much Wenlock Limestone Formation is the earliest, with eight specimens known; the four most complete examples all having 13 rays (see Chapter 2). *L. grayi* has long been the only known pre-Devonian multiradiate starfish, but a second 13-rayed species, as yet undescribed, has been recently discovered in the Kilmore Siltstone (Ludlow) of Victoria, Australia (D. J. Holloway, pers. comm. 2001).

Absent from the Ordovician and scarce in the Silurian, multiradiate asterozoans are relatively abundant in the Devonian. The most prolific horizon is the Hunsrückschiefer (Lower Devonian) of Germany. Six species were erected in the latter half of the 19th Century – *Helianthaster rhenanus* Römer, 1863, *Medusaster rhenanus* Stürtz, 1890, *Palaeosolaster gregoryi* Stürtz, 1899, *Echinasterias spinosus* Stürtz, 1899, *Echinodiscus multidactylus* Stürtz, 1899, and *Echinostella traquairi* Stürtz, 1899 – but both Schuchert (1915, p. 209) and Spencer (1925, p. 237) decided that *E. spinosus*, *E. multidactylus* and *E. traquairi* were synonyms of *P. gregoryi*. Lehmann (1957) redescribed the material, listing five multiradiate taxa: *H. rhenanus*, *H. rhenanus* var. *microdiscus*, *M. rhenanus*, *P. gregoryi* and *Kentrospondylus decadactylus* Lehmann, 1957. Except *K. decadactylus*, all were placed in the Asteroidea. In their account of the fossils of the Hunsrückschiefer, Bartels *et al.* (1998) included *H. rhenanus*, *H. rhenanus* var. *microdiscus* and *P. gregoryi* in the asteroids and

TABLE 3.1. Palaeozoic multiradiate asteroids.

Age	Species	Rays
Permian	None known	-
Carboniferous (Namurian)	*Lepidasterella montanensis* Welch, 1984	27-35
Carboniferous (Visean)	*Schondorfia fungosa* Blake and Guensburg, 1989	10
Carboniferous (Tournaisian)	*Lacertasterias elegans* Blake and Guensburg, 1989	19 or 20
Devonian (Upper)	*Lepidasterella gyalum* (Clarke, 1908)	23-25
Devonian (Upper)	*Devonistella filiciformis* (Woodward, 1874)	11
Devonian (Middle)	*Arkonaster topororum* Kesling, 1982	28
Devonian (Middle)	*Michiganaster inexpectatus* Kesling, 1971	17-25
Devonian (Lower)	*Palaeosolaster gregoryi* Stürtz, 1899	25-29
Devonian (Lower)	*Helianthaster rhenanus* Römer, 1863	14-16
Silurian (Ludlow)	Unidentified Australian form	13
Silurian (Wenlock)	*Lepidaster grayi* Forbes, 1850	13
Ordovician	None known	-

classified *M. rhenanus* and *K. decadactylus* as ophiuroids, but much uncertainty remains over the systematics. Current research suggests that all five species, with the possible exception of *P. gregoryi*, are ophiuroids (A. Glass, pers. comm. 2001) but pending further study the assignments of Bartels *et al.* (1998) are followed here.

Elsewhere, *Michiganaster inexpectatus* Kesling, 1971 and *Arkonaster topororum* Kesling, 1982 were found in the Middle Devonian of Michigan and Ontario respectively, and *Devonistella filiciformis* (Woodward, 1874) in the Upper Devonian of Harberton, near Totnes, Devon (see Spencer 1927, p. 369). The Upper Devonian of New York State also contains multiradiate asteroids, but their taxonomy is more problematical. Initially assigned to one species – *Helianthaster gyalum* Clarke, 1908 – Schuchert (1915, p. 160) reinterpreted the largest of Clarke's (1908) specimens as *Lepidasterella babcocki*, a new species belonging to a new, monospecific genus, with the other material assigned to *Palaeosolaster*? *gyalum* (Clarke, 1908). Ruedemann (1916) thought the specimens all belonged to the same genus, transferring *P*? *gyalum* to *Lepidasterella*, whilst Spencer (1927, p. 384) was uncertain whether there were 'true specific differences in the material.' Spencer and Wright (1966, p. U65) decided there were not, that *Lepidasterella* was monospecific and, as Clarke (1908) named the type material before Schuchert (1915), his *L. gyalum* took priority.

Multiradiate asteroids were not known from the post-Devonian Palaeozoic until Welch (1984) described *Lepidasterella montanensis* from the Bear Gulch Limestone

(Namurian) of Montana. Then Blake and Guensburg (1989) named *Lacertasterias elegans* from the Gilmore City Formation (Tournaisian) of Iowa, and *Schondorfia fungosa* from the Haney Formation (Visean) of Illinois. At present, no multiradiate starfish are known from rocks of Permian age.

3.3. ORIGIN OF THIRTEEN RAYS IN *LEPIDASTER GRAYI*

Lawrence and Komatsu (1990) showed that the number of rays in multiradiate species can be either constant or variable, but that the highest constant number appeared to be 11. Species with a higher number of rays show a higher degree of variance; this is true of modern asteroids such as *Heliaster* (see P. Sanchez 2000) and a similar trend is seen in Palaeozoic forms (see Table 3.1). With only eight specimens, it is impossible to be certain that *Lepidaster grayi* always had 13 rays, but no specimen exceeds this number.

Following the 'FIVE-PLUS' hypothesis (Hotchkiss 1998*a*, 2000), *L. grayi* has five primary rays and eight supernumerary rays. The locus (or loci) of extra ray addition is not known, but modern multiradiate asteroids exhibit two broad patterns. The first is the addition of all supernumerary rays in the same interradius, intercalated between primary rays C and D (Carpenter letters as assigned by Moore and Fell 1966). This is the more common pattern, seen in genera such as *Acanthaster*, *Pycnopodia, Solaster* and *Crossaster*, although the precise sequence of ray addition is different for each genus (see Hotchkiss 2000, fig. 1). The second is the addition of supernumerary rays in generations in four of the five primary interradii, a phenomenon observed by P. Sanchez (2000) in *Heliaster* and *Labidiaster*, two of the most numerously rayed genera (up to 50 rays present in *Labidiaster annulatus*, Dearborn *et al*. 1991). Based on the work of Hotchkiss (2000) and P. Sanchez (2000), two possible models – the 'all-in-one' model and the 'quadrants' model – are proposed here for the acquisition of 13 rays by *Lepidaster grayi*.

3.3.1 THE 'ALL-IN-ONE' MODEL

The 'all-in-one' model (Text-fig. 3.1A), based primarily upon the common sun-star *Crossaster papposus* (Linnaeus), hypothesizes that *L. grayi* added all eight supernumerary rays in one interradius. *C. papposus* was chosen because it is morphologically similar to *L. grayi*, having an R:r ratio of around two and a modal ray number of 13 (57% of specimens: M'Intosh *in* Lawrence and Komatsu 1990). *C. papposus* is one of a group of asteroids that add all supernumerary rays in interradius C-D. In extant asteroids the anus lies in this interradius and
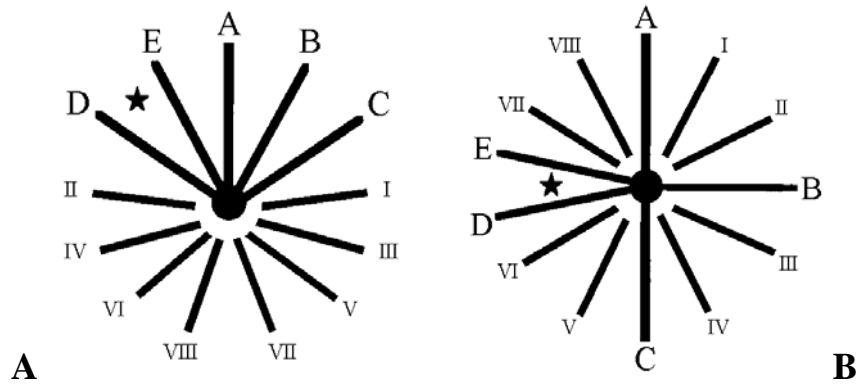
TEXT-FIG. 3.1. Possible models for the acquisition of supernumerary rays in *Lepidaster grayi* Forbes, 1850. A, The 'all-in-one' model. B, The 'quadrants' model. Five primary rays denoted by letters A-E, with madreporite between rays D and E; supernumerary rays denoted by Roman numerals I-VIII; diagrams after Hotchkiss (2000).

can be used as a marker to observe the exact pattern of supernumerary ray addition, but the anus is not known from any specimen of *L. grayi*. Thus it is not possible to establish whether the supernumerary rays were all added to one side of the anus, as in *Crossaster*, or added alternately either side of the anus, as in *Acanthaster*.

All supernumerary rays in *C. papposus* are added early in ontogeny, forming before the ring canal has completely developed (Gemmill *in* Hotchkiss 2000). A similar timing occurs in species of *Solaster*, where all rays have been added before the starfish is 1.5 mm in diameter (Carson 1988). Thus, if *L. grayi* followed the 'all-in-one' model, it is likely that the eight supernumerary rays would have been present when the starfish was no more than a few millimetres across.

3.3.2 THE 'QUADRANTS' MODEL

The 'quadrants' model (Text-fig. 3.1B) predicts that *L. grayi* added two rays in each of four interradii. This is based primarily on the Pacific sun-star *Heliaster helianthus*, which reaches a modal number of 33 rays (Tokeshi 1991) by adding seven supernumerary rays in each of four interradii (P. Sanchez 2000). Interestingly, however, Sanchez showed that *H. helianthus* adds a first generation of four rays, but then adds generations of eight rays, such that it begins with five primary rays, then successively nine, 17, 25 and 33. It does not have a 13-rayed stage. However, this does not necessarily negate the model, as it is possible that *L. grayi* added either one generation of eight rays (two rays in four primary interradii) or two generations of four rays (one ray in four primary interradii).

The only interradius in which supernumerary rays are not added is D-E, which contains the madreporite. To add supernumerary rays in the madreporitic interradius would require a fundamental alteration of the body plan because the madreporite is an integral part of the water vascular system. This is particularly pertinent for *L. grayi* with a large madreporite occupying the whole of the D-E interradius (see Text-fig. 2.1): it would have been impossible to intercalate supernumerary rays there.

In contrast to the early addition of supernumerary rays predicted by the 'all-in-one' model, asteroids that follow the 'quadrants' model continue producing rays well into adult life. *Heliaster*, for example, adds rays up to a diameter of 100 mm (Clark 1907). No specimen of *L. grayi* has any rays that are distinctly shorter than others, suggesting that all rays were added early in development.

3.3.3 APPLICATION OF MODELS TO *LEPIDASTER GRAYI*

In addition to differences in the pattern and timing of ray addition, there is a clear distinction between the 'all-in-one' model and the 'quadrants' model in terms of the end-number of rays – asteroids following the latter growth pattern normally have far more rays than those following the former. With 13 rays it would thus seem more likely that *L. grayi* followed the 'all-in-one' model. However, specimen BU 673 (Text-fig. 2.4) suggests that this may not have been the case. BU 673 is the smallest example of *L. grayi* and is imperfectly preserved, but had a diameter of between 25 and 30 mm, well within the size range at which *Heliaster* is still adding rays. This may be significant because Spencer (1918) was certain that BU 673 did not have 13 rays. He thought it had between eight and ten, and was an immature form that would have added the remaining rays later in development. Although this is difficult to verify, given the distorted nature of BU 673, the interradius between rays 2 and 3 (Text-fig. 2.4) is the least disturbed and forms an angle of 40º. If this is the true arc, it suggests that BU 673 had nine rays (360º/40º = 9). This fits neatly into the 'quadrants' model, with *L. grayi* adding one set of four rays to reach nine, then four more at a later stage to reach thirteen. However, if Lawrence and Komatsu (1990) are correct and the highest constant ray number in multiradiate asteroids is 11, it is equally plausible to explain BU 673 as evidence that all supernumerary rays were added early in the ontogeny of *L. grayi*, but that the total ray number was not fixed at 13. Further specimens are needed to fully clarify the matter.

3.4 REGENERATION OF RAYS IN MULTIRADIATE ASTEROIDS

As noted above, the ability to regenerate lost body parts is a feature seen in all extant classes of echinoderms. It was also suggested that the origin of supernumerary rays in asteroids might derive from the ability of starfish to grow new rays: that, in a broad sense, multiradiate asteroids are five-rayed forms that have generated 'replacement' rays without the primary rays having been lost. It is noteworthy, then, that, as well as showing distinct patterns of supernumerary ray addition, different multiradiate asteroids have markedly different regenerative abilities.

In *Heliaster*, ray regeneration is a common occurrence (P. Sanchez 2000) involving part or all of the ray, the latter often being associated with autotomy, and a large number of rays can be regenerated at the same time (see P. Sanchez 2000, fig. 2). In contrast, the genus *Solaster* does not appear to possess the same capabilities. Specimens of *S. dawsoni* and *S. stimpsoni* from the north-west coast of North America were observed to have regenerating rays (Engstrom *in* Lawrence 1992) but recent laboratory experiments (J. M. Lawrence, pers. comm. 2001) have shown that the body form of *Solaster* makes regeneration of rays difficult in that the wound of a severed ray does not always close. Thus a replacement ray cannot form and the starfish may become infected and die. A tentative correlation can therefore be made between the method of supernumerary ray addition and regenerative ability, with asteroids that follow the 'quadrants' model having greater capacity for regeneration. Multiradiate starfish using the 'all-in-one' model do not all have the same regenerative powers, though. *Acanthaster planci* is able to autotomize and re-grow many rays: McCallum *et al.* (1989) recorded specimens with seven, nine, or even ten regenerating rays.

If a modified ray regeneration mechanism is behind the origin of multiradiate asteroids, it is difficult to explain this variation of regenerative ability across multiradiate forms. P. Sanchez (2000, p. 573) argued that the multiradiate forcipulate asteroid genera *Pycnopodia*, *Rathbunaster*, *Heliaster* and *Labidiaster* add rays 'in a manner that is distinctive from other multiradiate starfish, possibly indicating a new taxonomic unit.' There can be little doubt that there are, at the very least, two separate origins for the acquisition of supernumerary rays in asteroids.

With so few specimens, and none that show rays of differing lengths that could be interpretable as undergoing regeneration, it cannot be established whether Silurian starfish such as *Lepidaster grayi* could regenerate rays. However, Silurian crinoids were capable of growing new arms (C. Franzén, pers. comm. 2001), and Bartels *et al.* (1998) showed that Devonian asteroids and ophiuroids could regenerate part, if not all, of a lost ray. Since regeneration of body-parts is a plesiomorphic feature of echinoderms, it is logical to assume that Wenlock asteroids also had regenerative capabilities. The absence of preserved evidence is almost certainly an artefact of the small number of fossil specimens, although there may

also have been fewer organisms that preyed on starfish in the Palaeozoic compared with the present day.

3.5 FUNCTIONAL AND ECOLOGICAL IMPLICATIONS OF SUPERNUMERARY RAYS IN *LEPIDASTER GRAYI*

3.5.1 PREVIOUS INTERPRETATIONS

Although there has been little previous work on *Lepidaster grayi*, its morphology has provoked some unusual interpretations regarding possible function. Forbes (1850) noted that the holotype was morphologically very similar to modern solasterids, particularly *Crossaster papposus*, but then stated that closer examination revealed *L. grayi* to have features 'so peculiar as to…render doubtful its position among true star-fishes' (Forbes 1850, p. 1). He speculated that *L. grayi* might in fact be a separate kind of echinoderm, part-starfish, part-crinoid, but it is unclear why Forbes reached this conclusion, since his account does not specify which aspects of the fossil were especially unusual.

Spencer (1918) had no doubt that *L. grayi* was a true starfish, but his interpretation of its life position retained an element of Forbes's suggestion that it had affinities with crinoids. *L. grayi*, Spencer (1918, p. 123) argued, was a non-predatory, sessile asteroid that lay with its aboral surface against the substrate, collecting food from the water column, an interpretation later generalized to all Palaeozoic multi-rayed starfish (Spencer and Wright 1966, p. U24). For *L. grayi*, he based this hypothesis on three pieces of evidence: firstly, that all known specimens were preserved showing their oral surfaces; secondly, that the presence of strong muscles between the adambulacrals 'must have bent the arms upwards' (Spencer 1918, p. 124); and thirdly, that the tube feet could not have been used for locomotion due to their small size. Spencer did not explain how he inferred the dimensions of the tube feet, but it is presumed that it was based on his conclusion that the arm cavity was small (Spencer 1918, p. 122). Additionally, Spencer argued that an upside-down mode of life would explain the madreporite being positioned in an oral interradius, rather than on the aboral surface as in modern forms. If *L. grayi* lived in the normal orientation for asteroids with its oral surface against the substrate, a madreporite on that surface 'would obviously have been useless functionally' (Spencer 1918, p. 124).

Blake and Guensburg (1989) disagreed with Spencer's interpretation, and suggested instead that *L. grayi* was in most respects similar to modern multiradiate asteroids, both in life position and feeding behaviour. They argued that it was unlikely *L. grayi* lived with its aboral surface against the seabed since this behaviour is undocumented in modern species, and

asteroids are anatomically arranged to function with the oral surface against the substrate (Blake and Guensburg 1989, p. 336). Furthermore, large interadambulacral muscles do not preclude flexible movement of the rays, the madreporite could still have functioned even if facing the seabed, and small tube feet would not necessarily have prevented locomotion. They also noted that the way-up of the specimens known to Spencer was likely to reflect the depositional conditions rather than the life position of *L. grayi*, and questioned the purpose of having a heavily plated aboral surface if it were pressed against the substrate.

It is proposed here that the madreporite was neither oral nor aboral, but truly interradial. The madreporite of the best-preserved specimen of *L. grayi* (BGS 27515) is wholly on the oral surface, but only touches the inferomarginals in the proximal part of the interbrachial arc. A short distance further along its perimeter the madreporite is in contact with a row of displaced aboral ossicles, and at its distal-most end it is not adjacent to any ossicles. Clearly it is not in its natural position and has been at least partly displaced onto the oral surface. The most likely mechanism to explain this is that the specimen lived with its oral surface against the substrate, was buried either whilst alive or recently dead, and that the combination of post-mortem collapse and weight of overlying sediment forced the madreporite from an originally interradial position. Such a position for the madreporite would have enabled it to function normally, as it would have been facing into the water, approximately perpendicular to the substrate.

The fact that specimens of *L. grayi* invariably show the oral surface is intriguing, but unlikely to represent evidence of an upside-down mode of life. Given that the best-preserved fossils in the Much Wenlock Limestone Formation occur in storm-generated obrution deposits, the suggestion by Blake and Guensburg (1989) that specimens were transported and inverted prior to burial is perfectly feasible (see also Jones and Portell 1988). Conversely, it is quite likely that some specimens are preserved the right way-up at the base of the lithology that buried them, thus showing their oral surface. This is supported by evidence of way-up seen in the matrix surrounding specimen NOTNH FS03795. The specimen is preserved in a thin horizon of siliciclastic mudstone that forms a veneer on one surface of a bioclastic limestone, and the geopetal infill of a brachiopod close to the junction of the two lithologies (see Appendix) indicates that the mudstone underlies the limestone. Thus, NOTNH FS03795 lies at the base of the bed, and is preserved upside-down, although a note of caution must be raised because reworked and inverted geopetals are found in parts of the Much Wenlock Limestone Formation.

3.5.2 MULTIRADIATE ADVANTAGES

In terms of biomass, being multiradiate represents a drastic change from being five-rayed. A 13-rayed starfish of the same diameter as one with five will need more food to support its greater body mass. This implies that there must be some advantage associated with having supernumerary rays.

The most obvious consequence of having more than five rays is an increase in the number of tube feet. As tube feet are used for locomotion, attachment and feeding, the implication is that multiradiate asteroids ought to be more mobile, more able to resist being detached from the seabed, and more successful feeders.

3.5.2.1 Mobility

Lawrence (1988) reviewed the functional consequence of asteroids being multiradiate rather than five-rayed in an attempt to explain why, if it is advantageous, the multiradiate state is not dominant in modern starfish. With regard to mobility, Lawrence stated that there is no evidence that multiradiate forms have greater locomotive capacities; Feder and Christiansen (1966) showed that five-rayed species of the family Astropectinidae are able to move as quickly as multiradiate forms. That said, the sunflower star *Pycnopodia helianthoides* is extremely mobile, being able to reach speeds of 1.6 m per minute in pursuit of prey (Lambert 1995).

3.5.2.2 Attachment

Verrill (1914) thought that a greater number of rays increased the ability of a starfish to attach itself firmly to the substrate in high-energy environments. Again, Lawrence (1988) argued that there was no firm evidence to support this, because both multiradiate forms such as *Heliaster* and five-rayed genera such as *Pisaster* live in high-energy conditions, and there are numerous multiradiate species living in quiet marine environments. However, compared with multiradiate starfish from low-energy conditions, *Heliaster* has a large central disk, and short rays that are fused proximally, which Lawrence (1988, p. 598) speculated might be 'an adaptation necessary for the multiarmed condition in a rigorous environment'. For the Pacific South American species *H. helianthus*, Tokeshi (1991) noted that small individuals (<100 mm diameter) had a weaker grip on the substrate than their larger counterparts.

3.5.2.3 Feeding

Most extant asteroids are carnivorous, either as scavengers or predators (Sprinkle 1987, Tudge 2000). A multiradiate starfish of the same diameter as a five-rayed form has a greater body mass and, assuming a similar metabolic rate, needs a larger quantity of food. There are two ways in which this can be achieved: either by out-competing the five-rayed species for the same food source, or by adapting to feed on a separate one. For many multiradiate

asteroids it is the latter – a prime example is shown by the order Brisingida, taxa of which capture plankton by forming a crinoid-like feeding fan with their long, thin rays (see e.g. Emson and Young 1994).. However, most multiradiate forms are specialized predators: the crown-of-thorns starfish *Acanthaster planci* is notorious for its ability to decimate coral communities (Blake 1979); the common sun-star *Crossaster papposus* eats echinoderms, in particular echinoids and other starfish (Hayward *et al*. 1996); the Antarctic sun-star *Labidiaster annulatus* catches krill, amphipods and small fish from the water column (Dearborn *et al*. 1991); *Solaster stimpsoni* eats only holothurians, but is itself the staple diet of *Solaster dawsoni* (Tudge 2000); and *Pycnopodia helianthoides* is capable of capturing large, mobile prey, such as crabs and octopuses, as well as spending days burrowing for infaunal bivalves (Shivji *et al*. 1983). Supernumerary rays enable these starfish to catch active prey and to manipulate sessile organisms that five-rayed forms cannot.

At first glance, *Heliaster helianthus* appears to be an exception to this rule, since it feeds on the same prey types – mussels, gastropods and barnacles (Tokeshi 1991) – as many five-rayed species. However, Vermeij (1990) stated that *Heliaster* is the only asteroid genus that is known consistently to feed on such organisms in a tropical environment, sympatric genera feeding either on small prey that can be swallowed whole, or on immobile animals with exposed soft parts, like corals and sponges. Again, its multiradiate body shape enables *Heliaster* to feed in a different way to pentaradial asteroids.

3.5.2.4 All-round senses
One functional aspect of the multiradiate state not discussed by Lawrence (1988) is its closer approximation to radial symmetry than being five-rayed. Simplistically, a pentaradial starfish has an arc of 72º between each ray, whereas a thirteen-rayed starfish reduces that arc to 27.7º. Like all echinoderms, asteroids have no brain or true centre of organization and no front or back, which means that the rays act rather like individual organisms in a moving colony: each ray has sensory devices and can lead the animal in a chosen direction. Both in terms of prey detection and predator avoidance, supernumerary rays would appear to be an advantage in that they give more complete coverage of the area around the starfish, especially since asteroid rays, unlike those of ophiuroids, are relatively inflexible in a lateral plane.

3.5.3 FUNCTIONAL MORPHOLOGY OF PALAEOZOIC ASTEROIDS

Dean (1999*a*) showed that there are many difficulties in assigning Palaeozoic asterozoans to the classes Asteroidea and Ophiuroidea, particularly in the Ordovician, but by the Ashgill the diagnostic body plan of each class had evolved (Dean 1999*b*, p. 8). Some Silurian asterozoans (e.g. *Palasterina* – see Chapter 2) remain problematical, but *Lepidaster grayi* is

unequivocally an asteroid and its functional morphology can be interpreted on that basis. The question is then whether Palaeozoic multiradiate starfish functioned in the same way as extant forms. As noted above, extant starfish with more than five rays are often active, voracious and very specialized predators. With an abundance of potential prey in Wenlock reef and inter-reef environments, the morphological similarity of *L. grayi* to living multiradiate species might lead automatically to the assumption that it too was carnivorous. However, there has been much debate over whether Palaeozoic asteroids were capable of feeding in the same way as modern forms, and particularly whether they were capable of extra-oral consumption. This is an extraordinary technique whereby the starfish extrudes its stomach over or into prey that is too large to fit into the mouth and digests the organism externally. The best-known exponent of this is the common starfish *Asterias rubens* Linnaeus, which eats mussels by positioning itself over the bivalve and using its tube feet to prise the valves open, forcing its stomach between them and consuming the unfortunate mollusc within its shell (see e.g. Norberg and Tedengren 1995; Sommer *et al*. 1999).

Gale (1987), Donovan and Gale (1990) and Gale and Donovan (1992) argued that all Palaeozoic asteroids were deposit-feeders, scavengers or predators of small, inactive benthic organisms, with Gale (1987, p. 129) stating that early Palaeozoic starfish were 'rather inflexible animals' without suckered tube feet, muscular rays or a flexible mouth-frame. The capture of mobile or irregularly shaped prey was thus precluded, as was predation on organisms larger than the mouth opening, with extra-oral feeding not evolving until the Mesozoic (Gale 1987; Donovan and Gale 1990; Gale and Donovan 1992). This was supported by Dean (1999*a, b*) in her analysis of the functional morphology of Ordovician asterozoans, and she concluded that the predominant mode of life was deposit-feeding, with occasional predation of sessile animals. Blake and Guensburg (1988, 1989, 1990, 1994) disagreed, arguing that, by the mid-Ordovician, asteroids had developed the same range of behavioural traits as modern forms, including extra-oral predation, a purported example of which was described from the Upper Ordovician of Ohio (Blake and Guensburg 1994). As the first multiradiate asteroid, *L. grayi* represents a significant change in starfish morphology, with the implication of an associated change in behaviour, and can be used to evaluate the competing hypotheses.

3.5.4 FEEDING BEHAVIOUR OF *LEPIDASTER GRAYI*

Although Blake (1987) and Gale (1987) produced different interpretations of asteroid phylogeny, it is generally agreed that there was a major diversification of the class in the Mesozoic (Donovan and Gale 1990; Blake and Guensburg 1990; Blake, Janies and Mooi 2000). The earliest example of a starfish belonging to an extant family is from the Late

Triassic (Blake, Tintori and Hagdorn 2000), although Gale (1987) and Donovan and Gale (1990) argued that neoasteroids were present also in the Middle Triassic, but no close relationship has been established between any Palaeozoic taxon and a crown-group family (Donovan and Gale 1990; Blake, Tintori and Hagdorn 2000). Morphological similarities between Palaeozoic and extant forms are therefore attributed to convergence – Gale (1987, p. 129) explained the resemblance of the Ordovician genus *Platanaster* to living paxillosids in this way, as did Blake and Guensburg (1994, p. 235), who noted the similarity of form between another Ordovician genus, *Promopalaeaster*, and modern asteriids.

As *Lepidaster grayi* is not closely related to any extant multiradiate starfish, its morphological similarity to taxa such as *Crossaster papposus* must be the result of convergence. Most extant multiradiate asteroids are active predators, but Gale (1987) argued that this feeding strategy was not available to Palaeozoic starfish because they did not have suckered tube feet, sufficient body or ray flexibility, and were not able to evert their stomachs. Thus, either *L. grayi* was not functionally convergent with living multiradiate species, or Gale (1987) was incorrect and at least some Palaeozoic starfish were active predators. The null hypothesis is the latter – it must be demonstrated that *L. grayi* could not have used similar feeding techniques to extant forms.

3.5.4.1 Tube feet morphology

All extant echinoderms have tube feet (podia). Following the Extant Phylogenetic Bracket hypothesis of Witmer (1992), they are an homologous feature derived from the same ancestor, rather than an homoplastic character that evolved independently in all five classes. Since tube feet occur in all living echinoderms, and there are no features of Silurian starfish to suggest secondary loss, *Lepidaster grayi* and other Silurian asteroids possessed tube feet. According to Gale (1987), the tube feet of Palaeozoic starfish were not suckered, so they could not grip the valves of shelled prey in the way that extant starfish do when feeding extra-orally on bivalves. Additionally, they would have been incapable of gripping the substrate during high energy conditions. However, in a statement that applies equally well to asteroids in general, Gale and Donovan (1992, p. 346) concluded that the poor preservation potential of echinoderm soft-parts made it unlikely that fossilized tube feet of the Ordovician genus *Promopalaeaster* would ever be found. Without their preservation, it is impossible to verify the claim that the tube feet of Palaeozoic starfish were not suckered, but even if they were not, this does not rule out active predation (Blake and Guensburg 1988). Vickery and McClintock (2000) showed that modern asteroids of the families Luidiidae and Astropectinidae lack suckered tube feet, yet the genus *Luidia* includes multiradiate species that are active predators of mobile prey (Blake and Guensburg 1988, 1990; Hayward *et al*. 1996). Finally, work by Thomas and Hermans (1984, 1985), Flammang *et al*. (1994) and Flammang (1995) has

revealed that at least some starfish tube feet do not use suction to gain hold of prey items or substrates, but instead employ a form of chemical adhesion.

3.5.4.2 Body and ray flexibility

Describing early Palaeozoic asteroids as being 'rather inflexible animals' (Gale 1987, p. 129) is inexplicit and ambiguous. Extant starfish are generally regarded as flexible, but are slow-moving, and their rays have little capacity for lateral flexure, with most movement restricted to the vertical plane. Thus, living asteroids could be described in the same way. Although some Palaeozoic starfish do have larger ossicles than extant forms, this does not mean that their bodies were incapable of flexure – a relative displacement of just a few degrees between adjacent ossicles, extrapolated over a whole series, would have given substantial flexibility to a ray, for example. As noted by Blake and Guensburg (1988), the asteroid body is inherently flexible, being formed of unfused skeletal elements joined by connective tissues, and differences in ray musculature between Palaeozoic and extant forms (Gale 1987) do not alter this basic interpretation. *Lepidaster grayi* might not have had the ray flexibility for it to have been able to capture swift-moving organisms, but it was probably able to manipulate many of the same types of prey as modern starfish.

3.5.4.3 Mouth-frame flexibility and stomach eversion

One of the primary reasons Gale (1987) concluded that Palaeozoic starfish were detritivores and scavengers was his argument that they had inflexible mouth-frames, and could only have eaten food of smaller size than the buccal opening. As with body flexibility, this is difficult to accurately determine, but even if the mouth-frame of species such as *Lepidaster grayi* was incapable of being opened to any great degree, this does not necessarily rule out stomach eversion as a means of consuming larger prey. Living species of *Asterias* have a buccal opening of only a few millimetres (Tokeshi 1991), but are extra-oral predators, whilst *Luidia* can only partially extrude its stomach (Blake and Guensburg 1990) but is an active predator of organisms larger than its mouth diameter. Additionally, a small mouth-frame and inability to evert its stomach would not necessarily have meant *L. grayi* could only eat items that fitted into the mouth whole – the supernumerary rays and tube feet could have been used to manipulate larger food that was then eaten in stages intra-orally.

3.6 SUMMARY AND CONCLUSIONS

Lepidaster grayi is the earliest-known species of starfish to deviate from pentameral symmetry, but with the low preservation potential of asteroids it is quite possible that there

were species with supernumerary rays prior to the Wenlock. Without Ordovician examples, it is not possible to be certain that starfish have been able to break away from pentamerism throughout their evolutionary history, but *L. grayi* shows that they have been able to do so for most of that time. It is also clear that the multiradiate condition is homoplastic, having evolved independently in unrelated taxa on more than one occasion (Hotchkiss 2000). Whether the same developmental pathway, such as a modification of the mechanism that enables many asteroids to regenerate rays, led to the acquisition of supernumerary rays in different taxa is unclear. It is also unclear how a thirteen-rayed Silurian starfish evolved from pentaradial Ordovician species – the addition of eight rays is a drastic change in body morphology that apparently arose suddenly and without any known intermediate stage. Nonetheless, the evolution of *L. grayi* and other Palaeozoic multiradiate asteroids is a significant event in asteroid phylogeny, and would have had major ecological implications.

At least during the early Ordovician, asteroids showed little variation from the primitive body plan of small, five-rayed forms, suggesting that they had a limited range of modes of life, interpreted by Dean (1999*a*, *b*) as predominantly deposit-feeding and scavenging. By the Wenlock, however, starfish had developed a much more diverse range of body shapes (see Chapter 2), from the first species to show a cushion-star body shape, *Doliaster brachyactis*, to *Lepidactis wenlocki* with its long, thin rays, as well as the multi-rayed *L. grayi*. The precise timing of this morphological diversification is unknown, but it shows that, at least by the early Silurian, asteroids had begun to develop the variety of body shapes seen in present day species. By functional convergence, it can thus be inferred that they had also begun to develop a similar variety of life habits and feeding behaviour.

In terms of required technique, there is little to distinguish the whole-prey consumption of small immobile animals, such as brachiopods, from deposit-feeding, since both methods involve ingestion of material containing edible and inedible portions. Deposit-feeding is the more primitive strategy (see Table 3.2) in that much inedible material is consumed in order to extract small edible particles, whereas predation of sedentary animals guarantees a larger package of nutrients in one place, even if the inedible components of the prey must also be consumed. Gale's (1987) argument that asteroids used only these two relatively inefficient methods of nutrient-gathering for the first 240 Ma of their evolutionary history is possible, but improbable, given the morphological diversifications that occurred. Ordovician asteroids show primitive morphologies, so probably had primitive modes of life, but from the Silurian onwards there is an obvious diversification of body form, which must represent a similar diversification of behaviour.

If Gale (1987) is correct, and Palaeozoic asteroids did not have suckered tube feet, flexible rays, body or mouth-frame, and could not evert their stomach, it is difficult to explain the repeated occurrence of multiradiate asteroids prior to the Mesozoic, as they would have

been ecologically incomparable with extant multiradiate taxa. The hypothesis that Palaeozoic

TABLE 3.2. Evolution of feeding types utilized by asteroids. Not all feeding methods utilized by extant asteroids are listed, and the numbers applied to the derived states are not intended to represent an evolutionary progression, where type 3a is derived from type 2b, type 3b is derived from type 3a, or so on. However, they do represent a sequence of increasing complexity in terms of required characteristics – intra-oral predation of small, shelled benthos is achievable without a particularly flexible mouth frame or body, an eversible stomach, or adhesive tube feet, whereas extra-oral predation of active organisms requires a flexible body and rays, an eversible stomach and adhesive tube feet.

State	Feeding strategy	Modern example (with food)
Primitive	Intra-oral deposit-feeding/scavenging	*Asterina gibbosa* (detritus)
Derived (1)	Intra-oral predation of small benthos	*Heliaster helianthus* (barnacles)
Derived (2a)	Extra-oral predation of unshelled benthos	*Acanthaster planci* (coral)
Derived (2b)	Extra-oral predation of shelled benthos	*Asterias rubens* (mussels)
Derived (3a)	Intra-oral predation of active organisms	*Luidia ciliaris* (echinoderms)
Derived (3b)	Extra-oral predation of active organisms	*Crossaster papposus* (asteroids)

multiradiate asteroids were suspension-feeders (Spencer and Wright 1966) could be supported if taxa such as *L. grayi* had a morphology similar to that of extant filter-feeders, but brisingids, the only extant multiradiate starfish known to filter-feed, have long, very thin rays and a small central disc (Emson and Young 1994): *L. grayi* was not a filter-feeder. If Gale's (1987) functional interpretations of Palaeozoic asteroids are applied to *L. grayi*, all of the multiradiate advantages outlined in section 3.5.2 are inapplicable, and there is no obvious explanation for *L. grayi* having eight extra rays.

With an abundance of immobile benthic epifauna in the Much Wenlock Limestone Formation, *L. grayi* may not have needed to hunt active prey (derived states 3a and 3b), but that is not to say it was incapable of doing so. With a large central disk composed of numerous small ossicles, *L. grayi* has an inherent flexibility that would have enabled it to tackle larger benthic organisms, either swallowing them whole or extruding its stomach over them. Another possibility is a mode of life like that of *Acanthaster planci*, which feeds on corals: Blake (1979) showed that the supernumerary rays of *A. planci* are an adaptation to living and feeding on the irregular coralline surfaces. The abundance of rugose and tabulate corals in the Much Wenlock Limestone Formation raises the possibility that the supernumerary rays of *L. grayi* served a similar function.

CHAPTER FOUR

AN UNUSUAL NEW CRINOID FROM THE SILURIAN OF ENGLAND

ABSTRACT. *Calyptocymba mariae* gen. et sp. nov. is described from the Wenlock (Homerian) of Dudley, England. Unlike any other known Silurian crinoid, the small cup of *C. mariae* is only weakly mineralized. Because of this, the arrangement of the calycal plates is difficult to ascertain, and neither basal nor infrabasal ossicles are seen. However, the incorporation of the fixed brachials into the top of the cup, the uniserial, pinnulate arms and the cirri-bearing stem indicate that it is a member of the Subclass Camerata. All specimens of *C. mariae* are from a mudstone belonging to the Nodular Beds Member of the Much Wenlock Limestone Formation, deposited below fair weather wave-base, and their articulation shows that they were not transported far, if at all, prior to burial. Thus, the thinly plated cup and delicate body morphology of *C. mariae* are interpreted as adaptations to living in an environment of low velocity currents, the crinoids being stenotopic rheophiles.

ALTHOUGH isolated skeletal elements can be of great palaeontological value, particularly for biostratigraphy, a more complete understanding of the biology and ecology of extinct organisms is dependent on the discovery of articulated specimens. This is especially true of Palaeozoic crinoids, individual ossicles of which occur in vast, sometimes rock-forming quantities, but which are rarely found complete. Horizons of exceptional preservation, such as those found in the Silurian limestones that crop out in and around Dudley in the English Midlands, are thus of considerable significance. There, particularly during the Wenlock (~425 Ma), storm-generated obrution deposits smothered a diverse reef and inter-reef fauna that contained many echinoderms, including asteroids, cystoids, ophiocistioids and carpoids. Crinoids are by far the most numerous, however, and 56 species have been described from the Much Wenlock Limestone Formation (Widdison 2002), many preserved in exquisite detail.

Prior to microscopic examination, the specimens of *Calyptocymba mariae* gen. et sp. nov. had been identified as ophiuroids, since only the rays and central disc are obvious to the naked eye. Closer study revealed the presence of calycal plates and, in three cases, stems, such that the fossils are undoubtedly crinoids, but quite unlike any of the forms described by Widdison (2002). The most prominent distinguishing characteristics are the small calyx, thinly plated almost to the point of being unmineralized, and the long, slender arms and cirri-bearing stem.

4.1 MATERIAL, LOCALITY AND HORIZON

No specimens of *Calyptocymba mariae* are known other than those in the Holcroft collection of the Lapworth Museum, suggesting that *C. mariae* was preserved at a very small number of horizons, and possibly on only a single bedding plane. This is supported by all material having been found in 1890 in the same quarry, described in the catalogue of the Holcroft collection as 'Pit SS of Trindle House, Dudley'. The exact location of the quarry is unclear – Trindle House was the Dudley headquarters of The Mines Drainage Commissioners, who owned pits across the West Midlands – but the lithology in which the crinoids are preserved is a well-bedded, dark grey mudstone most probably representative of the upper part of the Nodular Beds Member of the Much Wenlock Limestone Formation. Thus, although the provenance of the specimens remains uncertain (see Appendix for further discussion), *C. mariae* is interpreted as being of Wenlock age.

4.2 SYSTEMATIC PALAEONTOLOGY

Terminology used follows Sprinkle (1987, pp. 573-577); all specimens are in the Lapworth Museum of Geology, University of Birmingham, UK; prefixed by BU.

<div align="center">

Class CRINOIDEA Miller, 1821

Subclass CAMERATA Wachsmuth and Springer, 1885

?Order MONOBATHRIDA Moore and Laudon, 1943

</div>

Remarks. The incorporation of the proximal brachial ossicles into the calyx and the presence of pinnules and cirri indicate that *Calyptocymba* belongs to the Camerata (*sensu* Ubaghs 1978). However, the indistinct nature of the calyx makes accurate ordinal and familial placement of the genus difficult. Camerates are separated into two orders – Monobathrida with monocyclic calyces and Diplobathrida with dicyclic calyces – but neither basal nor infrabasal plates are known in *Calyptocymba*. Because of the proximity of the radial plates to the stem, it is probable that the calyx of *Calyptocymba* was monocyclic, comparable in ossicular arrangement with *Clematocrinus retiarius* (Phillips *in* Murchison, 1839), a monobathrid from the Much Wenlock Limestone Formation (see Widdison 2002, pl. 5; text fig. 23), but until specimens are discovered that show the calyx in greater detail, this cannot be confirmed.

The thinly plated, almost unmineralized calyx of *Calyptocymba* is apparently unique amongst crinoids. It might therefore be argued that *Calyptocymba* is distinctive not only

generically, but also at a higher systematic level. However, all other morphological characters present, from the cirri-bearing stem to the pinnulate arms, can be found in members of the Camerata, so, pending a full phylogenetic analysis of the group, it is preferable to interpret *Calyptocymba* as an unusual monobathrid camerate rather than a member of a previously unknown higher clade.

Genus CALYPTOCYMBA gen. nov.

Derivation of name. From the Greek words '*kalyptos*', covered or concealed, and '*kymbe*', cup, in reference to the calyx being absent or only faintly delineated in all specimens. Gender feminine.

Type and only known species. *Calyptocymba mariae* gen. et sp. nov.

Diagnosis. Camerate crinoid with small, very thinly plated calyx; radials incorporating two fixed brachials beneath axillary. Brachia long, slender, uniserial, branching once immediately above cup to form ten arms; each brachial with pair of filamentous pinnules. Stem long, thin, with pairs of cirri spaced regularly along column.

*Stratigraphical range*. Known only from the Wenlock of central England.

Calyptocymba mariae sp. nov.
Text-figs 4.1–4.4

Derivation of name. In memory of my maternal grandmother, Marie Stead, whose enthusiasm for natural history inspired my own.

Holotype. BU 3752, from the Much Wenlock Limestone Formation (Silurian: Wenlock: Homerian) of Dudley, England.

Paratypes. BU 3751, 3753, 3754, 3755, 3756 (counterpart of BU 3755), 3757–62 (six individuals on same slab as BU 3755), 3763, 3764, all from same locality as holotype.
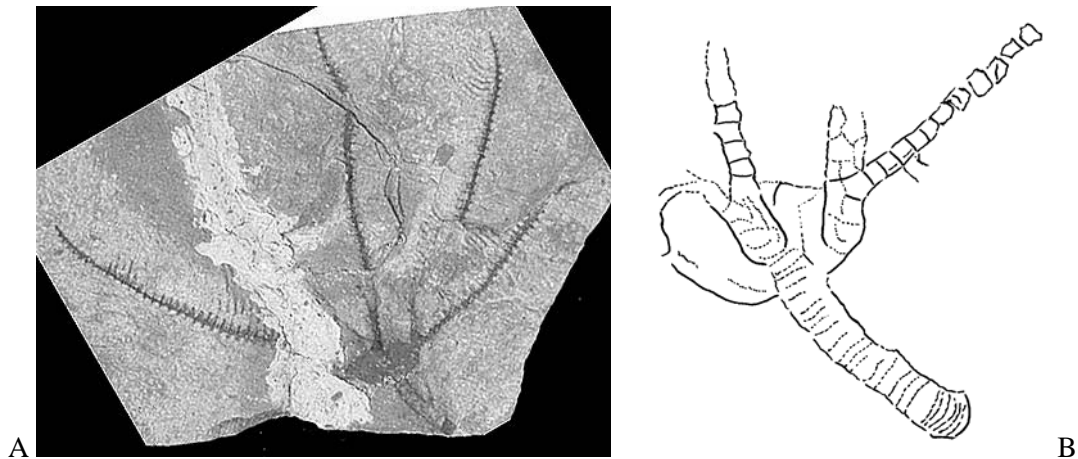
TEXT-FIG. 4.1. *Calyptocymba mariae* gen. et sp. nov., BU 3752 (holotype), Much Wenlock Limestone Formation, Dudley. A, photograph showing calyx, part of stem, and four pinnulate brachia, x 2; B, *camera lucida* drawing of calyx and stem, x 5.

Diagnosis. As for genus.

Description.

Calyx. Cup small (4–5 mm diameter) with thinly mineralized plates delineated only by suture lines. Calyx probably monocyclic, basal plates not seen. Radial plates large, octagonal; fixed brachials incorporated into top of cup, interbrachials not seen. Tegmen unknown.

Brachia. Brachia up to 30 mm long, thin (~0.3 mm), composed of up to 35 brachials. Isotomous branching occurs once immediately above cup, producing ten arms. First two brachial ossicles incorporated into radial plate, axillary triangular, all with granular/pustulate ornamentation. Brachials arranged uniserially, each with pair of long (up to 10 mm), filamentous pinnules.

Column. Like brachia, column long (up to 45 mm) and slender (1–1.5 mm diameter). Columnal ossicles round, 0.5–1 mm thick, bearing pair of cirri approximately every eighth columnal. Cirri up to 10 mm long with cirral ossicles 0.5 mm thick, 0.2 mm in diameter. Holdfast, if present, not seen.

The holotype (BU 3752; Text-fig. 4.1) shows part of the stem, a calyx with radial plates, and four almost complete brachia with pinnules. The most complete stem, with cirri, is that of specimen BU 3758 (Text-figs 4.3B, 4.4), whilst a shorter example is seen on BU 3759 (Text-fig. 4.3A), joined to the calyx on which suture lines of two radial plates are visible. The size,
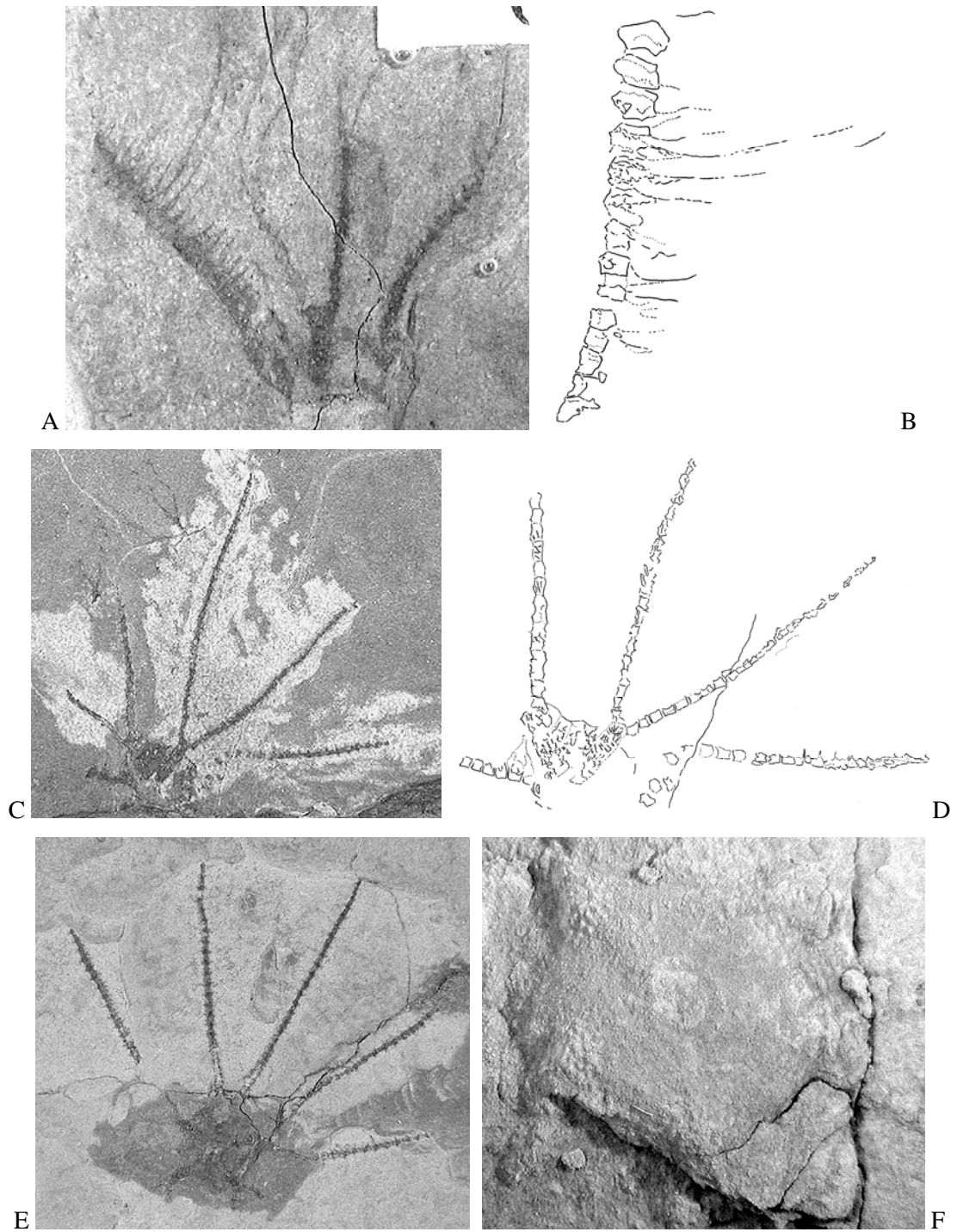
TEXT-FIG. 4.2. *Calyptocymba mariae*, gen. et sp. nov., Much Wenlock Limestone Formation, Dudley. A, photograph, and B, *camera lucida* drawing of paratype BU 3753, showing well-preserved pinnules, A, x 3.5, B, x 4; C, photograph, and D, *camera lucida* drawing of paratype BU 3754, C, x 2.5, D, x 3; E, paratype BU 3755, x 2.5; F, BU 3755, close-up of calyx, showing pustulose texture of fixed brachials, x 8.
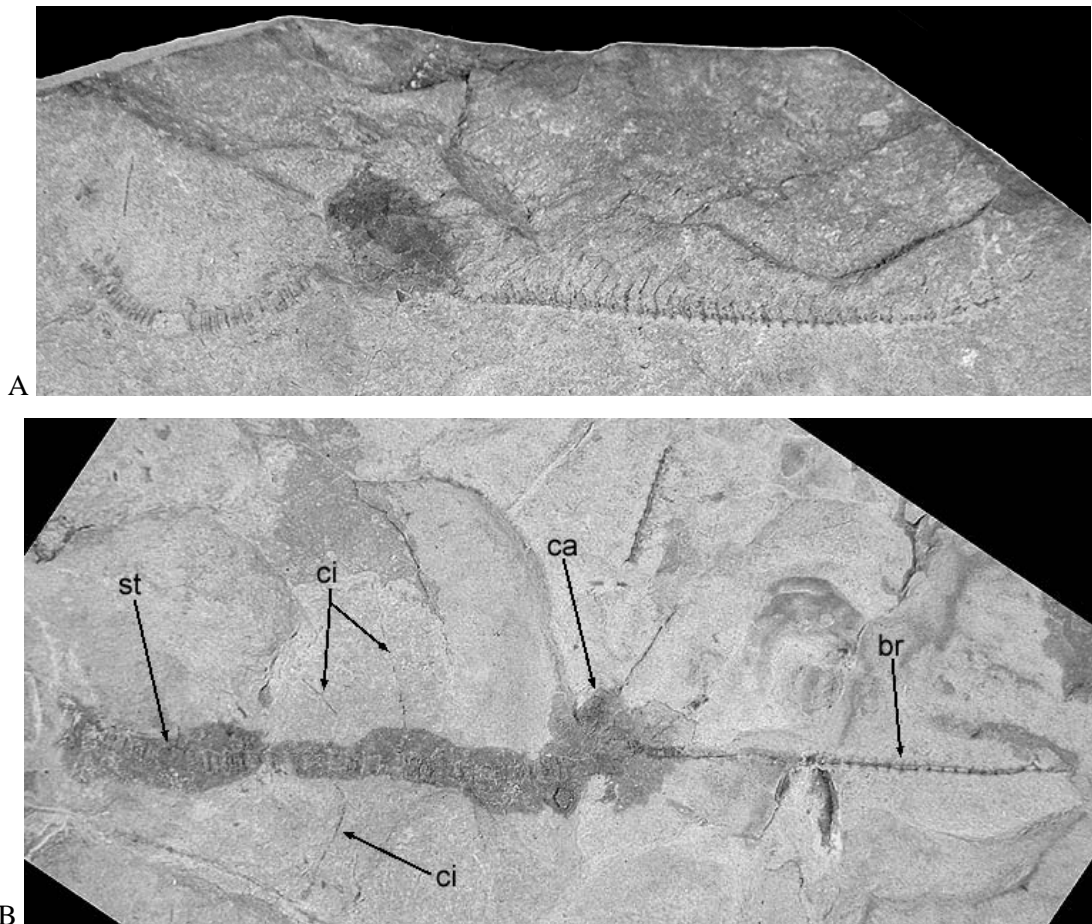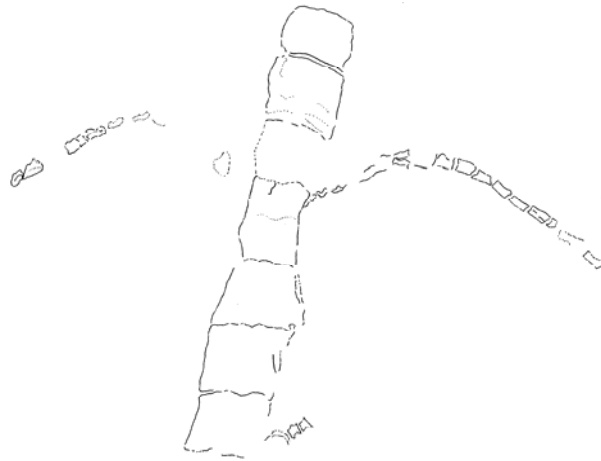
TEXT-FIG. 4.3. *Calyptocymba mariae* gen. et sp. nov., Much Wenlock Limestone Formation, Dudley. A, paratype BU 3759, showing stem, calyx and brachium, x 3; B, paratype BU 3758, showing stem (st) with cirri (ci), calyx (ca) and brachium (br), x 2.5.

ossicular organization and relationship to the brachials of the calyx is most clearly delineated on BU 3755 (Text-fig. 4.2E, F), whereas the longest pinnules are seen on BU 3753 (Text-fig. 4.2A). The longest, most complete brachium is preserved in BU 3754 (Text-fig. 4.2C).

Remarks. Two further Lapworth Museum specimens (BU 3765-6) are probably examples of *C. mariae*, but have been coated in a resinous substance of unknown composition that prevents detailed examination of characters. They cannot therefore be unquestionably assigned to the same species.

Of the crinoids described from the Much Wenlock Limestone Formation by Widdison (2002), the form that most closely resembles *Calyptocymba mariae* is the monobathrid *Clematocrinus retiarius* (Phillips *in* Murchison, 1839). Compared with *C. mariae*, *Cl. retiarius* (Text-fig.

TEXT-FIG. 4.4. *Calyptocymba mariae* gen. et sp. nov., Much Wenlock Limestone Formation, Dudley. BU 3758, *camera lucida* drawing of stem, showing columnals and cirri in detail, x 10.

4.5) is more stoutly constructed, with a much more thickly calcified calyx, and occurs in two morphotypes, one with ten arms and one with twenty (Widdison 2002), but the two species are the only crinoids from the Much Wenlock Limestone Formation to possess cirri along the entire length of the stem. Most specimens of *Cl. retiarius* were collected from a single stratigraphical horizon, a buff-coloured bed 4.58 m from the top of the Nodular Beds Member on Wren's Nest Hill (Widdison 2002).

4.2.1 Cup calcification of *Calyptocymba mariae*

The thin-plated cup of *C. mariae* is distinctive: the calyx functions to protect the internal organs, and is normally formed of robustly calcified ossicles. Thinner calycal plates would make a crinoid more vulnerable to mechanical damage and to attack by predators, so it is necessary to determine whether the calyx of *C. mariae* was really as thinly mineralized as it seems or whether its delicate appearance reflects taphonomic processes.

No complete specimens of *C. mariae* are known, but, considering how easily and rapidly echinoderm skeletons disarticulate after death – individual ossicles separate within days, and can be moved by very weak currents (Watkins and Hurst 1977, p. 211) – the preservation is still exceptional. All examples display articulation of small ossicles, even down to sub-millimetric cirral elements (e.g. BU 3758, Text-figs 4.3B, 4.4), proving that the crinoids were buried quickly, either while alive or soon after death, and could not have undergone significant transportation. Thus, the disparity between the degree of

55
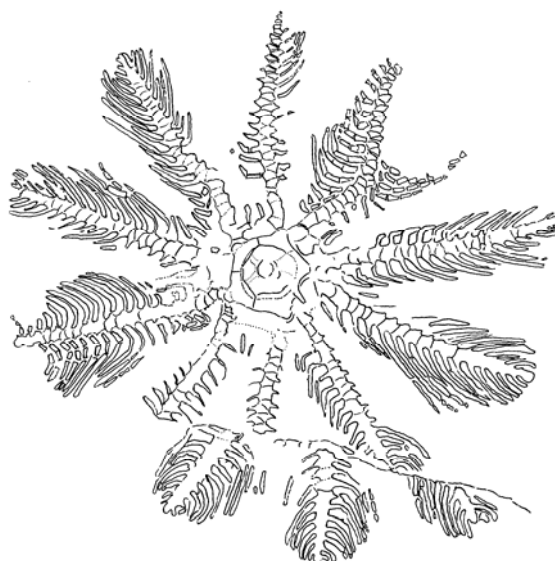
TEXT-FIG. 4.5. *Clematocrinus retiarius* Phillips *in* Murchison, 1839, Much Wenlock Limestone Formation, Dudley. *Camera lucida* drawing of BU 4393, x 4.

mineralization of the calycal plates and, for example, the brachial ossicles of *C. mariae* cannot be the result of differential abrasion – any currents of sufficiently high energy to erode the calyx would have acted also upon other parts of the crinoid.

Similarly, the articulated nature of the specimens, and the association of BU 3756-3762 on the same small slab of rock, indicates that the diagenetic processes affecting them must have been broadly the same. Small-scale taphonomic variations could have occurred, but consistent selective decalcification of the calyx is improbable. Notably, at the very base of each arm, the fixed brachials are distinctly calcified, with a pustulose or granular texture, whereas the remainder of the radial plate is barely discernible (see e.g. Text-fig. 4.2F). Only the presence of suture lines, and a slight difference in colour compared with the matrix, indicates that the radial plates are there at all. Support for the hypothesis that the calyx was thinly plated is provided by the pinnules, which display a similar style of preservation, being noticeable through a colour difference rather than an obvious calcification of elements. As with the calyx, they are connected to brachials that are clearly mineralized. Given that the full thickness of the pinnules is visible, there is no doubt that they were extremely slender, and their similarity in appearance to the calyx suggests strongly that it too was composed of thin plates.

With the weak development of calycal plates a primary rather than taphonomic feature, biological and functional morphological implications for *Calyptocymba mariae* arise. As all specimens are small, though, it must be considered first whether they were juveniles,

whose calyces would have become more robustly mineralized later in life. During crinoid ontogeny, the first skeletal elements to form are those of the calyx, with brachial and columnal elements appearing subsequently (Bodenbender and Ausich 2000). As the animal ages, brachials and columnals are added one by one, the former growing by distal addition of ossicles, coupled with deposition of calcite on existing plates (Brower 1995). Thus, if the crinoids were juveniles one would expect the number of brachial and columnal ossicles to be low, but the arms of *C. mariae* have up to 35 brachials (e.g. BU 3754; Text-fig. 4.2c) and the most complete stem, on specimen BU 3758 (Text-fig. 4.3b), has more than 40 columnals. The possibility of the specimens being juveniles is therefore excluded and, since the thickness of calyx plates normally increases by the addition of calcite increments throughout life (Smith 1990), the reduced calcification of *C. mariae* must be a derived character rather than a juvenile one.

4.3 PALAEOECOLOGY AND FUNCTIONAL MORPHOLOGY

4.3.1 Palaeoenvironmental setting

The lithology in which the specimens of *C. mariae* occur is a dark grey mudstone, probably from the Nodular Beds Member of the Much Wenlock Limestone Formation, and the articulation of the crinoids shows that they are autochthonous. This part of the Much Wenlock Limestone Formation sequence is thought to have been deposited below fair weather wave-base, and below storm wave-base in part (see Ratcliffe and Thomas 1999, fig. 5). In their study of crinoid communities in the Much Wenlock Limestone Formation of Dudley, Watkins and Hurst (1977) argued that the presence of articulated crinoids in the Nodular Beds Member was unusual. Based on the collections of the Lapworth Museum, they concluded that almost all specimens were from the Upper Quarried Limestone Member, which overlies the Nodular Beds Member and was deposited in shallower, higher energy conditions. The only species from the Nodular Beds Member to be discussed was *Clematocrinus retiarius*, described by Watkins and Hurst (1977, p. 214) as 'the dominant species of a very rare, low-diversity assemblage'. The overall hypothesis of crinoid distribution in the Much Wenlock Limestone Formation was questioned by Widdison (2002), but the ecological interpretation of *Cl. retiarius* was supported, and the similarities in morphology and occurrence between it and *C. mariae* suggests that their ecological requirements were similar.

4.3.2 Palaeoecology

With a total body length of 75–80 mm, a small, thinly plated calyx, long, slender arms with filamentous pinnules, and a thin, cirri-bearing stem, *Calyptocymba mariae* was a delicate, diminutive crinoid. The relationship between morphology and environment in Palaeozoic crinoids has been examined by many authors (e.g. Brower 1975, 1994; Baumiller 1993; Holterhoff 1997; Kammer *et al.* 1998; Meyer *et al.* 2002) with the generalization that large, robust species inhabited turbulent shallow waters, whereas smaller, more slender forms lived in deeper, lower energy conditions. However, following the work of Kammer (1985) and Kammer and Ausich (1987) on Carboniferous crinoids, Baumiller (1993) argued that, being pinnulate, camerates were restricted to high energy environments, as their dense mesh filtration fans could not have functioned efficiently in current velocities below 40 mm s^{-1} (Baumiller 1993, p. 312). Quieter, deeper water conditions were therefore dominated by the non-pinnulate disparids, cladids and flexibles, utilizing an open-fan feeding system.

Brett (1984, p. 97), however, noted that some species of finely pinnulate Silurian camerates were known solely from mudstone facies, whilst other, open-fanned forms were found only in lithologies deposited under high energy conditions. Similarly, Brower (1975) showed that in the Llandovery of the Pentland Hills, Scotland, a crinoid fauna from a quiet, soft-bottom environment contained three species of camerates, two species of disparids, and just one cladid. The camerates were delicate forms with small calyces, morphologically comparable with both *Cl. retiarius* and *C. mariae*. This evidence, combined with the information on the palaeoenvironment of *C. mariae*, indicates that Baumiller's (1993) hypothesis is erroneous, at least with regard to Silurian forms. *C. mariae* may not have inhabited especially deep water – the local shelf topography during the Wenlock was such that storm wave-base lay at a relatively shallow depth, approximately coincident with the base of the photic zone (Ratcliffe and Thomas 1999, fig. 5) – but it certainly lived in quiet conditions. It is clear that, although they were probably uncommon, Palaeozoic crinoids with pinnulate, narrow-grooved arms were not absent from sediments laid down close to storm wave-base, and the Camerata cannot be regarded as exclusively high energy crinoids.

Paradoxically, this conclusion was indirectly predicted by Baumiller (1993). He argued that, compared with flexible and inadunate forms, camerate crinoids were ecological specialists adapted to feeding on small food particles (see also Kammer and Ausich 1987; Kammer *et al.* 1998). The presence of *Calyptocymba mariae* in a low energy, low diversity assemblage can be explained using the same hypothesis – its small, thinly plated calyx would not have required as high a nutrient supply as a species with a larger, more robustly plated calyx, and coupled with the efficiency of the filtration fan feeding system (see below), this enabled *C. mariae* to live in much lower energy conditions than typical camerates.

4.3.3 Functional morphology

4.3.3.1 Feeding

Extant crinoids are filter-feeders, traditionally divided into two groups by the particular feeding method they utilize. Rheophiles are reliant on currents for nutrient supply, positioning their arms perpendicular to the flow direction in a brachial filtration fan. Rheophobes, meanwhile, live in conditions of extremely low energy, collecting their food passively by forming a horizontally aligned 'collecting bowl' with their arms and picking up nutrients that settle from suspension. Using this classification, therefore, it would seem likely that *C. mariae* was a rheophobe, avoiding currents of any significance.

However, most living crinoids, whether inhabiting shallow, high energy conditions or deep water with little current activity, employ a rheophilic mode of life, with different species being sensitive to currents of different strength. This renders the term rheophile imprecise, and led Ausich (1977) to propose a subdivision of rheophilic crinoids into high and low energy varieties. True rheophobes (in the strict sense of crinoids that do not or cannot gather their food actively from currents, relying instead on detrital 'rain' falling out of suspension) are rare today and were probably scarce in the Silurian (Brett 1984). One of the few likely rheophobes from the Silurian is *Petalocrinus*, an inadunate with rigidly fused arms that formed an inflexible bowl (Frest and Strimple 1977).

The dominance of rheophilic crinoids is the result of the extraordinary efficiency of the filtration fan feeding method, even in very low energy currents. This pre-eminence can be traced back to a mid-Ordovician crinoid diversification that saw the first appearance of forms with densely pinnulate arms and narrow ambulacral grooves (Guensburg and Sprinkle 1992). In the Silurian, filtration fans were restricted to camerates and highly ramulate inadunates (Brett 1984). Non-pinnulate Silurian crinoids with few arms (e.g. flexibles and most inadunates) were incapable of forming efficient fans, instead relying on wide ambulacral grooves and numerous tube feet to capture larger items of food, although most were rheophilic in the sense that they were reliant on currents to supply nutrients.

Although it lived in an environment affected only intermittently by notable currents, *C. mariae* was not a rheophobe. Rather, its small, slender body morphology and long, pinnulate arms would have formed a sensitive filtration fan suited to gathering food even when current activity was extremely weak. This is as predicted by aerosol filtration theory, where different fan arrays are tailored for optimal function under different current strengths (see e.g. Baumiller 1997; Holterhoff 1997), enabling specialized (stenotopic) rheophiles to thrive in apparently unsuitable locations. Food particles in a low energy environment such as the one *C. mariae* inhabited would also have been smaller and perhaps in shorter supply than in shallower waters. Additionally, the filtration fan of *C. mariae* is large relative to the calyx, implying a high level of feeding efficiency.

4.3.3.2 Protection

Although a proportionally small calyx is to be expected in a species living like *C. mariae*, the thinly mineralized cup is problematical, particularly because there is no close analogue in either fossil or extant crinoids. Brett (1984) showed that Silurian crinoids from low energy environments often had less robustly plated cups than those from turbulent waters, and *C. mariae* may have developed this trend to an extreme degree. The implication is that the risk of damage to the calyx was sufficiently low that plate thickness could be minimized. *C. mariae* lived in conditions where mean current strength was never strong enough to carry harmfully large clasts, but the potential threat of predation is harder to determine.

It has often been assumed that crinoids were not subjected to any great degree of predation pressure until the Mesozoic, when diversification of durophagous organisms led to the migration of stalked crinoids into deeper marine environments (see e.g. Oji 1996; Aronson *et al*. 1997; McClintock *et al*. 1999; Aronson and Blake 2001). However, mobile predators were significant by the early Palaeozoic (Lacalli 2001) and many could have preyed on crinoids (see discussions in Brett 1984; Donovan and Schmidt 2001). It is unlikely that predation on crinoids began only as part of the Mesozoic Marine Revolution (Donovan and Schmidt 2001, p. 268), and although predation may have been less intense, its effect on crinoid ecological distribution during the Palaeozoic may have been underestimated.

4.3.3.3 Attachment

It is unclear how *Calyptocymba mariae* was attached to the seabed, but the absence of a holdfast may not be due to incomplete preservation. Terminal holdfasts were lacking in most Silurian camerates (Brett 1984, p. 95), and attachment was commonly by distal cirri and modification of the column base, forming a root-like structure (see also Watkins and Hurst 1977, p. 212). The absence of a holdfast in *Clematocrinus retiarius*, coupled with the stem being short and cirri-bearing, led Watkins and Hurst (1977) to suggest that the crinoid might have been mobile, and capable of repositioning itself on the soft substrate using the cirri. A similar function may have been served by the cirri of *C. mariae*, but Donovan (1993) argued that evidence from ossicle articulation indicated that the ability to relocate did not evolve until the Mesozoic. Widdison (2002, p. 198) considered the cirri of *Cl. retiarius* to have possibly been for stability via an even distribution of body mass, as with extant isocrinids, or that they assisted in regulation of currents around the crinoid. With its stem being relatively long, indicating a predominantly upright life position, it is likely that the cirri of *C. mariae* served a similar purpose, but their use as support for a more reclined life position cannot be excluded.