Evolutionary and ecological significance of *Lepidaster grayi*, the earliest multiradiate starfish

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*Lepidaster grayi* Forbes, 1850, from the Much Wenlock Limestone Formation (Silurian: Wenlock) of England, is the earliest species of starfish (Echinodermata: Asteroidea) to deviate from pentaradial symmetry, having 13 rays rather than five. Based on the patterns of supernumerary ray development seen in extant multiradiate asteroids, two possible models are evaluated for the origin of the eight additional rays seen in *L. grayi*. In the ‘all-in-one’ model, all rays were added in the same interradius, whereas in the ‘quadrants’ model generations of rays would have been added in each of four interradii. The smallest specimen of *L. grayi*, apparently having only nine rays, suggests that the ‘quadrants’ model is most probable for the species. The presence of supernumerary rays in Silurian starfish, coupled with the existence of numerous other Palaeozoic multiradiate taxa, shows that asteroids have been able to deviate from pentamerism for most of their evolutionary history, and the variety of methods of supernumerary ray addition indicates that the multiradiate condition is homoplastic. The ecological significance of multiradiate Palaeozoic starfish is reviewed: the mouth frame of *L. grayi* had considerably greater flexibility than that of contemporaneous five-rayed species and, in combination with its supernumerary rays, enabled *L. grayi* to manipulate and consume larger food items. It is probable that Silurian starfish utilized a similar range of trophic guilds as those exploited by extant taxa. © 2007 The Linnean Society of London, Zoological Journal of the Linnean Society, 2007, 150, 743–754.


INTRODUCTION

Despite a fossil record stretching back nearly 500 million years, the evolutionary history of starfishes (Echinodermata: Asteroidea) is not well understood. This is due primarily to their scarce and sporadic occurrence as fossils. The asteroid skeleton is formed of numerous individual ossicles connected by soft tissues that decay swiftly after death, so that preservation requires exceptionally rapid burial. There is consequently much controversy over the biology and ecology of Palaeozoic taxa, with some authors (e.g. Blake & Guensburg, 1988, 1989, 1990, 1994) interpreting them as comparable with extant forms, but others (e.g. Gale, 1987; Donovan & Gale, 1990; Gale & Donovan, 1992) regarding them as having been ecologically restricted. The earliest multiradiate starfish (asteroids with more than five rays) are of particular interest in this regard, as their modern equivalents are among the most ecologically specialized asteroids, many being voracious predators.

In a paper describing two Mississippian species, Blake & Guensburg (1989) examined the palaeobiological implications of supernumerary rays, while Hotchkiss (2000) provided a comprehensive review and analysis of the possible origins of multiradiate asteroids. These studies apart, there has been very little work on the origin and ecological significance of early multiradiate taxa. This paper examines *Lepidaster grayi* Forbes (Fig. 1), the oldest known multiradiate asteroid, from the Wenlock (Silurian) of England. The evolution of its 13-rayed body morphology is discussed, along with the possible impact of asteroids
with such morphologies on Palaeozoic marine ecosystems.

ECHINODERM SYMMETRY AND PALAEOZOIC MULTIRADIATE ASTEROIDS

The five extant classes of the Echinodermata – Asteroidea, Crinoidea, Echinoidea, Holothuroidea and Ophiuroidea – display an array of extraordinary morphological characteristics. Perhaps the most striking of these is the five-fold body symmetry of adult echinoderms. The origin and nature of echinoderm pentamerism has been well debated (see, for example, Nichols, 1967a, b; Stephenson, 1967, 1974, 1979; Lawrence, 1988; Lawrence & Komatsu, 1990; Hotchkiss, 1998a, b, 2000) but remains contentious, particularly because a number of early taxa (e.g. carpoids: Smith, 2005; helicoplacoids: Sprinkle & Wilbur, 2005) were not pentaradial. All extant classes of echinoderm, however, show five-fold symmetry. Echinoids and holothurians are the most consistent, always having five ambulacral grooves, although holothurians and some echinoids may also have a superposed bilateral symmetry. Many crinoids have supernumerary arms, but these normally occur in multiples of five due to bifurcation of the five primary brachia. Asteroids and, to a lesser extent, ophiuroids are the exception: although most species are five-rayed, many deviations are encountered, 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 exclusively multiradiate (Hotchkiss, 2000). As most of the multiradiate forms have ray numbers indivisible by five, questions are raised about the nature of pentamerism, both in starfish and across the echinoderms as a whole.

From their first appearance in the Tremadoc and throughout the Ordovician, all species of asteroid are essentially pentaradial (see Shackleton, 2005). Very occasional six-rayed individuals are known, but these are believed to be teratological (J. D. Shackleton, pers. comm.) and it is not until the Silurian that multiradiate species are recorded. _Lepidaster grayi_ from the Much Wenlock Limestone Formation (Silurian), Dudley, England is the oldest, with eight specimens known (for full systematics see Herringshaw, Thomas & Smith, in press). The holotype and largest specimen (NHM 40215, Natural History Museum, London) has a diameter of 102 mm; it and the three other most complete specimens all appear to have had 13 rays (Table 1).

Table 1. Specimen sizes and number of rays seen in _Lepidaster grayi_ Forbes, 1850. Where necessary, diameter calculated from radius measured along most distorted ray. Specimen NOTNH FS03800 has only 11 rays preserved, but ossicles of mouth region indicate at least 12, probably 13, originally present; DUDMG 606 not located, measurements based on illustrations of Spencer (1918); OUM C00515 too poorly preserved to determine size or number of rays. Institutional abbreviations as follows (all UK): BGS – British Geological Survey, Keyworth; BU – Lapworth Museum of Geology, University of Birmingham; DUDMG – Dudley Museum & Art Gallery, Dudley; NHM – Natural History Museum, London; NOTNH – Nottingham Museum of Natural History, Wollaton Hall, Nottingham; OUM – Oxford University Museum of Natural History; SM – Sedgwick Museum, University of Cambridge.

<table>
<thead>
<tr>
<th>Specimen</th>
<th>Diameter (mm)</th>
<th>No. of rays</th>
</tr>
</thead>
<tbody>
<tr>
<td>NHM 40215</td>
<td>102</td>
<td>13</td>
</tr>
<tr>
<td>NOTNH FS03800</td>
<td>83   &gt; 11</td>
<td></td>
</tr>
<tr>
<td>DUDMG 606</td>
<td>82</td>
<td>13</td>
</tr>
<tr>
<td>NOTNH FS03795</td>
<td>73   &gt; 8</td>
<td></td>
</tr>
<tr>
<td>BGS GSM27515</td>
<td>68</td>
<td>13</td>
</tr>
<tr>
<td>SM A5496</td>
<td>48</td>
<td>6 (incomplete)</td>
</tr>
<tr>
<td>BU 673</td>
<td>24</td>
<td>&gt; 7</td>
</tr>
<tr>
<td>OUM C00515</td>
<td>?</td>
<td>&gt; 4</td>
</tr>
</tbody>
</table>

Figure 1. _Lepidaster grayi_, Much Wenlock Limestone Formation (Silurian), Dudley, England. Specimen BGS GSM27515 (British Geological Survey, Keyworth, England), showing oral surface; m = madreporite. Scale bar = 10 mm.
(Table 2), the most prolific source being the Hunsrückschiefer (Lower Devonian) of Germany. Bartels, Briggs & Brassel (1998) recognized five species, three of which – *Helianthaster rhenanus* Römer, *H. rhenanus* var. *microdiscus* Lehmann and *Palaeosolaster gregoryi* Stürtz – they placed in the Asteroidea, the other two – *Medusaster rhenanus* Stürtz and *Kentrospondylus decadactylus* Lehmann – being interpreted as ophiuroids. Current research suggests all five taxa may be ophiuroids (A. Glass, pers. comm.), but this remains to be confirmed. Elsewhere, *Michiganaster inexpectatus* Kesling, 1971, and *Arkonaster topororum* Kesling, 1982, were found in the Middle Devonian of Michigan and Ontario, respectively, while the Upper Devonian has yielded *Devonistella filiciformis* Woodward, 1874 from Devon, and *Lepadasterella gyalum* (Clarke, 1908) from New York State. Multiradiate asteroids were not known from the post-Devonian Palaeozoic until Welch (1984) described *Lepadasterella montanensis* from the Bear Gulch Limestone (Namurian) of Montana. Subsequently, Blake & Guensburg (1989) recognized *Lacertasterias elegans* from the Gilmore City Formation (Tournaisian) of Iowa and *Schondoria fungosa* from the Haney Formation (Visean) of Illinois. At present, no multiradiate starfish are known from rocks of Permian age.

**ORIGIN OF THIRTEEN RAYS IN LEPIDASTER**

The five-part body symmetry of all five extant echinoderm classes indicates that it is ‘rigidly programmed into the developmental process’ (Lawrence, 1987: 7). Most species of starfish are five-rayed and this is tightly regulated developmentally, such that deviation from pentamerism is rare in five-rayed species (Lawrence & Komatsu, 1990). However, the occasional occurrence of non-pentameral individuals in such species, combined with the number of multiradiate taxa known, indicates that starfish have a capability for symmetry variations not present in other echinoderms. Some authors (e.g. Dawkins, 1996) have used this variability to argue that pentamerism is not a fundamental character of crown-group echinoderms, but a more widely accepted hypothesis is that of Hotchkiss (1998a, b, 2000). His research into echinoderm pentamerism (Hotchkiss, 1995, 1998b) led to the proposal of a ‘rays-as-appendages’ model (Hotchkiss, 1998b) for its origin, one of the predictions of which was that asteroids that are multiradiate as adults actually begin with five rays, adding supernumerary rays later in development. The number of rays varies both within and between multiradiate species: Lawrence & Komatsu (1990) showed that ray number is generally constant in taxa with 11 or fewer rays, but variable above that. Hotchkiss’s prediction was supported by studies of the metamorphosis of extant multiradiate asteroids (see summary in Hotchkiss, 2000) and led to the proposal of the ‘Five-Plus’ hypothesis (Hotchkiss, 1998a, 2000), which states 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 uncertain, but Hotchkiss (2000) suggested post-generation of rays in the incompletely developed starfish or intercalated regeneration of rays in the ‘imago’ (*sensu* Hotchkiss, 2000) as two possibilities.

The ability to regenerate lost body parts is a feature seen in all extant classes of echinoderms. Thus, it is possible that supernumerary rays derive from the ability of starfish to grow new rays: essentially, multiradiate asteroids could be five-rayed forms that have generated ‘replacement’ rays without the primary rays having been lost. With such a small number of speci-
The ‘all-in-one’ model

The ‘all-in-one’ model (Fig. 2A), 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 (\( R \) being the distance from the centre of the disc to the tip of the ray, \( r \) the distance from the centre of the disc to the interradius) and a modal ray number of 13 (57% of specimens: M’Intosh in Lawrence & 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 can be used as a marker to observe the exact pattern of supernumerary ray addition: in *Crossaster*, supernumerary rays are all added to one side of the anus, whereas in *Acanthaster* they are added alternately either side of the anus. As the anus is not visible in any available specimen of *L. grayi* (and may have been absent from Palaeozoic asteroids: Jangoux, 1982), it is not possible to assess which of these patterns, if either, is more plausible.

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.

**Figure 2.** Models for the acquisition of supernumerary rays in *Lepidaster grayi* (after Hotchkiss, 2000). A, the ‘all-in-one’ model. B, the ‘quadrants’ model. Five primary rays denoted by letters A–E; eight supernumerary rays denoted by Roman numerals I–VIII; \( m \) = madreporite.

The 'quadrants' model

The ‘quadrants’ model (Fig. 2B) predicts that *L. grayi* added two rays in each of four interradii. This is based primarily on the Pacific sun-star *Heliaster helianthus* (Lamarck), which reaches a modal number of 33 rays (Tokeshi, 1991) by adding seven supernumerary rays in each of four interradii (Sanchez, 2000). Sanchez showed that *H. helianthus* adds a first generation of four supernumerary rays, but then adds rays in generations of eight, 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 invalidate the model, because *L. grayi* could have added either one generation of eight rays (two rays in each of four primary interradii) or two successive generations of four rays in these interradii.

The only interradius in which supernumerary rays are not added is D–E, which contains the madreporite. The madreporite is an integral part of the asteroid water vascular system, such that the addition of supernumerary rays in the madreporitic interradius would necessitate a fundamental modification of the body. This is particularly pertinent for *L. grayi* with a large madreporite occupying the whole of the D–E interradius (Fig. 1).
In contrast to the early addition of supernumerary rays predicted by the ‘all-in-one’ model, asteroids that follow the ‘quadrants’ model may continue producing rays well into adult life. The addition of rays in *Heliaster*, for example, is known to occur when the asteroid has a body diameter of up to 100 mm (Clark, 1907). The absence of shorter rays from any specimen of *L. grayi* suggests that all rays were added early in development, although this would be expected in a taxon with only eight supernumerary rays.

**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 commonly have far more rays than those following the former. Of the eight known specimens of *Lepidaster grayi*, four are sufficiently complete to show the number of rays. Ranging in diameter from 68 to 102 mm (Table 1), all four had 13 rays, indicating that this was the typical adult number. As such, it might seem more likely that *L. grayi* followed the ‘all-in-one’ model, but specimen BU 673 (Fig. 3) suggests that this was not the case. BU 673 is the smallest example of *L. grayi* and is imperfectly preserved, but its diameter of approximately 25 mm is well within the size range at which *Heliaster* is still adding rays, and beyond that at which *Crossaster* and *Solaster* have added all supernumerary rays. This may be significant because BU 673 does not appear to have 13 rays: Spencer (1918) thought it had between eight and ten, and that it was an immature form that would have added the remaining rays later in development. Although the specimen is distorted, BU 673 certainly had more than seven rays. The interradius between rays 2 and 3 (Fig. 3) is the least disturbed and forms an angle of not less than 40°. If this is the true arc, it indicates that BU 673 had nine rays (360°/40° = 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 13. Additional small specimens are required to test this possibility.

**SIGNIFICANCE OF SUPERNUMERARY RAYS**

In terms of biomass, the multiradiate condition represents a drastic change from being five-rayed: if similar ray and central disc proportions are maintained, the volume of the body is approximately doubled. Assuming a similar metabolic rate, a 13-rayed starfish of the same diameter as one with five rays will thus need more food to support its greater body mass: for multiradiate taxa to have become so successful, 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 could be more mobile, more able to resist being detached from the seabed, and/or more successful feeders. In terms of both mobility and attachment...
there is no convincing evidence that multiradiate taxa are better equipped than pentaradial forms (see Lawrence, 1988), but there is at least some disparity in feeding behaviour.

Extant asteroids exploit an extremely wide range of food sources (see Sloan, 1980; Jangoux, 1982). Of the six feeding categories defined for benthic marine invertebrates by Walker & Bambach (1974: table 6) – suspension feeding, deposit feeding, browsing, carnivory, scavenging, and parasitism – all except parasitism are exploited by living starfish (Jangoux, 1982: table 2). The additional food required by multiradiate taxa could be obtained either by out-competing pentaradial species for the same food source, or by specializing to feed on a separate one. Within the asteroid trophic groups, multiradiate taxa exhibit some of the most unusual modes of feeding, suggesting that in many cases it is the latter. Members of the order Brisingida, for example, capture plankton by forming a crinoid-like feeding fan with their long, thin rays (e.g. Novodinia antillensis: Emson & Young, 1994), whilst many other multiradiate specialists are active carnivores. The crown-of-thorns starfish Acanthaster planci (Linnaeus) is notorious for its ability to destroy coral communities (Blake, 1979); Labidiaster annulatus catches krill, amphipods and small fish (Dearborn et al., 1991); Crossaster papposus preys commonly on other asteroids, inducing them to automate rays which it then consumes (Jangoux, 1982); Solaster stimpsoni Verrill eats holothurians, but is itself the chief prey of Solaster dawsoni Verrill (Mauzey, Birkeland & Dayton, 1968); and Pycnopodia helianthoides (Brandt) is capable of capturing large, mobile prey such as crabs and octopuses, as well as burrowing for infaunal bivalves (Shivji et al., 1983). It is inferred that supernumerary rays enable multiradiate asteroids to capture and manipulate food that five-rayed asteroids cannot, although it should be noted also that multiradiate starfish often have larger mouth frames (Jangoux, 1982: 143). This is particularly true of taxa with many supernumerary rays, where the central disc (and hence its oral surface) is larger as a consequence of accommodating the additional rays.

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

One further aspect of the multiradiate state is its closer approximation to radial symmetry than that of a five-rayed body plan. In simple geometrical terms, a pentaradial starfish has an arc of 72° between each ray, whereas a 13-rayed starfish reduces that arc to 27.7°. Like all echinoderms, asteroids have no brain or true centre of organization and no front or back, such that the rays act rather like individual elements of a moving colony: each ray has sensory devices and can lead the animal in a chosen direction. In terms of both prey detection and predator avoidance, supernumerary rays may therefore be advantageous in giving more complete coverage of the area around the starfish, especially as asteroid rays, unlike those of ophiuroids, are relatively inflexible in a lateral plane.

**IMPLICATIONS OF SUPERNUMERARY RAYS IN LEPIDASTER**

As shown by Dean (1999) and Shackleton (2005), there can be difficulties in assigning asterozoans from the Early Ordovician to the classes Asteroidea and Ophiuroidea but, by the Ashgill, the diagnostic body plan of each class had evolved (see also Blake & Guensburg, 2005). Lepidaster is unequivocally an asteroid and its functional morphology can be interpreted on that basis.

Gale (1987), Donovan & Gale (1990) and Gale & Donovan (1992) interpreted Palaeozoic asteroids as lacking various morphological characters present in extant starfish, including suckered tube feet and complex ray musculature, such that they were restricted to deposit feeding, scavenging or predation of small, immobile benthos. This conclusion was supported, at least with regard to the earliest asteroids, by Shackleton (2005) who documented a morphological conservatism among Ordovician taxa and suggested that they ‘probably remained dominantly deposit-feeders throughout the period’ (Shackleton, 2005: 60). However, Blake & Guensburg (1988, 1989, 1990, 1994) disagreed, arguing that Ordovician asteroids utilized a range of feeding methods similar to those of modern forms, including extra-oral predation (see Blake & Guensburg, 1994). This is the technique observed in living asteroids of the orders Valvatida, Spinulosida and Forcipulatida (Jangoux, 1982), whereby the starfish extrudes its stomach over or into prey too large to fit into the mouth, and digests the organism externally.

The basis for much of the controversy over the functional morphology of Palaeozoic starfish is that the phylogenetic relationships of the Asteroidea are poorly understood. It is generally agreed that all Palaeozoic taxa belong to the stem (Blake, 1987; Gale, 1987; Blake & Guensburg, 1990; Donovan & Gale, 1990;
Blake, Janies & Mooi, 2000; Blake & Hotchkiss, 2004; Shackleton, 2005), with crown-group starfish known only from the post-Permian, but no consensus has been reached as to which are the most basal extant asteroids. Some authors (e.g. Jangoux, 1982; Gale, 1987) have interpreted paxillosids as the most primitive living order, whilst other analyses (e.g. Blake, 1987; Knott & Wray, 2000) have contradicted this. Hence it is unclear which morphological features are primitive, and which derived. For example, depending on which phylogeny is accepted, tube feet can be interpreted as either primitively suckered or primitively non-suckered, with the tube feet of Palaeozoic asteroids interpreted accordingly. Since Jangoux (1982: 140–141) stated that all starfish with suckered tube feet feed extra-orally and all with non-suckered tube feet feed intra-orally, their likely morphology in Palaeozoic taxa has been used as a palaeoecological proxy. However, a number of additional important factors need to be considered, some of which have not been adequately addressed by previous studies. Firstly, despite the work of Walker & Bambach (1974) and Jangoux (1982), no explicit definition of the trophic guilds potentially available to Palaeozoic starfish has ever been produced. Secondly, most extant starfish are ‘fundamentally polytrophic’ (Jangoux, 1982: 117), regardless of whether they feed extra-orally or have suckered tube feet. Finally, as shown in Table 3, there are few instances in which asteroid morphology can be associated unequivocally with specific types of feeding behaviour, making ecological interpretations of extinct taxa more problematical.

In the absence of close phylogenetic relationships, morphological similarities between Palaeozoic and extant forms are attributed to convergence: Gale (1987) explained the resemblance of the Ordovician genus Platanaster to living paxillosids in this way, as did Blake & Guensburg (1994), who noted the similarity of form between another Ordovician taxon, Protopalaeaster, and modern asteroids. Hence, 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. However, Crossaster is an active carnivore capable of extra-oral feeding, behaviour that Gale (1987) argued was not available to Palaeozoic starfish because they did not have suckered tube feet, sufficient mouth or ray flexibility, and were not able to evert their stomachs. Thus, Lepidaster either was morphologically but 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 Lepidaster could not have used similar feeding techniques to extant forms.

As noted above, a wide spectrum of feeding modes exists in living starfish: Jangoux (1982) showed that asteroids utilize five of the six trophic groups defined for benthic invertebrates by Walker & Bambach (1974), and refined this into eight asteroid feeding categories (Jangoux, 1982: table 2). These were as follows: carnivores on epifaunal macroprey (Group I), carnivores on small sessile or colonial epifauna (Group II), carnivores on infaunal macroprey (Group III), deposit feeders on epibenthic or substrate films (Group IV), deposit feeders on sediment (Group V), algivores (Group VI), suspension feeders (Group VII) and scavengers (Group VIII). This is further modified here (Table 3), with 11 groups recognized, including six categories of carnivory. The food types available and morphological features required for each feeding category are assessed and examples given, where they exist, of extant multiradiate taxa that utilize each method.

Most of the trophic groups utilized by living starfish are available to both intra-orally and extra-orally feeding species. There are many specializations within feeding categories (see Jangoux, 1982) but only two categories – soft-part carnivory of sessile, protected epifauna, and carnivory of fast-moving epifauna – are apparently restricted entirely to asteroids with specific morphological adaptations. The critical morphological features identified by Gale (1987) are clearly of significance to the feeding behaviour of extant taxa, but few can be correlated directly with particular trophic groups: most categories include asteroids using a diversity of feeding methods. In this light, the potential utilization of each feeding category by Lepidaster is critically examined.

**Deposit Feeding**

Deposit feeding was not documented in multiradiate asteroids by Jangoux (1982), being a trophic group characterized by five-rayed starfish primarily living on soft substrates in deep water (e.g. porcellanasterids). However, it is perhaps the simplest method of feeding available to asteroids, with the tube feet used to push nutrient-rich sediment into the mouth cavity and, as such, would certainly have been available to a multiradiate taxon such as Lepidaster.

**Scavenging**

No living starfishes are specialist scavengers, but most scavenge opportunistically or in times of necessity (Jangoux, 1982). Scavenged food can be consumed intra- or extra-orally, the size of the item being governed by flexibility of the mouth frame. Gale (1987) argued that Palaeozoic asteroids had inflexible mouth frames and could only have eaten food items smaller

than the buccal opening. This argument (see also Gale & Donovan, 1992) was based on the arrangement of the interradial marginal ossicles relative to those of the mouth frame. In Palaeozoic taxa, where a single axillary ossicle is present it forms part of the marginal series and its proximal surface abuts directly against the mouth ossicles, indicating a much-reduced flexibility of the mouth frame (Gale, 1987; Gale & Donovan, 1992). In crown group asteroids, this axillary has moved to a position between the marginal ossicles and the mouth frame and is interpreted as having provided greater oral flexibility.

Although the ossicular arrangement described by Gale (1987) and Gale & Donovan (1992) is undoubtedly present in most Palaeozoic asteroids, *Lepidaster* is different, having a mouth frame that is distinctly separated from the axillary marginals. As illustrated in Figure 4, the best-preserved specimen of *Lepidaster* shows that numerous small actinal ossicles of the central disc lie between the fan-shaped array of axillary ossicles and the mouth frame. Preservational imperfection does not enable the exact arrangement of ossicles to be determined, but it is clear that the mouth plates do not abut directly against the axillary marginals. As such, an oral flexibility more like that of extant asteroids is indicated; *Lepidaster* would have been able to consume larger food items than sympatric pentaradial asteroids.

**Table 3.** Starfish feeding categories (after Walker & Bambach, 1974; Jangoux, 1982)

<table>
<thead>
<tr>
<th>Feeding category</th>
<th>Example food types</th>
<th>Specialized features required</th>
<th>Multiradiate examples (Jangoux, 1982)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Deposit feeding</td>
<td>Detritus</td>
<td>None shared by all taxa</td>
<td>None identified</td>
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<tr>
<td>Scavenging</td>
<td>Carrion</td>
<td>None shared by all taxa</td>
<td>Common</td>
</tr>
<tr>
<td>Grazing/browsing</td>
<td>Algae</td>
<td>Stomach eversion</td>
<td>None identified</td>
</tr>
<tr>
<td>Ciliary feeding</td>
<td>Substrate films</td>
<td>Body ciliature</td>
<td>None identified</td>
</tr>
<tr>
<td>Suspension feeding</td>
<td>Plankton</td>
<td>Flexibility to extend and align rays with currents</td>
<td>Rare – e.g. brisingids</td>
</tr>
<tr>
<td>Carnivory – sessile epifauna with exposed soft tissues</td>
<td>Sponges, coral, sea pens</td>
<td>Stomach eversion in some taxa</td>
<td>Common – <em>Luidia Acanthaster</em></td>
</tr>
<tr>
<td>Carnivory – whole-prey consumption of sessile, protected epifauna</td>
<td>Bivalves, gastropods</td>
<td>None shared by all taxa</td>
<td>Common – <em>Luidia, Heliaster</em></td>
</tr>
<tr>
<td>Carnivory – digging for infauna</td>
<td>Bivalves</td>
<td>Flexible rays</td>
<td>Common – <em>Luidia, Pycnopodia</em></td>
</tr>
<tr>
<td>Carnivory – slow-moving epifauna</td>
<td>Echinoderms</td>
<td>None shared by all taxa</td>
<td>Common – <em>Solaster, Crossaster</em></td>
</tr>
<tr>
<td>Carnivory – soft-part consumption of sessile, protected epifauna</td>
<td>Bivalves, gastropods</td>
<td>Suckered tube feet, eversible stomach</td>
<td>Rare – asteriids only</td>
</tr>
<tr>
<td>Carnivory – fast-moving epifauna and nekton</td>
<td>Crustaceans, fish</td>
<td>Pedicellariae, flexible rays</td>
<td>Very rare – e.g. <em>Labidiaster</em></td>
</tr>
</tbody>
</table>

**Figure 4.** Camera lucida illustration of arrangement of oral ossicles in *Lepidaster grayi* (specimen BGS GSM27515, British Geological Survey, Keyworth). Dark grey ornament indicates mouth ossicles; medium grey ornament indicates inferomarginal and axillary ossicles; light grey indicates matrix; mp = mouth-angle plates, t = tori.
Grazing/Browsing
Few extant asteroids feed on living plants, but many consume microscopic algae or decaying plant matter (Jangoux, 1982). As with deposit feeding, such food can be passed directly into the mouth using the tube feet or consumed by eversion of the stomach, the latter method enabling larger quantities to be eaten. Benthic marine algae were present in the Silurian and potentially available to Lepidaster, although no multitradate herbivores were recorded by Jangoux (1982).

Ciliary Feeding
Jangoux (1982: 148) defined ciliary feeding as the collection of small particulate food directly from the substratum using ciliation of the ventral body surface and/or of the everted stomach. It is not known whether Lepidaster possessed cilia, but no living multitradate starfish are known to feed in this way and the five-rayed exponents of ciliary feeding live mainly in deep water. The lithofacies of the Much Wenlock Limestone Formation in which Lepidaster is preserved are indicative of moderate to shallow water depth (see Ratcliffe & Thomas, 1999), with the holotype of Lepidaster grayi occurring in the crinoidal grainstone lithofacies of Ratcliffe & Thomas (1999), a bioclastic limestone interpreted as having been deposited in high-energy conditions above fair-weather wave base.

Suspension Feeding
Suspension feeding in asteroids was considered by Jangoux (1982) to be a specialization of ciliary feeding, where particulate material is collected from the water column rather than the substrate. Multitradate asteroids of the order Brisingida are specialized suspension feeders (Emson & Young, 1994) but their crinoid-like body morphology of tiny central disc and long, slender rays is quite unlike that of Lepidaster. However, asteroids with a variety of body shapes are known to use suspension feeding (see Jangoux, 1982: 149–151) with the main requirement being flexible rays that can be aligned with nutrient-bearing currents.

Carnivory
In previous discussions of Palaeozoic asteroid palaeoecology, the most contentious subject has been that of carnivory. Prey available to marine carnivores can be categorized into five types: sessile prey with exposed soft parts, sessile prey with protected soft parts, slow-moving prey, fast-moving prey and buried prey. With regard to carnivorous asteroids, each of these is defined as a feeding category (Table 3), but with two methods of predation defined for sessile, protected prey: whole prey consumption and consumption of soft parts only. The latter technique involves the opening of the prey’s protective shell and is seen only in asteroids (Jangoux, 1982), which have suckered tube feet and an eversible stomach.

The flexible mouth frame and supernumerary rays of Lepidaster would have enabled it to manipulate and consume relatively large food items. An abundance of sessile benthos was present in the Much Wenlock Limestone Formation, many of which would have been potential prey items (e.g. brachiopods, gastropods) either by intra- or extra-oral feeding. Sessile epifauna with exposed soft tissues, such as corals, sponges and bryozoans, might also have been preyed on: extant multitradate starfish are capable of feeding both intra- and extra-orally on such organisms.

All extant echinoderms have tube feet: extinct phylogenetic bracketing (Witmer, 1992) allows us to infer their presence in Palaeozoic asteroids. Based on his phylogeny of crown group asteroids, Gale (1987) interpreted the tube feet of Palaeozoic starfish as not having been suckered, and that they could neither have gripped prey in the way that extant asteroids do when attacking bivalves or operculate gastropods, nor have lived on hard substrates. Tube feet apparently lacking suckers have recently been described in an asterozoan from the Herefordshire Lagerstätte (Wenlock) of England (Sutton et al., 2005) but the tube foot morphology of Lepidaster is unknown. However, even its tube feet were not suckered, this would not preclude Lepidaster from being a carnivore. Asteroids of the families Luidiidae and Astropectinidae lack suckered tube feet (Vickery & McClintock, 2000), yet the genus Luidia is ‘rather strictly carnivorous’ (Jangoux, 1982: 118) and includes multitradate species that are active predators of large, mobile prey. Furthermore, work by Thomas & Hermans (1984, 1985), Flammang, Demeu- lenaere & Jangoux (1994) and Flammang (1995) has revealed that, in at least some starfish, the tube feet use chemical adhesion rather than suction to gain hold of prey items or substrates, suggesting that suckers may not be essential to extra-oral feeding.

Of the infaunal organisms preyed on by extant starfish, primarily bivalves, few existed in the Wenlock, making the exploitation of that feeding category by Lepidaster relatively improbable. Carnivory of fast-moving epifauna, such as crustaceans and fish, is extremely uncommon in asteroids (Jangoux, 1982) and, given the abundance of sessile or slow-moving benthos in the Much Wenlock Limestone Formation, also unlikely to have been utilized by Lepidaster.

Conclusions
The palaeoecology of Palaeozoic asteroids has proved a contentious topic in the last two decades, with the Blake and Gale schools of thought providing different
interpretations. However, it is apparent that, regardless of which hypothesis is preferred, most of the feeding categories utilized by living starfish were available to Palaeozoic forms: other than asteroid-type predation, none is dependent directly on both suckered tube feet and an eversible stomach. Additionally, even if it were functionally possible, asteroid-type predation would probably have been extremely rare in Palaeozoic taxa, given the abundance of small, sessile or slow-moving benthic organisms available as prey. However, the greater mouth-part flexibility apparent in *Lepidaster* suggests that extra-oral predation might have been possible in the earliest multiradiate starfish.

The morphological conservatism of Ordovician asteroids was interpreted by Shackleton (2005) as indicating their ecological restriction, but the presence of *Lepidaster* in a morphologically varied fauna from the Wenlock of England (see Herringshaw et al., in press) suggests that Silurian starfish were more ecologically diverse. Too few data are available presently to determine whether the asteroids of the Much Wenlock Limestone Formation were an endemic fauna or to determine whether the asteroids of the Much Wenlock Limestone Formation were an endemic fauna or representative of a global diversification and, given the poor preservation potential of asteroids, it is also possible that more diverse morphologies, including multiradiate taxa, existed in the Ordovician.

Without an accepted phylogeny of the Asteroidea, it is difficult to evaluate completely the degree of convergence between Palaeozoic multiradiate asteroids such as *Lepidaster* and morphologically similar extant taxa such as *Crossaster*. Further investigation is required, both of post-Ordovician members of the stem Asteroidea and of the clade as a whole, to determine which characters are homologous and which convergent. However, *Lepidaster grayi* is the earliest known asteroid with supernumerary rays, a large central disc and, most crucially in terms of functional morphology, a mouth frame dissociated from the marginal ossicles. This greater oral flexibility is interpreted as having enabled *Lepidaster* to consume larger quantities or items of food, with the extra rays assisting in its manipulation. The feeding categories it exploited will probably never be known, but there are no convincing reasons for regarding *Lepidaster* as ecologically restricted: as with modern multiradiate starfish, a diverse range of feeding behaviour, including active predation, was potentially available.

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