A starfish with three-dimensionally preserved soft parts from the Silurian of England

M. D. Sutton^{1,*}, D. E. G. Briggs², David J. Siveter³,
Derek J. Siveter^{4,5} and D. J. Gladwell³

¹Department of Earth Sciences and Engineering, South Kensington Campus, Imperial College London, London SW7 2AZ, UK

²Department of Geology & Geophysics, Yale University, PO Box 208109, New Haven, CT 06520-8109, USA

³Department of Geology, University of Leicester, Leicester LE1 7RH, UK

⁴Department of Earth Sciences, University of Oxford, Parks Road, Oxford OX1 3PR, UK

⁵Geological Collections, University Museum of Natural History, Oxford OX1 3PW, UK

Palaeozoic asteroids represent a stem-group to the monophyletic post-Palaeozoic Neoasteroidea, but many aspects of their anatomy are poorly known. Using serial grinding and computer reconstruction, we describe fully articulated Silurian (*ca* 425 Myr) specimens from the Herefordshire Lagerstätte, preserved in three dimensions complete with soft tissues. The material belongs to a species of *Bdellacoma*, a genus previously assigned to the ophiuroids, but has characters that suggest an asteroid affinity. These include a pyloric system in the gut, and the presence of large bivalved pedicellariae, the latter originally described under the name *Bursulella* from isolated valves. Ampullae are external and occur within podial basins; the radial canal is also external. Podia are elongate and lack terminal suckers. The peristome is large relative to the mouth. Aspects of the morphology are comparable to that of the extant Paxillosida, supporting phylogenetic schemes that place this order at the base of the asteroid crown group.

Keywords: Asteroidea; *Bdellacoma*; *Bursulella*; Herefordshire Lagerstätte; Wenlock Series

1. INTRODUCTION

Asteroids (starfish or sea-stars) are a diverse and ecologically important group of marine invertebrates. Palaeozoic fossil starfish are of special interest because there is now a consensus that most, if not all, were stem-group rather than crown group Asteroidea (Blake 1987, 2000; Gale 1987). However, a phylogenetic framework for this stem-group has yet to be resolved (although see Gale 1987; Dean 1999), and the phylogeny of the crown group also remains controversial (e.g. Knott & Wray 2000), not least because of problems with rooting and the polarity of characters such as the presence/absence of podial suckers. Well-preserved stem-group fossils are required to help resolve these problems, but are rare. Fossils are typically partly or entirely disarticulated, and while ossicles are often preserved in three-dimensions, preservation of entire animals in the round is rare; the resulting conflation of adoral and aboral ossicles hinders description. Preservation of labile tissues such as tube-feet is very unusual (although see Gale 1987, fig. 7f; Dean 1999).

Here, we describe new asteroid fossil material from the lower Silurian (Wenlock Series; *ca* 425 Myr) Herefordshire Lagerstätte of England (Briggs *et al.* 1996). Fossils from this deposit are preserved as three-dimensional calcite in-fills in nodules in a volcanoclastic ash (Orr *et al.* 2000), and preserve high-fidelity details of soft tissues that can be studied through serial grinding and computer reconstruction (Sutton *et al.* 2001b). The deposit has yielded a diversity of sponges; radiolarians (Orr *et al.* 2002); an aplacophoran-like mollusc, *Acaenoplax hayae*

(Sutton *et al.* 2001a, 2004); several arthropods including *Offacolus kingi* (a stem group chelicerate; Orr *et al.* 2000; Sutton *et al.* 2002), *Colymbosathon ecplecticus* (a myodocopid ostracod crustacean; Siveter *et al.* 2003), *Cinerocaris magnifica* (a phyllocarid crustacean; Briggs *et al.* 2004), and *Haliestes dasos* (a pycnogonid; Siveter *et al.* 2004); a polychaete worm, *Kenostriachus clementsii* (Sutton *et al.* 2001c); and an array of as yet undescribed species, including several more echinoderms.

The starfish material described here is closely comparable with *Bdellacoma vermiformis* (Salter 1857). *B. vermiformis*, most recently studied by Spencer (1940), is the only described species of *Bdellacoma*, and is known only from the Leintwardine Group, Ludlow Series of Church Hill Quarry in the Leintwardine area of the Welsh Borderland (Siveter 2000, p. 357). The material described here resembles *Bdellacoma* in its gross anatomy (a relatively small disc and long arms; compare figure 1a with figure 1e) and the morphology of its spines. Most significantly, it also possesses the same distinctive pedicellariae (compare figure 1b with figure 2d,e). These structures were described as ‘clavate tubercles’ by Salter (1857) and ‘squat, thick spines’ by Spencer (1940), but are clearly identifiable as bivalved structures on well-preserved specimens in the Oxford University Museum collection (e.g. arrow, figure 1b). Slight differences in the outline of the pedicellariae suggest that the Herefordshire material may represent a new species, but a full systematic treatment and analysis of the affinities of *Bdellacoma* is deferred to a future paper; here, we treat the Herefordshire Lagerstätte material as *Bdellacoma* sp.

* Author for correspondence (m.sutton@imperial.ac.uk).

Figure 1. (a), (b) *Bdellocoma vermiformis* Salter 1857; Lower Leintwardine Formation, Ludlow Series, Silurian; Church Hill Quarry, Leintwardine, Herefordshire, UK. (a) OUM C.17124, sub-complete specimen (contrast on specimen improved digitally), $\times 1.5$. (b) Detail of OUM C.17109 showing moulds of pedicellariae, $\times 4.8$. Arrow indicates external mould of a pair of conjoined pedicellaria valves. (c)–(g) *Bdellocoma* sp. Wenlock Series, Herefordshire Lagerstätte, OUM C.29573; (c), (d), (f) and (g) are stereo-pairs of reconstructions from serial-grinding. (c) Oblique view of adoral surface of proximal part of arms and disc, $\times 3$. Green, podia; blue, pedicellariae; orange, spines (undifferentiated); white, other fossil material. (d) Adoral view of disc with spines and podia removed, three ambulacral grooves and intervening mouth-angle plates labelled, $\times 5$. Note that two arms without labelled ambulacral grooves (lower part of figure) have lost material in the reconstruction process; see §2. (e) Idealized reconstruction based on serial sawing; the mouth is directed upwards and the arms reflexed aborally, with ambulacral grooves on the outside; position of serial-grinding disc reconstruction indicated; approximately $\times 1$. (f) Adoral view of internal sediment-filled gut inside disc, $\times 9$. (g) Lateral view of disc with spines and podia removed, rendered translucent to show gut placement, $\times 5$. AG, ambulacral groove; CS, cardiac stomach; MAP, mouth angle plates; PC, pyloric caeca; Pe, pedicellariae; PR, peristomial ridge (?taphonomic artefact); Ps, peristome; Po, podia; Sp, spines (undifferentiated).

2. MATERIAL AND METHODS

Of 14 available specimens of *Bdellocoma* sp. (OUM C.29572–85), parts of two (OUM C. 29572–3) have been reconstructed digitally. OUM C.29573 (figure 1c–g) was initially serially sawn at 4 mm intervals using a 0.3 mm blade (see Electronic Appendix) to generate a low-resolution reconstruction of the gross body-form, of which figure 1e is a stylised version.

The two resulting 3.7 mm slices that comprised the disc were subsequently serially ground and digitally photographed at 20 μ intervals, and these datasets (see Electronic Appendix) were combined and used to generate 3D computerized ‘virtual fossils’ by the method detailed in Sutton *et al.* (2001b). The resulting model thus contains a 0.3 mm gap immediately adoral to the peristome, and ‘arm’ material (including

Figure 2. (a)–(g) *Bdellacoma* sp., Wenlock Series, Herefordshire Lagerstätte; section of arm from OUM C.29572; (a)–(e) are reconstructions from serial grinding, (a)–(c) are stereo pairs. Green, soft tissues; blue, pedicellariae; orange, adambulacral spines; white, other fossil material. (a) Sub-adoral view, $\times 14$. (b) Sub-adoral view (identical viewpoint to (a)), with pedicellariae, adambulacral spines and soft tissue (except one podium) removed, $\times 14$. (c) Oblique view of aboral surface of arm, $\times 10$. Arrow indicates pedicellaria isolated in (d), (e). (d), (e) Isolated single valve of pedicellaria (indicated in (c)), with soft tissue, $\times 20$; (d) lateral view, (e) interior view. (f) Slice 166 from serial grinding sequence, $\times 10$. (g) Interpretation of (f), $\times 10$. Green, soft tissue; lilac, Stereom. Arrow indicates soft tissue in ambulacral groove. (h) Diagrammatic cross-section of neoasteroidean arm (after Ruppert and Barnes 1994). Light green, connective soft tissue; dark green, water–vascular system; mid green, other soft tissue; lilac, Stereom. AbS, aboral spine; AbO, aboral ossicle; AdO, adambulacral ossicle; Am, ampulla; AmO, ambulacral ossicle; AS, adambulacral spine; C, coelom; LC, lateral canal; Pa, papulae; PB, podial basin; Pe, pedicellariae; Po, podia; PST, pedicellarial soft tissue; RC, radial canal; RN, radial nerve; SG, skeletal gap.

a mouth-angle plate) is also missing from the bottom of [figure 1d](#). A section of arm from OUM C.29572 ([figure 2a–g](#)) was also reconstructed. Abradial–adradial polarity is not known for this model. Both specimens are fully three-dimensional with the exception of the podia, which are preserved as thin sheets ([figure 2f,g](#)) except at their bases and, in some cases, their tips. All the podia extend into the matrix, and are collapsed to two dimensions in a manner consistent with a simple compressive force. We thus interpret their collapse as post-burial, related to decay or to loss of pressure in the water-vascular system immediately subsequent to death, combined with weak compression by the weight of overlying ash. The model of OUM C.29572 ([figure 2a–c](#)) reveals that it is preserved asymmetrically, with the bulk of the arm volume to one side (the right in [figure 2f,g](#)) of the ambulacral groove. This is interpreted as a result of *in vivo* flexibility. Stereom in both specimens has recrystallized, and hence plate boundaries are not apparent.

Images were edited prior to reconstruction to remove extraneous material, resolve fossil/matrix ambiguities, and to improve the continuity of collapsed podia in reconstruction. In OUM C.29572, distinct dark and light ‘phases’ are distinguishable ([figure 2f,g](#)). These preserve soft-part (organic) and hard-part (skeletal) structures, respectively, and have been reconstructed as separate components. Areas of indeterminate phase were colour coded as ‘hard part’, except where clearly contiguous with soft tissue (e.g. collapsed podia). OUM C.29573 lacks clear distinction between phases but contains a sediment filled gut inside the disc, also reconstructed separately ([figure 1f,g](#)). Specimens have also been colour-coded to identify components and structures. This refinement (Sutton *et al.* 2002) enables the computer to reconstruct each structure separately and render them in different colours to aid visualization, and to hide structures selectively in order to perform ‘virtual dissections’. It is important to note that the exact point at which the colour changes where one structure meets another (e.g. at a spine base) is somewhat arbitrary, and it has not always been possible to maintain consistency. The virtual specimens were studied using a custom on-screen visualization system with stereo viewing capabilities. Specimens and datasets are housed in the University Museum of Natural History, Oxford (OUM).

3. DESCRIPTION

This description concentrates on aspects of morphology upon which the Herefordshire material casts new light. Gross body form has been determined only in outline (see [figure 1e](#)). The arms are long in comparison to the disc and appear to have been relatively mobile; OUM C.29573 is preserved with arms directed aborally. Interpretation of plating structure is hampered by recrystallization but details, where apparent, are described below.

The lateral and aboral surfaces of the arms consist of a reticulate network of quadriradiate ossicles. Organic material fills the arm and extends through the gaps in this lattice, often protruding above the surface in stubby projections interpreted as papulae (respiratory/excretory evaginations; [figure 2c,f,g](#)). Each node in the lattice bears a short radially symmetrical spine, flared and concave distally ([figure 2a–c,f,g](#)). These spines (referred to here as ‘aboral’) appear immobile. A series of spines (referred to

here as ‘adambulacral’) are associated with the transverse ridges of the ambulacral groove (see below; [figure 2c,f,g](#)). These have a circular cross-section basally, but extend into weakly concavo-convex oar-blade-like structures. They are preserved in different orientations ([figure 2a](#)) and are thus interpreted as articulated basally. There are six per transverse ridge. Three originate where each ridge meets the ambulacral groove edge; the largest of these is directed sub-adorally. Three smaller examples attach approximately halfway down each ridge and are directed sub-medially.

The aboral surface sporadically bears distinctive bivalved pedicellariae ([figures 1c](#) and [2a,c–g](#)). Valves are roundedly subtriangular in outline, their distal apex bearing paired spines diverging at approximately 60°. In profile, they are strongly but not evenly convex, with distinct facets (near perpendicular to the commissural plane) laterally and especially distally between the divergent spines. The valves have small tooth-like serrations on their commissural margins. The pedicellariae are preserved with differing gapes (compare the two complete examples in [figure 2c](#)), which indicates that they were articulating structures, presumably capable of closure. Soft tissue is consistently preserved in the basal half of the valve cavity. The top of this material is saddle-shaped, convex in sagittal section ([figure 2d,e](#)). The pedicellariae are attached to the ossicular network by a stubby calcite ‘boss’, much shorter than the aboral spines. This structure contains a core of soft tissue connected to that of the arm interior, but connected only tenuously to that between the valves.

The ambulacral groove consists of deep podial basins, partially roofed laterally and separated by transverse ridges offset from each other across the midline ([figure 2b](#)). Half of the lateral basin wall is open to the arm interior. This is consistently the same half, but might be either abradial or adradial (see §2). Each basin is filled by a mass of soft tissue (interpreted as an ampulla) from which a long and flat projection (a collapsed podium) emerges ([figure 2b,f,g](#)). The ampullae extend to the midline of the groove, which also preserves a substantial thickness of external soft tissue ([figure 2f,g](#)). Podia are elongate and have weakly pointed distal terminations. Although typically collapsed, a few ([figure 1c](#)) preserve a sub-circular cross-section distally.

The aboral surface of the small disc is incompletely known. It lacks pedicellariae and bears spines similar to the aboral spines of the arms. The madreporite is not known. The mouth frame comprises five two-piece mouth-angle plates ([figure 1d](#)), each bearing probably eight spines directed inwards, and nearly converging medially ([figure 1c](#)). These spines are similar in morphology to the adambulacral spines described above. A thin membrane (peristome) covers the adoral surface of the disc abradial of the mouth frame ([figure 1d](#)). The peristome does not preserve an opening, but possesses a sub-median keel-like ridge ([figure 1c,d](#)). This structure is approximately co-planar with the collapsed podia and probably represents a taphonomic ‘pinching’ artefact that conceals the mouth; the peristome is thus interpreted as relatively loose and ‘baggy’.

Much of the disc is occupied by a sediment filled structure, interpreted as a cardiac stomach (see [figure 1f,g](#), Electronic Appendix), which is congruent with

the peristome adorally (although it does not reach into the peristomial ridge) and extends to near the aboral surface of the disc. The stomach is undivided and rectal caecae and an anus are not apparent. A single out-pocketing is preserved, connected to the stomach adorally but extending aborally for about half of the thickness of the disc. It consists of two subplanar structures (figure 1f) connected along one edge. This structure corresponds in position with an arm and is interpreted as a pyloric caeca. The absence of other corresponding structures is interpreted as a result of incomplete sediment penetration.

4. DISCUSSION

Pyloric caecae, pedicellariae, papulae and an external radial canal (figure 2h) are all crown-group asteroid characters, absent in crown-group ophiuroids. Hard-part fossil evidence suggests that the last two characters were primitive to the stelleroids; their presence in *Bdellacoma* is thus not clear evidence of asteroid affinities. However, comparable pedicellariae and a pyloric system are not known in any echinoderms other than asteroids and these appear to be asteroid apomorphies. Spencer (1940) and Spencer & Wright (1966) placed *Bdellacoma* within the proturid ophiuroids, but we consider this unlikely in the light of our new data and instead treat it as a stem-group asteroid with a convergently ophiuroid-like body-form. *Bdellacoma* has offset (alternating) ambulacral plates, which previous authors (e.g. Spencer & Wright 1966; p. U13; Dean 2005) have treated as a typically ophiuroid character. However, the Herefordshire Lagerstätte material casts doubt on this, and highlights the difficulty in assigning early Palaeozoic stelleroids to the stem of either extant group.

The adambulacral spines of *Bdellacoma* are clear homologues of similarly positioned spines in Recent asteroids, but differ in their distally-broad bladed morphology and overlapping habit. These differences may reflect a requirement for a greater degree of protection of the external ampullae. The aboral spines of *Bdellacoma* are similar to the paxillae of certain Recent asteroids, but homology cannot be established in the absence of microstructural data.

The pedicellariae of *Bdellacoma* are 'elementary pedicellariae' according to the classification of Jangoux & Lambert (1987), in that they are not associated with a foramen and lack a discrete basal piece. They belong within the 'élémentaires droits' subcategory, and the calcite boss on which they rest is probably to be homologous with the 'protrubérance développée par la plaque squelettique sous-jacente' ('protruberance developed by the subjacent skeletal plate'; Jangoux & Lambert 1987; p. 49). However, the morphology of these pedicellariae differs in detail from Recent examples, notably in their unusually large size relative to the arms, in the development of distal spines and in lacking a lateral gape when closed. Similar valves have been recorded as isolated fossils in Silurian to Carboniferous rocks (Boczarowski 2001), and are presumably indicative of a relatively long-lived clade comprising a significant number of taxa. These were first described from the upper Wenlock of Gotland, Sweden (Jones 1887), under the monotypic generic name *Bursulella*, and interpreted as ostracods. Using Devonian material, Boczarowski (2001) re-interpreted similar valves as echinoderm pedicellariae,

although he assigned them to the Echinoidea. The structures are large and robust with strongly serrated valves that can completely close. Some crown-group asteroids use articulating pedicellariae in prey-capture (Chia & Koss 1994), and we infer a similar function in *Bdellacoma*. However, the absence of a substantial soft-part connection to the arm rules out the pedicellariae as sites of digestion, and we suggest that the pedicellarial soft tissue is primarily adductor muscle.

Taphonomic 'pinching' of the peristome complicates interpretation of the oral region, but the peristome in *Bdellacoma* appears to have been large relative to the mouth. The absence of a sediment fill in the mouth implies that it remained closed after death, suggesting that the sphincter muscles that operate the mouth of crown group asteroids may have been absent. The sac-like gut of *Bdellacoma* is simpler than that of many Recent asteroids, with neither a clear cardiac/pyloric division, nor apparently any pouches or evaginations other than the pyloric caecae. While the absence of rectal caecae or an anus may be an artefact of incomplete sediment penetration, we tentatively interpret the digestive system as blind.

Recent asteroids possess internal ampullae, their podia emerging through pores in the ambulacral ossicles (figure 2h). Most Palaeozoic asteroids lack podial pores, but instead have external hollows (podial basins). These have normally been inferred to hold external ampullae, although several authors (Schuchert 1915; Spencer 1919–1940; p. 184; Kesling 1962; Branstrator 1975; Haude 1995) have argued instead for internal ampullae, suggesting that gaps in the walls of podial basins functioned as podial pores (see discussion in Blake 2000; p. 320). Our material demonstrates that podial basins in *Bdellacoma* accommodated external ampullae despite the presence of such gaps, which presumably contained articular tissue (option 3 of Blake 2000; p. 321). Soft tissue is also preserved medially in the ambulacral groove (arrow in figure 2g), but discrete radial and lateral canals are not evident; we interpret this material as an amalgamation of tissues including the ambulacral musculature, radial nerve cord and water-vascular canals.

The long and weakly pointed podia of *Bdellacoma* lack terminal suckers. This morphology is similar to that of the calcified Ordovician somasteroid tube feet figured by Dean (1999). There is considerable variation in the morphology of tube foot terminations within extant asteroids, and the traditional view of a straightforward distinction between 'flat-tipped, suckered' and 'pointed, non-suckered' morphologies has been shown to be oversimplistic (Vickery & McClintock 2000). Nonetheless, the podia of *Bdellacoma* clearly belong in the 'pointed, non-suckered' category of these authors, in which there is less variation than the other. The extended position of the tube-feet in both specimens is noteworthy, as extant starfish withdraw their podia when threatened (A.B. Smith, personal communication.). This might represent attempted escape behaviour following burial.

The soft parts of *Bdellacoma* are most closely comparable to those of the Paxillosida among extant orders of asteroids. 'Pointed, non-suckered' tube feet are restricted to paxillosids except for one example of 'semi-pointed, non-suckered' podia in the deep-sea order Notomyotida (Vickery & McClintock 2000). A sac-like and undivided blind gut is also typical of the Paxillosida (although an

anus is sometimes present; see Jangoux 1982), and 'élémentaires droits' pedicellariae occur only in paxillosids and valvatids (Jangoux & Lambert 1987). This is consistent with phylogenies that place the Paxillosida at the base of the crown group asteroids (Mortensen 1922, 1923; Gale 1987; Smith 1997), rather than those (MacBride 1921, 1923a,b; Blake 1987; Knott & Wray 2000) that suggest that this order is derived.

We thank the Leverhulme Trust (F/08581/E), the Natural Environment Research Council (GR3/12053) and English Nature for their support, K. Saunders for technical work, D. Blake, A. Gale and S. Bengtson for helpful discussion, A. B. Smith and two anonymous referees for helpful reviews and T. Hall and J. Sinclair for general assistance.

REFERENCES

- Blake, D. B. 1987 A classification and phylogeny of post-Palaeozoic sea stars (Asteroidea: Echinodermata). *J. Nat. Hist.* **21**, 481–528.
- Blake, D. B. 2000 The class Asteroidea (Echinodermata): fossils and the base of the crown group. *Am. Zool.* **40**, 316–325.
- Boczarowski, A. 2001 Isolated sclerites of Devonian non-pelmatozoan echinoderms. *Palaeontol. Pol.* **59**, 1–216.
- Branstrator, J. W. 1975 Podial efficacy of some Ordovician asteroids (Echinodermata) from North America. *Bull. Am. Paleont.* **67**, 57–69.
- Briggs, D. E. G., Siveter, D. J. & Siveter, D. J. 1996 Soft-bodied fossils from a Silurian volcanoclastic deposit. *Nature* **382**, 248–250.
- Briggs, D. E. G., Sutton, M. D., Siveter, D. J. & Siveter, D. J. 2004 A new phyllocarid (Crustacea: Phyllocarida) from the Silurian Fossil-Lagerstätte of Herefordshire, England. *Proc. R. Soc. B* **271**, 131–138.
- Chia, F. S. & Koss, R. 1994 Asteroidea. In *Microscopic anatomy of invertebrates*, vol. 14 (ed. F. W. Harrison & F. S. Chia), pp. 169–246. New York: Wiley-Liss.
- Dean, J. 1999 Evolutionary diversification of asteroids and ophiuroids (Echinodermata). Unpublished Ph.D. thesis, Cambridge University.
- Dean, J. 2005 Skeletal homologies, phylogeny and classification of the earliest asterozoan echinoderms. *J. Syst. Palaeontol.* **3**, 29–114.
- Gale, A. S. 1987 Phylogeny and classification of the Asteroidea (Echinodermata). *Zool. J. Linn. Soc.* **89**, 107–132.
- Haude, R. 1995 Echinodermen aus dem Unter-Devon der argentinischen Präkordillere. *N. Jahrb. Geol. Paläont. Abh.* **197**, 37–86.
- Jangoux, M. 1982 Digestive systems: Asteroidea. In *Echinoderm nutrition* (ed. M. Jangoux), pp. 235–272. Rotterdam: A.A. Balkema.
- Jangoux, M. & Lambert, A. 1987 Étude comparative des pédicellaires des astéries (echinodermes). *Bull. Soc. Sc. Nat. Ouest Fr. Suppl. H.S.* 1987, 47–58.
- Jones, T. R. 1887 *Notes on some Silurian Ostracoda from Goulard*, 8 pp. Stockholm: Norstedt and Söner.
- Kesling, R. V. 1962 Notes on *Protopalaeaster narrawayi* Hudson. *J. Paleontol.* **36**, 933–942.
- Knott, K. E. & Wray, G. A. 2000 Controversy and consensus in asteroid systematics: new insights to ordinal and familial relationships. *Am. Zool.* **40**, 382–392.
- MacBride, E. W. 1921 Echinoderm larvae and their bearing on evolution. *Nature* **108**, 529–530.
- MacBride, E. W. 1923a Echinoderm larvae and their bearing on evolution. *Nature* **111**, 47.
- MacBride, E. W. 1923b Comment on T. Mortensen, Echinoderm larvae and their bearing on classification. *Nature* **111**, 323–324.
- Mortensen, T. 1922 Echinoderm larvae and their bearing on evolution. *Nature* **110**, 806–807.
- Mortensen, T. 1923 Echinoderm larvae and their bearing on evolution. *Nature* **111**, 322–323.
- Orr, P. J., Briggs, D. E. G., Siveter, D. J. & Siveter, D. J. 2000 Three-dimensional preservation of a non-biomineralized arthropod in concretions in Silurian volcanoclastic rocks from Herefordshire, England. *J. Geol. Soc. Lond.* **57**, 173–186.
- Orr, P. J., Siveter, D. J., Briggs, D. E. G., Siveter, D. J. & Sutton, M. D. 2002 Preservation of radiolarians in the Herefordshire Konservat-Lagerstätte (Wenlock, Silurian), England, and implications for the taphonomy of the biota. *Spec. Pap. Palaeontol.* **67**, 205–224.
- Ruppert, E. E. & Barnes, R. D. 1994 *Invertebrate zoology*, 6th edn, 1056 pp. Orlando: Saunders College Publishing.
- Salter, J. W. 1857 On some new Palaeozoic starfishes. *Ann. Mag. Nat. Hist.* **20**, 321–334.
- Schuchert, C. 1915 Revision of Paleozoic Stelleroidea with special reference to North American Asteroidea. *Bull. Am. Nat. Mus.*, **88**, 312 pp.
- Siveter, D. J. 2000 The Ludlow series. In *British silurian stratigraphy* (ed. R. J. Aldridge, D. J. Siveter, D. J. Siveter, P. D. Lane, D. Palmer & N. H. Woodcock), pp. 327–425. Peterborough: Joint Nature Conservation Committee.
- Siveter, D. J., Sutton, M. D., Briggs, D. E. G. & Siveter, D. J. 2003 An ostracode crustacean with soft parts from the lower Silurian. *Science* **302**, 1749–1751.
- Siveter, D. J., Sutton, M. D., Briggs, D. E. G. & Siveter, D. J. 2004 A Silurian sea-spider. *Nature* **431**, 978–980.
- Smith, A. B. 1997 Echinoderm phylogeny: how congruent are morphological and molecular estimates? In *Geobiology of echinoderms* (ed. J. A. Waters & C. G. Maples) *Pal. Soc. Pap.*, **3**, 337–355.
- Spencer, W. K. 1919–1940 *A Monograph of the British Palaeozoic Asteroidea*. *Palaeont. Soc. Lond. Mem.* 540 pp.
- Spencer, W. K. & Wright, C. W. 1966 Asterozoans. In *Treatise on invertebrate paleontology, Pt U, Echinodermata 3* (ed. R. C. Moore), pp. U4–U107. Geological Society of America and University of Kansas.
- Sutton, M. D., Briggs, D. E. G., Siveter, D. J. & Siveter, D. J. 2001a An exceptionally preserved vermiform mollusc from the Silurian of England. *Nature* **410**, 461–463.
- Sutton, M. D., Briggs, D. E. G., Siveter, D. J. & Siveter, D. J. 2001b Methodologies for the visualization and reconstruction of three-dimensional fossils from the Silurian Herefordshire Lagerstätte. *Paleontol. Elec.* **4**. (http://palaeo-electronica.org/2001_1/s2/issue1_01.htm)
- Sutton, M. D., Briggs, D. E. G., Siveter, D. J. & Siveter, D. J. 2001c A three-dimensionally preserved fossil polychaete worm from the Silurian of Herefordshire, England. *Proc. R. Soc. B* **268**, 2355–2363.
- Sutton, M. D., Briggs, D. E. G., Siveter, D. J., Siveter, D. J. & Orr, P. J. 2002 The arthropod *Offacolus kingi* (Chelicerata) from the Silurian of Herefordshire, England: computer based morphological reconstructions and phylogenetic affinities. *Proc. R. Soc. B* **269**, 1195–1203.
- Sutton, M. D., Briggs, D. E. G., Siveter, D. J. & Siveter, D. J. 2004 Computer reconstruction and analysis of a three-dimensionally preserved vermiform mollusc (*Acaenoplax hayae*) from the Silurian Herefordshire Lagerstätte (Wenlock, England), and implications for molluscan phylogeny. *Palaeontology* **47**, 293–318.
- Vickery, M. S. & McClintock, J. B. 2000 Comparative morphology of tube feet among the Asteroidea: phylogenetic implications. *Am. Zool.* **40**, 355–364.

The supplementary Electronic Appendix is available at <http://dx.doi.org/10.1098/rspb.2004.2951> or via <http://www.journals.royal.soc.ac.uk>.