

A SILURIAN OPHIUROID WITH SOFT-TISSUE PRESERVATION

by REECE P. CARTER¹ , MARK D. SUTTON^{1,*} , DEREK E. G. BRIGGS² ,
IMRAN A. RAHMAN³ , DAVID J. SIVETER⁴  and DEREK J. SIVETER^{3,5} 

¹Department of Earth Sciences & Engineering, Imperial College London, London, SW7 2BP, UK; m.sutton@imperial.ac.uk;

²Department of Earth & Planetary Sciences, Yale Peabody Museum of Natural History, Yale University, New Haven, CT 06520-8109, USA

³Oxford University Museum of Natural History, Parks Road, Oxford, OX1 3PW, UK

⁴School of Geography, Geology & the Environment, University of Leicester, Leicester, LE1 7RH, UK

⁵Department of Earth Sciences, University of Oxford, South Parks Road, Oxford, OX1 3AN, UK

*Corresponding author

Typescript received 21 January 2021; accepted in revised form 29 April 2021

Abstract: Most Palaeozoic brittle stars lack the fused arm ossicles (vertebrae) that facilitate the remarkable mode of walking that characterizes living forms. Here we describe a stem ophiuroid from the Herefordshire Lagerstätte (Silurian, Wenlock Series), which is exceptional in preserving the body cavity uncompact and the long tube feet. We assign the specimen to the order Oegophiurida. The morphology of the arms and attitude of the

specimen suggest that locomotion may have been achieved by arm propulsion combined with podial walking. This ophiuroid increases the diversity of echinoderm higher taxa with preserved soft parts represented in the Herefordshire Lagerstätte.

Key words: Asterozoa, Herefordshire Lagerstätte, Silurian, Ophiuroidea, Soft tissues.

LIVING representatives of the echinoderm subphylum Asterozoa are divided into two classes: Ophiuroidea (brittle stars) and Asteroidea (sea stars). A new ophiuroid from the Silurian Herefordshire Lagerstätte (Briggs *et al.* 1996; Siveter *et al.* 2020) preserves the body cavity in three dimensions and retains soft tissues including the tube feet and internal structures (Carter 2019). The body cavity in fossil asteroids has normally collapsed through decay and compaction (Mah & Blake 2012) and the same applies to fossil ophiuroids, such as Palaeozoic oegophiurids, which possessed a large disc. Tube feet were previously described in a Herefordshire asterozoan assigned to *Bdellacoma* (Sutton *et al.* 2005) in which they are preserved, as in the ophiuroid reported here, as void fills following soft-tissue decay. Sutton *et al.* (2005) assigned *Bdellacoma* to Asteroidea based on the presence of a pyloric system in the gut and the presence of pedicellariae. Blake (2013), however, included *Bdellacoma* in Stenuroidea, which he elevated to class level alongside Somasteroidea, Ophiuroidea and Asteroidea. These reassignments remain the subject of discussion: Gladwell (2018) retained Order Stenurida including *Bdellacoma* within Ophiuroidea in the absence of a wider phylogenetic analysis. The position of *Bdellacoma* remains uncertain but the discovery of an oegophiurid clearly establishes the occurrence of ophiuroids in the

Herefordshire Lagerstätte. The Herefordshire biota has yielded tube feet in other echinoderms, the edrioasteroid *Heropyrgus disterrminus* Briggs *et al.*, 2017 and the ophiocystioid *Sollasina cthulhu* Rahman *et al.*, 2019, although those of *Sollasina* are covered in calcite plates.

Echinoderm fossils rarely preserve soft tissues. The first report of preserved tube feet in a Palaeozoic asterozoan was from the Lower Devonian Hunsrück Slate of Germany, where the soft tissues in *Bundenbachia benecke* (Protasteridae) are replaced by pyrite (Glass & Blake 2004). Pyritized tube feet are known in other Hunsrück Slate echinoderms: a crinoid (Ausich *et al.* 2013) and a holothurian (Smith & Reich 2013). Pyritized tube feet are also known in *Protasterina flexuosa* (Protasteridae) from the Upper Ordovician of Kentucky (Glass 2006), which preserves internal features of the water vascular system (Clark *et al.* 2017). The ophiocystioid *S. cthulhu* is the only Herefordshire echinoderm known to preserve evidence of an internal canal (Rahman *et al.* 2019). Tube feet reported in the stylophoran *Thoralicystis* sp. nov. from the Lower Ordovician Fezouata Shale of Morocco are preserved in iron oxide pseudomorphs of pyrite (Lefebvre *et al.* 2019). The Herefordshire Lagerstätte provides the only known Palaeozoic setting in which echinoderm soft tissues are preserved through a taphonomic pathway that does not involve pyritization.

Well-preserved tube feet may provide evidence of the nature of feeding and locomotion in fossil asterozoans (Gale 1987; Vickery & McClintock 2000; Blake 2013). Although rare, they are more commonly preserved than soft internal features of the water vascular system. When they project beyond the test they can be entombed in sediment before they decay, and the exceptional taphonomic conditions of the Herefordshire deposit have preserved them as a calcite-filled void (Orr *et al.* 2000). The preservation of tube feet in pyrite at other localities is also facilitated by their external position, which expedites diffusion of iron (Briggs 2003).

MATERIAL AND METHOD

A single specimen was serially ground at 20 µm intervals. The 718 exposed surfaces were submerged under a thin layer of water and photographed with a Leica DFC420 digital camera mounted on a Leica MZ8 binocular microscope. The SPIERS software suite was used to remove extraneous material from the images to reconstruct (Fig. 1) a three-dimensional ‘virtual fossil’ (Sutton *et al.* 2001, 2012, 2014; Spencer *et al.* 2020). Datasets from the serial grinding, together with the final three-dimensional model in VAXML/STL format, are held by the Oxford University Museum of Natural History (OUMNH), and are also available in Carter *et al.* (2021).

SYSTEMATIC PALAEOLOGY

Phylum ECHINODERMATA Bruguière, 1791 (*ex* Klein, 1734)

Class OPHIUROIDEA Gray, 1840

Order OEGOPHIURIDA Matsumoto, 1913

Suborder LYSOPHIURINA Gregory, 1896

Family PROTASTERIDAE? Miller, 1889

Genus PROTASTER? Forbes, 1849

Type species. *Protaster sedgwickii* Forbes, 1849, by monotypy, from the Silurian, Ludlow Series of Kendal, Lake District, UK.

Material. OUMNH PAL-C.36516, a complete specimen reconstructed as a virtual fossil. Three other unground specimens, OUMNH PAL-C.36029, PAL-C.36517, and PAL-C.36518, probably belong to this taxon.

Locality and horizon. Coalbrookdale Formation, Wenlock Series, Silurian, Herefordshire, UK.

Description. The central disc is *c.* 5 mm in diameter, and pentagonal to subcircular in outline (Fig. 1A, B). The specimen is unusual among Palaeozoic asterozoans in having undergone

negligible compaction and preserving the dorsal body wall of the disc above, rather than collapsed, onto the proximal part of the arms. The preserved height of the body is *c.* 40% of the diameter of the disc (Fig. 1C, D). The oral surface is convex, but this may be largely due to flexure of the arms dorsally (Fig. 1A, C). The aboral (dorsal) surface of the disc is convex except in one direction, where it is slightly depressed and perforated in places (Fig. 1B). The arms are clearly distinguished from the disc by the relief of the ossicles (Fig. 1A, G): *c.* 55% of the arm length extends beyond the disc margin (Fig. 1A, B, G). One arm shows more pronounced evidence of folding (Fig. 1C, F, H), which is interpreted, based on the different attitude of this arm compared with the others, as the result of flexibility *in vivo* rather than a taphonomic artefact. The arms could clearly be flexed both vertically and laterally. There is a pentagonal space in the position of the mouth (Fig. 1A, G) but the outlines of the plates in this region, which are more prominent than those of the arm, are indistinct. The arms widen slightly from the mouth to the margin of the disc and taper gradually beyond it to terminate in a point (Fig. 1A, G). We did not distinguish a terminal plate; it may not have been captured by the reconstruction. Extrapolation indicates that there are *c.* 18 pairs of tube feet, and therefore rows of ossicles, in each arm (Fig. 1I, J).

The ambulacral ossicles, as viewed from the oral side, appear to be *c.* 50% longer than wide and accommodate a small embayment, interpreted as the podial basin, from which the tube feet arise (Fig. 1I, J). The ambulacral ossicles are offset on either side of the perradial suture (Fig. 1I, J); this offset is more pronounced distally than proximally. The ambulacra are flanked and partially overlapped by narrower adambulacral ossicles (Fig. 1F). The adambulacral ossicles are thicker than those of the ambulacra. Short, paired groove spines are preserved in the distal part of the arm inclined toward its tip at *c.* 20° (Fig. 1K). A shallow ambulacral groove runs along the axis of each arm (Fig. 1F, I), narrowing and closing as the tip is approached. This closure is particularly obvious in the arm that is folded distally.

The tube feet (Fig. 1A, C, F–I, K) are long and thin, longest near the mid-length of the arm and becoming shorter toward the mouth and the arm tip. They show little morphological detail but appear to be of constant width (Fig. 1I, K). The tube feet were clearly subject to partial collapse (Fig. 1I, K) but there is no clear evidence of a basal expansion or a distal sucker. Internal features of the water vascular system are not preserved.

There is no ambital framework (Blake & Guensburg 2015) or thickening around the margin of the disc, which is irregular and perforated in places as a result of damage during fossilization (Fig. 1B). On the oral side the plates in the interradial portions of the disc lack visible boundaries; they are interpreted as small and thin, with little relief at their boundaries. Evidence of a madreporite has not been confirmed (*contra* Carter 2019). The boundaries of the aboral plates, like those on the oral side, are not evident; these are also interpreted as small and thin, and lacking relief at their boundaries (Fig. 1D). There is no evidence of an anus (Fig. 1B), which is also absent in living ophiuroids.

Three poorly preserved apparently sac-like internal structures are located interradially (Fig. 1E). There is no evidence that they are part of the water vascular system or connected to the mouth.

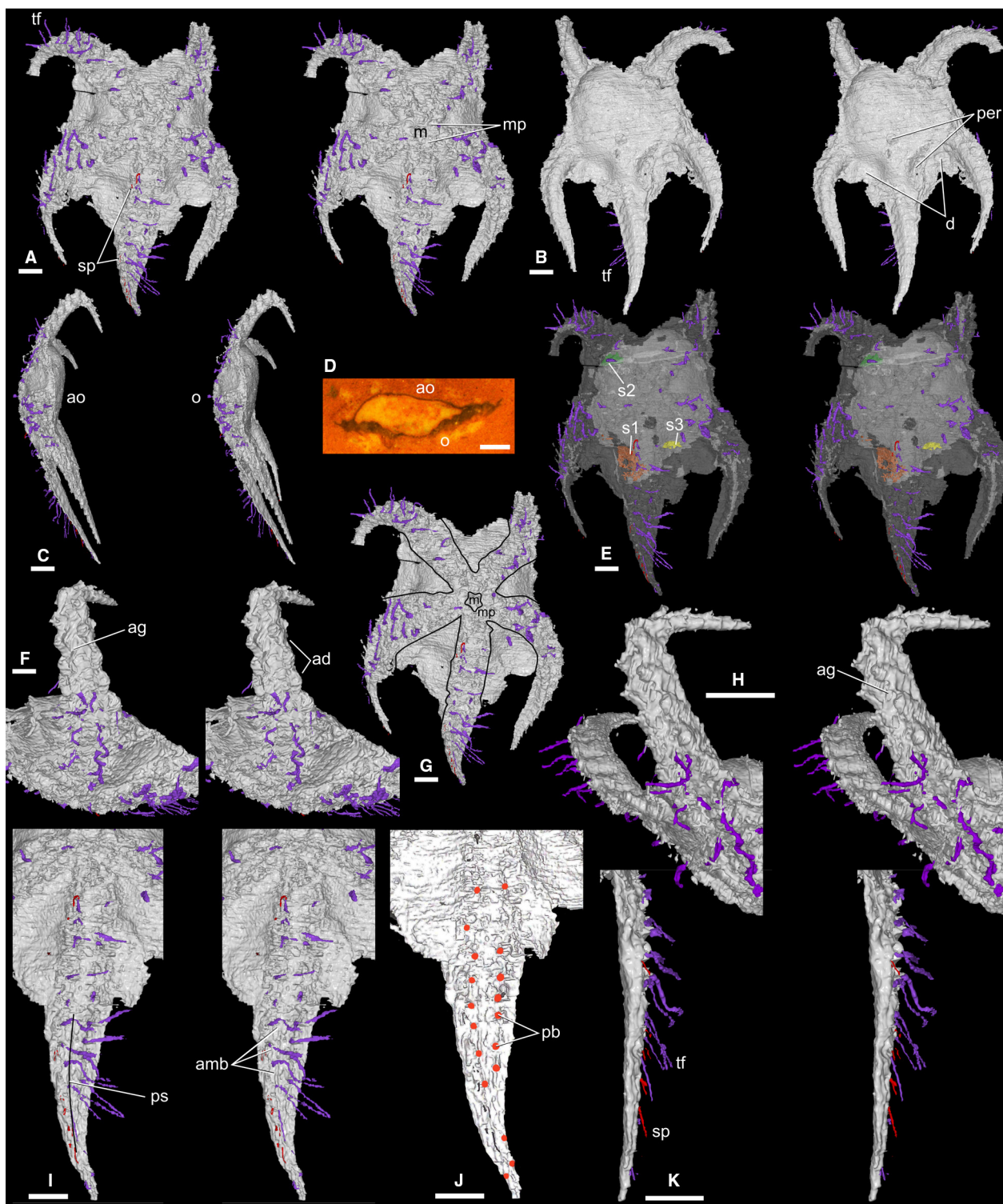


FIG. 1. *Protaster?* sp. (OUMNH PAL-C.36516). A–C, E–F, H–I, K, virtual reconstructions as stereo-pairs. A, oral; B, aboral; C, lateral view. D, section through disc showing body cavity. E, transparent view to highlight tube feet and internal soft tissues. F, sharply folded arm in oral view. G, oral view with arms outlined. H, sharply folded arm (and adjacent arm) in lateral view. I, ‘posterior’ arm in oral view showing tube feet; and J, their points of origin (podial basins: red circles) displaying the offset of ambulacral plates. K, lateral view showing extension of tube feet and some groove spines. *Abbreviations:* ad, adambulacral plate; ag, ambulacral groove; amb, ambulacral plate; ao, aboral surface; d, depressed part of aboral surface with ragged disc margins; m, mouth; mp, mouth plates; o, oral surface; pb, podial basin; per, perforations; ps, perradial suture; s1–s3, sac-like internal structures 1–3; sp, groove spine (red); tf, tube foot (purple). Scale bars represent 1 mm.

They show no consistency in size or shape. It is not known whether there were other such structures, not preserved, that would complete the pentamerous symmetry. Structures flanking one arm (Fig. 1E, s1 and s3) might be a pair, in which case their position corresponds approximately to the expected location of the bursae or associated gonads, which are large organs in some asterozoans, and may be relatively decay resistant compared with other organs (Briggs & Kear 1993).

Remarks. We assign the Herefordshire specimen to the Order Oegophiuroida, a group of stem ophiuroids known only from the Palaeozoic. The relationships of Palaeozoic ophiuroids remain an area of investigation (Blake & Guensburg 2015; Blake *et al.* 2015; Hunter *et al.* 2016; Gladwell 2018). The Herefordshire specimen is difficult to assign to a genus, and does not contribute sufficient data to allow a phylogenetic analysis. The diagnostic features of asterozoans lie mainly in the detailed morphology of the arm ossicles and interradial plates. The methodology and resolution of our reconstructions are sufficient to resolve plate-boundary morphology, if it were preserved. Plate boundaries are difficult to discern in this case, however, as a result of the pervasive recrystallization typical of echinoderm fossils from the Herefordshire deposit (Sutton *et al.* 2005; Briggs *et al.* 2017; Rahman *et al.* 2019), and because the ossicles are partially concealed by the outer body wall. In addition, the outer (abradial) margin of the ambulacra (and therefore their outline), which is important for distinguishing genera (Glass & Blake 2004; Hunter *et al.* 2016), is obscured by the adambulacra (laterals).

DISCUSSION

Systematic position

The Herefordshire specimen shares a number of characters with Protasteridae, most recently diagnosed by Dean Shackleton (2005; see Blake *et al.* 2016), including an obvious interradial disc without marginalia, elongate gradually tapering arms, and alternating ambulacra with a slightly zig-zag perradial suture (Spencer 1934; Dean Shackleton 2005). The apparently light nature of the plating may be taphonomic. Similarly, the possible absence of vertical spines is probably an artefact of taphonomy or due to these structures not being captured in the reconstruction. *Protaster sedgwickii* is the only ophiuroid taxon recorded from the Wenlock Shales (i.e. Coalbrookdale Formation) in the British Isles (Lewis *et al.* 2007). We tentatively assign the Herefordshire specimen to *Protaster* but there is insufficient information to attempt a species assignment.

Locomotion

Extant ophiuroids have evolved a musculoskeletal method of locomotion based on fusion of the arm

ossicles into vertebrae and coordinated movements of the snake-like arms (Clark *et al.* 2018), which give the group its name. The interpretation of locomotion in fossil asterozoans, especially those outside crown group Ophiuroidea and Asteroidea, is not straightforward; morphology may not be a definitive guide to function (Dean Shackleton 2005, p. 59; Clark *et al.* 2020). Oegophiurids such as *Protaster* had offset ambulacra and their arms were presumably less flexible than those of living ophiuroids. Spencer & Wright (1966) regarded oegophiurids as largely sessile and capable of only slow locomotion. The flexure of the arms in the Herefordshire ophiuroid, however, probably reflects their movement in life. Their arrangement (Fig. 1A, B, G) corresponds to that in reverse rowing (Astley 2012), one of two major modes of walking in extant ophiuroids. Some living ophiuroids such as *Ophiogeron granulatus* rely on podial walking on their large tube feet, and such taxa may be an analogy for Palaeozoic forms (Byrne & Hendler 1988; who refer to *O. granulatus* as *O. supinus*). On this basis Glass & Blake (2004) inferred that podial locomotion was likely for the Devonian protasterid *Bundenbachia beneckeii*, and Clark *et al.* (2020) extended this to Palaeozoic ophiuroids without fused segments. Movement in the Herefordshire specimen may have been facilitated in the same way although the tube feet are slender, as in living ophiuroids, compared with those of *B. beneckeii*. Sutcliffe (1997) described a new trace fossil, *Arcichnus saltatus*, from the Hunsrück Slate as a product of this mode of locomotion in the protasterid *Taeniaster* but it is not clear that protasterids were capable of moving in this manner (Glass & Blake 2004). Spencer (1951; see also Spencer & Wright 1966) considered that at least some Palaeozoic ophiuroids were infaunal but it is doubtful that they lived permanently in burrows (Glass & Blake 2004). The orientation of the concretion containing the Herefordshire fossil relative to the host sediment is unknown. The dorsal curvature of the arms, however, is most reminiscent of escape movements of the asteroid *Astropecten* following burial (Ishida *et al.* 2019), rather than those of the ophiuroid *Ophiophthalmus* (Ishida & Fujita 2001), perhaps reflecting the lower flexibility of the arms compared with those in living ophiuroids. The Silurian ophiuroid may have moved with some combination of arm propulsion, even in the absence of fused ambulacra, and podial walking, in contrast to the musculoskeletal walking used by living ophiuroids.

Feeding

Modern ophiuroids include detritivores and scavengers, suspension feeders and predators. The tube feet in the

Herefordshire protasterid are long and thin, similar to those of the protasterid *B. beneckeii* from the Hunsrück Slate. The ampullae were presumably external and protected by the ossicles flanking the open groove or furrow. The ability of arms to fold adorally around the ambulacral groove may have provided a further protective mechanism. The size of the mouth as preserved and the lack of details for the mouth plate morphology (Fig. 1A, G) provide no evidence for or against deposit feeding, even though there is a large body cavity. The tube feet lacked suckers, as in all ophiuroids. Such tube feet in Palaeozoic forms may have facilitated a range of feeding modes including trapping suspended particles and coiling the arm to capture larger food items in scavenging or predation (Glass & Blake 2004). Thus there is no definitive evidence for the feeding strategy used by the Herefordshire ophiuroid.

CONCLUSION

The new Silurian ophiuroid preserves the body in three dimensions and has arms that are flexible in any direction and slender tube feet similar to those in living ophiuroids. Although the lack of preserved details of the plates prevents a definitive genus and species assignment, the fossil is clearly an ophiuroid and, as such, increases the diversity of taxa known from the Herefordshire Lagerstätte. In the absence of additional evidence of the morphology or multiple specimens showing the attitude of the arms, the potential for constraining the ecology of the Silurian ophiuroid is limited.

Acknowledgements. We thank Carolyn Lewis for technical support and David Edwards and the late Roy Fenn for general assistance. Our research was funded by the Natural Environment Research Council (grant NE/F018037/1), the Leverhulme Trust (grant EM-2014-068), the Yale Peabody Museum of Natural History Invertebrate Palaeontology Division, and Natural England. RPC was supported by the Palaeontological Association through its Undergraduate Research Bursary scheme (grant PA-UB201905). We are grateful for comments from Fred Hotchkiss and an anonymous reviewer, which resulted in important improvements to the paper.

Author contributions. DeJS, DaJS, DEGB and MDS conceived the study; MDS and DeJS curated the data; DeJS, DaJS, DEGB, MDS and RPC acquired the funding; RPC, MDS, DEGB, IAR, DaJS and DeJS carried out the investigation; MDS, DeJS and DaJS devised the methodology; DeJS carried out the project administration; MDS implemented the software; MDS and IAR supervised RPC; RPC, MDS and DEGB created Figure 1; RPC, MDS and DEGB prepared the first draft of the paper; and DEGB, MDS, IAR, DeJS, DaJS and RPC reviewed and edited the paper.

DATA ARCHIVING STATEMENT

The raw serial-grinding data and triangle-mesh model of the holotype specimen OUMNH PAL-C.36516 (in VAXML/STL format), are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.wdbrv15nc>

Editor. George Sevastopulo

REFERENCES

- ASTLEY, H. C. 2012. Getting around when you're round: quantitative analysis of the locomotion of the blunt-spined brittle star, *Ophiocoma echinata*. *Journal of Experimental Biology*, **215**, 1923–1929.
- AUSICH, W. I., BARTELS, C. and KAMMER, T. W. 2013. Tube foot preservation in the Devonian crinoid *Codiocrinus* from the Lower Devonian Hunsrück Slate, Germany. *Lethaia*, **46**, 416–420.
- BLAKE, D. B. 2013. Early asterozoan (Echinodermata) diversification: a paleontologic quandary. *Journal of Paleontology*, **87**, 353–372.
- and GUENSBURG, T. E. 2015. The class Somasteroidea (Echinodermata, Asterozoa): morphology and occurrence. *Journal of Paleontology*, **89**, 465–486.
- — and LEFEBVRE, B. 2016. New early Paleozoic Asterozoa (Echinodermata) from the Armorican Massif, France, and the Western United States. *Annales de Paléontologie*, **102**, 161–181.
- ZAMORA, S. and GARCÍA-ALACALDE, J. L. 2015. A new Devonian asteroid-like ophiuroid from Spain. *Geologica Acta*, **13**, 335–343.
- BRIGGS, D. E. G. 2003. The role of decay and mineralization in the preservation of soft-bodied fossils. *Annual Review of Earth & Planetary Sciences*, **31**, 275–301.
- and KEAR, A. J. 1993. Decay of *Branchiostoma*: implications for the interpretation of soft-tissue preservation in conodonts and other primitive chordates. *Lethaia*, **26**, 275–287.
- SIVETER, D. J. and SIVETER, D. J. 1996. Soft-bodied fossils from a Silurian volcanoclastic deposit. *Nature*, **382**, 248–250.
- — SIVETER, D. J., SUTTON, M. D. and RAHMAN, I. A. 2017. An edrioasteroid from the Silurian Herefordshire Lagerstätte of England reveals the nature of the water vascular system in an extinct echinoderm. *Proceedings of the Royal Society B*, **284**, 20171189.
- BRUGUIÈRE, J. G. 1791. *Tableau encyclopédique et méthodique des trois règnes de la nature. Contenant l'helminthologie, ou les vers infusoires, les vers intestins, les vers mollusques, &c.* Panckoucke, Paris.
- BYRNE, M. and HENDLER, G. 1988. Arm structures of the ophiomyxid brittlestars (Echinodermata: Ophiuroidea: Ophiomyxidae). 687–695. In *Echinoderm biology: Proceedings of the Sixth International Echinoderm Conference, Victoria, 23–28 August 1987*. A.A. Balkema, Rotterdam.
- CARTER, R. 2019. Analysing an exceptionally-preserved Silurian asterozoan. *Palaeontology Newsletter*, **102**, 79–82.

- SUTTON, M. D., BRIGGS, D. E., RAHMAN, I. A., SIVETER, D. J. and SIVETER, D. J. 2021. Data from: A Silurian ophiuroid with soft-tissue preservation. *Dryad Digital Repository*. <https://doi.org/10.5061/dryad.wbrv15nc>
- CLARK, E. G., BHULLAR, B.-A. S., DARROCH, S. A. F. and BRIGGS, D. E. G. 2017. Water vascular system architecture in an Ordovician ophiuroid. *Biology Letters*, **13**, 20170635.
- HUTCHINSON, J. R., DARROCH, S. A. F., MONGIARDINO KOCH, N., BRADY, T. R., SMITH, S. A. and BRIGGS, D. E. G. 2018. Integrating morphology and in vivo skeletal mobility with digital models to infer function in brittle star arms. *Journal of Anatomy*, **233**, 696–714.
- — and BRIGGS, D. E. G. 2020. Three-dimensional visualization as a tool for interpreting locomotion strategies in ophiuroids from the Devonian Hunsrück Slate. *Royal Society Open Science*, **7**, 201380.
- DEAN SHACKLETON, J. 2005. Skeletal homologies, phylogeny and classification of the earliest asterozoan echinoderms. *Journal of Systematic Palaeontology*, **3**, 29–114.
- FORBES, E. 1849. Figures and descriptions illustrative of British Organic Remains. *Memoirs of the Geological Survey of the United Kingdom*, **Decade 1**, 1–64.
- GALE, A. S. 1987. Phylogeny and classification of the Asterozoa (Echinodermata). *Zoological Journal of the Linnean Society*, **89**, 107–132.
- GLADWELL, D. 2018. Asterozoans from the Ludlow Series (upper Silurian) of Leintwardine, Herefordshire, UK. *Papers in Palaeontology*, **4**, 101–160.
- GLASS, A. 2006. Pyritized tube feet in a protasterid ophiuroid from the Upper Ordovician of Kentucky, USA. *Acta Palaeontologica Polonica*, **51**, 171–184.
- and BLAKE, D. B. 2004. Preservation of tube feet in an ophiuroid (Echinodermata) from the Lower Devonian Hunsrück Slate of Germany and a redescription of *Bundembachia benecke* and *Palaeophiomys grandis*. *Paläontologisches Zeitschrift*, **78**, 73–95.
- GRAY, J. E. 1840. *Synopsis of the contents of the British Museum*, 42nd edition. Woodfall and Son, London, 370 pp.
- GREGORY, J. W. 1896. On the classification of the Palaeozoic echinoderms of the group Ophiuroidea. *Proceedings of the Zoological Society of London*, **1896**, 1028–1044.
- HUNTER, A., RUSHTON, A. and STONE, P. 2016. Comments on the ophiuroid family Protasteridae and description of a new genus from the Lower Devonian of the Fox Bay Formation, Falkland Islands. *Alcheringa*, **40**, 429–442.
- ISHIDA, Y. and FUJITA, T. 2001. Escape behaviour of epibenthic ophiuroids buried in the sediment: observations of extant and fossil *Ophiura sarsii sarsii*. 285–292. In BARKER, A. N. (ed.) *Echinoderms 2000*. Swets and Zeitlinger, Lisse.
- — KOHTSUKA, H., MANABE, M. and OHARA, M. 2019. A new example of the trace fossil *Asteriacites quinquefolius* from Japan and its process of production as revealed by observations of an extant sea star. *Paleontological Research*, **23**, 1–9.
- KLEIN, J. T. 1734. *Naturalis dispositio echinodermatum. Accessit lucubratiuncula de aculeis echinorum marinorum, cum spicilegio de belemnitis*. Schreiber, Gedani [Gdańsk], Poland.
- LEFEBVRE, B., GUENSBURG, T. E., MARTIN, E. L. O., MOOI, R., NARDIN, E., NOHEJLOVÁ, M., SALEH, F., KOURİSS, K., EL HARIRI, K. and BRUNO, D. 2019. Exceptionally preserved soft parts in fossils from the Lower Ordovician of Morocco clarify stylophoran affinities within basal deuterostomes. *Geobios*, **52**, 27–36.
- LEWIS, D. N., DONOVAN, S. K., CRABB, P. and GLADWELL, D. J. 2007. A field guide to Silurian Echinodermata of the British Isles: part 1 – Eleutherozoa and Rhombifera. *Scripta Geologica*, **134**, 27–59.
- MAH, C. L. and BLAKE, D. B. 2012. Global diversity and phylogeny of the asterozoa (Echinodermata). *PLoS One*, **7**, e35644.
- MATSUMOTO, H. 1913. Evolutionary history of the class Ophiuroidea and a note on the new classification of the class. *Zoological Magazine*, **25**, 521–527. [in Japanese]
- MILLER, S. A. 1889. *North American geology and palaeontology for the use of amateurs, students and scientists*. Western Methodist Book Concern, Cincinnati, OH, 664 pp.
- ORR, P. J., BRIGGS, D. E. G., SIVETER, D. J. and SIVETER, D. J. 2000. Three-dimensional preservation of a non-biomineralized arthropod in concretions in Silurian volcaniclastic rocks from Herefordshire, England. *Journal of the Geological Society*, **157**, 173–186.
- RAHMAN, I. A., THOMPSON, J. R., BRIGGS, D. E. G., SIVETER, D. J., SIVETER, D. J. and SUTTON, M. D. 2019. A new ophiocistoid with soft-tissue preservation from the Silurian Herefordshire Lagerstätte, and the evolution of the holothurian body plan. *Proceedings of the Royal Society B*, **286**, 20182792.
- SIVETER, D. J., BRIGGS, D. E. G., SIVETER, D. J. and SUTTON, M. D. 2020. The Herefordshire Lagerstätte: fleshing out Silurian marine life. *Journal of the Geological Society of London*, **177**, 1–13.
- SMITH, A. B. and REICH, M. 2013. Tracing the evolution of the holothurian body plan through stem-group fossils. *Biological Journal of the Linnean Society*, **109**, 670–681.
- SPENCER, A. R. T., GARWOOD, R. J. and SUTTON, M. D. 2020. palaeoware/SPIERS: SPIERS v3.1.0. Zenodo. <https://doi.org/10.5281/zenodo.3859623>
- SPENCER, W. K. 1934. British Palaeozoic Asterozoa. Part 9. *Palaeontographical Society Monographs*, **87**, 437–494, plates 25–28. [for 1993]
- 1951. Early Palaeozoic starfish. *Philosophical Transactions of the Royal Society B*, **235**, 87–129.
- and WRIGHT, C. W. 1966. Asterozoans. 4–107. In MOORE, R. C. (ed.) *Treatise on invertebrate paleontology. Part U. Echinodermata 3*. Geological Society of America & University of Kansas Press.
- SUTCLIFFE, O. E. 1997. An ophiuroid trackway from the Lower Devonian Hunsrück Slate, Germany. *Lethaia*, **30**, 33–39.
- SUTTON, M. D., BRIGGS, D. E. G., SIVETER, D. J. and SIVETER, D. J. 2001. Methodologies for the visualization and reconstruction of three-dimensional fossils from the Silurian Herefordshire Lagerstätte. *Palaeontologia Electronica*, **4**, 2.
- — — — and GLADWELL, D. 2005. A starfish with three-dimensionally preserved soft parts from the

- Silurian of England. *Proceedings of the Royal Society B*, **272**, 1001–1006.
- GARWOOD, R., SIVETER, D. J. and SIVETER, D. J. 2012. SPIERS and VAXML: a software toolkit for tomographic visualisation and a format for virtual specimen interchange. *Palaeontologia Electronica*, **15**, 5T.
- RAHMAN, I. A. and GARWOOD, R. J. 2014. *Techniques for virtual palaeontology*. Wiley-Blackwell, 209 pp.
- VICKERY, M. S. and McCLINTOCK, J. B. 2000. Comparative morphology of tube feet among the Asterozoa: phylogenetic implications. *American Zoologist*, **40**, 355–364.