

An edrioasteroid from the Silurian Herefordshire Lagerstätte of England reveals the nature of the water vascular system in an extinct echinoderm

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Abstract

Echinoderms are unique in having a water vascular system with tube feet, which perform a variety of functions in living forms. Here, we report the first example of preserved tube feet in an extinct group of echinoderms. The material, from the Silurian Herefordshire Lagerstätte, UK, is assigned to a new genus and species of rhenopyrgid edrioasteroid, *Heropyrgus distermimus*. The tube feet attach to the inner surface of compound interradial plates and form two sets, an upper and a lower, an arrangement never reported previously in an extant or extinct echinoderm. Cover plates are absent and floor plates are separated along the perradial suture, creating a large permanent entrance to the interior of the oral area. The tube feet may have captured food particles that entered the oral area and/or enhanced respiration. The pentameral symmetry of the oral surface transitions to eight columns in which the plates are vertically offset resulting in a spiral appearance. This change in symmetry may reflect flexibility in the evolutionary development of the axial and extraxial zones in early echinoderm evolution.

Keywords: Echinodermata, Edrioasteroidea, Herefordshire Lagerstätte, Silurian, water vascular system.

1. Introduction

The water vascular system is a defining feature of echinoderms which, via the tube feet, performs a diversity of functions in living forms including feeding, locomotion and respiration. Here, we present evidence of tube feet in an edrioasteroid, representing one of the most basal groups of pentaradial echinoderms [1,2]. Edrioasteroids appeared in the Cambrian and persisted until the Permian [3], occurring worldwide, mostly in shallow-water settings. They are characterized by a disc-like to globular theca with five ambulacra and do not possess erect plated feeding appendages (i.e. arms or brachioles). Rare examples, such as the

1 rhenopyrgids, have an elongate conical peduncle and lived on soft substrates [4]. Here, we
2 report a new genus and species, *Heropyrgus disterminus*, from the lower Silurian Wenlock
3 Series Herefordshire Lagerstätte (~430 Ma) of England [5,6].

4 Fossil echinoderms rarely preserve soft tissues, and the only other records of tube foot
5 preservation are confined to representatives of the extant classes, which has limited our
6 understanding of the evolutionary history of the water vascular system. These include
7 asteroids from the Upper Ordovician of Kentucky [7] and of Shropshire, England [8,9], as
8 well as ophiuroids, a crinoid, and a holothurian from the Lower Devonian Hunsrück Slate of
9 Germany [10–12]. The only other echinoderm described from the Herefordshire Lagerstätte
10 to date, the asteroid *Bdellacoma* sp., also revealed evidence of tube feet [13]. *Heropyrgus*
11 *disterminus* gen. et sp. nov., like the other exceptionally preserved fossils from Herefordshire
12 [14 and references therein], is preserved as three-dimensional calcite in-fills in nodules in a
13 volcanoclastic ash [15]. Select specimens were studied through serial grinding and computer
14 reconstruction [16–18].

16 2. Material and methods

17 Three specimens (figure 1*a–h*, *k–s*) were chosen from ~20 available examples and serially
18 ground at 30 µm intervals (20 µm for the coriaceous sac of OUMNH C.36003). Each surface
19 was captured digitally and the resulting tomographic datasets were reconstructed with the
20 SPIERS software suite and studied as three-dimensional virtual fossils [16,18]. This
21 destructive approach is necessary as the calcite void fill that preserves fossils from the
22 Herefordshire Lagerstätte is very similar in composition to the host rock [15], and the density
23 contrast is insufficient to allow X-ray-based imaging techniques to yield the high fidelity
24 results required. Interpretation of the virtual fossils was facilitated on screen by variable
25 magnification, rotation, virtual dissection, and stereoscopic viewing. Specimens were also

examined using screen-captured images and 3-D prints. Full details of the locality and datasets from serial-grinding tomography of the specimens are housed in the Oxford University Museum of Natural History (OUMNH). Serial-grinding datasets and triangle-mesh models in VAXML/STL format are also available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.561tg> [19]. The tube feet of a modern asteroid in the collections of the Yale Peabody Museum of Natural History (YPM) were studied for comparative purposes.

3. Systematic palaeontology

Phylum Echinodermata [20] (ex [21])

Class Edrioasteroidea [22]

Order Edrioasterida [23]

Suborder Edrioblastoidina [24]

Family Rhenopyrgidae [25]

Genus *Heropyrgus* gen. nov.

Type species: *Heropyrgus distermminus* sp. nov.

Other species: None.

(a) Etymology

Herefordshire, for the locality where the taxon occurs; *pyrgos* (Greek) = tower, referring to the long erect peduncle. *Distermminus* (Latin) = separated, referring to the permanent gape between the floor plates.

(b) Diagnosis of genus (monotypic) and species

Rhenopyrgid lacking cover plates; oral plates fringed by nine floor plates with narrow ridges

on their inner surface; floor plates separated along perradial suture; oral and floor plates fused into compound interrarial plates; constricted elongate zone of imbricate plates between oral surface and suboral collar; long peduncle composed of numerous imbricate plates organized into eight columns.

(c) Material

Holotype: OUMNH C.36043 (figure 1*c, e–h, k–p*). Paratypes: OUMNH C.36044 (figure 1*d, s*), OUMNH C.36003 (figure 1*a, b, q, r*). Other (unground) specimens: OUMNH C.36045–36058, 29683, 29685, 29687, 29688.

(d) Locality and horizon

Herefordshire, England, UK; Wenlock Series, Silurian.

(e) Description

OUMNH C.36003 (figure 1*a*) reveals the complete morphology of *Heropyrgus disterrminus*. The theca is 27 mm long, and the oral surface ranges from 2.4 mm (OUMNH C.36044) to 4.2 mm (OUMNH C.36043) in maximum width. The oral surface sits atop a suboral constriction, which is irregularly plated and transitions into the collar. There is a pronounced gutter where the collar inserts into the plated peduncle, which terminates distally in a holdfast structure, the coriaceous sac.

The oral surface is highly domed and comprises five large compound interrarial plates (figure 1*c, d*), each consisting of a central oral plate and several marginal floor plates fused into a single structure (figure 1*o*). The oral plates are subtriangular in outline, with a wide base. The floor plates are rectangular in outline and are oriented at an angle to the oral plate such that the compound interrarial plates are highly concave with a scalloped margin (figure

1 1o). The axial floor plate is the longest and those lateral to it are successively shorter. High
2 narrow ridges run along the length of the inner surface of the floor plates, decreasing in
3 height from axial to lateral (figure 1c, d). Although the boundaries between the floor plates
4 and the adjacent oral plate are not distinct, linear traces on the external surface (e.g. BC
5 interradial plate in OUMNH C.36043: figure 1o), the arrangement of indentations in the
6 scalloped margin (figure 1k–o), and the spacing of the ridges on the inner surface (figure 1f),
7 demonstrate that nine floor plates surround each oral plate, one median, the others flanking it;
8 the outermost floor plates are evident where the oral surface meets the suboral constriction
9 (e.g. BC interradial plate in OUMNH C.36043: figure 1o). There are five straight ambulacra,
10 which are apparently arranged into a slight 2–1–2 symmetry (figure 1c, d, g): the largest
11 angle subtended by the oral surface is in ambulacrum A (~116°; figure 1g). Cover plates are
12 absent and the floor plates are separated along the perradial suture, resulting in a wide
13 permanent gape (figure 1c, d).

14 OUMNH C.36043 preserves elongate tentacle-like structures situated on the inner
15 surface of the compound interradial plates (figure 1e–g). These structures are widest at their
16 base, becoming narrower distally until they reach a pointed tip. They are arranged in two sets:
17 an upper set attaches about half-way up each compound interradial plate (near the top of the
18 oral plate), and a lower set attaches close to the base. Both sets of structures extend upwards
19 along the inside of the interradial plates; those in the upper set are generally longer than those
20 in the lower and are roughly aligned with the slots bounded by the narrow ridges on the inner
21 surface of the floor plates (figure 1f). Based on the best-preserved examples associated with
22 the CD interradial plate, there appear to be nine structures in each set, i.e. one upper and one
23 lower corresponding to each floor plate.

24 In specimen OUMNH C.36043, two elongate branching thread-like structures attach to
25 two different interradial plates, but are not part of *Heropyrgus distermimus*. The first of these

structures is attached to the exterior surface of a floor plate (AB interradius) and extends well above the oral surface (figure 1*l, n*). The second is much shorter and attaches to the inner surface of a floor plate (CD interradius), adjacent to one of the internal ridges (figure 1*m*).

The arrangement of plates in the collar is essentially 5-fold (figure 1*k, n*). The plates alternate in position in successive rows which overlap proximally. There are at least six rows but the margins of the plates adjacent to the oral surface are difficult to discern. Smaller plates are occasionally intercalated in a row. Three smaller plates are evident between the five large ones that make up the most distal row in OUMNH C.36043 (figure 1 *k, n*), for example, presumably filling in spaces (two others, making up the complement of five, may be concealed where the larger plates overlap laterally). This roughly symmetrical arrangement breaks down in the CD interradius towards the oral surface. Here, there is a somewhat disorganized configuration, including an elongate medial plate that slightly overlaps the oral plate and likely marks the position of the periproct (figure 1*n*). A small circular notch to the right of this plate presumably indicates the position of the hydropore and/or gonopore (figure 1*n, p*). The specimens available show no evidence of contraction or expansion of the collar.

A series of widely spaced, narrow short ridges is present at the base of the larger plates that form the distalmost row of the collar, where it inserts into the peduncle (figure 1*s*). These ridges are eight in number, corresponding to the number of columns in the peduncle itself. Thus, three of the collar plates bear two ridges and two others just one, reflecting their alignment with the peduncle columns. These ridges are clearly evident in OUMNH C.36044 (figure 1*s*) but more subdued in OUMNH C.36043. They are not evident on OUMNH C.36003 but this may be because the slices are oriented along the length of the specimen.

The peduncle is subcircular in cross-section, and its surface is covered by regularly spaced, plates arranged in eight columns (figure 1*a, b, n*). The plates within each column

1 overlap proximally (i.e. toward the oral surface) and are offset vertically resulting in a spiral
2 appearance. The complete specimen, OUMNH C.36003, shows that the columns may consist
3 of up to 25 plates (figure 1*a*). The peduncle of this specimen is gently curved (figure 1*a*).
4 Sections through OUMNH C.36003 (e.g. G148, H172 in [19]) suggest that the peduncle was
5 a hollow structure (figure 1*b*).

6 Beyond a slight constriction at its distal termination the peduncle transitions abruptly
7 into the holdfast ('basal coriaceous sac' in [26]) (figure 1*a, q, r*). OUMNH C.36003 reveals
8 spine-like 'plates' embedded in the dermis of this bulbous structure, projecting normal to its
9 surface (figure 1*q, r*). The holdfast accommodates a deep circular depression in the center
10 into which the spines project (figure 1*q, r*). These spines become less densely spaced
11 proximally until they are no longer present near the boundary with the plated peduncle. The
12 holdfast is anchored by eight laterally projecting lobes (figure 1*q, r*).

14 **4. Discussion**

15 **(a) Systematic position**

16 The Family Rhenopyrgidae includes several species that have been assigned to the genus
17 *Rhenopyrgus*. Following Sumrall *et al.* [27], we consider *R. coronaeformis*, *R. flos*, *R.*
18 *piojensis* and *R. whitei* the only unambiguous members of this genus. *Heropyrgus* gen. nov.
19 shares a number of characters with *Rhenopyrgus* including a domed oral surface,
20 differentiated suboral collar, long peduncle, and holdfast (coriaceous sac) composed of
21 numerous small plates; these features clearly identify it as a rhenopyrgid edrioasteroid. A
22 major difference between *Heropyrgus* and *Rhenopyrgus*, however, is the absence of cover
23 plates, which distinguishes the Herefordshire taxon as a new genus. The remarkable
24 preservation of the Herefordshire material, including the non-biomineralized tentacle-like
25 structures (figure 1*e–g*), indicates that the specimens were buried alive and were not

1 significantly impaired by decay. There is no evidence of cover plates, either in place,
2 separated and lying within the gape, or otherwise associated with any of the three specimens
3 that were serially ground [19]. The scalloped margin of the compound interrarial plates
4 would not have readily accommodated the articulating margin of a series of cover plates
5 (compare, for example, with the straight proximal margins of cover plates in species of
6 *Rhenopyrgus* illustrated in [27], fig. 1). Thus, the available evidence indicates that cover
7 plates were absent in life as opposed to lost and not preserved.

8 The assignment of rhenopyrgids to the Edrioasteroidea has never been in doubt and
9 they are generally acknowledged to lie closest to cyathocystids and edrioblastoids. Holloway
10 and Jell [25] erected the Family Rhenopyrgidae to accommodate *Rhenopyrgus*, but did not
11 assign it to either of the edrioasteroid orders defined by Bell [23], designating it as Order
12 uncertain. Smith and Jell's [4] cladistic analysis of Cambrian edrioasteroids and related taxa
13 grouped *Rhenopyrgus* with the Cambrian genera *Totiglobus* and *Cambroblastus*. Guensburg
14 and Sprinkle [28] revised the formal classification of Edrioasteroidea, placing *Rhenopyrgus*
15 in a Subfamily Rhenopyrginae of the Family Cyathocystidae (together with cyathocystids),
16 Suborder Edrioblastoidina, Order Edrioasterida. Sumrall *et al.* [27] favoured the same
17 scheme, based on a cladistic analysis, but resurrected Holloway and Jell's [25] Family
18 Rhenopyrgidae alongside the Family Cyathocystidae. We assign *Heropyrgus* to the
19 Rhenopyrgidae as it differs from other members of this family only in the (secondary) loss of
20 the cover plates. Sumrall *et al.*'s [27, fig. 2A] cladogram grouped *Rhenopyrgus* in a polytomy
21 with *Cyathotheca* and *Lampteroblastus* (i.e. a clade equivalent to the Suborder
22 Edrioblastoidina).

23 24 **(b) The water vascular system**

1 The tentacle-like structures evident on the interior of the compound interrarial plates of
2 *Heropyrgus disterrminus* in OUMNH C.36043 (figure 1e–g) have never been described in any
3 edrioasteroid. These structures are elongate with pointed tips, similar morphologically to the
4 tube feet of many extant echinoderms including the knob-ending tube feet in certain asteroids
5 (figure 1j) [29,30]. They are also similar to structures interpreted as non-suckered tube feet in
6 the Herefordshire asteroid *Bdellacoma* sp. (figure 1i) [13]. Moreover, the structures in *H.*
7 *disterrminus* are situated on either side of each ambulacrum, as are the tube feet of all other
8 echinoderms. For these reasons, we interpret the structures in *H. disterrminus* as tube feet.

9 The tube feet of *H. disterrminus* are arranged into upper and lower sets and roughly
10 aligned with the floor plates (figure 1f). No other elements of the water vascular system are
11 preserved, but we infer that it was similar to that in extant echinoderms. Thus, the tube feet
12 were presumably joined by lateral canals to five radial canals that were aligned with the
13 ambulacra in a 2–1–2 pattern [31] and connected by the ring canal [32]; if the circular notch
14 at the bottom right of the CD interradius (figure 1n, p) represents a hydropore, this was
15 presumably connected to the ring canal by the stone canal (figure 2). The placement of the
16 tube feet indicates that the lateral canals were longer toward the center and gradually reduced
17 in length toward the periphery of the oral surface (figure 2).

18 The arrangement of the tube feet into upper and lower sets is radically different from
19 anything previously documented in echinoderms. It also contrasts with all previous
20 reconstructions of the edrioasteroid water vascular system, which inferred a one-to-one
21 correspondence between tube feet and floor plates [e.g. 26,33,34], whereas there are two tube
22 feet per floor plate in *H. disterrminus*. We find no evidence that the tube feet were closely
23 associated with pores between adjacent floor plates [26,33,34]; the tube feet in *H. disterrminus*
24 are roughly aligned with ridges on the inner surface of the floor plates (figure 1f) and are not
25 close to the floor plate margins. However, our material provides some support for Bell's [33]

inference that the radial canals were internal. There is no evidence of grooves to accommodate canals on the exterior surface of the theca of *H. distermimus* and the floor plates could not have supported the radial canals because they are separated along the perradial suture. We infer that the radial canals were suspended within the thecal cavity, where they would have been protected in the absence of overlying cover plates. It is not clear whether a similar arrangement was present in other edrioasteroids.

The position of the narrow ridges on the inner surface of the floor plates would have prevented the compound interrarial plates from meeting at the perradial suture. The remarkable preservation of the soft tissues (tube feet), never previously seen in any edrioasteroid, strongly suggests that the absence of cover plates and the spacing between the floor plates are real features, rather than artefacts of taphonomy. Thus, the large star-shaped opening onto the interior of the oral area was a permanent feature in life. The attachment of a thread-like structure, which we interpret as an epibiont, to the inner surface of a floor plate (figure 1*m*) is consistent with the absence of cover plates and a permanent gape. The tube feet are short and, even when fluid filled, almost certainly did not extend beyond the margin of the interrarial plates. Consequently, it is unlikely that they could have captured food particles directly from the water column, as in crinoids. It seems more likely that *H. distermimus* captured suspended food particles that entered the oral area. The tube feet may have served to sort and transport food particles towards the mouth, as do the knob-ending tube feet in paxillosid asteroids [30]. The tube feet may also have played a role in respiration; the flow of water over tube feet in *H. distermimus* was facilitated by the large permanent opening onto the oral area, and would have enhanced gas exchange.

(c) Symmetry

Edrioasteroids originated in the Cambrian and the majority lived on the sediment surface during the early Cambrian before transitioning to hard substrates [35] or developing a peduncle for anchoring in soft sediment, the strategy adopted by *Rhenopyrgus* [4] and *Heropyrgus*. *H. distermius* offers an opportunity to consider the evolution (and evolutionary development) of symmetry changes in echinoderms. The oral surface is pentameral and shows a slight 2–1–2 symmetry (figure 1c, g). The arrangement of plates in the collar is less regular, but essentially 5-fold, particularly where it inserts into the peduncle. The plates of the peduncle are arranged in eight columns; adjacent plates are offset laterally resulting in a spiral appearance. An 8-fold arrangement is also evident in projecting swellings at the end of the coriaceous sac. The most distal row of plates in the collar, which is dominated by five large plates, is marked by ridges, probably for muscle attachment [26]. Three of the five large plates bear two widely spaced ridges each, and the other two large plates bear just one, yielding a total of eight, which correspond in position to the eight columns in the peduncle. In this way the symmetry shifts from pentameral in the crown to 8-fold in the peduncle.

Following the model of Mooi and David [36] we can posit the origins of the three regions in the body of rhenopyrgids. The oral surface belongs to the axial zone, and the collar and peduncle are extraxial. The axial zone of *Helicocystis*, the most primitive pentaradial echinoderm known [1], includes a spiral arrangement. In rhenopyrgids, the ambulacra are pentaradial but the plates of the extraxial peduncle form eight columns which are offset laterally, resulting in a spiral appearance. This illustrates the persistence of developmental flexibility in edrioasteroids.

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Data accessibility: Serial-grinding datasets and triangle-mesh models in VAXML/STL format are available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.561tg> [19].

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References

1. Smith AB, Zamora S. 2013 Cambrian spiral-plated echinoderms from Gondwana reveal the earliest pentaradial body plan. *Proc. R. Soc. Lond. B* **280**, 20131197. (doi:10.1098/rspb.2013.1197)
2. Zamora S, Rahman IA. 2014 Deciphering the early evolution of echinoderms with Cambrian fossils. *Palaeontology* **57**, 1105–1119. (doi:10.1111/pala.12138)
3. Sumrall CD. 2009 First definite record of Permian edrioasteroids: *Neosorophusella maslennikovi* n. sp. From the Kungurian of Northeast Russia. *J. Paleont.* **83**, 990–993. (doi:10.1666/09-063.1)
4. Smith AB, Jell PA. 1990 Cambrian edrioasteroids from Australia and the origin of

- 1 starfishes. *Mem. Queensland Mus.* **28**, 715–778.
- 2
- 3 5. Briggs DEG, Siveter DJ, Siveter DJ. 1996 Soft-bodied fossils from a Silurian
- 4 volcanoclastic deposit. *Nature* **382**, 248–250. (doi:10.1038/382248a0)
- 5
- 6 6. Briggs DEG, Siveter DJ, Siveter DJ, Sutton MD. 2008 Virtual fossils from 425 million-
- 7 year-old volcanic ash. *Am. Sci.* **96**, 474–481.
- 8
- 9 7. Glass A. 2006 Pyritized tube feet in a protasterid ophiuroid from the Upper Ordovician of
- 10 Kentucky, U.S.A. *Acta Pal. Pol.* **51**, 171–184.
- 11
- 12 8. Spencer WK. 1916 A monograph of the British Palaeozoic Asterozoa, Part II. *Palaeont.*
- 13 *Soc. Monograph* **69**, 57–108.
- 14
- 15 9. Gale AS. 1987 Phylogeny and classification of the Asteroidea (Echinodermata). *Zool. J.*
- 16 *Linn. Soc.* **89**, 107–132. (doi:10.1111/j.1096-3642.1987.tb00652.x)
- 17
- 18 10. Glass A, Blake DB. 2004 Preservation of tube feet in an ophiuroid (Echinodermata) from
- 19 the Lower Devonian Hunsrück Slate of Germany and a redescription of *Bundenbachia*
- 20 *benecke* and *Palaeophiomyxa grandis*. *Pal. Zeit.* **78**, 73–95.
- 21
- 22 11. Ausich WI, Bartels C, Kammer TW. 2013 Tube foot preservation in the Devonian crinoid
- 23 *Codiocrinus* from the Lower Devonian Hunsrück Slate, Germany. *Lethaia* **46**, 416–420.
- 24 (doi:10.1111/let.12023)
- 25

12. Smith AB, Reich M. 2013 Tracing the evolution of the holothurian body plan through stem-group fossils. *Biol. J. Linn. Soc.* **109**, 670–681. (doi:10.1111/bij.12073)
13. Sutton MD, Briggs DEG, Siveter David J, Siveter Derek J, Gladwell DJ. 2005 A starfish with three-dimensionally preserved soft-parts from the Silurian of England. *Proc. R. Soc. Lond. B* **272**, 1001–1006. (doi:10.1098/rspb.2004.2951)
14. Siveter DJ, Briggs DEG, Siveter DJ, Sutton MD, Legg D. 2017 A new crustacean from the Herefordshire (Silurian) Lagerstätte, UK, and its significance in malacostracan evolution. *Proc. R. Soc. Lond. B* **284**, 20170279. (doi:10.1098/rspb.2017.0279)
15. Orr PJ, Briggs DEG, Siveter DJ, Siveter, DJ. 2000 Three-dimensional preservation of a non-biomineralised arthropod in concretions in Silurian volcanoclastics from Herefordshire, England. *J. Geol. Soc. Lond.* **157**, 173–186. (doi:10.1144/jgs.157.1.173)
16. Sutton MD, Briggs DEG, Siveter DJ, Siveter DJ. 2001 Methodologies for the visualization and reconstruction of three-dimensional fossils from the Silurian Herefordshire Lagerstätte. *Palaeont. Electron.* **4**, art. 2. (http://palaeo-electronica.org/2001_1/s2/issue1_01.htm).
17. Sutton MD, Briggs DEG, Siveter DJ, Siveter DJ. 2002 The arthropod *Offacolus kingi* (Chelicerata) from the Silurian of Herefordshire, England: computer based morphological reconstructions and phylogenetic affinities. *Proc. R. Soc. Lond. B* **269**, 1195–1203. (doi:10.1098/rspb.2002.1986)

18. Sutton MD, Garwood RJ, Siveter DJ, Siveter DJ. 2012 SPIERS and VAXML: a software toolkit for tomographic visualisation, and a format for virtual specimen exchange. *Palaeont. Electron.* **15**, Issue 2; 5T, 14 pp. (<http://palaeo-electronica.org/content/issue-2-2012-technical-articles/226-virtual-palaeontology-toolkit>)
19. Briggs DEG, Siveter DJ, Siveter DJ, Sutton MD, Rahman IA. 2017 Data from: An edrioasteroid from the Silurian Herefordshire Lagerstätte of England reveals the nature of the water vascular system in an extinct echinoderm. *Dryad Digital Repository*. (doi:10.5061/dryad.561tg)
20. Bruguière JG. 1791 *Tableau encyclopédique et méthodique des trois règnes de la nature, Vol. 7, L'helminthologie*. 83 pp. Paris: Charles–Joseph Panckoucke.
21. Klein JT. 1734 *Naturalis dispositio echinodermatum. Accessit lucubrationum de aculeis echinorum marinarum, cum spicilegio de belemnitis*. Tab. I–XXXV. Gedani.
22. Billings E. 1858 On the Asteriadae of the Lower Silurian rocks of Canada. *Geological Survey of Canada, Figures and descriptions of Canadian organic remains* Decade **3**, 75–85.
23. Bell BM. 1976 A study of North American Edrioasteroidea. *New York State Mus. Mem.* **21**, 1–476.
24. Fay RO. 1962 Edrioblastoidea, a new class of Echinodermata. *J. Paleont.* **36**, 201–205.

25. Holloway DJ, Jell PA. 1983 Silurian and Devonian edrioasteroids from Australia. *J. Paleont.* **57**, 1001–1016.
26. Smith AB. 1985 Cambrian eleutherozoan echinoderms and the early diversification of edrioasteroids. *Palaeontology* **28**, 715–756.
27. Sumrall CD, Heredia S, Rodríguez CM, Mestre AI. 2013 The first report of South America edrioasteroids and the paleoecology and ontogeny of rhenopyrgid echinoderms. *Acta Pal. Pol.* **58**, 763–776. (doi:10.4202/app.2011.0108)
28. Guensburg TE, Sprinkle J. 1994 Revised phylogeny and functional interpretation of the Edrioasteroidea based on new taxa from the Early and Middle Ordovician of western Utah. *Fieldiana (Geol.)* **29**, 1–43. (doi:10.5962/bhl.title.3313)
29. Vickery MS, McClintock JB. 2000 Comparative morphology of tube feet among the Asteroidea: phylogenetic implications. *Amer. Zool.* **40**, 355–364. (doi:10.1093/icb/40.3.355)
30. Hennebert E, Jangoux M, Flammang P. 2013 Functional biology of asteroid tube feet. In *Starfish: Biology and Ecology of the Asteroidea* (ed. JM Lawrence), pp. 24–36. Baltimore, USA: Johns Hopkins University Press.
31. Sprinkle J. 1973 *Morphology and evolution of blastozoan echinoderms*. Museum of Comparative Zoology Special Publication. 283 pp. Cambridge, Massachusetts: Harvard University.

- 1 32. Nichols D. 1972 The water vascular system in living and fossil echinoderms.
2 *Palaeontology* **15**, 519–538.
3
- 4 33. Bell BM. 1977 Respiratory schemes in the Class Edrioasteroidea. *J. Paleont.* **51**, 619–
5 632.
6
- 7 34. Paul CRC, Smith AB. 1984 The early radiation and phylogeny of echinoderms. *Biol.*
8 *Rev.* **59**, 443–481. (doi:10.1111/j.1469-185X.1984.tb00411.x)
9
- 10 35. Zamora S, Deline B, Álvaro JJ, Rahman IA. 2017 The Cambrian substrate revolution and
11 the early evolution of attachment in suspension-feeding echinoderms. *Earth-Science Reviews*
12 **171**, 478–491. (doi:10.1016/j.earscirev.2017.06.018)
13
- 14 36. Mooi R, David B. 2008 Radial symmetry, the anterior/posterior axis, and echinoderm
15 Hox genes. *Ann. Rev. Ecol. Evol. Syst.* **39**, 4–62.
16 (doi:10.1146/annurev.ecolsys.39.110707.173521)

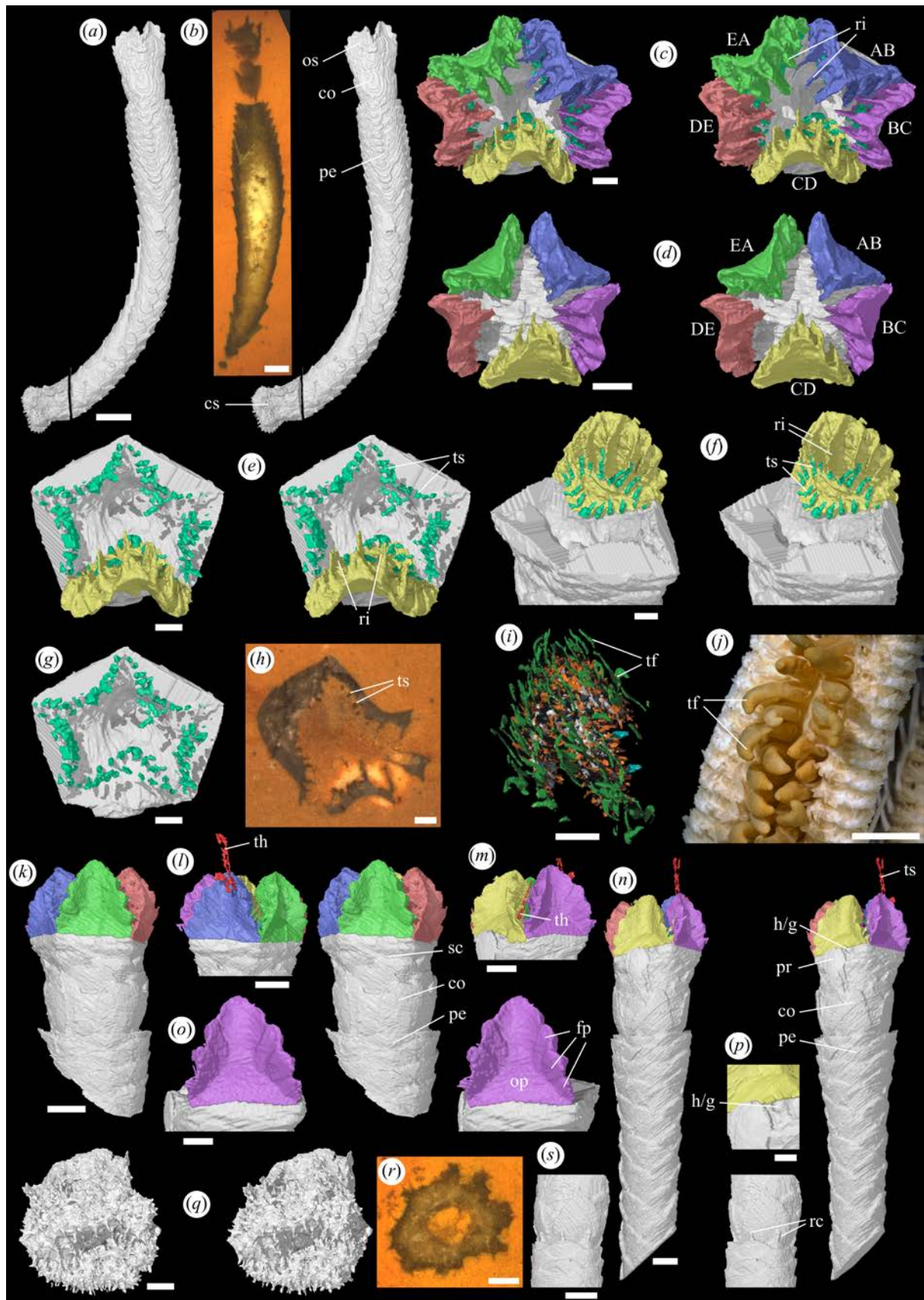


Figure 1. *Heropyrgus disterminus* (a–h, k–s) and other echinoderms (i, j). (a, c–g, i, k–q, s) ‘virtual’ reconstructions (a, c–f, k, n, o, q, s are stereo-pairs), (b, h, r) specimen in rock, (j)

1 photograph. (a) OUMNH C.36003 lateral view showing division of theca into oral surface,
 2 collar, peduncle and coriaceous sac. (b) OUMNH C.36003, section through the oral surface,
 3 collar and proximal peduncle showing crystalline calcite filling the void. (c) OUMNH
 4 C.36043, oral surface. (d) OUMNH C.36044, oral surface. (e) OUMNH C.36043, oral
 5 surface showing tentacle-like structures and compound interradial plate CD (other interradial
 6 plates removed). (f) OUMNH C.36043, oral surface in oblique view showing compound
 7 interradial plate CD and associated tentacle-like structures (all other features removed). (g)
 8 OUMNH C.36043, oral view with compound interradial plates removed to show 2–1–2
 9 symmetry revealed by the larger angle in ambulacrum A. (h) OUMNH C.36043, section
 10 through oral area showing tentacle-like structures interpreted as tube feet. (i) OUMNH
 11 C.29573, tube feet in the fossil asteroid *Bdellacoma* sp. from the Silurian of Herefordshire
 12 (from [13]). (j) YPM IZ 008378.EC, tube feet in the extant paxillosid asteroid *Luidia*
 13 *barbadensis*. (k) OUMNH C.36043, lateral view facing interradial plate EA showing suboral
 14 constriction, collar and proximal part of peduncle. (l) OUMNH C.36043, lateral view of oral
 15 surface showing thread-like structure attached to compound interradial plate AB. (m)
 16 OUMNH C.36043, lateral view of oral surface showing thread-like structure attached to
 17 compound interradial plate CD. (n) OUMNH C.36043, lateral view showing junction of
 18 collar and peduncle, and the spiral arrangements of the plates on the latter. (o) OUMNH
 19 C.36043, compound interradial plate BC. (p) OUMNH C.36043, lateral view showing
 20 hydropore/gonopore. (q) OUMNH C.36003, coriaceous sac showing spine-like plates and
 21 central depression. (r) OUMNH C.36003, coriaceous sac in oblique section showing
 22 evidence of lateral projections. (s) OUMNH C.36044, base of collar showing two ridges on a
 23 single collar plate. Abbreviations: AB–EA, interradial plates; co, collar; cs, coriaceous sac;
 24 fp, floor plates; h/g, hydropore/gonopore; op, oral plate; os, oral surface; pe, peduncle; pr,
 25 periproct; rc, ridges on collar plate; ri, ridges on inner surface of floor plates; sc, suboral

constriction; tf, tube feet; th, thread-like structure; ts, tentacle-like structures interpreted as tube feet. Scale bars: (a) is 2 mm; (b, l–n, p, s) are 1 mm; (c–h, o, q, r) are 0.5 mm; (i, j) are 5 mm.

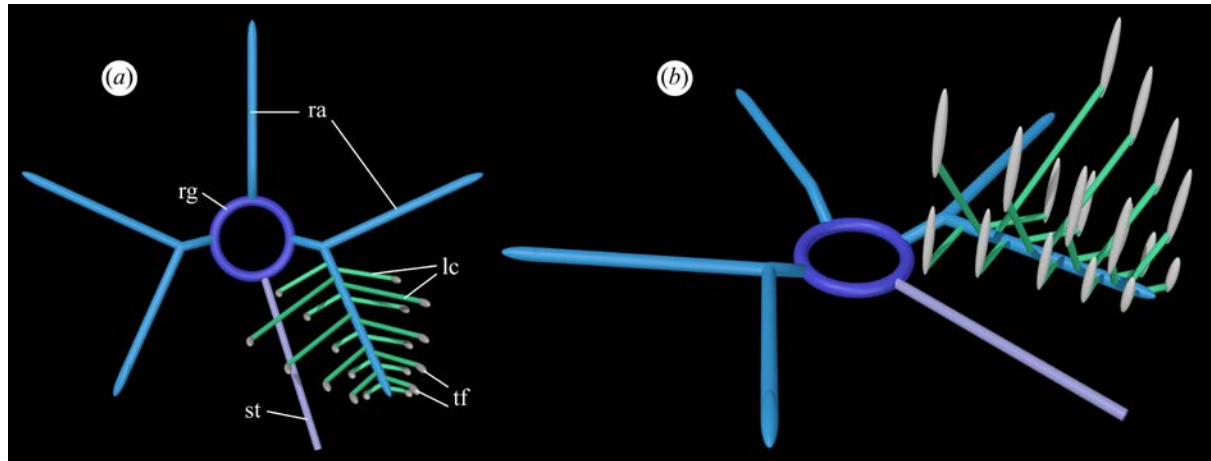


Figure 2. Reconstruction of the water vascular system in *Heropyrgus disterminus*. (a) Upper view. (b) Angled view. Abbreviations: lc, lateral canals; ra, radial canals; rg, ring canal; st, stone canal; tf, tube feet.