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Authors: Rahman, Imran A., Stewart, Sarah E., and Zamora, Samuel

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The youngest ctenocystoids from the Upper Ordovician of the United Kingdom and the evolution of the bilateral body plan in echinoderms

IMRAN A. RAHMAN, SARAH E. STEWART, and SAMUEL ZAMORA

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During the early Palaeozoic, echinoderm body plans were much more diverse than they are today, displaying four distinct types of symmetry. This included the bilateral ctenocystoids, which were long thought to be restricted to the Cambrian. Here, we describe a new species of ctenocystoid from the Upper Ordovician of Scotland (*Conollia sporranoides* sp. nov.). This allows us to revise the genus *Conollia*, which was previously based on a single poorly-known species from the Upper Ordovician of Wales (*Conollia staffordi*). Both these species are characterized by a unique morphology consisting of an elongate-ovoid body covered in spines, which clearly distinguishes them from their better-known Cambrian relatives; they are interpreted as infaunal or semi-infaunal burrowers from deep-water environments. This indicates that the ctenocystoid body plan was not fixed early in the evolution of the group, and they most likely modified their structure as an adaptation to a new mode of life in the Ordovician.

Key words: Echinodermata, Ctenocystoidea, evolution, bilateral symmetry, body plans, Ordovician, United Kingdom.

Imran A. Rahman [imran.rahman@bristol.ac.uk], School of Earth Sciences, University of Bristol, Life Sciences Building, 24 Tyndall Avenue, Bristol BS8 1TQ, UK.
Sarah E. Stewart [sarah.stewart@nms.ac.uk], Department of Natural Sciences, National Museum of Scotland, Chambers Street, Edinburgh EH1 1JF, UK.
Samuel Zamora [samuel@unizar.es], Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington DC, 20013-7012, USA; and Museo Geominero, Instituto Geológico y Minero de España, C/ Manuel Lasala, 44-9º B, 50006 Zaragoza, Spain.

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Introduction

The initial diversification of echinoderm body plans was extremely rapid, with bilateral, asymmetrical, spiral and pentaradiate forms appearing together in some of the oldest known (Cambrian) echinoderm faunas (Smith et al. 2013). Out of these four clearly differentiated body plans, only pentaradiate clades remain today; all other forms became extinct during the Palaeozoic, over 250 million years ago (Sprinkle 1983; Sumrall and Wray 2007).

The bilateral body plan is perhaps the most intriguing organization in the phylum Echinodermata, recalling their bilaterian ancestry, and it is represented by a single early Palaeozoic group, the ctenocystoids (Fig. 1). While several other groups display bilateral symmetry superimposed on a pentaradiate body plan (e.g., pleurocystitid rhombiferans and irregular echinoids), only ctenocystoids lack any trace of underlying radiality. Some have argued that ctenocystoids indicate the plesiomorphic condition for echinoderms (Ubaghs 1975; Rahman and Clausen 2009; Zamora et al. 2012), while others interpret them as secondarily derived, with the most primitive known echinoderms pentaradiate (Sumrall 1997; David et al. 2000; Sumrall and Wray 2007). This debate has been fuelled, in part, by their unusual character combination; ctenocystoids are stem-less and have a strongly bilaterally symmetrical body (theca), which is typically flattened and framed by one or, more often, two rings of marginal plates. Both the upper and lower thecal surfaces are covered by flexible, tessellated membranes. At the anterior of the theca, a specialized organ called the ctenidium covers the mouth; this

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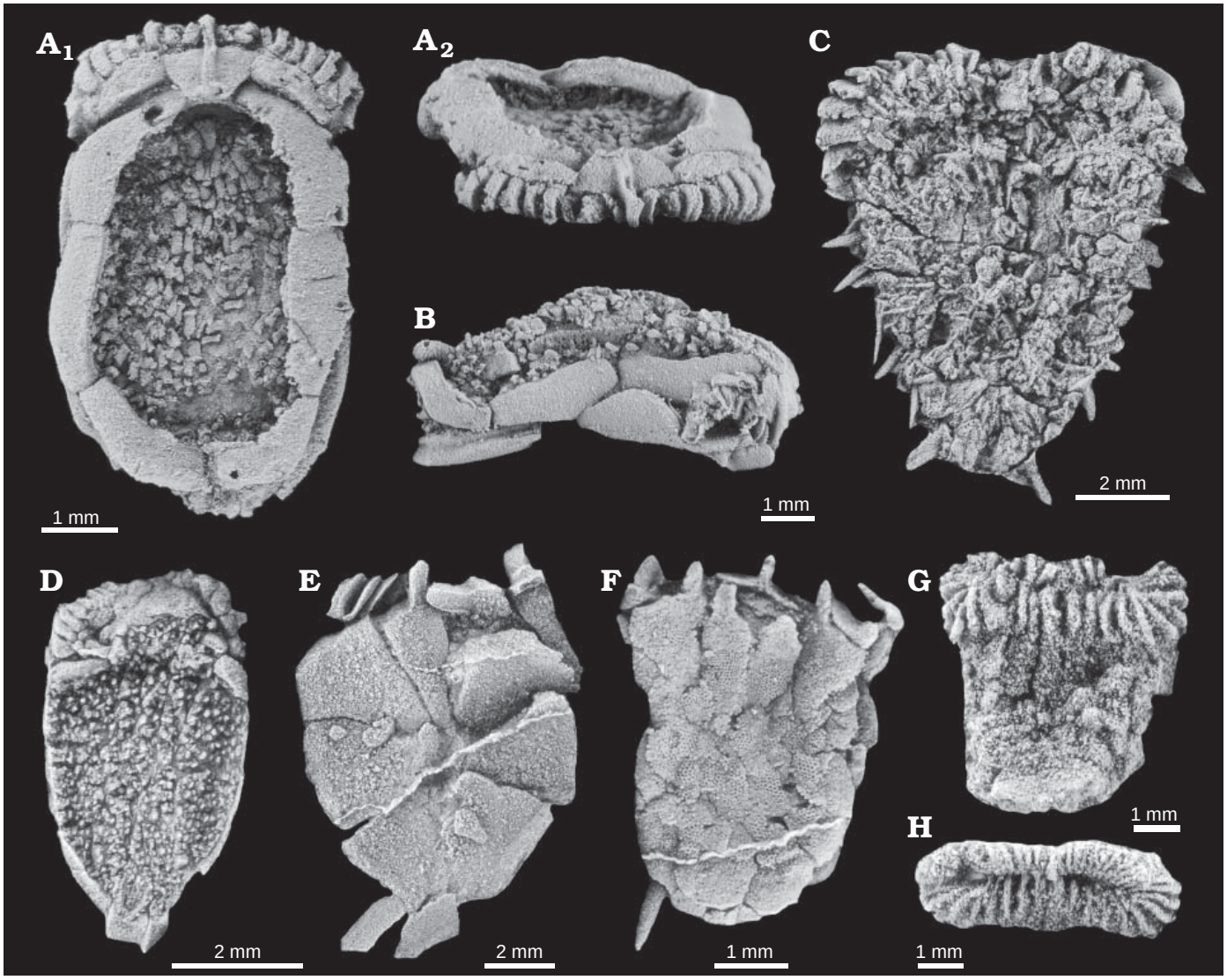


Fig. 1. Representative Cambrian ctenocystoid echinoderms. **A**, **B**. *Ctenocystis utahensis* Robison and Sprinkle, 1969 from Cambrian Series 3 of the United States. USNM 163252 in dorsal (A_1) and anterior (A_2) views; USNM 595079 in right lateral view (B). **C**. Undescribed ctenocystoid (Ctenocystoid gen. et sp. nov 1 in Smith et al. 2013) from Cambrian Series 3 of Morocco. NHMUK EE 15428 in dorsal view. **D**. *Courtessolea moncereti* Domínguez Alonso, 2004 from Cambrian Series 3 of France. MNHN F.A45783 in dorsal view. **E.** *Courtessolea* sp. from Cambrian Series 3 of Spain. MPZ 2009/1234b in ventral view. **F**. Undescribed ctenocystoid (Ctenocystoid gen. et sp. nov 2 in Smith et al. 2013) from Cambrian Series 3 of Morocco. NHMUK EE 15317 in ventral view. **G**, **H**. *Jugoszovia archaeocyathoides* Dzik and Orłowski, 1995 from Cambrian Series 3 of Poland. ZPAL Ec1/9 in ventral view (G); ZPAL Ec1/1 in anterior view (H). All specimens are latex casts whitened with ammonium chloride sublimate.

is composed of a series of distinctive blade-like plates. At the posterior, the anus is represented by a cone-shaped aperture (Robison and Sprinkle 1969; Rahman and Clausen 2009).

Ctenocystoids were geographically widespread in the Cambrian (reported from Baltica, Laurentia, East Gondwana, and West Gondwana), but had a limited stratigraphical range, being restricted to Stage 5 and the Drumian (Smith et al. 2013; Zamora et al. 2013). In addition, a single enigmatic species has been reported from post-Cambrian rocks, *Conollia staffordi* Domínguez Alonso, 2004 from the Upper Ordovician of Wales. Here, we report a new species of ctenocystoid, *Conollia sporranoides* sp. nov., from the Upper Ordovician of Scotland, and accordingly reconsider the anatomy of the genus. This provides novel insights into the functional morphology and mode of life of *Conollia* Domínguez Alonso, 2004.

Institutional abbreviations.—GLAHM, Hunterian Museum, Glasgow, UK; MNHN, Muséum National d'Histoire Naturelle, Paris, France; MPZ, Museo de Paleontología, Universidad de Zaragoza, Zaragoza, Spain; NHMUK, Natural History Museum, London, UK; USNM, Smithsonian Institution National Museum of Natural History, Washington, D.C., USA; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

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Geological setting, material, and methods

Approximately 26 specimens of *Conollia sporranoides* sp. nov. (GLAHM 131255/1–GLAHM 131255/26) were collected from the Laggan Member of the Balclatchie Formation at Dalfask Quarry in Girvan, northwest Scotland, UK (Fig. 2). This locality is part of a deep-water Konservat Lagerstätte, which is early Caradoc (Sandbian, Upper Ordovician) in age. Dalfask Quarry exposes a succession of blue-grey, calcareous, laminated siltstone and mudstone beds, representing a localized low-oxygen environment below the photic zone, perhaps with an unconsolidated muddy substrate (Stewart and Owen 2008). It contains a diverse, unusual fauna of benthic invertebrates, which is dominated by the odontopleurid trilobite *Diacanthaspis trippi*, the orthid brachiopod *Onniella williamsi*, the polyplacophoran *Solenocaris solenoides*, a possible new species of the stylophoran *Anatifopsis* and the ctenocystoid *Conollia sporranoides* sp. nov. (Stewart and Owen 2008). Ctenocystoids occur on a single slab of laminated siltstone (along with complete specimens of *Diacanthaspis trippi*). The fossils are preserved as moulds and are sometimes partially pyritized.

In addition, we studied all 34 known specimens of *Conollia staffordi* (NHMUK EE 5903–NHMUK EE 5933), which came originally from a small quarry near the village of Clarbeston, southwest Wales, UK. This probably corresponds to the lower part of the Mydrim Shale Formation, which is lower Caradoc (Sandbian, Upper Ordovician) in age. The quarry consists of fissile black shales and subordinate mudstone, which were likely deposited in a relatively deep-water, possibly anoxic basin. Ctenocystoids are associated with trilobites, ostracods, and abundant graptolites (Fortey 2006). Similar to *Conollia sporranoides* sp. nov., all specimens of *Conollia staffordi* are preserved as moulds in grey-brown shale.

In order to accurately describe the morphology of *Conollia sporranoides* sp. nov. and *Conollia staffordi*, specimens were cast in latex; these casts were whitened with ammonium chloride sublimate and photographed, and subsequently coated in gold and imaged with scanning electron microscopy. Furthermore, X-ray micro-tomography was used to image the slab of siltstone containing multiple specimens of *Conollia sporranoides* sp. nov. This sample was scanned on a Nikon XT H 225 ST cabinet scanner at the Natural History Museum, London, using a current/voltage of 180 kV/150 μA. This generated a dataset of 1950 slice images with a voxel size of about 30 μm (SOM 1: Supplementary Online Material available at http://app.pan.pl/SOM/app60-Rahman_etal_SOM.pdf). This dataset was then digitally reconstructed using the freely available SPIERS software suite (Sutton et al. 2012). An inverted linear threshold was applied, creating binary images with all pixels darker than a user-defined grey level turned "on" (white). The "on" pixels identified as belonging to the fossils were manually assigned to distinct regions-of-interest, which were then rendered as separate isosurfaces to give an interactive three-dimensional virtual reconstruction (SOM 2). High-quality images (Fig. 3G–I) were produced in the open-source program Blender (www.blender.org).

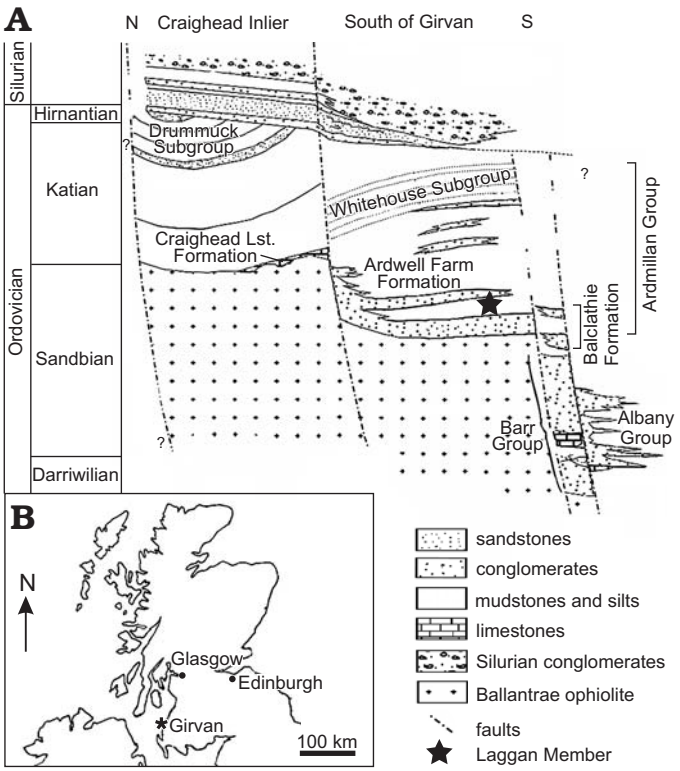


Fig. 2. Stratigraphical position (**A**) and geographical location (**B**) of the site where *Conollia sporranoides* sp. nov. was collected. Adapted from Ingham (1992).

Systematic palaeontology

Phylum Echinodermata Bruguière, 1791 (ex Klein, 1734)

Class Ctenocystoidea Robison and Sprinkle, 1969

Genus *Conollia* Domínguez Alonso, 2004

Type species: *Conollia staffordi* Domínguez Alonso, 2004; Upper Ordovician (Sandbian) of Wales, UK.

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Emended diagnosis.—A ctenocystoid with an elongate-ovoid theca, no marginal frame and thecal ossicles expanded at the posterior as thin spines. Ctenidial plating weakly or undifferentiated, consisting of multiple small radially-oriented blade-like ctenoid plates. Long, serrated spines situated at the base of the ctenidium.

Remarks.—The genus and type species were erected by Domínguez Alonso (2004), but have largely been overlooked in subsequent discussions of early Palaeozoic echinoderms. This might be because there was some doubt about the validity of this work for zoological nomenclature. However, because (i) the work was issued for the purpose of providing a public and permanent scientific record, (ii) the work was obtainable free of charge when first issued in 2004, and (iii) identical and simultaneously obtainable copies are available as PDFs from the Universidad Complutense de Madrid E-Prints repository (http://eprints.ucm.es/5270) and printed on paper from six major publicly-accessible libraries (Universidad Complutense de Madrid; Museo Nacional de Ciencias Naturales; Natural History Museum, London; Smithsonian Institution National Museum of Natural History; Museum für Naturkunde; Muséum National d'Histoire Naturelle), it meets the criteria of what constitutes published work (for the purposes of zoological nomenclature) according to the International Code of Zoological Nomenclature (articles 8 and 9, ICZN 1999, 2012). The taxonomic names introduced in Domínguez Alonso (2004) are therefore considered valid.

Geographic and stratigraphic range.—Northwest Scotland and southwest Wales, UK. Lower Caradoc (Sandbian), Upper Ordovician.

Conollia sporranoides sp. nov.

Fig. 3; SOM 1, 2.

Etymology: From the Scottish Gaelic *sporran*, purse, pouch, and the Greek *eidos*, form, likeness; in reference to the similarity of the body to a traditional Scottish pouch.

Holotype: GLAHM 131255/2, complete specimen preserved as a mould in siltstone.

Type locality: Dalfask Quarry in Girvan, northwest Scotland, UK.

Type horizon: Laggan Member, Balclatchie Formation, lower Caradoc (equivalent to the Sandbian), Upper Ordovician.

Material.—GLAHM 131255/1–GLAHM 131255/26, approximately 26 specimens preserved as moulds in siltstone from the Laggan Member of the Balclatchie Formation at Dalfask Quarry in Girvan, northwest Scotland, UK.

Diagnosis.—A species of *Conollia* with undifferentiated ctenidial plating. Serrated spines at the base of the ctenidium are long and fine.

Description.—Small (approximately 4–6 mm long), bilaterally symmetrical ctenocystoid; elongate-ovoid in outline, with a prominent ctenidium situated at the anterior of a thinly-plated theca covered in spines.

The ctenidium is circular in anterior aspect and hemispherical in dorsal view, and measures approximately 1–3 mm in width. It comprises a dorso-ventrally compressed ring of at least 16–18 small (up to about 1 mm in diameter), thin, blade-like ctenoid plates (Fig. 3B–E). These plates are not differentiated in terms of morphology or size; they are hemispherical in outline, with posterior rectangular projections that have flat outer faces (Fig. 3C, I). There are no other specialized ctenidial plates. Long, fine, serrated spines, measuring up to about 1 mm in length, are located adjacent to the ctenidium (Fig. 3D, F). These spines might have articulated with the outer faces of the posterior bases of the ctenoid plates.

The theca is elongate with a rounded posterior margin. It is composed of multiple thin polygonal plates, with no marginal frame. There is no clear differentiation between the plating of the dorsal and ventral surfaces. Numerous fine, hair-like spines cover the entire theca; they measure up to about 0.5–0.8 mm in length (typically longer towards the anterior) and are curved rearwards (Fig. 3A, B). The nature of the transition between the ctenidium and the theca is ambiguous. The anus cannot be identified.

Remarks.—*Conollia sporranoides* sp. nov. can be confidently assigned to the genus *Conollia* on the basis of its small, spiny, elongate-ovoid theca, which lacks a marginal frame. However, this species differs from *Conollia staffordi* (Fig. 4) in having undifferentiated ctenidial plating, lacking the large dorso-central ossicle that is characteristic of the type species (Fig. 4B, C). Moreover, the body is slightly shorter and the spines (both thecal and serrated) generally finer compared to *Conollia staffordi*. Finally, there is no clear differentiation of the dorsal and ventral surfaces in *Conollia sporranoides* sp. nov., but in *Conollia staffordi* the spines can be noticeably thicker on the ventral surface (Fig. 4C).

Geographic and stratigraphic range.—Girvan, northwest Scotland, UK; Lower Caradoc (Sandbian), Upper Ordovician.

Discussion

Comparison with other ctenocystoids.—The presence of an anterior ctenidium and the strong bilateral symmetry of the skeleton clearly identify *Conollia* as a ctenocystoid. However, *Conollia staffordi* and *Conollia sporranoides* sp. nov. are distinguished from all other ctenocystoids by the complete absence of a marginal frame, the weakly or undifferentiated nature of the ctenidial plating and the elongate-ovoid theca covered in spines. Out of all the formally described ctenocystoid genera, *Conollia* is most similar to *Jugoszovia* (Fig. 1G, H), which has a greatly reduced marginal frame and near-perfect bilateral symmetry; however, the ctenidial plating is more differentiated in *Jugoszovia*, and moreover the theca is sub-triangular, flattened and lacks spines (Dzik and Orłowski 1995). *Courtessolea* (Fig. 1D, E) displays strong bilateral symmetry, like *Conollia*, but is otherwise rather different, possessing a well-developed,

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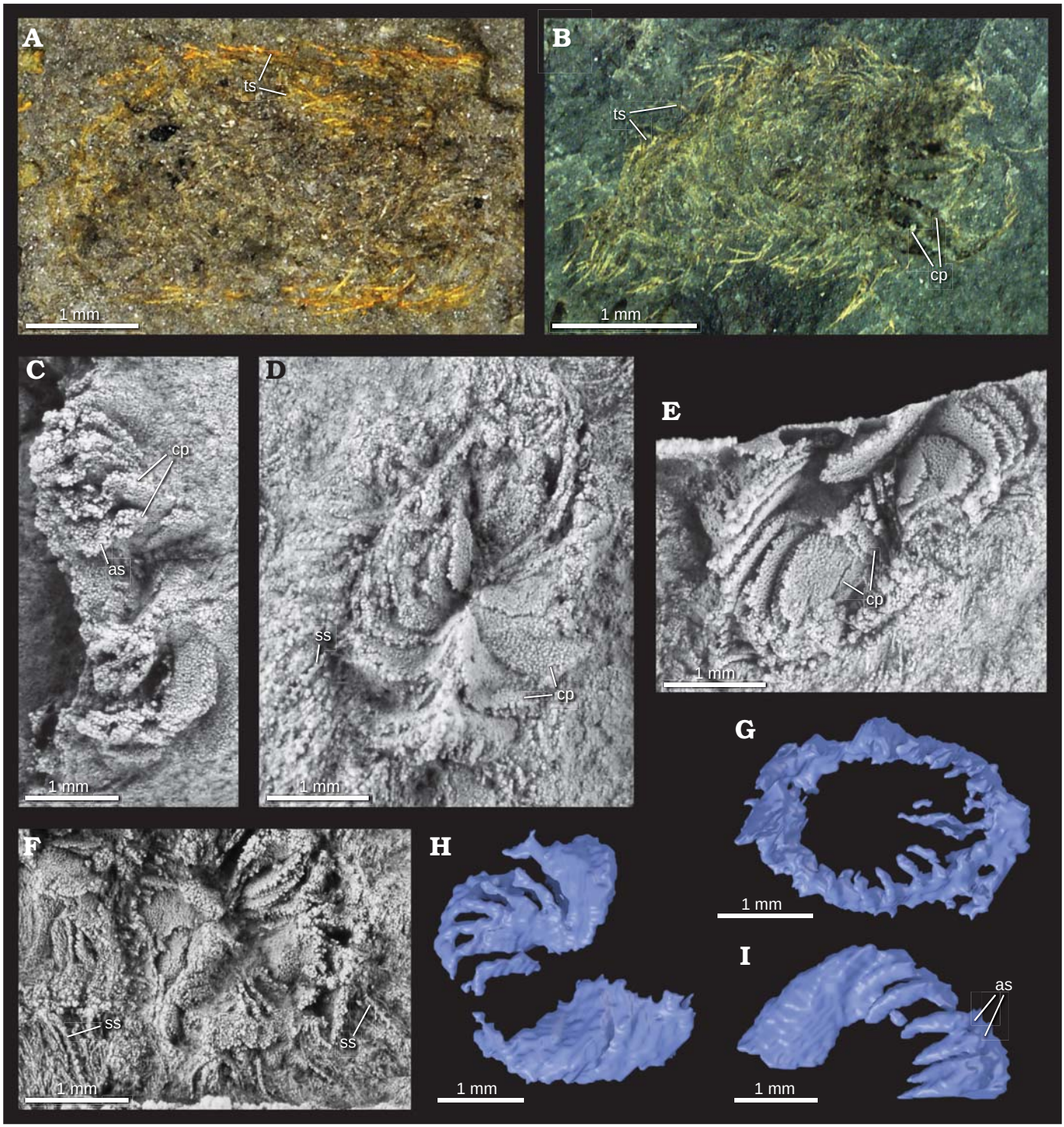
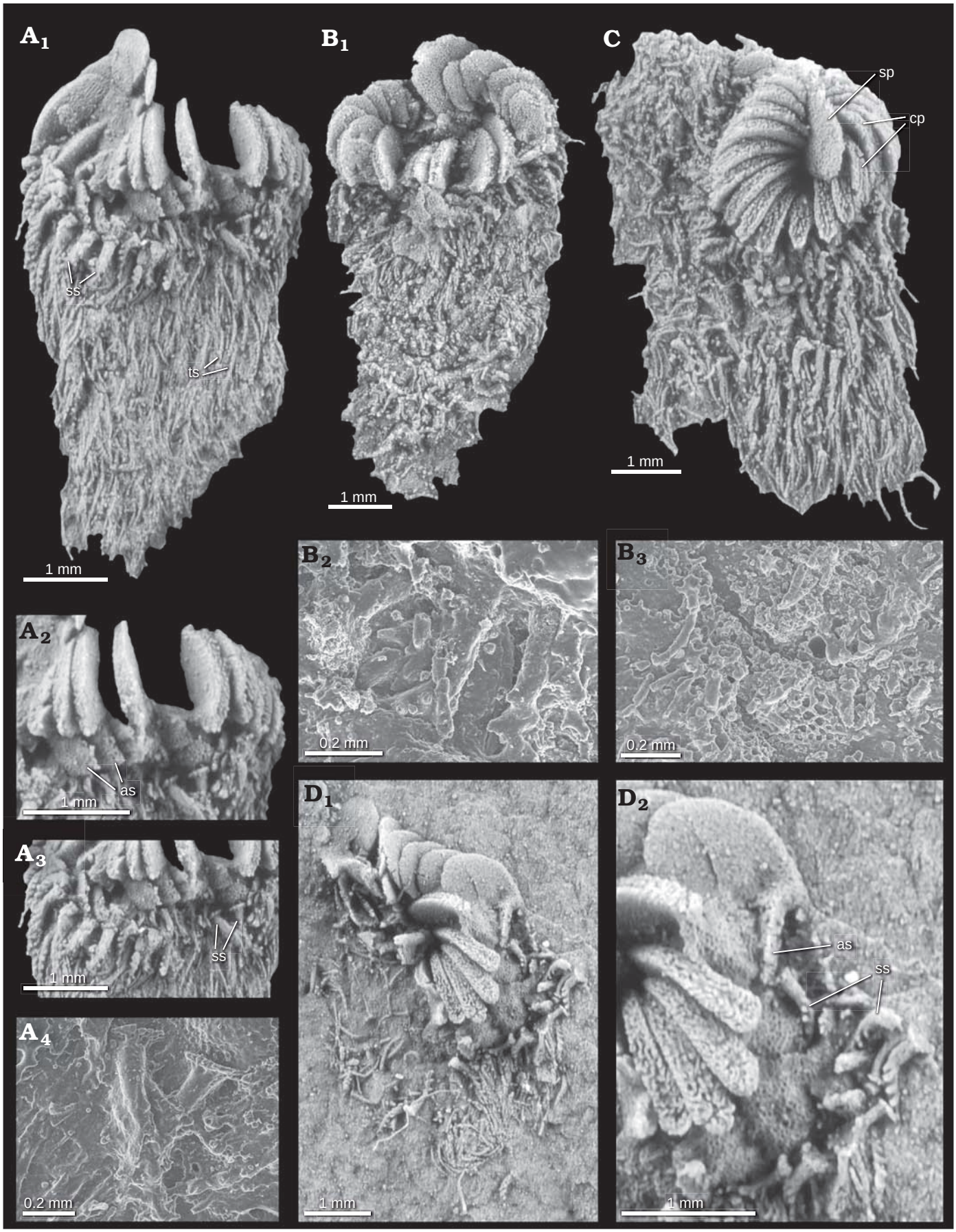


Fig. 3. Ctenocystoid echinoderm *Conollia sporranoides* sp. nov. from the Upper Ordovician of Scotland, UK. **A**. GLAHM 131255/1, partial specimen. **B**. GLAHM 131255/2, complete specimen. **C**. GLAHM 131255/3, partial ctenidium in lateral view. **D**. GLAHM 131255/4, partial ctenidium in adoral view. **E**. GLAHM 131255/5, partial ctenidium. **F**. GLAHM 131255/6, partial ctenidium. **G**. GLAHM 131255/7, complete ctenidium in anterior view. **H**. GLAHM 131255/8, partial ctenidium in anterior view. **I**. GLAHM 131255/9, partial ctenidium in anterior view. Photographs of original specimens (A, B), latex casts whitened with ammonium chloride sublimate (C–F), and virtual reconstructions (G–I). Abbreviations: as, articulations for serrated spines; cp, ctenoid plates; ss, serrated spines; ts, thecal spines.

single-layered marginal frame, a flattened theca and clearly differentiated plating of the ctenidium (Domínguez Alonso 2004). Finally, *Ctenocystis*, *Etoctenocystis*, *Gilcidia*, and *Pembrocystis* are most dissimilar to *Conollia*, being characterized by double-layered marginal frames, flattened, weakly asymmetrical thecae, and differentiated ctenidial plating (Robison and Sprinkle 1969; Sprinkle and Robison 1978; Fatka and Kordule 1985; Jell et al. 1985; Ubaghs 1987;

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Ubaghs and Robison 1988; Domínguez Alonso 2004; Rahman and Clausen 2009).

Smith et al. (2013) reported two ctenocystoids from Morocco (awaiting formal description) that can be compared with *Conollia*. Ctenocystoid gen. et sp. nov. 1 (Smith et al. 2013: fig. 4f; Fig. 1C) resembles *Conollia* in having a bilaterally symmetrical body covered with spines, and might also lack a differentiated marginal frame (the ctenidial plating is unclear), but its flattened, sub-triangular theca is similar to other, more typical ctenocystoids, particularly *Jugoszovia*. Ctenocystoid gen. et sp. nov. 2 (Smith et al. 2013: fig. 4b, h; Fig. 1F) possesses a robust, single-layered marginal frame, a flattened theca and clearly differentiated ctenidial plating, characters which are strongly dissimilar to *Conollia*. One final comparison can be made with the primitive, bilaterally symmetrical, ctenocystoid-like fossil *Ctenoimbricata*, which possesses spiny expansions of the thecal plates similar to those of *Conollia*. However, *Ctenoimbricata* is distinguished by the possession of a single-layered marginal frame, differentiated ctenidial plating and a flattened theca, and furthermore the spines of *Conollia* are much more widely distributed across the skeleton than those of *Ctenoimbricata* (which are restricted to the dorsal integument and marginal frame) (Zamora et al. 2012). Based on its morphology and stratigraphic position, we suggest that *Conollia* is a derived ctenocystoid, perhaps most closely related to *Jugoszovia* and ctenocystoid gen. et sp. nov. 1 from Smith et al. (2013).

Mode of life.—*Conollia* possesses a unique anatomical structure, which comprises a ctenidium with weakly or undifferentiated plating and an elongate-ovoid theca covered in spines and lacking a marginal frame. Below, we consider the functional significance of these characters and discuss the implications for the animal's mode of life.

Owing to their bilateral symmetry, most workers that have studied ctenocystoids have argued that they were motile animals. Robison and Sprinkle (1969), Sprinkle and Robison (1978), Jefferies et al. (1996) and Domínguez Alonso (1999, 2004) suggested that ctenocystoids were capable of propelling themselves forward by jet propulsion—presumably through strong muscular contraction of the body cavity, causing water to be forcefully expelled out the posterior anus. This is, however, extremely unlikely on morphofunctional grounds; thecal flexion was greatly restricted by the rigid frame in typical Cambrian ctenocystoids, which were most probably sessile in life (Rahman and Clausen 2009). In contrast, the absence of marginal plates in *Conollia* implies a significantly higher degree of thecal flexibility compared to other ctenocystoids; taken together with its strong bilateral symmetry, this points towards a more active mode of life. We consider jet propulsion (as outlined above) an improbable means of locomotion because the numerous long spines and the bulky ctenidium (Figs. 3A, B, 4A–C) would likely have created high drag and low stability in the water column. Furthermore, the worm-like body of *Conollia* is quite unlike that of jet propulsors such as cephalopods, jellyfish and scallops (Daniel 1984). Parsley (1999) and Parsley and Prokop (2004) suggested that ctenocystoids might have been able to move using the ctenidium, but the lack of specialized ventral plates (i.e., the robust suboral plates, which could plausibly have been used to displace the sediment) argues strongly against this for *Conollia*. Instead, we propose that *Conollia* was able to move slowly by contracting the body-wall musculature of the theca in peristaltic waves, similar to some modern holothurians, annelids and nemerteans (Heffernan and Wainwright 1974; Clark 1981; Turbeville and Ruppert 1983).

The numerous long, fine spines that cover the theca of *Conollia* have been interpreted as adaptations to a semi-infaunal mode of life, aiding penetration into the substrate (Domínguez Alonso 1999, 2004). An alternative possibility is that the spines enhanced stability on the seafloor by increasing the surface area of the animal; however, if this was true then substantial dorsoventral differentiation would be expected, and there is only very limited variation between spines on the upper and lower thecal surfaces in *Conollia staffordi* (Fig. 4A, C) and no differentiation in *Conollia sporranoides* sp. nov. Moreover, the rounded outline of the theca would have meant that only a small part of the body was in contact with the substrate at any given time, conveying poor stability on the sediment surface (in contrast to other ctenocystoids, which are characterized by flattened lower surfaces that seem well adapted to life resting on the seafloor; Rahman and Clausen 2009). The spiny, ovoid theca of *Conollia* is more compatible with an active, burrowing mode of life, and therefore we agree with Domínguez Alonso (1999, 2004) that *Conollia* was at least partly infaunal. Several modern holothurians, annelids and nemerteans penetrate the substrate using peristaltic locomotory waves (Heffernan and Wainwright 1974; Clark 1981; Turbeville and Ruppert 1983; Bromley 1996), and a similar mechanism is hypothesized for *Conollia*. The spines of *Conollia* are strongly curved backwards (Figs. 3A, B, 4A, C), and this suggests that movement was preferentially in the forward direction. In some modern burrowing polychaetes and echinoids, comparable fine structures (chaetae and spines) serve to aid locomotion and/or sediment excavation (Nichols 1959; Smith and Crimes 1983; Fauchald and Rouse 1997; Merz and Woodin 2006); however, this function seems un-

← Fig. 4. Ctenocystoid echinoderm *Conollia staffordi* Domínguez Alonso, 2004 from the Upper Ordovician of Wales, UK. **A**. NHMUK EE 5913, complete specimen in ventral view (A_1), detail of ctenidium (A_2) and detail of neck spines (A_3, A_4). **B**. NHMUK EE 5929a, complete specimen in ventral view (B_1) and detail of spines (B_2, B_3). **C**. NHMUK EE 5916 (holotype), complete specimen in anteroventral view. **D**. NHMUK EE 5910, partial specimen in lateral view (D_1) and detail of neck (D_2). Photographs of latex casts whitened with ammonium chloride sublimate (A_1, A_2, A_3, B_1, C, D_1, D_2) and scanning electron microscope images of latex casts coated in gold (A_4, B_2, B_3). Abbreviations: as, articulations for serrated spines; cp, ctenoid plates; sp, suroral plate; ss, serrated spines; ts, thecal spines.

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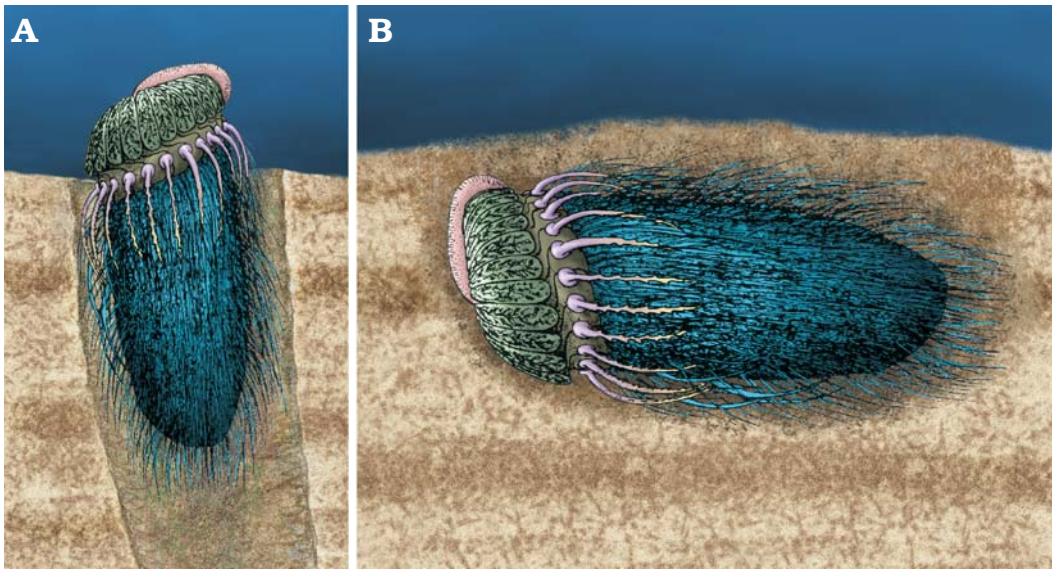


Fig. 5. Reconstructions of two possible modes of life of *Conollia*. **A**. A semi-infaunal mode of life. **B**. An infaunal mode of life. Adapted from Domínguez Alonso (2004).

likely for *Conollia* as the spines did not have muscular articulations and, hence, were not independently motile. Instead, the spines most probably helped to keep mud away from the body and brace *Conollia* within the burrow (similar to the capillary chaetae in certain infaunal polychaetes; Merz and Woodin 2006).

The feeding mechanism and tiering position of *Conollia* are unclear. If it used the ctenidium to passively capture resuspended organic particles just above the seafloor, as has been suggested for other ctenocystoids (Rahman and Clausen 2009; Zamora et al. 2012) and similar to some modern holothurians (Bromley 1996), a semi-infaunal mode of life is necessitated so that the anterior feeding apparatus could maintain contact with the sediment surface (Fig. 5A). Alternatively, *Conollia* could have actively fed on organic detritus within the sediment, similar to some modern annelids (Bromley 1996), in which case a permanent opening to the sediment—water interface might not have been required and, hence, a fully infaunal mode of life would be feasible (Fig. 5B). The reduction/loss of the suroral plate, which is thought to have controlled currents into and out of the body in other ctenocystoids (Rahman and Clausen 2009; Zamora et al. 2012), might indicate a lower degree of feeding selectivity in *Conollia*, perhaps more compatible with a subsurface deposit-feeding mode of life. Additional material, particularly any associated trace fossils, could shed further light on the mode of life of this animal.

Palaeoenvironment.—*Conollia sporranoides* sp. nov. comes from calcareous laminated siltstone/mudstone beds that were deposited in a deep-shelf environment, as implied by the associated fauna of deep-water trilobites (including the blind *Diacanthaspis trippi*) and brachiopods (Stewart and Owen 2008). *Conollia staffordi* is also from rocks inferred to have been deposited in a relatively deep-water environment, based on the accompanying deep-water trilobites (with no or reduced eyes) and graptolites (Fortey 2006). The presence of fairly complete, articulated specimens of both *Conollia sporranoides* sp. nov. and *Conollia staffordi*, including several individuals with spines in life position (Figs. 3A, B, 4A–C), strongly suggests that post-mortem transport was minimal (i.e., specimens are autochthonous or parautochthonous); anything more extensive would most likely have caused disarticulation of the fragile skeleton (as is the case for other weakly articulated fossil echinoderms; Brett et al. 1997). Furthermore, there is no evidence of abrasion-induced skeletal damage, which can be indicative of long-distance transportation in echinoderms (Gorzelak and Salamon 2013). The fauna associated with both *Conollia* species also implies minimal transport, notably the occurrence of complete, articulated trilobites, stylophorans and chitons (Fortey 2006; Stewart and Owen 2008). For these reasons, we suggest that *Conollia* almost certainly inhabited a deep-water environment in life.

The apparent 40-million-year gap in the ctenocystoid fossil record, from the widespread occurrence of genera in Cambrian Series 3 to the first appearance of *Conollia* in the Upper Ordovician, probably reflects a taphonomic bias related to their palaeoenvironment. Deep-water lagerstätten from the upper Cambrian and Ordovician are relatively rare (although see e.g., Van Roy et al. 2010; Botting et al. 2011), meaning that the likelihood of ctenocystoids being preserved intact and articulated was very low. Isolated plates probably occur in greater numbers, but might be difficult to recognise as ctenocystoids (or could otherwise have been overlooked due to their small size).

Conclusions

In this paper, we describe a new ctenocystoid from the Upper Ordovician of Scotland (*Conollia sporranoides* sp. nov.) and revise the genus that this species belongs to. These fossils demonstrate that the bilateral body plan of ctenocystoids

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persisted for over 50 million years following its first appearance in the Cambrian (Smith et al. 2013). Ctenocystoids show considerable morphological disparity, and there are significant differences between Cambrian and Ordovician forms. The steps involved in the evolutionary transition from a typical Cambrian ctenocystoid such as *Jugoszovia* to the derived genus *Conollia* included the complete loss of the marginal frame (and associated inflation of the theca), the reduction/loss of differentiated ctenidial plating and the pronounced development of spines. These changes most likely reflect the new infaunal or semi-infaunal mode of life adopted by *Conollia* in the Ordovician, which contrasts with the epifaunal habits of typical Cambrian taxa (Rahman and Clausen 2009).

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