Exceptionally preserved soft parts in fossils from the Lower Ordovician of Morocco clarify stylophoran affinities within basal deuterostomes.

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Abstract

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Keywords	deuterostomes; echinoderms; Fezouata Lagerstätte; Morocco; phylogeny.
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**Exceptionally preserved soft parts in fossils from the Lower Ordovician of
Morocco clarify stylophoran affinities within basal deuterostomes**

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ABSTRACT

The extinct echinoderm clade Stylophora consists of some of the strangest known deuterostomes. Stylophorans are known from complete, fully articulated skeletal remains from the middle Cambrian to the Pennsylvanian, but remain difficult to interpret. Their bizarre morphology, with a single appendage extending from a main body, has spawned vigorous debate over the phylogenetic significance of stylophorans, which were long considered modified but bona fide echinoderms with a feeding appendage. More recent interpretation of this appendage as a posterior "tail-like" structure has literally turned the animal back to front, leading to consideration of stylophorans as ancestral chordates, or as hemichordate-like, early echinoderms. Until now, the data feeding the debate have been restricted to evaluations of skeletal anatomy. Here, we apply novel elemental mapping technologies to describe, for the first time, soft tissue traces in stylophorans in conjunction with skeletal molds. The single stylophoran appendage contains a longitudinal canal with perpendicular, elongate extensions projecting beyond hinged biserial plates. This pattern of soft tissues compares most favorably with the hydrocoel, including a water vascular canal and tube feet found in all typical echinoderms. Presence of both calcite stereom and now, an apparent water vascular system, support echinoderm and not hemichordate-like, affinities.

Keywords: deuterostomes, echinoderms, Fezouata Lagerstätte, Morocco, phylogeny

1. Introduction

Phylogenetic relationships among the main clades of deuterostomes (Swalla and Smith, 2008; Erwin et al., 2011; David and Mooi, 2014) and in particular, the earliest chordates (including the vertebrates) (Jefferies, 1986; Holland et al., 2015; Janvier, 2015) represent long-debated issues. In recent years, however, the combination of molecular, embryological, and anatomical data has made it possible to establish a robust phylogeny for extant deuterostomes. With the Hemichordata (acorn worms), the echinoderms (sea lilies, starfish, sea urchins, and related forms) are now considered to belong to a clade, the Ambulacraria, as the sister-group of chordates (cephalochordates, tunicates and vertebrates) (Bottjer et al., 2006; Swalla and Smith, 2008; David and Mooi, 2014; Holland et al., 2015; Janvier, 2015; Lowe et al., 2015). This phylogenetic scenario provides insights not only into the distinctive morphological features (apomorphies) acquired within each clade of deuterostomes, but also into the primitive characters (plesiomorphies) inherited from their common ancestors (Bottjer et al., 2006; Swalla and Smith, 2008; David and Mooi, 2014; Lowe et al., 2015). For example, the occurrence of gill slits in both extant hemichordates and chordates strongly supports the view that these structures were very likely present in earliest deuterostomes (Smith, 2005; Bottjer et al., 2006; Swalla and Smith, 2008; Lowe, 2015). Their absence in echinoderms is most parsimoniously regarded as a secondary loss during the course of echinoderm evolution (Smith, 2005; Bottjer et al., 2006; Swalla and Smith, 2008; Zamora and Rahman, 2014), or perhaps at the origin of the phylum itself (Mooi and David, 1998, 2008).

Integrating fossil data into the phylogeny of deuterostomes offers the opportunity to document the sequential acquisition of key characters through time and to provide minimum dates for lineage divergences. The interpretation of the earliest known deuterostomes (Shu et al., 2001, 2004; Caron et al., 2010, 2013) (Cambro-Ordovician, 541–443 Myr) is particularly challenging

because their morphologies are often bizarrely unlike those of modern forms, with unexpected combinations of anatomical features. Along with cambroernids (Caron et al., 2010), conodonts (Briggs, 1992), vetulicolians (Shu et al., 2001) and vetulicystids (Shu et al., 2004), stylophorans belong to the bestiary of extinct, enigmatic early deuterostomes.

Stylophorans (cornutes and mitrates), a group of unusual middle Cambrian–Pennsylvanian (509–300 Myr) fossils, are small (typically one or two centimeters in length), bipartite organisms consisting of a single, articulated appendage inserted into a flattened, asymmetric to bilaterally symmetric body made of a multiplated, internal skeleton, or test (Ubaghs, 1968; Clausen and Smith, 2005; Smith, 2005; David et al., 2000; Dominguez et al., 2002; Lefebvre, 2003) (Fig. 1A, C). The appendage comprises two distinct parts: a highly flexible proximal region (partially inserted into the test) of telescopic, imbricate rings; and a relatively stiff distal region consisting of opposing, delicate biserial platelets mounted on massive, uniserial elements (ossicles). The two platelet biseries form a roof over a longitudinal median groove running along the upper surfaces of the ossicles. Some interpretations suggest that the biserial platelets are fixed (Fig. 1F), but others show them as hinged, movable elements, much like cover plates in modern sea lilies and their kin (crinoids) (Fig. 1C). In life, the test likely contained the viscera, and in some taxa, bears a series of pores interpreted either as respiratory (Ubaghs, 1968; David et al., 2000; Lefebvre, 2003) or pharyngeal structures (Jefferies, 1986; Dominguez et al., 2002; Shu et al., 2004; Clausen and Smith, 2005; Smith, 2005; Bottjer et al., 2006) (Fig. 1A, C). Both the appendage and the test consist of numerous calcitic skeletal elements possessing the same microstructure (called stereom) found in all echinoderms (Ubaghs, 1968; Jefferies, 1986; David et al., 2000; Dominguez et al., 2002; Lefebvre, 2003; Clausen and Smith, 2005; Smith, 2005; Bottjer et al., 2006; Zamora and Rahman, 2014).

The phylogenetic position of stylophorans within deuterostomes has been a contentious matter for decades. In the early 1960s, the stylophoran appendage was interpreted as a feeding arm, comparable in morphology to the feeding structures of various extant echinoderms (Ubaghs, 1968; David et al., 2000; Lefebvre, 2003). In this hypothesis, stylophorans are considered *bona fide* echinoderms, with their appendage bearing a single ambulacral ray of the water vascular system (Figs. 1A–C, 2). In the late 1960s, the stylophoran appendage was reinterpreted as a chordate-like tail, containing a notochord and serially arranged muscle blocks (Jefferies, 1986; Dominguez et al., 2002). Thereby, stylophorans were designated calcichordates, ancestral members of all three modern chordate lineages. This interpretation implies that the stereom skeleton of extant echinoderms was an apomorphy of all deuterostomes and therefore secondarily and independently lost in all lineages with the exception of echinoderms. Most recently, the stylophoran appendage has been interpreted as a muscular, hemichordate-like stalk (Shu et al., 2004; Clausen and Smith, 2005; Smith, 2005; Bottjer et al., 2006; Swalla and Smith, 2008; Caron et al., 2010) (Figs. 1D–F, 2). In this interpretation, stylophorans remained echinoderms (because of the presence of the distinctive stereom), but are among the earliest members of the phylum, because they retain plesiomorphic features lost in all more derived taxa (e.g., locomotory stalk), and lack apomorphies present in more derived taxa (e.g., water vascular system).

Two basic assumptions of the calcichordate interpretation have previously been falsified. First, the purported sister-group relationship between echinoderms and chordates was not confirmed by molecular phylogenetics, which indicated that echinoderms are more closely related to hemichordates than they are to chordates (Bottjer et al., 2006; Swalla and Smith, 2008; Erwin et al., 2011; Lowe et al., 2015). Second, available evidence supports the view that stereom

is an echinoderm synapomorphy that first appeared in the early Cambrian (Bottjer et al., 2006; Kouchinsky et al., 2012; Zamora and Rahman, 2014). The last two remaining, current hypotheses both agree that stylophorans are echinoderms (Fig. 2), but differ markedly in the interpretation of their appendage: feeding arm constructed like a typical echinoderm ray [H1] versus tail constructed like a hemichordate-like stalk [H2].

Here we report the first evidence for soft part preservation in stylophorans. These data make it possible to test, for the first time, soft anatomies predicted by H1 and H2. The feeding arm hypothesis (H1) requires that: (1) the longitudinal median groove contained a water vascular canal, with lateral tube feet; (2) biserial platelets are cover plates that opened to expose the tube feet; (3) the mouth was located at the proximal end of the food groove; and (4) the fore-gut (esophagus) was located within the proximal rings. The locomotory stalk scenario (H2) implies that: (1) the longitudinal median groove contained a peduncular nerve; and (2) biserial platelets are integrated, contiguous body wall elements sutured to each other so as to enclose a coelom.

2. Material and methods

All figured specimens are housed in the collections of Cadi-Ayyad University (Faculté des Sciences et Techniques, Guéliz), Marrakesh, Morocco. Locality details are indicated on specimen labels, and can be provided on request. Specimens were prepared with scalpels and needles under high magnification using a Zeiss SteREO Discovery.V8 stereomicroscope. Interpretative drawings were made using a camera lucida attached to a Zeiss SteREO Discovery.V8 stereomicroscope. Photographs were made with a Zeiss AxioCam MRc5 digital

camera mounted on a Zeiss SteREO Discovery.V8 stereomicroscope. Digital photographs were processed in Adobe Photoshop Elements 9. Figs. 3A–B and Figs. S2A, S4A–B are composite images stitched together using Adobe Photoshop Elements 9. Elemental composition was analysed in a FEI Quanta 250 scanning electron microscope (SEM) equipped with an energy X-ray analyser (EDX) at the Centre Technologique des Microstructures, plateforme de l'Université Claude Bernard Lyon 1.

3. Results

Stylophorans with soft parts were collected in the Lower Ordovician Fezouata Konservat-Lagerstätte, in a small excavation along the western flank of Bou Izargane hill, approximately 18 km north of Zagora (central Anti-Atlas, Morocco; Fig. 3). Here, the Fezouata Shale corresponds to a 1,000 m-thick, repetitive succession of argillaceous siltstones, unconformable over the middle Cambrian sandstones of the Tabanite Group (Destombes et al., 1985; Martin et al., 2016). The excavation is approximately 270 m above the base of the Ordovician series and within the lower stratigraphic interval (about 80 m thick) yielding soft-bodied faunas typical of the Fezouata Biota (Vinther et al., 2008, 2017; Van Roy et al., 2010, 2015; Van Roy and Briggs, 2011; Lefebvre et al., 2016; Martin et al., 2016) (Fig. 3). Nearby graptolites indicate a late Tremadocian age (*A. murrayi* Zone) (Gutiérrez-Marco and Martin, 2016; Lefebvre et al., 2016, 2018; Martin et al., 2016).

All specimens were collected from a single, small, 3 cm-thick lens of dark blue mudstones. Three fossiliferous intervals occur within the lens: a lower layer with many densely packed,

complete, and fully articulated marrellomorphs (*Furca* sp.; Fig. 4A), an intermediate horizon with a low-diversity assemblage of trilobites (*Anacheirurus* sp., *Bavarilla* sp.) with soft parts (Fig. 4B–C), and an upper, low-diversity assemblage comprising almost exclusively cornute stylophorans (more than 300 specimens belonging to two taxa, *Hanusia* n. sp. and *Thoralicystis* n. sp.; Figs 5–9). Deposition is interpreted as rapid burial of autochthonous communities by distal storm deposits in relatively shallow environmental conditions (Martin et al., 2016; Vaucher et al., 2016). In this level, arthropods and echinoderms are typically preserved as faint, flattened impressions on the dark rock. As in the Burgess Shale, echinoderm skeletons are indicated as impressions without preservation of actual stereom. In contrast, their soft tissues appear as colorful structures, resulting from the oxidation of original pyrite into yellow, red to purple iron oxide pseudomorphs (Figs. 5A, 6A, 7A, 8A, C). This type of preservation is not unique to the Bou Izargane cornutes (Vinther et al., 2008, 2017; Van Roy et al., 2010, 2015; Lefebvre et al., 2016). Similarly preserved soft parts (e.g. guts) have been described in arthropods (Gutiérrez-Marco et al., 2017), hyolithids (Marti Mus, 2016), and machaeridian annelids (Vinther et al., 2008) occurring in the same stratigraphic interval of the Fezouata Shale. In the cornutes, the identification and precise distribution of Fe-rich soft tissues were obtained by chemical analyses and elemental mapping under SEM (Figs. 5B, E, 6).

At least one specimen of *Thoralicystis* n. sp. shows clear evidence of soft-bodied structures in the distal part of its appendage (Figs. 5–6). Preserved soft tissues consist of: (1) two superimposed longitudinal canals housed in the continuous, median groove on the upper surface of ossicles, and extending from the stylocone cavity (proximally) to the distal end of the appendage; (2) numerous small, lateral tube-like extensions branching regularly from the external longitudinal canal and protruding outward from between widely open, hinged plates.

Several specimens of *Thoralicystis* n. sp. and *Hanusia* n. sp. exhibit strong evidence of soft tissues preserved within the proximal part of their appendage (Figs. 7–8). All these specimens display a spindle-shaped, elongate cavity extending throughout the proximal rings of the appendage from the stylocone cavity (distally), to the main body cavity (proximally). All these soft-bodied structures are described for the first time in stylophorans.

4. Discussion

4.1. The stylophoran appendage is a feeding arm

On the basis of this new evidence, it is possible to evaluate critically the two current interpretations of the stylophoran appendage. In the stalk model (H2), the outermost of the two longitudinal canals could be interpreted as the peduncular nerve housed in a fully enclosed body cavity, or coelom. However, H2 must be rejected because of the presence of open plates that precludes such a coelom, and the presence of lateral extensions that branch regularly from the external longitudinal canal and protrude externally in between the open plates. This organisation is incompatible with that of a stalk-, or tail-like structure, but fits requisites of the feeding-arm model (H1). The evidence strongly supports H1, in which the external longitudinal canal is interpreted as an ambulacral canal of the water vascular system, and the lateral, tube-like structures as ambulacral tube feet (Figs. 5–6, 9), the morphology of which is strikingly similar to that of exceptionally preserved tube feet described from Paleozoic arm-bearing forms (Glass and Blake, 2004; Sutton et al., 2005; Glass, 2006; Clark et al., 2017). As a consequence, the mouth of

stylophorans is most parsimoniously located at the proximal end of this ambulacral groove (Fig. 5C), the spindle-shaped cavity extending from the mouth (distally) and connected to the main body cavity (proximally) representing the anterior part of the gut (Figs. 5, 7–8). Comparison with the situation in the arms and pinnules of modern crinoids suggests that the internal longitudinal canal internal to the space above the water vascular system is a coelomic canal (Figs. 5–6). There is no evidence that what are interpreted here as tube feet represent some sort of musculature, because they project as free-standing structures extending from the longitudinal canal, and protrude outside of the body wall into the external medium.

Labyrinthic meshwork has been described in the proximal cavity of the stylocone (large, cone-shaped, uniserial ossicle located at the proximal end of the distal part of the appendage) of the primitive stylophoran *Ceratocystis* (middle Cambrian) (Clausen and Smith, 2005). Similar observations in extant echinoderms suggest that this labyrinthic microstructure was associated with muscle insertion, implying that the stylocone cavity once housed musculature with functionality similar to that in hemichordates. However, living echinoderms express muscles as well, so this trait is compatible with both H1 (Fig. 1B) and H2 (Fig. 1E), and cannot be used to provide evidence for or against either.

Finally, the putative locomotory function of the stylophoran appendage has been frequently considered as incompatible with its interpretation as a feeding arm and the presence of a water-vascular canal (Rahman et al., 2009; Rozhnov and Parsley, 2017). As this is the case in many extant arm-bearing echinoderms (e.g. asteroids, ophiuroids, comatulids), it is very likely that stylophorans used their appendage not only for nutrition, but also locomotion (Lefebvre, 2003).

4.2. Implications for echinoderm phylogeny

230 Preserved soft tissues in cornutes from the Fezouata Shale provide strong evidence suggesting
231 the existence of ambulacral structures in the stylophoran appendage. The evidence supports the
232 view that this extinct group of ambulacrarians possessed at least two of the major apomorphies
233 supporting recognition of the phylum Echinodermata: (1) a multi-element endoskeleton, made of
234 calcitic plates displaying the typical, three-dimensional, stereomic microstructure; and (2) a
235 water vascular system. However, the precise phylogenetic position of stylophorans within
236 echinoderms remains so far unresolved because they do not display any evidence of the radial,
237 five-fold symmetry generally considered a synapomorphy of the phylum (Shu et al., 2004;
238 Smith, 2005; Bottjer et al., 2006; Swalla and Smith, 2008; Zamora and Rahman, 2014). If this
239 absence is original, stylophorans would then represent a relatively early branch of pre-radial
240 echinoderms (Ubaghs, 1968, 1975; Shu et al., 2004; Smith, 2005; Bottjer et al., 2006; Swalla and
241 Smith, 2008; Zamora and Rahman, 2014). Such an interpretation requires that anatomically
242 similar, arm-like, feeding structures were acquired independently in stylophorans in the middle
243 Cambrian, and again, in later forms such as asteroids and crinoids, in the Early Ordovician
244 (Ubaghs, 1968, 1975).

245 Alternatively, the late appearance of stylophorans in the fossil record 10-12 m.y. after radial
246 taxa (e.g., eocrinoids, helicoplacoids, and edrioasteroid-like forms such as stromatocystitoids)
247 (Kouchinsky et al., 2012; Zamora et al., 2013) and their unusual, flattened morphology more
248 parsimoniously suggest that stylophorans are relatively derived echinoderms descended from
249 pentaradial ancestors (David et al., 2000). This interpretation is supported by embryological data,
250 which provide no evidence suggesting that 5-part radial symmetry is preceded by stages with
251 fewer rays (Mooi and David, 2008). In this context, the possession of arm-like, ambulacral

structures containing coelomic extensions other than the hydrocoel could represent an apomorphy uniting stylophorans with forms such as crinoids (David et al., 2000; Lefebvre, 2003).

4.3. Implications for early deuterostome phylogeny

The exceptionally preserved cornute specimens from Morocco bring revolutionary new evidence to consider. That evidence actually reverses the anterior-posterior axis suggested by some very recent interpretations seeking to revive a modified version of the calcichordate interpretation (Shu et al., 2001, 2004; Clausen and Smith, 2005; Smith, 2005; Bottjer et al., 2006; Swalla and Smith, 2008; Zamora and Rahman, 2014). Since the early 2000s, molecular phylogenies have strongly supported an ambulacrarian clade that unites hemichordates and echinoderms as sister-group to the chordates (Bottjer et al., 2006; Swalla and Smith, 2008; David and Mooi, 2014; Holland et al., 2015; Janvier, 2015; Lower et al., 2015). As a consequence of this new phylogenetic framework, several authors reinterpreted stylophorans as early members of the Echinodermata, morphologically extremely close to the last common ancestor of both hemichordates and echinoderms (Shu et al., 2001, 2004; Clausen and Smith, 2005; Smith, 2005; Bottjer et al., 2006; Swalla and Smith, 2008). In this interpretation, stylophorans would possess a single echinoderm apomorphy: the calcite, stereom skeleton. They would not yet have acquired two other significant echinoderm apomorphies: the water-vascular system and the radial, five-fold symmetry.

In a surprising parallel to the calcichordate hypothesis, stylophorans would share with other (early) ambulacrarians and deuterostomes (1) a bipartite body organization, with a head and a muscular, locomotory tail (or stalk); and (2) the presence (plesiomorphic retention) of gill slits (Shu et al., 2001, 2004; Conway Morris, 2003; Clausen and Smith, 2005; Smith, 2005; Bottjer et al., 2006; Swalla and Smith, 2008; Caron et al., 2010; Conway Morris and Caron, 2012; Zamora and Rahman, 2014; Conway Morris et al., 2015). As a consequence, this interpretation of stylophorans as hemichordate-like, early echinoderms with a bipartite organization (anterior head and posterior, tail-like appendage) has in the last 15 years caused many comparisons of early deuterostomes to stylophorans, i.e. *Herpetogaster* and cambroernids (Caron et al., 2010), *Pikaia* and other putative early chordates (Donoghue et al., 2003; Gee, 2006; Conway Morris and Caron, 2012), vetulicolians (Shu et al., 2001; Conway Morris, 2003; Vinther et al., 2011; Ou et al., 2012), and vetulicystids (Shu et al., 2004; Conway Morris et al., 2015).

Our study demonstrates that: (1) stylophorans had a water-vascular system; and (2) that their appendage was not a locomotory, muscular tail. By bringing new, unequivocal evidence that the stylophoran appendage is an echinoderm feeding arm (comparable in morphology to a crinoid feeding arm) and not a hemichordate-like tail (or stalk), our discovery shows that the interpretation of these fossils as early echinoderms retaining features of basal ambulacrarians and/or hemichordates can be definitively rejected. In fact, any suggestion that stylophorans can tell us something about common ancestry of echinoderms with other deuterostomes is seriously compromised by the solid evidence that such conclusions rely on a reconstruction that has the animal the wrong way around. The bipartite body organization of stylophorans (theca and feeding arm) is not homologous to the bipartite body organization of *Herpetogaster*, vetulicolians, vetulicystids, early chordates and/or hemichordates (head and post-anal tail).

Whatever the precise phylogenetic position of stylophorans within the Echinodermata, the significance of the Fezouata fossils lies in the picture they give of the remarkable diversity within the phylum throughout its evolution, and not of the supposed origins of the phylum itself.

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Figure captions

Fig. 1. The two current interpretations of stylophoran morphology and their implications for soft-tissue anatomy, based on the cornute *Phyllocystis blayaci* (Lower Ordovician, France). **A–C.** H1, stylophorans as typical echinoderms with a single feeding arm. **D–F.** H2, stylophorans as pre-radial echinoderms with a hemichordate-like stalk. **A, D.** Basic anatomical features deduced from skeletal morphology. **B, E.** Reconstructions of soft tissue anatomy along a longitudinal

section of the stylophoran appendage. **C, F.** Three-dimensional reconstructions of the soft tissue anatomy in the distal part of the stylophoran appendage.

Fig. 2. The two current interpretations of stylophoran phylogenetic position within ambulacrarian deuterostomes. H1, stylophorans as typical echinoderms with a single feeding arm. H2, stylophorans as pre-radial echinoderms with a hemichordate-like stalk.

Fig. 3. Geographic and geologic context of Bou Izargane locality. On the maps (left), Ordovician outcrops in north-western Africa and in the Zagora area are indicated in green. The red star shows the location of Bou Izargane hill. On the right, partial stratigraphic column of the Fezouata Shale, showing the position of the Bou Izargane excavation. The left column indicates sea level changes. Numbers along the right column indicate the height (in meters) above the Cambrian/Ordovician boundary. The colors used in the log correspond to those of outcropping rocks.

Fig. 4. Arthropods with soft-tissue preservation collected in the same lens as cornute stylophorans with soft parts, late Tremadocian (Lower Ordovician), Bou Izargane, Zagora area (Morocco). **A.** Two associated specimens of the marrellomorph *Furca* sp. (AA.BIZ15.OI.364). **B–C.** Two specimens of the trilobite *Bavarilla zemmourensis*. **B.** Arrows indicate four locomotory appendages below the thorax (AA.BIZ15.OI.181). **C.** The arrow shows one frontal appendage at the anterior extremity of the cephalon (AA.BIZ15.OI.16). Scale bars, 5 mm (A, C); 2 mm (B).

Fig. 5. *Thoralicystis* n. sp. from the Fezouata Shale, Lower Ordovician, Morocco (AA.BIZ15.OI.259). **A–C.** Complete specimen in lateral view. **A.** Composite photographic reconstruction. **B.** Composite SEM elemental map of Fe. **C.** Composite reconstruction of soft part anatomy based on camera lucida drawings, SEM elemental maps (Fe) and back-scattered electron micrographs. **D–F.** Magnified views of parts of the distal appendage outlined in (A–C). **D.** Back-scattered electron micrograph. The arrows indicate the position of tube feet. **E.** SEM elemental map showing the distribution of Fe. **F.** Reconstruction of the soft parts based on camera lucida drawings, SEM elemental maps (Fe) and back-scattered electron micrographs. pr. cavity, proximal cavity; pr. rings, proximal rings; styl., stylocone; wvs, water vascular system. Scale bars, 5 mm (A–C); 1 mm (D–F).

Fig. 6. Soft-tissue preservation in the distal appendage of the cornute stylophoran *Thoralicystis* n. sp. (AA.BIZ15.OI.259), late Tremadocian (Lower Ordovician), Bou Izargane, Zagora area (Morocco). **A.** Photographic view of the magnified area. **B.** Back-scattered electron micrograph showing the water vascular system (ambulacral canal, tube feet) and the second, more internal, longitudinal canal. Skeletal elements (biserial platelets, ossicles) are not visible. **C–J.** SEM elemental maps of Al (**C**), C (**D**), Fe (**E**), K (**F**), Mg (**G**), Na (**H**), O (**I**) and Si (**J**). Scale bars, 1 mm.

Fig. 7. Soft-tissue preservation in the test and proximal appendage of the cornute stylophoran *Hanusia* n. sp. (AA.BIZ15.OI.110), late Tremadocian (Lower Ordovician), Bou Izargane, Zagora area (Morocco). **A.** Composite photographic reconstruction of the specimen in lateral view. **B.** Composite reconstruction based on back-scattered electron micrographs. **C.** Reconstruction of

the soft parts based on camera lucida drawings and back-scattered electron micrographs. bis.
platelets, biserial platelets. Scale bars, 5 mm.

Fig. 8. Soft-tissue preservation in the proximal appendage of the cornute stylophoran *Hanusia* n. sp. (AA.BIZ15.OI.80), late Tremadocian (Lower Ordovician), Bou Izargane, Zagora area (Morocco). **A.** Specimen in upper view. **B.** Reconstruction of (A), based on camera lucida drawings. **C.** Closer view of the proximal region of the appendage outlined in (A). **D.** Reconstruction of (C), based on camera lucida drawings. pr. cavity, proximal cavity; pr. rings, proximal rings. Scale bars, 1 mm.

Fig. 9. Reconstruction of the cornute stylophoran *Thoralicystis* n. sp., late Tremadocian (Lower Ordovician), Zagora area (Morocco), with the tube feet protruding beyond the cover plates. The appendage is about 20 mm long.