A hyolithid with preserved soft parts from the Ordovician Fezouata Konservat-Lagerstätte of Morocco

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Abstract

Hyolithids are an extinct group of early lophotrochozoans with an external skeleton consisting of a conical conch, an externally fitting operculum, and a pair of long, lateral spines named helens. Their phylogenetic position within the lophotrochozoans is unclear, although traditionally they have been regarded as molluscs. Although hyolithids occur in Konservat-Lagerstätten, their soft-part preservation had so far been restricted to the gut. The few known examples suggested that a simple U-shaped gut was characteristic of the group, but new occurrences show a diversity of gut configurations suggesting certain ecological diversity within the group. Here is reported an exceptionally preserved hyolithid specimen from the Ordovician Fezouata Konservat-Lagerstätte of Morocco with a relatively complete gut possibly including an oesophagus, a mouth and a faecal string. Uniquely for hyoliths, other soft parts, likely those associated with the inner surface of the operculum, appear to be preserved as well protruding from the aperture. The anatomy of the preserved soft parts is in accordance with inferences from skeletal anatomy suggesting that hyolithid soft parts did not extend much beyond the aperture, and that only the internal portion of the helens was associated with soft tissues. It is also compatible with lophotrochozoan affinities, but

molluscan apomorphies, such as a foot or a radula are not present in the specimen. Taken together, the newly available information suggests that hyolithids may have had a relatively generalized feeding organ, which could adapt to various feeding modes in the suspension-detritus-deposit feeding spectrum. A specialized deposit feeding strategy would be at odds with what is known about hyolithid functional morphology, therefore the presence of a sediment-like infill in the posterior part of the gut of the presently described specimen is puzzling and, as it has been suggested for some Chengjiang taxa, may represent a taphonomic "artefact".

1. Introduction

Hyoliths are an extinct group of early lophotrochozoans with an external skeleton consisting of a conical conch and an operculum. Their phylogenetic position within the lophotrochozoans is unclear (Runnegar et al 1974), although traditionally they have been regarded as molluscs (e.g. Marek and Yochelson, 1976). Their stratigraphic range extends from the early Cambrian to the Permian, although they are only abundant and diverse in the early Palaeozoic. Two groups have been recognized within the Hyolitha, orthothecids and hyolithids (see Marek and Yochelson, 1976). Hyolithids have a four-pieced external skeleton consisting of a conical conch of subtriangular cross section (although the precise outline can be variable), an externally fitting operculum with a complex inner surface, and a pair of flattened spines (helens) that grow internally and extend laterally through the conch-operculum commissure. The conch has a ventral shelf called ligula, and the operculum is folded to fit the angular aperture. Orthothecids are more diverse morphologically and characterized by a conch of varied cross section

51 and a retractable operculum. Their symmetry is also diverse, with species that are
52 radially symmetrical and others showing bilateral symmetry. As presently defined, they
53 form a heterogeneous group, which could even be polyphyletic. This is particularly true
54 for the lower Cambrian, where the distinction between orthothecids and other "tubular
55 problematica" is blurred. However, many orthothecids have relatively complex opercula
56 similar to those of hyolithids, and it is likely that at least some "orthothecids" are
57 closely related to hyoliths.

58 Although hyoliths occur in soft-part preservation localities, so far their soft-part
59 preservation had been restricted to their guts, and the observation that their body wall was
60 never preserved in Burgess-type assemblages has been interpreted as evidence that hyoliths
61 had an acuticular, cellular integument (Butterfield, 2003). Reported hyolithid soft parts from
62 the Hunsrück Slate, Germany (Houbriek et al., 1988; Bartels et al., 1998) are intriguing but
63 contentious (only one specimen is illustrated, and the relevant structures are ambiguous). A
64 report of soft part preservation in a hyolithid from the Kaili Fm, China (Mao et al., 1992) is
65 also questionable (the relevant structures are likely cracks in the conch).

66 Hyolith guts, however, are relatively common occurrences. Until recently, folded,
67 sediment filled guts, had only been described in orthothecids (e.g. Thoräl, 1935; Runnegar et
68 al., 1975; Malinky, 2003), while morphologically simpler, U-shaped guts seemed to
69 characterize hyolithids (e.g. Butterfield, 2001, 2003). This picture is starting to change, with
70 new occurrences showing a diversity of gut configurations in both groups which points to a
71 certain ecological diversity of the hyoliths as a whole (e.g. Chen, 2004; Wilson, 2006;
72 Devaere et al., 2014).

73 Here I describe an exceptionally preserved hyolithid specimen from the Ordovician
74 Fezouata Konservat-Lagerstätte of Morocco with a relatively complete gut, possibly
75 including an oesophagus, a rounded mouth and a faecal string. Uniquely for hyoliths, other

soft parts, likely those associated with the inner surface of the operculum appear to be preserved as well, protruding from the aperture.

2. Material and methods

The specimen was collected from the upper part of the Lower Fezouata Formation in the Tamagrout area, ca 20 km N of Zagora in south-eastern Morocco (see Supplementary Material for more detailed information about the geological setting) and is housed in the Yale Peabody Museum of Natural History, with the number YPM 515750

The specimen was photographed using two different techniques: (1) coated with ammonium chloride and illuminated with natural light, to enhance relief, and (2) under water and with polarized light to enhance colour contrast. All images are one-frame-photographs, except for the image in Figure 3A which is a composite image obtained with the computer software Combine ZP (after a stack of images in different focal planes). Images in Figures 1B and 3A are originally colour photographs (taken under water and with polarized light), and the B&W conversion was controlled (with Photoshop) to enhance certain features of the specimen. Energy dispersive X-ray spectroscopy (EDS) was used to analyse the elemental composition of the fossils. In the description, the terms left, right, anterior, posterior, etc., refer to the inferred life orientation of the organism.

3. Preservation

The specimen is flattened but preserves some three-dimensionality (Fig. 1A) and consists of part (Figs 1A-C, 2, 3A) and counterpart (Figs 1D, 3B). It has split along the ventral surface of the conch; therefore the structures contained within the conch are only preserved in the part, unless they have relief, in which case they are also preserved as an imprint in the counterpart. Much of the ventral apertural margin (the ligula margin) is not preserved in the part because the relevant area has chipped off exposing dorsally located structures (Figs 1A, 2A, 4C). The corresponding area in the counterpart is better exposed (after some preparation; Figs 1D, 4C), but the counterpart is generally less informative.

Skeletal elements are demineralized, and both skeletal and soft parts are mostly preserved as iron oxides (Fig. 2). A portion of the gut is preserved as a somewhat diffuse, black stain, which lacks relief and likely represents highly degraded organic matter (Figs 2, 3A, 4B-C). This portion of the gut is only preserved in the part, The rest of the gut is preserved as a "sediment" infill (the word sediment is written in inverted commas because its origin is uncertain; see section 5.3), lacking any evidence of remaining organic matter (Figs 1A, C-D, 4A). It is considerably wider than the organically preserved portion and has relief (Figs 1C-D). EDS analyses show no difference in composition between the gut and adjacent areas of the fossil. Spectra and elemental concentrations suggest that both consist mostly of silica, K-rich phyllosilicates and iron oxides.

4. Description of the specimen

The hyolithid is articulated and almost complete (Figs 1A-B, 2A, 4C), and missing parts

(such as the left helen) are probably present but not exposed. The specimen is exposed showing the ventral side. The operculum lies in front of the aperture, slightly displaced forward; only the conical shield is clearly visible. The right helen stretches between the conch and operculum, apparently not directly in contact with either of them (Figs 1B, 2A, 4C). The morphology of the skeletal parts is typical of hyolithids, although beyond this, there is little systematic information preserved.

4.1. Soft parts extending outside the aperture

Extending between conch and operculum, there is a trapezoidal red-yellow stain that connects the three skeletal elements (Figs 1B, 2, 4C). The stain has a well-defined outline that, in its anterior margin, replicates the curvature of the ventral margin of the operculum (and that of the ligula, since both margins come in contact to close the aperture). The stain is located dorsally relative to the gut, but ventrally relative to the operculum. All these features suggest that the stain represents soft parts of the animal. No comparable ventral tissues are preserved (although the ventral apertural area is only partly preserved; see Fig. 4C)

4.2. Gut

The gut is preserved as a conspicuous structure that occupies the upper half of the conch, extending beyond the dorsal apertural margin and into the ligula (Figs 1, 2, 3A, 4C). It is aligned with the plane of symmetry and does not occupy the full width of the conch. The organically preserved portion of the gut (Figs 2B, 3A, 4B-C) has a complex, difficult to

interpret, anterior region that includes what seems to be a rounded chamber ca. 1.3 mm in diameter. Anteriorly, the chamber continues in a straight band (width ca. 0.5 mm) that approaches the margin of the ligula; the band is faint and mostly preserved in iron oxides (organic matter if present appears very diffuse). Both chamber and band are almost aligned with the plane of symmetry of the conch, slightly displaced to the left (like the rest of the organically preserved portion of the gut), and are ventrally located with respect to other portions of the gut. Posteriorly, the chamber leads to a relatively wide (ca. 0.8-1.0 mm), perpendicularly oriented segment that extends towards the left side. The continuation of the gut is unclear in this area but the rest of the organically preserved gut consists of a thin (ca. 0.3 mm), winding band intertwined with a wider (ca. 1.2 mm), "sediment"-filled gut segment (segment 5; see next paragraph) located to the left of the organism (Figs 3A, 4B). The thin organic band fades posteriorly, along the margin of segment 5 (Figs 3A, 4B-C), and its presumed continuation with the rest of the gut is obscure.

There are several distinct segments in the "sediment"-filled portion of the gut whose connections with each other are not straightforward (Figs 1C-D, 3A, 4). To the left of the animal there is segment 5, intertwined with the organically preserved gut portion. Segment 5 has a sinusoidal curvature, anteriorly bends towards the left side of the aperture and fades away as it reaches the level of the dorsal aperture margin (Figs 1C, 4C). This segment shows several marked constrictions (arrowed in Fig. 1C), which coincide precisely with the course of the organically preserved portion of the gut that revolves around it (Figs 1C, 3A, 4A-B). Segment 1 is the most distal and appears to be continuous with segment 2 (Fig. 3A), which is the widest (ca. 1.8-2.1 mm) segment (Figs 2C-D, 4A-B). Anteriorly, segment 2 reaches the margin of the ligula and may continue slightly beyond, but the relevant area is incompletely preserved. Segment 4 is clearly located in a more dorsal position than segment 2, and therefore partly hidden behind it. Finally, a possible short segment 3 (Figs 1D, 3A, 4)

can be seen in the ligula area, to the left of segment 2)

4.3. Additional structures possibly associated with the gut

Two additional structures, both located at the aperture, may be related to the gut. One of them (arrowed in Figs 1D, 3B, and reconstructed in Fig. 4) is only preserved in the counterpart (as an imprint, in negative relief; although herein illustrated in positive relief, from a latex cast); the corresponding area in the part is broken. The structure is faint and difficult to see and illustrate. Therefore, its precise morphology is uncertain and the following description tentative. Described in positive relief (as seen in the latex cast; Figs 1D, 3B), it seems to consist of a raised ring of ca. 0.5-0.6 mm in diameter. Thin, radially arranged folds or ridges (ca. 0.4-0.5 in length) seem to stem from the ring. The structure is located at the margin of the ligula (Fig. 1D), coinciding with the plane of symmetry of the animal, and just ahead of the anterior band of the organically preserved portion of the gut (Fig. 4D).

A second structure is preserved at the left side of the ligula (white arrow in Fig. 2B; see also Figs 1B, 2A, 4C). It is a small band (ca. 1 mm long and 0.5 mm wide) preserved in iron oxides. Its lateral margins appear well defined but its distal end seems to be crumbling. It stems from the ligula margin with no clear continuation inside the conch. A possibly significant observation is that segment 5, interpreted as the terminal segment of the gut (see section 5.2), curves towards it (Fig. 4C), suggesting the structure may be related to the gut.

5. Interpretation and discussion

5.1. Soft parts extending outside the aperture

Hyolithid soft parts, besides the gut, have rarely been reported, and all reports to date are questionable (see Introduction). Therefore the preservation of soft parts extending beyond the aperture in the presently described specimen is a unique and important finding (Figs 1B, 2, 4C). The soft parts are dorsally located, connect the three skeletal elements and have a well-defined shape, which somewhat replicates that of the operculum. All of this suggests they represent the soft parts attached to the internal surface of the operculum. The whole body attitude of the specimen (with the different skeletal elements associated but with the helens and the operculum sequentially displaced forward) is typical of well-preserved, complete hyolithids (such as those from the Burgess Shale; Yochelson, 1961), suggesting that, although not preserved, the same soft tissues were holding the skeletal pieces together in those specimens. Also, this body attitude is compatible with the partial detachment (perhaps due to muscle relaxation) of the opercular soft parts.

An additional relevant feature of the preserved soft parts is that, as predicted on the basis of helen morphology and microstructure (see Martí Mus and Bergström, 2007, and references therein; Martí Mus et al., 2014), only the proximal portion of the helen is surrounded by soft parts; the rest extends as a thin, “naked” spine.

5.2. Reconstruction of the gut and associated structures

The gut has a relatively convoluted course, difficult to reconstruct in detail, since the connections between the different segments are not obvious; what follows is an attempt to

partially reconstruct the path of the digestive tube. It is here proposed that the organically preserved tube (Figs 2, 3A, 4B-C) is the beginning of the gut. Its ventral position, as well as its morphology, is consistent with this interpretation; particularly the presence of a straight tube (an oesophagus?), aligned with the plane of symmetry of the conch, that leads to the margin of the ligula. The organically preserved portion of the gut seems to disappear posteriorly behind segment 1 and its connection with the rest of the gut is not obvious (Figs 3A, 4B-C). Segment 1 appears to be continuous with segment 2, forming a long tube that reaches the ligula area (Figs 3A, 4B-C). Beyond this point the path of the gut is unclear (partly because the specimen is broken at the aperture area and because the gut is partly hidden from view on the dorsal side) and the connections between segment 3, 4 and 5 cannot be resolved (Figs 1C-D, 3A, 4A-B). Finally, segment 5 (which is intertwined with the organically preserved portion of the gut) may represent the terminal segment of the gut since in a convoluted, U-shaped gut, the beginning and the end of the tube are the most likely segments to run more or less parallel to each other. Segment 5 curves towards the left as it approaches the aperture suggesting that the anus may have opened somewhat laterally. This may be consistent with data from skeletal anatomy, since the articulation between conch and operculum (involving muscles and opercular processes) is located at the dorsal apertural margin, coinciding with the plane of symmetry of the organism (see Marti Mus and Bergström, 2005; and references therein), and may have caused the terminal portion of the gut to deviate to a lateral position.

There is a marked difference in thickness between the organically preserved and the "sediment"-filled portions of the gut (Figs 3A, 4B-C). This difference may be in good part taphonomic (see section 5.3); however, the hyolithid specimen illustrated by Chen (2004, fig. 304), whose gut seems uniformly preserved as a "sediment" infill, shows a thin anterior portion and a wider posterior one, suggesting that a variation in thickness between different

gut portions may be a characteristic of some hyolithids.

The preservation of the ring situated at the ligula margin is not informative enough to allow a definitive interpretation, however it seems to have the appropriate dimensions and position to represent the mouth (the ring has the same diameter as the oesophagus and is located just in front of it, inside the conch, at the ventral apertural margin; Figs 1D, 3B, 4). The radial structures diverging from the ring may represent radially arranged tentacles. Although uncommon in the fossil record, clear examples of tentacles, such as those forming the brachiopod lophophore, are known to be three-dimensionally preserved, occasionally as negative imprints, in Chengjiang (Zhang et al., 2009).

A possible interpretation for the short band extending from the ligula margin (Figs 1B, 2, 4C) is that it represents a faecal string, coming out from the terminal gut segment, segment 5, which seems to curve towards the string as it approaches the aperture.

5.3. Preservation of the gut

Preservation in the Fezouata Konservat-Lagerstätte has been compared with that of the early Cambrian Chengjiang localities (Van Roy et al., 2010, 2015) and the hyolith specimen described herein shares numerous preservational features with Chengjiang fossils (Gabbott et al., 2004). One characteristic of the Chengjiang Lagerstätte is the common preservation of guts as inflated, "sediment" infills. The co-occurrence of two types of preservation in a single gut is also common, with portions preserved as an organic film and portions preserved as an inflated "sediment" infill (this is particularly well illustrated for naraoiids; see Vannier and Chen, 2002, fig. 2). In Chengjiang, this type of gut preservation occurs in various taxa (e.g. Hou and Bergström, 1997, p.101), perhaps including hyolithids (Chen 2004, p. 201).

While a literal interpretation of these infills would suggest sediment ingestion, in some taxa this interpretation appears to be at odds with both biological and taphonomic data (Vannier and Chen, 2002; Butterfield, 2002), and some authors have argued for a diagenetic origin of the "sediment" infill (Butterfield, 2002; Butterfield et al., 2007). Although the actual mechanism that could lead to this type of gut preservation is still not understood, ingestion is ruled out in this scenario. This conflicting evidence has been thoroughly discussed in the case of naraoiids (Vannier and Chen, 2002; Butterfield, 2002; Wilson, 2006; Bergström et al., 2007; Lin and Briggs, 2010).

The partly "sediment"-filled, inflated gut of the specimen described herein raises the same kind of unresolved questions as those of naraoiids and other Chengjiang taxa, particularly because what is known about the functional morphology of hyolithids seems at odds with a specialized deposit feeding strategy (see section 6.3). The fact that the infill only occurs in the posterior half of the gut, which also appears highly distended if compared with the organically preserved first half of the gut both argues against ingestion as the origin of the infill, and likens it to the Chengjiang occurrences. An additional, possibly relevant observation is that the structure proposed to represent a faecal string (Figs 2B, 4C) is not preserved as a sediment string but as a stain of iron oxides (like the soft parts extending outside the aperture). Also, the width of the faecal string is comparable to that of the organically preserved portion of the gut and therefore considerably thinner than the apparently distended, "sediment"-filled, terminal portion of the gut.

6. Biology of hyolithids

6.1. Soft part anatomy

Hyolithids had numerous muscle scars around the conch aperture and all over the opercular inner surface (see Martí Mus and Bergström, 2005, and references therein), which indicates that soft parts were firmly attached around the aperture and could not retract deeply within the conch (as it occurs in most gastropods, for example). Pointing in the same direction, hyolithid opercula fitted the aperture externally, and could not be withdrawn into the conch. Therefore hyolithids must have lacked large protruding soft parts requiring space to be withdrawn inside the conch. The presence of an extended ventral shelf, the ligula, hindering the access of the soft parts to the substrate; and a pair of specialized lateral spines, the helens, likely adapted for movement and stabilization (see Martí Mus et al., 2014 and references therein), seem also incompatible with the existence of any ventral organ used for movement or substantial manipulation of the substrate. It is therefore likely that hyolithid soft parts did not extend much beyond the apertural margin, even when the shell was fully open (a possible exception being the presence of tentacles associated with the mouth). The soft parts preserved in the Fezouata specimen are entirely consistent with this, since they are restricted to internal structures (the gut), and the tissues associated with the operculum.

6.2. Hyolithid guts

Large, tightly packed, sediment filled guts with a characteristic morphology, and possibly associated with deposit feeding have only been described in orthocethid hyoliths (e.g. Thorall, 1935; Runnegar et al., 1975; Malinky, 2003). Orthothecids (even those species most likely to be closely related with hyoliths) differ from hyolithids in many ecologically relevant features (such as the absence of helens and ligula, or the presence of retractable opercula) and are likely to have had a different mode of life.

326 Regarding hyolithids, Babcock and Robison (1988) reported three specimens of the
327 hyolithid *Haplophrentis reesei* from the middle Cambrian Spence Shale with preserved guts.
328 The guts are reconstructed as a relatively wide central string. One of them is reported to be
329 filled with sediment, while the other two appear to be preserved as carbonaceous films.
330 Unfortunately the illustrations are not very informative and the details of the possible guts
331 remain obscure. An exceptionally preserved specimen with a simple, U-shaped gut was
332 illustrated by Butterfield (2001, 2003) from the middle Cambrian Mount Cap Formation.
333 The gut is thin, relatively long and shows a flexible, loose configuration inside a relatively
334 wide body cavity. Apparently similar but less well preserved, loop-shaped guts have also
335 been reported from several early Cambrian and an early Ordovician hyolithids (English and
336 Babcock, 2010; fig. 4e; the guts are said to be sediment-filled, but the only figured specimen
337 is poorly illustrated; Botting et al., 2015; fig. 3n). A less-known occurrence comes from the
338 early Cambrian Chengjiang Konservat-Lagerstätte (Chen, 2004, fig. 304). The specimen is a
339 hyolithid with a sinuously folded, apparently sediment filled gut. Unlike the tightly folded
340 gut of the orthothecids mentioned above, the folding in the Chinese specimen is looser and
341 somewhat irregular and the gut seems to occupy only the anterior half of the conch. Also,
342 different gut segments appear to vary in width. A specimen from the early Cambrian Kaili
343 biota illustrated in Zhao et al. (2011; fig. 117) shows a similar structure partially preserved.
344 The gut in the presently described hyolithid may represent the most complete so far,
345 possibly including the mouth and a terminal faecal string. It shares with the above-
346 mentioned Chinese specimens the "sediment" infill, but (although relatively convoluted)
347 does not show the "close-packed" folding of the Chinese examples (where the gut segments
348 are aligned perpendicularly to the conch axis). Also, uniquely for hyoliths as a whole, the
349 gut has two intertwined segments (perhaps representing the proximal and terminal segments
350 of the gut). This feature may not be phylogenetically relevant, but is typical of sipunculans, a

group of lophotrochozoans that has been compared with hyoliths (Runnegar et al., 1975).

6.3. Mode of life of hyolithids

Hyolithids are often regarded as filter or suspension feeders. The distinction between filter and suspension feeding is based on whether the water volume is passed through a body cavity or confined space within the body-shell, as in the filter feeding sponges, bivalves and brachiopods; or not, as in suspension feeding annelids, crinoids or bryozoans. Evidence supporting filter or suspension feeding in hyolithids comes mostly from the presence of bryozoans and tabulate corals living as epibionts on the conchs of various hyolithid species (Marek and Galle, 1976; Galle and Plusquellec, 2002; Galle and Parsley, 2005; Malinky, 2006). The tabulate corals restricted their distribution to the dorsal and lateral sides of the conch, but bryozoans grew on the ventral side as well, suggesting that hyolithids actively lifted their aperture above the substrate, conceivably using their helens. Both types of epibionts were oriented towards the conch aperture. The presence of epibionts and the details of their orientation and distribution suggest that hyoliths actively oriented themselves to currents. Shell morphology is also consistent with filter or suspension feeding, particularly the presence of a ligula (Marek et al., 1997), but also of the helens, both pointing to a reduced ability to manipulate the substrate with the soft parts (see section 6.1). The specimen illustrated by Butterfield (2001, 2003), with a simple U-shaped gut, was compatible with the view of hyolithids as filter-suspension feeders (particularly when compared with the tightly-packed, sediment-filled guts known in several orthothecids, which pointed to deposit feeding; see section 6.2). Other examples (Chen, 2004; Zhao et al., 2011; and herein), however,

show hyolithids with relatively long, convoluted guts, suggesting a diversity of feeding modes among hyolithids. The guts of all these specimens are at least partly filled with "sediment", but the Chinese occurrences (Chen, 2004; Zhao et al., 2011) have not been studied in detail and it is unclear whether any of these specimens could represent evidence for sediment ingestion (see section 5.3). It seems therefore likely that hyolithids as a group were not specialized filter feeders (in the sense mentioned above, such as brachiopods and many bivalve groups), and a possibility is that different species adopted different strategies within the suspension-detritus-deposit feeding continuum. A highly specialized deposit feeding strategy seems however at odds with hyolithid functional morphology, particularly because of the inferred reduced ability to manipulate the substrate with the soft parts (see section 6.1). Hyolithids, therefore, may have had a relatively generalized feeding organ, which could adapt to these various feeding strategies. This occurs in other lophotrochozoan groups, such as polychaetes and sipunculans, the feeding mode depending on modifications of the tentacles surrounding the mouth. The interpretation of the ring in the presently described specimen (Figs 1D, 3B, 4) as a mouth, perhaps surrounded by fine tentacles, is in accordance with this hypothesis.

6.4. Hyolithid phylogeny

Skeletal anatomy and mode of growth suggest lophotrochozoan affinities for hyolithids, but their phylogenetic position within the lophotrochozoans is unclear (Runnegar et al 1974). Traditionally they have been regarded as molluscs (e.g. Marek and Yochelson, 1976), although what is known about their anatomical organization

seems to depart considerably from that of molluscs (Runnegar 1975, 1980).

The new data about the soft parts reported here, particularly the possible presence of a circular mouth surrounded by tentacles, supports lophotrochozoan affinities, but molluscan apomorphies such as a foot or a radula are not present in the specimen. This would indicate that hyolithids do not belong to the crown group Mollusca, not to the crownward part of their stem group.

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525 Figure captions.

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527 Fig. 1. Specimen YPM 515750. A-C, specimen (part) photographed using different
528 techniques and magnification. A, C, specimen coated with ammonium chloride, and
529 photographed under incident light. A, general view of the specimen. C, close up of the
530 gut; black arrows point to constrictions on segment 5 of the gut. B, specimen
531 photographed under water and with polarized light; originally a colour photograph, the
532 image has been processed in Photoshop to enhance particular features of the specimen
533 (see methods). D, latex cast of counterpart coated with ammonium chloride and
534 photographed under natural light; note that the ligula is more completely preserved than
535 in the part; white arrow points to a circular structure preserved close to the margin.
536 Arrowheads in C and D mark the level of the dorsal apertural margin. Numbering in C
537 and D refers to the distinct gut segments discussed in the text. Scale bar in A represents
538 5 mm for A-B; scale bar in C represents 2 mm for C-D.

539

540 Fig. 2. Specimen YPM 515750 (part). Specimen photographed under water and with
541 polarized light; note part of the gut preserved as a black stain. A, complete specimen;
542 note that oxidation colours (yellow-red) are restricted to the fossil; B, Close up of
543 central area of the specimen; black arrow points to level of dorsal apertural margin;
544 white arrow points to structure interpreted as a possible faecal string. Abbreviations: ch:
545 chamber, co: conch, op: operculum, rh: right helen. Scale bar in A represents 5 mm;
546 scale bar in B represents 2 mm.

547

548 Fig. 3. Specimen YPM 515750. A, close up of the specimen (part) at the gut area;
549 photographed under water and with polarized light; originally a colour photograph, the

550 image has been processed in Photoshop to enhance particular features of the specimen
551 (see methods); black arrow points to the area where the segment of the gut preserved as
552 organic matter “disappears” from view; numbering refers to the distinct gut segments
553 discussed in the text; arrowhead mark the level of the dorsal apertural margin. B, close
554 up of the circular structure preserved on the counterpart (see Fig. 1D); note the fine,
555 radially arranged ridges. Scale bar in A represents 2 mm. Scale in B represents 1 mm.

556

557 Fig. 4. Reconstruction of preserved soft parts in specimen YPM 515750; all drawings
558 are composites, combining structures preserved in the part, in the counterpart or in both.
559 A, structures preserved in relief; all but the anterior ring (labelled "m") are preserved
560 both in the part and counterpart, and are interpreted to represent the "sediment-filled"
561 part of the gut; the anterior ring (m) is only preserved in the counterpart and is
562 tentatively interpreted as a mouth. B, the portion of the gut preserved as a carbonaceous
563 film (only preserved in the part) has been added to the reconstruction of the gut; note
564 how the organically preserved gut revolves around segment 5, precisely fitting its
565 constrictions; note as well how its anterior-most portion (oe) reaches the anterior ring
566 (m). C, complete specimen with the gut located centrally and anteriorly within the
567 conch, and the ring (m) close to the margin of the ligula; the somewhat trapezoidal stain
568 that connects the three skeletal elements is interpreted to represent the soft parts
569 associated with the internal surface of the operculum; the narrow band that stems from
570 the left side of the ligula (fs) is tentatively interpreted as a faecal string. Hachured lines
571 indicate a break on the ligula area (on the part), and the hachures are directed
572 downslope. Numbering refers to the distinct gut segments discussed in the text.
573 Abbreviations: ch: chamber, co: conch, dam: dorsal apertural margin, fs: faecal string,

574 li: ligula, m: mouth, op: operculum, rh: right helen, spo: soft parts of the operculum.

575 Scale bars represent 2 mm.

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580 **Graphical Abstract**

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583 **Figure 1**

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585 **Figure 2**

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587 **Figure 3**

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589 **Figure 4**