Hyoliths are Palaeozoic lophophorates

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Hyoliths – orthothecids and hyolithids – are abundant and globally distributed 'shelly' fossils that appear early in the Cambrian and occur throughout the 280 million year span of Palaeozoic strata[1,2]. The ecological and evolutionary significance of this group has remained unresolved, largely because of their idiosyncratic scleritome (operculum, conical shell, and paired 'helens' in hyolithids) and poorly constrained soft anatomy[3-5]. Since their first description over 175 years ago, hyoliths have most often been regarded as *incertae sedis*[4,6], allied with molluscs[7,8] or assigned their own phylum[1,2]. Here, we examine over 1500 specimens of the mid-Cambrian hyolithid *Haplophrentis* from the Burgess Shale and Spence Shale *Lagerstätten*. We reconstruct *Haplophrentis* as a semi-sessile epibenthic suspension feeder that was capable of using its helens to elevate its tubular body above the sea floor[3,9-12]. Exceptionally preserved soft tissues include an extendable, gullwing-shaped, tentacle-bearing organ surrounding a central mouth, which we interpret as a lophophore, and a U-shaped digestive tract ending in a dorsolateral anus. Together with opposing bilateral sclerites and a deep ventral visceral cavity, these features indicate an affinity with the lophophorates (brachiopods, phoronids and tommotiids), substantially increasing the early disparity of this prominent group. This study reiterates the importance of soft-tissue preservation from Burgess Shale-type deposits in elucidating the evolutionary history of long-problematic taxa.

The radiation of biomineralized skeletons ranks among the most important and conspicuous records of the Cambrian Explosion. These 'shelly' Cambrian fossils track the evolution of animal body plans – but many have proved difficult to interpret from a biological perspective[6]. One enigmatic group, particularly widespread and diverse in Cambrian sediments, are the hyoliths. Orthothecid hyoliths possess a conical shell (previously referred to as "conch") and cap-like operculum, each of which were putatively aragonitic and grew by basal-marginal accretion[1]. Hyolithid hyoliths are additionally characterized by a pair of logarithmically curving lateral spines ('helens') and a non-planar operculum with a more extensive array of internally directed processes and muscle scars[13,14]. Hyoliths have generally been considered as close allies of molluscs due to the presence of a bulb-shaped larval 'protoconch'[15] and purported mineralogical and microstructural similarities between their shells[7] – though recent studies have questioned both the validity and the significance of these observations[1,16]. Beyond this, the peculiar hyolith scleritome affords few opportunities for comparison with extant organisms. The only abundant evidence of non-mineralized anatomy comes from putative muscle scars, but these do little to constrain the affinities of hyoliths[11,14]. Rarer traces of U-shaped guts[3-5] are also phylogenetically uninformative due to their widespread occurrence among lophotrochozoans[19].

Here, we revisit the systematic affinity of the hyolithid *Haplophrentis* based on over 1500 specimens, 254 of which preserve soft tissues (SI Discussion and Tables 1-2). The specimens include *Haplophrentis carinatus* from the Burgess Shale (principally from the Stanley Glacier[17] and Marble Canyon[18] localities, B.C., Canada) and *H. reesei*[5] from the Spence Shale (Utah, U.S.A.), and are housed at the Royal Ontario Museum (ROM) and the Kansas University Museum of Invertebrate Paleontology (KUMIP), respectively.

Description. A gullwing-shaped band below the operculum emits as many as 12 (*H. carinatus*) to 16 (*H. reesei*) elongate elements that exhibit variable orientation and curvature ('tentacles' herein; Figs 1b, 2; Extended Data Figs 1-4). The lateral regions of the band may curve slightly posteriad or anteriad. The flared basal portion of each tentacle is followed by a longer, gently tapering section, up to half the length of the operculum and about 7% as wide as long. Two shorter medial tentacles attach proximally around a centrally located mouth. We interpret this tentaculate band as a lophophore.

The lophophore connects to a wide medially situated structure that splays anteriorly from a narrow central tube with the mouth at the distal end. We interpret this tube as a pharynx with muscular walls. Variations in the length and width of this pharyngeal organ indicate that it, along with the attached lophophore, was protrusible. In some specimens, the pharyngeal organ is less than half the length of the operculum, and the distally attached tentacles are almost entirely concealed beneath the operculum (Fig. 2a-b; Extended Data Fig. 1). In others, the pharynx extends from the posterior of the operculum almost to its anterior margin, resulting in the tentacles projecting through the commissure (Figs 1b, 2c-d; Extended Data Figs 2-4). The aboral end of the pharyngeal organ was evidently attached to the operculum, as the pharynx and tentacles remain medially located when the operculum is displaced from the conical shell aperture (Fig. 1b; Extended Data Figs 1-4).

The pharynx narrows as it passes under the posterior margin of the operculum, joining with the gut (Fig. 1b; Extended Data Fig. 5). The undifferentiated, U-shaped gut is contained within the conical shell. It extends to at most 75% of the depth of the conical shell before looping back along the functional dorsum (Fig. 1b-c; Extended Data Fig. 5). The anus opens near the commissure, slightly left of the midline[3] and outside the crown of tentacles (Fig. 1c; Extended Data Fig. 5a-b).

Paired, kidney-shaped traces in the carbon film, often surrounded by dark, carbonaceous rims, occur below the operculum, dorsal to the pharynx (Fig. 2a, c; Extended Data Figs 1a, b, 3, 6f). A dark, radial structure of equivalent constitution occurs below the umbo of the operculum, (Fig. 2a, c; Extended Data Figs 1a-b, 3, 6d-f). Muscle scars occupy a similar position in other hyolithids[14], suggesting that the surrounding carbon is preserved connective tissue.

A symmetrical pair of large grey structures flanks the gut, along the functional dorsum of the conical shell, terminating near the posterior margin of the operculum (Fig. 1; Extended Data Figs 2c, 3b, 5a, 6a-c, 7b). At this point, each structure is nearly half the width of the operculum. The structures taper apically and – decay notwithstanding – extend as far as the loop of the gut. The biological identity of these visceral organs is unclear.

A thin and deformable layer, possibly the body wall, circumscribes the inside of the conical shell. It stops short of the apex of the conical shell, apparently leaving the apical region unoccupied (Extended Data Fig. 1c, 6c).

The helens of *Haplophrentis* emerge at a slight downward angle from a lateral notch at the commissure of the conical shell and operculum, growing as open logarithmic spirals that twist helically along their length and pointing either anteriad or posteriad[10,11,14,20] (Extended Data Fig. 7). Brachiopods are attached to the helens of four *Haplophrentis* specimens that have tightly articulated skeletons and preserved soft tissues: strong evidence that these associations occurred when both animals were alive (Extended Data Fig. 8). As such, the helens could not have been submerged below the sediment-water interface, and “retracted” helens observed within conical shells[5] are likely a taphonomic artefact.

Discussion. The lophophore of *Haplophrentis* resembles the characteristic tentacular feeding organs of several suspension feeding taxa, particularly Entoprocta and Lophophorata (i.e. Brachiopoda and Phoronida, possibly including Ectoprocta)[21]. This indicates that *Haplophrentis* was a benthic suspension feeder[3,9,12] rather than a deposit feeder[5,22]. The downward-directed helens[10,14] may have been rotated to elevate the commissure from the sediment-water interface (Fig. 3, Extended Data Fig. 7, SI Discussion), consistent with observations of encrusting organisms on both the dorsal and ventral surfaces of hyolithid conical shells[9].

The disposition of the mouth and anus at the anterior and posterior margins of the hyolithid commissure indicates that the operculum and conical shell were dorsoventrally opposed – contrasting with molluscs, which typically secrete only dorsal skeletal elements (shells, opercula)[10]. As in brachiopods, the lophophore is contained in the mantle cavity formed by dorsal and ventral bilateral sclerites[23]. The combination of characters present in *Haplophrentis* and the lack of molluscan apomorphies[3] decisively supports an affinity with the lophophorates, particularly the brachiopods.

The simple arrangement of tentacles in the *Haplophrentis* lophophore is strikingly similar to that in brachiopod larvae (Extended Data Figs 1d, 2e), but distinct from the complex lophophore arrangements that characterise most adult brachiopods[23]. Neither does the *Haplophrentis* lophophore form the closed loop characteristic of crown-group brachiopods[23], instead diverging laterally in a manner that recalls the primitive phosphatic-shelled brachiopod *Heliomedusa orienta*[24].

The partial attachment of the lophophore to the hyolithid operculum supports a homology with the dorsal (brachial) valve of brachiopods[23], identifying the opposing conical shell as ventral and potentially homologous with the brachiopod pedicle valve (Fig. 4). Although opposing valves are common to both hyolithids and brachiopods, the deep extension of the hyolithid visceral area into the conical shell differs markedly from the condition in most crown-group brachiopods, where the viscera are reduced to the space between the valves. This arrangement is found in some fossil taxa, notably lingulellotretids, which are close to the linguliform members of the brachiopod crown group[25]; *Yuganotheca*, which is thought to represent an intermediate between phoronid and the brachiopod body plans[26]; and *Lingulosacculus*, whose phylogenetic position is ambiguous[27]. Hyolith shell microstructure lacks an obvious equivalent amongst brachiopods, though shell penetrating canals of similar size and preservation in both hyoliths[1] and obolellids (putatively basal calcareous brachiopods)[28] potentially support comparable skeletal secretion in these groups.

While a position within total group Lophophorata is well supported, the ultimate placement of hyolithids will depend on the order of character acquisition in the brachiopod body plan. The dominant viewpoint suggests that brachiopods diverged from among the problematic tommotiids[29,30], and as such their ancestral ground-plan is inferred to have included a multi-element phosphatic scleritome. Working under this hypothesis, the conical shell, operculum and helens of hyolithids might be homologised with the sclerites of a *Micrina*-like tommotiid, resolving hyolithids (potentially including *Lingulosacculus*) in the brachiopod stem lineage (Fig. 4). *Yuganotheca* – in which the lophophore is enclosed by unmineralized mantle lobes that protrude above a single ventral sclerite[26] – could then be interpreted as having undergone a secondary loss of mineralization. The ventrally extended viscera of these taxa conceivably characterise the ancestral form of crown group Brachiopoda, providing a link with the phoronid body plan[26]. Under this interpretation, the elongated visceral cavity of lingulellotretids[25] may have been retained from the ancestral brachiopod state, with the more restricted visceral area of modern brachiopods arising once in linguliforms and again in rhynchonelliforms.

This hypothesis must remain somewhat speculative and incomplete, not least because a detailed comparison of hyolithids and tommotiids is made difficult by differences in sclerite mineralogy and microstructure[1,30] (Extended Data 9-10, SI Discussion). Similar issues have frustrated attempts to interpret the evolution of morphologically distinct phosphatic- and calcitic-shelled brachiopod lineages[28]. The addition of purportedly aragonitic hyoliths to the lophophorate tree further complicates the evolution of biomineralization in this group, emphasising the many details of deep lophotrochozoan phylogeny that remain ambiguous. Even so, the recognition of hyoliths as members of this clade settles a longstanding palaeontological debate, and emphasizes the high level of disparity and ecological dominance achieved by lophophorates in marine communities throughout the Palaeozoic Era.

Methods

The fossil material studied herein is deposited at the Royal Ontario Museum, Toronto (ROM) and the Kansas Museum of Invertebrate Paleontology, Kansas (KUMIP). Some ROM specimens were mechanically prepared using a tungsten-tipped micro-engraving tool. Specimens were photographed under various lighting conditions and with ammonium chloride coating to enhance contrast, and imaged using backscatter and secondary electron microscopy. Measurements were taken using ImageJ.

Data availability statement. Data generated or analysed during this study are included in this published article (and its supplementary information files).

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Supplementary Information is available in the online version of the paper.

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Figures

Figure 1 | *Haplophrentis carinatus* from the Burgess Shale. Specimens oriented anterior to the top, fossil images (top row) and associated line drawings (bottom row). **a,** Royal Ontario Museum (ROM) 62928.5 from Marble Canyon, dorsal view with partially broken operculum, showing the gut and paired visceral organs within the conical shell. **b,** ROM63981.1 from Stanley Glacier, dorsal view (composite image of part and counterpart) showing the lophophore attached to the pharynx and most of the gut. **c,** ventral view of ROM63982.1 from Stanley Glacier, showing the U-shaped gut and anus. Scale bars = 2 mm. Abbreviations: a, anus; ag, anal branch of gut; c, conical shell; cl, clavicle; cp, cardinal process; lh, left helen; m, mouth; o, operculum; og, oral branch of gut; p, pharynx; rh, right helen; t, tentacle; vo, visceral organ.

Figure 2 | Soft tissues associated with the *Haplophrentis* operculum. Dorsal view of specimens, anterior to the top. **a,** ROM63983.1, *H. carinatus* from Stanley Glacier, lophophore in retracted position with at least 6 tentacles on the left side, showing muscle scars. **b,** Kansas Museum of Invertebrate

Paleontology (KUMIP) 366447, *H. reesei* from the Spence Shale, showing retracted lophophore with 16 tentacles. **c,** ROM59943.1, *H. carinatus* from Stanley Glacier, showing partially extended lophophore with tentacles beyond the operculum margin. **d,** KUMIP 204340, *H. reesei* from the Spence Shale, with a fully extended pharynx and lophophore. Scale bars = 2 mm. Abbreviations: ct, connective tissue; g, gut; ms, muscle scar; mt, medial tentacle; pl, pharynx lumen; other abbreviations as in Figure 1.

Figure 3 | Anatomical reconstruction of *Haplophrentis*. a-d, lophophore extended, helens in anteriad position. **a,** dorsal profile; **b,** left lateral profile; **c,** ventral profile, ligula of conical shell cut away; **d,** frontal profile, operculum removed. **e-f,** lophophore retracted, helens in posteriad (resting) position. **e,** left lateral profile; **f,** ventral profile, ligula of conical shell cut away. **g,** life reconstruction on the Cambrian sea floor. Abbreviations: bw, body wall; other abbreviations as in Figures 1, 2.

Figure 4 | Possible position of hyolithids within total group Lophophorata. Dashed lines indicate hypothesized lophophorate relationships. The inclusion of Ectoprocta within Lophophorata remains ambiguous[21], hence they are omitted from this figure. 1 = lophophore, U-shaped gut curving ventrally, multielement phosphatic scleritome; 2 = dorsal and ventral valves enclosing lophophore chamber; 3 = aragonitic(?) sclerite mineralogy; 4 = pedicle with coelomic cavity, lateral elongation of lophophore arms; 5 = calcitic shell mineralogy, extreme reduction of visceral area, loss of anus. Colour scheme of diagrams: pink, visceral area; green, lophophore; purple, gut; blue, ventral valve; yellow, dorsal valve. Extinct taxa marked by a cross.

Extended Data Figure 1 | Retracted lophophore of *Haplophrentis*. a, b, *H. carinatus*, dorsal view of ROM63983.1 from Stanley Glacier. **a,** entire specimen photographed dry with polarized light; **b** detail of tissue associated with the operculum. **c,** dorsal view of KUMIP366447 from the Spence Shale photographed wet with polarized light. **d,** Larva of the extant brachiopod *Glottidia* with retracted lophophore; image reprinted from fig.1b in Strathmann, R. Ciliary sieving and active ciliary response in capture of particles by suspension-feeding brachiopod larvae. Acta Zoologica. Wiley. © 2005 The Royal Swedish Academy of Sciences. Scale bars: **a-c,** 2 mm; **d,** 0.2 mm. Abbreviations: bw, body wall; c, conical shell; cl, clavicle; cp, cardinal process; ct, connective tissue; es, embryonic shell; g, gut; lh, left helen; ls, larval shell; ms, muscle scar; mt, medial tentacle; o, operculum; pd, pedicle; rh, right helen; t, tentacle.

Extended Data Figure 2 | *Haplophrentis carinatus* from Stanley Glacier (ROM63981.1). a, operculum, showing extended pharynx and lophophore photographed dry with polarized light. **b**, interpretive drawing. **c,** part, photographed wet with polarized light; **d**, counterpart, photographed wet with polarized light. **e,** larva of the extant brachiopod *Glottidia* with extended lophophore; image reprinted from fig. 1a in Strathmann, R. Ciliary sieving and active ciliary response in capture of particles by suspension-feeding brachiopod larvae. Acta Zoologica. Wiley. © 2005 The Royal Swedish Academy of Sciences. Scale bars: **a-d,** 2 mm; **e,** 0.2 mm. Abbreviations: ag, anal branch of gut; bw, body wall; cl, clavicle; cp, cardinal process; m, mouth; og, oral branch of gut; p, pharynx; pl, pharynx lumen; t, tentacle.

Extended Data Figure 3 | *Haplophrentis carinatus* from Stanley Glacier (ROM 59943.1). a, part photographed dry with polarized light; **b,** counterpart, photographed wet with polarized light. **c,** operculum (composite image of part and counterpart) showing extended tentacles, photographed dry with polarized light. Scale bars = 2 mm. Abbreviations: cl, clavicle; cp, cardinal process; ct, connective tissue; g, gut; ms, muscle scar; pl, pharynx lumen; t, tentacle; vo, visceral organ.

Extended Data Figure 4 | *Haplophrentis reesei* from the Spence Shale (KUMIP204340). a-b, operculum, showing extended pharynx and lophophore. **a,** photographed dry with polarized light. **b,** wet, with polarized light. **c-e,** whole specimen. **c,** dry, unpolarized light. **d,** dry with polarized light. **e,** wet with polarized light. Scale bars: **a-b,** 2 mm; **c-e,** 5 mm. Abbreviations: c, conical shell; ct, connective tissue; g, gut; lh, left helen; m, mouth; o, operculum; p, pharynx; pl, pharynx lumen; rh, right helen; t, tentacle.

Extended Data Figure 5 | U-shaped digestive tract of *Haplophrentis carinatus*. a, b, ROM63982.1 from Stanley Glacier, ventral view, photographed wet with polarized light; **b** corresponds to area boxed in **a**. **c,** ROM63984.1, dorsal view, photographed dry with polarized light. Scale bars = 1 mm.

Abbreviations: a, anus; ag, anal branch of gut; og, oral branch of gut; p, pharynx; t, tentacle; vo, visceral organ.

Extended Data Figure 6 | Musculature and visceral area of *Haplophrentis carinatus*. a, ROM63985.1 from Marble Canyon, laterally oriented specimen showing the position of visceral organs and gut within the conical shell, photographed wet with polarized light. **b,** ROM62928.5 from Marble Canyon, dorsal view showing paired visceral organs flanking the gut, photographed wet with polarized light. **c,** ROM63986.1 from Marble Canyon, dorsal view with paired visceral organs adjacent to the gut, photographed dry with polarized light. **d, e,** ROM63987.1 from Mount Odaray, photographed wet with polarized light. **d,** ventral view of the operculum, showing connective tissue dorsal to the pharynx; **e,** detail of area boxed in **d**. **f,** ROM63988.1 from Stanley Glacier, dorsal view of operculum with preserved muscle scars and connective tissue, dorsal to the pharynx, photographed dry with polarized light. Scale bars = 1 mm. Abbreviations: bw, body wall; ct, connective tissue; g, gut; m, mouth; ms, muscle scar; og, oral branch of gut; p, pharynx; t, tentacle; vo, visceral organ.

Extended Data Figure 7 | *Haplophrentis* scleritome. a, ROM62968.4 from Marble Canyon, lateral view; note downward disposition of right helen, which emerges from the commissure just above the ligula of the conical shell, photographed dry with polarized light. **b,** ROM62968.2, obliquely preserved specimen with anteriorly directed helens, showing the shape of the aperture of the conical shell, photographed dry with polarized light. **c,** Backscatter Scanning Electron Microscope image showing the bulb-shaped larval shell at apex of conical shell in ROM63989.1 from Marble Canyon. **d,** ROM63991.1 from Marble Canyon, with a slightly displaced operculum and the helens directed anteriorly and curving below the body, photographed dry with polarized light. **e,** ROM63993.1 from Marble Canyon, operculum closing the conical shell aperture, both helens directed posteriorly with the left one preserved in the same plane as the body and the right one curving below, photographed dry with polarized light. **f,** two specimens (ventral views) from Marble Canyon showing variation in the curvature and twist of the helens (visible portion is in the same plane as the conical shell in both), photographed wet with polarized light.

f_1, ROM64005.1; **f_2,** ROM63989.1. **g,** dorsal view of the right helen of ROM63992.1 from the Raymond Quarry, curving posteriad (inserting into the body on the upper right side) with the direction of twist indicated by the arrow; photographed using unpolarized light. **h,** ROM63994.1 from the Walcott Quarry, backscatter SEM image of a helen showing ornament of transverse ribs. **i, j,** ROM63995.4 from the Walcott Quarry, photographed wet with polarized light. **i,** whole specimen; **j,** detail of area boxed in **i**, ornament of transverse ribs on the conical shell. Scale bars: **a, b, d, e, g, i,** 2 mm; **c,** 0.5 mm; **f_1, f_2, h, j,** 1 mm. Abbreviations: c, conical shell; cp, cardinal process; g, gut; lh, left helen; o, operculum; p, pharynx; rh, right helen; vo, visceral organ.

Extended Data Figure 8 | Brachiopod epibionts on *Haplophrentis*. Arrows indicate brachiopods. **a**, ROM63996.1, *H. carinatus* with *Nisusia? burgessensis*, photographed using ammonium chloride sublimates. **b-c,** ROM63997.1, *H. carinatus* with an acrotretid brachiopod, note soft tissue preserved below operculum, photographed dry with polarized (**b**) and unpolarized light (**c**). **d-f,** KUMIP314211, *H. reesei* with *Micromitra sp.*, photographed using unpolarized light. **g-h,** KUMIP304352, *H. reesei* with *Nisusia sp.*, photographed using unpolarized light. Scale bars: **a-b,** 2 mm; **c, e, f, h,** 1 mm; **d, g,** 5 mm.

Extended Data Figure 9 | Elemental distribution in *Haplophrentis carinatus* from Marble Canyon (ROM63998.1). Scale bars = 2 mm. Abbreviations: PL, polarized light (photographed wet); SE, secondary electron micrograph; C, carbon; S, sulfur; Mg, magnesium; Fe, iron; K, potassium; P, phosphorous; Ca, calcium; Al, aluminum; Na, sodium; O, oxygen; Si, silicon; Ti, titanium.

Extended Data Figure 10 | Detail of elemental composition of *Haplophrentis carinatus* from Marble Canyon. a-d, ROM63998.1. **a, b,** carbon maps of part and counterpart; note the concentration of carbon in the transverse shell ornament, clavicles and cardinal processes – evidence of an organic component of the skeleton; **c,** sulfur map (composite image of part and counterpart), showing, soft tissues, including tentacles, partially replaced by pyrite. **d,** phosphorous map (composite image of part and counterpart), showing phosphatized gut. **e-f,** ROM63999.1, carbon maps of part and counterpart, note that carbon surrounding the clavicles and cardinal processes may be related to the attachment of muscles and connective tissue in these regions. Scale bars = 1 mm. Abbreviations: cl, clavicle; cp, cardinal process; g, gut; lh, left helen; p, pharynx; t, tentacle; vo, visceral organ.