

Original Article

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Exceptionally preserved hyolithids from the middle Cambrian of North China

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Abstract

Hyoliths are extinct enigmatic organisms of early lophotrochozoan affinity known globally from the Palaeozoic Era and were especially diverse and abundant in the Cambrian Period. However, the commonly incomplete preservation of hyolith exoskeletons and our limited knowledge of their soft anatomy makes their ecological and biological aspects unclear. Konservat-Lagerstätte are crucial windows to unlock the mysteries of hyoliths. Here we report a new occurrence of exceptionally preserved hyolithid hyoliths from the middle Cambrian Mantou Formation (Miaolingian, Wuliuan) in Shandong Province, North China. The preserved soft organs of the new species *Novakotheca weifangensis* sp. nov. include a U-shaped gut and possible pharynx, oesophagus, stomach and digestive gland, which provide significant new information for the reconstruction of the digestive system of hyolithids. Two taphonomic modes of hyoliths described herein are recognized: soft tissue preservation through pyritization and three-dimensional shell preservation through phosphatization. Morphological variations due to different preservational pathways in the same species are revealed, highlighting the taphonomic bias on taxonomy. The ecological association between hyoliths and small brachiopod epibionts is a direct example of species interactions, providing insights into the ecological structures and adaptability of early animals during Cambrian time.

1. Introduction

Hyoliths are among the first biomineralized bilaterians to occur in the Cambrian Period, living throughout the entire Palaeozoic Era until their Permian extinction. These enigmatic animals, subdivided into the morphologically distinct orders Orthothecida and Hyolithida, comprise a conical shell associated with a cap-like operculum and, in hyolithids, an additional pair of logarithmically curving lateral helens and a ventral ligula on the conch (Martí Mus *et al.* 2014). However, hyoliths are usually preserved as simple conical shells, and the lack of other significant skeletal and anatomical information tends to render speculative their systematics, phylogeny, biomechanics, palaeoecology and other aspects. The biological relationships of hyoliths have long been debated, and the group has variously been treated as a lineage close to molluscs (Malinky & Yochelson, 2007), sipunculans or a separate phylum (Runnegar *et al.* 1975; Sun *et al.* 2016). Recently, the preserved remains of soft tissue associated with hyoliths likely support the notion that these animals may have been lophophorates (Moysiuk *et al.* 2017; Sun *et al.* 2018a). However, this idea has been challenged by later work on skeletal microstructures and soft anatomy (Li *et al.* 2019, 2020; Liu *et al.* 2020b).

Burgess Shale-type biotas offer deep insights into Cambrian life. Exceptionally preserved hyoliths have been commonly documented in the Konservat-Lagerstätten of South China, mainly those from the lower Cambrian (Chen, 2004; Sun *et al.* 2017, 2018a; Liu *et al.* 2020a, b, 2021), with the exceptions of the Cambrian Wuliuan Kaili Biota (Mao *et al.* 1992; Chen *et al.* 2003), Guzhangian Fulu Biota (Peng *et al.* 2020) and Jiangshanian Guole Biota (Zhu *et al.* 2016); however, little is known from North China, despite abundant hyolith skeletons occurring as part of the small shelly fauna that has been documented from the lower Cambrian strata of this block (Pan *et al.* 2019). Here, we report a new finding of exceptionally well-preserved hyoliths, *Novakotheca weifangensis* sp. nov., from the Mantou (alternatively ‘Manto’) Formation (Cambrian Miaolingian, Wuliuan) in the Longgang section of Weifang City in Shandong Province, North China. The exceptionally well-preserved soft parts of this new taxon provide important new data for reconstructing the complete digestive system of hyolithids. The different taphonomic modes of the soft organs and conical shells of the same species highlight the taphonomic bias and their effect on taxonomy. The biological association of hyoliths and brachiopod epibionts provides insights into their ecological interactions and the adaptability of early metazoans during Cambrian time.

2. Material and methods

The material described in this study was collected from the Upper Shale Member of the Mantou Formation in the Longgang section, Linqu County, Shandong Province, China. Trilobites from this interval are indicative of the *Bailiella lantenoisi* Zone (uppermost Wuliuan, Cambrian Miaolingian) (Sun, Z. X. *et al.* 2020a,b). The hyolith-bearing interval also yields brachiopods, vermiform animals, diverse arthropods, sponges, cancelloriids, algae and other problematic fossils of uncertain affinity (Sun, Z. X. *et al.* 2015, 2020a,b). For detailed information on geography, stratigraphy and sedimentology of this section see Sun, Z. X. *et al.* (2020a,b). All the specimens in this paper are housed in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (NIGPAS).

Specimens were examined and imaged by standard light microscopy, scanning electron microscopy (SEM; instrument model SU3500) with energy dispersive X-ray (EDX) spectroscopy and a Carl Zeiss SteREO Discovery V12 microscope linked to an AxioCam HR3 digital microscope CCD camera. Specimen NIGPAS173866 was scanned by a three-dimensional X-ray microscope (Zeiss Xradia 520 Versa) in the Micro-CT Lab of the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences. The volume data were processed using VGStudio MAX software.

3. Systematic palaeontology

Class HYOLITHA Marek, 1963
 Order HYOLITHIDA Sysoyev, 1957
 Family HYOLITHIDAE Sysoyev, 1958
 Genus *Novakotheca* Malinky, 1990
Novakotheca weifangensis sp. nov.
 Figures 1–5

Etymology. Named for Weifang City, Shandong Province, China, where the species occurs.

Type material. Holotype: NIGPAS173868c (Fig. 1b); paratypes: NIGPAS173866 (Figs 1f, 3), NIGPAS173867 (Fig. 1a), NIGPAS173870 (Fig. 1d), NIGPAS173875 (Fig. 1k), NIGPAS173876 (Fig. 2a), NIGPAS173877 (Fig. 2e), NIGPAS173879–NIGPAS173883 (Fig. 4).

Additional material. 118 specimens in total, including seven slabs with three-dimensional phosphatized conical shells in a shale matrix; the rest are highly compressed specimens in shale. Most of them are incompletely preserved.

Occurrence. Cambrian Miaolingian Wuliuan, the Upper Shale Member of the Mantou Formation (*Bailiella lantenoisi* Zone) in Weifang, Shandong Province, North China.

Diagnosis. Hyolithid with subtriangular cross-section; aperture orthogonal; dorsum of intermediate height and narrowly rounded in the centre; a pair of shallow longitudinal furrows along each margin of dorsum; lateral margins gently rounded. Operculum roughly ovate and platyclavicate.

Description. Conical shell small with thin body wall; the dorsal length of complete specimens ranges from 6.7 to 16.2 mm (mean = 9.8 mm, $n = 6$), and the ventral length varies from 9 to 19 mm (mean = 11.6 mm, $n = 7$). Shell surface covered with faint growth lines, slightly arched on the venter. Cross-section subtriangular (Figs 3d, f, 4d, e). Aperture orthogonal, dorsal apertural rim unflared; apertural width ranges from 2.2 to 5.8 mm (mean = 3.3 mm, $n = 12$). Dorsum of intermediate height and narrowly

rounded in the centre; adjacent slopes nearly flat (Figs 3a, d, f, 4d, e), terminating in a pair of lateral furrows (Fig. 3c, d, f) and transitioning into adjacent convex flanks (Figs 3f, 4e); lateral margins broadly rounded (Fig. 4e). Venter gently inflated (Fig. 4e); ventral ligula short with broadly rounded anterior edge (Figs 1d–f, 2h); the ligula length varies from 1.6 to 2.4 mm (mean = 1.8 mm, $n = 7$), which is approximately 54 % of the apertural width and 16 % of the ventral shell length. Apex pointed; apical termination slightly turned to the left; apical angle averages 21.5° ($n = 13$), ranging from 19.3° to 25.5°.

Operculum roughly ovate (Figs 1b, d, g, h, i, k, 2a, b); width of operculum ranges from 2.4 to 4.2 mm (mean = 3.5 mm, $n = 4$). Clavicles platyclavicate, covered with longitudinal ridges (Fig. 1b, g, i, k), divergence averaging 97.4° ($n = 5$, min. = 87.7°, max. = 102.3°); length of clavicles ranges from 1 to 1.6 mm (mean = 1.4 mm, $n = 5$). Summit bluntly pointed. Conical shield large, subovate to fan-shaped, lateral sides straight. Cardinal shield small and subtriangular. Cardinal processes subconical, small and projecting divergently.

Helens tapering distally with pointed tips of variable curvature, protruding forward (Figs 1b, c, h, i, 2a, b), laterally (Fig. 1c, e) or backward (Fig. 1j).

Remarks. Compression can be a significant factor secondarily shaping shell morphology, which complicates the precise taxonomy of specimens preserved in shale. The cross-section, medial axis, inflation of dorsum and venter and lateral margins, etc. of *N. weifangensis* vary with the degree of compression. Sharper and more distinct dorsal medial axes (e.g. Figs 1b, c, g, 3a, d, 4a, b, 5d), less inflated venters (Figs 3f, 4d), lower dorsa (Figs 3d, f, 4d) and sharper lateral margins (Figs 3f, 4d) are observed in the compressed specimens compared to those in rocks that exhibit little or no compression (e.g. Fig. 4e). The specimens described here exhibit a range of shell deformations and provide enough information for the recognition of their biological features.

The fossils described here are assigned to *Novakotheca* based on its diagnostic characters including an orthogonal aperture and dorsum with flattened, steeply dipping slopes, terminating in a pair of longitudinal sulci near the lateral margins (Malinky, 1990). The specimens from the Mantou Formation possess the first known examples of an operculum and helens for *Novakotheca*. The general morphology of the new species is quite similar to that of *N. crebescens*, but the latter has sharper lateral margins and more prominent lateral furrows than in *N. weifangensis* (Malinky, 1990, figs 1.2, 1.7, 2.5, 2.14). Specimens of *N. crebescens* preserved in limestone expose enough detail of its original characteristics (Malinky, 1990) to ensure the validity of comparison between these two species.

A pair of horn-shaped structures are present on the lateral sides of one operculum of *N. weifangensis* (Fig. 2a, b), which possibly represent muscle scars. Hyolithid hyoliths are suggested to share a common skeleto-muscular system with similar arrangements of muscle scars (Martí Mus & Bergström, 2005). The morphology of the scars in this study is different from that known from other species, but their lateral occurrence and location partially overlap with the clavicles, indicating a similarity with the 'd' scars described in the conical shield of *Gompholites* and *Maxilites* (Martí Mus & Bergström, 2005), even though their precise correspondence in their relative position remains speculative (Martí Mus & Bergström, 2005). Although the horn-shaped structures of *N. weifangensis* merely appear on a single specimen, the possibility of muscle scars cannot be ruled out.



Fig. 1. (Colour online) *Novakotheca weifangensis* sp. nov. from the Mantou Formation in the Longgang section, North China. (a) NIGPAS173867, ventral view, almost complete conical shell with an operculum, showing a sinuous U-shaped gut and brachiopod epibionts near the apex. (b) NIGPAS173868c, dorsal view, a hyolith with an articulated operculum and right-side helen and preserved partial intestine. (c) NIGPAS173869a, dorsal view, incomplete conical shell with an operculum and a pair of helens. (d) NIGPAS173870, ventral view, conical shell with an operculum, a preserved U-shaped gut and other soft parts. (e) NIGPAS173871, ventral view, a hyolith shell with a helen, showing secondarily mineralized but unrecognizable soft parts. (f) NIGPAS173866, ventral view, a conical shell with a partial operculum. (g) NIGPAS173872, dorsal view, a hyolith with an operculum preserved in association with brachiopods. (h) NIGPAS173873a, dorsal view, a conical shell with an operculum, a left-side helen and a possible gut, preserved in association with a brachiopod valve. (i) Close-up of the boxed area in (h). (j) NIGPAS173874, ventral view, a deformed shell with an articulated operculum and one helen. (k) NIGPAS173875, the interior of an operculum showing clavicles and cardinal processes. Scale bars are 1 mm. Abbreviations: br – brachiopod; cl – clavicle; cp – cardinal process; ct – connective tissue; g – gut; he – helen; op – operculum; vo – visceral organ.

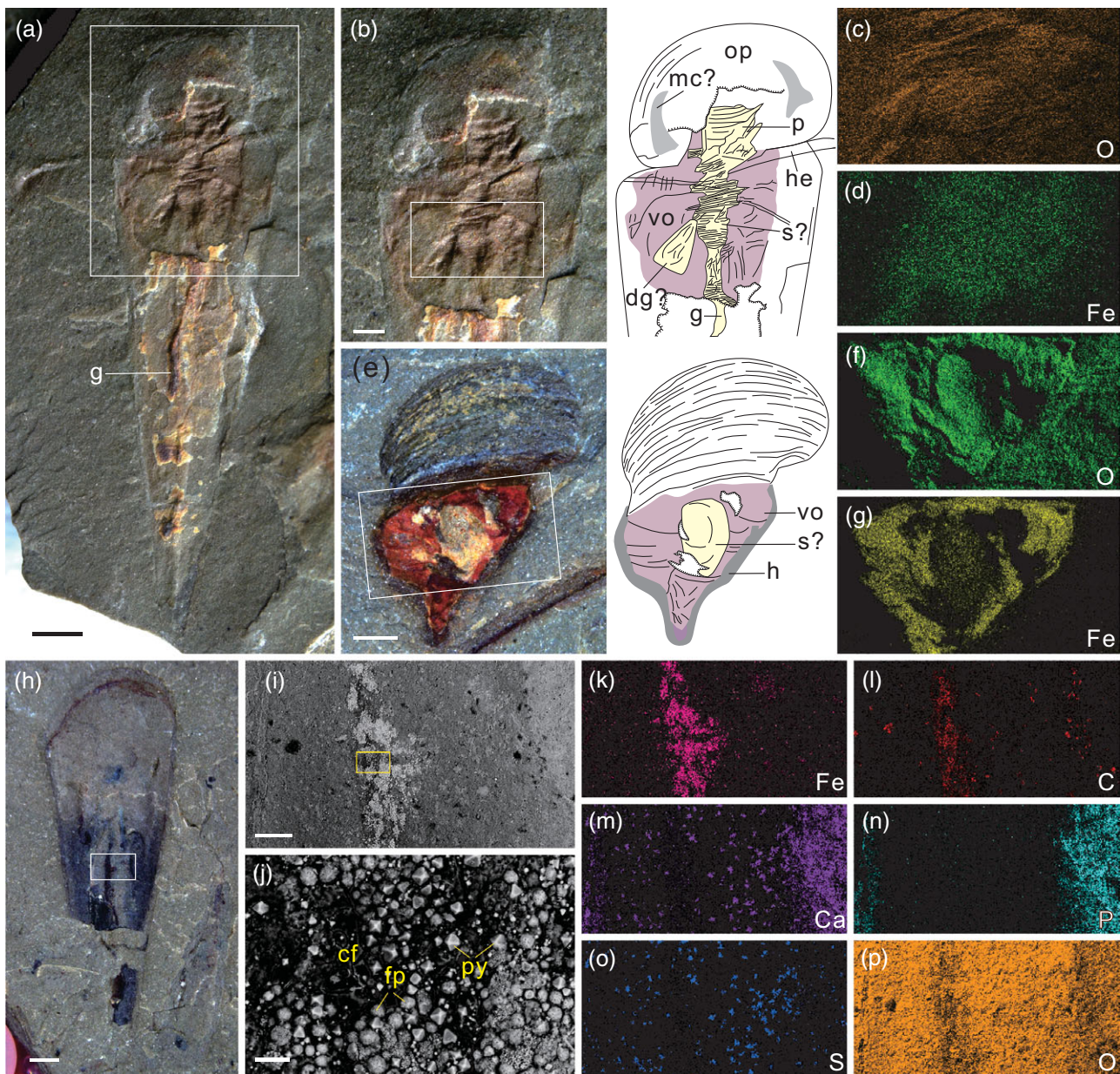


Fig. 2. (Colour online) *Novakotheca weifangensis* sp. nov. from the Mantou Formation in the Longgang section, North China. (a) NIGPAS173876, ventral view, a conical shell with an operculum and a helen, showing a curving gut and other soft organs. (b) Magnified image and interpretive drawing of the boxed area in (a). (c, d) Elemental distribution of the boxed area in (b). (e) NIGPAS173877, ventral view, an incomplete shell with secondarily mineralized soft organs and an interpretive drawing on the right side. (f, g) Elemental composition of the boxed area in (e). (h) NIGPAS173878, ventral view, an incomplete shell preserved with part of the intestine. (i) SEM image of the boxed area in (h). (j) Close-up of the boxed area in (i), showing the dark carbonaceous film, bright euhedral pyrite crystals and framboidal pyrites in the gut. (k–p) Elemental distribution of the area in (i). Scale bars are 1 mm for (a, h), 500 μm for (b, e), 200 μm for (i), and 20 μm for (j). Abbreviations: cf – carbonaceous film; dg – digestive organ; g – gut; h – halo; he – helen; mc – muscle scar; op – operculum; p – pharynx; py – euhedral pyrite; fp – framboidal pyrite; s – stomach; vo – visceral organ.

4. Discussion

4.a. Taphonomy

The hyoliths were discovered as exceptionally well-preserved articulated specimens with soft parts (Figs 1a–j, 2, 3) and as clusters of shell fragments (Fig. 4a–c), which represent event-induced rapid burial of the assemblage and time-averaging background accumulation, respectively (Zhao *et al.* 2012). Two taphonomic modes of the hyoliths from the Mantou Formation of the Longgang section have been recognized:

(1) *Pyritization of nonmineralized tissue.* Soft parts of the hyoliths, mostly alimentary canals, show preservation as a dark carbon film associated with pyrite (Figs 1a, h, i, 2a, h–l) or yellow to reddish imprints enriched in iron oxides (Figs 1d, e, 2a–d, e–g). Pyrites are present as both euhedral crystals and framboids (Fig. 2j), possibly indicating oxygenated bottom waters but anoxic or dysoxic conditions after burial or during late diagenesis, as in the Guanshan Biota (Forchielli *et al.* 2014; Liu *et al.* 2021). The EDX analysis reveals iron minerals with little to no sulfur (Fig. 2o), representing pseudomorphic alteration of pyrites during

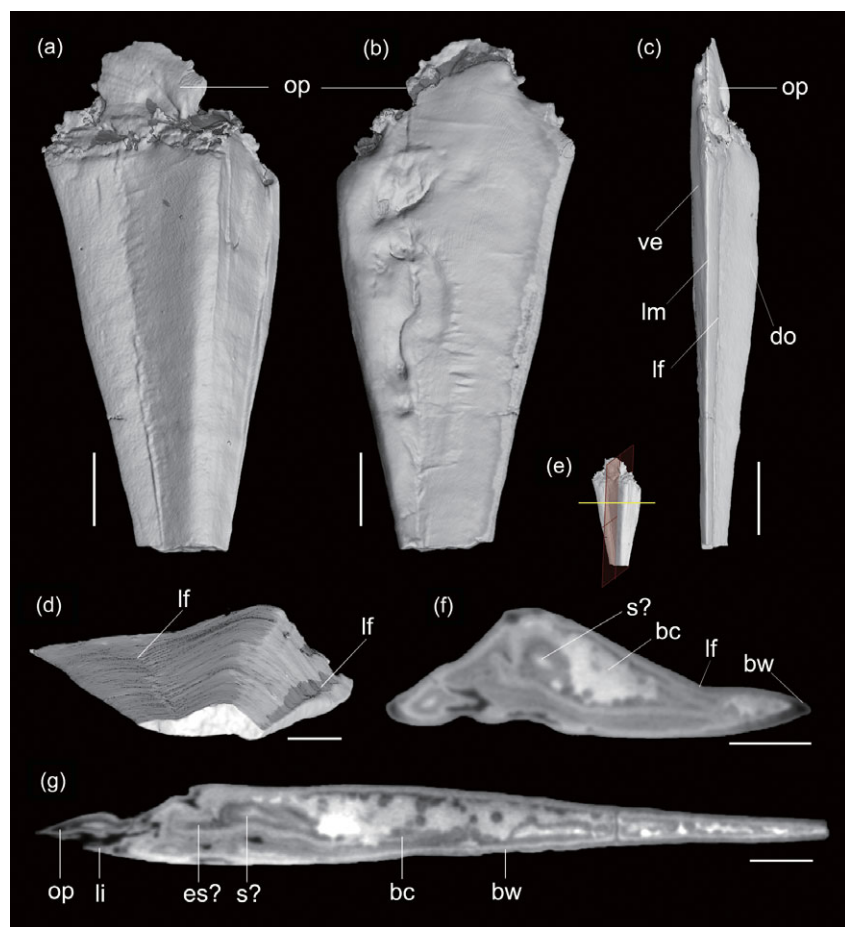


Fig. 3. Micro-CT images of *Novakotheca weifangensis* sp. nov. from the Mantou Formation in the Longgang section, North China, NIGPAS173866. (a) Dorsal view. (b) Ventral view. (c) Lateral view. (d) Posterior view showing the cross-section. (e) Slicing positions. The yellow line and red plane indicate the slicing sites of (f) and (g), respectively. (f) Cross-section of the shell. (g) Longitudinal section of the shell. Scale bars are 1 mm for (a–c) and 500 μ m for (d, f, g). Abbreviations: bc – body cavity; bw – body wall; do – dorsum; es – oesophagus; lf – lateral furrow; li – ligula; lm – lateral margin; op – operculum; s – stomach; ve – venter.

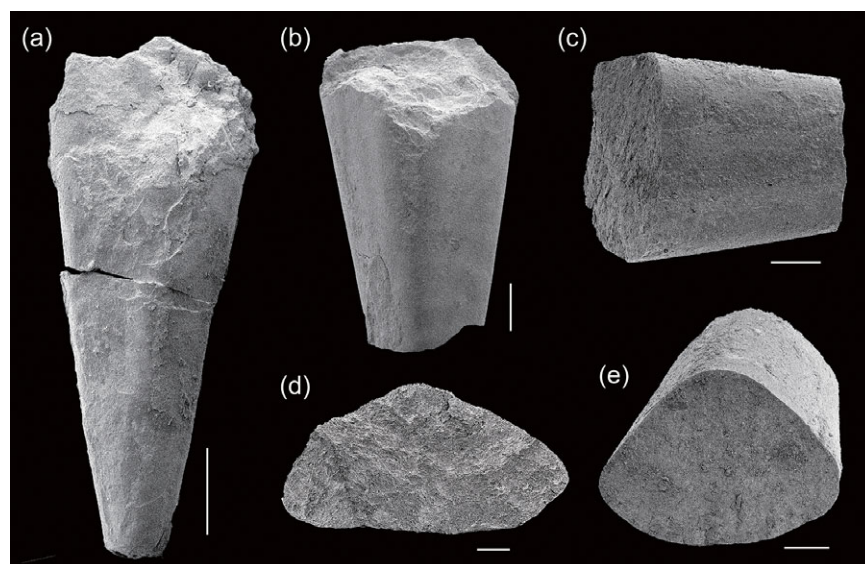


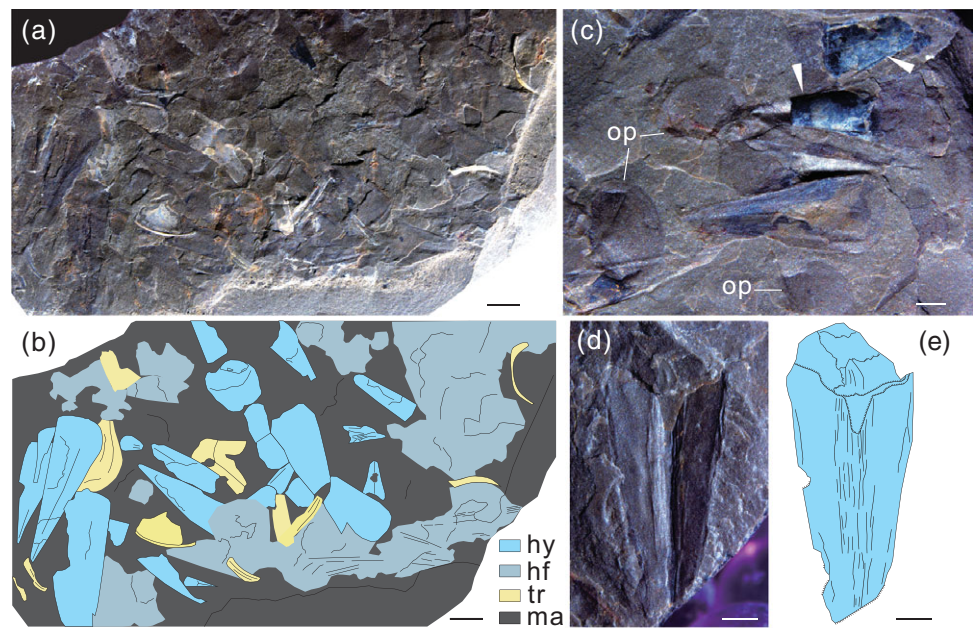
Fig. 4. SEM images of three-dimensionally preserved *Novakotheca weifangensis* sp. nov. from the Mantou Formation in the Longgang section, North China. (a) NIGPAS173879, dorsal view. (b) NIGPAS173880, dorsal view. (c) NIGPAS173881, anterior-lateral view. (d) NIGPAS173882, cross-section. (e) NIGPAS173883, anterior view showing the cross-section. Scale bars are 1 mm for (a), 600 μ m for (b), 300 μ m for (c, e), and 200 μ m for (d).

weathering processes (Zhu *et al.* 2005; Forchielli *et al.* 2014). Pyritization is a common pathway for the replication of soft tissues of organisms throughout the Phanerozoic Eon (Szczezanik & Sawłowicz, 2005; Farrell *et al.* 2013; Farrell, 2014; Schiffbauer *et al.* 2014), and the pyritization process revealed herein is a characteristic preservational mode in the Cambrian Burgess Shale-type

biotas of China (Zhu *et al.* 2005; Gaines *et al.* 2008; Forchielli *et al.* 2014).

(2) *Phosphatization of conical shells.* Small shelly fossils (SSFs) dominated the early Cambrian diversity, but witnessed a decline from the middle Cambrian onwards (Porter, 2004). The

Fig. 5. (Colour online) *Novakotheca weifangensis* sp. nov. from the Mantou Formation in the Longgang section, North China. (a) NIGPAS173884, a cluster of hyolith shells and trilobite fragments. (b) Line drawing of (a). (c) NIGPAS173875, a cluster of hyoliths with opercula and shells; conical shells display the combination of compression and three-dimensional phosphatization (indicated by the white arrowheads). (d) NIGPAS173885, dorsal view, an incomplete shell showing compressed wrinkles. (e) Sketch of (d). Scale bars are 2 mm for (a, b) and 1 mm for (c–e). Abbreviations: hf – undistinguishable hyolith fragments; hy – hyolith shell; ma – matrix; op – operculum; tr – trilobite fragments.



phosphatic replacement of skeletons usually occurs in shallow water carbonates (Li *et al.* 2004; Creveling *et al.* 2014; Yang *et al.* 2015; Skovsted *et al.* 2021), with scattered records from deeper shelf environments (Steiner *et al.* 2003; Yang *et al.* 2014). Little is known about phosphatized skeletal fossils from siliciclastic facies (Sun, H. J. *et al.* 2020). The phosphatized internal moulds of hyolith shells herein (Fig. 4) are preserved in three dimensions in shale of the Mantou Formation in the Longgang section (Fig. 5c). Organic matter and iron minerals are two vital reactive phosphorus fluxes to sediments in both modern and ancient marine environments (Delaney, 1998; Dornbos *et al.* 2006; März *et al.* 2008; Creveling *et al.* 2014). Decayed soft tissues or phosphatic skeletons possibly provided additional dissolved phosphorus in pore water. The formation of phosphatized hyoliths possibly underwent the following process (Creveling *et al.* 2014): phosphorus was delivered to the sediments by organic and iron-bound shuttles, and then hyolith skeletons trapped P-laden anoxic pore waters and facilitated the nucleation and precipitation of phosphate minerals via microbial metabolic pathways.

Taphonomic processes can significantly impact on taxonomy and our understanding of the fossil record (Hughes, 1995; Allison & Bottjer, 2011; Kammerer *et al.* 2020), but this issue has received little attention in hyoliths. Taphonomic deformation creates abiotic changes in biological structures, obscuring original diagnostic morphological characteristics, including the cross-section, height of the dorsum, inflation of the venter, sharpness of the median ridge and divergence angle, etc. To improve the resolution of hyolith systematics for broader research on other palaeobiological aspects, the following approaches might be considered: (1) assess the taphonomic condition of specimens; (2) evaluate the taphonomic distortion of the morphology and introduce quantitative analysis (e.g. geometric morphometrics) to correct deformation in fossils (Kammerer *et al.* 2020), if the quality and quantity of material available is sufficient; and (3) learn more about morphological variations at the species level across different facies and taphonomic windows.

4.b. Soft anatomy of hyolithids

In addition to muscle scars (Martí Mus & Bergström, 2005), soft parts of hyoliths have been extensively documented but are mainly restricted to their guts. The digestive tracts of orthothecids are zig-zag-folded and sediment-filled (Thorl, 1935; Runnegar *et al.* 1975; Malinky, 2003; Devaere *et al.* 2014), while simpler U-shaped guts seem to be characteristic of hyolithids (Meshkova & Sysoev, 1981; Babcock & Robison, 1988; Butterfield, 2003; Moysiuk *et al.* 2017; Liu *et al.* 2021) with a few exceptions displaying a variety of gut configurations (Chen, 2004; Martí Mus, 2016; Sun *et al.* 2016). Soft organs other than the intestines of hyolithids have rarely been described. Martí Mus (2016) reported a hyolithid specimen preserving a relatively complete gut including a possible oesophagus and a tentacled mouth, as well as other soft parts associated with the operculum from the Ordovician Fezouata Konservat-Lagerstätte, Morocco. Recently, the hyolithid *Haplophrentis* described from the Burgess Shale and Spence Shale was illustrated with a pharynx that expands anteriorly and is connected to a tentacled gullwing-shaped band encircling a mouth, connected posteriorly to a U-shaped gut surrounded by plausible visceral organs (Moysiuk *et al.* 2017). Other reports of hyolithid soft organs (Houbrick *et al.* 1988; Mao *et al.* 1992) are questionable (Martí Mus, 2016).

Soft tissues of *N. weifangensis* include a pharynx with a wrinkled muscular wall protruding forward towards the anterior of the operculum (Fig. 2a, b), and likely connected with tentacles as described in the hyolithids *Haplophrentis reesei* and *H. carinatus* (Moysiuk *et al.* 2017) and the orthothecid *Triplicatella opimus* (Liu *et al.* 2020a,b). The pharyngeal organ extends posteriorly, connected to a relatively narrow tube, possibly the oesophagus (Fig. 3g); this is joined with a swollen structure (Figs 2a–g, 3f, g), which is the assumed stomach with wrinkled muscular walls (Fig. 2a–c), and the stomach narrows downward to a U-shaped gut (Figs 1d, 2a). A triangular structure connected to the lower lateral side of the stomach may represent a digestive gland (Fig. 2a, b). The digestive system is encompassed by visceral organs (Figs 1d, 2a, b, e).

The stomach and digestive gland are essential digestive organs of lophotrochozoans (Williams *et al.* 1997; Lobo-da-Cunha, 2019); however, knowledge of these organs in hyoliths is very limited. The speculative stomach of *N. weifangensis* possibly served as an area that sorted food particles captured by the tentacles, as in brachiopods and some molluscs (Reid, 1965; Williams *et al.* 1997; Lobo-da-Cunha, 2019). Once the nutrient substances entered the stomach, suspended particles were rotated under the effect of the stomach fluid and mechanical action through relaxation and contraction of muscles. Then, fine partially digested grains flowed towards the digestive gland, and the U-shaped intestine received the residues coming from the stomach for further digestion, which is inferred from the smaller aperture between the digestive gland and the stomach than that between the intestine and the stomach (Fig. 2b). The digestive gland may have performed multiple functions, including secretion of digestive enzymes, nutrient absorption and energy storage, as suggested in molluscs (Lobo-da-Cunha, 2019). The digestive system of hyolithids seems more complicated and efficient than previously thought. Although hyolithids have been commonly reconstructed as suspension or filter feeders (Marek *et al.* 1997; Butterfield, 2001; Moysiuk *et al.* 2017), supported by the absence of sediments in the guts of the individuals described here, the effective digestive system likely adapted to a wide range of food resources (Martí Mus, 2016; Sun *et al.* 2018b), such as organic particles in the water column, microorganisms, animal corpses, detritus and deposits, which, as passive prey, were especially beneficial in nutrient-stressed environments. Although the new material does not resolve the precise phylogeny of hyoliths, it provides significant additional information for reconstructing the complete digestive system of hyolithids.

4.c. Epibionts and their palaeoecological implications

Biom mineralized skeletons serve as hard substrates for sessile invertebrates throughout the Phanerozoic Eon (Topper *et al.* 2015; Taylor, 2016; Zhang *et al.* 2020; Zicha *et al.* 2020), and the host/epibiont association provides direct evidence for species interactions and ecological strategies (Topper *et al.* 2015). Hyoliths were one of the main preferred hosts from the Cambrian to the Devonian (Marek & Galle, 1976; Galle & Plusquellec, 2002; Galle & Parsley, 2005; Malinky, 2006; Sun *et al.* 2017; Zicha *et al.* 2020). Epibionts living on hyoliths included echinoderms (Sun *et al.* 2017; Zicha *et al.* 2020), molluscs (Zicha *et al.* 2020), brachiopods (Topper *et al.* 2015; Moysiuk *et al.* 2017), encrusting bryozoans and tabulate corals (Marek & Galle, 1976; Galle & Plusquellec, 2002; Galle & Parsley, 2005; Malinky, 2006).

Some specimens of articulated hyoliths from North China are preserved with brachiopods (Fig. 1g–i). These specimens show no sign of attachment, suggesting chance superimposition during burial. However, one example displays two brachiopod specimens fixed to the hyolith, close to the apex, and the latter shows articulation with soft parts (Fig. 1a), indicating a live association. Previous work suggests that hyoliths had the ability to actively orient themselves to currents (Marek *et al.* 1997) and to be movable on or partly in substrates (Sun *et al.* 2018b). The sessile–mobile association benefitted brachiopods by increased nutrient availability, stabilization from benthic turbidity and possible anti-predation (Topper *et al.* 2014). However, the increasing body mass of brachiopods could have become burdensome to the hyoliths; thus, their relationship might have shifted from commensalism to resulting in a negative impact on the host during ontogeny.

5. Conclusions

The specimens from the Cambrian (Wuliuan) Mantou Formation, Longgang section, North China described herein are exceptionally well preserved with soft parts including a U-shaped gut, a possible pharynx, an oesophagus, a stomach and a digestive gland, providing important information for the reconstruction of the complete digestive system of hyoliths, which may have contributed to the effective digestion and absorption of food particles. Hyoliths possibly benefitted from this effective digestive system to adapt to a variety of feeding strategies on the suspension–detritus–deposit–scavenging spectrum and to survive in a nutrient-poor environment. Pyritization and phosphatization are recognized taphonomic modes for the preservation of soft tissues and shells in three dimensions, respectively. The different preservational pathways highlight the taphonomic impact on the morphological variations of hyoliths, thus affecting the taxonomic evaluation. Assessing taphonomic conditions, degrees of deformation and morphological variations at the species level across different facies is necessary to achieve high-resolution hyolith systematics. Brachiopods attached to hyoliths in live associations provide direct evidence for species interactions, indicating the complexity of Cambrian marine ecosystems and the ecological adaptation of animals.

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