

Palaeobiology of orthothecide hyoliths from the Cambrian Manto Formation of Hebei Province, North China

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Newly discovered specimens of the orthothecide hyoliths in Hebei Province of North China reveal new data on diversity, skeletal microstructure and palaeoecology of the order Orthothecida. *Decoritheca cyrene* possesses a well-defined skeletal structure consisting of rows of tubercles in the shell wall, which correspond to dimples on the internal surface of the conch. We describe a new species *Cupitheca convexa* sp. nov. characterised by a planar and interior convex operculum with a pair of bilobate cardinal processes, which differs from the more widespread *C. holocyclata* in opercular morphology and overall ornamentation of the conch, highlighting the significance of operculum in the classification of hyoliths. First discovery of the presumed unusual protoconch of *C. convexa* sp. nov. implies a possible lecithotrophic development to adapt to nutrient-fluctuant environments. Pitting structure on the operculum and shell as well as lamellar-fibrillar structure on the internal mould of *C. convexa* sp. nov. are observed herein.

Key words: Hyolitha, Orthothecida, ontogeny, larval conch, skeletal microstructure, Cambrian, China.

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Introduction

Orthothecide hyoliths are one of the two main groups within the Hyolitha. They are most abundant and diverse worldwide in the Cambrian, with a progressive decline until their extinction in the Middle Devonian (Malinky 2009). They are characterized by a calcareous conical shell with a generally planar aperture and a retractable planar or slightly concave operculum. The boundary between the dorsal and ventral portions of the operculum is indistinct, although near the dorsal margin the operculum possesses an elevated knob-like structure referred to as the summit. The interior is ordinarily smooth except for a pair of cardinal processes that radiate from below the summit. The morphology of the gut tract as well as its sediment infilling suggests a benthic, deposit feeding life habit of some orthothecides (Marek 1967; Runnegar et al. 1975; Devaere et al. 2014), rather than suspension feeding as suggested for the hyolithides (Marek et al. 1997; Galle and Parsley 2005; Moysiuk et al. 2017).

Orthothecide hyoliths have been known from China for more than a century (Walcott 1905, 1911, 1913) with additional reports by Resser and Endo (1937) and Endo (1937). Interest in the group was revived by Qian (1977, 1978, 1983) and Qian et al. (1979) with more taxa being described (Xiao and Zhou 1984; Malinky 1987; Qian 1989; Jiang 1992; Xiao and Duan 1992; Qian et al. 2003; Steiner et al. 2007; Parkhaev and Demidenko 2010; Pan et al. 2015). Here we report a new occurrence of hyoliths from the Cambrian of North China. The specimens described here derive from the Cambrian Manto Formation (around the boundary of Cambrian Stage 4/ Stage 5) in the Zuojiawu section of Tangshan City in Hebei Province, North China (see SOM 1, Supplementary Online Material available at http://app.pan.pl/SOM/app63-Sun_et_al_SOM.pdf). Two species are recognised at the locality: *Cupitheca convexa* sp. nov. and *Decoritheca cyrene* (Walcott, 1905). *Cupitheca* Duan in Xing et al., 1984 is characterised by a generally tubular conch with a bluntly rounded apical

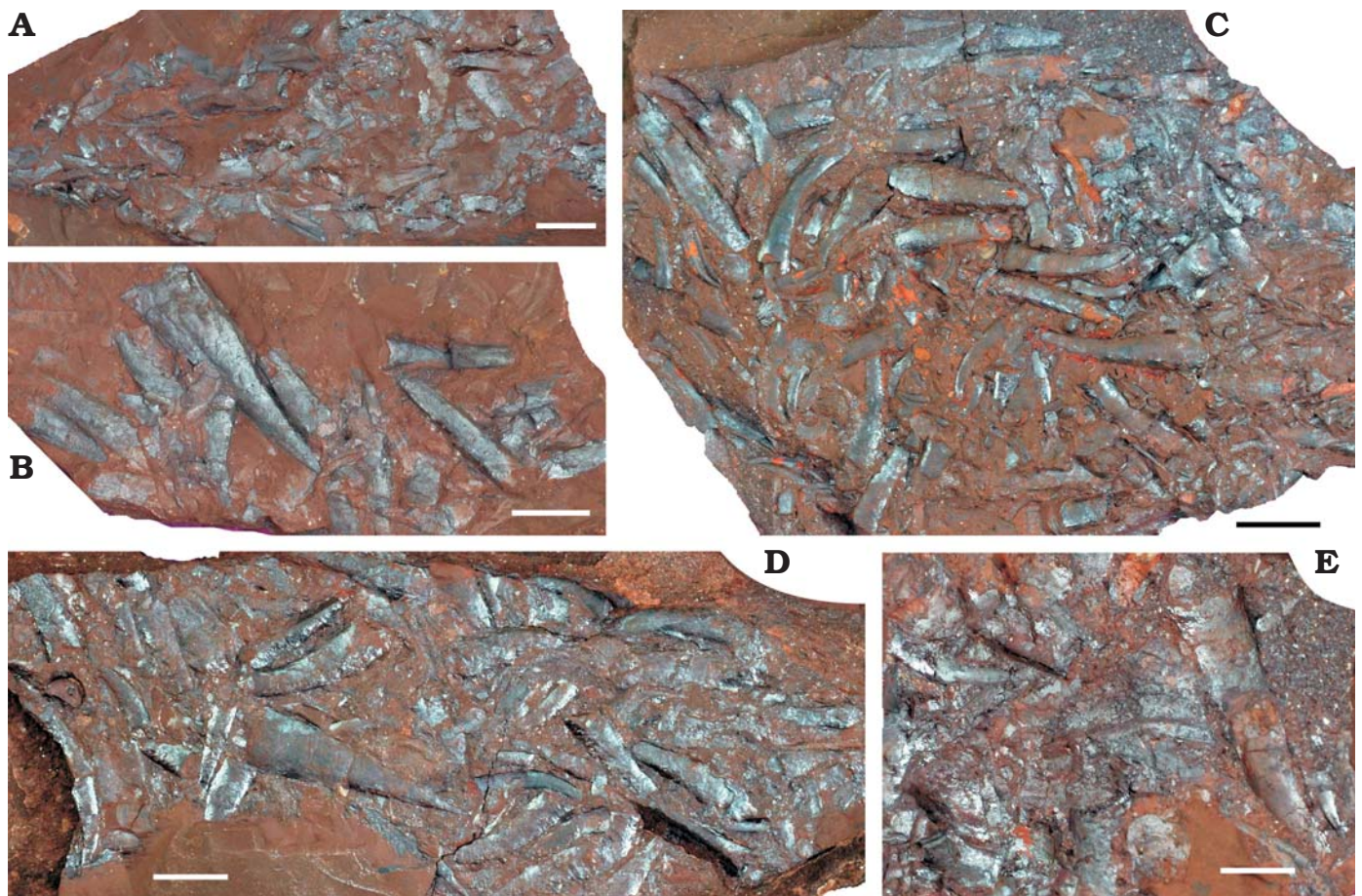


Fig. 1. Aggregations of orthothecide hyoliths preserved in purplish-red shales from the Manto Formation (Cambrian Stage 4/5) in the Zuojiawu section of Tangshan, China. A. NIGPAS 166336. B. NIGPAS 166345. C. NIGPAS 166334. D. NIGPAS 166341b. E. NIGPAS 166346. Scale bars 5 mm, except E, 2 mm.

termination and circumferential furrow. It ranges from the Cambrian Fortunian to Cambrian Stage 5 (Xing et al. 1984; Duan 1984; Bengtson et al. 1990; Pan et al. 2015) (see SOM 2). Owing to its unusual decollating ontogeny and lack of a convincing operculum, *Cupithec*a has long been excluded from the hyoliths and treated as a problematica form of uncertain affinity (Bengtson et al. 1990; Demidenko 2001; Wrona 2003; Malinky and Skovsted 2004; Pan et al. 2015), whereas others suggest a hyolith affinity and more close to Orthothecida (Kruse et al. 2004; Skovsted et al. 2016). The present material tends to support orthothecide affinity of *Cupithec*a.

*Decorithec*a is a globally distributed orthothecide ranging from the Cambrian Stage 3 to Stage 10 (Qian 1989; Qian and Xiao 1995; Malinky 2014; see also SOM 2), rendering it one of the longest ranging orthothecide genera. Here we report an unusual skeletal microstructure seen in *D. cyrene* that consists of tubercles covered the surface of internal mould of the shell.

Institutional abbreviations.—NIGPAS, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, China.

Geological setting

The hyolith specimens described in this paper were collected from the purplish-red shale of the Manto Formation at the Zuojiawu section, Fengrun District of Tangshan City, Hebei Province, located in the northeastern region of the North China Platform (see SOM 1). The Manto Formation is a heterogeneous succession characterised by purplish-red shale intercalated with limestone, marlstone, dolostone, and sandstone, which was generally considered to have been deposited in tidal flat or lagoon environments under arid conditions (Xiang et al. 1999). It crops out extensively in the northern and eastern parts of the North China Platform. The concept of this formation was revised and restricted to the lower part of the originally described unit (Lu and Dong 1953; Lu 1962). Subsequently, Xiang et al. (1999) reverted to the initial definition of the Manto Formation, which is followed herein. It includes nine trilobite zones, in ascending order, they are *Redlichia nobilis*, *Qiaotouaspis*, *Yaojiayuella*, *Shantungaspis*, *Hsuehuangia–Ruichengella*, *Ruichengaspis*, *Sunaspis*, *Poriagraulos*, and *Bailiella–Lioparia* zones (Wang et al. 2014), ranging from Cambrian Series 2 Stage 4 to Series 3 Stage 5 (Lungwangmiaoan to Hsuehuangian in

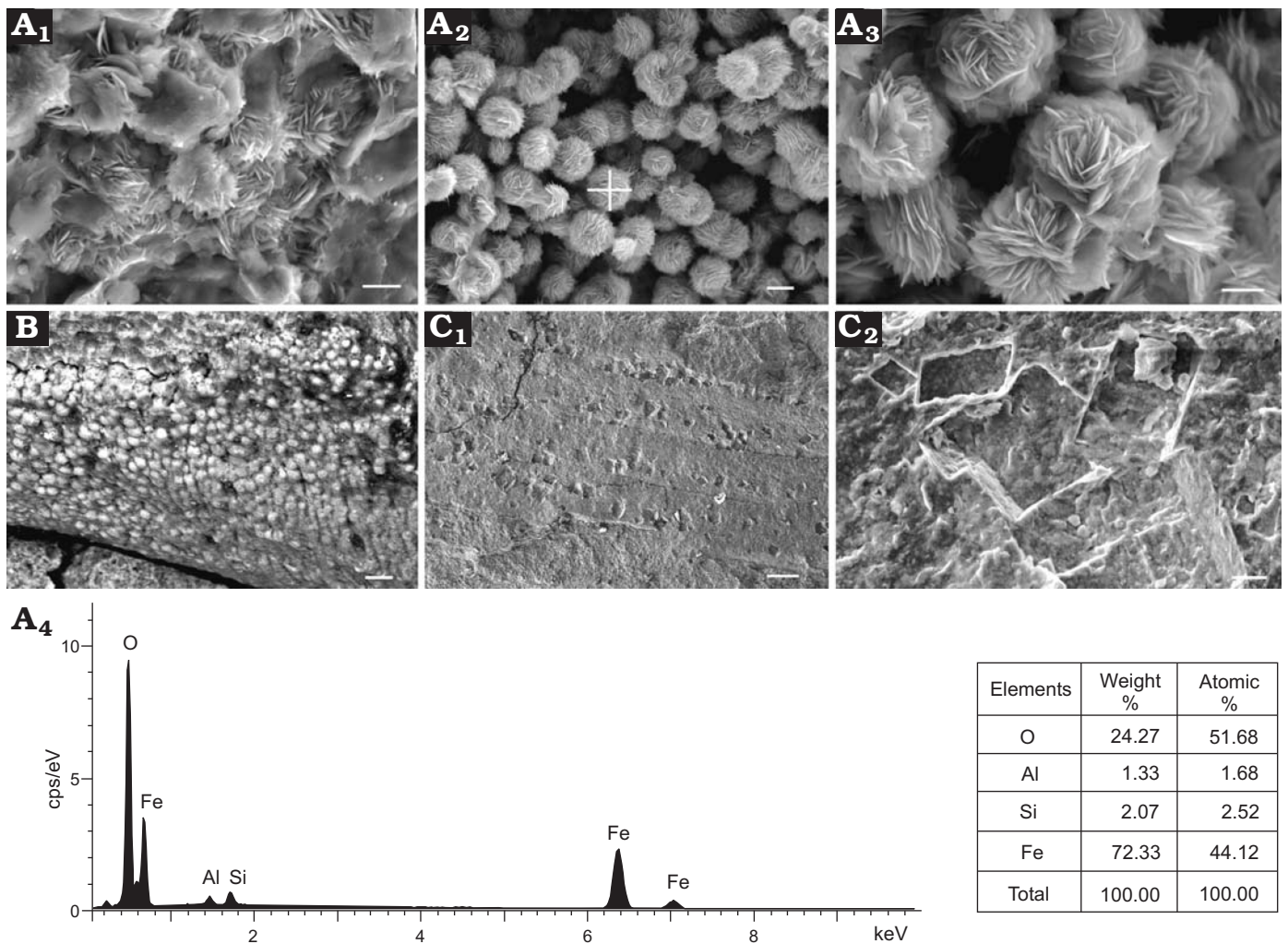


Fig. 2. Scanning electron micrographs of shell and shale fabrics as well as mineral elemental analyses of matrix from the Manto Formation (Cambrian Stage 4/5) in the Zuojiauwu section of Tangshan, China. **A**. NIGPAS 166334, fine grained clay minerals and hematite crystals in the matrix (A_1). Tabular crystals of hematite forming rosette-shaped aggregations in the matrix (A_2 , A_3); the cross in A_2 shows the location of elemental analysis (A_4). **B**. NIGPAS 166339a, skeleton coated with hematite. **C**. NIGPAS 166337, halite pseudomorphs distributed on the surface of undetermined fossil (C_1), calcite imprints in the matrix (C_2). Scale bars: A_1 , A_2 , C_2 , 2 μm ; A_3 , 1 μm ; **B**, 10 μm ; C_1 , 50 μm .

age) based on Peng (2009) and Peng et al. (2012). The hyolith-yielding interval contains abundant trilobites including *Luaspides linyuanensis* Duan, 1966 indicative of the *Shantungaspis* Zone (Duan et al. 2005), which was recently correlated with the Cambrian Stage 5 (Taijiangian) (Peng 2009; Wang et al. 2014). However, the precise age of the *Shantungaspis* Zone is uncertain, it could be late Stage 4 or early Stage 5 (Shanchi Peng, personal communication 2017). The hyolith-bearing interval also yields fragments of anomalocaridids and brachiopods (Huang et al. 2012) as well as other problematic fossils of uncertain affinity.

Material and methods

The specimens analysed herein were collected from the Manto Formation exposures of Tangshan, and the fossils are usually preserved as internal moulds with limited skeletal

material. All specimens described here are deposited in NIGPAS under repository numbers 166329–166377.

Two types of preservation are recognised among the skeletal fossils from the Manto Formation. One style is represented by dense concentrations of shells preserved on the bedding planes (Fig. 1). These fossils consist of opercula, discarded segments and conchs of *C. convexa* sp. nov. in association with a few shells of *D. cyrene* (Fig. 1B, D), and numerous trilobite fragments and bioclasts of unidentified fossils. This assemblage is preserved as a non-size-sorted association that has a chaotic orientation without individuals being fully intact, suggesting rapid deposition from storm-induced density currents (O'Brien et al. 1980; Brett and Baird 1986; Simões and Aceñolaza 2009; Cherns et al. 2011). Mineral structures (Fig. 2A₁–A₃) and elemental analyses (Fig. 2A₄) indicate that the pigment mineral hematite (diameter of hematite rosette 1–4 μm) accounts for the reddish colour of the shale and fossils (Ziegler and McKerrow

1975; Turner 1979), specifically the coating of the hyolith conchs (Fig. 2B). The presence of halite pseudomorphs (Fig. 2C₁) and calcite impressions (Fig. 2C₂) support the inference of an arid inner shelf/ lagoonal-mud flat depositional setting for the reddish shale (Xiang et al. 1999).

A second type of preservation is characterized by individual conchs of orthothecids without opercula attached (Fig. 3B₃, F, H), but associated with both fragmented and rare articulated trilobites, appendages and mouthparts of anomalocaridids, disarticulated brachiopods with convex-up oriented single valves, sponges and coprolitic material in purplish-red shales. No preferred orientation can be observed in this case. These fossil associations represent time-averaged assemblages (Zhao et al. 2009, 2014) and a few shells covered with algae (Fig. 3I) suggest a period of exposure on the seafloor prior to burial.

Specimens were examined using SU3500 Scanning Electron Microscopy (SEM) with Electron Dispersive X-ray (EDX) under UVD and BSE-COMP modes to observe the mineral and skeletal morphology in the Public Technology Service Center of NIGPAS. Illustrated fossils were imaged by Canon EOS 5D MarkIII with a Canon MP-E 65mm f/2.8 Macro lens and some of the specimens were coated with magnesium oxide to reduce reflection. Digital macrophotographs were edited and rendered using Adobe Photoshop CS6 and Coreldraw X4 softwares. Fossils were measured by using Digimizer software.

Systematic palaeontology

Phylum uncertain

Remarks.—Affinity of hyoliths has long been controversial. Previous works on the earliest developmental pattern of hyoliths and molluscs demonstrated a similarity between these groups to each other and to the annelids (e.g., Martí Mus et al. 2014). However, other studies of internal anatomy tend to favour a close relationship between hyoliths and sipunculans (Pojeta 1987; Sun et al. 2016). Recently, a novel idea that hyoliths are lophophorates close to the brachiopod-phoronid clade has been proposed by Moysiuk et al. (2017). However, the phylogenetic position of the hyoliths within the Lophotrochozoa, and whether these organisms constitute a monophyletic group remain open questions.

Class Hyolitha Marek, 1963

Order Orthothecida Marek, 1966

Family Novitatidae Sysoyev, 1968 (emended Malinky 1987)

Genus *Decoritheca* Sysoyev, 1972

Type species: *Hyolithus (Orthotheca) excavatus* Holm, 1893; middle Cambrian, Sweden.

Diagnosis.—See Berg-Madsen and Malinky (1999).

Remarks.—*Decoritheca* is morphologically similar to *Contitheca* Sysoyev, 1958, but they are separated by the prominent ridge present on the dorsum of the latter, giving rise to a heart-shaped cross section. The former possesses a rounded dorsum and lacks the middle dorsal ridge, creating a reniform cross section. Specimens described herein match well the traits of *Decoritheca* and are therefore assigned to that genus. *Decoritheca* also resembles *Nephrotheca* Marek, 1966 in cross section, but differs from the latter in solely having transverse lines (Malinky 1987), although, to some degree, ornamentation may not be the best criterion to differentiate taxon ranking above species. So far no operculum for *Decoritheca* has been documented. *Decoritheca cyrene* was described from the “middle Cambrian” (Cambrian Series 3) Changhsia Formation and the “upper Cambrian” (Cambrian Furongian) Chaomitien Formation (Walcott 1905; Malinky 1987); the long span of the species may also reflect a taxonomic problem. Until better fossil material is available to address the relationship between *Nephrotheca*, *Decoritheca*, and some other similar taxa, specimens described below are provisionally placed under *Decoritheca*.

Stratigraphic and geographic range.—Cambrian Series 2 Stage 3 to Furongian Stage 10. Distributed in China, Greenland, Sweden, British Columbia, Texas, Montana, possibly South Dakota, and New York State (Malinky 1987; 1990; 2014; see also SOM 2).

Decoritheca cyrene (Walcott, 1905)

Fig. 3.

1905 *Orthotheca cyrene* sp. nov.; Walcott 1905: 19.

1905 *Orthotheca cyrene dryas* sp. nov.; Walcott 1905: 19.

1913 *Orthotheca cyrene* Walcott, 1905; Walcott 1913: 94, pl. 5: 21, 21a.

1913 *Orthotheca cyrene dryas* Walcott, 1905; Walcott 1913: 93, pl. 5: 22, 22a–c.

1946 *Hyolithes (Orthotheca) cyrene* (Walcott), 1905; Sinclair 1946: 75.

1946 *Hyolithes (Orthotheca) dryas* (Walcott), 1905; Sinclair 1946: 75.

1987 *Decoritheca cyrene* (Walcott, 1905); Malinky 1987: 948–951, figs. 2.4, 6.1–6.6, 6.14.

Material.—Thirty-seven specimens (NIGPAS 166329–35, 166337, 166338, 166341, 166344, 166349–74) preserved as internal moulds of conchs.

Diagnosis.—See Malinky (1987: 948).

Description.—Conch straight with a planar (orthogonal) aperture, length of conchs ranges from 7.1–20.1 mm, and apertural width ranges from 2.9–5.5 mm. The dorsum is broadly rounded and covered with rows of tubercles (Fig. 3C), with diameters of 6–10 µm. Venter developed with a prominent longitudinal median concavity, becoming shallower from aperture to apex. Sub-rounded ridges adjacent to the concavity grade into narrowly rounded lateral margins (Fig. 3B₁, B₃, D, F, H) and lateral margins are straight in dorsal view. Ventral external surface is covered with closely spaced transverse lines (Fig. 3B₂). The morphology of dorsum and venter gives rise to a reniform cross section, but only one specimen displays the full image of transverse section (Fig. 3E), the apertural height is 0.7 mm, apertural width is

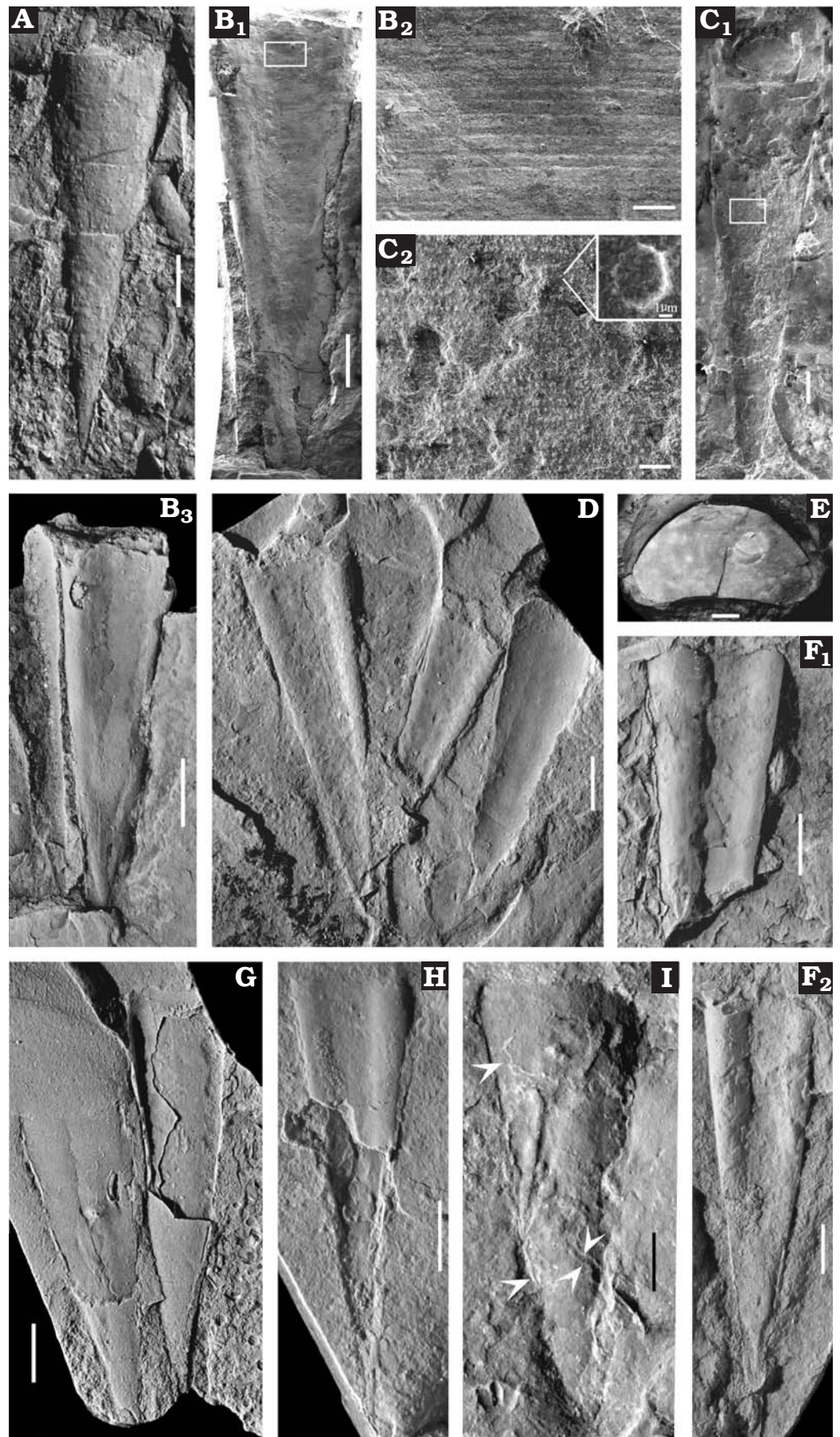


Fig. 3. Novitatid hyolith *Decoritheca cyrene* (Walcott, 1905) from the Manto Formation (Cambrian Stage 4/5) in the Zuojiawu section of Tangshan, China. **A.** NIGPAS 166338 in dorsal view. **B.** NIGPAS 166335 in ventral (**B₁**) and ventro-lateral (**B₃**) views; detail showing transverse lines on the external surface of venter (**B₂**). **C.** NIGPAS 166337 in dorsal view, conch of *Decoritheca cyrene* with operculum of *Cupitheca convexa* sp. nov. in apertural region (**C₁**); rows of tubercles (**C₂**), inset shows enlarged individual tubercle with nearly flat top. **D.** NIGPAS 166329 in ventral view. **E.** NIGPAS 166341b, aperture with reniform cross section. **F.** NIGPAS 166331 in ventral view; **F₁**, incomplete shell showing well developed median concavity and adjacent ridges; **F₂**, nearly complete shell with broken aperture and adapically shallowing median concavity. **G.** NIGPAS 166330, both shells display partial venter and partial dorsum from dorsal view. **H.** NIGPAS 166333 in ventral view. **I.** NIGPAS 166332 in dorsal view, white arrows indicate algae. Scale bars: **A, D, B₃, F₁–I,** 2 mm; **B₁, C₁,** 1 mm; **B₂,** 100 μ m; **C₂,** 20 μ m; **E,** 200 μ m.

1.4 mm, and apertural width/height ratio is 2. Conchs terminate in pointed apex, and angle of divergence at apex ranges from 15–18°. Operculum and helens unknown.

Remarks.—This species bears resemblance to *D. lineatula* (Holm, 1893) from Sweden, but the presence of only longitudinal sculpture on the latter serves to distinguish it from the former. *D. cyrene* also bears limited resemblance to the Swedish *D. excavata* (Holm, 1893), but the two species can be differentiated by the absence of rounded ridges at the ventral lateral margins in the latter.

One specimen of this species (Fig. 3C₁) appears to preserve a conch with an unattached operculum near the aperture. Given that the operculum is nearly circular but the cross section of *D. cyrene* is reniform, it is unlikely that the conch and operculum represent the same taxon. It is more likely that these specimens are coincidentally located next to each other as result of movement by currents or perhaps bioturbation. Circular opercula such as these are usually found in clusters of *C. convexa* sp. nov. shells, and therefore we suggest that these circular or oval opercula more reasonably belong to *C. convexa* sp. nov.

Stratigraphic and geographic range.—Cambrian Series 3 Stage 5 to Furongian Stage 10. The Manto Formation of Tangshan, Hebei Province (herein), the Chaomitien and Changhsia formations of Yantai, Shandong Province (Walcott 1905), and the Changhsia Formation in Anhui Province, China (Qian and Xiao 1995); Snowy Range Formation of Gallatin, Montana; Wilberns Formation of Burnet County, Texas (Malinky 1987; see also SOM 2).

Family Cupithecidae Duan, 1984

Genus *Cupitheca* Duan in Xing et al., 1984

Type species: *Cupitheca brevituba* Duan in Xing et al., 1984, lower Cambrian, South China.

Diagnosis.—See Bengtson et al. (1990: 203).

Remarks.—For detailed discussion and taxonomic history see Malinky and Skovsted (2004: 568–569), Pan et al. (2015: 388) and Skovsted et al. (2016: 125).

Stratigraphic and geographic range.—Cambrian; Terreneuvian Fortunian to Series 3 Stage 5; since the biostratigraphic correlation of “Lower Limestone” (= Maseong Formation) is not clear (Lee 2008), the age of *C. cf. mira* reported by Lee (2008) should be questioned. Distributed in China (Pan et al. 2015), Korea (Lee 2008), Australia (Kruse et al. 2004; Skovsted et al. 2016), Antarctica (Wrona 2003), Greenland (Malinky and Skovsted 2004), Newfoundland (Skovsted and Peel 2007), Spain (Jensen et al. 2010), India (Gilbert et al. 2016; Hughes 2016), possibly Kazakhstan and England (Malinky and Skovsted 2004; see also SOM 2).

Cupitheca convexa sp. nov.

Figs. 4–8.

Etymology: From Latin *convexus*, in reference to the convex nature of the interior of the operculum at the cardinal process area.

Type material: Holotype NIGPAS 166339a (Fig. 6D); Paratypes NIGPAS 166334, 166336–43 (Figs. 4, 6A–C) from the type locality.

Type locality: Zuojiaiwu section, Fengrun District of Tangshan City, Hebei Province, North China.

Type horizon: The purplish-red shales of the Manto Formation, Cambrian Stage 4/5.

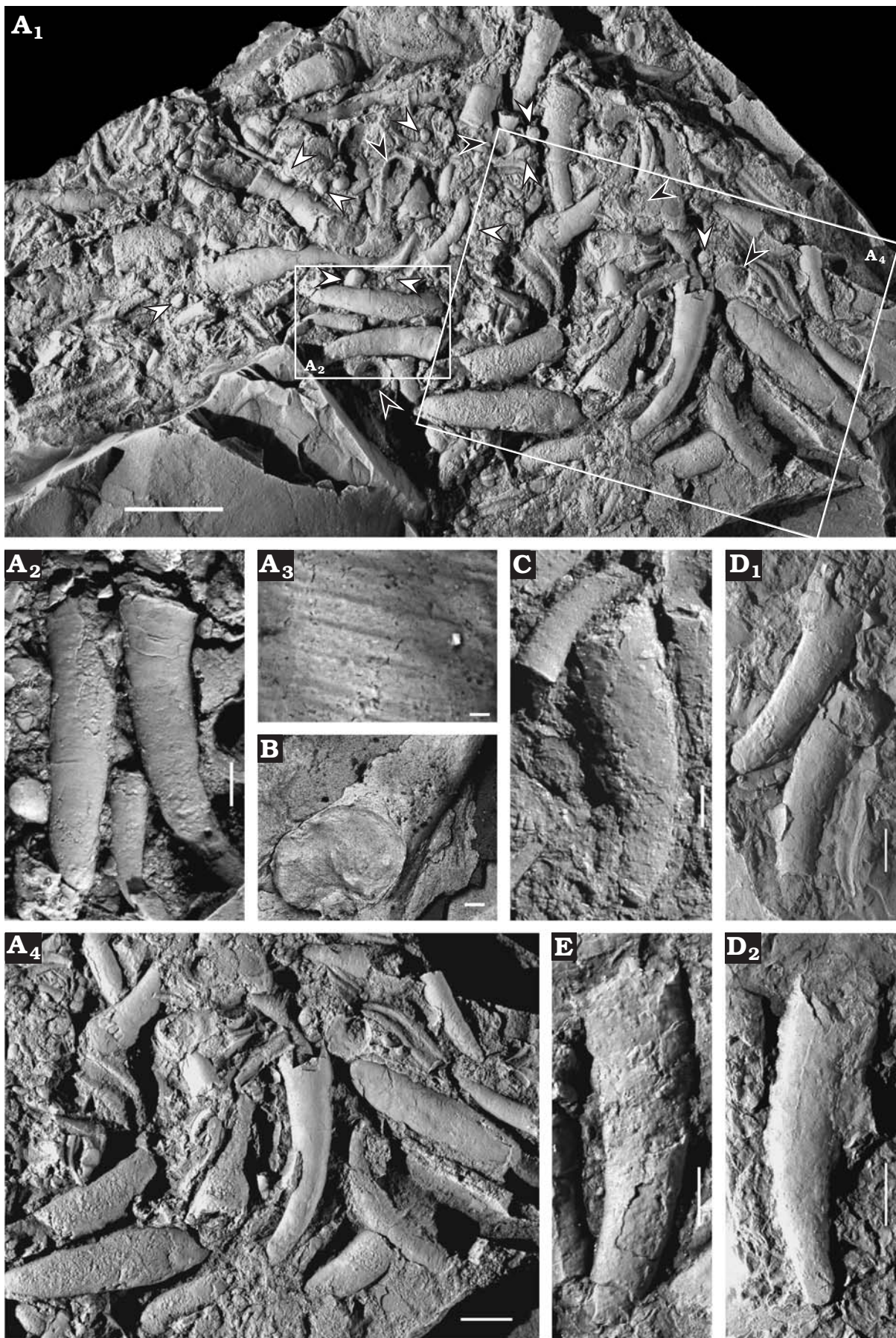
Material.—Thirteen specimens in total, preserved as clusters of moulds of conchs and opercula (NIGPAS 166336–39a, b, 166340, 166341a, b, 166342–47), and 3 specimens (NIGPAS 166375–77) preserved as inarticulate shells. All are decalcified.

Diagnosis.—*Cupitheca* with interior surface of operculum convex near cardinal processes; cardinal processes are moderately well-developed and bilobate; conch cyrtoconic; ornamentation on conch is merely transverse lines, and both interior and exterior surfaces of operculum covered by concentric ribs.

Description.—Conchs cyrtoconic with pronounced curvature, degree of curvature slightly varies in different specimens (Fig. 4A, C–E); transverse lines on exterior surface (Figs. 4A₃, 5A₇) with intervening spaces 2–15 µm wide; cross section circular to oval (Fig. 4B); apical angle of divergence small (14–16°); sculpture at apical termination varies (Fig. 5A₄, A₅, B), with some having radial lines that probably represent the original microstructure of the shell (Fig. 5A₄, A₅), while others possess a smooth terminus with no lines or other features (Fig. 5A₁–A₃, A₆, A₇, C₃); and still others have irregularly radiating, branching ornamentation (Fig. 5B), which may be an artefact of preservation. A circumferential furrow separates the apical region from the remainder of the shell.

Operculum circular to sub-circular or slightly oval (opercular width and length are subequal, Fig. 7A); protooperculum nearly flat (Fig. 6A₂, A₃) and circular (Fig. 6A, B₁, B₃), 250–530 µm in diameter (Fig. 7A), with a location toward the dorsal margin. Bilobate cardinal process can be observed near the dorsal margin of the operculum on the interior surface, forming a convex area and grading downward into a flattened marginal area (Fig. 6B₄, C, D₁, D₃), impressions of cardinal processes can also be observed on the exterior of the operculum (Fig. 6A, B₁–B₃), which may be the result of high compression; these structures are generally rectangular in shape, and terminate at the distal end in a bluntly rounded surface. Angles of divergence of cardinal processes are 99–113° and 100° on average. Cardinal processes are

Fig. 4. Cupithecoid hyolith *Cupitheca convexa* sp. nov. from the Manto Formation (Cambrian Stage 4/5) in the Zuojiaiwu section of Tangshan, China. **A.** NIGPAS 166334, accumulation of conchs and opercula (A₁), white arrows suggest discarded cylindrical segments, black arrows indicate opercula; three almost complete shells with apical parts buried in the matrix (A₂); transverse lines on the dorsal surface of conch (A₃); aggregation of skeletal parts with chaotic orientation (A₄). **B.** NIGPAS 166336, incomplete conch shows full aperture. **C–E.** More or less complete conchs. **C.** NIGPAS 166338. **D.** NIGPAS 166340, two adjacent shells, the left one displays full apex (D₁); single conch with partial broken aperture (D₂). **E.** NIGPAS 166341b. Scale bars: A₁, 5 mm; A₂, C, 1 mm; A₃, 5 µm; B, 100 µm; A₄, D, E, 2 mm. →



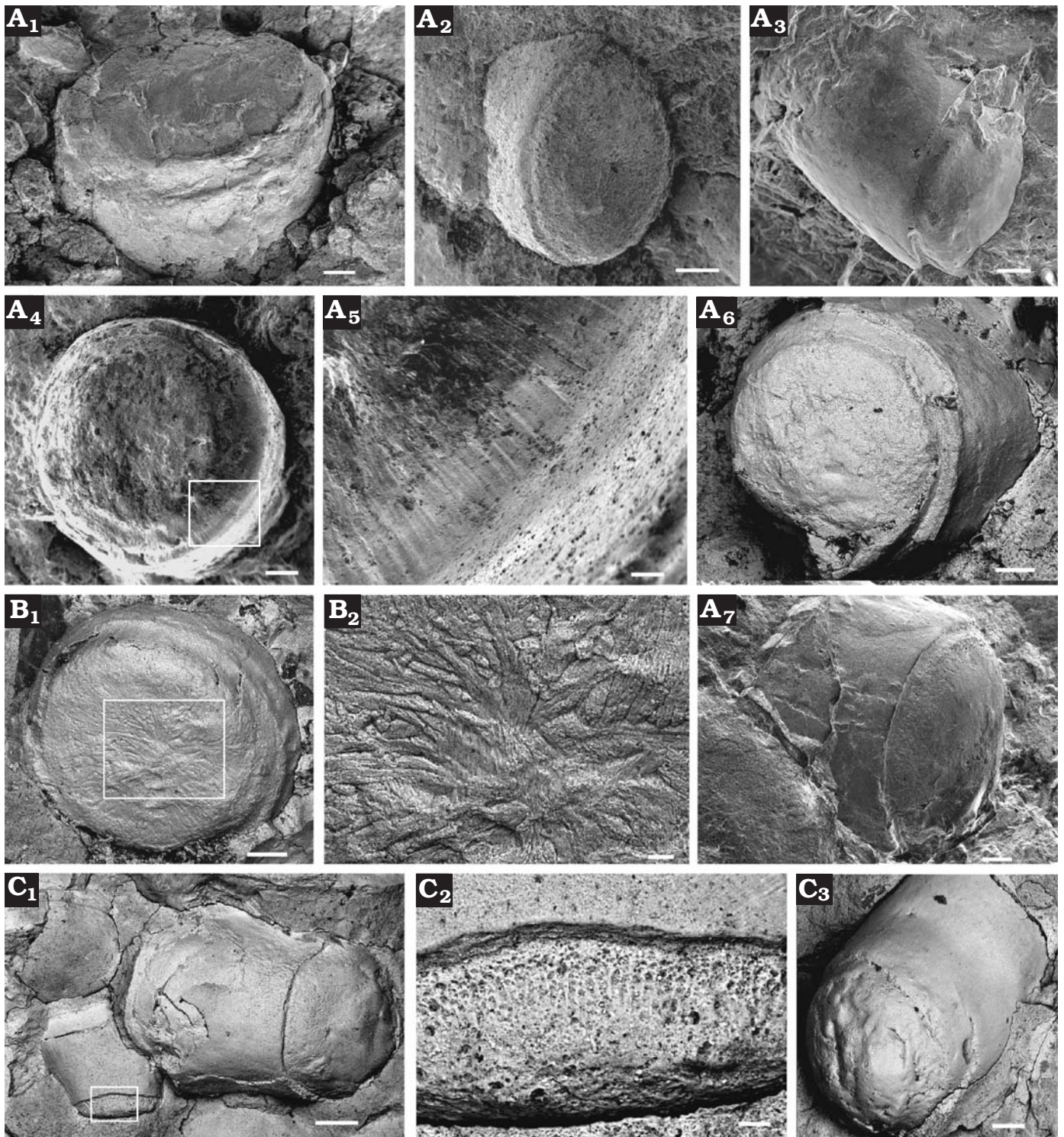


Fig. 5. Internal moulds of decollated segments of cupithecoid hyolith *Cupithecica convexa* sp. nov. from the Manto Formation (Cambrian Stage 4/5) in the Zuojiaiwu section of Tangshan, China. **A.** NIGPAS 166334, discarded apical segments with smooth surface (A₁–A₃, A₆); bottom of the apex (A₄); apical bottom covered with radial sculptures (A₅); discarded segment preserves faint transverse lines on the surface of conch (A₇). **B.** NIGPAS 166343, decollated segment displaying apical bottom, probable diagenetic artefacts on the bottom of apex (B₁); branching ornamentation on the bottom of apex (B₂). **C.** NIGPAS 166339a, decollated segments two segments preserved together the left one exhibits pits and longitudinal groove structures on the surface of terminal part (C₁); detail (C₂); discarded apical segments with smooth surface (C₃). Scale bars: A₁, A₃, A₆, A₇, B₁, C₃, 100 µm; A₂, A₄, 50 µm; C₁, 200 µm; A₅, B₂, C₂, 20 µm.

covered from proximal to distal terminations with scattered sub-circular pits (shown as tubercles on the counterparts; e.g., Fig. 6D), 4–9 µm in diameter. Exterior of operculum is

covered by a series of concentric lamellae or ribs (Fig. 6A₁, A₃, B₁–B₃). Interior also covered with concentric lines or ribs (Fig. 6B₄, D₁, D₃) that correspond to those on the exterior.

Remarks.—Specimens of *Cupithec*a recovered from the Manto Formation on the North China Platform are distinctive from the more widely distributed and therefore better known *C. holocyclata* Bengtson in Bengtson et al., 1990 (Bengtson et al. 1990; Skovsted et al. 2016) in terms of ornamentation of the conch and overall shape of the operculum. *C. holocyclata* from Australia (Bengtson et al. 1990) and several individuals reported from North China from Cambrian Stage 4 (Skovsted et al. 2016) have a dominant transverse ornament, with minimal to subordinate longitudinal overprint. In addition, the interior of the operculum of *C. holocyclata* is concave, while that of *C. convexa* sp. nov. is convex, and cardinal processes seen in *C. holocyclata* appear to be more robust than those of *C. convexa* sp. nov.. The protooperculum of the former is a circular elevated platform with a concave base and marginal rim (Skovsted et al. 2016), which is different from the flattened and circular protooperculum in *C. convexa* sp. nov.. The new species is distinguished from *C. costellata* Xiao and Zhou, 1984 by possession of distinct longitudinal ornament in the latter. Our material also resembles *C. manicae* Duan, 1984 from the Lower Cambrian of Hubei Province, South China (Duan 1984) in general morphology and cross section of the shell, but the latter possesses no ornament on the conch (possibly a taphonomic bias) and no known operculum, which makes detailed comparison difficult. This is also the case with the similar taxa *C. brevituba* Duan in Xing et al., 1984, *C. intermedia* (Duan, 1984), and *C. mira* (He in Qian, 1977) from the lower Cambrian of South China (Xiao and Zhou 1984; Duan 1984). These previous identifications as *Cupithec*a were based mainly on the ornament on the conchs, here we highlight the importance of the operculum in the classification of this group. The occurrence of *C. holocyclata* without opercula preserved should be questioned (see SOM 2).

The conch of specimen NIGPAS 166334 (Fig. 8A) possesses two distinct zones that are separated by a transverse discontinuity. The adapertural portion is characterised by transverse lines (Fig. 8D), whereas the adapical tapering zone is covered by longitudinal to sub-radial ornament (Fig. 8C). Although the apical termination cannot be well separated from the matrix, based on the distinct ornamentation covering of the two zones, the adapertural region is regarded as early juvenile portion of the conch, whereas the adapical portion is the presumed protoconch. Therefore the transverse discontinuity or furrow is possible the site where the first septum-like structure developed (Bengtson et al. 1990). Furthermore, the diameter of the shell at the furrow is 450 μm , which overlaps with the ranges of diameters of the protoopercula in this collection (Fig. 7C). No weakening points or septum-like structures have been observed on the presumed protoconch. The ridge-like structure (Fig. 8C) seems to be deceptive, appearing as a biological structure, but in fact is most likely the result of mechanical damage because the outmost layer is squeezed to form an uneven ridge (Fig. 8C) rather than a dissolved groove (Fig. 8B). Although the apex is partially broken and peeled away, part

of the lateral sub-radial lines could still be observed on the mould (Fig. 8E).

Stratigraphic and geographic range.—The Manto Formation, late Cambrian Series 2 Stage 4 or early Series 3 Stage 5, Hebei Province, North China (see SOM 2).

Discussions

Mode of growth, early life habit, and affinity of *Cupithec*a.—Bengtson in Bengtson et al. (1990) presented evidence for an unusual manner of growth for *Cupithec*a in which the animal decollated portions of its conch at various times by the development of a septum-like transverse wall in the apical region, which may have been a strategy similar to coiling in order to avoid reaching an extreme length. *Cupithec*a *convexa* sp. nov. probably evolved a new life habit with a preference for shallow, nearshore environments where the availability of resources may have periodically fluctuated. The decollating life habit would have been especially well suited to this type of environment, in that by shortening itself, the animal would have required fewer resources in order to survive. The decollating mode of growth is similar to that of some extant terrestrial and littoral-fringe gastropods (Vermeij 1973; Gittenberger and Povel 1995; Páll-Gergely and Németh 2008) as well as gastropods from deep-water hot vents and cold seeps (Kaim et al. 2008). The functions of decollation for these animals include repair of an incidentally damaged apex or protection against desiccation by evaporation (Gittenberger and Povel 1995). *Cupithec*a *convexa* sp. nov. having lived in shallow water, may also have developed decollation for repair of injured apex. Regarding this mode of growth, it is questionable as to whether the presumed gastropod ancestor of the extant decollating forms possessed the ability to shed portions of its shell or whether decollation evolved within this group, convergent with *Cupithec*a.

The protoconch of *Cupithec*a remained unknown until now. Although orthothecide protoconchs have been frequently documented (Dzik 1980; Duan 1984; Qian and Zhang 1985; Qian 1989; Wrona 2003; Steiner et al. 2007; Topper et al. 2009), most were described for taxonomic purposes. The protoconchs observed on *Bactrotheca*, *Conotheca*, *Neogloborilus* and some other orthothecide taxa either have a smooth sub-spherical apex (Dzik 1978, 1980; Qian and Zhang 1985; Qian 1989; Wrona 2003; Steiner et al. 2007; Topper et al. 2009) or fusiform with a pointed apex (Dzik 1978, 1980; Duan 1984; Qian and Zhang 1985; Martí Mus et al. 2014), separated by a constriction of variable size from the remainder of the conch. In this case the constriction is well-defined on the internal mould and this type of feature ordinarily has been interpreted as having recorded hatching or the beginning of metamorphosis (Martí Mus et al. 2014). However, the presumed protoconch of *Cupithec*a described herein differs from the protoconchs mentioned above in

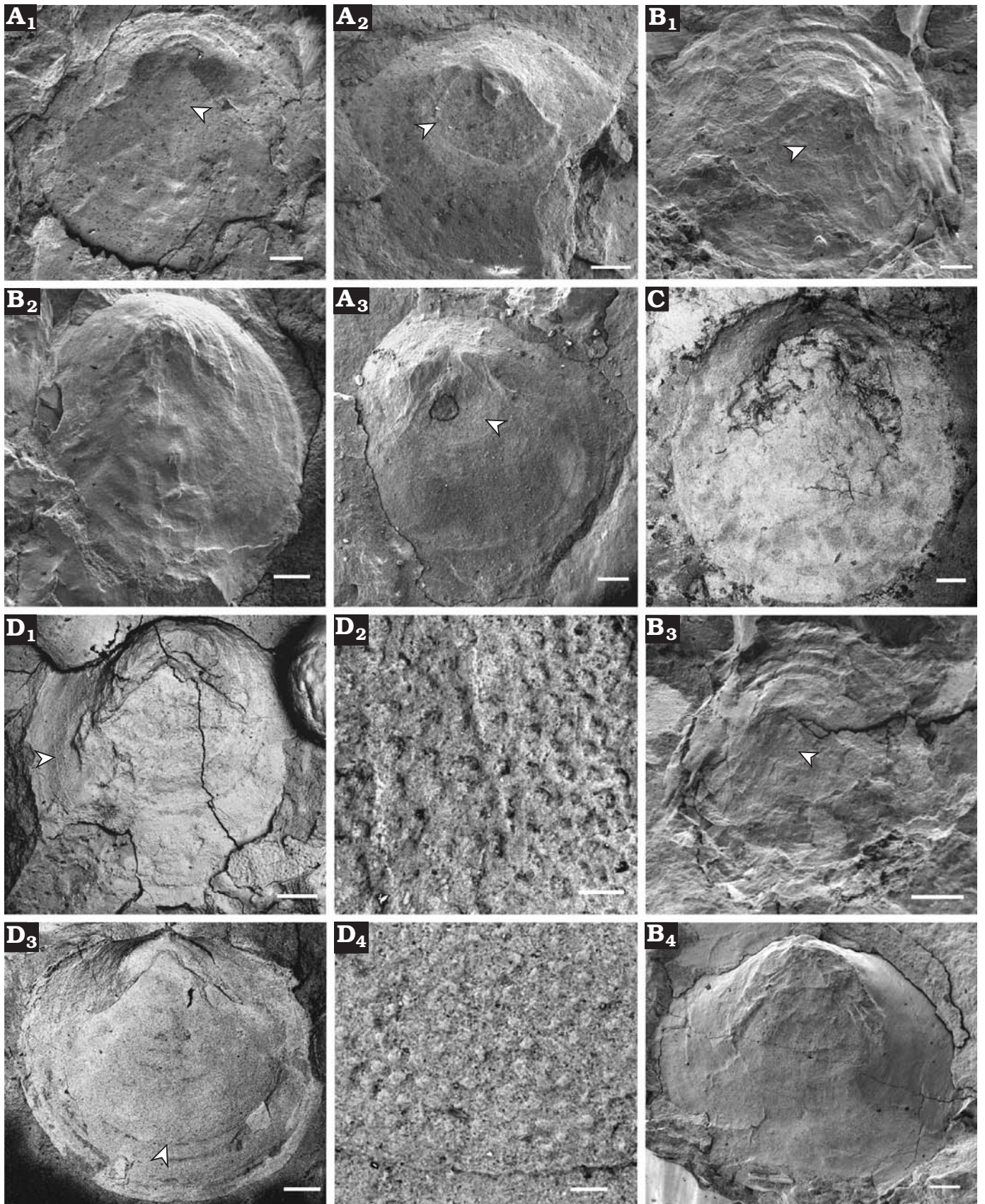


Fig. 6. Opercula of cupithecoid hyolith *Cupitheca convexa* sp. nov. preserved as internal or external moulds, which are prepared from natural casts, collected from the Manto Formation (Cambrian Stage 4/5) in the Zuojiawu section of Tangshan, China. **A, B.** Internal moulds of opercula, NIGPAS 166337 (**A**) and NIGPAS 166342 (**B**); showing exteriors covered with concentric ribs, protoopercula (indicated by white arrows) and imprints of bilobate cardinal →

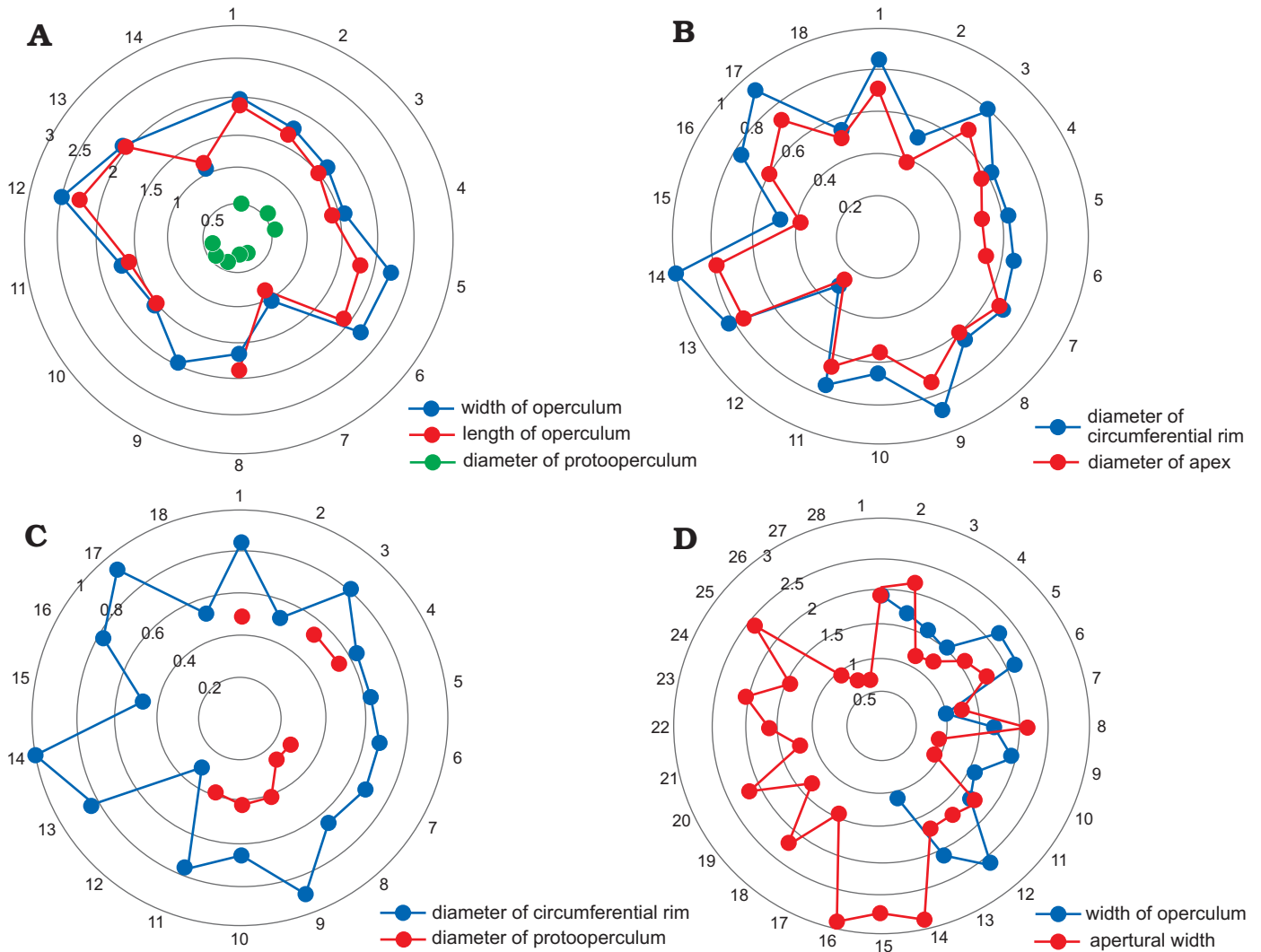


Fig. 7. Statistical distribution of different skeletal parts, junctions of the outermost ring represent the number of data, and concentric circles represent length (in mm).

terms of overall shape (fusiform versus rounded). The size of the *C. convexa* sp. nov. protoconch, however, surpasses the dimensions of all other members of hyoliths (Bengtson et al. 1990; Martí Mus et al. 2014), and hence must be considered unusual among Cambrian hyoliths, which implies a possible lecithotrophic development as suggested for other metazoan groups (Allen and Pernet 2007; Laibl et al. 2017). Lecithotrophy of this group may decrease reliance on exogenous nutrition associated with unpredictable food resources (Laibl et al. 2017) and thereby maximize chances of survival (Allen and Pernet 2007; Mercier et al. 2013). The protooperculum of *C. convexa* sp. nov. is flat rather than elevated as in *C. holocyclata* (Skovsted et al. 2016), indicating that an attachment or anchoring larval lifestyle is unlikely and that the

larva was possibly free-lying on the sea floor, with limited locomotion or passively movable by currents.

The presumed protoconch of *C. convexa* sp. nov. does not show abrupt morphological change, and the larval period terminated with a juvenile body form that gradually acquired adult characteristics, as in previously documented groups (Martí Mus et al. 2014). With the growth of the conch, *C. convexa* sp. nov. graded into the decollating stage (see SOM 3). Observed diameters of protoopercula are usually smaller than those of the circumferential rims of the discarded segments (Fig. 7C), which suggests that decollation started following metamorphosis. Some discarded fragments that have a circumferential diameter similar to that of protoopercula (Fig. 7C), might be indicative of early decollating stages.

processes (A₁–A₃, B₁–B₃); interior preserved concentric ribs and cardinal processes (B₄). C, D. Counterparts of internal moulds of opercula displaying interior with imprints of bilobate cardinal processes, NIGPAS 166343 (C) and NIGPAS 166339a (D, holotype). Internal mould exhibiting interior surface of the operculum with concentric ribs and cardinal processes preserved (D₁), arrow indicates the location of D₂; pitting structure on the surface near opercular margin (D₂); specimen showing opercular interior covered by concentric ribs and tubercles on the surface near margin (D₃), arrow indicates position of D₄; rounded tubercles (D₄), which correspond to pits on the surface of interior of operculum, as they are shown in (D₂). Scale bars: A, B₂, B₄, C, D₁, D₃, 200 µm; B₁, B₃, 100 µm; D₂, D₄, 20 µm.

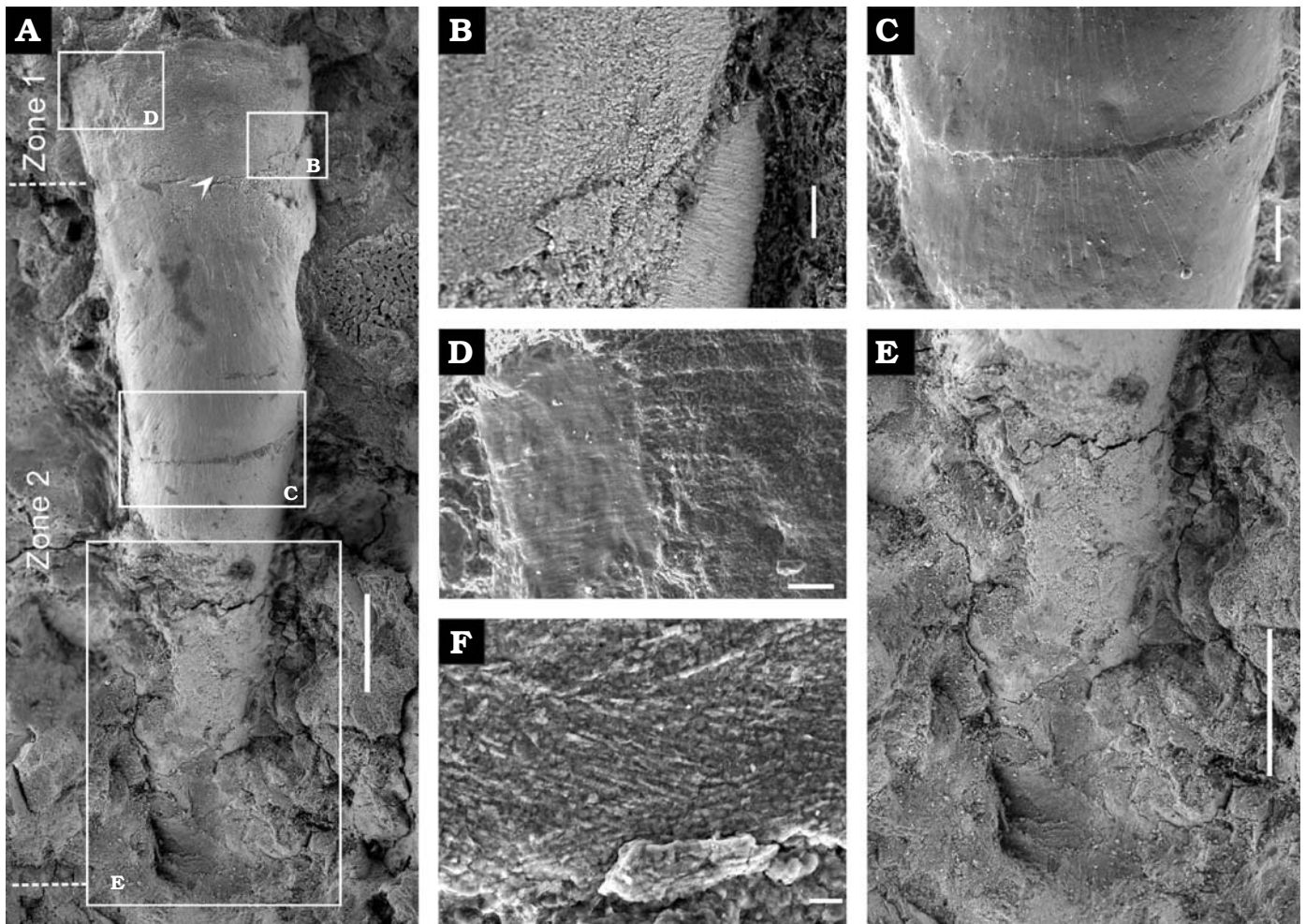


Fig. 8. Internal mould of the conch of cupithecoid hyolith *Cupithec convexa* sp. nov. (NIGPAS 166334) from the Manto Formation (Cambrian Stage 4/5) in the Zuojiauwu section of Tangshan, China. **A.** General view. **B.** Boundary between presumed protoconch and the rest of the shell. **C.** Transverse lines preserved on the surface of the conch. **D.** Conch covered with longitudinal to sub-radial ornament and mechanical compression forming a transverse ridge-like structure. **E.** Apical portion. **F.** Lamellar-fibrillar structure (indicated by white arrow in **A**). Scale bars: **A, E**, 200 μm ; **B**, 20 μm ; **C**, 2 μm ; **D**, 50 μm ; **F**, 5 μm .

The hyolith affinity of *Cupithec* is clearly established (Skovsted et al. 2016), and it has been proposed that *Cupithec* is closer to the orthothecoid hyoliths as has been suggested previously by Kruse et al. (2004). This suggestion is based mainly on the lack of helens and clavicles, although the presence of a cardinal shield in *C. holocyclata* is more reminiscent of hyolithides than the orthothecoids (Skovsted et al. 2016). As is typical for orthothecoids, the operculum of *C. convexa* sp. nov. possesses cardinal processes only and is planar without differentiation of cardinal or conical shields. One characteristic trait of orthothecoids not yet seen in *Cupithec* is an operculum that may be retracted a short distance into the conch (Marek 1963, 1966, 1967; Malinky 2009; Valent and Fatka 2013), which is thought to have been a strategy for minimizing sediment intake into the shell, given the absence of a ligula in that group. Although no specimens of *Cupithec* possess an attached operculum, the width range of opercula matches that of the apertures (Fig. 7D), which in some degree may provide a proxy of the supposed retractable manner of *C.*

convexa sp. nov. Consequently, an assignment of *Cupithec* to Orthothecida is suggested.

Skeletal microstructures of *Cupithec* and *Decorithec*.—

Most of the specimens studied herein were entirely decalcified and the original skeletal microstructures have been largely destroyed by diagenesis or erosion. However, some shells fortunately preserve replicas of the original microstructures.

One specimen (NIGPAS 166339a) of *C. convexa* sp. nov. has well preserved pits and longitudinal gutters connecting them on the outer surface of the cylindrical rim (Fig. 5C₁, C₂). The pits correspond to the radial tubules in the rim of the convex wall, which may have functioned as channels for releasing shell-dissolving fluid to the specific area of transverse wall formation (Bengtson et al. 1990). The gutters connected to the pits may be the result of erosion by groundwater and therefore are a taphonomic rather than biologic feature. Lamellar-fibrillar microstructure commonly seen in Cambrian molluscan forms (Feng and Sun 2003; Vendrasco et al. 2010) has been observed on one

internal mould of *C. convexa* sp. nov. (Fig. 8F) with crystal bundles oriented at varying angles. Whether this structural resemblance is the result of homology or convergence remains an open question, as the lamellar-fibrillar structure has evolved convergently several times even within the molluscs (Vendrasco et al. 2010). Some opercula of *C. convexa* sp. nov. exhibit scattered sub-circular, shallow and nearly flat-bottomed pits (preserved as nodules on the counterparts; e.g., Fig. 6D) on the marginal area of the internal surface. The pits documented here may correspond to the terminations of rods in the opercula (Kouchinsky 2000b) whereas similar structures on the exterior of some brachiopod shells are interpreted as impressions of biomineralised tablets in the primary layer (Cusack et al. 1999).

The skeletal microstructure of *Decoritheca* has been reported only once before (Dzik 1980) as consisting of phosphatized rods in the shell body wall. However, the conch of *D. excavata* illustrated by Dzik (1980) possesses a sharply triangular cross section unlike the reniform cross section of typical *Decoritheca*, therefore the identification as *Decoritheca* by Dzik (1980) is doubtful. Despite generally good preservation of most specimens of *D. cyrene* the shell microstructure has been unknown until now. One internal mould from the Manto Formation exhibits rows of tubercles on the dorsal surface of *D. cyrene* (Fig. 3C). The tubercles are circular to sub-circular with a nearly flat top, which correspond to dimples on the internal surface of the conch. These have been interpreted as casts of tubules in the shell wall that provided a framework to reinforce the skeleton (Kouchinsky 2000b), and they are similar to those of some molluscs (Kouchinsky 2000a). Tubercles are also common structures in trilobites, and some that are smooth and circular may even be comparable to sensory organs of extant arthropods (Størmer 1980). Similar structures such as sensory protrusions (papillae) can also be observed beneath the cuticle of sipunculans (Cutler 1994). To function as sensors, the tubercles would need to reach the external surface of the shell, which is not the case for *D. cyrene* and the sensory function seems unlikely.

Conclusions

Newly discovered hyoliths from the Manto Formation (Cambrian Stage 4/5) in the Zuojiawu section in Hebei Province, North China are assigned to the species *Cupitheca convexa* sp. nov. and *Decoritheca cyrene* (Walcott, 1905). Cardinal processes on opercula of *C. convexa* sp. nov. support a hyolith affinity for this group (Skovsted et al. 2016). The absence of helens and the planar outline of the operculum without clavicles would argue for its placement within the order Orthothecida. *C. convexa* sp. nov. and *C. holocyclata* exhibit strong morphological differences in their opercula, whereas their conchs are far less dissimilar, highlighting the crucial role of the operculum in taxonomy. Discovery of the presumed protoconch of *C. convexa* sp. nov. demon-

strates that this feature is distinct from those of other hyoliths which suggests a strong adaptability and a diversity of early life habit of Cambrian orthothecids. Replicates of the original skeletal microstructures (pits and lamellar-fibrillar structure) of *C. convexa* sp. nov. bear similarities with those of brachiopods and molluscs, however, whether this is the result of convergence or homology remains an open question. The function of decollation of the conch in *C. convexa* sp. nov. may have been to repair injuries to the animal, or as an alternative of coiling to avoid an extreme length to deal with the fluctuation of nutrient resources. Specimens of the orthothecid *D. cyrene* from the Manto Formation possess tubercle structures on the dorsum and these may represent casts of tubules in the shell wall, which possibly have provided a framework to reinforce the skeleton. Our results affirm the diversity of skeletal structure and ecology of Cambrian orthothecids.

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