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Morphometric analysis of stem-group mollusks from the northern Yangtze Craton, China

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Abstract.—Cap-shaped skeletal fossils are the earliest undisputed body fossils of mollusks appearing in the basal Cambrian. A study on the morphometry of cap-shaped fossils from the Nanjiang area (North Sichuan, China) is undertaken to understand the origin and evolution of the early mollusks. The distribution of these fossil cap-shaped mollusks indicates a stepwise increase in their diversity during the early Cambrian. *Maikhanella* Zhegallo in Voronin et al., 1982 co-occuring with the spinose sclerites of siphogonuchitids, is regarded as the earliest scleritized mollusk. It is followed by other maikhanellids, e.g., *Purella* Missarzhevsky, 1974 and *Yunnanopleura* Yu, 1987, which co-occur with the earliest univalved helcionellids, e.g., *Igorella* Missarzhevsky in Rozanov et al., 1969. Cluster analysis of their morphometric characteristics shows that the *Maikhanella* group is similar to the *Purella* and *Yunnanopleura* groups, but is less comparable with univalved helcionellids. The maikhanellids are interpreted as representatives of the stem group Aculifera, although it remains uncertain if one or two larger cap-shaped shell plates were present on the elongate slug-like body, comparable to those of *Halkieria* Poulsen, 1967 or *Orthrozanclus* Conway Morris and Caron, 2007. Maikhanellids are characterized by the prominent protrusions or scales on the cap-shaped shell plates arranged in a concentric pattern around the shell apex. Evolutionarily, the protrusions or scales are reduced in younger strata, whereas subsequently a typically concentric ornament developed, the cap-shaped shell plates developed higher profiles, and the apical region became increasingly bare of scales. Meanwhile, the cap-shaped shell plates gradually evolved into a helcionellid-like appearance with an anteroposteriorly inclined apex. The morphological evolution of the earliest sclerotized mollusks reflects biotic evolution and environmental adaption among the stem-group mollusks during the early Cambrian.

Introduction

Maikhanellids are early Cambrian small shelly fossils (SSFs) with cap-like shells generally decorated with scales and/or brick-tiled protrusions. They are widely distributed in the Terreneuvian Series strata in many regions including China (Yang and He, 1984; Qian and Bengtson, 1989; Ding et al., 1992; Feng et al., 2001; Steiner et al., 2004, 2020; Guo et al., 2014; Yang et al., 2014; Yu, 2014; Shao et al., 2015; Liu et al., 2016; Pang et al., 2017a), Mongolia (Zhegallo, 1982; Bengtson, 1992; Esakova and Zhegallo, 1996), Siberia (Qian, 1999; Kouchinsky et al., 2017; Parkhaev, 2017), France (Kerber, 1988; Devaere et al., 2013), and Iran (Hamdi et al., 1989).

Despite some uncertainties, general phylogenetic opinions consider maikhanellids to be related to mollusks (Bengtson, 1992; Li et al., 2007), a conclusion that has been supported by studies on the microstructure of their shells (Kouchinsky, 1999; Parkhaev, 2004, 2014; Vendrasco et al., 2009, 2010, 2011; Vendrasco and Checa, 2015). Previous studies considered the maikhanellids to be related to monoplacophorans (Qian and Bengtson, 1989; Feng et al., 2001; Yu, 2014) due to general morphological similarities in shell shape, although a detailed analysis based on muscle scar imprints or ultrastructure never established this relationship. However, it is understood that maikhanellids are among the oldest stem-group mollusks with mineralized shells (Feng et al., 2001; Ponder et al., 2007; Parkhaev and Demidenko, 2010; Parkhaev, 2017; Vinther et al., 2017; Qin et al., 2019).

A detailed study of the morphological evolution among different maikhanellid groups would facilitate our understanding of molluscan origination and early evolution. Here, we present our

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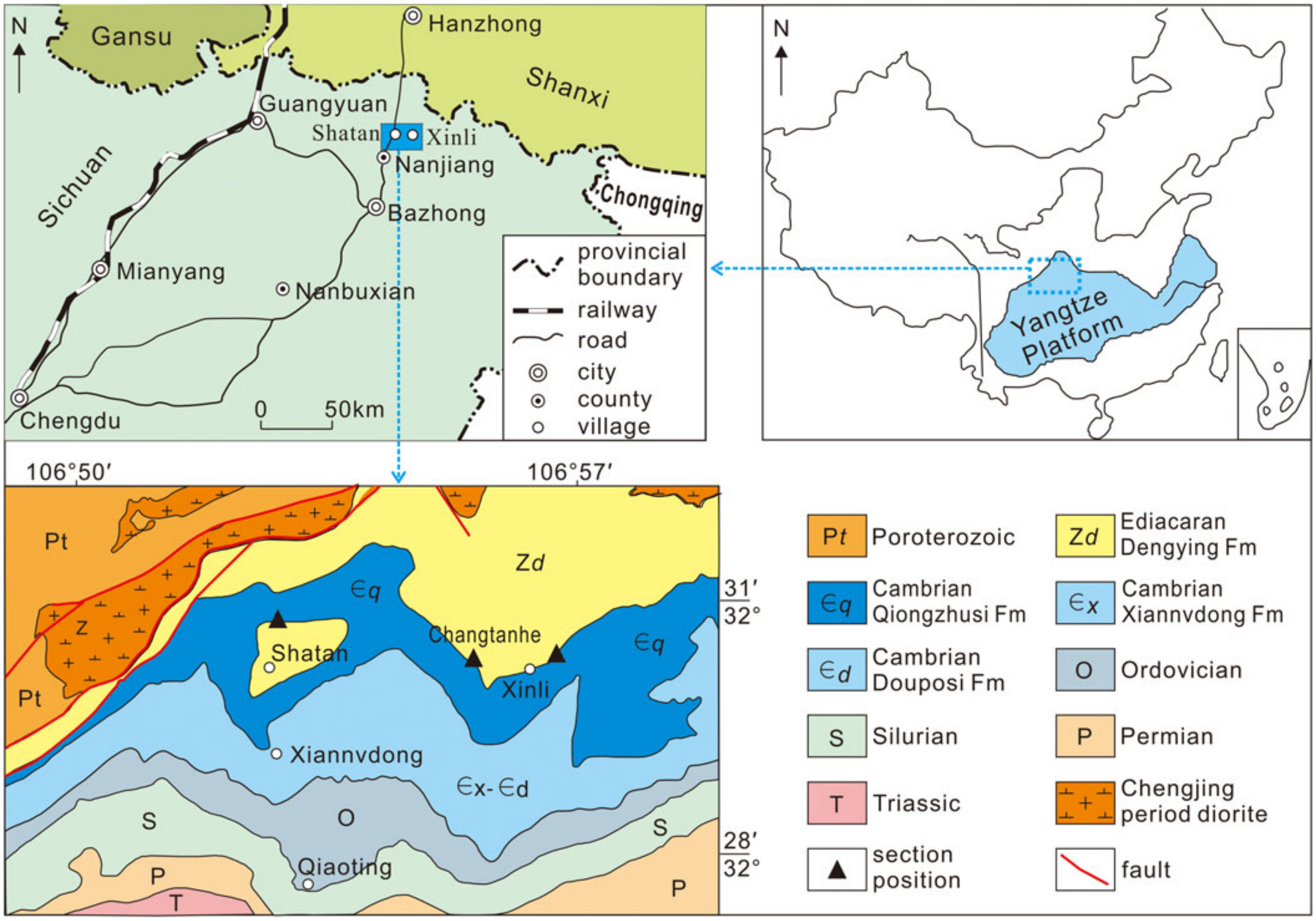

Figure 1. Map of localities of SSF-bearing sections in northeast Sichuan, China (modified from Pang et al., 2010, 2017b).

study on the morphological features and temporal variations of cap-shaped molluscan shells from the Terreneuvian deposits at the northern margin of the Yangtze Platform with the purpose to better understand their taxonomic and evolutionary relationships.

Geological setting

The studied sections at North Shatan (32°30′43″N, 106° 52′49″E), Changtanhe (32°29′54″N, 106°55′41″E), and Xinli (32°31′20″N, 106°58′03″E) are located in Nanjiang County of northeastern Sichuan Province, China, on the northern margin of the Yangtze Platform (Fig. 1).

The Dengying, Kuanchuanpu, and overlying Qiongzhusi formations are exposed in these sections (Fig. 2). The uppermost portion of the Dengying Formation has previously been subdivided, in ascending order, into the Beiwan, Xinli, and Mofangyan members. The Xinli and Mofangyan members are herein assigned to the Kuanchuanpu Formation due to the presence of a significant amount of phosphatic bio- and lithoclasts (Steiner et al., 2020), although the basal Cambrian carbonates can be locally dolomitized. The Beiwan Member is composed of silicified dolostone. The Xinli Member is mainly composed of dolostone containing phosphatic or collophanite layers with well-developed chert beds or laminae as well as siliceous interbeds at the base and a variable thickness of 5–16 m. The overlying 4.5–9.5 m of Mofangyan Member is mainly composed of dark gray limestone with bitumen tar and dolomitic limestone and with well-developed siliceous bands or laminae. New stratigraphic data show that the Xinli and Mofangyan members represent a continuous sequence and have a gradual relationship, however, they can be lithologically distinguished by the degree of dolomitization. In some areas, the strata at the top of the Mofangyan Member are missing. The black shales of the Qiongzhusi Formation (a synonym of Guojiaba Formation; Steiner et al., 2004) overlie the Kuanchuanpu Formation with a disconformity (Fig. 2). The Kuanchuanpu Formation is mostly of Terreneuvian age, based on SSF assemblages.

Materials and methods

Field and laboratory methods.—The fossils were extracted from the carbonates of the Kuanchuanpu Formation of the northern Shatan and Changtanhe sections and from limy collophanite at the Changtanhe and Xinli sections. The carbonates were dissolved in 3–15% buffered acetic acid and then sieved for fossil residues. SSFs were picked and observed under a binocular microscope (Olympus SZX7). Selected fossils were

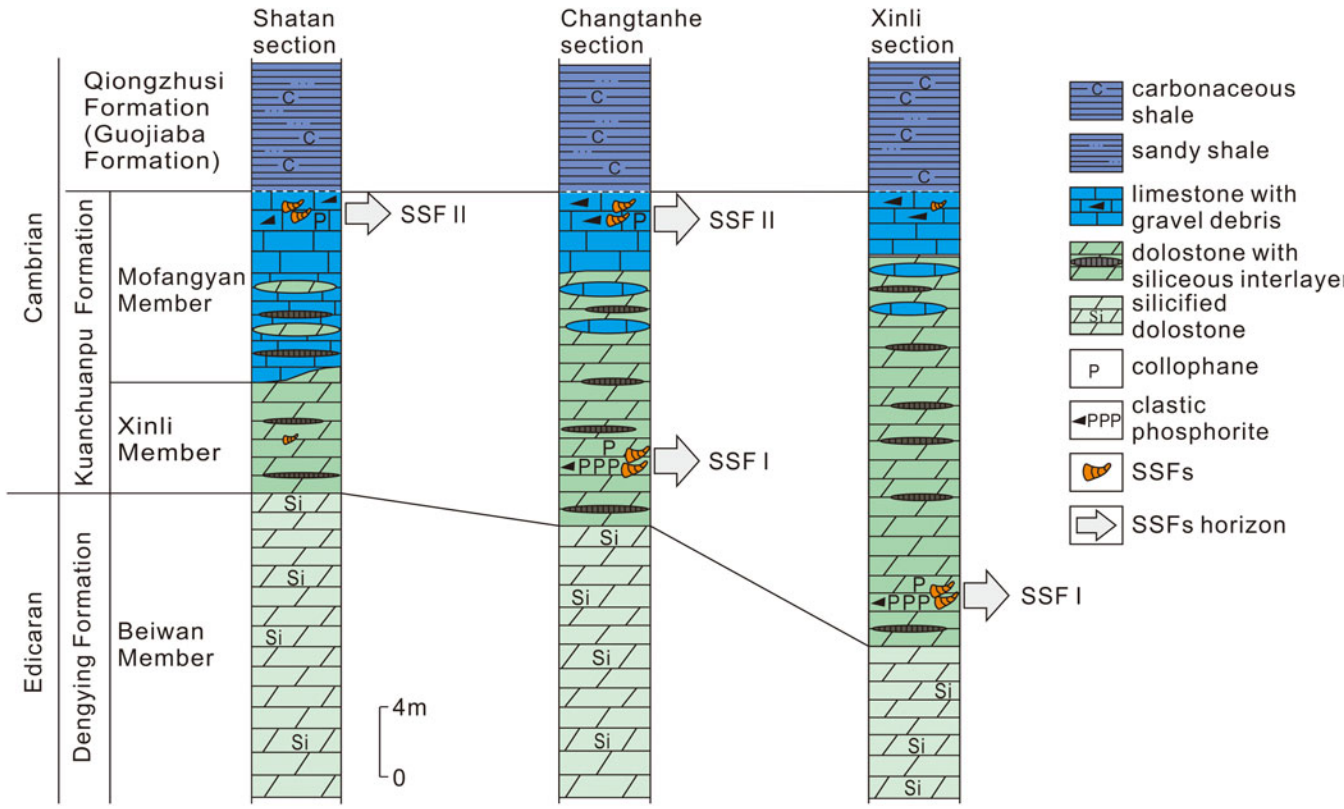

Figure 2. Stratigraphic columns of the cap-shaped molluscan shell-bearing sections in northeastern Sichuan, China.

studied under a Quanta250 FEG scanning electron microscope (SEM) at the State Key Laboratory of Oil Gas Reservoir Geology and Exploitation, Chengdu University of Technology.

Repository and institutional abbreviation.—All fossil specimens are deposited in the Palaeontology and Historical Geology Laboratory at the Institute of Sedimentary Geology, Chengdu University of Technology (CDUT), China. Station numbers in the text identify areas, sections, and identification numbers of the fossil samples, e.g., NC01-4-3 indicates Nanjiang area, Changtanhe section, and fossil sample 01-4-3.

The distribution of cap-shaped mollusks

Maikhanellids and other cap-shaped molluscan fossils collected from Fortunian stata in the Nanjiang region are assigned to the upper part of the first SSF assemblage zone (SSF I, the *Anabarites trisulcatus-Protohertzina anabarica* Assemblage Biozone). A younger bed contains many typical SSFs of SSF assemblage II (SSF II, *Paragloborilus subglobosus-Purella squamulosa* Assemblage Biozone).

SSF I occurs in the phosphatic beds of the Kuanchuanpu Formation (Xinli Member) in the Changtanhe and Xinli sections of the Nanjiang area. The cap-shaped mollusks of this assemblage exclusively consist of maikhanellids (Fig. 3), including *Maikhanella pristinis* (Jiang, 1980), *M. multa* Zhegallo in Voronin et al., 1982, *M. perelegans* Feng, Sun, and Qian, 2001, *M. cambrina* (Jiang in Luo et al., 1982), *M. superata* Feng, Sun, and Qian, 2001, and *M.* cf. *M. superata*.

Abundant cap-shaped molluscan shells were recovered from the upper bed of the Kuanchuanpu Formation (Mofangyan Member) in the northern Shatan and Changtanhe sections of Nanjiang County. The assemblage contains maikhanellids (Fig. 4), including *Purella tianzhushanensis* Yu, 1979, *Purella squamulosa* Qian and Bengtson, 1989, *Purella* sp., *Yunnanopleura longidens longidens* Feng, Sun, and Qian, 2001, *Y. biformis* Yu, 1987, and helcionellid univalved shells, e.g., *Igorella oblatis* Jiang, 1980 (see Table 1 for complete faunal list).

The distribution of maikhanellids in the two studied assemblages is generally consistent with those in other regions of the Yangtze Platform. At the southwestern margin of the Yangtze Platform, the maikhanellids are distributed in SSF Assemblage zones I and II (Fig. 5). In SSF I, cap-shaped molluscan shells are exclusively represented by *Maikhanella* Zhegallo in Voronin et al., 1982 in eastern Yunnan and Hubei (Luo et al., 1984; Feng et al., 2001; Yang et al., 2014; Steiner et al., 2020). However, the few *Maikhanella* species that range into SSF II are accompanied by other maikhanellid genera, such as *Purella* Missarzhevsky, 1974 and univalved helcionellids (Jiang, 1980; Luo et al., 1984; Feng et al., 2001; Yang et al., 2014). *Protoconus crestatus* Yu, 1979 always co-occurs with species of *Maikhanella* (Yang et al., 2014) and likely represents the steinkern preservation of *Maikhanella*. Here, we report *Maikhanella* occurring in the upper SSF I in Nanjiang County, confirming its range from SSF I to SSF II in other regions (Fig. 5). Other maikhanellid taxa, including *Purella* and *Yunnanopleura* Yu, 1987, and the helcionellid *Igorella* Missarzhevsky in Rozanov et al., 1969 occurred in

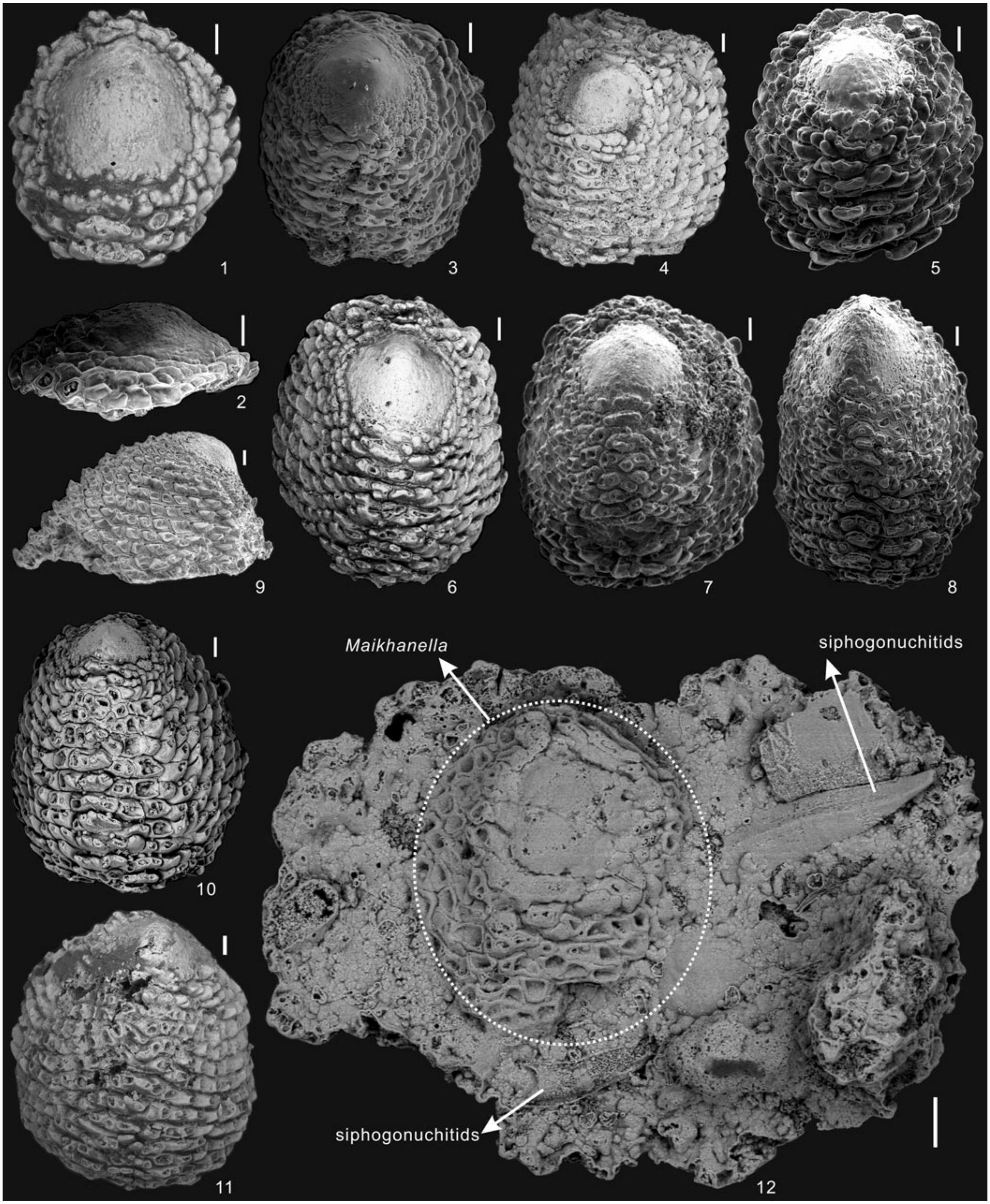

Figure 3. SEM micrographs of maikhanellid cap-shaped shells from the *Anabarites trisulcatus-Protohertzina anabarica* Assemblage Zone of the Changtanhe section, Nanjiang County, Sichuan: (**1, 2**) *Maikhanella pristinis* (Jiang, 1980) (NC01-04-1-2); (**3–5**) *Maikhanella multa* Zhegallo in Voronin et al., 1982: (**3**) NC01-04, from Pang et al., 2017a (reproduced with permission); (**4**) NC01-04-1-3; (**5**) NC01-04-1-4; (**6, 7**) *Maikhanella perelegans* Feng, Sun, and Qian, 2001: (**6**) NC01-04-2-9; (**7**) NC01-04-2-10; (**8**) *Maikhanella cambrina* (Jiang in Luo et al., 1982) (NC01-04-3-7); (**9, 10**) *Maikhanella superata* Feng, Sun, and Qian, 2001: (**9**) NC01-04-5-22; (**10**) NC01-04-5-23; (**11**) *Maikhanella* cf. *M*. *superata* (NC01-04-4-2); (**12**) a specimen of *Maikhanella* (NC01-04-3) preserved in a cluster with some spiphogonuchitid spines. Apical views (**1, 3, 4–8, 10, 11**), lateral views (**2, 9**). Scale bars = 0.1 mm.

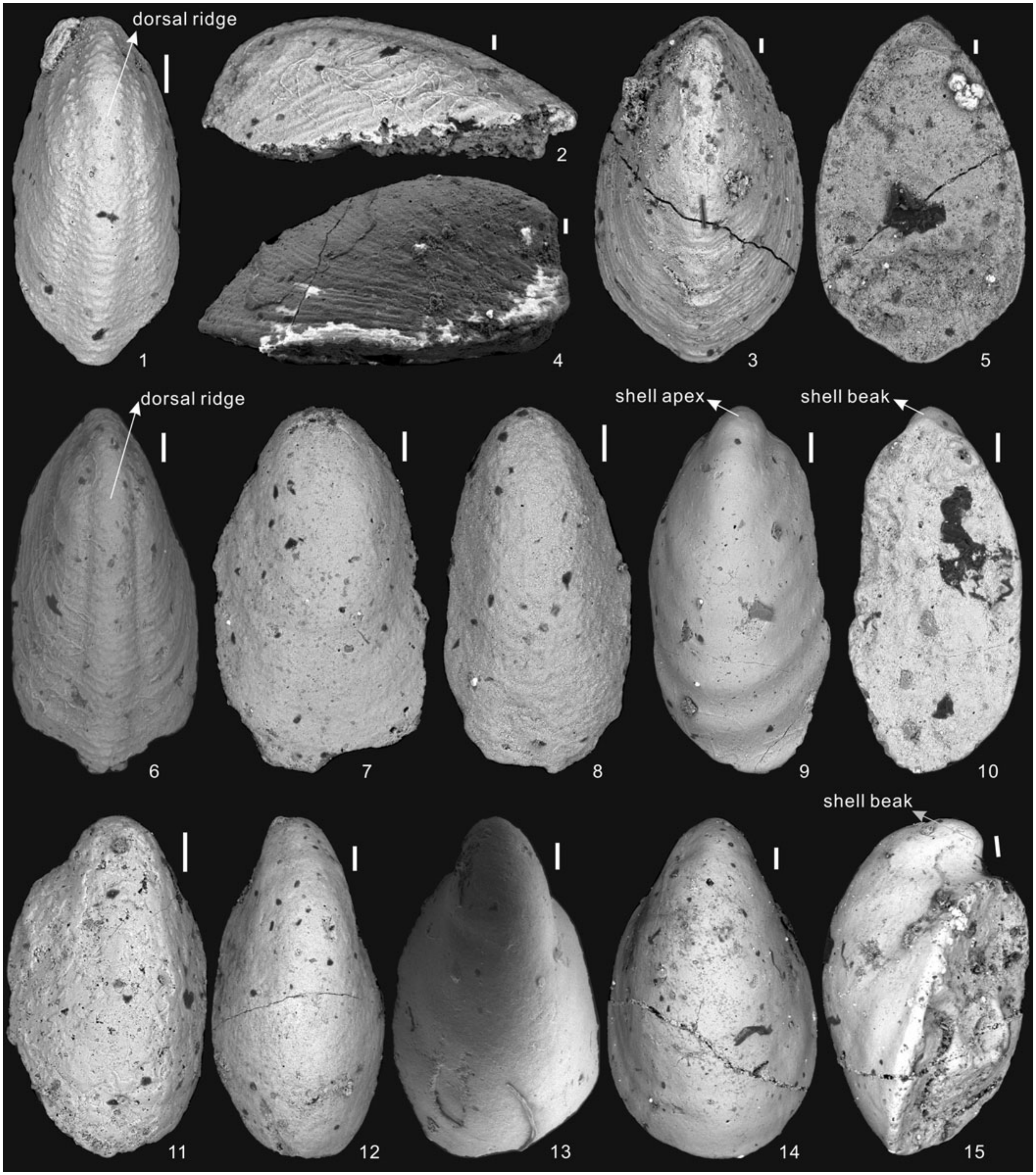

Figure 4. SEM micrographs of cap-shaped mollusks from the *Paragloborilus subglobosus- Purella squamulosa* Assemblage Zone of the northern Shatan section, Nanjiang County, Sichuan: (**1, 6**) *Purella tianzhushanensis* Yu, 1979: (**1**) NSQ6-10-3; (**6**) NSQ6-17; (**2–5**) *Purella squamulosa* Qian and Bengtson, 1989 (NSQ6-13-1); (**7, 8**) *Yunnanopleura biformis* Yu, 1987: (**7**) NSQ6-11-3; (**8**) NSQ6-11-4; (**9, 10**) *Yunnanopleura longidens* Feng, Sun, and Qian, 2001 (NSQ6-15-1); (**11**) *Igorella* sp., (NSQ6-18-1); (**12**) *Igorella oblatis* Jiang, 1980 (NSQ6-14-2); (**13–15**) *Igorella mioribis* Jiang, 1980: (**13**) NSQ6-S063, from Pang et al., 2017a (reproduced with permission); (**14, 15**) NSQ6-12-1. Apical views (**1, 3, 6–9, 11–14**), apertural views (**5, 10**), lateral view (**2, 4, 15**). Scale bars = 0.1 mm.

Table 1. The complete fauna list in these two fossil assemblage zones from the Nanjiang area of northern Sichuan.

Zone	cap-shaped molluscan fossils	other co-occurring SSF
SSF II	*Emeithella testudinaria* Qian, 1977 *Igorella mioribis* Jiang, 1980 *Igorella oblatis* Jiang, 1980 *Igorella* sp. *Obtusoconus paucicostatus* Yu, 1979 *Papilloconus explanatus* Feng, Sun, and Qian, 2001 *Purella* sp. *Purella squamulosa* Qian and Bengtson, 1989 *Purella tianzhushanensis* Yu, 1979 *Yunnanopleura biformis* Yu, 1987 *Yunnanopleura longidens* Feng, Sun, and Qian, 2001	*Chancelloria altaica* Romanenko, 1968 *Chancelloria irregularius* (Qian, 1989) *Coleolella fangxianensis* Li in Ding et al., 1992 *Conotheca nana* Qian, 1978 *Hexaconularia* sp. *Hyolithellus micans* (Billings, 1871) *Olivooides* cf. *O. alveus* Qian, 1977 *Paragloborilus mirus* He in Qian, 1977 *Paragloborilus subglobosus* Qian, 1977 *Parazhijinites guizhouensis* Qian and Yin, 1984 *Protohertzina unguliformis* Missarzhevsky, 1973 *Rhadochites scissus* Yang and He, 1984 *Siphogonuchites triangularis* Qian, 1977 *Turcutheca lubrica* Qian, 1978 *Zhijinites lubricus* Qian, Chen, and Chen, 1979
SSF I	*Maikhanella pristinis* (Jiang, 1980) *Maikhanella multa* Zhegallo in Voronin et al., 1982 *Maikhanella perelegans* Feng, Sun, and Qian, 2001 *Maikhanella cambrina* (Jiang in Luo et al., 1982) *Maikhanella superata* (Feng, Sun, and Qian, 2001) *Maikhanella* cf. *M. superata* (Feng, Sun, and Qian, 2001)	*Anabarites trisulcatus* Missarzhevsky in Voronova and Missarzhevsky, 1969 *Conotheca longiconia* Qian, 1978 *Conotheca subcurvata* Yu, 1974 *Conotheca* sp. *Hexaconularia* sp. *Hyolithellus tenuis* Missarzhevsky in Rozanov et al., 1968 *Lopochites* sp. *Protohertzina anabarica* Missarzhevsky, 1973 *Protohertzina unguliformis* Missarzhevsky, 1973 *Siphogonuchites chordoides* (Jiang, 1980) *Turcutheca lubrica* Qian, 1978

SSF II, of which only the helcionellid *Igorella* has been reported to range into the even higher SSF Assemblage Zone III (Fig. 4). Generally, it can be confirmed that *Maikhanella* is the earliest known shell-bearing molluscan taxon, succeeded by *Purella*, *Yunnanopleura*, and many univalved helcionellids, e.g., *Igorella*.

Morphological terminology and features

Cambrian small shelly fossils of the Yangtze Platform generally have undergone diagenesis, e.g., secondary phosphatization (Zhu et al., 1996; Chen et al., 2016; Pang et al., 2017b; Ji et al., 2019). Therefore, their primary shell ultrastructure is mostly obliterated by diagenesis and generally the soft tissues have decayed. Fortunately, the external morphological features of their cap-shaped shell plates are often relatively well preserved (Figs. 3, 4). Thus, it is tested here whether evolutionary relationships can be inferred from a morphometric analysis of early molluscan shells, even though their soft-tissue organization can be fundamentally different. Description of the characters for the morphometric analysis is given in Table 2.

Quantitative and qualitative characters.—The morphometric measurements include linear dimensions such as shell length (Ls), width (Ws), and height (Hs), and aperture length (La) and width (Wa) (see Table 2 for comparison).

The morphological terms of Jacquet and Brock (2016) have been applied: categorization of size is noted as micro (Ls < 5 mm), macro/small (≥ 5 mm to < 10 mm), or macro/large (≥ 10 mm). Height-length ratio (Hs:Ls) is used to define categories of height profiles, including low (≥ 0. 25 to < 0. 5), moderate (≥ 0. 5 to < 0. 75), high (≥ 0. 75 to < 1. 0), or tall (≥ 1. 0). Width-length ratio (Wa:La) of the aperture provides a measure of apertural outline and can be differentiated as laterally compressed (< 0. 25), elliptical (≥ 0. 25 to < 1), or circular (= 1). The ratio (Ls-La)*10/Ls represents the developing beak. In addition, the term ‘ovoid’ expresses that the aperture expands toward one end, and ‘subrectangular’ means with parallel sides.

Comparison of morphological characteristics.—Most taxa of maikhanellids, e.g., *Maikhanella* and *Purella,* have a highly radially symmetrical shell (Figs. 3, 4, 6). They all have ornament arranged in a concentric pattern around the shell apex. The apices are well developed and are located at the center or at the anterior/posterior edges of cap-shaped shells (the anterior/posterior orientation of apices remains uncertain until complete scleritomes are recovered). Some maikhanellids, e.g., *Maikhanella superata* (Feng, Sun, and Qian, 2001) and *Purella* spp., developed an inclined apex with a beak-like appearance. They all have a large aperture, the width of which is equal to the width of the shell. The inside of the shell did not preserve imprints of muscles or cells.

The maikhanellid taxa and univalved helcionellids of the different stratigraphical horizons show systematic differences in morphological characteristics. Later species of maikhanellids, e.g., *Maikhanella superata* (Figs. 3.9, 3.10, 6) are cyrtoconic to various degrees, whereas early species show low cap-shaped shells without cyrtoconic construction. The protrusions or scales on the surface of early maikhanellids are arranged in a concentric pattern around the shell apex, whereas later maikhanellids forms (e.g., *Purella*) have typical concentric ribs. The apex position and the morphological features of the beaks vary among taxa. The apices of *Maikhanella pristinis* and *M. multa* are located near the center of the relatively large and convex shells without beaks (Figs. 3.1–3.5, 6). The apices

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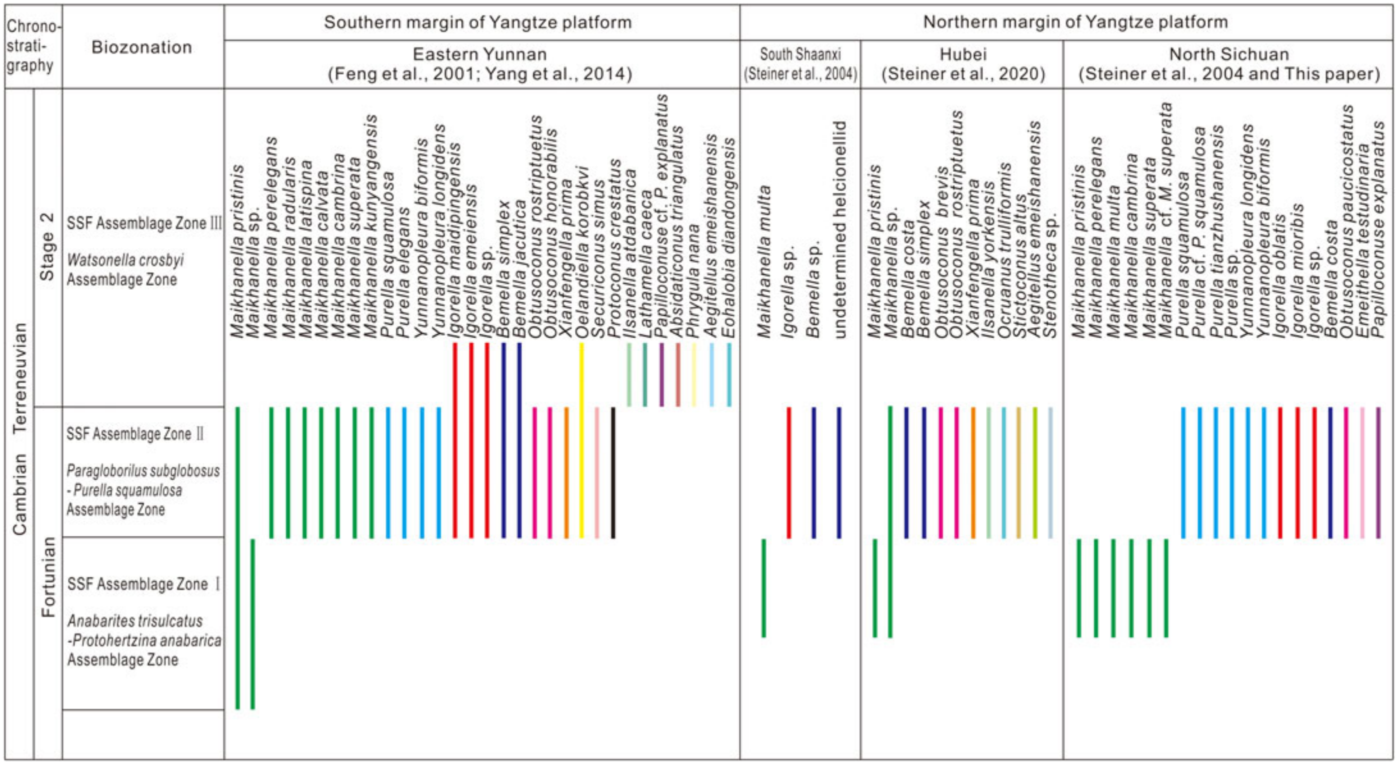

Figure 5. Stratigraphic distribution of univalve molluscan fossils on the Yangtze Platform. Taxa that do not otherwise appear in the text are: *Absidaticonus triangulatus* Yue in Xing et al., 1983, *Aegitellus emeishanensis* He in Yin et al., 1980, *Bemella costa* Zhou and Xiao, 1984, *Bemella jacutica* Missarzhevsky in Rozanov and Missarzhevsky, 1966, *Bemella simplex* Yu, 1979, *Igorella emeiensis* (Yu, 1987), *Igorella maidipingensis* (Yu, 1974), *Ilsanella atadabanica* (Missarzhevsky in Rozanov and Missarzhevsky, 1966), *Lathamella caeca* Liu, 1979, *Maikhanella calvata* (Jiang in Luo et al., 1982), *M. kunyangensis* (Feng, Sun, and Qian, 2001), *M. latispina* (Feng, Sun, and Qian, 2001), *M. radularis* (Qian and Bengtson, 1989), *Obtusoconus honorabilis* (Qian, Chen, and Chen, 1979), *Obtusoconus rostriptuetus* (Qian, 1978), *Oelandiella korobkvi* Vostokova, 1962, *Phrygula nana* (Chen and Zhang, 1980), *Purella elegans* Yu, 1979, *Strictoconus altus* Qian and Bengtson, 1989, and *Xiafengella prima* He and Yang, 1982.

Table 2. Features of maikhanellid and some other cap-shaped molluscan shells of SSF Assemblages I and II from Nanjiang County, Sichuan.

Zone	Genus	Shell	Aperture	Apex and Beak	Ornament
SSF II lower	*Igorella*	Almost symmetrical or slightly asymmetric cyrtoconic. Micro length (Ls = 0.65–1.61 mm), moderate height (Hs:Ls = 0.39–0.61). Steep and narrow anterior.	Ovoid (Wa:La = 0.48–0.90). Aperture length < shell length. Aperture width = shell width.	Apex large, smooth. Hooked beak-like apex bends toward anterior edge of aperture.	No protuberances or scales. Some concentric ornament evident.
	Yunnanopleura	Almost perfectly symmetrical cyrtoconic or ladle-shaped. Micro length (Ls = 0.72–1.65 mm) and low (Hs:Ls = 0.24–0.44). With steep, narrow anterior facet.	Ovoid (Wa:La = 0.49–0.76). Aperture length slightly smaller than or equal to shell length. Aperture width = shell width.	Apex large, smooth. Pointed beak-like apex at or slightly protruding from anterior edge of aperture.	No protuberances or scales. Small amount of concentric ornament.
	Purella	Almost perfectly symmetrical cyrtoconic or ladle-shaped. Micro length (Ls = 0.50–1.30 mm) and moderate height (Hs:Ls = 0.40–0.59). Highest part of shell often near posterior edge of apex. With steep, narrow anterior part.	Ovoid (Wa:La = 0.46–0.68). Aperture length slightly smaller than or equal to shell length. Aperture width = shell width.	Apex small, smooth. Pointed beak-like apex at or slightly protruding from anterior edge of aperture.	Protuberances or scales are long strips arranged in a concentric pattern. Larger scales present in subapical field. Large, protuberant dorsal ridge on center of shell surface.
SSF I upper	*Maikhanella*	Almost perfectly symmetrical cyrtoconic. Micro length (Ls = 1.10-1.70 mm) and moderate height (Hs:Ls = 0.46-0.65. Highest part of shell often near posterior edge of apex.	Elliptical, subrectangular, or ovoid (Wa:La = 0.57–0.87). Aperture length slightly smaller than or equal to shell length. Aperture width = shell width.	Apex often near anterior edge; exposed area varying in size. A tip like a shell beak present on anterior side of apex.	Prominent protuberances or scales on surface, concentric around apex.
lower	*Maikhanella*	Almost perfectly symmetrical cap-shaped. Micro length (Ls = 0.82–1.38 mm) and low height (Hs:Ls = 0.27–0.45. Highest part of shell usually near center of apex.	Circular or elliptical (Wa:La = 0.76–0.96). Aperture length = shell length. Aperture width = shell width.	Apex typically subcentral to anterior; most with larger exposed areas. No prominent beak-like apex.	Prominent protuberances or scales on surface, arranged in concentric pattern around apex.

of the later species of *Maikhanella*, e.g., *M. superata,* lie near the anterior/posterior edge of the shell with a prominent tip creating a beak-like structure (Figs. 3.9, 3.10, 6). The apices of *Purella* and *Yunnanopleura* lie at the anterior/posterior edge of the shell with a small, sharp beak-like appearance (Figs. 4.1–4.10, 6).

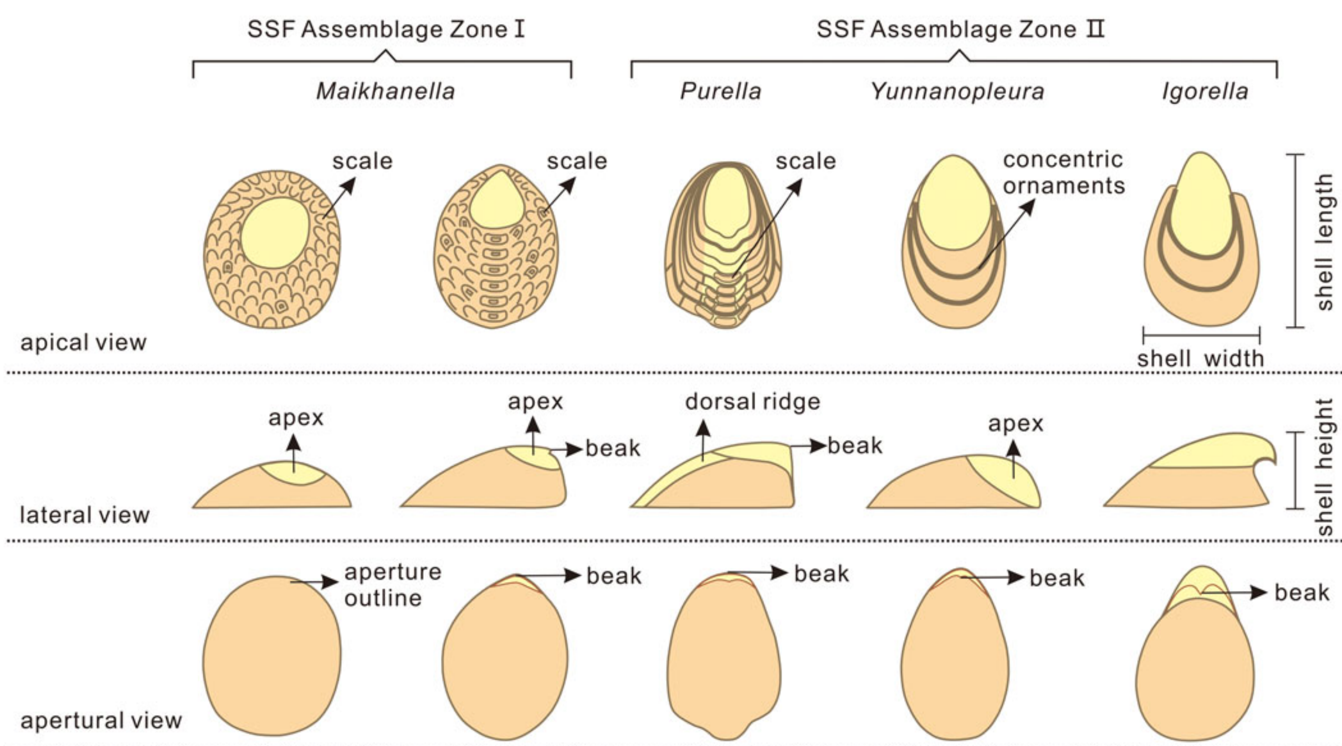

Figure 6. Comparison of morphological aspects of the apices and beaks of cap-shaped mollusks from the Fortunian Age of the early Cambrian.

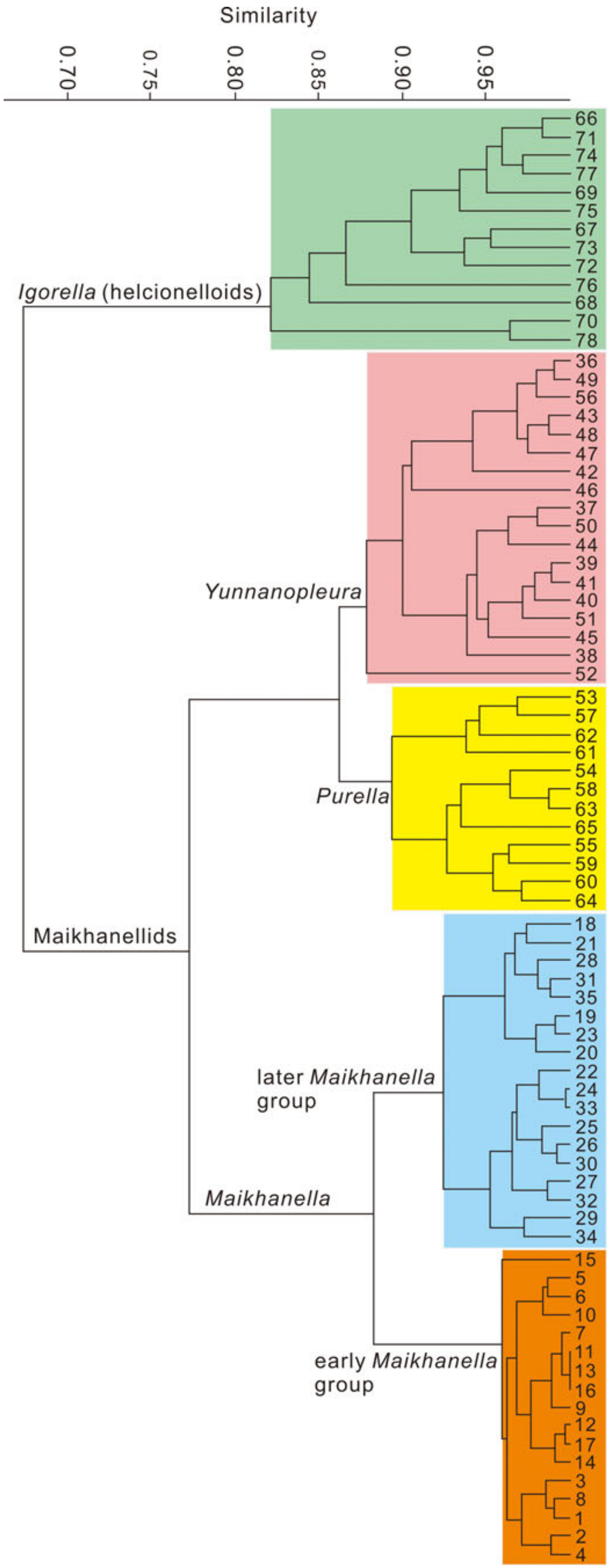

Figure 7. Cluster analysis chart of the shell characteristics of the main univalve fossils from Fortunian strata (see Supplemental Table 1 for the data).

Cluster analysis.—A cluster analysis based on the character matrix in Supplementary Table 1 was carried out using Past 3 software (Huang et al., 2013) with Bray-Curtis Distance. The clustering results (Fig. 7) show that the studied fossils can be categorized into five groups, the early *Maikhanella* (*M. multa, M. pristinis*, etc.), the later *Maikhanella* (*M. cambrina, M. superata*, etc.), the *Purella*, the *Yunnanopleura*, and the *Igorella* groups. This clustering result is consistent with the results of empirical morphological observations (Table 2). Among them, the early and the late *Maikhanella* groups are closely related to each other and the *Purella* group is clustered with the *Yunnanopleura* group (similarity > 0.75). In contrast, the *Igorella* group is clustered more distantly from all maikhanellid groups (similarity > 0.65).

The similarity pattern presented in Figure 7, together with stratigraphic occurrences, suggests that the *Igorella* group (helcionelloids) is not a direct descendant of maikhanellids, although the cap-shaped shells bear some similarity. The shell structure of *Maikhanella*, with a mesh-like pattern on the inner side of shell, is quite different from that of *Igorella*.

Morphological evolution in early Cambrian cap-shaped mollusks

In general, the diversity of cap-shaped mollusks increased throughout the Terreneuvian Epoch (Fig. 5). In the first assemblage, maikhanellids (e.g., *Maikhanella*) developed large cap-shaped shells with some prominent ornament of spinose structures (Fig. 3). Studies on molluscan sclerites demonstrate the high morphological variability in biomineralized molluscan skeletons (Parkhaev, 2008). Studies of *Halkieria* Poulsen, 1967 and *Maikhanella* resulted in a reconsideration of the idea that coeloscleritophoran and molluscan exoskeletons are not homologous (Bengtson, 1992). The scales of maikhanellid shells are in principle comparable to the co-occurring tubular sclerites of siphogonuchitids (Qian, 1999; Liu et al., 2016), but are strikingly different from the ornamentation of univalved helcionellid shells. Here, we also report a specimen of *Maikhanella* preserved in a cluster with some spiphogonuchitid spines (Figs. 3–12), which supports the hypothesis that sclerites of *Maikhanella* and *Lopochites* Qian, 1977 or *Siphogonuchites* Qian, 1977 belonged to the same scleritome.

The apical parts of maikhanellid shells did not reveal protoconchs, as is typical in many helcionellid species (Parkhaev, 2017). This indicates that the early ontogenetic development of maikhanellids and helcionellids was different. The helcionellids developed a single shell early that covered the larva, whereas the potentially multiple biomineralized shells of maikhanellids might have developed at a slightly later stage, covering only part of the dorsal integument. In particular, maikhanellids are distinct from helcionellids by their scaly shell ultrastructure, the lack of a protoconch, and symmetric construction.

It is assumed here that the scleritome of maikhanellids was organized as in other stem-group aculiferans, with one or two of the large, cap-shaped shells anteroposteriorly positioned on a slug-like soft body. Besides the large cap-shaped shell plates, the maikhanellid scleritome had numerous hollow and elongated

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sclerites of siphogonuchitids, e.g., *Lopochites* and *Siphogonuchites,* arranged in concentric zones, and covered the dorsal side of mantle between the cap-shaped maikhanellid plates. Although no complete scleritomes or soft parts have been found for maikhanellids with high cap-shaped shells, such cap-shaped shell plates have been documented in many scleritomes, e.g., *Halkieria* (Vinther, 2015), *Calvapilosa* Vinther et al., 2017, *Oikozetetes* Conway Morris, 1995 (Paterson et al., 2009; Jacquet et al., 2014), and *Orthrozanclus* Conway Morris and Caron, 2007 (Zhao et al., 2017). Other enigmatic cap-shaped shells of SSF II and SSF III, e.g., *Ocruranus finial* Liu, 1979, *Ocruranus trulliformis* (Jiang, 1980), and *Eohalobia diandongensis* Jiang in Luo et al., 1982, could represent cap-shaped shell plates of the stem group Aculifera as well. This preliminary hypothesis is supported by the fact that maikhanellids and siphogonuchitids (e.g., *Lopochites*, *Siphogonuchites*) co-occur in the same strata and are closely associated in some specimens (Figs. 3–12). The morphology of the larger protrusions or scales of the maikhanellids is very similar to the morphology and construction of siphogonuchitids.

In SSF II, the diversity of maikhanellids (e.g., *Purella* and *Yunnanopleura*) and in particular those of the helcionellids (e.g., *Igorella* and *Obtusoconus* Yu, 1979) increased considerably (Fig. 4), thereby demonstrating a stepwise expansion in generic diversity. The stepwise increase in generic diversity in northern Sichuan is consistent with the early–mid Meishucunian trend in diversity increase on the Yangtze Platform (Li et al., 2007). Moreover, this diversity increase is comparable with the global diversity increase through the Nemakit-Daldynian to the Tommotian (Li et al., 2007; Maloof et al., 2010; Kouchinsky et al., 2012, Guo et al., 2014). This pretrilobitic diversity increase, which is mainly due to the diversification of SSFs, has been interpreted as the first stage (Qian, 1999) or the first pulse (Maloof et al., 2010) of the Cambrian Bioradiation Event.

The overall shape, symmetry, apical appearance, and scaly ornamentation of the maikhanellids provide key parameters for the discussion of the morphological evolution.

(1) Most maikhanellids developed one or two symmetric cap-shaped shell plates with a low profile. Later forms of maikhanellids have higher, symmetric cap-shaped shells with stronger inclination of the apex toward the anterior/posterior edge, e.g., in *Maikhanella superata*. This kind of higher cap-shaped shell plate is also common in univalved helcionellids, e.g., *Igorella oblatis* or *Securiconus simus* Jiang, 1980; in addition, these univalved shells are often slightly asymmetric.

(2) The position of the apex and the development of a beak-like apex varied among different genera. The apex of *Maikhanella multa* (or *M. pristinis*) is located near the center of the shell with no evident beak. The apex of the later species of *Maikhanella*, e.g., *M. superata,* lies near the anterior/posterior facet of the shell, which is laterally contracted resulting in a beak-like apex on the anterior/posterior side. The apices of *Purella* and *Yunnanopleura* lie at the anterior/posterior facet of the shell forming a small but prominent beak-like apex. The univalved shell developed in *Igorella* is similarly cap-shaped with a beak-like apex, however, the apex noticeably extends beyond the front edge of the aperture and bends toward the front part of the aperture.

(3) The protrusions or scales on the surface of maikhanellid shells are arranged in concentric pattern around the shell apices, which culminate in the appearance of typical concentric ornamentation. The protrusions and scales have a similar construction as the co-occurring disarticulated sclerites of sinosachitids. The inner side of slightly eroded *Maikhanella* shells appears like a mesh. Other enigmatic cap-shaped shells of SSF II and SSF III, e.g., *Ocruranus finial, O. trulliformis*, and *Eohalobia diandongensis*, could represent cap-shaped shell plates of the stem group Aculifera as well. These taxa developed shell plates with concentric ornamentation typical of *Igorella* or other related helcionellids. The cap-shaped plates grew by marginal accretion, adding mineralized areas in a concentric pattern.

Generally, it can be recognized that *Maikhanella* is the earliest known shell-bearing molluscan taxon, succeeded by *Purella*, *Yunnanopleura*, and many univalved helcionellids, e.g., *Igorella*. The morphological similarity study (Fig. 7), the dissimilarity in shell structure (mesh vs. solid shell), and the stratigraphic occurrence pattern suggest that the *Igorella* group (helcionelloids) is not a direct descendant of the maikhanellids. These distinctive features and progressive changes of the earliest molluscan shells provide new evidence that the genus *Maikhanella* is the most primitive stem group of aculiferan discovered so far. An evolutionary trend is proposed for cap-shaped mollusks during the Fortunian Age of the Cambrian on the Yangtze Platform, based on the overall shape, symmetry, appearance of apex, and the presence of scaly ornamentation in maikhanellids (Fig. 8). The earliest molluscan stem group representatives in the Ediacarian and earliest Cambrian likely had a slug-like body plan organized in concentric zones, similar to that of *Kimberella* Wade, 1972. This was likely a plesiomorphic character shared with the brachiopod stem group (Steiner et al., 2021). One main apomorphy of all molluscan clades is the presence of a radula (Fig. 9). Two lineages have been derived from soft-bodied Ediacaran ancestors without sclerites: one developing unmineralized multiple scales (wiwaxiids clade), and the other developing a chitinous cuticle with multiple carbonatic sclerites and aesthete canal systems (stem group Aculifera) (Fig. 9). The earliest representatives of the stem group Aculifera were the maikhanellids and related siphogonuchitids. Maikhanellid animals had slug-like bodies covered by numerous spinose and one or two platy, cap-shaped sclerites. The cap-shaped sclerites of the early maikhanellids were covered by coarser scaly ornamentation. In later maikhanellids (e.g., *Purella*) the scaly ornamentation was reduced and more solid cap-shaped sclerites formed. As the protrusions (scales), apices, and beak-like structures were transformed chronologically, the diversity of molluscan taxa increased. The apical location in these shells shows a gradual progression as it shifted from a subcentral position to the anterior edge of shell. Simultaneously, the apex changed from a convex circle into a pointed shape, with a progressively more pronounced beak-like structure and development of a moderately high cyrtoconic morphology. Later, the helcionellids developed a single solid shell without an aesthete canal system (Fig. 9) beginning to appear slightly asymmetric compared to the symmetric cap-shaped sclerites of maikhanellids. This is likely related to the fact that the soft tissues had to be completely covered by a single shell and the body plans and organ placement were adapted to

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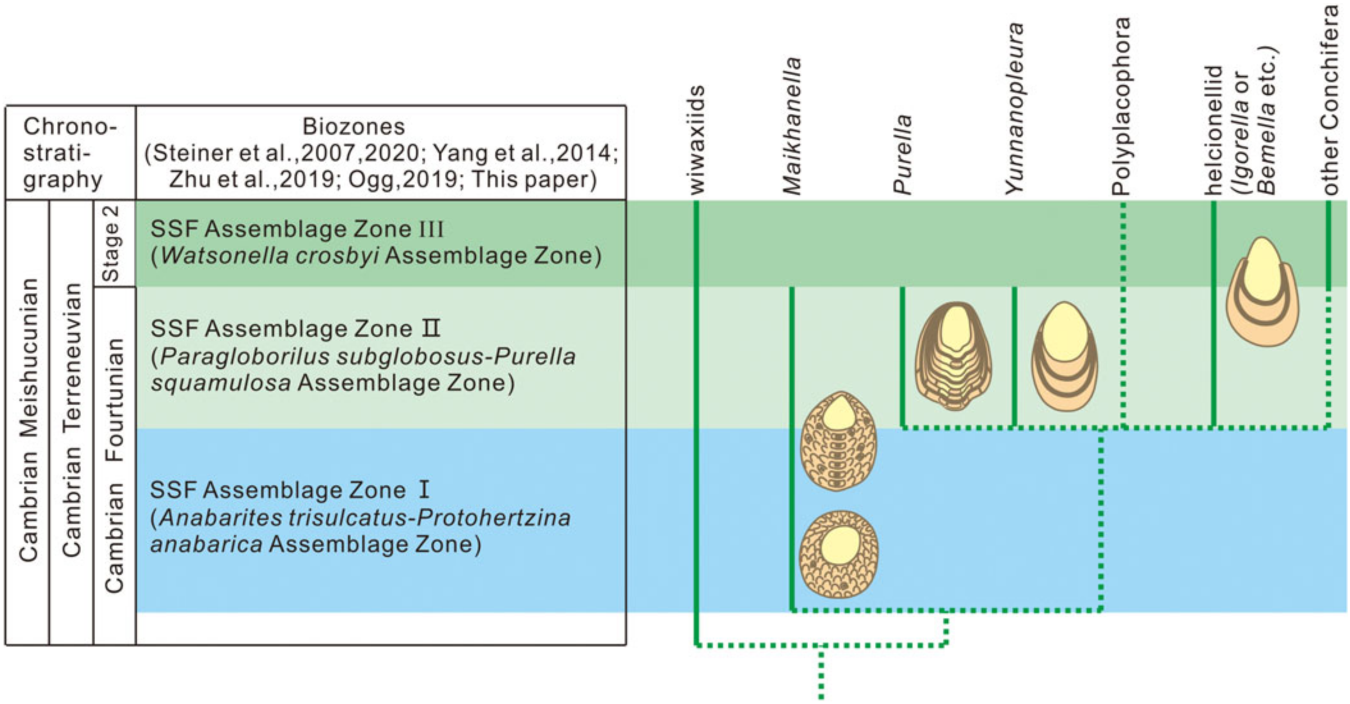

Figure 8. Hypothetical evolutionary trend of cap-shaped mollusks during the Fortunian Age of the Cambrian on the Yangtze Platform.

this. The general trend from unmineralized slug-like ancestral mollusks, via stem group aculiferans (partially covered by spinose and few larger cap-shaped sclerites of loosely or more consolidated tubular scales) toward helcionellids (with a single solid shell) was likely driven by the strongly increasing predatory pressure during the Cambrian Bioradiation Event.

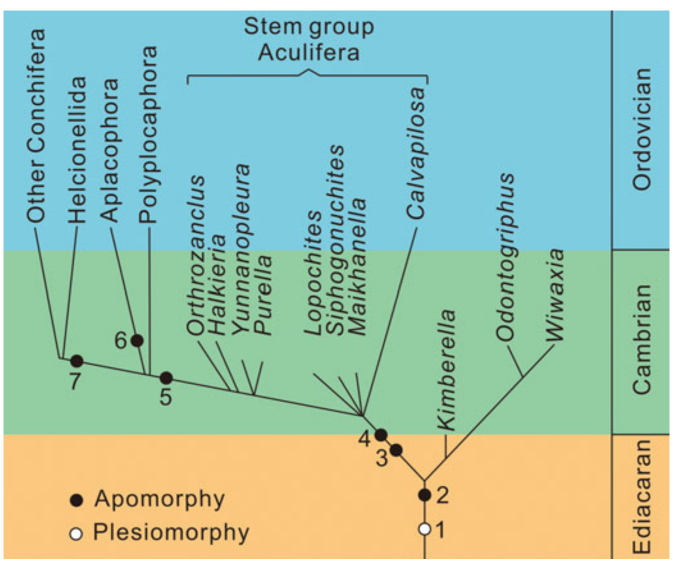

Figure 9. Phylogenetic tree of aculiferan evolution based on the record of cap-shaped mollusks from the Fortunian Age of the Cambrian and the hypothesis of evolution of apomorphic characters: (**1**) slug-like body plan organized in concentric zones; (**2**) radula; (**3**) dorsal chitinous/ proteinaceous cuticle with multiple carbonatic sclerites and a ventral foot and mantle; (**4**) aesthete canal system; (**5**) differentiation of hypostracum for a fixation of platy sclerites; (**6**) reduction of carbonatic sclerites; (**7**) single sclerite with hypostracum of nacre and reduction of aesthete canals (modified from Vinther et al., 2017). Taxa that do not otherwise appear in the text are: *Lopochites* Qian, 1977, *Odontogriphus* Conway Morris, 1976, and *Wiwaxia* Walcott, 1911.

In general, the stratigraphic analysis of the sclerites of early Cambrian mollusks shows a continuous increase in taxonomic diversity and morphological evolution of various aspects. The variations possibly indicate environmental and ecological adaptions during the Cambrian Bioradiation Event. In contrast to the biomineralized mollusks that first occurred in early Cambrian carbonate settings, the Ediacaran biota with the potential soft-bodied stem group mollusk inhabited sandy environments commonly sealed by microbial mats. Predatory pressure during this time was low, so that biomineralized skeletons did not provide an advantage in selectivity. The early Cambrian Mollusca, e.g., the maikhanellids, began to secrete calcareous (mostly aragonitic) skeletons to protect their soft bodies from oceanic predators. This hypothesis unifies the existence of the enigmatic soft-bodied Ediacaran stem group mollusk and the early Cambrian biomineralized mollusks, which can help resolve Darwin's paradox about the unique biological evolution at the Precambrian-Cambrian boundary.

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Data availability statement

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.vt4b8gtts.

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