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New Early Cambrian Maikhanellids (Mollusca) from Zhangjiagou Section, South Shaanxi, China

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Abstract: A new maikhanellid genus, *Totornatus* gen. nov., from the Lower Cambrian (Fortunian Stage) of Zhangjiagou section at Xixiang County, southern Shaanxi Province, South China, is based on a new taxon *T. strigatus* gen. et sp. nov. Although showing similar morphology with a cap-shaped shell and an oval aperture to other members of the family, the new species differs from previous maikhanellids in its smooth apex. The apical field consists of dense, small, round or oval granules, which gradually merge to bigger, elongated, scale-like protrusions toward the apertural margin. On this basis, we establish *Totornatus strigatus*, which shows a transverse groove in two-ninths of its shell. This result enriches the diversity of the earliest mollusks and maikhanellids.

Key words: invertebrate paleontology, mollusks, Maikhanellidae, Fortunian, Zhangjiagou, Shaanxi Province

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1 Introduction

The unique event and the reasons behind the Cambrian explosion have been an intriguing subject for paleontologists during the past decades (e.g., Zhang and Shu, 2014; Bicknell and Paterson, 2018). At the beginning of this Cambrian event, abundant skeletonized microfossils emerged, i.e., small shelly fossils (SSFs) (Erwin et al., 2011). Of these, many early mollusks have been found near the Precambrian–Cambrian boundary (Li et al., 2011). But whether a single fossil specimen is an individual animal or, alternatively, a part of an unknown or known animal's anatomy has been challenging to determine (Feng et al., 2001). Moreover, the preservation forms of these fossil types are initially chitin or a biomineralized exoskeleton, lacking evidence of soft-body structures. Therefore, the exact taxonomic position, classification and phylogenetic relationships of many are still controversial. The diagnostic features of a maikhanellid comprise an SSF with peculiar scaly ornamentation (Yu, 1987) and two or three shell layers within the complete shell wall (Voronin et al., 1982; Bengtson, 1992; Feng et al., 2001, 2002); furthermore, each scale also have two layers (Yu, 1987; Feng and Sun, 2003).

The family Maikhanellidae was established in 1989 by Russian paleontologist V. V. Missarzhevsky (Missarzhevsky, 1989) based on the genus *Maikhanella* Zhegalo (in Voronin et al., 1982). Originally, maikhanellids were thought to include *Purella* Yu, 1979, when fossils were found in Tomotian strata of the Siberian platform and preserved in the form of an inner mold without ornamentation (Missarzhevsky, 1974). Later, further taxa such as *Lepidites* (Zhong, 1977), *Purella* (Yu, 1979), *Cassidina* (Jiang, 1980), *Ramenta*, *Canopoconus*, *Maikhanella* (Jiang, 1982; Voronin et al., 1982) were subsequently discovered in Yunnan, Hubei and Shaanxi provinces, China. According to the different shell shapes, heights, and ornamentation feature types of the Maikhanellidae: *Maikhanella* and *Purella* (Bengtson, 1992), two subfamilies with six (Feng et al., 2001) or seven genera (Ponder et al., 2007; Parkhaev and Demidenko, 2010) have been described.

Scholars have recently found abundant and beautifully preserved maikhanellids from the Kuanchuanpu Formation (Fm.; ca. 535 Ma) at Zhangjiagou section, Xixiang County, southern Shaanxi province, South China (Fig. 1). Six genera had previously been identified there by individual shell shape, ornamentation types, and morphological measurements (Shao et al., 2015; Liu et al., 2016; Qin et al., 2019).

Here we describe a new maikhanellid, *Totornatus strigatus* gen. et sp. nov., from the Kuanchuanpu Fm. at Zhangjiagou section. This discovery will impact the diversity of maikanellids and provide significant evidence regarding the earliest evolution of mollusks.

2 Geological Setting and Methods

Specimens were extracted from a phosphatic limestone in the lower part of the second member of the Kuanchuanpu Fm., Zhangjiagou section, Xixiang County, southern Shaanxi Province, South China (Fig. 1). The lithostratigraphy and biostratigraphy of the Zhangjiagou section were studied by Li (1984) and Steiner et al. (2004; 2007). The same locality and horizon have previously

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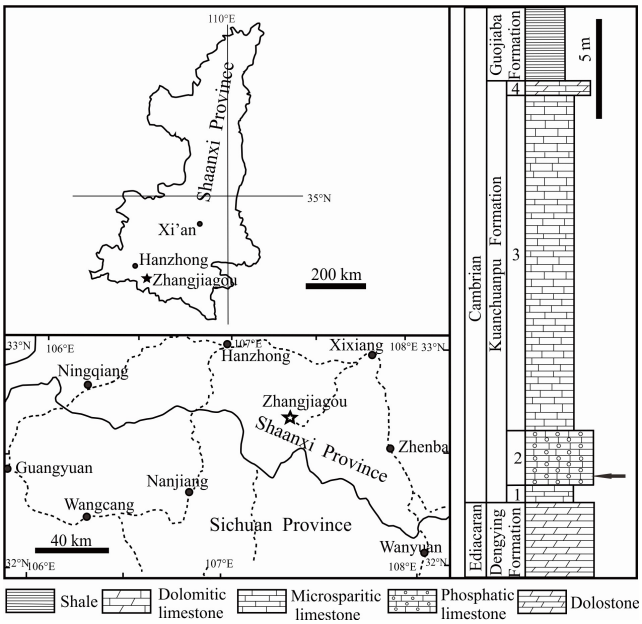

Fig. 1. Location map and stratigraphic column of the Zhangjiagou section in southern Shaanxi Province.
The key horizon yielding the current specimens is denoted by an arrow.

yielded abundant and beautifully preserved microfossils, such as specimens of *Olivooides* (Liu et al., 2014a; Steiner et al., 2014); Liu et al., 2017; Shao et al., 2018; Shao et al., 2019a; Steiner et al., 2014), *Pseudooides* (Shao et al., 2018), the oldest known priapulid-like cycloneuralian, as well as other scalidophorans (Liu et al., 2014b, 2019; Shao et al., 2016, 2018, 2019b; Wang et al., 2019, 2020) and a plausible deuterostomian (Han et al., 2017). The fossil-bearing horizon correlates to the *Anabarites trisulcatus–Protohertzina anabarica* assemblage biozone (Steiner et al., 2007), which has an estimated date of about 535 Ma (Steiner et al., 2007, 2014) and falls within the Fortunian Stage (Peng et al., 2012).

Rock samples from the key horizon at the Zhangjiagou section (Fig. 1) were cracked into football-sized pieces. Each rock sample was put in a plastic pail or basin with a capacity of 20 L and then macerated using ~8% dilute acetic acid; the cycle of sieving and changing acid requires three to seven days, depending on the temperature (ambient temperature ~40°C in summer, ~20°C in winter). The undissolved residues were dried naturally and then handpicked under a binocular microscope. Microfossils were picked out and mounted on aluminum stubs for observation under a Hitachi S4800 environmental scanning electron microscope at Chang'an University, Xi'an. The figures were processed using Adobe Photoshop CS5.

The studied specimens are now deposited at the University Museum of Chang'an University.

3 Systematic Paleontology

3.1 Taxonomy of Maikhanellidae

The classification of the maikhanellids has been controversial since they were first reported. Moreover, the preservation forms of these fossils are in chitin or as biomineralized exoskeletons, and they lack evidence of soft body structure (Feng et al., 2001). The specimens were initially classified as Monoplacophora mollusks because of the unique shell shape (Jiang, 1980). In more recent times, some researchers have still used the classification as monoplacophorans (Voronin et al., 1982; Yang and He, 1984; Feng et al., 2001; Ponder et al., 2007; Parkhaev and Demidenko, 2010). Latterly, they have been considered to belong to the Polyplacophora (Yu, 1987) or Gastropoda (Luo et al., 1982; Liu, 1987). Then, the Maikhanellidae was established as a family within a polyphyletic group of order rank (Missarzhevsky, 1989). Later research showed that the cross-laminar layer of the shell is typical of various molluskan groups (Feng and Sun, 2003).

Bengtson (1992) proposed that *Maikhanella* is probably a junior synonym of *Siphogonuchites* or *Lopochites*, both of which are derived from halkieriids. Halwaxiids, including *Australohalkieria*, *Drepanochites*, *Eohalobia*, *Halkieria*, *Lomasulcachites*, *Ninella*, *Ocruranus*, *Oikozetetes* (Jacquet et al., 2014), *Orthrozanclus*, *Sinosachites*, and *Siphogonuchites*, have been assigned variously to stem-group mollusks, stem-group annelids or brachiopods, so that the maikhanellids were not considered to be in the crown group for mollusks (Conway Morris and Caron, 2007). Later research assumed that *Halkieria* and *Siphogonuchites* were stem-group Polyplacophora and Aplacophora (Vinther et al., 2017). However, some scholars still identified halkieriids as stem-group mollusks, or both stem-group brachiopods and phoronids (Zhao et al., 2017), or just stem-group brachiopods (Sun et al., 2018).

In summary, there is still great controversy about the phylogenetic relationship of maikhanellids. For now, we leave the taxon in open nomenclature regarding the phylum, class and order level until more conclusive evidence is available.

3.2 Taxonomy of new taxon

Phylum, Class and Order uncertain

Family Maikhanellidae Missarzhevsky, 1989

Type genus *Maikhanella* Zhegallo in Voronin et al., 1982.

Other genera *Purella* Missarzhevsky, 1974; *Xiadongoconus* Yu, 1979; *Ramenta* Jiang, 1982; *Yunnanopleura* Yu, 1987; *Mediata* Feng (in Feng et al., 2001).

New genus: *Totornatus* gen. nov.

Derivation of name: Latin: *Toti-*, the entire surface of the shell, and *ornatus*, 'ornate' for the scaly ornamentation.

Type and only species: *Totornatus strigatus* gen. et sp. nov.

Diagnosis: The same as for new species (below) with scales on the edge more slender and parallel to the shell margin.

Remarks: The most striking difference between this new monotypic genus and other previously described maikhanellids is the scaly ornamentation that covers the

entire external shell surface (Fig. 3a–d). The characteristics of new genus are clear: the apical field of the shell consists of dense, small, round, or oval granules that gradually pass into larger, elongated, scale-like protrusions toward the apertural margin.

***Totornatus strigatus* gen. et sp. nov.**

(Fig. 2; Fig. 3e–m)

Derivation of name: Latin: *strigatus*, meaning 'a transverse band', for the transverse groove.

Diagnosis: Small low-capped shell, with all lengths are less than 1 mm. Aperture from circular to oval, elliptical or pyriform. Anterior margin flat, straight or slightly concave. Ornamentation of slightly convex or flat scales (15–150 μm) covers entire external surface; small and dense spherulitic texture on the apical field changing to elongate protrusions on apertural margin with a central concavity having one to three smaller papillate protrusions. Shell divided into two parts by a transverse groove that straddles the shell and is fused to both sides; anterior part of shell accounting for about two-ninths. Each scale nearer towards the apertural margin contains one or two holes filled with phosphate matrix.

Holotype: UMCU XXMH1458 (Fig. 2a).

Material: 11 specimens; paratypes XXMH1457; XXMH1459–1467.

Occurrence: Lower Cambrian Kuanchuanpu Fm. (Fortunian Stage: Terreneuvian Series), Zhangjiagou

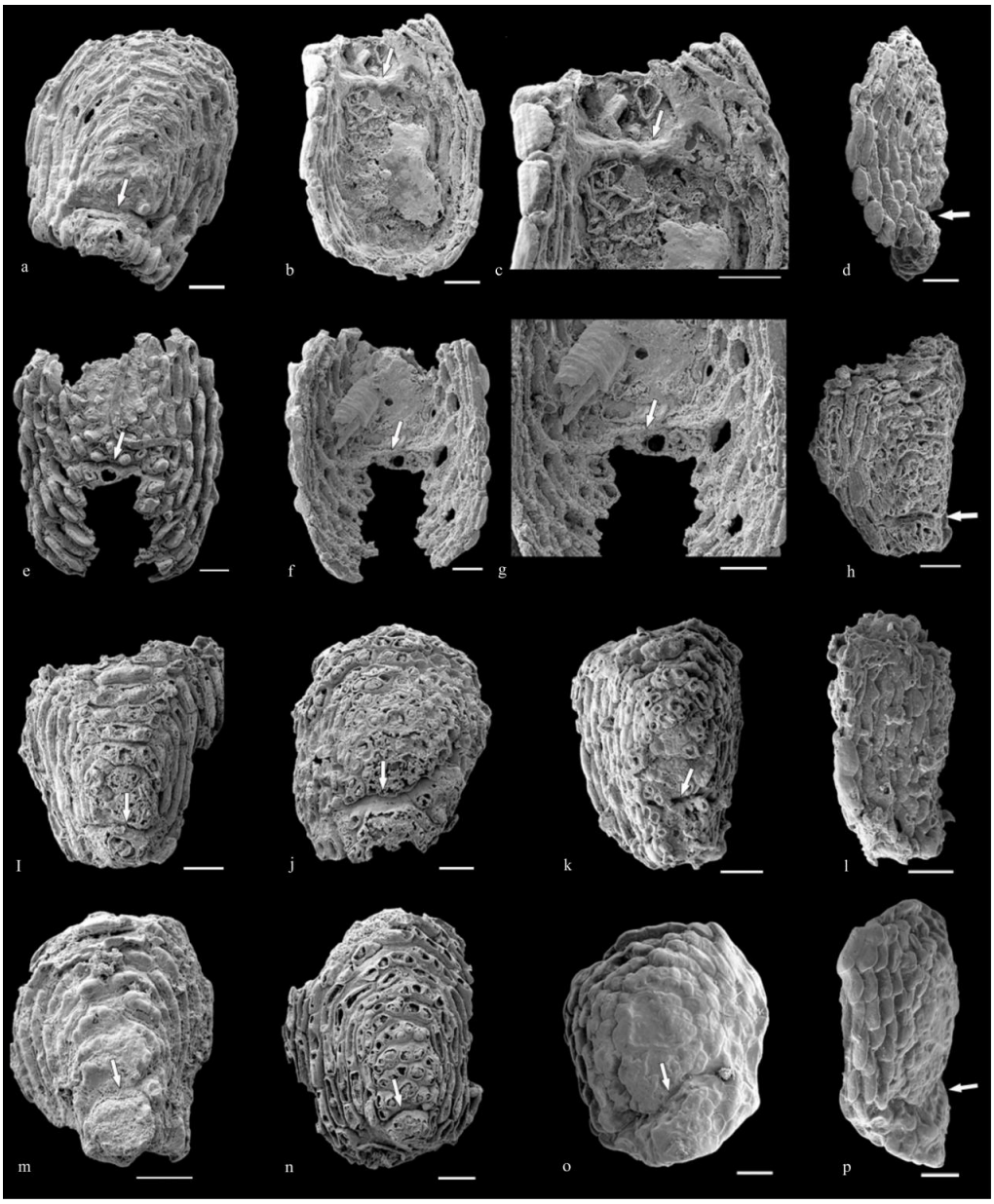

Fig. 2. Characteristics of *Totornatus strigatus* gen. et sp. nov. from the Zhangjiagou section, Xixiang, southern Shaanxi.
Valves oriented with anterior to top (b, c) or bottom of photographs: (a) XXMH1458; (e) XXMH1459; (i) XXMH1460; (j). XXMH1461; (k) XXMH1462; (m) XXMH1463; (n) XXMH1464; (o) XXMH1465; (b, f) are an internal view of (a, e); (c, g) enlarged images of (b, f); (d, h, l, p) are the lateral view of (a, i, k, o); marked by white arrows, respectively, showing a transverse groove. The entire surface of the shell is covered with characteristic scales. Scale bar = 100 μm.

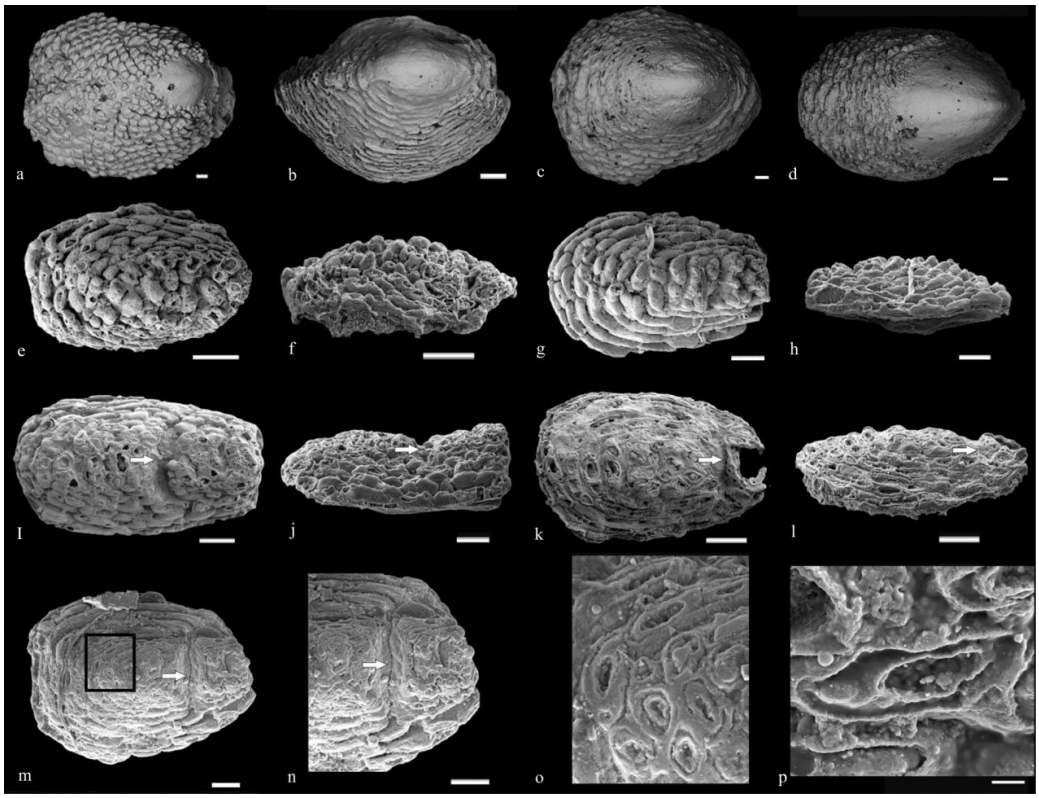

Fig. 3. Characteristics of other maikhanellids compared with the new taxon from the Zhangjiagou section.
Valves with anterior to right of photographs: (a) *Maikhanella* sp., XXMH1451; (b) *Maikhanella* sp., XXMH1452; (c) *Mediata xixiangensis* Shao, 2015 (in Shao et al. 2015), XXMH1453; (d) *Mediata kunyangensis* Feng, 2001, XXMH1454; (e, g) *Totornatus strigatus* gen. et sp. nov., XXMH1455, XXMH1456; (i, k, m) entire shell surface covered with scales, XXMH1466; XXMH1467; XXMH1457; (n) enlarged images of m showing the transverse groove at the anterior field; (o) detailed view (see box in m) showing two layers of scales; (p) enlarged images of (i); (f, h, j, l) lateral view of (e, g, i, k); white arrows point to transverse groove. Scale bar = 100 μm except for 10 μm in (p).

section, Xixiang, southern Shaanxi, China.

Description: As demonstrated by the holotype specimen XXMH1458, *Totornatus strigatus* gen. et sp. nov., the shells resemble a low cap with a rounded, elongated aperture and a length:width ratio of 1.2–1.6. The length is 400–800 μm, width 270–650 μm, and height 200–280 μm. The height of the shell is 0.32–0.53 times of the length. The aperture can be circular to oval, elliptical or pyriform. The anterior margin of the shell is straight or slightly convex. Distinctive scaly ornamentation covers the entire surface of the shell; on the apical field this has a small and dense spherulitic texture and nearer towards the apertural margin, the sculpture passes into elongate rectangular protrusions that contain one to three smaller papillary projections. As shown herein (Fig. 2j, n), each scale contains one or two holes filled with phosphate matrix. The periphery of each scale is raised, and the central concavity has papillate protrusions (Fig. 3o, p). Some scales exhibit interior hollow spaces when broken during preservation or lab preparation (Fig. 2a, e, n) and then they can also be filled with a mineral. The internal shell surface also bears rhomboid ornamentation that forms a grid structure (Fig. 2b, f).

Each shell has a transverse groove that divides the specimen into two parts, the front part of which accounts for most of the specimen (about two-ninths). The transverse groove straddles the apex of the shell body and is fused to both sides of the elongated scale. The transverse groove is significantly more extensive and deeper than the space between the two adjacent plates (Figs. 2, 3i–n). The groove is more prominent inside the shell (Fig. 2b, f) and is approximately parallel to the anterior margin.

4 Comparison

The diagnostic feature of maikhanellids is the peculiar scaly ornamentation of the shell, which distinguishes them from all other Cambrian univalved mollusks. The shell is relatively simple, mainly cap-shaped or limpet-like. The apex is always smooth. The position and size of the apex vary between and within genera. Except for the apex, the rest is covered by scales that are tile-like, tongue-like, rhomboid, or elongate granules. The aperture varies from circular to oval, elliptical or pyriform. Previously, the maikhanellids were usually divided into different genera and species according to the various shell shapes and ornamentation types (Li et al., 2007; Yang et al., 2014). Here, we compare the new fossil taxon with other genera (Table 1).

First of all, the newly discovered fossils are generally smaller than earlier described mikhanellids, with a lower

Table 1 Comparison between different maikhanellid genera

	Apex	Height	Scaly ornamentation
Maikhenella	Exposed, blunt circle, near central	Medium	Square or rectangular granules stacked like scales, one side parallel to the shell margin, and the other side is oblique
Ramenta	Smooth, wide, round, near the front	Low	Rhomboidal granules stacked like scales and oblique with the shell margin
Purella	Smooth, small, round, convex, near the front	High	Elongate scales aligned in comarginal rows
Xiadongoconus	Smooth, big, straight or slightly inclined anteriorly	Low	Comarginally aligned rhomboid granules
Yunnannopleura	Smooth, small	Low	Long scales arranged in a concentric manner
Mediata	Smooth, round, convex	Medium	Dense, long, ovate, oblong protuberances. A prominent middorsal buttress from posterior to anterior
Totornatus	Covered with scales, slightly convex or flat	Low	Apical field of dense, small, round, or oval granules. Scales on the edge more slender and parallel to the shell margin. A transverse groove appears at two-ninths of the body

shell (200–280 μm). Secondly, the anterior margin of the shell is flatter. Third, although the new genus retains a cap -shaped profile and oval aperture as the other genera, they lack a smooth apex. Scale-like protrusions also cover the shell in the new genus. The peak of other maikhanellids have a distinct boundary from the scaly surface (Fig. 3a–d). The shell of the new taxon is completely covered with scales, and the apical field consists of dense, small, round, or oval granules. The tiny granules pass into larger, elongated, scale-like protrusions from the apex to the aperture margin. Remarkably, the scales on the edge are slenderer than those of the previously discovered maikhanellids, with a length:width ratio of 9–13. Near the apertural margin, the scales are elongate rectangles and contain one to three smaller papillary projections (Fig. 2n).

Besides, maikhanellid shells generally consist of two parts: apex and scaly shell ornamentation. Only *Mediata* can be distinguished by a prominent middorsal buttress from posterior to anterior (Feng et al., 2001). *Totornatus strigatus* gen. et sp. nov. has a visible transverse groove at the anterior, which is observed internally as a deeper and broader trench than the space between the two adjacent scales (Fig. 2b, f). The transverse groove straddles the apical of shell and separates two-ninths of the body of the shell, dividing it into two unequal parts: smaller anterior and bigger posterior.

5 Conclusions

We report 13 specimens of three-dimensionally phosphatized maikhanellid shells from the Lower Cambrian (Fortunian Stage) Zhangjiagou section, Xixiang County, in South China. The shell structures of these specimens are described in detail. The new taxon, *Totornatus* gen. nov. has a smooth apex, and the shell is completely covered with scales. The apical field consists of dense, small, round, or oval granules. *Totornatus strigatus* gen. et sp. nov. has a transverse groove in the anterior area separating about two-ninths of the shell. The new taxon exhibits the typical cap-shaped profile and oval aperture, whereas the apex is covered by scale-like protrusions, which are different from the smooth apex of other maikhanellids.

The new taxon enriches the diversity of maikhanellids and provides further material support for the evolution of the family and the phylogenetic relationships between maikhanellids and other univalved shells.

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