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Early Cambrian *Anabarella plana* from Three Gorges area, South China

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Anabarella, a conspicuous taxon of early mollusc, is widely distributed in the early Cambrian strata and is considered an important link in the evolutionary lineage that reflects a transitional form from helcionelloids to bivalves. In South China, *Anabarella* has mainly been documented from Yunnan, Shaanxi, Sichuan, and Hubei provinces. However, the taxonomy of *Anabarella* is questionable, which has implications for the interpretation of the genus' temporal and spatial distribution. New and abundant well-preserved specimens of the helcionelloid mollusc *Anabarella* were recovered from the Member 5 of the Yanjiahe Formation in the Three Gorges area. Through morphological study, these specimens can be definitely identified as *A. plana*. On the basis of this new material, the species of *Anabarella* previously reported in the literature from South China were taxonomically revised, and, with the exception of *A. plana* from the Yanjiahe Formation, other species should be assigned to *Igorella*. Therefore, at present, *A. plana* is the only valid species of the genus *Anabarella* in South China and is limited to Cambrian Stage 2. Study of the available specimens of *A. plana* reveal three types of microstructures: convex polygonal impressions, concave polygons, and lamello-fibrillar microstructure. In addition, the thicker shell of the sub-apical area and the three different structures of the sub-apical area provide more evidence that *A. plana* might have adapted a semi-infaunal mode of life and indicate that *Anabarella* is a likely ancestor of *Watsonella*.

KEYWORDS

Anabarella plana, taxonomic revision, microstructures, Yanjiahe Formation, Cambrian Stage 2, South China

1 Introduction

The abrupt appearance of small shelly fossils (SSFs) in the Cambrian strata is one of the most crucial evolutionary bio-events in Earth's history (Shu, 2008; Maloof et al., 2010; Erwin et al., 2011). As an important component of SSFs, microscopic molluscs play an important role in deciphering the radiation and evolution of early animals (Qian, 1999; Parkhaev, 2000; Parkhaev, 2001; Parkhaev, 2002; Parkhaev, 2008). The fossil record of molluscs in the lower Cambrian of South China provides an important archive for studying their diversity and affinity (Luo et al., 1982; Xing et al., 1983; Yu, 1987; Parkhaev and Demidenko, 2010; Yang et al., 2014; Steiner et al., 2020). In addition, this abundant molluscan constituent is useful for the stratigraphic correlation of the lower Cambrian (Li et al., 2011; Guo et al., 2021). Nevertheless, due to brief morphological descriptions and low-resolution images (Parkhaev

and Demidenko, 2010; Li et al., 2019), the taxonomy of molluscs in the Cambrian strata was over-split and has subsequently produced many junior synonyms. This has hampered the further study of their paleobiology and applications in the correlation of lower Cambrian strata. Taxonomic revision of the Cambrian molluscs is necessary for reconstructing molluscan evolutionary lineages (Qian et al., 2009).

Anabarella Vostokova, 1962, one of the earliest univalve mollusc fossils exhibiting a laterally compressed shell, is an important genus that is widely distributed in early Cambrian strata (Fortunian to Stage 4) of North China (He et al., 1984; Feng et al., 1994; Li et al., 2019), Siberia (Vostokova, 1962; Rozanov et al., 1969; Gubanov and Peel, 2003; Kouchinsky et al., 2017), Australia (Bengtson et al., 1990), Mongolia (Esakova and Zhegallo, 1996), Baltica (Isakar and Peel, 2007), Avalonia (Landing, 1989), and Germany (Elicki, 1994). However, it is uncommon in South China (Steiner et al., 2020; Guo et al., 2021). *Anabarella* has been suggested as being a transitional form from univalve helcionelloids to bivalves (Gubanov, 1998; Gubanov and Peel, 2003; Vendrasco et al., 2011a). In addition, the strongly laterally compressed shell of *Anabarella* led to it being considered as the first mollusc adapted to a semi-infaunal mode of life (Gubanov, 1998; Gubanov et al., 1999; Gubanov and Peel, 1999; 2003). Based on morphological variations, 16 nominal and several indeterminate species were described. However, the diagnostic characters of most species have been regarded as intraspecific variations of the type species, *A. plana* (Landing, 1989). *Anabarella* shares a laterally compressed shell with *Mellopegma Runnegar and Jell, 1976* and *Stenotheca Salter in Hicks, 1872*, which makes correct determination of the materials difficult (Vendrasco et al., 2011b). Although the coiled degree and expansion ratio of the shells are different, several species have been imprecisely assigned to *Anabarella*, such as *A. indecora* (= *Mellopegma indecora*), *A. drepanoida* (= *Stenotheca drepanoida*), *A. simesi* (= *M. simesi*), and *A. cheleta* (= *M. cheleta*). Therefore, the classification of the laterally compressed molluscs and the taxonomic revision of *Anabarella* in the previous publications are confusing, and the species assigned to *Anabarella* have not been systematically investigated, especially those found in South China.

Recently, hundreds of specimens of *Anabarella* were collected from the Member 5 of the Yanjiahe Formation in the Three Gorges area, South China. These new collections allow us to describe these specimens in detail and to further revise the species of *Anabarella* previously reported in South China. Meanwhile, the microstructures and the morphology of *A. plana* are studied and the importance of *Anabarella* in the context of early molluscan evolution are here discussed.

2 Locality, material, and methods

The rock samples were collected from the Member 5 of the Yanjiahe Formation (*Watsonella crosbyi* assemblage zone) in the Gunziao and Yanjiahe sections, Yichang, Hubei Province (Figure 1). SSFs' distribution and the stratigraphy of the Yanjiahe Formation has been systematically investigated in recent years (Guo et al., 2014; Guo et al., 2020; Steiner et al., 2020; Guo et al., 2021). More than 100 specimens of *A. plana* have been collected from the insoluble residues of siliceous-

phosphatic, intraclastic limestone digested in 5%–10% acetic acid. All specimens were manually picked from the residues under a binocular microscope. Selected specimens were coated with gold and photographed using an FEI Quanta 650 Scanning Electron Microscope (SEM) at Chang'an University.

All specimens are catalogued and deposited in Chang'an University (CU), Xi'an, China.

3 Systematic paleontology

Phylum Mollusca Cuvier, 1797
 Class Helcionelloida Peel, 1991
 Order Helcionellida Geyer, 1994
 Family Helcionellidae Wenz, 1938
 Genus *Anabarella Vostokova, 1962*

- 1962 *Anabarella Vostokova*, p.56.
 1969 *Anabarella Vostokova*; Rozanov et al., p. 144.
 1976 *Anabarella Vostokova*; Runnegar and Jell, p.130.
 1990 *Anabarella Vostokova*; Bengtson et al., p. 244.
 1994 *Planutenia Elicki*, p. 81.
 1996 *Anabarella Vostokova*; Esakova and Zhegallo, p. 169.
 2001 *Anabarella Vostokova*; Gravestock et al., p.184.
 2003 *Anabarella Vostokova*; Gubanov and Peel, p. 1077.
 2004 *Anabarella Vostokova*; Gubanov et al., p. 721.
 2017 *Anabarella Vostokova*; Kouchinsky et al., p. 340.
 2019 *Anabarella Vostokova*; Li et al., p. 30.

Type species—*Anabarella plana Vostokova, 1962*; lower Cambrian, Siberia.

Species included—See Table 1.

Diagnosis—See (Gubanov and Peel, 2003).

Remarks—*Anabarella Vostokova, 1962* was firstly designated as a univalve mollusc—due to its strongly laterally compressed shell—from the early Cambrian. *Anabarella*, *Mellopegma*, *Stenotheca*, and *Watsonella* can easily be distinguished from most other univalve molluscs by their strongly laterally compressed shell. Even so, *Stenotheca* differs from *Anabarella* in its taller, loosely coiled, moderately expanding shell, and slightly curved aperture margin (Vendrasco et al., 2011b, Figure 15). *Mellopegma* differs from *Anabarella* in having a less coiled, longer shell, a pronounced sub-apical shelf, and a greater curvature of the aperture margin (Vendrasco et al., 2011b, Figures 5–8). *Igorella* is also similar to *Anabarella* in lateral view (Figures 2A,B) but differs from *Anabarella* in its slightly laterally compressed shell, elliptic aperture, and loosely coiled shell. *Watsonella* differs from *Anabarella* in its unremarkable apex, a greater curvature of the aperture margin, and short sub-apical area (Figures 2C,D; Guo et al., 2021). *Planutenia Elicki, 1994* was established based on the internal molds from the upper Ludwigsdorf member in Germany (Elicki, 1994). This genus has been regarded as a junior synonym of *Anabarella*, according to its similar morphology (Gravestock et al., 2001). Hence, *Planutenia flectata* and *P. inclinata* have been assigned to *A. australis* (Parkhaev, 2004; Li et al., 2019). The taxonomic revision of other species is shown in Table 1.

Distribution—Cambrian Fortunian-Stage 4, South China, North China, Siberia, Mongolia, Australia, Antarctica, Baltica, Avalonia.

Anabarella plana Vostokova, 1962

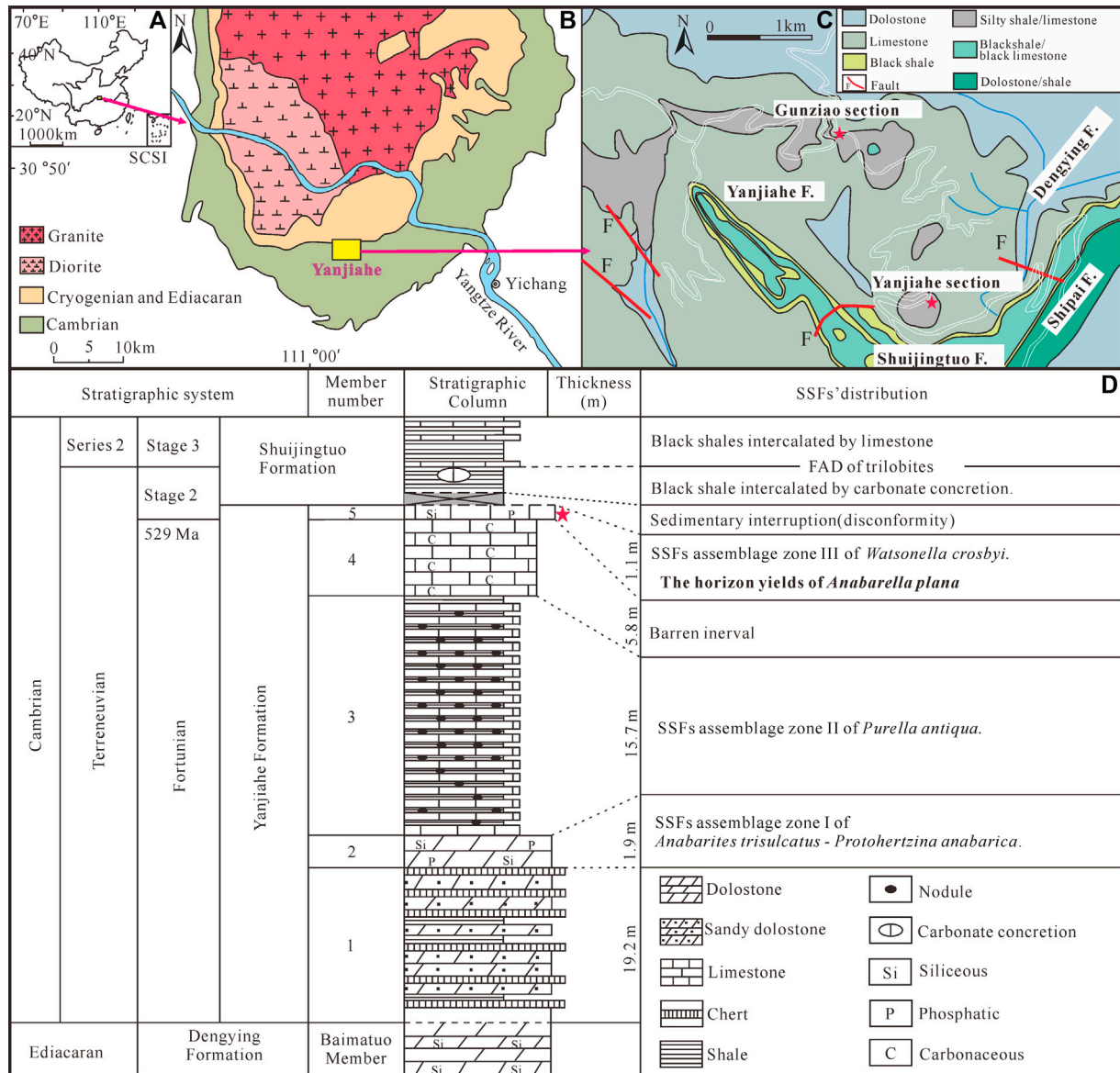


FIGURE 1 Location and stratigraphy of the Terreneuvian Yanjiahe Formation in the Three Gorges area, Hubei Province, China (modified from Guo et al., 2021). (A) Sketch map of the People's Republic of China, the rose-red arrow showing the position of the collecting locality in Hubei Province. (B) Simplified geological map of the Three Gorges area, Hubei Province, showing the outcrops of the Cambrian strata, the rose-red arrow showing the position of the Yanjiahe area. (C) Detailed geological map of the Yanjiahe area, showing the outcrops of the Yanjiahe Formation, red stars showing the locations of the Yanjiahe Section and Gunziao Section. (D) Lithostratigraphic column and biostratigraphy of key SSFs from the Yanjiahe Formation in the Yanjiahe section, Three Gorges area, red star indicating the horizon where specimens of *A. plana* were collected.

1962 *Anabarella plana* Vostokova, p.56, pl. 2, **Figures 1**.
 1969 *Anabarella plana* Vostokova; Rozanov et al., p. 144, pl. 2, **Figure 3**; pl.6, **Figures 4–6**.
 1982 *Anabarella plana* Vostokova; Zhegallo in Voronin et al., p. 45, pl. 1, **Figures 6–7**.
 1982 *Anabarella exigua* Zhegallo in Voronin et al., p. 45, pl. 1, **Figure 8**.
 1983 *Anabarella plana* Vostokova; Lenzion and Posti, p. 126, pl. 94, **Figure 8**.
 1987 *Anabarella plana* Vostokova; Val'kov, p.121, pl. 16, **Figures 2–3**.
 1989 *Anabarella plana* Vostokova; Landing, pp. 755–756, **Figures 9.4, 10.11–12**.
 1995 *Anabarella plana* Vostokova; Easkova and Ermak in Pospelov et al., p. 204.
 1996 *Anabarella plana* Vostokova; Zhegallo in Esakova and Zhegallo, p. 170, pl. 20, **Figures 1–2**.
 1996 *Anabarella exigua* Zhegallo; Zhegallo in Esakova and Zhegallo, p. 170, pl. 20, **Figure 3**.
 1999 *Anabarella* sp. cf. *A. plana* Vostokova; Gubanov in Vidal et al., p. 142, **Figures 4–5**.
 2003 *Anabarella plana* Vostokova; Gubanov and Peel, p. 1077, pl. 1–3; text-**Figure 3**.
 2007 *Anabarella* cf. *A. plana* Vostokova; Isakar and Peel, pp. 260–261, **Figure 4**.

TABLE 1 Species taxonomic revision checklist of *Anabarella*.

Nominal species of <i>Anabarella</i>	Taxonomy after revision
<i>Anabarella plana</i> Vostokova, 1962	Type species
<i>Anabarella indecora</i> Missarzhevsky in Rozanov et al., 1969	<i>Mellopegma indecora</i> (Missarzhevsky, 1989)
<i>Anabarella exigua</i> Zhegallo in Voronin et al., 1982	<i>Anabarella plana</i> (Gubanov and Peel, 2003)
<i>Anabarella lentiformis</i> Yue in Xing et al., 1983	<i>Igorella maidipingensis</i> (Parkhaev and Demidenko, 2010)
<i>Anabarella gyprhynchosa</i> He in Xing et al., 1983	<i>Igorella maidipingensis</i> (Parkhaev and Demidenko, 2010)
<i>Anabarella drepanoidea</i> He and Pei, 1984	<i>Stenotheca drepanoidea</i> (Gravestock et al., 2001)
<i>Anabarella simesi</i> Mackinnon, 1985	<i>Mellopegma simesi</i> (Vendrasco et al., 2011b)
<i>Anabarella aplanta</i> Jermak in Jermak et Pelman, 1986	Valid species
<i>Anabarella emeiensis</i> Yu, 1987	<i>Igorella emeiensis</i> (Parkhaev and Demidenko, 2010)
<i>Anabarella australis</i> Runnegar in Bengtson et al., 1990	Valid species
<i>Anabarella argus</i> Runnegar in Bengtson et al., 1990	<i>Anabarella australis</i> (Gravestock et al., 2001)
<i>Planutenia inclinata</i> Elicki, 1994	<i>Anabarella australis</i> (Parkhaev, 2004)
<i>Planutenia flectata</i> Elicki, 1994	<i>Anabarella australis</i> (Parkhaev, 2004)
<i>Anabarella tshitaensis</i> Parkhaev, 2004	Valid species
<i>Anabarella cheleta</i> Skovsted, 2006	<i>Mellopegma cheleta</i> (Peel et al., 2016)
<i>Anabarella navaranae</i> Peel, 2021	Valid species

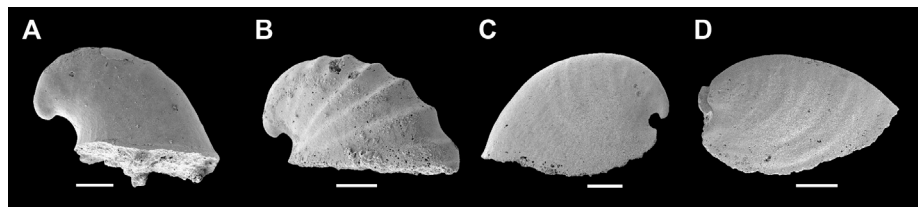


FIGURE 2

Representative members of Cambrian univalve molluscs from the Yanjiahe Formation. (A) *Igorella emeiensis*, internal mold, CUBar58-21. (B) *I. maidipingensis*, internal mold, CUBar119-4. (C) *A. plana*, internal mold, CUBar246-4. (D) *Watsonella crosbyi*, internal mold, CUBar186-6. (A,B,D) from the Member 5 of the Yanjiahe Formation in Yanjiahe section. (C) From the Member 5 of the Yanjiahe Formation in Gunziao section. Scale bars: 500 µm.

2011a *Anabarella plana* Vostokova; Vendrasco et al., pl. 6, Figures 1–6.

2015 *Anabarella plana* Vostokova; Budd and Jackson, Figure 6e.

2017 *Anabarella plana* Vostokova; Kouchinsky et al., pp. 340–343, Figures 14, 15.

2020 *Anabarella plana* Vostokova; Steiner et al., Figures 5A, B, F.

2021 *Anabarella plana* Vostokova; Guo et al., Figures 3E, F.

Holotype—CNIGRM No. 8361–8 from the lower Cambrian of the Kenyada River, western tributary of the Olenek River, North Siberia.

Material—More than 100 specimens (internal molds) collected from the Yanjiahe and Gunziao sections, Yichang, Hubei Province; Member 5 of the Yanjiahe Formation.

Diagnosis—Small, cyrtconic, rapidly expanding, strongly laterally compressed, bilaterally symmetrical univalve shell. Shell coiled to one

whorl, sub-apical side concave and short, dorsal margin broadly rounded, lateral surface flat. Aperture curved, narrow. Apex hook-shaped, curved to the posterior aperture margin. Shell smooth or slightly ornamented with growth lines and regularly spaced comarginal rugae.

Description—Univalve shell, up to 3,000 µm in length and 2000 µm in height (Figure 3A), rapidly expanding from the apex to aperture (Figures 4A,B,C1,H1,I1), strongly laterally compressed, bilaterally symmetrical (Figures 4C2,D2,E2), isostrophically coiled about one whorl. Apex hook-shaped, tightly coiled (Figures 4H1,I1,J1). Sub-apical side very short, dorsal side long and round (Figures 4A,B,C1,D1,E1,H1,I1). Aperture narrow (Figures 4D3,E3,F4,H3,I2,J2), elongated oval with length/width ratio about 4:1 in planar view (Figure 3B), always wider anteriorly and narrower posteriorly (Figures 4H3,I2,J2). Apertural margin convex in lateral view (Figures 4C1,H1,I1). Lateral sides flat

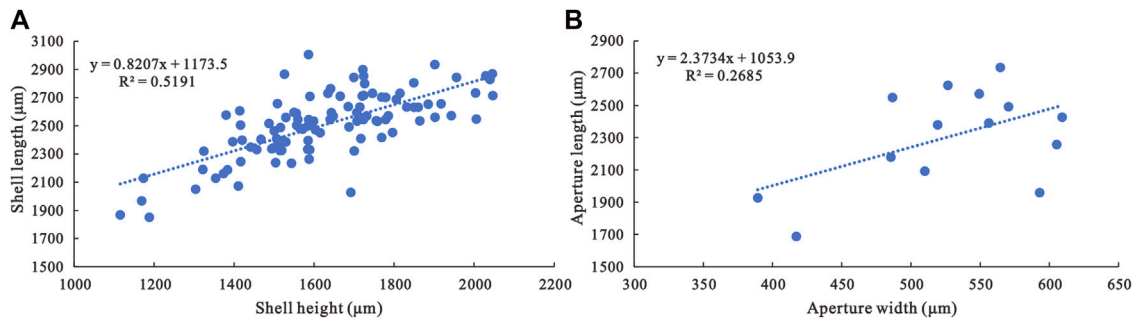


FIGURE 3
Morphological parameter analyses of *A. plana*. (A) Shell length/shell height ratio of *A. plana* (N=105). (B) Aperture length/aperture width ratio of *A. plana* (N=14).

(Figures 4D2,E2,F3). Shell ornamented with growth lines. Internal mold smooth (Figures 4A,C1,G1) ornamented with shallow comarginal folds on the lateral side (Figures 4B,D1,F1,H1,I1,J1) or faint thin ribs parallel to dorsal margin (Figure 4F2). Dorsum of internal mold usually bears two shallow grooves (Figures 4G2,G3,H2). Sub-apical side short and open, almost circular in outline (Figure 4H1). Apex overhanging on the apertural margin or even projecting over it. Sinus below the apex on the internal mold (Figures 4B,C1,H1,I1,J1).

Three types of microstructure are present on the surface of internal molds: convex polygonal impressions, concave polygonal textures, and lamello-fibrillar microstructures. Convex polygonal impressions are restricted to the apical areas (Figures 5A1,A2,B1,B2,C1,C2), up to 40 µm in width. The convex polygons vary in shape and are separated by shallow grooves (Figure 5C2). The concave polygonal textures occur near the apertural and dorsal margins (Figures 5D1,D2,E3,E4), which is much clearer on the ridge near the aperture (Figures 5E1,E2). The width of these concave polygons is small, approximately 10 µm. Additionally, rarely preserved lamello-fibrillar microstructures appear on the apical and sub-apical areas (Figures 6A1,B1,C1,D1).

Remarks—*A. plana* belongs to the univalve molluscs, with a stratigraphic range restricted to the Cambrian strata of upper Fortunian to Stage 2. Landing (1989) regarded the morphological differences of *Anabarella* as intraspecific variability and revised all species to *A. plana*. This opinion was not accepted by some researchers. According to Gubanov and Peel (2003), only *A. exigua* can be regarded as a junior synonym of *A. plana*. Among the five valid species, *A. plana* differs from *A. australis* Runnegar in Bengtson et al., 1990 by the rapidly expanding, tightly coiled shell and shorter sub-apical side (dorsal side length/sub-apical side length ratio 7:1–8:1 vs. 2:1–4:1 in *A. australis*); from *A. tshitaensis* Parkhaev, 2004 by the hook-shaped apex, rapidly expanding, tightly coiled shell, and the semicircular sinus under the apex; from *Anabarella navaranae* Peel, 2021 by the lower (shell length/shell height ratio ca. 1.5:1 vs. 1:1 in *A. navaranae*), tightly coiled, rapidly expanding shell; from *A. applanta* Jermak in Jermak and Pelman, 1986 by a larger shell (2,500 µm vs. 700 µm in *A. applanta*) and its hooked apex.

Occurrence—Upper Fortunian and lower part of Cambrian Stage 2; Siberia, western Mongolia, Baltica, South China, Spain, Avalonia.

4 Discussion

4.1 Records of *Anabarella* in South China

In South China, the fossil records of *Anabarella* were mainly documented from Yunnan (Luo et al., 1982; Yu, 1987), Sichuan (Xing et al., 1983; Yu, 1987), Shaanxi (Xing et al., 1983), and Hubei provinces (Steiner et al., 2020; Guo et al., 2021). With the exception of the type species *A. plana* (Luo et al., 1982; Steiner et al., 2020; Guo et al., 2021), three nominal species of *Anabarella* were previously named from South China: *A. emeiensis* Yu, 1987, *A. lentiformis* Yue in Xing et al., 1983, and *A. gypirhynchosa* He in Xing et al., 1983 (Table 1; Xing et al., 1983; Yu, 1987).

Anabarella plana in South China was initially discovered by Luo et al. (1982) from the Dahai Member of the Zhujiqing Formation in Huize, Yunnan Province, based on a single specimen. This specimen (Luo et al., 1982, plate 20, Figures 11, 11a), however, shows a small, cyrtconic, cap-shaped, moderately high, slightly laterally compressed shell, with an obtuse apex and an elliptical aperture—features more consistent with the genus *Igorella* Missarzhevsky in Rozanov et al., 1969, and hence is herein identified as *I. emeiensis* Yu, 1987. In addition, *A. plana* was also reported without description from the Member 5 of the Yanjiahe Formation in the Three Gorges area of South China (Steiner et al., 2020; Guo et al., 2021). In this study, based on numerous specimens, the morphology, taxonomy, and stratigraphic distribution of *A. plana* in the Yanjiahe Formation are systematically analyzed.

Anabarella emeiensis Yu in Lu, 1979 (plate III, Figures 12–15) was originally proposed based on specimens from the Maidiping Formation in the Emei region, Sichuan Province (Lu, 1979). However, this material was illustrated without associated descriptions of the taxon; hence, *A. emeiensis* is considered a nomen nudum. Yu (1987) formally described and reassigned the taxon as *A. emeiensis* Yu, 1987 based on the former specimens (plate 39, Figures 7–9) and other specimens (plate 40, Figures 7–9) from the Zhongyicun Member in Xundian, Yunnan Province. Subsequently, *A. emeiensis* is regarded as a junior synonym for *Stenotheca emeiensis* based on specimens collected from the Xinji Formation of Henan Province (Feng et al., 1994). However, based on the description and illustrations, the diagnostic features of “S.

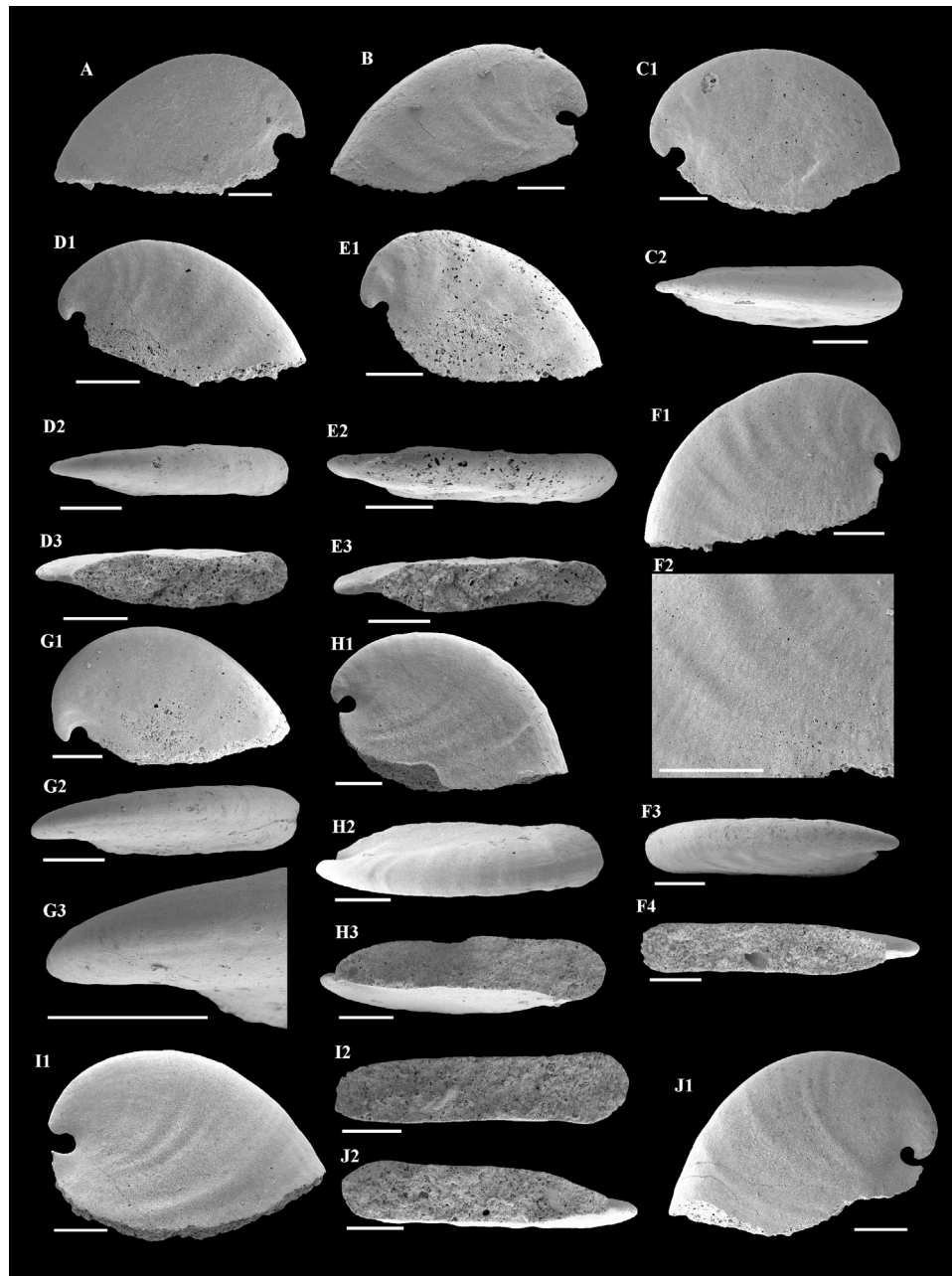


FIGURE 4

A. plana from the Member 5 of the Yanjiahe Formation. (A,B) Internal molds, lateral view, CUBar23-1, CUBar41-1. (C1) Internal mold, lateral view, CUBar235-1; (C2) dorsal view of (C1). (D1) Internal mold, lateral view, CUBar241-2; (D2) dorsal view of (D1), (D3) apertural view of (D1). (E1) Internal mold, lateral view, CUBar241-3; (E2) dorsal view of (E1), (E3) apertural view of (E1). (F1) Internal mold, lateral view, CUBar243-2; (F2) magnification of (F1) showing the faint thin ribs, (F3) dorsal view of (F1), (F4) apertural view of (F1). (G1) Internal mold, lateral view, CUBar241-5; (G2) dorsal view of (G1), (G3) magnification of (G2) showing the shallow grooves on the dorsum. (H1) Internal mold, lateral view, CUBar242-1; (H2) dorsal view of (H1), (H3) apertural view of (H1). (I1) Internal mold, lateral view, CUBar242-2; (I2) apertural view of (I1). (J1) Internal mold, lateral view, CUBar243-5; (J2) apertural view of (J1). (A,B) From the Yanjiahe Section, (C1–J1) from the Gunziao Section. Scale bars: 500 μm .

emeiensis” described by Feng et al. (1994) are more consistent with the diagnostic features of *A. australis* described by Bengtson et al. (1990). Hence, *S. emeiensis* should be assigned to *A. australis*. Nevertheless, the length/width ratio of the aperture in the specimens of *A. emeiensis* illustrated by Yu (1987) is approximately 2:1, much smaller than in other forms of *Anabarella* (ca. 4:1) and inconsistent with the character of a laterally compressed shell—a distinct diagnostic feature of *Anabarella*. Additionally, the taller and less coiled shell is much

closer to *Igorella*. Therefore, we agree with Parkhaev and Demidenko (2010) that *A. emeiensis* should be assigned to *I. emeiensis*.

Anabarella lentiformis Yue in Xing et al., 1983 (plate 26, Figures 24–26) was discovered in the upper Kuanchuanpu Formation in the Ningqiang country of Shaanxi Province. The internal molds shown in the original illustration are small, recurved, cyrtoconic, coiled less than one whorl, and slightly laterally compressed. The apex is hook-shaped, projecting over the apertural margin. The aperture is lenticular, with a

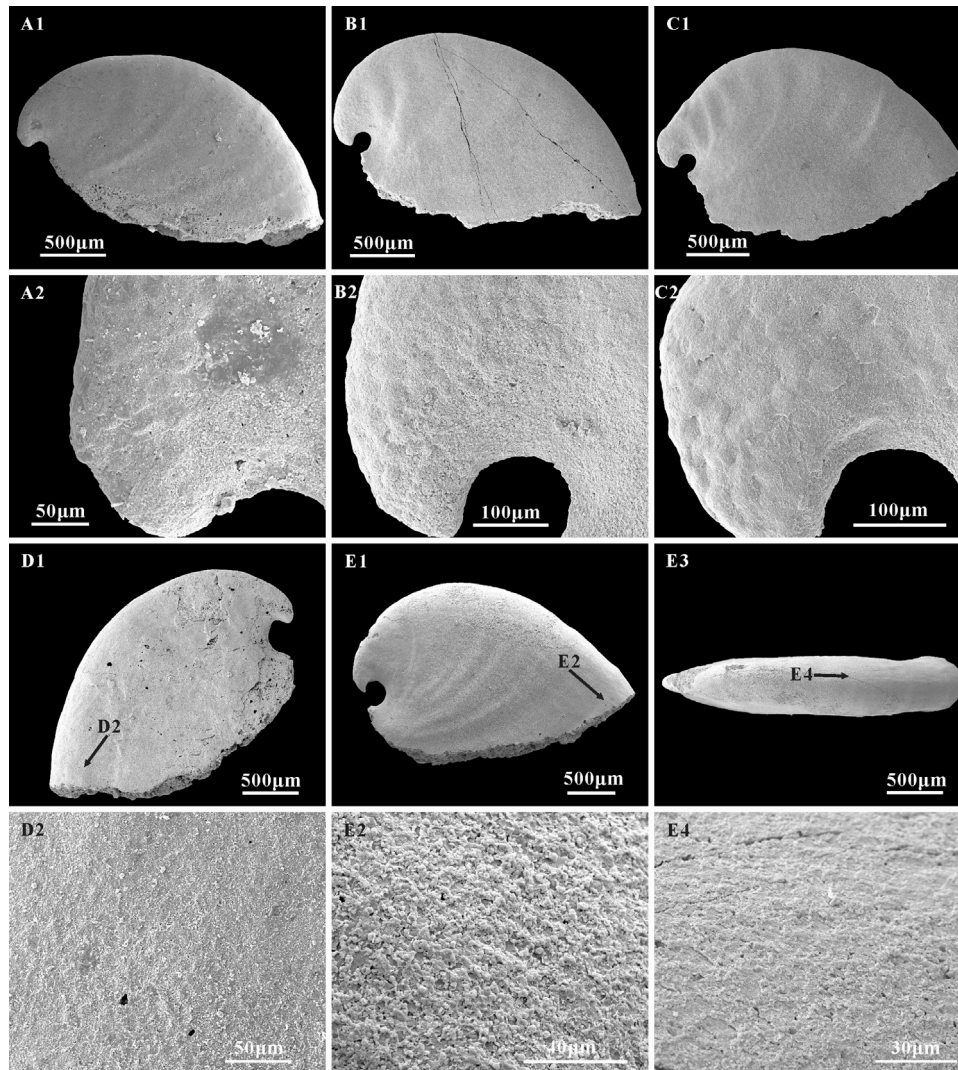


FIGURE 5

Polygonal impressions on the internal molds of *A. plana*. (A1,B1,C1) internal molds, lateral view, CUBar241-6, CUBar244-3, CUBar244-10, respectively; (A2,B2,C2) magnifications of (A1,B1,C1), showing the convex polygonal impressions on the apical area, represent the cell imprints of the outer mantle epithelium. (D1,E1) Internal molds, CUBar75-38, CUBar242-3; (D1,E1) lateral view, (E3), dorsal view of (E1); (D2,E2,E4), magnifications of (D1,E1,E3), showing the concave polygonal impressions on the apertural and dorsal areas, representing the inner ends of shell prisms. (A1,B1,C1,E1) from the Member 5 of the Yanjiahe Formation in Gunziao Section, (D1) from the Member 5 of the Yanjiahe Formation in Yanjiahe Section. Arrows show magnified locations.

length/width ratio of about 2.5:1. The coarser comarginal rugae occur near the dorsal areas. These features were previously regarded as intraspecific variability of *A. plana* (Landing, 1989). However, compared to the diagnostic features of *Anabarella*, the less coiled, slightly laterally compressed shell is more similar to *Igorella*. Hence, *A. lentiformis* has been regarded as a junior synonym of *I. maidipingensis* Yu, 1974 (Parkhaev and Demidenko, 2010).

Anabarella gypirhynchosa He in Xing et al., 1983 (plate 13, Figure 7) was established based on a broken specimen from the Niuniuzhai Member (=Maidiping Formation) of the Hongchunping Formation, Sichuan Province. The specimen is semicircular in lateral view. A hook-shaped apex curves to the aperture margin. The aperture shape is unknown. Irregular comarginal folds are present on the internal mold surface. According to these features, we follow Parkhaev and Demidenko (2010) and assign *A. gypirhynchosa* to *I. maidipingensis*.

After revisions, the valid identification of *A. plana* in South China is only from the Member 5 of the Yanjiahe Formation. Given the co-occurrence of *Aldanella attleborensis* and *W. crosbyi* in the Member 5 of the Yanjiahe Formation, the stratigraphic range of *A. plana* in South China is limited to the Cambrian Stage 2. This changes the traditional understanding that *A. plana* appeared earlier than *W. crosbyi* in South China (Gubanov and Peel, 2003). *A. plana* also appeared in the *W. crosbyi* assemblage zone (Cambrian Stage 2) of Avalonia (Landing, 1989) and Estonia (Mens and Isakar, 1999; Isakar and Peel, 2007), but the earliest record of it was discovered from the upper *Purella antiqua* assemblage zones (Fortunian) of Siberia (Khomentovsky and Karlova, 1993; Gubanov and Peel, 2003; Kouchinsky et al., 2017), Mongolia (Esakova and Zhegallo, 1996), and Spain (Gubanov and Peel, 2003).

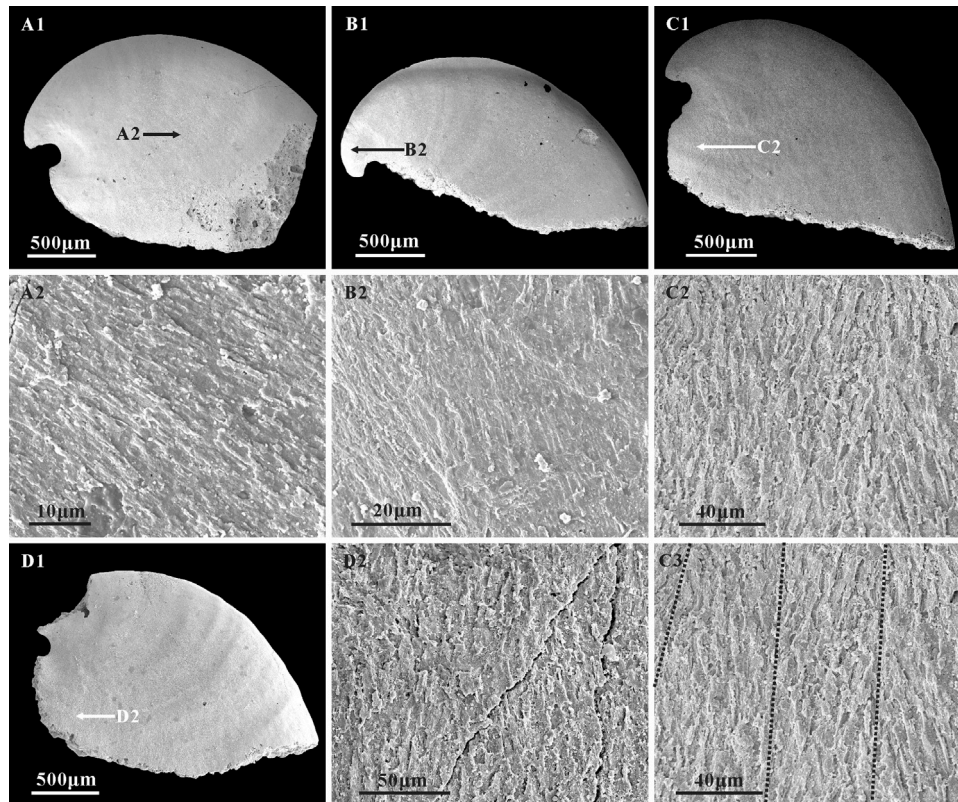


FIGURE 6

Lamello-fibrillar microstructure in the internal molds of *A. plana*. (A1,B1,C1,D1) Internal molds, lateral view, CUBar204-4, CUBar205-2, CUBar244-14, CUBar241-13, respectively. (A2,B2,D2) magnifications of (A1,B1,D1) respectively, (C2,C3) magnifications of (C1), showing the lamello-fibrillar microstructures. Black dotted lines on (C3) showing the convergence of different orientation fibers. Specimens from the Member 5 of the Yanjiahe Formation in Gunziao Section. Arrows indicate magnified locations.

4.2 Microstructures of *Anabarella plana*

Study of the microstructure of Cambrian fossils provides significant characteristics that could be used to better understand the degree of diversification, phylogeny, and shell strength of the early molluscs (Vendrasco et al., 2010). To date, extensive work has been done based on Cambrian molluscan microstructure (Runnegar, 1985; Kouchinsky, 1999; Kouchinsky, 2000; Vendrasco et al., 2010; Vendrasco et al., 2011a; Li et al., 2022). Three types of microstructure (i.e., polygonal impressions, stepwise texture, and lamello-fibrillar microstructure) have been studied on the laterally compressed internal molds of *A. plana* and *W. crosbyi* to reveal their phylogenetic relationships (Kouchinsky, 1999; Vendrasco et al., 2011a; Li et al., 2011; Guo et al., 2021). These microstructures, observed on the internal molds of *A. plana* from the Yanjiahe Formation, are similar to those of *Anabarella* and *Watsonella* (Bengtson et al., 1990; Kouchinsky, 1999; Vendrasco et al., 2011a; Li et al., 2019), such as an outer layer of polygonal impressions and inner layer lamello-fibrillar microstructure, but no sign of stepwise texture. The polygonal impressions are common microstructures that appear on the internal molds of *A. plana*, *W. crosbyi*, *Pojetaia runnegari*, and other Cambrian molluscs (Kouchinsky, 1999; Vendrasco et al., 2011a; Li et al., 2011; Guo et al., 2021). Several interpretations of the polygonal impressions on Cambrian molluscs have been made,

such as muscle scars (Parkhaev, 2006), imprints of shell prisms (Kouchinsky, 1999; Vendrasco et al., 2010; Li et al., 2011; Guo et al., 2021), or cell imprints of the outer mantle epithelium (Ushatinskaya and Parkhaev, 2005; Parkhaev and Karlova, 2011). Herein, the polygonal impressions on *A. plana* appear as convex (Figures 5A2,B2,C2) and concave structures (Figures 5D2,E3,E4). On the new material of *Anabarella*, the convex polygons vary in shape: mainly circular or nearly circular, up to 40 μm in width, and separated by shallow grooves (Figure 5C2). Unlike the positive relief of *A. plana* described by Kouchinsky (1999, Figure 2B), the convex polygons illustrated herein are restricted to the apical areas (Figures 5A2,B2,C2) and no tubercles in the polygons. In addition, a convex polygon with such a large diameter has never been found in the apical area of *Anabarella*. Similar convex polygonal impressions have been described on the apex of *Aldanella*, *Oelandiella*, and *Securiconus*, and are mostly interpreted as imprints of shell prisms (Isakar and Peel, 2007; Vendrasco et al., 2010). However, the much larger diameter and specific position of such polygons are different from prismatic imprints. Therefore, we agree that the convex polygons could be interpreted as the impressions of cells of the outer epithelium (Ushatinskaya and Parkhaev, 2005; Parkhaev and Karlova, 2011). The concave polygonal texture is more common on the internal molds of *Anabarella* and appears on the apical and dorsal areas of *A. plana* (Kouchinsky, 1999) and sub-apical area of *A. australis*

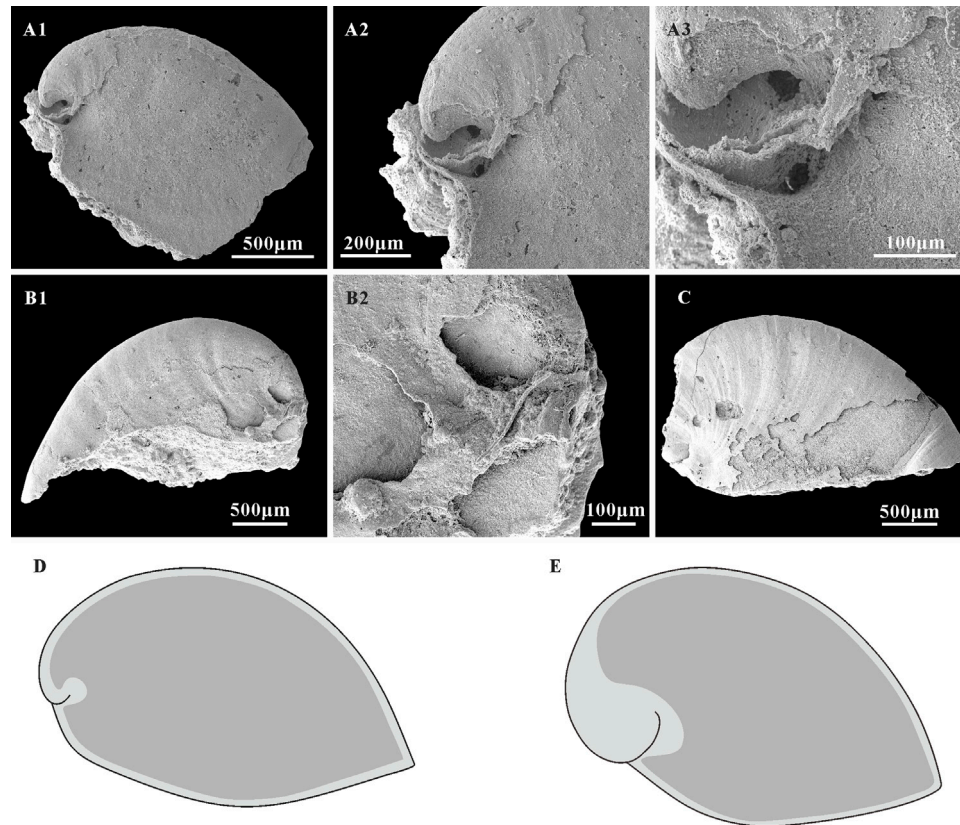


FIGURE 7

A. plana with external coating and associated schematic of shells and internal mold extent in *Anabarella*. **(A1,B1,C)** Internal molds, lateral view, CUBar128-24, CUBar243-6, CUBar246-15, respectively. **(A2,A3)** magnifications of **(A1)** showing the morphological variation of external coating and internal mold on the apical areas of *A. plana*. **(B2)** Magnification of **(B1)**, showing the shell morphology of *A. plana* on apical area. **(D)** Sketch of *A. plana*. **(E)** Sketch of *A. australis*, according to the specimens showed in Li et al., 2019 (Figures 3I,H). Dark gray, morphology of internal mold; light gray, morphology of shell. **(A1)** From the Member 5 of the Yanjiahe Formation in Yanjiahe Section, **(B1,C)** from the Member 5 of the Yanjiahe Formation in Gunziao Section.

(Bengtson et al., 1990). The concave polygonal textures on the internal mold of *A. plana* from the Yanjiahe Formation are small—approximately 10 μm in diameter. They appear near the apertural and dorsal margin (Figures 5D1,D2,E3,E4) and are much clearer on the ridge near the aperture (Figures 5E1,E2). Compared to the concave polygons of *W. crosbyi* (Li et al., 2011; Guo et al., 2021), *A. plana* (Kouchinsky, 1999), and *A. australis* (Bengtson et al., 1990), the concave polygons here are less pronounced and frequent, which might be correlated with preservational bias. Concave polygonal textures have been interpreted as inner ends of the prismatic shell layer (Kouchinsky, 1999; Li et al., 2011; Guo et al., 2021).

Although inner layer lamello-fibrillar microstructures are common in early Cambrian molluscs such as *W. crosbyi* (Guo et al., 2021) and *A. australis* (Li et al., 2019), this structure is rarely reported on the internal molds of *A. plana*. In the specimens of the Yanjiahe Formation, lamello-fibrillar textures consisting of bundles of fibers occur on the lateral fields, and the apical and sub-apical areas (Figures 6A2,C2,D2). Fibers are arranged at the same orientation (Figure 6A2) or intersect at low angles (Figures 6C2,C3) but belong to different layers (Figure 6B2).

The similarities in microstructures between *Anabarella* and *Watsonella*—such as polygonal impressions, stepwise texture and lamello-fibrillar microstructure—taken together with their shell

form, were the important evidence for *Anabarella* being a likely ancestor of *Watsonella* (Kouchinsky, 1999; Vendrasco et al., 2011a).

4.3 Morphological variations of the *Anabarella* shell

The preservation forms of SSFs strongly depend on facies, diagenesis, and the methods of fossil extraction in the lab (Gubanov and Peel, 2003; Jacquet et al., 2019; Li et al., 2019). Among SSFs, molluscs are usually extracted as secondarily replaced shells, internal molds, external molds, or external coatings in phosphatized calcareous rocks treated with acetic acid. However, it is widely known that the morphology of molluscs preserved as listed above show varying fidelity to their characteristic features, depending on the mode of preservation (Bengtson et al., 1990; Skovsted, 2004). Morphological variation between external coatings and internal molds is a common in univalve SSFs, particularly in *Anabarella*. For instance, the internal molds of *Anabarella* are always smooth and ornamented with gentle rugae, but the external coatings are only ornamented with growth lines. In addition, the main difference between internal molds and external coatings focuses on the shape and size of the shell sub-apical areas, and has been ascribed to preservational artifacts—a

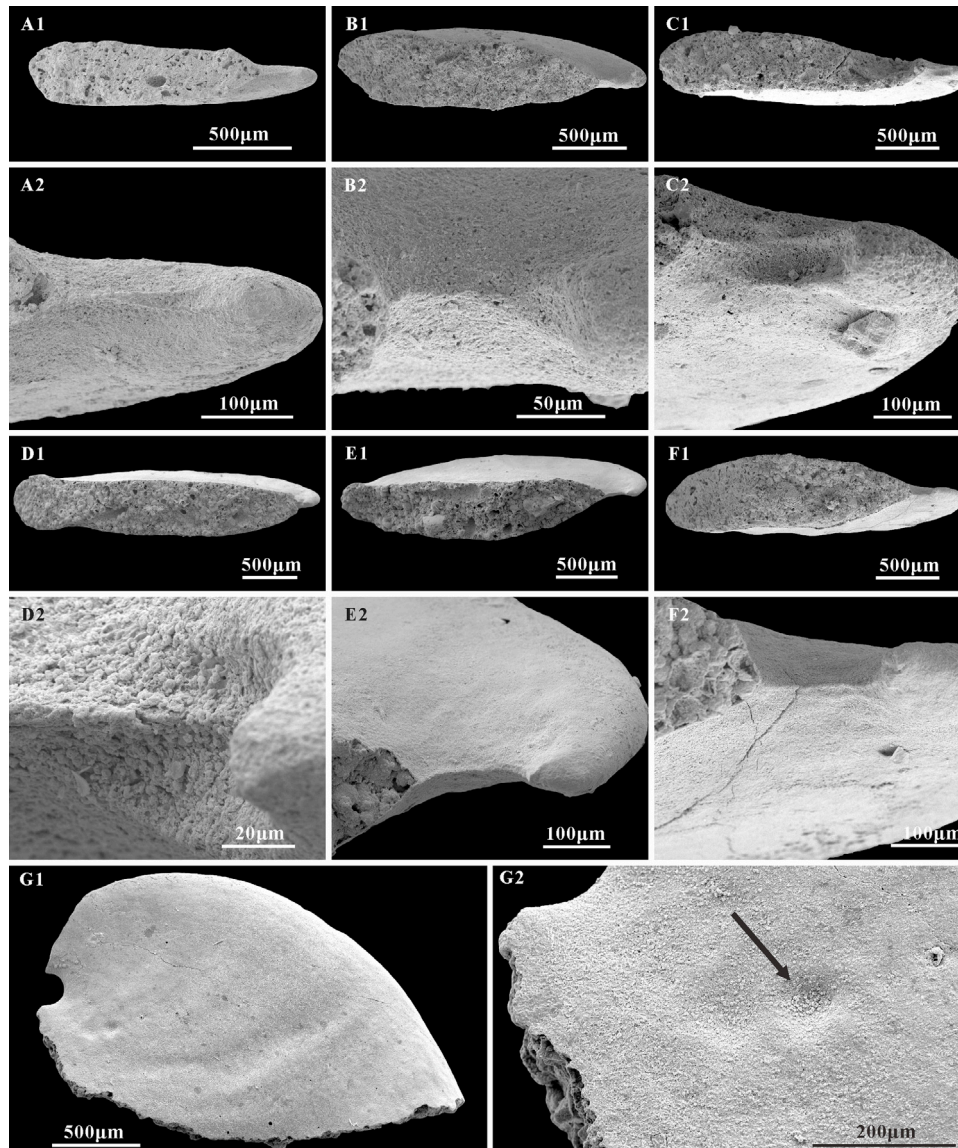


FIGURE 8

Structures on the sub-apical area of *A. plana* and possible imprint of scar. (A1,B1,C1,D1,E1,F1) Internal molds, apertural view, CUBar217-7, CUBar241-7, CUBar241-1, CUBar242-3, CUBar241-4, CUBar241-10, respectively. (A2,B2,C2,D2,E2,F2) magnifications of (A1,B1,C1,D1,E1,F1), showing the structures of sub-apical side. (G1) internal mold, lateral view, CUBar242-7. (G2) magnification of (G1), showing the possible imprint of scar. Arrow shows the location of scar. Specimens from the Member 5 of the Yanjiahe Formation in Gunziao Section.

heavily phosphatized shell and degree of recrystallization (Gubanov and Peel, 2003; Li et al., 2019). However, the observed morphological variation is not necessarily caused by preservational bias. The new materials of *A. plana* in the Yanjiahe Formation may reveal another interpretation of the cause of morphological variation between external coating and internal mold.

Thin phosphatic coatings are preserved on some specimens of *A. plana* from the Member 5 of the Yanjiahe Formation (Figures 7B2,C) which replicate the external shell morphology well. The morphology of internal molds is extremely different to external phosphatic coatings, especially on the sub-apical area (Figures 7A1–A3,B1,B2,C). In contrast to the Spanish specimens (from the lower Cambrian of Sant Lorenzo de Calatrava, Sierra Morena) that

have heavily phosphatized shells (Gubanov and Peel, 2003, plate 3), the material studied here is lightly phosphatized. The well-preserved growth lines in the thin external coating (Figures 7A2,C) and the imprints of the shell microstructures (Figures 5, 6) in the internal mold surfaces suggest that the free space between the external coating and internal mold (Figures 7D,E; Li et al., 2019) represents the morphology of the original shell, and do conform to being phosphatization overgrowths around the original shell. It is worth noting that the sub-apical shell of *Anabarella* is thicker than the rest of the shell (Figure 7A3; Li et al., 2019, Figures 3H,I). This might be related to the adaptive strategy of *Anabarella* (Gubanov, 1998; Figure 2). As possibly the first molluscan taxon to adapt the semi-infaunal mode of life, it has been suggested *Anabarella* burrowed to softer substrates

for food or to avoid predators (Gubanov, 1998; Gubanov et al., 1999). In this mode of life, the posterior of the shell would always be exposed above the substrate and be easily damaged by predators in the sediment. *Mellopegma*, another mollusc interpreted to have adapted to a burrowing lifestyle, shows concentrated damage in the sub-apical area (Vendrasco et al., 2011b), which indicates that this portion of the shell is more susceptible to damage or attack. Although the scar is rarely preserved on the internal molds, a possible scar imprint appeared on the sub-apical area of *A. plana* (Figure 8G1,G2). Hence, the thicker original shell in sub-apical area of *Anabarella* might be adapted to resist the attacks of predators and sediments. Hence, the morphological differences between the external coatings and internal molds of *Anabarella*, especially of the sub-apical area, were caused by the variation in thickness of the original shell, not merely by preservational bias.

4.4 Implications of *Anabarella* for molluscan evolution

Based on the stratigraphic distribution, morphology, and shell microstructures, a hypothetical evolutionary lineage from the uppermost Fortunian *Oelandiella* via *Anabarella* to the Stage 2 *Watsonella*, and even to the Stage 3 earliest bivalves *Pojetaia* and *Fordilla* has been suggested (Runnegar and Pojeta, 1974; Gubanov, 1998; Gubanov et al., 1999; Kouchinsky, 1999; Vidal et al., 1999; Gubanov and Peel, 2000; Gubanov and Peel, 2003; Vendrasco et al., 2011a; Vendrasco et al., 2011b; Li et al., 2011; Guo et al., 2021). The evolutionary lineage from *Oelandiella* via *Anabarella* to *Watsonella* is accompanied by a loss of the strong comarginal ornamentation and increased lateral compression (Gubanov and Peel, 1999). In addition to these evolutionary trends, the sub-apical structures of *A. plana* in the new materials of the Yanjiahe Formation also appear transitional.

Unlike most helcionelloids with a gentle sub-apical area, the well-preserved sub-apical areas of *A. plana* show three different types of structures in internal molds: a V-shaped convergence (Figures 8A1,A2,B1,B2), two sinuses separated by a ridge (Figures 8C1,C2,D1,D2), and a raised ridge (Figures 8E1,E2,F1,F2). These structures may indicate that the shell sub-apical areas of *A. plana* have a tendency to separate in order to extend the aperture, which is consistent with *W. crosbyi* having a relatively short sub-apical field and a strong upward posterior aperture. Compared to the wide aperture of *Oelandiella*, that of *Anabarella* and *Watsonella* is narrow but more curved in lateral view, which elongates the aperture's length and improves efficiency of movement and foraging. This is accompanied by the gradual disappearance of the apex. In addition, the narrower and longer aperture of *Anabarella* and *Watsonella* makes it easier to burrow into the softer substrate. Hence, we suggest that the dorsal elongate structures of *Anabarella* (Figures 4G2,G3,H2) are analogous to the median furrow of *Watsonella* (Gubanov et al., 1999), which might be the ligament precursor of bivalves (Li et al., 2011). From a functional perspective, the morphological variation observed in *Oelandiella*, *Anabarella*, and *Watsonella* may reflect the change of adaptive life strategy—for example, epifaunal, semi-infaunal, and infaunal. The similarities in morphology, as well as the earlier occurrence of *A. plana* (upper Fortunian) in Cambrian strata, indicate the possibility that *W. crosbyi* is the descendent of

Anabarella, although the systemic position of *W. crosbyi* is uncertain. In summary, the similarity in morphology and shell microstructure between *A. plana* and *W. crosbyi* implies their close relationship and supports the hypothesis of an evolutionary lineage from *Oelandiella* (uppermost Fortunian) through *Anabarella* (uppermost Fortunian-Stage 2) and *Watsonella* (Stage 2) to *Pojetaia* and *Fordilla* (Stage 3) (Vendrasco et al., 2011b). *A. plana* from the Member 5 of the Yanjiahe Formation provides important information about the intermediate morphological transition during the evolutionary process between helcionelloids and bivalves.

5 Conclusion

This taxonomic study of *Anabarella* in South China was performed on the basis of abundant new materials. Investigation shows that the only reliable species of *Anabarella* in South China is *A. plana*, which is only recognized in the Yanjiahe Formation of western Hubei, and its age is limited to Cambrian Stage 2. The studied specimens provide important information about the morphology and microstructures of *A. plana*. The well-preserved growth lines on the external coating and microstructures on the internal mold indicate that the phosphatization around the original shell is slight, and the morphological variations between shells and internal molds of *A. plana* may be caused by the variation in original shell thickness, not just by preservational bias. Three types of microstructure are identified on the internal mold of *A. plana*: convex polygonal impressions, concave polygons, and a lamello-fibrillar microstructure. The convex polygonal impressions on the apical area are interpreted as the cast of the cellular epithelium of the mollusc, but the concave polygons may correlate with the inner ends of shell prisms. Lamello-fibrillar microstructures consisted of fibers mostly related to the inner layer. The comparability of the microstructures and morphology of *A. plana* with *W. crosbyi* provides important evidence that supports a hypothetical evolutionary lineage from *Anabarella* to *Watsonella*.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material, and further inquiries can be directed to the corresponding author.

Author contributions

Conceptualization: JG and YQ, writing-original draft: YQ; writing-review and editing: JG, GL, and JH; sample collection: YQ, JP, JS, ZS, and XZ.

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