



Diversity and systematics of calcified cyanobacteria and associated microfossils in Cambrian Series 2 shallow-marine carbonates, Yangtze Platform, South China

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Abstract. Calcified cyanobacteria and associated microfossils were systematically investigated in 10 shallow-marine carbonate sections – reefal and non-reefal – from Cambrian Series 2 of the Yangtze Platform, South China. A total of 15 species in 10 genera of calcified cyanobacteria and 5 species in 3 genera of Microproblematica were identified, including 2 new species (*Streptubularia robustus* sp. nov. and *Xianella mollis* sp. nov.). *Girvanella*, *Subtifloria*, *Razumovskia*, *Acuasiphonoria*, *Xianella*, and *Streptubularia* are attributed to Oscillatoriales (cyanobacteria); *Kordephyton*, *Bija*, *Hedstroemia*, and *Botomaella* are attributed to Nostocales (cyanobacteria); *Renalcis*, *Izhella*, and *Epiphyton* are attributed to Microproblematica. This is the first report of *Acuasiphonoria*, *Razumovskia*, *Subtifloria*, *Xianella*, *Bija*, and *Botomaella* from South China, and it advances the fossil record of *Acuasiphonoria* from the Late Ordovician to the Cambrian Series 2. Comparisons indicate that these calcified assemblages from the Yangtze Platform show close resemblances to those of the Siberian Platform and North China. This establishes a global distribution of at least 15 genera of calcified cyanobacteria in the early Cambrian. These results support the view that cyanobacterial calcification was widespread in shallow-marine environments during the early Cambrian, suggesting significant links to paleo-oceanic and paleo-atmospheric conditions.

1 Introduction

Cyanobacterial photosynthesis can increase pH in and near the extracellular polysaccharide sheath, promoting the likelihood of inducing CaCO₃ precipitation on or within the sheath and favoring their preservation as calcified fossils (Pentecost and Riding, 1986). Since cyanobacterial marine calcification can depend on seawater carbonate saturation and atmospheric CO₂ level, secular variations in calcified cyanobacterial abundance and diversity may reflect changes in paleo-oceanic and paleo-atmospheric conditions (Riding, 1992; Arp et al., 2001; Riding, 2006a; Liu et al., 2021). Riding (1992) proposed the concept of cyanobacterial cal-

cification episodes (CCEs) to describe intervals of enhanced marine cyanobacterial calcification, alternating with reduced calcification episodes (RCCs).

During the Precambrian–Cambrian transition (~560–520 Ma), numerous animal phyla appeared in marine environments, including ancestors of many modern animal lineages (e.g., Conway Morris, 1989, 1993; Qian and Bengtson, 1989; Crimes, 1992; Valentine, 2004; Li et al., 2006; Shu, 2008). Rapid ecological differentiation and expansion across animal phyla led to complex animal-dominated marine ecosystems (Shu, 2008; Erwin and Tweedt, 2012; Zhang et al., 2014), laying the foundations for Phanerozoic animal evolution. There were also changes in much simpler organ-

isms. Proliferation of calcified cyanobacteria since the very beginning of the Cambrian has been widely documented in reef and associated carbonate facies (Chuvashov et al., 1987; Korde, 1973; Luchinina and Tikhomirova, 1987; Maslov, 1956; Riding and Voronova, 1984; Riding, 1991a; Vologdin, 1932, 1937, 1939; Wray, 1977). Extensive carbonate deposition and the rapid diversification of calcified cyanobacteria led to the designation of the Cambrian and Early Ordovician as major CCEs (Riding, 1992).

Cambrian calcified cyanobacteria have been widely reported, e.g., in Mongolia (Drozдова, 1980; Wood et al., 1993), North America (Kobluk and James, 1979; James, 1981; Read and Pfeil, 1983; McMenamin et al., 2000; Pratt, 2001), Spain (Álvaro et al., 2000, 2006), Mexico (Noriega-Ruiz et al., 2024), France (Debrenne et al., 2002), Australia (Riding, 2006b), South China (Sun et al., 1985; Zhang and Yuan, 1994; Zheng, 1996; Ye and Yang, 1996; Hicks and Rowland, 2009; Adachi et al., 2014a, b), and North China (Woo et al., 2008; Lee et al., 2014; Qi et al., 2013; Adachi et al., 2023; Xiao et al., 2025), with additional, more isolated occurrences elsewhere. However, detailed systematic investigations of these fossils – pioneered by Russian scientists in particular – have remained relatively limited. Moreover, whereas previous studies of early Cambrian calcified cyanobacteria have predominantly focused on reef facies, their occurrences in other shallow-marine carbonate environments have often remained less well documented.

During the early Cambrian, the Yangtze Platform of South China was characterized by widespread shallow-marine carbonate deposition and experienced multiple phases of archaeocyath and microbial reef development. Previous studies described a variety of calcified cyanobacteria within these reefs, e.g., *Girvanella* from the Xiannüdong Formation (Ye and Yang, 1995; Hicks and Rowland, 2009; Li et al., 2021); *Girvanella*, *Botomaella*, *Kordephyton*, and *Proaulopora*-like filaments from the Tianheban Formation (Debrenne et al., 1991; Zhang and Yuan, 1994; Adachi et al., 2014a); and a diverse assemblage comprising *Girvanella*, *Razumovskia*, *Batenevia*, *Proaulopora*, *Subtifloria*, and *Hedstroemia* from the Qingxudong Formation (Sun et al., 1985; Zheng, 1996; Adachi et al., 2014b). These studies are scattered and primarily descriptive, warranting a more systematic investigation. For example, several key taxa, such as *Batenevia*, *Proaulopora* (Zheng, 1996), *Hedstroemia*, and *Subtifloria* (Sun et al., 1985), remained poorly illustrated or unfigured. Consequently, the overall diversity of early Cambrian calcified cyanobacteria in South China remains poorly constrained.

We examined 10 shallow-marine carbonate sections – both reefal and non-reefal – from Cambrian Series 2 in five regions (western Hunan, northeastern Guizhou, eastern Hubei, southern Shaanxi, and northern Sichuan) of the Yangtze Platform, South China. Thin-section analyses identified 15 species and 10 genera of calcified cyanobacteria, with 2 new species. This includes the first report of *Acuasiphonoria*, *Razumovskia*, *Subtifloria*, *Xianella*, *Bija*, and *Botomaella* in

South China. Additionally, this advances the fossil record of *Acuasiphonoria* from the Late Ordovician to the Cambrian Series 2. These assemblages closely resemble those from the Siberian Platform and North China. Our comprehensive study reveals significant new details, increases the global diversity of Cambrian calcified cyanobacteria, and provides data that support the concept of a cyanobacterial calcification episode (CCE) that commenced during the early Cambrian.

2 Geological setting and outcrop sections

2.1 Geological setting

Current reconstructions suggest that, during the Cambrian, the Yangtze Platform was located in tropical latitudes of the Southern Hemisphere (Fig. 1A), close to northern Gondwana (Li et al., 2008). It is generally accepted that the Yangtze Platform can be divided into three paleogeographic units: Upper, Middle, and Lower (Zhu et al., 2021). Studies of Cambrian shallow-marine carbonate facies have concentrated on the Middle–Upper Yangtze region (Fig. 1B).

Early Cambrian sea level rise preserved late Ediacaran sedimentary patterns and established widespread shallow-water facies in the Middle–Upper Yangtze (Pu et al., 1993), grading from tidal flats westward to shallow carbonate shelves. During the Fortunian to Cambrian Age 2, tidal-flat facies (phosphorite–dolostone–siliceous sediments) prevailed, while, near the southeastern margin, deep-water carbonaceous and siliceous shales accumulated, and anoxia promoted organic matter preservation (Mou et al., 2011). Coeval shallow shelves contain phosphoritic nodule-bearing siliceous mudstones. Peak transgression extended the deep-water basin northwestward during Series 2 (Stage 3). Uplift of the Hannan–Kangtien “Old Lands” introduced clastic sediments, forming shallow-marine successions of siltstone and sandy shale with localized fine sandstones (Feng et al., 2001). The southeastern basin margin persisted, accumulating interbedded carbonaceous shale and siliceous sediments. During Series 2 (Stage 4), regressive–transgressive cycles established carbonate-dominated environments (Fig. 1D; Mou et al., 2012; Zhang et al., 2010; Li and He, 2014).

2.2 Outcrop sections studied

We investigated Cambrian Series 2 carbonate strata in 10 outcrop sections in the northwestern and central regions of the Yangtze Platform (Fig. 1C). Collectively, the strata studied span all stages of calcified cyanobacterial evolution in Cambrian Series 2 shallow-marine carbonates in this region. The Daheba, Beiba-Fucheng, Yangjiagou, Tangjiahe, and Shatan sections are situated in the northwestern region (southern Shaanxi and northern Sichuan provinces), and the strata studied there correspond to the Xiannüdong Formation (ϵ_2x). The Xiachazhuang section in the central region of the Yangtze Platform exposes the Tianheban Formation (ϵ_2t). Similarly,

the Yutang, Limei, Panshi, and Panxin sections, also within the central region of the Yangtze Platform, expose the Qingxudong Formation (ϵ_2q). In accordance with recent advances in Cambrian stratigraphy (Zhu et al., 2021), the Xiannüdong Formation is assigned to Cambrian Series 2, Stage 3, and the Tianheban and Qingxudong formations are assigned to Cambrian Series 2, Stage 4 (Fig. 2).

The Xiannüdong Formation mainly consists of massive, relatively pure or clastic-rich, oolitic, microbial, and reef limestones, with occasional layers of sandstone and siltstone (Zeng, 2020) (Fig. 2). The Xiannüdong Formation contains a relatively higher amount of terrigenous input. The overlying Yanwangbian Formation has thin- to medium-bedded calcareous siltstone and fine sandstone at its base, overlain by light- to dark-red claystone, siltstone, and fine sandstone. The underlying Guojiaba Formation comprises grayish-green siltstone and claystone with abundant trace fossils. The Xiannüdong Formation (Cambrian Stage 3) is predominantly carbonate with some siliciclastics (Shen, 2015). In the Beiba-Fucheng section of southern Shaanxi, a large reef complex (Fig. 3A) contains *Archaeopharetra chengkouensis* and calcimicrobes (*Epiphyton*, *Renalcis*) as primary reef-building organisms, accompanied by trilobite and echinoderm bioclasts. Its cement contains a minor amount of quartz sand. The middle part of the Shatan section in northern Sichuan contains a prominent reef (Fig. 3B) with well-preserved archaeocyaths exposed on weathering surfaces, together with calcimicrobes and echinoderm and trilobite bioclasts. In the Tangjiahe section, a small reef (Fig. 3C) shows densely packed archaeocyaths on weathered surfaces (Fig. 3D), together with echinoderm and trilobite bioclasts. The Yangjiagou section is predominantly microbial carbonate (thrombolite and stromatolite); a small number of archaeocyaths are visible in the outcrop. In the Daheba Formation, oolite beds are frequently interbedded with fragmented archaeocyaths.

The Tianheban Formation has conformable contacts with the underlying yellowish-green silty shale of the Shipai Formation and with overlying massive dolostones of the Shilongdong Formation (Fig. 2). It is composed of thin- to medium-bedded argillaceous-banded limestone, intercalated with oolitic and conglomeratic limestones and silty shale. The middle–upper intervals of the formation contain archaeocyath-bearing reefs, interpreted as open-platform deposits (Wang, 1986). Microbial-archaeocyath reef facies, well developed in the Xiachazhuang section (Fig. 3E), contain abundant fossils (Fig. 3F) such as *Archaeocyathus yichangensis*, calcified cyanobacteria, calcimicrobes of uncertain affinity, and bioclasts (trilobites, cancelloriids, echinoderms).

The Qingxudong Formation, conformably overlying the Palang Formation, is composed of alternating layers of gray-green to yellow-green clay-rich shale, light-gray calcareous shale, and silty shale, with thin argillaceous limestone interbeds, transitioning upward into the Gaotai or Aoxi formations (Fig. 2), which consist predominantly of laminated

dolostone. The Qingxudong Formation in the Yutang section comprises four members: (i) basal light-gray micrite grading upward into (ii) dark-gray limestone, (iii) light-gray mottled limestone, and (iv) dark-gray to black argillaceous-banded limestone. Within the lower part of the upper argillaceous-banded limestone unit, thick-bedded intervals contain calcimicrobe reef limestone (Fig. 3H). The upper part transitions to thin-bedded argillaceous-banded limestone. In the Panxin section, the lower member of the Qingxudong Formation consists of limestone grading upward into limestone-bearing dolomite, suggesting a tidal-flat environment or an exposure event (inner-ramp facies). The upper member includes limestone intervals of oolitic limestone containing calcified cyanobacteria, indicating transformation into a high-energy bank environment (mid-ramp facies). In the Panshi section, the lower member of the Qingxudong Formation is limestone; the middle member is limestone-bearing dolomite, with its top part missing; and the upper member is argillaceous limestone, reflecting a distal open-platform environment (outer-ramp facies). In the Limei section, the Qingxudong Formation is predominantly limestone. An interval of bioclastic grainstone is present at the base, and limestone-bearing dolomite forms the upper part. Numerous calcified cyanobacteria occur in the upper–middle section.

3 Material and methods

A total of 13 094 thin sections were prepared from samples collected at 10 outcrop sections and examined using a Canon DSLR camera coupled with an OLYMPUS BX53 transmitted-light polarizing microscope. Detailed microscopic observations of calcified cyanobacteria and problematic calcimicrobial fossils were conducted, with comprehensive documentation and acquisition of over 4000 photomicrographs. Fossil identification was based on diagnostic characteristics, including filament diameter, length and branching, sheath thickness, and overall morphology, following taxonomic criteria based on previous studies (e.g., Debrenne et al., 1991; Riding, 1991a; Liu et al., 2016a, 2021). Systematic classification incorporated both fossil and present-day cyanobacterial features. All specimens and thin sections are housed in the Department of Geology, Northwest University.

4 Systematic paleontology

Overall, 20 species in 13 genera of calcified cyanobacteria and associated microfossils, including 2 new species, were identified. *Girvanella*, *Subtifloria*, *Xianella*, *Acuasiphonaria*, *Razumovskia*, and *Streptubularia* are attributed to the Oscillatoriales (cyanobacteria); *Hedstroemia*, *Kordephyton*, *Botomaella*, and *Bija* are attributed to Nostocales (cyanobacteria). In addition, associated *Epiphyton*, *Renalcis*, and *Izhella* are reported and attributed to calcified Micropro-

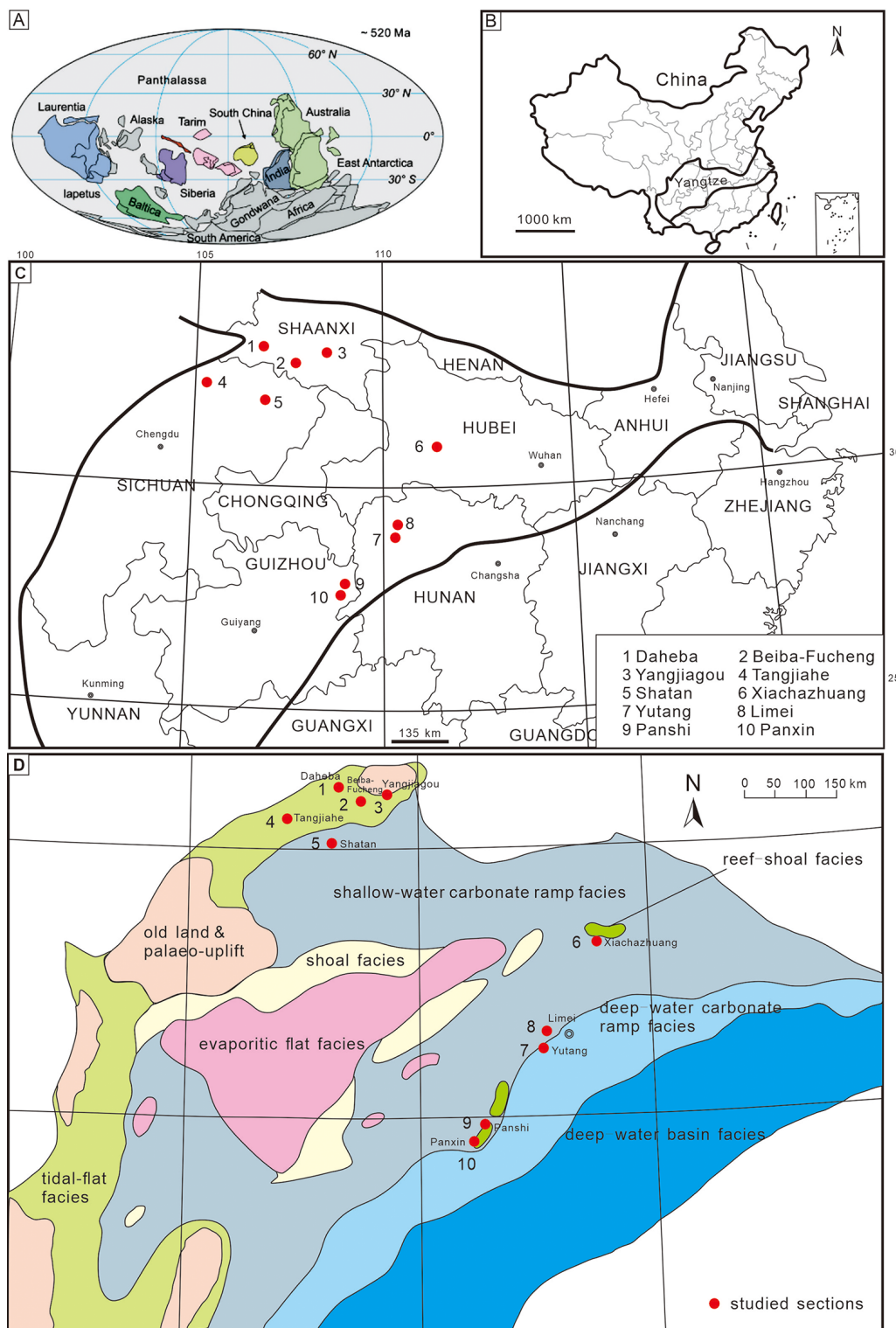


Figure 1. Maps showing the sections studied and depositional facies in the Middle–Upper Yangtze Platform region during Cambrian Series 2. (A) Early Cambrian (520 Ma) paleocontinental reconstruction (Li et al., 2021, fig. 1). (B) Location of the Yangtze region within China. (C) Locality map showing the sections studied. (D) Lithofacies paleogeographic map of the Middle–Upper Yangtze region during Cambrian Series 2. Red dots indicate study sections discussed in this paper, after Zhang et al. (2016). Paleogeographic facies adapted from Mou et al. (2012).

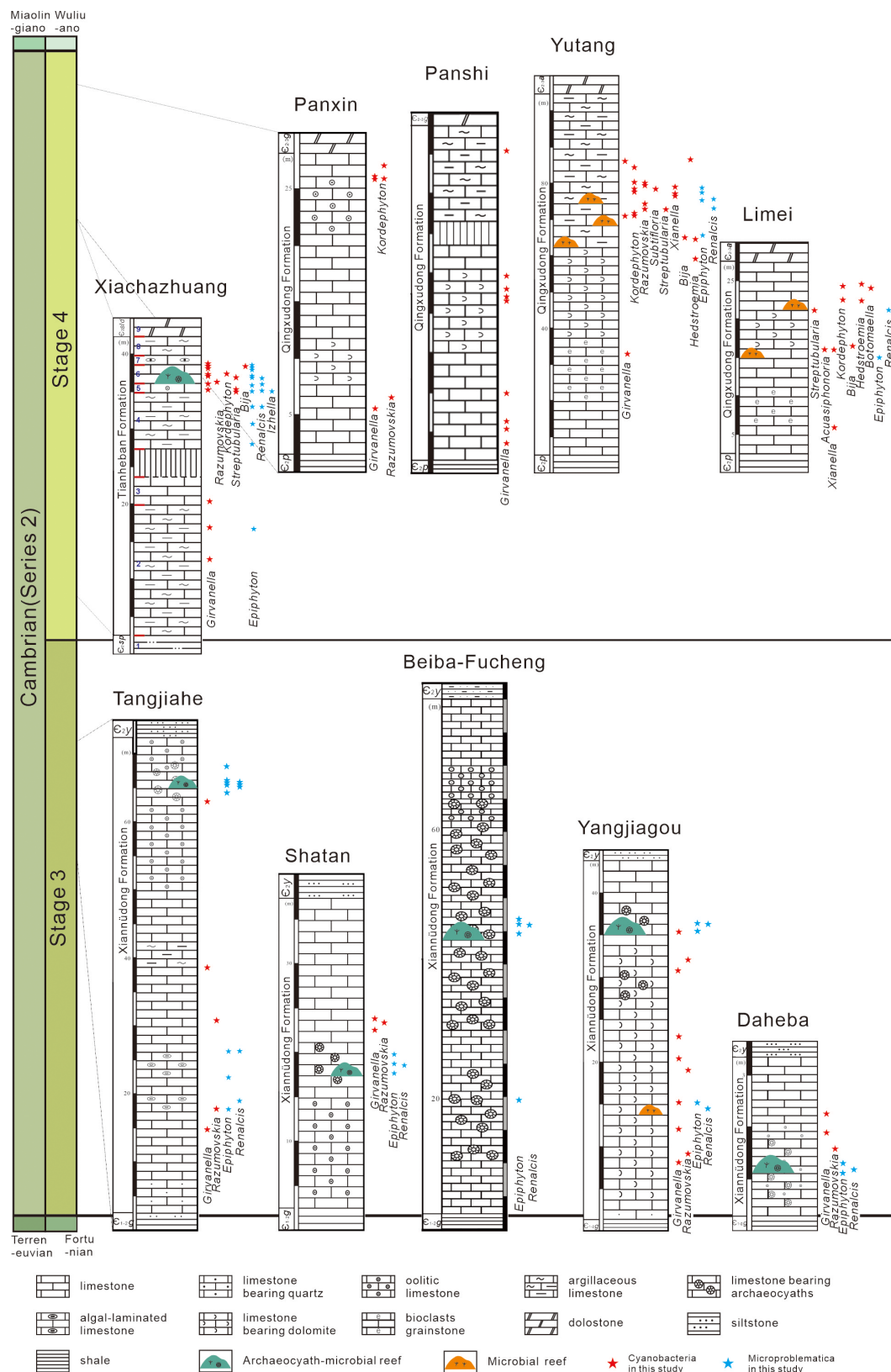


Figure 2. Stratigraphic column of 10 shallow marine carbonate sections, both reefal and non-reefal, from Cambrian Series 2 of the Yangtze Platform, showing horizons with calcified cyanobacteria and associated microfossils.

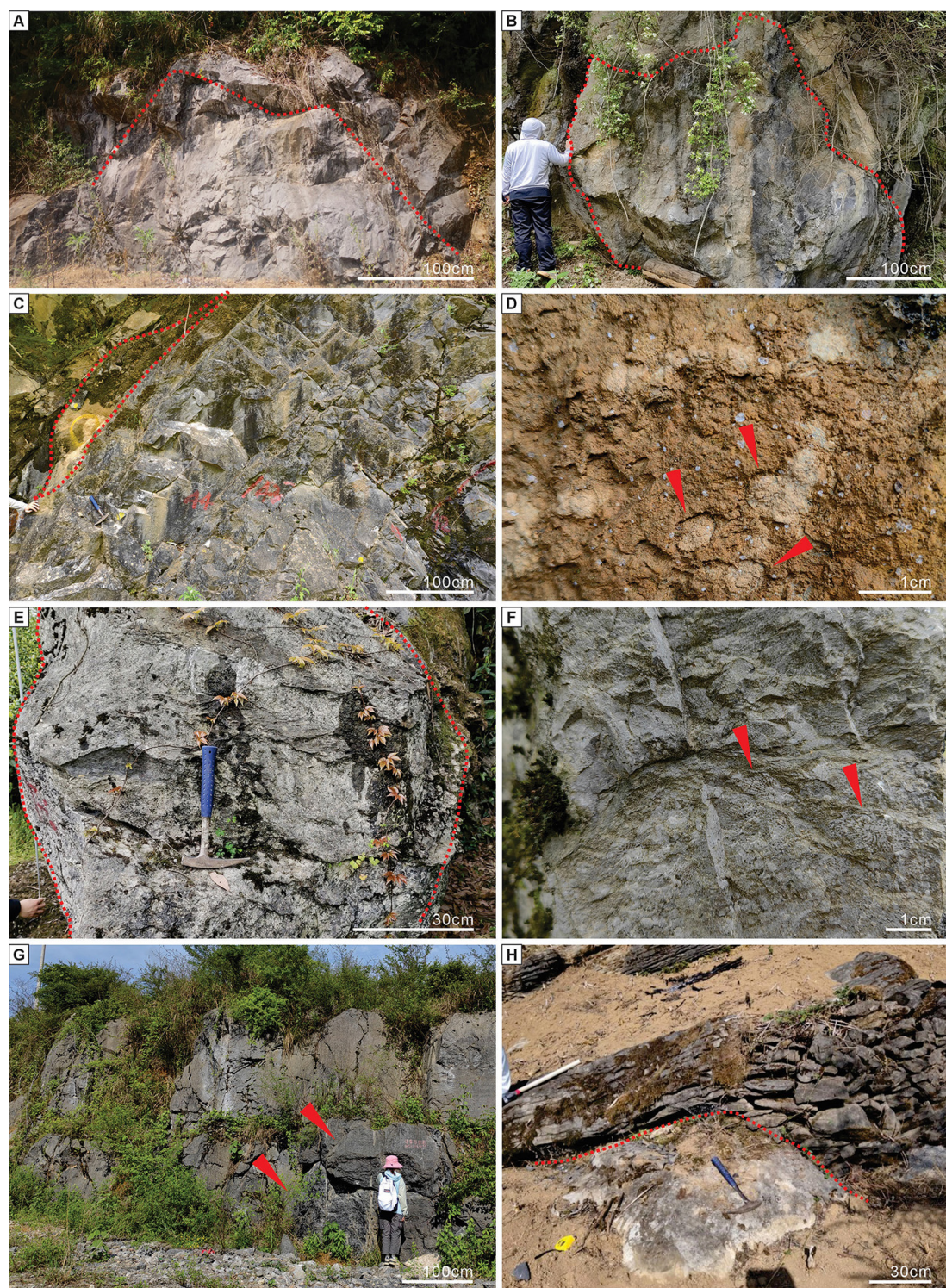


Figure 3. Cambrian Series 2 reef outcrops in the sections studied. Large reef (outlined in red) in the Xiannüdong Formation, Fucheng section. (B) Reef (outlined in red) in the lower–middle Xiannüdong Formation, Shatan section. (C) Archaeocyath-bearing reef in the Xiannüdong Formation, Tangjiahe section (small archaeocyath reef outlined in red). (D) Weathered surface of the reef in (C) showing distinct archaeocyaths (red arrows). (E) Calcimicrobe–archaeocyath reef (outlined in red) in the Tianheban Formation, Xiachazhuang section. (F) Weathered surface of the reef in (E) showing archaeocyaths (red arrows). (G) Argillaceous-banded limestone (red arrows), Qingxudong Formation, Pan-shi section. (H) Dome-shaped calcimicrobial reef (partially exposed) in dark-gray argillaceous-banded limestone (Member 4, Qingxudong Formation), Yutang section.

lematica. Most of these fossils are from the Qingxudong and Tianheban formations. The locations, horizons, and sedimentary facies of these calcified cyanobacteria and Microproblematica are illustrated in Fig. 2; the taxa are illustrated in Fig. 4.

Cyanobacteria Stanier, 1974

Order Oscillatoriales Elenkin, 1949

Genus *Girvanella* Nicholson and Etheridge, 1878 (Fig. 5)

1973 *Nicholsonia* Korde: 212, pl. 43, fig. 3; pl. 44, fig. 1; pl. 45, fig. 1.

Type species. *Girvanella problematica* Nicholson and Etheridge, 1878; Upper Ordovician, Scotland.

Diagnosis. Calcareous tubular filaments; long and curved; loosely to tightly tangled; micritic thin wall; filament diameters usually range from a few microns to tens of microns.

Comparison. *Girvanella* is one of the most widely known calcified cyanobacteria of the Paleozoic (Danielli, 1981). *Girvanella* species are mainly distinguished based on the overall diameter of the filament and the wall thickness. Korde (1973) distinguished *Nicholsonia* from *Girvanella*, but *Nicholsonia* was subsequently considered to be a synonym of *Girvanella* (Danielli, 1981) due to the lack of difference between some species of *Nicholsonia* and *Girvanella*. *Batenevia* and *Botominella* (which has been considered to be a synonym of *Subtifloria*; see Luchinina, 1975) are distinguished from *Girvanella* by their sarciniform (bundled) filament arrangement.

Affinity. *Girvanella* is generally regarded to be cyanobacterial (Bornemann, 1886; Pollock, 1918; Frémy and Dangéard, 1935). Riding's (1977b) comparison of it with calcified cyanobacterial sheaths, as in present-day *Plectonema*, has been widely accepted (Feng et al., 2010; Min et al., 2019, 2024; Liu et al., 2016a, 2021; Zheng et al., 2024; Zhang et al., 2024; Xiao et al., 2025).

Species. Conventionally, species of *Girvanella* are primarily distinguished by filament diameter and wall thickness (Wood, 1957). Zhang et al.'s (2024) revision of *Girvanella* species, by combining statistical analysis of their diameters with the taxonomic criteria of Mamet and Roux (1975), recognized four *Girvanella* species: *kasakiensis*, *problematica*, *wetheredii*, and *staminea*.

Girvanella kasakiensis Maslov, 1949 emend. Mamet and Roux, 1975 (Fig. 5E)

1949 *Girvanella ducii* var. *kasakiensis* Maslov: 6.

1965 *Girvanella* aff. *ducii* Chuvashov: 74, pl. 17, fig. 3.

1967 *Girvanella ducii* Wethered; Wray: 34, pl. 7, fig. 5.

1975 *Girvanella kasakiensis* Maslov; Mamet and Roux: 142, pl. 4, fig. 10; pl. 5, figs. 1, 2, 9, 10.

2011 *Girvanella kasakiensis* Maslov; Liu et al.: 495, pl. 1, fig. 3.

2016a *Girvanella kasakiensis* Maslov; Liu et al.: 188, fig. 4A.

2021 *Girvanella kasakiensis* Maslov; Liu et al.: 7, figs. 4.2, 4.3.

Material. Rare in the Xiannüdong Formation (ϵ_2x) at the Yangjiagou section, Hanzhong City, southern Shaanxi Province.

Description. Calcareous unbranched tubular filaments, long and loosely tangled; wall thin, micritic; external diameter 23–28 μm , wall thickness 4–6 μm (Fig. 5E).

Girvanella problematica Nicholson and Etheridge, 1878 emend. Wood, 1957(= *Girvanella ducii* Wethered, 1890 (Fig. 5A–D))

1878 *Girvanella problematica* Nicholson and Etheridge: 23, pl. 9, fig. 24.

1890 *Girvanella ducii* Wethered: 280, pl. 11, fig. 2a–c.

1932 *Girvanella problematica* Nicholson and Etheridge; Høeg: 64, pl. 1, figs. 4–6.

1981 *Girvanella problematica* Nicholson and Etheridge; Bourque et al.: 95, pl. 1, figs. 2–4.

2001 *Girvanella problematica* Nicholson and Etheridge; Riding and Fan: 789, fig. 3B, C.

2011 *Girvanella problematica* Nicholson and Etheridge; Liu et al.: 495, pl. I, fig. 4.

2016a *Girvanella problematica* Nicholson and Etheridge; Liu et al.: 188, fig. 4B.

2021 *Girvanella problematica* Nicholson and Etheridge; Liu et al.: 7, fig. 4.1.

Material. Abundant in the Xiannüdong Formation (ϵ_2x) at the Yangjiagou section, southern Shaanxi Province, and in the Qingxudong Formation (ϵ_2q) at the Yutang section, Yangtze Platform, Hunan Province, South China.

Description. Calcareous tubular filaments, curved and wound into a loose mass; wall thin, micritic; external diameter 13–22 μm , wall thickness 2–4 μm (Fig. 5A–D).

Girvanella wetheredii Chapman, 1908 (= *Girvanella in-crustans* Wethered, 1890, non Bornemann, 1886) (Fig. 5F)

1975 *Girvanella wetheredii* Chapman; Mamet and Roux: 141, pl. 1, figs. 9–12, pl. 161, pl. 2, figs. 1–5.

1995 *Girvanella wetheredii* Chapman; Mamet and Shalaby: 233, pl. 1, fig. 3.

2011 *Girvanella wetheredii* Chapman; Liu et al.: 495, pl. 1, fig. 1.

2016a *Girvanella wetheredii* Chapman; Liu et al.: 188, fig. 4C.

Material. Locally present in the Qingxudong Formation (ϵ_2q) at the Yutang section, Yangtze Platform, Hunan Province, South China.

Taxo- nomy	Num- ber	Genus	Species	Occurrence	Sketch		Suggested modern analogues	
Cyanobacteria	1	<i>Girvanella</i>	<i>G. kasakiensis</i> <i>G. wetheredii</i> <i>G. problematica</i>	Є2x, Є2t, Є2q			Oscillatoriacean cyanobacterium	<i>Plectonema</i>
	2	<i>Streptubularia</i>	<i>S. tenuitubus</i> <i>S. robustus</i> sp. nov.	Є2t, Є2q				<i>Borzia</i>
	3	<i>Acuasiphonoria</i>	<i>A. ordovica</i>	Є2q			Phormidiaceae cyanobacterium	<i>Phormidium breve</i>
	4	<i>Subtifloria</i>	<i>S. sp.</i>	Є2q				<i>Microcoleus</i>
	5	<i>Xianella</i>	<i>X. hongii</i> <i>X. mollis</i> sp. nov.	Є2q				<i>Symploca</i>
	6	<i>Razumovskia</i>	<i>R. hispida</i> <i>R. lata</i>	Є2x, Є2q, Є2t				<i>Phormidium</i>
	7	<i>Hedstroemia</i>	<i>H. sp.</i>	Є2q			Rivulariaceans cyanobacterium	<i>Rivularia</i>
	8	<i>Bija</i>	<i>B. sibirica</i>	Є2t, Є2q				
	9	<i>Botomaella</i>	<i>B. sp.</i>	Є2q				
	10	<i>Kordephyton</i>	<i>K. crinitum</i>	Є2t, Є2q				
Microproblematica	11	<i>Renalcis</i>	<i>R. granosus</i>	Є2t, Є2q			uncertain	
	12	<i>Izhella</i>	<i>I. nubiformis</i>	Є2t, Є2q				
	13	<i>Epiphyton</i>	<i>E. parapusillum</i> <i>E. flabellatum</i> <i>E. sp.</i>	Є2q				

Figure 4. Taxa of calcified cyanobacteria and associated calcified Microproblematica recognized in this study, with suggested present-day analogues. Species in bold are new (sketches of fossils and modern analogues are based on Liu et al., 2016a).

Description. Calcareous tubular filaments, curved and wound into a loose mass; wall thin, micritic; external diameter 8–12 µm, wall thickness about 1–2 µm (Fig. 5F).

Genus **Razumovskia** Vologdin, 1939 (Fig. 6A–C)

1937 *Razumovskia* Vologdin; Krasnopeeva: 19, pl. III, fig. 24.
1990 *Trichophyton* Bian and Zhou: 6. pl. 4, fig. 8.

2016a *Razumovskia* Vologdin; Liu et al.: 189, pl. 4, fig. G.
Type species. *Razumovskia uralica* Vologdin in Krasnopeeva, 1937; Lower Cambrian; South Urals, Russia.
Diagnosis. Calcareous tubular filaments, long and curved, arranged in a parallel or vertically alternating pattern, and grouped into a mat; distal tubes can extend vertically from the mat, bending into different lengths; wall thin micritic.

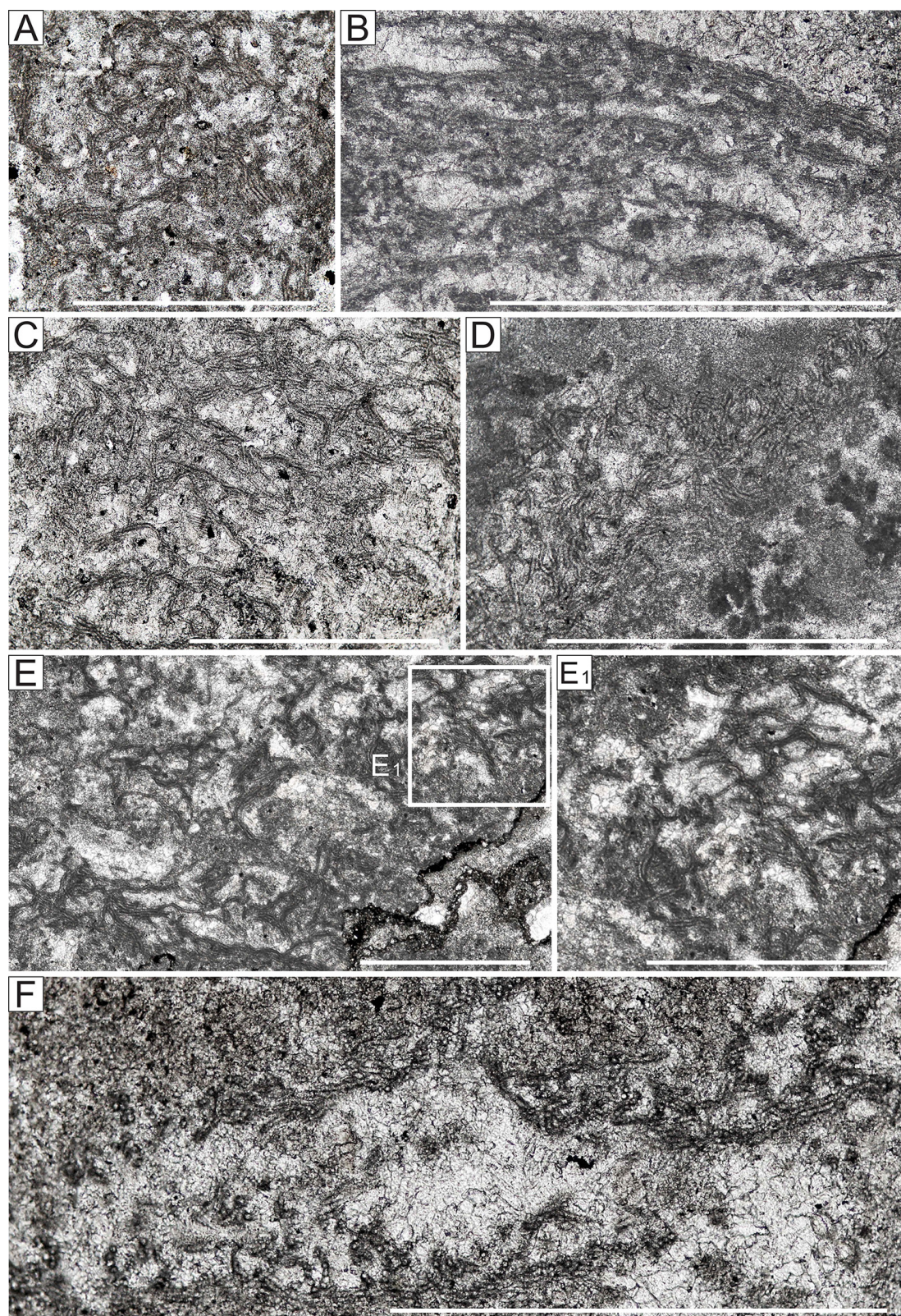


Figure 5. Photomicrographs of *Girvanella* in the early Cambrian of South China. (A–D) *Girvanella problematica*. (A) Yangjiagou section, sample no. 2-29, oblique longitudinal sections. (B) Xiachazhuang section, sample no. 6-S32, oblique longitudinal sections. (C) Yangjiagou section, sample no. 2-22, oblique longitudinal sections. (D) Xiachazhuang section, sample no. 3-2, oblique longitudinal sections. (E) *Girvanella kasakiensis*, Yangjiagou section, sample no. 2-6, longitudinal sections. (F) *Girvanella wetheredii*, Yutang section, sample no. 4-2, longitudinal and cross-sections. All scale bars equate to 1 mm.

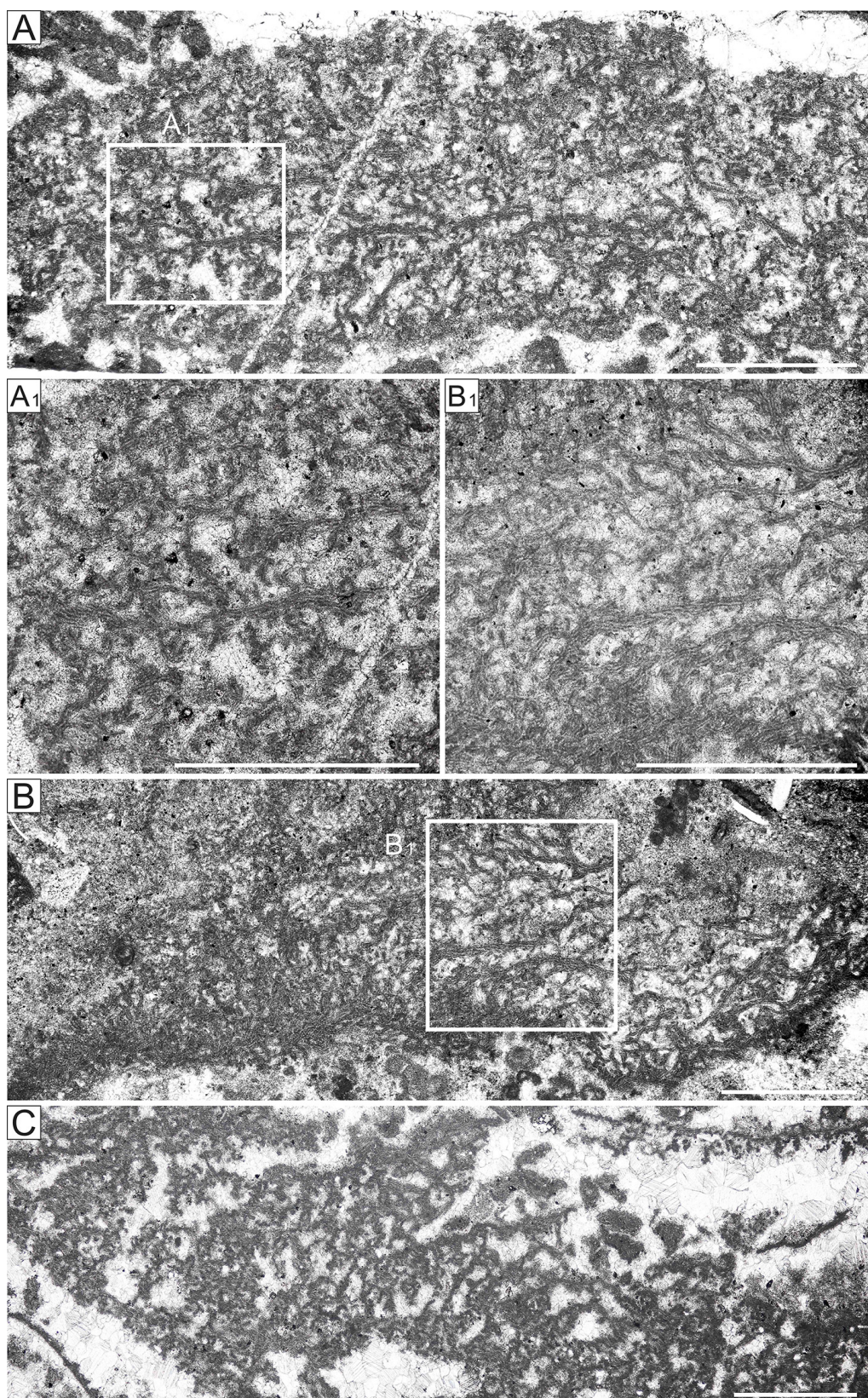


Figure 6. Photomicrographs of *Razumovskia* fossils, early Cambrian, South China. (A–B) *Razumovskia hispida*. (A) Yangjiagou section, sample no. 2-6. (A₁), enlargement of part of (A). (B) Xiachazhuang section, sample no. 6-S04. (B₁) Enlargement of part of (B). (C) *Razumovskia lata* Yangjiagou section, sample no. 2-31. All scale bars equate to 1 mm.

Comparison. *Razumovskia* has been reported from the early Cambrian (Vologdin, 1939; Korde, 1973; Drosdova, 1980; Adachi et al., 2023; Zheng et al., 2024), Late Cambrian (Lee and Riding, 2022) and Late Ordovician (Liu et al., 2016a). *Razumovskia* and *Girvanella* are similar in terms of basic filament morphology; the main difference is filament arrangement. *Girvanella* filaments are commonly irregularly tangled, whereas *Razumovskia* filaments are typically arranged in parallel or vertically alternating, with a tendency to curve upward at the end. *Trichophyton*, proposed by Bian and Zhou (1990) and also reported from the Ordovician of the Ordos Basin of North China (Ye et al., 1995), is considered to be a junior synonym of *Razumovskia* (Liu et al., 2016a).

Affinity. Liu et al. (2016a) compared the filament arrangement in *Razumovskia* to that of present-day *Phormidium*.

Species. Korde (1961, 1973) recognized five species based on filament diameter: *R. kyanica*, *R. multispora*, *R. seriate*, *R. hispida*, and *R. grandis*. *Razumovskia* species recognized in the present study are *R. hispida* and *R. lata*, as described by Drosdova (1980).

Razumovskia hispida Korde, 1973

1973 *Razumovskia hispida* Korde: 128, pl. 10, fig. 1; pl. 11, fig. 1a.

Material. Widespread in the Xiannüdong Formation (ϵ_2x) at the Yangjiagou section, southern Shaanxi Province, and locally present in the Tianheban Formation (ϵ_2t) at the Xiachazhuang section, Hubei Province, South China.

Description. Short filaments extending from the mat, diameter 10–15 μm , wall thickness 2 μm (**Fig. 6A–B**).

Razumovskia lata Drosdova, 1980

1980 *Razumovskia lata*; Drosdova: pl. IV, fig. 3; Plate V, figs. 1, 3, 5.

1990 *Trichophyton changshanensis*; Bian and Zhou: 6, pl. 4, fig. 8, IV.

1995 *Trichophyton* sp.; Ye et al.: 16, pl. 8, fig. 7.

2014 *Razumovskia lata*; Liu: 57, pl. 4–4, fig. B.

Material. Only observed in the Xiannüdong Formation (ϵ_2x) at the Yangjiagou section, Hanzhong City, southern Shaanxi Province.

Description. Short filaments extend from longer and more curved mat-like filaments, with diameter $\sim 8 \mu\text{m}$ (**Fig. 6C**).

Genus *Subtifloria* Maslov, 1956 (**Fig. 7A**)

1959 *Botominella* Reitlinger: 25, pl. 10, figs. 1–7.

2009 *Girvanella* Nicholson and Etheridge; Wang et al.: fig. 2a.

2014 *Girvanella* Nicholson and Etheridge; Rong et al.: fig. 5a, b.

Type species. *Subtifloria delicata* Maslov, 1956; Lower Cambrian; Siberian Platform, Russia.

Diagnosis. Calcified tubular filaments, nearly parallel and clustered into bundles, uniform filament diameter, thin micritic wall.

Comparison. Calcified *Subtifloria* has mainly been reported from the early–middle Cambrian (Maslov, 1956; Luchinina, 1975; Luchinina and Terleev, 2003; Mei et al., 2020; Li and Cong, 2025) and the Middle–Late Ordovician (Riding and Fan, 2001; Liu et al., 2016a, 2021; Tang, 2024). Rare examples of *Subtifloria* have been described from the Middle–Late Devonian in southern China (Feng et al., 2010). Unlike *Batenevia*, in which the filaments are also in bundles; *Subtifloria* filaments do not branch. Luchinina (1975) considered *Botominella* to be a junior synonym of *Subtifloria*. *Subtifloria* resembles *Girvanella* in terms of tube size but differs in terms of the subparallel arrangement of its filaments in bundles and its possible branching. Specimens regarded to be *Girvanella* from the Middle–Upper Ordovician of the Tarim Basin (Wang et al., 2009; Rong et al., 2014) have since been identified as *Subtifloria* (Feng et al., 2010; Liu et al., 2016a; Xiao et al., 2025). *Subtifloria latissima* Luchinina from the Lower Carboniferous of the Kuzbass (Bogush et al., 1990, pl. 3, fig. 1) may be *Girvanella* (Feng et al., 2010; Liu et al., 2016a; Xiao et al., 2025).

Affinity. Luchinina (in Chuvashov et al., 1987) compared *Subtifloria* with present-day *Microcoleus*, which shows filaments arranged in parallel bundles, supporting a cyanobacterial affinity, and this has been endorsed (Feng et al., 2010; Liu et al., 2016a).

Species. *Subtifloria* currently consists of two species, *S. delicata* and *S. latissima* (Bogush et al., 1990). *S. delicata* filaments can be up to 12 mm long, with an outer diameter of $\sim 27 \mu\text{m}$ and a wall thickness of around 5 μm ; *Subtifloria latissima* resembles *Girvanella*; its taxonomic status is uncertain.

Subtifloria sp.

Material. Rarely present in the Qingxudong Formation (ϵ_2q) at the Yutang section, Hunan Province, South China.

Description. Filaments, almost parallel and clustered into bundles, with external diameter 34–40 μm .

Remarks. Due to its unusually large diameter, much greater than currently recognized *Subtifloria* species (**Fig. 7A**), its classification remains uncertain.

Genus *Acuasiphonoria* Liu et al., 2016 (**Fig. 7B**)

1973 *Kordephyton* Korde: 289, pl. 13, fig. 2; pl. 14, figs. 2, 3.

Type species. *Acuasiphonoria ordovica* Liu et al., 2016; Upper Ordovician, Katian, Lianglitag Formation; Tarim Basin, Xinjiang Province, Northwest China.

Diagnosis. Straight to gently curved, calcified long tubular filaments, appearing to end in a sharp point; possibly branched at an acute angle, tube wall micritic.

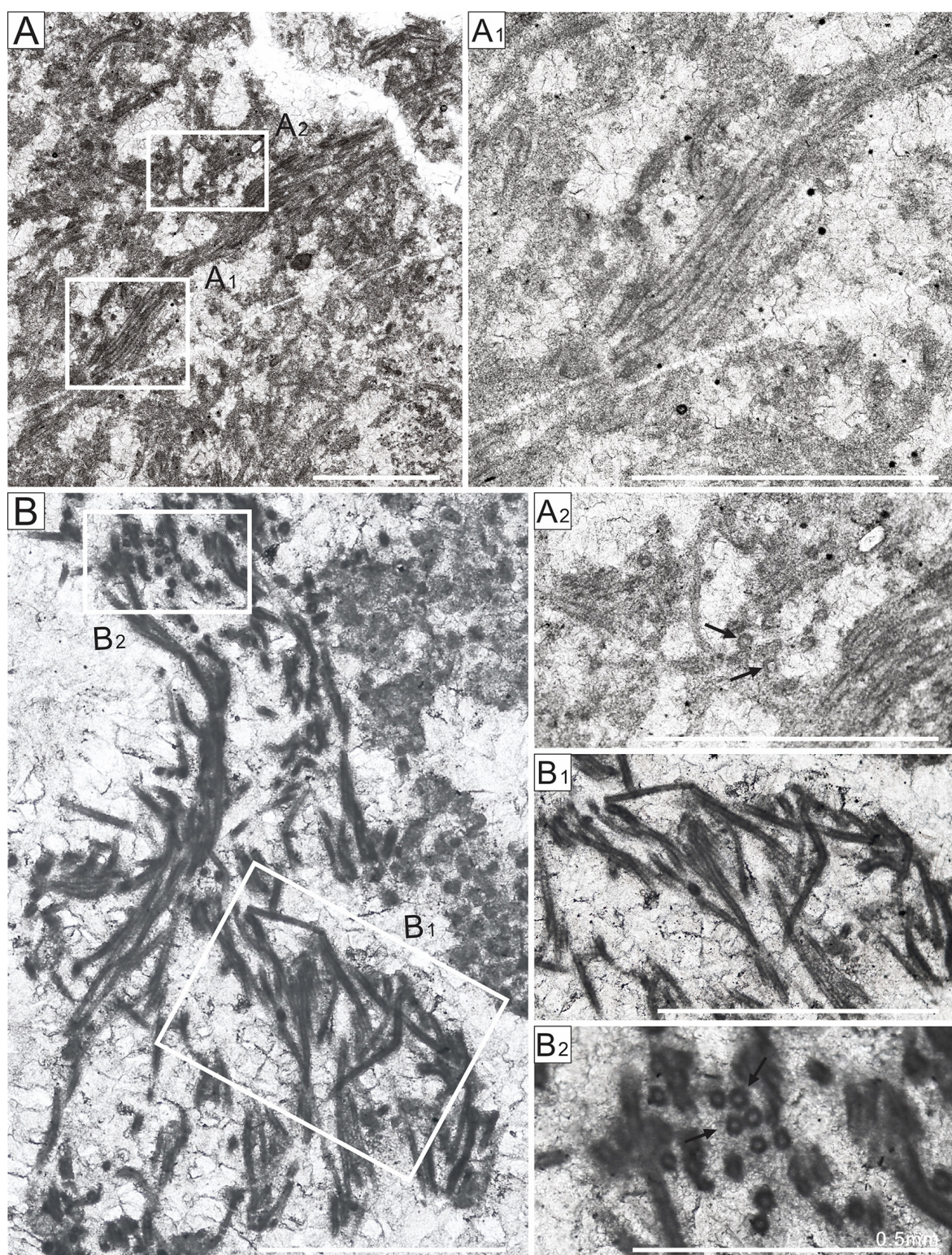


Figure 7. Photomicrographs of *Subtifloria* and *Acuasiphonoria* fossils, early Cambrian, South China. A, *Subtifloria* sp., Yutang section, sample no. 5-S17, longitudinal section. (A₁) Enlargement of part of (A) longitudinal section. (A₂) Enlargement of part of (A). Arrows indicate cross-sections. (B) *Acuasiphonoria ordovica*, Limei section, sample no. 3-DLC-1, longitudinal section. (B₁) Enlargement of part of (B) longitudinal section. (B₂) Enlargement of part of (B). Arrows point to cross-sections. All scale bars equate to 1 mm, except where indicated.

Comparison. *Acuasiphonoria* has previously been reported from the Late Ordovician (Liu et al., 2016a, 2021); this is its first report from the Cambrian. *Acuasiphonoria* is distinguished from *Girvanella* and *Subtifloria* by long straight or only slightly curved filaments that appear to taper, needlelike. *Acuasiphonoria* can resemble branched, bushy forms of *Proaulopora* in its macroscopic morphology. However, *Acuasiphonoria* is morphologically distinct from *Tubophyllum* and the *Proaulopora* Group (Proauloporaceae) as a whole since it lacks a multilayered wall structure and distinctive whorl-like collars which are characteristic of the *Proaulopora* Group. Moreover, its sizes differ considerably: members of the *Proaulopora* Group are much larger, generally 50–100 µm in diameter, whereas the filament diameter of *Acuasiphonoria* is 22–24 µm.

Affinity. *Acuasiphonoria* is interpreted as an oscillatoriacean sheath (Liu et al., 2016a). By terminating in a sharp point, *Acuasiphonoria* is similar to *Phormidium breve* (Phormidiaceae), whose trichomes similarly show abrupt apical attenuation (Fig. 4).

Species. *Acuasiphonoria* currently consists of only one species, *Acuasiphonoria ordovica*.

Acuasiphonoria ordovica Liu et al., 2016

2016a *Acuasiphonoria ordovica* Liu et al., p. 191, fig. 5A–C.

2021 *Acuasiphonoria ordovica* Liu et al.: 6, pl. 4, figs. 6–7.

Material. Rarely present in the Qingxudong Formation (ε_{2q}) of the Limei section, Yangtze Platform, Hunan Province, South China.

Description. Elongate straight, separated cylindrical filaments, slightly curved, ending in a sharp point; extending straight for up to 1 mm; external diameter 22–24 µm; wall thickness 4–6 µm, micritic (Fig. 7B₂).

Genus ***Streptubularia*** Zheng, Xiao, and Liu, 2025

Type species. *Streptubularia tenuitubus* Xiao et al., 2025; Cambrian, Series 2, Jianchang and Zhushadong Formation, Liaoning and Shandong provinces, North China.

Diagnosis. Robust curved micritic tube with thick micritic wall; length-to-width ratio 3 : 1 to 6 : 1; irregularly constricted; Y-shaped dichotomous branching.

Comparison. *Streptubularia* has previously been reported from the early Cambrian of North China (Xiao et al., 2025). In morphology, *Streptubularia* is somewhat similar to *Girvanella* Nicholson and Etheridge, 1878, but is unusually large. Lee et al. (2014) reported a large-diameter *Girvanella*-like fossil. However, in addition to being large, *Streptubularia* shows branching. A species of *Nicholsonia*, *N. grandis*, can show branching and reach a diameter of 50 µm (Korde 1973, p. 212), closely resembling *Streptubularia*. *Nicholsonia* was considered to be a synonym of *Girvanella* (Danielli, 1981, p. 96) due to an apparent lack of difference in illustrations (Korde, 1973, pl. XLV). Nonetheless, *Nicholsonia* does

appear to exhibit morphological differences among its constituent species, although its features are difficult to recognize from the original illustrations. We suggest that *Nicholsonia* may be a composite taxon, possibly a heterogeneous association of *Girvanella* and other organisms. Further work is required to elucidate the distinction between *Streptubularia* and *Nicholsonia*.

Affinity. Xiao et al. (2025) compared *Streptubularia* from the early Cambrian Jianchang Formation in the North China Plate with extant *Borzia* (Borziaceae, Oscillatoriales), citing short filaments with cross-wall constrictions (Hu et al., 2006). However, *Streptubularia* is larger than *Borzia* and resembles a calcified sheath, not a cellular filament. We suggest that *Streptubularia* could be an oscillatoriacean sheath, as for *Girvanella*.

Species. Two species of *Streptubularia* are distinguished, based on tube diameter, relative thickness of the wall, and growth habit.

Streptubularia tenuitubus Zheng, Xiao, and Liu, 2025 (Fig. 8A–B)

1973 *Nicholsonia grandis* Korde: 215, pl. 45, fig. 1.

2014a *Girvanella* Adachi et al.: 709, pl. 6, fig. C.

2014b *Girvanella* Adachi et al.: 51, pl. 6, figs. E, F.

2025 *Streptubularia tenuitubus* Xiao et al.: 13, pl. 6 figs. A–E.

Material. Holotype: thin section NWU XCZS02-2-33 from the Xiachazhuang Section (Tianheban Formation, Cambrian Series 2 Stage 4), Yangtze Platform, Hubei, South China.

Description. Curved short tubes, external diameter 60–75 µm, tube length 300–600 µm, micritic wall, internal sparsely filled. Often occurs in association with archaeocyaths and the calcified Microproblematica *Renalcis* and *Epiphyton* (Fig. 8A–B).

Streptubularia robustus sp. nov.

(LSIDurn:lsid:zoobank.org:act:1D577D03-C9B1-4D60-9DBD-071B5B017F7A) (Fig. 8C–D)

Etymology. *robustus*; robust.

Material. Holotype: thin section NWU YTS03-1-15 from Yutang section; Cambrian Series 2 Stage 4, Qingxudong Formation; Yangtze Platform, Hunan Province, South China. Abundant in the Limei and Yutang sections.

Description. Curved calcareous thick tubes, external diameter 85–125 µm, wall thickness 9–18 µm, micritic wall (Fig. 8C–D).

Remarks. *Streptubularia* often occurs in association with *Kordephyton*. Adachi et al. (2014a) referred to filaments up to 100 µm in diameter to large *Girvanella*. Similar filaments were described by Lee et al. (2014) and Adachi et al. (2023) as “tubiform microbe” without addressing their systematic position. These fossils resemble *Streptubularia*.

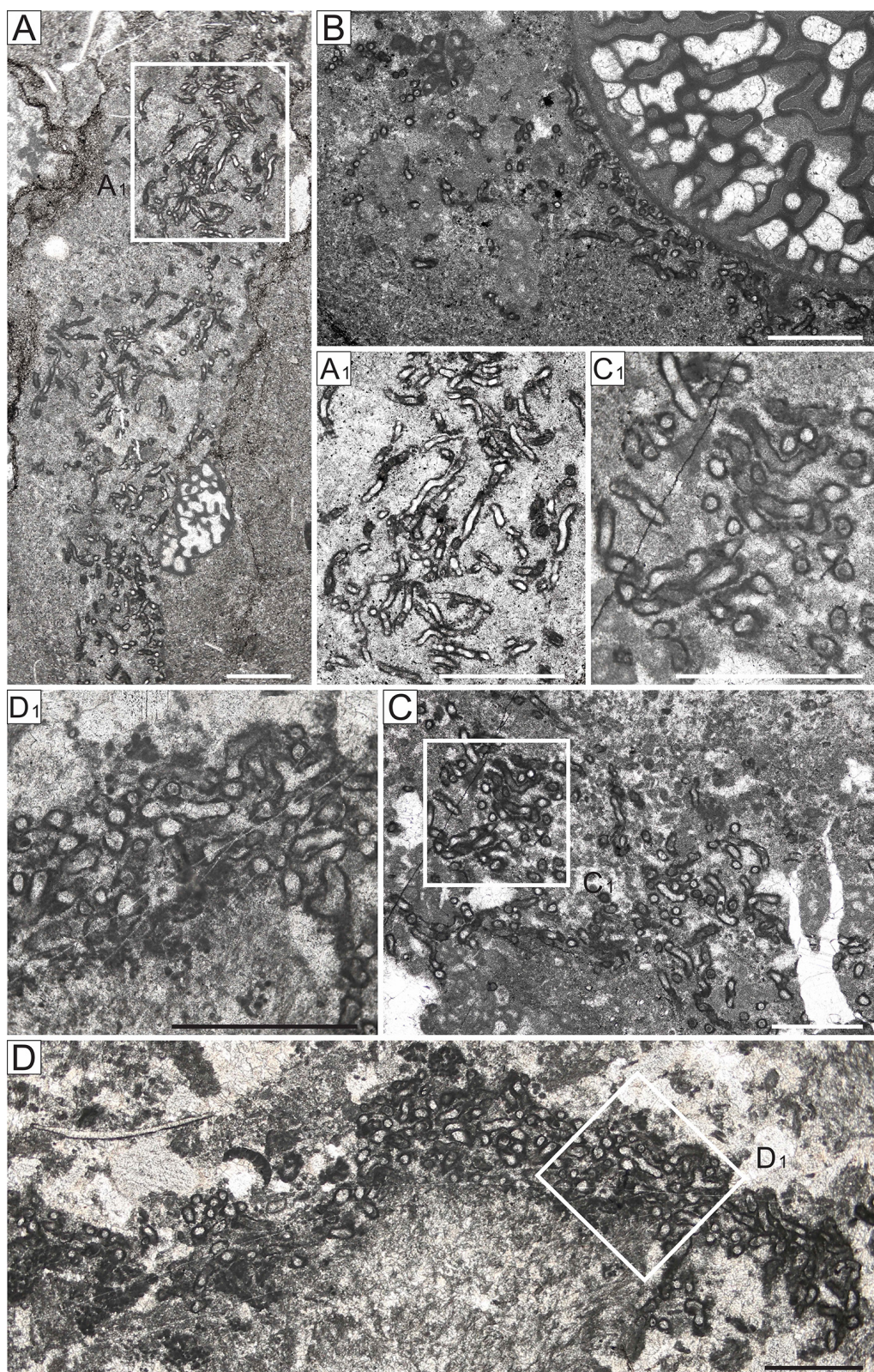


Figure 8. Photomicrographs of *Streptubularia*, early Cambrian, South China. (A–B) *Streptubularia tenuitubus*; (A) *Streptubularia tenuitubus* sp. et gen. nov., Xiachazhuang section, sample no. 6-S02 longitudinal section and cross-section. (A₁) Enlargement of part of (A). (B) *Streptubularia tenuitubus* with archaeocyath and *Renalcis*, Xiachazhuang section, sample no. 6-1. (C–D) *Streptubularia robustus* n. sp.; (C) *Streptubularia robustus* n. sp., longitudinal section and cross-section. (D) *Streptubularia robustus* sp. nov., Yutang section, sample no. 5-S03, longitudinal section and cross-section. D₁ Enlargement of part of (D). All scale bars equate to 1 mm.

Genus *Xianella* Lee and Riding, 2016
(Fig. 9A–C)

Type species. *Xianella hongii* Lee and Riding, 2016; Upper Ordovician Beiguoshan Formation, Ordos Basin, Northwest China.

Diagnosis. Calcareous microfossil; narrow unbranched tubular filaments forming prostrate and erect anastomosing cable-like strands; wall micritic.

Comparison. *Xianella* has been reported from the Ordovician (Lee and Riding, 2016; Liu et al., 2021) and the early Cambrian of North China (Xiao et al., 2025). The filaments of *Xianella* form wide cord-like threads, similarly to *Cladogirvanella* Ott, 1966, with the difference being that *Xianella* tubes are larger in diameter and are arranged both horizontally and vertically. Bundled filamentous structure also occurs in *Subtifloria* Maslov, 1956, and in similar genera such as *Botominella* Reitlinger, 1959, and *Batinevia* Korde, 1966, but these are not known to form such long branching cables. Ordovician *Acuasiphonoria* Liu et al., 2016, also consists of arrays of elongate filaments. However, its long, gently curved tubes are pointed and possibly branch at acute angles (Liu et al., 2016a). These features and the lack of anastomosed bundles distinguish *Acuasiphonoria* from *Xianella*, which has narrow, unbranched, thin, single-layered-wall tubules (20–45 µm); forms cable-like strands and cavities; and lacks whorl collars. The *Proaulopora* Group, in general, exhibits thick filaments (up to 70 µm) with multilayered walls, whorl collars, minor branching, and clustered growth.

Affinity. As with *Girvanella*, *Xianella* has been interpreted as the calcified sheath of filamentous cyanobacteria (Lee and Riding, 2016; Liu et al., 2021; Xiao et al., 2025). Based on its cable-like strands composed of filament bundles, *Xianella* was compared by Lee and Riding (2016) with present-day mat-forming cyanobacteria with multiple trichomes in a common sheath, such as *Microcoleus*. Our specimens support this interpretation (Fig. 11C–a).

Species. The genus is monospecific.

Xianella hongii Lee and Riding, 2016
(Fig. 9A–C)

2016 *Xianella hongii* Lee and Riding, p. 4, figs. 4, 5.

2021 *Xianella hongii* Lee and Riding; Liu et al.: 9, pl. 5, figs. 1–6.

Material. Abundant in the Qingxudong Formation (ε₂q) of the Yutang section, Hunan Province, South China.

Description. Filaments aggregated into mats, inter-filament cavities of varying sizes, cavity diameters range from 100 to 1000 µm, tube diameters range from 20 to 30 µm (Fig. 9A–C).

Xianella mollis sp. nov.
(LSIDurn:lsid:zoobank.org:act:B9A502AA-54DC-4117-B7DE-181101E02DA5)
(Fig. 10A–B)

Etymology. *Mollis* (Latin) means soft.

Material. Holotype: thin section NWU YT S18-2-13 Qingxudong Formation (Cambrian Series 2 Stage 4) Yutang section; Yangtze Platform, Hunan Province, South China. *X. mollis* occurs locally in the Yutang section.

Description. Calcified tubes, unbranched, straight to slightly curved, or wavy. Locally subparallel (Fig. 10A–B). Wall micritic, thick. Wall thickness of 5–10 µm, tubes usually 200–600 µm in length, external diameter 25–45 µm, forming filament bundles with widths of 500–800 µm and lengths up to 3.3 mm; filament bundles can be curved into a U shape (Fig. 10A–B). Mat-like growth.

Remarks. Filaments of *X. mollis* and *X. hongii* are very similar. The main distinction is that, in *X. hongii*, the bundles of filaments usually enclose spar-filled cavities (Lee and Riding, 2016), whereas, in *X. mollis*, they typically show mat-like growth, and the bundles of filaments are characteristically curved into a U shape and lack anastomose strands (Fig. 11A, C).

The characteristic subparallel arrangement of the tubes in filament bundles somewhat resembles that of *Subtifloria* (Fig. 11B). *Xianella mollis* is distinguished by its thick mat-like filament arrangement and concentric annular cross-section (Fig. 11A). *X. mollis* tubes are similar in size to those of *Girvanella* and *Pachytibia* Zheng, Xiao, and Liu, 2025, from the early Cambrian of North China but are distinguished from *Girvanella* by being more straight. *Pachytibia* has thicker walls and lacks a subparallel filamentous structure (Fig. 11D) (Xiao et al., 2025).

Affinity. The dense and subparallel arrangement of mat-like filaments in *X. mollis* can be compared with present-day Phormidiaceae Kützing ex Gomont 1893, such as *Symploca* and *Phormidium*. The filament bundles of *Symploca* can form intertwined, entangled, or parallel aggregates of filaments like those of *X. hongii* (Fig. 11C–b), whereas, in *Phormidium*, the bundles of filaments typically have a curved growth pattern similar to that of *X. mollis* (Fig. 11A). We interpret *X. mollis* to be the calcified sheath of a cyanobacterium and tentatively assign it to the Phormidiaceae.

Order Nostocales (Borzi) Geitler, 1925

Genus *Kordephyton* Radugin and Stepanova, 1964
(Fig. 12)

1973 *Kordephyton* Korde: 289, pl. 13, fig. 2; pl. 14, figs. 2, 3.

Type species. *Kordephyton crinitum* Korde, 1973; Middle Cambrian (Amgan), Elanskoe Formation, Elanskoe, Lena River, Sakha (Yakutia), Russia.

Diagnosis. Thin micritic filaments, long and delicate, in a fan-like pattern. Most filaments appear to be solid; tubular structure is observed in a few micritic filaments and shows relatively thick micritic walls (Fig. 12B).

Comparison. *Kordephyton* is currently only confirmed from the Cambrian (Riding and Voronova, 1984; Latham and

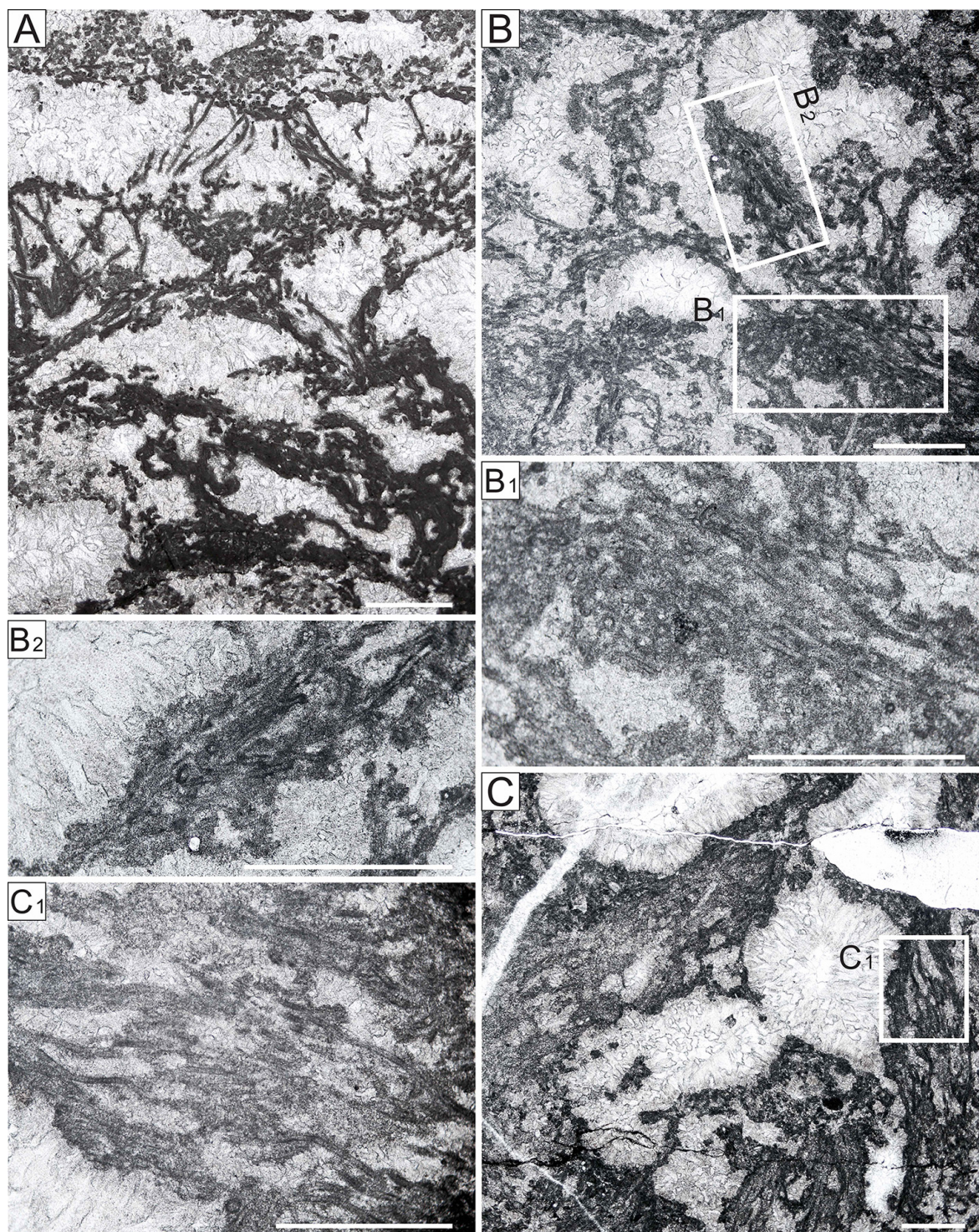


Figure 9. Photomicrographs of *Xianella hongii*, early Cambrian, South China. (A) Overall morphology, Limei section, sample no. 3-DLC-1, longitudinal sections and cross-sections. (B) Medium-sized fenestrae bounded by bundles of *Xianella* filaments, Yutang section, sample no. 5-S18. (B₁) Enlargement of part of (B), cross-section. (B₂) Local enlargement of (B), longitudinal section. (C) Yutang section, sample no. 5-S19. (C₁) Enlargement of part of (C), longitudinal section. All scale bars equate to 1 mm.

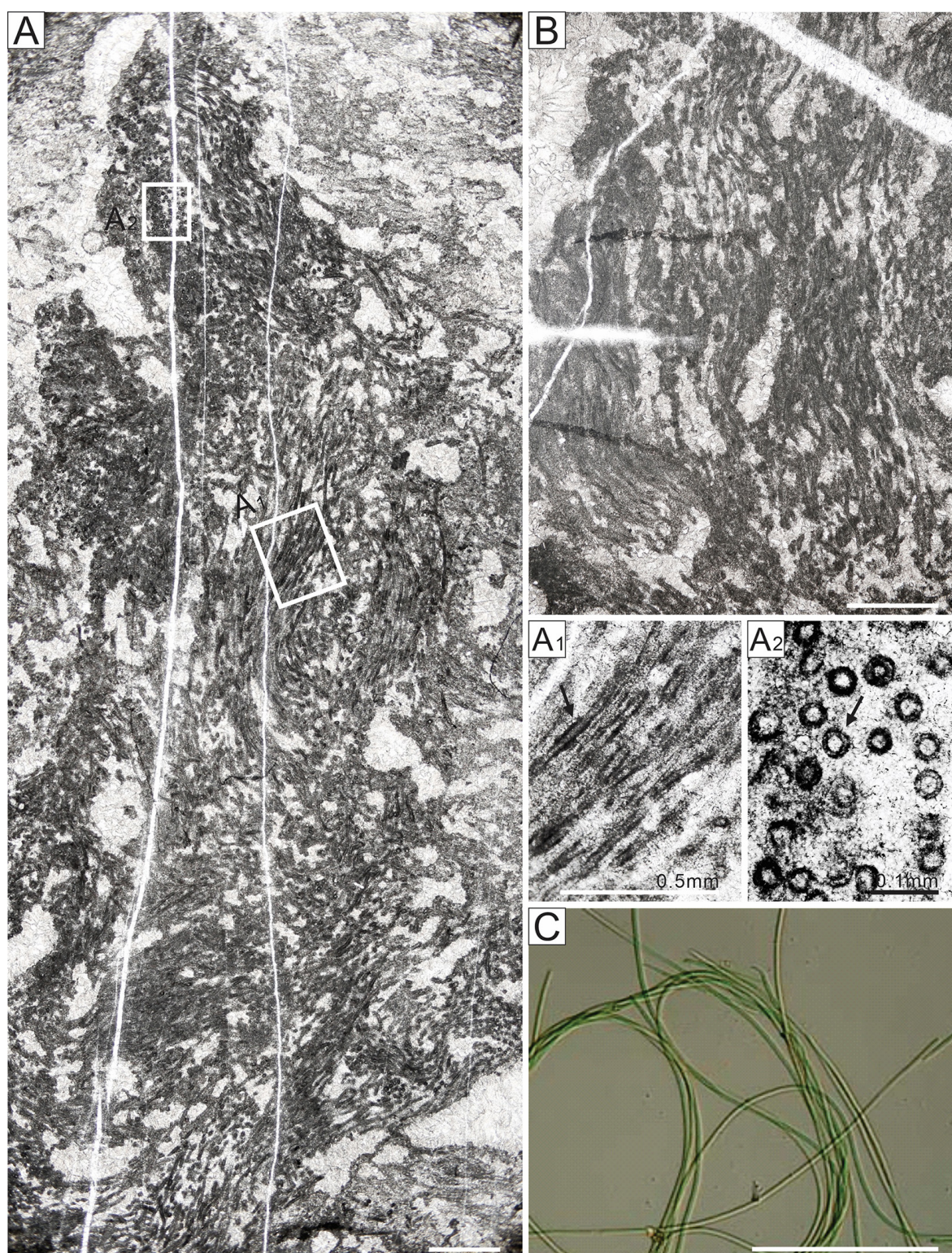


Figure 10. Photomicrographs of *Xianella mollis* sp. nov., early Cambrian, South China. (**A–B**) *Xianella mollis* sp. nov. **A**, overall morphology, Yutang section, sample no. 5-S18, longitudinal sections and cross-sections. (**A₁**) Enlargement of (**A**), micritic wall (arrowed), longitudinal sections. (**A₂**) Enlargement of (**A**), concentric ring-like structure (arrowed), cross-sections. (**B**) Yutang section, sample no. 5-S19, longitudinal section. (**C**) Extant *Phormidium* sp. Scale bars equate to 1 mm, except where indicated.

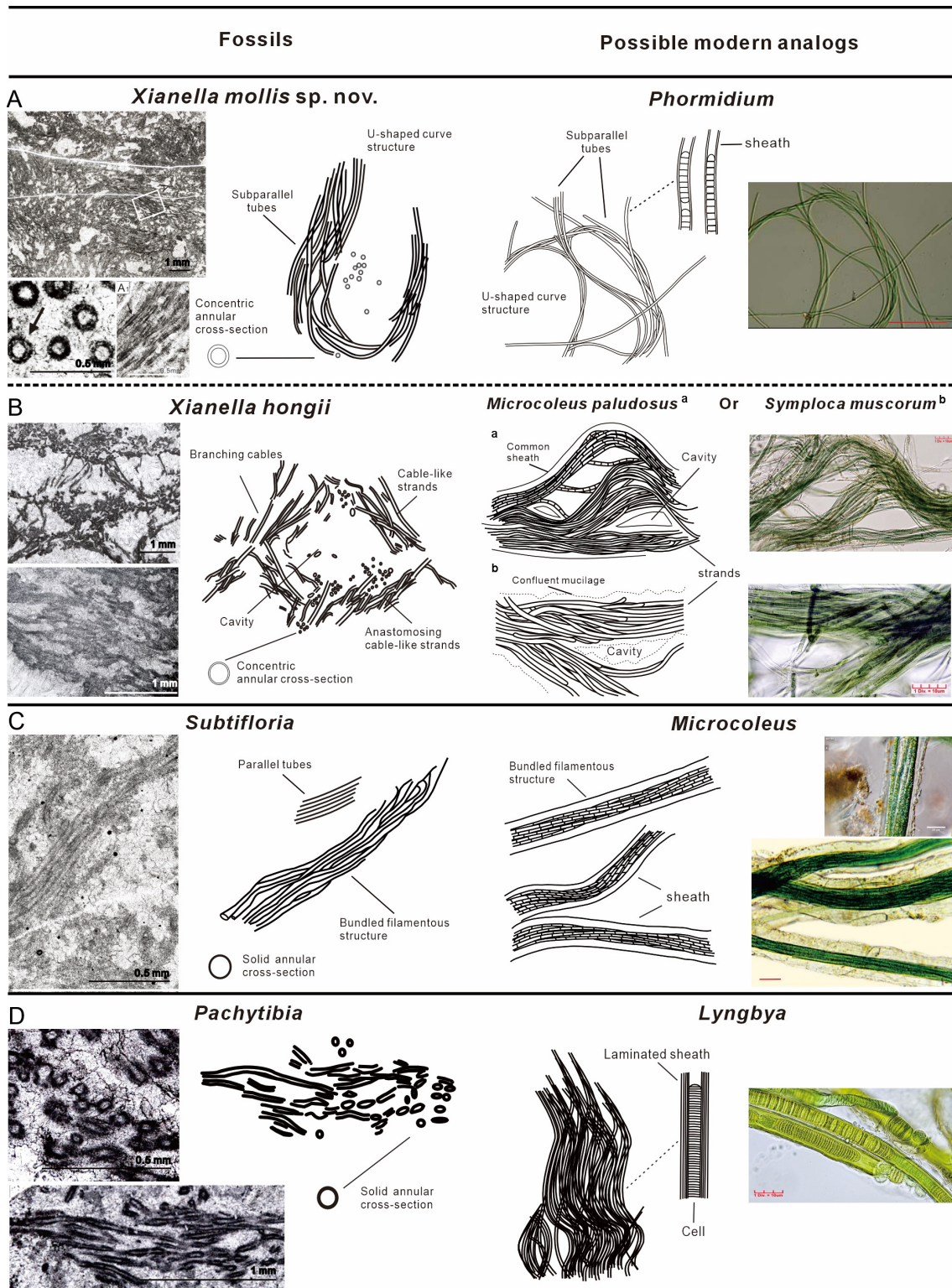


Figure 11. (A–D) *Xianella mollis* sp. nov. compared with taxa such as *Xianella hongii*, *Subtifloria*, and *Pachytibia* from the early Cambrian and possible extant morphological analogs, namely *Phormidium*, *Microcoleus*, *Symploca* (Phormidiaceae, Cyanobacteria), and *Lyngbya* (Oscillatoriaceae, Cyanobacteria). Photomicrographs and sketches: (A) *Xianella mollis* sp. nov. from this study and present-day *Phormidium* sp.; arrows indicate U-shaped structure in the fossil and *Phormidium*. (B) *Xianella hongii*, extant *Microcoleus paludosus*, and *Symploca muscorum*; arrows indicate cable-like strands, branching cables, and cavities. (C) *Subtifloria* and extant *Microcoleus*. (D) *Pachytibia* (from Xiao et al., 2025) and extant *Lyngbya*. Note the laminated sheath in *Lyngbya*. Photographs of present-day species are from <https://www.atlasofcyanobacteria.com> (last access: 11 June 2026)

Riding, 1990; Mankiewicz, 1992; Elicki, 1999; Adachi et al., 2023, 2014a, b), although possible occurrences have been reported from the Ordovician (Li et al., 2015). *Kordephyton* shares a general overall appearance with rivulariacean-like calcified microfossils (e.g., *Zonotrichites*, *Ortonella*, *Botomaella*), characterized by a delicate, micritic, tubular, branched filament arrangement in fan-like radiating clusters, mutually distinguished by details of their filaments, branching patterns, thallus shape, and size. For example, *Kordephyton* differs from *Botomaella* in having more slender tubular filaments, with relatively thick micritic walls and a large overall thallus size. *Kordephyton*'s layered, bush-like structure resembles that of some *Epiphyton* species, and Riding and Voronova (1985) regarded both genera to share “dendroid” morphology. However, the delicate filaments of *Kordephyton* differ from those of *Epiphyton*, in which the filaments are generally both wider and shorter.

Affinity. Riding (2001) placed *Kordephyton*, together with *Bija*, *Bajanophyton*, and *Botomaella*, in the *Botomaella* Group based on morphological characteristics and supported their likely cyanobacterial affinity. We suggest that *Kordephyton* is comparable in terms of organization and appearance with some rivulariaceans based on delicate filaments with relatively wide sheaths.

Species. Criteria for distinguishing *Kordephyton* species include differences in filament diameter, morphology, branching, and shape of notional protosporangia. Three species of *Kordephyton*, described or revised by Korde (1973), are the most widely recognized (Mankiewicz, 1992): *K. crinitum* (type species), *K. crispum* (Korde, 1961) from Kuznetsk Alatau, and *K. conglutinatum* (Korde, 1973) from East Sayan. In addition, we recognize *Kordephyton australis*, characterized by continuous, non-laminated filaments, from the Middle Cambrian (Ordian) of the Douglas River, Northern Territory, Australia (Kruse and Reitner, 2014), as a distinct species.

***Kordephyton crinitum* Korde, 1973**
(Fig. 12A–D)

Material. Abundant in the Qingxudong Formation (ϵ_2q) at the Yutang section, Hunan Province, and locally present in the Tianheban Formation (ϵ_2t) of the Xiachazhuang and Qingxudong formations (ϵ_2q) at the Limei sections, Yangtze Platform, South China.

Description. Long thin filaments, densely arranged in fan shapes and with blurred filament outlines, can be difficult to mutually distinguish (Fig. 12A–D); branches occur distally on filaments; basal protuberances are tentatively interpreted as putative holdfast structures; protosporangial structures are absent.

Remarks. Discontinuities between constituent filaments and layered bushes, in this species as in other Siberian species, distinguish it from *Kordephyton australis* (Kruse and Reitner, 2014). Due to often blurred outlines, it can be difficult to confirm that filaments branch and also to distinguish

inferred protosporangial structures. The fine and delicate filaments in our specimens are distinct from the coarser filaments typical of *K. conglutinatum* and resemble *K. crinitum* (Korde, 1973).

Genus *Bija* Vologdin, 1932

Type species. *Bija sibirica* Vologdin, 1932; Lower Cambrian; Siberian Platform, Russia.

Diagnosis. Basal cross-section rounded to polygonal, composed of closely spaced long tubular filaments, filaments radially dispersed from the base; irregularly dichotomously branched from one another, with a tendency for filament diameter to decrease distally.

Comparison. *Bija* is known from the Cambrian (Vologdin, 1932) and Late Ordovician (Liu et al., 2016a). It shows similarities with *Hedstroemia* Rothpletz, 1913, both having filaments that are circular–polygonal in cross-section. Riding (1991b) suggested that *Bija* may be a junior synonym of *Hedstroemia*, differing only in that *Bija* filaments are longer, and their diameters are less uniform.

Affinity. *Bija* was placed in the Cyanobacteria by Luchina (1975). Potential synonymy with *Hedstroemia* implies shared affinity and comparison with Rivulariaceae (Riding, 1991b). Nonetheless, facies analysis (Liu et al., 2016b, 2017) suggests ecological disparity: *Bija* is reef- and/or bank-adapted, whereas *Hedstroemia* is lagoon-adapted. Such environmental differences could suggest distinct ecomorphs or taphonomic effects.

Species. Based on filament diameter and angle of branching, *Bija* is divided into two species: *Bija grandis* (Korde, 1973) and *Bija sibirica* (Vologdin, 1932).

***Bija sibirica* Vologdin, 1932**
(Fig. 13A–B)

1932 *Bija sibirica* Vologdin: 16, fig. 11.

1962 *Bija sibirica* Vologdin: 486, pl. 6, fig. 5

1973 *Bija sibirica* Vologdin; Korde: 37, figs. 2–4; 38, figs. 1, 2.

2016a *Bija sibirica* Vologdin; Liu et al., p. 194, fig. 5I, J.

Material. Rarely present in the Qingxudong Formation (ϵ_2q) at the Limei and Yutang sections, Hunan Province, South China.

Description. Filaments 2–3 mm long, round to polygonal in cross-section, with tubular filaments radiating from the base, tending to become thinner distally, with diameters of $\sim 100\ \mu\text{m}$ at the base and $\sim 60\ \mu\text{m}$ towards the termination (Fig. 13A–B).

Remarks. Filaments of *Bija grandis* are robust, reaching diameters of 0.15–0.20 mm. In contrast, the filaments and branched angle of *Bija* in this study are notably narrower and conform better with dimensions characteristic of *Bija sibirica*.

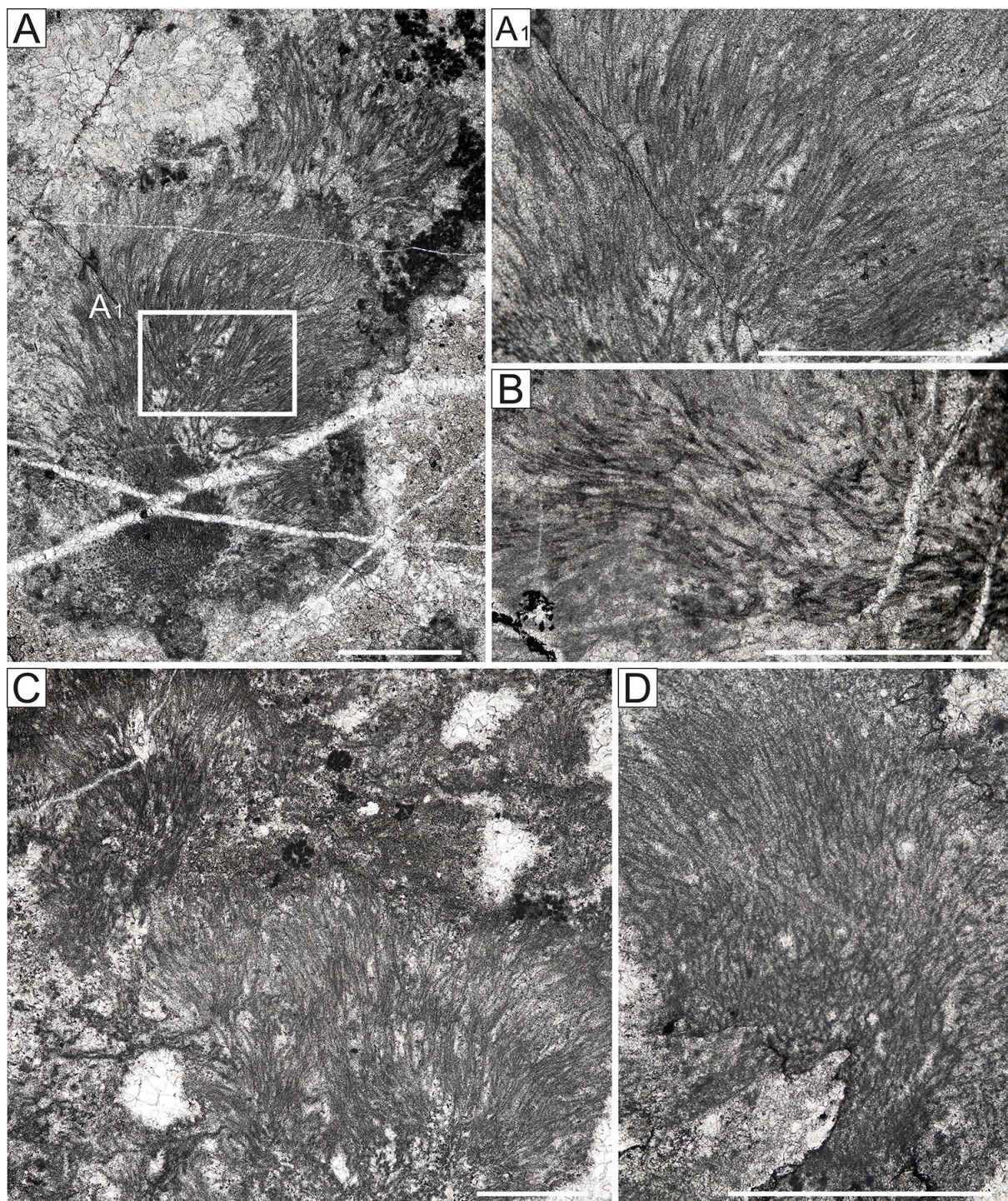


Figure 12. Photomicrographs of *Kordephyton*, early Cambrian, South China. (A–D) Overall morphology, Yutang section, sample no. 5-S08, longitudinal sections and cross-sections. (A₁) Enlargement of part of A, radial filaments in longitudinal section. (B) Possible tube structure, Yutang section, sample no. 5-S03, longitudinal section. (C) Radial filaments with *Epiphyton* (darker micritic masses), Yutang section, sample no. 5-7, longitudinal section. (D) Radial filaments, Yutang section, sample no. 5-7, longitudinal section. All scale bars equate to 1 mm.

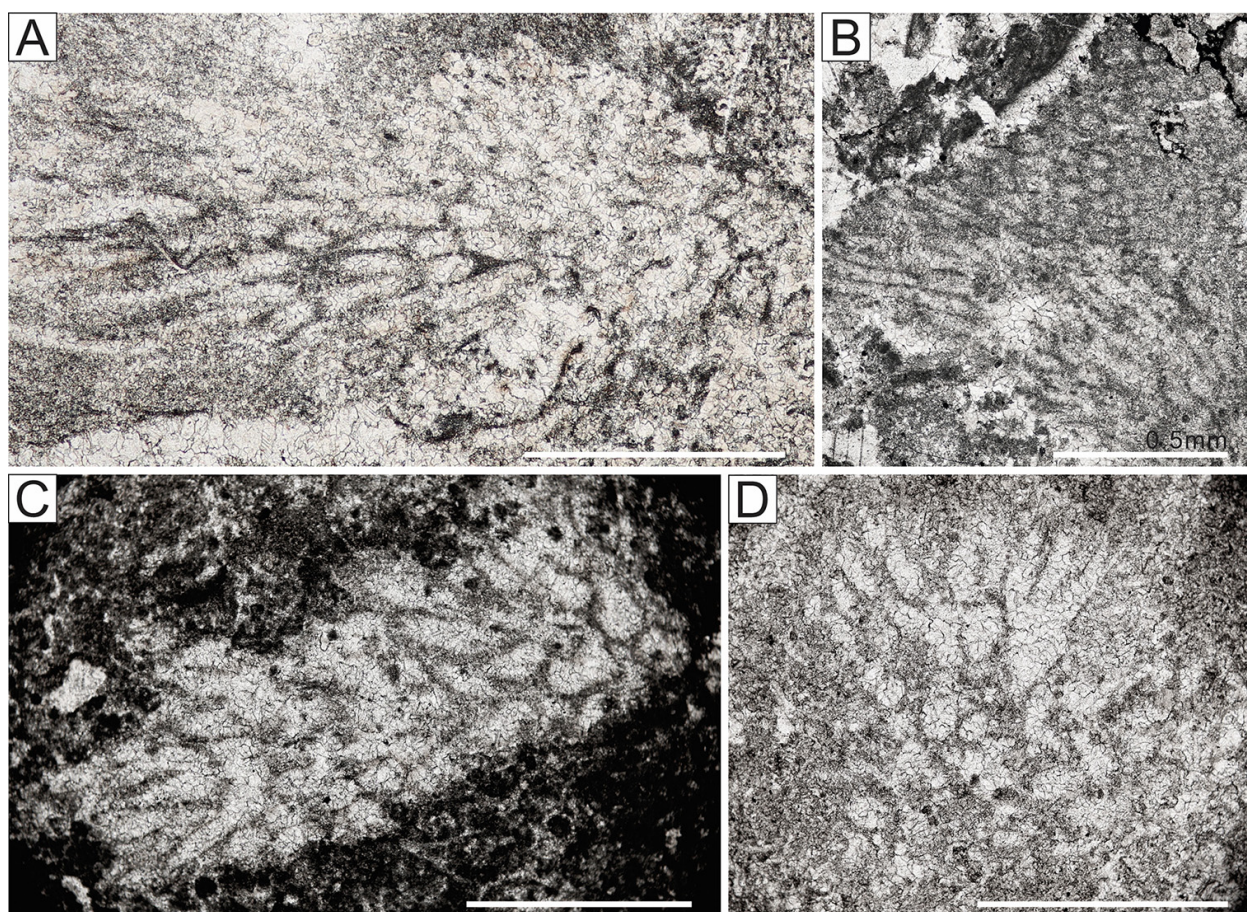


Figure 13. Photomicrographs of *Bija* and *Hedstroemia*, early Cambrian, South China. (A–B) *Bija sibirica*. (A) Overall morphology, Yutang section, sample no. 4-4, longitudinal sections and cross-sections. (B) Yutang section, sample no. 5-5, longitudinal sections and cross-sections. (C) Possible *Hedstroemia*, Yutang section, sample no. 3-11, oblique longitudinal sections. (D) Poorly preserved *Hedstroemia*, Yutang section, sample no. 4-2. All scale bars equate to 1 mm.

Genus *Hedstroemia* Rothpletz, 1913
(Fig. 13C–D)

Type species. *Hedstroemia halimedoidea* Rothpletz, 1913; Silurian, Wenlock, Gotland, Sweden.

Diagnosis. Calcareous microfossil composed of closely packed tubes, more or less radially arranged, dichotomously branched at a low angle, and expanding distally.

Comparison. *Hedstroemia* is well known from the Cambrian (Riding and Voronova, 1985), Late Ordovician (Liu et al., 2016a, 2021), and Silurian (Rothpletz, 1913). Its filament arrangement very broadly resembles that of *Botomaella* Korde (1958) and *Bija* Vologdin (1932), with fan-shaped radial clusters of tubular branching filaments. In comparison, filaments of *Hedstroemia* are generally thicker and show large variations in width.

Affinity. *Hedstroemia* and similar erect to radial filamentous fossils (*Ortonella*, *Garwoodia*) were placed in the subgroup Porostromata, under Schizophyceae (Pia, 1927), and attributed to the Codiaceae (Chlorophyta) (Pia, 1937), a

view followed by several authors (e.g., Elliott, 1956, 1975; Guilbault and Mamet, 1976). However, this assignment has been contested. Riding (1977a, b) argued against classifying *Cayeuxia*, *Garwoodia*, *Hedstroemia*, and *Ortonella* in Codiaceae due to their simple thallus organization. Dragastan (1985, 1993) considered *Hedstroemia* to be a pseudoudoteacean green alga. Luchinina (in Chuvashov et al., 1987) placed the *Hedstroemia* Group, including *Bija*, *Hedstroemia*, *Ortonella*, and others, in cyanobacteria under Garwoodiaceae. Riding and Voronova (1985) and Riding (1991a) drew attention to morphological similarities between *Hedstroemia* and calcified sheaths of the extant cyanobacterium *Rivularia*. Subsequently, Liu et al. (2016b) suggested that *Hedstroemia* and extant rivulariaceans shared a preference for lagoonal habitats, possibly further supporting their mutual affinities. We propose that *Hedstroemia* and *Hedstroemia*-like taxa observed in this study, including *Bija* and *Botomaella*, may be calcified sheaths of cyanobacteria, such as extant rivulariaceans.

***Hedstroemia* sp.**

Description. Tubes subrounded in transverse section, 90–140 µm in diameter; filaments radially arranged, expanding distally and dichotomously branched from base and then showing multiple branching into clusters at acute angles near 10°; filaments are short.

Remarks. The fossils we observed are mostly fragments, resembling *Hedstroemia biofilosa* based on their longitudinal sections and circular to oval transverse sections (Fig. 13C, D) but with larger tubes. Our specimens are scarce and affected by recrystallization, challenging species assignment.

Genus ***Botomaella*** Korde, 1958
(Fig. 14A–C)

- 1958 *Botomaella* Korde; pp. 117, pl. 4, fig. 11.
1973 *Fistulella* Korde; 217, pl. 46, 2a; pl. 47, 1.
1976 *Botomaella* Voronova; 81, pl. 10, 1.
1985 *Botomaella* Sun et al.; 54, pl. 2–5.
2014a *Botomaella*? Adachi et al.; 7, fig. 6.
2024 *Botomaella*? Zheng et al.; 318, fig. 5.

Type species. *Botomaella zelenovi* Korde, 1958, pl. 117, pl. 4, fig. 11.

Diagnosis. Erect tubular filaments, branching irregular or dichotomous, straight to slightly curved, forming radial fan-like masses; subcircular in cross-section; wall thin, micritic.

Comparison. *Botomaella*, named by Korde (1958) after the Botoma River, is currently only reported from the early Cambrian. *Botomaella* has tubular, branched filaments characteristically arranged in fan-like radiating clusters, broadly similar to *Kordephyton*, *Apophoretella*, *Hedstroemia*, and *Ortonella*. Riding (2001) classified *Kordephyton*, *Bija*, and *Botomaella* together under the “*Botomaella* group” based on their morphological characteristics. Dragastan (1985) suggested that *Botomaella* may have a dendritic branching structure with primary and secondary branches. Several secondary branches can emerge sequentially from the primary branch, and these secondary branches may undergo further asymmetrical dichotomous branching, although with a relatively low frequency of bifurcation. Compared with *Kordephyton*, *Botomaella* has larger filament diameters but a smaller overall thallus size. It can be distinguished from *Apophoretella*, which shows dichotomous branching at a smaller angle and has obvious arcuate bands. Filaments of *Hedstroemia* are both wider and more variable in width than those of *Botomaella*. *Ortonella* has narrower and distinctly dichotomously branched tubes, whereas, in *Botomaella*, the tubes are less well defined and less regularly branched.

Affinity. Dragastan (1985) suggested that *Botomaella* resembles recent filamentous cyanophytes such as *Scytonema*, and it has also been compared with extant *Rivularia* (Korde, 1973; Riding, 1991a).

***Botomaella* sp.**

Description. Diameters range from 38 to 48 µm; dichotomously branched, branching angles around 35° (Fig. 14A, A₁); filaments are long, sometimes up to 5 mm (Fig. 14B).

Remarks. In these specimens, the filaments are larger in diameter prior to branching and smaller after branching, suggesting the presence of main and secondary branches (Fig. 14A). This differs from *Ortonella*, in which tube diameters remain relatively unchanged after branching. Subradial bundles occur, with branching angles ranging from approximately 25 to 40°. These branching angles appear to be larger than those reported in current species of *Botomaella*; therefore, we do not assign a species.

5 Calcified Microproblematica

Genus ***Epiphyton*** Bornemann, 1886
(Fig. 15A–D)

1967 *Paraepiphyton* Wray: 41

Type species. *Epiphyton flabellatum* Bornemann, 1886

Diagnosis. Calcified dendritic microfossil, filaments circular, typically micritic, diameter can increase slightly distally, branching often dichotomous at relatively small angles.

Comparison. Korde (1973) described numerous genera broadly similar to *Epiphyton*, which may include junior synonyms (Riding, 1991b). Nonetheless, despite similarities, several distinct genera can be distinguished (e.g., *Gordonophyton*, *Korilophyton*, *Tharama*, *Tubomorphophyton*). These have been attributed to the family Epiphytaceae (Korde, 1959, 1973; Chuvashov et al., 1987) and to the *Epiphyton* Group (Riding, 1991a; Luchinina, 2009).

Affinity. Bornemann (1886) described *Epiphyton* as a green alga belonging to the Siphonales (Chlorophyta), but its taxonomic attribution remains unresolved. Pia (1927, p. 39) placed *Epiphyton* in the cyanobacteria. Korde (1959) and Luchinina and Terleev (2008) suggested that *Epiphyton* is a rhodophyte. Riding and Voronova (1982) suggested that *Epiphyton* fossils could represent a heterogeneous group. Woo and Chough (2010) provided direct evidence for photosynthesis in *Epiphyton* fossils from the Middle Cambrian in China. The difficulty of identifying definitive modern analogues, together with the likely heterogeneity of these fossils, has often led to the provisional placement of *Epiphyton* among calcimicrobes or Microproblematica (Riding, 1991a; Liu et al., 2016a). Min et al. (2019) interpreted *Epiphyton* as a cyanobacterium based on specimens from the Dengying Formation (Neoproterozoic) at the Lijiagou section in China. However, their material is preserved through phosphatization, which cannot be directly compared with calcified *Epiphyton*. Ibarra and Sanon (2019) suggested a chlorophyte affinity for *Epiphyton*.

Species. *Epiphyton* comprises numerous species, typically based on subtle morphological differences, such as branching

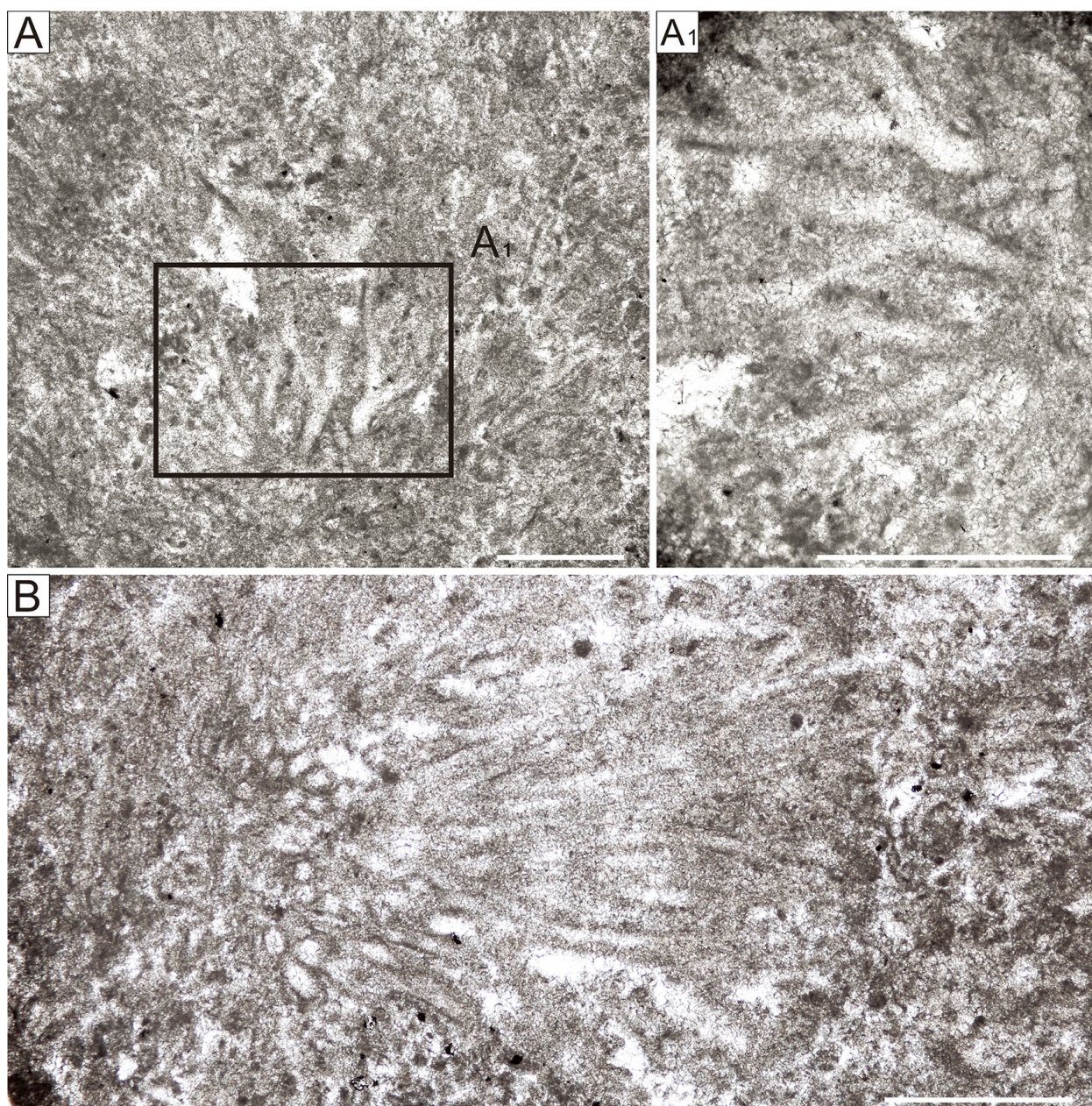


Figure 14. (A–B) *Botomaella* sp. A, Limei section, sample no. BP12-2, longitudinal sections. (A₁) Enlargement of part of (A) showing branches in longitudinal section. (B) Overall morphology, Limei section, sample no. BP12-2, longitudinal and cross-sections. Scale bars: (A) 0.2 mm; (A₁) and (B) 0.5 mm.

angle (Luchinina, 1975; Woo et al., 2008). We distinguish three varieties in our samples.

***Epiphyton flabellatum* Bornemann, 1886
(Fig. 15A, B)**

1886 *Epiphyton flabellatum* Bornemann: 18, pl. 1.10.

1973 *Epiphyton flabellatum* Bornemann; Korde, 306, pl. 30.3.

2008 *Epiphyton flabellatum* Bornemann; Woo et al., 59, fig. 5.c.

2024 *Epiphyton flabellatum* Bornemann; Zhu et al., 8, fig. 7.

2024 *Epiphyton flabellatum* Bornemann; Zheng et al., 63 (10), fig. 6A.

2025 *Epiphyton flabellatum* Bornemann; Xiao et al., fig. 10D, E.

Description. Bush-shaped thalli, with radiating micritic branches that are distinct and rounded in transverse sec-

tion; filament diameter ~50–60 µm; branching is normally dichotomous at 15–20°; rarely segmented.

Remarks. Bifurcating rodlike branches and overall shrub-like form are defining features of *Epiphyton flabellatum*. Its overall characteristics and dimensions are similar to *E. pseudoflexuosum*, *Epiphyton naturale*, and *E. tuberculatum*. One or more of these may prove to be a synonym of the form described here.

***Epiphyton parapusillum* Korde, 1973**

(Fig. 15C)

Description. Thallus hemispheric; outer boundaries of the small bushes are well defined; filament diameter ~50 µm; branching dichotomous at small angles ~10°; filaments lack segmentation.

Remarks. In overall structure and thallus characteristics, this *E. parapusillum* closely resembles *Epiphyton furcatum* and *Epiphyton fruticosum*. It is distinguished by its branching pattern (exhibiting only two to three orders of branching), larger chambers in the fan-shaped sections of the thalli, and exceptionally small size.

***Epiphyton* sp.**

(Fig. 15D)

2014 *Epiphyton* sp.; Liu, 72, fig. 4-9A

Description. Filaments densely arranged, creating dendritic radiating clusters up to 4 mm in diameter; individual filaments locally appear to be tubiform with diameter 40–50 µm; branching normally dichotomous at 10–15°; segmentation lacking.

Remarks. Hollow tubes are consistent with *Epiphyton* sp. reported by Liu et al. (2016a) and can be compared to *Tubomorphophyton* (see Riding and Voronova, 1982). Scarcity of these fossils in our material (Fig. 15D) makes it difficult to assign this microfossil to a particular species.

Genus *Renalcis* Vologdin, 1932

Type species. *Renalcis granosus* Vologdin, 1932; Middle Cambrian; Altai Mountains, Russia.

Diagnosis. Calcified, clusters of thick-walled, well-defined, irregularly spherical chambers, forming swollen, hollow aggregates.

Comparison. *Nephelostroma* Dangéard and Doré, 1957, is regarded as a junior synonym of *Renalcis* (Reitlinger, 1960).

Affinity. *Renalcis* has been suggested to be a chroococcalean cyanobacterium (Hofmann, 1975; Pratt and Schlaifer, 1984; Luchinina in Chuvashov et al., 1987; Riding, 1991b; Turner et al., 2000), but its affinities and formation have also long been regarded to be problematic and remain unclear. For example, it has also been suggested to have been produced by precipitation induced by communities of phototrophic and heterotrophic bacteria (Chafetz and Guidry, 1999) or heterotrophic bacteria only (Stephens and Sumner, 2002). Due to a lack of definite present-day analogs, *Renalcis* and similar genera, such as *Izhella*, are often broadly regarded to be

possible bacterial-calcified Microproblematica (Feng et al., 2010; Liu et al., 2016a, 2017).

***Renalcis granosus* Korde, 1961**

(Fig. 15E)

1932 *Renalcis granosus* Vologdin, p. 15, pl. 9.

1972 *Renalcis* sp. Riding and Toomey: 514, pl. 2, figs. 1–3.

1973 *Renalcis granulatus* Korde, p. 112, pl. 2, figs. 2–3.

1973 *Renalcis erbinatus* Korde, p. 114, pl. 1, fig. 4.

1990 *Renalcis devonicus* Bian and Zhou: pl. 1, figs. 2, 5.

1995 *Renalcis* sp. Ye et al.: 15, pl. 8, fig. 6.

2009 *Renalcis* Vologdin; Wang et al.: fig. 2d.

2009 *Izhella* Antropov; Wang et al.: fig. 2e.

2011 *Renalcis* sp. Liu et al.: 501, pl. 5, fig. 6.

2016 *Renalcis granulatus* Liu et al.: 201, fig. 9A.

2021 *Renalcis granulatus* Liu et al.: 18, pl. 9, fig. 7.

Description. Branches of superposed chambers arise from a common base; basal chambers up to 0.55 mm in external diameter. Walls ~50 µm thick and can exhibit poorly developed clefts on their inner surfaces.

Remarks. Relatively large chambers, ranging 200 to 500 µm in external diameter. Recognition of *R. granosus* is based on morphology, size, and structure, including superimposed chambers, large chamber cavities, and branches arising from a common base.

Genus *Izhella* Antropov, 1955

Type species. *Izhella nubiformis* Antropov, 1955; Upper Devonian; Russia.

Diagnosis. Subspherical to botryoidal hollow vesicles with thick, micritic walls, aggregated into clusters.

Comparison. *Izhella* closely resembles *Renalcis* (Riding 1991a; Feng et al. 2010), and the two often occur intergrown, leading to frequent confusion and/or misidentification in reports (Wray, 1967; Korde, 1973; Wang et al., 2009). The wall of *Izhella* is characteristically thick with deep, narrow clefts on its inner surface, whereas the wall of *Renalcis* can often be thinner with poorly developed or no clefts.

***Izhella nubiformis* Antropov, 1955**

(Fig. 15F)

1955 *Izhella nubiformis* Antropov: 47.

1967 *Renalcis turbitus* Wray: 46, pl. 11, fig. 1.

1983 *Renalcis* Adams: 330, figs. 1, 2.

1973 *Renalcis tuberculatus* Korde: 113, pl. 3, fig. 1.

2011 *Izhella* sp. Liu et al.: 501, pl. 5, fig. 5.

2016 *Izhella nubiformis* Liu et al.: 201, fig. 9C.

Description. Aggregations of thick-walled micritic chambers. The walls contain deep clefts extending outward from the interior surface through approximately up to two-thirds of the wall thickness. In the longitudinal section, the chambers appear to be lunate; basal chambers up to 0.57 mm in

external diameter, with compound lobate cavities ~ 0.3 mm wide; walls ~ 0.1 mm thick with clefts up to $60\text{ }\mu\text{m}$ deep.

Remarks. In our specimens, narrow inner clefts extend two-thirds of the way through the wall, matching diagnostic features of the *Izhella* type species.

6 Discussion

6.1 Global distribution of early Cambrian calcified cyanobacteria

Previous detailed reports of Cambrian calcified cyanobacteria predominantly originated from studies of well-preserved specimens in the Ural Mountains, Siberia, and in North China (Vologdin, 1932, 1937, 1939; Maslov, 1956; Korde, 1961, 1973; Voronova et al., 1969; Luchinina, 1975; Luchinina and Tikhomirova, 1987; Voronova, 1976, 1979; Xiao et al., 2025), with relatively fewer studies in the Americas, Australia, China, Europe, and India, although *Epiphyton* was initially described from Sardinia (Bornemann, 1886). Detailed distributions are compiled in Table 1.

Historically, the Siberian record of calcified cyanobacteria is the most thoroughly studied and has led to major contributions (e.g., Vologdin, 1932; Maslov, 1956; Korde, 1973). Subsequent taxonomic advances regarded *Vologdinella* Korde, 1957, and *Amganella* Reitlinger, 1959, as junior synonyms of *Proaulopora* Vologdin, 1937, and subsumed *Botominella* Reitlinger, 1959, within *Subtifloria* Maslov, 1956. Detailed studies (Vologdin, 1932, 1939, 1962; Maslov, 1956; Luchinina, 1975; Korde, 1957, 1973; Voronova, 1976, 1979; Wood et al., 1993; Drozdova, 1980; Kobluk and James, 1979; Riding, 1991a, 2001) have recognized at least 10 genera of early Cambrian calcified microfossils comparable with calcified cyanobacteria: *Girvanella*, *Razumovskia*, *Subtifloria*, *Obruchevella*, *Batenevia*, *Bija*, *Botomaella*, *Hedstroemia*, *Kordephyton*, and *Proaulopora* (Table 1). In contrast, early Cambrian calcified microfossils documented from North America and Europe are relatively limited in diversity, with only *Girvanella* and *Botomaella* (Table 1) commonly being identified (Pfeil and Read, 1980, 1983; Kobluk and James, 1979; James, 1981; Álvaro et al., 2000; Pratt, 2001; Debrenne et al., 2002; Noriega-Ruiz et al., 2024).

Additional occurrences of early Cambrian calcified cyanobacteria and related microfossils have been reported from the North China Block, with genera including *Girvanella*, *Streptubularia*, *Razumovskia*, *Subtifloria*, *Xianella*, *Apophonetella*, *Pachytibia*, *Hedstroemia*, *Kordephyton*, and *Bija* (Qi et al., 2013; Lee et al., 2014; Adachi et al., 2023; Xiao et al., 2025) (Table 1).

In addition, *Girvanella*, *Kordephyton*, *Hedstroemia*, and *Streptubularia* have been documented from South China, including the provinces of Hunan, Hubei, and Guizhou (Sun et al., 1985; Zhang and Yuan, 1994; Ye and Yang, 1995; Hicks and Rowland, 2009; Adachi et al., 2014a, b; Li et al., 2021) (Table 1). Among these, *Proaulopora* and *Botomaella*

cannot be confirmed in the Yangtze Platform from previous studies (Zhang and Yuan, 1994) (lack of figures and/or poor preservation). A study of an archaeocyath reef in the Xiachazhuang section, Hubei Province, reported *Botomaella* (Zheng et al., 2024); however, re-inspection suggests that these specimens are poorly preserved and may more likely represent *Apophoretella* (Table 1).

6.2 New discovery of early Cambrian calcified cyanobacteria in South China

Based on the above systematic paleontological studies, 15 species within 10 genera of calcified cyanobacteria and 5 species within 3 genera of Microproblematica are identified in this study from Cambrian Series 2 of South China, including two new species (*Streptubularia robustus* sp. nov. and *Xianella mollis* sp. nov.) (Table 1). Thus, our study confirms the presence of four previously reported distinct genera in the early Cambrian of the Yangtze Platform, namely *Girvanella*, *Kordephyton*, *Hedstroemia*, and *Streptubularia* (Table 1), together with the first documented occurrences of *Bija*, *Botomaella*, *Acuasiphonoria*, *Razumovskia*, *Subtifloria*, and *Xianella*. Recognition of *Acuasiphonoria*, previously only recognized in Late Ordovician strata, therefore extends its fossil record to the Cambrian.

In addition, previous studies of early Cambrian calcified cyanobacteria have largely focused on reef facies. Our research demonstrates, for the first time, that calcified cyanobacteria also existed in non-reef shallow-marine carbonate facies in South China during this period. The taxonomic composition of the calcimicrobial genera closely follows changes in sedimentary environments. In non-reefal facies, calcimicrobes are very depauperate and typically occur in low-energy hydrodynamic settings. In reef facies, by contrast, calcimicrobe diversity and abundance increase markedly and vary according to the nature of the additional reef builders.

During deposition of the Xiannüdong Formation (Cambrian Series 2, ϵ_2x), microbial–archaeocyath reefs developed in South China. Calcified cyanobacteria and problematic calcimicrobes are low in abundance, and the most typical microbial association consists of *Epiphyton* and *Renalcis*. The substantial terrigenous clastic input during this period likely influenced the development of calcified cyanobacteria. These microbes either encrust archaeocyaths or occur sporadically in inter-archaeocyath spaces, playing a relatively minor role in reef construction. In contrast, in the Tianheban Formation (ϵ_2t), archaeocyaths still serve as framework builders, but the proportion of calcified cyanobacteria is higher. *Kordephyton*, *Streptubularia*, and *Bija* are present and played an important role in reef construction as encrusters and binders. When archaeocyaths became extinct in the Qingxudong Formation (ϵ_2q), reefs were subsequently built entirely by calcimicrobes, which show a marked increase in diversity and abundance. Widespread and abundant forms – such as *Gir-*

Table 1. Outline of global distribution of principal calcified cyanobacteria and associated calcimicrobe floras during the Cambrian Fortunian–Age 4. Genera in boldface represent new additions from this work.

Regions		Cyanobacteria	Associated calcified microfossils	Facies	Age	References
Siberia	Russia	<i>Subtifloria</i> (misidentified as <i>Botominella</i>), <i>Girvanella</i> (synonym of <i>Nicholsonia</i>), <i>Hedstroemia</i> , <i>Botomaella</i> (misidentified as <i>Fistulella</i>), <i>Proaulopora</i> (misidentified as <i>Amganella</i>), <i>Obruchevella</i> , <i>Batenevia</i> , <i>Kordephyton</i> , <i>Bija</i> , <i>Razumovskia</i>	<i>Gordonophyton</i> , <i>Epiphyton</i> , <i>Renalcis</i> , <i>Tubomorphophyton</i> , <i>Tarthinia</i> , <i>Gemma</i> , <i>Korilophyton</i> , <i>Chabakovia</i>	reef	Fortunian–Age 4	Maslov (1956); Korde (1961, 1973); Vologdin (1962); Voronova and Missarzhevsky (1969); Voronova (1976, 1979); Luchinina (1975); Bogush et al. (1990)
North America	USA	<i>Girvanella</i>	<i>Renalcis</i> , <i>Gordonophyton</i> , <i>Tarthinia</i>	reef	Age 4	Pfeil and Read (1980, 1983); Mark et al. (2000); Pratt (2001)
	Canada	<i>Girvanella</i>	<i>Epiphyton</i> , <i>Renalcis</i>	reef	Age 3	Kobluk and James (1979); James (1981)
	Mexico	<i>Girvanella</i>	<i>Epiphyton</i> , <i>Renalcis</i>	reef	Age 3–Age 4	Noriega-Ruiz et al. (2024)
Europe	Spain	<i>Girvanella</i>	<i>Epiphyton</i> , <i>Renalcis</i>	reef	Age 4	Álvaro et al. (2000)
	France	<i>Girvanella</i> , <i>Botomaella</i>	<i>Epiphyton</i> , <i>Renalcis</i>	reef	Age 3	Debrenne et al. (2002)
Asia	Mongolia	<i>Girvanella</i> , <i>Batinevia</i> (unfigured), <i>Razumovskia</i>	<i>Gordonophyton</i> , <i>Epiphyton</i> , <i>Renalcis</i> , <i>Tubomorphophyton</i> , <i>Tarthinia</i>	reef	Age 3	Drozdzova (1980); Wood et al. (1993)
	Tarim Basin	vesicular Cyanobacteria, calcified oscillatoriacean cyanobacterium	<i>Epiphyton</i>	reef	Age 3–Age 4	Song et al. (2012, 2014); Chen et al. (2024)
	North China	<i>Girvanella</i> , <i>Apophoretella</i> , <i>Hedstroemia</i> , <i>Razumovskia</i> , <i>Bija</i> , <i>Kordephyton</i> , tubiform microbe (identified as <i>Streptubularia</i> in this study)	<i>Renalcis</i> , <i>Epiphyton</i> , <i>Tarthinia</i> , <i>Amgaina</i>	peritidal flats and ooid shoals	Age 3	Qi et al. (2013); Lee et al. (2014); Adachi et al. (2023)
	North China	<i>Girvanella</i> , <i>Kordephyton</i> , <i>Apophoretella</i> , <i>Hedstroemia</i> , <i>Subtifloria</i> , <i>Xianella</i> , <i>Streptubularia</i> gen. nov., <i>Pachytibia</i> gen. nov.	<i>Renalcis</i> , <i>Epiphyton</i>	reefal and non-reefal shallow carbonate	Age 4	Xiao et al. (2025)
	South China	<i>Girvanella</i>	<i>Epiphyton</i> , <i>Renalcis</i> , <i>Tarthinia</i>	reef	Age 3	Ye and Yang (1996); Hicks and Rowland (2009); Li et al. (2021)
	South China	<i>Proaulopora</i> (uncertain) (unfigured), ? <i>Apophoretella</i> (may be misidentified as <i>Botomaella</i>), ? <i>Botomaella</i> (poor preservation), <i>Kordephyton</i> , <i>Hedstroemia</i> (unfigured), <i>Girvanella</i> , <i>Streptubularia</i> (misidentified as <i>Girvanella</i>),	<i>Epiphyton</i> , <i>Chabakovia</i> , <i>Renalcis</i>	reef, open platform	Age 4	Debrenne et al. (1991); Sun et al. (1985); Zhang and Yuan (1994); Zheng (1996); Adachi et al. (2014a, b)
	South China	? <i>Botomaella</i> (unidentifiable due to poor preservation), <i>Kordephyton</i> , <i>Girvanella</i> , tubiform microbe(reidentified as <i>Streptubularia</i> in this study)		reef	Age 4	Zheng et al. (2024)
	South China	<i>Girvanella</i> (<i>G. kasakiensis</i> ; <i>G. problematica</i> ; <i>G. wetheredii</i>), <i>Razumovskia</i> (<i>R. hispida</i>; <i>R. lata</i>) , <i>Subtifloria</i> (<i>S. sp.</i>) , <i>Xianella</i> (<i>X. hongii</i>; <i>X. mollis sp. nov.</i>) , <i>Bija</i> (<i>B. sibirica</i>) , <i>Acuasiphonoria</i> (<i>A. ordovica</i>) , <i>Kordephyton</i> (<i>K. crinitum</i>), <i>Streptubularia</i> (<i>S. tenuitubus</i> ; <i>S. robustus</i>), <i>Botomaella</i> (<i>B. sp.</i>), <i>Hedstroemia</i> (<i>H. sp.</i>)	<i>Epiphyton</i> , <i>Renalcis</i> ; <i>Bizhella</i>	reefal and non-reefal shallow carbonate	Age 3–Age 4	This study (bold portions indicate first report in the Yangtze Platform)
Worldwide calcified cyanobacteria		<i>Acuasiphonoria</i> , <i>Apophonetella</i> , <i>Batenevia</i> , <i>Girvanella</i> , <i>Obruchevella</i> , <i>Pachytibia</i> , <i>Proaulopora</i> , <i>Razumovskia</i> , <i>Subtifloria</i> , <i>Streptubularia</i> , <i>Xianella</i> , <i>Bija</i> , <i>Botomaella</i> , <i>Hedstroemia</i> , <i>Kordephyton</i> ,			Fortunian–Age 4	Bold indicates the first reports in the Yangtze Platform by this study

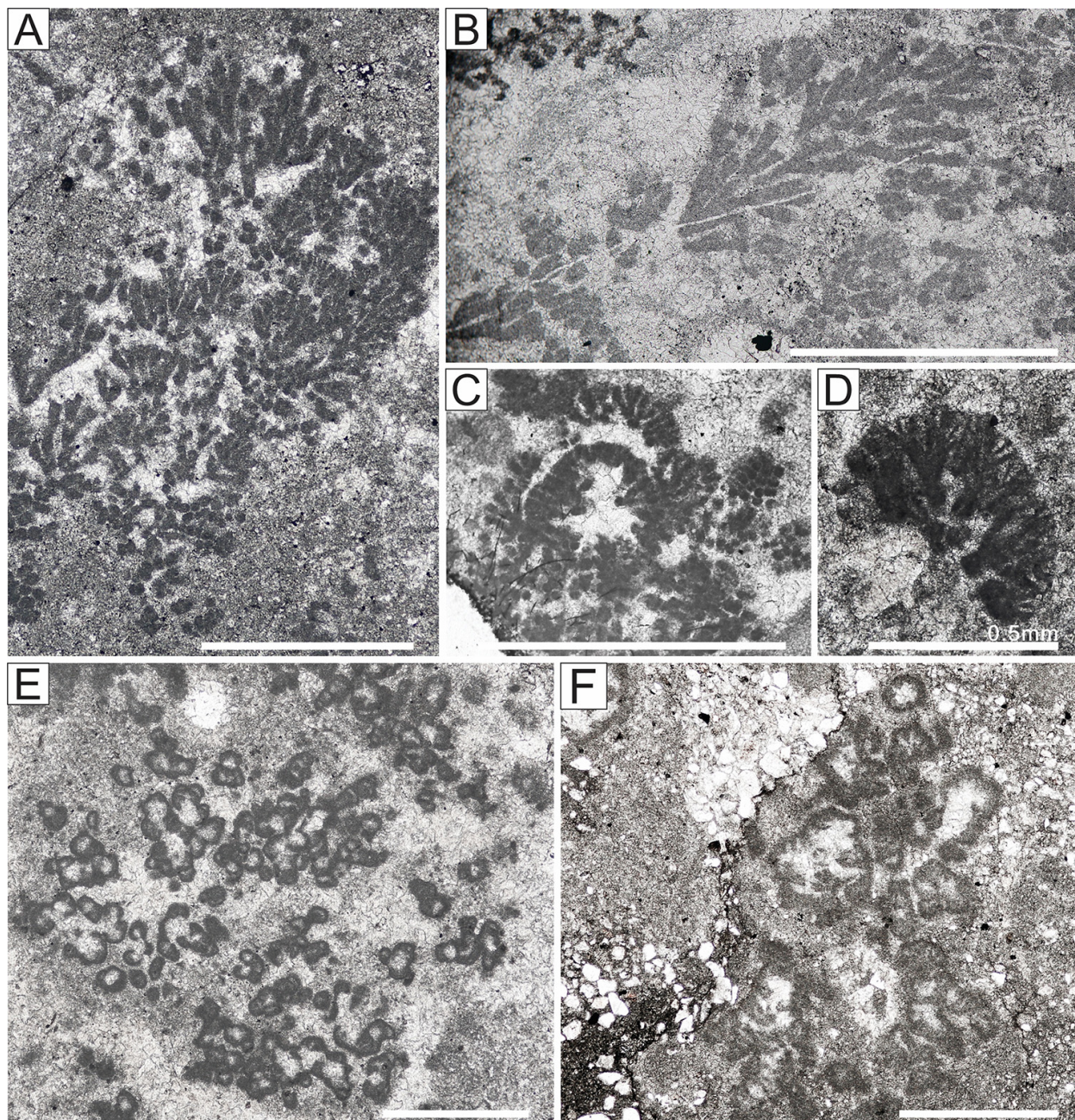


Figure 15. (A–D) *Epiphyton*. (A) *Epiphyton flabellatum*. Limei section, sample no. LZB-1, longitudinal sections. (B) *E. flabellatum*. Limei section, sample no. LZB-1, longitudinal sections. (C) *Epiphyton parapusillum*. Xiachazhuang section, sample no. 6-2, longitudinal and cross-sections. (D) *Epiphyton* sp., Yutang Section, sample no. 1-11, longitudinal sections. (E) *Renalcis granosus*, Xiachazhuang section, sample no. 5-1, cross-sections. (F) *Izhella nubiformis*. Xiachazhuang section, sample no. 6-1, cross-sections. All scale bars equate to 1 mm.

vanella, *Razumovskia*, *Xianella*, *Huayuanella*, *Kordephyton*, and dendritic *Epiphyton* – reduced water flow velocity, trapped sedimentary particles, and formed the reef framework. Smaller forms (e.g., *Girvanella*, *Razumovskia*, *Streptubularia*) acted as binders, whereas chambered *Epiphyton* and *Renalcis* clusters reinforced the framework and occupied interstitial spaces.

6.3 Early Cambrian cyanobacterial calcification episode (CCE) and its implications

During early Cambrian Series 2, calcified cyanobacteria in South China reefal facies gradually evolved from a few relatively simple types, dominated by Oscillatoriaceae, to more diverse assemblages that included Phormidiaceae and Rivulariaceae. This trend may have been driven by ecological

competition with archaeocyaths (i.e., an inverse relationship between two reef builders) and by changes in sedimentary environments (i.e., reduction in inputs of terrigenous detrital particles) or both.

Overall, the number of early Cambrian cyanobacterial genera recognized in North China and South China is comparable with that of the Siberian Platform (Table 1). These floras now include 15 genera of calcified cyanobacteria (Table 1): *Girvanella*, *Acuasiphonoria*, *Batenevia*, *Razumovskia*, *Subtifloria*, *Obruchevella*, *Streptubularia*, *Xianella*, *Pachytibia*, *Proaulopora*, *Bija*, *Botomaella*, *Hedstroemia*, *Kordephyton*, and *Apophoretella*. Of these, *Acuasiphonoria* is the first report of this genus from the Cambrian. In addition, we report two new species (*Streptubularia robustus* sp. nov. and *Xianella mollis* sp. nov.). Our findings expand the diversity of early Cambrian cyanobacteria, supporting the observation that high diversity of calcified cyanobacteria in Cambrian Series 2 is a globally recognizable phenomenon.

Cyanobacterial calcification was widespread and occurred across a variety of shallow-marine environments in the Early Cambrian, likely reflecting a significant and widespread change in environmental conditions: a global early Cambrian cyanobacterial calcification episode (CCE). Such episodes have been linked to oceanic and atmospheric conditions that influence marine carbonate precipitation, such as atmospheric $p\text{CO}_2$ and oceanic carbonate saturation state (Riding, 1991a, 2006, 2009; Kah and Riding, 2007; Liu et al., 2020). Continued studies of these globally distributed assemblages will provide further new insights into the evolution, biogeographic distribution, and environmental significance of cyanobacterial calcification for understanding early Cambrian marine life and conditions.

7 Conclusions

Comprehensive systematic taxonomic analysis of reef-associated calcified cyanobacteria from Cambrian Series 2 strata of the Yangtze Platform identified 10 genera, namely *Acuasiphonoria*, *Bija*, *Botomaella*, *Girvanella*, *Hedstroemia*, *Kordephyton*, *Razumovskia*, *Streptubularia*, *Subtifloria*, and *Xianella*, including two new species (*Streptubularia robustus* sp. nov. and *Xianella mollis* sp. nov.). In addition, we recognized three commonly associated genera of uncertain affinity: *Epiphyton*, *Izhella*, and *Renalcis*. This allows recalibration of the inception of the stratigraphic range of *Acuasiphonoria*, from the Late Ordovician to the Cambrian Series 2. These findings substantially expand the documented diversity of early Cambrian calcified cyanobacteria in non-Siberian terranes and the recognized diversity of their habitats in shallow-marine environments, thereby providing robust evidence to support recognition of the early Cambrian cyanobacterial calcification event. These results improve understanding of Cambrian shallow-marine carbonate communities and sediments and are relevant to the interpretation

of factors that influenced seawater chemistry, atmospheric $p\text{CO}_2$ levels, and global climate at the inception of the Phanerozoic.

Code availability. We confirm that no new custom software code was developed or used for the data analysis and interpretation presented in this study. All instrumental data (SEM, EDS, and XRD) were acquired and processed using the standard commercial software packages integrated with the respective instruments (ZEISS Sigma 300 SEM with Bruker Quantax EDS system, and PANalytical Empyrean diffractometer software). These are routine, off-the-shelf tools employed solely for basic data acquisition and standard peak/spectral identification; no custom scripts, macros, or algorithms were written specifically for this research. Therefore, there is no underlying software code that requires deposition in a public repository. All relevant instrument parameters and analytical procedures have been thoroughly described in the Methods section (Sect. 3) of our manuscript, ensuring full reproducibility of the results.

Data availability. We confirm that all data supporting the findings of this study are presented within the article and its supplementary materials. The primary data include field photographs, polished slab images, thin-section microphotographs, scanning electron microscopy (SEM) images, energy-dispersive X-ray spectroscopy (EDS) spectra, and X-ray diffraction (XRD) patterns, all of which are fully displayed in the main figures (Figs. 1–10) and described in the corresponding figure captions and Methods section (Sect. 3). No raw data were deposited in external public repositories because the key observational and analytical results have been comprehensively documented in the published figures, making the data fully accessible and reproducible from the article itself. Should further details be required, the raw data are available from the corresponding author upon reasonable request.

Author contributions. LL: conceptualization, project administration, supervision, investigation resources, writing (review and editing). JS: preparation, visualization, writing (original draft preparation, review and editing). JZ: visualization, writing (original draft preparation, review and editing). RR: writing (review and editing).

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