



Body reconstruction, taxonomy, and biostratigraphy of a ‘problematic’ chancelloriid

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Abstract

Chancelloriids are a group of ‘problematic’ fossils characterized by bag-shaped body equipped with mineralized sclerites on the external surface. Among the chancelloriid taxa, the genus *Dimidia* was known only by isolated sclerites from small shelly faunas and once regarded as a junior synonym of *Allonnia*. The complete body of *Dimidia simplex* Jiang is described herein for the first time, based on well-preserved specimens from the Chengjiang biota (Cambrian Stage 3) of South China. The name *Dimidia* is resurrected since the characteristic sclerites in the scleritome are distinctive within all known chancelloriid genera with complete bodies. The sclerites of *Dimidia* are densely arranged, each composed of two symmetrical, acute rays that pointed out with their long axes nearly vertical to the body surface, structurally representing an intermediate type between the single-rayed and the common rosette-like composite sclerites of chancelloriids. The remains of *Dimidia* were previously found across South China, Gondwana, and Laurentia, and stratigraphically ranging from the upper Stage 2 to Wuliuan Stage of the Cambrian. The discovery of complete bodies of *Dimidia* contributes to revealing the diversity and clarifying the ‘problematic’ taxonomy of chancelloriids, and emphasizes the necessity to scrutinize more scleritome fossils to interpret the taxonomy and phylogenetic affinity of other small shelly fossils.

Keywords Chancelloriids · Scleritome · Small shelly fossils · Chengjiang biota · South China

Introduction

The Cambrian explosion is characterized by a relatively rapid appearance of animal body plans alongside an episodic biomineralization of metazoans (Erwin and Valentine 2013; Zhang and Shu 2021). During the event, the most extensive biomineralization happened within the Terreneuvian Epoch of Cambrian, represented by mineralized skeletons of a

wide range of lophotrochozoan and non-bilaterian metazoan clades (Zhuravlev and Wood 2008; Kouchinsky et al. 2012; Wood and Zhuravlev 2012; Zhang and Shu 2021). These mineralized skeletons, including a variety of shells, sclerites, spines, spicules, and other fragments, were collectively referred to as small shelly fossils (SSFs) (Matthews and Misarzhevsky 1975; Bengtson 2004). Interestingly, a number of SSFs were assigned to unidentified or ‘problematic’ taxa with controversial phylogenetic states, since it is difficult to restore their affinities based only on isolated and incomplete body parts (Bengtson 1985, 1986). Until recent decades, a series of comparative studies on both isolated skeletal elements and their corresponding scleritome (and soft bodied) fossils have contributed to further understanding the morphology, taxonomy, and phylogeny of these early biomineralizing metazoans (e.g. Bengtson and Conway Morris 1984; Conway Morris and Peel 1990; Ivantsov and Wrona 2004; Bengtson 2005; Skovsted et al. 2009).

Chancelloriids are one of the ‘problematic’ groups that witnessed the Cambrian explosion as well as the extensive biomineralization (Qian 1989; Bengtson et al. 1990; Steiner et al. 2004; Han et al. 2019; Yun et al. 2019b, 2021a, b;

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Moore et al. 2021). Although cancelloriids were firstly described based on complete body fossils (Walcott 1920) and have been discovered in many exceptionally preserved biotas as scleritomes (e.g. Bengtson and Hou 2001; Janussen et al. 2002; Bengtson and Collins 2015; Zhao et al. 2018; Yun et al. 2019a), their skeletal remains are more common in geologic records and have attracted more attention from palaeontologists (e.g. Luo et al. 1982; Vassiljeva and Sayutina 1988; Bengtson et al. 1990; Moore et al. 2014). As a result, there are many separate studies on the isolated sclerites and articulated scleritomes, causing difficulties in resolving cancelloriid taxonomy (Yun et al. 2019b). Based on the morphology of isolated sclerites from the small shelly faunas, at least twelve genera of Chancelloriida were established (Parkhaev and Demidenko 2010). However, there are only four genera ever discovered in the soft bodied or scleritome fossil assemblages, including *Chancelloria* Walcott, 1920, *Allonnia* Doré and Reid, 1965, *Archiasterella* Sdzuy, 1969, and *Nidelric* Hou et al., 2014 (Bengtson and Hou 2001; Hou et al. 2014; Bengtson and Collins 2015; Cong et al. 2018; Zhao et al. 2018; Yun et al. 2018, 2019a). It is noted that many sclerite-based genera, such as *Dimidia* Jiang in Luo et al., 1982, *Aldania* Vassiljeva, 1985, and *Rosella* Vassiljeva in Vassiljeva and Sayutina, 1988, were abandoned and regarded as synonyms of the three common genera:

Allonnia, *Archiasterella*, and *Chancelloria* (Qian and Bengtson 1989; Qian et al. 1999; Parkhaev and Demidenko 2010). This is reasonable since there were no counterparts of these ‘problematic’ taxa existed or dominated in the scleritomes. Nevertheless, the discovery of new scleritomes and soft bodies could always improve and rectify the knowledge on the morphology and taxonomy of cancelloriids.

The specimens described herein represent a new type of cancelloriid scleritome with mainly double-rayed sclerites morphologically resembling *Dimidia* from the SSFs. The preservation, taxonomy, and distribution of this scleritome-based genus are investigated, which help interpreting the early evolution and biostratigraphy of the cancelloriid group.

Material and methods

Totally 23 specimens were collected from 5 localities, including Mafang (MF), Erjie (EJ), Jianshan (JS), Shankou (SK) and Sanjiezi (SJZ) sections, of the Chengjiang biota (Yu’anshan Formation; Cambrian Stage 3) around Kunming area, Yunnan Province, China (Table 1; see Zhang et al. 2001 for geologic setting). All specimens are deposited in

Table 1 Specimens of *Dimidia simplex* Jiang in Luo, Jiang, Wu, Song, and Ouyang, 1982 from localities of the Chengjiang biota

Outcrop	Specimen	Preservation			
		Middle part	Upper part	Lower part	Fragments
Sanjiezi (SJZ)	SJZ-B00-001	✓			
	SJZ-B00-002	✓			
	SJZ-B04-001				✓
	SJZ-B04-002				✓
	SJZ-B05-014				✓
	SJZ-B05-024				✓
	SJZ-B05-027	✓			
	SJZ-B05-030				✓
	SJZ-B05-036				✓
	SJZ-B04-102				✓
	SJZ-B05-182				✓
	SJZ-B05-200		?	✓	
	SJZ-B10-235	✓		✓	
	SJZ-B06-472			✓	
	Mafang (MF)	MF-001	✓		
MF-097				✓	
Jianshan (JS)	JS-268		✓		
	JS-305				✓
	JS-315				✓
Erjie (EJ)	EJ-747				✓
Shankou (SK)	SK-818				✓
	SK-819				✓
	SK-823		✓		

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Specimens were examined and prepared under a Nikon SMZ800 stereomicroscope and then photographed with a Canon EOS 5D Mark II camera. The images were re-levelled and processed with Affinity Photo 1.10 and CorelDRAW X8. Energy-dispersive spectroscopic (EDS) analysis with a FEI Quanta 450 scanning electron microscope (SEM) and X-ray fluorescence (XRF) with a Bruker's M4 TORNADO spectrometer were performed to investigate the elemental composition. Micro-Computed X-Ray Tomography (Micro-CT) under an X-ray microscope ZEISS Xradia 520 Versa was performed (under a 70 kV condition) to reconstruct the internal structure of the fossils. The Micro-CT data were processed with VG Studio 2.2 Max for tomographic analysis and 3D visualization.

Fossil preservation

The fossils are all preserved in greyish-yellow mudstones of the Yu'an-shan Formation (Chengjiang biota) and highlighted by a reddish or brownish colour (Fig. 1a). The XRF and EDS analyses reveal that the specimens are rich in O, Al, Si, K, Mg, Fe, S, and C (Fig. 1), indicating the dominance of clay minerals and iron oxides. Specifically, Fe (from iron oxides) is remarkably concentrated (Fig. 1b, c, k), and C and P are slightly concentrated (Fig. 1d, m) in fossils, when compared to the surrounding rock matrix. This composition implies that the fossils were originally preserved as carbon films (with later pyritization), representing a typical Burgess-Shale type preservation (Forchielli et al. 2014; Gaines 2014).

The sclerites are densely distributed in specimens and manifest as compressed reliefs on the surface of the rock. While the Micro-CT analysis reveals that, at least in some specimens, there are also acute sclerites deeply embedding into the rock (Fig. 2; see Supplementary material for the video of Micro-CT result), reflecting a three-dimensional preservation. In one specimen, there is a narrow gap between the surficial and embedded sclerites (Fig. 2b, c), representing the internal cavity of the organism. However, there are no organs, appendages, or tentacles within the cavity or in any other parts of the fossil.

Systematic palaeontology

Basal Epitheliozoa (Ax 1995), while phylum and class uncertain

Order **Chancelloriida** Walcott, 1920

Family **Chancelloriidae** Walcott, 1920

Genera known from scleritome preservation (updated after Bengtson and Collins 2015). *Chancelloria* Walcott, 1920, *Allonnia* Doré and Reid, 1965, *Archiasterella* Sdzuy, 1969, *Nidelric* Hou et al., 2014, and *Dimidia* Jiang in Luo et al., 1982.

Genus ***Dimidia*** Jiang in Luo, Jiang, Wu, Song, and Ouyang, 1982

1982 *Dimidia* n. gen.—Jiang in Luo et al.: p. 198–199

1984 *Diminia* [sic] Jiang—Jiang: p. 17.

?1989 *Onychia* Jiang—Qian: p. 254 (pro parte).

1989 *Allonnia* Doré and Reid—Qian and Bengtson: p. 19 (pro parte)

2004 *Allonnia* Doré and Reid—Wrona: p. 26 (pro parte).

2006 *Allonnia* Doré and Reid—Clausen and Álvaro: p. 226 (pro parte).

?2006 *Eremactis* Bengtson and Conway Morris—Skovsted: p. 1099 (pro parte).

Type species. *Dimidia simplex* Jiang in Luo, Jiang, Wu, Song, and Ouyang, 1982, based on isolated sclerites from the Shiyantou Formation (Cambrian Stage 2) in eastern Kunming, Yunnan Province, China.

Emended diagnosis. (after Luo et al. 1982). Chancelloriids with a scleritome characterized by densely distributed sclerites that composed of two symmetrical, conical hollow rays.

Remarks. The genus *Dimidia* was originally proposed based on phosphatized, isolated doubled-rayed sclerites (Luo et al. 1982) and subsequently regarded as a junior synonym of *Allonnia* (Qian and Bengtson 1989; Qian et al. 1999). However, the scleritome dominated by doubled-rayed sclerites described herein is distinct from the *Allonnia* scleritome that contains mostly three-rayed sclerites (Yun et al. 2019b). Therefore, the genus *Dimidia* is resurrected.

Dimidia simplex Jiang in Luo, Jiang, Wu, Song, and Ouyang, 1982

Figures 3, 4

1982 *Dimidia simpleca* [sic] n. sp.—Jiang in Luo et al.: p. 199.

1982 *Diminia simplex* [sic] n. sp.—Jiang in Luo et al.: p. 259, pl. 23, figs. 5, 6.

1984 *Diminia simplex* [sic] Jiang—Jiang: p. 22, pl. 4, Fig. 13.

?1986 *Dimidia simpleca* [sic] Jiang—Jiang and Huang: p. 322, pl. 1, Fig. 13.

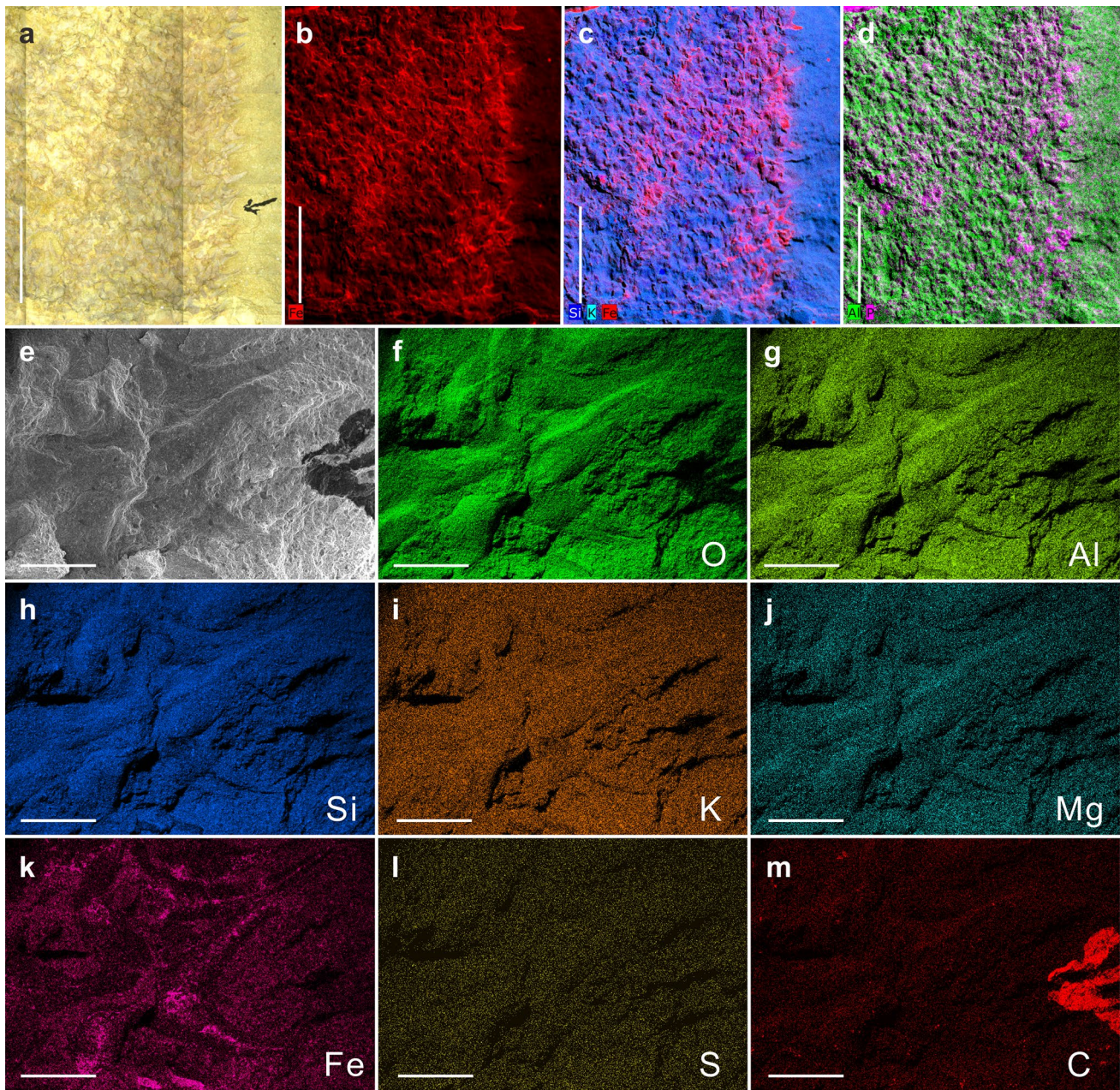


Fig. 1 Elemental distribution in the specimens of *Dimidia simplex* Jiang in Luo, Jiang, Wu, Song, and Ouyang, 1982 from the Chengjiang biota. **a** Specimen SJZ-B05-036A, showing a middle lateral part of a scleritome with jagged margins. **b–d** Elemental distribution in the area shown in **a**, analysed by using X-Ray Fluorescence (XRF). **e**

Scanning Electronic Microscopic (SEM) image of a sclerite indicated by a black arrow in **a**. **f–m** Elemental distribution in the area shown in **e**, analysed by using Energy Disperse Spectroscopy (EDS). Scale bars: 10 mm for **a–d** and 1 mm for **e–m**

- ?1989 *Dimidia simplex* [sic] Jiang—Bhatt: p. 67, pl. 1, Fig. 8.
 ?1989 *Onychia simplex* (Jiang)—Qian: p. 254–255, pl. 96, fig. 2.
 1989 *Allonnia? simplex* (Jiang)—Qian and Bengtson: p. 19–20, fig. 6I.
 ?2004 *Allonnia* sp.—Wrona: p. 26–28, Fig. 6Q.

- ?2006 *Allonnia* cf. *simplex* (Jiang)—Clausen and Álvaro: p. 226, fig. 3H, i.
 ?2006 *Eremactis conara* Bengtson and Conway Morris—Skovsted: p. 1099, Fig. 9.3.
 2020 *Allonnia simplex* (Jiang)—Sun et al.: p. 3, fig. 2AF.

Remarks on nomenclature. The species name was inconsistently spelled as '*Dimidia simplex*' and '*Diminia simplex*'

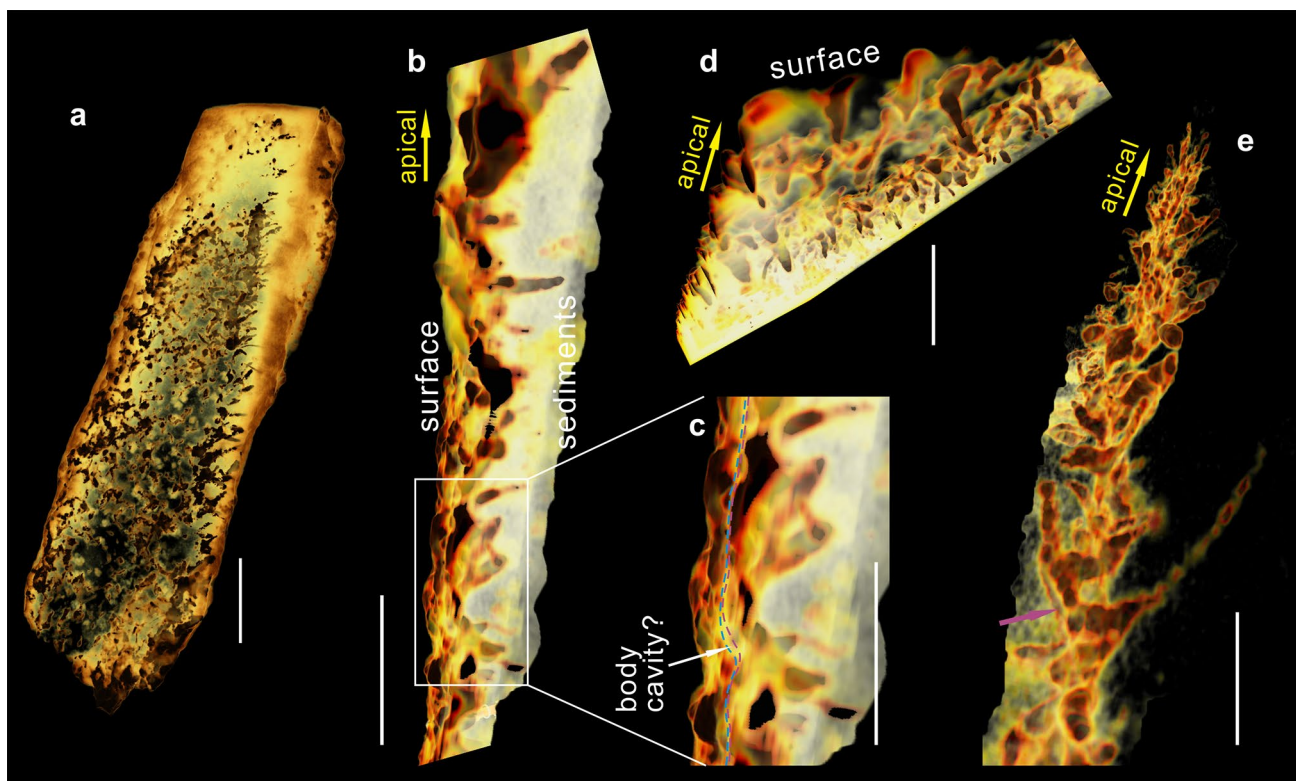


Fig. 2 Micro-Computed X-Ray Tomographic (Micro-CT) images of *Dimidia simplex* Jiang in Luo, Jiang, Wu, Song, and Ouyang, 1982 from the Chengjiang biota. **a–d** Specimen SK-823B, see Supplementary material for detail; **a** front view of the specimen; **b** lateral view of an internal longitudinal section, showing conical rays embedded in the sediments and nearly perpendicular to the specimen surface (as well as the animal body surface); **c** enlargement of the area

indicated by a white frame in **b**, in which the longitudinal narrow gap that divided sclerites to two layers probably reflects the original internal cavity of the animal; **d** lateral bottom view of an internal section, showing sclerite rays under the specimen surface. **e** Specimen SK-823A, lateral view of an internal section; purple arrow indicates a distinctive double-rayed sclerite. Scale bars: 10 mm for **a** and 0.5 mm for **b–d**

in different parts of the primary publication, and no etymology was given (Luo et al. 1982). In a subsequent publication of the same author, it was spelled as '*Diminia simplex*' (Jiang 1984). According to the original Chinese version, the genus name means 'bi-partite' and was based on the Latin *dimidius* (half); the species name means 'simple' and was from the Latin adjective *simplex* (simple; this adjective takes the same ending in all three genders) (Qian and Bengtson 1989). Therefore, after removing inadvertent errors in spelling, the correct Latin name of the species should be '*Dimidia simplex*', as also suggested by Qian and Bengtson (1989).

Paratypes from scleritome preservation. SJZ-B00-001, SJZ-B10-235, and MF-001 from localities of the Chengjiang biota (Cambrian Stage 3) in Kunming area, Yunnan Province, China (described herein).

Diagnosis. As emended diagnosis for the genus.

Description. The overall body is subcylindrical or biconical in shape, with a wide middle part that gradually tapered

towards both ends (Fig. 3a, e–g). Sclerites are densely arranged and imbricated on the body surface (the density reaching 100 per cm²) (Figs. 3, 4). The integument bearing the sclerites is mostly obscured by the dense sclerites.

Specimens SJZ-B10-235 and MF-001 are largest bodies that over 8.5 cm in height and 3.2 cm in width at the widest part (Fig. 3a, e). The apex of the body is preserved in specimens SJZ-B10-235 and JS-268B, and likely in SK-823 (Fig. 3a, d, f), which are characterized by a tuft-like structure (apical tuft around the orifice) that is composed of robust single-rayed sclerites at the top (Fig. 3b–d). Specimens SK-823 and MF-097 reveal an upper and a lower part of the body, respectively. The former is partly preserved and shows a jagged outline (Fig. 1f), and the latter represents a stalk-like basal end that tapers downward (Fig. 1g), likely rooting into the sea floor in life. Other specimens are mostly body fragments characterized by densely distributed sclerites and jagged outlines (Figs. 3h, 4). Sclerites arrange in an imbricating appearance and thus partly obscure each other for a high density (Fig. 4a, b, e, f).

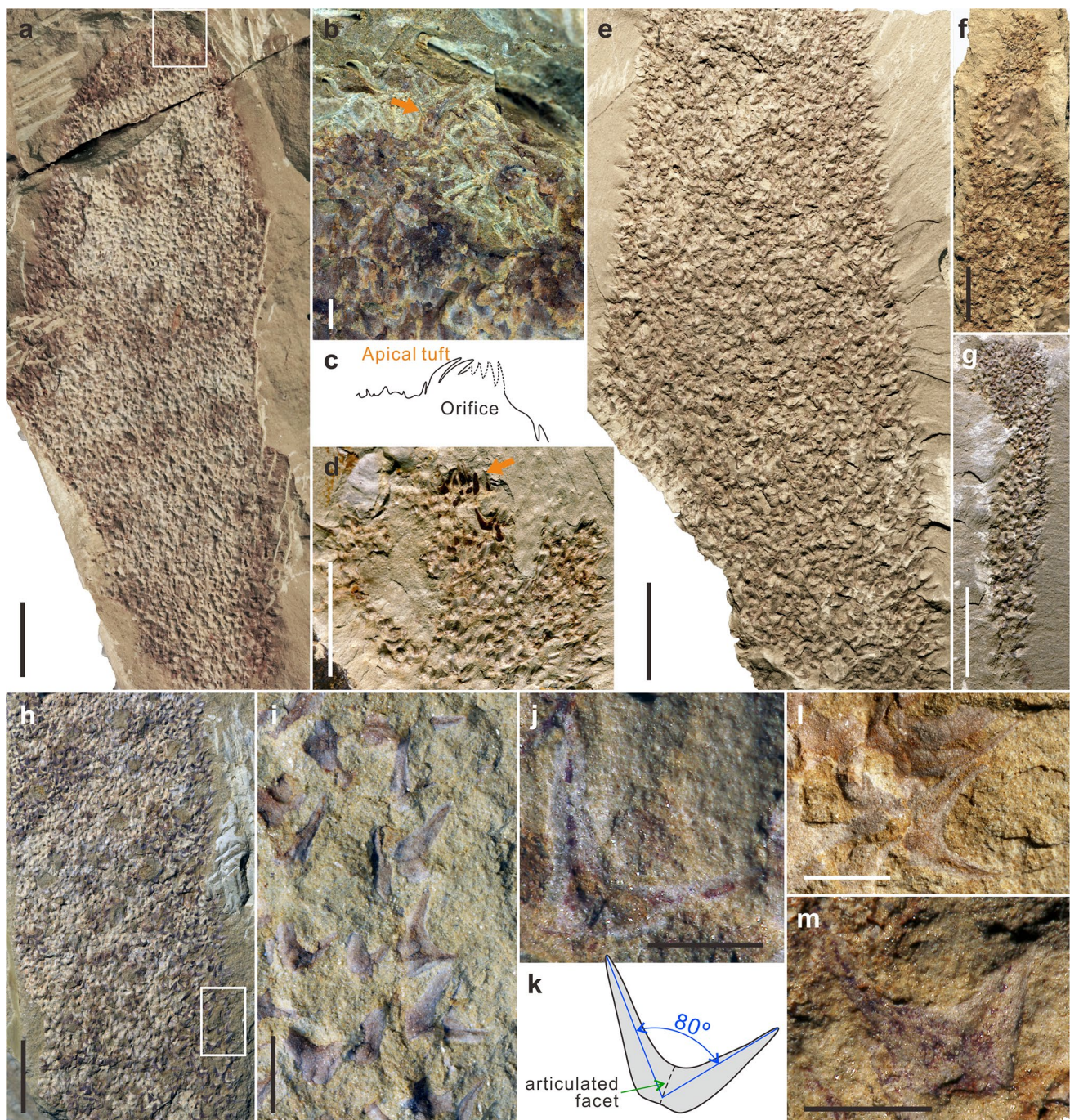


Fig. 3 Scleritomes of *Dimidia simplex* Jiang in Luo, Jiang, Wu, Song, and Ouyang, 1982 from the Chengjiang biota. **a** Specimen SJZ-B10-235A, showing a relatively complete scleritome. **b** Detail of the apical region that indicated by a white frame in **a**; the orange arrow indicates the stout single-rayed sclerites of the apical tuft. **c** Sketch of the apical tuft revealed in **b**. **d** Specimen JS-268B, showing an upper part of a scleritome with suspected tuft-like structure. **e** Specimen MF-001A, a scleritome that slightly tapers apically. **f** Specimen SK-823B,

an upper part of a scleritome. **g** Specimen MF-097, a lower part of a scleritome. **h** Specimen SJZ-B00-001A, a middle lateral part of a scleritome with a jagged margin. **i** Detail of the marginal area that indicated by a white frame in **h**, showing clear shape and structure of the sclerites. **j–m** Detail of sclerites; **j**, **m** sclerites in the specimen SJZ-B04-102; **k** sketch of **j**; **l** sclerites in the specimen SJZ-B05-036A, showing dark maroon ray axes. Scale bars, 10 mm for **a**, **d–f**, **h**, 1 mm for **b**, **i**, and 0.5 mm for **g**, **j**, **l**, **m**

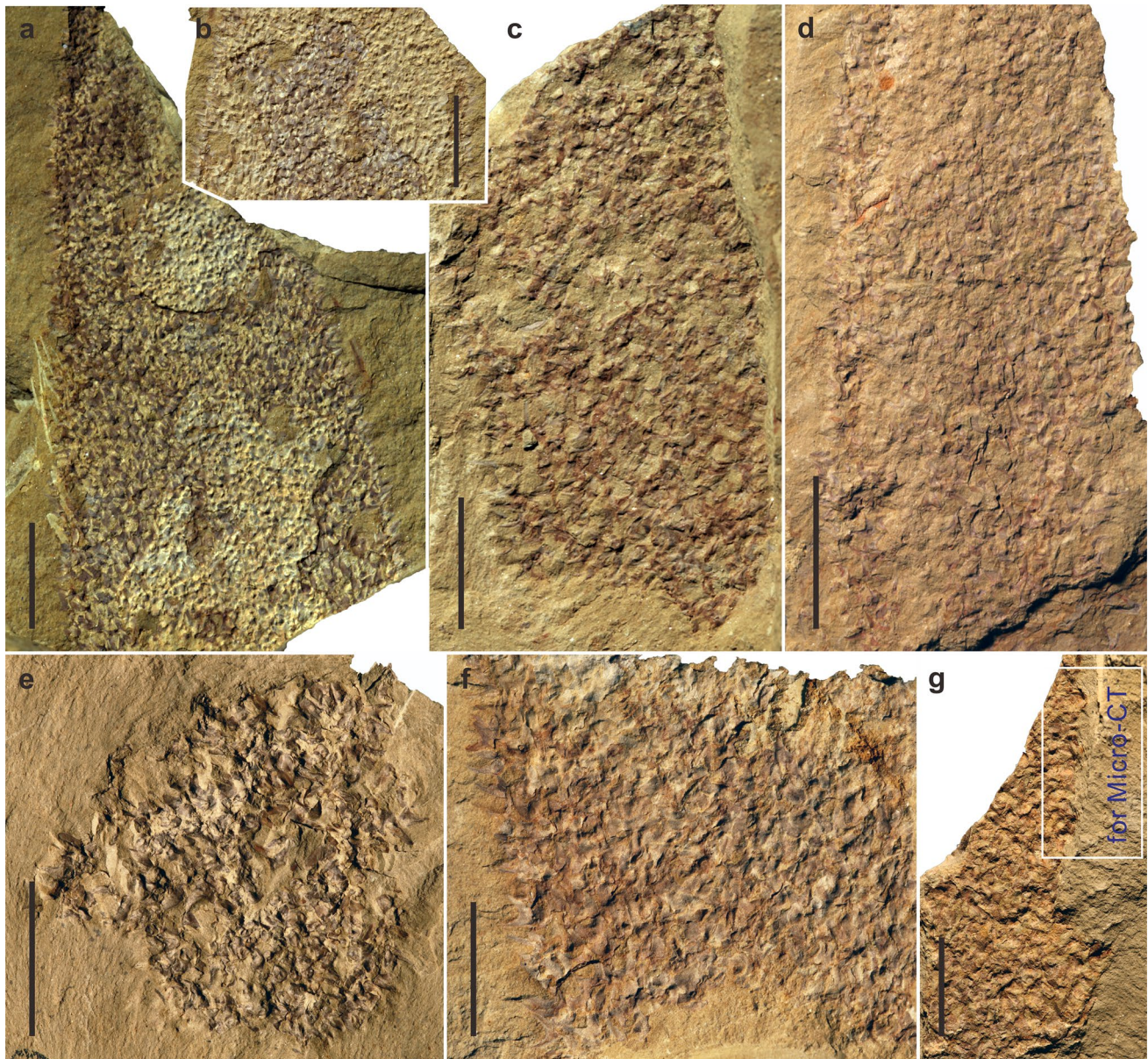


Fig. 4 Fragmental scleritomes of *Dimidia simplex* Jiang in Luo, Jiang, Wu, Song, and Ouyang, 1982 from the Chengjiang biota. Specimen SJZ-B00-002, part (a) and counterpart (b), showing a middle part of a scleritome with a jagged margin and scale-like dense sclerites. Middle and lateral parts of the scleritome, showing jagged

margins formed by dense, outward-pointing sclerites; c specimen SJZ-B05-030A; d specimen SJZ-B05-027B; e specimen SK-818A; f specimen SJZ-B05-036B; g specimen SK-823A, the area covered by sediments (indicated by a white frame) was analysed by using Micro-CT (Fig. 2e). Scale bars represent 10 mm

Each sclerite is V- or crescent-shaped, composed of two conical, symmetrical, and isometric rays that are generally 0.5–0.8 mm in length and articulate at their swollen proximal bases with an angle around 80° (Fig. 3h–m). The articulated facet between the two rays is situated within the symmetry plane and usually preserved as a thin groove (Fig. 3i, j, k). The core (lumen) along the long axis of the rays is different from the peripheral parts in primary composition, manifesting as a distinctive maroon colour (Fig. 3j, l,

m), corresponding to the concentration of the iron dioxides (Fig. 1k).

Comparison. The sclerites on scleritome specimens from the Chengjiang biota are morphologically congruent with the holotype of *D. simplex* from the Shiyantou Formation (Cambrian Stage 2) (Luo et al. 1982; Qian and Bengtson 1989) and the phosphatized double-rayed sclerites from the small shelly fauna of the Yu'an shan Formation (Cambrian Stage 3; the horizon of the Chengjiang biota) in eastern

Yunnan, China (Sun et al. 2020). They are also similar to the double-rayed sclerites (including suspected ones) from other small shelly assemblages in South China, India, Antarctica, Spain, and Greenland (Bhatt 1989; Qian 1989; Wrona 2004; Clausen and Álvaro 2006; Skovsted 2006) in general shape and structure. In addition, the sclerite density of the scleritome specimens is generally comparable with that of the cancelloriid *Nidelric* from Chengjiang and Guanshan biotas, whereas sclerites of the latter are solely single-rayed in structure (Hou et al. 2014; Zhao et al. 2018).

Discussion

Body reconstruction

Chancelloriids generally have a constricted apex with a noticeable orifice and an obconical basal end anchoring to the seafloor substrate; the apical orifice surrounded by a palisade-like apical tuft comprising a suite of modified single-rayed sclerites, which can obstruct large particles or predators from invading the body cavity (Bengtson and Collins 2015; Yun et al. 2018, 2019a). The body surface is bedecked by a series of mineralized (aragonitic) sclerites that characterized by different numbers and positions of hollow rays in different genera: for examples, *Chancelloria* is characterized by sclerites with 5–8 lateral rays plus a central ray, *Allonnia* dominated by 3-rayed sclerites, *Nidelric* by single-rayed sclerites (Yun et al. 2019b, 2021b). In consideration of the simple cylindrical or conical body shape, as well as the absence of internal organs, the studied fossils reveal and corroborate the sessile, radially symmetrical body plan of the Chancelloriida (Fig. 5). However, the domination of dense sclerites composed of a pair of acute rays in one scleritome reflects a different structural and arrangement pattern of sclerites from other known genera with complete bodies. Since the sclerite structure (reflected by the number and articulated mode of hollow rays) and their arrangement in the scleritome are phylogenetically significant traits of the group (Qian and Bengtson 1989; Yun et al. 2019b), *Dimidia* represents a distinctive genus possesses an intermediate type of structural complexity of sclerites between the genera dominated by single-rayed sclerites (such as *Nidelric*) and other taxa characterized by rosette-like composite sclerites.

Distribution and biostratigraphy

Although the scleritome (or complete body) of *Dimidia* is hitherto only discovered in the Chengjiang biota of South China, sclerites of this genus (double-rayed sclerites) were previously reported from a number of Cambrian skeletal assemblages that distributed in South China, Gondwana and Laurentia (Luo et al. 1982; Bhatt 1989; Qian 1989; Wrona



Fig. 5 Body reconstruction of *Dimidia simplex* Jiang in Luo, Jiang, Wu, Song, and Ouyang, 1982

2004; Clausen and Álvaro 2006; Skovsted 2006) (Fig. 6a). The common chancelloriids, including *Chancelloria*, *Allonnia*, and *Archiasterella*, have a worldwide distribution and a variety of patterns of preservation (e.g. Qian 1989; Bengtson et al. 1990; Moore et al. 2014, 2021; Yun et al. 2016, 2019a, 2019b). Comparatively, *Dimidia* and other uncommon taxa such as *Nidelric*, were only distributed within the tropical and subtropical zones, indicating that these genera probably had more strict requests (such as the warm sea water) to the habitat.

The oldest chancelloriids (sclerites belonging to *Chancelloria* and undefined taxa) were reported from the lower to middle Fortunian Stage of Siberia, Mongolia, and South China (Khomentovskiy and Gibsher 1990; Khomentovskiy and Karlova 1993; Brasier et al. 1996; Steiner et al. 2004; Zhu et al. 2017). While the youngest chancelloriids (*Chancelloria* and suspected *Archiasterella*) were discovered

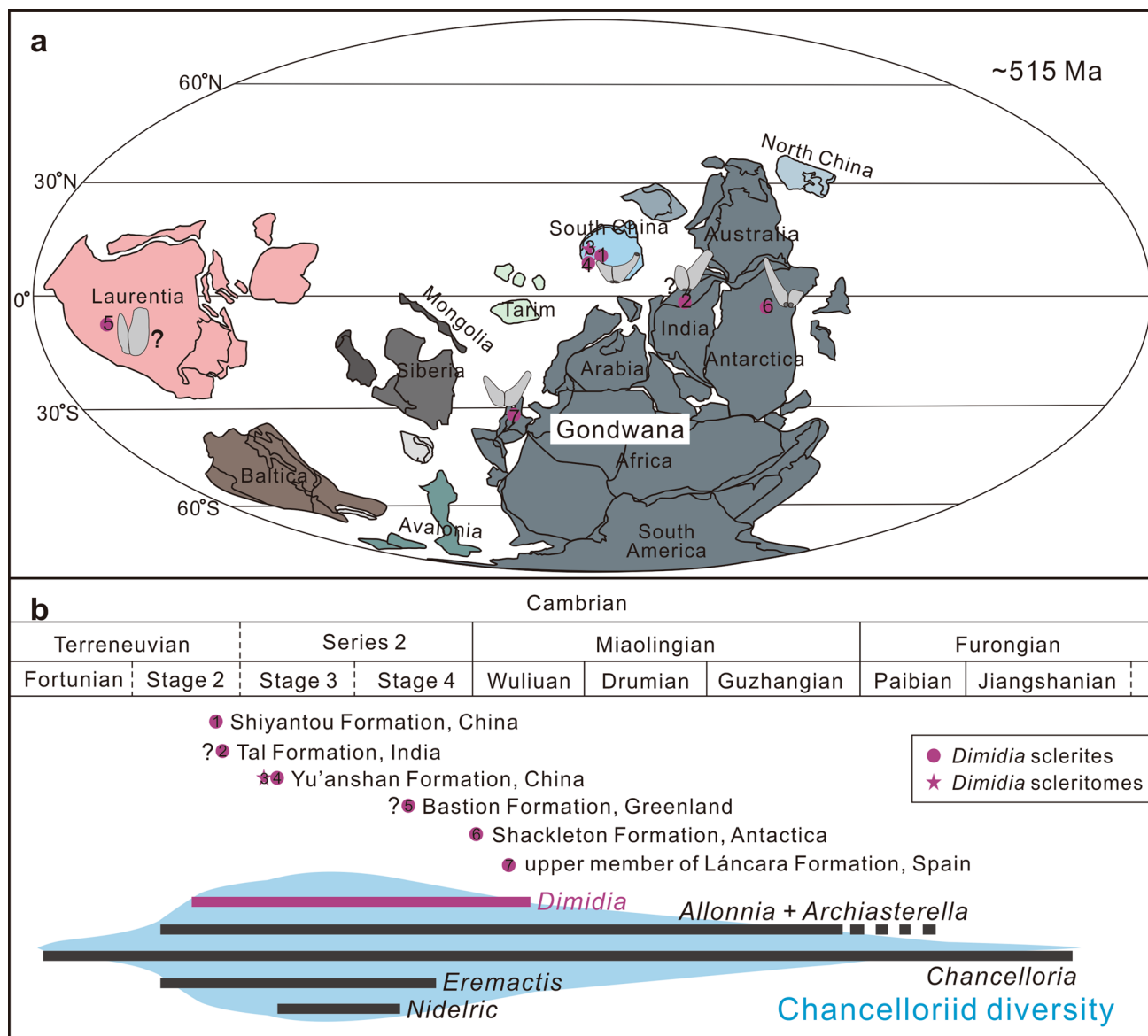


Fig. 6 Distribution and existing range of the cancelloriid *Dimidia*. **a** Paleogeographic distribution of *Dimidia*, including the double-rayed cancelloriid sclerites from small shelly faunas. The paleogeographic map is modified from Yun et al. (2016), Pan et al. (2018) and Zhao et al. (2020). **b** Stratigraphical range of *Dimidia* and a general

range of other representative cancelloriid genera, revealing a change of genus-level diversity through time. 1, Luo et al. (1982); 2, Bhatt (1989); 3, this paper; 4, Sun et al. (2020); 5, Skovsted (2006); 6, Wrona (2004); 7, Clausen and Álvaro (2006)

in the Paibian to Jiangshanian Stages of Laurentia, Peri-Gondwana, and North China (Mostler and Mosleh-Yazdi 1976; Hohensee and Stitt 1989; Han et al. 2019). The stratigraphical range of the genera *Allonnia* and *Archiasterella*, though not as long as *Chancelloria*, is from middle Stage 2 (Luo et al. 1982; Missarzhevsky 1989; Jacquet et al. 2017) and lasted at least to the end of Miaolingian Series (Beresi and Rigby 2013; Sun et al. 2022). However, *Dimidia* ranges only from upper Stage 2 to Wuliuan Stage (Fig. 6b). It is noted that a number of special types of cancelloriids,

such as *Nidelric*, *Eremactis*, *Diffusasterella* Demidenko in Alexander, Jago, Rozanov, and Zhuravlev, 2001, *?Chancelloriella* Demidenko, 2000, and so on, other than the common genera (*Chancelloria*, *Archiasterella*, and *Allonnia*), are also restricted within the Cambrian stages 2 to Wuliuan (Bengtson et al. 1990; Alexander et al. 2001; Skovsted 2006; Hou et al. 2014; Zhao et al. 2018; Moore et al. 2014, 2021). Therefore, the stratigraphical range of *Dimidia* generally corresponds to a flourishing period (with highest genus-level diversity) of the cancelloriid group (Fig. 6b).

Implication for the study of small shelly fossils

The Cambrian small shelly fossils are represented by a series of fragmental, mineralized body parts of many ‘miscellaneous’ and ‘problematic’ taxa (Matthews and Missarzhevsky 1975; Qian and Bengtson 1989; Qian et al. 1999; Bengtson 2004; Yun et al. 2016). Admittedly, specific investigations on the disarticulated skeletons themselves are significant in interpreting the skeletal structure and biomineralization of these taxa (e.g. Wood and Zhuravlev 2012; Vendrasco et al. 2017; Li et al. 2019; Yun et al. 2021b). However, the knowledge about overall morphology, integrated skeletal framework, and phylogenetic relationship of these ‘problematic’ early animals relies more on discovering counterparts of the SSFs in complete scleritome or soft bodied fossils. For examples, based on related complete body fossils, a group of plate- and tubercle-like sclerites were proven to be skeletal elements of palaeoscolecid worms (Ivantsov and Wrona 2004; Skovsted et al. 2011); some enigmatic coniform and sellate sclerites were assigned to stem group brachiopods (Skovsted et al. 2009; Kouchinsky et al. 2010); most members of the polyphyletic group ‘Coeloscleritophora’ (such as *Halkieria*) are now considered as stem or crown group molluscs (Conway Morris and Peel 1990; Caron et al. 2006; Vinther et al. 2017). As to cancelloriids, the discovery of complete bodies of different species and genera, including the *Dimidia* herein, could reveal the diversity of this group and contribute to clarify their ‘problematic’ taxonomy and potentially the enigmatic phylogeny (Bengtson and Collins 2015; Cong et al. 2018; Yun et al. 2018, 2021b; Zhao et al. 2018). In a similar way, it is necessary to scrutinize more scleritome fossils to find clues for understanding the taxonomy and phylogenetic affinity of other ‘problematic’ SSFs, such as zhijinitids and cambroclavids.

Conclusions

The cancelloriid genus *Dimidia*, once regarded as a junior synonym of *Allonnia*, is resurrected based on well-preserved, distinctive scleritomes from the Chengjiang biota. The scleritome of *Dimidia* is dominated by densely arranged sclerites composed of two symmetrical rays, representing a possible intermediate structural type between the single-rayed and other composite sclerites. The paleogeographic distribution of *Dimidia*, associated with other special cancelloriid taxa, is within the tropical and subtropical zones; their stratigraphical range generally corresponds to a flourished period of all cancelloriids. Furthermore, the discovery of the new scleritome corroborates that each genus of Chancelloriida is characterized by specific structures of

sclerites and helps clarifying the ‘problematic’ taxonomy of the small shelly fossils.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s12542-023-00660-y>.

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Data availability statement All data are provided in the text, figures, and supplementary materials.

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