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A tale of three taphonomic modes: the Ediacaran fossil *Flabellophyton* preserved in limestone, black shale, and sandstone

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Abstract

Ediacaran macrofossils are typically preserved in three taphonomic modes: casts/molds in siliciclastic rocks, casts/molds in carbonate rocks, and carbonaceous compressions in black shales. Only a few taxa are known to be preserved in more than one of these taphonomic modes. *Flabellophyton* is a genus that has been previously reported from lower Ediacaran black shale of the Lantian Formation (635–551 Ma) in South China and upper Ediacaran sandstone of the Ediacara Member (560–550 Ma) in South Australia. Here we report *Flabellophyton* from upper Ediacaran limestone of the Shibantan Member of the Dengying Formation (551–539 Ma) in South China, making *Flabellophyton* the only genus that occurs in all three taphonomic modes. We also provide a systematic description of *Flabellophyton* based on material from the Lantian and Dengying formations in South China, recognizing three

morphospecies—*F. lantianense*, *F. typicum* sp. nov., and *F. obesum* sp. nov. *Flabellophyton* is reconstructed as an erect epibenthic marine organism attached to sandy, carbonate, and muddy substrates. Its phylogenetic affinity remains ambiguous though it was historically interpreted as an algal fossil. The wide environmental and stratigraphic distribution of *Flabellophyton* allow comparative taphonomic and paleoecological analysis. Taphonomic analysis of *Flabellophyton* indicates that multiple taphonomic pathways can facilitate the preservation of Ediacaran macrofossils. As a window into Ediacaran paleoecology, *Flabellophyton* and other Ediacaran fossils played a crucial role in the construction of epibenthic communities in Ediacaran oceans, and helps to understand the ecological migration and evolutionary expansion from deeper to shallower oceans during the Ediacaran Period.

Keywords: *Flabellophyton*, Ediacaran Period, Lantian Formation, Dengying Formation, South China

1. Introduction

The Ediacara biota in the middle–late Ediacaran Period represents some of the earliest macroscopic and morphologically complex multicellular eukaryotes (Droser et al., 2017; Laflamme et al., 2013; Liu et al., 2014; Narbonne, 2005; Xiao and Laflamme, 2009). Most Ediacara-type fossils are preserved as casts and molds in sandstone successions (Fedonkin et al., 2007), but several recent studies have shown that some taxa of the Ediacara biota can also be preserved as casts and molds in carbonate successions (Bykova et al., 2017; Chen et al., 2014; Grazhdankin et al., 2008; Narbonne and Aitken, 1990) or as carbonaceous compressions in black shales (Xiao et al., 2013; Zhu et al., 2008). For example, *Arborea*, *Hiemalora*, *Pteridinium*, and *Rangea* are found in both sandstone and limestone facies (Chen et al., 2014; Wang et al., 2020), and *Beltanelliformis*, *Eoandromeda*, *Gesinella*, *Flabellophyton*, *Liulingjitaenia*, *Longifuniculum*, and *Orbisiana* in sandstone and black shale facies (Wan et al., 2014; Xiao et al., 2013). In addition, some of these taxa also extend to the early Ediacaran Period (Wan et al., 2014; Xiao et al., 2013). Various Ediacaran strata

in South China, including black shales in the Doushantuo/Lantian Formation and limestones in the Shibantan Member of the Dengying Formation, are known to preserve Ediacara-type fossils and they offer an opportunity to broaden our view of the stratigraphic, environmental, and taphonomic distributions of the Ediacaran macrofossils.

In this study, we report the discovery of *Flabellophyton* preserved in limestone of the Shibantan Member of the Dengying Formation in the Yangtze Gorges area of South China, making it the only genus that occurs in all three taphonomic windows. *Flabellophyton* and its synonymous forms were first described from the early–middle Ediacaran (635–580 Ma) Lantian Formation (Bi et al., 1988; Chen et al., 1994; Yan et al., 1992). Several systematic studies of this genus from the Lantian Formation have been published (Wan et al., 2013; Yuan et al., 1999). Subsequently, Xiao et al. (2013) reported *Flabellophyton* from upper Ediacaran (ca. 560–550 Ma) sandstone of the Ediacara Member in South Australia. Thus, the discovery of *Flabellophyton* from the 551–539 Ma Shibantan Member not only expands the environmental and taphonomic ranges of this genus, but also extends its stratigraphic range. The main objectives of this paper are to document the taxonomic diversity, and to discuss the taphonomy and paleoecology of this genus, based on material from the Lantian Formation and Shibantan Member.

2. Geological setting, material and methods

Flabellophyton fossils were collected from the Lantian and Dengying formations in South China (Fig. 1A–D). A total of 3250 *Flabellophyton* specimens were collected from Member II black shale of the Lantian Formation at two excavation sites near the village of Piyuan in Xiuning County (29°55′25.7″ N, 118°06′0.7″E) and near the village of Shiyu in Yixian County (29°57′09.1″ N, 118°03′22.2″ E), both in southern Anhui Province. In addition, 12 specimens of *Flabellophyton* were recovered from limestone of the Shibantan Member of the Dengying Formation at an excavation site near the Wuhe village (30°47′14.9″ N, 110°03′18.2″ E) in the Yangtze Gorges area, Hubei Province. All illustrated specimens are reposited in Nanjing Institute of

Geology and Palaeontology, Chinese Academy of Science (NIGPAS).

The Lantian Formation in southern Anhui Province rests on terminal Cryogenian glacial diamictite of the Leigongwu Formation and can be divided into four lithostratigraphic members (Fig. 1C). The total thickness of the Lantian Formation varies from ~150 m (Guan et al., 2014; Wan et al., 2014; Wan et al., 2016) to 190 m in southern Anhui Province (Wang et al., 2017). At our study site, these four members are, in ascending order, Member I representing the cap dolostone (4 m), Member II consisting of 23-m-thick siltstone, 8.6-m-thick mudstone and 34-m-thick fossiliferous black shale, Member III with 26 m of dolostone intercalated with black shales in the lower part and 40 m of limestone in the upper part, and Member IV with 20 m of black mudstone (Wan et al., 2014; Wan et al., 2016). The Lantian Formation is overlain by siliceous rock of the upper Ediacaran Piyuancun Formation, which contains macrofossils described as *Palaeopascichnus* sp. (Dong et al., 2012). The Piyuancun Formation is in turn overlain by the lower Cambrian Hetang Formation that contains small shelly fossils (Steiner et al., 2003), articulate sponge fossils (Tang et al., 2019c; Xiao et al., 2005a; Yuan et al., 2002a), and the problematic animal fossil *Cambrowania* (Tang et al., 2019a, b).

The Lantian biota, including *Flabellophyton*, occurs in the fossiliferous black shale in the upper part of Member II (Fig. 1C). The lithostratigraphic sequence of the Lantian Formation is similar to that of the Doushantuo Formation in the Yangtze Gorges area (Yuan et al., 2011), which also consists of four members of similar lithologies and has been constrained between 635 Ma and 551 Ma (Condon et al., 2005). Based on a zircon U–Pb age of 632.5 ± 0.8 Ma from an ash bed in lower Member II (Condon et al., 2005) and a Re–Os age of 593 ± 17 Ma from the lower Member IV of the Doushantuo Formation in the Yangtze Gorges area (Zhu et al., 2013), Yuan et al. (2011) estimated that the fossiliferous Member II of the Lantian Formation is probably between 632 Ma and 576 Ma. Attempts to directly data the fossiliferous black shales from Member II of the Lantian Formation produced additional constraints: Lan et al. (2019) reported a maximum age of 590 ± 7 Ma based on detrital zircon U-Pb dating, whereas Liu et al. (2020) reported a minimum age of

612 ± 29 Ma based on diagenetic monazite U-Pb dating.

The Dengying Formation in the Yangtze Gorges area overlies the 635–551 Ma Doushantuo Formation and consists of three members. These are, in an ascending order, the Hamajing, Shibantan, and Baimatuo members (Fig. 1D). The Hamajing (20.4-m-thick) and Baimatuo (58.7-m-thick) members both consist of light gray thick-bedded peritidal dolostone, whereas the intervening Shibantan Member consists of 157.4-m-thick dark gray thin-bedded bituminous limestone. The Dengying Formation is overlain by the Yanjiahe Formation, which contains early Cambrian small shelly fossils (Guo et al., 2014) and acanthomorphic acritarchs (Ahn and Zhu, 2017; Dong et al., 2009). Given that the Ediacaran–Cambrian boundary is estimated to be ~539 Ma (Linnemann et al., 2019), the Dengying Formation is constrained between 551 Ma and 539 Ma.

The Shibantan assemblage was hosted in the Shibantan Member limestone of the Dengying Formation. Ediacara-type fossils including *Arborea*, *Hiemalora*, *Pteridinium*, and *Rangea* (Chen et al., 2014; Wang et al., 2020), abundant bilaterian trace fossils (Chen et al., 2018; Chen et al., 2013; Chen et al., 2019; Meyer et al., 2017; Meyer et al., 2014; Xiao et al., 2019), vendotaenid macrofossils (Zhao et al., 1988), and enigmatic fossils such as *Yangtziramulus* and *Curviacus* (Shen et al., 2017; Shen et al., 2009; Xiao et al., 2005b) have been reported from the Shibantan Member. The tubular fossil *Sinotubulites* has been reported from the uppermost Shibantan and lower Baimatuo members (Cai et al., 2015; Zhao et al., 1985). The *Flabellophyton* specimens presented in this paper also came from the Shibantan Member (Fig. 1D), from the lower 25 m interval of this unit.

Fossil specimens were examined and photographed under a reflected light microscope. In order to understand the taphonomy of the fossils, petrographic thin sections perpendicular and parallel to bedding surface were prepared for a selected number of specimens. The thin sections were examined under a petrographic microscope. A small number of specimens and thin sections were also examined using a LEO1530VP field-emission environmental scanning electron microscope (FE-ESEM) equipped with an integrated EDAX Genesis 2000 and a SUTW–Sapphire

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detector. Energy dispersive X-ray spectroscopy (EDS) elemental maps were generated for the fossil specimens and surrounding matrix using the EDAX system (acquisition time 90–120 s). In order to determine whether the fossils have distinct organic carbon isotope compositions, organic material was physically removed from the fossils and rock matrix for $\delta^{13}C_{org}$ analysis on an Isoprime isotope ratio mass spectrometer. Finally, organic material in the fossils and rock matrix was characterized using a JY Horiba LabRam HR800 Raman spectrometer (514 nm Ar laser at room temperature and atmospheric pressure).

3. Results

3.1. Systematic Palaeontology

Genus *Flabellophyton* Steiner, 1994, emended

Cyathophyton Bi et al., 1988 (nomen nudum).

Huizhouella Yan et al., 1992 (nomen nudum).

Flabelliphyton Yan et al., 1992 (nomen nudum).

Flabellophyton Chen et al., 1994. (nomen nudum)

Flabellophyton Steiner, 1994.

non Flabellophyton strigata Yuan et al., 1999.

Type species: *Flabellophyton lantianense* Steiner, 1994, emended, nomen correctum

Other recognized species: *Flabellophyton typicum* sp. nov.; *Flabellophyton obesum* sp. nov.

Original diagnosis: Narrow fan-shaped impressions; originally membraneous, probably tubular to cup-shaped organisms or colonies of organisms; basal part often with a slightly wider and rounded structure; longitudinally often with band-shaped structures along which the body may be torn apart. [Translated from Steiner (1994)].

Emended diagnosis: Conical thallus, often preserved as fan-shaped compressions on bedding surface, consisting of regularly and closely bundled filaments. Filaments are unbranched and radiate from a basal holdfast.

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Discussion: This form was first reported by Bi et al. (1988) from the Lantian Formation in southern Anhui Province, and described under the genus *Cyathophyton*, with two constituent species—*C. formosum* and *C. simplicis*. Similar fossils from the Lantian Formation in the same region were later described by Yan et al. (1992) as *Huizhouella* (including *H. typicus*, *H. longifolius*, and *H. scoparius*) and *Flabelliphyton formosus*. However, neither a diagnosis nor a type species was provided for *Cyathophyton* (Bi et al., 1988). Although a diagnosis and a type species were provided for *Huizhouella* and *Flabelliphyton*, no holotype was designated for the type species (Yan et al., 1992). Thus, *Cyathophyton*, *Huizhouella*, and *Flabelliphyton* are regarded as invalid genera. The genus *Flabellophyton* and four constituent species—*F. lantianensis* (type species), *F. scopijormis*, *F. cancellatum*, and *F. piyuancunensis*—were erected by Chen et al. (1994) to accommodate fan-shaped macrofossils from the Lantian Formation. Because Chen et al. (1994) did not specify the repository of type specimens and thus violated ICBN (Tokyo Code, 1994) article 37.5 (corresponding to IAPT Shenzhen Code, 2018, article 40.7), Steiner (1994) later validated *Flabellophyton* by designating a new holotype for its type species *F. lantianensis*, essentially creating a new genus *Flabellophyton* Steiner, 1994. Yuan et al. (1999) argued that Steiner's (1994) taxonomic procedure was unjustified because they deemed that the original diagnosis and type specimen designation by Chen et al. (1994) was sufficient despite no specification of repository. However, as stipulated in the IAPT Art. 9.2 (Shenzhen Code, 2018), "omissions of required information under Art. 40.6–40.8 are not correctable". Thus, we consider *Flabellophyton* Chen et al., 1994 invalidly published and it cannot be validated by subsequent taxonomic actions. As such, *Flabellophyton* Chen et al., 1994 has no status according to IAPT Art. 12.1, and it does not compete with *Flabellophyton* Steiner, 1994 for the earlier homonym (IAPT Art. 53.1), even though the former was effectively published prior to the latter. Therefore, *Flabellophyton* Steiner, 1994 is the first and only validly published genus available to accommodate the material described in this paper.

The four species of *Flabellophyton* of Chen et al. (1994) are differentiated on the basis of general shapes and "transverse septa" on the filaments. However, the

"transverse septa" are likely related to taphonomic shrinkage during carbonization, which produced a grainy texture on the carbonaceous filament (Yuan et al., 1999). Both Steiner (1994) and Yuan et al. (1999) argued that the four species of *Flabellophyton* Chen et al., 1994 are synonymous and should be synonymized with the type species. Steiner (1994) diagnosed *Flabellophyton* as membraneous, but our observations suggest that it likely represents a conical thallus. Thus, the diagnosis of *Flabellophyton* is here emended to emphasize its conical thallus and to remove taphonomic structures such as "transverse septa" as diagnostic features.

Yuan et al. (1999) erected the species *Flabellophyton strigata*, which is characterized by transverse nodes or bands across the thallus. However, Wan et al. (2013) argued that such transverse nodes represent horizontal carbonaceous filaments or bands (Fig. 2K–L), and thus *F. strigata* was featured by characteristic skeletal body framed by longitudinal and horizontal carbonaceous filaments or bands, which warrants a different genus and should be removed from the genus *Flabellophyton*. Therefore, we tentatively exclude *Flabellophyton strigata* from the genus *Flabellophyton* until Wan et al.'s (2013) claims are verified in future investigation.

A quantitative morphological analysis of *Flabellophyton* showed that several morphospecies may be recognized on the basis of thallus divergence angle from the apical end (Wan et al., 2013). Here, we formally recognized three morphospecies of *Flabellophyton*: *F. lantianense* characterized by a slender thallus, *F. typicum* sp. nov. by a conical thallus; and *F. obesum* sp. nov. by an obtuse and broad thallus.

Flabellophyton lantianense Steiner, 1994, emended, nomen correctum

Figure 2A–F

Huizhouella longifolius Yan, Xing, and Xu *in* Yan et al., 1992, pp. 44–45, pl. 21, figs. 2–3; pl. 22, fig. 4; pl. 24, fig. 2. (nomen nudum)

Flabellophyton piyuancunensis Chen, Lu, and Xiao *in* Chen et al., 1994, p. 264, fig. 33. (nomen nudum)

Flabellophyton lantianensis Steiner, 1994, p. 127, pl. 16, figs. 6, 8–9.

Baculiphyca sp.; Yuan et al., 1999, p. 150, fig. 4A.

Flabellophyton lantianensis Chen, Lu and Xiao; Wan et al., 2013, fig. 3a–c.

Flabellophyton sp. 1; Yuan et al., 2016, p. 44, figs. 3.24–3.26.

Emended Diagnosis: A species of *Flabellophyton* with a slender thallus and an apical divergence angle less than 12 degrees.

Holotype: MLa 069, reposited at Institute of Geology and Palaeontology of Berlin University, Germany.

Material: 311 specimens in our collection.

Description: Slender compression consisting of closely and regularly arranged filamentous structures, with an apical divergence angle of 5–12 degrees. Thallus straight (Fig. 2B–D, F) or slightly bent (Fig. 2A, E), but never fold. The compressed thallus has a consistent width along much of its length, but tapers basally to form a stipe connected with the holdfast, and has a rounded or flat upper end.

Orthography: Both Chen et al. (1994) and Steiner (1994) adopted *lantianensis* as the species epithet. However, as *Flabellophyton* is considered neuter, the correct declension of the species epithet should be *lantianense*. According to IAPT Article 60.1, this orthographical error is here corrected, and *Flabellophyton lantianense* should be used in the future.

Remarks: Chen et al. (1994) erected *Flabellophyton piyuancunensis* to describe slender fan-shaped fossils from the Lantian Formation, but this species is invalid because the repository of its holotype was not specified. *Flabellophyton lantianensis* Steiner, 1994 was typified by a specimen (MLa 069) very similar to the holotype of *F. piyuancunensis*. In our opinion, *F. piyuancunensis* Chen et al., 1994 and *F. lantianensis* Steiner, 1994 are synonymous. Considering that *F. piyuancunensis* Chen et al., 1994 is invalid, we choose *F. lantianensis* Steiner, 1994 to accommodate the slender form of *Flabellophyton.*

Flabellophyton is the dominant genus in the Lantian biota (Wan et al., 2013; Yuan et al., 1999). Measurements of divergence angles, based on 1286 specimens of *Flabellophyton* from the Lantian Formation, show that, although there is a continuous range from 5 to 60 degrees, there are multiple modes (Fig. 4A). An outline analysis of

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156 *Flabellophyton* specimens (see Wan et al., 2013)—including 107 specimens measured on six field quadrats (black lines in Fig. 4B) and 49 specimens measured in the laboratory (red lines in Fig. 4B)—indicates that there are three morphotypes that are respectively characterized by slender clavate, intermediate, and obtuse fan-shaped compressions (Fig. 4B). Integrating the apical divergence angle measurements (Fig. 4A) and the shape analysis results (Fig. 4B), we proposed three *Flabellophyton* morphospecies: *F. lantianense* characterized by a slender clavate thallus with an apical divergence angle of 5–12˚; *F. typicum* sp. nov. by an intermediate conical thallus with an apical divergence angle of 12–45˚; and *F. obesum* sp. nov. by an obtuse conical thallus with an apical divergence angle of 45–60˚ (Fig. 4A–C). Of these species, *F. typicum* sp. nov. is most abundant, *F. lantianense* is rarer, and *F. obesum* sp. nov. is the least common (Fig. 4A).

Flabellophyton lantianense differs from other species of *Flabellophyton* by its slender thallus with a smaller apical divergence angle and clavate shape. The general morphology of *Baculiphyca taeniata* Yuan et al. 1995 from the Ediacaran Miaohe biota is somewhat similar to *Flabellophyton lantianense*, but it is characterized by a truly parenchymatous thallus rather than bundled filaments (Xiao et al., 2002). Thus, the specimen described as *Baculiphyca* sp. in Yuan et al. (1999) should be regarded as *Flabellophyton lantianense* because of its bundled filamentous construction.

Occurrence: Lower Ediacaran Lantian Formation in Xiuning and Yixian counties, Anhui Province, South China.

Flabellophyton typicum **sp. nov.**

Figure 2G–J; Figure 3A–H; Figure 6A; Figure 9A

Cyathophyton formosum Xing, Bi, and Wang *in* Bi et al., 1988, p1. 4, fig. 2. (nomen nudum)

Cyathophyton simplicis Xing, Bi, and Wang *in* Bi et al., 1988, p1. 4, fig. 7. (nomen nudum)

Huizhouella typicus Yan, Xing, and Xu *in* Yan et al., 1992, p. 44, pl. 18, figs. 4, 8–9; pl. 19, figs. 1–4, 6; pl. 20, fig. 9; pl. 23, fig. 3. (nomen nudum)

Huizhouella scoparius Yan, Xing, and Xu *in* Yan et al., 1992, p. 45, pl. 18, figs. 1–3, 5, 7; pl. 20, fig. 11; pl. 22, fig. 3. (nomen nudum)

Flabellophyton lantianensis Chen, Lu, and Xiao *in* Chen et al., 1994, p. 263, figs. 27, 30–31, 37. (nomen nudum)

Flabellophyton scopiformis Chen, Lu, and Xiao *in* Chen et al., 1994, p. 263, figs. 21–22. (nomen nudum)

Flabellophyton cancellatum Chen, Lu, and Xiao *in* Chen et al., 1994, pp. 263-264, figs. 17, 24–26. (nomen nudum)

Flabellophyton piyuancunensis Chen, Lu, and Xiao *in* Chen et al., 1994, p. 264, figs. 18, 28, 35–36, 38. (nomen nudum)

Flabellophyton lantianensis Steiner, 1994, p. 127, pl. 16, figs. 1, 3, 7, 10.

Huizhouella typicus Yan, Xing, and Xu; Tang et al., 1997, pl. Ⅱ, figs. 1–3; pl. Ⅲ, figs. 2–4a.

Flabellophyton lantianensis Chen, Lu, and Xiao; Yuan et al., 1999, p. 152, figs. 2F, 5A–C, 6H.

Flabellophyton lantianensis Chen, Lu, and Xiao; Yuan et al., 2002b, p. 47, figs. 43–44.

Flabellophyton lantianensis Chen, Lu, and Xiao; Yuan et al., 2011, fig. 2d.

Flabellophyton lantianensis Chen, Lu, and Xiao; Wan et al., 2013, fig. 3d–j, l.

Flabelophyton sp. Chen, Lu, and Xiao; Xiao et al., 2013, fig. 1C–F.

Flabellophyton lantianensis Chen, Lu, and Xiao; Yuan et al., 2016, p. 41, figs. 3.20–3.22.

Etymology: Latin "*typicus*", typical, referring to the intermediate conical shape of this species.

Diagnosis: A species of *Flabellophyton* with the basal divergence angle of 12–45 degrees, forming a conical body with a stipe connected to the basal holdfast.

Holotype: NIGP–PB22446, field collection number 12LT–8418 (Fig. 2G), reposited at NIGPAS.

Material: 2817 specimens in our collection.

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Description: Fossil consists of a basal holdfast, lower stipe, and upper conical body. The holdfast is globose to subspherical in shape, often preserved as a round disk (Fig. 2G–H), sometimes with additional organic matter or structures attached to it (Fig. 2I–J and possibly Fig. 3A, I–J). Filaments are tightly bundled in the lower part to form a thin stipe, and then expand in the upper part to form a conical body that is preserved as a fan-shaped compression. Filamentous structures are smooth, and they do not branch or cross each other. The distal end of the conical body is rounded and sometimes asymmetrically lopsided (Fig. 2G–H), although it is sometimes irregularly shaped due to taphonomic degradation or disruption of the filaments (Fig. 2I–J; Fig. 3A–B, J). Fossils are mostly straight and can be bent occasionally (Fig. 2I).

Fossil specimens have an apical divergence angle of 12–45 degrees. For specimens from the Lantian Formation, the conical bodies are 10–70 mm in height and 4–20 mm in maximum width (Fig. 5), and the filamentous structures are 0.01–0.2 mm in thickness. These measurements are 100–150 mm, 15–40 mm, and 0.5–3 mm, respectively, for specimens from the Shibantan Member, and 100–250 mm, 30–50 mm, and 0.5–2 mm, respectively, for specimens from the Ediacara Member (Fig. 5).

Remarks: The intermediate conical form of *Flabellophyton* is the dominant and representative taxa in the Lantian biota, which was traditionally described as *Flabellophyton lantianensis*. However, as discussed above, the *Flabellophyton lantianensis* Chen, Lu, and Xiao, 1994 is invalid and *Flabellophyton lantianensis* Steiner, 1994 represents the slender form. Thus, here we establish *Flabellophyton typicum* sp. nov. to describe the intermediate conical form.

Xiao et al. (2013, their fig. 1G–H) illustrated two specimens from the Ediacara Member of the Rawnsley Quartzite of South Australia and compared them with *Flabellophyton* from the Lantian Formation. The Australian specimens (Fig. 3I–J) are similar to *Flabellophyton typicum* in divergence angle, however they are larger (Fig. 5) and have a thinner stipe (Fig. 3J). Although they may also belong to *Flabellophyton typicum*, at the present we tentatively place them in an open nomenclature (*Flabellophyton* sp.) pending further investigation.

Flabellophyton specimens from the Shibantan Member are also larger in size

than the Lantian specimens (Fig. 5), but they share the basic morphological features of *Flabellophyton*, including a basal holdfast, a short and relatively thick stipe, and upper fan-shaped (conical) body. Their general shape and apical divergence angles are most similar to *typicum* sp. nov. from the Lantian Formation. Thus, *Flabellophyton* specimens from the Shibantan Member are identified as *F. typicum* sp. nov.

F. typicum sp. nov. is superficially similar to the putative animal fossil *Lantianella laevis* from the Lantian Formation, except for the absence of a tentacular crown (Wan et al., 2016). The Lantian algal fossil *Huangshanophyton fluticulosurn* shares a fan-like shape with *F. typicum*, but its filaments are sparsely arranged (Chen et al., 1994; Yuan et al., 1999). *F. typicum* also resembles the conical to tubular algal fossil *Gesinella* Steiner et al. (1992) from the Ediacaran Liuchapo Formation in South China, but the latter is a tubular thallus with a membraneous wall but without filamentous structures, it has a rhizoidal holdfast, and it shows evidence of episodic growth (Steiner, 1994; Wu et al., 2012; Zhao et al., 2004).

Occurrence: Lower Ediacaran Lantian Formation in Xiuning and Yixian counties, Anhui Province, South China; upper Ediacaran Shibantan Member of Dengying Formation in Yangtze Georges, South China.

Flabellophyton obesum sp. nov.

Figure 2M–P

Flabelliphyton formosus Yan, Xing and Xu in Yan et al., 1992, p. 45, pl. 21, fig. 1; pl. 22, fig. 1. (nomen nudum)

Flabellophyton sp.; Yuan et al., 2011, fig. 2G–I.

Flabellophyton lantianensis Chen, Lu and Xiao; Wan et al., 2013, fig. 3k.

Flabellophyton sp.2; Yuan et al., 2016, p47, figs. 3.28–3.30.

Etymology: Latin "obesus", referring to the obtuse conical shape of fossils

Holotype: NIGP–PB22452, field collection number 11LT–8239 (Fig. 2M), reposited at NIGPAS.

Material: 51 specimens in our collection.

Diagnosis: A species of *Flabellophyton* with a broadly or obtusely conical thallus and an apical divergence angle greater than 45 degrees.

Description: Broad fan-like carbonaceous compressions consisting of closely and regularly arranged filamentous structures, with an apical divergence angle of 45–60 degrees. A holdfast is present (Fig. 2M–O), but the stipe is poorly differentiated. The upper end is hollowed (Fig. 2M) or rounded (Fig. 2O–P).

Remarks: *Flabellophyton obesum* sp. nov. differs from other species of *Flabellophyton* in its greater divergence angle and obtuse conical shape. Some obliquely compressed specimens of the tufted algal fossil *Anhuiptyton lineatum* (e.g. fig. 2c in Yuan et al., 2011) from the Lantian Formation are similar to *F. obesum*, but they have a greater number of filaments (up to 1000 in each specimen) that branch dichotomously.

Occurrence: Lower Ediacaran Lantian Formation in Xiuning and Yixian counties, Anhui Province, South China.

3.2. Preservation

3.2.1. Specimens from the lower Lantian Formation

Flabellophyton from Member II black shale of the Lantian Formation is preserved as carbonaceous compressions. It occurs more or less continually in a 34 m stratigraphic interval, and specimens are randomly distributed or clustered on bedding surfaces (Wan et al., 2016). Most specimens are completely preserved with intact holdfasts, indicating that they were erect benthic organisms preserved in situ. The fossils are not preferentially oriented, suggesting that they were preserved in a quiet sedimentary environment.

Weathered specimens (Fig. 2) are dark gray to dark brown in color, contrasting with the lighter color of the matrix. Due to high degree of carbonization, specimens mostly consist of carbonaceous grains, making it impossible to extract intact specimens using acid maceration techniques. Such carbonaceous grains likely resulted from volume reduction of carbonaceous material due to devolatilization, with gaps between carbonaceous grains filled with clay minerals. Such gaps are often irregularly

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distributed in the thallus, although they are sometimes regularly distributed, giving a false impression of septate structure on longitudinal filaments (Chen et al., 1994). Despite carbonization, however, the longitudinal filamentous structures are easily discernable as they are outlined by a greater concentration of carbonaceous material.

Fresh and better-preserved specimens, on the other hand, have no septate structures, and they are nearly black and hardly distinguishable in color from the matrix. Thus, it is difficult to photograph them under reflected light (Fig. 6A), but they can be easily imaged under SEM because of their higher concentration of organic carbon relative to the matrix (Fig. 6B). The longitudinal filamentous structures can be seen under both reflected light microscopy (Fig. 6C) and SEM (Fig. 6D). In transverse cross-sections perpendicular to the bedding plane, the fossils consist of homogeneous carbonaceous material with a thickness of 200–300 μm (Fig. 6J–K), and the filamentous structures are only seen as ridges (Fig. 6L), suggesting that these filamentous structures are either surface sculptures or more likely they were amalgamated during carbonization to form a homogeneous carbonaceous sheet. Honeycomb-like structures with cavities ~10 μm in size are pervasive in carbonaceous material of the fossils (Fig. 6H–I), and these likely represent oxidative molds of pyrite framboids (Wang et al., 2014; Yuan et al., 2001), suggesting that pyritization played a role in the preservation of *Flabellophyton*. It seems that a thin layer of fibrous aluminosilicate clay minerals (Fig. 6G), which are brighter than carbonaceous material in BSE-SEM images (Fig. 6D, F, J–K) and are enriched in O, Si, Al, and K (Fig. 7A–I), envelops the carbonaceous material of the fossil. This suggests that clay minerals may have also played a role in fossilization. Similar clay minerals also fill cracks within carbonaceous material of the fossil (Fig. 6M; Fig. 7J–R), but this does not necessarily rule out a constructive taphonomic role of clay minerals, particularly if the cracks were formed during early diagenesis. Taken together, the data seem to suggest that kerogenization, pyritization, and aluminosilicification may have all contributed to the preservation of *Flabellophyton* in the Lantian Formation. This mode of preservation is different from typical Burgess Shale-type (BST) preservation, where the role of pyritization is limited, but

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kerogenization and aluminosilicification are important (Butterfield, 2003; Gaines et al., 2008; Lin and Briggs, 2010). It also echoes the view that kerogenization, pyritization, and aluminosilicification are not mutually exclusive and can sometimes reinforce each other in ensuring preservation of soft tissues (Cai et al., 2012; Schiffbauer et al., 2014).

Raman spectroscopic analysis of *Flabellophyton* fossils revealed two peaks at 1365 cm^{-1} and 1594 cm^{-1} (Fig. 8A), and the thermal maturity is estimated to be around 235℃ using the Raman geothermometer developed by Kouketsu et al. (2014). This degree of thermal maturity is consistent with the amalgamation of filamentous structures of *Flabellophyton* to form a homogenized carbonaceous sheet. Organic carbon isotope analysis shows that *Flabellophyton* fossils and matrix have similar $\delta^{13}C_{org}$ values around −30‰ (VPDB; two-tailed pooled Student's t-test, p = 0.15, N = 4) (Fig. 8B). The carbon isotope data are consistent with an algal interpretation of *Flabellophyton*.

3.2.2. Specimens from the Shibantan Member

Flabellophyton from the Shibantan Member is preserved as casts/molds in limestones. It co-occurs with Ediacara-type macrofossils and trace fossils (Chen et al., 2018; Chen et al., 2013; Chen et al., 2014; Chen et al., 2019; Meyer et al., 2014; Wang et al., 2020). No preferred orientation of *Flabellophyton* has been observed in the Shibantan Member, likely because of the small number of specimens (n = 12) preserved on several bedding surfaces. Thus, the biostratinomy and paleo-environment of *Flabellophyton* in the Shibantan Member can only be inferred with the help of co-existing Ediacara-type macrofossils. One of the co-existing fossils is *Wutubus,* which is an erect benthic conotubular organism. Specimens of *Wutubus* are preferentially oriented on the bedding surface (Chen et al., 2014), suggesting a depositional and paleoecological environment with greater hydrodynamic energy than the Lantian Formation, where specimens of *Flabellophyton* are randomly oriented.

Thin sections cut parallel and perpendicular to bedding plane show that the matrix is characterized by an intercalation of microlaminated and intraclastic layers

(Fig. 9B, E). The microlaminated layers are rich in organic matter and clay minerals, as indicated by a slight enrichment in Si, Mg and Al (Fig. 9G–L). They are interpreted as microbial mats based on their similarity to crinkled microlaminae in modern and fossil stromatolites (Seong-Joo et al., 2000). The distribution of these clay minerals follows the crinkled microlaminae, suggesting that they are either detrital material trapped in microbial mats or authigenic minerals preferentially precipitating in microbial mats; it has been experimentally demonstrated that microbial activities can facilitate the formation of authigenic clays in microbial mats or biofilms (Darroch et al., 2012). The intraclastic layers, on the other hand, contains very little clay minerals or organic carbon. Instead, they mainly consist of intraclastic material, peloids, and calcitic cement. *Flabellophyton* fossils are cast by intraclasts and calcite cement (Fig. 9F), similar to the matrix intraclastic layer but with a greater amount of cement. This style of preservation clearly suggest that sediment can be introduced into the body of *Flabellophyton* through an opening (see section 3.3. "Morphological reconstruction and phylogenetic affinity"). *Flabellophyton* fossils are often associated with crinkled microlaminae (Fig. 9B, E, F), suggesting an ecological or taphonomic relationship between *Flabellophyton* and microbial mats in the Shibantan Member.

3.3. Morphological reconstruction and phylogenetic affinity

Flabellophyton specimens are preserved on the bedding surface as compressed two-dimensional remains with a fan-shaped morphology. Thus, *Flabellophyton* could have been either a fan-shaped or a conical organism when alive. Based on the following observations, we reconstruct *Flabellophyton* as an epibenthic organism with a hollow conical morphology (Fig. 4C). First, the presence of a basal holdfast indicates that *Flabellophyton* was an epibenthic marine organism (Xiao et al., 2013). Second, as *Flabellophyton* has a more or less terete stipe (Fig. 6A, J) that can be bent (Fig. 2A, E, I) but never folded, the stipe is more likely a three-dimensional terete structure. Third, a two-dimensional fan-shaped blade would have been hydrodynamically unstable as an erect epibenthic organism with a relatively simple holdfast, and would likely have been folded when buried (e.g., fig. 3.3 in Xiao et al.,

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2002). Thus, it is more likely that *Flabellophyton* was a conical rather than a fan-shaped organism when alive. Furthermore, because the distal end of the fan-shaped compressions of *Flabellophyton* can be bulged (i.e., distally convex; Fig. 2D–E, G, O–P) or hollowed (i.e., distally concave; Fig. 2H, M–N), but never flatly truncated, *Flabellophyton* was likely a conical organism with a hollow central cavity and an upper circular aperture, which can be compressed laterally or obliquely to form either a bulged or a hollowed rim. Importantly, this aperture may have allowed intraclastic sediment to infill the central cavity (Fig. 9E–F) and preserve the fossils as casts and molds. Consequently, we infer that *Flabellophyton* was an epibenthic organism with a holdfast, a differentiate stipe, a hollow conical body, and an upper aperture (Fig. 4C).

Although the phylogenetic affinity of *Flabellophyton* remains ambiguous, it was historically interpreted as an algal fossil. An algal interpretation is consistent with the presence of longitudinal filamentous structures, which are common among modern and Ediacaran benthic algae (Steiner, 1994; Xiao et al., 2002; Yuan et al., 1999). On the other hand, *Flabellophyton* resembles the conical fossil *Lantianella* from the Lantian biota, which is interpreted as a putative animal (Wan et al., 2016). The lack of an upper crown of tentacle-like structures in *Flabellophyton* may represent incomplete preservation or ontogenetic variations, but these possibilities remain to be confirmed. The open conical morphology of *Flabellophyton* is broadly similar to several conical or tubular Ediacaran fossils such as *Ausia fenestrata* (Hahn and Pflug, 1985), *Theatardis avalonensis* (Clapham et al., 2004), and *Wutubus annularis* (Chen et al., 2014), some of which have been interpreted as sponges or sponge-related animals (Antcliffe et al., 2014; Clapham et al., 2004; Erwin et al., 2011; Fedonkin, 1996; Laflamme et al., 2013). However, none of these Ediacaran fossils are constructed by filaments. Thus, the similarity in gross morphology is likely due to evolutionary convergence. At the present, it is best to regard *Flabellophyton* as an enigmatic Ediacaran genus with unknown phylogenetic affinity.

4. Discussion

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4.1. Taphonomic implications

Classical Ediacara-type taxa can be preserved in three different taphonomic windows—sandstones, black shales, and limestones (Chen et al., 2014; Grazhdankin et al., 2008; Narbonne and Aitken, 1990; Wan et al., 2014; Xiao et al., 2013; Zhu et al., 2008). However, few Ediacaran macrofossils are known to be preserved in all three taphonomic windows, and *Flabellophyton* represents a rare exception, as this genus is recovered from early Ediacaran black shales of the Lantian Formation, late Ediacaran sandstones of the Ediacara Member, and terminal Ediacaran limestones of the Shibantan Member. The new discovery of *F. typicum* from the Shibantan Member thus complements and expands the taphonomic range of this taxon and of Ediacaran macrofossils in general.

Our taphonomic analysis of *Flabellophyton* shows that multiple taphonomic pathways may have contributed to its preservation. In particular, the precipitation of authigenic minerals such as pyrite, clay minerals, calcite, and possibly silica may have contributed to the preservation of *Flabellophyton* in a certain degree of three-dimensionality. *Flabellophyton* from the Lantian Formation preserves carbonaceous remains, but pyritization and aluminosilicification apparently also facilitated fossil mineralization, allowing the preservation of rather thick carbonaceous remains (~200 μm in thickness). In the Shibantan Member, *Flabellophyton* is cast by intraclastic sediment introduced to the central cavity through the upper aperture and cemented by authigenic calcite, which allowed the preservation of *Flabellophyton* in a degree of three-dimensionality (Fig. 9B, E, F). Sealing by microbial mats above and below the fallen bodies of *Flabellophyton* may have made it possible to conserve the fine structures of longitudinal filaments, although the filaments are still poorly preserved relative to those in the Lantian Formation where they are replicated by much finer-grained clay minerals. *Flabellophyton* in the Ediacara Member is cast by sandstone (Xiao et al., 2013), and the three-dimensional preservation was likely facilitated by authigenic silica precipitation (Tarhan et al., 2016), or by authigenic pyrite precipitation in masking microbial mats (Gehling, 1999; Liu et al., 2019). This style of preservation is

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somewhat similar to the taphonomic mode of putative seaweeds in the Sonia Sandstone of the Marwar Supergroup in western India (Pandey and Sharma, 2017). To summarize, not only Ediacaran macrofossils can be preserved in multiple taphonomic modes, but multiple taphonomic pathways or processes can facilitate their preservation.

4.2 Paleoecological implications

Environmental factors such as water depth exert a strong control, through taphonomic and/or paleoecological processes, on the distribution of Ediacara-type fossils (Gehling and Droser, 2013; Grazhdankin, 2004; Muscente et al., 2017). At face value, currently available data seem to suggest that *Flabellophyton* migrated or expanded from deeper to shallower environments during the Ediacaran Period. *Flabellophyton* populations in the early Ediacaran Lantian biota lived in a relatively deep and quiet slope-basinal environment, whereas those in the upper Ediacaran assemblage of South Australia lived in a shallow littoral environment and those in the terminal Ediacaran Shibantan assemblage in a subtidal shelf environment. Because the data have limited environmental and temporal coverage, we are uncertain whether this apparent environmental shift represents an evolutionary-ecological migration, an expansion, and simply a sampling bias. However, the *Flabellophyton* data are consistent with an evolutionary-ecological shift of Ediacaran organisms from deeper to shallower environments during the middle-late Ediacaran Period (Fedonkin, 2003; Narbonne et al., 2014; Xiao, 2004), a pattern hypothesized to have been driven by the synergistic interactions between temperature-dependent oxygen supply and demand (Boag et al., 2018). Regardless, the wide geographic and environmental distribution of *Flabellophyton* points to an unusual capability of *Flabellophyton* to evolutionarily adapt to different environments.

Other environmental factors such as sediment substrates and redox conditions may have also played a role in controlling the distribution of Ediacaran macrofossils. In this regard, it is important to note that *Flabellophyton* was able to colonize muddy, sandy, and carbonate substrates, as demonstrated by fossil material from the Lantian

Formation, Ediacara Member, and Shibantan Member, respectively. Again, this wide range of substrates suggest a remarkable adaptability and versatility of the genus *Flabellophyton*. The impact of oceanic redox conditions on the distribution of *Flabellophyton* is more difficult to evaluate, because of the time averaging effect of geochemical samples and geochemical processes at the water-sediment interface (Wang et al., 2017). Nevertheless, geochemical data indicate that fossiliferous black shales in the Lantian Formation were deposited in largely anoxic but rapidly oscillating redox conditions (Guan et al., 2014; Wang et al., 2017), and the Lantian fossils including *Flabellophyton* probably lived in brief oxic episodes but were decimated and preserved in anoxic and euxinic environments (Yuan et al., 2011). The redox conditions of the Ediacara Member in South Australia are uncertain because of the lack of redox proxies applicable in sandstone facies. *Flabellophyton* in the terminal Ediacaran Shibantan Member probably also lived in an era characterized by dynamic oceanic redox conditions (Bowyer et al., 2017). Geochemical proxies (e.g., uranium isotopes) for global redox conditions indicate a global expansion of oceanic anoxia during the terminal Ediacaran Period (Tostevin et al., 2019; Wei et al., 2018; Zhang et al., 2018). However, geochemical proxies (e.g., Fe speciation data) for local redox conditions indicate strong redox variations both temporally and spatially in the terminal Ediacaran Period (Wood et al., 2015). Systematic Fe speciation data are not available from the Shibantan Member. However, preliminary and yet unpublished data indicate that the fossiliferous limestone in the Shibantan Member has extremely low Fe and Mn concentrations, suggesting locally oxic conditions.

Finally, as the most abundant and possibly a keystone taxon in the Lantian biota, *Flabellophyton* played a crucial role in the construction of epibenthic communities in early Ediacaran oceans. Specimens of *Flabellophyton* in the Lantian biota (dominated by *F. typicum* sp. nov.) are always profusely distributed on the bedding plane forming a dense fossil population (Fig. 10). Because of their similar sizes and in-situ preservation, these specimens probably represent a single cohort of individuals showing synchronous aggregate growth and sexual reproduction (Droser and Gehling, 2008; Yuan et al., 2013). Together with other erect epibenthic taxa in the Lantian

biota, including macroalgae and putative animals, these fossil populations constituted communities dominated by erect epibenthic organisms in the early Ediacaran, shortly after the Snowball Earth event. This primitive erect epibenthic ecosystem has critical ecological significance, because it replaced the sheet-like ecosystem dominated by microbial mats in a level-bottom marine environment prior to the Ediacaran Period, and formed the basis of the complex erect ecosystem after the Ediacaran Period (Butterfield, 2007). We also note that the size and hence tiering height of *Flabellophyton* increased from centimeters in the early Ediacaran Lantian biota to over a decimeter in the later Ediacara and Shibantan assemblages (Fig. 5). It would be interesting to investigate whether this size trend is representative in other Ediacaran organisms and, if yes, whether such trends are related to evolutionary migration/expansion from deeper to shallower environments or influenced by nutrient availability. As a window into Ediacaran paleoecology, *Flabellophyton* and other epibenthic Ediacaran organisms hold the promise to unlock evolutionary and ecological trends in the Ediacaran Period.

5. Conclusions

A number of Ediacara-type macro-organisms (e.g., *Arborea*, *Eoandromeda*, *Hiemalora*, *Pteridinium*, and *Rangea*) are known to have remarkable stratigraphic, environmental, ecological and taphonomic ranges, which allow comparative ecological and taphonomic analyses. Here we report a new occurrence of *Flabellophyton* from terminal Ediacaran limestones of the Shibantan Member in the Yangtze Gorges area of South China. Together with previously reported occurrences of *Flabellophyton* from early Ediacaran black shales in the Lantian Formation in South China and late Ediacaran sandstones in South Australia, the new data provide a more complete picture of the morphological, environmental, ecological, stratigraphic, and taphonomic ranges of *Flabellophyton*. *Flabellophyton* is subdivided into three morphospecies, *F. lantianense*, *F. typicum* sp. nov., and *F. obsum* sp. nov. It is reconstructed as an epibenthic organism with a holdfast, a stipe, and a hollow conical body with an upper aperture. Its phylogenetic affinity remains ambiguous, though it

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has long been interpreted as an algal fossil. *Flabellophyton* occurs in multiple taphonomic windows in black shales, sandstones, and limestones, and multiple taphonomic and fossil mineralization processes (e.g., kerogenization and authigenic precipitation of pyrite, aluminosilicates, calcite, and possibly silica) may have contributed to the different modes of preservation. The wide geographic and environmental distribution of *Flabellophyton* indicates its unusual capability of evolutionary adaptation to different environments, which may have contributed to the evolutionary and ecological migration or expansion of *Flabellophyton* from deeper to shallower oceans during the Ediacaran Period.

Acknowledgements

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Figure captions

Fig. 1. Geological maps and stratigraphic columns. (A) Simplified tectonic map of China showing the Yangtze Block (YB) in relation to North China Block (NCB), Cathaysia Block (CB), and Tarim Block (TB). (B) Geological map of the Yangtze Block showing *Flabellophyton* localities (stars) in the Lantian area (29°55'25.7" N, 118°06'0.7" E) and Yangtze Gorges area (30°47'18.9" N, 111°03'1.5" E). (C–E) Stratigraphic columns showing Ediacaran successions in the Lantian area of South China (C), Yangtze Gorges area of South China (D), and Flinders Ranges area of South Australia (E), with stars denoting *Flabellophyton* horizons. The ID-TIMS zircon U-Pb radiometric ages of 635.2 ± 0.6 Ma, 632.5 ± 0.5 Ma, and 551.1 ± 0.7 Ma are from Condon et al. (2005), the SHRIMP zircon U-Pb age of 614.0 ± 9.0 Ma is from Liu et al. (2009), and the Re-Os isochron age of 593 ± 17 Ma is from Zhu et al. (2013). Modified after Jiang et al. (2011) and Xiao et al. (2013).

Fig. 2. *Flabellophyton* from the early Ediacaran Lantian Formation of South

China. Fossils are preserved as carbonaceous compressions in Member II black shale of the Lantian Formation in southern Anhui Province, South China. (A–F) *F. lantianense*. (A) NIGP-PB22441 (field collection number12LT-4411). (B) NIGP-PB22442 (field collection number 10LT-3212). (C) NIGP-PB22443 (field collection number 12LT-4312). (D) NIGP-PB22444 (field collection number 09LT-5770). (E) NIGP-PB22445 (field collection number 11LT-8276). (F) NIGP-PB22446 (field collection number 12LT-0091). (G–J) *F. typicum* sp. nov. (G) NIGP-PB22447 (field collection number 12LT-8418), holotype. (H) NIGP-PB22448 (field collection number 17LT-7418). (I) NIGP-PB22449 (field collection number 12LT-0451). (J) NIGP-PB22450 (field collection number 10LT-3966). (K) *F. strigata* Yuan et al. 1999 NIGP-PB22451 (field collection number 15LT-8430), showing the skeletal-like body construction by longitudinal filaments and transverse bands, different from *F. typicum* that has only longitudinal filaments; (L) Magnified view of dashed rectangle in (K). (M–P) *F. obesum* sp. nov. (M) NIGP-PB22452 (field collection number 11LT-8293), holotype. (N) NIGP-PB22453 (field collection number 09LT-4647). (O) NIGP-PB22454 (field collection number 12LT-0467). (P) NIGP-PB22455 (field collection number 10LT-4815). Scale bars 5 mm. All illustrated specimens are reposited at the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Science (NIGPAS).

Fig. 3. *Flabellophyton* from the late Ediacaran Period. (A–H) *F. typicum* sp. nov. from the terminal Ediacaran Shibantan Member of the Dengying Formation in the Yangtze Gorges area, South China. Fossils are preserved as casts and molds in limestone. (A) NIGP-PB22457 (field collection number 15WH-7950). (B) NIGP-PB22458 (field collection number 14WH-5936). (C) NIGP-PB22459 (field collection number 14WH-7464). (D) NIGP-PB22460 (field collection number 14WH-7470). (E) NIGP-PB22461 (field collection number 14WH-7474). (F) NIGP-PB22462 (field collection number 14WH-7437). (G) NIGP-PB22463 (field collection number 14WH-6070). (H) NIGP-PB22464 (field collection number 14WH-8605). (I–J) *Flabellophyton* sp. from the upper Ediacaran System in South

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Australia. Fossils are preserved as casts and molds in the Ediacara Member sandstone of the Rawnsley Quartzite Formation in the Flinders Ranges area. (I) After fig. 1G in Xiao et al. (2013). (J) After fig. 1H in Xiao et al. (2013). Scale bars 10 mm. All illustrated specimens from South China are reposited at the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Science (NIGPAS).

Fig. 4. Morphological distinction among the three species of *Flabellophyton*. (A) Frequency distribution of divergence angles of 1286 specimens from the Lantian biota (Modified after Wan et al., 2013). Different shades differentiate the three species: *F. lantianense* (divergence angles 5–12 degrees), *F. typicum* sp. nov. (divergence angles 12–45 degrees), and *F. obesum* sp. nov. (divergence angles 45–60 degrees). (B) Superposition of rescaled outlines of *Flabellophyton* specimens from the Lantian Formation (black lines: 107 specimens measured in six field quadrats; red lines: 49 specimens measured in the laboratory). Modified from Wan et al. (2013). Overall three morphospecies of *Flabellophyton* can be recognized. (C) Morphological reconstruction of *F. lantianense*, *F. typicum* sp. nov., and *F. obesum* sp. nov., shown here from left to right.

Fig. 5. Cross-plot of height and maximum width of *Flabellophyton*. Different colors represent specimens from the Lantian Formation, Shibantan Member, and Ediacara Member. Data of specimens from the Lantian Formation after Wan et al. (2013).

Fig. 6. Microstructures of *Flabellophyton typicum* sp. nov. from Member Ⅱ black shale of the Lantian Formation. (A–B) Reflected light and backscattered-electron scanning electron microscopy (BSE-SEM) microphotographs of a well-preserved specimen, 11LT-1856. (C–D) Enlargements of (A–B, rectangle labeled "C" in A), showing filamentous structures. (E–F) Enlargements of (A–B, rectangle labeled "E" in A), showing enveloping clay minerals (light color in F). (G–I) Magnified views of labeled rectangles in (F), showing fibrous clay minerals (G) and molds of pyrite

framboids (H–I). (J–K) BSE-SEM microphotographs of thin sections cutting along labeled lines in (A). (L–M) Enlargements of labeled rectangles in (K). Arrows in (L) point out surface irregularity related to filamentous structures (see also C).

Fig. 7. EDS elemental maps of thin sections of a well-preserved specimen of *Flabellophyton typicum* sp. nov.. (A) BSE-SEM micrograph of labeled rectangle in Fig. 6J. (B–I) EDS elemental maps corresponding to (A). (J) BSE-SEM micrograph of labeled rectangle in Fig. 6M. (K–R) EDS elemental maps corresponding to (J). Elements are marked on upper left of elemental maps. Scale bars 50 μm.

Fig. 8. Raman spectrum and organic carbon isotope compositions of *Flabellophyton typicum* sp. nov. from Member Ⅱ black shale of the Lantian Formation. (A) A representative Raman spectrum. Thermal maturity of the carbonaceous material is estimated to be ~235 ℃ using the Raman geothermometer published by Kouketsu et al. (2014). (B) Organic carbon isotope compositions of fossil and corresponding matrix, which show no significant differences (two-tailed pooled Student's t-test, p=0.15, N=4).

Fig. 9. Microstructures and EDS elemental maps of *Flabellophyton typicum* sp. nov. from the Shibantan Member of the Dengying Formation. (A) Reflected light photograph of specimen 14WH-7884. (B) Transmitted light photomicrograph of a transverse thin section cut perpendicular to bedding surface and along labeled line in (A). White and black brackets mark, respectively, microlaminated and intraclastic layers in matrix. (C) Enlargement of labeled rectangle in (A). (D) Transmitted light photomicrograph of longitudinal section cut parallel to bedding surface and corresponding to (C). (E) Transmitted light photomicrograph of transverse thin section cut perpendicular to bedding surface and along labeled line in (A), with white and black brackets marking, respectively, microlaminated and intraclastic layers in matrix. (F) Enlargement of labeled rectangle in (E). (G) BSE-SEM micrograph of labeled rectangle in (F). (H–L) EDS elemental maps corresponding to (G).

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Fig. 10. Paleoecological reconstruction of *Flabellophyton.* (A) A slab with approximately 70 specimens of *Flabellophyton typicum* sp. nov. from the early Ediacaran Member Ⅱ black shale of the Lantian Formation, NIGP-PB22456 (field collection number 15-LT0256). The specimens were likely preserved in situ and, because of their similar sizes, they probably represent a single cohort of individuals showing synchronous aggregate growth. It is thus possible that *Flabellophyton typicum* sp. nov. was able to reproduce sexually. (B) Same as (A), but with each fossil specimen resurrected while being kept its original site, shape, and location. (C) Same as (B), but with slab removed, showing a *Flabellophyton* community on Ediacaran ocean floor.

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Declaration of interests

☒ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐ The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Highlights

- *Flabellophyton* is reported from upper Ediacaran limestone of the Shibantan Member of the Dengying Formation (551–539 Ma) in South China.

- *Flabellophyton* is the only genus that occurs in all three Ediacaran taphonomic modes.

- *Flabellophyton* is subdivided into three morphospecies, and is reconstructed as an epibenthic organism with ambiguous phylogenetic affinity.

- *Flabellophyton* indicates that multiple taphonomic pathways can facilitate the preservation of Ediacaran macrofossils.

- *Flabellophyton* helps understand the ecological migration and evolutionary expansion from deeper to shallower oceans during the Ediacaran Period.
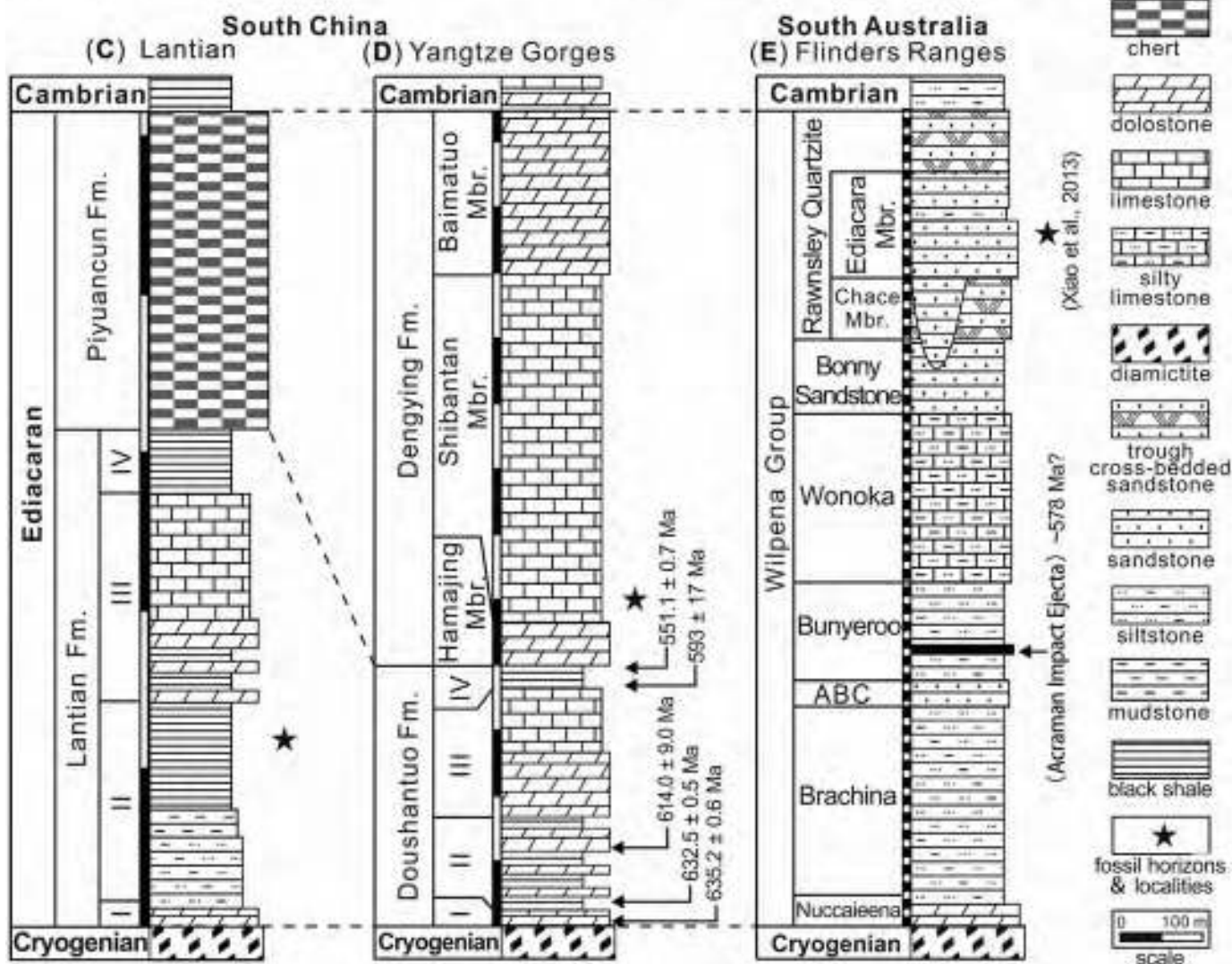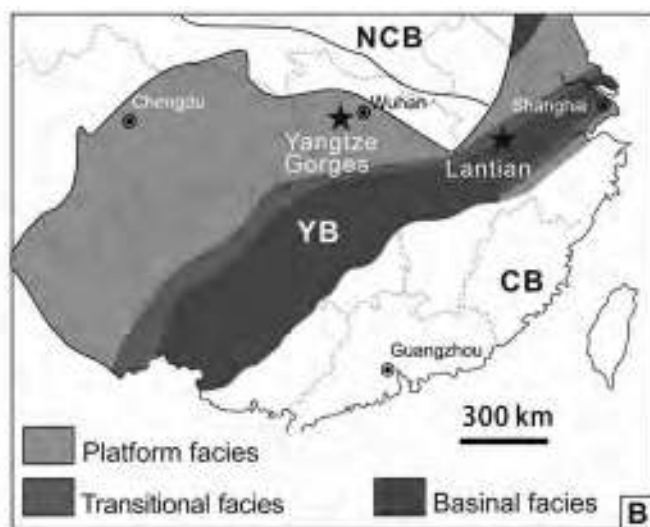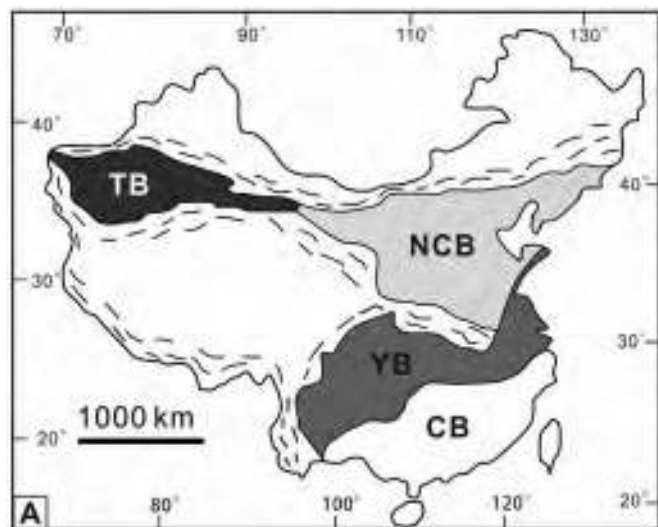
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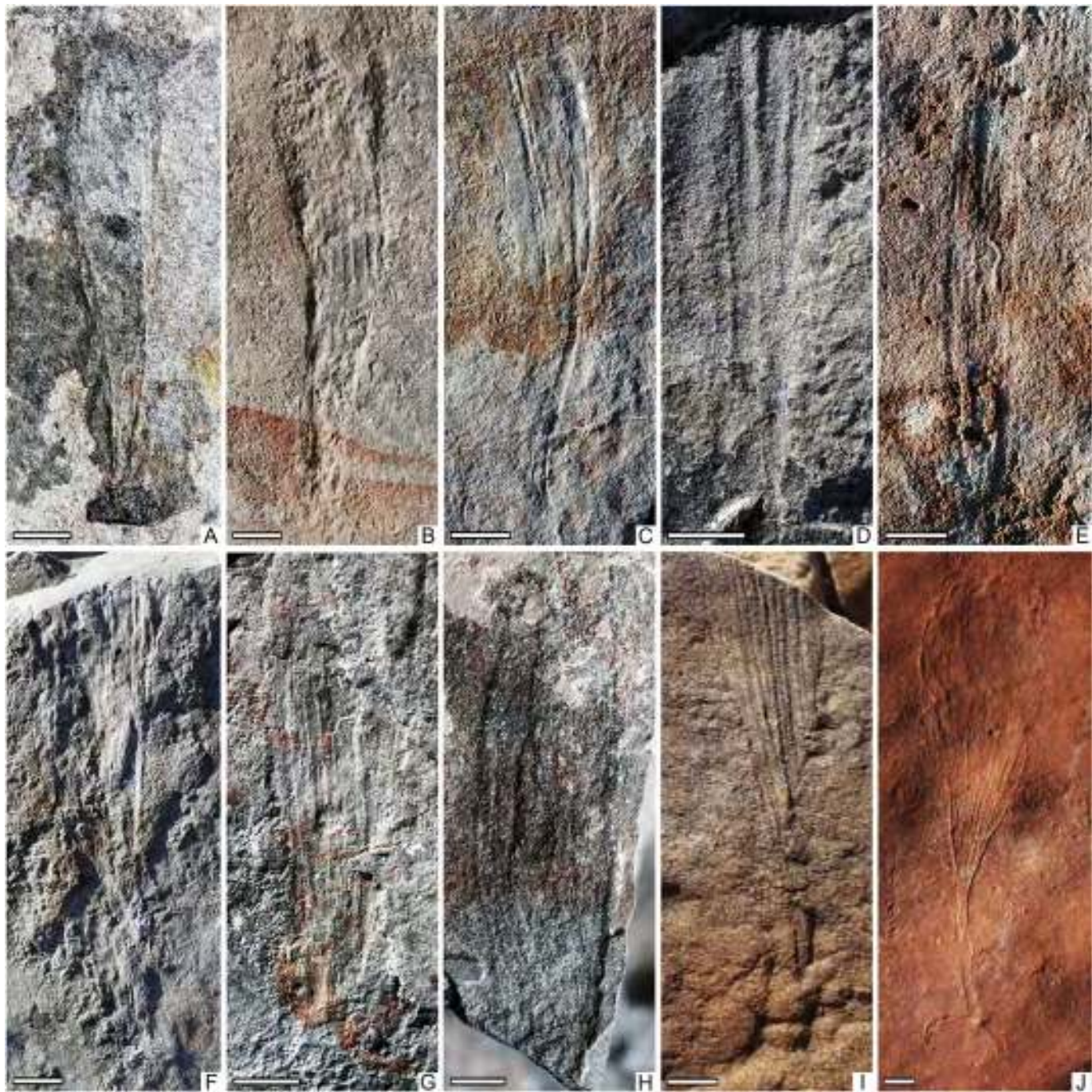
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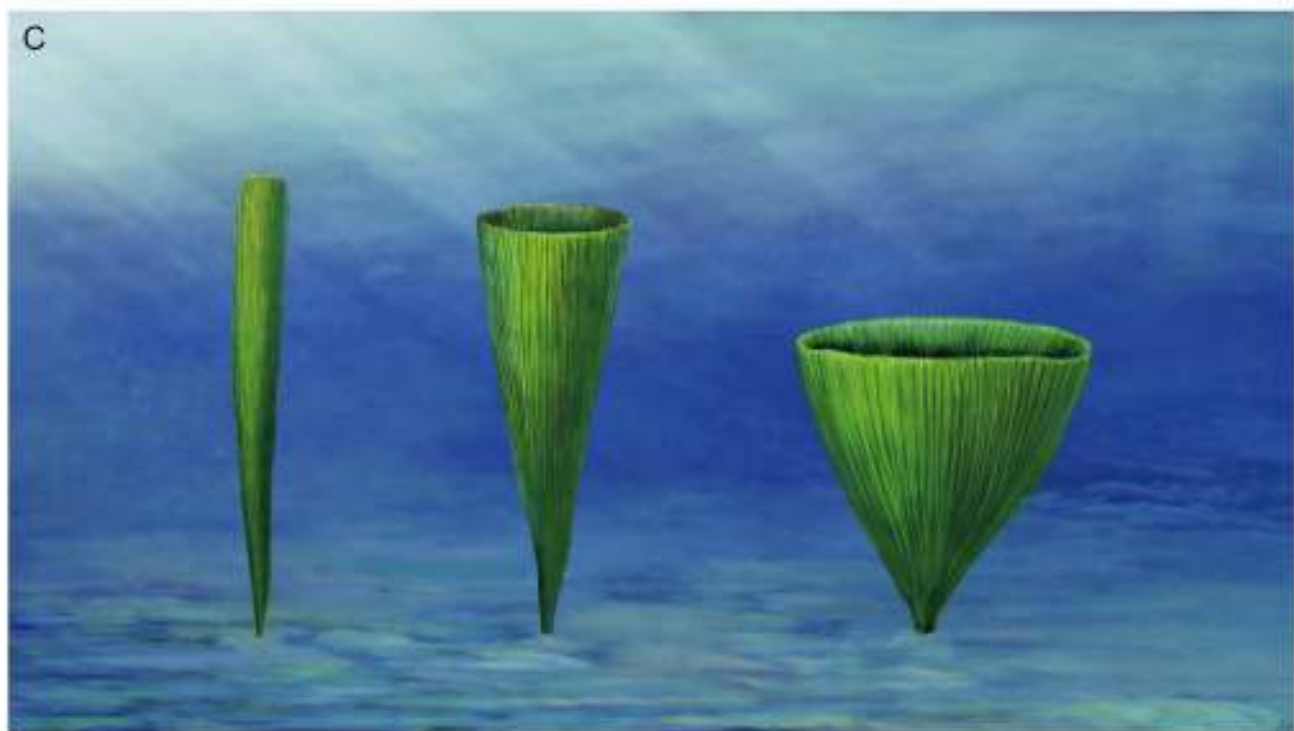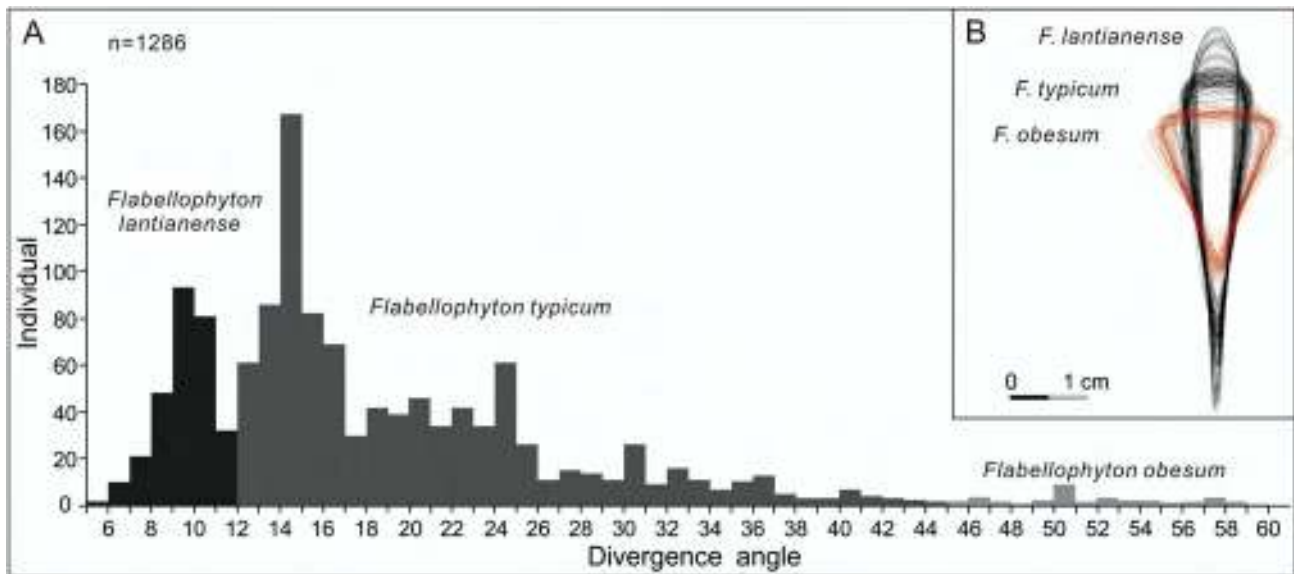
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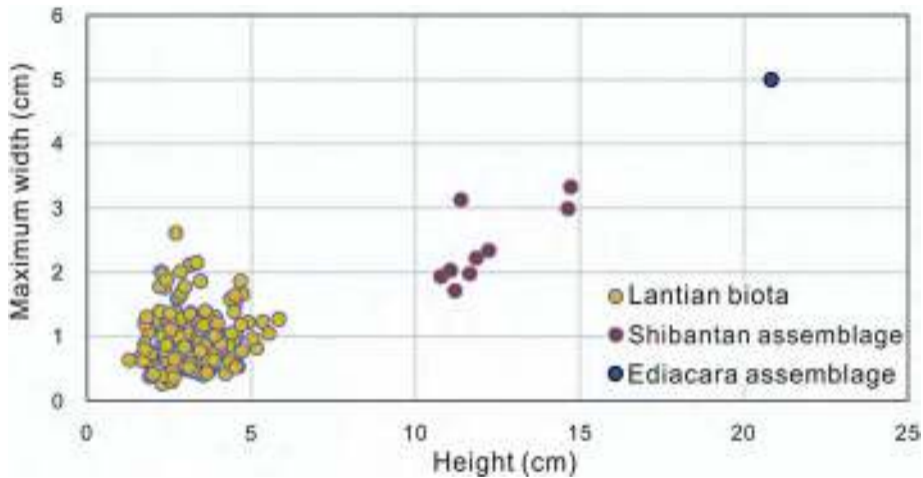
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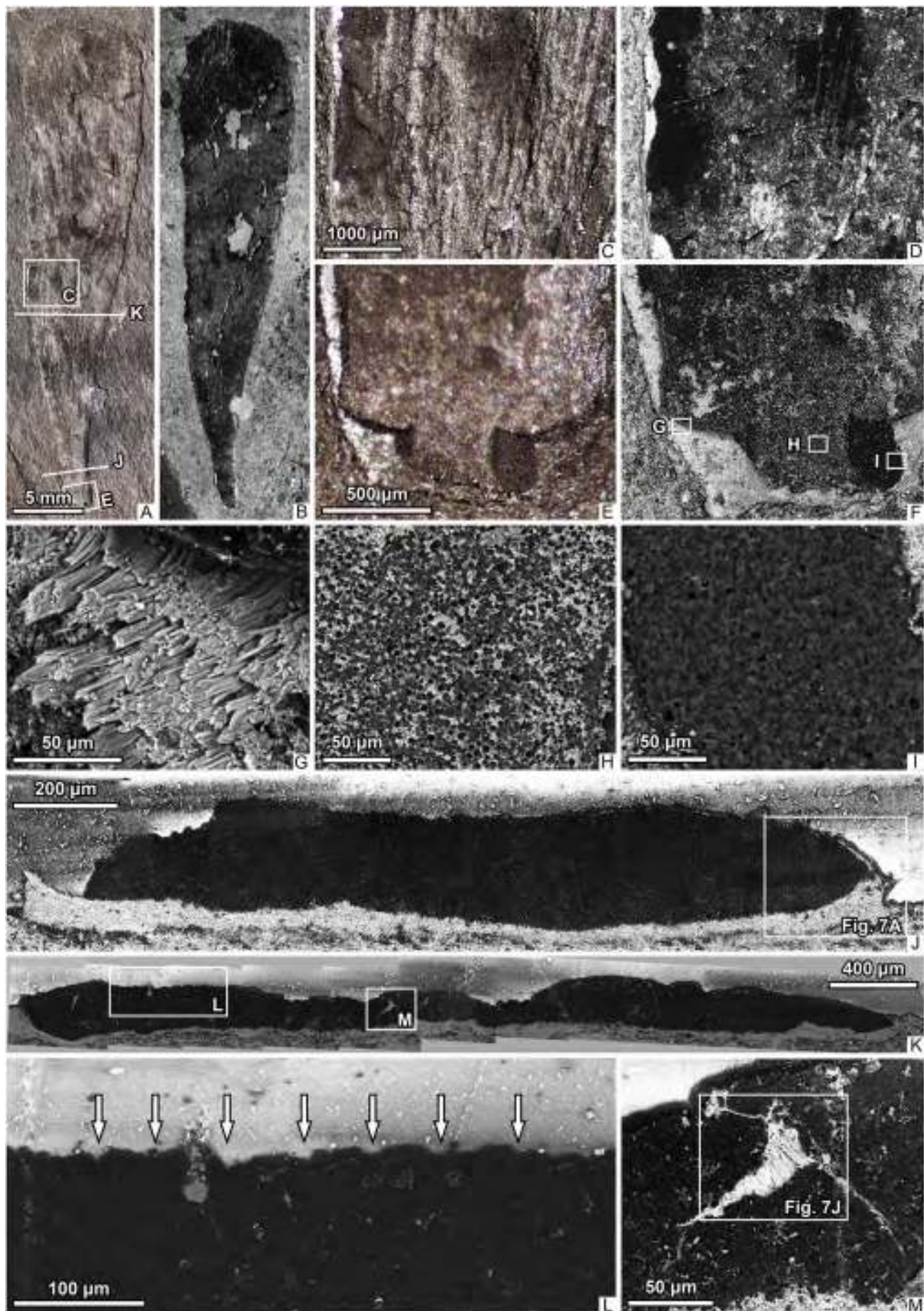
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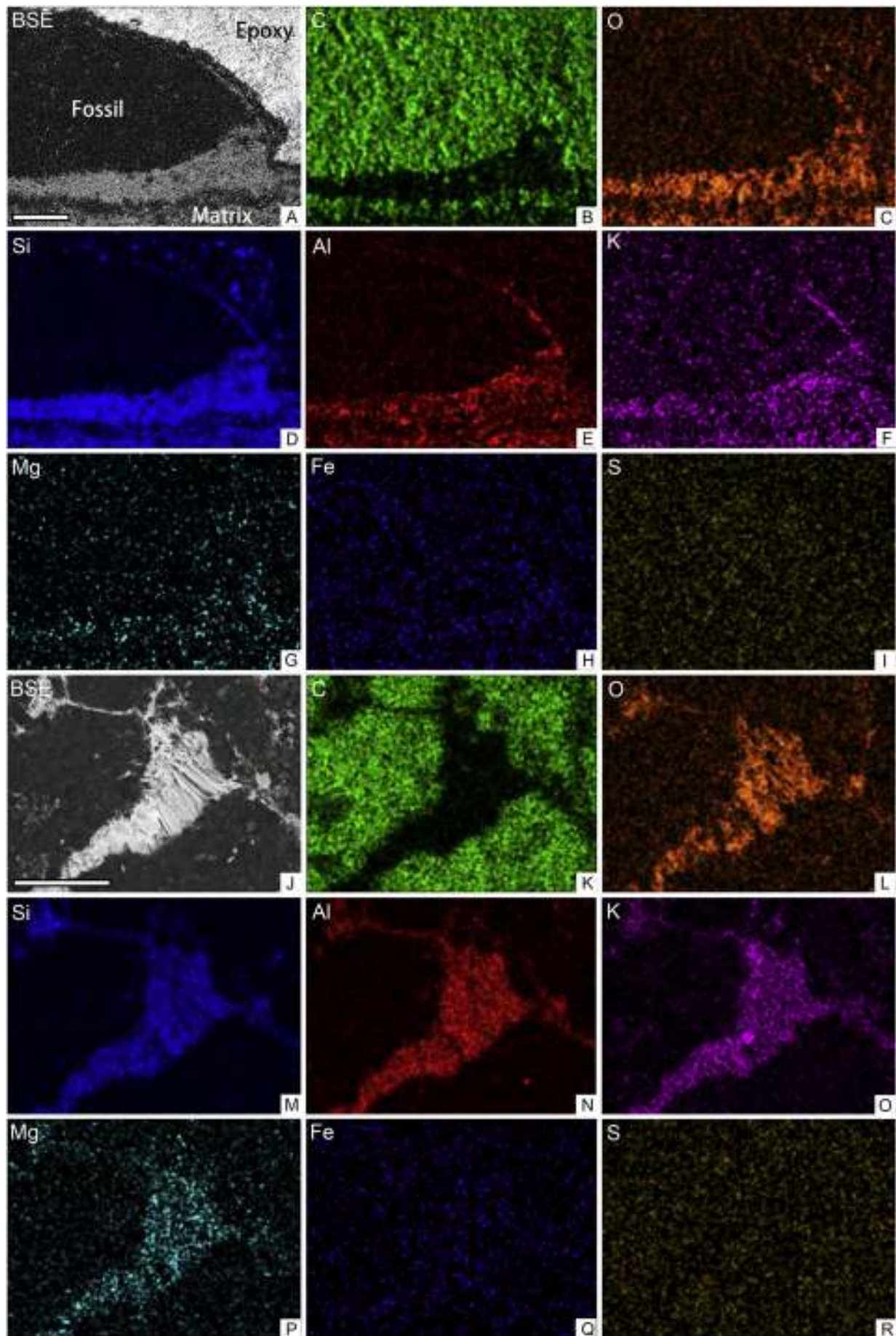
Figure 7
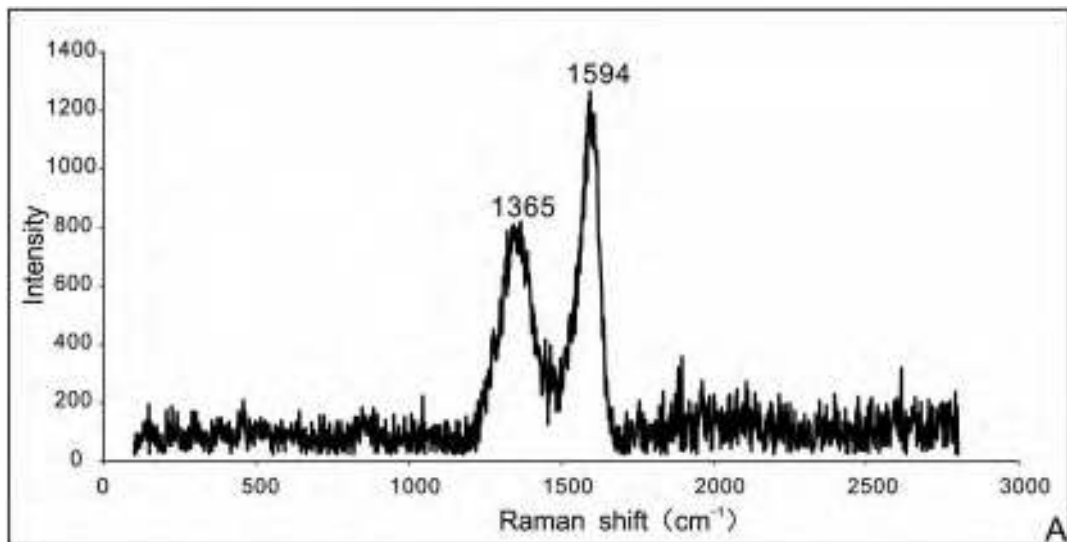
Fossil $\delta^{13}C_{org}$ (‰, VPDB)		Matrix $\delta^{13}C_{org}$ (‰, VPDB)	
LT-1-A-1	-29.9	LT-1-A-2	-30.1
LT-1-A-3	-30.3	LT-1-A-4	-30.1
LT-1-B-1	-29.7	LT-1-B-2	-30.5
LT-1-B-3	-30.1	LT-1-B-4	-31.0
Mean	-30.0	Mean	-30.4

Figure 8

Figure 9

Figure 10