The Quanjishan *Charnia* assemblage from the northern Qaidam Basin, Tibetan Plateau, and implications for palaeoecology and taphonomy of Ediacaran fronds

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Abstract

The late Ediacaran Quanjishan macrofossil assemblage of northwest China is one of the oldest fossil assemblages yet discovered in the Tibetan Plateau. It contains numerous specimens of the iconic and long-ranging soft-bodied rangeomorph *Charnia*, and the terminal Ediacaran candidate index fossil *Shaanxilithes*, preserved in siliciclastic rocks of the Zhoujieshan Formation from the Quanjishan area, northern Qaidam Basin, Tibetan Plateau. Here, we present a detailed description of *Charnia* fossils recently excavated from the Quanjishan assemblage, including specimens of *Charnia masoni* and *Charnia gracilis*, which are distinguished by the shape of their first-order branches and their divergence angle from the axial midline. Most Quanjishan *Charnia* specimens are small individuals (some are left in open nomenclature), some of which are comparable to juvenile fronds from other global Ediacaran localities, and

are interpreted here as juvenile specimens. Sedimentary characteristics suggest that the Quanjishan *Charnia* lived in marine depositional environments somewhere between shoreface and offshore transition, and under low-to-moderate energy hydrodynamic conditions, which supports the suggestion that *Charnia* preferred calmer habitats. Three-dimensional preservation exhibiting both surfaces of the frondose fossils is recognized in the Quanjishan assemblage, providing a new taphonomic window into three-dimensional preservation of Ediacaran soft-bodied organisms. The Quanjishan assemblage extends the palaeogeographic distribution of *Charnia* as well as rangeomorphs, and emphasizes that *Charnia* is one of the longest-ranging genera amongst the Ediacaran macrobiota.

Keywords: Qaidam Basin; Ediacaran; Zhoujieshan Formation; *Charnia*; fronds; rangeomorph

1. Introduction

The Ediacaran macrobiota (~574–539 Ma; ages from Linnemann et al., 2019; Matthews et al., 2021) documents a radiation of complex, largely soft-bodied, macroscopic organisms prior to the Cambrian Explosion. Although the phylogenetic placement of many Ediacaran macro-organisms remains to be determined, multiple lines of evidence suggest that several of them were metazoans (e.g. Fedonkin and Waggoner, 1997; Bobrovskiy et al., 2018; Chen et al., 2019; Dunn et al., 2021; Wang et al., 2024). These soft-bodied organisms are usually preserved as impressions beneath or within event beds (Gehling, 1999; Narbonne, 2005; O'Connell et al., 2024), and can occur as mono-specific (e.g. Zhang et al., 2022; Psarras et al., 2023) or highly diverse bedding-plane assemblages (e.g. Droser et al., 2019; Stephenson et al., 2024).

Efforts to track evolutionary transitions within the Ediacaran macrobiota draw upon global compilations of fossil occurrence data, with multivariate analyses dividing the biota into three biotic assemblages (e.g., Waggoner, 2003; Boag et al., 2016; Wu et al., 2021; Wood et al., 2023), namely the Avalon (~574–560 Ma), White Sea (~560–

550 Ma), and Nama (~550–539 Ma) assemblages (though some suggest a fourth assemblage represented by the Miaohe biota; Muscente et al., 2019). However, the extent to which various environmental, temporal, palaeolatitudinal or taphonomic controls shape these assemblages remains debated (e.g. Grazhdankin, 2004, 2014; Gehling and Droser, 2013; Laflamme et al., 2013; Boag et al., 2016; Droser et al., 2017; Muscente et al., 2019; Boddy et al., 2022; Evans et al., 2022; Darroch et al., 2023; Bowyer et al., 2024). In such analyses, taxa that occur within multiple lithologies (e.g. *Charnia*, Wu et al., 2024a), and 'intermediate' assemblages that contain representative taxa from multiple biotic assemblages (e.g. the Shibantan assemblage, Xiao et al., 2020), are particularly important, providing opportunities to test hypotheses that seek to explain Ediacaran macrofossil distributions in time and space. The newly reported Quanjishan assemblage of northwest China (Pang et al., 2021) may represent another intermediate assemblage, containing two taxa (*Charnia* and *Shaanxilithes*) that are rarely found in together in other global Ediacaran localities.

Charnia is an iconic frondose taxon assigned to the Rangeomorpha (Jenkins, 1985), and since its initial description in England (Ford, 1958), it has become one of the most extensively studied Ediacaran organisms (e.g. Ford, 1962; Glaessner and Wade, 1966; Glaessner, 1984; Laflamme et al., 2007; Antcliffe and Brasier, 2008; Dunn et al., 2018, 2019, 2021; Butterfield, 2022; Wu et al., 2024a). It has been reported from the Yangtze Gorges area (Wu et al., 2024a) and Qaidam Basin (Pang et al., 2021) of China, Charnwood Forest in the U.K. (Wilby et al., 2011), Newfoundland (Narbonne, 2004; Laflamme et al., 2007; Hofmann et al., 2008; Liu et al., 2012; Dunn et al., 2019; Matthews et al., 2021) and the Mackenzie Mountains (Narbonne et al., 2014) of Canada, north-central Siberia (Grazhdankin et al., 2008) and the White Sea region (Martin et al., 2000; Grazhdankin, 2003) of Russia, and South Australia (Gehling and Droser, 2013), in addition to a possible occurrence from Ukraine (Grytsenko, 2016). This global distribution across deep- and shallow-marine facies, spanning around 25 million years from beds ~575 Ma in Newfoundland (Liu et al., 2012; Matthews et al., 2021) to <550 Ma in the Shibantan Member of South China (Condon et al., 2005; Yang et al., 2021;

Wu et al., 2024a), makes *Charnia* one of the longest-ranging and most cosmopolitan Ediacaran taxa, and a key taxon of interest when considering controls on Ediacaran taxonomic distributions and diversity. As one of the earliest known representatives of the Ediacaran biota (Matthews et al., 2021), *Charnia* also holds significant importance in elucidating the phylogeny and developmental patterns of rangeomorphs. The phylogenetic affinities, feeding strategy, systematics, and lifestyle of *Charnia* are long debated (refer to summary in Wu et al., 2024a), but researchers are gravitating towards a general consensus that *Charnia* is a total-group metazoan (Xiao and Laflamme, 2009; Budd and Jensen, 2017; Darroch et al., 2018) or eumetazoan (Dunn et al., 2018, 2021; Butterfield, 2022; Runnegar, 2022). Feeding may have been via filter-feeding or osmotrophy (see discussions in Laflamme et al., 2009; Liu et al., 2015; Butterfield, 2022), and although most studies consider it to have been tethered to the seafloor and standing upright in the water column (e.g., Laflamme et al., 2007; Narbonne et al., 2014; Wilby et al., 2015; Droser et al., 2017), some workers favor a non-erect lifestyle (e.g., Grazhdankin, 2004; McIlroy et al., 2021). There is evidence to suggest that at least some charniid reproductive cycles involved stolon formation (Liu and Dunn, 2020; Delahooke et al., 2024).

Charnia fossils preserved in siliciclastic rocks of the Zhoujieshan Formation from the Quanjishan area, northern Qaidam Basin, Tibetan Plateau, Northwest China (Fig. 1A, B) were first reported by Pang et al. (2021), who provided only a brief description based on a limited number of specimens. A selection of these specimens was subsequently mentioned in Wu et al., (2024b). Here we describe 69 *Charnia* specimens recently collected from multiple horizons at this locality, including examples of both *Charnia masoni* and *Charnia gracilis*, and offer detailed systematic descriptions as well as palaeoecological and taphonomic analyses of these fossils. The depositional facies containing the Quanjishan *Charnia* are also assessed. The co-occurrence of *Shaanxilithes* (a candidate index fossil of the terminal Ediacaran, see Hua et al., 2004; Hua et al., 2020; Chai et al., 2021) and *Charnia* in the Quanjishan assemblage demonstrates that *Charnia* is likely to have persisted into the latest Ediacaran.

2. Geological setting

There are several microcontinents between the Tarim and North China paleocontinents, e.g., the Alxa massif, Central Qilian terrane, Olongbuluke terrane, and Qaidam Block (Lu et al., 2002, 2008; Sun et al., 2020; Fig. 1A, B). The Olongbuluke terrane (also known as the Quanji massif) is geographically located in the northern margin of the Qaidam Basin, Tibetan Plateau, and to the east of the Tarim Block and the west of the North China Craton (Fig. 1A, B). The Olongbuluke terrane is mainly composed of a medium to high grade metamorphosed crystalline basement which could date back to the Archean-Paleoproterozoic Era, and overlying unmetamorphosed sedimentary succession among which preserves a discontinuous sedimentary record of the Proterozoic spanning more than 1 billion years (Sun et al., 2022; Wu et al., 2024). Previous studies also indicated that the Olongbuluke terrane has recorded the history of the assembly and breakup processes of the Columbia and the Rodinia supercontinents (Gong et al., 2012; Chen et al., 2013; Yu et al., 2017; Sun et al., 2019; Sun et al., 2022).

The metamorphic crystalline basement of the Olongbuluke terrane is formed at ~2.46–1.80 Ga, and in ascending order is composed of the Delingha complex (~2.46–2.37 Ga), the Dakendaban Group (~2.32–1.90 Ga), and the Mesoproterozoic Wandonggou Group (Lu et al., 2002; Gong et al., 2012; Chen et al., 2013). The Delingha complex is a set of metamorphic deformed granite containing enclaves of amphibolite and mafic granulite (Lu et al., 2008; Gong et al., 2012; Zhang et al., 2014). The Dakendaban Group contains a set of migmatitic granite, and can be further divided into the lower Dakendaban Group (a set of amphibolite-facies volcano-sedimentary units formed during ~2.32–2.24 Ga, Chen et al., 2012) and the upper Dakendaban Group (the khondalite-like supracrustal rocks formed during ~2.2–1.9 Ga, Chen et al., 2013; Zhang et al., 2014; Sun et al., 2019). The Wandonggou Group is a set of low graded metamorphosed volcanic–sedimentary rocks (Gong et al., 2012).

The Proterozoic sedimentary strata, which were developed on the metamorphic crystalline basement with an angular unconformity, are mainly distributed in the

Quanjishan, Shihuigou, and Olongbuluke areas in the northern margin of the Qaidam Basin. The newly defined Quanji Group (containing the Mahuanggou, Kubaimu, Shiyingliang and Hongzaoshan formations) mainly comprises conglomerates and sandstones in the lower part, and dolostones in the upper part (Sun et al., 2019; Sun et al., 2022; Wu et al., 2024b). The Quanji Group was deposited between ~1780 Ma and ~1600 Ma, corresponding to the late Paleoproterozoic, constrained by U-Pb ages of detrial zircons from the basal Quanji Group and volcanic rocks from the lower Hongzaoshan Formation (Zhang et al., 2016; Sun et al., 2019; Sun et al., 2022). The Heitupo Formation, unconformably overlying the Hongzaoshan Formation, is mainly composed of greenish-gray mudstones. The depositional age of the Heitupo Formation is less than 751 Ma, constrained by detrial zircon U-Pb age, but whether it is Tonian in age remains to be further confirmed (Sun et al., 2022).

Ediacaran sedimentary rocks in the Olongbuluke terrane are exposed at the Quanjishan and Shihuigou areas (Fig. 1C), and comprise the Hongtiegou and Zhoujieshan formations (Fig. 2) (Sun et al., 2022; Wu et al., 2024b). The Hongtiegou Formation is composed of yellowish-green, purple-grey, to greenish-grey massive and stratified diamictites (Fig. 2). Common dropstones and striated clasts imply a glaciogenic origin for the Hongtiegou Formation (Ma et al., 2019). The Zhoujieshan Formation is the youngest Neoproterozoic stratigraphic unit in the Olongbuluke terrane, conformably overlying the Hongtiegou Formation and disconformably underlying the Cambrian Olongbuluke Group. The Zhoujieshan Formation is about 57 m in thickness in the Quanjishan area, and consists of a ca. 7 m thick cap dolostone unit at the base, followed by ca. 50 m of siliciclastic rocks (Fig. 3A, B, C, G). The cap dolostone unit comprises basal massive, pebble-bearing dolostones, which gradually transitions to pebble-free, thick–medium bedded dolostones (Fig. 2; Shen et al., 2010; Sun et al., 2022). The siliciclastic and dolomitic clasts in the lower part of the cap dolostone unit are interpreted to be either debris falling from ice rafts during the deglacial period, or products of transgressive reworking of the underlying unlithified diamictites of the Hongtiegou Formation, indicating a continuous transition between these two units (Sun

et al., 2022; Wu et al., 2024b).

The siliciclastic part of the Zhoujieshan Formation begins with a layer of thin-bedded, yellowish-green siltstones of less than 1 m in thickness, and is followed by ~49 m of red, thin, parallel- to cross-laminated fossiliferous silty feldspathic and quartz-rich fine sandstones and interbedded siltstones (Fig. 3A–G). *Charnia* occurs in the lower siliciclastic portion of this sedimentary package, ranging between ~5 m and ~20 m above the cap dolostone unit, while *Shaanxilithes* occurs throughout the entire siliciclastic portion of the Zhoujieshan Formation (Fig. 2; Pang et al., 2021). The compositional maturity of *Charnia*-bearing fossiliferous beds is low, whereas textural maturity is high (Fig. 3F). Outcrop planar cross bedding (Fig. 3A, B) and parallel bedding (Fig. 3C, G), semi-centimeter-scaled planar cross lamination in thin section (Fig. 3D–F), parallel lamination in thin section (Fig. 3D–E), low-angled truncation of laminae (Fig. 3E), as well as possible microbially induced sedimentary structures (Fig. 3H, I), also appear in the lower siliciclastic beds of the Zhoujieshan Formation. Less rounded grains in the sediment (Fig. 3F) suggest that these grains have experienced limited influence from wave activity. These lines of lithological evidence (fine sandstones and siltstones with poor roundness) and sedimentary structures (parallel to low-angle cross bedding, and a lack of clear wave ripples) are consistent with multidirectional to unidirectional flow, and we infer that the Zhoujieshan Formation was deposited somewhere between lower shoreface and the offshore transition, where hydrodynamic conditions are typically moderate to low, with occasional influxes of higher energy sediment from storm events.

Specimens were mostly collected from ~5–11 m above the cap dolostone unit of the Zhoujieshan Formation (Fig. 2) at Quanjishan section A (37°25′55.2″N, 95°48′0.2″E), Qaidam Basin (Fig. 1C). Although the precise geochronological age of the Zhoujieshan Formation is lacking, it can be roughly constrained to between ca. 550 Ma and 539 Ma by the common presence of *Shaanxilithes*, which has been considered to be a candidate index fossil for the terminal Ediacaran (Hua et al., 2004, 2020; Chai et al., 2021), both above and below the *Charnia*-bearing horizons. As a result, the

Zhoujieshan Formation and the seemingly conformable underlying Hongtiegou Formation are likely to be late Ediacaran in age. The Hongtiegou Formation thus likely represents late Ediacaran glacial deposition (Pang et al., 2021), correlative with the nearby Luoquan and Zhengmuguan glacial deposits (Le Heron et al., 2018; Wu et al., 2024c), occurring after the ~580 Ma Gaskiers glaciation (Pu et al., 2016), and potentially being related to the 'Great Ediacaran Glaciation' (sensu Wang et al., 2023; though see also Niu et al., 2024).

3. Materials and methods

A total of 69 collected specimens from the Zhoujieshan Formation are identified as *Charnia*. Among them, 36 specimens preserve at least two sets of clear and well-preserved first-order branches that can be measured. Other specimens are too poorly or incompletely preserved to generate effective measurements. 21 specimens preserve a clear and complete petalodium (Figs. 4, 5). A Nikon D810 digital camera was used to photograph all specimens. Measurements of measurable specimens (Table 1) were obtained from photographs using *FIJI* software (Schindelin et al., 2012). Cross plots were produced using *PAST* version 4.03 software (Hammer et al., 2001) to assess body size and growth stage (Fig. 6). The specimens (Figs. 4, 5, 7, 8) are accessioned in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (NIGPAS), with NIGPAS museum catalog numbers (prefix NIGP-), as stated below for each specimen.

4. Results

Two species of the genus *Charnia*, including twenty specimens of the type species *C. masoni* Ford, 1958, emended Wu et al., 2024a (Figs. 4C, 5D) and twelve specimens of *C. gracilis* Wu et al., 2024a (Fig. 4), are here recognized from the Quanjishan assemblage. Differentiation between these two species is primarily based on quantitative characteristics of the first-order branches (Fig. 6A), including mean

divergence angle and the parameter X (defined as | (a − b)/ (a + b) |, where “a” and “b” represent the angles between the diagonal line and borderlines at the distal end of first-order branches; sensu Wu et al., 2024a), which can effectively distinguish between sigmoidal and straight morphologies. The 37 remaining specimens are referred to the genus *Charnia* (e.g. Figs. 5A–C, 7, 8) based on their overall frondose shapes, alternating first-order branching, and the absence of a central stalk. Nevertheless, they are either too small (e.g. Fig. 5B), incomplete (e.g. Fig. 8C) or poorly preserved (e.g. Fig. 7), to permit confident identification to species level, and so we refer to them as *Charnia* sp. Among these specimens, there are a small number of tiny *Charnia* fronds (Fig. 5) that possess petalodia that are 10.1–13.4 mm in total length (mean = 11.6 mm; n = 5) and 3.9–8.8 mm in width (mean = 5.7 mm; n = 7), with usually 4–5 first-order branches per row. For comparison, the petalodia of the remaining specimens with complete petalodia are 20.0–123.4 mm in length (mean = 46.8 mm; n = 16) and 4.7–18.6 mm in width (mean = 11.5 mm; n = 16). The number of first-order branches for these larger specimens with a complete petalodium is usually 6–8 per row (Fig. 6D).

The Quanjishan *Charnia* specimens are typically preserved as two-dimensional positive hyporelief or negative epirelief casts, with only one side of the petalodium preserved (e.g. Figs. 4, 5). Preserved holdfasts (if present) are often preserved in opposite relief to their associated petalodium (e.g. Figs. 4A–B; 5C–D), but there are also exceptions where holdfast and petalodium are preserved in the same relief (e.g. Fig. 4D). Fronds of all *Charnia* species are often oriented in a similar direction when they occur together on individual slabs (Figs. 4C–D, 5A–B). A particular specimen of *Charnia* sp. also displays a raised petalodium margin with higher topographic relief relative to the middle portion of the specimen (Fig. 7). Furthermore, one *Charnia* sp. specimen, which exhibits a fracture across the middle of petalodium, presents both positive and negative reliefs on two different but adjacent laminae (Fig. 8A–B), indicating preservation of a three-dimensional cast and mold (i.e., full relief or endorelief), with both sides of the frond preserved and a sediment infill. Two other specimens of *Charnia* on a separate bedding plane are preserved in opposite reliefs (Fig.

4C), with a *C. gracilis* specimen (lower left) preserved as positive hyporelief and a *C. masoni* specimen (upper right) as negative hyporelief, adding further support to the presence of full relief preservation within the assemblage.

5. Systematic Palaeontology

Genus *Charnia* Ford, 1958, emended Dunn et al., 2019

Type species: *Charnia masoni* Ford, 1958

Diagnosis: As per Dunn et al., 2019

Remarks: Since *Charnia grandis* Glaessner & Wade, 1966 has been considered as a synonym of *Charnia masoni* (Wilby et al., 2011; Brasier et al., 2012), and *Charnia wardi* Narbonne & Gehling, 2003 and *Charnia antecedens* Laflamme et al., 2007 were reassigned to *Trepassia* Narbonne et al., 2009 and *Vinlandia* Brasier et al., 2012, respectively, *C. masoni* was regarded as the only species of the *Charnia* genus for a decade. Recently, a new species *Charnia gracilis* Wu et al., 2024a, was erected based on specimens from the Shibantan Member of South China, differing from the type species *C. masoni* in its slender, straighter, and lower-angled first-order branches. Such a taxonomic treatment is further supported by morphological measurements of *Charnia* specimens from the Quanjishan assemblage herein (Table 1; Fig. 6A), for example measurements of mean divergence angle of first-order branches ($> 20°$ for *C. masoni* and $\leq 20°$ for *C. gracilis*) and the parameter X (≥ 0.3 for *C. masoni*, and $0 \leq X < 0.3$ for *C. gracilis*). In addition, *C. gracilis* has a larger L/W (length/width) ratio for its longest first-order branches (mean = 6.0, n = 7) than *C. masoni* (mean = 4.7, n = 13; Fig. 6C), suggesting that *C. gracilis* possessed more slender first-order branches than *C. masoni*.

Charnia masoni Ford, 1958, emended Wu et al., 2024a

Figures 4C (partim), 5D

1958 *Charnia masoni* Ford, pp. 212–213, pl. 13, fig. 1.

?1959 *Charnia* sp.; Glaessner, p. 1472, text-fig. 1b.

?1959 *Rangea*?; Glaessner, in Glaessner & Daily, pp. 387–388, pl 46, fig. 2.

1961 *Charnia* sp.; Glaessner, p. 75, text-fig.

1962 *Charnia* sp.; Glaessner, pp. 484–485, pl. 1, fig. 4 (non fig. 5).

1962 *Charnia masoni*; Ford, fig. 4 (non fig. 5).

1966 *Rangea grandis*; Glaessner & Wade, p. 616, pl. 100, fig. 5.

1973 *Glaessnerina grandis*; Germs, p. 5, fig. 1D.

1976 *Charnia* ex gr. *masoni*; Sokolov, p. 141, text-fig.

1977 *Charnia* ex gr. *masoni*; Sokolov, p. 441.

1978 *Charnia* sp.; Fedonkin, fig. 3 (9).

1979 *Charnia masoni*; Glaessner, p. A99, fig. 12 (3).

1981a *Charnia masoni*; Fedonkin, p. 66, pl. 3, figs. 5, 6; pl. 29, fig. 1.

1981a *Zolotytsia biserialis*; Fedonkin, pp. 67–68, pl. 3, fig. 7.

1981b *Charnia masoni*; Fedonkin, p. 100.

1981 *Charnia masoni*; Sokolov & Brekhovskikh, p. 3, text-fig.

1981 *Glaessnerina grandis*; Glaessner & Walter, fig. 6.11C.

1983a *Charnia masoni*; Fedonkin, pl. 1, fig. 1.

1983b *Charnia masoni*; Fedonkin, fig. 37.

1983 *Charnia masoni*; Sokolov & Fedonkin, p. 13, fig. 9.

1984 *Charnia masoni*; Sokolov, p. 6, text-fig.

1984 *Charnia masoni*; Sokolov & Fedonkin, fig. 3f.

1984 *Charnia* cf. *C. masoni*; Glaessner, fig. 2.21B.

1984 *Charnia masoni*; Glaessner, fig. 2.21A.

1984 *Glaessnerina grandis*; Glaessner, fig. 2.21C.

1985 *Charnia masoni*; Fedonkin, p. 99, pl. 12, fig. 4; pl. 13, figs. 2–4.

1985 *Charnia* cf. *C. masoni*; Jenkins, fig. 7C.

1985 *Charnia masoni*; Jenkins, fig. 7B.

1987 *Charnia masoni*; Fedonkin, pl. 15.

1987 *Glaessnerina grandis*; Preiss, fig. E.

1990 *Charnia masoni*; Fedonkin, p. 110, pl. 12, fig. 4; pl. 13, figs. 2–4.

1992 *Charnia masoni*; Fedonkin, figs. 28–30.

1992 *Charnia masoni*; Runnegar & Fedonkin, figs. 7.5.5A, 7.5.10A.

1994 *Charnia masoni*; Fedonkin, fig. 2A, B.

1995 *Charnia grandis*; Boynton & Ford, p. 168, fig. 1.

1996 *Glaessnerina grandis*; Jenkins, p. 35, fig. 4.1.

1997 *Charnia masoni*; Grazhdankin & Bronnikov, fig. 2a, d.

1999 *Charnia grandis*; Ford, p. 231, figs. 1, 3.

2000 *Charnia*; Martin et al., fig. 4A.

2004 *Charnia*; Grazhdankin, fig. 2.

2005 *Charnia masoni*; Narbonne et al., figs. 2b, 3g.

2005 *Charnia*; Grazhdankin et al., fig. 3d.

2007 *Charnia masoni*; Laflamme et al., pp. 252–253, fig. 4A–J.

2007 *Charnia* cf. *masoni*; Fedonkin et al., fig. 276 (partim).

2007 *Charnia* cf. *masoni*; Fedonkin et al., figs. 304, 314 (partim).

2007 *Charnia masoni*; Fedonkin et al., p. 265, fig. 354.

2008 *Charnia masoni*; Hofmann et al., p. 16, fig. 13.1, 13.2.

2008 *Charnia grandis*?; Hofmann et al., pp. 16–18, fig. 14.

2009 *Charnia masoni*; Bamforth & Narbonne, fig. 7.5.

2011 *Charnia masoni*; Wilby et al., figs. 2A, 3A.

2011 *Charnia masoni*; Grazhdankin, fig. 3a–d.

2012 *Charnia masoni*; Liu et al., figs. 4b, 5a.

2012 *Charnia* aff. *masoni*; Liu et al., fig. 4a.

2013 *Charnia* aff. *masoni*; Liu et al., fig. 1d.

2013 *Charnia masoni*; Liu et al., fig. 2a–d.

2013 *Charnia* sp.; Gehling & Droser, fig. 2Q.

2014 *Charnia* cf *masoni*; Narbonne et al., pp. 215, 216, fig. 5.1–5.4.

2015 *Charnia masoni*; Noble et al., fig. 4A, G.

2015 *Charnia masoni*; Wilby et al., fig. 5.

2015 *Charnia masoni*; Liu et al., fig. 2D.

2016 *Charnia masoni*; Liu et al., fig. 3D.

2017 *Charnia masoni*; Antcliffe et al., fig. 4E.

2018 *Charnia masoni*; Dunn et al., figs. 1E, 3.

2018 *Charnia masoni*; Kenchington et al., figs. 1A, D, 7E (partim).

2019 *Charnia masoni*; Dunn et al., pp. 16–17, figs. 1–3, 5–8, 10.

2020 *Charnia masoni*; Liu & Dunn, fig. 4d.

2020 *Charnia masoni*; McIlroy et al., fig. 10f.

2021 *Charnia masoni*; Matthews et al., fig. 2B.

2021 *Charnia masoni*; McIlroy et al., fig. 1b.

2021 *Charnia masoni*; Pang et al., figs. 3A–3C, S2A–S2E.

2021 *Charnia masoni*; Dunn et al., figs. 1 (A-2), S1–S2.

2022 *Charnia masoni*; Butterfield, figs. 1a, 2.

2022 *Charnia masoni*; Mussini and Dunn, fig. 1A.

2023 *Charnia masoni*; Pasinetti and McIlroy, fig. 3C.

2024a *Charnia masoni*; Wu et al., fig. 2.1.

Holotype: LEIUG 2328, from Bed B (Wilby et al., 2011), North Quarry, Charnwood Forest, UK.

Materials: Twenty specimens from the Zhoujieshan Formation at Quanjishan section A (Fig. 1C).

Diagnosis: As Wu et al. (2024a).

Description: Quanjishan specimens are characterized by a centimeter to decimeter-scale uniterminal bifoliate frond, which comprises a typically incompletely preserved petalodium with first-order branches alternately arranged along the two sides, forming a zig-zag central axis (Figs. 4C, 5D). The complete preserved petalodia are 10.9–85.7 mm in length (mean = 35.3 mm, n = 9) and 6.0–17.9 mm in width (mean = 10.1 mm, n = 10) and consist of 4–8 first-order branches per row. The longest first-order branch in each measurable specimen is 5.1–29.0 mm (mean = 15.1 mm, n = 20) in length and 1.2–5.9 mm in width (mean = 3.2 mm, n = 20), with a L/W ratio ranging

from 3.3–6.5 (mean = 4.7, n = 20). First-order branches are highly constrained and sigmoidal in shape, with a mean divergence angle of 27.7° (n = 20). The first-order branches consist of approximately a dozen second-order branches, arranged in parallel and forming near-rectangular shapes (Figs. 4C, 5D). Third-order branches are rarely observed. One tiny *C. masoni* specimen in our collection preserves a basal discoidal structure (Fig. 5D), although its stem is not distinct.

Occurrence: Zhoujieshan Formation, Quanjishan area, Northwest China (Pang et al., 2021); Shibantan Member, Dengying Formation, Yangtze Gorges area, South China (Xiao et al., 2020; Wu et al., 2024a); Bradgate Formation, Charnian Supergroup, Charnwood Forest, UK (Wilby et al., 2011); Conception and St. John's groups, Newfoundland, Canada (Narbonne, 2004; Laflamme et al., 2007; Hofmann et al., 2008; Liu et al., 2012; Dunn et al., 2019; Matthews et al., 2021); Nadaleen Formation (previously known as "June Beds", Moynihan et al., 2019), Mackenzie Mountains, northwestern Canada (Narbonne et al., 2014); Khatyspyt Formation, Olenek Uplift, north-central Siberia, Russia (Grazhdankin et al., 2008); Verkhovka Formation, White Sea region, Russia (Martin et al., 2000); Rawnsley Quartzite, Flinders Ranges, South Australia (Gehling and Droser, 2013).

Remarks: *Charnia masoni* from the Zhoujieshan Formation was first reported by Pang et al. (2021). The specimens herein are classified in the genus *Charnia* based on their constrained and alternately arranged first-order branches, as well as their single-sided (*sensu* Narbonne et al., 2009) rangeomorph units. Due to incomplete preservation of the specimens, further morphological measurements and verification of their developmental patterns are not possible. However, these specimens are mainly identified as *C. masoni* based on the morphology of their first-order branches, which possess moderate divergence angles and sigmoidal shapes (Fig. 6), as described by Wu et al (2024a).

Charnia gracilis Wu et al., 2024a

Figure 4A–B, C (partim), D (partim)

?1972a *Rangea sibirica*; Sokolov, p. 50.

?1972b *Rangea sibirica*; Sokolov, pl. I, fig. 3.

?1979 *Glaessnerina sibirica*; Glaessner, p. A99, fig. 12 (1).

?1984 *Glaessnerina sibirica*; Glaessner, fig. 2.21D.

?1998 *Charnia masoni*; Nedin & Jenkins, p. 315, fig. 1.

2007 *Charnia* sp.; Fedonkin et al., fig. 232 (partim).

2008 *Charnia masoni*; Grazhdankin et al., fig. 2A.

2014 *Charnia masoni*; Grazhdankin, fig. 2.3.

2020 *Charnia* sp.; Xiao et al., fig. 4f.

?2024 *Charnia* cf. *gracilis*; McKean et al., fig. 12a.

2024a *Charnia gracilis*; Wu et al., figs. 2.2–2.8, 3.

Holotype: NIGP161629, from the Shibantan Member, Dengying Formation, Wuhe, Yangtze Gorges area, South China (Wu et al., 2024a).

Materials: Twelve specimens from the Zhoujieshan Formation at Quanjishan section A (Fig. 1C).

Diagnosis: As per Wu et al. (2024a).

Description: Among the seven specimens identified as *Charnia gracilis* (Fig. 4), three are complete and well-preserved, including the petalodium, stem, and holdfast (Fig. 4A, B, D). The specimens exhibit features of a uniterminal bifoliate frond, ranging from centimeter to decimeter scale. The completely preserved petalodia are 22.0–123.4 mm in length (mean = 59.2 mm, n = 7) and 6.3–18.6 mm in width (mean = 13.4 mm, n = 8), and consist of 5–7 first-order branches per row. These specimens consist of a nearly parallel-sided and spicate petalodium that gradually tapers at its apical end. The petalodium is constructed by highly constrained, thin, straight, and low-angled (mean = 17.4°, n = 12) first-order branches, which are alternately arranged along the petalodium, creating a zig-zag central axis. The longest first-order branches in all measurable specimens are 7.7–49.0 mm in length (mean = 23.2 mm, n = 12) and 1.6–7.1 mm in width (mean = 3.8 mm, n = 12), with a L/W ratio ranging from 4.2–9.0 (mean

= 5.9, n = 12). The first-order branches are formed by 10–20 second-order branches, which are arranged parallel to each other in near-rectangular (e.g. Fig. 4B, C) to parallelogrammatic (e.g. Fig. 4A, D) arrangements. Third-order branches are rarely seen. The stem, which is 5.0–11.8 mm in length (mean = 9.5 mm, n = 3), connects the petalodium and the rounded holdfast. Three specimens possess a holdfast (Fig. 2A, B, D), with a diameter of between 4.5 mm and 23.4 mm (mean = 11.3 mm).

Occurrence: Zhoujieshan Formation, Quanjishan area, Northwest China; Shibantan Member, Dengying Formation, Yangtze Gorges area, South China (Wu et al., 2024a); Khatyspyt Formation, Olenek Uplift, north-central Siberia, Russia (Grazhdankin et al., 2008); Verkhovka Formation, White Sea region, Russia (Fedonkin et al., 2007); possible occurrences in the Rawnsley Quartzite, Flinders Ranges, South Australia (Nedin and Jenkins, 1998) and St. John's Group, Avalon Peninsula, Newfoundland (McKean et al., 2024).

Remarks: These specimens can be recognized as *Charnia gracilis* because of their low-angled (< 20°) and straight first-order branches (Fig. 6A). The overall shape of their petalodium as well as their first-order branches resembles *C. gracilis* specimens from South China, but the Quanjishan *C. gracilis* specimens can be more completely preserved, with stems and holdfasts. The petalodium and holdfast are often preserved in opposite reliefs within individual specimens (e.g. Fig. 4A–B), although there are rare exceptions (e.g. Fig. 4D). The apex of the petalodium on these fronds (e.g. Fig. 4A) is not as rounded as that of *Charnia masoni*. There seem to be fewer second-order branches on the first-order branch located at the very apex of the frond (approximately four second-order branches) compared to the first-order branch below (at least six second-order branches, e.g. Fig. 4A), which is consistent with previous findings that there is a "differentiation" stage during the initial growth of first-order branches in *Charnia* (Wilby et al., 2015; Dunn et al., 2019).

6. Discussion

Charnia specimens from the Quanjishan assemblage extend the palaeogeographic

distribution of this genus (Pang et al., 2021), particularly for *C. gracilis*, which is here newly described on a palaeocontinent close to the North China Craton, augmenting its existing occurrence on the South China Craton from the Shibantan Member of the Dengying Formation (~550–543 Ma) in the Yangtze Gorges area (Wu et al., 2024a). *C. gracilis* currently exhibits a narrower palaeogeographic distribution than *C. masoni*, and a shorter stratigraphic range, although a single figured specimen in McKean et al. (2024) may extend this taxon to the Avalon Terrane. In any case, considering the long stratigraphic range and global palaeogeographic distribution of the genus *Charnia*, it becomes evident that *Charnia* represents one of the longest-ranging Ediacara-type macro-organisms, ranging over ~30 million years (Wu et al., 2024a). The co-occurrence of *Charnia* and terminal Ediacaran fossil *Shaanxilithes* in the Zhoujieshan Formation suggests that these *Charnia* specimens may be younger than the Shibantan specimens in South China (Wu et al., 2024a), considering that those beds hosting *Shaanxilithes* (at the top of the Shibantan Member, An et al., 2020) are above the occurrence of *Charnia* (at the base of the Shibantan Member) in South China. This further suggests that the Quanjishan area (alongside the Khatyspyt Formation of Siberia, where *Charnia* and *Shaanxilithes* may be contemporaneous; Psarras et al., 2023), was one of the youngest *Charnia* localities worldwide.

6.1 An assemblage dominated by small-sized *Charnia* specimens

Most *Charnia* specimens from the Quanjishan assemblage exhibit a relatively smaller size in comparison to material from other localities, as reflected by lower values of length and width in both their petalodia and longest first-order branches (Fig. 6B–C). For example, the length of most measurable *Charnia* specimens in our collection is no larger than 100 mm (with one specimen exceeding this and reaching 123.4 mm), while specimens in other localities can easily grow longer than 100 mm or even reach 450 mm (Fig. 6B). Meanwhile, the L/W ratios for both their petalodia and longest first-order branches are similar to other *Charnia* materials worldwide (Fig. 6B, C). The smaller size of the Quanjishan *Charnia* specimens does not seem to result from an

493 evolutionary trend, since *Charnia* from the terminal Ediacaran Shibantan assemblage
494 (~550–543 Ma) can be more than 25 cm (*C. masoni*; e.g. fig. 2.1 in Wu et al., 2024a)
495 or over half a meter long (*C. gracilis*; e.g. fig. 3.1 in Wu et al., 2024a). The number of
496 first-order branches for the Quanjishan *Charnia* specimens (≤ 16) is generally less than
497 is seen in *Charnia* specimens from other localities (16–30 first-order branches, see Fig.
498 6D), whereas their ratio of petalodium length to number of first-order branches is
499 similar (Fig. 6D). It is therefore reasonable to interpret that these Quanjishan *Charnia*
500 specimens reflect an earlier growth stage characterized by differentiation of new first-
501 order branches, prior to the subsequent inflation stage of first-order branches (Wilby et
502 al., 2015; Dunn et al., 2019; Wu et al., 2024a). In comparison, some of the Quanjishan
503 *Charnia* sp. and *C. masoni* specimens (Fig. 5) possess a tiny petalodium (10.1–13.4
504 mm in length) and even fewer first-order branches (4–5 in each row). The number of
505 first-order branches as well as their body size in these cases is comparable to some
506 previously reported juvenile fronds (e.g. fig. 4 in Liu et al., 2012), and so we here
507 consider them as juvenile individuals, possibly in an even earlier development stage
508 than is seen in other specimens (e.g. Fig. 4).

509 The numerical abundance of small-sized *Charnia* specimens in the Quanjishan
510 assemblage is not likely to result from sampling artefacts, since specimens were
511 collected from multiple horizons of the Zhoujieshan Formation. However, it is not yet
512 clear whether the small size of the Quanjishan *Charnia* specimens results from
513 taphonomic bias (e.g. size sorting during burial), or reflects a snapshot of genuine
514 *Charnia* palaeocommunities dominated by small-sized specimens. Benthic sessile
515 organisms with a smaller body size have been shown to be favored in settings with
516 relatively strong drag forces of water currents, as their small size can reduce the risk of
517 being uprooted (Denny et al., 1985; Denny, 1999; Gaylord, 2000; Pratt and Johnson,
518 2002). Since this portion of the Zhoujieshan Formation was interpreted to have been
519 deposited in between shoreface and offshore transition environment, where the
520 hydrodynamic conditions should not be too high except in storm or sediment-deposition
521 events, the smaller size of the Quanjishan specimens is unlikely to reflect such a trend

(though it is possible that strong hydrodynamic conditions or transportation may have filtered and size-sorted these assemblages, stripping out larger individuals). Further sedimentological work is required to investigate this possibility.

6.2 Palaeoecological implications

Frondose organisms, such as *Charnia*, are susceptible to hydrodynamic influence given their anticipated benthic and erect lifestyle (though see Grazhdankin, 2004; McIlroy et al., 2021). Taphonomic and morphological characteristics of the Quanjishan *Charnia* specimens, such as fronds on the same slab being aligned in the same direction (Figs. 4C–D, 5A–B) and some fronds preserving a holdfast (e.g. Figs. 4A–B, D, 5C–D), are consistent with such a benthic and erect lifestyle. In one particular slab, tiny *Charnia* sp. specimens (presumed early juveniles) and relatively larger *Charnia* sp. specimens are preserved together with a consistent alignment (Fig. 5A–B), further suggesting that *Charnia* can be easily influenced by water currents, even if they originally resided in a calm setting. Theoretically, the common orientation of frondose organisms can serve as evidence that they were influenced by water currents and can be used to infer the current direction (e.g., Seilacher, 1992), although the phenomenon of fronds possessing different or opposite orientations exists in other localities (e.g., fig. 5 in Vixseboxse et al., 2021; fig. 7C in McKean et al., 2023).

In our thin sections of the fossiliferous rocks (where *Charnia* occurs), we observed centimeter-scale low-angled cross beds (Fig. 3D–F), including both examples that lie directly underneath a fossiliferous bed (Fig. 3E, F), and in one example, low-angled truncation of laminae above that same fossiliferous bed (Fig. 3E). The related *Charnia* specimen is preserved as positive hyporelief, so this individual lived on top of the low angled planar cross bedding after it had been deposited, and before the formation of low-angled truncation of laminae. As a result, this specimen likely grew in the interval between two higher-energy depositional events, in a relatively calm setting indicated by interbedded siltstones. On the basis of heterolithic sediments and evidence for current activity, the bed where this *Charnia* specimen lay was probably deposited

somewhere close to or below the fair-weather wave base. We thus suggest that the *Charnia* assemblage in Quanjishan resided in between lower shoreface and offshore transition settings.

In other localities worldwide, *Charnia* occurs in both shallow and deep marine environments (Grazhdankin, 2004; Liu et al., 2015; Dunn et al., 2019), including but not limited to offshore (Gehling and Droser, 2013), offshore transition (Wu et al., 2024a), middle shoreface (Grazhdankin, 2004), low-energy carbonate ramp environments (Grazhdankin et al., 2008), and deep-water slope (Wood et al., 2003). As a result, it seems that the environments that *Charnia* could tolerate can range from middle shoreface to deep water settings.

At the Quanjishan section, rocks hosting *Shaanxilithes* occur in the same siltstone and fine-grained sandstone lithologies as *Charnia*, providing further evidence that *Shaanxilithes* and frondose organisms could live in close association (as predicted by Darroch et al., 2016). *Shaanxilithes* from other localities could, however, also occur in silty mudstone (Chai et al., 2021; Wang et al., 2021), slaty siltstone (Shen et al., 2007), siltstone (Hua et al., 2004; Zhuravlev et al., 2009; Tarhan et al., 2014; Zhang et al., 2015), fine-grained sandstone (Darroch et al., 2016), muddy limestone (Fang et al., 2021), and dolostone (Tarhan et al., 2014), perhaps suggesting a wide tolerance of *Shaanxilithes* for different environments. However, it should be noted that at least some of those occurrences reflect body fossil coquinas of *Shaanxilithes* tubes, and not original in-life depositional settings (Psarras et al., 2023).

6.3 Taphonomic insights of *Charnia*

Fronds of *Charnia* from the Quanjishan assemblage can be preserved in two- and three-dimensions (Fig. 9). In most cases, petalodia of the Quanjishan *Charnia* are preserved as two-dimensional positive hyporelief and/or negative epirelief (Fig. 9B–C). In this two-dimensional preservational style, only the mold of the lower surface of petalodia is preserved after burial. Such a preservation style is typically found in Ediacara-type macrofossil localities such as Charnwood Forest and Newfoundland

(Laflamme et al., 2007; Wilby et al., 2011). In contrast, discoidal holdfasts of Ediacaran fronds are more often preserved three-dimensionally in various lithologies (Tarhan et al., 2015; Bykova et al., 2017). It has been suggested that the holdfast of *Charnia* should be deeply buried in the substrate based on its generally smaller size and rare occurrence (Laflamme et al., 2007; Burzynski and Narbonne, 2015), giving it a greater chance to be preserved three-dimensionally. As a result, the bedding layer near the holdfast may curve and bulge along its edge (Fig. 9A), whereas the petalodium causes the layer underneath to be depressed after compression of the organism into the substrate, creating opposite reliefs to the holdfast (Fig. 9C). In our collections, this phenomenon is indicated by a small pit that connects with the positively preserved petalodium through a stem (Figs. 4A, B, 5C, D). This phenomenon is also observed in some Newfoundland specimens (e.g. fig. 5 in Narbonne et al., 2009). Because of the three-dimensional preservation of the holdfast, it is also possible that the holdfast and petalodium are in the same relief (e.g. Fig. 4D), as the holdfast is compressed and represents the layer of sediment beneath the layer where the petalodium lies (Fig. 9B).

Three-dimensional preservation, though relatively rare in Ediacara-type soft-bodied macrofossils, has been reported from the White Sea (Grazhdankin, 2004) and Nama (Crimes and Fedonkin, 1996; Vickers-Rich et al., 2013) assemblages. Particularly for the Nama assemblage, examples of three-dimensional preservation frequently result from specimens having undergone transportation prior to burial (O'Connell et al., 2024), suggesting that passive sediment infill may play an important role in three-dimensional preservation (see also Grazhdankin, 2004). The White Sea *Charnia* specimen studied by Dunn et al. (2021) using microCT, synchrotron, and SEM techniques, also clearly demonstrates that sedimentary infill is a key factor in its three-dimensional preservation, and emphasizes that the branches of *Charnia* were highly interconnected, allowing sediment to circulate within the organism once the external walls had been breached.

The Quanjishan assemblage contains more rare examples of three-dimensional preservation of Ediacara-type macrofossils. One *Charnia* sp. specimen is preserved in

three-dimensional cast and mold style, with both the upper and lower sides of the fossil cast before lithification (Fig. 8A, B). The fossil layer was then fractured across the middle of the specimen during excavation, presenting opposite reliefs in different layers (Fig. 9D). This could also apply to other fronds preserved as positive epirelief or negative hyporelief (e.g. Fig. 4C), which could actually represent three-dimensional rather than two-dimensional preservation (Fig. 9D). Casting both sides of the frond seems to be more challenging than casting a single side, because the carcass needs to remain intact and uncompressed before casting is finished, and thus more time is required to complete the process. A low energy depositional setting may favor this slow process, but when and how the sediment entered the organism remains to be explored. Theoretically, some of the Quanjishan *Charnia* specimens without a holdfast might have been transported before burial, which may also lead to their three-dimensional preservation (*sensu* O'Connell et al., 2024).

7. Conclusion

As a component of the oldest macrofossil assemblage so far discovered in the Tibetan Plateau, newly described *Charnia* fossils from the Quanjishan assemblage, northern Qaidam Basin in northwest China represent one of the youngest occurrences of *Charnia* in the world, as they occur alongside *Shaanxilithes*, enriching our understanding of *Charnia* and the Ediacaran macrobiota. This assemblage contains many small *Charnia* specimens that generally possess a smaller petalodium and fewer first-order branches than *Charnia* fossils from other localities. There are also small specimens of ~1 cm in length, exhibiting both numbers of first-order branches and body sizes comparable to previously reported juvenile *Charnia* specimens. *Charnia* in the Zhoujieshan Formation likely lived in a subtidal marine environment, somewhere between lower shoreface and the offshore transition. This suggests that *Charnia* may have preferred relatively calm hydrodynamic conditions in life, and when taken together with other global occurrences, implies that *Charnia* could tolerate environments ranging from middle shoreface to deep water settings. Both two- and

three-dimensional preservation, as well as low to high reliefs, are present within the Quanjishan *Charnia* assemblage. As one of the longest-ranging genera within the Ediacaran biota, *Charnia* seemingly endured across a wide spectrum of temporal, spatial, and environmental settings.

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Figure and Table captions

Fig. 1. Geological maps showing the Olongbuluke terrane, northern Qaidam Block, northwest China. (A) Tectonic subdivision of China. (B) Simplified geological map of the northern Tibetan Plateau. (C) Simplified geological map of the Quanjishan-Shihuigou area in the Olongbuluke terrane and the locations of the main Proterozoic sections. Section numbers 1, 2, and 3 represent Quanjishan section A, Quanjishan section B, and Shihuigou section, respectively. Modified from Pang et al. (2021), Sun et al., (2020), and Sun et al. (2022).

Fig. 2. Stratigraphic column at Quanjishan section A (left column) with the Ediacaran portion (middle column) magnified. Geochronological data for the Hongzaoshan and Heitupo formations are derived from Zhang et al. (2016) and Sun et al. (2022). Lithology of the major fossiliferous horizons (marked by black dots) from the lower Zhoujieshan Formation (5–11 m above cap dolostone unit) is shown in detail (right column). Modified from Pang et al. (2021) and Sun et al. (2022). Abbreviations: Cam. = Cambrian, SSFs = Small Shelly Fossils, OLB Gp. = Olongbuluke Group, ZJS Fm. = Zhoujieshan Formation, HTG Fm. = Hongtiegou Formation, HTP Fm. = Heitupo Formation.

Fig. 3. Sedimentary structures in the lower Zhoujieshan Formation of Quanjishan section A. (A) Outcrop photo of planar cross bedding within a siltstone bed of the lower Zhoujieshan Formation. (B) Outcrop photo of planar cross bedding within a fine sandstone bed of the lower Zhoujieshan Formation. (C) Outcrop photo of parallel bedding of the lower Zhoujieshan Formation. (D–E) Thin sections of rocks from the lower Zhoujieshan Formation, showing low-angled planar cross lamination (dashed rectangle). Black arrows mark the horizons where *Charnia* occurs. White arrow in (E) marks a truncation of laminae. Yellow arrows point towards the top bedding surface. Scale bar = 10 mm. (F) Magnified view of the dashed rectangle area in (E), showing

the details of low-angled planar cross lamination as well as less rounded grains. Scale bar = 1 mm. (G) General lithology of the fresh rock of the lower Zhoujieshan Formation, 6–7 m above cap dolostone unit, showing interbedded fine sandstone, siltstone, and muddy siltstone. (H) Possible microbially induced sedimentary structures observed on medium-grained sandstone from the lower Zhoujieshan Formation. (I) Possible microbially induced sedimentary structures from siltstone of the lower Zhoujieshan Formation. Scale bar = 5 cm.

Fig. 4. *Charnia* specimens from the Quanjishan assemblage, with their stem and holdfast (white arrows) preserved. Note that fronds on the same slab are all oriented in the same direction (C, D). Petalodia of specimens in (A) and (B), both of which are *C. gracilis*, are preserved as positive hyporelief and their holdfasts as negative hyporelief. Specimens in (C) are preserved as different reliefs (yellow arrows), where *C. gracilis* (lower left) is preserved as positive hyporelief, and *C. masoni* (upper right) is preserved as negative hyporelief. Petalodia and holdfasts of specimens in (D) are preserved as positive relief with their stratigraphic orientations unknown. Specimen on the right of (D) is *C. gracilis* and specimen on the left of (D) is *Charnia* sp. All scale bars = 1 cm. A: NIGP204060 (arrowed specimen); B: NIGP204061; C: NIGP204062 (lower left) and NIGP204063 (upper right); D: NIGP204064 (right) and NIGP204065 (left).

Fig. 5. Small *Charnia* specimens from the Quanjishan assemblage. (A, B) Multiple *Charnia* specimens (NIGP204066–NIGP204072, from left to right), preserved as positive hyporelief, with two incomplete *Charnia* sp. specimens (white arrows) adjacent to five tiny *Charnia* sp. specimens (dashed rectangle), which may represent early juvenile forms. Note that they all lie in the same orientation. (B) Magnified view of the dashed rectangle area in (A), showing details of five tiny *Charnia* sp. specimens (white arrows), less than 1 cm in frond width. (C) *Charnia* sp. specimen (NIGP204073), the petalodium of which is preserved as positive relief and its holdfast (white arrow)

preserved as negative relief, with the stratigraphic orientation unknown. (D) *Charnia masoni* specimen (NIGP204074), the petalodium of which is preserved as positive relief and its holdfast (white arrow) preserved as negative relief, with the stratigraphic orientation unknown. Scale bars = 5 cm (A); 1 cm (B–D).

Fig. 6. Biometric plots of *Charnia* from the Quanjishan assemblage and other localities worldwide. (A) Cross-plot of mean divergence angle versus mean value of X = |(a − b)/(a + b)| (sensu Wu et al., 2024a) of *Charnia* from different localities, revealing how these metrics can distinguish *Charnia* species, supporting the suggestion that *Charnia* with measurable first-order branches preserved from the Quanjishan assemblage comprise both *Charnia gracilis* (X value <0.3; mean diverging angle ≤20°) and *Charnia masoni* (X value ≥0.3; mean diverging angle >20°) specimens. (B) Cross-plot of petalodium length versus width. (C) Cross-plot of length versus width of the longest first-order branch. (D) Cross-plot of petalodium length versus countable number of first-order branches, with plots of Quanjishan specimens magnified. Hollow symbols represent measurements of *C. gracilis*, whereas filled symbols represent measurements of *C. masoni*. Purple cross symbols represent the indeterminate *Charnia* sp. in Quanjishan assemblage. Measurement data for the Quanjishan specimens can be found in Table 1. Data from other localities are derived from Wu et al. (2024a).

Fig. 7. Part and counterpart of *Charnia* sp. (NIGP204075) displaying a raised petalodium margin with higher topographic relief compared with the middle part. The petalodium is mainly preserved as negative epirelief (A) and positive hyporelief (B), but it is important to note that the edge of the petalodium and the second-order branches (arrows in B) are in opposite reliefs. Scale bars = 1 cm.

Fig. 8. Three-dimensional preservation of *Charnia* specimens. (A) and (B) Part and

counterpart of *Charnia* sp. (NIGP204076). In different laminae, the specimen is expressed in opposite reliefs, suggesting that the *Charnia* is preserved in three-dimensions with sediment trapped within the body cavity. (C) *Charnia* sp. (NIGP204077) preserved as higher relief, where the surface of the fossil is distinctly elevated above its surrounding layer. Abbreviations: ne = negative epirelief, pe = positive epirelief, ph = positive hyporelief, nh = negative hyporelief. Scale bars = 1 cm.

Fig. 9. Sketch showing the proposed two- and three-dimensional preservation process. (A) Proposed living state of *Charnia masoni*. Note the draping of sediments around the holdfast (magnified). (B) A two-dimensional preservation scenario where both petalodium and holdfast are preserved as positive hyporeliefs. (C) A two-dimensional preservation scenario where only the mold of the lower surface of a petalodium (after burial) is preserved, and the sediment surrounding the holdfast may be elevated slightly along its upper surface due to ponding of sediment around the holdfast, causing an opposite relief relationship. (D) A three-dimensional preservation scenario where there are theoretically equal chances for either the upper or lower surface of the petalodium to be exposed during excavation. The sketch for three-dimensional preservation shows the circumstance of the specimen in Figure 8A–B, which preserves both positive relief and negative relief in adjacent laminae.

Table 1. Measurements of *Charnia* specimens from the Quanjishan assemblage, China.