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ORIGINAL ARTICLE

Applications of fossil taxonomy in palaeoenvironmental reconstruction: a case study of ostracod identification and diversity in Permian–Triassic boundary microbialites

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Abstract

The value of taxonomy as a tool in palaeoenvironmental analysis depends on accuracy of determination of relevant taxa; in cases where taxa present unresolved problems of distinction (identification uncertainty and overlap), difficulties may exist in their application in facies studies. A prime example is found in ostracods of the Permian–Triassic boundary interval, considered here in sequences from south China. Low-latitude shallow-marine carbonate facies in the immediate aftermath of the end-Permian extinction (EPE) have common widespread microbialite biostromes containing abundant shelly fossils including ostracod assemblages not found elsewhere, stimulating the earlier idea that the microbialite was a refuge from stressors of extinction. These assemblages are dominated by the Family Bairdiidae that are mostly smooth-shelled ostracods notoriously difficult to resolve into sub-familial taxonomic units. Studies of ostracod taxonomy require a careful approach of integrating cornerstone aspects of their biology such as ontogenetic development and sexual dimorphism to disentangle taxonomically discrete groups. These significant difficulties of taxonomic resolution have a knock-on impact on application of the faunas in facies analysis; several studies remain open to interpretation because of these issues. Resolution of ostracod taxonomy is critical to the refuge hypothesis, because ostracods (mostly as complete closed carapaces, including juveniles and adults) accumulated in the microbialite; thus shell morphology is critical to analysis of ostracods in the microbialites so understanding the taxonomy is vital. The microbialites comprise two main facies where ostracods are abundant: (1) layers consisting of microbial components and intervening micrite; (2) uncommon shell-rich lenses of packstone-grainstone fabric between microbial layers. The refuge hypothesis is considered unlikely by some authors, who instead interpret the microbialites as a taphonomic window for imported ostracod shell preservation. However, post-extinction microbialite sheets are extensive on shallow marine carbonate platforms in Tethys and show little evidence of physical damage. We deduce that, instead of a taphonomic window, the well-preserved ostracod assemblages lived on the microbialite, and that the 'refuge hypothesis' remains viable. The concepts discussed in this study may be applicable to other fossil groups where taxonomic problems are acute.

Keywords Ostracods · Bairdiidae · End-Permian extinction · Microbialites · Taphonomic window

Introduction

Recent years have seen growing interest amongst the scientific community towards microbial deposits developed in the aftermath of the end-Permian extinction (EPE), resulting in a plethora of studies (e.g., Baud et al. 1997, 2005, 2007; Ezaki et al. 2003; Hips and Haas 2006; Yang et al. 2011; Jiang et al. 2014; Lehrmann et al. 2015; Adachi et al. 2017; Bagherpour et al. 2017; Tang et al. 2017; Wu et al. 2017; Heindel et al. 2018; Martindale et al. 2019; Wang et al. 2019; Zhang et al. 2020). Increasing attention has focused on the abundant ostracod assemblages reported from these

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deposits worldwide and the associated refuge hypothesis (Forel et al. 2013a), which proposed that the microbialite environment provided a protected setting for their survival in the aftermath of the extinction. The refuge hypothesis became a topic of further discussion with questions regarding its validity, leading to alternative interpretations for the presence of ostracods in the microbialite (e.g., Hautmann et al. 2015; Martindale et al. 2019; Qiu et al. 2019; Wan et al. 2021). Such questions raise the necessity of clarifying how ostracods came to be present in sediment between the calcareous microbial constructing framework within the microbialites. Thus the aims of this study are (1) to clarify and discuss the critically important taxonomic features of ostracods as essential background to their application in sedimentological interpretations and then (2) to attempt to resolve the nature of ostracod assemblages associated with Permian–Triassic boundary microbialites in relation to the sedimentary environments and processes of the microbialites. We provide a detailed treatment of taxonomic problems of ostracods essential to understanding interpretations of microbialite facies immediately after the EPE. Applications in environmental analysis of other fossil groups that have complex taxonomic problems may benefit from the ideas presented in this study.

Ostracods in post-EPE ecosystems

Taxonomic concepts

As outlined above, to demonstrate the importance of ostracod taxonomy in palaeoenvironmental reconstruction, it is necessary to explore the details of taxonomic issues. The identification of living ostracods relies on morphological characters of soft parts and appendages, as well as morphology and characters visible on the external and internal surfaces of the valves. In contrast, preservational factors mean that the vast majority of fossil ostracods can be determined using only characters of the conjoined two valves (carapace) or disarticulated valves once they are extracted from the enclosing matrix by diverse mechanical or chemical processes. In most cases, scanning electron microscope (SEM) images of fossil ostracods provide information about only the external morphology because inner surface structures are not accessible in closed carapaces; and the inner surfaces of disarticulated valves are often abraded or covered by sediment. The carapace/valve-based morphological classification (and therefore identification) of fossil ostracods is established through the observation of the outline in lateral, dorsal, ventral, anterior and posterior views (see Lord 2020 for a recent discussion on external and internal carapace characters important in ostracod species definition), implying that specimens glued for SEM imaging should be turned several times, with a high risk of loss or breakage. This difficulty has resulted in a high number of species frequently pictured in only right lateral view, imposing a first important limitation to classification/identification: diagnostic characters of certain taxa cannot be seen in lateral view, such as the flat and parallel flanks of the Late Palaeozoic to Early Triassic genus *Orthobairdia* Sohn (1960) that are visible in only dorsal view (see below for further discussion on this genus).

The taxonomic determination of fossil ostracods from the Permian–Triassic transition is of particular complexity as most are smooth-shelled, rounded/ovoid and lack strong diagnostic features (see Fig. 1 for examples). This observation is especially true for ostracods obtained from post-EPE microbialites because the ostracods are exceptionally abundant and small, as a result of the presence of relatively high abundances of juvenile specimens and the post-extinction Lilliput Effect (e.g., Forel 2014; Forel et al. 2015). Examples of juveniles are shown in Fig. 2. It is now widely acknowledged that ostracods associated with post-EPE microbialites are largely dominated by the Bairdiidae (informally termed bairdiids), chiefly *Bairdia* and *Bairdiacypris* (e.g., Crasquin-Soleau et al. 2004, 2006; Forel 2012, 2014; Forel et al. 2009, 2013a, b, 2015; Liu et al. 2010; Wan et al. 2019). Bairdiidae have been components of marine ecosystems since Ordovician time (e.g., Cabioch et al. 1986; Titterton and Whatley 1988; Meidla 1996; Truuver et al. 2012; Maddocks 2013). *Bairdia* McCoy (1842) was established from Carboniferous strata of Ireland, but subsequent work showed this genus is a complex of genera. Intense efforts have partly clarified the '*Bairdia* dynasty' (Malz 1988) in modern environments with the establishment of the genera *Bairdoppilata* Coryell et al. (1935), *Neonesidea* Maddocks (1969), *Paranesidea* Maddocks (1969) and *Triebelina* van den Bold (1946) (e.g., Maddocks 1969, 2013, 2015). Numerous authors have since emended the morphological criteria of specific significance in *Bairdia* (e.g., Kellett 1934; Sohn 1960). Many issues remain but it is generally accepted that *Bairdia* is restricted to the Palaeozoic Era and that 'to include other forms under this name violates its morphologic and quite possibly its phyletic homogeneity' (Maddocks 1969, p. 1). Nonetheless, *Bairdia* continues to be reported even in Cenozoic strata and modern marine environments, these reports being here considered as easy solutions to the complicated taxonomy of smooth-shelled bairdiids often due to limited material (e.g., Guernet 1982, 1985; Babinot and Degaugue-Michalski 1996; Bossio et al. 2006; Perçin-Paçal et al. 2015; Angue-Minto'o et al. 2016; Uffenorde 2016; Moorea Biocode database http://www.mooreabiocode.org). These taxonomic issues related to smooth-shelled bairdiids are particularly important in fossil material for which internal features are not accessible and identifications rely on the interpretation of external

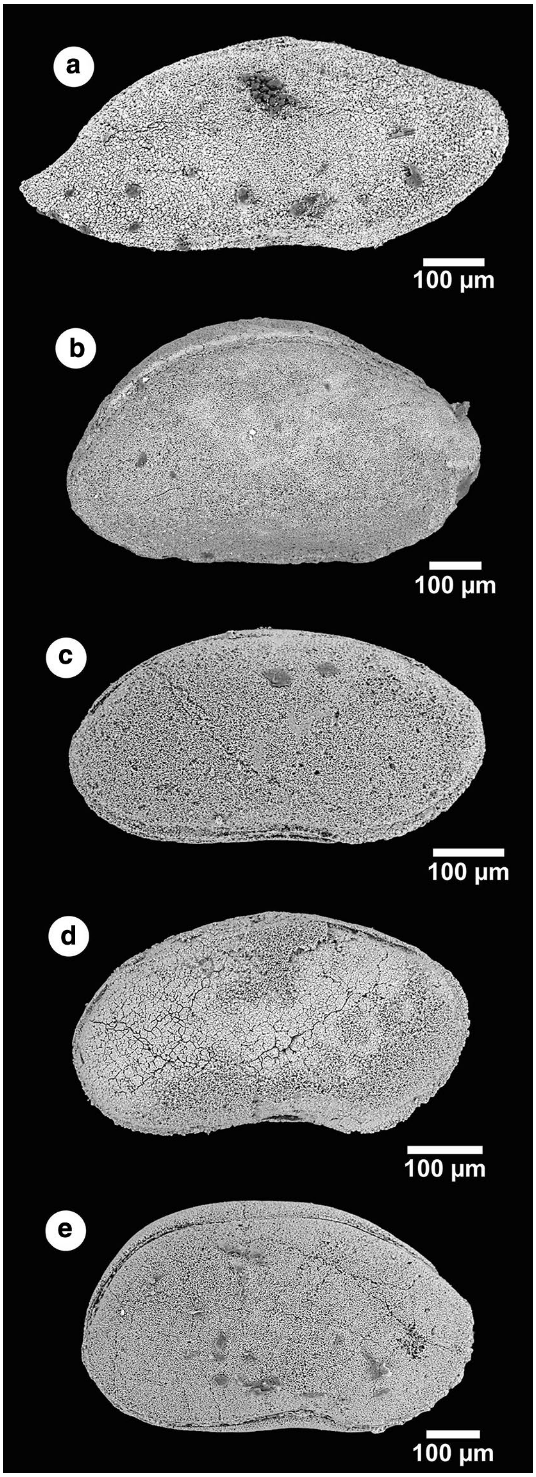

Fig. 1 Bairdiidae from post-EPE microbialites illustrating the transitional morphologies between *Bairdia* (**a**) and *Bairdiacypris* (**e**). A, *Bairdia* from Runbao site, Guizhou; **b–d** transitional forms that depending on the authors may be identified as *Bairdia* or *Bairdiacypris*, respectively from Baizhuyuan (Sichuan), Laolongdong (Sichuan), and Dajiang (Guizhou) sites; **e** *Bairdiacypris* from Dongwan site, Sichuan

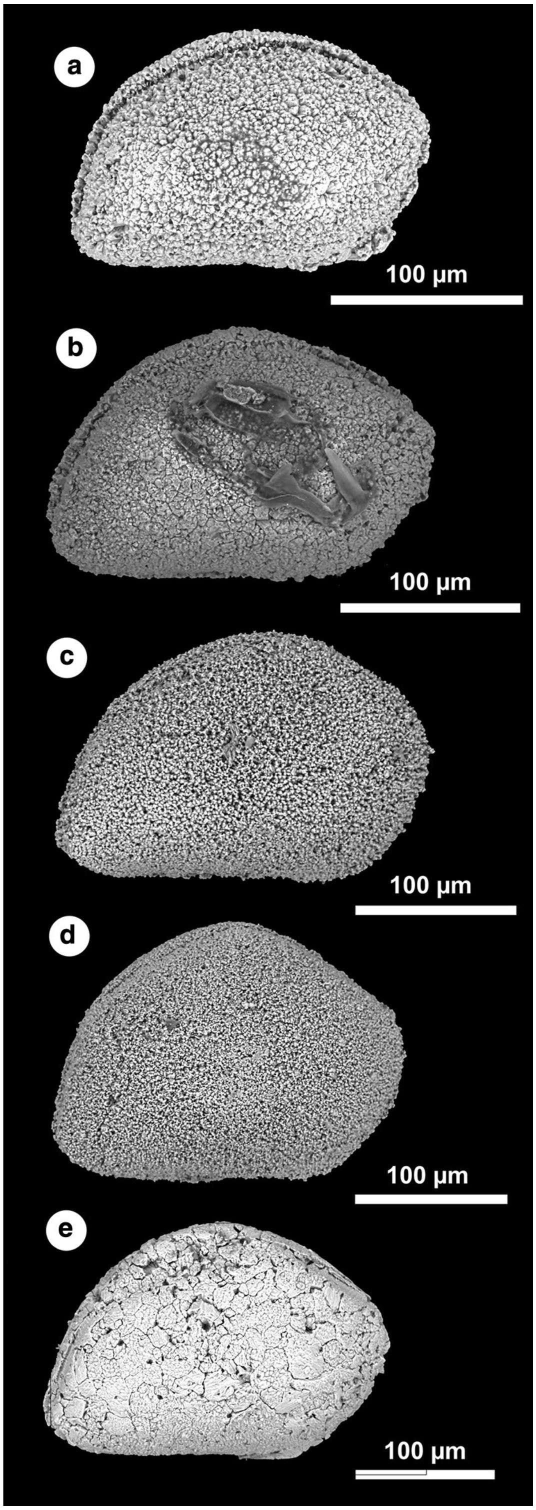

Fig. 2 Juveniles of Bairdiidae from post-EPE microbialites illustrating the high degree of convergence of the carapace morphology in bairdiid juveniles that are hardly attributed to associated species without the study of a suite of specimens. **a**, **b** from Laolongdong site (Sichuan); **c**, **d** from Dajiang site (Guizhou); **e** from Rungbao site (Guizhou)

features only. Since the first description of *Bairdia*, a series of allied genera have been described, including *Cryptobairdia*, *Rectobairdia* and *Orthobairdia*, all from Middle Devonian-Permian strata of USA (Sohn 1960). However, these genera did not meet a specialist consensus: *Orthobairdia* has been considered as a synonym of *Bairdia* by Becker (2001) while *Cryptobairdia* and *Rectobairdia* are regarded as subgenera of *Bairdia,* for instance by Becker et al. (1989, 1990), Becker (2001) and Forel and Crasquin (2020), although not considering the questionable status of subgenera in the fossil record.

Another issue arises from the growing confusion of the discrimination of several genera (*Bairdia* and *Bairdiacypris*, *Bairdiacypris* and *Fabalicypris*) at the EPE: Lord (2020) summarized the case of *Bairdiacypris* Bradfield (1935) and *Fabalicypris* Cooper (1946), a genus also reported from post-EPE assemblages, although less abundant (e.g., Crasquin-Soleau et al. 2004; Crasquin et al. 2010; Forel et al. 2015; Gliwa et al. 2020). Both genera have been described from the Carboniferous of the USA and are very similar, although they differ in the lateral outline and nature of the ventral overlap. Here again, opinions have varied, with Becker (2001) considering *Fabalicypris* as a subgenus of *Bairdiacypris* while others (e.g., Sohn 1983; Hoare et al. 1999) regarded *Fabalicypris* as a junior synonym of *Bairdiacypris*. *Bairdia* accommodates bairdiids with a more or less distinctly arched mid-dorsal margin while *Bairdiacypris* gathers elongate species with a tripartite dorsal margin and rounded posterior end (e.g., Becker 2001). The distinction between *Bairdia* (Fig. 1a) and *Bairdiacypris* (Fig. 1e) is thus complex and the source of major uncertainties related, for instance, to the subjectivity of what should be considered as elongate and to the existence of transitional forms from arched to tripartite dorsal margins (Fig. 1b–d). Through time, this distinction has become more uncertain, with transitional forms and species inadequately described and/or illustrated to support generic attribution. The distinction between *Bairdia* and *Bairdiacypris* is today more unclear than ever as the subjectivity in the generic attributions reaches unprecedented levels. Similarly, *Fabalicypris* is now largely reported for specimens in which the ventral offset of the overlap is not documented. Distinguishing these features is exceptionally important because of proliferation of ovoid taxa in the immediate post-EPE interval where the occupation of the morphospace by the thriving post-extinction taxa changed with the near disappearance of Palaeocopida and the proliferation of very ovoid taxa (e.g., Forel et al. 2015). This pattern has led to an exceptionally high number of species published under open nomenclature, many of which may be artificial. Conversely, numerous species may be chimaeras (sensu Danielopol et al. 2019), thereby representing groupings of specimens of different biological species resulting from the high degree of convergence in bairdiids, leading to difficulties of identification in the fossil record. Thus, achieving even a basic assessment of taxonomic diversity is both difficult and subjective between workers.

Taxa duration

Several taxa reported from the EPE have aberrant stratigraphic ranges, leading to major issues regarding biodiversity dynamics. *Fossocytheridea mosbyense* Tibert et al. (2003) (*Fossocytheridea mosbyensis* [*sic*] of Liu et al. 2010) was reported from Late Permian microbialite deposits from the Chongyang section, Hubei Province, China (Liu et al. 2010). *F. mosbyense* was originally described from the Cenomanian of the Western Interior Basin, Utah, USA and the genus *Fossocytheridea* Swain and Brown (1964) itself is known from the Aptian to Maastrichtian (e.g., Tibert et al. 2003; Bergue et al. 2011). Its report from Late Permian deposits implies a duration of ~ 175 my for this genus and ~ 150 my for this species (based on the latest chronostratigraphic chart in Cohen et al. 2020). Such aberrant durations have recently been pointed out for Jurassic (and even older) occurrences of the living genus *Bythocypris* (Lord 2020). Although complex, the question of the geological longevity of taxa is of key importance as it may lead to aberrant records and thus to major bias in evolutionary and biodiversity studies. For instance, species' duration of certain Cretaceous bivalves is estimated to be about 2 my (Koch 1984); for Cenozoic gastropod species duration is about 2.1 my and those with planktic larvae have a mean duration of about 4.4 my (Hansen 1980). In the Late Cenozoic, echinoid species duration lasted for 2 my or more (Stanley 1979). The median species longevity of numerous marine invertebrate taxa, such as bivalves, gastropods, and Foraminifera, approaches or exceeds 10 my (Stanley 1979, 1982). Approximately 50% of marine diatom species from 13 Ma are alive today; this means that an average species lasts much longer than 13 my (Andrews 1976; Stanley 1982). For fossil invertebrates, it has been shown that the mean species duration is about 11 my and that it is substantially the same throughout the Phanerozoic (Raup 1978). Cronin (1985, 1987) provided the longevity ranges of several ostracod species of the marine genus *Puriana*, based on biostratigraphic data, most of the species duration ranges being of 3.5–8 my in the Cenozoic. In the Ordovician, species duration has been reported to range from 1 to 2 my (Swain 1996). For Cenozoic non-marine ostracod species, the duration of species appears to have been of the order of 1–5 my; more highly ornamented species had typically shorter life spans than did the simpler forms (Swain 1990). The extension of *Fossocytheridea mosbyense* from the Late Cretaceous down to the Late Permian is therefore aberrant and violates biological reality. Independently from this temporal aspect, *Fossocytheridea* is mainly diagnosed by characters visible on the inner part of the valves (see Tibert et al. 2003 for revision) and by an anterior-dorsal sulcus as well as sieve pores that are absent from the Late Permian specimen illustrated in Liu et al. (2010). The example of *Fossacytheridea* demonstrates the caution required before attributing long evolutionary time-spans to generic and subgeneric taxa: such aberrant generic and specific extensions constitute major biases in long-term biodiversity trends and should be identified and avoided.

Palaeobiology of ostracods

The palaeobiology of ostracods plays a major role in their application for stratigraphy and palaeoenvironmental interpretations. There are three key aspects, considered as follows.

(1) Ostracods, as for other crustaceans, grow by successive moulting (ecdysis) until they reach adult stage. The ontogenetic development of ostracods records numerous changes, especially regarding soft parts, carapace and size (e.g., Smith and Kamiya 2002, 2005). The carapaces and/or valves that constitute fossil ostracod assemblages thus correspond to adults and juveniles in which adults are discriminated by their well-developed hinge teeth and inner lamellae in many modern taxa (van Morkhoven 1962, fig. 69; Athersuch et al. 1989, fig. 16). As stated earlier, the soft parts of fossil ostracods are only very rarely preserved, so that valves are assigned to their corresponding ontogenetic stage by identifying discrete clusters of size in diagrams where valve length is plotted against height (e.g., Bolz 1969; Hunt and Chapman 2001; Watabe and Kaesler 2004; Retrum and Kaesler 2005; Forel 2014; Forel et al. 2015). Sexual dimorphism in ostracods, i.e., biological and morphological differences between males and females, is known from the Ordovician onwards (Siveter et al. 2014) and sexual reproduction has probably been present since the origin of the group (pers. com. David Siveter 12-03-2021). Three parts of ostracods are prone to display as sexually dimorphic structures (Ozawa 2013):

- soft parts (male hemipenes and female genital organs) and appendages, with certain males displaying asymmetric or larger limbs, presence/absence of substructures on some limbs of living Podocopida and Myodocopida, different eye structures in some Myodocopida (Abe and Vannier 1991, 1993; Ikeya and Abe 1996);
- heavier surface ornamentation in certain female Podocopida than in male counterparts (Tsukagoshi 1998; Kamiya et al. 2001; Smith and Kamiya 2005);
- size and shape of the carapaces which generally reflect the presence of (potential) brood chambers in the presumed female carapaces in Palaeocopida that can occur posteriorly, ventrally or anteroventrally/anteriorly (e.g., Henningsmoen 1965). In certain recent Podocopida, the female carapaces are larger with a more inflated posterior border (e.g., Maddocks and Illiffe 1986; Maddocks 1991; Smith and Hiruta 2004; Smith and Kamiya 2005; Sato and Kamiya 2007) although in some living podocopid examples (e.g., *Cyprideis torosa*) posterior dimensions can be related to large male copulatory appendages (e.g., Fernandes Martins et al. 2017).

(2) A second major issue is that the change of shell shape during ontogeny is commonly not considered in most of the recent ostracod taxonomic works investigating the EPE transition and all by-products such as size analysis and community dynamics, as has already been highlighted by Forel and Crasquin (2015). This issue is of extreme importance as the number of open nomenclature species that are actually juveniles is increasingly recognised, probably of associated species because the juvenile morphology of Bairdiidae is highly convergent (Fig. 2). For instance, *Bairdiacypris ottomanensis* Crasquin-Soleau et al. (2004) has been reported from one Early Triassic sample of the Chongyang section, Hubei Province, China (Liu et al. 2010, fig. 4). The only specimen illustrated is seemingly a very young juvenile from its small dimensions, about 410 µm in length (Liu et al. 2010, fig. 3.1; adults exceed 900 µm in length: Forel 2014; Gliwa et al. 2020). Nevertheless, the report (Liu et al. 2010) of this important Permian-Triassic species is problematic and really needs study of a suite of specimens to develop better understanding; this unique juvenile could be any one of a number of species. This specimen is also an example of excessive taxonomic splitting as we consider it to be conspecific with *Bairdiacypris* sp. 1 and 2 from the same section, all being extremely small, thus lowering the diversity counts. The same observation applies to the taxonomy used by Wan et al. (2019) who described high-resolution changes in the species composition of ostracod assemblages through the Permian-Triassic event in Zuodeng section, Guangxi, China. Taxonomic changes through the EPE have been reported previously, for instance from the Aras Valley section in north-west Iran where a complete turnover occurred from a pre-EPE low-diversity *Fabalicypris*-dominated community to a more diverse *Bairdiacypris*-dominated post-EPE

community in the absence of microbialites (Gliwa et al. 2020). This major turnover has been characterized on generic trends that are much less biased than specific ones, although also problematic for reasons explained above. The high-resolution changes proposed by Wan et al. (2019) rely uniquely on the changes in bairdiid species dominance, the identification of which remain open to interpretation. *Bairdia davehornei* Forel et al. (2013b) and *Bairdia*? *kemerensis* Crasquin-Soleau et al. (2004) are the dominant characteristic species of the Assemblage 1 (Wan et al. 2019, fig. 6). Each of these two species is illustrated by one specimen in Wan et al. (2019), respectively, an apparently broken specimen and a broken encrusted specimen: the identification of these species used as markers of one assemblage therefore requires further supporting specimens. *Bairdia fengshanensis* Crasquin-Soleau et al. (2006) in Wan et al. (2019) is a juvenile specimen with even smaller dimensions than those provided by Crasquin-Soleau et al. (2006) and could be attributed to any other member of the bairdiids as detailed above. The proposed 'clear indication of the evolution of the family Bairdiidae' (Wan et al. 2019, p. 11) remains an open question in the light of these issues.

(3) Several aspects regarding the lifestyles of ostracods used in recent discussions are also problematic. Wan et al. (2021, p. 7) state that '… Mesozoic pioneers, especially some proposed filter-feeding ostracods belonging to Metacopina (i.e., *Hungarella* and *Silenites*), were opportunists that evolved under reduced competitive pressure (Boomer et al. 2008; Forel et al. 2011)'. Boomer et al. (2008, p. 48) made clear that the speculation by Lethiers and Whatley (1994), that extinct metacopes are filter-feeders, is based only on the comparison of carapace characteristics with those of the extant Platycopina that are filter-feeders, and we know that carapace characteristics can mislead taxonomic attributions (e.g., Siveter et al. 2013). Similarly, Forel et al. (2011, pp.165–6) made it very clear that Lethiers and Whatley only *postulated* that metacope ostracods were filter feeders. Subsequently a Devonian metacope with soft parts has been reported (Olempska et al. 2012) but unfortunately did not reveal its mode of feeding. The case for late metacopes as filter-feeders is at best unproven, and a group that existed from late Ordovician to Early Jurassic (c. 270 my) may well represent a variety of lifestyles. As recently discussed by Forel et al. (2020) this issue is not restricted to Metacopina and to microbial facies through the EPE. Zhang et al. (2017) reported changes in benthic palaeocommunities through the EPE in a clastic sequence at the Zhongzhai section using the classification of suspension-feeders for Palaeocopida and deposit-feeders for Podocopida based on hypotheses of Adamczak (1969), Whatley (1991) and Lethiers and Whatley (1994). However, Palaeocopida as a whole should no longer be classified as filter-feeders since the discovery of a fulcral point and mandibular scars in early Carboniferous Beyrichioidea imply that these ostracods were deposit-feeders (Olempska 2008). Conversely, Podocopida are not all deposit-feeders as shown for instance by the filtering structures in the extant genus *Vitjasiella* (Schornikov 1976).

On the use of morphometric analysis

Morphometry is the quantitative description, analysis and interpretation of shape and shape variation in organisms (Rohlf 1990). Morphometrical analyses have been extensively used in ostracod research (see a summary in Baltanás and Danielopol 2011), for instance investigating the distribution of landmarks (e.g., Karanovic et al. 2017), semi-landmarks (e.g., Wrozyna et al. 2016), Eigenshape analysis (e.g., Schweitzer et al. 1986) and Fourier analysis (e.g., Tanaka 2009). Wan et al. (2021) addressed the decoupling of taxonomic diversity and morphological disparity of ostracods (see below) through the EPE in microbial facies by performing a morphometric analysis using semi-landmarks on two-dimensional valve shapes. However, we have identified four key aspects of the study by Wan et al. (2021) which we consider to be unresolved, and important because they have significant bearing on the palaeoecological interpretations of ostracods in the post-extinction microbialite:

(1) The relationship between morphological disparity (the range of morphological variations within a clade) and taxonomic diversity (the number of species within that clade) is the subject of evolutionary studies for many years (e.g., Minelli 2016; Hopkins and Gerber 2017), with a focus on the discrimination between these two concepts, often expressed as decoupling of diversity and disparity, that may occur in relation to extinction events. The study by Wan et al. (2021) investigated 373 specimens representing 349 species, so that most species in their sample set are represented by single specimens. Unfortunately, owing to the generic and specific issues discussed above, the morphological boundary between species through the EPE is often hard to define, which creates a problem of reliably recognizing the decoupling of diversity and disparity. Taxonomic issues regarding fossil Bairdiidae are abundant and may not be solved until molecular tools and still-unexplored characters are involved. These difficulties are related to the palaeontological material itself, which is comprised of morphospecies, wherein taxonomic discrimination

is affected by high convergence and tenuous characters visible on the carapaces and valves of smooth-shelled Bairdiidae. Similarly, taxonomic diversity cannot be investigated without at least establishing standards. The Wan et al. (2021) investigation incorporates material that was published and identified by other authors, implying the use of several standards of classification, noting that the classification of Bairdiidae is still very subjective in many aspects (see discussion above and Lord 2020). Independent of the taxonomic issues described above, standardizing the identifications would at least have allowed a consistent clustering of the taxonomic units that otherwise appear as chimaeras in the current state.

(2) Simple morphometrics of valve lateral outlines used in Wan et al. (2021) are likely poor indicators of morphological disparity and body size. Shell volume would be a more realistic measure of body size but it would be time-consuming and challenging to quantify. In the fossil record, valve outline (requiring uncompacted original 3D preservation) is often the only accessible proxy for morphological disparity assessment, but a comparative analysis of a wider range of characteristics, such as outline in dorsal/ventral view, calcified inner lamella features (when accessible) might be of key importance. Such a more complete and robust analysis cannot be performed by relying on published data but requires new material and a consistent data-collection method aimed at morphometric analysis.

(3) The establishment of clearly defined criteria for landmark placement to ensure objective comparability and reproducibility of morphometric analyses is vital, although on smooth ostracods is understandably problematic. Wan et al. (2021, p. 4) stated that 'First, two type III landmarks (LM 1 and 2) were defined by the maximum curvature at the anterior and posterior portions of the valve.' However, inspection of fig. 2 in Wan et al. (2021) shows that LM 1 is not on the site of maximum anterior curvature, and the position of LM 2 is questionable; if anywhere, LM 1 should be placed between LM 3 and LM 4. Fig. 2 in Wan et al. (2021) is only an example of the methodology used but shows that LM 29 is located on a broken portion of the anteroventral margin and that the whole anterior margin itself is damaged, resulting in the uncertain outline of the valve. Because the only illustrated specimen is broken, it then raises a key question of the reliability of measurements of specimens that are not illustrated. This reliability is also questioned by the integration in the analysis of measurements of valves that are tilted (e.g., Wan et al. (2019), fig. 4.17), broken (e.g., Wan et al. 2019, fig. 3.11, fig. 3.18, fig. 4.7) or partly covered with sediment (e.g., Wan et al. 2019, fig. 3.13, fig. 3.15).

(4) Ontogeny of ostracods is a key parameter that requires determination using dedicated, rigorous collection and analysis of ostracod assemblages. Wan et al. (2021, p. 4) stated that 'A generalized Procrustes analysis (GPA) with a minimized bending algorithm was used to remove the effects of size, location, and orientation of the specimen images…'. Unfortunately, removing the effect of size does not eliminate the issue of ontogeny. The ontogeny of ostracods is not limited to a size increase (and appendages addition); outline changes are also major features of their development, including in Bairdiidae, as was illustrated and discussed for instance by Smith and Kamiya (2002) on the living *Neonesidea oligodentata*. Understanding ontogenetic change also does not solve the too-often overlooked problem of sexual dimorphism of carapaces that also occurs in Bairdiidae (e.g., Maddocks 2013, 2015) that represent the vast majority of ostracod assemblages from microbial facies. Typically, sexual dimorphism of the carapaces of Bairdiidae is reflected in the elongation of the specimens, and thereby questions the variations along PC 1 that 'correspond to changes in the elongation of the ostracod carapaces' (Wan et al., 2021, p. 5).

In this general context, ontogeny and sexual dimorphism challenge the morphological disparity patterns determined by Wan et al. (2021). Because ontogenetic development of ostracods is marked by important morphological changes, it is reasonable to wonder how much of the observed high morphological disparity within the microbial facies is related to an unknown number of juveniles in their studied material.

Microbialite facies, ostracods and taphonomic window concept

The microbialite facies, in which ostracods are found, formed in low-latitude shallow marine carbonate facies in the immediate aftermath of the end-Permian extinction (EPE) (e.g., Kershaw et al. 2012; Martindale et al. 2019). The microbialites occur as thin, widely distributed carbonate sheets that covered large areas of several separated shallow marine carbonate platforms throughout Palaeo-Tethys, the principal areas being the South China Block and Western Tethys (Turkey and Iran, with minor occurrences in the UAE and elsewhere, summarised by Kershaw et al. 2012). Microbialite sheets comprise many layers (e.g., Fig. 3a) that developed on top of pre-extinction diversely fossiliferous carbonate platforms and effectively represent microbial biostromes that grew *in-situ*. Numerous studies have documented and discussed the nature of the microbialite biostromes and demonstrate their diverse nature (e.g., Ezaki et al. 2003; Baud et al. 2005; Yang et al. 2011; Heindel et al. 2018).

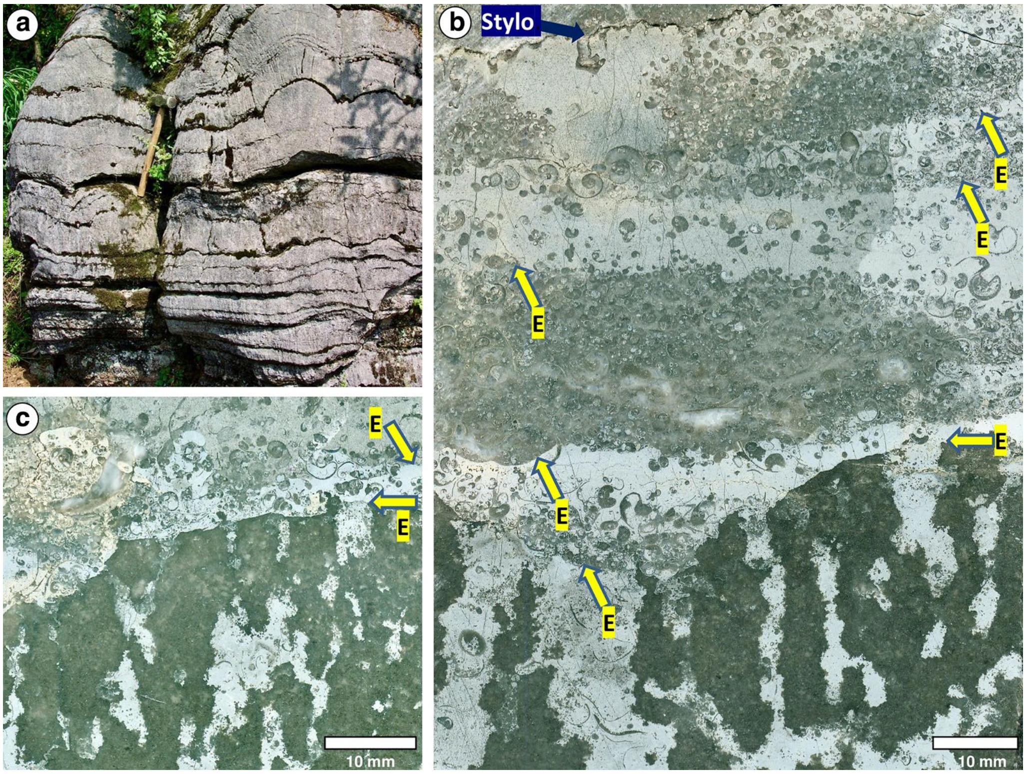

Fig. 3 Post-EPE microbialites from Dongwan site, Sichuan, China. **a** field image of layered microbialite; **b** vertical polished slab near the top of the microbialite, showing eroded microbialite head (dark), the top of which is eroded (E), overlain by several thin layers of shelly packstones-grainstones, each of which has an eroded top, see text for discussion; the rock is affected a little by pressure solution at the top (Stylo); **c** detail of another specimen near to (**b**), showing more detail of eroded microbialite and overlying shell-rich micrite

Those in South China (eastern Tethys) were dominated by narrow-branched calcimicrobial structures that are extensively recrystallized; in some places there are also stromatolites. Microbialites in South China have a significantly different architecture from those of western Tethys (principally Turkey and Iran, see Kershaw 2017). In Turkey, there is a mixture of interbedded stromatolites and thrombolites; in Iran, stromatolites and thrombolites are abundant in different sites; stromatolites in Iran are commonly narrow columns, unlike those of Turkey and South China. Despite the variation in nature of the microbialite biostromes, they contain abundant shelly fossils including ostracod taxa not found elsewhere, stimulating the idea of Forel et al. (2013a) that the microbialite was a refuge from the adverse effects of the extinction event. The South China microbialites comprise two main facies: (1) layers consisting of microbial components and intervening micrite; (2) between layers are uncommon shell-rich lenses of packstone-grainstone fabric (Figs. 2, 3). Ostracods are abundant in both facies.

The refuge hypothesis has experienced a mixed reception. It is considered unlikely by some authors (e.g., Hautmann et al. 2015). Wan et al. (2021) interpreted the microbialites as a taphonomic window in respect of the ostracods, where the lower energy of the microbialite environment provided an ideal location for preservation of imported ostracod shells, transported by current action from a life location outside the microbial setting. The concept of a taphonomic window is well known as a means to preserve components of an ecosystem in other locations or mineralogies, otherwise these components are lost to the fossil record (e.g., Cherns et al. 2008). For their proposal, Wan et al. (2021) drew on the interpretations of the depositional history of the microbialite and noted that the ostracod faunas are part of lenses of shelly debris deposited on microbialite layers (see also Hautmann et al. 2015).

In the field, the microbialite biostromes are seen as continuous sheets without much lateral change. In most field sites there is no evidence of the margins of the biostromes, a notable exception being the Great Bank of Guizhou, where the microbialite forms a sheet across the shallow marine top of the bank and the microbialite disappears at its margins; even so, in the field these margins are rarely observed because of outcrop vegetation cover. Consequently, ideas about the possibility of ostracods living *not* on the microbialite, but nearby, are not supported by field evidence. Furthermore, Hautmann et al. (2015) described a scenario of autochthonous to para-autochthonous shell layers interbedded with microbialite layers, with a clear indication that the shells lived on the microbialite, either in between heads and branches of microbialite components or on the eroded tops of individual layers of microbialite. However, examination of logs of the latest Permian to earliest Triassic facies (e.g., Kershaw et al. 2012; Hautmann et al. 2015) reveals that micrite sediment dominates the matrix in microbialite layers and shell lenses are uncommon. Furthermore, there is little evidence of physical damage of microbialite components (calcimicrobes, stromatolites, thrombolites and others) because of the low energy setting (Fig. 4). Nevertheless, some microbialite layer tops show minor erosion of both the microbial calcite (Fig. 3c) and micrite sediment, indicating early (sea-floor) lithification of microbialite layers, with shell lenses deposited in topographic lows across tops of microbialite layers, presumably during storms (see Kershaw 2015, figs. 3–5). Shell-layer contacts are commonly sharp, indicating early consolidation of individual shelly deposits (Fig. 3b). Taphonomically, ostracods are relatively well preserved in both facies, with only minor breakage to valve margins. The high number of juveniles present as carapaces in the microbialite facies illustrates the importance of juvenile mortality, and thus the persistence of relatively deleterious conditions in spite of all adaptations to cope with this context (Forel 2014; Forel et al. 2015). The overall dominance of carapaces, both adults and juveniles, is indicative of the lack of post-mortem transportation (e.g., Boomer et al. 2003) that would have disarticulated most of them. Because of the large area of distribution of microbialite biostromes, it is difficult to imagine that the ostracods were not living in the microbialite facies, and instead they likely inhabited quiet places between microbialite calcite heads and branches, and on the eroded tops of individual microbialite layers. Thus any assessment of the microbialite as a taphonomic window for ostracod preservation needs to take into account the complexity of the sedimentary component of the microbialite. In our opinion, the presence of small erosion surfaces between microbialite layers and also within sediment fills (Figs. 3, 4) indicate that early lithification likely prevented use of the microbialite as a taphonomic window.

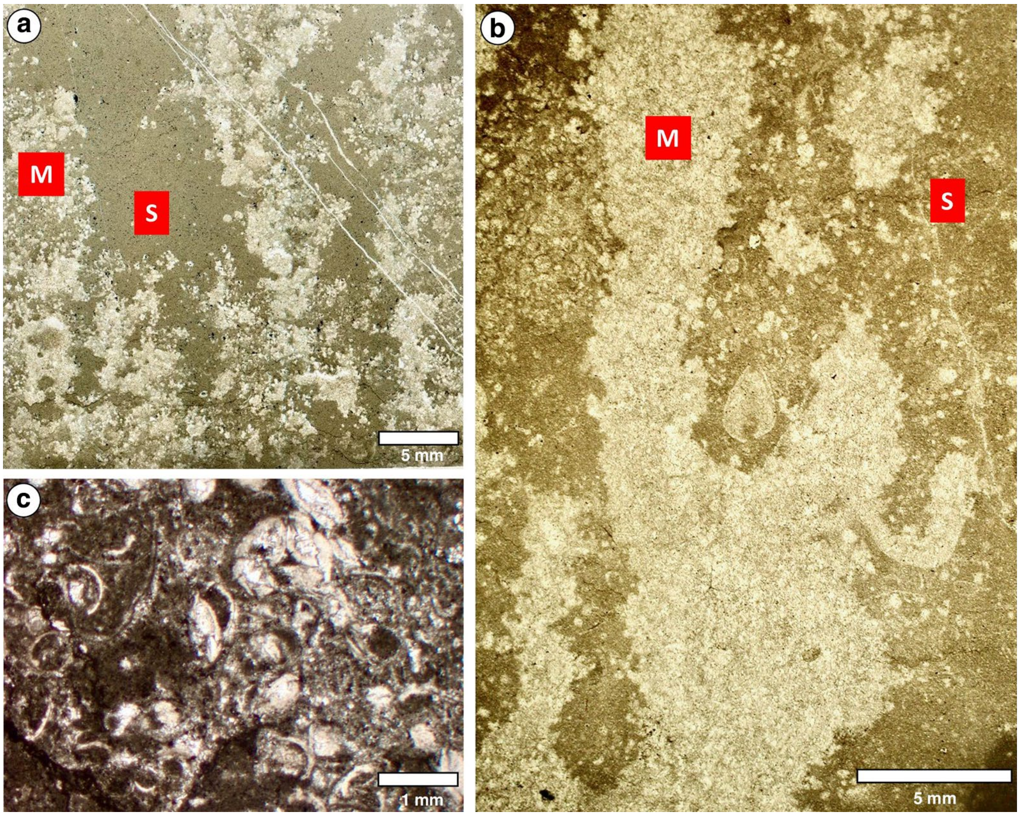

Fig. 4 Details of post-EPE microbialite from South China, showing branches and sedimentary fill, all vertical thin section views. **a** large thin section view of several microbialite branches (M) with micrite fill (S), Baizhuyuan site, Sichuan; **b** detail of another thin section, of recrystallised microbialite (M) with delicate margins preserved in contact with micrite and bioclastic fill; a complete ostracod is shown in the centre, Jianshuigou site, Sichuan; **c** detail of another thin section showing abundant complete ostracods, Dajiang Site, Guizhou

Conclusions

Reconsideration of ostracod taxa in microbialite facies in the immediate aftermath of the end-Permian extinction, reveals that:

1. Ostracod taxonomy and ontogeny (with associated changes in body shape and size) are complex and critical aspects that require careful consideration to establish a robust taxonomic system, which is a pre-requisite to any analysis of taxonomic diversity, morphological disparity and taphonomy.
2. The high abundance of commonly articulated ostracods in the widely distributed microbialites in shallow marine environments in South China after the EPE is considered evidence that the ostracods lived on the sea floor amongst microbial masses. The low-energy environment and well-established facies patterns of the post-extinction microbialite that contains ostracod taxa unique to the microbialite, remains a possible refuge for ostracods after the extinction. Thus the 'refuge hypothesis' remains viable and the concept of a taphonomic window is not needed.
3. The reliability of data (measurements of ostracod shells) in the light of taxonomic, ontogenetic and preservation issues is a major challenge. Poor, unreliable or over-refined data are a growing problem and the most sophisticated data manipulation cannot solve the basic problem of basing conclusions on misleading generalisations, in particular the (over)assessment of past biological diversity.
4. Although this study has considered only ostracods, the principles applied here may have relevance to other fossil groups with complex taxonomic issues.

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