

# Thoughts on the Late Paleozoic–Early Mesozoic records of deep-sea ostracods

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**ABSTRACT:** The nature and timing of mechanisms and events that shaped the deep-sea biodiversity are still debated. The present contribution provides an analysis and discussion of the distribution of off-shelf ostracods in the Late Paleozoic–Early Mesozoic. A taxonomic revision introduces *Kozuria* gen. nov. to accommodate Triassic species of *Acanthoscapha*, traditionally seen as Devonian–Carboniferous holdover archetypal of the Middle Triassic deep-sea of the western Tethys. The taxonomic composition as well as the temporal and geographic distribution of Permian and Triassic off-shelf assemblages are summarized and discussed in the light of climatic and biotic events. This analysis illustrates the Triassic uniformization of the composition of off-shelf assemblages and two possible periods of offshore migration in the late Permian (Changhsingian) and Middle Triassic (Anisian).

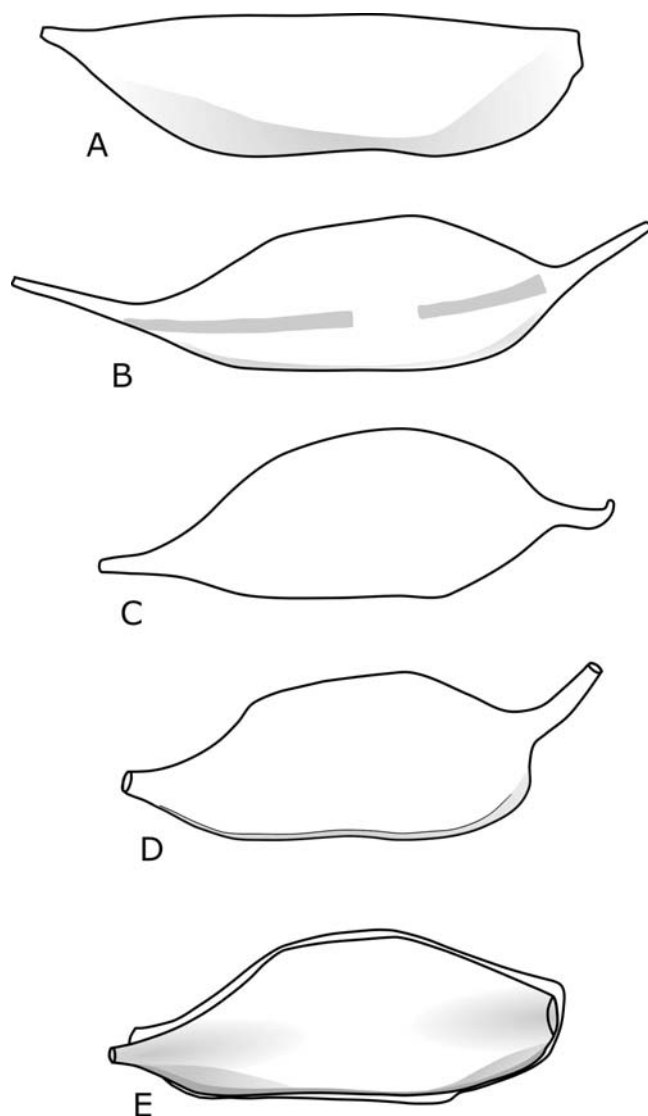
**Keywords:** Deep-sea ostracods, Permian, Triassic, survival, radiation, migration

## INTRODUCTION

It is now largely accepted that the deep-sea supports one of the highest levels of biodiversity on Earth and that it greatly differs from shallow marine and terrestrial ecosystems (e.g., Gray et al. 1997; Ramirez-Llodra et al. 2010; Rex and Etter 2010). However, the mechanisms and events that shaped this diversity are still debated. The idea that deep-sea diversity results from shallow-water dispersers is common (e.g., Moseley 1880; Jablonski et al. 1983; Vermeij 1995; Jacobs and Lindberg 1998) but taxa are also known to have dispersed from deep to shallow seas (e.g., Jablonski and Bottjer 1991; Jablonski 2005; Lindner et al. 2008). The apparent offshore migration of marine benthos over time implies the antiquity of at least part of the deep-sea fauna (e.g., Lethiers and Raymond 1991; Vermeij 1995; Jablonski 2005; Smith and Stockley 2005; Thuy et al. 2014). Debates have also increasingly focused on how the Cretaceous Oceanic Anoxic Events and Cenozoic cooling of deep-water masses may have hindered the colonization of deep habitats (e.g., Jacobs and Lindberg 1998; Horne 1999; McLain and Hardy 2010; Rex and Etter 2010). Therefore, the modern deep-sea fauna either survived anoxic events by moving to oxygenated shallow-water refuges or arose from colonization by shallow-water fauna after the Paleocene (e.g., Jacobs and Lindberg 1998; Horne 1999; Wilson 1999; Benton and Twitchett 2003; McLain and Hardy 2010). Estimates of the timing of deep-sea colonization by isopods based on molecular clock calibrated against the fossil record indicate that anoxic events at the Permian/Triassic boundary and during the Mesozoic did not cause the extinction of the entire deep-sea fauna (Lins et al. 2012). Others have proposed that the ancestors of some deep-sea lineages colonized this environment prior to or during the Mesozoic and survived the subsequent multiple anoxic events (e.g., Wilson 1999; McLain and Hardy 2010). Biogeographic patterns and molecular clock estimates calibrated against the fossil record of shallow-water sister groups of the modern deep-sea

fauna provided dates from Early Mesozoic to Pleistocene, most converging to a latest Mesozoic or Cenozoic origin (Menzies et al. 1973; Wilson 1999; Smith and Stockley 2005; Strugnell et al. 2008). Rather than being a cause of extinction, anoxia may have contributed to speciation in these lineages (e.g., McLain and Hardy 2010). In these debates, understanding the rise of Mesozoic deep-sea ecosystems is a major crucible. However, the subduction of oceanic crust into the mantle results in the relatively young Mesozoic–Cenozoic age of the current oceanic basins (Müller et al. 2008) and older remains are limited to fragments preserved as ophiolites. The discovery of Carboniferous oceanic crust within the eastern Mediterranean Sea (Granot 2016) may create new investigation perspectives. This project is further complicated by the fact that the deep-sea is actually a complex mosaic of diverse environments including continental slopes, abyssal plains, oceanic trenches, mid-ocean ridges, seamounts, hydrothermal fields, cold-seeps, each being highly heterogeneous (e.g., Riehl et al. 2020).

What can be the contribution of ostracods to this discussion? Ostracods have inhabited deep-water bodies during their entire history (e.g., Blumenstengel 1965a, b; Schallreuter 1971) and their Paleozoic fossil record documents massive migration from shelves to off-shelf areas after the end-Devonian extinction (e.g., Lethiers and Feist 1991; Lethiers and Raymond 1991; Crasquin and Horne 2018). Hence, ostracods are ideal for unlocking events and patterns that may have structured the deep-sea faunas in the Late Paleozoic–Early Mesozoic as they are abundant, diverse and share a long history with deep-sea environments. The Late Paleozoic–Early Mesozoic interval has been pivotal in the history of marine ecosystems with two major biological crises, at the end of the Permian (EPE; c. 252 million years ago) and at the end of the Triassic (TJE; c. 201 million years ago). The Permian and Triassic evolution of neritic ostracods is progressively understood (see Crasquin and Forel 2015; Forel and Crasquin 2020 for recent summaries) and that



TEXT-FIGURE 1

Lateral profiles of *Acanthoscapha* type species and species of the Permian and Triassic re-attributed to *Kozuria* Forel gen. nov. Drawings not to scale.

A. *Acanthoscapha navicula* (Ulrich 1891), right lateral view of a carapace, Early Devonian.

B. *Kozuria bogschi* (Kozur 1970), external view of a right valve, Anisian.

C. *Kozuria veghae* (Kozur 1970), external view of a right valve, Anisian.

D. *Kozuria mersinella* (Forel in Forel et al. 2019a), external view of a right valve, Carnian.

E. *Kozuria amphialata* (Kristan-Tollmann 1973), right lateral view of a carapace, Norian.

characterizing the TJE and Jurassic interval still requires efforts, but the evolution of off-shelf taxa remains a no man's land.

Reports of Permian and Triassic bathyal and possibly abyssal ostracod assemblages have accumulated in the last 50 years, all characterized by remnants of distinctive deep-sea Paleozoic families (e.g., Kozur 1970; Yuan et al. 2007, 2009; Forel et al.

2019a). Conversely, the recognition of off-shelf assemblages in the Jurassic is problematic because of the absence of such groups considered as endemic to off-shelf conditions. Here we perform a standardization of taxonomic identifications: *Kozuria* gen. nov. is introduced to accommodate Triassic species previously attributed to *Acanthoscapha* Ulrich and Bassler 1923. We describe the distribution of off-shelf assemblages and taxa at the Late Paleozoic–Early Mesozoic transition and question the paradigm that the environmental distribution of Beecherellidae, Rectoriidae, Bythocytheridae and Tricorninidae did not change from the Devonian, in the light of growing evidence of offshore-onshore exchanges, including for ostracods (e.g., Smith and Stockley 2005; Thuy 2013; Forel et al. 2019b).

## TAXONOMIC REMARKS AND UPDATES

Before discussing the composition and distribution of deep-sea ostracod assemblages from the Late Paleozoic and Early Mesozoic interval, a taxonomic standardization is necessary to avoid artificially extending the range of Devonian–Carboniferous taxa for which diagnostic conceptions have gradually shifted from one identification to another.

Class OSTRACODA Latreille 1806

Subclass PODOCOPA Müller 1894

Superfamily BAIRDIOIDEA Sars 1887

Family BEECHERELLIDAE Ulrich 1894

**Preliminary remarks:** Beecherellidae Ulrich 1894 are diagnosed as “Bairdiacea with elongate, subrectangular, trapezoid to triangular outline; valves marginally depressed or ventrally flattened; mostly marginally spines developed on one or both valves, hinge undifferentiated; (in post-Silurian genera) distinct duplicatures common, showing conspicuous vestibula” (p. 370 in Becker 2001). *Acanthoscapha* Ulrich and Bassler 1923, type species: *Acanthoscapha navicula* (Ulrich 1891; text-fig. 1A), was described from the Early Devonian of Albany County, New York (Ulrich and Bassler 1923) and its earliest known occurrence is of Late Ordovician age (Baldis and Cabaleri 1988). Following discussions and revisions by Berdan (1960) and Becker (2001), *Acanthoscapha* is diagnosed as follows: “with more-or-less elongate, rectangular, trapezoid to spindle-like outline; carapace with flattened ends, greatest length dorsally; spines (or horn-like extensions) posteriorly and/or anteriorly developed on larger valve or on both valves, lateral spines known occasionally; lateral surface smooth or with delicate ornament; ventral overlap distinct” (p. 371 in Becker 2001). At the time of writing, seven *Acanthoscapha* species have been documented from the Permian and Triassic interval: *A. amphialata* Kristan-Tollmann 1973, *A. blessi* Kozur 1990, *A. bogschi* Kozur 1970, *A. mersinella* Forel in Forel et al. 2019, *A. veghae* Kozur 1970, *A. sp. 1* in Tanaka et al. 2018, *A. sp. 2* in Tanaka et al. 2018.

Genus ***Kozuria*** Forel n. gen.

Text-figure 1B–E

**Type species:** *Kozuria bogschi* (Kozur 1970).

**Etymology:** In reference to Dr. Heinz Kozur, who was the first to document this genus (identified as *Acanthoscapha*) in Triassic marine deposits of Hungary.

**Diagnosis:** Elongate, laterally asymmetric Beecherellidae with tapered posterior end, tripartite dorsal margin, maximal length

located below mid-height, anterior and posterior borders prolonged by spines oriented upward.

*Species included:*

• *Acanthoscapha bogschi* Kozur 1970 from the Anisian of Hungary (Kozur 1970; text-fig. 1B), later documented in Romania (Salaj and Jendrejáková 1984; Mirăuță et al. 1991, 1993; Crasquin-Soleau and Grădinaru 1996; Sebe et al. 2013) and Austria (Mette et al. 2015), and from the Ladinian of Hungary (Monostori and Tóth 2013);

• *Acanthoscapha veghae* Kozur 1970 from the Anisian of Hungary (Kozur 1970; text-fig. 1C), later documented in Romania (Mirăuță et al. 1991 1993; Crasquin-Soleau and Grădinaru 1996; Sebe et al. 2013), and from the Ladinian of Hungary (Monostori and Tóth 2013);

• *Acanthoscapha mersinella* Forel in Forel et al. 2019 from the Carnian of Turkey (Forel et al. 2019a; text-fig. 1D);

• *Acanthoscapha amphialata* Kristan-Tollmann 1973 from the Norian of Austria (Kristan-Tollmann 1973; text-fig. 1E).

*Remarks:* The first record of *Acanthoscapha* for the Permian and Triassic interval was provided by Kozur (1970) who erected *Acanthoscapha bogschi* (text-fig. 1B) and *Acanthoscapha veghae* (text-fig. 1C) from the Anisian, Middle Triassic, of Hungary. These two species and more largely this concept of the genus *Acanthoscapha* were subsequently considered as emblematic of Middle Triassic deep-sea assemblages in western Tethys (Salaj and Jendrejáková 1984; Mirăuță et al. 1991, 1993; Crasquin-Soleau and Grădinaru 1996; Monostori and Tóth 2013; Sebe et al. 2013; Mette et al. 2015) with rarer occurrences in the Late Triassic (Kristan-Tollmann 1973; Forel et al. 2019a). However, most of these Permian and Triassic species radically differ from *Acanthoscapha* by the maximum of length systematically located below mid-height, resulting in a much more pronounced bairdiid outline with tapered posterior end (text-fig. 1). The observed shift in the notion of *Acanthoscapha* was introduced by Kozur (1970) and paved the way for subsequent misidentifications. *Acanthoscapha blessi* Kozur 1990 from the Wuchiapingian of Hungary (Kozur 1990) is excluded from *Kozuria* because of its massive and symmetric subrectangular outline with maximal length close to dorsal margin. *Acanthoscapha* sp. 1 from the Sakmarian of Japan (Tanaka et al. 2018) is also excluded from *Kozuria* because of its massive subquadrate lateral outline with maximal length close to dorsal margin. *Acanthoscapha* sp. 2 from the same locality (Tanaka et al. 2018) does not belong to *Acanthoscapha* because of its very ventral maximal length. This species also does not belong to *Kozuria* because its anterior and posterior ends are caudate rather than prolonged by spines. This taxonomic re-evaluation of the Permian and Triassic identifications in the light of the original and emended diagnoses of *Acanthoscapha* implies that this genus did not range higher than the Carboniferous.

*Occurrence:* Anisian, Middle Triassic of Hungary (Kozur 1970), Romania (Salaj and Jendrejáková 1984; Mirăuță et al. 1991, 1993; Crasquin-Soleau and Grădinaru 1996; Sebe et al. 2013) Austria (Mette et al. 2015), to Norian, Late Triassic of Austria (Kristan-Tollmann 1973).

Family BAIRDIIDAE Sars 1887

Genus *Processobairdia* Blumenstengel 1965b

Type species: *Processobairdia anteroцерата* Blumenstengel 1965b

*Remarks:* *Processobairdia* species have been reported from off-shelf ostracod assemblages from the Frasnian and Fammenian stages of the Upper Devonian (e.g., Blumenstengel 1965b; Bless and Michel 1967; Dreesen et al. 1985; Becker and Blumenstengel 1992). It was recently reported from the Anisian, Middle Triassic, of Hungary (Mette et al. 2015). The original diagnosis of *Processobairdia* reports horns on the latero-dorsal area of each valve, which cannot be confirmed for the Anisian material as only left valves were found. In the absence of complete carapaces, this Triassic occurrence should not be taken as valid to avoid the artificial extension of the stratigraphic range of *Processobairdia*, as previously suggested in Forel et al. (2019a). We therefore consider that *Processobairdia* did not range to the Middle Triassic.

DEEP-SEA ASSEMBLAGES IN THE LATE PALEOZOIC-EARLY MESOZOIC

How are deep-sea ostracod assemblages recognized?

The Thuringian ecotype is considered as a Devonian–Carboniferous off-shelf fauna characterized by taxa with distinctively prominent spines occurring in bathyal facies: a summary and characteristic taxa are provided and discussed in Crasquin and Horne (2018). Lethiers and Raymond (1991) introduced a triangular diagram to estimate the bathymetric attribution of assemblages from the Famennian–Dinantian using the relative proportions of species of the genus *Bairdia*, Thuringian ecotype and other groups. In this model:

- assemblages with more than 50% of Thuringian species and less than 15% of *Bairdia* represent bathyal conditions,

- for proportions between 12 to 50% of Thuringian species and 15 to 22% of *Bairdia*, the assemblages are attributed to the outer neritic-upper bathyal area.

Since the first discovery of remnants of the Thuringian ecotype in Middle Triassic deposits of Hungary by Kozur (1970), this model has been applied several times for the Permian and Triassic interval (e.g., Crasquin-Soleau and Grădinaru 1996; Yuan et al. 2007; Crasquin et al. 2008; Sebe et al. 2013; Forel et al. 2018). Thuringian taxa documented in Permian and Triassic belong to Beecherellidae (*Kozuria*), Rectoriidae (e.g., *Ortho-naria*, *Anahuacia*, *Triplacera*), Bythocytheridae (e.g., *Paraberounella*, *Striatobythoceratina*; including Berounellidae following the revision of Schornikov 1990), Tricorninidae (*Tricornina*, *Ovornina*, *Bohemina*), as well as other taxa exhibiting “deep-sea diagnostic” characters (e.g., *Bairdia*, *Acratia*, certain healdiids). These taxa are absent from the Jurassic fossil record, leading to the impossibility to recognize off-shelf assemblages except by their dissimilarity with coeval material (e.g., Lord and Lambourne 1991; Honigstein et al. 2014). The implicit paradigm that underlies the use of the Lethiers and Raymond (1991) diagram for Permian and Triassic assemblages is that the environmental distribution of Beecherellidae, Rectoriidae, Bythocytheridae and Tricorninidae was comparable in the Devonian and in the Late Paleozoic–Early Mesozoic time interval. Does this fixist view remain correct and acceptable in



TABLE 1

Summary of outer neritic-upper bathyal, bathyal and bathyal- abyssal ostracod assemblages of the Permian and Triassic time interval. In 4 of the investigated contributions (Yuan et al. 2007, 2009; Crasquin et al. 2008; Sebe et al. 2013), two distinct types of ostracod assemblages are recognized (outer neritic-upper bathyal, bathyal).

Epoch	Stage	Country	Standardized environment	References
Late Triassic	Carnian	Turkey	outer neritic-upper bathyal	Forel et al., 2017
Middle Triassic	Ladinian	Hungary	bathyal	Monostori & Tóth 2013
	Anisian	Turkey	bathyal	Kozur et al. 2000
		Romania	bathyal	Crasquin-Soleau & Grădinaru, 1996; Sebe et al. 2013
			outer neritic-upper bathyal	Sebe et al. 2013; Forel & Grădinaru 2018
		Hungary	bathyal	Kozur 1970; Monostori 1995
		Austria	outer neritic-upper bathyal	Mette et al. 2014
Early Triassic	Spathian	Romania	outer neritic-upper bathyal	Sebe et al. 2013
Late Permian	Changhsingian	South China	bathyal	Yuan et al., 2007, 2009
			outer neritic-upper bathyal	Yuan et al., 2007, 2009
	Wuchiapingian	Sicily	bathyal-abyssal	Kozur 1991
Early Permian	Kungurian	Sicily	bathyal	Crasquin et al. 2008
			outer neritic-upper bathyal	Crasquin et al. 2008
		Thailand	bathyal	Burrett et al., 2014 (age precised in PBDB)

the context of growing evidence of offshore-onshore exchanges (e.g., Thuy 2013; Forel et al. 2019b)?

How far do sedimentological and other paleontological records support the ostracod evidence for Permian and Triassic off-shelf conditions? Permian off-shelf assemblages have been reported from the Sakmarian–Artinskian of Indonesia (Bless 1987; Gründel and Kozur 1975), Kungurian of Sicily (Crasquin et al. 2008) and Thailand (Burrett et al. 2014), Wuchiapingian of Sicily (Kozur 1991), Changhsingian of China (Yuan et al. 2007, 2009) (Table 1). Triassic ones are known from the Anisian of Austria (Mette et al. 2015), Romania (Crasquin and Grădinaru 1996; Sebe et al. 2013; Forel and Grădinaru 2018), Hungary (Kozur 1970; Monostori 1995) and Turkey (Kozur et al. 2000), Ladinian of Hungary (Monostori and Tóth 2013) and Carnian of Turkey (Forel et al. 2019a) (Table 1). Sedimentological and other paleontological data obtained for most of the studied samples/assemblages are in line with ostracod information (e.g., Flügel et al. 1991 for the Permian of Sicily; He et al. 2005 for the Late Permian of China; Grădinaru 2000 for the Middle Triassic of North Dobrogea, Romania; Budai et al. 2001 for the Ladinian of Hungary; Chantong et al. 2013 for the Kungurian of Thailand; Bechstädt and Mostler 1974 for the Anisian of Austria). However, the Lower Permian assemblages from Indonesia are problematic because they were regarded as recording bathyal conditions by Gründel and Kozur (1975) and Bless (1987) but as corresponding to shallow marine flysch sediments by Audley-Charles (1965). The samples analyzed by Gründel and Kozur (1975) and Bless (1987) have been collected from Bitauai, Mutis, Nono Ofien in western Timor (Indonesia) and have also been processed for conodont analysis (van den Boogaard 1987). According to Charlton et al. (2002) and Haig et al. (2014), all samples are issued from the Bitauai beds of the Maubisse Formation, largely representing shallow marine environments deposited on topographic highs (Charlton et al. 2002). The structural complexity of Lower Permian successions in Timor makes it hard to ascertain the position and age of the samples studied for ostracods: a complete re-analysis based on sedimentary structures, microfacies and ostracod content from well-positioned samples in terms of local litho-stratigraphy is an absolute necessity for future works.

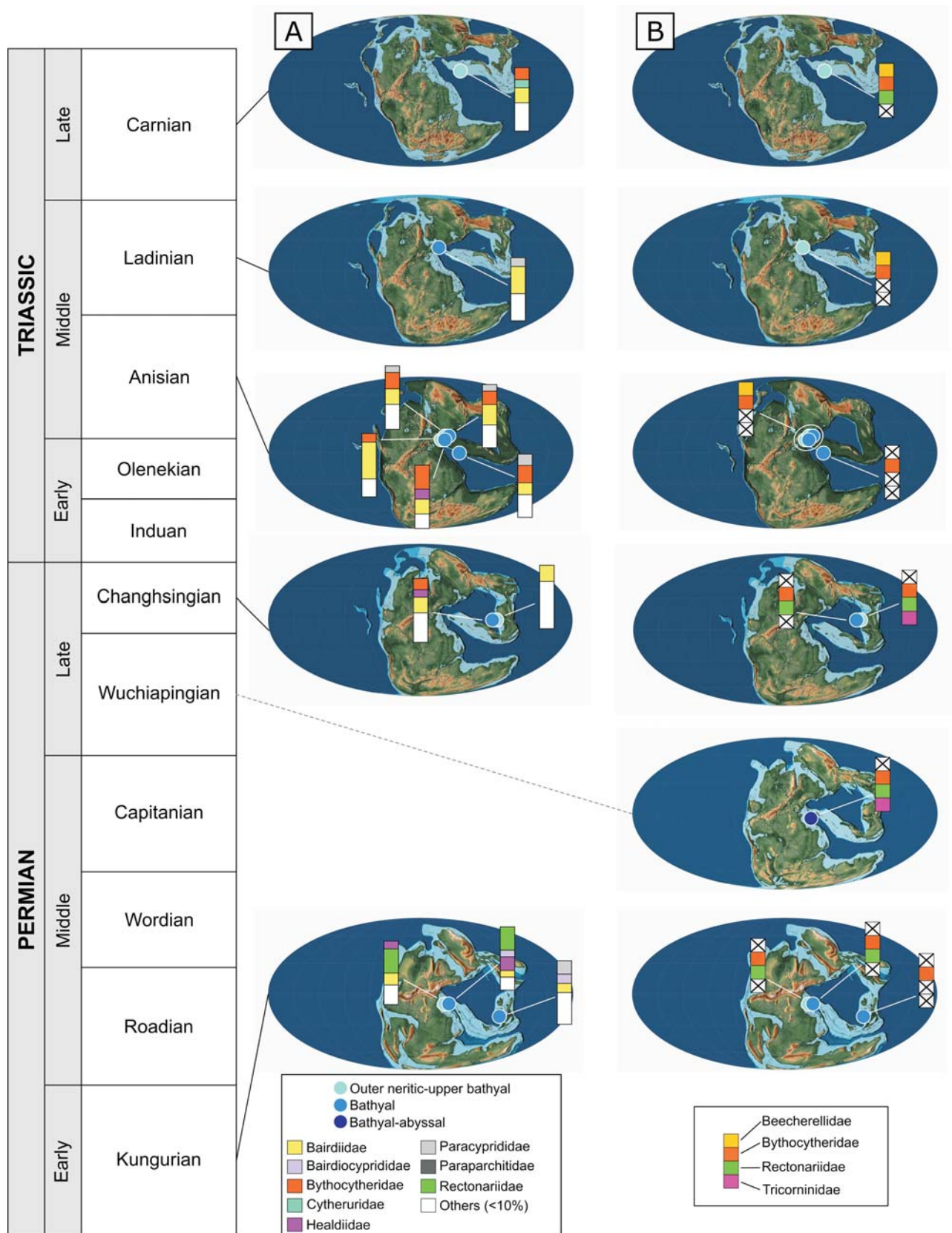
### Geographic and stratigraphic distributions

In the present contribution, all assemblages referred to as “deep-sea” in the literature have been gathered, without considering isolated occurrences (e.g., Kozur 1971 1972, 1973; Tanaka et al. 2014) and incomplete assemblages (e.g., Kristan-Tollmann 1978). Sebe et al. (2013) referred to “bathyal-abyssal” conditions for assemblages with more than 50% of deep-sea species without discussion so that we do not consider this attribution and only refer to bathyal conditions. Ostracods from “lower bathyal and abyssal zones in water-depths well below 1000 m” have been described for two distinct samples of the Wuchiapingian of Sicily (Kozur 1991) but it is unclear whether the entire assemblages are described thus they are not included in the discussion of familial composition. The late Kungurian–Radian age of the bathyal assemblage from Thailand (Burrett et al. 2014) has been revised for Kungurian following the Palaeobiology Database updates (accessed in November 2020). As detailed in the previous paragraph, ostracods from the Sakmarian–Artinskian of Timor (Gründel and Kozur 1975; Bless 1987) are problematic: they are excluded from this analysis but considered in the discussion paragraph.

The assemblages are referred to the following standardized categories: outer neritic-upper bathyal (ON-UB), bathyal (upper limit around 700 m depth), bathyal-abyssal (more than 2000 m deep; Table 1). The proportions of families that account for at least 10% of the genera of each assemblage are shown in text-fig. 2A (complete familial compositions and proportions are provided in Supplementary data) and the presence/absence of deep-sea families Beecherellidae, Bythocytheridae, Rectonariidae, Tricorninidae is shown in text-fig. 2B.

### The Permian and Triassic assemblages

Five ON-UB and eight bathyal ostracod assemblages have so far been documented for the Permian and Triassic time interval, all located within the Tethyan area (Figs 2A, B). ON-UB and bathyal assemblages from same area and age (Kungurian of Sicily, Changhsingian of China, Anisian of Hungary and Romania; text-fig. 2A) only differ by their respective proportions of domi-



TEXT-FIGURE 2

Distribution and composition of off-shelf ostracod assemblages in the Permian and Triassic interval. (A) Relative proportions of families of each assemblage, with details of the families that account for more than 10% of the genera. (B) Presence/absence of Beecherellidae, Bythocytheridae, Rectonariidae, Tricorninidae. Palaeogeographic maps generated from the GPlatesdatapack (Müller et al. 2018).

nant families, pointing to gradual shifts rather than drastic changes from one bathymetric compartment to another. Major changes are observed through space and time but Bairdiidae are invariable members of dominant families. The dominant components of ON-UB communities are more heterogeneous in the Permian than in the Triassic, possibly illustrating the influence of important climatic changes that occurred during this period, as discussed later. Bythocytheridae and Rectoriidae are constant components of Permian assemblages: Bythocytheridae only exceed 10% in bathyal conditions in the Sakmarian–Artinskian of Timor and Changhsingian of China (Yuan et al. 2007), Rectoriidae are dominant only in the Early Permian when they range from 10% and 37%. The unusual composition of the bathyal assemblage of the Kungurian of Thailand (absence of Rectoriidae, co-dominance of Bairdiidae and Bairdiocyprididae) may largely illustrate transportation from shallower waters as hypothesized by Burrett et al. (2014). Triassic off-shelf assemblages record:

- The homogenisation of their composition (text-fig. 2A) with the overall dominance of Bairdiidae and Bythocytheridae and the frequent occurrence of Paracyprididae (*Spinocypris*), they mainly differ by the accessory taxa and relative proportions of dominant families;
- The disappearance of Tricorninidae from the fossil record;
- The re-emergence of Beecherellidae and Rectoriidae respectively in the Anisian of western Tethys (Romania, Hungary, Austria; Kozur 1970; Crasquin-Soleau and Grădinaru 1996; Sebe et al. 2013; Mette et al. 2015) and the Carnian of Turkey (Forel et al. 2019a). The latest Rectoriidae occurrence in the Changhsingian, Late Permian, of China (Yuan et al. 2007, 2009) has therefore been followed by a gap that lasted most of the Triassic. Conversely, the latest Permian occurrence of Beecherellidae is of Sakmarian age (Tanaka et al. 2018), implying an extremely long Lazarus record during most of the Permian and the Early Triassic. These gaps may be filled by future studies.

#### **The case of Devonian–Carboniferous remnants in the Permian and Triassic**

Over the studied interval, Tricorninidae experienced their highest diversity in the Artinskian–Sakmarian with three genera that were all previously known from the Devonian–Carboniferous interval (text-fig. 3; see Crasquin and Horne 2018). *Ovornina* and *Bohemina* residually extended to the Late Permian but failed to develop in the Triassic (text-fig. 4).

Thirteen Rectoriidae occurred in the Permian and Triassic interval and their highest diversity is observed in the Kungurian (text-figs. 3, 4). During most of the Early Permian, they were restricted to neotethyan neritic associations of Sicily and Indonesia (Crasquin et al. 2008; Bless 1987; Gründel and Kozur 1975). The Kungurian saw their extension to ON-UB and bathyal deposits followed by a Middle Permian gap and their re-emergence in the Late Permian in bathyal and bathyal-abysal conditions of China (Yuan et al. 2007) and Sicily respectively (Kozur 1991). Following another gap for the entire Early and Middle Triassic, they re-entered the fossil record in the ON-UB deposits of the Carnian of Turkey (Forel et al. 2019a). Their last known occurrence is reported from Upper Triassic outer neritic deposits of Romania (Forel and Grădinaru 2020; text-fig. 4).

In the Permian, Beecherellidae only occurred in seamount deposits of the Sakmarian of Japan (Tanaka et al. 2018). Following a major gap, they re-entered the fossil record in ON-UB and bathyal assemblages from the Anisian of western Tethys (Salaj and Jendrejáková 1984; Mirăuță et al. 1991, 1993; Crasquin-Soleau and Grădinaru 1996; Monostori and Tóth 2013; Sebe et al. 2013; Mette et al. 2015) to the Carnian of Turkey (Forel et al. 2019a) and their last record occurred in Norian outer neritic sediments of Austria (Kristan-Tollmann 1973). Only two genera have been reported for this interval: *Kozuria* n. gen., that may have radiated in the Permian, and *Gencella* with unclear roots as it is restricted to the Carnian of Turkey.

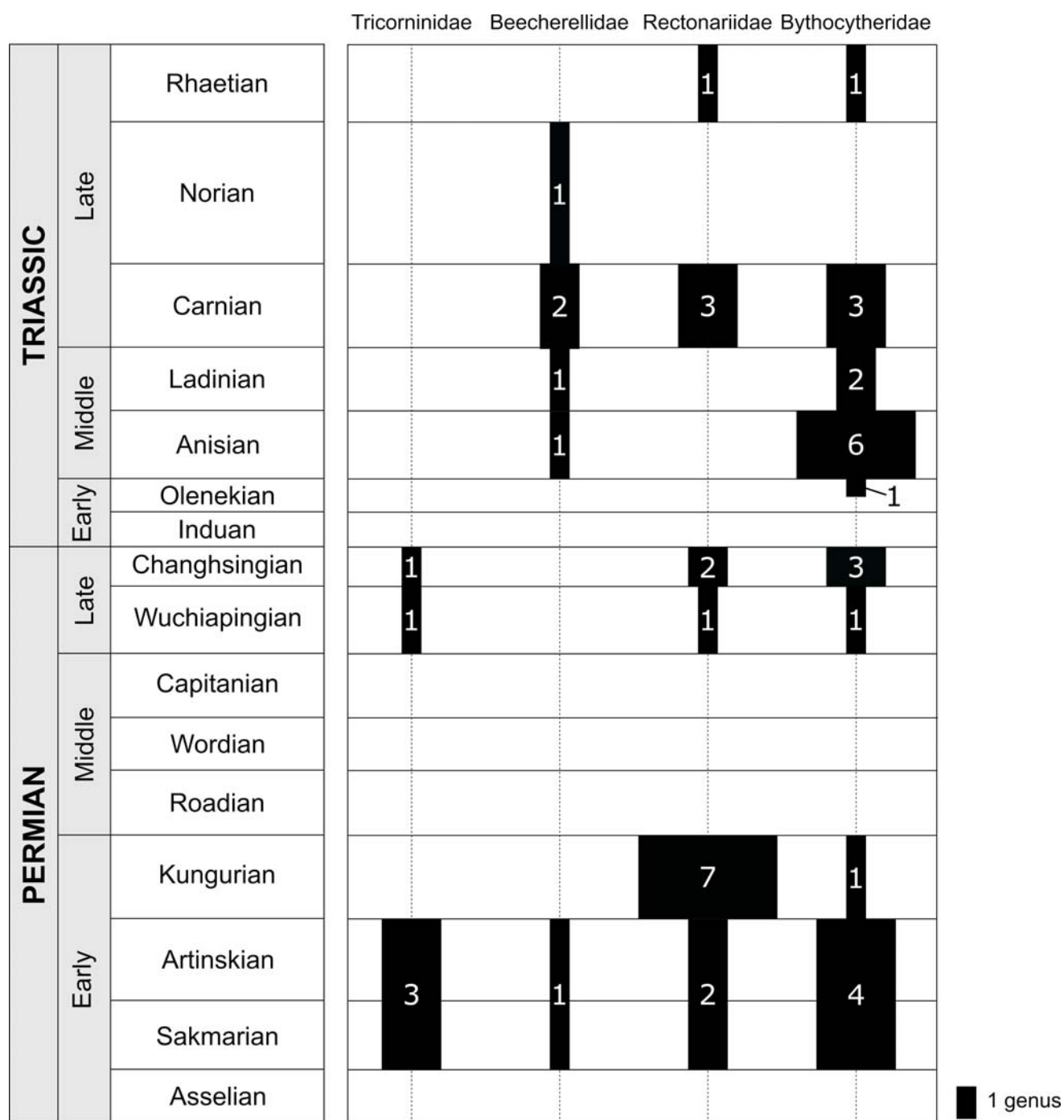
Nine deep-sea Bythocytheridae spanned the Permian and Triassic with a relatively complex history (text-figs 2A, 2B, 3). During this interval, Bythocytheridae have not been restricted to off-shelf environments (e.g., *Callicythere*; Wei 1981; Forel 2014). However *Bythoceratina*, *Monoceratina*, *Nagyella*, *Nemoceratina*, *Paraberounella*, *Striatobythoceratina*, *Triassocythere* and *Tuberoceratina* are traditionally found in off-shelf settings (text-fig. 4). Following a Wordian–Capitanian gap, Bythocytheridae re-entered the fossil record in the Late Permian and have been major components of Middle and Late Triassic assemblages. As a whole, most of their Early Permian history appears to have taken place in neritic conditions. *Paraberounella* occurred mainly in bathyal areas in the Permian and was restricted to ON-UB zones in the Ladinian and Carnian. The Late Carboniferous (Moscovian; Kozur 1990) and Late Permian (Changhsingian; Crasquin et al. 2010) records of *Triassocythere* correspond to purely neritic conditions. During the Triassic, *Triassocythere* had a mainly off-shelf history with its latest occurrence in the outer neritic area in the Rhaetian of Romania being the shallowest (Forel and Grădinaru 2020) but the state of preservation of this specimen indicates that it may have been transported. The pre-Triassic history of this genus is still poorly documented but it could illustrate a migration toward greater depths through the EPE. The oldest known occurrence of *Monoceratina* is from the Late Devonian (Frasnian; Becker and Wang 1992) and its entire Paleozoic history has been reported from purely neritic environments (e.g., Sohn 1969; Dreesen et al. 1985; Becker and Wang 1992). In the Permian and Triassic interval, two periods of off-shelf presence are recognized for this genus (text-fig. 4): in the Late Permian (Changhsingian; Yuan et al. 2007) and in the Middle Triassic (Anisian and Ladinian to a lesser extent; Kozur 1970; Monostori 1995; Crasquin-Soleau and Grădinaru 1996; Sebe et al. 2013). Owing that *Monoceratina* has never been recognized from off-shelf conditions outside these periods, the observed Permian and Triassic patterns cannot be considered as environmental restriction to one part of its habitability range. As *Monoceratina* was only known from shelf habitats, we consider that these patterns may also illustrate a migration toward greater depths.

## **DISCUSSION**

### **Survival and radiations in the Permian and Triassic**

The deep-sea has long been considered as a refuge for lineages excluded from continental shelf habitats by predators, competitors or unsuitable conditions (e.g., Vermeij 1995) and numerous discussions have questioned whether global oceanic anoxic events may have prevented the establishment of deep-sea fauna before the Late Cretaceous (e.g., Jacobs and Lindberg 1998; Horne 1999). The contribution of ostracodology that documents the long range of Paleozoic taxa is of utmost significance when





TEXT-FIGURE 3  
Generic diversity of Tricorninidae, Beecherellidae, Rectonariidae and deep-sea Bythocytheridae in the Permian and Triassic interval.

wondering about the survivorship of organisms through the EPE and the origin of Mesozoic deep-sea fauna.

The distributions of Rectonariidae, deep-sea Bythocytheridae, Tricorninidae and Beecherellidae in ON-UB and bathyal assemblages of the Permian and Triassic varied greatly (text-fig. 2B, 3, 4), possibly indicating distinct paleobiologies and paleoenvironmental requirements. The present contribution shows that *Acanthoscapha*, generally seen as archetypal of

Middle Triassic off-shelf conditions in western Tethys, did not occur in the Triassic. In the current state of our knowledge, Beecherellidae residually ranged up to the Carnian with sustained radiations that allowed for the emergence of *Kozuria* and *Gencella* in the Middle and Late Triassic respectively. The Permian record of Rectonariidae is characterized by the large amount of genera inherited from the Devonian–Carboniferous interval with only few new taxa in the Kungurian (text-fig. 4). Conversely, all Triassic Rectonariidae are new although kept in

open nomenclature because of their rarity. This feature also illustrates the sustained radiations within Rectonariidae through the EPE and in the Triassic. It may furthermore indicate that a major shift in the radiation rates of Rectonariidae occurred through the EPE, from low in the Permian to relatively high in the Triassic, although it is still difficult to clarify when exactly this shift occurred as they are unknown from Early and Middle Triassic deposits. The notion of survival therefore has to be used with caution as the occurrences of these families in the Permian and Triassic interval has been supported by relatively important radiation rates. Conversely, the very residual presence of Tricorninidae in the Permian and their absence from all Triassic assemblages illustrate the insufficiency of radiations to support the emergence of new genera. Tricorninidae can thus be considered, at the familial and generic levels, as long-term holdovers in the Permian and victims of the EPE. In terms of diversity, the Anisian has not only been the period of highest diversity for Bythocytheridae, but also a period of major radiation (text-fig. 4). However, this has not been the case for Rectonariidae, further accentuating the idea of distinct paleobiologies and/or the establishment of distinct paleoceanographic conditions in the Middle Triassic, as discussed below.

#### Linking the Permian and Triassic ostracod records to paleoclimatic and paleoenvironmental changes?

The Paleozoic ended with a prolonged glaciation known as the Late Paleozoic Ice Age, which lasted for more than 80 Myr between 338 and 256 Ma (e.g., Crowell 1999; Stephenson et al. 2007; Frank et al. 2008). The Late Paleozoic Ice Age comprised multiple glacial-deglacial episodes reflected by the advance and retreat of glaciers under drier and wetter climate conditions (Isbell et al. 2003; Kochhann et al. 2020). The deglaciation began in the Early Permian: most of the global climate change occurred between the start of widespread deglaciation in the Sakmarian and the onset of greenhouse conditions in the Kungurian (e.g., Isbell et al. 2003; Montañez et al. 2007). This glaciation may have initiated or intensified the thermohaline circulation in the world's oceans by the formation of cold, oxygenated water in polar regions mainly in the southern hemisphere (e.g., Frakes et al. 1992; Uchman 2004). Such cold-water masses affected Panthalassa and the southeastern parts of the Paleo-Tethys and in contrast, warm-to-temperate climates surrounded the western parts of the Paleo-Tethys (e.g., Frakes et al. 1992; Scotese 1997; Uchman 2004). The ostracods from the Sakmarian–Artinskian of Indonesia (Timor) are exceptional in that they illustrate the presence of Thuringian taxa in neritic conditions, following the most recent works on Lower Permian successions of the area detailed earlier. Bless (1987) proposed that:

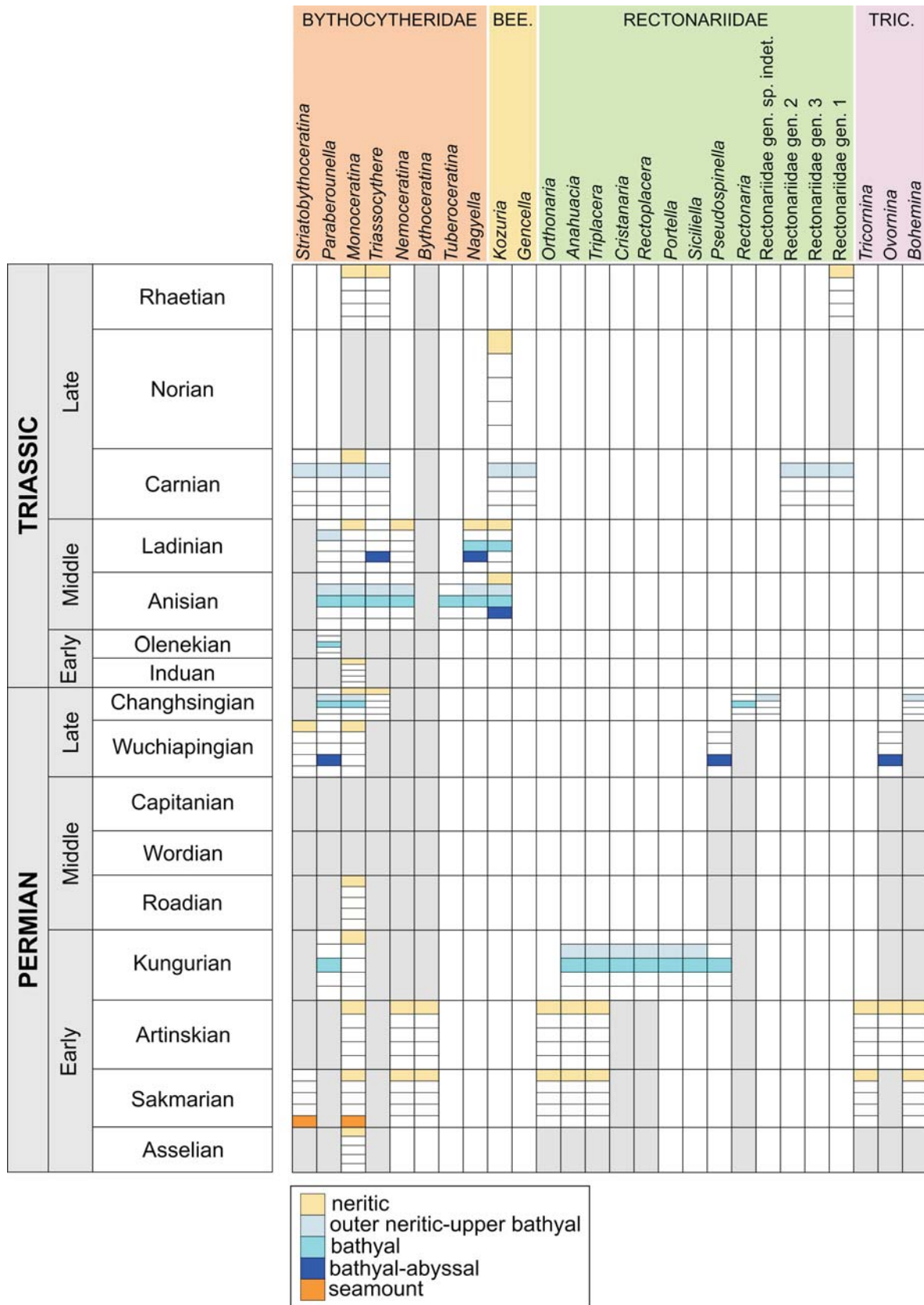
- off-shelf ostracods may have been transported onto the shelf by upwelling or currents,
- temperature controlled their distribution rather than depth or hydrodynamic conditions,
- slow competition pressure in the area may have allowed Thuringian ostracods to occupy shallow waters.

Only a precise re-analysis of assemblages in their geological context may help evaluating the degree of taphonomic mixing of these assemblages. The expansion of deep cold waters on continental margins associated with upwelling may have been of major importance in the observed pattern. The observed important proportion of Rectonariidae (text-fig. 2A) may relate to

the proximity of Pangea and nutrient influx by continental weathering, further increased by the end of the Late Paleozoic Ice Age but only precise samplings of Timor successions and neighbouring localities will allow deeper discussion.

The end of the Permian witnessed the onset of a superanoxic ocean from the Changhsingian to the Early Triassic (e.g., Isozaki 2007; Bond and Wignall 2010; Payne and Clapham 2012) and an episode of global warming during the Late Permian (e.g., Kearsy et al. 2009; Joachimski et al. 2012; Sun et al. 2012) that may have led to ocean stratification and ultimately to the formation of a chemocline (e.g., Kump et al. 2005; Isozaki 2009). This chemocline may first have been restricted to deep-sea areas and could have triggered the bathymetry-dependent differential temporal pattern of brachiopod and radiolarian disappearance and miniaturization across the EPE in China (e.g., Feng and Algeo 2014; He et al. 2015). The warming trend further developed during the Early Triassic and culminated in the late Smithian (Retallack 2002; Kidder and Worsley 2004; Kiehl and Shields 2005; Sun et al. 2012; Romano et al. 2013) followed by a major cooling event at the Smithian–Spathian boundary that actually began in the late Smithian (Goudemand et al. 2019). This intense warming caused the intensification of oceanic stratification with the expansion of the oxygen minimum zone and the upward migration of the chemocline (e.g., Riccardi et al. 2007), which resulted in the main extinction event of shallow faunas. The hypotheses formulated in this contribution of offshore migration for *Triassocythere* and *Monoceratina* may be new evidence for a massive event of off-shelf colonization at the brink of the EPE also documented for brachiopods (He et al. 2005; Chen et al. 2006) and isopods (Lins et al. 2012). This event must have taken place prior to the onset of the massive oxygen depletion through the EPE. All ostracods of the present contribution being benthonic through their ontogeny, their dispersal might have been achieved by active locomotion across barriers that have disappeared or were no longer effective. The Pliocene history of shallow water ostracods in the Mediterranean Sea shows that depth is not a sufficient barrier to colonization of deep waters (Benson 1972). In the Atlantic Ocean, boundaries between water masses have diverse effects on ostracod migration depending on species, with for instance *Bosquetina mucronulatum* (Brady 1880) and *Cytherella serratula* (Brady 1880) associated with at least two distinct water masses while the genus *Abyssocythere* Benson 1971 is confined to a specific water mass (Dingle and Lord 1990). The rapid decrease of temperatures with depth may have prevented certain taxa from descending into depths so that the thermocline may have been an almost hermetic barrier in a two-layered ocean (Benson 1975). The pre-EPE migration of these ostracods may thus have required changes in the thermocline and/or degradation of environmental conditions on the platforms or off-shelf zones. The thermal tolerance of ostracods has been a long-term research topic as temperature is an essential factor controlling the ostracod distribution in recent marine environments (e.g., Elofson 1941; Benson et al. 1983; Penney 1993). Phanerozoic climatic changes have been involved in several extinctions and profound reorganizations of marine ostracod communities for instance during the Toarcian (e.g., Boomer et al. 1998; Gómez and Arias 2010) or the Aptian (e.g., Wilkinson 2011; von Bargen et al. 2016). Crustaceans can be considered as poikilothermic, i.e. that their body temperature closely follows that of their environment, and ostracods are among crustaceans that also display avoidance of extreme temperatures of klinokinetic type (Lagerspetz and Vainia 2006).





TEXT-FIGURE 4

Environmental distribution of deep-sea Bythocytheridae, Beecherellidae, Rectoriariidae and Tricorinidae in the Permian and Triassic. Uncertain environmental attribution of taxa occurring in the Artinskian-Sakmarian of Timor (Bless 1987; Gründel and Kozur 1975) are marked by '?'. Environmental attributions and references of each corresponding assemblage are available in Table 1.

When possible, ostracods might hence move away from the area where they encounter or approach their thermal tolerance. The pre-EPE offshore migration may therefore illustrate a response to increasing temperature in neritic areas. However, the increasing temperature surface during the Late Permian might have strengthened the thermic barrier of the thermocline (e.g., Wei et al. 2015), which might rather have precluded ostracods from migrating. The migration of organisms toward deeper water bodies is hence only conceivable in association with the deepening of the thermocline as has been proposed by Grasby et al. (2016). In that matter, the temperature may have exerted a strong selective pressure on ostracods through the EPE. It should be stressed that Changhsingian off-shelf ostracods are only known from China which also provided important deep-sea brachiopods that witnessed a regional abrupt event in late Changhsingian (He et al. 2005; Chen et al. 2006). However, the molecular data obtained on isopods is evidence that this trend might have been more ubiquitous (Lins et al. 2012). Evidence of speciation through the Permian and the Triassic described for Bythocytheridae, Rectoriariidae and Beecherellidae are in line with the idea that anoxia may not have been a cause of extinction for all ostracod taxa but may have rather contributed to speciation in these lineages (e.g., McLain and Hardy 2010).

Following the EPE, a major resurgence of bathyal ostracods occurred in the Anisian and the Ladinian along the western Tethys margin (Figs 2A, B). How can this feature be explained? A recent study reported that “megamonsoon”-driven intense eastward winds along the western Tethys margin (Transdanubian range, Hungary) caused the upwelling of cold, oxygen-depleted, nutrient-rich waters (Budai et al. 2017). This important amount of nutrients may have led to the explosive peak of ammonoid diversity and radiolarians observed in the Middle and Late Anisian (Pelsonian, Illyrian; Budai et al. 2017). The Austrian assemblage described in Mette et al. (2015) is of Pelsonian age (Late Anisian) and may be related to the same event. However, the high diversity of off-shelf ostracods in Romania (North Dobrogea) pre-dates the establishment of this phenomenon as they are of Aegean and Bithynian age, Early and Middle Anisian (Crasquin-Soleau and Grădinaru 1996; Sebe et al. 2013). Different opinions on the paleogeography of western Tethyan realm in the Middle Triassic can be found in the literature, from that shown in Marcoux and Baud (1996) or Budai et al. (2017) of the Transdanubian range located on the western margin of Neotethys to that for instance shown in Moix et al. (2007, 2008) of the Transdanubian range on the margin of the Meliata basin and North Dobrogea on the margin of the Küre basin opening on the northern margin of Paleo-Tethys. In spite of their very patchy fossil record, the distribution of common taxa in these areas points to the presence of distribution pathways. The diachronous pattern of ostracod distribution may be related to the lack of Aegean and Bithynian report of off-shelf ostracods in Hungary.

The observed increase of the contribution of Bairdiidae to off-shelf assemblages from the Changhsingian upward is puzzling but the scarcity of Late Permian assemblages and the Early Triassic gap do not allow to go further in the characterisation of this feature. However, Middle and Late Triassic off-shelf assemblages undeniably document a much more homogenous composition than the Permian ones. The great homogeneity of the bathyal ostracod species in the early Anisian has been noticed by Crasquin-Soleau and Grădinaru (1996) and is here

shown at the familial level. Crasquin-Soleau and Grădinaru (1996) however considered that this feature related to the conservatism of the deep-sea environment but the present contribution shows that:

- numerous genera radiated in the Permian and the Triassic,
- a familial homogeneity of the off-shelf assemblages is only visible in the Triassic.

This uniformity of Tethyan fauna is reminiscent of that reported by Kristan-Tollmann (1988) for neritic assemblages in the Late Triassic, which has recently been shown to be related to the opening of the communication between the Paleo-Tethys and Neo-Tethys in the Tuvanian, Early Carnian (Forel and Moix 2020). Only analyses of new assemblages from both oceans will allow further discussing the possibility of extending this idea to off-shelf assemblages.

#### SUPPLEMENTARY DATA AVAILABILITY

Complete familial compositions and proportions of Permian and Triassic off-shelf ostracod assemblages are available online at <https://www.micropress.org/microaccess/micropaleontology/issue-380>, a free online repository hosted by Micropaleontology Press.

#### CONCLUSION

The present analysis and discussion provide new evidence that the diversity of deep-sea ostracods at the Paleozoic–Mesozoic transition has been shaped by colonization events from adjacent neritic areas (*Triassocythere*, *Monoceratina*), *in-situ* radiations among Beecherellidae, Bythocytheridae (except *Triassocythere* and *Monoceratina*) and Rectoriariidae, as well as long-term Paleozoic survivorship. Beecherellidae, Bythocytheridae and Rectoriariidae are traditionally considered as evidence for the existence of a deep-sea refuge or for the stability of environmental conditions in deep areas of the Permian and Triassic oceans: could they also illustrate the view that anoxia stimulated speciations for certain taxa?

Two periods of deep-sea colonization by ostracods are here proposed to have occurred in the Late Permian (Changhsingian) and Middle Triassic (Anisian). The colonization of off-shelf areas by neritic ostracods at the end of the Permian might have been made possible by the deepening of the thermic barrier constituted by the thermocline in association with warming climate. As for ostracods, this end-Permian migration may have been an escape mechanism to avoid increasing temperatures in neritic areas. Several questions are still pending: is the Middle Permian gap related to climatic/circulation conditions, to the lack of studies on this interval or to preservation issues? As stated in the introduction, molecular clocks indicate that anoxic events at the Permian–Triassic boundary and during the Mesozoic did not cause the extinction of the entire deep-sea fauna: if this can be considered as true for ostracods through the EPE, the Jurassic record of off-shelf assemblages remains enigmatic and future studies should clarify this aspect.

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