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Late Triassic ostracods from the Lycian Nappes, southwestern Turkey: implications on taxonomy and palaeobiogeographical distribution

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Abstract – The first ostracods known from the Lycian Nappes in southwestern Turkey are here reported, adding to the scientific understanding of marine ostracods during the Cordevolian, early Carnian, Late Triassic. The Karapınar Formation exposed at the Ağlıovası Yayla section yielded five species, including the typical Late Triassic *Mirabairdia longispinosa* Kristan-Tollmann, *Nodobairdia mammilata* Kollmann and *Polycope pumicosa schleiferae* Kozur. Their taxonomy is discussed and the ontogenetic development of *Nodobairdia mammilata* is described for the first time. In spite of the limited significance of this poor fauna for palaeoenvironment reconstitution, it points to a deposition in the offshore subtidal zone under moderate water depth, in line with previous interpretations. The palaeobiogeographical distribution of marine ostracods during the Late Triassic is updated and discussed. It implies that communication ways between the Palaeotethys and Neotethys oceans were already opened during the Cordevolian, slightly earlier than the Julian as previously proposed.

Keywords: ostracods / Carnian / Lycian Nappes / Turkey / taxonomy / palaeobiogeography

Résumé – Ostracodes du Trias supérieur des Nappes Lyciennes, Turquie du sud-ouest: implications taxinomiques et paléobiogéographiques. Les premiers assemblages d'ostracodes connus des Nappes Lyciennes au sud-ouest de la Turquie sont ici rapportés, apportant à la compréhension scientifique des ostracodes marins du Cordévolien, Carnien inférieur, Trias supérieur. La Formation Karapınar affleurant à Ağlıovası Yayla a livré cinq espèces, dont *Mirabairdia longispinosa* Kristan-Tollmann, *Nodobairdia mammilata* Kollmann et *Polycope pumicosa schleiferae* Kozur, typiques du Trias supérieur. Leur taxinomie est discutée et le développement ontogénétique de *Nodobairdia mammilata* est décrit pour la première fois. En dépit des limites de cette faune pauvre pour la reconstitution du paléoenvironnement, elle indique un milieu de dépôt dans la zone subtidale sous une colonne d'eau modérée, en accord avec les interprétations antérieures. La distribution paléobiogéographique des ostracodes marins au Trias supérieur est mise à jour et discutée. Elle implique que les voies de communication entre les océans Paléotéthys and Néotéthys étaient ouvertes dès le Cordévolien, légèrement plutôt qu'au Julien comme proposé auparavant.

Mots clés : ostracodes / Carnien / Nappes Lyciennes / Turquie / taxinomie / paléobiogéographie

1 Introduction

The Triassic period is one of the most significant intervals of time in the macroevolutionary history of organisms, with the rise of the modern fauna and the emergence of modern ecosystems in sea and on land (e.g. [Spekoski, 1984](#); [Van Valen, 1984](#); [Brusatte et al., 2011](#); [Chen and Benton, 2012](#); [Benton](#)

[et al., 2013](#)). Most of the new predators later involved in the Mesozoic marine revolution ([Vermeij, 1977](#)), such as predatory gastropods, decapods, neopterygian fishes and marine reptiles, were already established in the Triassic (e.g. [Chen and Benton, 2012](#) and references therein for a review). Middle and Late Triassic occurrences of drill holes on mollusks, brachiopods ([Klompaker et al., 2016](#)) and ostracods ([Forel et al., 2018](#)) are rare but witness the establishment of typically Mesozoic drilling activity as early as Anisian, Middle Triassic.

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Ostracods are millimetre-size crustaceans that today live in various aquatic environments, from temporary freshwater ponds to hydrothermal sources or cold methane seep sites (e.g. Horne *et al.*, 2002; Maddocks, 2005; Karanovic, 2012; Yasuhara *et al.*, 2018). The deepest known living species has been reported from 9307 m water depth (Brandão *et al.*, 2019). Ostracods have dwelt in marine waters since the Early Palaeozoic (e.g. Salas *et al.*, 2007; Siveter, 2008). They were significantly affected by the end-Permian crisis and their recovery is considered as complete during the Anisian, Middle Triassic (Crasquin-Soleau *et al.*, 2007; Crasquin and Forel, 2015). The Triassic period is of paramount importance in their macroevolution with the turnover from the Palaeozoic to the Meso-Cenozoic faunas (e.g. McKenzie, 1982; Crasquin-Soleau *et al.*, 2007; Crasquin and Forel, 2015). However, this period stays enigmatic with the challenging temporary dominance of heavily sculpted Bairdiidae (e.g. Kollmann, 1960, 1963; Bolz, 1971a, b; Kristan-Tollmann, 1978) or residual occurrence of Palaeozoic taxa in deep waters up to the Carnian (Forel *et al.*, 2019a). These features, together with the still poor understanding of their geographical, environmental and taxonomic distribution, challenge our understanding of their survival mechanisms and diversity structuration during the Triassic, prior to their Mesozoic rediversification.

Here we report on ostracods from the Cordevolian, early Carnian, Late Triassic, of the Lycian Nappes (Karadağ Unit, Karapınar Formation) in southwestern Turkey. Five species are recognized, of which three are already known from the Upper Triassic marine successions: *Mirabairdia longispinosa* Kristan-Tollmann (1978), *Nodobairdia mammilata* Kollmann (1963) and *Polycope pumicosa schleiferiae* Kozur in Bunza and Kozur (1971). The taxonomy of the species is discussed and the development of *Nodobairdia mammilata* is described for the first time, with the identification of five ontogenetic stages. This faunule from the northern margin of the Neotethys adds new data to the knowledge of the palaeobiogeographical distribution of ostracods during the Late Triassic. The comparison of their updated distribution through time with the three main hypotheses of the origin of Tethyan ostracods, here termed “western America”, “eastern Tethys” and “western Tethys” (e.g. Bate, 1977; Kristan-Tollmann and Tollmann, 1981, 1982; Kristan-Tollmann, 1986a, b, 1988a; Lord, 1988; Ketmuangmoon *et al.*, 2018), documents a mixture of distribution pathways depending on the taxonomic level under scrutiny. The large distribution of *Mirabairdia longispinosa* and *Nodobairdia mammilata* in the Cordevolian, early Carnian, implies that they might have radiated at the end of the Ladinian and that communication ways between the Palaeotethys and Neotethys oceans were opened earlier than generally proposed (Julian; e.g. Kozur, 2000; Stampfli and Kozur, 2006; Moix *et al.*, 2007, 2013).

2 Geological setting and stratigraphy

The studied area was described in details by Moix *et al.* (2013): only a short overview is provided here and the reader is referred to this key contribution and references therein for all tectonostratigraphic details on the Lycian Nappes.

2.1 The Lycian Nappes

The Lycian Nappes represent a vast area in southwestern Turkey between the Menderes Massif to the northwest and the Beydağları platform to the southeast (Fig. 1). They are subdivided into three main tectonic units (de Graciansky, 1968, 1972; Brunn *et al.*, 1971; Bernoulli *et al.*, 1974; Poisson, 1977), in ascending order:

- The autochthonous series of the Menderes Massif and the Beydağları/Susuz Dağ/Göcek domains;
- The intermediate complex, which is composed of imbricated thrust sheets, viz. Karadağ, Teke Dere, Haticeana Dağ and Köyceğiz units;
- The peridotite Marmaris Nappe, of Late Cretaceous age, at the top of the tectonic pile.

The Lycian Nappes are composed of the Bodrum, Domuzdağ, Dumanlıdağ, Gülbahar, Marmaris and Tavas nappes (Senel *et al.*, 1994; Fig. 1). The Tavas Nappe is itself composed of the Karadağ and Teke Dere units (Fig. 2).

The Karadağ Unit is of Middle Carboniferous to Late Triassic age and is composed of bioclastic limestones with sandy and pelitic intercalations (de Graciansky, 1968, 1972; see Moix *et al.*, 2013 for further precisions). Thick outcrops of quartzites were attributed to the Early Triassic or late Ladinian (de Graciansky, 1972; Bernoulli *et al.*, 1974). The Karadağ Unit is subdivided into six formations, in ascending order (Senel *et al.*, 1994; Fig. 2): Sazak Fm. (possibly Late Devonian shales and limestones, not shown in Fig. 2), Kiloluk Fm. (Middle Carboniferous bioclastic limestones, dolomites and dolomitic limestones, not shown in Fig. 2), Akkavak Fm. (Early Permian crystalline limestones, dolomites and shales), Sarıtas Fm. (possibly late Anisian to early Ladinian sandstones), Karapınar Fm. (black limestones with Middle Triassic foraminifers and early Carnian conodonts; Moix *et al.*, 2013) and Belenkavak Fm. (Carnian-Norian sandstones, siltstones and shales).

The Teke Dere Unit is of Early and Late Permian age and is composed of white dolomites and massive limestones followed by green arkosic sandstones and greywackes (de Graciansky, 1968, 1972). Pillow-lavas, black and russet folded radiolarites and Permian limestones locally intersperse the green arkoses. This interval is capped by Late Permian dolomites and limestones, unconformably overlain by the red continental to shallow-marine Cenger Fm. of Late Triassic age as shown by lungfish and reptile remains (Monod *et al.*, 1983; Buffetaut *et al.*, 1988). These red conglomerates, sandstones and siltstones are molassic deposits followed by a thick carbonate sequence ranging from the Triassic to the Late Cretaceous (Ağaçlı and Badadağ formations), which is itself overlain by a Late Paleocene to Lutetian flysch (Senel, 1997). The Teke Dere Unit is composed of the following formations in ascending order (Senel *et al.*, 1994; Fig. 2): Çatakdere Fm. (crystalline limestones), Incirbeleni Fm. (shales, sandstones, limestone lenses, lydites and volcanics) and Nisangahtepe Fm. (dolomites and limestones). These three formations were considered as early to middle Wordian in age, but Kozur *et al.* (1998) indicated a Mississippian age for the Incirbeleni Fm. and microfauna and microflora from the Nisangahtepe Fm.

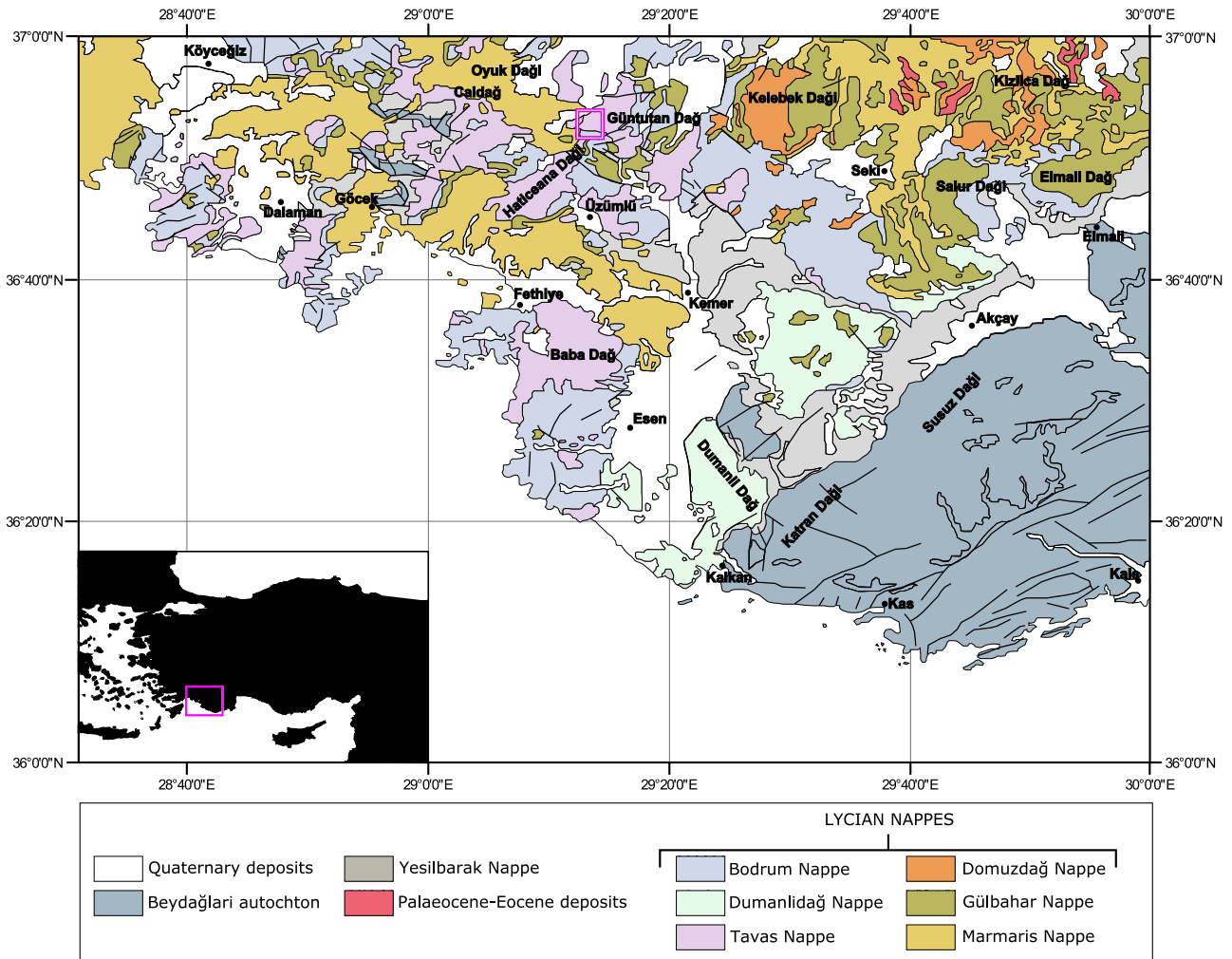


Fig. 1. Simplified structural map of southwestern Turkey showing the tectonic units of the Fethiye quadrangle (modified from Senel, 1997). The pink square indicates the location shown in Figure 2.

rather point to a Kubergandian age (Tethyan equivalent of the Roadian; Vachard and Moix, 2013).

2.2 The Ağılıovaş Yayla section

The investigated area is located north of the Teke Peninsula in southwestern Turkey, northeast of Fethiye Gulf and close to the road between Fethiye and Çameli (Fig. 1). The Ağılıovaş Yayla series are located between 1600 and 2000 m of altitude, 4 km south of Tascilar village, north of the Karadağ (2233 m) and about 1 km east of a pasture known as Ağılıovaş Yayla. The composite succession of the Ağılıovaş Yayla section permits the recognition of the Karadağ and Teke Dere units (Fig. 2). All carbonate microfacies correspond to shallow inner-ramp deposits that have been little displaced to preserved as *in situ* thanatocenoses or proximal tempestites (Moix et al., 2013).

The oldest shallow marine sediments in the Ağılıovaş Yayla area belong to the Kiloluk Fm. The base of the sequence is composed of dolomites, cherty limestones and bioclastic limestones that contain early Kasimovian fusulinids (Vachard and Moix, 2011; Moix et al., 2013). Recent tectonics brought

the Late Carboniferous succession close to a 160-m thick platform-like development of Early Permian to Late Triassic age.

The Ağılıovaş Yayla autochthonous series start with grey fusulinid-rich limestones. It is transitional to alternating thin-bedded black limestones, massive grey to black limestones, middle-bedded sandy limestones with pelitic horizons, thick-bedded black laminated limestones and thin-bedded black limestones interspersed by argillites (Akkavak Fm.). All fossil assemblages indicate a Sakmarian age (Moix et al., 2013). It is followed by the Sarıtaş Fm., which is a thick-bedded interval of white quartzites. It is capped by the Karapınar Fm., composed of thick-bedded gray limestones and thin-bedded bioclastic black nodular limestones, locally with cherts. The limestones levels indicate a Middle-Late Triassic age (Moix et al., 2013). The upper part of the section is marked by the siliciclastic Belenkavak Fm., corresponding to a wildflysch-like sequence composed of shales, silstones, sandstones, conglomerates, with various blocks of Permian age (de Graciansky, 1972; Vachard and Moix, 2011).

The sample investigated in this work (labelled 328/07) belongs to the Karadağ Unit and was previously studied by

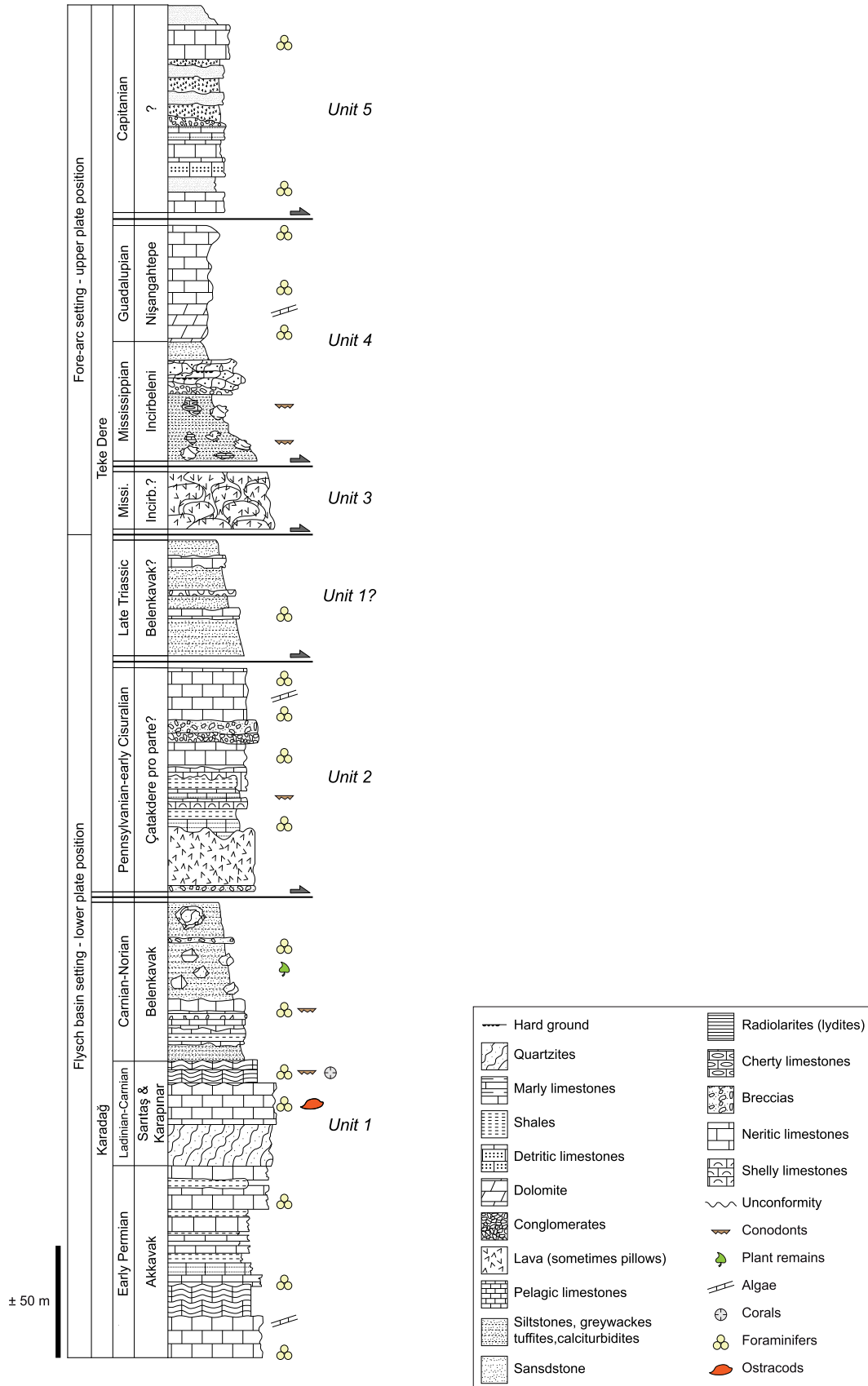


Fig. 2. Synthetic composite lithostratigraphic succession of the Ağlıhovası Yayla section (modified after Moix *et al.*, 2013) and position of the studied sample.

Moix *et al.* (2013). It is issued from dark limestones at the top of the Karapınar Fm. (Fig. 2) that yielded *Pseudofurnishius murcianus murcianus* van den Boogaard (1966), a conodont indicative of the Cordevolian, early Carnian, Late Triassic (based on the three-folded Carnian subdivision of Kozur and Mostler, 1994, 1996; Kozur, 2003). This conodont is also a typical indicator for the Neotethyan domain, showing that the Karadağ Unit belongs to the Cimmerian Taurus terrane and was part of the northern passive margin of the Neotethys (Moix *et al.*, 2013). Ostracods have been mentioned in this sample by Moix *et al.* (2013) with two specimens illustrated and identified as “Sculptured Bairdiidae” and “*Polycoopsis* n. sp. ex gr. *cincinnata* (Apostolescu)”. The occurrence of other sculptured bairdiids was mentioned and discussed in terms of palaeoenvironmental implication in Moix *et al.* (2013) but no taxonomic list was provided.

3 Material and methods

The sample 328/07 was processed using acetic acid for conodont extraction (Moix *et al.*, 2013) and also yielded an ostracod faunule of eight specimens representing five species distributed into four genera (Plate 1). Although not abundant, their preservation is good enough to identify three species already known from the Late Triassic, viz. *Mirabairdia longispinosa* Kristan-Tollmann (1978), *Nodobairdia mammilata* Kollmann (1963) and *Polycope pumicosa schleiferae* Kozur in Bunza and Kozur (1971). The other two species are kept in open nomenclature because of the lack of material and of distinctive characters.

In this contribution, we follow the general classification of Moore (1961) and Horne *et al.* (2002). For the three species already known during the Triassic, we provide and discuss the complete list of synonyms and kresonyms in order to build a suitable basis for the palaeobiogeographical investigation performed here. The height/length diagram of *Nodobairdia mammilata* Kollmann (1963) gathers the dimensions of all specimens from the literature and this work (Fig. 3). In this diagram, right and left valves are distinguished for isolated valves and complete carapaces, following the method of Urlichs (1971), Harloff (1993) and Forel *et al.* (2019b) for instance. For each of the species scrutinized in this work, we follow the updated stratigraphic framework available on the Paleobiology Database (accessed on the 01/10/2019) and their original and revised stratigraphic information are summarized in Table 1.

An important point in the discussion of the palaeobiogeographical implications of the ostracods from the Lycian Nappes is which is the adopted definition of the Carnian. The subdivisions of the Carnian stage have been a matter of debate, between a two-fold and a three-fold Carnian (see Chen *et al.*, 2016 and Rigo *et al.*, 2018 for recent summaries). The three-fold Carnian subdivision is here followed and the recovered species are of Cordevolian age, early Carnian, as shown by the occurrence of the conodont *Pseudofurnishius murcianus murcianus* (Moix *et al.*, 2013). All figured specimens are deposited in the micropalaeontology collections of the Muséum national d’Histoire naturelle (Paris), under catalogue numbers MNHN.F.F63332–MNHN.F.F63339.

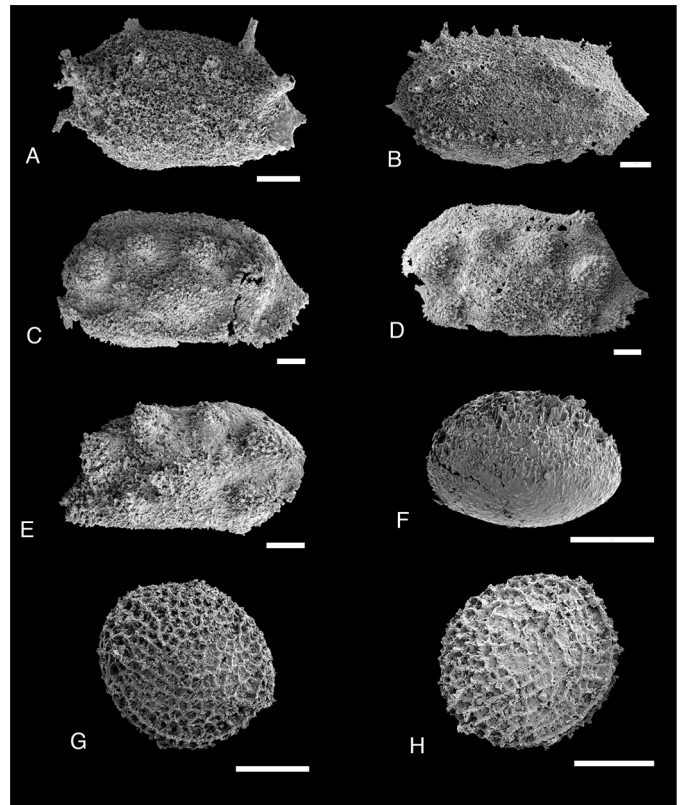


Plate 1. Ostracods from the sample 328/07, Karapınar Formation, Lycian Nappes, southwestern Turkey, Cordevolian, Early Carnian, Late Triassic (MNHN: Muséum national d’Histoire naturelle, Paris). A: *Mirabairdia longispinosa* Kristan-Tollmann (1978), lateral view of a left valve, MNHN.F.F63332; B: *Mirabairdia* sp., lateral view of a left valve, MNHN.F.F63333; C–E: *Nodobairdia mammilata* Kollmann (1963); C: lateral view of a left valve, MNHN.F.F63334; D: lateral view of a right valve, MNHN.F.F63335; E: lateral view of a right valve, MNHN.F.F63336; F: *Hungarella* sp.: lateral view of a left valve, MNHN.F.F63337; G, H: *Polycope pumicosa schleiferae* Kozur in Bunza and Kozur (1971); G: lateral view of a right valve, MNHN.F.F63338; D: lateral view of a left valve, MNHN.F.F63339. All scale bars are 100 μ m.

4 Systematic palaeontology (by Marie-Béatrice Forel)

Class Ostracoda Latreille (1806)
 Subclass Podocopa Müller (1894)
 Superfamily Bairdioidea Sars (1887)
 Family Bairdiidae Sars (1887)
 Subfamily Bairdiinae Sars (1923)
 Genus *Mirabairdia* Kollmann (1963)

1973a *Vavilovella* Kozur: 21–24, pl. 3, figs. 4, 5.

Type species. *Mirabairdia pernodosa* Kollmann (1963) by original designation.

Preliminary remarks. *Vavilovella* Kozur (1973a) (type species: *Vavilovella psychrosphaerica* Kozur (1973a); Sevatian, late Norian, Austria) was erected to accommodate bairdiids with “dorsal outline clearly divided into three parts;

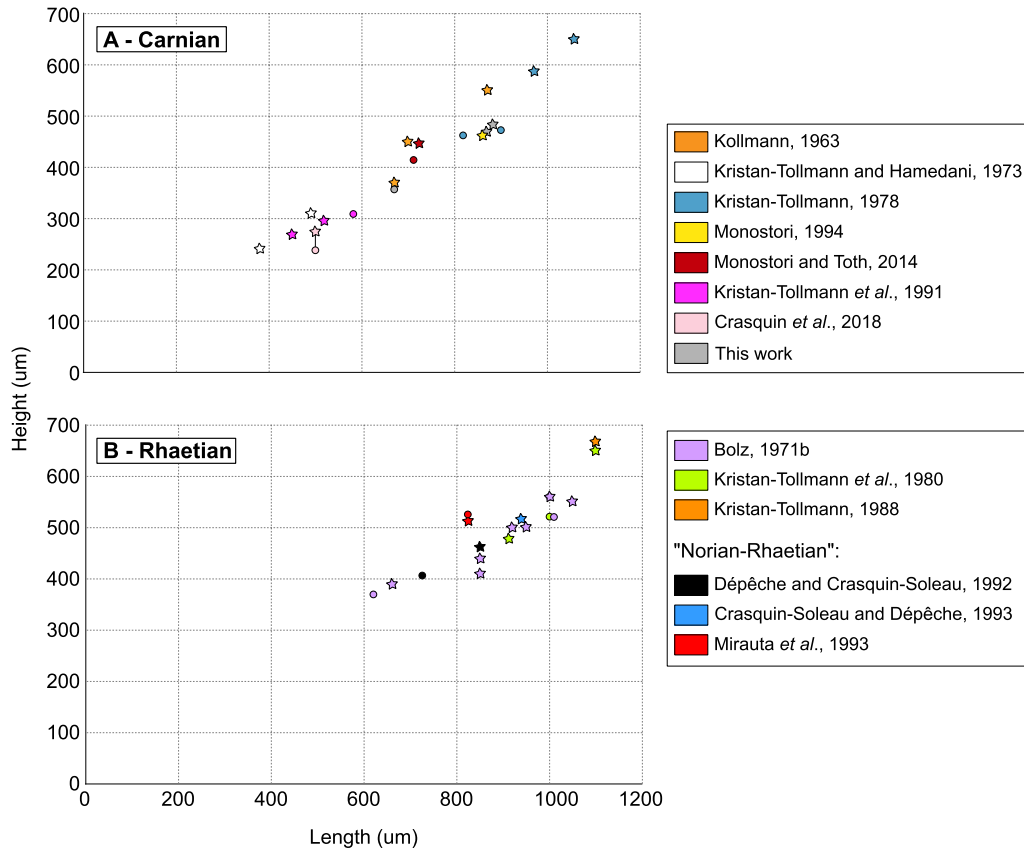


Fig. 3. Height/Length scatter plot of *Nodobairdia mammilata* Kollmann (1963) for the Carnian (A) and Rhaetian (with “Norian-Rhaetian”; B). The dimensions of right and left valves of the complete carapace are linked. Right valves and left valves are represented respectively by circles and stars.

Table 1. Updated stratigraphic information of studied and cited species, following the Palaeobiology Database, accessed on the 01/10/2019.

Species and reference considered	Occurrence in original reference	PBDB update	This work
<i>Mirabairdia pernodosa</i> Kollmann (1963)	Ladinian-lower Carnian	Julian-Tuvalian, Carnian	Cordevolian-Tuvalian, Carnian
<i>Mirabairdia longispinosa</i> Kristan-Tollmann (1978) in Liebermann (1979)	“Niveau mit Trachyceras aon”, Julian, middle Carnian	–	Cordevolian, early Carnian
<i>Nodobairdia mammilata</i> Kollmann (1963)	Ladinian	aon subzone, Julian, middle Carnian	Cordevolian, early Carnian
<i>Nodobairdia mammilata</i> Kollmann (1963) in Liebermann (1979)	Julian, middle Carnian	aon subzone, Julian, middle Carnian	Cordevolian, early Carnian
<i>Triebelina (Nodobairdia) triassica</i> Bolz (1971a)	Norian-Rhaetian	Rhaetian	Rhaetian
<i>Triebelina</i> sp. G in Bolz (1971a)	Norian-Rhaetian	Rhaetian	Rhaetian

anterior end terminated by long thorns; surface occupied by long, forked thorns, with small nodules between them” (Kozur, 1973a; translated from German). Kozur (1973a) distinguished *Vavilovella* from *Mirabairdia* Kollmann (1963) by the extreme sculpture of *Vavilovella*, all lateral elements being transformed into thorns while they are only single spines in *Mirabairdia*. Kristan-Tollmann (1978) underlined that the general arrangement of the ornaments in the two genera is strictly similar and that their morphology, varying from short lobes to

pedunculated nodes or spines, should only be used for specific separation. Kristan-Tollmann (1978) therefore considered *Vavilovella* as a junior synonym of *Mirabairdia*. This opinion has been followed in all publications since the work of Kristan-Tollmann (1978) and is followed here.

***Mirabairdia longispinosa* Kristan-Tollmann (1978) (Plate 1A)**

1978 *Mirabairdia longispinosa* Kristan-Tollmann: 94–96, pl. 3, figs. 1–3; pl. 7, fig. 5.

1979 *Mirabairdia longispinosa* Kristan-Tollmann; Liebermann: 106.

2018 *Mirabairdia longispinosa* Kristan-Tollmann; Forel *et al.*: 10, figs. 4.20, 4.21.

Material. One left valve.

Dimensions. L = 518 μm , H = 327 μm , H/L = 0.63 (this material).

Occurrences. South Tyrol, Italy, Cordevolian, early Carnian, Late Triassic (Kristan-Tollmann (1978)); Cave del Predil (Raibl), Italy, Julian Alps, Cordevolian, early Carnian, Late Triassic (Liebermann, 1979; see stratigraphic update in Tab. 1); Tavusçayiri Block, Sorgun Ophiolitic Mélange, Huğlu Tuffite, southern Turkey, *Spongortilispinus moixi* radiolarian Zone, lower Tuvallian, late Carnian, Late Triassic (Forel *et al.*, 2018); sample 328/07, Karapınar Formation, Karadağ Unit, Ağılıovası Yayla section, Lycian Nappes, southwestern Turkey, Cordevolian (*Pseudofurnishius murcianus murcianus* conodont), early Carnian, Late Triassic (this work).

Remarks. In the studied sample, *Mirabairdia longispinosa* occurs as a single LV, the dimensions of which indicate that it is a relatively young juvenile (see below for further discussion). Despite these abundance and size limitations, the lateral outline, absence of nodes and morphology of the horns exclude this species from *Mirabairdia pernodosa* Kollmann (1963) (Carnian, Late Triassic, Austria), *Mirabairdia plurinodosa* Mette *et al.* (2014) and *Mirabairdia praepsychrosphaerica* Mette *et al.* (2014) (the latter two species being from Pelsonian, middle Anisian, Middle Triassic, Austria).

The specimen from the Lycian Nappes displays:

- Two dorsal thorns;
- A subdorsal row of three thorns, the posterior one being thicker, and a relatively large pedunculated anterior wart;
- An anterior bifurcated spine;
- Three poorly preserved sub-ventral warts.

This species is therefore attributed without doubt to the typically Carnian *Mirabairdia longispinosa* Kristan-Tollmann (1978) that is diagnosed by a lateral ornamentation made of thorns and warts, while it is exclusively composed of thorns in *Mirabairdia psychrosphaerica* (Kozur, 1973a) known from the Rhaetian, Late Triassic, of Austria. The present specimen is much smaller than the holotype (L = 1130 μm , H = 580 μm ; Kristan-Tollmann (1978)) and corresponds to a relatively young instar. Only few specimens of this species are known so that its ontogenetic development is complex to assess. However, the difference in H/L ratio between the holotype (0.51) and the present specimen (0.63) indicates that one feature of the ontogeny of *Mirabairdia longispinosa* is an overall elongation of the carapace. Furthermore, the occurrence of already well-developed diagnostic ornamental features on the juvenile from the Lycian Nappes indicates that they appear relatively early in the ontogeny of this species.

***Mirabairdia* sp.**

(Plate 1B)

2013 Sculptured Bairdiidae; Moix *et al.*: pl. 5, fig. 6.

Material. One left valve.

Dimensions. L = 750 μm , H = 437 μm , H/L = 0.58.

Occurrences. Sample 328/07, Karapınar Formation, Karadağ Unit, Ağılıovası Yayla section, Lycian Nappes, southwestern Turkey, Cordevolian (*Pseudofurnishius murcianus*

murcianus conodont), early Carnian, Late Triassic (Moix *et al.*, 2013; this work).

Remarks. The present specimen was illustrated in Moix *et al.* (2013; pl. 5, fig. 6) with the following description: “Sculptured Bairdiidae, left valve, former ventral rib and former elongated oblique anterodorsal and posterodorsal ribs disintegrated in lines of short hollow spines, such a feature occurs only in such sculptured Bairdiidae which lived below the storm wave base” (p. 433). It was only identified at the familial level, without discussion on possible generic attribution. It is here attributed to *Mirabairdia*.

Mirabairdia sp. is a thin and delicate LV. The DB bears a series of straight spines that apparently do not extend to the PDB and only slightly to the ADB. The lateral surface is characterized by:

- A series of small hollow spines in the ventro-lateral area, parallel to the ventral margin, extending from the AVB to the PVB;
- Two straight rows of four larger hollow spines below the antero-dorsal and postero-dorsal angles, respectively bent anteriorly and posteriorly.

This lateral ornamentation relates *Mirabairdia* sp. to *Mirabairdia pernodosa* Kollmann (1963) from the Carnian of the Alps (Kollmann (1963); see stratigraphic update in Tab. 1). However, *Mirabairdia* sp. lacks the horizontal and vertical rows of spines in the median and dorsal areas developed on *Mirabairdia pernodosa*. The morphology of this species from the Lycian Nappes mainly differs from all other *Mirabairdia* species from the literature by its more delicate and thinner lateral ornaments, which could relate to the fact that the obtained LV may be a relatively young instar. This hypothesis is reinforced by the comparison of its dimensions with that of species from the literature:

- *Mirabairdia pernodosa* Kollmann (1963):
Adult: L = 810–820 μm , H = 440–460 μm ;
Juveniles: L = 670–700 μm , H = 370–410 μm ;
- *Mirabairdia longispinosa* Kristan-Tollmann (1978):
Adult: L = 1130 μm , H = 580 μm ;
- *Mirabairdia plurinodosa* Mette *et al.* (2014):
RV: L = 920–1130 μm , H = 460–560 μm ;
LV: L = 950–1070 μm , H = 460–570 μm ;
- *Mirabairdia praepsychrosphaerica* Mette *et al.* (2014):
RV: L = 1120–1270 μm , H = 490–530 μm ;
LV: L = 1120–1270 μm , H = 520–640 μm .

This species is new to science but its diagnostic characters cannot be reliably described until more material is found.

Until now, the ontogeny of *Mirabairdia* species stays poorly described. Kozur (1973a) indicated that juveniles of *Mirabairdia psychrosphaerica* (Kozur, 1973a) from the Rhaetian of Austria slightly differ from adults in being squat, with anterior extremity longer, more weakly rounded and ventral margin straighter, with short dorso-median, ventro-median and antero-ventral spines. Juveniles of *Mirabairdia pernodosa* illustrated in Kollmann (1963) show that large nodules bearing smaller nodules are already present in the earliest juvenile recovered. *Mirabairdia* sp. is devoid of large

nodules, which would imply that small nodules may appear earlier than larger ones during the ontogenetic development and/or may be diagnostic features of the new species. Only additional material allowing for the characterization of the ontogenetic development of this species will clarify this issue.

Genus *Nodobairdia* Kollmann (1963)

Type species. *Nodobairdia mammilata* Kollmann (1963) by original designation.

Preliminary remarks. The taxonomic history of Triassic sculptured Bairdiidae is complex with a strong volatility of opinions on the significance of characters used for their classification. *Nodobairdia* Kollmann (1963) was erected to accommodate bairdiids with four large sub-dorsal warts and a longitudinal latero-ventral ridge undivided or divided into three parts (Kollmann (1963)). Contrary to the generic scheme established by Kollmann (1963) that was later followed by diverse authors, Bolz (1971a, b) considered that the presence/absence of marginal ornamentations is more significant than their morphology (e.g. nodular, annular, spinose). In Bolz generic scheme, *Nodobairdia* is considered as a subgenus of the extant genus *Triebelina* van den Bold (1946). Kristan-Tollmann (1978), more recently followed by Mette *et al.* (2014), suggested that the ornamentation of *Nodobairdia* and *Mirabairdia* shows a gradual pattern so that these genera may be synonyms. It is beyond the scope of the intention of this paper and its material to attempt a revision of the Bairdiidae at the generic level. The important variations of the opinions of the diverse authors on the generic classification of Bairdiidae resulted in an intricate situation, with the alternative use of Kollmann and Bolz schemes by the same authors, for instance in Urlichs (1972), Hillebrandt *et al.* (2007, 2013) and Urlichs and Krystyn (2016). To avoid adding noise factor to the already confuse classification of Triassic ornate Bairdiidae and until their systematic and phylogeny are clarified, the generic scheme of Kollmann (1963) is followed in considering primary ornamentation as relevant generic character, owing that ornamentation is widely used as generic marker for other families (e.g. Trachyleberididae; Moore (1961); more recently Warne and Whatley, 2016).

Nodobairdia mammilata Kollmann (1963)

(Plates 1C–E)

1963 *Nodobairdia mammilata* Kollmann: 174, 175, pl. 7, figs. 6–15.

1971a *Triebelina* sp. G; Bolz: pl. 2, fig. 9.

1971b *Triebelina* (*Nodobairdia*) *triassica* Bolz: 216–218, pl. 16, figs. 229–232.

1971 *Nodobairdia mammilata* Kollmann; Kristan-Tollmann: 61, pl. 1, fig. 1.

non 1973 *Nodobairdia mammilata* Kollmann; Kristan-Tollmann and Hamedani: pl. 12, fig. 9, pl. 13, fig. 1.

1978 *Nodobairdia mammilata* Kollmann; Kristan-Tollmann: 84, pl. 8, figs. 1–6.

1979 *Nodobairdia mammilata* Kollmann; Liebermann: 105, 106.

1980 *Nodobairdia mammilata* Kollmann; Kristan-Tollmann *et al.*: 185, pl. 7, figs. 11–13.

1986b *Nodobairdia mammilata* Kollmann; Kristan-Tollmann: 209, 210, fig. 4.

1988a *Nodobairdia mammilata* Kollmann; Kristan-Tollmann: fig. 6/6.

1991 *Nodobairdia mammilata* Kollmann; Kristan-Tollmann *et al.*: 201, pl. 1, figs. 1–3.

1992 *Nodobairdia mammilata* Kollmann; Dépêche and Crasquin: 2, figs. 1–4.

1993 *Nodobairdia mammilata* Kollmann; Crasquin and Dépêche: pl. 1, fig. 12.

1993 *Nodobairdia mammilata* Kollmann; Mirăuță *et al.*: 95, pl. 3, figs. 22a, b.

1994 *Nodobairdia mammilata* Kollmann; Monostori: 316, 318, fig. 4/3.

2010 *Nodobairdia mammilata* Kollmann; Zorn: 271, pl. 7, figs. 8–11.

2014 *Triebelina* (*Nodobairdia*) *mammilata* (Kollmann); Monostori and Tóth: 28, pl. 2, figs. 9, 10.

2015 *Nodobairdia mammilata* Kollmann; Hausmann and Nützel: 241.

2016 *Nodobairdia triassica* (Bolz); Urlichs and Krystyn: 21.

2018 *Nodobairdia mammilata* Kollmann; Crasquin *et al.*: 137, fig. 7G.

Material. Two left valves, one right valve (this material).

Dimensions. Fig. 3.

Occurrences. South Tyrol, Italy, Cordevolian, early Carnian, Late Triassic (Kollmann (1963); Kristan-Tollmann, 1971; Zorn, 2010; see stratigraphic update in Tab. 1); Northern Calcareous Alps, Rhaetian, Late Triassic (Bolz, 1971a, b; Urlichs and Krystyn, 2016; see stratigraphic update in Tab. 1); South Tyrol, Italy, Cordevolian, early Carnian, Late Triassic (Kristan-Tollmann (1978)); Cave del Predil (Raibl), Italy, Julian Alps, Cordevolian, early Carnian, Late Triassic (Liebermann, 1979; see stratigraphic update in Tab. 1); Iran, Rhaetian, Late Triassic (Kristan-Tollmann *et al.*, 1980; Kristan-Tollmann, 1988a); Australia, early Norian, Late Triassic (Kristan-Tollmann, 1986b); Hungary, upper Julian-Tuvalian, middle-late Carnian, Late Triassic (Kristan-Tollmann *et al.*, 1991; Monostori, 1994); Australia, late Norian-mid-Rhaetian, Late Triassic (Dépêche and Crasquin, 1992; Crasquin and Dépêche, 1993); Hungary, Carnian-Rhaetian, Late Triassic (Monostori and Tóth, 2014); Stuoeres Wiesen, Italy, Carnian, Late Triassic (Hausmann and Nützel, 2015); Sicily, *Tropites dilleri* zone, Tuvalian, late Carnian, Late Triassic (Crasquin *et al.*, 2018); sample 328/07, Karapınar Formation, Karadağ Unit, Ağılıovası Yayla section, Lycian Nappes, southwestern Turkey, Cordevolian (*Pseudofurnishius murcianus murcianus* conodont), early Carnian, Late Triassic (this work).

Remarks. We follow Kristan-Tollmann (1978) in considering *Triebelina* (*Nodobairdia*) *triassica* Bolz (1971b), later identified as *Nodobairdia triassica* (Bolz) in Urlichs and Krystyn (2016), as a junior synonym of *Nodobairdia mammilata* Kollmann (1963). Similarly, we follow Kristan-Tollmann *et al.* (1980) in re-attributing *Triebelina* sp. G in Bolz (1971a) to *Nodobairdia mammilata* Kollmann (1963). Specimens from the Norian-Rhaetian of Romania (Mirăuță *et al.*, 1993) are poorly illustrated and their lateral characters are not observable: here we questionably attribute them to *Nodobairdia mammilata* Kollmann (1963). Kristan-Tollmann and Hamedani (1973) identified two valves from the late Carnian of Austria as *Nodobairdia mammilata* without providing the reasons for their doubt on the specific attribution.

Later, Kristan-Tollmann *et al.* (1980), followed by Kristan-Tollmann *et al.* (1991) and Monostori and Tóth (2014), re-attributed these specimens to *Nodobairdia mammilata* and considered them as very early juveniles with diagnostic ventral longitudinal ridge only suggested by anterior and posterior tiny nodules and two small dorsal nodes hardly visible due to preservation. Here we do not follow this re-attribution for the reasons detailed hereafter. In the smallest specimens attributed to *Nodobairdia mammilata* (Fig. 3A), those from Sicily (Crasquin *et al.*, 2018) and Hungary (Kristan-Tollmann *et al.*, 1991) already have well-developed dorsal and sub-dorsal nodes. Those from the Northern Calcareous Alps (Kristan-Tollmann and Hamedani, 1973) are of similar dimensions but have a much weaker lateral ornamentation for which elements are hardly distinguished, a fact that can not only be attributed to their preservation state. We consider that the Alpine specimens have been wrongly re-attributed to *Nodobairdia mammilata* because of their very common juvenile bairdiid contour that is hardly attributable to any precise species. The comparison of their morphology and size with those that may belong to the same ontogenetic stage leads us to formally exclude them from *Nodobairdia mammilata*.

Nodobairdia mammilata has been documented from the Carnian to the Rhaetian and the dimensions of all specimens from the literature are plotted in Figures 3A and 3B. The dimensions of Carnian and Rhaetian (with “Norian-Rhaetian”) specimens are plotted separately in Figure 3A and Figure 3B respectively. The carapace shown in Kristan-Tollmann (1986b) lacks information on magnification or size and is therefore not included. Similarly, Liebermann (1979), Hausmann and Nützel (2015) and Urlichs and Krystyn (2016) did not illustrate any specimen and Kristan-Tollmann (1971) only illustrated the dorsal area of a right valve. The smallest known specimen of *Nodobairdia mammilata* is a left valve from the middle Carnian of Hungary (Kristan-Tollmann *et al.*, 1991) while the largest ones are LV from the Rhaetian of Iran (Kristan-Tollmann *et al.*, 1980; Kristan-Tollmann, 1988a). Only one complete carapace has been illustrated to date, from the late Carnian of Sicily (Crasquin *et al.*, 2018). Another complete carapace was shown by Kollmann (1963) but it is covered with sediment and the contour of RV is hardly visible so that it is treated as a LV. The size range of Carnian and Rhaetian material indicates the presence of several ontogenetic stages (Figs. 3A and 3B).

During the Carnian (Fig. 3A), LV are more abundant than RV and a unique complete carapace has been illustrated to date (Crasquin *et al.*, 2018). This carapace shows that the overlap of LV on RV is only developed along the dorsal and ventral margins and we postulate that LV and RV may roughly plot together in the H/L diagrams throughout the ontogeny. With the additional hypothesis that the largest specimens may be adults, all Carnian specimens of *Nodobairdia mammilata* are distributed into five scatter plots corresponding to five stages (A-4 to Adult; Fig. 3A). During the Carnian, adults are only known from the Cordevolian of Tyrol (Kristan-Tollmann 1978). Stage A-3 is only represented by a RV from Hungary (Kristan-Tollmann *et al.*, 1991) and the available carapace (Crasquin *et al.*, 2018) corresponds to a stage A-4. The LV from the Lycian Nappes (Plates 1C and 1D) are both A-1 stages and the RV (Plate 1E) may be an A-2 juvenile.

LV are also more abundant than RV during the Rhaetian (Fig. 3B). All dimensions of *Nodobairdia mammilata* from the

literature are distributed into five scatter plots (Figs. 3A and 3B), in line with Bolz (1971b) observation of five ontogenetic stages for *Triebelina (Nodobairdia) triassica*. Bolz (1971b) added that the ventral ridge is only apparent at the adult stage in *Triebelina (Nodobairdia) triassica*. The present observations of the entire range of specimens of *Nodobairdia mammilata* rather indicate that the ventral ridge appears quite early in the ontogeny as it is already clearly expressed on specimens attributed to the A-4 stage (e.g. Crasquin *et al.*, 2018).

Suborder Metacopina Sylvester-Bradley (1961)

Superfamily Healdioidea Harlton (1933)

Family Healdiidae Harlton (1933)

Genus *Hungarella* Méhes (1911)

Type species. Hungarella problematica Méhes (1911) by original designation.

***Hungarella* sp.**

(Plate 1F)

Material. One left valve.

Dimensions. L = 232 μm , H = 164 μm , H/L = 0.7.

Occurrences. Sample 328/07, Karapınar Formation, Karadağ Unit, Ağlıovası Yayla section, Lycian Nappes, southwestern Turkey, Cordevolian (*Pseudofurnishius murcianus murcianus* conodont), early Carnian, Late Triassic (this work).

Remarks. The specimen is very small compared to contemporaneous species (e.g. Urlichs, 1971; Forel *et al.*, 2019b), which leads us to conclude that it is a rather young juvenile.

Order Myodocopida Sars (1866)

Suborder Myodocopina Sars (1866)

Superfamily Polycopoidea Sars (1866)

Family Polycopidae Sars (1866)

Genus *Polycope* Sars (1866)

Type species. Polycope orbicularis Sars (1866) by original designation.

***Polycope pumicosa schleiferae* Kozur in Bunza and Kozur (1971)**

(Plates 1G and 1H)

1971 *Polycope pumicosa schleiferae* Kozur in Bunza and Kozur: 14, pl. 2, fig. 17.

2013 *Polycopsis* n. sp. ex gr. *cincinnata* (Apostolescu); Moix *et al.*: pl. 5, fig. 7.

Non 2013 *Polycope pumicosa schleiferae* [sic] Kozur; Monostori and Tóth: 308, pl. 1, fig. 2.

2019a *Polycope pumicosa schleiferae* Kozur; Forel *et al.*: 36, fig. 24D.

Material. Two valves.

Dimensions. L = 234–251 μm , H = 215–220 μm , H/L = 0.88–0.9 (this material).

Occurrences. Hungary, Cordevolian, early Carnian, Late Triassic (Bunza and Kozur 1971); Tavusçayırı Block, Sorgun Ophiolitic Mélange, Huğlu Tuffite, southern Turkey, *Tetraporobrachia haeckeli* radiolarian Zone, Julian, middle Carnian, Late Triassic (Forel *et al.*, 2019a); sample 328/07, Karapınar Formation, Karadağ Unit, Ağlıovası Yayla section, Lycian Nappes, southwestern Turkey, Cordevolian (*Pseudofurnishius murcianus murcianus* conodont), early Carnian, Late Triassic (Moix *et al.*, 2013; this work).

Rejected occurrence. Hungary, Ladinian, Middle Triassic (Monostori and Tóth, 2013).

Remarks. The present specimens have first been discussed by Moix *et al.* (2013), who attributed them to *Polycopsis*

Müller (1894). *Polycopsis* was erected based on modern material mainly using soft body characters, which led several authors to point out the impossibility to distinguish between *Polycope* and *Polycopsis* in the absence of soft parts (e.g. Urlichs, 1972; Neale, 1983). For this reason, Urlichs (1972) chose to re-assign Triassic species to *Polycope* Sars (1866), and was later followed for instance by Kolar-Jurkovšek (1990) or implicitly by Monostori and Tóth (2013), Sebe *et al.* (2013) and Forel *et al.* (2019a). We are in line with Urlichs (1972) and subsequent authors in considering that records of *Polycopsis* in the Triassic are unreliable and that *Polycopsis* species in Kozur (1970), Bunza and Kozur (1971), Kozur *et al.* (2000) should be re-assigned to *Polycope*.

Specimens attributed to *Polycope pumicosa schleiferae* from the Ladinian, Middle Triassic, of Hungary (Monostori and Tóth, 2013) are here excluded from this species because the illustrated specimen (Pl. 1, fig. 2 in Monostori and Tóth, 2013) is rostrate anteriorly and lacks the diagnostic narrow ridge along the free margin. The dimension range of this material is also larger than that of the type material (a diameter ranging from 800 to 860 µm; type material ranging from 274 to 297 µm in length and from 250 to 270 µm in height, Bunza and Kozur (1971)) but this feature is not discriminant enough as it may relate to ontogeny. Monostori and Tóth (2013) also re-attributed *Polycope* cf. *pumicosa schleiferae* from the early Anisian, Middle Triassic, of Romania (Crasquin and Grădinaru, 1996, later reported from the same area by Sebe *et al.*, 2013) to *Polycope pumicosa schleiferae*. However, this taxonomic choice was not discussed. Here we do not subscribe to this re-attribution as the material from the Dobrogea has smaller reticulations dominated ventrally by a series of concentric ridges parallel to the ventral margin and lacks the narrow ridge along free margin. Consequently, *Polycope pumicosa schleiferae* is here considered as restricted to the Carnian and has been reported from Hungary (Bunza and Kozur (1971)) and Turkey (Forel *et al.*, 2019a; this work). The precise age of the type material of *Polycope pumicosa schleiferae* is problematic as it is only attributed to the early Carnian (Unterkaarn) from Bakonyszűcs in Hungary (p. 14 in Bunza and Kozur (1971)), with no further information. Bunza and Kozur (1971) subscribe to the three-fold subdivision of the Carnian but in the absence of precise elements or information to discuss this age attribution, the Hungarian occurrence of *Polycope pumicosa schleiferae* is questionably attributed to the Cordevolian.

Morphologically, it is worth noting that the valve shown in Plate 1H displays rows of small pores arranged parallel to each reticula wall, which were never observed previously.

5 Results and discussion

5.1 Diversity and palaeoenvironment

All specimens obtained from the Cordevolian, early Carnian of the Karapınar Formation in the Lycian Nappes (southwestern Turkey), are isolated valves, implying that they may not be autochthonous (e.g. Oertli, 1971; Boomer *et al.*, 2003). The small dimensions of the material seem to reinforce this hypothesis, as detailed in the systematic palaeontology chapter of this contribution: *Hungarella* sp. and all Bairdiidae of this study are interpreted as juveniles and *Polycope pumicosa schleiferae* is only slightly smaller than the type material. It is therefore quite difficult to build strong

palaeoenvironmental interpretations because of the scarceness of the material and of its possible allochthonous origin but some elements are nevertheless significant.

Nodobairdia mammilata and *Mirabairdia longispinosa* are subtidal species that have been previously recorded from lagoonal/restricted shallow subtidal (Liebermann, 1979) to basinal settings during the Carnian (*Nodobairdia mammilata*: Hausmann and Nützel (2015); *Mirabairdia longispinosa*: Kristan-Tollmann (1978)). Bunza and Kozur (1971) did not provide information on the environmental preferences of *Polycope pumicosa schleiferae*, but it has been reported from contemporaneous offshore areas (Forel *et al.*, 2019a). This species, previously identified as *Polycopsis* n. sp. ex gr. *cincinnata* (Apostolescu) [referring to Apostolescu (1959)] in Moix *et al.* (2013), has been reported as occurring in “moderately deep water below the storm wave base and in deep water” (p. 419 in Moix *et al.*, 2013). However, it is not clear on which data or references this assertion relies. Nevertheless, the absence of typical deep-water taxa such as those from the Julian of the Mersin Mélange (Turkey; Forel *et al.*, 2019a) and the characteristics of the three species detailed above, point to a relatively offshore subtidal palaeoenvironment under moderate water depth. Moix *et al.* (2013, p. 419) add that “the presence of several typical sculptured Bairdiidae without disintegration of the nodes and ribs indicates that the water depth was around 100 m, estimating warm water in a water depth at 70 to 100 m or not much deeper”. This sentence is problematic because:

- No details of the occurring Bairdiidae are provided;
- The only specimen figured in Moix *et al.* (2013, here re-identified as *Mirabairdia* sp.) lacks nodes or ribs;
- These explanations are themselves problematic as ribs and nodes are most of the time relatively low-lying ornamental features so that this deduction should be used for spines rather than ribs and nodes.

5.2 On the palaeobiogeographical distribution of ostracods during the Carnian

5.2.1 Mesozoic Neotethys

The conodont *Pseudofurnishius murcianus murcianus* van den Boogaard (1966), retrieved from the studied sample, is a typical indicator for the Neotethyan domain and shows that the Karadağ Unit belongs to the Cimmerian Taurus terrane and was part of the northern passive margin of the Neotethys (Fig. 4; Moix *et al.*, 2013).

The Palaeotethys existed between Eurasia and Gondwana in the Late Palaeozoic and was subducted northwards during the Middle-Late Triassic (e.g. Robertson and Dixon, 1984, Dercourt *et al.*, 1986, 1993, 2000; Moix *et al.*, 2008). Its closure triggered the opening of the Neotethys by the rifting of continental fragments (Taurides, Cimmerian blocks) from the northern margin of the Gondwana. In parallel, the northward subduction of the Palaeotethys beneath Eurasia opened up a series of back-arc basins along the southern area of Eurasia (Fig. 4). The closure of the Palaeotethys was terminated by the collision of the Taurides and Eurasia in the latest Triassic, known as the Cimmerian orogenic event. In the mean time, the Neotethys was opening to the south.

The geodynamic evolution of the Neotethys during the Mesozoic is currently described by two main models. The first

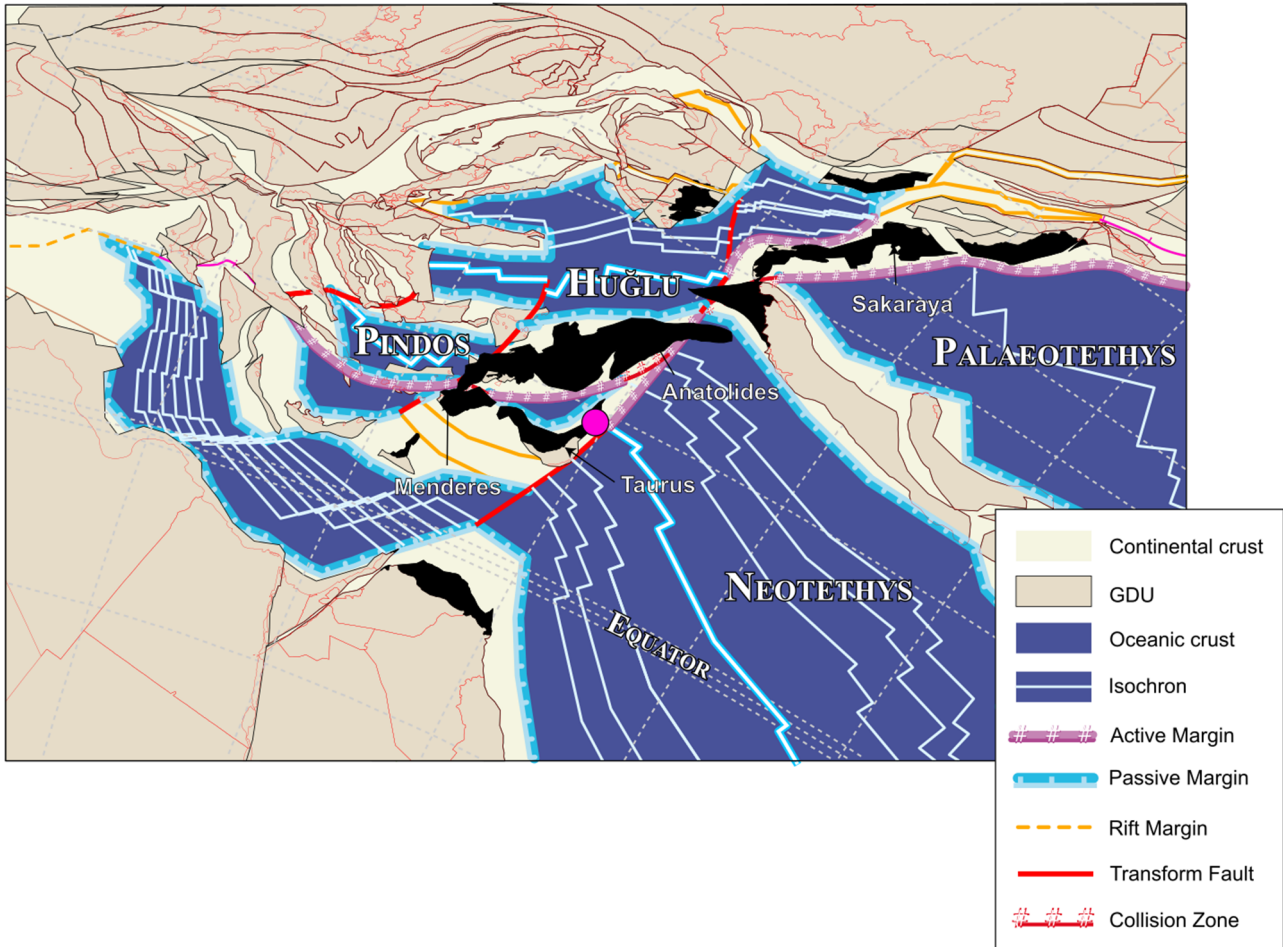


Fig. 4. Palaeogeographic map of the western Tethyan area for the Late Triassic (230 Ma). In black are the dispersed parts of Turkey (modified from Moix *et al.*, 2013). The pink circle indicates the position of the studied area.

model, termed “one-ocean thesis”, was introduced by Bernoulli and Laubscher (1972) and later reworked by Neubauer and von Raumer (1993), Schmid *et al.* (2008) and Bortolotti *et al.* (2013). The second one proposes multiple oceanic basins and microcontinents (*e.g.* Sengör, 1984; Robertson and Dixon, 1984; Stampfli and Borel, 2004; Stampfli and Kozur, 2006; Moix *et al.*, 2008; Robertson *et al.*, 2009, 2013). A relatively simple one-ocean model has been proposed for the Alpine-Dinaric-Hellenic belt, but comparisons with Eastern Mediterranean and Middle East led to more complicated scenarios (*e.g.* Robertson *et al.*, 2009). The close similarity of the upper Julian-lower Tuvlian radiolarian faunas from the Northern Calcareous Alps through the Lagonegro Basin, Sicily, Greece and farther east in the Antalya nappes, in the Mersin Mélange and in Elbistan (Turkey) may confirm the idea of a single oceanic basin (Ozsvárt *et al.*, 2017).

5.2.2 Origin and palaeobiogeography of ostracods during the Triassic: state of the art

The area of origin of Mesozoic tethyan ostracods has been considered by three main schools of thoughts:

- The “western America” hypothesis, which considers that they radiated in western America, particularly in British

Columbia, with a subsequent westward trans-pantalassic dispersion (Kristan-Tollmann and Tollmann, 1981, 1982; Kristan-Tollmann, 1986a, b, 1988a);

- The “western Tethys” hypothesis that has for instance been proposed for *Polycope cincinnata* Apostolescu (1959) that occurs in the western Tethys during the Middle and Late Triassic and became cosmopolitan, reaching Timor, in the Early Jurassic (Lord, 1988). Bate (1977) considered that the European Province may have been the radiation place of the majority of important Mesozoic families;
- The “eastern Tethys” hypothesis that has been proposed for several taxa such as the vallate healdiid *Hermiella* (Kristan-Tollmann, 1993), cytheroids (Bate, 1977; Lord, 1988 based on Kristan-Tollmann, 1983) or ornate bairdiids (Ketmuangmoon *et al.*, 2018; discussed below). Lord (1988) hypothesized that typical Jurassic taxa might have originated on the eastern side of the Tethys, migrated to the western Tethys during the Late Triassic transgression and diversified there up to the known Jurassic record. Recently, it has been proposed that *Carinobairdia* and Schulerideidae may have radiated on the Chinese coasts during the Tuvlian, late Carnian, and migrated westward later during the Late Triassic (Forel *et al.*, 2019b). At the generic level, this Chinese record also represents the oldest known

occurrence of *Carinobairdia* that may thus have colonized western tethyan areas through the *Carinobairdia cabralae-Carinobairdia alpina* lineage.

The knowledge of the origin of Mesozoic marine ostracods and their diffusion ways is still heterogeneous. For Early Jurassic ostracods, five provinces have been recognized (European, Tethyan, North African, American, East African; Bate, 1977) as well as important changes in their provincialism (Arias, 2007). The Early Jurassic provincialism has been related to the spread of cosmopolitan species, extinction of endemic species, disappearance of geographical barriers, warmer climate conditions and rising sea level (Arias and Whatley, 2009).

The palaeobiogeographical distribution of ostracods during the Triassic has been discussed mainly during the 70's and 80's, but was never really reconsidered since this relatively prolific period. In 1973, Kozur (1973b) distinguished three distinct conodonts and ostracods provinces during the Triassic: southern boreal, tethyan (subdivided into nevadian, asiatic, dinarian, austroalpine, westmediterranean and german subprovinces) and northern boreal provinces. Kozur (1973b) also proposed successive faunal connexions within the tethyan province, which might have been connected to the northern boreal province through the german subprovince during the Early Triassic. A westward migration of brackish water and euryhaline ostracods in the Middle Triassic (upper Illyrian-Ladinian) is finally proposed from the asiatic subprovince through the eastern Carpathians and northern margin of the Black Sea. Later, Kristan-Tollmann and Tollmann (1981, 1982) and Kristan-Tollmann (1986a, 1988a, b, 1991) analysed the distribution of diverse fossil groups (algae, crinoids, foraminifers, holothurians, anomuran coprolites, halobids, brachiopods, ammonoids and ostracods) concluded that it was homogeneous within the Tethys during the Late Triassic. On the opposite, six provinces have been identified for foraminifer species in the Late Triassic (Chablais *et al.*, 2011): the peri-Tethys, eastern Gondwana, eastern Laurasia, central Pacific, Sambosan and other seamounts. However, no evident palaeobiogeographic restrictions is observed at the generic level. More recently, Chen *et al.* (2016) proposed the existence of two distinct provinces for conodonts during the Middle and Late Triassic, viz. tethyan and panthalassan domains. These diverse views are relatively challenged by recent works that rather document an increasing differentiation occurred between the Neotethyan and the Palaeotethyan faunas, with a maximum in the Cordevolian (e.g. Moix *et al.*, 2007). During this interval, the conodont, ostracod, holothurian sclerite and sponge spicule faunas show that the Apulian-Tauride High clearly separated (e.g. Kozur, 2000; Stampfli and Kozur, 2006; Moix *et al.*, 2007, 2013; Fig. 4):

- The Neotethyan fauna to the south, for instance marked by *Pseudofurnishius murcianus* van den Boogaard (1966) and *Theelia tubercula* Kristan-Tollmann (1963);
- The northern Tethyan fauna in the Huğlu-Pindos Ocean and its shelves (including the Antalya Nappes), to the north.

After the breakup of the Apulian-Tauride High that may have occurred in the Julian, the faunas of the Neotethys and these of the Tethyan areas (Palaeotethyan back-arcs) immediately north of the Tauric Autochthon became almost identical (Kozur, 2000; Moix *et al.*, 2007).

Since these early works, this major issue has not been further discussed in details. The present work, following Forel *et al.* (2019b), aims at characterizing migration patterns underlying the observed Late Triassic tethyan homogeneity.

5.2.3 The Lycian Nappes record

Of the five species we document from the Lycian Nappes, three are known from other Triassic marine successions: *Mirabairdia longispinosa* Kristan-Tollmann, *Nodobairdia mammilata* Kollmann and *Polycope pumicosa schleiferae* Kozur. Their Cordovelian occurrences in the Lycian Nappes revive the discussion on palaeogeographical distribution during the Late Triassic, homogeneity of tethyan communities, dispersal routes as well as radiation areas. In this discussion, we considered as a necessary condition to be able to verify and confirm the conspecificity of all specimens attributed to the studied species. For this reason, articles that record but not illustrate the species are here excluded as they may introduce artificial occurrences. Therefore, the following references are omitted from this discussion:

- Liebermann (1979; Cordevolian, early Carnian, Italy): *Mirabairdia longispinosa*;
- Liebermann (1979; Cordevolian, early Carnian, Italy) and Hausmann and Nützel (2015; Carnian, Italy): *Nodobairdia mammilata*.

The updated palaeogeographical distribution of the three species through time is summarized in Table 2. *Polycope pumicosa schleiferae* and *Mirabairdia longispinosa* are both restricted to the Carnian of the western Tethys *sensu lato*. In the present state of our knowledge, *Polycope pumicosa schleiferae* is known from the early and middle Carnian and does not extend in the late Carnian. During the Cordevolian, it occurs on the northern portion of the Neotethys (Moix *et al.*, 2013; this work) and possibly on the northern margin of the Huğlu Basin (Hungary; Bunza and Kozur (1971)). During the middle Carnian, it is only known from the southern margin of the Huğlu Basin (Turkey; Forel *et al.*, 2019a). *Mirabairdia longispinosa* is known from the early and late Carnian (Tab. 2), possibly illustrating the lack of data for the middle Carnian. During the Cordevolian, *Mirabairdia longispinosa* occurs on the northern margin of the Huğlu Basin (Kollmann (1963); Kristan-Tollmann, 1971, 1978; Zorn, 2010) and in the Neotethys (this work). It is last documented in the late Carnian on the southern margin of the Huğlu Basin (Forel *et al.*, 2018).

Nodobairdia mammilata has a longer history, ranging from the early Carnian to the Rhaetian (Tab. 2). Until the present record, this species was restricted to the Alpine area during its entire Carnian history (Kristan-Tollmann, 1971, 1978; Kollmann (1963); Zorn, 2010; Kristan-Tollmann *et al.*, 1991; Monostori, 1994; Kristan-Tollmann and Hamedani, 1973). Occurrences in Sicily during the late Carnian (Crasquin *et al.*, 2018) and in Australia later during the Norian (Kristan-Tollmann, 1986b) and upper Norian-Rhaetian (Dépêche and Crasquin, 1992; Crasquin and Dépêche, 1993) could have witnessed a large diffusion of *Nodobairdia mammilata* in the Neotethys after the Carnian. However, the present report indicates that *Nodobairdia mammilata* was already present in the Huğlu Basin and on the northern area of the Neotethys

Table 2. Stratigraphical and palaeogeographical ranges of ostracod species recorded outside the Lycian Nappes during the Triassic; stages durations not to scale. Light grey squares: literature-based distribution; dark grey squares: new distribution from the Lycian Nappes.

	<i>M. longispinosa</i>		<i>N. mammilata</i>	<i>P. pumicosa schleiferae</i>
RHAETIAN			Northern Calcareous Alps Australia Hungary	
NORIAN		Iran	Australia	
		Hungary		
	Tuvalian	Turkey (Huğlu)	Hungary Sicily	
CARNIAN	Julian		Hungary	Turkey (Huğlu)
	Cordevolian	Italy	Italy	Hungary?
		Turkey (Lycian Nappes)	Turkey (Lycian Nappes)	Turkey (Lycian Nappes)

Abbreviations: A: Austria; C: China; G: Germany; H: Hungary; I: Iran; R: Romania; S: Slovakia; T: Turkey; Ti: Tibet.

Ocean in the Cordevolian, at the base of the Carnian. Consequently, *Polycopse pumicosa schleiferae*, *Mirabairdia longispinosa* and *Nodobairdia mammilata* were already largely distributed during the Cordevolian, early Carnian, implying that they may have radiated earlier, possibly at the end of the Ladinian. Although data are still lacking to propose a robust hypothesis on the radiation areas of these species, it is reasonable to consider their early evolutive history as purely western-tethyan. Only a larger geographical coverage of the Middle-Late Triassic transition will clarify whether they radiated in neotethyan or palaeotethyan waters. As described earlier, the disaggregation of the Apulian-Tauride High that separated neotethyan and palaeotethyan faunas is traditionally placed in the Julian, Middle Carnian (e.g. Kozur, 2000; Stampfli and Kozur, 2006; Moix *et al.*, 2007, 2008, 2013). Yet, the ostracod record indicates that communication ways were already present and provided stable palaeoenvironmental conditions for these benthic organisms to spread from one ocean to the other at the base of the Cordevolian.

During the Late Triassic, the Cimmerian continent, the width of which is still unknown, was crossed by major faults (Fig. 4) that could have served for faunal exchanges between the Palaeotethys and Neotethys during the collision phase. The migrating flexural bulge and development of a foreland basin demonstrate that the Tauric-Anatolian and Beydağları-Apulian domains were separated at least by a few hundred kilometers, this separation being placed in the Julian (e.g. Kozur, 2000; Moix *et al.*, 2008). These flexural structures may have been relatively deep corridors allowing faunal relations as early as in the Cordevolian as shown by the ostracods reported here. At some places and before it was completely overlapped by the accretionary prism, the Cimmerian block may have been brought at already important depth to allow faunal exchanges before the closure of the Palaeotethys (Fig. 5). We propose here that the opening of the communication between the Palaeotethys and the Neotethys may have initiated already during the Cordevolian, and became more widely established during the Julian for more intense, and therefore more visible, faunal exchanges (pers. comm. Prof. Dr. Gérard Stampfli, Université de Lausanne).

Following these observations and interpretations, it is necessary to confront the idea of homogeneity of tethyan

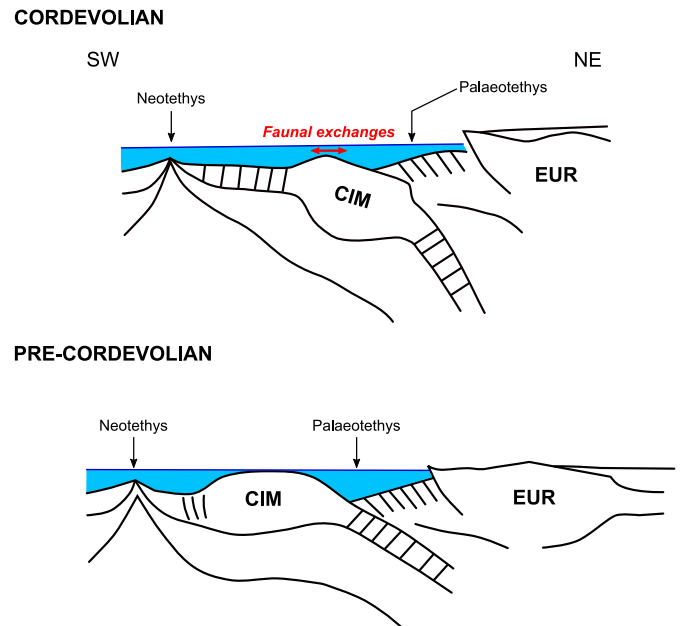


Fig. 5. Sketch illustrating the successive pre-Cordevolian (bottom) and Cordevolian (top) position of the Cimmerian block allowing for faunal exchanges only from the Cordevolian onwards. CIM: Cimmerian block. EUR: Europe.

ostracods during the Late Triassic (e.g. Kristan-Tollmann and Tollmann, 1981, 1982; Kristan-Tollmann, 1986a, 1988a, b, 1991) with that of the opening of Neotethys and Palaeotethys communication during the Cordevolian. These two conceptions of Late Triassic ostracod faunas may seem antithetical but they need to be replaced in a stratigraphical context to get insight into the temporal dynamism of ostracods distribution. The synthesis on the homogeneity of tethyan marine communities of Kristan-Tollmann (1988a) offered a static summary of the large-scale distribution of diverse algae, crinoid, holothurian, ostracod and anomouran coprolite species from the Middle Triassic (Late Ladinian, down to Late Anisian for ostracods) to the end of the Late Triassic (Rhaetian). *Nodobairdia mammilata* is part of the typical tethyan taxa that

led Kristan-Tollmann (1988a) to conclude to the relative homogeneity of the tethyan communities during the Late Triassic. The present record is in line with this observation in showing a large distribution of this species during the Cordevolian. As detailed above, several hypotheses were brought for the geographical trend of tethyan colonization but none was replaced in a temporal context. It is only later that temporalization was brought with the proposal of uniformization of palaeotethyan and neotethyan faunas during the Julian (e.g. Kozur, 2000; Stampfli and Kozur, 2006; Moix *et al.*, 2007, 2008, 2013). Here, the initiation of this uniformity is placed in the Cordevolian. The homogenization of the ostracod faunas reported by several authors during the Late Triassic (e.g. Kristan-Tollmann and Tollmann, 1981, 1982; Kristan-Tollmann, 1986a, 1988a, b, 1991) might therefore relate to the opening of communications between the Neotethys and the Palaeotethys oceans during the Cordevolian, early Carnian. However, Kristan-Tollmann (1988a) states that the uniformity was already recognizable at the end of the Ladinian, and even at the end of the Anisian for ostracods. This early uniformity needs to be carefully re-considered as it cannot be explained by the same tectonic event and may correspond to different diversity dynamics.

5.2.4 Generic versus specific palaeogeographical patterns

The purely western-tethyan history of *Polycopse pumicosa schleiferae*, *Mirabairdia longispinosa* and *Nodobairdia mammilata* and the opening of the oceanic communication reactivate the discussion on the origin of tethyan ostracods and on their palaeogeographical homogeneity during the Late Triassic (e.g. Kristan-Tollmann and Tollmann, 1981, 1982; Kristan-Tollmann, 1986a, 1988a; Lord, 1988; Forel *et al.*, 2019b). The distribution pathways are also important to discuss as they may provide insights into the history of radiation, colonization events and associated environmental conditions.

The oldest occurrences of *Nodobairdia* are from the Anisian *lato sensu* of the Suhkothai terrane (Ketmuangmoon *et al.*, 2018) and late Anisian of South China (Kristan-Tollmann, 1983). It is known up to the Rhaetian (Bolz, 1971a, b; Kristan-Tollmann *et al.*, 1979, 1980, Kristan-Tollmann, 1988a; Dépêche and Crasquin, 1992; Crasquin and Dépêche, 1993; Mette *et al.*, 2012; Monostori and Tóth, 2014). These palaeogeographical and stratigraphical ranges led Ketmuangmoon *et al.* (2018) to propose that Southeast Asia may have been an important area of generic origination during the Middle Triassic, with *Nodobairdia* later spreading to the entire tethyan areas. This observation was recently extended to *Carinobairdia* (Forel *et al.*, 2019b). When considering the species distribution, *Nodobairdia mammilata* colonized most of the western Tethys to Iran but it apparently did not extend to the easternmost areas.

The history of *Mirabairdia* drastically differs from that of *Carinobairdia* and *Nodobairdia*. Its first attested occurrence is of Capitanian age, Middle Permian, in South China (Zazzali *et al.*, 2015). During its entire Permian history, *Mirabairdia* has been restricted to South China, with a maximum of diversity during the Changhsingian, Late Permian (e.g. Shi and

Chen, 1987, 2002; Hao, 1994, 1996; Yi, 2004; Yuan *et al.*, 2009; Crasquin *et al.*, 2010). During the Triassic, a westward trend similar to that reported for *Nodobairdia* is documented for *Mirabairdia*, with records in South China during the Anisian (Kristan-Tollmann, 1983) and all around the Huğlu Basin during the Middle and Late Triassic: Turkey (Julian, middle Carnian, Forel *et al.*, 2019a; Tuvalian, late Carnian, Forel *et al.*, 2018), Italy (Julian, middle Carnian, Kollmann (1963); Liebermann, 1979; Cordevolian, early Carnian, Kristan-Tollmann (1978)), Hungary (Anisian, Middle Triassic, Kozur, 1971), Austria (Julian, middle Carnian, Kollmann (1963); Rhaetian, Kozur, 1973a; Anisian, Middle Triassic, Mette *et al.*, 2014). This record may imply a westward migration along the northern margin of the Palaeotethys up to the Anisian. It may have been followed by the colonization of the Huğlu Basin during the Carnian with an extension to the north of the Neotethys at the very beginning of the Carnian as shown by the present record of the Cordevolian of the Lycian Nappes. The history of the genus *Mirabairdia* therefore implies much older roots than for *Carinobairdia* and *Nodobairdia* and survival to the end-Permian extinction. However, the present contribution provides the first known record of *Mirabairdia* in the Neotethys.

This mixture of endemism between generic and specific levels has also been reported during the Late Triassic for foraminifers (Chablais *et al.*, 2011). These distinct generic and specific patterns show that these problematics need to be studied in their full complexity. It is interesting to note that generic patterns rather show a westward trend for all these taxa.

6 Conclusions

Ostracods of Cordevolian, early Carnian, Late Triassic, age have been retrieved from the Karapınar Formation cropping out at the Ağılıovası Yayla section, located in the Lycian Nappes in southwestern Turkey. Five species are found, including three typical Late Triassic species: *Mirabairdia longispinosa* Kristan-Tollmann (1978), *Nodobairdia mammilata* Kollmann (1963) and *Polycopse pumicosa schleiferae* Kozur in Bunza and Kozur (1971). We discuss the taxonomy of the species recovered, describe the ontogeny of *Nodobairdia mammilata* and observe five stages for the Carnian and Rhaetian material. We discuss the palaeoenvironmental implications of the assemblage, pointing toward a deposition in the relatively offshore subtidal zone under moderate water depth. We finally discuss the palaeobiogeographical distribution of marine ostracods during the Late Triassic: it implies that communications between the Neotethys and the Huğlu Basin might have been already open during the Cordevolian.

Abbreviations

RV	Right valve
LV	Left valve
DB	Dorsal border
AD	Bantero-dorsal border
PDB	Postero-dorsal border
H	Height
L	Length

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