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 Ağilovası Yayla section yielded five species, including the typical Late Triassic Mirabairdia longispinosa Kristan-Tollmann, Nodobairdia mammilata Kollmann and Polycopae punicosa 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

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 (Klompmaker 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 re-diversification.

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: Mirabraria longispinosa Kristan-Tollmann (1978), Nodobairdia mammilata Kollmann (1963) and Polycop e pumicosa schleiferae 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 fauna 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 Mirabraria 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/Susz Dağ/Göçek 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), Kololum Fm. (Middle Carboniferous bioclastic limestones, dolomites and dolomitic limestones, not shown in Fig. 2), Akkavak Fm. (Early Permian crystalline limestones, dolomites and shales), Sarrtas 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 ( Ağacı and Badada 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, lyclites 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.
rather point to a Kubergandian age (Tethyan equivalent of the Roadian; Vachard and Moix, 2013).

2.2 The Ağlıovası 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 Ağlıovası 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 Ağlıovası Yayla.

The composite succession of the Ağlıovası 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 Ağlıovası 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 Ağlıovası 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 argilites (Akkavak Fm.). All fossil assemblages indicate a Sakmarian age (Moix et al., 2013). It is followed by the Sarıtas 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 Ağılıovası Yayla section (modified after Moix et al., 2013) and position of the studied sample.
Chen et al. (2013). It is issued from dark limestones at the top of the Karapınar Fm. (Fig. 2) that yielded Pseudofurnishius mucianus mucianus 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 Karadag 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 “Polycopsis n. sp. ex gr. cinctimata (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 Polycopsis 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 specimens. In this way, 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 denomination 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 mucianus mucianus (Moix et al., 2013). All figured specimens are deposited in the micropaleontology collections of the Muséum national d’Histoire naturelle (Paris), under catalogue numbers MNHN.F.63332–MNHN.F.63339.

4 Systematic palaeontology
(by Marie-Béatrice Forel)

Class Ostracoda Latreille (1806)
Subclass Podocopa Müller (1894)
Superfamily Bairdioidae 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); Sevati-an, late Norian, Austria) was erected to accommodate bairdiids with “dorsal outline clearly divided into three parts;
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.

**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 |
|--------------------------------|---------------------------------|-------------|-----------|
| *Mirabairdia pernodosa* Kollmann (1963) | Ladinian-lower Carnian | Julian-Tuvalian, Carnian | Cordevolian-Tuvalian, Carnian |
| *Mirabairdia longispinosa* Kristan-Tollmann (1978) in Liebermann (1979) | “Niveau mit Trachyceras aon”, Julian, middle Carnian | – | Cordevolian, early Carnian |
| *Nodobairdia mammilata* Kollmann (1963) | Ladinian | aon subzone, Julian, middle Carnian | Cordevolian, early Carnian |
| *Nodobairdia mammilata* Kollmann (1963) in Liebermann (1979) | Julian, middle Carnian | aon subzone, Julian, middle Carnian | Cordevolian, early Carnian |
| *Triebelina* (Nodobairdia) *triassica* Bolz (1971a) | Norian-Rhaetian | Rhaetian | Rhaetian |
| *Triebelina* sp. G in Bolz (1971a) | Norian-Rhaetian | Rhaetian | Rhaetian |

antior 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); Tavuşçayırı Block, Sorgun Ophiolitic Mélange, Huğlu Tuflite, southern Turkey, *Spongotorillispinus moixi* radiolarian Zone, lower Tuvalian, late Carnian, Late Triassic (Forel et al., 2018); sample 328/07, Karapınar Formation, Karadağ Unit, Ağılovası 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 postero-dorsal 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 pernodoso* 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 pernodoso*. 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 pernodoso* 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 plurinodoso* Mette et al. (2014):
  - RV: L = 920–1130 µm, H = 460–560 µm;
  - LV: L = 950–1070 µm, H = 460–570 µm;

- *Mirabairdia praephyrropsephaerica* 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, venter-median and antero-ventral spines. Juveniles of *Mirabairdia pernodoso* 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 spines on the ventral margins and sub-ventral warts.
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, spinoise). 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 Whately, 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); Stuores 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, Karapinar Formation, Karadag Unit, Ağılıovasi 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 Nüttel (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 Healdtioidae Harlton (1933)

Family Healdtiidae 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 \(\mu\)m, H = 164 \(\mu\)m, H/L = 0.7.

**Occurrences.** Sample 328/07, Karapınar Formation, Karadaağ Unit, Ağılıvovasi Yayla section, Lician 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 schleferae* Kozur in Bunza and Kozur (1971)

(Plates 1G and 1H)

**Material.** Two valves.

**Dimensions.** L = 234–251 \(\mu\)m, H = 215–220 \(\mu\)m, H/L = 0.88–0.9 (this material).

**Occurrences.** Hungary, Cordevolian, early Carnian, Late Triassic (*Bunza and Kozur* 1971); Tavuşçayırı Block, Sorgun Ophiolitic Mélange, Huğlu Tufaite, southern Turkey, *Tetraporobrachia haeckeli* radiolarian Zone, Julian, middle Carnian, Karapınar Formation, Karadaağ Unit, Ağılıvovasi Yayla section, Lician 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 *Polycope*...
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 *Polycype* and *Polycopsis* in the absence of soft parts (e.g. Ulrichs, 1972; Neale, 1983). For this reason, Ulrichs (1972) chose to re-assign Triassic species to *Polycype* 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 Ulrichs (1972) and subsequent authors in considering that records of *Polycosi* 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 *Polycype*.

Specimens attributed to *Polycype 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 *Polycype cf. pumicosa schleiferae* from the early Anisian, Middle Triassic, of Romania (Crásquin and Grădinaru, 1996, later reported from the same area by Sebe et al., 2013) to *Polycype 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, *Polycype 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 *Polycype pumicosa schleiferae* is problematic as it is only attributed to the early Carnian (Unterkarn) from Bakonyszics 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 *Polycype 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 Bairdiidæ of this study are interpreted as juveniles and *Polycype pumicosa schleiferae* is only slightly smaller than the type material. It is therefore quite difficult to build strong palaeoenvironmental interpretations because of the scariness 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 *Polycype 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 Bairdiidæ 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 Bairdiidæ 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 Karadag 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
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 Tuvalian radiolarian faunas from the Northern Calcareous Alps through the Lagonegro Basin, Sicily, Greece and farther east in the Antalyan 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-panthalassic 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 Tuvalian, 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, halobiids, brachiopods, ammonoids and ostracods) and 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 (Chabrais et al., 2011): the peri-Tethys, eastern Gondwana, eastern Laurasia, central Pacific, Sambosan and other seamounts. However, no evident palaeobiogeographical 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 *Theelita 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 latu*. 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.
Ocean in the Cordevolian, at the base of the Carnian. Consequently, *Polycope 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 waters is traditionally placed in the Julian, Middle Carnian (e.g. Kozur, 2000; Stampfl 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 Stampfl, Université de Lausanne).

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

**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.

|        | *M. longispinosa* | *N. mammilata* | *P. pumicosa schleiferae* |
|--------|------------------|----------------|--------------------------|
| RHAETIAN |                  |                |                         |
|        | Iran             |                | Northern Calcareous Alps |
| NORIAN | Hungary          |                | Australia                |
|        | Tuvalian         |                | Hungary                  |
|        | Turkey (Huğlu)  |                | Sicily                   |
| CARNIAN| Julian           |                | Hungary                  |
|        | Cordevolian      |                | Italy                    |
|        | 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.

![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.](image)
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; Stampfi 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 Polycop e 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 Sukhothai 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 origin 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 Ağlıovası 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 Polycop e 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

| Abbreviation | Meaning        |
|--------------|----------------|
| 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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