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Bounded by crises: An overview of the evolution of marine ostracods during the Triassic

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Abstract

The Triassic has been a turning in the history of biodiversity: bracketed by two major biotic crises, characterized by major biotic, climatic and tectonic events, it has seen the transition from the Palaeozoic to the Modern evolutionary faunas. We propose the first synthetic analysis of the diversity of marine and brackish-water ostracods over the entire Triassic, in the light of palaeoecological, palaeoenvironmental and palaeogeographical contexts. Although general diversity trends witness poor ostracod communities during most of the Early Triassic after the end-Permian crisis, the roots of their Triassic taxonomic rediversification are visible as early as the Dienerian. The explosive diversification of the Spathian and Anisian is followed by a high-diversity plateau up to the brink of the end-Triassic extinction. A “morphological phylogeny” proposes that all Permian and Triassic ornate Bairdiidae derived from Petasobairdia in the Kungurian, with the emergence of the Ceratobairdia-lineage and Abrobairdia-lineage. While they are generally the “poor cousin” of trophic chains analyses, traces of typical Mesozoic drilling predation on Late Triassic ostracods unexpectedly document the increase of the efficiency of predators drilling abilities through the Triassic. Finally, the palaeogeographical distribution of ostracods as been very dynamic during this interval, with distinct peri-palaeo-tethyan and peri-neo-tethyan biotas in the Early Triassic, followed by a dispersal and thus a relative homogenization from the Anisian onwards.

Keywords	Ostracods; Early, Middle, Late Triassic; Diversity; Palaeogeography; Ornate Bairdiidae
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Research Data Related to this Submission

There are no linked research data sets for this submission. The following reason is given:
These data correspond to the 2 supplementary files that accompany the manuscript

Dr. Marie-Béatrice Forel
Associate Professor
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Paris, April 20, 2020

Dear Editor,

Please find here the manuscript entitled '*Bounded by crises: an updated view of the evolution of marine ostracods during the Triassic*' (Forel M.-B. & Crasquin S.) we would like to propose for publication in *Marine Micropaleontology*, for the Ostracoda special issue edited by M. Yasuhara.

This contribution is the first review of the diversity of marine and brackish-water ostracods during the Triassic, a major period in the history of biodiversity worldwide. Thanks to a large database of all ostracod taxa documented during this interval, we describe their diversity from assemblages recovering from the end-Permian extinction to those going extinct at the end of the Triassic. We summarize and discuss their characteristics, importance to reconstruct the early roots of the Mesozoic marine revolution and describe their geographic distribution through time. Finally, we propose a phylogeny of ornate Bairdiidae that display a still challenging explosive diversification during this interval.

On behalf of my collaborator, thank you for giving this work your consideration.

Marie-Béatrice Forel

Highlights

- Explosive diversification of ostracods during the Spathian and Anisian, Triassic.
- Ornate Bairdiidae derived from *Petasobairdia* in the Kungurian.
- Ostracods show increasing drilling abilities of Triassic predators.
- Homogenization of geographical distribution from the Anisian onwards.

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4 crises, characterized by major biotic, climatic and tectonic events, it has seen the transition
5 from the Palaeozoic to the Modern evolutionary faunas. We propose the first synthetic
6 analysis of the diversity of marine and brackish-water ostracods over the entire Triassic, in
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14 ornate Bairdiidae derived from *Petasobairdia* in the Kungurian, with the emergence of the
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21 Anisian onwards.
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40 **Keywords:**

41 Ostracods

42 Early, Middle, Late Triassic

43 Diversity

44 Palaeogeography

45 Ornate Bairdiidae
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Bounded by crises: an updated view of the evolution of marine ostracods during the Triassic

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ABSTRACT

The Triassic has been a turning in the history of biodiversity: bracketed by two major biotic crises, characterized by major biotic, climatic and tectonic events, it has seen the transition from the Palaeozoic to the Modern evolutionary faunas. We propose the first synthetic analysis of the diversity of marine and brackish-water ostracods over the entire Triassic, in the light of palaeoecological, palaeoenvironmental and palaeogeographical contexts.

Although general diversity trends witness poor ostracod communities during most of the Early Triassic after the end-Permian crisis, the roots of their Triassic taxonomic rediversification are visible as early as the Dienerian. The explosive diversification of the Spathian and Anisian is followed by a high-diversity plateau up to the brink of the end-Triassic extinction. A “morphological phylogeny” proposes that all Permian and Triassic ornate Bairdiidae derived from *Petasobairdia* in the Kungurian, with the emergence of the *Ceratobairdia*-lineage and *Abrobairdia*-lineage. While they are generally the “poor cousin” of trophic chains analyses, traces of typical Mesozoic drilling predation on Late Triassic ostracods unexpectedly document the increase of the efficiency of predators drilling abilities through the Triassic. Finally, the palaeogeographical distribution of ostracods as been very dynamic during this interval, with distinct peri-palaeo-tethyan and peri-neo-tethyan biotas in

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1. Introduction

The end-Permian extinction (EPE), ~252 Ma (Burgess et al., 2014; Baresel et al., 2017), has been the largest biological crisis in Earth's history, with the extinction of more than 90% of marine species (e.g., Raup, 1979; Erwin, 1994; Alroy et al., 2008; Stanley, 2016). The emission of the Siberian continental flood basalts is currently considered as the main trigger for the crisis, and the associated release of aerosols and/or CO₂ and their feedbacks on oceanic and terrestrial systems may have intensified its environmental and ecological stresses (e.g., Campbell et al., 1992; Renne et al., 1995; Reichow et al., 2009; Saunders and Reichow, 2009). The Triassic is one of the most significant intervals of time in the history of biodiversity with the stepwise restoration of land and sea ecosystems after the EPE, the rise of the modern fauna and the emergence of modern ecosystems (e.g., Sepkoski, 1984; Brusatte et al., 2010; Chen and Benton, 2012; Benton et al., 2013). Most of the new predators that have been 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 drill holes on mollusks and brachiopods (Klompmaker et al., 2016; Tackett and Tintori, 2019) document the establishment of a typical Mesozoic drilling activity early in the Mesozoic and thus the rooting of the Mesozoic marine revolution deep into the Triassic.

Marine ostracods have been documented through the entire Permian and Triassic systems worldwide (e.g., Wang, 1978; Chen and Shi, 1982; Shi and Chen, 1987; Yi, 1992; Hao, 1994; Crasquin-Soleau et al., 2006; Yuan et al., 2007, 2009; Mette, 2008, 2010; Crasquin et al., 2010; Forel and Crasquin, 2011a, b; Forel et al., 2013a, b, 2015, 2019a, b; Forel, 2012, 2014). They went through severe losses and a deep restructuration of their communities through the EPE (Crasquin-Soleau et al., 2007; Crasquin and Forel, 2014 for review). The Triassic period has also been of paramount importance in the macroevolution for ostracods,

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179
180 with the turnover from the Palaeozoic fauna to the Meso-Cenozoic one (e.g., [McKenzie](#),
181 [1982](#); [Crasquin-Soleau et al., 2007](#); [Crasquin and Forel, 2014](#)). However, this period stays
182 enigmatic with the temporary and challenging dominance of Platycopida and heavily sculpted
183 Bairdiidae (e.g., [Kollmann, 1960, 1963](#); [Bolz, 1971a, b](#); [Kristan-Tollmann, 1978](#)), the
184 explosive radiation of early Cytheroidea (e.g., [Gründel, 1978](#); [Whatley and Boomer, 2010](#)) or
185 the residual occurrence of Palaeozoic taxa in deep-waters up to the Rhaetian ([Forel and](#)
186 [Grădinaru, under review](#)). In that sense, the Triassic ostracod fauna is neither Palaeozoic nor
187 truly Mesozoic. These features, together with the still limited knowledge of their geographical,
188 environmental and taxonomic distribution, challenge our understanding of the mechanisms
189 underlying their survival and diversity structuration during the Triassic, prior to their Mesozoic
190 re-diversification.

201
202 Here we propose the first analysis of the evolution of ostracod diversity (genera and families)
203 during the entire Triassic, placing our discussion in palaeogeographical and
204 palaeoenvironmental contexts. Their continuous record through the EPE and the Triassic
205 provides unique insights into the marine environments and timing of the post-extinction
206 survival and recovery. We discuss the deep intrication of micro- and macro-evolution for
207 marine and brackish ostracods, from the restructuration of assemblages after the EPE to the
208 brink of the end-Triassic biological crisis.

217 **2. A brief state of the art**

221 *2.1. Ostracods through the end-Permian extinction*

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225 Marine ostracods greatly suffered from the EPE, with a species extinction rate of about 80%
226 ([Crasquin and Forel, 2014](#)). Several species spanning the Permian document continuous
227 environmental stress over this interval, as revealed by substantial reduction of the body size
228 and growth rates that culminated at the EPE ([Forel et al., 2015](#)). The EPE was peculiarly a
229 major strike for taxa such as Palaeocopida that were widespread and diverse during the
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239 entire Palaeozoic in both neritic and deep waters (e.g., [Kozur, 1985](#); [Becker and Wang,](#)
240 [1992](#)) but barely survived until their last known occurrence at the beginning of the Late
241
242 Triassic (Carnian; [Forel et al., 2019a](#)).

243
244
245 Distinct recovery phases have been described for ostracod assemblages in the Early and
246
247 Middle Triassic ([Fig. 1A](#)). Diverse types of ostracod survival have been reported from the
248
249 *survival phase*, directly after the EPE (Early Triassic, Griesbachian). A short-lived survival of
250
251 abundant Bairdiidae is associated with post-extinction microbial mats thriving around the
252
253 Palaeo-Tethys, that were exploited for O₂ and food resources ([Forel et al., 2009, 2013a, b,](#)
254 [2015](#); [Forel, 2012, 2014](#); [Hautmann et al., 2015](#); [Martindale et al., 2019](#)). Bairdiidae are
255
256 traditionally considered as restricted to stable and normal marine water bodies (e.g., [Melnyk](#)
257 [and Maddocks, 1988](#)) but these post-EPE assemblages challenge this paradigm in
258
259 illustrating unexpected adaptive faculties including modifications of reproduction, growth
260
261 rates and body sizes ([Forel, 2014](#); [Forel et al., 2013a, b, 2015](#); [Forel, 2018](#)). The second
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263 type is the abundant survivorship of Hollinellidae (Palaeocopida) in very proximal clastic
264
265 zones, under the influence of high detrital input that has, to date, only been reported from
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267 Vietnam ([Crasquin et al., 2018](#)) and South China ([Forel et al., under review](#)). The last
268
269 survival type is that of abundant Cavellinidae only observed from northwest Iran ([Gliwa et al.,](#)
270 [2020](#)) and that is currently under description. These diverse patterns highlight the necessity
271
272 of shifting paradigm from a unique phenomenon to a wide range of survivals that need to be
273
274 considered in their entire taxonomic and environmental complexities ([Forel et al., under](#)
275 [review](#)). Following this period of survival, the Dienerian and Smithian interval yielded very
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277 rare ostracods worldwide, earning it the name of *maximum of poverty* ([Crasquin-Soleau et](#)
278 [al., 2007](#); [Crasquin and Forel, 2014](#)). The recovery of ostracods is considered as complete in
279
280 the Anisian, Middle Triassic ([Crasquin and Forel, 2014](#)).

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286 Our current knowledge is therefore quite detailed regarding the biodiversity characteristics of
287
288 ostracods through the extinction and to the Anisian, during which the full recovery of the
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290 assemblages is assumed to have occurred. However, this Early-Middle Triassic dynamic
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292 has, until now, never been discussed in the light of palaeogeographical and
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298 palaeoenvironmental conditions, and never been replaced in the context of the entire
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300 Triassic. The Triassic is of crucial importance in the history of biodiversity as it was bounded
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302 by two of the five major extinctions of the Phanerozoic. However, global understanding of the
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304 diversity and evolution of ostracods during the Late Triassic, at the brink of the end-Triassic
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306 crisis, is still lacking. Many questions are still pending and in the context of increasing proofs
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308 of Mesozoic marine revolution being rooted down to the Triassic, what new information
309
310 ostracods may provide?
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312

313 314 *2.2. The Triassic*

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318 The Triassic period lasted from ~252 to 201 Ma (Cohen et al., 2013, updated version 2020;
319
320 Fig. 1A) and was bracketed by two major biological crises. It has been critical in the origin of
321
322 marine and continental modern ecosystems, with the origin of key vertebrates including
323
324 dinosaurs (e.g., Brusatte et al., 2010), frogs, turtles, rhynchocephalians, crocodylomorphs
325
326 and mammals (Benton 2016 and references therein for a review). In the Triassic, all
327
328 continents were fused into the supercontinent Pangaea, incised on its eastern by the Tethys
329
330 forming a large embayment side and surrounded by the Panthalassa Ocean that covered
331
332 more than 70% of Earth's surface (Fig. 1B). The fragmentation of the Pangaea began near
333
334 the end of the Triassic with the outpouring of the massive Central Atlantic magmatic province
335
336 (e.g., Marzoli et al., 1999; Davies et al., 2017). Triassic climates were warm and equable,
337
338 with no polar icecaps. In the Early-Middle Triassic, the sea level was similar to or 10-20 m
339
340 higher than the present-day mean sea level. An important rise occurred at the end of the
341
342 Ladinian and culminated in the late Carnian, representing the highest Triassic sea level (~50
343
344 m above present-day mean sea level). The late Norian recorded a decline, followed by stable
345
346 levels close to present-day until the mid-Rhaetian when the decline further accentuated to
347
348 about 50 m below present-day in the latest Triassic and earliest Jurassic (Haq, 2018).
349
350 The Triassic has been marked by two major events. The first one, at the Smithian-Spathian
351
352 boundary, is generally considered as the most significant event within the post-EPE recovery
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356
357 (e.g., [Galfetti et al., 2007](#); [Stanley, 2009](#)). This interval is marked by severe global climate
358
359 changes ([Hermann et al., 2012](#)) and major extinction of nektonic organisms ([Orchard, 2007](#);
360
361 [Brühwiler et al., 2010](#)). A strong debate is on-going on the temperature pattern at this
362
363 interval, between tenants of extremely high temperatures ([Sun et al., 2012](#)) and those of a
364
365 major cooling event ([Goudemand et al., 2019](#)). The second event correspond to the most
366
367 important climate change within the Triassic and occurred in the Carnian (e.g., [Preto et al.,](#)
368
369 [2010](#)). In shallow marine areas of the western Tethys, this episode is characterized by the
370
371 demise of early Carnian carbonate platforms and the sudden deposition of coarse
372
373 siliciclastics (e.g., [Simms and Ruffell, 1989](#)). Recognized from deltaic to shallow marine
374
375 successions of the Dolomites (e.g., [Krystyn, 1978](#); [Breda et al., 2009](#)) to deep-water settings
376
377 of the Himalayas and Lagonegro Basin ([Hornung et al., 2007a](#); [Rigo et al., 2007](#)), it has been
378
379 attributed to an increase in rainfall and is associated with extinction and biotic turnover (e.g.,
380
381 [Simms and Ruffell, 1989, 1990](#); [Roghi et al., 2010](#)). This event has been given several
382
383 names: “Carnian Wet Intermezzo” in the Germanic Basin, “Carnian Pluvial Event” in northern
384
385 Europe, “Reingraben turnover” in the Northern Calcareous Alps, “Raibl Event” in the Italian
386
387 Dolomites (e.g., [Schlager and Schöllnberger, 1974](#); [Simms & Ruffell, 1989, 1990](#); [Hornung](#)
388
389 [and Brandner 2005](#); [Hornung et al., 2007a, b](#); [Kozur and Bachmann, 2010](#); [Dal Corso et al.,](#)
390
391 [2012](#); [Ogg, 2015](#)).

392 393 394 **3. Methods**

395 396 397 398 **3.1. Data**

399
400
401
402 For the present analysis, all Triassic occurrences of marine and brackish ostracod genera
403
404 were gathered from the literature and our own data (the complete literature list is given in
405
406 [Supplementary File 1](#)). For each occurrence, we provide palaeogeographical and
407
408 stratigraphic information at the stage level that were eventually updated from additional
409
410 literature and Palaeobiology Database (accessed in March 2020). Following the taxonomic
411
412
413

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415
416 harmonization described below, one hundred seventy-six genera distributed into forty-one
417
418 families span from the Griesbachian (Early Triassic) to the Rhaetian (Late Triassic) (Table 1).
419
420 Genera reported from the “Early Triassic”, “Middle Triassic” or “Late Triassic” have been
421
422 considered as occurring during all stages of the epoch considered: *Judahella* (Early Triassic,
423
424 Tunisia; Kamoun et al., 1994); *Simeonella* (Early Triassic, China; Wei et al., 1983); *Cavellina*
425
426 and *Liuzhinia* (Middle Triassic, China; Wei et al., 1983); *Gombasekella* (Middle Triassic,
427
428 India; Agarwal, 1992); *Cypridina* (Middle Triassic, Bosnia and Italy; Late Triassic, Brasil;
429
430 Kornicker et al., 2006); *Cytherella*, *Fabanella*, *Hungarella* (Late Triassic, Iraq; Al-Khahab and
431
432 Al-Halawachi, 2018). Conversely, *Triadocypris* reported from the Triassic of Vietnam
433
434 (Kornicker et al., 2006) was not considered because of this large age uncertainty.
435
436
437

438 3.2. Taxonomic harmonization

439
440
441 The classification of Triassic Cytheruridae follows the revisions of Whatley and Boomer
442
443 (2000), that of Limnocytheridae follows Whatley and Moguevsky (1998) and the
444
445 classification of Bythocytheridae follows Schornikov (1988, 1990). Punciidae are attributed to
446
447 the Punciocopida following Danielopol and Swanson (2019) rather than to Palaeocopida
448
449 (e.g., Horne et al., 2002).
450

451 For the present investigation, the following generic adjustments have been necessary.

452
453 *Polycopsis* Müller, 1894 was erected based on modern material mainly using soft body
454
455 characters and several authors pointed out the impossibility to distinguish between *Polycope*
456
457 Sars, 1866 and *Polycopsis* in the absence of soft parts (e.g., Urlichs, 1972; Neale, 1983). We
458
459 follow Urlichs (1972) and subsequent authors as Kolar-Jurkovšek (1990), Monostori and Tóth
460
461 (2013), Sebe et al. (2013), Forel and Moix (in press) in considering that Triassic reports of
462
463 *Polycopsis* are unreliable. *Polycopsis* species in Kozur (1970), Bunza and Kozur (1971),
464
465 Kozur et al. (2000) are therefore re-attributed to *Polycope*.
466

467 The classification of Triassic Healdiidae and Bairdiidae still problematic but it is beyond the
468
469 scope of this paper to attempt a revision of these major ostracod groups. The original
470
471
472

473
474
475 classification of Triassic ornate bairdiids proposed by [Kollmann \(1960, 1963\)](#) is thus followed
476
477 in considering the primary ornamentation as relevant generic character. *Triebelina* van den
478
479 Bold, 1946 was also described from modern material and its affinities to other present-days
480
481 bairdiids is complex, as shown by discussion in [Maddocks and Wouters \(1991\)](#) and by the
482
483 different opinions on its synonymy with *Glyptobairdia* Stephenson, 1946 summarized in [Malz](#)
484
485 [and Lord \(1988\)](#). Because of the high level of homeomorphy in ornate Bairdiidae (e.g.
486
487 [Maddocks and Wouters, 1991](#)), Triassic occurrences of *Triebelina* are not considered as
488
489 valid (e.g., [Bolz 1971a, b](#); [Ulrichs, 1972](#); [Dépêche and Crasquin-Soleau, 1992](#)) and are here
490
491 re-attributed to their respective subgeneric identifications.

492
493 For the phylogenetic analysis of Permian the Triassic ornate Bairdiidae we perform,
494
495 *Lanczichebairdia* Gramm, 1997 and *Arcibairdia* Gramm, 1997 from the Capitanian of USSR
496
497 ([Gramm, 1997](#)) are considered respectively as junior synonyms of *Petasobairdia* Chen *in*
498
499 Chen and Shi, 1982 and *Bairdiolites* Croneis and Gale, 1939. *Praelobobairdia* Kozur, 1985 is
500
501 considered as a junior synonym of *Petasobairdia*, following [Becker \(2001\)](#). Following [Becker](#)
502
503 ([2001](#)), the smooth bairdiid *Rectobairdia* Sohn, 1960 and *Cryptobairdia* Sohn, 1960 are
504
505 considered as subgenera of *Bairdia* McCoy, 1844.

506
507 The possible synonymy of the Healdiidae *Ogmoconcha* Triebel, 1941 and *Hungarella*
508
509 (Méhes, 1911) has long been debated. Here we follow [Kristan-Tollmann \(1977a, b\)](#), [Lord](#)
510
511 ([1982](#)), [Boomer and Jellinek \(1996\)](#), among others, in considering this synonymy as unlikely
512
513 given the distinct central muscle scar field patterns observed in these genera. We also follow
514
515 [Lord \(1972\)](#) in considering that until the relationship of *Ogmoconcha* and *Hungarella* is
516
517 clarified, *Hungarella* should only been used for Triassic species to avoid artificially rooting
518
519 *Ogmoconcha* down to the Triassic. Morphologically, the left and right valves of *Hungarella*
520
521 are asymmetrical contrary to those of *Ogmoconcha* ([Kristan-Tollmann, 1977a, b](#); [Lord,](#)
522
523 [1982](#)): in the absence of observable central muscle scars, all Triassic occurrences of
524
525 *Ogmoconcha* and *Ogmoconchella* are here re-attributed to the genus *Hungarella*.

528 **4. Insights into the Triassic evolution of marine ostracod diversity**

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530
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4.1. Global diversity patterns

During the Triassic, the global diversity of ostracods ranges from 11 genera in the Smithian (Early Triassic) to 82 in the Anisian and from five to 23 families in the Smithian and the Griesbachian respectively (Fig. 3A). The first peak of diversity in the Griesbachian (53 genera, 23 families) documents the decoupling of generic and familial diversity in the aftermath of the EPE as this Triassic maximum of familial diversity is not paralleled by that of genera, recorded later in the Anisian. A severe loss in diversity occurs in the Dienerian with 15 genera distributed into nine families. This pattern further develops in the Smithian that records the lowest diversity of the Triassic, at all taxonomic levels considered, with 11 genera and five families. These two patterns respectively illustrate the Griesbachian survival period, followed by a pauperisation of the assemblages that covers the entire Dienerian and Smithian, as discussed by [Crasquin-Soleau et al. \(2007\)](#) and [Crasquin and Forel \(2014\)](#). A progressive rediversification occurs in the Spathian (35 genera, 12 families) and further develops in the Anisian with a peak that reaches 83 genera, the maximum recorded for the Triassic interval. Here again, the familial and generic diversity are decoupled and may indicate that high taxonomic levels react more slowly than lower levels during periods of taxonomic restructuring. This observation further substantiates the previous reports of [Crasquin-Soleau et al. \(2007\)](#) and [Crasquin and Forel \(2014\)](#) in placing the first burst of the rediversification during the Spathian and its acme during the Anisian. The subsequent interval spanning from the Ladinian to the Rhaetian is for the first time characterized here in term of global ostracod diversity and records a seesawing diversity within a high-level plateau ranging from 60 (Norian) to 78 genera (Carnian), and from 17 (Ladinian, Norian) to 23 (Carnian) families.

These trends are underlain by varied patterns of extinction of survivors and emergence of newcomers that are for the first time described here (Fig. 3A). From the Griesbachian to the Smithian, only few new genera emerged, with a drop from 10 newcomers in the

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593 Griesbachian to three in the Smithian. The observed declining diversity for this interval
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595 therefore relates to rare radiations coupled with numerous extinctions in the Griesbachian,
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597 corresponding to the disappearance of Permian holdovers (24 genera). The subsequent low
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599 diversity maintained in the Dienerian and Smithian mainly reflects the stasis of newcomers
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601 and extinctions. On the opposite, the Spathian and Anisian rising diversity appears as the
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603 consequence of a burst of radiating genera, with a maximum in the Anisian (34). The entire
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605 Middle and Late Triassic interval is characterized by sustained extinctions, ranging from 19
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607 genera during the Ladinian to 35 at the end of the Rhaetian, with the exception of the Norian
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609 during which only eight genera went extinct. This interval is also marked by the overall stable
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611 amount of radiating genera. This relative balance of extinctions and radiations resulted in the
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613 overall high plateau observed for this interval.
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615 616 617 4.2. Taxonomic features underlying diversity trends 618

619
620 In terms of taxonomic structuration, the diversity loss from the Griesbachian to the Dienerian
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622 is related to three phenomena. The first is the final disappearance of seven of the eight
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624 Griesbachian palaeocopid families at the end of this stage (Aechminellidae, Buregiidae,
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626 Hollinellidae, Indivisiidae, Kloedenellidae, Knoxitidae, Paraparchitidae; Fig. 3B). No other
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628 family ends up in the Griesbachian (Fig. 2). The second feature relates to genera that are
629
630 uniquely known in the Griesbachian and geographically restricted to China (*Anxiania*,
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632 *Beichuania*, *Paramicrocheilinella*) and Australia (*Truncobairdia*; Table 1). The third
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634 component is the last occurrence of numerous genera from diverse families as Bairdiidae
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636 (*Orthobairdia*), Bairdiodyprididae (*Baschkirina*, *Silenites*), Cavellinidae (*Sulcella*),
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638 Cytherissinellidae (*Arqoviella*), Healdiidae (*Cytherellina*), Pontocyprididae (*Haworthina*).
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640 Important Triassic taxa nevertheless root as early as in the Griesbachian: *Hungarella*
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642 (Healdiidae), *Kerocythere* (Cytheruridae), *Mockella* (Cytheruridae), *Triassinella*
643
644 (Limnocytheridae). All these genera are restricted to the Triassic as none range up to the
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646 Jurassic. As for the families, only Limnocytheridae (*Triassinella*) radiated during this interval.
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652 The close analysis of the taxonomic structuration of Dienerian communities once again
653 documents the decoupling of familial and generic trends as well as the very first roots of the
654 rediversification. This stage is virtually neutral in terms of familial events, with only the
655 disappearance of Amphissitidae. However, the generic rediversification is already visible with
656 the emergence of 4 genera, *Triassocythere* (Bythocytheridae), *Bektasia* (Cavellinidae),
657 *Ptychobairdia* (Bairdiidae), *Lutkevichinella* (Limnocytheridae).
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662 The ostracod record shows no influence of this Smithian-Spathian event at the time of
663 writing: this observation may relate to the fact that most of taxa at this time interval are
664 benthic while this biotic event has affected nektonic organisms, as detailed earlier. An
665 increased investigation of planktonic taxa during this interval, possibly in Romania and
666 Hungary that already yielded promising observations (e.g., [Forel and Grădinaru, 2018](#); [Tóth
667 and Cséfan, 2018](#)), may provide new elements. The peculiarity of the Spathian diversification
668 is that it is largely the result of genera returning to the fossil record after having been Lazarus
669 through the EPE and/or the beginning of the Early Triassic. As a whole, they represent 19 of
670 the 35 genera (54%) recorded during the Spathian. Four genera re-enter the fossil record
671 from the Late Permian: *Spinocypris* and *Triassocypris* (Paracyprididae), *Paraberounella*
672 (Bythocytheridae) and *Urobairdia* (Bairdiidae). Those re-entering the fossil record from the
673 Triassic are Kirkbyidae (*Carinaknightina*), Bairdiidae (*Petasobairdia*, *Bairdiacypris*,
674 *Ptychobairdia*), Cytheruridae (*Kerocythere*), Healdiidae (*Hungarella*) and Cavellinidae
675 (*Bektasia*), to cite only the most representative. This phenomenon is a less important
676 contribution to the Anisian burst of diversity (17 of 82 genera, 21%) and the Lazarus pattern
677 is therefore of major importance to understand the dynamic of early recovery during the
678 Triassic. The Spathian also documents the roots of the diversification of Cytheruridae and
679 Limnocytheridae, both families further developing in the Anisian ([Fig. 4; Table 1](#)), as well as
680 the maximal diversity of the Paracyprididae, that lasted until the Ladinian.
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685 This diversification further develops in the Anisian, which is of major importance in the
686 macroevolution of ostracods during the Triassic as it records, for instance ([Fig. 4](#)): (1) the
687 maximum of diversity of Bythocytheridae (18 genera including 13 newcomers) and of
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711 Cavellinidae (four genera including two newcomers), (2) the first Triassic occurrence of
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713 Beecherellidae following an important gap in their fossil record, (3) the on-set of the
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715 diversification of Cytherellidae and the true rediversification of Healdiidae, (4) the emergence
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717 and diversification of typically Triassic ornate Bairdiidae, which are further discussed later,
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719 (5) the first high point of the high diversity plateau for Cytheruridae, that will develop until the
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721 end of the Triassic in an overall increasing diversity trend. It records the highest radiation rate
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723 for this family, with three new genera (*Blomella*, *Eucytherura*, *Gruendelicypthere*).

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725 As part of the high-diversity plateau encompassing the Middle and Late Triassic, the Ladinian
726
727 witnessed only few important biotic events for ostracods. The major event is the peak in
728
729 diversity of Limnocytheridae (15 genera), that contrasts with all other families observed to
730
731 date during this interval (Fig. 4). Most of the Ladinian Limnocytheridae were already present
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733 in the Anisian (e.g. *Triassinella*, *Lutkevichinella*, *Renngartenella*, *Casachstanella*,
734
735 *Simeonella*) but three new genera emerged (*Cytherissinella*, *Christellocythere*,
736
737 *Reversiocythere*). The Ladinian sees the emergence of the Mandelstaminidae
738
739 (*Rhombocythere*) that will last, with this unique genus, until the Rhaetian.

740
741 The Carnian stage is a high-point of the Middle-Late Triassic diversity plateau that relates to
742
743 the emergence of seven Bairdiidae genera, five ornate (*Edithobairdia*, *Eisobairdia*,
744
745 *Carinobairdia*, *Medwenitschia*, *Parurobairdia*) and two smooth (*Isobythocypris*, *Hiatobairdia*).
746
747 The re-entrance in the fossil record of *Ceratobairdia* and *Parurobairdia* is worth mentioning
748
749 as it represents one of the longest Lazarus period known to date for ostracods during this
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751 interval (Changhsingian to Carnian). It also corresponds to the on-set of maximal diversity of
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753 Cytherellidae, with three genera (*Cytherella*, *Issacharella*, *Leviella*): this feature is maintained
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755 until the Rhaetian with the replacement of *Issacharella* by *Cytherelloidea*. Together with the
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757 Rhaetian, the Carnian constitutes the highest diversity for Cytheruridae (eight genera), of
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759 which only *Metacytheropteron* is new. A very peculiar aspect of the Carnian is the re-
760
761 emergence of Rectonariidae (three genera) that were Lazarus since their latest occurrence in
762
763 the Changhsingian of South China (Yuan et al., 2009): the implications of this observation
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765 are discussed below. The Carnian sees the survivorship of a unique Cavellinidae (*Bektasia*),
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770 that will stay the last representative of this family until its disappearance at the end of the
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772 Rhaetian. It finally witnesses the roots of Protocytheridae (*Klinglerella*). Although several
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774 ostracod assemblages witness the degradation of environmental conditions related to the
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776 Carnian Humid Episode (e.g., [Keim et al., 2001](#)), the influence of this event on marine
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778 ostracod fauna still needs to be thoroughly studied. Typical Carnian taxa, such as
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780 *Renngartenella sanctaecrusis* or *Simeonella brotzenorum* Sohn, 1968, witness salinity issues
781
782 related to the Carnian Pluvial event (e.g., [Kristan-Tollmann and Hamenadi, 1973](#); [Gerry et](#)
783
784 [al., 1990](#); [Monostori, 1994](#); [Keim et al., 2001](#); [Forel et al., in press](#)), but these works only
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786 focus on the western tethyan zone and data are still lacking from eastern area (e.g., [Forel et](#)
787
788 [al., 2019b](#)).

789
790 The Norian is also a period of great stability with no peculiar event in terms of ostracod
791
792 biodiversity except the unique Triassic occurrence of Punciidae (*Triassopuncia*,
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794 *Triassomanawa*; [Kozur, 1996](#)). Prior to the end-Triassic extinction, the Rhaetian records the
795
796 acme of several families, including Bairdiidae, Cytheruridae and Healdiidae. It also records
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798 the earliest known occurrences of major groups such as Progonocytheridae (*Kinkelinella*)
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800 and Cytheridae (*Aparchitocythere*, *Parariscus*). Finally, it yielded the latest known occurrence
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802 of Beecherellidae (*Acantoscapha*) and Rectonariidae (open nomenclature genera).

803 804 805 **5. Discussion**

806 807 808 809 *5.1. Triassic occurrences of Palaeozoic taxa*

810 811 812 813 *5.1.1. Palaeocopida*

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817 Palaeocopida were major components of the Palaeozoic ostracod fauna and were
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819 widespread from shallow to deep marine waters (e.g., [Jones, 1989](#); [Becker and Wang, 1992](#);
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821 [Casier and Lethiers, 1998](#); [Olempska and Chauffe, 1999](#); [Chitnarin et al., 2012](#)). They were
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823 traditionally thought to have gone extinct at the EPE (e.g., [Moore, 1961](#)) but since the 80's, a
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829 growing body of literature documented their survival into the Early Triassic (Crasquin and
830 Forel, 2014 and references therein). The persistence of living Palaeocopida has been
831 evoked, Kirkbyoidea being considered by some as the forerunners of the Cretaceous to
832 recent Punciidae (e.g., Schallreuter, 1968; Swanson, 1991). This question is still debated:
833 some consider that there might be no living Palaeocopida and that Punciidae should rather
834 be attributed to Cytherellidae (e.g., Whatley et al., 1993; Becker, 1997; Martens et al., 1998;
835 Martin and Davis, 2001) while others recently revived the order Punciocopida Schallreuter,
836 1968 (Danielopol and Swanson, 2019). It is out of the scope of the present contribution to
837 discuss this issue and the Punciidae documented from the Norian (Kozur, 1996) have been
838 here attributed to the Punciocopida.

839 Eight Palaeocopida families survived in the Griesbachian (Fig. 2; Table 1) and in the direct
840 aftermath of the EPE, they are part of all survival patches described earlier. When present,
841 Paraparchitidae, Kirkbyidae, Kloedenellidae and Knoxitidae are only accessory components
842 of the communities surviving in association with microbial deposits (e.g., Crasquin-Soleau
843 and Kershaw, 2005; Forel, 2012, 2014; Forel et al., 2013a, b; Crasquin-Soleau et al., 2004a,
844 b). Conversely, Hollinellidae (*Hollinella*) proliferate through the EPE in littoral clastic areas of
845 South China (Forel et al., under review) and northern Vietnam (Crasquin et al., 2018). This
846 phenomenon documents different adaptative abilities to peculiar environmental conditions to
847 which these organisms were adapted. As such, *Hollinella* may radically differ from Bairdiidae
848 in terms of adaptative abilities in being able to cope with high detrital influx.

849 Of the eight families occurring in the Griesbachian, only Kirkbyidae range higher in the
850 Triassic (Fig. 2). They then disappear from the fossil record until their last known occurrence
851 during the Carnian, Late Triassic (Forel et al., 2019a). An analysis of their generic diversity
852 and environmental distribution in the Permian and Triassic reveals a unique pattern (Fig. 5).
853 Over the studied interval, the Kirkbyidae's diversity reaches its acme in the Changhsingian
854 with eight genera. Their diversity rapidly decreases through the EPE with residual
855 occurrences in the Griesbachian, Dienerian (*Carinaknightina*; Sohn, 1970) and Spathian
(*Carinaknightina*; Crasquin-Soleau et al., 2006). They are for the last time reported from the

886
887
888 Carnian, corresponding to their highest Triassic generic diversity with *Carinaknightina*,
889 *Kirkbya* and *Tubulikirkbya*, the latest two genera re-entering the fossil record since their last
890 occurrence in the Changhsingian (Yi, 2004; Yuan et al., 2007). In terms of environmental
891 distribution, Permian Kirkbyidae are known from marginal to basinal conditions (Fig. 5). Their
892 early Triassic distribution appears to correspond to a restriction to subtidal and basinal areas.
893
894 This pattern further develops in the Late Triassic, when their last known occurrence is
895 restricted to slope environments while they are totally absent from shallower localities. This
896 pattern may indicate the narrowing of the distribution of Kirkbyidae through time to deeper
897 and more stable environments. Kirkbyidae were members of both neritic and deep-sea
898 assemblages throughout their histories (e.g., Becker and Wang, 1992; Chitnarin et al., 2012)
899 and it is reasonable to consider that they were capable of such deep-water survival which
900 therefore does not correspond to a migration but truly to a restriction of their environmental
901 distribution.

902
903 Apart from the Kirkbyidae, *Triassicindivisia* occurs in the Spathian and Anisian of the subtidal
904 zone in southern Tibet (Forel and Crasquin, 2011a; Forel et al., 2011). Although of uncertain
905 superfamilial and familial attribution, this genus is the unique Palaeocopida genus known to
906 date that radiated in the Triassic.

907 908 909 910 911 912 913 914 915 916 917 918 919 920 921 922 923 *5.1.2. Deep-sea taxa*

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927 The diversity of Triassic deep-sea ostracods, their taxonomic structuration, links to Permian
928 taxa and palaeogeographical distribution are still poorly understood. In most cases, these
929 ostracods have been secondarily silicified so that their occurrence in the fossil record
930 requires sufficient amounts of available silica. The Permian and Triassic interval was marked
931 by an interruption of the siliceous bioproduction, labelled “Early Triassic chert gap”, related to
932 the abrupt collapse of the thermohaline circulation (Beauchamp and Baud, 2002). It is
933 assumed to have lasted until the late Spathian or Anisian (Kakuwa, 1996; Isozaki, 1997;
934 Kozur, 1998a, b). Radiolarians that have been documented from the earliest Triassic of
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947 South China (Yang et al., 2012), Early Triassic of Japan (Sashida, 1991), Smithian-Spathian
948 of New Zealand (Hori et al., 2003, 2011), Spathian of Japan (Kamata, 1999), early Spathian
949 of Vietnam (Takahashi et al., 2017), to cite only a few, nevertheless demonstrate that
950 siliceous productivity was maintained but may have been insufficient to allow the secondary
951 silicification of ostracods during this interval. Most Palaeozoic deep-sea taxa reported from
952 the Triassic, described and discussed below, may consequently have entered the Lazarus
953 record through the EPE and its aftermath because of the low preservation potential of these
954 poor faunas in a context of low dissolved silica.

955
956 Deep-sea ostracods from Triassic deposits have been increasingly documented since Kozur
957 (1970) and the reader is referred to Crasquin and Forel (2014) for details and discussion on
958 their Early and Middle Triassic distribution. Only recent discoveries of unquestionable and
959 relatively diverse taxa in the Late Triassic, Carnian (Forel et al., 2019a) and Rhaetian (Forel
960 and Grădinaru, under review) are here discussed. Typical Palaeozoic deep-sea taxa
961 reported to date from the Triassic are *Spinomicrocheilinella* in the Anisian (Mette et al.,
962 2014), Beecherellidae (*Acanthoscapha*) and Berounellidae from bathyal and abyssal
963 environments of the entire Middle Triassic (Kozur, 1970, 1971, 1972; Crasquin-Soleau and
964 Grădinaru, 1996; Sebe et al., 2013). These taxa have all been extended up to the Carnian
965 and a new genus of Becherellidae (*Gencella*) implied that radiations were maintained,
966 although at low rates (Forel et al., 2019a).

967
968 Rectonariidae are Palaeozoic deep-sea taxa in essence: they have been associated with
969 deep-water masses in the Devonian-Carboniferous interval (e.g., Gründel, 1961; Olempska,
970 1981; Sanchez de Posada, 1987; Blumenstengel, 1992; Nazik et al., 2012) and they
971 residually range to the uppermost Permian (Yuan et al., 2007). Until recently, they were
972 considered as deep-sea victims of the EPE and have never been reported from previous
973 analysis of Triassic deep-sea deposits. However, three genera, that are new to science but
974 kept in open nomenclature because of the lack of material, unquestionably document their
975 persistence in the Carnian (Forel et al., 2019a) and up to the Rhaetian (Forel and Grădinaru,
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1006 [under review](#)). These observations first indicate that Rectonariidae survived the EPE and that
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1008 they have been Lazarus taxa during the entire Early-Middle Triassic time interval.

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1010 Owing to the great sensitivity of deep-sea ostracods (e.g., [Yasuhara et al., 2009](#)), strong
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1012 hypotheses are needed to explain the exceptional persistence of such residual Palaeozoic
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1014 taxa through the EPE and up to the brink of the end-Triassic crisis. Two hypotheses are
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1016 here considered. The first evokes a long-term yet unidentified refuge, which may have been
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1018 located in the deep sea as these taxa were restricted to bathyal and abyssal zones through
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1020 their fossil record and that they have never been observed from neritic deposits through the
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1022 Permian and Triassic interval ([Forel et al., 2019a](#)). This refuge differs from those
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1024 documented from neritic areas in the aftermath of the EPE by its much longer duration, from
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1026 the Late Permian to the Rhaetian, and by its larger taxonomic composition. The second
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1028 hypothesis implies the environmental stability of deep-sea areas around the Palaeo-Tethys
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1030 and Neo-Tethys oceans where these assemblages have been described, through the EPE
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1032 and more widely through the Triassic. This ostracod record has to be replaced within the
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1034 discussion on the oceanic anoxia reported from the late Middle Permian to the early Middle
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1036 Triassic, that may have occurred as several phases in the Early Triassic in northwestern
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1038 Pangaea, South China, Japan, Turkey (late Changhsingian-early Dienerian, Smithian-early
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1040 Spathian and middle Spathian; e.g., [Isozaki, 1997](#); [Grasby et al., 2012](#); [Song et al., 2012](#);
1041
1042 [Lau et al., 2016](#); [Wignall et al., 2016](#); [Huang et al., 2017](#)) and in the Middle Triassic in Japan
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1044 and South China, including in deep-sea areas ([Kubo et al., 1996](#); [Sugitani and Mimura, 1998](#);
1045
1046 [Wignall et al., 2010](#); [Huang et al., 2017](#); [Song et al., 2012](#); [Fujisaki et al., 2016](#); [Soda and](#)
1047
1048 [Onoue, 2018](#)). This lengthy anoxia is considered as an important factor of the delayed
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1050 recovery of marine biota after the EPE (e.g., [Chen and Benton, 2012](#); [Hallam, 1991](#)). The
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1052 present record of long-term survivorship of ostracods in the deep-sea is restricted to the
1053
1054 Tethyan area as no such event is known from Panthalassa, possibly related to fundamental
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1056 environmental differences between these oceanic realms. Long-term anoxia and ostracod
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1058 persistence are only compatible in the deep-sea if pulses of anoxia themselves consisted of
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1060 alternating anoxic and dysoxic intervals, or the refuge hypothesis should be favoured.
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5.2. A focus on Bairdiidae: diversity and “phylogeny”

Bairdiidae have been components of marine ecosystems from all time slices from the Ordovician (e.g., [Truuver et al., 2012](#); [Meidla, 1996](#)) to present-days (e.g., [Titterton and Whatley, 1988](#); [Maddocks, 2013](#)). Intense efforts have partly clarified the taxonomy of modern representatives of the “*Bairdia* dynasty” ([Malz, 1988](#)) with the establishment and/or revision of *Neonesidea* Maddocks, 1969, *Paranesidea* Maddocks, 1969, *Bairdoppilata* Coryell *et al.*, 1935 and *Triebelina* van den Bold, 1946 (e.g., [Maddocks, 1969](#); [Maddocks, 2013, 2015](#)). In the history of bairdiids, the Triassic is a unique interval with the explosive radiation of ornate taxa worldwide (e.g., [Kollmann, 1960, 1963](#); [Kristan-Tollmann, 1971a](#); [Bolz, 1971a, b](#)), most of which do not range into the Jurassic. The classification and phylogeny of Bairdiidae are major issues that the modern ostracodology needs to solve. Because of their importance in Triassic marine microfaunas, Bairdiidae are here treated separately and we discuss in detail the dynamics of their Triassic diversity and propose a “morphological phylogeny” of the ornate forms during the Permian and the Triassic.

5.2.1. Triassic diversity

Thirty-two Bairdiidae genera occur during the Triassic ([Table 1](#)). *Bairdia*, *Acratia*, *Bythocypris* have been termed “panchronic” taxa in [Crasquin-Soleau et al. \(2007\)](#). However, this notion of panchronism is problematic as it mistakenly implies the persistence of these taxa through the Phanerozoic and would, for instance for *Bairdia*, carry on and justify its abusive usage up to modern environments: we rather consider them as Palaeozoic-Early Mesozoic in essence. In terms of diversity dynamics, most patterns are similar to those described for the entire ostracod fauna during the Triassic ([Fig. 3](#)). Bairdiidae nevertheless significantly differ in that the Ladinian-Rhaetian interval rather witnesses a seesawing diversity within a general increase, resulting in their observed highest diversity in the Rhaetian ([Fig. 6](#)). Only few

1122
1123
1124 bairdiids radiated during the entire Early Triassic. Two peaks of radiation occur during the
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1126 Anisian and the Carnian, while the remaining of the Late Triassic is marked by rare radiations
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1128 and important extinction at the end of the Rhaetian. When comparing the relative diversity of
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1130 ornate *versus* smooth Bairdiidae along the Triassic, a reversal of the dominance occurred
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1132 when entering the Late Triassic, from smooth-dominated during the entire Early and Middle
1133
1134 Triassic, to ornate-dominated during the Late Triassic (Fig. 6).

1135
1136 Except for *Truncobairdia* which is restricted to the Griesbachian of Australia, all Griesbachian
1137
1138 bairdiids (11 genera) are survivors from the Late Permian. Three of these genera went
1139
1140 extinct during the Griesbachian, all of which are smooth in morphology (*Orthobairdia*,
1141
1142 *Praezabythocypris*, *Truncobairdia*). The only ornate form during the Griesbachian is the
1143
1144 Permian survivor *Petasobairdia* that went extinct at the end of the Rhaetian. The Dienerian
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1146 and Smithian record the lowest bairdiid diversity (four genera) with the radiation of
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1148 *Ptychobairdia* during the Dienerian, which is the only recorded ornate genera for this interval.
1149
1150 Two main periods of radiation of ornate bairdiids are recorded: Anisian and Carnian,
1151
1152 respectively with three (*Margarobairdia*, *Mirabairdia*, *Nodobairdia*) and five new genera
1153
1154 (*Edithobairdia*, *Eisobairdia*, *Carinobairdia*, *Medwenitschia*, *Parurobairdia*). The distribution of
1155
1156 ornate Bairdiidae in the Permian and Triassic is summarized in Fig. 7.

1157 1158 1159 5.2.2. Ornate bairdiids: elements of “morphological phylogeny” 1160

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1162
1163 The classification of sculpted Bairdiidae is still subject to debates, mainly regarding the use
1164
1165 of external sculptures as robust characters for generic scheme. Here, and until a complete
1166
1167 phylogenetic analysis can be performed, we follow the original scheme of Kollmann (1960,
1168
1169 1963) as stated above. Any attempt to conceptualize the evolution of ornate bairdiids during
1170
1171 the Triassic requires to be placed in perspective of the Permian record. Three groups are
1172
1173 distinguished among Permian and Triassic ornate bairdiids, characterized by the temporal
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1175 distribution and by the enhancement and growing complexity and sophistication of carapace
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1177 ornamentation through time (Fig. 7):
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- Group 1: genera that originated prior or during the Permian and do not range into the Triassic. They are characterized by simple and not combined ornamentation structures: unique spine or knob (*Xixionopsis*, *Spinobairdia*, *Sinabairdia*), latero-ventral ridge (*Vanganardia*) or vertical lateral ridges (*Arcibairdia*). Only *Abrobairdia* displays a combination of ornate dorsal margin at left valve (ridge, nodes, spines) and ornamental structures (ridges, nodes) on the antero-central and postero-central area of each valve.

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- Group 2: genera that radiated prior or during the Permian and range into the Triassic. *Bairdiolites*, *Ceratobairdia*, *Mirabairdia* and *Parurobairdia* went through the EPE as Lazarus taxa. They document an increasing complexity of the carapace ornamentation with more frequent combined structures as in *Ceratobairdia*, *Mirabairdia* and *Ptychobairdia*. This group also sees the strong development of ornament made of longitudinal and unstructured ridges as in *Ceratobairdia* and *Ptychobairdia*.

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- Group 3: genera that originated during the Triassic. They display the highest sophistication of lateral combined ornaments. The pinnacle of this pattern is the fused ornament of *Coronabairdia*, that corresponds to the fusion of dorso-lateral and ventro-lateral ridges into a peripheral ring.

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Owing to the temporal distribution of these groups, we propose the following scheme for the phylogeny of Triassic ornate Bairdiidae based on their ornament structures (Fig. 8). This scheme is rooted into the Kungurian and proposes that all subsequent ornate Bairdiidae derived from *Petasobairdia*. *Petasobairdia* Chen in Chen and Shi, 1982 ranges from the Sakmarian to the Rhaetian (Fig. 7) and is diagnosed by its ornate dorsal margin at left valve (ridge, nodes, horns) without combined lateral elements. During the Kungurian, *Abrobairdia* and *Ceratobairdia* may have derived from *Petasobairdia*: *Abrobairdia* by the development of dorso-lateral ridges and *Ceratobairdia* by the acquisition of latero-ventral structures. We propose that these two genera gave path to two distinct lineages: *Ceratobairdia*-lineage characterized by ridged ornaments and *Abrobairdia*-lineage with nodulose ornamentation. *Abrobairdia* ranges from the Kungurian to the Changhsingian, and is, as stated above, the earliest ornate bairdiid with combined ornamentation. Owing to this ornamental complexity

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1242 compared to contemporaneous genera, *Abrobairdia* may have been the origin all subsequent
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1244 genera with robust combined ornamentation. *Abrobairdia* seems closely related to
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1246 *Mirabairdia*, which is the second oldest genera with combined ornament (oldest attested
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1248 occurrence in the Changhsingian), therefore phylogenetically relating the groups 1 and 2 of
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1250 our analysis. It is worth noting that *Mirabairdia* from the Capitanian of South China (*M. sp. 1*
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1252 *in Zazzali et al., 2015*) is re-attributed to *Ceratobairdia* because of its latero-ventral ridge. The
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1254 earliest record of *Mirabairdia* may date back to the Wuchiapingian (*M. sp. 2 in Zazzali et al.,*
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1256 *2015*) but the dorso-lateral features characteristic of this genus are not well expressed so
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1258 that we consider that the earliest attested record of *Mirabairdia* is of Changhsingian age. The
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1260 *Abrobairdia-Mirabairdia* evolutive unit sees the progressive restriction of dorsal
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1262 ornamentation from several denticulations to 2 nodes or spines and the development of
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1264 latero-ventral ornament structure in the Early Triassic. Subsequent genera with ornaments
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1266 located at similar positions but of different morphologies, mainly *Nodobairdia* and
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1268 *Margarobairdia*, may have derived from that *Abrobairdia-Mirabairdia* evolutive unit.
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1270 The *Ceratobairdia*-lineage first saw the radiation of *Vanganardia* in the Capitanian,
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1272 independently followed by the emergence of *Parurobairdia*. We consider that *Ptychobairdia*
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1274 may have originated from *Parurobairdia* rather than from *Vanganardia* because
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1276 *Parurobairdia* possesses both sub-ventral and dorsal/sud-dorsal structures contrary to
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1278 *Vanganardia* that lacks dorsal elements. Rooting *Ptychobairdia* into *Vanganardia*, itself
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1280 rooted into *Ceratobairdia* would imply the loss of dorsal structures from *Ceratobairdia* to
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1282 *Vanganardia* and their subsequent re-development from *Vanganardia* to *Ptychobairdia*, we
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1284 exclude this more complex scenario. In this hypothesis, *Vanganardia* and *Parurobairdia* -
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1286 *Ptychobairdia* constitute independent lineages that derived from *Ceratobairdia*. *Vanganardia*
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1288 radiated in the Capitanian while the *Parurobairdia-Ptychobairdia* evolutive unit is rooted in
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1290 the Changhsingian and diversified in the Spathian with the radiation of *Ptychobairdia*. It is
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1292 worth noting that ventral structures of the Dienerian *Ptychobairdia* species shown in
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1294 [Crasquin-Soleau et al. \(2006\)](#) are not clear so we exclude this record. Similarly, the
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1301 occurrence of *Ceratobairdia* from the Carnian of Italy ([Kristan-Tollmann, 1978](#)) is questioned
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1303 because of the apparent lack of ventro-lateral structure.
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1305 This proximity between *Abrobairdia* and *Mirabairdia* was already noted by [Chen and Shi](#)
1306 ([1982](#)), who considered *Mirabairdia* and *Parurobairdia* as transitional forms between
1307 Palaeozoic and Mesozoic ornate bairdiids. The main elements of the phylogenetic model
1308 proposed here are in line with this opinion but provide details rather considering the
1309 development of ornate bairdiids by two distinct lineages.
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1317 *5.3. Rooting the Mesozoic Marine Revolution down to the Triassic*

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1321 The Mesozoic marine revolution changed the ecological structure of benthic communities
1322 and allowed for the rise of the Modern Fauna ([Vermeij, 1977](#)). During this major evolutionary
1323 episode, the development of durophagy and boring predation in marine predators triggered
1324 the colonization of infaunal habitats and the diversification of organisms with greater mobility
1325 and durophagous-resistant shells. This coevolution between marine predators and preys is
1326 traditionally considered to have taken place in the Jurassic and the Cretaceous (e.g.,
1327 [Roopnarine, 2006](#); [Baumiller et al., 2010](#)). However, the Triassic is increasingly regarded as
1328 the setting stage for the Mesozoic marine revolution as it marks the rise of the Modern Fauna
1329 and possibly of modern modes of predation (e.g., [Tackett, 2016](#); [Greene et al., 2011](#); [Ros](#)
1330 [and Echevarría, 2011](#); [Buatois et al., 2016](#); [Klomp maker et al., 2016](#); [Tackett and Tintori,](#)
1331 [2019](#)). Recent discoveries made on Late Triassic ostracods illustrate the important role
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1347 *5.3.1. Triassic: the first step in the emergence of Modern ostracods*

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1350 As for other marine organisms, the Triassic is a period of major importance for the rise of
1351 typically Meso-Cenozoic, or Modern, ostracod fauna. To understand all mechanisms involved
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1360 in this evolutive process, it is pivotal to clearly position the transition interval, which
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1362 corresponds to the interval spanning from the emergence of the first typical representative of
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1364 the Meso-Cenozoic forms, to the disappearance of the very last typical Palaeozoic taxa. Until
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1366 recently, it was identified from the Wuchiapingian to the Anisian for marine ostracods
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1368 ([Crasquin-Soleau et al., 2007](#); [Crasquin and Forel, 2014](#)). However, the observations
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1370 described in the previous paragraphs imply that the upper limit of this transition interval is
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1372 asynchronous for neritic and deep-sea taxa: in the Anisian for neritic taxa (*Triassicindivisia*;
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1374 [Forel and Crasquin, 2011a](#)), in the Rhaetian for deep-sea ones (Rectonariidae; [Forel and](#)
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1376 [Grădinaru, under review](#)). The position of the lower boundary of the transition interval for
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1378 neritic ostracods is also moving with the description of new assemblages and understanding
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1380 of the phylogeny of the typically Mesozoic ostracods and of their Permian roots. [Crasquin-](#)
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1382 [Soleau et al. \(2007\)](#) considered the first typical strongly shelled and ornamented Bairdiidae to
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1384 occur in the Wuchiapingian (*Sinabairdia*: [Becker and Wang, 1992](#); [Fig. 7](#)). Such ornate forms
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1386 have nevertheless recently been documented down to the Capitanian ([Zazzali et al., 2015](#);
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1388 see above) and work currently in progress documents the occurrence of *Petasobairdia* and
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1390 *Ceratobairdia* down to the Roadian of Texas, USA (work in progress). The Late Permian
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1392 indeed appears as the acme of *Petasobairdia* as shown by the abundant records for this
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1394 interval (e.g., [Kozur, 1985](#); [Shi and Chen, 1987](#); [Crasquin-Soleau and Baud, 1998](#); [Yi, 2004](#);
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1396 [Yuan et al., 2007](#); [Crasquin et al., 2010](#); [Forel, 2012](#)). A recent report from the Sakmarian of
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1398 Japan ([Tanaka et al., 2018](#)) roots this genus, as well as the origin of ornate Bairdiidae typical
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1400 for the Triassic according to the phylegenetic scheme proposed here, down to the base of
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1402 the Early Permian. We therefore consider that the lower boundary of the transition interval for
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1404 neritic ostracods roots deep in the Early Permian. Conversely, the position of the lower
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1406 boundary for deep-sea assemblages is more problematic as typical Jurassic deep-sea taxa
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1408 and assemblages are virtually unrecognizable from their neritic counterparts as stated by
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1410 [Lord \(1988\)](#). [Lord and Lambourne \(1991\)](#) documented a Pliensbachian, Early Jurassic,
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1412 assemblage from Turkey related to a possible bathyal habitat owing to the dominance of
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1414 *Ptychobairdia* and absence of Metacopina. More recently, an Early Jurassic assemblage
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1419 indicative of the photic zone at water depth significantly shallower than calcite lysocline has
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1421 been reported from Austria ([Honigstein et al., 2014](#)). The palaeobathymetry of this
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1423 assemblage was inferred by its composition (dominance of bairdiid, near absence of
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1425 cytheroids, lack of taxa that are important in coeval deposits such as Cladocopina,
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1427 Healdiidae and Platycopina) rather than by the occurrence of taxa that unquestionably point
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1429 to deep water zones. Inferring the emergence of typical deep-sea Mesozoic taxa possibly in
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1431 the Triassic or before is therefore complex in the present state of our knowledge.

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1433 As detailed earlier in this work, the Triassic ostracod fauna is clearly distinct from the
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1435 Palaeozoic one by the progressive disappearance of Palaeozoic components (e.g.
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1437 Palaeocopida, deep-sea taxa) and the rise of taxa that will become typical of the Mesozoic
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1439 and Modern marine assemblages. However, the massive diversification of ornate Bairdiidae
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1441 is only known at this interval and also distinguishes it from the Mesozoic fauna. Conversely,
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1443 the essentially Palaeozoic Metacopina (Healdiidae) diversified in the Triassic and the early to
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1445 mid part of the Early Jurassic. They went extinct during the Early Toarcian Oceanic Anoxic
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1447 Event ([Boomer et al., 2008](#)), which allowed for the Cytheroidea to further diversify until their
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1449 dominance as seen in modern marine microfauna. The Triassic events therefore correspond
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1451 to one step of this sequential on-set of the Mesozoic features of ostracod assemblages.

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1453 The present analysis also documents the Triassic roots of Mesozoic families through several
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1455 successive waves of radiation. Of them, Schulerideidae is an important component of Middle
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1457 and Late Jurassic assemblages of Europe (e.g., [Bate, 1977](#)). Some have considered that it
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1459 derived from the *Pulviella*-group [Speluncellini according to [Kozur \(1973a\)](#)], from the oldest
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1461 representative of *Praeschuleridea* Bate, 1963 reported by [Bate and Coleman \(1975; Bate,](#)
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1463 [1977\)](#) or the Jurassic genus *Ektyphocythere* Bate, 1963 ([Boomer et al., 2009](#)). However, an
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1465 undeniable Schulerideidae, attributed with doubt to *Schuleridae*, in the Carnian of South
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1467 China documents the Late Triassic origins of this family ([Forel et al., 2019b](#)). The Carnian
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1469 stage is also the period of radiation of *Isobythocypris* that later became widespread. To date,
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1471 the oldest representatives of the *Cardobairdia* are from the Early Jurassic of England, Wales,
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1473 Ireland and Australia ([Ainsworth, 1986, 1987; Lord and Boomer, 1988; Boomer, 1991; Lord](#)
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1478 [et al., 1993](#)). Several species have nevertheless been recognized from the Rhaetian of the
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1480 Black Sea and also root this genus down to the end of the Late Triassic ([Forel and](#)
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1482 [Grădinaru, under review](#)).

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1484 As for important families, Cytheruridae are settled down in the Anisian with the roots of
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1486 *Eucytherura* ([Table 1; Fig. 4](#)). An important discussion is needed here regarding *Callicythere*
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1488 Wei, 1981 described from the Dienerian of South China ([Wei, 1981](#)). Originally attributed to
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1490 Cytherissinellidae, *Callicythere* was later re-attributed to Bythocytheridae because of its mid-
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1492 valve sulcus and latero-ventral structures ([Forel et al., 2013b](#)). The inner structures and
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1494 mainly muscular patterns of *Callicythere* have never been observed to date. However,
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1496 considering the view of [Whatley and Boomer \(2000\)](#) that Bythocytheridae gave rise directly
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1498 or indirectly to Cytheroidea during the Late Palaeozoic or Early Mesozoic interval and that
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1500 one of the earliest cytheroid is Cytheruridae, we propose that the tethyan-wide *Callicythere*
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1502 that occurs from the Capitanian to the Spathian with an acme in the Changhsingian may
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1504 represent the link between Bythocytheridae and Cytheruridae.

1505 1506 1507 *5.3.2. Ostracods: pivotal proxies to the Early Mesozoic-type food-webs*

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1511 Ostracods compose the diet of diverse organisms including bivalves, gastropods, echinoids,
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1513 turtles, amphibians, fishes, annelids and other crustaceans (e.g., [Lowndes, 1930](#); [Harding,](#)
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1515 [1962](#); [Reyment, 1966](#); [Robertson, 1988](#); [Penchaszadeh et al., 2004](#); [Costa et al., 2006](#);
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1517 [Ghioca-Robrecht and Smith, 2008](#); [Leal, 2008](#); [Alcalde et al., 2010](#); [Rossi et al., 2011](#);
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1519 [Vandekerkhove et al., 2012](#)). Identifiable traces of predation on ostracods in the fossil record
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1521 are related to drilling Naticidae and Muricidae gastropods (e.g., [Maddocks, 1988](#); [Reyment](#)
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1523 [and Elewa, 2002](#)), the oldest record being of Early Albian, Early Cretaceous, age ([Maddocks,](#)
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1525 [1988](#)). Predation on ostracods is most of the time disregarded and most works focus on
1526
1527 relatively young assemblages (e.g., [Reyment et al., 1987](#); [Ruiz et al., 2010, 2011](#); [Villegas-](#)
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1529 [Martin et al., 2019](#)). Because of the small size of ostracods, they provide an important food
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1531 source for juvenile gastropods as well as an alternative nutritive resource when regular preys
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1537 are lacking (e.g., [Reyment, 1967](#); [Maddocks, 1988](#)). They may thus be used as proxies for
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1539 the dynamics of juvenile predators, for periods of prey impoverishment, or for the emergence
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1541 of predation in the very first levels of marine trophic chains during the restructuring of
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1543 benthic ecosystems associated with the on-set of the Mesozoic Marine Revolution.
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1545 Until the end of the Cretaceous, drilling activity is erratic and it later increased in relation to
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1547 the rise of Muricidae and Naticidae (e.g., [Harper, 2006](#)), the oldest group including being of
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1549 Valanginian, Early Cretaceous age ([Kaim, 2004](#)). Occurrences of drill holes on macro-
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1551 invertebrates are rare in the Triassic, but present in the Carnian and Norian ([Klompaker et](#)
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1553 [al., 2016](#); [Tackett and Tintori, 2019](#)). Recently, the oldest evidence of drilling predation on
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1555 ostracods, corresponding to an incomplete and rather non-functional hole, has been
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1557 described on a left valve of a bairdiid ([Forel et al., 2018](#)). This observation also constitutes
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1559 the first indication of drilling activity on micro-organisms in the Triassic. Although not
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1561 functional, this pivotal evidence documents the onset of drilling abilities of juvenile predators,
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1563 owing to the small dimensions of the trace (outer borehole diameter: 51.4 μm , outer borehole
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1565 diameter: 18 μm). Furthermore, owing that Bairdiidae live above the sediment, the predator
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1567 involved might have been hunting at the sediment surface ([Forel et al., 2018](#)). Rhaetian
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1569 ostracods currently under description document the occurrence of two complete drill holes of
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1571 smaller size than that of the Carnian sediments, that may indicate the increase of the
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1573 efficiency of the drilling abilities of Triassic predators ([Forel and Grădinaru, under review](#)).
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1575 Specialized durophagous predators during the Norian, mainly fishes, sharks and reptiles,
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1577 have been considered as having an ecological influence on benthic communities ([Tackett](#)
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1579 [and Tintori, 2019](#)). However, the ostracod successive records from the Carnian ([Forel et al.,](#)
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1581 [2018](#)) and the Rhaetian ([Forel and Grădinaru, under review](#)) document the already advanced
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1583 structuration of micro-predators in the Late Triassic, possibly corresponding to still
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1585 unidentified gastropods as proposed by [Klompaker et al. \(2016\)](#).
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1588 *5.4. Geographical distribution*

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1596 *5.4.1. Patterns of distribution through time*
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1600 The dynamic of marine ostracod provincialism during the Triassic is poorly known and has
1601 mainly been discussed in the 70's and 80's. [Kozur \(1973b\)](#) distinguished the southern boreal,
1602 tethyan and northern boreal provinces for Triassic conodonts and ostracods. [Kristan-](#)
1603 [Tollmann and Tollmann \(1981, 1982\)](#) and [Kristan-Tollmann \(1986a, 1988a, b, 1991\)](#)
1604 proposed that the distribution of diverse fossil groups, including ostracods, was
1605 homogeneous within the Tethys during the Late Triassic. [Forel and Moix \(in press\)](#) recently
1606 dated the opening of communications between the Neo-tethys and Palaeo-tethys oceans of
1607 early Carnian rather than middle Carnian as generally suggested, and proposed that the
1608 previously described homogenization of ostracod faunas during the Late Triassic may relate
1609 to this early event. However, the statement of [Kristan-Tollmann \(1988a\)](#) that the uniformity
1610 was already recognizable as early as end of the Anisian is problematic.
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1612 Here we provide insight into the provincialism of ostracod genera at each stage of the
1613 Triassic, following the first quantitative approach proposed by [Forel and Grădinaru \(2018\)](#) for
1614 the Anisian. For each time slice, localities that provided less than 3 genera are not
1615 considered as their paucity may bias the analysis, with an exception for Dienerian and
1616 Smithian that we tentatively characterize in spite of their extreme low diversity. Nekto-benthic
1617 taxa are excluded ([Crasquin-Soleau and Grădinaru, 1996](#); [Sebe et al., 2013](#); [Forel and](#)
1618 [Grădinaru, 2018](#); [Tóth & Cséfan, 2018](#)). For each stage we follow the method used by [Forel](#)
1619 [and Grădinaru \(2018\)](#) and produced a similarity symmetric matrix, following Q-mode analysis
1620 ([Supplementary File 2](#); e.g., [Henderson and Heron, 1976](#); [Pielou, 1979](#); [Janson and](#)
1621 [Vegelius, 1981](#); [Digby and Kempton, 1987](#)). Following [Arias and Whatley \(2009\)](#), we use the
1622 Jaccard's similarity coefficient ([Jaccard, 1912](#)) as it ranges from zero to one, emphasises
1623 presence instead of absence and is not influenced by differences in sample size (e.g.,
1624 [Cheetham and Hazel, 1969](#); [Baroni-Urbani and Buser, 1976](#); [Wolda, 1981](#); [Magurran, 1988](#)).
1625 We use the agglomerative clustering method 'unweighted pair group method with arithmetic
1626 mean' (UPGMA) which provides an unweighted arithmetic average between individuals (e.g.,
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1655 Hazel, 1970; Anderberg, 1973; Podam, 1989; Shi, 1993). All analyses were done using the
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1657 statistical software package PAST (Hammer et al., 2001; Hammer and Harper, 2005). For
1658
1659 some of the time slices, groupings of localities were made based on the palaeogeographical
1660
1661 reconstructions of Scotese (2014). For each period of the Triassic, the classification of areas
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1663 scrutinized in terms of similarities to their ostracod assemblages is shown in Fig. 9.

1664
1665 During the Griesbachian, the highest similarity is observed between palaeotethyan (Hungary,
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1667 south China) and cimmerian (northern Iran, southern Turkey) localities, highlighting a core of
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1669 peri-Palaeo-Tethyan biotas from which northern Italy and Slovenia are excluded in spite of
1670
1671 their geographical closeness. Southern neotethyan communities from Himalaya (Tibet, India)
1672
1673 show the highest similarity to this peri-palaeotethyan group. Australian communities stand
1674
1675 aside with the lowest degree of similarity, which may relate to distinct climatic regimes.

1676 Dienerian communities are extremely poor but they document similar patterns with
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1678 Himalayan communities (Nepal, Pakistan) displaying more similarity with other the southern
1679
1680 neotethyan localities (Tunisia) than with south Chinese ones. The Smithian communities are
1681
1682 also very poor but document the exclusion of Tunisia and Russia that display no similarity
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1684 with other tethyan communities. The Spathian burst of diversity sees the reinforcement of the
1685
1686 similarity between peri-Palaeo-Tethyan biotas (Romania, Tibet, China), that record lower but
1687
1688 still significant similarity with Israel on the southern margin of Neo-Tethys. Interestingly, these
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1690 localities have no similarity with communities documented from Russia and Germany. This
1691
1692 seems best explained by the emergence of brackish water Limnocytheridae in these areas
1693
1694 (*Triassinella*, *Lutkevichinella*, *Pulviella*, *Telocythere*, *Renngartenella*, *Speluncella*). The
1695
1696 isolation of russian and german communities further develops during the Anisian, as does
1697
1698 the core of peri-Palaeo-Tethyan biotas (Hungary, Italy, Austria, Turkey, Romania) that
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1700 documents the highest degree of similarity for this stage. Thailand, Israel and Jordan
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1702 assemblages display a relatively high similarity corresponding to the possible emergence of
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1704 a neo-tethyan region. Other regions (Himalaya, south China) show relatively low levels of
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1706 similarity, that may be indicative of the dispersal of taxa related to the radiation stage. The
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1708 Ladinian sees the individualization of two distinct clusters, the first one gathers France,
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1714 Spain, Germany and Russia (with Scandinavia at a lesser level of similarity) and corresponds
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1716 to areas of maximal diversification of brackish water Limnocytheridae. The second cluster
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1718 corresponds to the enlargement of the peri-Palaeo-Tethyan region (Iran, Hungary, Balkan,
1719
1720 Alps) to southern-neotethyan areas (Israel and Jordan). The close similarity of Canadian
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1722 biota to this tethyan communities highlights the lack of data for this area during the Triassic
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1724 and the possible existence of earlier trans-panthalassic faunal communications. The isolation
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1726 of localities providing brackish water taxa further develops in the Carnian, as well as the
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1728 establishment of a wide peri-tethyan region encompassing northern palaeo-tethyan and
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1730 southern neo-tethyan areas. The high similarity of Canada with these tethyan localities
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1732 further develops while Indonesia shows weaker levels of similarity, perhaps partly because of
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1734 the lack of data. During the Norian, a relative uniformity of the biotas is observed within
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1736 tethyan and panthalassic oceans, possibly illustrating the homogeneity of faunas and free
1737
1738 migrations among oceans. Conversely, Germany and Slovenia stand aside with very low
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1740 levels of similarity. The highest degree of similarity occurs between Germany, UK and
1741
1742 Ireland, possibly illustrating a first type of biota of the Rhaetian Sea, which was a shallow
1743
1744 epicontinental sea that covered the northwestern Europe during the latest Triassic (e.g.,
1745 [Fischer et al., 2012](#)). Another type of Rhaetian Sea biota seems represented by the second
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1747 level of similarity observed between France and Hungary. A third large cluster with lower
1748
1749 similarities still documents the relative biotic uniformity within tethyan and panthalassic
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1751 oceans (Japan, Australia, Romania, Austria, Iran, Iraq).

1752 1753 1754 1755 *5.4.2. Thoughts on the palaeogeography of radiations*

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1759 During most of the Triassic, South China appears as a key area for radiations. In the
1760
1761 Griesbachian, the first occurrence of Limnocytheridae (*Triassinella*) in South China
1762
1763 documents the emergence of this family on the eastern side of the Tethys very early in the
1764
1765 Triassic. Conversely, the Griesbachian large distributions of *Kerocythere* and *Hungarella*
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1767 seem to point to an incompleteness of their records: they are documented from South China
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1773 and respectively from Italy and Hungary and India, and these large patterns indicate that they
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1775 may have radiated earlier during the Late Permian. During the Carnian, South China saw the
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1777 radiation of Schulerideidae, described higher, and *Carinobairdia*, a genus that was only
1778
1779 known from the Norian-Rhaetian interval of Tyrol, Greece and Iran (Kollmann, 1963; Bolz,
1780
1781 1971a, b; Urlichs, 1972; Kristan-Tollmann, 1988; Kristan-Tollmann et al., 1991; Mette and
1782
1783 Mohtat-Aghai, 1999; Hillebrandt et al., 2007; Urlichs and Krystyn, 2016; Mercier, 1966;
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1785 Kristan-Tollmann et al., 1979, 1980). They migrated to the western Tethys later in the Late
1786
1787 Triassic and diversified there. This pattern was coupled to a major palaeobathymetrical
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1789 change, from their radiation on the deep-shelf followed by colonisation and ultimately
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1791 distribution only in shallow waters (Forel et al., 2019b). These ostracod records are in line
1792
1793 with growing evidence of the macroevolutionary importance of offshore origination in marine
1794
1795 invertebrates (e.g., Lindner et al., 2008; Thuy, 2013; Bribiesca-Contreras et al., 2017; Hess
1796
1797 and Thuy, 2018).

1798
1799 In essence, the Triassic history of *Petasobairdia* is tethyan but it may have been panthalassic
1800
1801 in origin as shown by its earliest occurrence from a seamount of the Panthalassa (Japan)
1802
1803 during the Early Permian, Sakmarian stage (Tanaka et al., 2018). It may have subsequently
1804
1805 migrated to the Indochina Block, Thailand, as shown by its occurrence as early as the
1806
1807 Artinskian, Early Permian, and late Roadian? (Chitnarin et al., 2012). A subsequent
1808
1809 westerward expansion of the genus is illustrated by Capitanian, Middle Permian, occurrences
1810
1811 in Russia (Gramm, 1997) and Turkey (Crasquin-Soleau et al., 2004b) It subsequently
1812
1813 occurred in the Wuchiapingian of Greece (Crasquin-Soleau & Baud 1998), Hungary (Kozur,
1814
1815 1985), Wuchiapingian and Changhsingian of China (Yuan et al., 2007; Shi and Chen, 1987;
1816
1817 Crasquin et al., 2010; Yi, 2004; Forel, 2012; Li et al., 1989; Zazzali et al., 2015),
1818
1819 Changhsingian of Iran (Forel et al., 2015) and Italy (Crasquin et al., 2008), documenting the
1820
1821 colonization of the entire Palaeo-Tethys and Neo-Tethys appear as early as Wuchiapingian,
1822
1823 Late Permian. These geographical features may show that *Petasobairdia* radiated in
1824
1825 panthalassic waters during the Early Permian (Sakmarian) and that subsequently migrated
1826
1827 westward to colonize palaeotethyan waters with the first step being Indochina Block in the
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1831
1832 Artinskian. During the Triassic, it is restricted to tethyan waters *lato sensu* and no record of
1833
1834 this genus is known from Panthalassic deposits, possibly reflecting its palaeogeographical
1835
1836 restriction. The large record of *Petasobairdia* during the Spathian (Tibet, Israel) following its
1837
1838 last record restricted to China during the Griesbachian clearly indicates that dispersal
1839
1840 continued during the post-EPE poverty phase (Dienerian-Smithian) although not recorded
1841
1842 because of the lack of material. Middle and Late Triassic occurrences of this genus are still
1843
1844 poorly documented on the eastern side of the tethyan area because of the lack of work
1845
1846 carried on these areas, however its presence *a* in the Anisian, Middle Triassic, of Thailand
1847
1848 ([Ketmuangmoon et al., 2018](#)) shows the subsistence of this genus at least until the base of
1849
1850 the Middle Triassic in this area.

1851
1852 *Ceratobairdia* and *Parurobairdia* have been Lazarus taxa during the entire Early and Middle
1853
1854 Triassic and re-entered the fossil record during the Norian. *Mirabairdia* is Lazarus during the
1855
1856 entire Early Triassic and re-entered the fossil record in the Anisian. The geographical
1857
1858 distribution of this genus through time indicates that it radiated in South Chinese waters
1859
1860 during the Changhsingian, Late Permian. When it re-entered the fossil record in the Anisian,
1861
1862 it was already present along the entire northern margin of the Palaeotethys: dispersal may
1863
1864 have occurred during the Early Triassic and the Lazarus record of this genus may be related
1865
1866 to preservation bias.

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1868 *Ptychobairdia* appeared to have radiated on the eastern side of tethyan area (South China;
1869
1870 [Crasquin-Soleau et al., 2006](#)) where it was apparently confined during the entire early
1871
1872 Triassic. Contrary to *Petasobairdia*, the records of *Ptychobairdia* do not indicate a westward
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1874 migration until the Anisian, during which it colonized only the northern margin of the tethyan
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1876 area (Hungary, Romania, Austria); a southern migration within the Tethys occurs from the
1877
1878 Ladinian onwards. A final step of eastward migration took place in the Upper Late Triassic
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1880 (Norian and Rhaetian) when it occurs in Panthalassic areas. This eastward movement might
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1882 however have begun earlier as shown by its large panthalassic distribution in Japan and
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1884 Canada during the Norian.

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1891 **6. Conclusions**
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1895 A database of all genera and families of marine and brackish ostracods gave us the
1896 opportunity to describe their diversity through the Triassic, a key period in the evolution of
1897 organisms in being bounded by two major biological crises and providing the earliest traces
1898 of the on-set of the Mesozoic marine revolution. We furthermore explored this database at
1900 the light of palaeoenvironmental, palaeoecological and palaeogeographical contexts.

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1905 1. In terms of bulk diversity, the rediversification of ostracods following the EPE mainly
1906 occurred in a continuous burst spanning the Spathian and the Anisian. However, the
1907 taxonomic restructuring of ostracod communities began already in the Dienerian, during
1908 the poverty phase that followed the EPE. Although general diversity trends document the
1909 impoverished ostracod communities during most of the Early Triassic, the roots of their
1910 Triassic taxonomic rediversification are visible as early as the Dienerian. The entire Middle
1911 and Late Triassic document to a high-diversity plateau maintained by the equilibrium
1912 between extinctions and radiations.
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1920 2. The Triassic occurrences of Palaeozoic groups (Palaeocopida and deep-sea taxa) are
1921 reviewed and a restriction of the restriction of the environmental distribution of Kirkbyidae is
1922 reported in the Triassic. Deep-sea taxa, mainly Rectoriidae, residually range up the
1923 Rhaetian and point to the stability of environmental conditions through the EPE and the
1924 Triassic, in contrast with on-going discussion of long-term and widespread anoxia.
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1930 3. Ornate Bairdiidae radiated during two main phases, in the Anisian and in the Carnian. A
1931 “morphological phylogeny” proposes that all Permian and Triassic ornate Bairdiidae derived
1932 from *Petasobairdia* in the Kungurian. Two distinct lineages arose during the Permian:
1933 *Ceratobairdia*-lineage characterized by ridged ornaments and *Abrobairdia*-lineage with
1934 nodulose ornamentation.
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1940 4. The transition interval from the Palaeozoic to the Modern fauna appears as
1941 asynchronous for neritic and deep-sea taxa. It is here considered as spanning from the Early
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1950 Permian to the Anisian for neritic ostracods. This interval is more complex to characterize for
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1952 deep-sea taxa, in the absence of Jurassic taxa that may be facies-markers.
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1954 5. The importance of ostracods in exploring food-webs through time is highlighted. The
1955 recent discoveries of holes related to drilling predation of Carnian and Rhaetian ostracods
1956 are a unique opportunity to describe the very early stages of the structuration of typically
1957 Mesozoic predation type, in compartements of the trophic chains that are most of the time
1958 ignored. The characteristics of these holes on ostracods witness the increase of the
1959 efficiency of predators drilling abilities through the Triassic.
1960
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1962 6. In terms of palaeogeographical distribution, peri-palaeo-tethyan and peri-neo-tethyan
1963 biotas appear as relatively distinct during most of the Early Triassic. The diversification burst
1964 saw the individualisation of a northern European biota characterized by the emergence of
1965 brackish water Limnocytheridae. A homogenization, possibly related to the dispersal of taxa
1966 after their radiation, became visible in the Anisian. This feature further developed in the
1967 Carnian with the establishment of a wide peri-tethyan region. In the Rhaetian, this feature is
1968 widespread and includes panthalassic localities, while at least two distinct biotas typical of
1969 the Rhaetian Sea may have been identified for the first time.
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1982 **Acknowledgements**

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3661 **Figure captions**
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3665 **Figure 1.** A, End-Permian and Triassic timescale with absolute ages from [Cohen et al.](#)
3666 ([2013](#), updated version 2020) and recovery pattern of ostracods after the end-Permian
3667 extinction, modified from [Crasquin and Forel \(2014\)](#). B, palaeogeographical map of the
3668 Anisian, Middle Triassic, modified from [Angiolini et al. \(2013\)](#).
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3675 **Figure 2.** Stratigraphical distribution of ostracod families during the Triassic. Arrows indicate
3676 older ranges (directed downward) and younger ranges (directed upward).
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3680 **Figure 3.** A, Total generic diversity of ostracods given for each time slice of the Triassic
3681 (black curve). For each interval, the number of newly originated genera (orange) and
3682 genera going extinct at the end of each stage (blue) are shown as histograms. B,
3683 Proportion of families per orders for each time slice of the Triassic.
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3689 **Figure 4.** Total generic diversity of Cytheruridae, Limnocytheridae, Bythocytheridae,
3690 Cavellinidae, Cytherellidae given for each time slice of the Triassic (black line). For each
3691 interval, the number of newly originated genera is given in dashed line.
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3698 **Figure 5.** Total generic diversity and palaeoenvironmental distribution of Kirkbyidae for each
3699 time slice of the Permian and Triassic. \$
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3704 **Figure 6.** Total generic diversity of Bairdiidae given for each time slice of the Triassic (black
3705 line). For each interval, the number of newly originated genera (orange) and genera
3706 going extinct at the end of each stage (blue) are shown as histograms.
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3711 **Figure 7.** Stratigraphical distribution of ornate Bairdiidae for each time slice of the Permian
3712 and Triassic.
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Figure 8. Evolutionary trends in ornate Bairdiidae based upon external carapace morphology and stratigraphical occurrence.

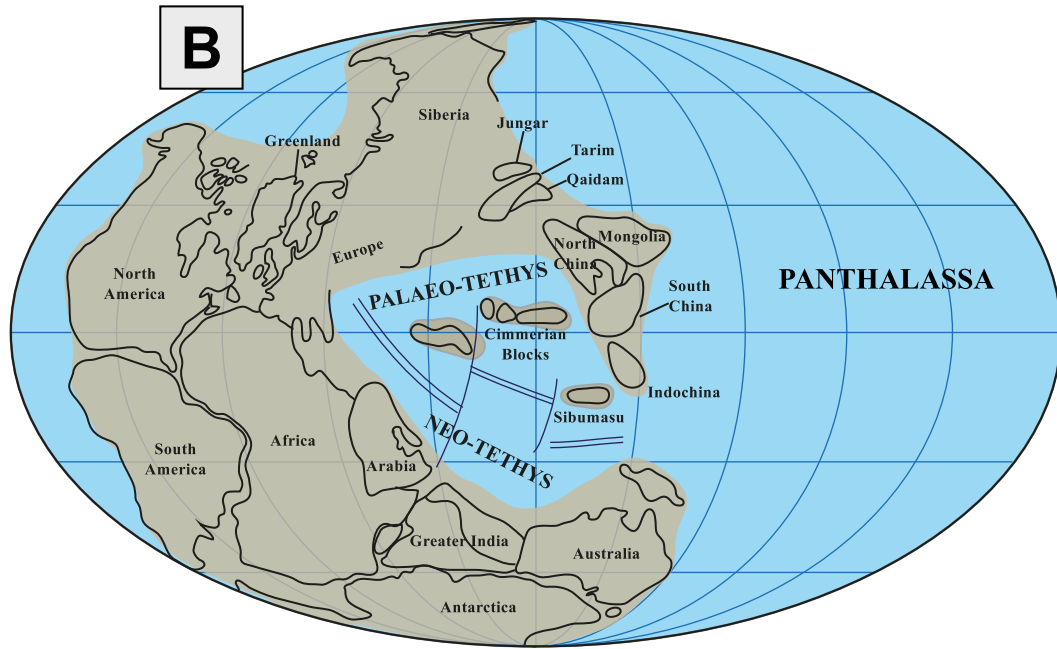
Figure 9. Dendrograms of UPGMA analysis based on diverse loci for each stage of the Triassic. B., S., S. (Ladinian) stands for Bosnia, Slovenia and Slovakia; S., Yu. (Carnian) stands for Slovenia and Yugoslavia.

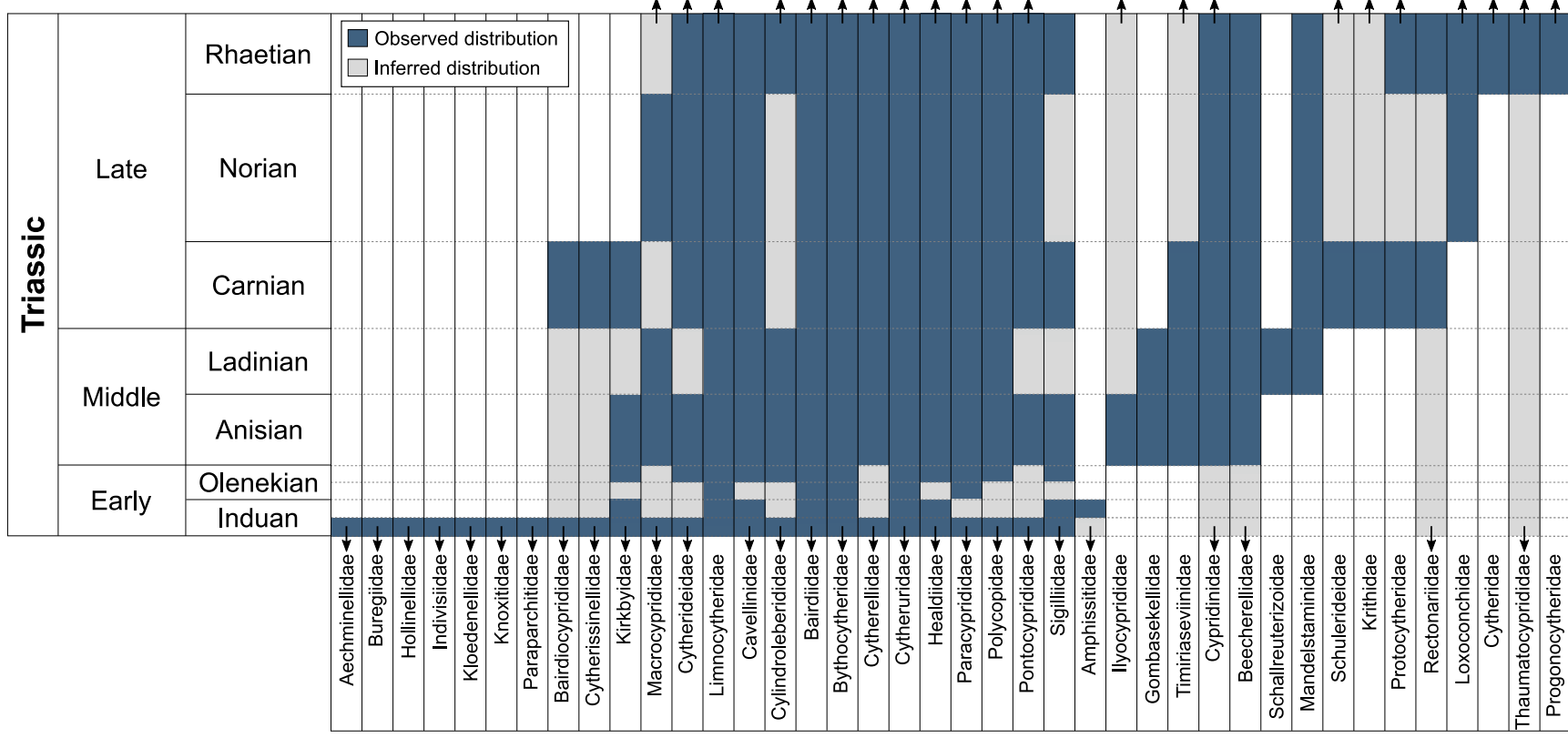
Table 1. Stratigraphical distribution of ostracod genera during the Triassic. Blue boxes indicate observed occurrences; grey boxes indicate inferred occurrences.

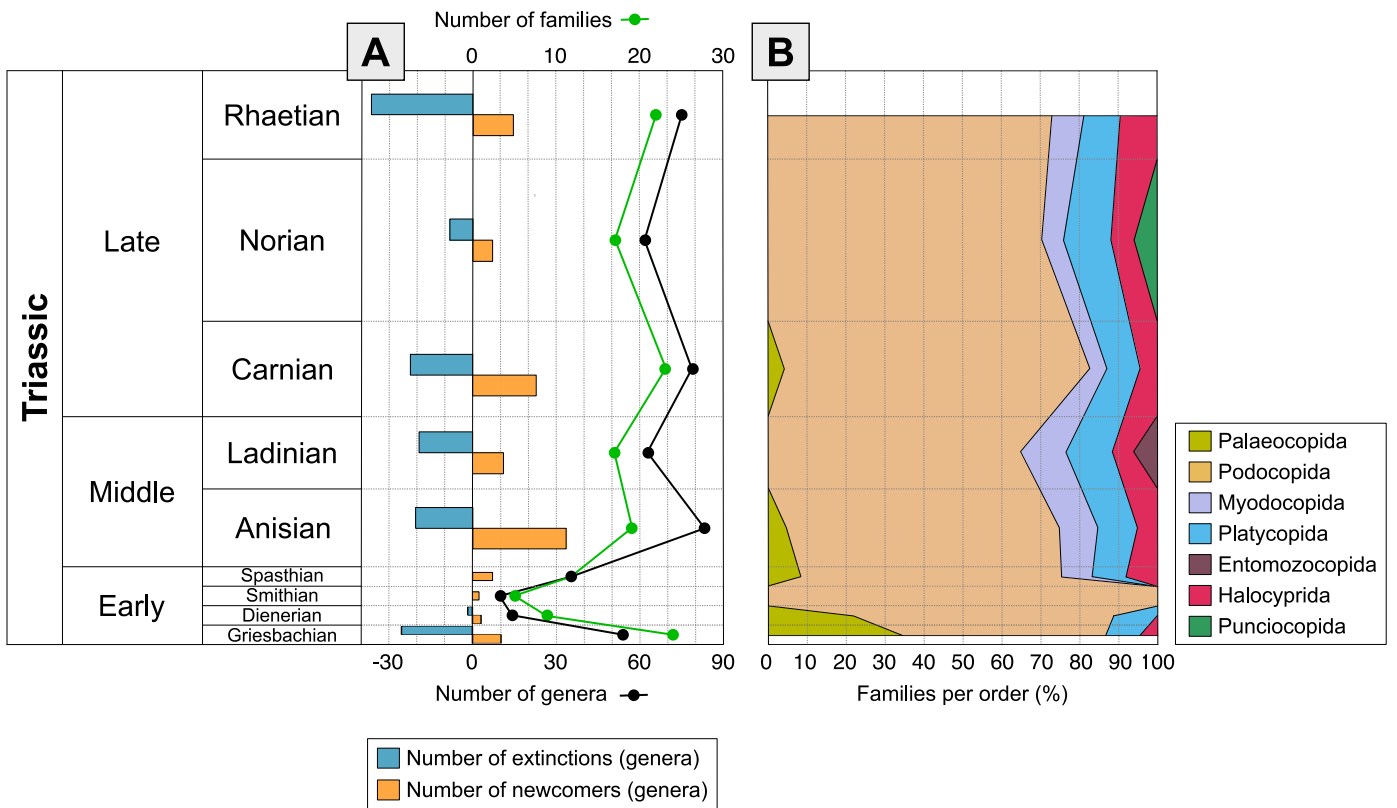
Supplementary File 1. Complete list of references used to create the database of Triassic ostracod genera and families.

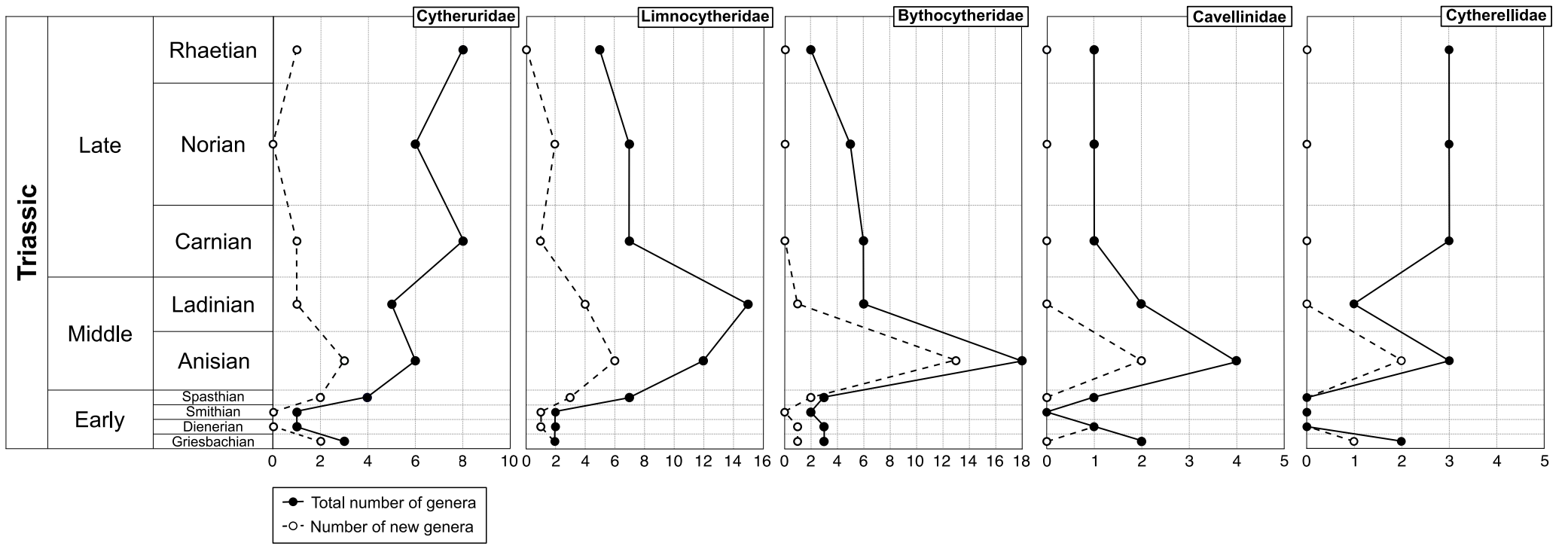
Supplementary File 2. Matrices of ostracod genera distribution during each stage of the Triassic.

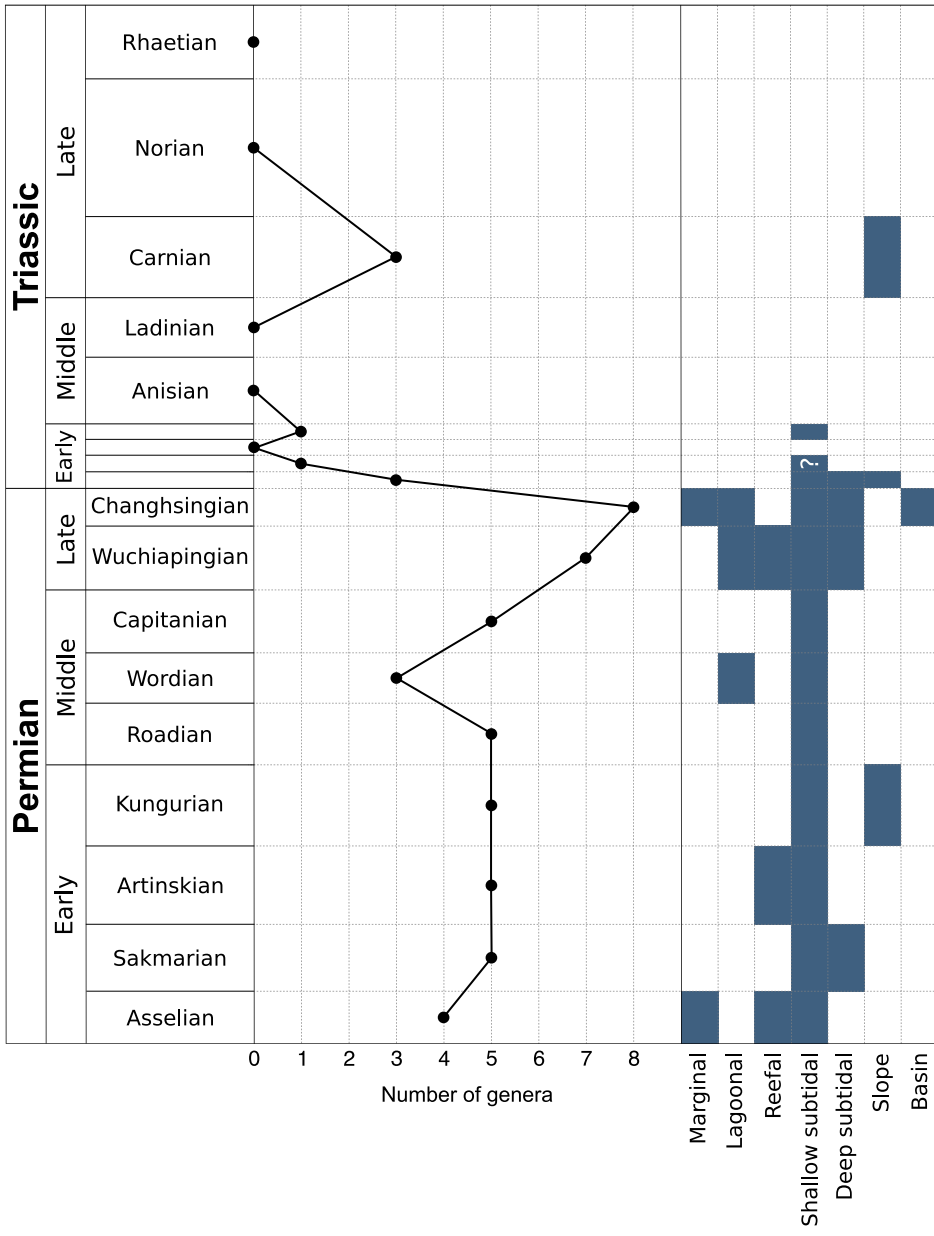
A	Triassic	201.3 ± 0.2		Rhaetian	<p>Radiation</p> <p>Initiation of the recovery</p> <p>Maximum of poverty</p> <p>Survival</p> <p>Maximum of extinction</p>				
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		227		Carnian					
		237		Ladinian					
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		247.2		Olenekian <table border="1" style="display: inline-table; vertical-align: middle;"> <tr><td>Spathian</td></tr> <tr><td>Smithian</td></tr> <tr><td>Dienerian</td></tr> <tr><td>Griesbachian</td></tr> </table>		Spathian	Smithian	Dienerian	Griesbachian
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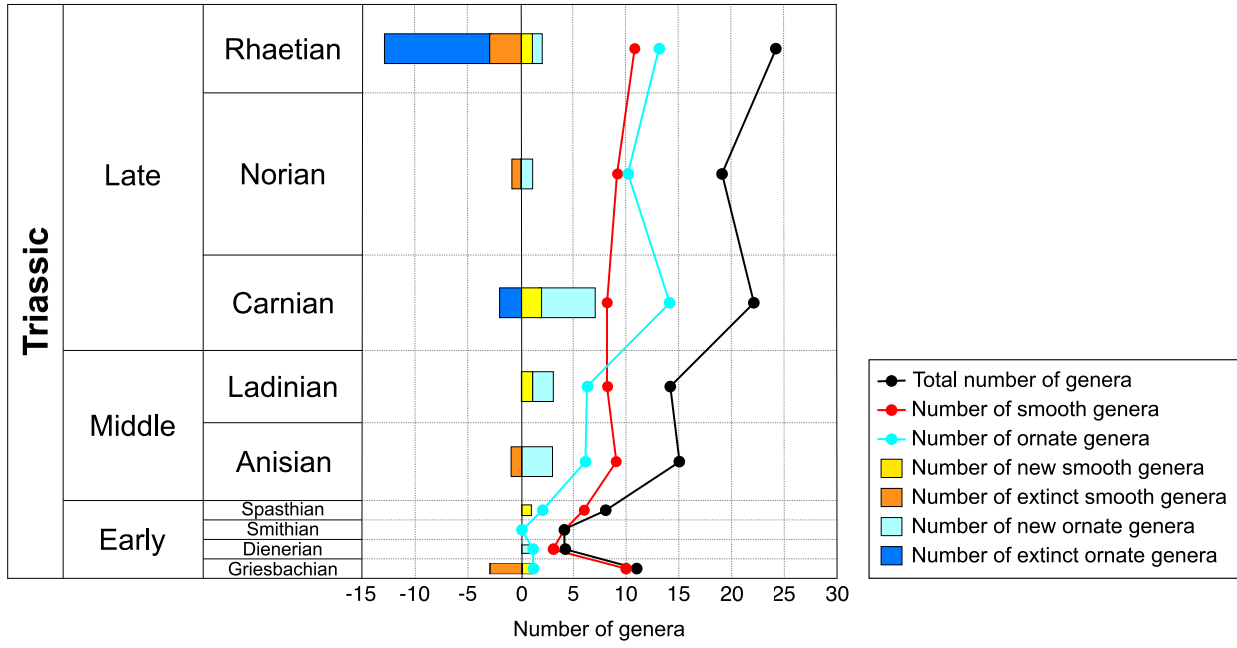


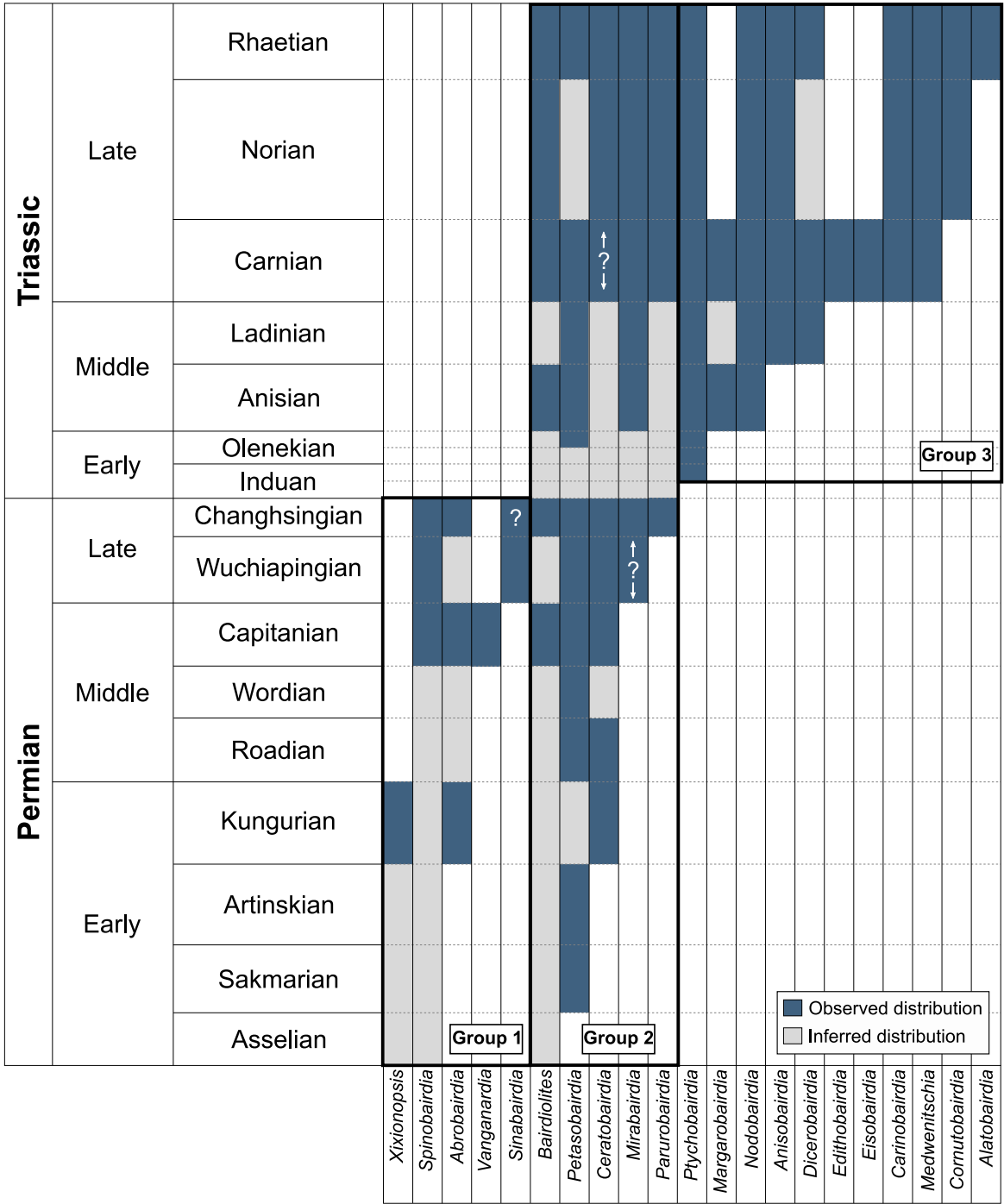










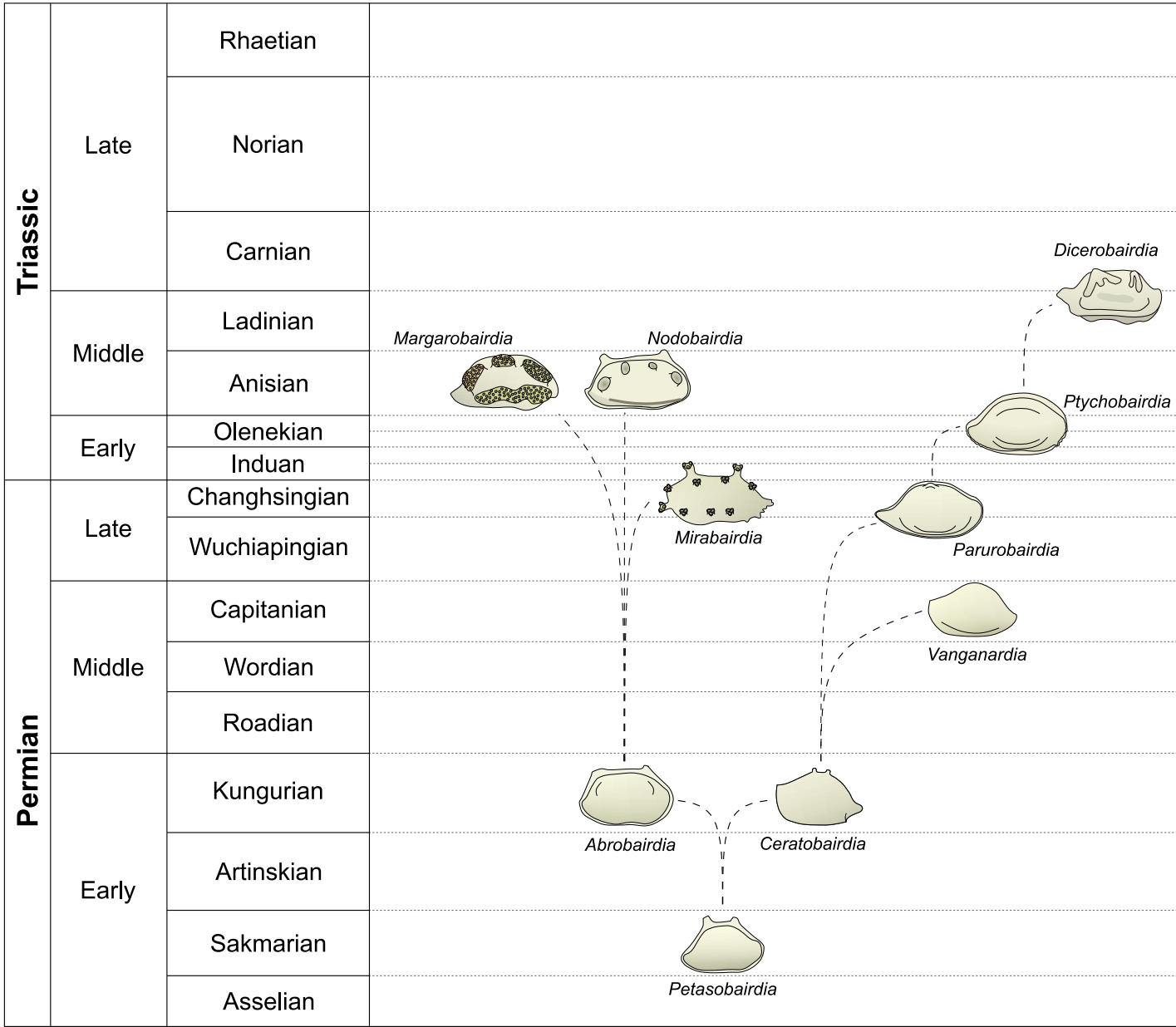


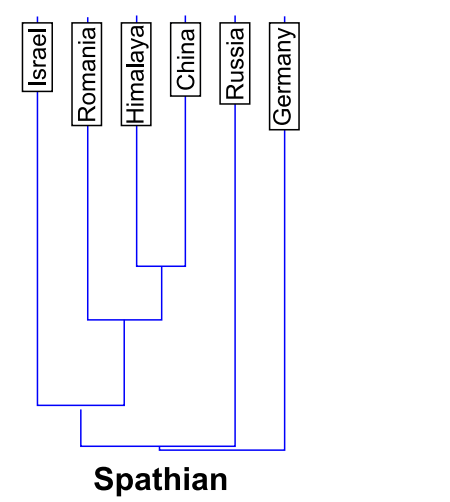
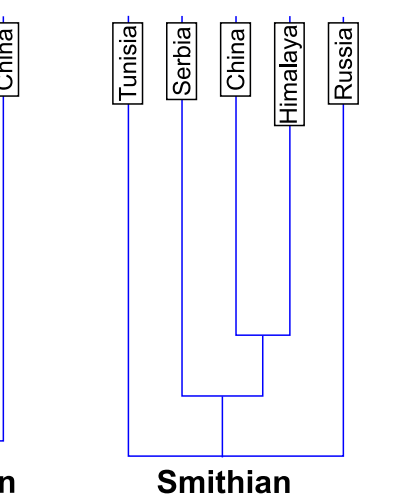
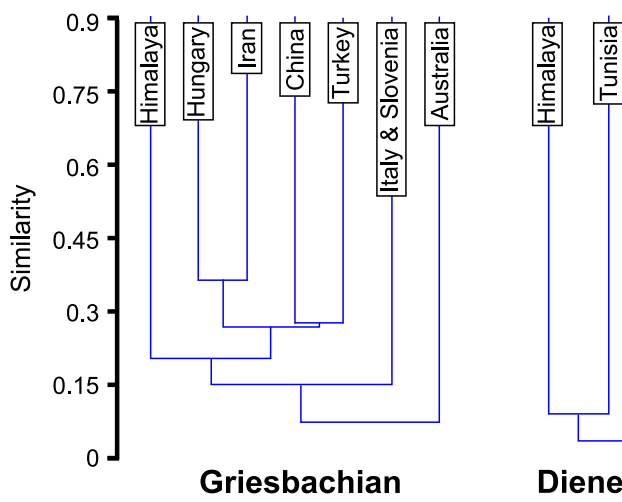
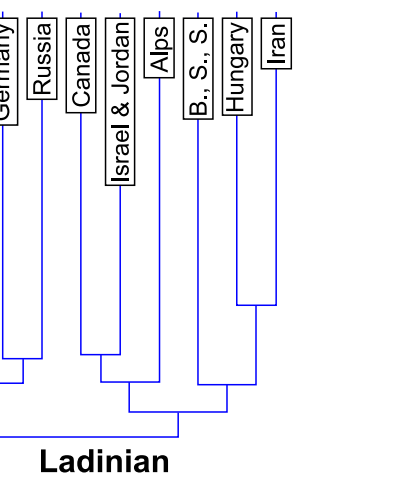
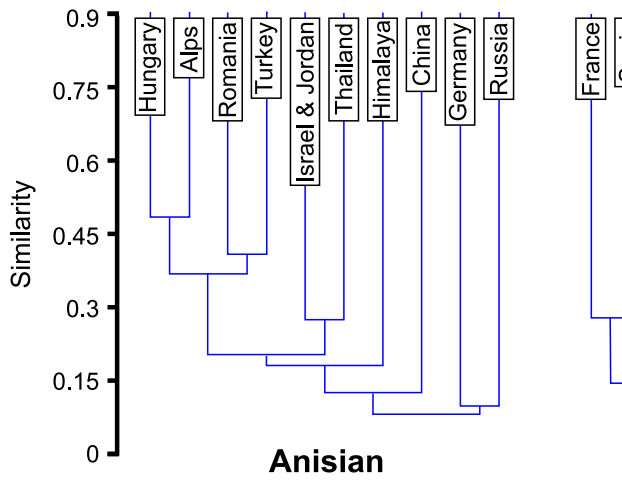
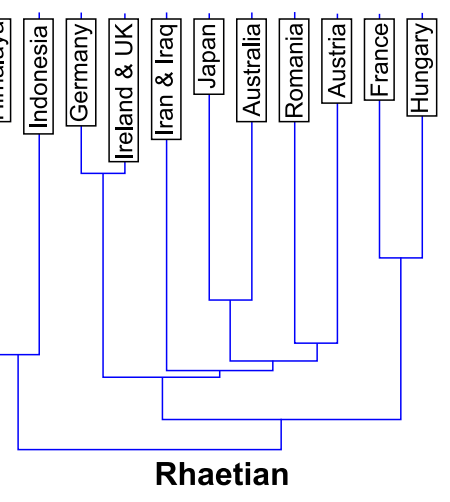
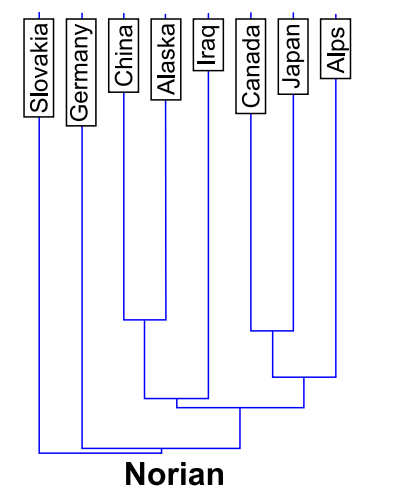
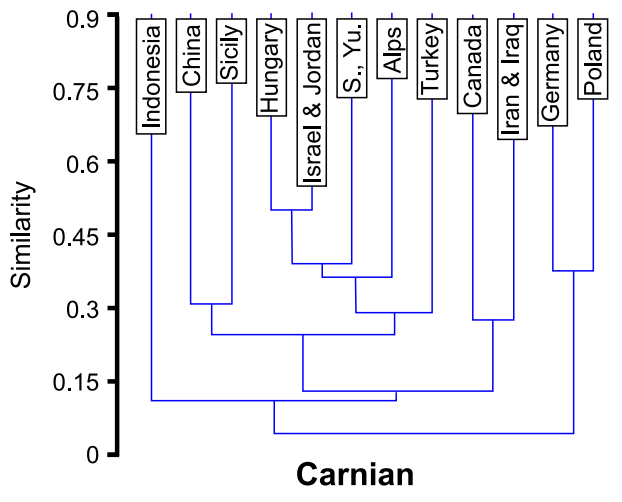
Group 3

Group 1

Group 2

Observed distribution
Inferred distribution





Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: