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Ostracod turnover during the Carnian Pluvial Episode (Late Triassic) in the Western Neotethys

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ABSTRACT

The Carnian Pluvial Episode (CPE) caused a biotic crisis and turnover in terrestrial and marine ecosystems in the Western Neotethyan realm. The expansion of deltaic systems on land and the increased siliciclastic input affected the distribution of benthic ostracods, both nearshore and offshore. Diversity changes of Carnian ostracod faunas from seven successions in the Transdanubian Range (TR), Western Hungary tracked the effects of the CPE, despite its distal hemipelagic depositional setting and position within an intraplatform basin. At the onset of CPE in the early Julian 2, the composition of the studied benthic ostracod assemblage was similar to that of the late Julian 1 communities albeit with decreased abundance of smooth bairdiids and healdiids. The ratio of healdiids and smooth bairdiids is likely related to the detrital supply with bairdiids colonizing primarily in intervals with decreased terrestrial input and carbonate platform progradation. During the maximum expansion of CPE in late Julian 2, the predominance of platycopid *Bektasia* indicates a shallowing trend, infilling of the Carnian basins and stressed environment due to clastic input and salinity stress. The Julian–Tuvalian boundary is characterized by high extinction rates among marine invertebrates simultaneously with the occurrence of a unique low diversity but abundant brackish water ostracod community with *Simeonella* and *Renngartenella* that can be traced along the entire Western Neotethys and northern Gondwana shelf. The appearance of this community is primarily linked to salinity variations during the CPE and the formation of restricted basin habitats in the TR with water stratification where the special community lived or was transported there with storms or river outflow. During the Tuvalian, fully open marine conditions were re-established with increased carbonate productivity in the platforms, favouring the colonization of stable shallow marine habitats with the appearance of ornate bairdiids in the ostracod faunas.

1. Introduction

The Carnian (Late Triassic) records a geologically short-lived climate change with a primary warming cycle (e.g., Trotter et al., 2015) and multiple, presumably, wet climatic phases, the so called Carnian Pluvial Episode (CPE) that lasted for ~1 myr (Simms and Ruffell, 1989, 1990; Kozur and Bachmann, 2010; Preto et al., 2010; Sun et al., 2016; Miller et al., 2017). The CPE is commonly linked to the eruption of the Wrangellia Large Igneous Province (Dal Corso et al., 2012; Jin et al., 2023) and carbon cycle perturbation from greenhouse-gas emission that affected the entire Earth-ocean-atmosphere system and intensified the Pangean megamonsoon circulation (Parrish, 1993; Hu et al., 2023). The global scale of the event is evidenced by the presence of multiple (four) negative carbon isotope excursions (Fig. 1) recorded both in marine and terrestrial organic matter, biomarkers, and marine carbonates across the Western and Eastern Neotethys and Gondwana locations (e.g., Dal Corso et al., 2012, 2015; Miller et al., 2017; Dal Corso et al., 2018, 2020; Jin et al., 2020; Mancuso et al., 2020; Jin et al., 2022). It was associated with enhanced hydrological cycle and continental runoff increasing the siliciclastic input into the ocean that led to the crisis of the carbonate factories in shallow seas, ocean acidification, and locally anoxic conditions in marginal marine settings of the Western Neotethys (e.g., Hornung et al., 2007; Rigo et al., 2007; Breda et al., 2009; Stefani et al., 2010; Rostási et al., 2011; Lukeneder et al., 2012).

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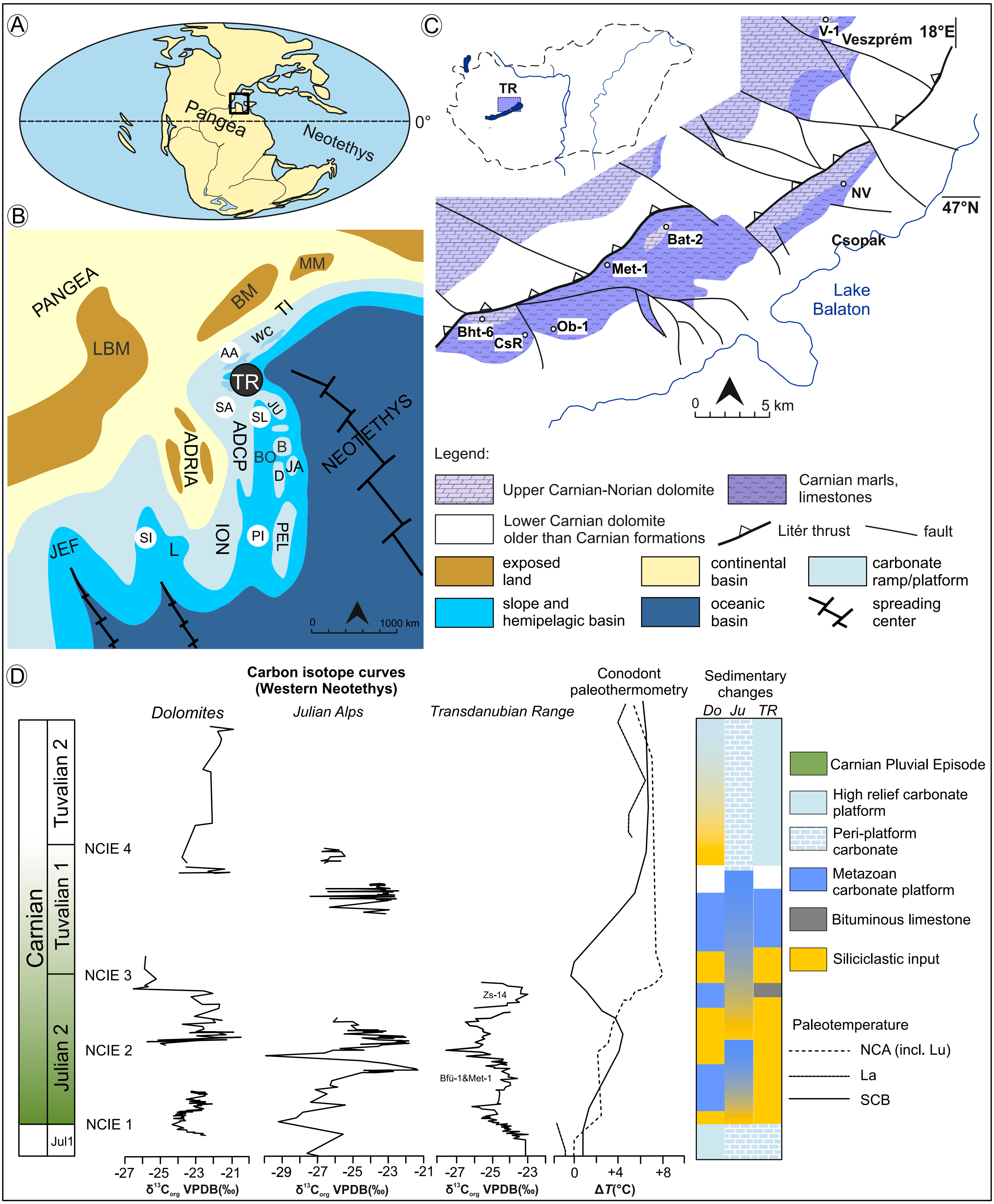

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Fig. 1. Paleogeographical setting of the Transdanubian Range (TR) during the Late Triassic A) Position of the Western Neotethys region. B) Position of the TR within the Western Neotethys region (after Haas et al., 2019). Abbreviations: LBM London-Brabant Massif, BM Bohemian Massif, MM Malopolska Massif, AA Austroalpine Units, WC Central and Inner West Carpathian Units, TI Tisza Unit, TR Transdanubian Range, SA Southern Alpine Unit, SL Slovenian basin, JU Julian Alps, B Bükk Unit, ADCP Adriatic Dinaridic Carbonate Platform, BO Bosnian Zone, D Drina–Ivanjica Unit, JA Jadar Block, SI Sicilian Basin, L Lagonegro Basin, JEF Jefra Basin, PI Pindos Basin, PEL Pelagonian-Subpelagonian Units. C) Simplified pre-Cenozoic geological map of the Balaton Highland showing the extension of the Carnian and Norian formations and studied sections (after Haas et al., 2010). Bat-2: Barnag Bat-2 well; Bht-6: Balatonhenye Bht-6 well; CsR: Csukrét Ravine outcrop; Met-1: Mencshely Met-1 well; Ob-1: Óbudavár Ob-1 well; NV: Nosztor Valley outcrop; V-1: Veszprém V-1 well. D) Overview of C cycle perturbations and associated sedimentological changes in the Western Neotethys during the CPE (modified after Dal Corso et al., 2018). Paleotemperature data from Hornung et al. (2007), Rigo and Joachimski (2010), Trotter et al. (2015), and Sun et al. (2016). Abbreviations: NCA Lu = Northern Calcareous Alps, Lunz. La = Lagonegro Basin. SCB=South China Block.

The carbon cycle perturbation and proposed climate change affected both the marine and the terrestrial ecosystems resulting in faunal and floral turnovers (e.g., Simms and Ruffell, 1989, 1990; Simms et al., 1995; Rigo et al., 2007; Roghi et al., 2010; Bernardi et al., 2018; Dal Corso et al., 2020). The CPE induced the onset of modern pelagic carbonate production with the mass occurrences of calcispheres (calcareous dinoflagellates) in the Western Neotethys (Preto et al., 2013; Dal Corso et al., 2021). In shallow marine habitats, modern-style scleractinian coral reefs radiated and replaced microbially dominated carbonate-producing ecosystems (Stanley, 2003; Hornung et al., 2007; Sun et al., 2016; Dal Corso et al., 2020). Principal biostratigraphical marker groups of the marine Triassic, such as ammonoids, underwent a major turnover during the CPE with high extinction rates during the Julian 2 and high origination rates in the early Tuvalian coincident with the third C-isotope excursion (Dal Corso et al., 2020). Conodonts have two extinction peaks, at the onset of the CPE in the early Julian 2 and at the Julian–Tuvalian boundary, while they diversified in the aftermath of the CPE in the late Tuvalian (Rigo et al., 2007, 2018; Chen et al., 2016; Tomimatsu et al., 2023). Among other invertebrate and vertebrate groups, high extinction rates are recorded for bryozoan and crinoids, bony fishes, sharks, and marine reptiles (Simms and Ruffell, 1989; Dal Corso et al., 2020).

Despite the fact that fossil ostracods are proven to be one of the most useful organisms for paleoenvironmental reconstructions (e.g., Boomer et al., 2003; Frenzel and Boomer, 2005), the paleoecological significance of Carnian faunas is less known. The Carnian stage also represents a turning point in ostracod evolution with the earliest occurrence of some typical Jurassic taxa in the Eastern Neotethys (Forel et al., 2019) and the oldest evidence of drilling predation (Forel et al., 2018). A few works present ostracod assemblages indicating brackish or hypersaline environments in the Carnian and connect these assemblages to a so-called 'salinity crisis' (Gerry et al., 1990; Kristan-Tollmann et al., 1991; Monostori, 1994; Keim et al., 2001, 2006; Monostori and Tóth, 2014; Forel et al., 2020), but the influence of the CPE on marine ostracods is still poorly understood.

In the Transdanubian Range (TR) numerous outcrops and boreholes document Carnian marine successions that provide a unique opportunity for investigating the environmental and ecological dynamics of marine habitats during the CPE (e.g., Budai and Haas, 1997; Budai et al., 1999; Haas et al., 2012; Dal Corso et al., 2015, 2018). The continuous stratigraphical record enables the temporally and spatially comprehensive investigation of the marine ostracod assemblages throughout the entire Carnian. Our goal is to detect diversity changes of the marine ostracod faunas in the Western Neotethys and to reveal links between biotic changes, salinity variations, nutrient supply, and oxygenation of the water column during the CPE.

2. Geological setting and studied sections

2.1. Depositional history of the Transdanubian Range during the Triassic

The area of the Transdanubian Range (TR) was situated on the Western Neotethys shelf during the Mesozoic between the Northern Calcareous Alps (NCA) and the Southern Alps (Haas et al., 1995) (Fig. 1A–C). The Triassic depositional history of the area starts with transgression, flooding of the Late Permian alluvial plains and the formation of shallow marine mixed clastic-carbonate ramp (Haas and Budai, 1995, 1999). The area was affected by extensional tectonics at the beginning of the middle Anisian (Budai and Vörös, 1993) corresponding to the Annaberg Event (Gawlick et al., 2021) and a second pulse at the end of the middle Anisian (late Pelsonian) attributed to the Reifling Event (Schlager and Schöllnberger, 1974; Gawlick et al., 2021) due to rifting and westward opening of the Neotethys, resulting in the formation of a horst-and-graben topography with uplifted blocks with shallow marine carbonate factories and downfaulted basins (Budai and Vörös, 1993; Bertotti et al., 1993; Budai and Vörös, 2006; Gaetani, 2010; Gawlick et al., 2012, 2021). The disintegration of the former carbonate ramp was followed by rapid subsidence during the late Anisian and Ladinian establishing deep-marine depositional environment on the Western Neotethys shelf (Vászoly and Buchenstein formations in the TR, Budai and Vörös, 2006; Gawlick et al., 2021; Karádi et al., 2022). The extensional tectonics was accompanied by volcanic activity leading to the deposition of volcanic tuffs ("pietra verde") in the entire Western Neotethys realm (Dunkl et al., 2019; Storck et al., 2019). The Carnian paleogeography was characterized by a dissected platform-basin system with great variety of facies depending on the proximity to carbonate platforms. Based on facies analogies with the Southern Alps, a rimmed shelf with steep slope and a 500–600 m deep basin can be envisaged for the early Carnian paleotopography of the TR (Nagy, 1999). In basinal settings the early Carnian is represented by the pelagic carbonates of the Füred Limestone Formation (FL) that was followed by the fine-grained mixed siliciclastic-carbonate sediments of the Veszprém Marl Formation (VMF) divided into a lower marl (Mencshely Marl Member) and upper marl unit (Csicsó Marl Member) that infilled the basin areas due to the intensifying terrigenous influx during the CPE (Fig. 2, Rostási et al., 2011, Haas et al., 2012). Episodic deposition of dolomites or calcareous skeletal toe-of-slope sediments indicates periods of platform progradation intercalated within the marl packages (Fig. 2). Metazoan carbonate platforms apparently prevailed longer in isolated areas that developed on uplifted paleo-highs of the TR e.g., in the Keszthely Mts. (Ederics Formation) and in the eastern part of the Bakony (Sédvölgy Dolomite Member) and prograded into the basin during highstand periods (Fig. 2) (e.g., Haas and Budai, 1995; Budai and Haas, 1997; Haas and Budai, 1999, 2014; Nagy, 1999).

The progressive sediment supply from the siliciclastic shoreline combined with relative sea-level variations and progradation of carbonate platforms, resulted in the infilling of the intraplatform areas with flattening of the paleotopography represented by the shallowing upward succession of the Sándorhegy Limestone Formation (SF, Fig. 2) in the late Julian–early Tuvalian (Nagy and Csillag, 2002). A shallow marine environment was formed where a shallow basin (~100–150 in depth) was connected by gentle slopes to isolated platforms that were built up by primarily metazoan reefs and encrusting binding organisms such as molluscs, foraminifers, and sponges (Nagy, 1999; Nagy and Csillag, 2002). Due to the inherited dissected bottom topography combined with the infill of the basins and a late Julian sea-level fall (Nagy, 1999; Pecorari et al., 2023), some parts of the shallow basins became separated with restricted circulation resulting in water column stratification represented by the Pécsely Member (Nagy, 1999; Nagy and Csillag, 2002). In the stagnant water column, anoxic-dysoxic conditions prevailed

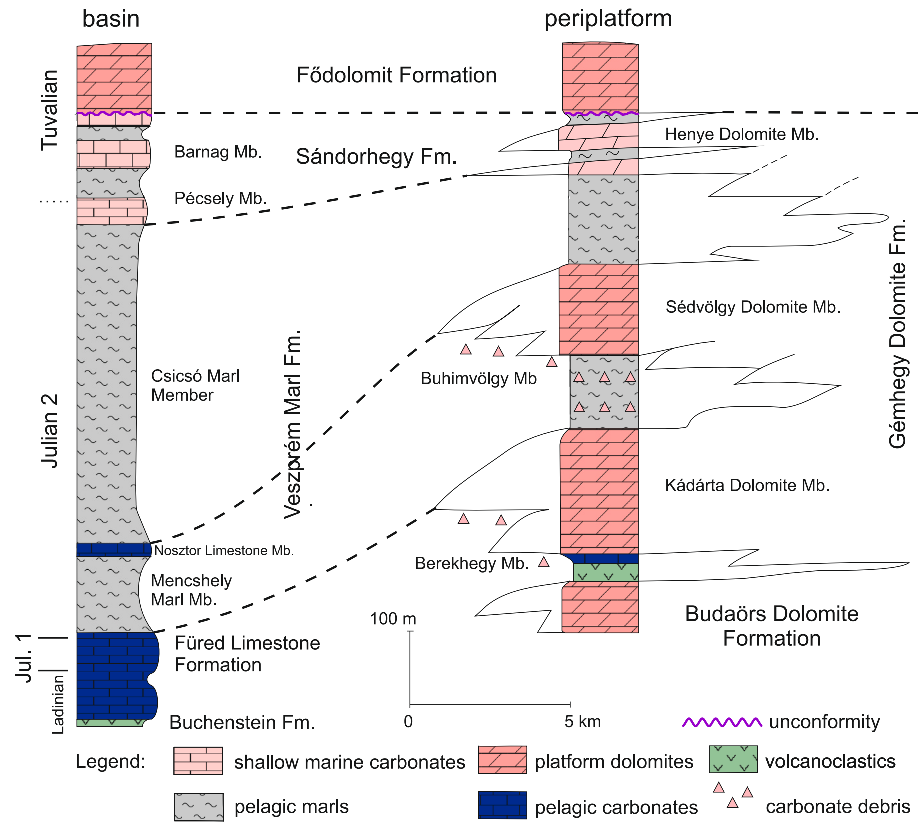

Fig. 2. Correlation of the coeval Carnian basin and periplatform facies of the TR in the strike of southern Bakony and Balaton Highland (modified after Haas and Budai, 1999).

leading to the deposition of organic rich bituminous limestone laminae with occasional subtidal microbial mats while pseudomorhps after dissolved gypsum in intercalating dolomite beds infer hypersaline bottom waters (Nagy, 1999). A subsequent sea level rise opened the basin marked by the deposition of mollusc and ostracod coquinas followed by progradation of the carbonate platforms and shallowing. Episodic increases of terrigenous input temporally diminished the activity of carbonate factories represented by relatively thick marl and clayey limestone packages within the Sándorhegy Formation assigned to the Barnag Member (Nagy, 1999; Nagy and Csillag, 2002).

As a consequence of the upfilling of the basins an extremely levelled topography came into being in the Tuvalian that initiated the evolution of the extensive carbonate platform of the Hauptdolomit/Dolomia Principale. Notably, the studied sequences of the TR are capped by a pronounced unconformity before the deposition of the Fődolomit Formation (Fig. 2, Hauptdolomit equivalent) (Nagy, 1999; Nagy and Csillag, 2002; Haas et al., 2012). See the Supplementary Material for detailed description of lithostratigraphical units.

2.2. *Age and biostratigraphical considerations*

Primary Triassic biostratigraphical markers, ammonites and conodonts only sporadically occur in the Carnian mixed clastic-carbonate sediments of the Transdanubian Range due to unfavourable environmental conditions during the CPE, thus the precise biostratigraphical correlation is often difficult and requires other fossil groups e.g., palynomorphs (Baranyi et al., 2019), benthic foraminifers (Oravecz-Scheffer, 1987; Góczán and Oravecz-Scheffer, 1996ab) or chemostratigraphical correlation (Dal Corso et al., 2015, 2018). An early Julian age for the Füred Limestone Formation is suggested by ammonoids, conodonts, and radiolarians (Dosztály et al., 1989; Dosztály, 1993; Budai et al., 1999). Palynological assemblages of the Veszprém Marl Formation (Góczán et al., 1991; Góczán and Oravecz-Scheffer, 1996a, 1996b; Baranyi et al., 2019) were correlated to the Julian 2 *Aulisporites astigmosus* assemblage sensu Roghi et al. (2010) and the *Duplicisporites continuus* assemblage sensu Roghi (2004) from the Alps. Ammonoid marker taxa were found only in the Nosztor Limestone Member (*Austrotrachyceras austriacum*) and Csicsó Marl Member (*Neoprotrachyceras baconicum*) both suggesting a Julian 2 age for the Veszprém Marl Formation (Budai et al. Nagy, 1999; Dal Corso et al., 2015). The position of the Julian–Tuvalian boundary has been tentatively placed in the lower part of the Sándorhegy Formation based on palynomorphs and benthic foraminifers (Fig. 3, Góczán et al., 1983, 1991; Góczán and Oravecz-Scheffer, 1996a). Yet it has to be noted that none of these groups provide a high precision biostratigraphy as accurate as ammonoids or conodonts and can be facies dependent, especially benthic foraminifers.

A broad NCIE has been recorded in the uppermost part of the Füred Limestone Formation that has been correlated to the onset of the globally synchronized CPE carbon cycle perturbation at the Julian 1–2 boundary (Figs. 1, 3, see in Dal Corso et al., 2015, 2018). A second NCIE has been recorded at the top of the lower marl unit in the TR (Mencshely Marl Mb) before the platform progradation period (Fig. 3), and a third is in the Sándorhegy Formation recovered so far only from the Zsámbék-14 well in the Gerecse Hills, NE part of the TR (Dal Corso et al., 2018). However, this third NCIE lacks firm biostratigraphical control and cannot be precisely correlated to the global C-isotope trends.

3. Materials and Methods

The Carnian formations of the study area can be traced along the southeastern limb of the syncline structure of the Transdanubian Range, along the compressional Alpine structure of the Litér overthrust. Five borehole successions and two outcrops have been selected for ostracod studies (Fig. 3). The Barnag Bat-2 -, Mencshely Met-1 - and Óbudavár

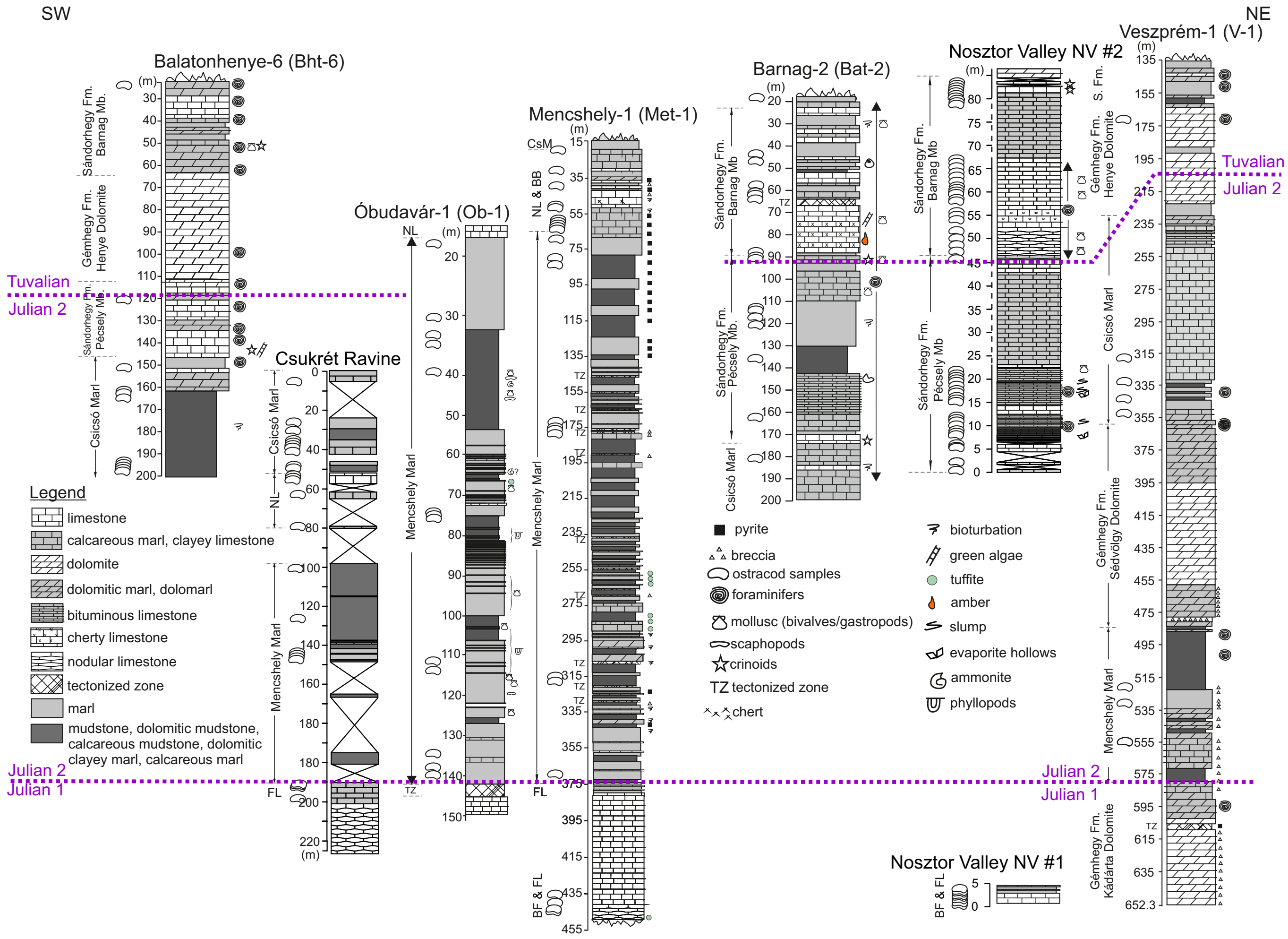

Fig. 3. Lithostratigraphical logs of the studied wells and outcrops in the TR showing the sampled horizons for ostracod analysis. The Julian–Tuvalian boundary is placed after Góczán and Oravecz-Scheffer (1996a, 1996b) but its position is uncertain due to the lack of reliable index fossils (ammonoids, conodonts). See the Supplementary Material for detailed description of lithostratigraphical units. Abbreviations: FL = Füred Limestone Formation, NL = Nosztor Limestone Member, BB=Buhimvölgy Breccia Member, BF=Buchenstein Formation.

Ob-1 boreholes, the outcrops Csukrét Ravine and Nosztor Valley represent Carnian intraplatform basin sequences while periplatform successions could be studied in the Balatonhenye Bht- and Veszprém V-1 boreholes (Table 1; Fig. 3).

Overall, a total of 155 microfossil-bearing samples were examined from various Carnian (Julian–Tuvalian) sedimentary successions (Supplementary Material Table S1): 12 from the uppermost Ladinian to lowermost Carnian (Julian 1) beds of Füred Limestone and 4 from the so-called “transitional beds” to the Veszprém Marl Formation, 35 from the Mencshely Marl Member, 10 from the Nosztor Limestone Member and 23 from the Csicsó Marl Member of the Veszprém Marl Formation (Julian 2). Thirty samples represent the Pécsely Member (Julian–Tuvalian transition) and 41 samples come from the Tuvalian Barnag Member of the Sándorhegy Formation (Fig. 3). Unfortunately, several layers of Veszprém Marl Formation were barren, or many samples yielded only very low number of specimens. The calcareous microfauna was mostly extracted with H_2O_2 from silts, silty and argillaceous marls. In the case of clayey limestones and limestones cold acetolysis was used, following the protocol by Lethiers and Crasquin-Soleau (1988). For the paleoecological interpretations, the original collections of Monostori (1994) from the Nosztor Valley and of Monostori and Tóth (2014) from the Met-1, Bat-2 and Bht-6 were used beside the new sampling. Scanning electron micrographs (SEM) of ostracods were taken at the Department of Petrology and Geochemistry, Eötvös Loránd University with AMRAY 1830 I/T6 Scanning Electron Microscope and in the Botanical Department of the Hungarian Natural History Museum in Budapest with a Hitachi S-2600 N Variable Pressure Scanning Electron Microscope.

To visualize compositional differences between the different ostracod assemblages and identify underlying environmental gradients, nonmetric multidimensional scaling (NMDS) was performed in PAST v.4.11 on a genera-based dataset (Supplementary Material Table S2, species were combined according to their corresponding genus) (Hammer et al., 2001). NMDS is the most robust unconstrained ordination method in ecology (e.g., Jardine and Harrington, 2008) as it does not make any assumption about linear or unimodal response to environmental gradients. For NDMS the Bray–Curtis dissimilarity was used and the row counted dataset was Wisconsin double standardized before the NMDS (Jardine and Harrington, 2008).

4. Results

A total of 34 marine benthic taxa are identified belonging to suborder Platycopina (families Cavellinidae and Cytherellidae), Metacopina (family Healdiidae), Bairdiocopina (families Bairdiocyprididae, Bairdiidae and Bythocyprididae), Cypridocopina (Paracyprididae and Pontocyprididae) and Cytherocopina (families Cytheruridae and Limnocytheridae). Classification of the ostracods follows Becker (2002),

Table 1
Summary of the studied successions (boreholes and outcrops) with their GPS coordinates, the main Carnian lithostratigraphical units and the key geological references on their sedimentological characteristics.

Locality	GPS coordinates	Lithostratigraphic units	Main references
Balatonhenye Bht-6	46°55′20.23” N 17°37′35.11″ E	Veszprém Marl Fm Csicsó Marl Mb Sándorhegy Fm Pécsely Mb Barnag Mb Gémhegy Fm Henye Dolomite Mb	Góczán and Oravecz-Scheffer (1996a) Nagy and Csillag (2002)
Csukrét Ravine	46°55′15,79” N 17°39′32.84″ E	Füred Limestone Fm Veszprém Marl Fm Mencshely Marl Mb Nosztor Limestone Mb Csicsó Marl Mb	Góczán et al. (1991)
Óbudavár Ob-1	46°55′19.21” N 17°41′05.56″ E	Veszprém Marl Fm Mencshely Marl Mb	Budai et al. (1999)
Mencshely Met-1	46°57′18.97” N 17°43′10.46″ E	Füred Limestone Fm Veszprém Marl Fm Mencshely Marl Mb Nosztor Limestone Mb Buhimvölgy Breccia Mb Csicso marl Mb	Budai et al. (1999)
Barnag Bat-2	46°58′44.61” N 17°46′21.23″ E	Veszprém Marl Fm Csicsó Marl Mb Sándorhegy Fm Pécsely Mb Barnag Mb	Góczán and Oravecz-Scheffer (1996a) Nagy and Csillag Nagy and Csillag (2002)
Nosztor Valley	47°00′03.45” N 17°54′53.42″ E	Füred Limestone Fm (NV #1) Sándorhegy Fm (NV #2) Pécsely Mb Barnag Mb	Góczán and Oravecz-Scheffer (1996a) Nagy (1999)
Veszprém V-1	46°55′20.23” N 17°37′35.11″ E	Veszprém Marl Fm Mencshely Marl Mb Csicsó Marl Mb Gémhegy Fm Kádárta Dolomite Mb Sédvölgy Dolomite Mb Henye Dolomite Mb Sándorhegy Fm	Góczán and Oravecz-Scheffer (1996a) Budai et al. (1999)

Horne et al. (2002) and Whatley and Boomer (2000). Taxonomical information is provided in the Supplementary Material. Ostracods are represented by both single valves and carapaces. The influence of transportation from shallower to deeper areas needs to be evaluated for the purpose of paleoenvironmental interpretation. The autochthonous or allochthonous nature of ostracod assemblages can be determined using the proportion of carapaces versus isolated valves as well as the demographic structure of populations (e.g., Boomer et al., 2003). In the studied samples, the majority of the specimens are articulated carapaces (98%) that indicates autochthonous 'in situ' preservation with little or no post-mortem transportation. However, the predominance of carapaces was not facies dependent, with similar overall distributions observed in tempestite beds and coquinas and in autochthonous sediments (marls and limestones). The preservation potential of the studied specimens is generally moderate given that most of the valves and carapaces are recrystallized and filled with sediment. The ostracod specimens are represented by older instars or adults in the studied successions. The number of specimens is very variable in the studied samples. Many samples are barren, the maximum specimen number can be ~20,000 in a single sample. Paleoecologically important ostracods are illustrated in Figs. 4–5.

4.1. Main faunal trends

The ostracod assemblages of the Carnian series of the Füred Limestone Formation (Fig. 6) are characterized by the predominance of metacopid healdiids (*Hungarella felsooersensis* and *H. problematica*) and smooth bairdiids (*Bairdia* (*Urobairdia*) *angusta*, *Bairdia balatonica, B. cassiana, B. parvula* and *Isobythocypris* sp.) The proportion of the metacopids forms ca. 35%, the bairdioids ca. 55–65% of the ostracod assemblage. Smooth bairdiocyprids (*Bairdiacypris triassica*) are only minor component of the fauna, their proportion is generally low, ca. 5–10%. The transitional interval between the Füred Limestone and Veszprém Marl formations (Fig. 6) is characterized by poor ostracod assemblages and the rare occurrence of cytherellids (*Bektasia*). The lower marly unit of the Veszprém Marl Formation (Mencshely Marl Member) yields a taxonomically similar albeit very poor ostracod assemblages with a significant decrease in abundance and diversity values compared to the Füred Limestone Formation (Fig. 6). The most common taxa, ca. 45–50%, belong to *Hungarella*, ca. 35–40% to *Bairdia* with both *Bairdiacypris* and *Bektasia* below 15%. The assemblage of the Nosztor Limestone Member slightly differs characterized by the dominance of the smooth bairdiids, ca. 50–70%, the appearance of *Bairdia* (*Urobairdia*) *angusta*, increase of bairdiocypridoids (*Bairdiacypris*), ca. 20%, and the decrease of *Hungarella* down to ca. 20% compared to the fauna of the Mencshely Marl Member (Fig. 6). The upper marl unit of the Veszprém Marl Formation (Csicsó Marl Member) contains an impoverished ostracod assemblage with ca. 30–40% of the specimens belonging to the smooth bairdiids (*Bairdia balatonica* and *B. cassiana*) and ca. 20–25% to the metacopid healdiids (*Hungarella felsooersensis, H. problematica*) with increasing abundance (up to 100%) of platycopids (*Bektasia gibbera, B. ivisensis, B. subcylindrical)* towards the top of the Veszprém Marl Formation (Figs. 6–7).

A significant faunal turnover is recorded in the lower part of the Sándorhegy Formation (Pécsely Member) in the interval of the Julian–Tuvalian transition where almost monogeneric ostracod assemblages are recorded with the predominance of limnocytherid-like *Renngartenella* or limnocytherid *Simeonella* depending on the facies (Fig. 7). In the lowermost part of the Pécsely Member *Renngartenella* dominates in the clayey limestone beds of the Nosztor Valley #2 section (at 9 m, 95%) that is followed by a bituminous laminated limestone unit with marly interlayers and ostracod coquinas. These tempestite beds between the limestone laminae contain an extremely abundant community (up to ~1400 specimens) with the predominance of *Simeonella* (*S. brotzenorum* and *S. reissi*, up to 96% of the assemblage) accompanied by *Kerocythere* (*K. raibliana, K. veghae*) and *Renngartenella sanctaecrucis* (Fig. 7). A thin calcareous marl bed at 121.7 m of the borehole Bht-6 yielded a profusion of ostracods (~ 20,000 specimen) similar in composition to the bituminous laminites in the Nosztor Valley. A single thin limestone horizon at 12.5 m intercalated with the overlaying lithologically varied bituminous laminites in Nosztor Valley #2 are characterized by the dominance of smooth bairdiids (*B. cassiana* and *Isobythocypris*?, ca. 50%) and limnocytherid *Simeonella* (ca. 40%) with low proportion (ca. 1–8%) of *Kerocythere* and *Renngartenella*. Higher up in the succession, thick-bedded nodular clayey limestone units of the Barnag Member (Nosztor Valley #2) are dominated by *Kerocythere* ca. 67–78% and *Renngartenella* ca. 22–34%.

The upper part of the Tuvalian sections (Fig. 7, Nosztor Valley #2, Bat-2) contains rich and diverse ostracod assemblages with the dominance of the platycopid *Bektasia* (*B. gibbera, B. ivisensis, B. subcylindrica*, ca. 60–90%). Ornate bairdiids (ca. 5–15%) such as *Dicerobairdia* (*D. bicornuta, D. latispinosa*), *Hiatobairdia* (*H. subsymmetrica*), *Nodobairdia* (*N. mammilata, N. ventronodosa*) and *Ptychobairdia* (*P. kuepperi*) first appear here (Fig. 7). Likewise, cypridoids (*Pontocypris*? and *Pontocyprella* sp.) and representatives of *Mostlerella nodosa* are recorded in this interval the first time from the TR successions (Fig. 7).

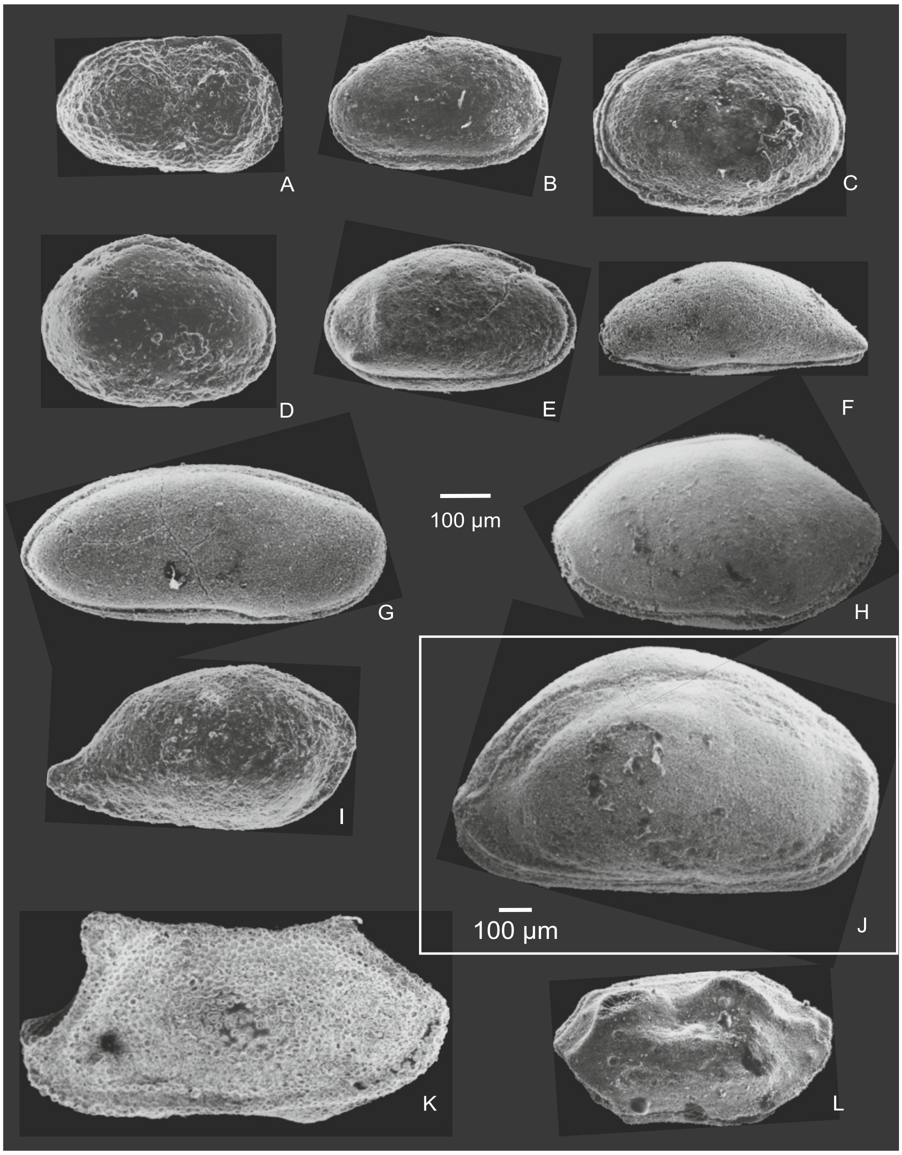

Fig. 4. SEM photoplate illustrating selected ostracod taxa. A) *Bektasia gibbera*, carapace in right view, Bht-6121.7 m. B) *B. subcylindrica*, carapace in right view, NV#2 sample NV-44. C) *B. ivisensis*, carapace in left view, NV#2 sample NV-43. D) *Hungarella problematica*, carapace in left view, Bht-6197.6 m. E) *H. felsooersensis*, carapace in right view, NV#2 sample NV-6. F) *Acratia nostorica*, carapace in left view, NV#2 sample NV-45. G) *Bairdiacypris triassica*, carapace in right view, NV#2 sample NV-2. H) *Bairdia cassiana*, carapace in right view, NV#1 sample 3. I) *B.* (*Urobairdia*) *angusta*, right valve, Met-1 56.8 m. J) *Bairdia balatonica*, carapace in right view, NV#1 sample 2. K) *Dicerobairdia latispinosa*, carapace in right view, Bat-2 64.5 m. L) *D. bicornuta*, carapace in right view, NV#2 sample NV-50.

4.2. NMDS (Non-metric multidimensional scaling)

The NMDS plot (Fig. 8) demonstrates that the ostracod samples in the TR are very variable in terms of composition. The ordination shows that Ladinian and Carnian pre-CPE assemblages from the Füred Limestone Formation have high axis 1 values and are dominated by healdiids (*Hungarella*) and smooth bairdiids (*Bairdia*, *Urobairdia*) and *Bairdiacypris* (Ladinian data for comparison from Litér, Kádárta, Katrabóca II and Felsőörs sections from the Balaton Highland from Monostori and Tóth, 2013 and Karádi et al., 2022, Supplementary Table S3). These taxa are shared with the Ladinian assemblages, yet a significant difference is established by the lack of Ladinian deep marine cytheroid taxa e.g., *Nagyella*, beecherellid *Acanthoscapha* and cypridoid *Praemacrocypris* in the Carnian. Ostracod faunas from the early CPE interval (Mencshely Marl Member) are taxonomically impoverished compared to pre-CPE assemblages with lower axis 1 values consisting mainly of *Hungarella* and/or smooth bairdiids. Samples from the Csicsó Marl Member and Sándorhegy Formation are separated in three groups by the NMDS. Late Julian and Tuvalian samples with periplatfrom ornate bairdiid taxa (e.g., *Nodobairdia, Dicerobairdia* and *Hiatobairdia*) are grouped together and have relatively low axis 1 and axis 2 values. *Bektasia* is characteristic for both samples in the Csicsó Marl Member and Sándorhegy Formation with similar axis 1 position to ornate bairdiids but much higher axis 2 values. Samples with *Renngartenella, Simeonella* and *Kerocythere* score the lowest axis 1 and varied axis 2 values in the NMDS plot indicating that they considerably differ from periplatform or early CPE, early Carnian and Ladinian assemblages.

5. Discussion

5.1. Late Ladinian–Carnian ostracod assemblages of the TR and their implications for depositional environment

The Ladinian–Carnian ostracod faunas recorded the biotic consequences of global climatic trends (CPE) simultaneously with regional-local sea level variations and changes in depositional setting. The TR

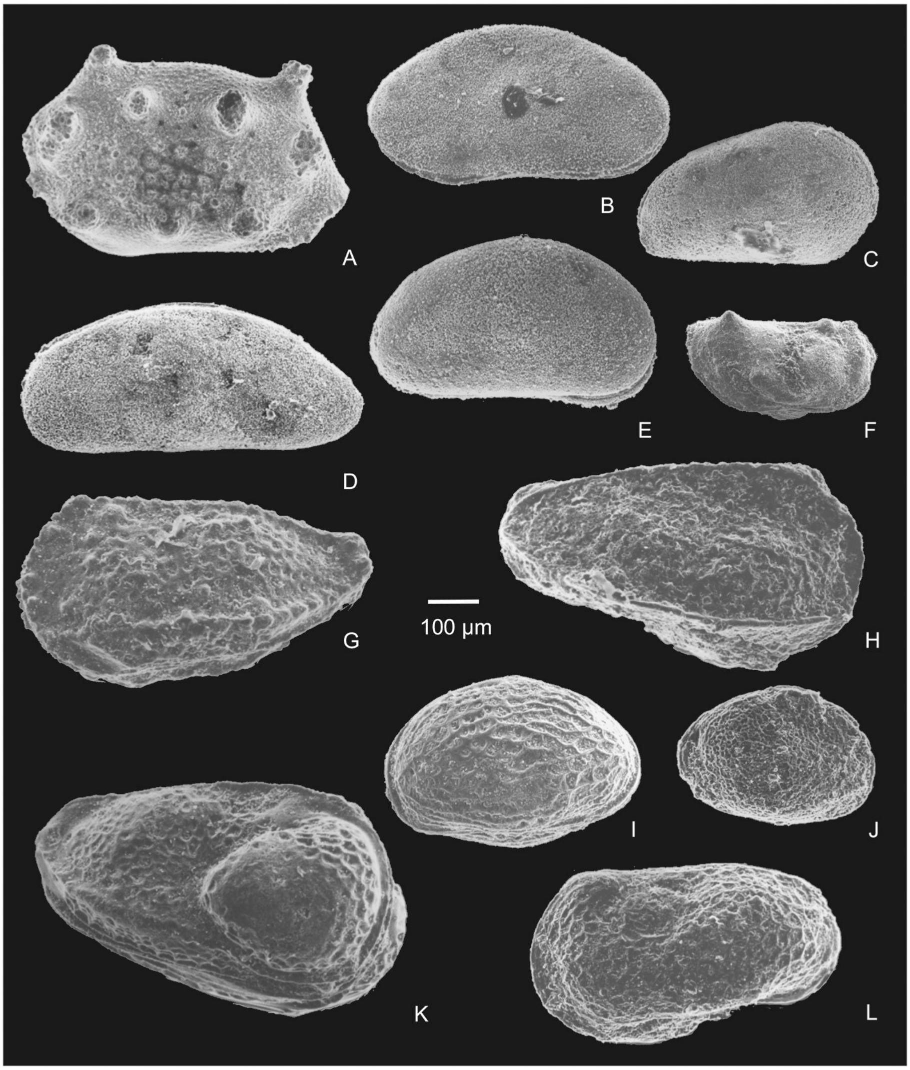

Fig. 5. SEM photoplate illustrating selected ostracod taxa. A) *Nodobairdia mammilata*, carapace in left view, Bat-2 64 m. B) *Bythocypris* sp., carapace in left view, NV#2 sample NV-2. C) *Spinocypris nostorica*, carapace in right view, NV#2 sample NV-45. D) *Pontocypris* sp., carapace in left view, NV#2 sample NV-45. E) *Pontocyprella* sp., carapace in right view, NV#2 sample NV-45. F) *Mostlerella nodosa*, carapace in right view, NV#2 sample NV-45. G) *Kerocythere raibliana*, carapace in left view, NV#2 sample NV-23. H) *K.* cf. *reticulata*, carapace in right view, Bht-6121.7 m. I) *Simeonella brotzenorum*, carapace in left view, NV#2 sample NV-11. J) *S. reissi,* carapace in right view, Bht-6121.7 m. K) *Kerocythere veghae*, carapace in right view, NV#2 sample NV-20. L) *Renngartenella sanctaecrucis*, carapace in left view, Bht-6121.7 m.

was in a more distal marine setting compared to the Dolomites and Julian Alps (Fig. 1B) thus the potential mixture of deep and shallow marine periplatform assemblages is to be expected. Overall, the ostracod faunas record a transition from deep marine neritic assemblages in the Ladinian–early Carnian to shallow marine periplatform associations in the Tuvalian (late Carnian) due to the infilling of the intraplatform basins by mixed clastic-carbonate sedimentary packages as a consequence of enhanced detrital input during the CPE and progradation of carbonate platforms.

5.1.1. Ladinian–early Carnian ostracod communities pre-CPE

Ladinian benthic ostracod faunas of the TR are dominated by deep marine to open shelf taxa represented by smooth bairdioids and bairdiocyprids (proportion of 25–70%), smooth healdioid *Hungarella* (15–50%) and the nektobenthic opportunistic polycopids (~15%) that lived in oligotrophic starved deep marine basin environments (Monostori and Tóth, 2013; Karádi et al., 2022). These open marine habitats (water depth > 200 m) hosted also unique deep-sea elements such as the bizarre spiny tricorninid *Nagyella*, beecherellid *Acanthoscapha* and cypridoid *Praemacrocypris* taxa that share modern analogies with ostracod assemblages living under the thermocline in modern oceans (Kozur, 1972, 1991).

The general composition of the earliest Carnian faunas recovered from the Füred Limestone Formation (Met-1, Nosztor Valley #1 section, Csukrét Ravine) with the predominance of healdiids and smooth bairdiids is similar to the Ladinian assemblages, however the bairdiocypridaceans became subordinate and nektobenthic polycopids and deep marine ostracods finally disappeared (Fig. 9A). The absence of deep-sea species but common presence of ornate bairdiids and cytheroids and that of smooth bairdiids such as *Bairdia, Bairdia* (*Urobairdia*)*, Bairdiacypris* indicate fully marine neritic waters in outer shelf or slope environment (e.g., Lethiers and Raymond, 1991; Forel et al., 2018). The change in the composition of the ostracod fauna suggests shallowing of the basin due to the beginning of the infilling in the Carnian intraplatform areas (e.g., Haas et al., 2012). The open marine character of the depositional setting in the lower part of the Füred Limestone Formation is further corroborated by its pelagic fossil assemblage including "flat clams", stemless microcrinoids (Roveacrinidae) and ammonoids (Góczán et al., 1991). The sessile encrusting *Tolypammina* and the infaunal *Pseudonodosaria* dominated benthic foraminiferal assemblages suggest the increase of

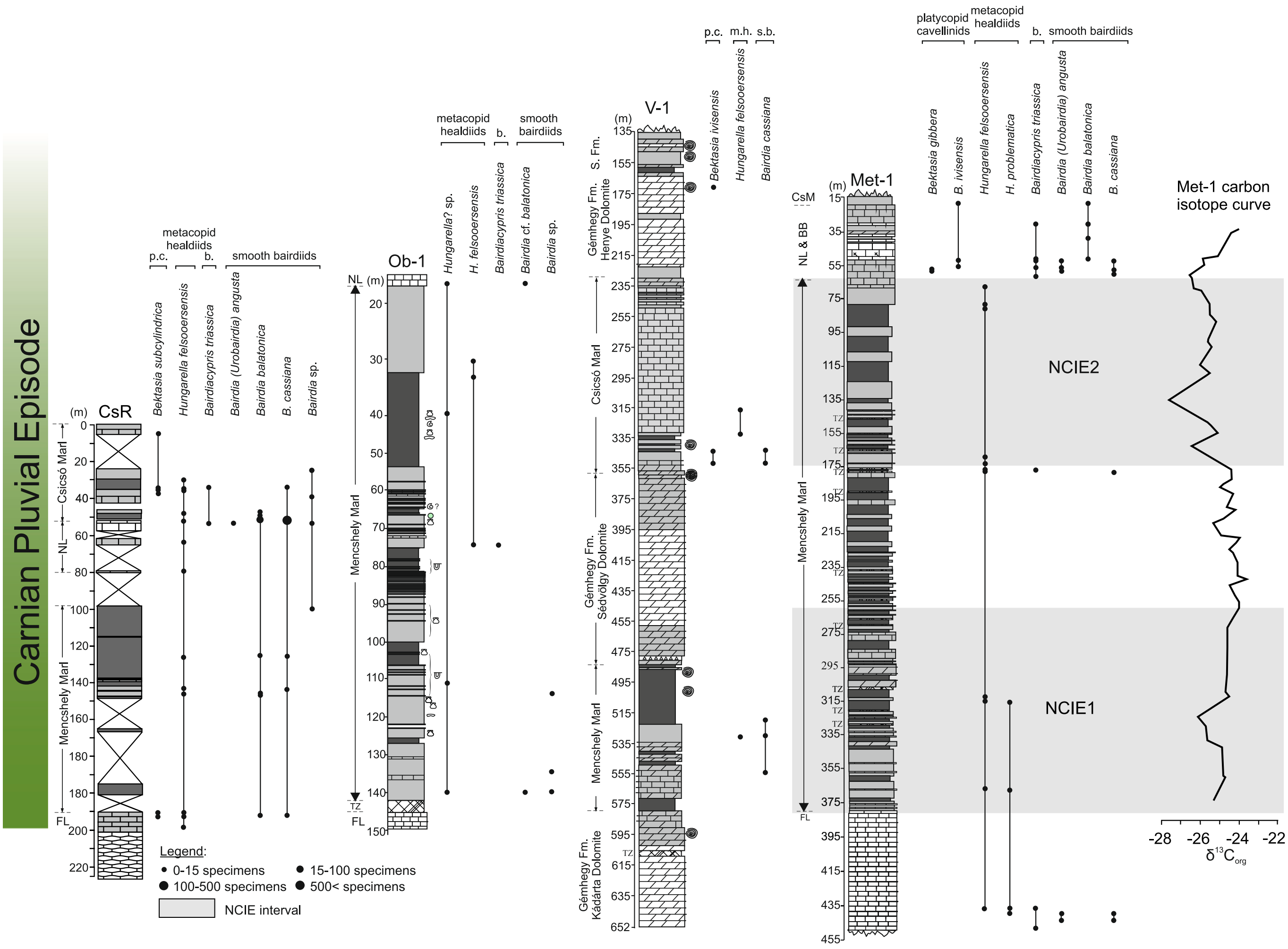

Fig. 6. Distribution of the identified ostracod taxa in the successions of the Csukrét Ravine (CsR) outcrop, Ob-1, Met-1 and V-1 wells. In Met-1 positions of NCIE-1 and NCIE-2 by Dal Corso et al. (2018) are indicated.

incoming detrital and organic flux in the starved basin of the TR (Rodríguez-Martínez et al., 2011). While the ostracods from the TR retained their neritic open marine character in the early Carnian, time-equivalent assemblages from the marls of the lower beds of the San Cassiano Formation in the Dolomites (Pralongia, Pedraces and Stuores-Wiesen sections, southern Tyrol, see Kristan-Tollmann, 1970; Urlichs and Oertli, 1971; Kristan-Tollmann, 1978) and in the Northern Calcareous Alps (NCA, Seelandalpe and Segen-Gottes Schacht section, Kollmann, 1960, 1963) contain mainly shallow water forms such as the ornate bairdiids *Ceratobairdia, Hiatobairdia, Nodobairdia* and *Mirabairdia* that indicate the proximity of shallow marine platform environments with well-agitated bottom waters (Urlichs, 1972).

5.1.2. Onset of the CPE (early Julian 2)

The initial phase of the CPE and the beginning of terrigenous influx is represented by the uppermost calcareous marl and clayey limestone beds of the Füred Limestone Formation transitioning into the Veszprém Marl Formation. These layers provided poor ostracod assemblages with mainly *Hungarella* and smooth bairdiids that are similar to the pre-CPE association in terms of faunal composition albeit with a severe drop in abundance values (Fig. 9B). The low number of the bairdiids and the appearance of the cytherellids (*Bektasia*) suggest a shallowing trend (Kristan-Tollmann and Hamedani, 1973; Forel et al., 2018). Among the benthic foraminifers, the specialized aragonitic trochospiral hyaline *Duostomina* is recorded first at the onset of the CPE in the successions of the TR (Kristan-Tollmann, 1960; Góczán et al., 1991). *Duostomina*-dominated foraminifer assemblages are associated with estuarine or embayment-type assemblages in the Triassic and siliciclastic facies (e.g., Apthorpe, 2003) and their appearance during the CPE is likely linked to the onset of terrestrial influx and stressed environment.

5.1.3. Ostracod assemblages during the main phase of the CPE (clastic pulse maximum, Julian 2)

The Julian 2 marly sedimentary packages of the Veszprém Marl Formation represent the maximum of clastic input in the Transdanubian Range during the CPE (Haas et al., 2012; Baranyi et al., 2019). Ostracod assemblages of the lower part of the marl sequence (Mencshely Marl Member) are characterized by the representatives of *Hungarella, Bektasia*, smooth bairdiids and bairdicypridaceans, with lower diversity compared to the fauna of the Füred Limestone Formation indicating stressed environment on the sea floor that is also corroborated by the predominance of eurytopic benthic foraminifers, *Duostomina*. The metacopid *Hungarella* formed monogeneric assemblages in the Met-1 well (at 325.9 to 260 m and 150 to 69 m) simultaneously with the Julian 2 NCIEs (Dal Corso et al., 2018), the increase of hygrophytic floral elements in the palynological data (Baranyi et al., 2019), and enhanced weathering rates based on clay minerals (Rostási et al., 2011; Baranyi et al., 2019). The monogeneric assemblages of metacopid *Hungarella* can be associated with the oxygen-poor conditions and there is some pyrite in the studied strata suggesting oxygen deficiency on the seafloor. Monospecific metacopid assemblages in Lower and Middle Liassic sites worldwide can be linked to extensive pyrite, is also a probable signal of

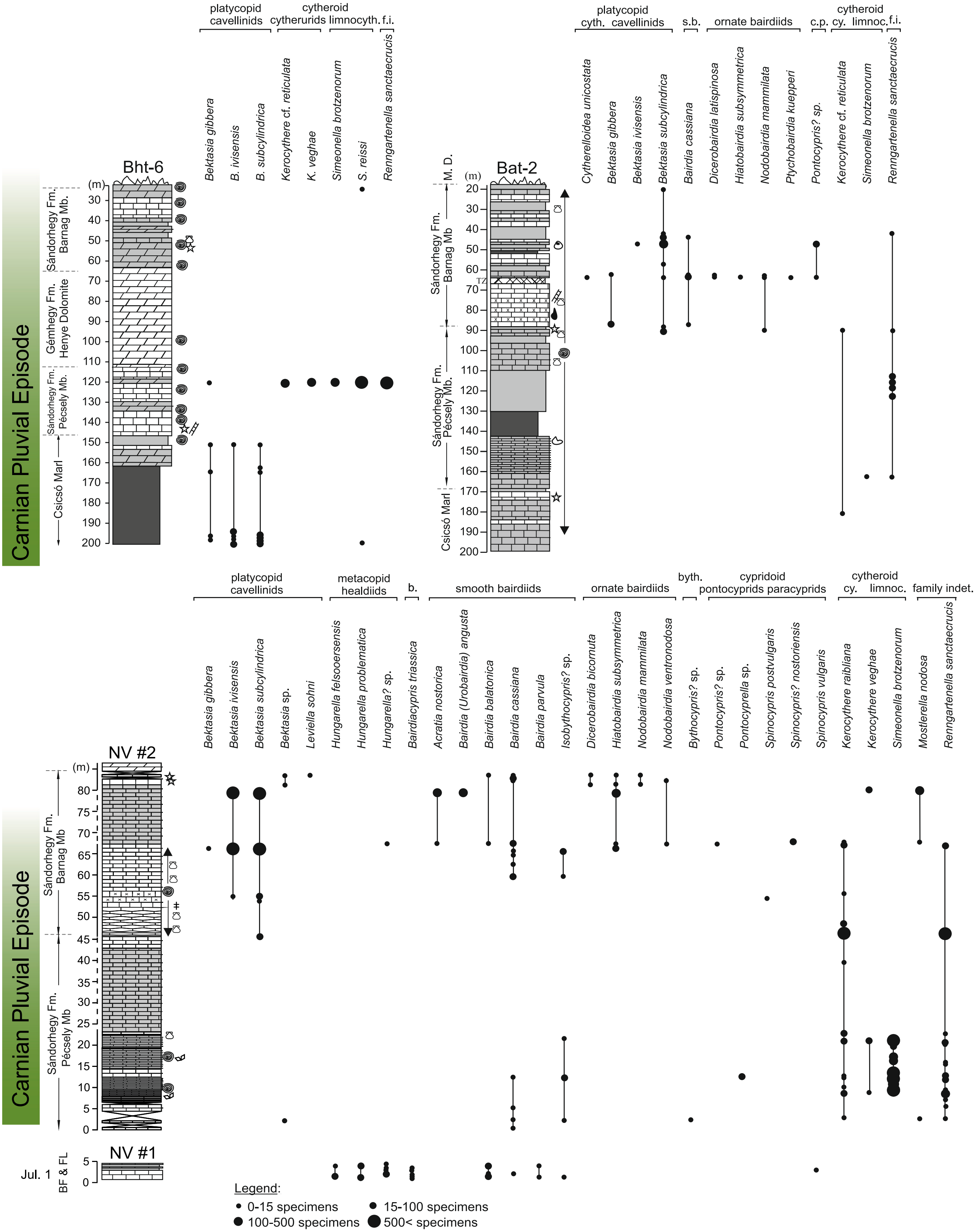

Fig. 7. Distribution of the identified ostracod taxa in the successions of Nosztor Valley #2 outcrop, Bht-6, and Bat-2 wells.

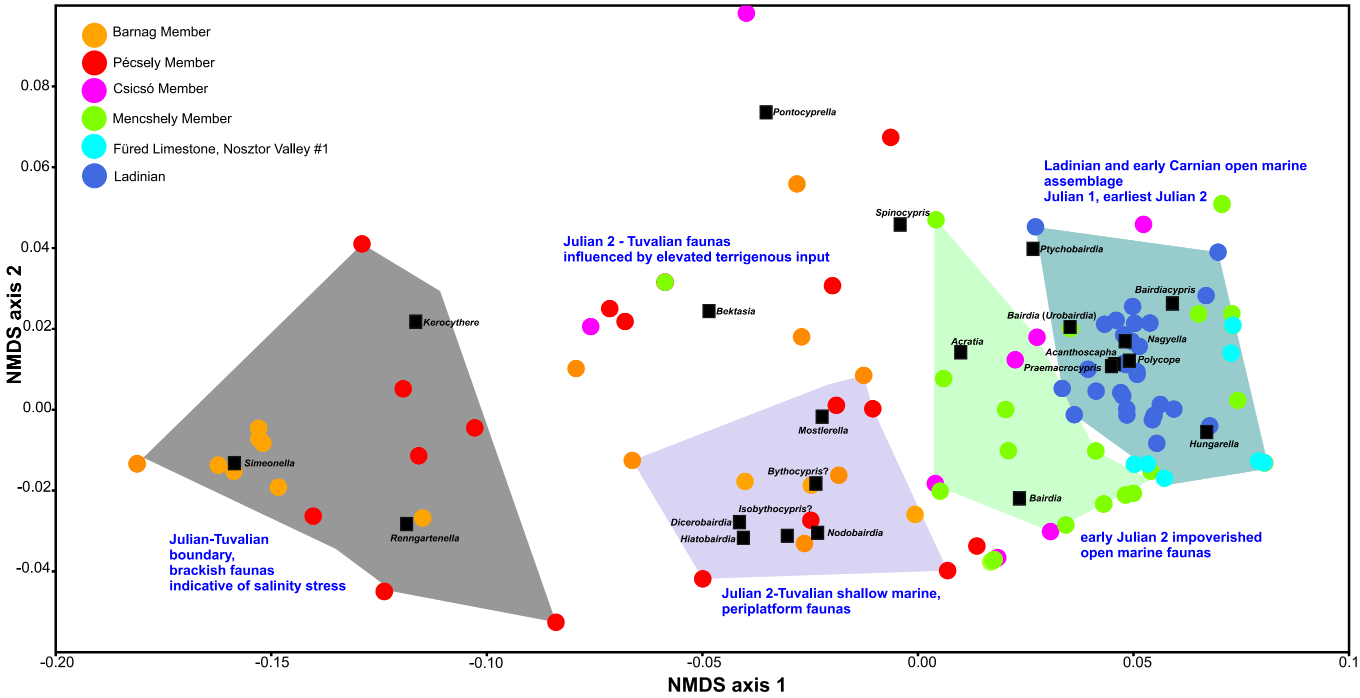

Fig. 8. NMDS biplot of Ladinian–Carnian ostracod samples from the TR, showing samples (circles in colour) together with genera (black squares). Input data from Supplementary Table S2. Ladinian data for comparison from Monostori and Tóth (2013) and Karádi et al. (2022). See Supplementary Table S3.

oxygen depletion (Whatley, 1991).

The recorded C-isotope excursions were related to multiple injections of the ^{13}C depleted carbon into the ocean-atmosphere, shifts in climate, and acceleration of the hydrological cycle with elevated terrestrial influx that only few ostracod taxa could tolerate. Between the NCIEs (~200 to 170 m) smooth bairdiids and bairdicypridaceans (*Bairdia cassiana, Bairdicypris triassica*) re-appeared which are characteristic in pre-CPE open marine environments and indicate temporal amelioration of environmental conditions for ostracod fauna. Similarly, the ostracod assemblage of the Nosztor Limestone Member is more diverse and consists mainly of smooth bairdioid elements with a rich pelagic fossil association including microcrinoids, holothuroids, radiolarians, and conodonts. The deposition of this carbonate unit overlying the Mencshely Marl Member indicates a platform progradation episode due to sea-level highstand and likely the decrease of siliciclastic influx (Haas and Budai, 1999).

During the late Julian 2 (Fig. 9C), the representatives of cavellinid *Bektasia* replace healdiid *Hungarella* in the ostracod assemblages of Csicsó Marl Member (V-1 and Bht-6 wells) indicating shallowing of the depositional setting and stressed environment due to the incoming siliciclastic material and possible salinity variations caused by freshwater influx (Kristan-Tollmann and Hamedani, 1973). The predominance of this opportunistic ostracod taxon and the low abundance of other carbonate secreting organisms suggest extreme environmental conditions and the crisis of carbonate factories in the period of the formation of the Csicsó Marl Member (Haas et al., 2012).

5.1.4. *Ostracod assemblages across the Julian–Tuvalian boundary*

In the interval with the Julian–Tuvalian boundary, the ostracod faunas underwent a significant turnover with the appearance of unique, almost monogeneric assemblages dominated by *Renngartenella-Simeonella-Kerocythere* opposed to the smooth bairdioids and healdiids typical of older Carnian beds. This ostracod community is linked to clayey limestone beds as well as marly tempestite beds with ostracod coquinas intercalated in the bituminous limestone laminites of the Pécsely Member (Sándorhegy Formation) (Fig. 9D). The bituminous limestone laminae and beds (0.1–2.0 m in thickness) in the TR (Nosztor Valley #2 and Bat-2 core) were deposited in restricted, stagnant basin with water stratification (Nagy, 1999; Nagy and Csillag, 2002). These bituminous limestone beds are barren of any microfauna in contrast to the marly interlayers and tempestite beds which contain ostracod coquinas with thousands of specimens of the limnocytherid *Simeonella*. By contrast, the thicker clayey limestone beds of the Nosztor Valley #2 section with limnocytherid-like *Renngartenella* and sculptured cytherurid *Kerocythere* dominated assemblages were densely packed with autochthonous bivalve remains and intensive bioturbation that indicates deposition in shallow basin environment beneath the normal wave base with low energy and well-oxygenated conditions (Nagy, 1999). The appearance of cytherurids is likely related to the shallowing of the marine basin as the Mesozoic representatives of this group are restricted to shallow marine shelf habitats with clear and well-oxygenated water (Ballent and Whatley, 2000, 2009). The majority of recent cytherurids e.g., from the Brazilian continental shelf prefer inhabiting a fine-grained sandy substrate in offshore environment (water depth between 50 and 100 m; Coimbra et al., 1999; Feijo Ramos et al., 1999). Their Triassic representatives e.g., *Kerocythere raibliana* and *K. veghae* were most likely also soft bottom-dwellers in shallow marine environments that benefitted from the shallowing trends in the TR during the latest Julian and early Tuvalian (Kozur, 1972).

The *Renngartenella-Simeonella* ostracod assemblage seems to be a marker horizon across the Western Neotethys in the late Julian 2 to early Tuvalian times that has been recorded from the Dolomites, Julian Alps, Northern Calcareous Alps (NCA) as well as from the northern Gondwana shelf (see references below). Despite the widespread occurrence of the assemblage, the environmental and ecological implications of the association are still uncertain. In the TR, the assemblage is generally associated with hypersaline bottom water, restricted basin and lowstand facies and tempestites (Nagy, 1999). By contrast, De Zanche et al. (2000) interpreted these ostracod bearing layers in the Julian Alps as highstand system tract (HST) deposits with shallowing environment and decreased salinity.

This ostracod assemblage was recorded in finely laminated organic-rich bituminous limestones of the Heiligkreuz Formation in the Heiligkreuz Hospiz/Santa Croce outcrop in the Dolomites together with the

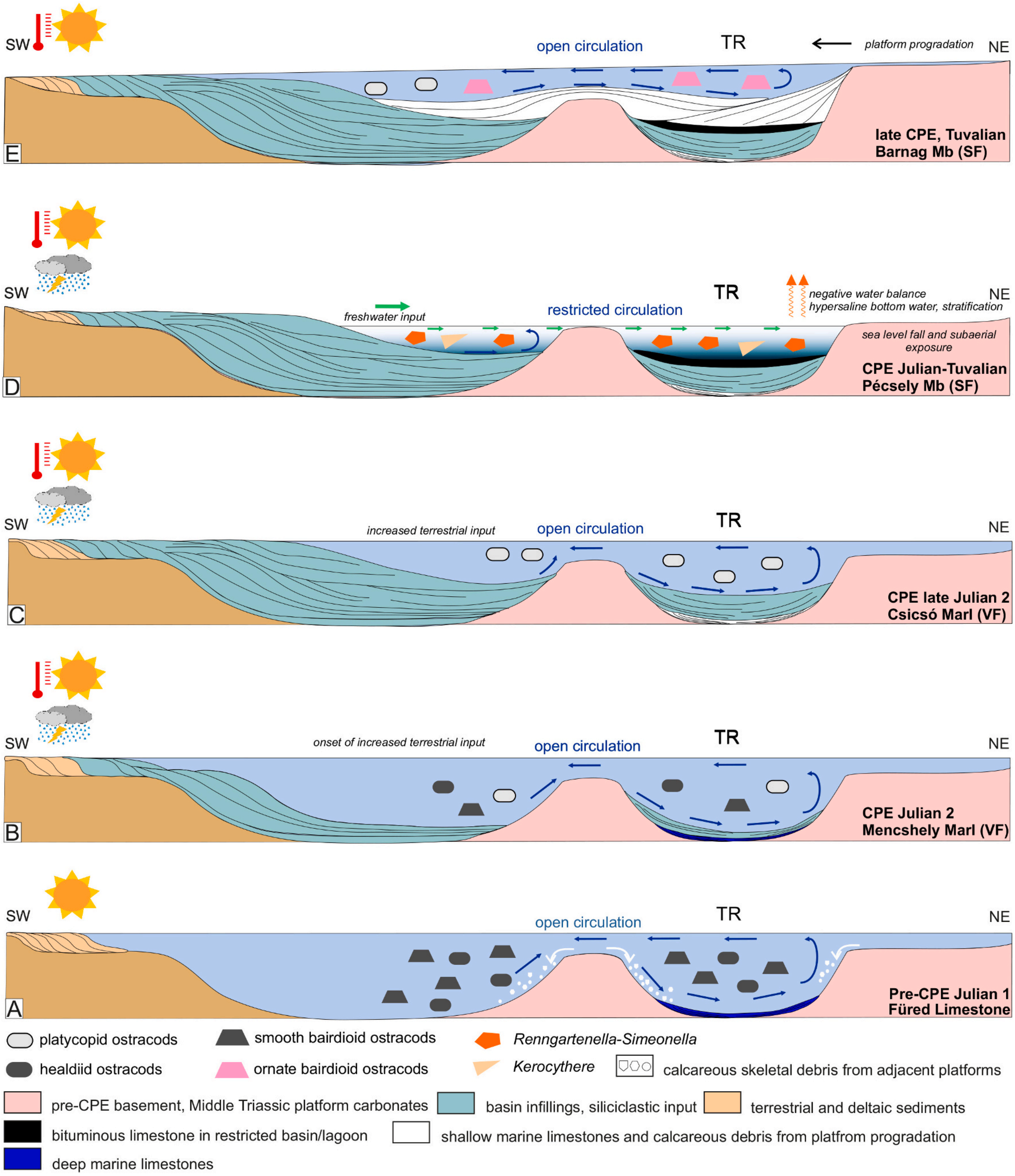

Fig. 9. Conceptual model of paleoenvironmental changes and their ostracod response during the Carnian Pluvial Episode in the TR. Sedimentological model is based on Nagy (1999) and Pecorari et al. (2023). A) Pre-CPE Carnian ostracod assemblages with mainly open marine taxa, healdiids and smooth bairdiids. B) Onset of the CPE and intensification of terrigenous input, decreased ostracod abundance and appearance of platycopids. C) High terrigenous input and stressed community with platycopid ostracods. D) Julian–Tuvalian boundary ostracod turnover with a unique low diversity ostracod assemblage with *Renngartenella*, *Simeonella*, and *Kerocythere*. E) Return of stable marine conditions with shallowing, and appearance of ornate bairdiids.

bivalve *Anaplophora münsteri* in a typical brackish faunal association (Keim et al., 2001). The exact timing (basal Julian 2–Tuvalian 1) of this brackish-water facies is uncertain, but the reconstructed environment is very similar to the depositional model of the Nosztor Valley #2 section in the TR with restricted oxygen deficient conditions, fluctuating salinity, possibly hypersaline bottom waters, and evidence for microbial (cyanobacterial) mats (Keim et al., 2001). A similar ostracod fauna was found in the upper grey to dark-grey thin-bedded micritic limestone and marly beds in the upper part of the Julian 2–Tuvalian Tor Formation of the Cave del Predil area in the Julian Alps (Lieberman, 1979). The stratigraphical position of the *Renngartenella* association in the Belca section (Forel et al., 2020) from the Raibl Beds′ in the Karavanke Mts (Slovenia) is better defined based on the monospecific *Nicoraella*? *budaensis* conodont fauna that is characteristic for the late Julian 2 to early Tuvalian 1 (Kozur and Mock, 1991; Rigo et al., 2018). The occurrence of this ostracod assemblage correlates well with that in the upper Tor Formation in Julian Alps spanning the late Julian 2–early Tuvalian interval (De Zanche et al., 2000; Kolar-Jurkovšek et al., 2005). At Belca, ostracod assemblages are dominated equally by *Renngartenella* and the cytherellid *Issacharella* but *Simeonella* was very rare there. Nevertheless, the high dominance of *Renngartenella* was associated there also with freshwater input and low salinity levels (Forel et al., 2020). In the Gerecse Hills represented by the Zsámbék-14 well ca. 100 km NE to the Balaton Highlands, coeval Carnian beds yielded a very similar ostracod assemblage to that of Belca with mainly *Issacharella, Judahella,* and *Grammicythere* (Kristan-Tollmann et al., 1991). These taxa are entirely absent in the Balaton Highland suggesting different environmental conditions and independent basin evolution.

In the NCA, the *Kerocythere-Renngartenella-Simeonella* association is present in the shallow marine series of the "Middle and Upper Marl-Sandstone-Limestone Members" of the Opponitz Formation close to the Julian–Tuvalian boundary (Stiegengraben section near Lunz am See, Kristan-Tollmann and Hamedani, 1973). Notably, *Bektasia* is more common here in the ostracod assemblage from the Opponitz Formation (Kristan-Tollmann and Hamedani, 1973) compared to the absence of the genus in the same layers from the TR or the Dolomites. The *Renngartenella-Simeonella* association can be traced southwards on the Western Neotethyan shelf as well. The same fauna can be found in Tuvalian marly clays and marly limestone series with tempestite beds of the Mufara Formation in Monte Gambanera (Sicily) (Crasquin et al., 2020).

The species *Simeonella brotzenorum* was originally described by Sohn (1968) from lower Carnian (Julian) beds of Har Gevanim, the type section of the Carnian (Julian) Saharonim Formation in Makthesh Ramon, Israel. Similar to the Nosztor Valley #2 section, *Simeonella* formed coquinas with thousands of specimens in marl beds intercalated into the sandy dolomite layers (Sohn, 1968; Korngreen and Benjamini, 2010; Bialik et al., 2012). Besides the Saharonim Formation, *Simeonella* was also recovered in large numbers from the overlying evaporite-carbonate-clastic complex of the Mohilla Formation in Israel together with *Renngartenella sanctaecrucis* in shallow marine, brackish to hypersaline lagoonal environment (Gerry et al., 1990) belonging to the Julian–Tuvalian interval (Bialik et al., 2012). Consequently, Gerry et al. (1990) connected the assemblage to the apparent Carnian salinity crises represented by the sediments of Mohilla Formation.

Similar faunas not only occurred on northern Gondwana shelf and margins of the Western Neotethys, but also in the Germanic and Polish basins. *Simeonella* (mainly *S. brotzenorum alpina*) occurred in large quantities in the lowermost layers of the Julian 2 Stuttgart Formation (=Schilfsandstein) in both basins (Wienholz and Kozur, 1970; Bunza and Kozur, 1971; Styk, 1982; Kozur and Bachmann, 2010) which were deposited in a shallow brackish water during the CPE under monsoonal climatic conditions with seasonal humid climate and droughts.

5.1.5. *Ostracod communities of the late CPE phase (Tuvalian)*

A sea-level rise opened the basin in the early Tuvalian and the subsequent highstand led to the carbonate platform progradation reconstructed by the shallowing upward trend (basin-slope-terrace) in the TR (Nagy, 1999; Nagy and Csillag, 2002). The higher diversity of the ostracod faunas of the Barnag Member (Sándorhegy Formation) in the Nosztor Valley (NV #2) section and Bat-2 core represents the re-establishment of stable open marine but shallower conditions compared to the early Carnian, indicated by the disappearance of *Simeonella* and increased abundance of the cytheroid *Kerocythere.* The co-occurrence of strongly sculptured bairdiids, *Bektasia* and neritic *Acratia* in the ostracod assemblages in the Barnag Member of the TR supported the shallowing trend (Urlichs, 1972; Forel et al., 2018; Crasquin et al., 2020). The diverse association of ornate bairdiids (*Dicerobairdia, Hiatobairdia, Nodobairdia,* and *Ptychobairdia*) indicate proximity to platform areas (Urlichs, 1972; Crasquin et al., 2018) that agrees well with the abundant macroinvertebrate remains from the same horizons (mollusc fragments, brachiopods, and crinoids) and the presence of large oncoids that were deposited in inner platform lagoonal and shallow subtidal environments (Nagy, 1999). The shallowing trend in the basin is further indicated by the predominance of the *Aulotortus-Triadodiscus-Nodosaria* foraminifer association (Góczán and Oravecz-Scheffer, 1996a, 1996b; Chablais et al., 2011), and the presence of small megalodontids (*Neomegalodon carinthiacus*). The proliferation of the genus *Bektasia* in the Nosztori Valley #2 suggests local renewal of detrital or/and freshwater input that was probably of lesser magnitude and thus could not completely eliminate the periplatform ostracod community.

5.2. *Ostracod response to the CPE in the TR — Paleoecological inferences*

Fossil ostracod assemblages of the TR were severely affected during the CPE evidenced by pronounced diversity and abundance variations especially in the marly sediments being in striking contrast with the diverse Middle Triassic (Monostori and Tóth, 2013; Karádi et al., 2022) and Carnian assemblages in the late CPE phase. The main environmental factors which determine the distribution and abundance of marine ostracod communities are water chemistry, salinity, substrate characteristics, temperature, oxygen and nutrient availability, and hydrodynamic conditions (e.g., Boomer and Eisenhauer, 2002; Frenzel and Boomer, 2005). Consequently, the complex environmental perturbation associated with the CPE i.e., global warming (e.g., Trotter et al., 2015; Sun et al., 2016), crisis of microbial carbonate factories (Hornung et al., 2007; Gattolin et al., 2015; Jin et al., 2020; Sun et al., 2020), elevated detrital and nutrient supply from the terrestrial influx (Rostási et al., 2011; Haas et al., 2012; Dal Corso et al., 2015, 2018) changes in water column oxygenation (Sun et al., 2016; Zhang et al., 2022; Tomimatsu et al., 2023) combined with sea level changes (e.g., Haas and Budai, 1999; Nagy, 1999; Pecorari et al., 2023) had a significant impact on the marine invertebrates including ostracods. Open marine taxa characterize the Ladinian and pre-CPE Carnian assemblages indicating oligotrophic deep-sea environments (Monostori and Tóth, 2013; Karádi et al., 2022). Species richness and abundance severely dropped at the onset of the CPE with the arrival of the clastic influx and these assemblages are characterized only by smooth bairdoids and healdiids (*Hungarella*) due to the disappearance of deep-sea taxa. Although they are both stenohaline neritic taxa inhibiting fully marine waters, their ratio is seemingly determined by the degree of siliciclastic influx and the carbonate supply during the CPE. Healdiids form almost monogeneric assemblages correlated to the NCIE 1 and 2 in the early CPE phase with the intensification of terrestrial supply while bairdiids flourished in the more stable intervals when the amount of detrital influx was decreasing e.g., during platform progradation periods (Nosztor Limestone Member). Cavellinids (*Bektasia*) appear at the onset of the CPE and their proportion is increasing in the upper marl unit (Csicsó Marl Member) towards the top of Veszprém Marl Formation simultaneously with the upfilling of intraplatform basins and elevated clastic influx. This taxon indicated shallowing as well as stressed conditions on the seafloor caused by the highest amount of detrital and freshwater influx (see chapter 5.1.3). The affinity to stressed conditions is also evident form the episodic increases of *Bektasia* in the Barnag Member linked to the revival of the clastic input. The shape and limen-like structure (=sulcus) of the carapace in *Bektasia* is very similar to that of extant platycopid ostracods which are well adapted to low oxygenated or oligotrophic conditions because of their filter-feeding strategy contrary to the deposit-feeding podocopids (Whatley, 1990, 1991). Probably, this filtering strategy provided a similar adaptive advantage in the ́murky ́ seawater during the CPE with large amount of detrital material in suspension.

The widespread and most likely simultaneous occurrence of the *Renngartenella sanctaecrucis-Simeonella* assemblage in the late Julian 2–early Tuvalian interval is the most characteristic ostracod event on the western Neotethyan shelf during the CPE. The interpretation of this assemblage is hampered by the unknown taxonomical assignment and ecology of *Renngartenella sanctaecrucis* but likely the occurrence of this assemblage is linked to salinity variations (e.g., Kristan-Tollmann and Hamedani, 1973; Gerry et al., 1990; Monostori, 1994; Keim et al., 2001). Monostori (1994) explained this abundant but low diversity assemblages with hypersaline bottom waters, water column stratification in the TR as a consequence of sea level fall and the development of intrabasinal sills that prohibited the circulation of normal marine waters (Nagy, 1999). The occurrence of *Simeonella* dominated fauna in ostracod coquinas in tempestite layers raises that question that they might represent allochthonous deposition within the Pécsely Member. It is possible that the limnocytherid *Simeonella* was transported with river outflow in times of floods and high-rainfall episodes from proximal brackish environments considering its occurrence in the brackish inland sea habitats of the Schilfsandstein as well (Kozur and Bachmann, 2010; Franz et al., 2019). This widespread distribution and extremely high abundance of *Simeonella* in nearly monogeneric associations are typical in recent brackish water ostracod communities as well (Frenzel and Boomer, 2005). The coeval occurrence of this special assemblage in marginal marine settings of the Western Neotethys also agrees with the rapid distribution of modern brackish water ostracod species in extant marginal marine settings that tend to occur pandemically and are distributed by water currents, drifting algae or storm activity (Boomer and Eisenhauer, 2002; Frenzel and Boomer, 2005).

The morphological similarity to the Middle Triassic *Lutkevichinella* might provide an alternative explanation for the possible in situ occurrence of *Simeonella* in restricted basins during the Carnian. The genus *Lutkevichinella* forms abundant assemblages in Middle Triassic sequences e.g., Germanic and Polish basins deposited under brackish conditions (Kozur, 1968a, 1968b, 1970; Diebel, 1965; Styk, 1982). Monospecific *Lutkevichinella* assemblage were also extracted from the Lower Anisian bituminous laminites of the TR (Iszkahegy Limestone, Szentkereszthegy section at Felsőörs, TR) where sedimentological features suggested deposition in a restricted lagoon with stratified water column (Tóth and Monostori, 2015). In the Anisian, the stratification was linked to freshwater influx and a short-lived humid climate period interrupting the early Anisian arid-semiarid climate (e.g., Kustatscher et al., 2010; Stefani et al., 2010). A similar explanation is easily conceivable for the CPE where the incoming freshwater and saline-hypersaline seawater was only partly mixing or not at all, leading to density stratification in the water column. A freshwater lense on the surface combined with the infilling (shallowing) of the basin and the Julian 2 sea level fall (Nagy, 1999) likely resulted in stagnant circulation in restricted basins that promoted the colonization of this special ostracod fauna that might have been resedimented due to tropical storms or hyperpycnal flows resulting in the formation of ostracod coquinas.

6. Conclusions

Ostracod assemblages of the TR record a major environmental shift through the Carnian. Changes in faunal composition reflect shallowing of the basin associated with the infilling of the Carnian intraplatform basins as well as the climatic perturbations during the Carnian. At the onset of the CPE in the early Julian 2, a diversity fall can be observed in the ostracod fauna due to the elevated clastic input. The ratio of smooth bairdioids and healdiids was controlled by the amount of clastic influx and the carbonate supply. In the late Julian 2, the predominance of cavellinid *Bektasia* and disappearance of baiirdiids suggest highly stressed environment and the crisis of carbonate factories likely coinciding with maximum clastic input, expansion of deltaic habitats and humid floras on land.

The Julian–Tuvalian boundary is marked by the most prominent faunal turnover during the CPE and is characterized by a unique low diversity ostracod assemblage dominated by brackish water taxa *Simeonella* and *Renngartanella* that tolerated subnormal marine as well as hypersaline waters. This assemblage occurs more or less simultaneously along the western and southern Neotethys shelf similar to the rapid colonization capabilities of modern brackish water ostracod species. In the TR they are linked to freshwater influence and density stratification in a restricted lagoon/basin that came into being after a Julian 2 sea level fall and infilling of the basins where ostracod shell rich sediments were received from proximal areas or in situ reworked during tropical storms or in periods of high-rainfall with enhanced river outflow.

During the early Tuvalian, diversification of the ostracod faunas and increase of ornate bairdiids signaled the return of open-marine conditions and the recovering of the shallow-marine carbonate factories linked to a global sea level rise followed by highstand platform progradation before the termination of the CPE in the Tuvalian 2.

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CRediT authorship contribution statement

Emőke Tóth: Writing – original draft, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Viktória Baranyi:** Writing – review & editing, Conceptualization. **Viktor Karádi:** Writing – review & editing, Conceptualization. **Xin Jin:** Writing – review & editing. **Tamás Budai:** Writing – review & editing.

Declaration of competing interest

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.

Data availability

All ostracod specimens are curated at the Department of Palaeontology of the Eötvös Loránd University in Budapest. Supplementary Material to this article can be found online.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.palaeo.2024.112379.

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