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Local versus global effects on changes of fossil diversity: paleoenvironmental interpretation of Triassic faunas of the Balaton Highland (Hungary)

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The formations of the Balaton Highland provide a high-resolution record of various fossil groups (ammonoids, bivalves, brachiopods) from the Early Triassic to the Carnian, with remarkable changes in taxonomic diversity. The local data differ considerably from the gradually increasing global diversity trends of the respective fossil groups. Ammonoids are rare in the Early Triassic; during the Anisian they reach a diversity maximum and remain rather diverse until the Carnian. This is connected to the considerable deepening of the sedimentary basin in the Middle Triassic. The benthic fossil groups show almost inverse local trends. In the Early Triassic, the proliferation of bivalves largely follows the transgressive pulses in the shallow marine setting; brachiopods are represented solely by *Lingula* specimens. Both the bivalve and the brachiopod diversity culminate in the middle Anisian what is interpreted in terms of extensional tectonic movements: the rocky escarpments of the disintegrated carbonate platforms provided favorable biotopes for sessile benthic organisms. The benthic diversities decreased significantly in the rest of Middle Triassic, which is due to the significant deepening of the local basin floor. The benthic groups reached maximum diversity in the Carnian. This is attributed partly to the filling up and shallowing of the local basin, partly to redeposition in the course of platform progradations, carrying rich fossil shell material from the neighboring shallow marine environments to the basin. Simultaneously, the sudden increase of the humidity ("Carnian pluvial event") created extensive river systems in the European continent; the increasing supply of organic matter was favorable for the benthos in the marine environments.

Key words: Triassic, diversity, ammonoids, bivalves, brachiopods, Balaton Highland, Hungary

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Introduction

The Balaton Highland is among the most important reference areas of the Tethyan Triassic stratigraphy (see Tozer 1984). Although this hilly terrain lacks the spectacular exposures and the Triassic sequences are far from being well-exposed, scattered and transient outcrops have yielded plenty of fossils, systematically collected over the past 150 years. Many ammonoid and brachiopod species were portrayed in the important pioneering monograph by Böckh (1872, 1873); thereafter the ammonoids were profusely illustrated by Mojsisovics (1882). The greatest contribution to the knowledge of the Triassic faunas of the Balaton Highland was made by the ambitious international project entitled "Wissenschaftliche Erforschung des Balatonsees" (Scientific Investigation of Lake Balaton) directed by L. Lóczy Sr. at the turn to the twentieth century. The product was a series of papers and monographs which provided records of numerous fossil groups, including microfossils. Special emphasis was given to the ammonoids (Diener, 1899, 1900; Arthaber 1903; Frech 1903), bivalves (Bittner 1901; Frech 1904, 1907; Kittl 1912), gastropods (Kittl 1900), and brachiopods (Bittner 1900; Frech 1904, 1907). The original fossil material described in the above-listed works has been deposited and is accessible in the collections of the Geological Institute of Hungary (MÁFI). The items of this repository were comprehensively enumerated by Szabó (1972).

In the last decades, partly in connection with the detailed geologic mapping project by the Geological Institute of Hungary, excavations and voluminous collections have been made in many important stratigraphic sections in the Balaton Highland. The Lower Triassic faunas, in comparison to those of the Southern Alps, were documented in detail by Broglio Loriga et al. (1990). After publishing some preliminary results (Vörös 1987, 1993; Vörös and Pálfy 1989), the Anisian to Carnian ammonoid record was presented in a stratigraphic context (Vörös 1998). The results have been integrated into a comprehensive volume on the geologic mapping (Budai et al. 1999). One part of the results contributed to the resurgence of the "Anisian/Ladinian boundary problem" (Vörös et al. 1996, 2003) where the Felsőörs section was a formal candidate for the Ladinian GSSP. Recently, the Middle Triassic Pelsonian Substage was re-evaluated and redefined (Vörös 2003a) and the fossil flora and fauna of the substage were documented in detailed systematic descriptions by Piros (2003, dasycladaceans), Vörös (2003b, ammonoids), Szente and Vörös (2003, bivalves), Pálfy (2003, brachiopods) and Kovács (2003, conodonts).

In summary, from the Balaton Highland we have a rather well-documented record of diverse fossil groups from the Early Triassic to the Carnian. Younger Triassic formations, e.g. the Carnian–Norian Main Dolomite (Fődolomit Formation) and the Norian-Rhaetian Dachstein Limestone locally abound in megalodontids, and the Rhaetian Kössen Formation also yielded a rich bivalve fauna. Since these occurrences lie mostly in the Bakony Mountains, outside the Balaton Highland, they are beyond the scope of the present paper.

A review of the Early Triassic to Carnian fossil documentation of the Balaton Highland reveals that three important fossil groups (ammonoids, bivalves and brachiopods) provide a more or less continuous record, with occurrences in almost all stages. It is also remarkable that their abundance and diversity (species richness) generally increases in time and the peak values are connected to specific stratigraphic levels. The general increase of diversity is consistent with the global change of the biosphere: the Triassic was a time of recovery after the end-Permian biotic catastrophe, when most fossil groups progressively diversified. On the other hand, the discrete episodes with diversity maxima (and minima) call upon local or regional paleoenvironmental causes, which override the global trends.

Data of fossil occurrences in stratigraphic units

The sources of data on ammonoid, bivalve and brachiopod diversity (species richness) of particular Triassic stratigraphic levels in the Balaton Highland, outlined in the introduction, are shown in Table 1, and will be detailed below. The Triassic (Induan to Carnian) formations of the Balaton Highland and the diversity values of ammonoids, bivalves and brachiopods in particular, in the selected stratigraphic levels, are shown in Fig. 1. The short descriptions of the formations are based mainly on the works by Budai and Haas (1997), Haas and Budai (1999, 2004).

1. Arács Formation (Induan). The 120 m-thick, mostly marine marl of this formation contains subordinate dolomitic and limestone interlayers and passes laterally (westward) into the supratidal Köveskál Dolomite. The locally abundant fossils (8 bivalve and 2 brachiopod taxa) of the Arács Marl were listed and figured by Broglio Loriga et al. (1990). Remarkably, the brachiopods are represented by two species of *Lingula*.

2. Zánka Sandstone Member (Hidegkút Formation, Lower Olenekian). The lower, 50 m-thick siliciclastic member of the Hidegkút Formation was previously called "Hidegkút Sandstone Member" and was attributed to the Upper Induan by Broglio Loriga et al. (1990). Recently, Budai and Haas (1997), Haas and Budai (1999, 2004) used the name Zánka Sandstone and assigned this member to the Lower Olenekian. This shallow marine, thinly laminated sandstone with limestone interlayers yielded only bivalves: 11 taxa were listed by Broglio Loriga et al. (1990). The upper member of the Hidegkút Formation, the mostly supratidal Hidegkút Dolomite, did not yield any fossils.

3. Csopak Formation (Upper Olenekian). This 200 m-thick, marl-dominated succession is the first formation of the Balaton Highland to have been deposited in a fully marine environment and reflects pelagic influence. Its fauna consists of 2 ammonoid, 12 bivalve and 1 brachiopod taxa, as demonstrated by Broglio Loriga et al. (1990). The single brachiopod taxon is a *Lingula* species. According to Budai and Haas (1997) the maximum flooding can be recognized in the middle

Table 1
Selected stratigraphic levels (Triassic, Balaton Highland) and the species numbers and data sources of the respective faunas

Ages/Formations	Ammonoidea species	Bivalvia species	Brachiopoda species	Sources
1. Induan Arács Formation	–	8	2	Broglio Loriga et al. (1990)
2. Early Olenekian Hidegkút Formation (Zánka Member)	–	11	–	Broglio Loriga et al. (1990)
3. Late Olenekian Csopak Formation	2	13	1	Broglio Loriga et al. (1990)
4. Early Anisian Iszkahegy Formation	–	2	–	Broglio Loriga et al. (1990)
5. Middle Anisian (Balatonicus Zone) Felsőörs Formation (lower part)	29	35	34	Vörös (2003b), Pálfy (1988, 2003) Szente and Vörös (2003)
6. Late Anisian (Trinodosus Zone) Felsőörs Formation (upper part)	24	8	18	Vörös and Pálfy (1989) Vörös (1998) + unpublished
7. Late Anisian (Reitzi Zone) Vászoly Formation	56	7	14	Vörös and Pálfy (1989) Vörös (1998) + unpublished
8. Early Ladinian Buchenstein Formation (lower part)	9	4	3	Szabó (1972), Vörös (1998)
9. Late Ladinian Buchenstein Formation (upper part)	31	17	8	Szabó (1972), Vörös (1998)
10. Carnian Veszprém Formation + Sándorhegy Formation	30	142	81	Szabó (1972)

part of the formation, coinciding with the occurrence of the ammonoids (*Tirolites, Dalmatites*).

4. Iszkahegy Formation (Lower Anisian). The lowermost Anisian, lagoonal-peritidal Aszófő Dolomite (200 m), devoid of megafossils, is followed by the bioturbated, gray limestone of the Iszkahegy Formation. This 250 to 300 m-thick succession was deposited in a restricted, partly anoxic basin on a carbonate ramp. The fauna of this shallow marine basin was very poor: Broglio Loriga et al. (1990) listed only two species of bivalves; ammonoids and brachiopods were not reported.

5. Felsőörs Formation, lower part (Middle Anisian, Balatonicus Zone). The carbonate ramp of the Lower to Middle Anisian, lagoonal Megyehegy Dolomite was affected by intensive extensional tectonics in the Middle Anisian, and a submarine topography of fault-bounded basins and horsts developed (Budai and

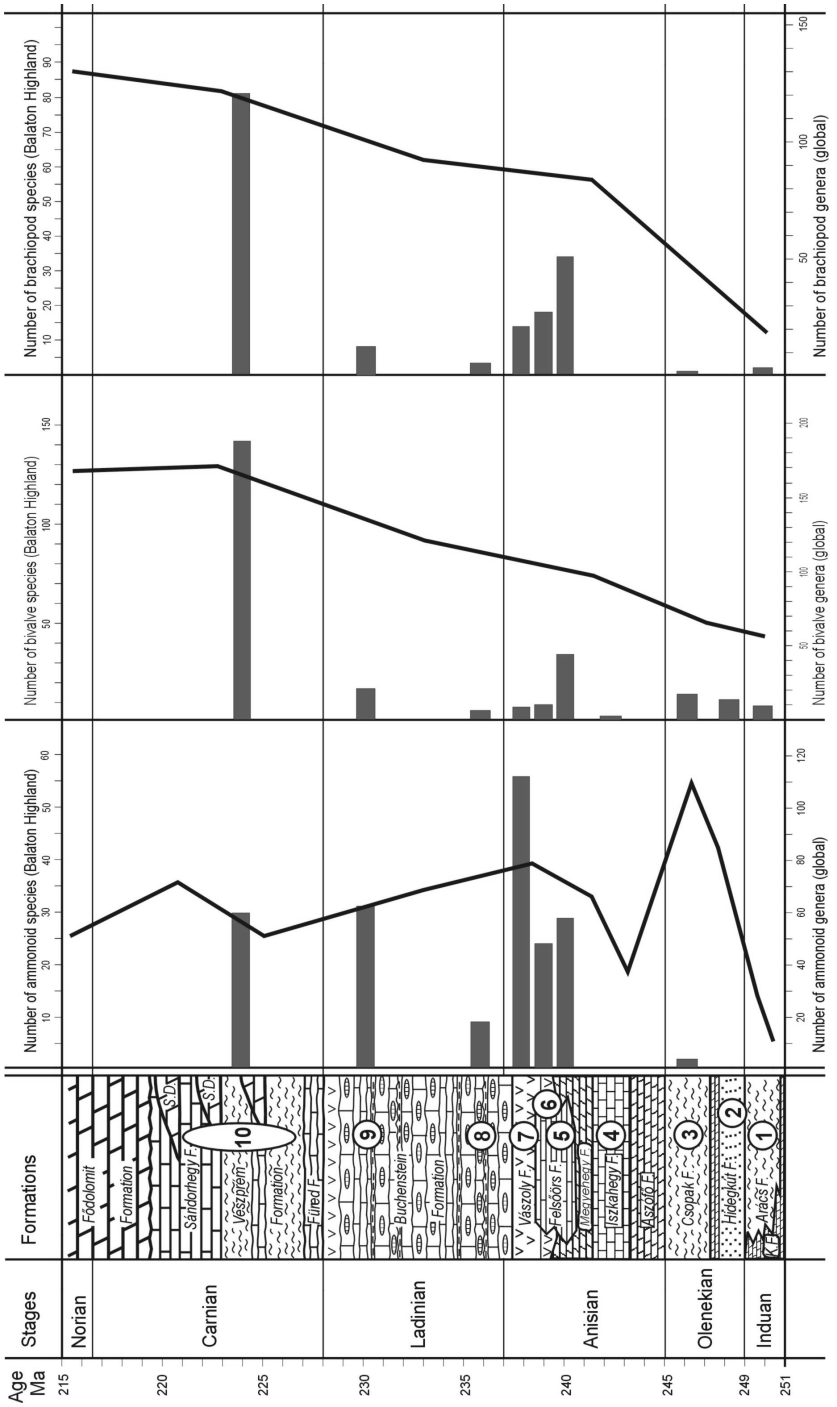

Fig. 1
The Triassic (Induan to lowermost Norian) formations of the Balaton Highland (after Budai and Haas, 1997) with the indication of selected fossiliferous levels with rich faunas (the numbers correspond to those listed in Table 1). The species richness of the ammonoid, bivalve and brachiopod faunas of the selected levels is displayed by horizontal bars. The curves (solid lines) represent the global changes in generic diversities of the respective fossil groups: ammonoids (after Brayard et al. 2009), bivalves (after McRoberts 2001) and brachiopods (compiled by the present author, see text for sources).
Abbreviations: K.F. – Köveskál Formation, S.D. – Sédvölgy Dolomite

Vörös 1992; Haas and Budai 1995). In the basins, well-bedded, partly bituminous or cherty, fossiliferous limestone layers with clayey interlayers (Felsőörs Formation) were deposited. Along the submarine fault scarps the "Recoaro-type" crinoidal-brachiopodal limestone of the Horoghegy Member, especially rich in benthic fossils (Vörös and Pálfy 2002), has accumulated. The 20 to 80 m-thick Pelsonian part of the formation (Balatonicus Zone) yielded 29 taxa of ammonoids (Vörös 2003b), 35 taxa of bivalves (Szente and Vörös 2003) and 34 taxa of brachiopods (Pálfy 1988, 2003).

6. Felsőörs Formation, upper part (Upper Anisian, Trinodosus Zone). The upper few tens of meters-thick part of this formation consist of gray, well-bedded, partly siliceous limestone with some tuffitic clay interlayers near the top. In consequence of its diachronous lower boundary, in some sections the deposition of the Vászoly Formation begins in the Trinodosus Zone; therefore these data were also included into this unit. The ammonoid fauna is very diverse (24 taxa: Vörös 1998). The bivalves are subordinate; 8 taxa, mostly at the genus level, have been identified by the present author. These data are in unpublished interim reports; therefore the taxa are listed here.

Palaeonucula sp.	*Filopecten* ? *rosaliae*
Daonella sp.	*Pteria* sp.
Posidonia sp.	*Plagiostoma* sp.
Entolium sp.	*Mysidioptera* sp.

The brachiopods are more diverse; the 18 taxa were identified partly by J. Pálfy (Vörös and Pálfy 1989), partly by the present author. The latter results are in unpublished interim reports; therefore the complete list is shown here.

Lingula sp.	*Schwagerispira speciosa*
Discinisca sp.	*Mentzelia mentzeli*
Norella refractifrons	*Mentzelia* aff. *ampla*
Holcorhynchella delicatula	*Koeveskallina koeveskalyensis*
Trigonirhynchella aff. *delecta*	*Koeveskallina ? pannonica*
Piarorhynchella trinodosi	*Angustothyris angustaeformis*
Volirhynchia vivida	*Angustothyris* aff. *suspecta*
Volirhynchia productifrons	*Pexidella sturi*
Schwagerispira schwageri	*Coenothyris* aff. *vulgaris*

7. Vászoly Formation (Upper Anisian, Reitzi Zone). With the onset of the pervasive volcanism, in the Reitzi Zone volcaniclastics became predominant over carbonates. In this, 2 to 20 m-thick part of the Vászoly Formation the siliceous, cherty and nodular limestone forms 5–20 cm-thick interlayers within the massive, greenish-gray to yellow tuffaceous strata. The limestone beds yielded plenty of ammonoids (56 species: Vörös 1998), which is the most diverse ammonoid fauna of the Balaton Highland. The bivalves are subordinate; 7 taxa

have been identified by the present author, mostly at the genus level. These data are in unpublished interim reports; therefore the taxa are listed here.

Palaeonucula sp.
Parallelodon cf. *elongata*
Daonella sp.
Posidonia sp.
Mysidioptera sp.
Myophoriopis sp.
Schafhaeutlia sp.

The brachiopod fauna is moderately diverse; the 14 taxa were identified partly by J. Pálfy (Vörös and Pálfy 1989), partly by the present author. The latter results are in unpublished interim reports; therefore the complete list is given here.

Discinisca sp.
Norella refractifrons
Norella aff. *rosaliae*
Trigonirhynchella aff. *delecta*
Piarorhynchella trinodosi
Volirhynchia vivida
Schwagerispira speciosa
Mentzelia mentzeli
Mentzelia mentzeli baconica
Mentzelia aff. *ampl*a
Koeveskallina ? *pannonica*
Tetractinella trigonella
Pexidella sturi
Angustothyris aff. *suspecta*

8. Buchenstein Formation, lower part (Lower Ladinian, Fassanian). In the deep pelagic basin prevailing in the Balaton Highland in Ladinian times, red or gray cherty limestone was deposited in less than 80 m total thickness. The 10 to 30 cm-thick beds of this Buchenstein Formation regularly contain thinner, clayey interlayers of volcanic origin. The diversity of ammonoids is considerably lower than in the underlying Vászoly Formation: 9 species were listed by Vörös (1998), though this scarcity may partly be due to preservational and collecting bias. The benthos was of extremely low diversity: the bivalves are represented exclusively by the genus *Daonella* (4 species: Szabó 1972); 3 brachiopod species were listed by Szabó (1972).

9. Buchenstein Formation, upper part (Upper Ladinian, Longobardian). The accumulation of the predominantly red, cherty limestone continued, but locally more fossiliferous, pure limestone was deposited. A major pulse of volcanism is marked by local appearance of massive tuffite layers. The pure, usually dark-red limestone yielded a very diverse ammonoid fauna (31 species: Vörös 1998). The shelly benthos shows also increasing diversity. Szabó (1972) listed 17 bivalve taxa (still predominated by the species of *Daonella*), and 8 brachiopod species.

10. Veszprém Formation, Sándorhegy Formation and Sédvölgy Members (Lower Carnian, Julian). The pelagic limestone succession of the Balaton Highland basin was terminated by the 10 to 60 m-thick Füred Limestone. Then, within the Julian, the lithology changed significantly and thick (200 to 600 m) marl was accumulated in the basin. The regional facies pattern became intricate: carbonate bodies, redeposited from a carbonate platform located to the east

(Sédvölgy Dolomite), created massive tongues (partly called Buhimvölgy Breccia) within the marl series. A time equivalent of one of these progradational tongues is called Nosztor Member; this pelagic limestone of 20 m thickness divides the Veszprém Formation into a lower (Mencshely Member) and an upper (Csicsó Member) part. With the filling up of the basin, the prograding platform gradually occupied the region and the partly hypersaline, partly normal marine, fossiliferous limestone of the Sándorhegy Formation became dominant. Finally, in the late Carnian, the uniform, peritidal beds of the "Main Dolomite" (Fődolomit Formation) started to be prevalent in the area and continued to be so up through most of the Late Triassic.

The above-described thick and lithologically complex series between the Füred Limestone and the Fődolomit Formation obviously represents various and very different paleoenvironments. Accordingly, its fossil fauna is extremely diverse: Szabó (1972) listed 30 ammonoid, 142 bivalve and 81 brachiopod taxa from the various members of the Veszprém Formation and the Sándorhegy Formation. This excessive richness of the bulk fauna is apparently due partly to paleoecological lumping because the fauna comprises fossils derived from various environments. The faunal lists of Szabó (1972) are based on the fossil material collected more than hundred years ago and deposited in the collections of the Geological Institute of Hungary (MÁFI). Most of the exposures of those times no longer exist, and the precise identification of the localities of the old fossil material was not yet possible. Moreover, neither taxonomic, nor nomenclatorial revisions of the listed taxa have been attempted. Thus it was not yet possible to undertake a revision of the Carnian fauna and, although the numbers of taxa given by Szabó (1972) are probably greatly exaggerated, they are used in the present paper without changes.

Discussion

Global versus local trends of fossil diversity

As a first step, the changes in diversity of ammonoids, bivalves and brachiopods recorded in the Balaton Highland were compared to global trends in diversity changes of the three fossil groups (Fig. 1). The species richness data given in Table 1 were used for measuring the local diversity. The global changes of diversity were plotted in terms of generic richness of the respective fossil groups. These data were taken from Brayard et al. (2009) for the ammonoids and from McRoberts (2001) for the bivalves; the brachiopod data were compiled by the present author, on the basis of recently revised volumes of the "Treatise on Invertebrate Paleontology", i.e. Savage et al. (2002), Alvarez and Rong (2002), Carter and Johnson (2006) and Lee et al. (2006). In most cases the local trends significantly deviate from the global ones.

The ammonoid trends, global and local, are more or less comparable in the Middle Triassic to Carnian period. Only the great Early Triassic global maximum

has left no trace in the Balaton Highland record, which is obviously due to local factors. The pelagic (nektonic) ammonoids were not able to enter the very shallow seas of the area, far from the oceans.

For the bivalves, the global diversity gradually and almost constantly increases through the Triassic. The local diversity values are rather low but seem to follow more or less the global trend from the Early Triassic until the middle Anisian. Afterward the local diversity of bivalves decreases abruptly, but reaches a new peak in the Carnian. The explanation for this Middle Triassic negative anomaly lies in local paleogeographic circumstances discussed below.

On the global scale the brachiopod generic richness, after an abrupt rise in the Early Triassic, increases gradually toward the end of the period. The local record is extremely poor in the Early Triassic. Only the rare occurrence of the genus *Lingula* is remarkable. This genus is regarded as an emblematic "disaster form" by Schubert and Bottjer (1995); its appearance shortly after the end-Permian catastrophe fits with the global model of biotic changes following a mass extinction. The middle Anisian peak in the local diversity of brachiopods is followed by a sharp decrease in the rest of the Middle Triassic. This phenomenon and the massive Carnian peak call for local factors in their interpretation.

In summary, the local diversity data recorded in the Balaton Highland, and their changes throughout the Triassic, differ considerably from the global diversity trends of the respective fossil groups.

Local factors governing the faunal changes

It is not surprising to find the cause of the local faunal changes in local paleoenvironmental factors. Yet the different trends in the diversities of the different (nektonic, benthonic) fossil groups of the Triassic of the Balaton Highland and their evaluation may provide valuable new insights.

One of the most obvious long-term paleogeographic changes in the Triassic history of the Balaton Highland is the deepening of the sedimentary basin in the Middle Triassic and the shallowing in the Carnian (Haas 1994; Haas et al. 1995). After the slow Early Triassic transgression water depth reached a depth in excess of 500 m in the late Anisian basins (Vörös 1996) and might have approached 1,000 m in the Ladinian (Budai and Haas 1997). The latter work is the source of the depth curve in Fig. 2, which shows the percentage of the ammonoid species against the proportion of the benthic species (i.e. the sum of the bivalve and brachiopod species) in the selected levels. The proportion of the ammonoids shows a distinct correlation with the depth curve. Remarkably, the first appearance of the ammonoids matches well with the late Olenekian transient deepening (level 3), when water depth exceeded 200 m for the first time in the Triassic. It seems that this transgression, resulting in the critical water depth, established the condition for the immigration of ammonoids from the Tethys Ocean into the shallow shelf basin of the Balaton Highland.

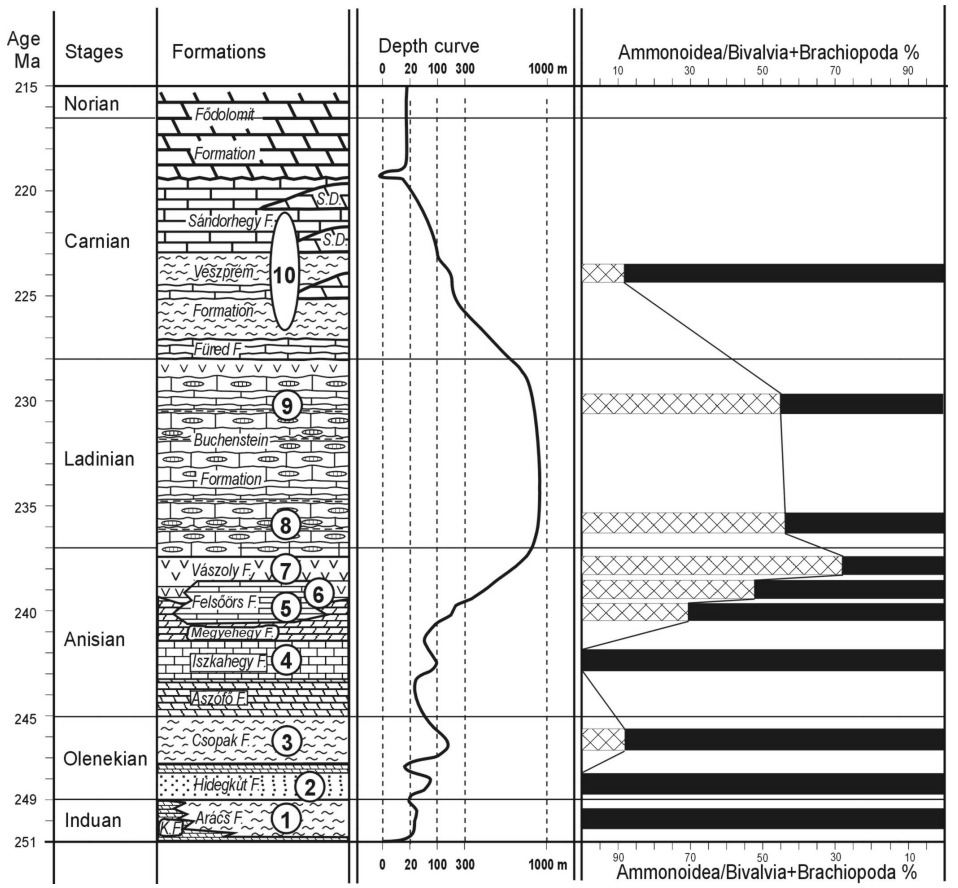

Fig. 2
The Triassic formations of the Balaton Highland with the indication of selected fossiliferous levels and the depth curve of the basinal areas (after Budai and Haas 1997), also showing the percentages of the ammonoid species (cross-hatched) against the proportion of the sum of the bivalve and brachiopod species (black) in the selected levels. Other sources and abbreviations as in Fig. 1

Figure 2 also shows the inverse relationship between the water depth and the proportion of the benthic species (bivalves and brachiopods). The obvious, generalized explanation is that the several hundred meters-deep sea-floor was unfavorable for the benthic organisms. In order to reveal some more specific causes of the diversity peaks of the benthic groups we must consider further local and regional environmental factors.

Some of the major local and regional events and environmental factors (except the depth of the sea water) of the Balaton Highland are illustrated in Fig. 3, and their correlation with the changes in lithology and the diversity peaks of the benthic fossil groups are also shown.

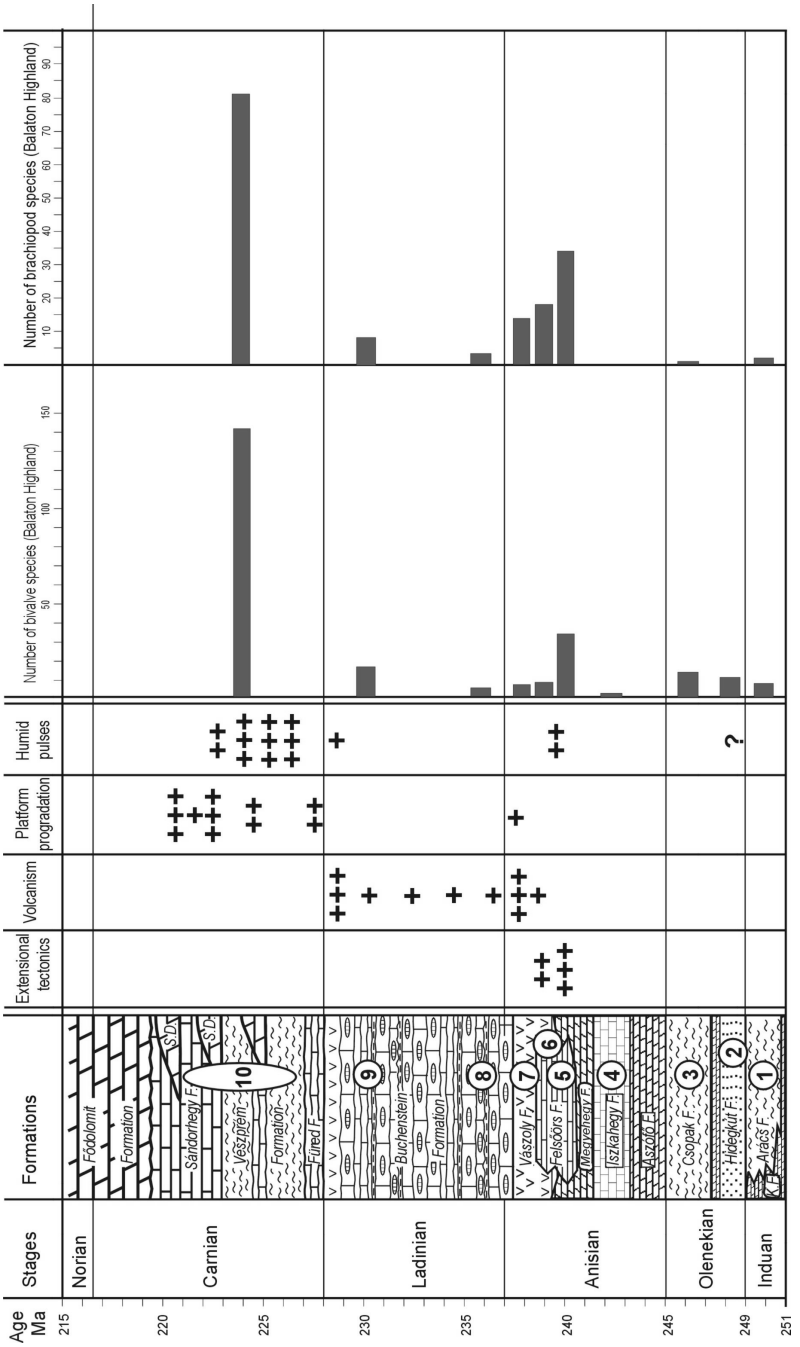

Fig. 3
The Triassic formations of the Balaton Highland with the indication of selected fossiliferous levels; the major local and regional events (crosses); and the species richness of the bivalve and brachiopod faunas of the selected levels (horizontal bars). The events of extensional tectonics, volcanism and platform progradations are taken (slightly modified) from Budai and Haas (1997), the humid pulses are from Preto et al. (2010). Other sources and abbreviations as in Fig. 1

In the Early Triassic, the benthos was represented mainly by the bivalves. The diversity peaks of these mostly cosmopolitan taxa are connected to the transgressive episodes in the shallow marine area of the Balaton Highland, as already pointed out by Broglio Loriga et al. (1990).

The Middle Anisian extensional tectonic movements seem to provide the first forceful effect on the benthic diversities. According to the paleogeographic models of Budai and Vörös (1992) and Vörös et al. (1997) the rocky escarpments and slopes of the disintegrated carbonate platforms could have served as favorable biotope for brachiopods, bivalves and other sessile benthic organisms. After death, the shells and skeletons were carried downslope to the neighboring basin and formed mass accumulations ("Recoaro-type" limestone) in the Felsőörs Formation. The regional humid climatic pulse, documented by Preto et al. (2010), might have resulted in increased fluvial influx, carrying extensive amounts of organic matter from the land areas. This input of food supply might have enhanced the proliferation of the benthic communities.

Later, in the course of the Middle Triassic, the diversity values of the benthic communities slowly but significantly decreased. This is obviously connected with the gradual and considerable deepening of the local basin floor. The rocky surfaces, i.e. the hard substrate, diminished and the basin reached a starved state, with very limited nutrient supply. The muddy bottom provided only limited possibilities for the burrowing organisms, whereas the sessile benthos largely disappeared. The Ladinian bivalve communities are dominated by "flat clams" or "paper pectens" (*Daonella* s. l.) which were commonly believed to belong to the pseudoplankton, i.e. living attached to floating objects (algae, etc.). Alternatively, Schatz (2005) argued for a benthic, pleurothetic mode of life ("snow-shoe strategy"), but in any case, the linkage of the daonellids to the soft sediments is obvious. The more or less continuous volcanism during the late Anisian and Ladinian had no detectable influence on the benthic diversity.

The massive peak of benthic diversity in the Carnian requires a complex explanation. As was emphasized in the previous chapter these data represent a "bulk fauna", once collected from diverse lithologies of several different formations of early and middle Carnian age. The presently used data base (Szabó 1972) contains faunal lists without modern revision. Although these two factors likely greatly exaggerate the taxonomic richness of the Carnian fauna, it may be confidently stated that it represents a true maximum in the local benthic diversity.

This real and significant diversity increase can be attributed to changes in three independent environmental factors. These are related to three specific features of the Carnian basin evolution of the Balaton Highland (Haas 1994; Budai and Haas 1997). (1) The rapid accumulation of several hundred meters-thick marly strata (Veszprém Marl) led to the shallowing of the basin, providing more favorable habitats for benthic life. (2) The increasing degree of platform progradation supplied large volumes of redeposited, platform-derived carbonates (Sédvölgy Dolomite tongues, Buhimvölgy Breccia) culminating in the widespread Sándor-

hegy Formation. The redeposited carbonates carried rich fossil assemblages from the neighboring shallow marine settings into the basin. This paleoecological mixing of faunas from various environments greatly increased the bulk diversity. (3) Both above factors might have been intensified by the sudden increase of humidity in the wider region. Although the paleobotanical evidence of this "Carnian pluvial event" in Europe was challenged by Visscher et al. (1994), recent studies support the idea of the "wet Carnian", also called the "Reingraben event" or "megamonsoon" (Bourquin and Guillocheau 1996; Rigo et al. 2007; Hornung et al. 2007; Preto et al. 2010). This large-scale humid pulse created extensive river systems in the European continent which greatly increased the supply of organic matter and enhanced benthic life in the surrounding marine basins, just as in the Balaton Highland.

Conclusions

The global diversity of the ammonoids, bivalves and brachiopods show a gradual increase throughout the Triassic, whereas the local diversity data recorded in the Balaton Highland, differ considerably from the global trend. These deviations are interpreted in terms of local paleoenvironmental changes.

The deepening of the sedimentary basin in the Middle Triassic and the shallowing in the Carnian is clearly expressed in the high percentage of the ammonoid species compared to the benthic species. It seems that a critical water depth of 200 m was necessary for immigration of ammonoids from the Tethys Ocean to the shallow shelf basin of the Balaton Highland.

The middle Anisian extensional tectonic movements increased the benthic diversities: the rocky escarpments of the disintegrated carbonate platforms provided biotopes for brachiopods, bivalves and other sessile benthic organisms. This is expressed in the middle and late Anisian diversity peaks.

The significant decrease in benthic diversity higher up in the Middle Triassic is obviously connected to the gradual and considerable deepening of the local basin floor.

The massive Carnian peak of benthic diversity can be attributed to three independent environmental factors. (1) The filling up and shallowing of the local basin was favorable for benthic life. (2) At times of platform progradation, the redeposited carbonates carried rich fossil assemblages from the neighboring shallow marine settings into the basin. (3) The sudden increase of humidity ("Carnian pluvial event") created extensive river systems in the European continent, greatly increasing the supply of organic matter and enhancing the proliferation of benthos in the marine environments.

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