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Abstract

Brachiopods, together with ammonoids, were collected bed-by-bed from several sections in the Bakony Mts. The sections, straddling the Jurassic-Cretaceous transition, yielded abundant and diverse brachiopod material (1277 specimens, 18 species), and this offered a possibility to determine the stratigraphic ranges of the brachiopod species. The ammonoid zonation, i.e the dating of the sections was supported by micropalaeontological (calpionellid and nannofossil) investigations. Three sections with proper ammonoid biostratigraphy, straddling the Jurassic-Cretaceous transition with continuous record, are documented in detail. It is demonstrated that, according to the stratigraphical distribution recorded in the Bakony sections, the most abundant brachiopod species range continuously from the Tithonian to the Berriasian, i.e. no change or turnover appears at the Jurassic/Cretaceous boundary. Our results endorse those published from the Klippen Belt of Poland and underscore that, at least in the intra-Tethyan realm, the brachiopod species invariably crossed the Tithonian/Berriasian boundary.

Keywords	Brachiopods, Jurassic–Cretaceous, biostratigraphy, Bakony Mts, Hungary
Taxonomy	Earth Sciences, Invertebrate Paleontology, Early Cretaceous, Late Jurassic

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Dear Editor,

Thank you for your letter with referees' opinions on our manuscript entitled: Brachiopod distribution through the Jurassic-Cretaceous transition in the western Tethyan pelagic realm: example from the Bakony Mountains (Hungary), Ref: YCRES_2019_121.

We, with my co-authors, considered carefully the corrections, amendments and suggestions by the referees, and corrected our manuscript accordingly.

We accepted the many linguistic and scientific corrections by referee M. R. Sandy. We formulated more correctly some sentences according to the criticism by Sandy (lines 267 to 273 and 311 to 319.
These changes we indicated in the „annotated version" of the resubmitted manuscript (Word file).

In the same file we included the few corrections suggested by referee M. Krobicki.
We did not accept the one suggestion by M. Krobicki, regarding missing references to some items in lines 159 to 170. There we indicated the authors of the respective species, e.g.: *Vjalovithyris rupicola* (Zittel, 1870); however these are not citations, therefore they were intentionally not listed in the references.

The figures and tables remained unchanged.

We acknowledge the positive opinions of the referees and are thankful for their very useful comments.

Here we attach two Word-files: an "annotated version" and a "clean version" of our revised manuscript.

We do hope that our paper will be accepted by and published in Createaceous Research.

Budapest, 11.06.2019

Yours sincerely,
Attila Vörös

Brachiopod distribution through the Jurassic–Cretaceous transition in the western Tethyan pelagic realm: example from the Bakony Mountains, Hungary

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Abstract

Brachiopods, together with ammonoids, were collected bed-by-bed from several sections in the Bakony Mountains. The sections, straddling the Jurassic–Cretaceous transition, yielded abundant and diverse brachiopod material (1277 specimens, 18 species), and this offered a possibility to determine the stratigraphic ranges of the brachiopod species. The dating of the sections by ammonoids was supported by micropalaeontological (calpionellid and nannofossil) investigations. Three sections straddling the Jurassic–Cretaceous transition with continuous record with good ammonoid biostratigraphic zonation are documented in detail. It is demonstrated that, according to the stratigraphical distribution recorded in the Bakony sections, the most abundant brachiopod species range continuously from the Tithonian to the Berriasian, i.e. no change or turnover appears at the Jurassic/Cretaceous boundary. Our results endorse those published from the Pieniny Klippen Belt of Poland and underscore that, at least in the intra-Tethyan realm, the brachiopod species invariably crossed the Tithonian/Berriasian boundary.

Key words

Brachiopods, Jurassic–Cretaceous, biostratigraphy, Bakony Mountains, Hungary

1. Introduction

The phylum Brachiopoda, after surviving the end-Permian and end-Triassic near-extinction events, exhibited a lesser but significant ~~secondary~~ bloom in the Jurassic. The last "fatal", order-level extinction of the rhynchonelliform brachiopods (Articulata, *auctt.*) in the Early Jurassic (early Toarcian) was followed by the last considerable diversity maximum of the subphylum in the Middle Jurassic (Vörös et al., 2016; Vörös et al., in press). Later in the Mesozoic (Late Jurassic – Early Cretaceous), the generic diversity of brachiopods shows definite decrease which is considerable among the rhynchonellides but only ~~minor~~ minor to non-existent among the terebratulides (Table 1). This significant deviation in the diversity trajectories of the two orders probably reflects the more advantageous anti-predatory strategy developed by the terebratulides (Vörös, 2010). The Late Jurassic to Early Cretaceous interval of terebratulid dominance was a quiet period in brachiopod history, at least in terms of diversity changes. The environmentally rather stable pelagic realm of the western Tethys was especially characterized by long-ranging brachiopod taxa. In the present paper we focus on a narrower part of the Jurassic~~-~~–Cretaceous transition and restrict the study to the Tithonian and Berriasian, and data on the stratigraphical distributions of brachiopod taxa in the Bakony Mountains~~-~~, Hungary. A comprehensive account on the stratigraphy and palaeontology of the Late Jurassic and Early Cretaceous formations of the region was given by Fülöp (1964), and more recently by Főzy (2017).

The beds of the Jurassic~~-~~–Cretaceous transition in the Bakony Mountain~~t~~s are extremely rich in brachiopods: more than 1200 specimens are available from this stratigraphical interval. This considerable number of fossils is mainly the result of detailed collecting by members of the Hungarian Geological Institute (HGI) in the 1960's. Brachiopods were almost always collected bed-by-bed, together with ammonites and this offered an exceptional possibility to record their stratigraphical distributions. Our present brachiopod data base is stratigraphically reliable and novel; similar results have been published only from the Polish Carpathians (Barczyk, 1991; Krobicki, 1994, 1996).

In this paper we focus on the stratigraphical distribution of brachiopods as recorded in the Bakony sections in the Tithonian~~-~~–Berriasian interval.

2. Geological setting

2.1. General

The geographical location and palaeogeographical setting of the studied localities are shown in Fig. 1. The Bakony Mountain~~t~~s belong to the Transdanubian Range, representing a key part of the Pelso Unit (Kovács et al., 2000; Haas, 2001), which in turn is part of the AlCaPa composite terrane (Csontos and Vörös, 2004). The Pelso/Bakony unit was part of the large system of intra-Tethyan (or Mediterranean) microcontinents in Jurassic and Early Cretaceous times (Vörös, 1993, 2016). The major part of this wide, submarine area was a pelagic plateau, but carbonate platforms and intervening deep basins also developed. These microcontinents were isolated by deep-sea/oceanic belts from the main continents, therefore dominantly pure limestones and other fine-grained sediments were deposited here during most of the Mesozoic. Accordingly, the Jurassic to Cretaceous transition, exposed in our studied sections, is represented by limestones of the Pálihálás Formation (of Ammonitico Rosso ~~Ammonitico~~ type) and the Szentivánhegy and Mogyorósdomb ~~Formations~~ formations (of Biancone type). As a rule, the lower, Tithonian part of the sections consists of reddish, nodular limestone, which becomes gradually less nodular, more compact and whiter in the higher, mostly Berriasian parts.

2.2. Localities and sections

From among the seven localities (Fig. 1), yielding important Tithonian and/or Berriasian brachiopod faunas, three sections were studied and are discussed in detail in the present paper. Two of these are located near the village of Hárskút, along the Közöskút Ravine. In section **HK-II** (No. 1 in Fig. 1; Geographical coordinates: 47°9′51.81″N, 17°47′3.98″E) the nearly horizontal beds form a prominent cliff around 15 m high known as Prédikálószék ("The Pulpit"). The Tithonian to Berriasian ammonite and calpionellid succession was discussed by Horváth and Knauer (1986) and Főzy (1990, 2017), and is under revision by two of the present authors (I. Főzy, O. Szives). The lithologic log, chronostratigraphy and the distribution of the most important brachiopod species for section HK-II are shown in Fig. 2.

Fig. 1. near here

Fig. 2. near here

Section **HK-12** is situated about a hundred meters north-eastward from HK-II (No. 2 in Fig. 1; Geographical coordinates: 47°9′56.97″N, 17°47′8.11″E); it is an artificially enlarged outcrop, excavated by the HGI, exposing gently dipping Berriasian and Valanginian strata. The ammonoid, belemnoid and calpionellid fauna and integrated isotope and biostratigraphy of this section was recently published by Főzy et al. (2010). The lithologic log, the chronostratigraphy and the distribution of the most important brachiopod species from section HK-12 are shown in Fig. 3. The Berriasian part of this section is rather condensed; the thickness of the fossiliferous Berriasian strata does not exceed 3 m. Within a ten metres distance to the east, there is an artificial outcrop, excavated by the HGI, (**HK-12a**) exposing

Tithonian red nodular limestones that are a few metres thick. This section yielded a scarce brachiopod fauna of low diversity.

The third section which yielded the most abundant and diverse brachiopod fauna, called **Szilas Ravine**, is close to the village of Borzavár (No. 4 in Fig. 1; Geographical coordinates: 47°16′26.35″N, 17°49′03.08″E). The detailed collection was made from a steep, rocky hillside, exposing a continuous series of beds more than 20 m thick of upper Kimmeridgian to lower Berriasian age. The ammonoid stratigraphy of the Szilas Ravine was published by Főzy (1990, 2017), and is under revision by two of the present authors (I. Főzy, O. Szives). The lithologic log, chronostratigraphy and distribution of the most important brachiopod species for Szilas Ravine are shown in Fig. 4.

Fig. 3 and 4. near here

Some other sections and localities in the northern Bakony Mountains also yielded Tithonian and/or Berriasian brachiopods. The Hárskút, **Édesvíz Key Section** (No. 3 in Fig. 1) is very important for Valanginian~~-~~–Hauterivian stratigraphy. Its lowermost few layers, with rather abundant brachiopod fauna, were dated as Tithonian and Berriasian, but the outcrop conditions do not allow drawing a log. A small, isolated outcrop, named **Zirc, Alsó-major** by Fülöp (1964) (No. 5 in Fig. 1), exposed Berriasian limestone layers with a few brachiopods. A famous locality at Olaszfalu, **Eperkés Hill** (No. 6 in Fig. 1) is an artificial trench, where masses of mostly disarticulated shells of brachiopods can be collected. Here a coarse grained, crinoidal-brachiopodal coquina limestone, the Szélhegy Formation, ~~is reminiscent of~~resembles the Lower Jurassic Hierlatz Limestone, but is dated as early Tithonian (Főzy 2017). The **Lókút, Key Section** (No. 7 in Fig. 1) has prime importance for Tithonian stratigraphy (Vigh 1984, Grabowski et al. 2010, 2017, Főzy et al. 2011, Főzy 2017). Detailed collecting in the 1960's yielded a very abundant and diverse Tithonian brachiopod fauna, but the lack of Berriasian forms does not allow us to include the section in this evaluation.

3. Material and methods

The studied material was collected from well-dated, measured sections and some other localities of Tithonian and/or Berriasian age in the northern Bakony Mountains (discussed above). The brachiopods are extremely abundant: from among the 1277 identified specimens 940 were collected from the Tithonian and 337 from the Berriasian (including indeterminable specimens, identified only to genus level) (Table 2). Specimens have been coated with ammonium chloride before photography. Specimens are deposited in the collection of the Department of Palaeontology and Geology of the Hungarian Natural History Museum (Budapest), under inventory numbers prefixed by M., or INV.

In the following part of the present paper we focus on the brachiopods identified to species level, and to the data from the sections HK-II, HK-12 and Szilas Ravine. The reasons for this restriction are that (1) the ammonoid biostratigraphy of these sections were recently re-evaluated, (2) from these sections, only HK-II and Szilas Ravine appear to straddle the Jurassic–Cretaceous transition with a continuous record. Although HK-12 section probably starts with lower Berriasian deposits, ammonites are extremely rare and in a poor state of preservation from this part. The upper part of this section yielded identifiable ammonites from the Berriasella occitanica and Berriasella boissieri zones of the middle and upper Berriasian, so this section is also included in the present evaluation. Because of reason (2) above, we do not illustrate a detailed log with the brachiopod data of the otherwise well-dated Lókút Key Section, where the brachiopod fauna is restricted to the Tithonian.

Even after this, the Tithonian–Berriasian brachiopod fauna of the three relevant sections is very diverse and abundant ~~at international standard~~: the remaining 565 specimens represent 21 species of 10 genera (Table 3). The overwhelming part belongs to the Pygopidae (~~456~~ 456 specimens); the most abundant genera of the family are: *Antinomia* (263), *Pygope* (129) and *Triangope* (~~64~~61). The family Nucleatidae is represented by ~~84~~ 82 specimens; rhynchonellides appear subordinately (10 specimens). It is worth mentioning that the brachiopod fauna of the Szilas Ravine is by far the most abundant and diverse from among the three investigated sections (346 well-identified specimens, 18 species). The representative elements of the studied Tithonian–Berriasian brachiopod fauna are illustrated in Fig. 5.

Fig.5 near here

In the brachiopod taxonomy we largely followed the revised volumes of the "Treatise" (Savage et al., 2002; Lee et al., 2006) with a few exceptions. The generic name *Vjalovithyris* Tkhorszhevsky, 1989 (synonymized with *Nucleata* in the Treatise) was retained for the species *V. rupicola* (Zittel, 1870) with laterally lobate shell. On the other hand, the more or less globose species *bouei* (Zejszner, 1846), originally included to *Vjalovithyris* by Tkhorszhevsky (1989), was removed from *Vjalovithyris* to *Nucleata* Quenstedt, 1868. The genus *Pygope* Link, 1830, in our opinion, was too widely interpreted in the revised Treatise (Lee et al. 2006). Here we returned to the narrower interpretation of the previous Treatise (Muir-Wood 1965) and Buckman (1906), and restrict *Pygope* to the perforate or bifidate forms with straight lateral commissures, without beak ridges and planareas. In this concept, the species *diphya* (Buch, 1834), *axine* (Zejszner, 1846), *janitor* (Pictet, 1867) and *vomer* Vigh, 1981 belong to *Pygope*. Moreover, here we restore the validity of the generic name *Antinomia* Catullo, 1851, following Buckman (1906) and Muir-Wood (1965), for the perforate and bifidate forms with arched or sinuous lateral commissures and well developed planareas. The species *catulloi* (Pictet, 1867), *diphoros* (Zejszner, 1846) and *sima* (Zejszner, 1846) are ranked to *Antinomia*.

The rich and bed-by-bed collected cephalopod fauna provided a firm biostratigraphic age-constraint for the brachiopod fauna under study. Although belemnites are also common in the studied stratigraphic interval, ammonites are far more abundant. About 3000 and 3550 ammonites were collected from the Hárskút section and the Szilas Ravine, respectively. Most of the ammonites belong to the long ranged phylloceratids and lytoceratids, which are typical for the Mediterranean faunal assemblages. The age diagnostic Late Jurassic–Early Cretaceous ammonite genera and species also clearly show Mediterranean distributions, and, accordingly, can be characterized within the frameworks of the ammonite zonation previously developed for the ~~Mediterranean~~ Tethyan palaeobiogeographic realm (Ogg et al., 2016).

Focusing on the Jurassic–Cretaceous transitional interval in the studied sections, we can say that the Lower Tithonian is generally rather complete and all of the Hybonoticeras hybonotum, Semiformiceras darwini, Semiformiceras semiforme, Semiformiceras fallauxi and Micracanthoceras ponti ammonite zones can be documented. In the lower part of the ~~Upper~~ upper Tithonian the "Durangites" and Micracanthoceras microcanthum zones can be recognized, but their separation is still problematic. Unfortunately, due to the impoverishment of the fauna in the latest Tithonian, the Jurassic/Cretaceous boundary cannot be precisely drawn in any of the studied sections by means of ammonites. At the HK-II section the boundary lies somewhere between beds 33~~-~~–36 (Fig. 2, grey band), bed 32 yields clearly Berriasian forms. Related to the Szilas Ravine ammonite assemblage, the boundary between the ~~Upper~~ upper Tithonian and the ~~Lower~~ lower Berriasian lies somewhere between beds 37~~-~~–43, bed 36 seems to contain a Berriasian assemblage (Fig. 4, grey band).

Table 1, 2, 3 near here

4. Results

Range charts have been constructed for the HK-II, HK-12 and Szilas Ravine sections with the occurrences of brachiopods in numbered beds of the respective sections indicated (Figs. 2, 3, 4). The scarce data set of the HK-II section suggests that the dominant brachiopod species (*Antinomia catulloi*, *Pygope diphya*) pass through the poorly defined Tithonian/Berriasian boundary (Fig. 2). The rather abundant and diverse brachiopod fauna of the HK-12 section is restricted to the Berriasian (Fig. 3). Yet, it is important to consider this section in the present study because it demonstrates the Berriasian re-appearance of a series of brachiopod species well known in the Tithonian (e.g. *Antinomia catulloi*, *A. diphoros*, *Pygope diphya*, *Triangope triangulus*, *Nucleata bouei*). The most profuse and robust brachiopod data were provided by the Szilas Ravine section (Fig. 4). Here at least ten brachiopod species cross the Tithonian/Berriasian boundary interval, though the biostratigraphical base of the Berriasian is ambiguous even in this section.

The stratigraphical ranges of the most significant (abundant and frequently occurring) brachiopod species, recorded in the well-dated sections through the Jurassic–Cretaceous transition in the Bakony Mountains, are shown in Fig. 6. Eleven species occur both in the Tithonian and in the Berriasian; while *Antinomia sima* seems to appear only in the late Berriasian. It must be noted that *Pygope axine* and *Vjalovithyris rupicola* are in fact very long ranging taxa, because (in the higher part of the HK-12 section) they are recorded again in the lower Valanginian.

Bed-by-bed investigation of the nannofossil assemblages of the three sections are in progress, but preliminary data revealed that nannofossils are in a poor to very poor state of preservation, showing clear signs of dissolution and diagenetic overprinting. Concerning the nannofossils of the nearby Lókút Key Section, which reveals the same stratigraphic units, Stoykova already concluded (in Grabowski et al. 2017) that they are in poor to very poor state of preservation and the best preserved forms are from the lower, Tithonian part of the section.

From HK-II and Szilas Ravine sections it seems that nannofossils will not provide accurate data to determine the exact age of the section due to the lack of age diagnostic forms such as nannoconids. Delicate nannofossil forms completely are lacking in both sections due to dissolution. Although nannoconids are considered among the most resistant, heavily calcitized forms (Thiersten, 1976), they show limited distribution in these sections which is in contrast to their usual dominance in pelagic carbonates (Busson and Noël, 1991). As Erba (1994) pointed out, nannoconids are considered as deep photic zone forms but temporarily may show very low abundance also in limestones with no sign of any disturbing environmental parameter such as dysoxia. According to her opinion, we may speculate that probably other, small scale environmental changes affected their abundance. Six smear slides from Szilas Ravine (beds 2, 37, 40, 43, 44, 48) yielded only dissolution resistant forms such as *Watznaueriales*, which does not allow us to perform quantitative statistical analysis. Nannofossil studies on the HK-II section have not yet been started. In relation to section HK-12, Báldi-Beke (1965) investigated the nannoconids of this site; however, we cannot correlate her sampling numbers with our bed numbering. The nannofossil assemblage is under revision.

5. Discussion

One of the remarkable features of the Tithonian–Berriasian brachiopod fauna of the Bakony Mountains is the extremely high diversity (18 species) and density (512 specimens) of the brachiopod assemblage of the Szilas Ravine as compared to the other investigated sections (Tables 2, 3). Without going into details of Late Jurassic palaeogeography of the

Bakony Mountains, here we suggest that this enrichment of the brachiopod fauna points to the effect of a nearby submarine elevation. A steep, rocky slope might provide favourable environments for brachiopods (Vörös 1986) and might drive nutrient-rich upwellings.

The brachiopod fauna, collected bed-by-bed, together with ammonoids from well-dated sections through the Tithonian–Berriasian in the Bakony Mountains, offered an exceptional opportunity to determine the stratigraphic ranges of the brachiopod species at the level of substage or even ammonoid zone. Our results demonstrate that the most abundant brachiopod species frequently occur both in the Tithonian and in the Berriasian, and no change appears around the Jurassic–Cretaceous boundary.

Our result is not unexpected; this subject was long-debated and perfectly summarized in a paper entitled ”Brachiopods at the Jurassic–Cretaceous boundary” by Ager (1975). He gave a “state-of-the-art” and concise review of the major brachiopod groups over the world in respect of the above topic. His main conclusions were: “there is certainly nothing noteworthy [faunal change] among the brachiopods at the conventional Tithonian/Berriasian level”, and “the brachiopods of the Berriasian are completely ‘Jurassic’ in character” (Ager 1975, p. 160, 161). It has to be noted however, that at that time, the bed-by-bed collections of brachiopods through the crucial interval, with detailed biostratigraphical control (ammonoid and/or micropalaeontological) were lacking.

In the last decades, due to the mentioned, advanced methods, the brachiopod record was greatly improved. The new results suggest that in the Euro-Boreal realm (i.e. in the territory of the contemporaneous European shelf and epicontinental seas) the brachiopod faunas changed at the Jurassic–Cretaceous boundary, even in species composition. For example, in Provence and elsewhere in the Euro-Boreal realm (Sandy 1986, fig. 21)), two of the nine recorded brachiopod species seem to disappear at the end of the Tithonian, and three appear in the Berriasian; the next remarkable faunal change appeared within the Valanginian.

Commented [1]: cf. Voros 1986 Palaeo3 ?

In Svalbard (Sandy et al. 2014, table 1), five brachiopod species, from among the 14 recorded, are restricted to the uppermost Jurassic (Volgian) and further seven species appear just in the lowermost Cretaceous (Ryazanian). However it must be remarked that here the brachiopods represent spot samples, collected from laterally discontinuous seep carbonates.

On the other hand, the new results from the Mediterranean or intra-Tethyan realm definitely endorse the conclusions by Ager (1975). Barczyk (1991) and Krobicki (1994, 1996) published particularly important data on brachiopod distributions across the Tithonian–Berriasian boundary from measured sections of the Pieniny Klippen Belt (Poland), supported by biostratigraphical dating (on the basis of ammonoids and calpionellids). This classic area (including the famous localities of Rogoźnik and Czorsztyn) supplied the brachiopods for the old and very first complex monograph on pygopides by Zejszner (1846). The bed-by-bed collections of Barczyk (1991) resulted in a range chart where six brachiopod species, from the 17 recorded, crossed the Tithonian–Berriasian boundary, and one species showed its first appearance in the Berriasian. Based on newly collected material and a partial taxonomical revision, Krobicki (1994, 1996) published a detailed and robust data base from the same sections. He showed that, though the brachiopod ranges seem to be interrupted within the Tithonian, from among the 13 brachiopod species recorded by him, 10 crossed the Tithonian–Berriasian boundary level, and no new species appeared in the Berriasian.

Our present results fit very closely to those of the Polish authors and underscore that, at least in the intra-Tethyan realm (where both the Bakony area and the Czorsztyn ridge once belonged), no significant change of brachiopod faunas can be recorded at the Tithonian–Berriasian boundary. We may add that a complete turnover of brachiopod species in the investigated sections of the Bakony Mountains was recorded in the Valanginian (at the Saynoceras verrucosum zone) in relationship with the Weissert oceanic anoxic event (see Főzy et al., 2010).

Finally, two further quotations from the old paper (Ager, 1975) by the wise master. “If the author was forced into . . . defining the Jurassic–Cretaceous boundary on the basis of brachiopod evidence, then he would be very tempted to do so within the Valanginian . . .” (l.c. p. 160). And also a warning (for the procedure of defining stage and system boundaries): “No special consideration should be given to the brachiopods, which are no better and no worse than the rest.” (l.c. p. 161).

6. Conclusions

It is suggested that the extremely high diversity and density of the brachiopod assemblage of the Szilas Ravine points to the effect of a nearby submarine elevation.

On the basis of the extremely abundant brachiopod material, collected from well-dated, measured sections, it is demonstrated that the most abundant brachiopod species occur both in the Tithonian and in the Berriasian, and no faunal break or turnover of species appears at the Jurassic/Cretaceous boundary.

Our results are in agreement with the robust data published from the Czorsztyn ~~zone~~ succession of the Pieniny Klippen Belt (Poland) and endorse the ~~old predicted assumption~~already observed phenomenon that ~~nothing happened to the~~no obvious extinction or diversification event in brachiopods appeared at the Tithonian–Berriasian boundary. This conclusion is valid for the intra-Tethyan realm, where both the Bakony M~~t~~ountains and the Czorsztyn ~~zone~~ succession belonged at the time in question. On the other hand, sparse data from the Euro-Boreal realm point to a turnover of brachiopod species at the Jurassic–Cretaceous boundary. This may suggest that the continuity of brachiopod species, crossing this boundary was connected to the continuity of the stable environment in the intra-Tethyan realm. whereas in other areas of Europe end-Jurassic regression and Early Cretaceous transgression impacted sedimentary and biotic environments.

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Figure captions

Fig. 1 A, B.

(A) The geographical setting of the localities yielding important Tithonian and/or Berriasian brachiopod faunas (sections studied in detail are in boldface in the following list). **1: Hárskút, HK-II, 2: Hárskút, HK-12** (and HK-12a), 3: Hárskút, Édesvíz, Key Section, **4: Borzavár, Szilas Ravine**, 5: Zirc, Alsó-major, 6: Olaszfalu, Eperkés Hill, 7: Lókút, Key Section; inset map with black box shows regional location of sections in western Hungary. (B) The palaeogeographical setting of the area in the Tithonian. Asterisk indicates the inferred palaeoposition of the Bakony area. (Modified from Csontos and Vörös 2004)

Fig. 2.

Lithologic log, chronostratigraphy and distribution of the most important brachiopod species in the Hárskút, HK-II section. For lithologic legend see Fig. 3. Ammonoid zones after Főzy (1990). Ki.: Kimmeridgian, Be.: Beckeri, Hybon.: Hybonotum, Darw.: Darwini, Semif.: Semiforme, Pon.: Ponti, “D.” Micr.: “Durangites” and Microcanthum. The grey rectangle indicates the approximate interval of the Berriasian base.

Fig. 3.

Lithologic log, chronostratigraphy and distribution of the most important brachiopod species in the Hárskút, HK-12 section. Lithologic log drawn by Damian Lodowski (Warsaw). Lithologic legend: 1: frequent ammonoids, 2: well-bedded white limestone, 3: thick-, or poorly-bedded light coloured limestone, 4: mostly red, nodular limestone, 5: radiolarite with calcareous nodules. Ammonoid zones after Főzy et al. (2010).

Fig. 4.

Lithologic log, chronostratigraphy and distribution of the most important brachiopod species in the Borzavár, Szilas Ravine section. For lithologic legend see Fig. 3. Ammonoid zones after Főzy (1990). Hyb.: Hybonotum, Pon.: Ponti, “D.” and Micr.: “Durangites” and Microcanthum. The grey rectangle indicates the approximate interval of the Berriasian base.

Fig. 5.

Representative species of the studied Tithonian~~–~~–Berriasian brachiopod fauna. Specimens have been coated with ammonium chloride before photography. Specimens are deposited in the collection of the Department of Palaeontology and Geology of the Hungarian Natural History Museum (Budapest), under inventory numbers prefixed by M., or INV. Scale bar = 2 cm.

(1) *Monticlarella* ? *tatrica* (Zejszner, 1846) (INV 2019.52.) Olaszfalu, Eperkés Hill, loose, ~~Lower~~ lower Tithonian; a: dorsal view, b: anterior view. (2) *Monticlarella* ? *agassizi* (Zejszner, 1846) (INV 2019.53.) Lókút, Key Section, Bed 4., ~~Upper~~ upper Tithonian, ~~;~~ a: dorsal view, b: anterior view. (3) *Pygope diphya* (Buch, 1834) (INV 2019.54.) Borzavár, Szilas Ravine, Bed 40, ~~Lower~~ lower Berriasian (?), a: dorsal view, b: lateral view. (4) *Pygope diphya* (Buch, 1834) (INV 2019.55.) Borzavár, Szilas Ravine, Bed 41, ~~Lower~~ lower Berriasian (?), a: dorsal view, b: lateral view. (5) *Pygope axine* (Zejszner, 1846) (INV 2019.56.) Borzavár, Szilas Ravine, Bed 60, ~~Upper~~ upper Tithonian, a: dorsal view, b: lateral view. (6) *Pygope axine* (Zejszner, 1846) (INV 2019.57.) Borzavár, Szilas Ravine, Bed 62, ~~Upper~~ upper Tithonian, a: dorsal view, b: lateral view. (7) *Pygope janitor* (Pictet, 1867) (INV 2019.58.) Borzavár, Szilas Ravine, Bed 97, ~~Lower~~ lower Tithonian, a: dorsal view, b: lateral view, c: anterior view. (8) *Antinomia catulloi* (Pictet, 1867) (INV 2019.59.) Hárskút, HK-12 section,

Bed 18, ~~Upper~~ upper Berriasian, a: dorsal view, b: lateral view. (9) *Antinomia catulloi* (Pictet, 1867) (M.87.067.), Hárskút, HK-II section, Bed 43, ~~Upper~~ upper Tithonian, a: dorsal view, b: lateral view. (10) *Antinomia catulloi* (Pictet, 1867) (INV 2019.60.) Borzavár, Szilas Ravine, Bed 71, ~~Lower~~ lower Tithonian, a: dorsal view, b: lateral view. (11) *Antinomia diphoros* (Zejszner, 1846) (INV 2019.61.) Borzavár, Szilas Ravine, Bed 39, ~~Lower~~ lower Berriasian, a: dorsal view, b: lateral view. (12) *Antinomia sima* (Zejszner, 1846) (INV 2019.62.) Hárskút, HK-12 section, Bed 18, ~~Upper~~ upper Berriasian, a: dorsal view, b: lateral view. (13) *Triangope triangulus* (Lamarck, 1819) (M.87.069.), Borzavár, Szilas Ravine, Bed 41, ~~Lower~~ lower Berriasian (?), a: dorsal view, b: lateral view. (14) *Triangope triangulus* (Lamarck, 1819) (INV 2019.63.) Lókút, Key Section, Bed 34, ~~Lower~~ lower Tithonian, a: dorsal view, b: lateral view. (15) *Nucleata bouei* (Zejszner, 1846) (INV 2019.64.) Hárskút, HK-12 section, Bed 20, ~~Upper~~ upper Berriasian, a: dorsal view, b: anterior view. (16) *Nucleata bouei* (Zejszner, 1846) (INV 2019.65.) Borzavár, Szilas Ravine, Bed 31, ~~Lower~~ lower Berriasian, a: dorsal view, b: anterior view. (17) *Vjalovithyris rupicola* (Zittel, 1870) (INV 2019.66.) Borzavár, Szilas Ravine, Bed 74, ~~Lower~~ lower Tithonian, a: dorsal view, b: anterior view. (18) *Oppeliella pinguicula* (Zittel, 1870) (INV 2019.67.) Hárskút, HK-12 section, Bed 21, ~~Upper~~ upper Berriasian, a: dorsal view, b: lateral view, c: anterior view.

Fig. 6.

Stratigraphical ranges of the most significant brachiopod species recorded in well-dated sections through the Jurassic~~-~~–Cretaceous transition in the Bakony Mountains ~~Hungary~~ (this paper). Dotted lines indicate that *Pygope axine* and *Vjalovithyris rupicola* appeared again in the early Valanginian.

Table captions

Table 1.

Number of brachiopod genera in the Middle Jurassic to Early Cretaceous interval – global data from Curry and Brunton, 2007.

Table 2.

Number of brachiopod specimens in the Tithonian and Berriasian sections from ~~Hungary~~the Bakony Mountains in the present study.

Table 3.

Number of Tithonian and Berriasian brachiopod species in the three sections studied in detail.

Brachiopod distribution through the Jurassic–Cretaceous transition in the western Tethyan pelagic realm: example from the Bakony Mountains, Hungary

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Abstract

Brachiopods, together with ammonoids, were collected bed-by-bed from several sections in the Bakony Mountains. The sections, straddling the Jurassic–Cretaceous transition, yielded abundant and diverse brachiopod material (1277 specimens, 18 species), and this offered a possibility to determine the stratigraphic ranges of the brachiopod species. The dating of the sections by ammonoids was supported by micropalaeontological (calpionellid and nannofossil) investigations. Three sections straddling the Jurassic–Cretaceous transition with continuous record with good ammonoid biostratigraphic zonation are documented in detail. It is demonstrated that, according to the stratigraphical distribution recorded in the Bakony sections, the most abundant brachiopod species range continuously from the Tithonian to the Berriasian, i.e. no change or turnover appears at the Jurassic/Cretaceous boundary. Our results endorse those published from the Pieniny Klippen Belt of Poland and underscore that, at least in the intra-Tethyan realm, the brachiopod species invariably crossed the Tithonian/Berriasian boundary.

Key words

Brachiopods, Jurassic–Cretaceous, biostratigraphy, Bakony Mountains, Hungary

1. Introduction

The phylum Brachiopoda, after surviving the end-Permian and end-Triassic near-extinction events, exhibited a lesser but significant bloom in the Jurassic. The last “fatal”, order-level extinction of the rhynchonelliform brachiopods (Articulata, *auctt.*) in the Early Jurassic (early Toarcian) was followed by the last considerable diversity maximum of the subphylum in the Middle Jurassic (Vörös et al., 2016; Vörös et al., in press). Later in the Mesozoic (Late Jurassic – Early Cretaceous), the generic diversity of brachiopods shows definite decrease which is considerable among the rhynchonellides but only minor to non-existent among the terebratulides (Table 1). This significant deviation in the diversity trajectories of the two orders probably reflects the more advantageous anti-predatory strategy developed by the terebratulides (Vörös, 2010). The Late Jurassic to Early Cretaceous interval of terebratulid dominance was a quiet period in brachiopod history, at least in terms of diversity changes. The environmentally rather stable pelagic realm of the western Tethys was especially characterized by long-ranging brachiopod taxa. In the present paper we focus on a narrower part of the Jurassic–Cretaceous transition and restrict the study to the Tithonian and Berriasian, and data on the stratigraphical distributions of brachiopod taxa in the Bakony Mountains, Hungary. A comprehensive account on the stratigraphy and palaeontology of the Late Jurassic and Early Cretaceous formations of the region was given by Fülöp (1964), and more recently by Főzy (2017).

The beds of the Jurassic–Cretaceous transition in the Bakony Mountains are extremely rich in brachiopods: more than 1200 specimens are available from this stratigraphical interval.

This considerable number of fossils is mainly the result of detailed collecting by members of the Hungarian Geological Institute (HGI) in the 1960's. Brachiopods were almost always collected bed-by-bed, together with ammonites and this offered an exceptional possibility to record their stratigraphical distributions. Our present brachiopod data base is stratigraphically reliable and novel; similar results have been published only from the Polish Carpathians (Barczyk, 1991; Krobicki, 1994, 1996).

In this paper we focus on the stratigraphical distribution of brachiopods as recorded in the Bakony sections in the Tithonian–Berriasian interval.

2. Geological setting

2.1. General

The geographical location and palaeogeographical setting of the studied localities are shown in Fig. 1. The Bakony Mountains belong to the Transdanubian Range, representing a key part of the Pelso Unit (Kovács et al., 2000; Haas, 2001), which in turn is part of the AlCaPa composite terrane (Csontos and Vörös, 2004). The Pelso/Bakony unit was part of the large system of intra-Tethyan (or Mediterranean) microcontinents in Jurassic and Early Cretaceous times (Vörös, 1993, 2016). The major part of this wide, submarine area was a pelagic plateau, but carbonate platforms and intervening deep basins also developed. These microcontinents were isolated by deep-sea/oceanic belts from the main continents, therefore dominantly pure limestones and other fine-grained sediments were deposited here during most of the Mesozoic. Accordingly, the Jurassic to Cretaceous transition, exposed in our studied sections, is represented by limestones of the Pálihálás Formation (of Ammonitico Rosso type) and the Szentivánhegy and Mogyorósdomb formations (of Biancone type). As a rule, the lower, Tithonian part of the sections consists of reddish, nodular limestone, which becomes gradually less nodular, more compact and whiter in the higher, mostly Berriasian parts.

2.2. Localities and sections

From among the seven localities (Fig. 1), yielding important Tithonian and/or Berriasian brachiopod faunas, three sections were studied and are discussed in detail in the present paper. Two of these are located near the village of Hárskút, along the Közöskút Ravine. In section **HK-II** (No. 1 in Fig. 1; Geographical coordinates: 47°9′51.81″N, 17°47′3.98″E) the nearly horizontal beds form a prominent cliff around 15 m high known as Prédikálószék ("The Pulpit"). The Tithonian to Berriasian ammonite and calpionellid succession was discussed by Horváth and Knauer (1986) and Főzy (1990, 2017), and is under revision by two of the present authors (I. Főzy, O. Szives). The lithologic log, chronostratigraphy and the distribution of the most important brachiopod species for section HK-II are shown in Fig. 2.

Fig. 1. near here

Fig. 2. near here

Section **HK-12** is situated about a hundred meters north-eastward from HK-II (No. 2 in Fig. 1; Geographical coordinates: 47°9′56.97″N, 17°47′8.11″E); it is an artificially enlarged outcrop, excavated by the HGI, exposing gently dipping Berriasian and Valanginian strata. The ammonoid, belemnoid and calpionellid fauna and integrated isotope and biostratigraphy of this section was recently published by Főzy et al. (2010). The lithologic log, the chronostratigraphy and the distribution of the most important brachiopod species from section HK-12 are shown in Fig. 3. The Berriasian part of this section is rather condensed; the thickness of the fossiliferous Berriasian strata does not exceed 3 m. Within a ten metres distance to the east, there is an artificial outcrop, excavated by the HGI, (**HK-12a**) exposing

Tithonian red nodular limestones that are a few metres thick. This section yielded a scarce brachiopod fauna of low diversity.

The third section which yielded the most abundant and diverse brachiopod fauna, called **Szilas Ravine**, is close to the village of Borzavár (No. 4 in Fig. 1; Geographical coordinates: 47°16′26.35″N, 17°49′03.08″E). The detailed collection was made from a steep, rocky hillside, exposing a continuous series of beds more than 20 m thick of upper Kimmeridgian to lower Berriasian age. The ammonoid stratigraphy of the Szilas Ravine was published by Főzy (1990, 2017), and is under revision by two of the present authors (I. Főzy, O. Szives). The lithologic log, chronostratigraphy and distribution of the most important brachiopod species for Szilas Ravine are shown in Fig. 4.

Fig. 3 and 4. near here

Some other sections and localities in the northern Bakony Mountains also yielded Tithonian and/or Berriasian brachiopods. The Hárskút, **Édesvíz Key Section** (No. 3 in Fig. 1) is very important for Valanginian–Hauterivian stratigraphy. Its lowermost few layers, with rather abundant brachiopod fauna, were dated as Tithonian and Berriasian, but the outcrop conditions do not allow drawing a log. A small, isolated outcrop, named **Zirc, Alsó-major** by Fülöp (1964) (No. 5 in Fig. 1), exposed Berriasian limestone layers with a few brachiopods. A famous locality at Olaszfalu, **Eperkés Hill** (No. 6 in Fig. 1) is an artificial trench, where masses of mostly disarticulated shells of brachiopods can be collected. Here a coarse grained, crinoidal-brachiopodal coquina limestone, the Szélhegy Formation, resembles the Lower Jurassic Hierlatz Limestone, but is dated as early Tithonian (Főzy 2017). The **Lókút, Key Section** (No. 7 in Fig. 1) has prime importance for Tithonian stratigraphy (Vigh 1984, Grabowski et al. 2010, 2017, Főzy et al. 2011, Főzy 2017). Detailed collecting in the 1960’s yielded a very abundant and diverse Tithonian brachiopod fauna, but the lack of Berriasian forms does not allow us to include the section in this evaluation.

3. Material and methods

The studied material was collected from well-dated, measured sections and some other localities of Tithonian and/or Berriasian age in the northern Bakony Mountains (discussed above). The brachiopods are extremely abundant: from among the 1277 identified specimens 940 were collected from the Tithonian and 337 from the Berriasian (including indeterminable specimens, identified only to genus level) (Table 2). Specimens have been coated with ammonium chloride before photography. Specimens are deposited in the collection of the Department of Palaeontology and Geology of the Hungarian Natural History Museum (Budapest), under inventory numbers prefixed by M., or INV.

In the following part of the present paper we focus on the brachiopods identified to species level, and to the data from the sections HK-II, HK-12 and Szilas Ravine. The reasons for this restriction are that (1) the ammonoid biostratigraphy of these sections were recently re-evaluated, (2) from these sections, only HK-II and Szilas Ravine appear to straddle the Jurassic–Cretaceous transition with a continuous record. Although HK-12 section probably starts with lower Berriasian deposits, ammonites are extremely rare and in a poor state of preservation from this part. The upper part of this section yielded identifiable ammonites from the Berriasella occitanica and Berriasella boissieri zones of the middle and upper Berriasian, so this section is also included in the present evaluation. Because of reason (2) above, we do not illustrate a detailed log with the brachiopod data of the otherwise well-dated Lókút Key Section, where the brachiopod fauna is restricted to the Tithonian.

Even after this, the Tithonian–Berriasian brachiopod fauna of the three relevant sections is very diverse and abundant: the remaining 565 specimens represent 21 species of 10 genera (Table 3). The overwhelming part belongs to the Pygopidae (456 specimens); the most abundant genera of the family are: *Antinomia* (263), *Pygope* (129) and *Triangope* (61). The family Nucleatidae is represented by 82 specimens; rhynchonellides appear subordinately (10 specimens). It is worth mentioning that the brachiopod fauna of the Szilas Ravine is by far the most abundant and diverse from among the three investigated sections (346 well-identified specimens, 18 species). The representative elements of the studied Tithonian–Berriasian brachiopod fauna are illustrated in Fig. 5.

Fig.5 near here

In the brachiopod taxonomy we largely followed the revised volumes of the "Treatise" (Savage et al., 2002; Lee et al., 2006) with a few exceptions. The generic name *Vjalovithyris* Tkhorszhevsky, 1989 (synonymized with *Nucleata* in the Treatise) was retained for the species *V. rupicola* (Zittel, 1870) with laterally lobate shell. On the other hand, the more or less globose species *bouei* (Zejszner, 1846), originally included to *Vjalovithyris* by Tkhorszhevsky (1989), was removed from *Vjalovithyris* to *Nucleata* Quenstedt, 1868. The genus *Pygope* Link, 1830, in our opinion, was too widely interpreted in the revised Treatise (Lee et al. 2006). Here we returned to the narrower interpretation of the previous Treatise (Muir-Wood 1965) and Buckman (1906), and restrict *Pygope* to the perforate or bifidate forms with straight lateral commissures, without beak ridges and planareas. In this concept, the species *diphya* (Buch, 1834), *axine* (Zejszner, 1846), *janitor* (Pictet, 1867) and *vomer* Vigh, 1981 belong to *Pygope*. Moreover, here we restore the validity of the generic name *Antinomia* Catullo, 1851, following Buckman (1906) and Muir-Wood (1965), for the perforate and bifidate forms with arched or sinuous lateral commissures and well developed planareas. The species *catulloi* (Pictet, 1867), *diphoros* (Zejszner, 1846) and *sima* (Zejszner, 1846) are ranked to *Antinomia*.

The rich and bed-by-bed collected cephalopod fauna provided a firm biostratigraphic age-constraint for the brachiopod fauna under study. Although belemnites are also common in the studied stratigraphic interval, ammonites are far more abundant. About 3000 and 3550 ammonites were collected from the Hárskút section and the Szilas Ravine, respectively. Most of the ammonites belong to the long ranged phylloceratids and lytoceratids, which are typical for the Mediterranean faunal assemblages. The age diagnostic Late Jurassic–Early Cretaceous ammonite genera and species also clearly show Mediterranean distributions, and, accordingly, can be characterized within the frameworks of the ammonite zonation previously developed for the Tethyan palaeobiogeographic realm (Ogg et al., 2016).

Focusing on the Jurassic–Cretaceous transitional interval in the studied sections, we can say that the Lower Tithonian is generally rather complete and all of the Hybonoticeras hybonotum, Semiformiceras darwini, Semiformiceras semiforme, Semiformiceras fallauxi and Micracanthoceras ponti ammonite zones can be documented. In the lower part of the upper Tithonian the "Durangites" and Micracanthoceras microcanthum zones can be recognized, but their separation is still problematic. Unfortunately, due to the impoverishment of the fauna in the latest Tithonian, the Jurassic/Cretaceous boundary cannot be precisely drawn in any of the studied sections by means of ammonites. At the HK-II section the boundary lies somewhere between beds 33–36 (Fig. 2, grey band), bed 32 yields clearly Berriasian forms. Related to the Szilas Ravine ammonite assemblage, the boundary between the upper Tithonian and the lower Berriasian lies somewhere between beds 37–43, bed 36 seems to contain a Berriasian assemblage (Fig. 4, grey band).

Table 1, 2, 3 near here

4. Results

Range charts have been constructed for the HK-II, HK-12 and Szilas Ravine sections with the occurrences of brachiopods in numbered beds of the respective sections indicated (Figs. 2, 3, 4). The scarce data set of the HK-II section suggests that the dominant brachiopod species (*Antinomia catulloi*, *Pygope diphya*) pass through the poorly defined Tithonian/Berriasian boundary (Fig. 2). The rather abundant and diverse brachiopod fauna of the HK-12 section is restricted to the Berriasian (Fig. 3). Yet, it is important to consider this section in the present study because it demonstrates the Berriasian re-appearance of a series of brachiopod species well known in the Tithonian (e.g. *Antinomia catulloi*, *A. diphoros*, *Pygope diphya*, *Triangope triangulus*, *Nucleata bouei*). The most profuse and robust brachiopod data were provided by the Szilas Ravine section (Fig. 4). Here at least ten brachiopod species cross the Tithonian/Berriasian boundary interval, though the biostratigraphical base of the Berriasian is ambiguous even in this section.

The stratigraphical ranges of the most significant (abundant and frequently occurring) brachiopod species, recorded in the well-dated sections through the Jurassic–Cretaceous transition in the Bakony Mountains, are shown in Fig. 6. Eleven species occur both in the Tithonian and in the Berriasian; while *Antinomia sima* seems to appear only in the late Berriasian. It must be noted that *Pygope axine* and *Vjalovithyris rupicola* are in fact very long ranging taxa, because (in the higher part of the HK-12 section) they are recorded again in the lower Valanginian.

Bed-by-bed investigation of the nannofossil assemblages of the three sections are in progress, but preliminary data revealed that nannofossils are in a poor to very poor state of preservation, showing clear signs of dissolution and diagenetic overprinting. Concerning the nannofossils of the nearby Lókút Key Section, which reveals the same stratigraphic units, Stoykova already concluded (in Grabowski et al. 2017) that they are in poor to very poor state of preservation and the best preserved forms are from the lower, Tithonian part of the section.

From HK-II and Szilas Ravine sections it seems that nannofossils will not provide accurate data to determine the exact age of the section due to the lack of age diagnostic forms such as nannoconids. Delicate nannofossil forms completely are lacking in both sections due to dissolution. Although nannoconids are considered among the most resistant, heavily calcitized forms (Thiersten, 1976), they show limited distribution in these sections which is in contrast to their usual dominance in pelagic carbonates (Busson and Noël, 1991). As Erba (1994) pointed out, nannoconids are considered as deep photic zone forms but temporarily may show very low abundance also in limestones with no sign of any disturbing environmental parameter such as dysoxia. According to her opinion, we may speculate that probably other, small scale environmental changes affected their abundance. Six smear slides from Szilas Ravine (beds 2, 37, 40, 43, 44, 48) yielded only dissolution resistant forms such as *Watznaueriales*, which does not allow us to perform quantitative statistical analysis. Nannofossil studies on the HK-II section have not yet been started. In relation to section HK-12, Báldi-Beke (1965) investigated the nannoconids of this site; however, we cannot correlate her sampling numbers with our bed numbering. The nannofossil assemblage is under revision.

5. Discussion

One of the remarkable features of the Tithonian–Berriasian brachiopod fauna of the Bakony Mountainss is the extremely high diversity (18 species) and density (512 specimens) of the brachiopod assemblage of the Szilas Ravine as compared to the other investigated sections (Tables 2, 3). Without going into details of Late Jurassic palaeogeography of the

Bakony Mountains, here we suggest that this enrichment of the brachiopod fauna points to the effect of a nearby submarine elevation. A steep, rocky slope might provide favourable environments for brachiopods (Vörös 1986) and might drive nutrient-rich upwellings.

The brachiopod fauna, collected bed-by-bed, together with ammonoids from well-dated sections through the Tithonian–Berriasian in the Bakony Mountains, offered an exceptional opportunity to determine the stratigraphic ranges of the brachiopod species at the level of substage or even ammonoid zone. Our results demonstrate that the most abundant brachiopod species frequently occur both in the Tithonian and in the Berriasian, and no change appears around the Jurassic–-Cretaceous boundary.

Our result is not unexpected; this subject was long-debated and perfectly summarized in a paper entitled ”Brachiopods at the Jurassic–Cretaceous boundary” by Ager (1975). He gave a “state-of-the-art” and concise review of the major brachiopod groups over the world in respect of the above topic. His main conclusions were: “there is certainly nothing noteworthy [faunal change] among the brachiopods at the conventional Tithonian/Berriasian level”, and “the brachiopods of the Berriasian are completely ‘Jurassic’ in character” (Ager 1975, p. 160, 161). It has to be noted however, that at that time, the bed-by-bed collections of brachiopods through the crucial interval, with detailed biostratigraphical control (ammonoid and/or micropalaeontological) were lacking.

In the last decades, due to the mentioned, advanced methods, the brachiopod record was greatly improved. The new results suggest that in the Euro-Boreal realm (i.e. in the territory of the contemporaneous European shelf and epicontinental seas) the brachiopod faunas changed at the Jurassic–Cretaceous boundary, even in species composition. For example, in Provence and elsewhere in the Euro-Boreal realm (Sandy 1986, fig. 21)), two of the nine recorded brachiopod species seem to disappear at the end of the Tithonian, and three appear in the Berriasian; the next remarkable faunal change appeared within the Valanginian.

In Svalbard (Sandy et al. 2014, table 1), five brachiopod species, from among the 14 recorded, are restricted to the uppermost Jurassic (Volgian) and further seven species appear just in the lowermost Cretaceous (Ryazanian). However it must be remarked that here the brachiopods represent spot samples, collected from laterally discontinuous seep carbonates.

On the other hand, the new results from the Mediterranean or intra-Tethyan realm definitely endorse the conclusions by Ager (1975). Barczyk (1991) and Krobicki (1994, 1996) published particularly important data on brachiopod distributions across the Tithonian–Berriasian boundary from measured sections of the Pieniny Klippen Belt (Poland), supported by biostratigraphical dating (on the basis of ammonoids and calpionellids). This classic area (including the famous localities of Rogoźnik and Czorsztyn) supplied the brachiopods for the old and very first complex monograph on pygopides by Zejszner (1846). The bed-by-bed collections of Barczyk (1991) resulted in a range chart where six brachiopod species, from the 17 recorded, crossed the Tithonian–Berriasian boundary, and one species showed its first appearance in the Berriasian. Based on newly collected material and a partial taxonomical revision, Krobicki (1994, 1996) published a detailed and robust data base from the same sections. He showed that, though the brachiopod ranges seem to be interrupted within the Tithonian, from among the 13 brachiopod species recorded by him, 10 crossed the Tithonian–Berriasian boundary level, and no new species appeared in the Berriasian.

Our present results fit very closely to those of the Polish authors and underscore that, at least in the intra-Tethyan realm (where both the Bakony area and the Czorsztyn ridge once belonged), no significant change of brachiopod faunas can be recorded at the Tithonian–Berriasian boundary. We may add that a complete turnover of brachiopod species in the investigated sections of the Bakony Mountains was recorded in the Valanginian (at the Saynoceras verrucosum zone) in relationship with the Weissert oceanic anoxic event (see Főzy et al., 2010).

Finally, two further quotations from the old paper (Ager, 1975) by the wise master. “If the author was forced into . . . defining the Jurassic–Cretaceous boundary on the basis of brachiopod evidence, then he would be very tempted to do so within the Valanginian . . .” (l.c. p. 160). And also a warning (for the procedure of defining stage and system boundaries): “No special consideration should be given to the brachiopods, which are no better and no worse than the rest.” (l.c. p. 161).

6. Conclusions

It is suggested that the extremely high diversity and density of the brachiopod assemblage of the Szilas Ravine points to the effect of a nearby submarine elevation.

On the basis of the extremely abundant brachiopod material, collected from well-dated, measured sections, it is demonstrated that the most abundant brachiopod species occur both in the Tithonian and in the Berriasian, and no faunal break or turnover of species appears at the Jurassic/Cretaceous boundary.

Our results are in agreement with the robust data published from the Czorsztyn succession of the Pieniny Klippen Belt (Poland) and endorse the already observed phenomenon that no obvious extinction or diversification event in brachiopods appeared at the Tithonian–Berriasian boundary. This conclusion is valid for the intra-Tethyan realm, where both the Bakony Mountains and the Czorsztyn succession belonged at the time in question. On the other hand, sparse data from the Euro-Boreal realm point to a turnover of brachiopod species at the Jurassic–Cretaceous boundary. This may suggest that the continuity of brachiopod species, crossing this boundary was connected to the continuity of the stable environment in the intra-Tethyan realm whereas in other areas of Europe end-Jurassic regression and Early Cretaceous transgression impacted sedimentary and biotic environments.

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Figure captions

Fig. 1 A, B.

(A) The geographical setting of the localities yielding important Tithonian and/or Berriasian brachiopod faunas (sections studied in detail are in boldface in the following list). **1: Hárskút, HK-II, 2: Hárskút, HK-12** (and HK-12a), 3: Hárskút, Édesvíz, Key Section, **4: Borzavár, Szilas Ravine**, 5: Zirc, Alsó-major, 6: Olaszfalu, Eperkés Hill, 7: Lókút, Key Section; inset map with black box shows regional location of sections in western Hungary. (B) The palaeogeographical setting of the area in the Tithonian. Asterisk indicates the inferred palaeoposition of the Bakony area. (Modified from Csontos and Vörös 2004)

Fig. 2.

Lithologic log, chronostratigraphy and distribution of the most important brachiopod species in the Hárskút, HK-II section. For lithologic legend see Fig. 3. Ammonoid zones after Főzy (1990). Ki.: Kimmeridgian, Be.: Beckeri, Hybon.: Hybonotum, Darw.: Darwini, Semif.: Semiforme, Pon.: Ponti, "D." Micr.: "Durangites" and Microcanthum. The grey rectangle indicates the approximate interval of the Berriasian base.

Fig. 3.

Lithologic log, chronostratigraphy and distribution of the most important brachiopod species in the Hárskút, HK-12 section. Lithologic log drawn by Damian Lodowski (Warsaw). Lithologic legend: 1: frequent ammonoids, 2: well-bedded white limestone, 3: thick-, or poorly-bedded light coloured limestone, 4: mostly red, nodular limestone, 5: radiolarite with calcareous nodules. Ammonoid zones after Főzy et al. (2010).

Fig. 4.

Lithologic log, chronostratigraphy and distribution of the most important brachiopod species in the Borzavár, Szilas Ravine section. For lithologic legend see Fig. 3. Ammonoid zones after Főzy (1990). Hyb.: Hybonotum, Pon.: Ponti, "D." and Micr.: "Durangites" and Microcanthum. The grey rectangle indicates the approximate interval of the Berriasian base.

Fig. 5.

Representative species of the studied Tithonian–Berriasian brachiopod fauna. Specimens have been coated with ammonium chloride before photography. Specimens are deposited in the collection of the Department of Palaeontology and Geology of the Hungarian Natural History Museum (Budapest), under inventory numbers prefixed by M., or INV. Scale bar = 2 cm. (1) *Monticlarella* ? *tatrica* (Zejszner, 1846) (INV 2019.52.) Olaszfalu, Eperkés Hill, loose, lower Tithonian; a: dorsal view, b: anterior view. (2) *Monticlarella* ? *agassizi* (Zejszner, 1846) (INV 2019.53.) Lókút, Key Section, Bed 4., upper Tithonian, a: dorsal view, b: anterior view. (3) *Pygope diphya* (Buch, 1834) (INV 2019.54.) Borzavár, Szilas Ravine, Bed 40, lower Berriasian (?), a: dorsal view, b: lateral view. (4) *Pygope diphya* (Buch, 1834) (INV 2019.55.) Borzavár, Szilas Ravine, Bed 41, lower Berriasian (?), a: dorsal view, b: lateral view. (5) *Pygope axine* (Zejszner, 1846) (INV 2019.56.) Borzavár, Szilas Ravine, Bed 60, upper Tithonian, a: dorsal view, b: lateral view. (6) *Pygope axine* (Zejszner, 1846) (INV 2019.57.) Borzavár, Szilas Ravine, Bed 62, upper Tithonian, a: dorsal view, b: lateral view. (7) *Pygope janitor* (Pictet, 1867) (INV 2019.58.) Borzavár, Szilas Ravine, Bed 97, lower Tithonian, a: dorsal view, b: lateral view, c: anterior view. (8) *Antinomia catulloi* (Pictet, 1867) (INV 2019.59.) Hárskút, HK-12 section, Bed 18, upper Berriasian, a: dorsal view, b: lateral view. (9) *Antinomia catulloi* (Pictet, 1867) (M.87.067.), Hárskút, HK-II section, Bed 43, upper

Tithonian, a: dorsal view, b: lateral view. (10) *Antinomia catulloi* (Pictet, 1867) (INV 2019.60.) Borzavár, Szilas Ravine, Bed 71, lower Tithonian, a: dorsal view, b: lateral view. (11) *Antinomia diphoros* (Zejszner, 1846) (INV 2019.61.) Borzavár, Szilas Ravine, Bed 39, lower Berriasian, a: dorsal view, b: lateral view. (12) *Antinomia sima* (Zejszner, 1846) (INV 2019.62.) Hárskút, HK-12 section, Bed 18, upper Berriasian, a: dorsal view, b: lateral view. (13) *Triangope triangulus* (Lamarck, 1819) (M.87.069.), Borzavár, Szilas Ravine, Bed 41, lower Berriasian (?), a: dorsal view, b: lateral view. (14) *Triangope triangulus* (Lamarck, 1819) (INV 2019.63.) Lókút, Key Section, Bed 34, lower Tithonian, a: dorsal view, b: lateral view. (15) *Nucleata bouei* (Zejszner, 1846) (INV 2019.64.) Hárskút, HK-12 section, Bed 20, upper Berriasian, a: dorsal view, b: anterior view. (16) *Nucleata bouei* (Zejszner, 1846) (INV 2019.65.) Borzavár, Szilas Ravine, Bed 31, lower Berriasian, a: dorsal view, b: anterior view. (17) *Vjalovithyris rupicola* (Zittel, 1870) (INV 2019.66.) Borzavár, Szilas Ravine, Bed 74, lower Tithonian, a: dorsal view, b: anterior view. (18) *Oppeliella pinguicula* (Zittel, 1870) (INV 2019.67.) Hárskút, HK-12 section, Bed 21, upper Berriasian, a: dorsal view, b: lateral view, c: anterior view.

Fig. 6.

Stratigraphical ranges of the most significant brachiopod species recorded in well-dated sections through the Jurassic–Cretaceous transition in the Bakony Mountains (this paper). Dotted lines indicate that *Pygope axine* and *Vjalovithyris rupicola* appeared again in the early Valanginian.

Table captions

Table 1.

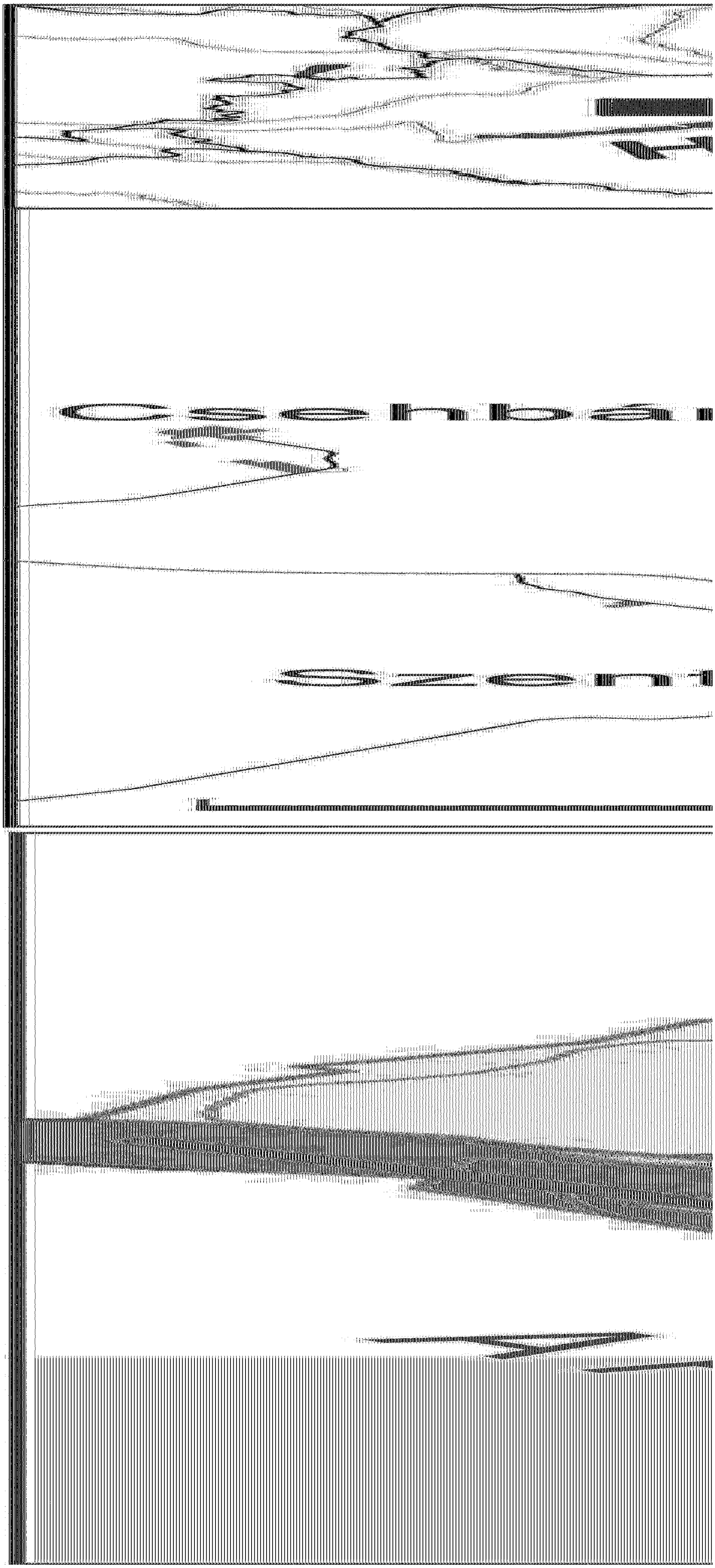
Number of brachiopod genera in the Middle Jurassic to Early Cretaceous interval – global data from Curry and Brunton, 2007.

Table 2.

Number of brachiopod specimens in the Tithonian and Berriasian sections from the Bakony Mountains in the present study.

Table 3.

Number of Tithonian and Berriasian brachiopod species in the three sections studied in detail.


Csehbán
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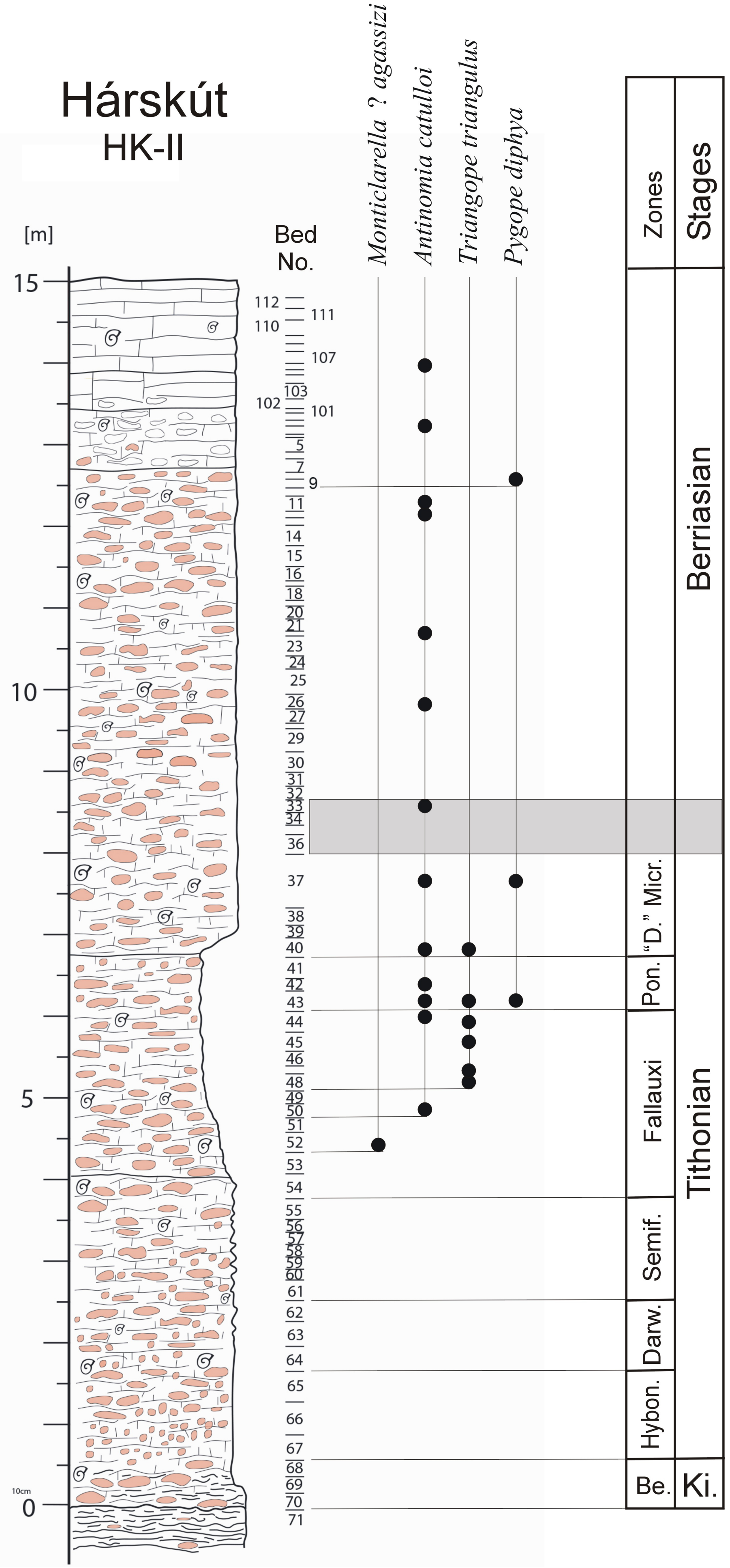

Hárskút
HK-II
[m]
15
10
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0
10cm
Bed No.
Monticlarella ? agassizi
Antinomia catulloi
Triangope triangulus
Pygope diphya
Zones
Stages
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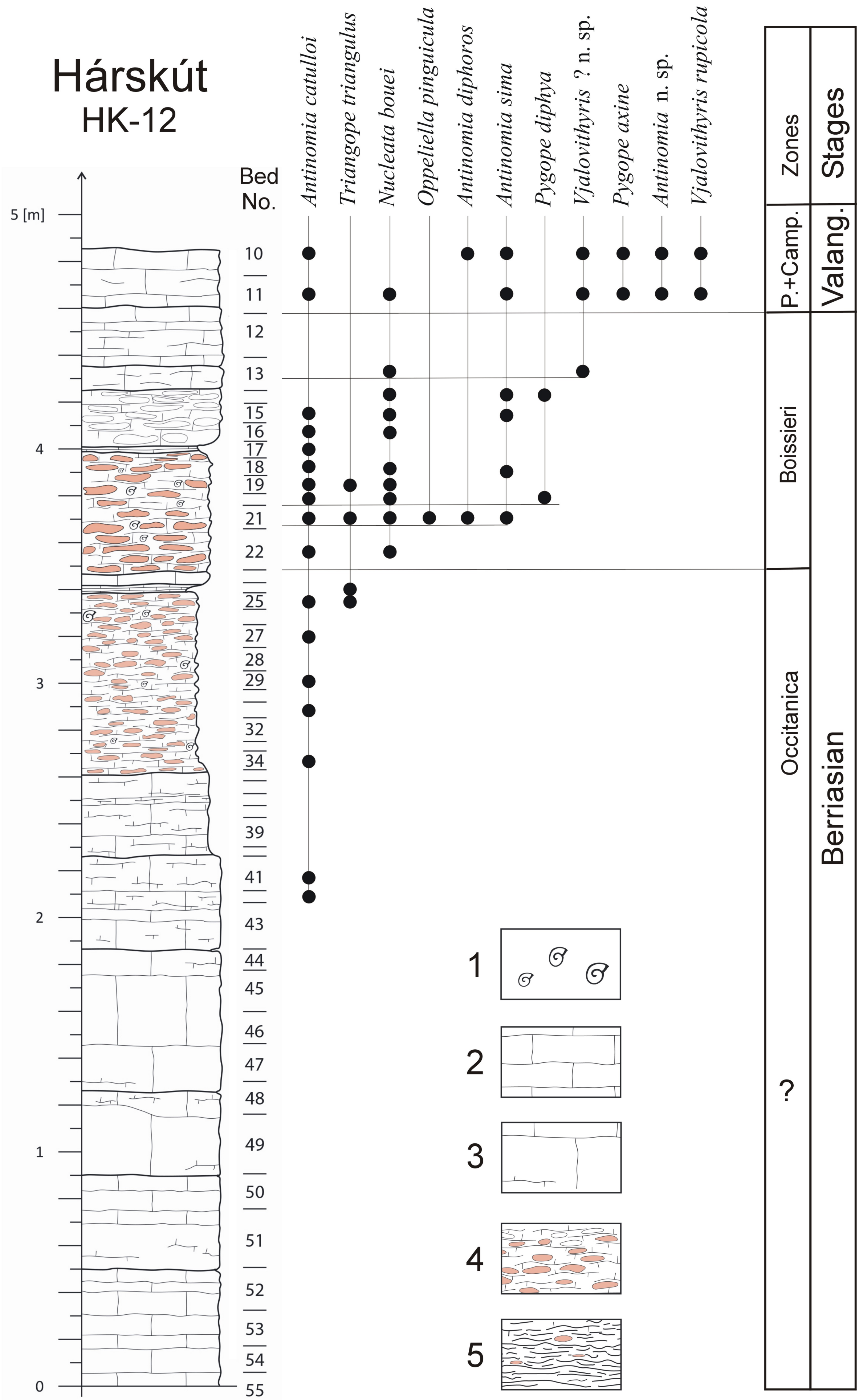
Pon.
Fallauxi
Semif.
Darw.
Hybon.
Be.



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55
Antinomia catulloi
Triangope triangulus
Nucleata bouei
Oppeliella pinguicula
Antinomia diphoros
Antinomia sima
Pygope diphya
Vjalovithyris ? n. sp.
Pygope axine
Antinomia n. sp.
Vjalovithyris rupicola
Zones
Stages
P.+Camp.
Valang.
Boissieri
Occitanica
?
Berriasian
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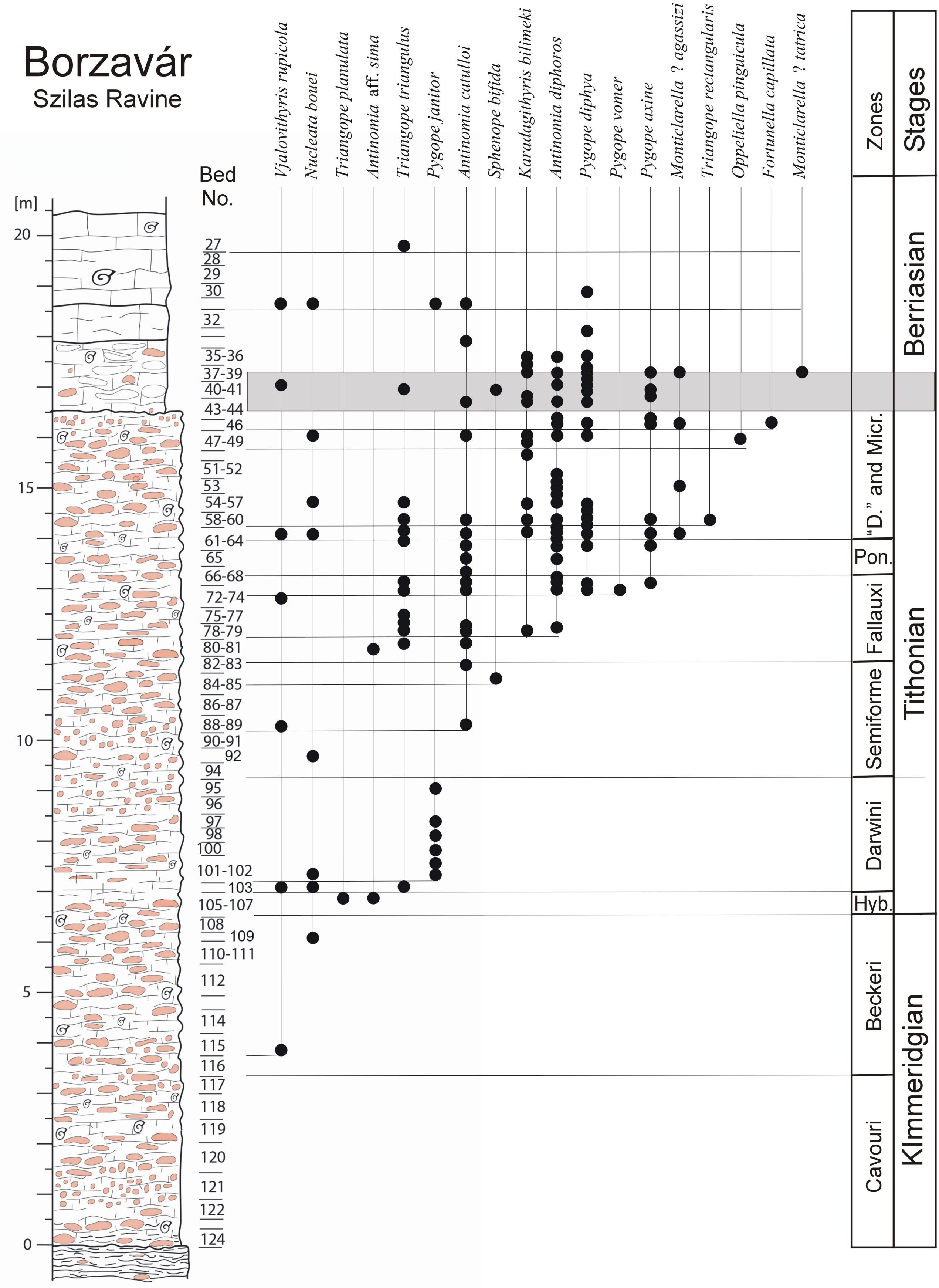
2
3
4
5



Borzavár
Szilas Ravine
[m]
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Bed No.
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Vjalovithyris rupicola
Nucleata bouei
Triangope planulata
Antinomia aff. sima
Triangope triangulus
Pygope janitor
Antinomia catulloi
Sphenope bifida
Karadagithyris bilimeki
Antinomia diphoros
Pygope diphya
Pygope vomer
Pygope axine
Monticlarella ? agassizi
Triangope rectangularis
Oppeliella pinguicula
Fortunella capillata
Monticlarella ? tatrica
Zones
Stages
Berriasian
"D." and Micr.
Pon.
Fallauxi
Semiforme
Tithonian
Darwini
Hyb.
Beckeri
Kimmeridgian
Cavouri

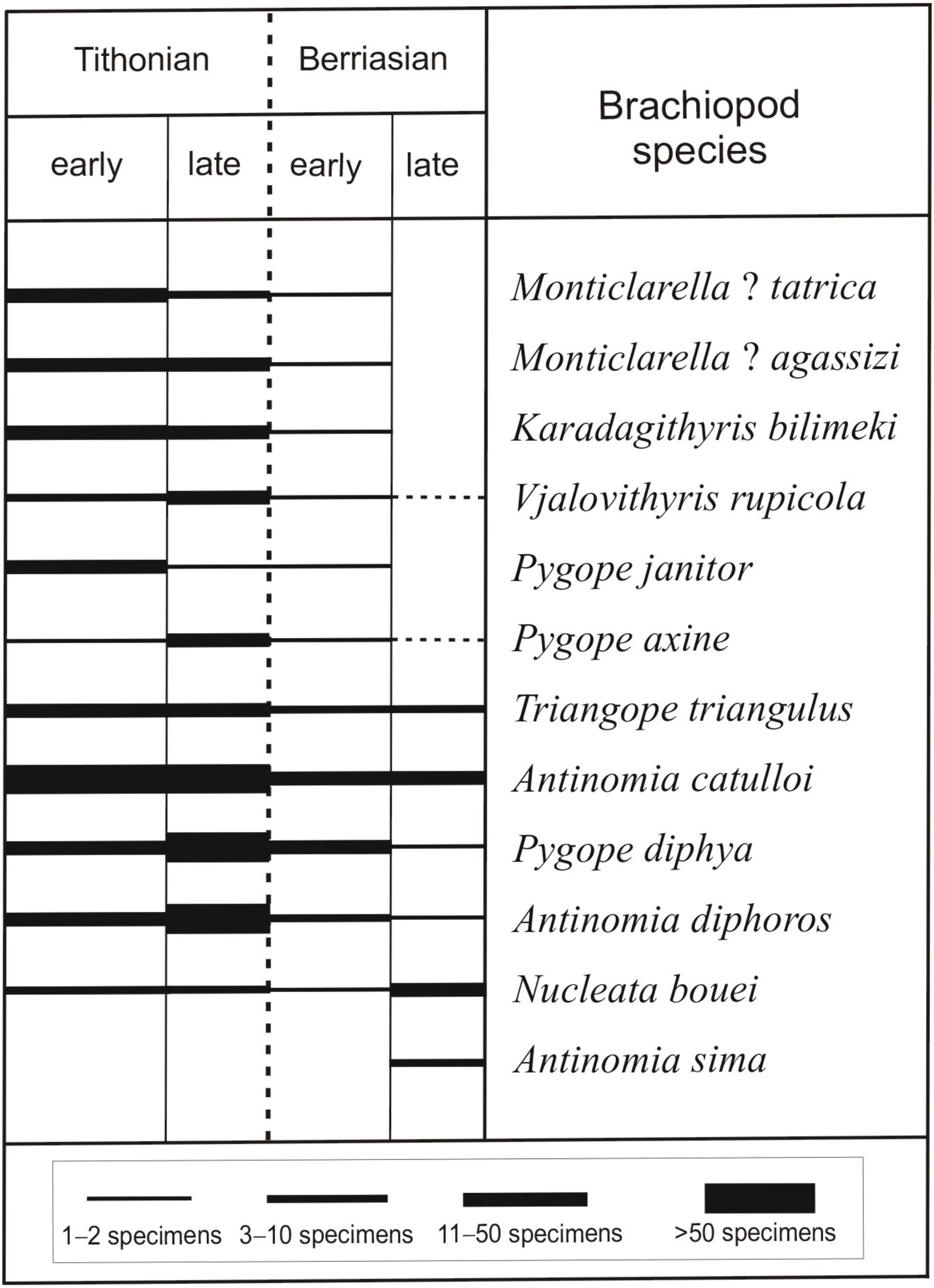
Tithonian
Berriasian
early
late
early
late
Brachiopod species
Monticlarella ? tatrica
Monticlarella ? agassizi
Karadagithyris bilimeki
Vjalovithyris rupicola
Pygope janitor
Pygope axine
Triangope triangulus
Antinomia catulloi
Pygope diphya
Antinomia diphoros
Nucleata bouei
Antinomia sima
1–2 specimens
3–10 specimens
11–50 specimens
>50 specimens

Table 1.
Number of brachiopod genera in the Middle Jurassic to Early Cretaceous interval (data from Curry & Brunton, 2007)

Epochs/Ages		Rhynchonellida	Terebratulida	**Total**
Early Cretaceous	Albian	9	58	**67**
	Aptian	11	55	**66**
	Barremian	14	54	**68**
	Hauterivian	17	61	**78**
	Valanginian	17	60	**77**
	Berriasian	18	59	**77**
Late Jurassic	Tithonian	22	46	**68**
	Kimmeridgian	24	52	**76**
	Oxfordian	33	56	**89**
Middle Jurassic	Callovian	49	57	**106**
	Bathonian	52	59	**111**
	Bajocian	57	64	**121**
	Aalenian	43	31	**74**

Table 2. Number of brachiopod specimens in the Tithonian and Berriasian sections considered in the present study

	Tithonian	Berriasian	total
Hárskút, HK-II	36	8	44
Hárskút, HK-12	0	179	179
Hárskút, HK-12a	16	0	16
Hárskút, Édesvíz, Key Section	31	40	71
Borzavár, Szilas Ravine	408	104	512
Zirc, Alsó-major	0	6	6
Olaszfalu, Eperkés Hill	172	0	172
Lókút, Key Section	277	0	277
total	940	337	1277

Table 3.
Specimen numbers of Tithonian and Berriasian brachiopod species in the three sections documented in detail

Brachiopod species	Hárskút HK-II	Hárskút HK-12	Borzavár Szilas Ravine
Monticlarella ? *tatrica* (Zejszner, 1846)			2
Monticlarella ? *agassizi* (Zejszner, 1846)	1		6
Fortunella capillata (Zittel, 1870)			1
Karadagithyris ? *bilimeki* (Suess, 1858)			15
Pygope diphya (Buch, 1834)	6	2	86
Pygope axine (Zejszner, 1846)		4	10
Pygope janitor (Pictet, 1867)			20
Pygope vomer Vigh, 1981			1
Antinomia diphoros (Zejszner, 1846)		3	84
Antinomia sima (Zejszner, 1846)		8	
Antinomia sp., aff. *sima* (Zejszner, 1846)			2
Antinomia catulloi (Pictet, 1867)	20	83	50
Antinomia n. sp.		13	
Triangope triangulus (Lamarck, 1819)	13	5	39
Triangope planulata (Zejszner, 1846)			3
Triangope rectangularis (Pictet, 1867)			1
Sphenope bifida Vörös, 2013			3
Nucleata bouei (Zejszner, 1846)		36	12
Vjalovithyris rupicola (Zittel, 1870)		7	10
Vjalovithyris n. sp.		17	
Oppeliella pinguicula (Zittel, 1870)		1	1
total	40	179	346