

Manuscript Details

Manuscript number	YCRES_2019_121_R1
Title	Brachiopod distribution through the Jurassic-Cretaceous transition in the western Tethyan pelagic realm: example from the Bakony Mountains (Hungary)
Article type	Full Length Article

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 Reviewers,
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 Cretaceous Research.

Budapest, 11.06.2019

Yours sincerely,
Attila Vörös

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

3
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9
10 Abstract

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

24

25

26 Key words

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

28

29 1. Introduction

30

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

49 The beds of the Jurassic–Cretaceous transition in the Bakony [Mountaints](#) are
50 extremely rich in brachiopods: more than 1200 specimens are available from this

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

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

59

60 2. Geological setting

61

62 2.1. General

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

76 nodular limestone, which becomes gradually less nodular, more compact and whiter in the
77 higher, mostly Berriasian parts.

78 *2.2. Localities and sections*

79 From among the seven localities (Fig. 1), yielding important Tithonian and/or
80 Berriasian brachiopod faunas, three sections were studied and are discussed in detail in the
81 present paper. Two of these are located near the village of Hárskút, along the Közöskút
82 Ravine. In section **HK-II** (No. 1 in Fig. 1; Geographical coordinates: 47°9'51.81"N,
83 17°47'3.98"E) the nearly horizontal beds form a prominent cliff around 15 m high known as
84 Prédikálószék ("The Pulpit"). The Tithonian to Berriasian ammonite and calpionellid
85 succession was discussed by Horváth and Knauer (1986) and Főzy (1990, 2017), and is under
86 revision by two of the present authors (I. Főzy, O. Szives). The lithologic log,
87 chronostratigraphy and the distribution of the most important brachiopod species for section
88 HK-II are shown in Fig. 2.

89 Fig. 1. near here

90 Fig. 2. near here

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

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

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

110

111 Fig. 3 and 4. near here

112

113 Some other sections and localities in the northern Bakony Mountains also yielded
114 Tithonian and/or Berriasian brachiopods. The Hárskút, **Édesvíz Key Section** (No. 3 in Fig. 1)
115 is very important for Valanginian–Hauterivian stratigraphy. Its lowermost few layers, with
116 rather abundant brachiopod fauna, were dated as Tithonian and Berriasian, but the outcrop
117 conditions do not allow drawing a log. A small, isolated outcrop, named **Zirc, Alsó-major** by
118 Fülöp (1964) (No. 5 in Fig. 1), exposed Berriasian limestone layers with a few brachiopods. A
119 famous locality at Olaszfalu, **Eperkés Hill** (No. 6 in Fig. 1) is an artificial trench, where
120 masses of mostly disarticulated shells of brachiopods can be collected. Here a coarse grained,
121 crinoidal-brachiopodal coquina limestone, the Szélhegy Formation, [is reminiscent](#)
122 [of](#) [resembles](#) the Lower Jurassic Hierlatz Limestone, but is dated as early Tithonian (Főzy
123 2017). The **Lókút, Key Section** (No. 7 in Fig. 1) has prime importance for Tithonian
124 stratigraphy (Vigh 1984, Grabowski et al. 2010, 2017, Főzy et al. 2011, Főzy 2017). Detailed

125 collecting in the 1960's yielded a very abundant and diverse Tithonian brachiopod fauna, but
126 the lack of Berriasian forms does not allow us to include the section in this evaluation.

127

128 3. Material and methods

129

130 The studied material was collected from well-dated, measured sections and some other
131 localities of Tithonian and/or Berriasian age in the northern Bakony Mountains (discussed
132 above). The brachiopods are extremely abundant: from among the 1277 identified specimens
133 940 were collected from the Tithonian and 337 from the Berriasian (including indeterminate
134 specimens, identified only to genus level) (Table 2). Specimens have been coated with
135 ammonium chloride before photography. Specimens are deposited in the collection of the
136 Department of Palaeontology and Geology of the Hungarian Natural History Museum
137 (Budapest), under inventory numbers prefixed by M., or INV.

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

149 Even after this, the Tithonian–Berriasian brachiopod fauna of the three relevant
150 sections is very diverse and abundant [at international standard](#): the remaining 565 specimens
151 represent 21 species of 10 genera (Table 3). The overwhelming part belongs to the Pygopidae
152 ([456–456](#) specimens); the most abundant genera of the family are: *Antinomia* (263), *Pygope*
153 (129) and *Triangope* ([6461](#)). The family Nucleatidae is represented by [84–82](#) specimens;
154 rhynchonellides appear subordinately (10 specimens). It is worth mentioning that the
155 brachiopod fauna of the Szilas Ravine is by far the most abundant and diverse from among
156 the three investigated sections (346 well-identified specimens, 18 species). The representative
157 elements of the studied Tithonian–Berriasian brachiopod fauna are illustrated in Fig. 5.

158 Fig.5 near here

159

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

174 planareas. The species *catulloi* (Pictet, 1867), *diphoros* (Zejszner, 1846) and *sima* (Zejszner,
175 1846) are ranked to *Antinomia*.

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

185 Focusing on the Jurassic–Cretaceous transitional interval in the studied sections, we
186 can say that the Lower Tithonian is generally rather complete and all of the *Hybonotoceras*
187 *hybonotum*, *Semiformiceras darwini*, *Semiformiceras semiforme*, *Semiformiceras fallauxi*
188 and *Micracanthoceras ponti* ammonite zones can be documented. In the lower part of the
189 Upper-upper Tithonian the “Durangites” and *Micracanthoceras microcanthum* zones can be
190 recognized, but their separation is still problematic. Unfortunately, due to the impoverishment
191 of the fauna in the latest Tithonian, the Jurassic/Cretaceous boundary cannot be precisely
192 drawn in any of the studied sections by means of ammonites. At the HK-II section the
193 boundary lies somewhere between beds 33–36 (Fig. 2, grey band), bed 32 yields clearly
194 Berriasian forms. Related to the Szilas Ravine ammonite assemblage, the boundary between
195 the Upper-upper Tithonian and the Lower-lower Berriasian lies somewhere between beds 37–
196 43, bed 36 seems to contain a Berriasian assemblage (Fig. 4, grey band).

197

198 Table 1, 2, 3 near here

199

200 4. Results

201

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

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

221 Bed-by-bed investigation of the nannofossil assemblages of the three sections are in
222 progress, but preliminary data revealed that nannofossils are in a poor to very poor state of
223 preservation, showing clear signs of dissolution and diagenetic overprinting. Concerning the

224 nannofossils of the nearby Lókút Key Section, which reveals the same stratigraphic units,
225 Stoykova already concluded (in Grabowski et al. 2017) that they are in poor to very poor state
226 of preservation and the best preserved forms are from the lower, Tithonian part of the section.

227 From HK-II and Szilas Ravine sections it seems that nannofossils will not provide
228 accurate data to determine the exact age of the section due to the lack of age diagnostic forms
229 such as nannoconids. Delicate nannofossil forms completely are lacking in both sections due
230 to dissolution. Although nannoconids are considered among the most resistant, heavily
231 calcitized forms (Thiersten, 1976), they show limited distribution in these sections which is in
232 contrast to their usual dominance in pelagic carbonates (Busson and Noël, 1991). As Erba
233 (1994) pointed out, nannoconids are considered as deep photic zone forms but temporarily
234 may show very low abundance also in limestones with no sign of any disturbing
235 environmental parameter such as dysoxia. According to her opinion, we may speculate that
236 probably other, small scale environmental changes affected their abundance. Six smear slides
237 from Szilas Ravine (beds 2, 37, 40, 43, 44, 48) yielded only dissolution resistant forms such
238 as *Watznaueriales*, which does not allow us to perform quantitative statistical analysis.
239 Nannofossil studies on the HK-II section have not yet been started. In relation to section HK-
240 12, Báldi-Beke (1965) investigated the nannoconids of this site; however, we cannot correlate
241 her sampling numbers with our bed numbering. The nannofossil assemblage is under revision.

242

243 5. Discussion

244

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

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

Commented [1]: cf. Voros 1986 Palaeo3 ?

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

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

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

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

278 On the other hand, the new results from the Mediterranean or intra-Tethyan realm
279 definitely endorse the conclusions by Ager (1975). Barczyk (1991) and Krobicki (1994, 1996)
280 published particularly important data on brachiopod distributions across the Tithonian—
281 Berriasian boundary from measured sections of the Pieniny Klippen Belt (Poland), supported
282 by biostratigraphical dating (on the basis of ammonoids and calpionellids). This classic area
283 (including the famous localities of Rogoźnik and Czorsztyn) supplied the brachiopods for the
284 old and very first complex monograph on pygopides by Zejszner (1846). The bed-by-bed
285 collections of Barczyk (1991) resulted in a range chart where six brachiopod species, from the
286 17 recorded, crossed the Tithonian—Berriasian boundary, and one species showed its first
287 appearance in the Berriasian. Based on newly collected material and a partial taxonomical
288 revision, Krobicki (1994, 1996) published a detailed and robust data base from the same
289 sections. He showed that, though the brachiopod ranges seem to be interrupted within the
290 Tithonian, from among the 13 brachiopod species recorded by him, 10 crossed the Tithonian-
291 —Berriasian boundary level, and no new species appeared in the Berriasian.

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

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

305

306 6. Conclusions

307

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

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

314 Our results are in agreement with the robust data published from the Czorsztyn ~~zone~~
315 succession of the Pieniny Klippen Belt (Poland) and endorse the ~~old-predicted~~
316 assumption already observed phenomenon that ~~nothing happened to the~~ obvious extinction
317 or diversification event in brachiopods appeared at the Tithonian—Berriasian boundary. This
318 conclusion is valid for the intra-Tethyan realm, where both the Bakony Mountains and the
319 Czorsztyn ~~zone~~ succession belonged at the time in question. On the other hand, sparse data
320 from the Euro-Boreal realm point to a turnover of brachiopod species at the Jurassic—
321 Cretaceous boundary. This may suggest that the continuity of brachiopod species, crossing
322 this boundary was connected to the continuity of the stable environment in the intra-Tethyan

323 realm- whereas in other areas of Europe end-Jurassic regression and Early Cretaceous
324 transgression impacted sedimentary and biotic environments.

325

326 Acknowledgements

327

328 The authors are indebted to Prof. B. Granier for inviting this paper to the special
329 volume of Cretaceous Research. The valuable comments of the reviewers M. R. Sandy and
330 M. Krobicki, and the editor E. Koutsoukos, are greatly acknowledged. The research was
331 supported by the grant OTKA/NKFI project no: K123762.

333

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440 Polish).

442

443 Figure captions

444

445 Fig. 1 A, B.

446 (A) The geographical setting of the localities yielding important Tithonian and/or Berriasian
447 brachiopod faunas (sections studied in detail are in boldface in the following list). **1:**

448 **Hárskút, HK-II, 2: Hárskút, HK-12** (and HK-12a), 3: Hárskút, Édesvíz, Key Section, **4:**

449 **Borzavár, Szilas Ravine**, 5: Zirc, Alsó-major, 6: Olaszfalu, Eperkés Hill, 7: Lókút, Key

450 Section; inset map with black box shows regional location of sections in western Hungary.

451 (B) The palaeogeographical setting of the area in the Tithonian. Asterisk indicates the inferred
452 palaeoposition of the Bakony area. (Modified from Csontos and Vörös 2004)

453

454 Fig. 2.

455 Lithologic log, chronostratigraphy and distribution of the most important brachiopod species

456 in the Hárskút, HK-II section. For lithologic legend see Fig. 3. Ammonoid zones after Főzy

457 (1990). Ki.: Kimmeridgian, Be.: Beckeri, Hybon.: Hybonotum, Darw.: Darwini, Semif.:

458 Semiforme, Pon.: Ponti, "D." Micr.: "Durangites" and Microcanthum. The grey rectangle

459 indicates the approximate interval of the Berriasian base.

460

461 Fig. 3.

462 Lithologic log, chronostratigraphy and distribution of the most important brachiopod species

463 in the Hárskút, HK-12 section. Lithologic log drawn by Damian Lodowski (Warsaw).

464 Lithologic legend: 1: frequent ammonoids, 2: well-bedded white limestone, 3: thick-, or

465 poorly-bedded light coloured limestone, 4: mostly red, nodular limestone, 5: radiolarite with

466 calcareous nodules. Ammonoid zones after Főzy et al. (2010).

467

468 Fig. 4.

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

473

474 Fig. 5.

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

480 (1) *Monticlarella ? tatica* (Zejszner, 1846) (INV 2019.52.) Olaszfalu, Eperkés Hill, loose,

481 ~~Lower-lower~~ Tithonian; a: dorsal view, b: anterior view. (2) *Monticlarella ? agassizi*

482 (Zejszner, 1846) (INV 2019.53.) Lókút, Key Section, Bed 4., ~~Upper-upper~~ Tithonian, a:

483 dorsal view, b: anterior view. (3) *Pygope diphya* (Buch, 1834) (INV 2019.54.) Borzavár, Szilas

484 Ravine, Bed 40, ~~Lower-lower~~ Berriasian (?), a: dorsal view, b: lateral view. (4) *Pygope diphya*

485 (Buch, 1834) (INV 2019.55.) Borzavár, Szilas Ravine, Bed 41, ~~Lower-lower~~ Berriasian (?), a:

486 dorsal view, b: lateral view. (5) *Pygope axine* (Zejszner, 1846) (INV 2019.56.) Borzavár,

487 Szilas Ravine, Bed 60, ~~Upper-upper~~ Tithonian, a: dorsal view, b: lateral view. (6) *Pygope*

488 *axine* (Zejszner, 1846) (INV 2019.57.) Borzavár, Szilas Ravine, Bed 62, ~~Upper-upper~~

489 Tithonian, a: dorsal view, b: lateral view. (7) *Pygope janitor* (Pictet, 1867) (INV 2019.58.)

490 Borzavár, Szilas Ravine, Bed 97, ~~Lower-lower~~ Tithonian, a: dorsal view, b: lateral view, c:

491 anterior view. (8) *Antinomia catulloi* (Pictet, 1867) (INV 2019.59.) Hárskút, HK-12 section,

492 Bed 18, Upper-upper Berriasian, a: dorsal view, b: lateral view. (9) *Antinomia catulloi* (Pictet,
493 1867) (M.87.067.), Hárskút, HK-II section, Bed 43, Upper-upper Tithonian, a: dorsal view, b:
494 lateral view. (10) *Antinomia catulloi* (Pictet, 1867) (INV 2019.60.) Borzavár, Szilas Ravine,
495 Bed 71, Lower-lower Tithonian, a: dorsal view, b: lateral view. (11) *Antinomia diphoros*
496 (Zejszner, 1846) (INV 2019.61.) Borzavár, Szilas Ravine, Bed 39, Lower-lower Berriasian, a:
497 dorsal view, b: lateral view. (12) *Antinomia sima* (Zejszner, 1846) (INV 2019.62.) Hárskút,
498 HK-12 section, Bed 18, Upper-upper Berriasian, a: dorsal view, b: lateral view. (13)
499 *Triangope triangulus* (Lamarck, 1819) (M.87.069.), Borzavár, Szilas Ravine, Bed 41, Lower
500 lower Berriasian (?), a: dorsal view, b: lateral view. (14) *Triangope triangulus* (Lamarck,
501 1819) (INV 2019.63.) Lókút, Key Section, Bed 34, Lower-lower Tithonian, a: dorsal view, b:
502 lateral view. (15) *Nucleata bouei* (Zejszner, 1846) (INV 2019.64.) Hárskút, HK-12 section,
503 Bed 20, Upper-upper Berriasian, a: dorsal view, b: anterior view. (16) *Nucleata bouei*
504 (Zejszner, 1846) (INV 2019.65.) Borzavár, Szilas Ravine, Bed 31, Lower-lower Berriasian, a:
505 dorsal view, b: anterior view. (17) *Vjalovithyris rupicola* (Zittel, 1870) (INV 2019.66.)
506 Borzavár, Szilas Ravine, Bed 74, Lower-lower Tithonian, a: dorsal view, b: anterior view.
507 (18) *Oppeliella pinguicula* (Zittel, 1870) (INV 2019.67.) Hárskút, HK-12 section, Bed 21,
508 Upper-upper Berriasian, a: dorsal view, b: lateral view, c: anterior view.

509

510 Fig. 6.

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

516

517 Table captions

518

519 Table 1.

520 Number of brachiopod genera in the Middle Jurassic to Early Cretaceous interval – global

521 data from Curry and Brunton, 2007.

522

523 Table 2.

524 Number of brachiopod specimens in the Tithonian and Berriasian sections from [Hungarythe](#)

525 [Bakony Mountains](#) in the present study.

526

527 Table 3.

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

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

3
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9
10 Abstract

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

24

25

26 Key words

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

28

29 1. Introduction

30

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

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

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

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

59

60 2. Geological setting

61

62 2.1. General

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

75 lower, Tithonian part of the sections consists of reddish, nodular limestone, which becomes
76 gradually less nodular, more compact and whiter in the higher, mostly Berriasian parts.

77 *2.2. Localities and sections*

78 From among the seven localities (Fig. 1), yielding important Tithonian and/or
79 Berriasian brachiopod faunas, three sections were studied and are discussed in detail in the
80 present paper. Two of these are located near the village of Hárskút, along the Közöskút
81 Ravine. In section **HK-II** (No. 1 in Fig. 1; Geographical coordinates: 47°9'51.81"N,
82 17°47'3.98"E) the nearly horizontal beds form a prominent cliff around 15 m high known as
83 Prédikálószék ("The Pulpit"). The Tithonian to Berriasian ammonite and calpionellid
84 succession was discussed by Horváth and Knauer (1986) and Főzy (1990, 2017), and is under
85 revision by two of the present authors (I. Főzy, O. Szives). The lithologic log,
86 chronostratigraphy and the distribution of the most important brachiopod species for section
87 HK-II are shown in Fig. 2.

88 Fig. 1. near here

89 Fig. 2. near here

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

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

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

109

110 Fig. 3 and 4. near here

111

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

124 yielded a very abundant and diverse Tithonian brachiopod fauna, but the lack of Berriasian
125 forms does not allow us to include the section in this evaluation.

126

127 3. Material and methods

128

129 The studied material was collected from well-dated, measured sections and some other
130 localities of Tithonian and/or Berriasian age in the northern Bakony Mountains (discussed
131 above). The brachiopods are extremely abundant: from among the 1277 identified specimens
132 940 were collected from the Tithonian and 337 from the Berriasian (including indeterminate
133 specimens, identified only to genus level) (Table 2). Specimens have been coated with
134 ammonium chloride before photography. Specimens are deposited in the collection of the
135 Department of Palaeontology and Geology of the Hungarian Natural History Museum
136 (Budapest), under inventory numbers prefixed by M., or INV.

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

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

157 Fig.5 near here

158

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

173 planareas. The species *catulloi* (Pictet, 1867), *diphoros* (Zejszner, 1846) and *sima* (Zejszner,
174 1846) are ranked to *Antinomia*.

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

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

196

197 Table 1, 2, 3 near here

198

199 4. Results

200

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

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

220 Bed-by-bed investigation of the nannofossil assemblages of the three sections are in
221 progress, but preliminary data revealed that nannofossils are in a poor to very poor state of
222 preservation, showing clear signs of dissolution and diagenetic overprinting. Concerning the

223 nannofossils of the nearby Lókút Key Section, which reveals the same stratigraphic units,
224 Stoykova already concluded (in Grabowski et al. 2017) that they are in poor to very poor state
225 of preservation and the best preserved forms are from the lower, Tithonian part of the section.

226 From HK-II and Szilas Ravine sections it seems that nannofossils will not provide
227 accurate data to determine the exact age of the section due to the lack of age diagnostic forms
228 such as nannoconids. Delicate nannofossil forms completely are lacking in both sections due
229 to dissolution. Although nannoconids are considered among the most resistant, heavily
230 calcitized forms (Thiersten, 1976), they show limited distribution in these sections which is in
231 contrast to their usual dominance in pelagic carbonates (Busson and Noël, 1991). As Erba
232 (1994) pointed out, nannoconids are considered as deep photic zone forms but temporarily
233 may show very low abundance also in limestones with no sign of any disturbing
234 environmental parameter such as dysoxia. According to her opinion, we may speculate that
235 probably other, small scale environmental changes affected their abundance. Six smear slides
236 from Szilas Ravine (beds 2, 37, 40, 43, 44, 48) yielded only dissolution resistant forms such
237 as *Watznaueriales*, which does not allow us to perform quantitative statistical analysis.

238 Nannofossil studies on the HK-II section have not yet been started. In relation to section HK-
239 12, Báldi-Beke (1965) investigated the nannoconids of this site; however, we cannot correlate
240 her sampling numbers with our bed numbering. The nannofossil assemblage is under revision.

241

242 5. Discussion

243

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

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

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

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

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

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

277 On the other hand, the new results from the Mediterranean or intra-Tethyan realm
278 definitely endorse the conclusions by Ager (1975). Barczyk (1991) and Krobicki (1994, 1996)
279 published particularly important data on brachiopod distributions across the Tithonian–
280 Berriasian boundary from measured sections of the Pieniny Klippen Belt (Poland), supported
281 by biostratigraphical dating (on the basis of ammonoids and calpionellids). This classic area
282 (including the famous localities of Rogóżnik and Czorsztyn) supplied the brachiopods for the
283 old and very first complex monograph on pygopides by Zejszner (1846). The bed-by-bed
284 collections of Barczyk (1991) resulted in a range chart where six brachiopod species, from the
285 17 recorded, crossed the Tithonian–Berriasian boundary, and one species showed its first
286 appearance in the Berriasian. Based on newly collected material and a partial taxonomical
287 revision, Krobicki (1994, 1996) published a detailed and robust data base from the same
288 sections. He showed that, though the brachiopod ranges seem to be interrupted within the
289 Tithonian, from among the 13 brachiopod species recorded by him, 10 crossed the Tithonian–
290 Berriasian boundary level, and no new species appeared in the Berriasian.

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

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

304

305 6. Conclusions

306

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

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

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

323

324 Acknowledgements

325

326 The authors are indebted to Prof. B. Granier for inviting this paper to the special
327 volume of Cretaceous Research. The valuable comments of the reviewers M. R. Sandy and
328 M. Krobicki, and the editor E. Koutsoukos, are greatly acknowledged. The research was
329 supported by the grant OTKA/NKFI project no: K123762.

330

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437 Polish).

439

440 Figure captions

441

442 Fig. 1 A, B.

443 (A) The geographical setting of the localities yielding important Tithonian and/or Berriasian
444 brachiopod faunas (sections studied in detail are in boldface in the following list). **1:**

445 **Hárskút, HK-II, 2: Hárskút, HK-12** (and HK-12a), 3: Hárskút, Édesvíz, Key Section, **4:**

446 **Borzavár, Szilas Ravine**, 5: Zirc, Alsó-major, 6: Olaszfalu, Eperkés Hill, 7: Lókút, Key

447 Section; inset map with black box shows regional location of sections in western Hungary.

448 (B) The palaeogeographical setting of the area in the Tithonian. Asterisk indicates the inferred
449 palaeoposition of the Bakony area. (Modified from Csontos and Vörös 2004)

450

451 Fig. 2.

452 Lithologic log, chronostratigraphy and distribution of the most important brachiopod species

453 in the Hárskút, HK-II section. For lithologic legend see Fig. 3. Ammonoid zones after Főzy

454 (1990). Ki.: Kimmeridgian, Be.: Beckeri, Hybon.: Hybonotum, Darw.: Darwini, Semif.:

455 Semiforme, Pon.: Ponti, "D." Micr.: "Durangites" and Microcanthum. The grey rectangle

456 indicates the approximate interval of the Berriasian base.

457

458 Fig. 3.

459 Lithologic log, chronostratigraphy and distribution of the most important brachiopod species

460 in the Hárskút, HK-12 section. Lithologic log drawn by Damian Lodowski (Warsaw).

461 Lithologic legend: 1: frequent ammonoids, 2: well-bedded white limestone, 3: thick-, or

462 poorly-bedded light coloured limestone, 4: mostly red, nodular limestone, 5: radiolarite with

463 calcareous nodules. Ammonoid zones after Főzy et al. (2010).

464

465 Fig. 4.

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

470

471 Fig. 5.

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

476 (1) *Monticlarella ? tatrlica* (Zejszner, 1846) (INV 2019.52.) Olaszfalu, Eperkés Hill, loose,
477 lower Tithonian; a: dorsal view, b: anterior view. (2) *Monticlarella ? agassizi* (Zejszner,
478 1846) (INV 2019.53.) Lókút, Key Section, Bed 4., upper Tithonian, a: dorsal view, b: anterior
479 view. (3) *Pygope diphya* (Buch, 1834) (INV 2019.54.) Borzavár, Szilas Ravine, Bed 40, lower
480 Berriasian (?), a: dorsal view, b: lateral view. (4) *Pygope diphya* (Buch, 1834) (INV 2019.55.)
481 Borzavár, Szilas Ravine, Bed 41, lower Berriasian (?), a: dorsal view, b: lateral view. (5)
482 *Pygope axine* (Zejszner, 1846) (INV 2019.56.) Borzavár, Szilas Ravine, Bed 60, upper
483 Tithonian, a: dorsal view, b: lateral view. (6) *Pygope axine* (Zejszner, 1846) (INV 2019.57.)
484 Borzavár, Szilas Ravine, Bed 62, upper Tithonian, a: dorsal view, b: lateral view. (7) *Pygope*
485 *janitor* (Pictet, 1867) (INV 2019.58.) Borzavár, Szilas Ravine, Bed 97, lower Tithonian, a:
486 dorsal view, b: lateral view, c: anterior view. (8) *Antinomia catulloi* (Pictet, 1867) (INV
487 2019.59.) Hárskút, HK-12 section, Bed 18, upper Berriasian, a: dorsal view, b: lateral view. (9)
488 *Antinomia catulloi* (Pictet, 1867) (M.87.067.), Hárskút, HK-II section, Bed 43, upper

489 Tithonian, a: dorsal view, b: lateral view. (10) *Antinomia catulloi* (Pictet, 1867) (INV 2019.60.)
490 Borzavár, Szilas Ravine, Bed 71, lower Tithonian, a: dorsal view, b: lateral view. (11)
491 *Antinomia diphoros* (Zejszner, 1846) (INV 2019.61.) Borzavár, Szilas Ravine, Bed 39, lower
492 Berriasian, a: dorsal view, b: lateral view. (12) *Antinomia sima* (Zejszner, 1846) (INV
493 2019.62.) Hárskút, HK-12 section, Bed 18, upper Berriasian, a: dorsal view, b: lateral view.
494 (13) *Triangope triangulus* (Lamarck, 1819) (M.87.069.), Borzavár, Szilas Ravine, Bed 41,
495 lower Berriasian (?), a: dorsal view, b: lateral view. (14) *Triangope triangulus* (Lamarck,
496 1819) (INV 2019.63.) Lókút, Key Section, Bed 34, lower Tithonian, a: dorsal view, b: lateral
497 view. (15) *Nucleata bouei* (Zejszner, 1846) (INV 2019.64.) Hárskút, HK-12 section, Bed 20,
498 upper Berriasian, a: dorsal view, b: anterior view. (16) *Nucleata bouei* (Zejszner, 1846) (INV
499 2019.65.) Borzavár, Szilas Ravine, Bed 31, lower Berriasian, a: dorsal view, b: anterior view.
500 (17) *Vjalovithyris rupicola* (Zittel, 1870) (INV 2019.66.) Borzavár, Szilas Ravine, Bed 74,
501 lower Tithonian, a: dorsal view, b: anterior view. (18) *Oppeliella pingucula* (Zittel, 1870)
502 (INV 2019.67.) Hárskút, HK-12 section, Bed 21, upper Berriasian, a: dorsal view, b: lateral
503 view, c: anterior view.

504

505 Fig. 6.

506 Stratigraphical ranges of the most significant brachiopod species recorded in well-dated
507 sections through the Jurassic–Cretaceous transition in the Bakony Mountains (this paper).

508 Dotted lines indicate that *Pygope axine* and *Vjalovithyris rupicola* appeared again in the early
509 Valanginian.

511

512 Table captions

513

514 Table 1.

515 Number of brachiopod genera in the Middle Jurassic to Early Cretaceous interval – global

516 data from Curry and Brunton, 2007.

517

518 Table 2.

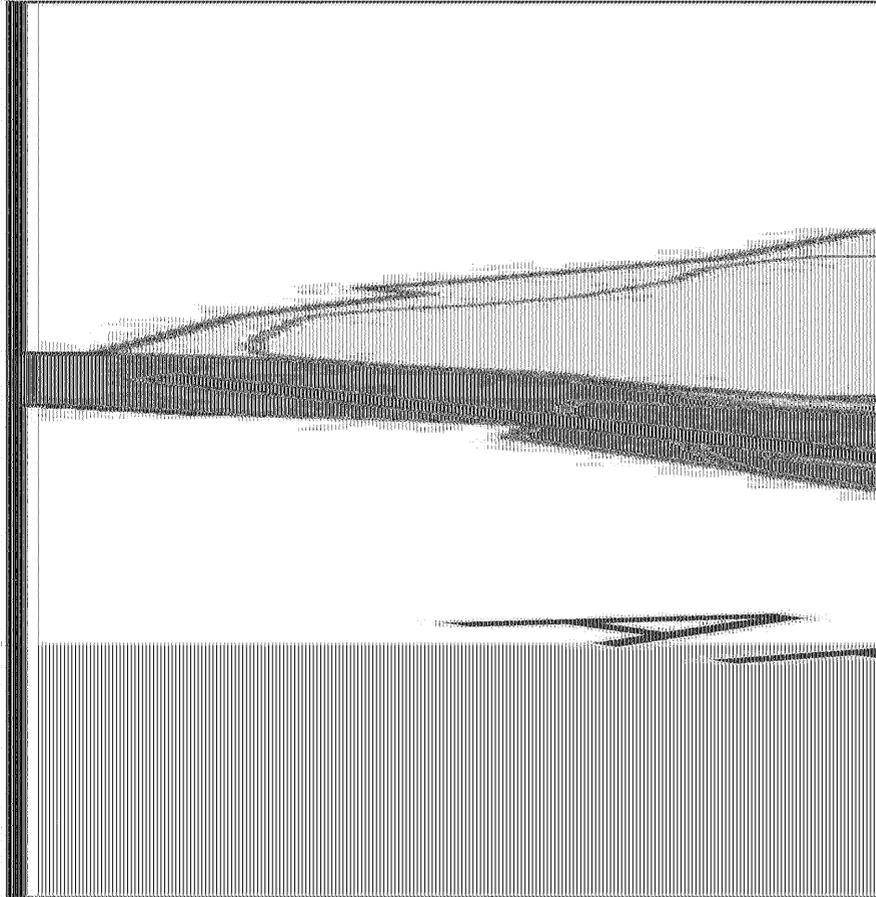
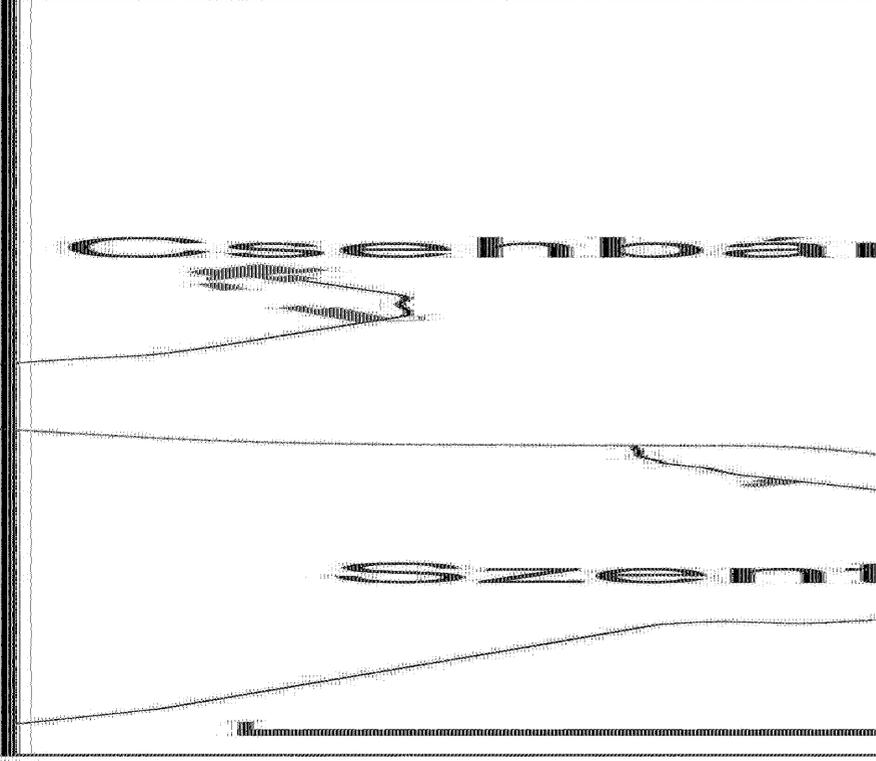
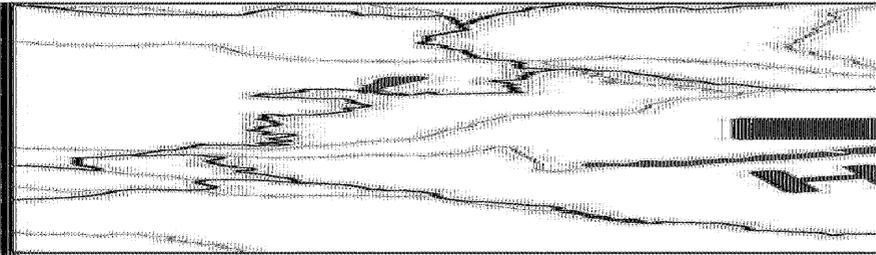
519 Number of brachiopod specimens in the Tithonian and Berriasian sections from the Bakony

520 Mountains in the present study.

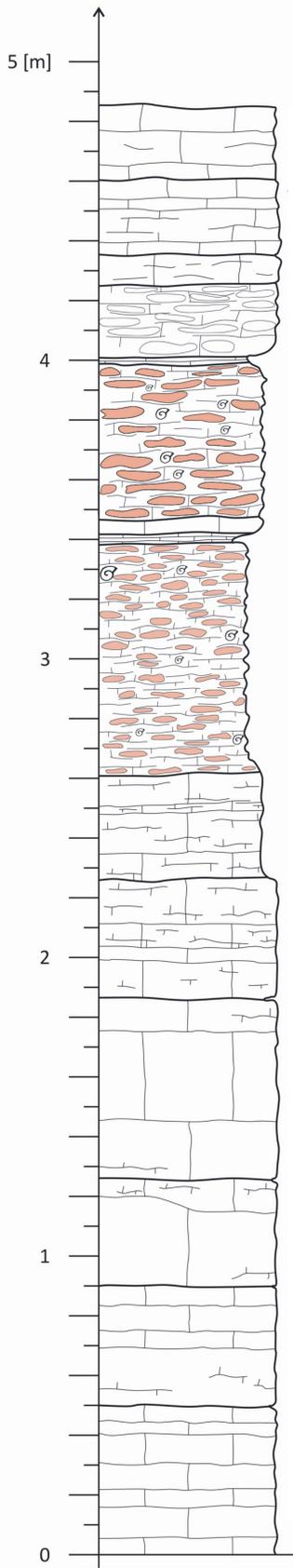
521

522 Table 3.

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

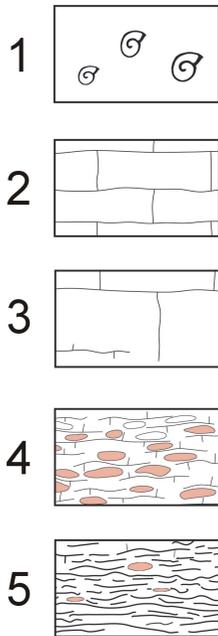
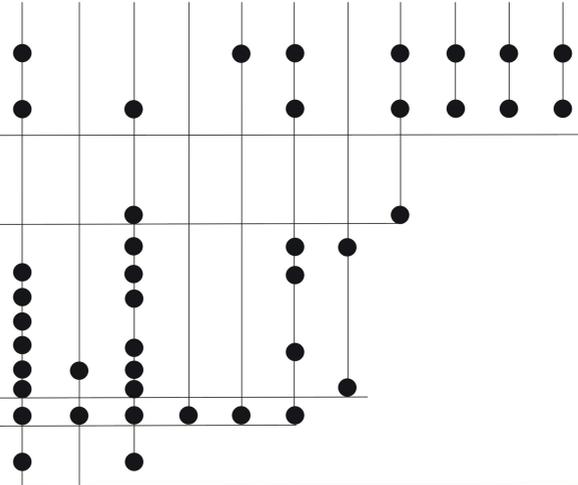


Hárskút HK-12



Bed No. 10, 11, 12, 13, 15, 16, 17, 18, 19, 21, 22, 25, 27, 28, 29, 32, 34, 39, 41, 43, 44, 45, 46, 47, 48, 49, 50, 51, 52, 53, 54, 55

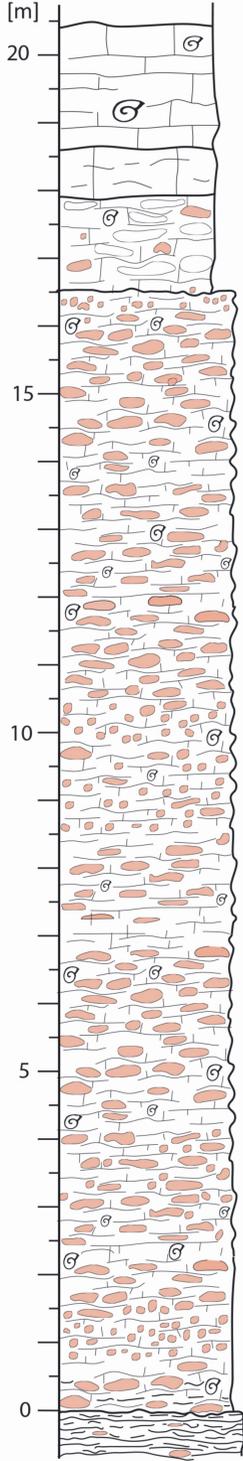
Antinomia catulloi
Triangope triangulus
Nucleata bouei
Oppeliella pinguicula
Antinomia diphoros
Antinomia sima
Pygope diphyha
Vjalovithyris ? n. sp.
Pygope axine
Antinomia n. sp.
Vjalovithyris rupicola



Zones	Stages
P.+Camp.	Valang.
Boissieri	Berriasian
Occitanica	
?	

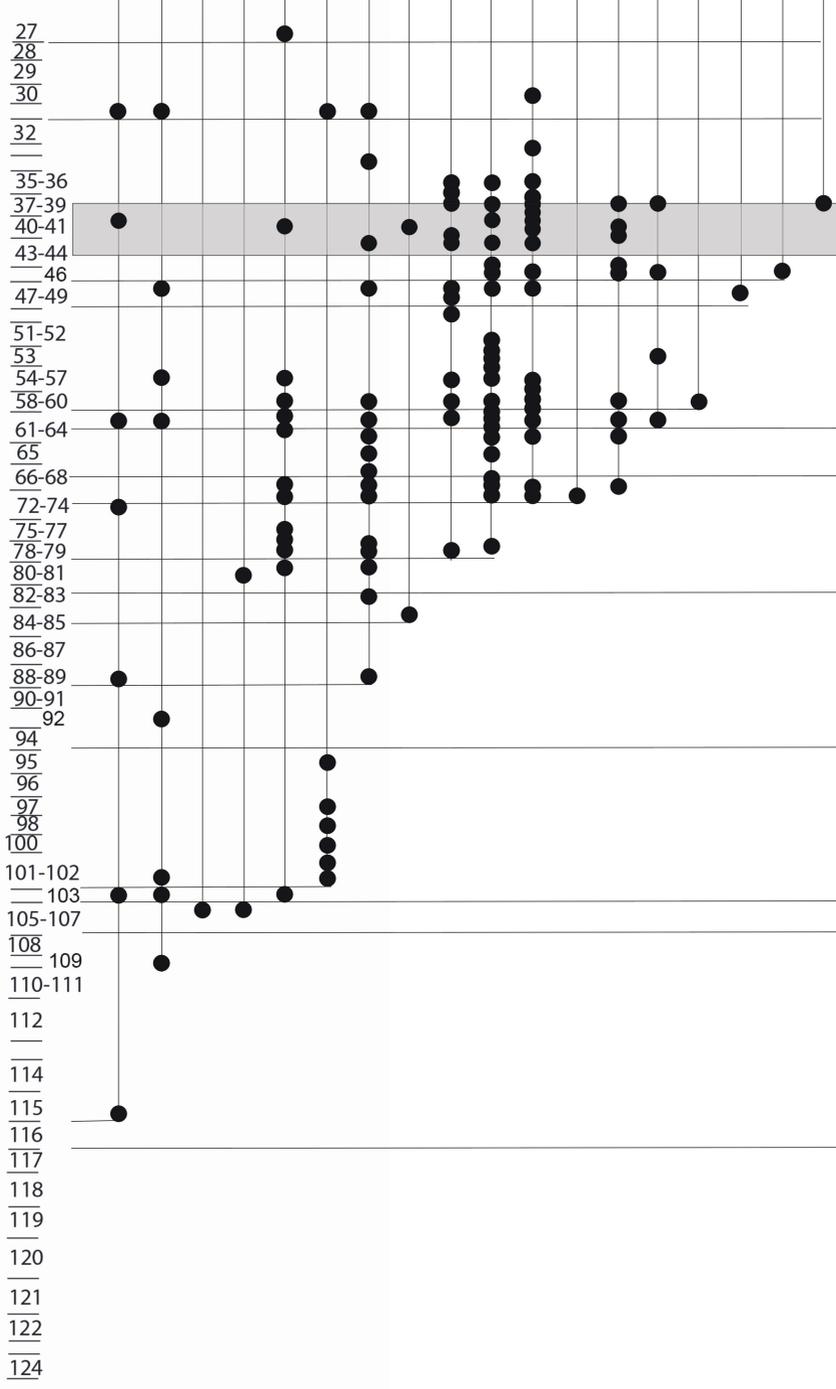
Borzavár

Szilas Ravine



Bed No.

- Vyalovithyris rupicola*
- Nucleata bouei*
- Triangope planulata*
- Aninomia* aff. *sima*
- Triangope triangulus*
- Pygope janitor*
- Aninomia catulloi*
- Sphenope bifida*
- Karadagithyris bilimeki*
- Aninomia diphoros*
- Pygope diphya*
- Pygope vomer*
- Pygope axine*
- Monticlarella ? agassizi*
- Triangope rectangularis*
- Oppeltella pinguicula*
- Fortunella capillata*
- Monticlarella ? tatrica*



Cavouri	Beckeri	Hyb.	Darwini	Semiforme	Fallauxi	"D." and Micr.	Berriasian	Zones
Kimmeridgian								Stages



Tithonian		Berriasian		Brachiopod species
early	late	early	late	
				<i>Monticlarella ? tatrlica</i>
				<i>Monticlarella ? agassizi</i>
				<i>Karadagithyris bilimeki</i>
				<i>Vjalovithyris rupicola</i>
				<i>Pygope janitor</i>
				<i>Pygope axine</i>
				<i>Triangope triangulus</i>
				<i>Antinomia catulloi</i>
				<i>Pygope diphya</i>
				<i>Antinomia diphoros</i>
				<i>Nucleata bouei</i>
				<i>Antinomia sima</i>



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