



1  
2 **A new polyglyphanodontine lizard (Squamata: Borioteiioidea) from the Late Cretaceous**  
3 **Iharkút locality (Santonian, Hungary)**

4  
5 **László Makádi**<sup>a, b</sup>

6  
7 <sup>a</sup> Department of Paleontology and Geology, Hungarian Natural History Museum, POB 137  
8 Budapest, H-1431 Hungary

9  
10 <sup>b</sup> Department of Paleontology, Eötvös University, Pázmány Péter sétány 1C, Budapest, H-  
11 1117, Hungary

12  
13  
14 \* Corresponding author, email address: iharkutia@yahoo.com  
15

16  
17  
18 **Abstract**

19  
20 In recent years the Late Cretaceous (Santonian) terrestrial vertebrate locality at Iharkút  
21 (western Hungary) has yielded well-preserved remains of lizard taxa besides the remains of fishes,  
22 amphibians, turtles, crocodiles, pterosaurs and dinosaurs. Previously the polyglyphanodontine  
23 lizard *Bicuspidon* aff. *hatzeiensis* has been reported from Iharkút. However, recent excavations at  
24 this site produced more lacertilian remains including new polyglyphanodontine material, namely a  
25 maxilla and two dentaries which suggest the presence of a new genus in the Iharkút fauna. This  
26 previously unknown lizard (described here as *Distortodon rhomboideus* n. g. n. sp.) is distinct  
27 from other polyglyphanodontines such as *Bicuspidon*, *Paraglyphanodon*, *Polyglyphanodon*,  
28 *Dicothodon* and *Peneteius*. It differs from these genera mainly in having the lingual cusp situated  
29 more distally compared to the labial one on its bicuspid teeth located in the distal part of the tooth  
30 row, thus the crowns having a unique rhomboidal shape in occlusal view. *Distortodon*  
31 *rhomboideus* further strengthens the dominance of borioteioid lizards in the Iharkút fauna. The  
32 growing presence of borioteioids in European localities supports previous theories which suggest  
33 some paleobiogeographic connections between the western Tethyan archipelago and North  
34 America in the Late Cretaceous.  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48

49 **Research highlights**

50  
51 New lizard remains have been found in the Late Cretaceous of Hungary. The remains show  
52 features typical of polyglyphanodontines. Based on some differences between these  
53 specimens and previously described genera a new genus and species is described.  
54  
55  
56  
57

58 **Keywords:** *Distortodon*, squamates, Polyglyphanodontinae, Iharkút, Late Cretaceous.  
59  
60  
61  
62  
63  
64  
65

## 1. Introduction

Squamates have a long worldwide evolutionary history dating back to the Early Jurassic, or even perhaps to the Late Triassic (Evans, 2003; Datta and Ray, 2006; Evans and Jones, 2010; Hutchinson et al., 2012). Within this long fossil record, terrestrial lizards from the Late Cretaceous western Tethyan archipelago of Europe are also represented by finds from several localities.

Squamate yielding French localities mostly range from the Campanian to the Maastrichtian (Buffetaut et al., 1996; Buffetaut et al., 1997; Gheerbrant et al., 1997; Buffetaut et al., 1999; Tabuce et al., 2004; Buffetaut, 2005) with a few Cenomanian exceptions (Vullo and Néraudeau, 2008; Vullo et al., 2011). Spanish sites basically belonged to the same Ibero-Armorican island in the Late Cretaceous (Pereda-Suberbiola, 2009) and are also dated to the Campanian and Maastrichtian (Rage, 1999; López-Martínez et al., 2000; Company, 2004; Blain et al., 2010; Narváez and Ortega, 2010; Houssaye et al., 2013).

Romanian localities in the Hațeg Basin and surrounding areas in Transylvania are even younger generally, from the Maastrichtian (Grigorescu et al., 1999; Codrea et al., 2002; Venczel and Csiki, 2003; Folie and Codrea, 2005; Grigorescu, 2005; Csiki et al., 2008; Codrea et al., 2010a,b; Grigorescu, 2010; Vasile and Csiki, 2010; Weishampel et al., 2010; Vasile and Csiki, 2011; Codrea et al., 2012; Jipa, 2012).

The Campanian Muthmannsdorf locality in Austria produced a single lacertilian vertebra (Seeley, 1881) and is presently inaccessible.

The remains found at these localities are mostly jaw fragments and isolated teeth, or scarce postcranium such as vertebrae, and usually do not allow precise taxonomic determination, though recently some (Pui Islaz locality, Early Maastrichtian, Hațeg Basin, Romania) yielded more complete or exceptional remains (Folie and Codrea, 2005; Codrea et al., 2012).

The Late Cretaceous (Santonian) terrestrial vertebrate locality at Iharkút (western Hungary) (Fig. 1) has yielded well-preserved remains of lizard taxa (Makádi, 2006, 2008) besides the remains of lepisosteid and pycnodontiform fishes (Ósi et al., 2012b), albanerpetontid and anuran amphibians (Szentesi and Venczel, 2010; Ósi et al., 2012b; Szentesi and Venczel, 2012), bothremydid turtles (Rabi et al., 2012), the first known freshwater mosasaur (Makádi et al., 2012), alligatoroid, ziphosuchian and heterodont eusuchian crocodiles (Ósi et al., 2007; Ósi et al., 2012b), azhdarchid pterosaurs (Ósi et al., 2005), a rhabdodontid ornithopod (Ósi et al., 2012a) the ceratopsian dinosaur *Ajkaceratops*

1 (Ősi et al., 2010), the basal nodosaurid ankylosaur *Hungarosaurus* (Ősi, 2005; 2 Ősi and Makádi, 2009), theropods (Ősi et al., 2010), and enantiornithine birds (Dyke and 3 Ősi, 2010).

4 Previously the presence of at least four different lacertilians was indicated based on 5 dentaries, maxillae and isolated teeth (Makádi, 2006, 2008). Among these, the most abundant 6 was *Bicuspidon* aff. *hatzeiensis* Folie and Codrea, 2005 represented by several jaw 7 fragments (including complete dentaries) (Makádi, 2006). 8

9  
10 Recent excavations at Iharkút produced more lacertilian material, including new 11 polyglyphanodontine material, namely maxillae, dentaries, and isolated teeth. Some of these 12 are identical to *B.* aff. *hatzeiensis* but there are at least two dentaries and a maxilla which, 13 based on dental characters, can be distinguished from *B.* aff. *hatzeiensis* (Makádi, 2006). 14 Moreover, it differs from other polyglyphanodontines such as *B. hatzeiensis* Folie and 15 Codrea, 2005 and *B. numerosus* Nydam and Cifelli, 2002, or *Paraglyphanodon*, 16 *Polyglyphanodon*, *Dicothodon* and *Peneteius* (Gilmore, 1940, 1942, 1943; Estes, 1969, 1983; 17 Nydam, 1999; Nydam et al., 2000; Nydam and Cifelli, 2002; Folie and Codrea, 2005; Nydam 18 et al., 2007). These new finds evidence the presence of another, previously unknown 19 polyglyphanodontine other than *Bicuspidon* in the Iharkút fauna, thus here I describe 20 *Distortodon rhomboideus* n. g. n. sp. 21  
22  
23  
24  
25  
26  
27  
28  
29  
30

## 31 32 33 **2. Stratigraphy and geological setting**

34  
35  
36 The locality is situated in the Bakony Mts, western Hungary, near the villages of 37 Némethánya and Bakonyjákó, at the place of Iharkút, a small village destroyed by the opening 38 of the mine in the late 1970s (Fig. 1A). At the fossil site the open-pit mining of the bauxite 39 exposed the Csehbánya Formation, which contains the bone-yielding layers. The Csehbánya 40 Formation is the overburden of the Nagytárkány Bauxite Formation and the Triassic Main 41 Dolomite Formation (Fig. 1B). It is a floodplain and channel deposit built up of variegated 42 clay, silt with interbedded grey and brown sand, sand and sandstone beds, and paleosols. In 43 the Iharkút-Némethánya area, the Csehbánya Formation is sometimes covered by the Eocene 44 Iharkút Conglomerate Formation or is situated immediately below Quaternary deposits (Fig. 45 1B); in other locations it is covered by the Oligocene–Miocene Csátka Formation (Haas et al., 46 1977; Mindszenty et al., 1984; Knauer and Siegl Farkas, 1992; Jocha-Edelényi, 1996; Ősi and 47 Mindszenty, 2009). Palynological studies suggest a Santonian age for the Csehbánya 48 Formation (Knauer and Siegl Farkas, 1992), this age is also confirmed by recent 49 paleomagnetic data (Szalai, 2005). 50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

1 At Iharkút, vertebrate remains, including those of *Distortodon*, were found throughout  
2 exposures of the Csehbánya Formation, but the SZ-6 site is the most important site (Fig. 1C).  
3 This outcrop is an approximately 2–3 m thick sequence of beds built up of coarse, pebbly  
4 sand and organic-rich silt and clay, which are interpreted as crevasse splay deposits (Fig. 1B.).  
5 The base of the sequence is clearly erosional as it forms noticeable erosional surfaces into the  
6 floodplain deposits. The bonebed at SZ-6 is a 10 to 50 cm thick, basal breccia composed of  
7 gray sand, siltstone, clay clasts, pebbles, and plant debris (also charcoal) that occasionally  
8 contains surprisingly complete bones, but more frequently yields fragmentary bones; the basal  
9 breccia is sometimes interrupted by finer sediments that settled out under calmer  
10 circumstances (Ősi et al., 2012b). As a result of these alternating energy conditions of  
11 deposition, bones in different states of preservation can be found in the same bed. Nearly 80%  
12 of the vertebrate remains from Iharkút were discovered in the bonebed of this site (Ősi and  
13 Mindszenty, 2009; Ősi et al., 2012b).  
14

15 The sandstone bed covering the basal breccia also contains vertebrate fossils, but the  
16 bones are fewer in number and more poorly preserved. However, two incomplete associated  
17 skeletons of the nodosaurid ankylosaur *Hungarosaurus tormai* Ősi, 2005 have been found in  
18 this bed. The overlying bed is a laminated, grayish siltstone of variable thickness (30 cm to  
19 1.5 m) and contains plant debris and only a few bones, but this bed also yielded two partial  
20 associated skeletons of *Hungarosaurus*. The sequence is closed by a greyish siltstone of  
21 several meters thickness in which vertebrate remains are extremely rare (Ősi and Mindszenty,  
22 2009; Ősi et al., 2012b).  
23

24 It is worth mentioning that several similar sequences are exposed within the mine. In  
25 most of these cases the basal breccia (bonebed) is missing and the cycle starts with sandstone,  
26 or, if present, the basal breccia is thin (only a few centimeters, containing no, or only a few  
27 vertebrate remains). Moreover, the cycles sometimes end with paleosoils, which also might  
28 contain vertebrate remains, mostly dinosaur and crocodile teeth, and bone and turtle shell  
29 fragments (Ősi and Mindszenty, 2009; Ősi et al., 2012b).  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50

### 51 **3. Material and methods**

52 In the present paper a partial right maxilla (MTM PAL2012.31.1.) (Fig. 2), a right  
53 dentary (MTM PAL2012.32.1.) (Fig. 3), and a partial left dentary (MTM PAL2012.33.1.)  
54 (Fig. 4) were studied. The specimens are the property of the Hungarian Natural History  
55 Museum (MTM).  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

1 The remains (similarly to almost all bones from the locality) are black of pyrite and  
2 organic material (Tuba et al., 2006), and are extremely fragile, but relatively well-preserved.  
3 Large scale screen-washing from the bone-bed (and from other sediments as well) is  
4 performed regularly, however, this method usually destroys lizard jaws held together by the  
5 matrix. Thus lacertilian maxillae and dentaries found by this method are mostly isolated teeth  
6 and indeterminate jaw fragments, and almost all lizard remains suitable for taxonomic  
7 purposes (including MTM PAL2012.31.1., MTM PAL2012.32.1., and MTM PAL2012.33.1.)  
8 were found by checking through the bonebed by hand while searching for larger vertebrate  
9 remains.  
10

11 The fragile specimens were fixed in the field with PVB (poly-vinyl butyral) and cracks  
12 were glued with cyanoacrylic. Preparation was done in the laboratory using a stereo-  
13 microscope with sharp needles and occasionally with local use of 10% acetic acid.  
14 Photographs were taken through a stereomicroscope using a Canon Eos 450D, while SEM  
15 micrographs were taken using the Hitachi 2360N environmental scanning electron  
16 microscope of the Department of Plant Anatomy, Eötvös Loránd University at an accelerating  
17 voltage of 20kV using primary electrons. Environmental Scanning Electron Microscopy  
18 (ESEM) was chosen to evade the need for coating the specimens in carbon or gold.  
19

20 In the Systematic Paleontology section the phylogeny of Nydam et al. (2007) was used.  
21 For the anatomical descriptions the orientation terminology proposed by Smith and Dodson  
22 (2003) was used. As used by other authors (Nydam and Cifelli, 2002), the description of the  
23 dentition is based on tooth positions numbered from mesial direction towards the distal end  
24 (e.g., 1st, 2nd, 3rd, etc.) for individual specimens, beginning with the most mesial tooth  
25 position which has been preserved. Since two of the three specimens are incomplete, position  
26 numbers do not have the same meaning in these specimens. Moreover, the number of teeth in  
27 a lizard jaw increases as the animal grows, and tooth count varies among individuals (Nydam  
28 and Cifelli, 2002). Thus these tooth position numbers are used only to help the description and  
29 comparison of successive teeth with different morphologies in the same specimens.  
30

## 31 **4. Results**

### 32 **4.1. Systematic Paleontology**

33 Order Squamata Oppel, 1811

34 Infraorder Scincomorpha Camp, 1923

35 Clade Borioteiioidea Nydam, Eaton and Sankey, 2007

36 Subfamily Polyglyphanodontinae Estes, 1983  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

*Distortodon* gen. nov.

*Derivation of name.* From Latin “*distortus*”, meaning distorted, and Greek “*odous*” [ὀ δούς], meaning tooth, refers to the distorted looking tooth crowns in occlusal view.

*Diagnosis.* As for the type and only known species.

*Type species.* *Distortodon rhomboideus*

*Distortodon rhomboideus* n. sp.

*Derivation of name.* New Latin “*rhomboideus*” (from Greek noun “*rhombos*” [ῥό μβος] meaning “rhombus”, and the Greek ending “*eidōs*” [εἶ δος], meaning “shape”), refers to the rhomboidal shape of the bicuspid teeth of the dentition in occlusal view.

*Holotype.* MTM PAL2012.31.1. partial right maxilla (Fig. 2).

*Type locality.* Iharkút open-pit bauxite mine, Bakony Hills, western Hungary (Ósi et al., 2012b)

*Stratigraphic horizon and age.* Upper Cretaceous (Santonian) Csehbánya Formation (Knauer and Siegl Farkas, 1992; Jocha-Edelényi, 1996)

*Referred specimens.* MTM PAL2012.32.1. right dentary (Fig. 3) and MTM PAL2012.33.1. partial left dentary (Fig. 4).

*Diagnosis.* Small polyglyphanodontine with characteristic tooth morphology. Lingual and labial cusps of distal teeth connected by ridge (probably V-shaped); teeth not greatly expanded transversally but rather mesiodistally; most distal large tooth in maxilla having “intermediate” form (larger labial cusp and smaller lingual cusp almost united, ridge between them short and blunt) in maxilla. Differs from all other polyglyphanodontines in the distal dentary teeth having the lingual cusps displaced more distally compared to the labial ones giving the crown a rhomboidal outline in occlusal view. Differs from *Peneteius* in the lack of mammal-like distal teeth with complex morphology. Differs from *Polyglyphanodon*, *Paraglyphanodon*, *Dicothodon* and *Peneteius* in the lack of suppressed tooth replacement. Differs from *Polyglyphanodon* and *Paraglyphanodon gazini* Gilmore, 1943 in teeth not expanded transversally. Differs from *Dicothodon* in that the lingual side of tooth is not mesiodistally wider than or equal to labial side; in the lack of well-developed accessory blades and associated basins on tooth crown. Differs from *Bicupidon*, *Dicothodon*, and *Polyglyphanodon* in having an apically widening tooth crown mesiodistally longer than tooth shaft. Differs generally from *Bicupidon* in having more tightly-fit, transversally not expanded teeth, which are also shorter projecting only one third of their height beyond labial wall of dentary and maxilla. Differs from *B. numerosus* also in the lack of caniniform anterior teeth but having posterior teeth with reduced lingual cusp.

### *Description and comparisons*

1  
2 *Maxilla*. Only a single partial right maxilla, MTM PAL2012.31.1. is known (Fig. 2). It is 6.5  
3 mm long, has a triangular shape in lateral view (Fig. 2A) and though its anterior portion is  
4 missing, it is obvious that the dorsal process was located more posteriorly than in *Bicuspidon*.  
5 The process also seems to have been much lower than in *Bicuspidon* or *Polyglyphanodon*  
6 (Gilmore, 1942; Nydam and Cifelli, 2002). The premaxillary process is not preserved. The  
7 lateral surface of the bone shows no ornamentation, but bears five large nutrient foramina in a  
8 single row, one above each tooth, and two additional foramina dorsal to them arranged  
9 irregularly. A small anterior opening of the superior alveolar canal is not visible above the 4<sup>th</sup>  
10 tooth in medial view, and the large posterior opening is located at the level of the 6<sup>th</sup> tooth and  
11 is well observable both in medial and dorsal views (Fig. 2B, C). The posterior end of the bone  
12 is broken and the articulation surface for the jugal is not preserved. The preserved part of the  
13 tooth row is straight in occlusal view (Fig. 2E).

14  
15  
16  
17  
18  
19  
20  
21  
22  
23 The maxilla has 7 preserved tooth positions, with teeth in the 3<sup>rd</sup>, 4<sup>th</sup>, 5<sup>th</sup> and 6<sup>th</sup> tooth  
24 positions, moreover, an extra tiny tooth is visible in a presumed last most distal 7<sup>th</sup> position, in  
25 contrast to the dentaries (Fig. 2). The robust teeth are subpleurodont with cementum  
26 deposition at their bases at an extent similar to *Bicuspidon* (Nydam and Cifelli, 2002; Folie  
27 and Codrea, 2005; Makádi, 2006). Similarly to *Bicuspidon*, the maxilla and the dentaries also  
28 differ from e.g. *Polyglyphanodon* or *Dicothodon bajaensis* (Nydam, 1999) which have  
29 suppressed tooth replacement and lack resorption pits (Nydam, 1999; Nydam and Cifelli,  
30 2002; Folie and Codrea, 2005; Makádi, 2006). The supradental shelf (at least where it is not  
31 broken) is wide similarly to teiids (Estes et al., 1988) and borioteioids (Nydam et al., 2007).  
32 The resorption pits of the teeth in the 3<sup>rd</sup>, 4<sup>th</sup>, 5<sup>th</sup> and 6<sup>th</sup> positions originally seem to have had  
33 subcircular shapes. However the apical edges of the pits were crushed (most probably before  
34 transportation and burial, as suggested by dull fracture edges) and thus those large elongated  
35 cavities were formed by the pit and the fractures and extend tapering in apical direction on the  
36 labial surface of the tooth shaft.

37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49 The teeth are closely packed similarly to *Paraglyphanodon utahensis* Gilmore, 1940 in  
50 contrast to *Bicuspidon* or *Dicothodon bajaensis* (Gilmore, 1940, 1943; Estes, 1983; Nydam,  
51 1999; Nydam and Cifelli, 2002; Folie and Codrea, 2005; Makádi, 2006). The degree of  
52 widening of the posterior teeth in transverse direction does not reach the extent observed in  
53 *Bicuspidon*, *Dicothodon*, or *Paraglyphanodon gazini* and is far from the condition seen in  
54 *Polyglyphanodon* but is more close to the posterior teeth of *Paraglyphanodon utahensis*,  
55 though the anterior teeth in *Polyglyphanodon* are also similar (Gilmore, 1940, 1942, 1943;  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

Estes, 1983; Nydam, 1999; Nydam and Cifelli, 2002; Folie and Codrea, 2005; Nydam and Cifelli, 2005; Makádi, 2006). Approximately one third of their height is projected beyond the lateral wall of the bone, which is less than in *B. numerosus* and *B. hatzeiensis* (Nydam and Cifelli, 2002; Folie and Codrea, 2005; Makádi, 2006) (Fig. 2B, D).

The crowns of the preserved teeth in the 3<sup>rd</sup>, 4<sup>th</sup>, 5<sup>th</sup> positions have the typical bicuspid appearance of transversally-toothed polyglyphanodontines (Nydam, 1999; Nydam and Cifelli, 2002): a large labial cusp and a slightly smaller lingual cusp are linked together by a transverse ridge which divides the tip of the crown to a mesial and a distal facet (Fig. 2D, E). This ridge, though worn, was probably V-shaped as in *Bicuspidon* or *Dicothodon moorensis* Nydam, 1999 and *Dicothodon cifellii* Nydam, Eaton and Sankey, 2007 (Nydam, 1999; Nydam and Cifelli, 2002; Folie and Codrea, 2005; Makádi, 2006; Nydam et al., 2007), in contrast to *Polyglyphanodon* and *Paraglyphanodon* (Gilmore, 1940, 1942, 1943; Estes, 1983; Nydam, 1999). They also differ from *Dicothodon* which, in addition to the V-shaped ridge (or U-shaped also known in *Dicothodon bajaensis*), has mesial and distal accessory blades on the tooth crowns (Nydam, 1999; Nydam et al., 2007), and are also completely different from the complex tooth morphology of *Peneteius* which has teeth with six cusps on the maxillary teeth and peg-like cusps on dentary teeth (Estes, 1969; Nydam et al., 2000; Nydam et al., 2007).

Moreover, the teeth of *Distortodon* differ from all other polyglyphanodontines in that they are “twisted” in labiomésial – linguodistal direction rather than expanded in labial – distal direction (Nydam and Cifelli, 2002; Folie and Codrea, 2005; Makádi, 2006). This is achieved by the lingual cusp having a slightly more distal position compared to the labial one, giving the crowns a “distorted”, rhomboidal shape in occlusal view (Fig. 2E). In labial view this “distortion” causes the crowns of the teeth in the 1<sup>st</sup> and 2<sup>nd</sup> positions to seem to be expanded mesiodistally and as a result of this, the crowns are very tightly packed, virtually contacting each other. Though this morphology resembles the condition seen in *Paraglyphanodon utahensis*, also lacking transversal widening of the teeth, the latter has symmetrical instead of distorted rhomboidal crowns in occlusal view (Gilmore, 1940, 1943; Estes, 1983; Nydam, 1999).

There is a distal large tooth, situated in the 6<sup>th</sup> position, which seems to have an intermediate form between bicuspid and monocuspid tooth morphology. The larger labial cusp and the smaller lingual cusp are almost united and the ridge between them is short and blunt. This morphology with a reduced lingual cusp is similar to that of the posterior maxillary teeth of *Polyglyphanodon* (and dentary teeth of *Polyglyphanodon* and *Paraglyphanodon utahensis*, as well) (Gilmore, 1942, 1943). This feature seen on the maxilla



1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

MTM PAL2012.31.1. differs from the morphology of the tooth in the same position (the last large tooth) in the dentaries (in MTM PAL2012.32.1. the 12<sup>th</sup>, in MTM PAL2012.33.1. the 7<sup>th</sup> positions), where the corresponding teeth are monocuspid. However, it is similar to the preceding tooth of the dentary, preserved in MTM PAL2012.32.1.

Distal to this last large tooth, a tiny conical tooth is visible distal to it and has a height app. 1/10 the height of the preceding one, being even smaller than in *B. aff. hatzegiensis* where it has a height app. fourth the height of the preceding tooth (Makádi, 2006), or than in *Polyglyphanodon sternbergi* Gilmore, 1940 and in the dentary of *Paraglyphanodon utahensis* (Gilmore, 1940, 1942, 1943). It has a relatively large (almost the same size as the tooth itself) resorption pit at its base.

*Dentary*. MTM PAL2012.32.1. is 10.5 mm long and bears 7 teeth and 5 empty tooth spaces. The preserved teeth occupy the 1<sup>st</sup>, 3<sup>rd</sup>, 5<sup>th</sup>, 7<sup>th</sup>, 9<sup>th</sup>, 11<sup>th</sup> and 12<sup>th</sup> positions (Fig. 3). The crowns of the first 4 preserved teeth are abraded, the crown of the tooth at the 5<sup>th</sup> position is crushed. The tooth at the 7<sup>th</sup> position has a crown more robust, and though it is abraded and no cusps are visible. At the base of the tooth a relatively small subcircular resorption pit is visible. The crown of the tooth at the 9<sup>th</sup> position is also worn but its bicuspid morphology is visible, while the teeth at the 11<sup>th</sup> and 12<sup>th</sup> positions are better preserved. In the case of these three last preserved teeth the resorption pits are subcircular and markedly larger than the one belonging to the tooth at the 7<sup>th</sup> position.

MTM PAL2012.33.1. is 8.5 mm long, the preserved portion is the posterior part of the bone bearing the most distal 7 tooth positions with 6 teeth more or less preserved (Fig. 4). The tooth in the 1<sup>st</sup> recognizable position has only its base intact, the crown is missing. The bone is crushed at the 2<sup>nd</sup> position and large parts are missing with only a small piece of bone holding together the anterior and posterior portions. The next tooth is situated in the 3<sup>rd</sup> position and its crown is crushed, while the following 4<sup>th</sup> and 5<sup>th</sup> positions, though worn, have their crowns preserved. The 6<sup>th</sup> position is empty, but the 7<sup>th</sup> position bears a relatively well-preserved tooth.

The ventral edge of MTM PAL2012.32.1. is convex in lateral and medial view (Fig. 3A, B, D), while in MTM PAL2012.33.1. it is straight (Fig. 4A, B, D). The Meckelian canal is open. The splenial was first thought to be partially preserved anteriorly in MTM PAL2012.32.1. but more careful examination revealed that the bone covering the Meckelian canal is just a dislocated part of the broken subdental shelf (Fig. 3B, D). Thus the splenial is not preserved in either specimens. The subdental shelf, though broken and partially displaced

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

closer to the tooth bases, must have been wide with the subdental gutter being high. Posterior to the last tooth an insertion facet for the anteromedial process of the coronoid is present. The lateral surface of the dentary shows no signs of ornamentation but small alveolar foramina are observable.

The teeth in the dentaries are subpleurodont with cementum deposition at their bases similarly to those in the maxilla, as common in teiids (Estes et al., 1988) and borioteiids (Nydham et al., 2007).

On MTM PAL2012.32.1. it is visible that the teeth at the 1<sup>st</sup> and 3<sup>rd</sup> positions probably had single cusped crowns similar to the mesial teeth of *Bicuspidon* aff. *hatzeziensis* from Iharkút (Makádi, 2006), the corresponding anterior part is missing in MTM PAL2012.33.1 (Figs. 3–4).

The crowns of the teeth in the middle of the dentary tooth row are similar to the maxillary teeth: they have a bicuspid morphology typical of most polyglyphanodontines, but with the rhomboidal shape in occlusal view caused by the slightly distal position of the lingual cusp compared to the labial one. Again similarly to the maxilla, in MTM PAL2012.33.1. the crowns of the 3<sup>rd</sup>, 4<sup>th</sup> and 5<sup>th</sup> teeth are very tightly packed and expanded mesiodistally, contacting each other (Fig. 4). This is not so obvious in MTM PAL2012.32.1. because only one (the one at the 9<sup>th</sup> position) tooth is preserved in the corresponding region of the dentition and its neighboring teeth are also missing (Fig. 3).

At the distal end of the tooth row, the typical bicuspid crown morphology described above transforms into a monocuspid form with the reduction of the lingual cusp, in contrast to *B. numerosus* but similarly to *B. hatzeziensis* and *B. aff. hatzeziensis* (Nydham and Cifelli, 2002; Folie and Codrea, 2005; Makádi, 2006). Similar reduction of the lingual cusp on the posterior teeth has been described also in *Paraglyphanodon utahensis* and in *Polyglyphanodon sternbergi* by Gilmore (1942, 1943). The crown of the tooth at the 11<sup>th</sup> position (the last but one large tooth) in MTM PAL2012.32.1. has a transitional form with overwhelmingly larger, conical labial cusp bearing apical striae on the lingual and labial sides (more pronounced on the former), this cusp is half encircled lingually by a cingulum which bears the protruding, apically striated much smaller lingual cusp. The ridge which connects the two cusps in the preceding teeth is virtually missing (Fig. 3). This crown is similar to the last large tooth in the maxilla. Unfortunately the same tooth position is empty in MTM PAL2012.33.1. (Fig. 4), but the next (in MTM PAL2012.32.1. the 12<sup>th</sup>) tooth is preserved in both dentaries. It has a monocuspid crown, similarly to *B. hatzeziensis* and *B. aff. hatzeziensis* (Folie and Codrea, 2005; Makádi, 2006), with distinct apical striae around the crown.

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

However, the cingulum encircling the apex is pronounced only on the mesial and distal sides, giving the crown a tricusate appearance in labial and lingual views (Figs. 3–4) similarly to *Socognathus unicuspis* Gao and Fox, 1991 (Nydam et al., 2010), or to the lingual cusp of distal teeth in larger specimens of *B. numerosus* (Nydam and Cifelli, 2002). Similar tricuspid outline of the crowns in labial view has been mentioned for *Paraglyphanodon utahensis* by Gilmore (1943). This tooth is the last in the dentaries, thus they differ from the maxilla MTM PAL2012.31.1., and also from *B. aff. hatzeiensis* in the lack of an ultimate, significantly smaller monocuspid tooth (Makádi, 2006). Unfortunately the holotype of Transylvanian *B. hatzeiensis* is broken behind the large monocuspid tooth (Folie and Codrea, 2005).

## 5. Discussion

The overall morphology of the maxilla and the dentaries as well as the subpleurodont teeth with cementum deposition at their bases, the heterodont dentition and the large subcircular resorption pits assigns the remains to Borioteiioidea (Nydam et al., 2007). Among borioteioids transversally expanded bicuspid teeth occur in polyglyphanodontines. The characteristic, distorted looking, rhomboidal bicuspid teeth, both in the maxilla and the dentaries, allow more precise determination.

“Transversely-toothed” genera like *Polyglyphanodon*, *Paraglyphanodon*, *Dicothodon*, *Peneteius* and *Bicuspidon numerosus* are known from North America (Gilmore, 1940, 1942, 1943; Estes, 1969, 1983; Nydam, 1999; Nydam et al., 2000; Nydam and Cifelli, 2002, 2005; Nydam et al., 2007) while *Bicuspidon hatzeiensis* and *Bicuspidon aff. hatzeiensis* were described from Europe (Folie and Codrea, 2005; Makádi, 2006). Several other taxa with different dentitions were described from Asia (Sulimski, 1975; Estes, 1983; Alifanov, 2000; Gao and Fox, 2000), these have radically different tooth morphology with polycusate, leaf-like, or obliquely widened polycusate, or bulbous tooth crowns in the distal part of the tooth row (Estes, 1983; Nydam, 1999; Alifanov, 2000; Nydam and Cifelli, 2002). They establish the sister group of transversely-toothed polyglyphanodontines, i.e. to the clade composed of Polyglyphanodontini+*Bicuspidon* (Nydam et al., 2007), though these relationships have been questioned recently (Conrad, 2008; Gauthier et al., 2012).

The maxilla MTM PAL2012.31.1. and the dentaries MTM PAL2012.32.1. and MTM PAL2012.33.1. can be easily distinguished from *Peneteius* since the latter has mammal-like distal teeth with accessory cusps and complex morphology (Estes, 1969; Nydam et al., 2000). *Dicothodon* has well-developed mesial and distal accessory blades on the tooth

1 crown, bordering deep antrum intercristatum anterior and posterior (Nydam, 1999; Nydam,  
2 2002; Nydam et al., 2007). *Polyglyphanodon* and *Paraglyphanodon gazini* have more  
3 widened teeth and between labial and lingual cusps a horizontal or U-shaped instead of the V-  
4 shaped blades of *Bicuspidon* (Gilmore, 1940, 1942, 1943; Estes, 1983; Nydam, 1999; Nydam  
5 and Cifelli, 2002). Though the tooth crowns on both the maxilla and the dentaries of  
6 *Distortodon* are more or less worn, in mesial or distal view it is obvious that the ridge  
7 between the cusps was markedly different from the condition seen in e.g. *Polyglyphanodon*  
8 *sternbergi*, the ridge does not have a straight horizontal section in the middle and short steep  
9 sections turning apically close to the cusps (Gilmore, 1942; Estes, 1983; Nydam, 1999). It is  
10 uncertain, whether it was V-shaped as in *Dicothodon moorensis* and *Bicuspidon* (Nydam,  
11 1999; Nydam and Cifelli, 2002; Folie and Codrea, 2005; Makádi, 2006), or had a more U-  
12 shaped curvature as in some *Dicothodon bajaensis* (Nydam et al., 2007), but it is worth to  
13 note that the ridge on the worn crowns look similar to the ridge on the worn specimens of  
14 *Bicuspidon* aff. *hatzegiensis* from Iharkút, which originally had V-shaped ridges as evidenced  
15 by well-preserved specimens (Makádi, 2006). This suggests that *Distortodon* also might have  
16 had more or less V-shaped, or at least not *Polyglyphanodon*-like ridges between the cusps.

17  
18 In the maxilla MTM PAL2012.31.1., teeth mesial to the last large tooth (the ones at the  
19 3<sup>rd</sup>, 4<sup>th</sup> and 5<sup>th</sup> positions) have the same morphology as corresponding ones in the dentaries,  
20 but the intermediate form of the tooth in the 6<sup>th</sup> position is different from the condition seen in  
21 the dentaries (MTM PAL2012.32.1. and MTM PAL2012.33.1.), where the last large teeth are  
22 clearly monocuspid. Thus it is possible that – as suggested here – *Distortodon rhomboideus*  
23 had a somewhat different dentition in the dentary and in the maxilla, or as another possibility,  
24 the morphology of this large most distal tooth can vary among individuals.

25  
26 The presence of the ultimate, most distal tiny tooth in MTM PAL2012.31.1. is similar to  
27 *B. aff. hatzegiensis*, however in specimens of the latter species it is significantly larger (1/4  
28 size of the preceding teeth) (Makádi, 2006). *Polyglyphanodon sternbergi* and  
29 *Paraglyphanodon utahensis* also have a small most distal tooth in their dentitions, however,  
30 those teeth are not so small compared to the preceding one, being half the size of that in  
31 *Paraglyphanodon utahensis* for instance (Gilmore, 1942, 1943). The partial reduction of the  
32 lingual cusp in the ultimate tooth is mentioned in *Paraglyphanodon utahensis* and in  
33 *Polyglyphanodon sternbergi* by Gilmore (1942, 1943).

34  
35 As seen in the maxilla of *Distortodon*, the tiny ultimate tooth has a large resorption pit  
36 having similar size to the tooth, indicating that the tooth was quite mature despite its small  
37 size. However, this tooth is not present in the dentaries. This might be caused by different  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
dental formulae of the maxilla and dentaries, or again simply due to variation among individuals, or can be the result of ontogenetic differences. Nonetheless, one of the dentaries (MTM PAL2012.32.1.) seems to originate from a slightly smaller individual than both the maxilla and the other dentary (this is indicated by comparison of the length of the distal portions of the tooth rows containing the last five large tooth places). Differences of the morphology, size, and number of teeth due to either ontogeny, intraspecific variation, and/or body size related to sexual dimorphism has been documented in recent teiids (Estes and Williams, 1984; Dessem, 1985; Anderson and Vitt, 1990) and fossil borioteioids, e.g. *Bicuspidon* itself (Nydam and Cifelli, 2002). However, as most times we lack enough information on ontogenetic and intraspecific variation and sexual dimorphism in Cretaceous lizards, moreover, “the structure and arrangement of the dentitions of these and related taxa are sufficiently complicated and predictable (i.e., “mammal-like”) within a taxon to represent a situation unique among lizards” as noted by Nydam et al. (2007: p. 538.), the practice is to use dental morphology of borioteioids for systematic determinations. As evidenced by more frequent *Bicuspidon* aff. *hatzeiensis* specimens from Iharkút (Makádi, 2006), bicuspid teeth in dentaries of different sizes have basically the same morphology, thus further strengthening the statement above.

31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65  
When the first specimen of *Distortodon* (MTM PAL2012.32.1. ) was found, at first sight it was suggested that it belongs to *B. aff. hatzeiensis* and the rhomboidal shape of the teeth was caused by lithostatic pressure. However, later excavations unearthed MTM PAL2012.31.1. and MTM PAL2012.33.1., both showing the characteristic rhomboidal tooth crowns in occlusal view. These specimens having the same morphology and their examination have shown that this tooth crown morphology is clearly not the result of geological processes because the morphology is the same as in all specimens, and hollow tooth bases are not compressed. Indeed, there are some unpublished fragmentary *B. aff. hatzeiensis* specimens from Iharkút which are actually compressed and do not exhibit the characteristic “distorted” tooth crowns described above. Thus it became evident that the specimens having teeth with rhomboidal crowns in occlusal view represented a species distinct from both *B. aff. hatzeiensis*, *B. hatzeiensis* and *B. numerosus* (Nydam and Cifelli, 2002; Folie and Codrea, 2005; Makádi, 2006). At first, it was suggested that this new species can be assigned to *Bicuspidon*, and with *B. aff. hatzeiensis* they are sympatric species in the Iharkút fauna. Nevertheless, the presence of new species of *Bicuspidon* in Europe other than *B. hatzeiensis* was already investigated in the first mention of *Bicuspidon* specimens from the Iharkút locality by Makádi (2006). The specific determination of those remains as “affinis

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

*hatzegiensis*” reflected the resemblance of the studied material to *Bicuspidon hatzegiensis* described from the Maastrichtian of Transylvania (Folie and Codrea, 2005), in contrast to *Bicuspidon numerosus* from the Albian-Cenomanian boundary of Utah (Nydam and Cifelli, 2002) but the possibility of *B. aff. hatzegiensis* being a new species was indicated by the use of the term *affinis* (Makádi, 2006). The explanation for this specific assignment was based on the fact that the holotype dentary of *B. hatzegiensis* from Transylvania shows at least one last monocuspid tooth at the distal end of the tooth row in contrast to *B. numerosus*, but while the bone is broken behind this last tooth in the holotype of *B. hatzegiensis* and other Hațeg specimens are even more fragmentary, it is uncertain whether more teeth were present (Nydam and Cifelli, 2002; Folie and Codrea, 2005). In contrast, *B. aff. hatzegiensis* dentaries from Iharkút (as well as yet unpublished maxillae) preserving the distal end of the dentition have another, smaller monocuspid tooth distal to the large one. Thus the lack of more complete material of *B. hatzegiensis* from Transylvania did not allow *B. aff. hatzegiensis* specimens from Iharkút to be either clearly distinguished from, or assigned to *B. hatzegiensis* (Folie and Codrea, 2005; Makádi, 2006). It should also be noted that if the presence/absence of the most distal tiny teeth in the dentition has less or no taxonomical meaning, then the specimens described from Iharkút previously as *B. aff. hatzegiensis* (Makádi, 2006) are probably identical with *B. hatzegiensis* from Transylvania (Folie and Codrea, 2005).

While investigating this problem, the discovery of MTM PAL2012.31.1., MTM PAL2012.32.1. and MTM PAL2012.33.1. came as a relevance and first seemed to evidence a certainly new species of *Bicuspidon*, distinct from either *B. aff. hatzegiensis* and *B. hatzegiensis*, as well as from *B. numerosus*. However more comparison with other polyglyphanodontines, especially *Paraglyphanodon* and *Dicothodon* indicated difference at generic level.

Based on the their morphology discussed above, the maxilla MTM PAL2012.31.1. and the dentaries MTM PAL2012.32.1. and MTM PAL2012.33.1. are recognized as belonging to a new genus and species, *Distortodon rhomboideus*. It is uncertain that *Distortodon* is more closely related to either *Bicuspidon*, or *Paraglyphanodon*, or perhaps *Dicothodon*. Unfortunately, the dentition of *Dicothodon* is not enough well known to make comparisons regarding to tooth positions, or differences in tooth size (Nydam, 1999; Nydam et al., 2007).

In some regards, the dentition of *Distortodon* is more similar to *Paraglyphanodon utahensis* than to *Bicuspidon* or *Dicothodon*. *P. utahensis* also has transversally not widened teeth, its tooth crowns have triangular outlines in labial view, the posterior teeth tend to have reduced lingual cusps and the ultimate tooth is smaller than the preceding tooth (though this is

1 similar in *B. aff. hatzegiensis*). Both *Distortodon* and *P. utahensis*, as well as *B. hatzegiensis*  
2 lack the caniniform anterior teeth described in *B. numerosus*. The teeth of *Distortodon* are  
3 closely spaced, not unlike of *P. utahensis*, but in contrast to *B. numerosus*, *B. hatzegiensis*,  
4 *Dicothodon bajensis*, and *P. gazini* as well (Gilmore, 1940, 1943; Estes, 1983; Nydam, 1999;  
5 Nydam and Cifelli, 2002; Folie and Codrea, 2005; Makádi, 2006; Nydam et al., 2007).  
6  
7

8  
9 The lack of more, especially cranial material makes a phylogenetic analysis unreasonable,  
10 but based on the similarities and differences discussed above, it is likely that *Distortodon* is  
11 closely related to *Bicuspidon*, and they are both outside Polyglyphanodontini as hypothesised  
12 for *Bicuspidon* by Nydam et al. (2007). Nevertheless, both *Bicuspidon* and *Distortodon* lack  
13 the diagnostic characters of Polyglyphanodontini, such as distinct ridges connecting labial and  
14 lingual cusps along mesial and distal margins of tooth crowns and the suppressed tooth  
15 replacement in adults (Nydam et al. 2007).  
16  
17

18  
19 The aim of this study is not the reconstruction of Late Cretaceous paleobiogeography of  
20 borioteiid lizards, or tetrapods in general, and more excessive work has been made for that  
21 purpose (e.g. (Pereda-Suberbiola, 2009; Weishampel et al., 2010). However, we have to  
22 examine the possible distribution of polyglyphanodontines in order to understand their  
23 evolutionary history. Polyglyphanodontines are known from the Late Albian until the end of  
24 the Cretaceous from North America, Asia and Europe (Nydam et al., 2007). Their oldest  
25 occurrence is *Dicothodon moorensis* is from the Upper Albian, but the other two species of  
26 that genus are younger, with *Dicothodon cifellii* from the Late Turonian of Utah and  
27 *Dicothodon bajensis* from the Campanian of Baja California, Mexico (Nydam, 1999; Nydam  
28 et al. 2007). *Bicuspidon* has even longer fossil record: *B. numerosus* was described from the  
29 Albian-Cenomanian boundary of Utah, (Nydam and Cifelli, 2002), while *B. aff. hatzegiensis*  
30 from the Santonian sediments from Iharkút represents a spatial and temporal intermediate  
31 station in the distribution of the genus (Makádi, 2006), and its youngest occurrence is *B.*  
32 *hatzegiensis* from the Maastrichtian of the Hațeg Basin, Romania (Folie and Codrea, 2005).  
33 *Distortodon* is now described also from the Santonian of Iharkút. *Peneteius* was described  
34 from the Upper Campanian of Utah and Texas and from the Upper Maastrichtian of Montana  
35 (Estes, 1969, Nydam et al., 2000; Nydam et al., 2007). *Paraglyphanodon* and  
36 *Polyglyphanodon* are both known from the Maastrichtian of Utah (Gilmore, 1940, 1942,  
37 1943; Estes, 1983; Nydam, 1999; Nydam et al., 2007). On the other hand, all the Asian  
38 polyglyphanodontines are from the Campanian (or possibly latest Santonian-Campanian) of  
39 the Gobi (Sulimski, 1975; Estes, 1983).  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

Already Nydam et al. (2007) were aware of the fact that *Bicuspidon*, though rare, was present in Europe, as evidenced by the Hațeg material (Folie and Codrea, 2005) and proposed the European dispersal of borioteioids. Now the growing number of new Hungarian finds such as *Distortodon* and *B. aff. hatzeiensis* can provide further support for this but our information about European Late Cretaceous lizards is still scarce. There is a significant gap in the European fossil record between the Cenomanian and the Santonian.

If we examine different Late Cretaceous terrestrial tetrapod groups at higher taxonomic levels (e.g. families) we find that they are members of an original Paleolaurasian or Euramerican bioprovince (Pereda-Suberbiola, 2009; Weishampel et al., 2010), not to mention taxa with Gondwanan origin like abelisaurids or ziphosuchians, though at lower taxonomic levels, such as genera, a lot of European Late Cretaceous taxa are more closely related to North American relatives than to Asian ones.

This is true for lizard such as borioteioids, taxa from Europe are close relatives of Albian-Cenomanian *B. numerosus* from North American and thus can be considered relicts in their own times, living contemporally with more derived polyglyphanodontines such as *Peneteius*. It seems reasonable that their ancestors were Paleolaurasian faunal elements, but Euramerican and Asian faunas quickly got separated by the epicontinental sea called the ‘Turgai Strait’ separating northern Europe, the western Tethyan archipelago and the Asian landmasses (Hay et al., 1999; Pereda-Suberbiola, 2009). Polyglyphanodontines evolved in North America and in Asia, and sometime between the Albian-Cenomanian and the Santonian representatives of the group arrived into the western Tethyan archipelago from the western part of North America through the Western Interior Seaway and the North Atlantic and probably island hopped to the Iharkút area, and later to the Hațeg Island. The approximately 14 million years between the ages of the North American and Iharkút localities was more than enough for this process. The migration to these areas was possible through pre-Santonian paleobiogeographic connections between North America and Europe, indicated by previous authors (e.g. Stampfli and Borel, 2002; Vullo and Néraudeau, 2008). The existence of similar routes is suggested even in the latest Maastrichtian (Martin et al., 2005). Moreover these dispersal routes must have also crossed the Western Interior Seaway to let lizards like *Distortodon* and *Bicuspidon* disperse to landmasses in the western Tethyan archipelago.

Another possible scenario for the European presence of borioteioids is that they are descended from an original Paleolaurasian (Pereda-Suberbiola, 2009) or Euramerican bioprovince (Weishampel et al., 2010) but when this province broke up due to the opening of the North Atlantic (Scotese, 2004), isolation lead to different genera or different species in



1  
2 North America (*Dicothodon*, *Paraglyphanodon*, *Polyglyphanodon*, *Peneteius*, *B. numerosus*)  
3 and Europe (*Distortodon*, *B. hatzeiensis*).

4 We have to consider that microplates that carry some European Late Cretaceous localities  
5 (e.g. Iharkút) originally drifted from far South, and were covered by water in pre-Santonian  
6 times, thus were excluded from this Paleolaurasian terrestrial fauna. It is hard to regard  
7 European Cretaceous localities as a single geographic unit since sometimes we have to deal  
8 with small landmasses like Iharkút, separated from the nearest landmass by thousands of  
9 kilometers and millions of years, drifting on microplates, rising from the closing Tethys  
10 Ocean and disappearing again leaving terrestrial sediments behind which span only a few  
11 hundred thousand years, and within those rocks only a single horizon yielding the vertebrate  
12 remains (Haas et al., 1977; Mindszenty et al., 1984; Knauer and Siegl Farkas, 1992; Jocha-  
13 Edelényi, 1996; Ósi and Mindszenty, 2009; Pereda-Suberbiola, 2009).

14 The Mussentuchit Member of the Cedar Mountain Formation (yielding *B. numerosus* in  
15 Utah) is interpreted as representing a series of floodplain overbank deposits of a meandering  
16 river system (Nydham and Cifelli, 2002), and similarly the Sânpetru Formation (yielding *B.*  
17 *hatzeiensis* in Transylvania) was deposited in a river system in an alluvial plain (Grigorescu,  
18 1983). These depositional environments were similar to the alluvial flood plain suggested for  
19 the Iharkút area where *Distortodon* and *B. aff. hatzeiensis* lived. This implies not only that  
20 these paleoenvironments were suitable for the fossilization of lizards, but also that  
21 polyglyphanodontines might have preferred similar environments, if remains are not much  
22 transported.

## 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42 **5. Conclusions**

43  
44  
45 Besides previously described *B. aff. hatzeiensis*, *Distortodon rhomboideus* adds a new  
46 genus and species to the Iharkút fauna and, concerning lacertilians, further strengthens the  
47 dominance of borioteioids in it. Moreover, it suggests that members of Polyglyphanodontinae  
48 were more abundant and diverse than previously thought. *B. aff. hatzeiensis* and *Distortodon*  
49 co-existed in the Iharkút area in the Santonian, being halfway in time and space between  
50 Albian-Cenomanian *B. numerosus* in North America and Maastrichtian *B. hatzeiensis* in  
51 Romania. The presence of these taxa in European localities supports previous theories which  
52 suggest some paleobiogeographic connections between the western Tethyan archipelago and North  
53 America in the Late Cretaceous.

1  
2  
3 **Acknowledgments**  
4  
5  
6

7 I thank Randall Nydam and Sebastián Apesteguía for helpful discussions; A. Ósi and the  
8 other members of the Iharkút Research Group, the staffs of the Dept. of Paleontology, Eötvös  
9 University and of the Dept. of Geology and Paleontology, Hungarian Natural History  
10 Museum for their help provided through the years. Randall Nydam and Marc Augé are  
11 gratefully acknowledged for critically reading the manuscript and making useful suggestions  
12 that greatly improved the work. The help of Károly Bóka in taking SEM photos is gratefully  
13 acknowledged. Fieldwork and the work of LM was supported by the MTA-ELTE Lendület  
14 (Dinosaur Research Group, grant n.: 95102); the OTKA T-39045, PD-73021, NF-84193  
15 grants; the National Geographic Society; the Jurassic Foundation; the MOL Plc. and the  
16 Hantken Foundation. Fieldwork was also supported by Bakonyi Bauxitbánya Ltd and Geovol  
17 Ltd.  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27

28 **References**  
29  
30  
31

- 32 Alifanov, V.R., 2000. The fossil record of Cretaceous lizards from Mongolia, in: Benton,  
33 M.J., Shishkin, M.A., Unwin, D.M., Kurochkin, E.N. (Eds.), *The age of dinosaurs in*  
34 *Russia and Mongolia*. Cambridge University Press, Cambridge, pp. 368-389.  
35  
36 Anderson, A.R., Vitt, L.J., 1990. Sexual selection versus alternative causes of sexual  
37 dimorphism in teiid lizards. *Oecologia* 84, 145-157.  
38  
39 Blain, H.-A., Canudo, J.-I., Cuenca-Bescós, G., López-Martínez, N., 2010. Amphibians and  
40 squamate reptiles from the latest Maastrichtian (Upper Cretaceous) of Blasi 2 (Huesca,  
41 Spain). *Cretaceous Research* 31, 433-446.  
42  
43 Buffetaut, E., 2005. Late Cretaceous Vertebrates from the Saint-Chinian area (Southern  
44 France): a review of previous research and an update on recent finds. *Acta*  
45 *Palaeontologica Romaniae* 5, 39-48.  
46  
47 Buffetaut, E., Costa, G., Le Loeuff, J., Martin, M., Rage, J.-C., Valentin, X., Tong, H., 1996.  
48 An Early Campanian vertebrate fauna from the Villeveyrac Basin (Hérault, southern  
49 France). *Neues Jahrbuch für Geologie und Paläontologie Monatshefte* 1996, 1-16.  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

- 1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65
- Buffetaut, E., Le Loeuff, J., Cavin, L., Duffaud, S., Gheerbrant, E., Laurent, Y., Martin, M., Rage, J.-C., Tong, H., Vasse, D., 1997. Late Cretaceous non-marine vertebrates from southern France: a review of recent finds. *Geobios* 20, 101-108.
- Buffetaut, E., Le Loeuff, J., Tong, H., Duffaud, S., Cavin, L., Garcia, G., Ward D., 1999. Un nouveau gisement de vertébrés du Crétacé supérieur á Cruzy (Hérault, Sud de la France). *Comptes Rendus de la Académie des Sciences, Sciences de la Terre* 328, 203-208.
- Camp, C., 1923. Classification of the lizards. *Bulletin American Museum of Natural History* 48, 289-481.
- Codrea, V., Barbu, O., Jipa-Murzea, C., 2010. Upper Cretaceous (Maastrichtian) landvertebrate diversity in Alba District (Romania). *Bulletin of the Geological Society of Greece* 43, 594-601.
- Codrea, V., Smith, T., Dica, P., Folie, A., Garcia, G., Godefroit, P., van Itterbeeck, J., 2002. Dinosaur egg nests, mammals, and other vertebrates from a new Maastrichtian site of the Hațeg Basin (Romania). *Comptes Rendus Palevol* 1, 173-180.
- Codrea, V., Venczel, M., Solomon, A.I., 2012. Squamate diversity of the Late Cretaceous „Hațeg Island”, Romania – Gondwanan links. 4th International Geologica Belgica Meeting – Moving Plates and Melting Icecaps – Processes and Forcing Factors in Geology, Abstract Book, 154.
- Codrea, V., Vremir, M., Jipa, C., Godefroit, P., Csiki, Z., Smith, T., Fărcaș, C., 2010. More than just Nopcsa's Transylvanian dinosaurs: A look outside the Hațeg Basin. *Palaeogeography, Palaeoclimatology, Palaeoecology* 293, 391-405.
- Company, J.R., 2004. Vertebrados continentales del Cretácico Superior (Campaniense-Maastrichtiense) de Valencia. PhD dissertation. Universitat de València, Valencia.
- Conrad, J.L., 2008. Phylogeny and systematics of Squamata (Reptilia) based on morphology. *Bulletin of the American Museum of Natural History* 310, 1-182.
- Csiki, Z., Ionescu A., Grigorescu, D., 2008. The Budurone microvertebrate site from the Maastrichtian of the Hațeg Basin – flora, fauna, taphonomy and paleoenvironment. *Acta Palaeontologica Romaniae* 6, 49-66.
- Datta, P.M., Ray, S., 2006. Earliest lizard from the Late Triassic (Carnian) of India. *Journal of Vertebrate Paleontology* 26, 795-800.
- Dessem, D., 1985. Ontogenetic Changes in the Dentition and Diet of Tupinambis (Lacertilia: Teiidae). *Copeia* 1985, 245-247.
- Dyke, G.J., Ősi, A., 2010. A review of Late Cretaceous fossil birds from Hungary. *Geological Journal* 45, 434-444.

- 1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65
- Estes, R., 1969. Relationships of two Cretaceous lizards (Sauria, Teiidae). *Breviora* 317, 1-8.
- Estes, R., 1983. Sauria terrestria, Amphisbaenia, in: Wellnhofer, P. (Ed.), *Encyclopedia of Paleoherpétology*. Gustav Fischer Verlag, Stuttgart and New York, pp. 1-249.
- Estes, R., de Queiroz, K., Gauthier, J., 1988. Phylogenetic relationships within Squamata, in: Estes, R., Pregill, G. (Eds.), *Phylogenetic relationships of the lizard families – Essays commemorating Charles L. Camp*. Stanford University Press, Stanford, pp. 119-281.
- Estes, R., Williams, E.E., 1984. Ontogenetic variation in the molariform teeth of lizards. *Journal of Vertebrate Paleontology* 4, 96-107.
- Evans, S.E., 2003. At the feet of the dinosaurs: the early history and radiation of lizards. *Biological Reviews of the Cambridge Philosophical Society* 78, 513-551.
- Evans, S.E., Jones, M.E.H., 2010. The origin, early history and diversification of lepidosauromorph reptiles, in: Bandyopadhyay, S. (Ed.), *New aspects of mesozoic biodiversity*. Springer, Berlin, pp. 27-44.
- Folie, A., Codrea, V., 2005. New lissamphibians and squamates from the Maastrichtian of Hațeg Basin, Romania. *Acta Palaeontologica Polonica* 50, 57-71.
- Gao, K., Fox, R.C., 1991. New teiids lizards from the Upper Cretaceous Oldman Formation (Judithian) of southwestern Alberta, Canada, with a review of the Cretaceous record of teiids. *Annals of the Carnegie Museum* 60, 145-162.
- Gao, K., Fox, R.C., 2000. Taxonomy and evolution of Late Cretaceous lizards (Reptilia:Squamata) from Western Canada. *Bulletin of Carnegie Museum of Natural History* 33, 1-107.
- Gauthier, J.A., Kearney, M., Maisano, J.A., Rieppel, O., Behlke A.D.B., 2012. Assembling the Squamate Tree of Life: Perspectives from the Phenotype and the Fossil Record. *Bulletin of the Peabody Museum of Natural History* 53, 3-308.
- Gheerbrant, E., Abrial, C., Capetta, H., 1997. Nouveaux sites a microvertébrés continentaux du Crétacé terminal des Petites Pyrénées (Haute-Garonne et Ariège, France). *Geobios* 20, 257-269.
- Gilmore, C.W., 1940. New fossil lizards from the Upper Cretaceous of Utah. *Smithsonian Miscellaneous Collections* 99, 1-3.
- Gilmore, C.W., 1942. Osteology of *Polyglyphanodon*, an Upper Cretaceous Lizard from Utah. *Proceedings of the United States National Museum* 92, 229-265.
- Gilmore, C.W., 1943. Osteology of Upper Cretaceous Lizards from Utah, with a description of a new species. *Proceedings of the United States National Museum* 93, 209-214.

- 1  
2 Grigorescu, D., 1983. A stratigraphic taphonomic and paleoecologic approach to a “forgotten  
3 land”: the dinosaur-bearing deposits from the Hațeg Basin (Transylvania–Romania). *Acta*  
4 *Palaeontologica Polonica* 28, 103-121.
- 5 Grigorescu, D., 2005. Rediscovery of a „forgotten land”: the last three decades of research on  
6 the dinosaur-bearing deposits from the Hațeg Basin. *Acta Palaeontologica Romaniaae* 5,  
7 191-204.
- 8  
9  
10 Grigorescu, D., 2010. The Latest Cretaceous fauna with dinosaurs and mammals from the  
11 Hațeg Basin – A historical overview, *Palaeogeography, Palaeoclimatology, Palaeoecology*  
12 293, 271-282.
- 13  
14  
15 Grigorescu, D., Venczel, M., Csiki, Z., Limborea, R., 1999. New latest Cretaceous  
16 microvertebrate fossil assemblages from the Hațeg Basin (Romania). *Netherlands Journal*  
17 *of Geosciences Geologie en Mijnbouw* 78, 301-314.
- 18  
19  
20 Haas, J., Jocha-Edelényi, E., Császár, G., 1977. Study of Mesozoic formations of the  
21 Transdanubian Central Mountains in Hungary [in Hungarian: *Mezozóos Formációk*  
22 *vizsgálata a Dunántúli-középhegységben*]. Annual Report of the Geological Institute of  
23 Hungary of the year 1975, 259-272.
- 24  
25  
26  
27  
28  
29 Hay, W.W., Deconto R.M., Wold, C.N., and Wilson, K.M., 1999. Alternative global  
30 Cretaceous paleogeography. *Geological Society of America Special Paper* 332(1999), 1-  
31 47.
- 32  
33  
34  
35 Houssaye, A., Bardet, N., Narváez, I., Ortega, F., 2013. Squamate finding in “Lo Hueco”  
36 (Late Campanian-Early Maastrichtian, Cuenca Province, Spain): the second non-marine  
37 pythonomorph lizard. *Paläontologische Zeitschrift*, available online, DOI 10.1007/s12542-  
38 013-0164-6
- 39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

1 bakonyi felső-kréta bauxitformációk szenon fedőképződményeinek palynosztratigráfiai  
2 helyzete]. Annual Report of the Geological Institute of Hungary of the year 1990, 463-  
3 471.  
4

5 López-Martínez, N., Canudo, J.I., Ardévol, L., Suberbiola, X.-P., Orue-Etxebarria, X.,  
6 Cuenca-Bescós, G., Ruiz-Omenaca, J.I., Murelaga, X., Feist, M., 2000. New dinosaur  
7 sites correlated with Upper Maastrichtian pelagic deposits in the Spanish Pyrenees:  
8 implications for the dinosaur extinction pattern in Europe. *Cretaceous Research* 22, 41-61.  
9

10 Makádi, L., 2006. *Bicuspidon* aff. *hatzegiensis* (Squamata: Scincomorpha: Teiidae) from the  
11 Upper Cretaceous Csehbánya Formation (Hungary, Bakony Mts). *Acta Geologica*  
12 *Hungarica* 49, 373-385.  
13

14 Makádi, L., 2008. A new insight into the Late Cretaceous lizard fauna of Europe: the  
15 exceptionally preserved specimens from the Santonian of Hungary. Abstract Volume of  
16 the 6<sup>th</sup> Annual Meeting of the EAVP, Spišska Nová Ves, pp. 60-61.  
17

18 Makádi, L., Caldwell, M.C., Ósi, A., 2012. The First Freshwater Mosasauroid (Upper  
19 Cretaceous, Hungary) and a New Clade of Basal Mosasauroids. *PLoS ONE* 7, e51781.  
20 doi:10.1371/journal.pone.0051781  
21

22 Martin, J.E., Case, J.A., Jagt, J.W.M., Schulp, A.S., Mulder, E.W.A., 2005. A new European  
23 marsupial indicates a Late Cretaceous high-latitude transatlantic dispersal route. *Journal of*  
24 *Mammalian Evolution* 12, 495-511.  
25

26 Mindszenty, A., Knauer, J., Szantner, F., 1984. Sedimentological features and the conditions  
27 of accumulation of the Iharkút bauxite [in Hungarian: Az iharkúti bauxit üledékföldtani  
28 jellegei és felhalmozódási körülményei]. *Földtani Közlöny* 114, 19-48.  
29

30 Narváez, I., Ortega, F., 2010. Análisis preliminar de los restos de Iguanidae indet. del  
31 Cretácico Superior de Lo Hueco (Fuentes, Cuenca). *Cidaris* 30, 205-209.  
32

33 Nydam, R.L., 1999: Polyglyphanodontinae (Squamata: Teiidae) from the medial and Late  
34 Cretaceous: new taxa from Utah, U.S.A. and Baja California del Norte, Mexico, in  
35 Gillette, D.D. (Ed.), *Vertebrate Paleontology in Utah*. Utah Geological Survey  
36 *Miscellaneous Publication* 99-1. Utah Geological Survey, Salt Lake City, pp. 303-317.  
37

38 Nydam, R.L., 2002. Lizards of the Mussentuchit Local Fauna (Albian-Cenomanian  
39 boundary) and comments on the evolution of the Cretaceous lizard fauna of North  
40 America. *Journal of Vertebrate Paleontology* 22, 645-660.  
41

42 Nydam, R.L., Caldwell, M.W., Fanti, F., 2010. Borioteiioidean lizard skulls from Kleskun  
43 Hill (Wapiti Formation; Upper Campanian), West-Central Alberta, Canada. *Journal of*  
44 *Vertebrate Paleontology* 30, 1090-1099.  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

- 1  
2 Nydam, R.L., Cifelli, R.L., 2002. A new teiid lizard from the Cedar Mountain Formation  
(Albian–Cenomanian boundary) of Utah. *Journal of Vertebrate Paleontology* 22, 276-285.
- 3  
4 Nydam, R.L., Cifelli, R.L., 2005. New data on the dentition of the scincomorphan lizard  
5 *Polyglyphanodon sternbergi*. *Acta Palaeontologica Polonica* 50, 73-78.
- 6  
7 Nydam, R.L., Eaton, J.G., Sankey, J., 2007. New taxa of transversely-toothed lizards  
8 (Squamata: Scincomorpha) and new information on the evolutionary history of „teiids”  
9 *Journal of Paleontology* 81, 538-549.
- 10  
11 Nydam, R.L., Gauthier, J., Chiment, J.J., 2000. The mammal–like teeth of the Late  
12 Cretaceous lizard *Peneteius aquilonius* Estes, 1969 (Squamata, Teiidae). *Journal of*  
13 *Vertebrate Paleontology* 20, 628-631.
- 14  
15 Oppel, M., 1811. Die Ordnungen, Familien und Gattungen der Reptilien als Prodom einer  
16 Naturgeschichte derselben. Joseph Lindauer Verlag, München.
- 17  
18 Ösi, A., 2005. *Hungarosaurus tormai*, a new ankylosaur (Dinosauria) from the Upper  
19 Cretaceous of Hungary. *Journal of Vertebrate Paleontology* 25, 370-383.
- 20  
21 Ösi, A., Apesteguía, S., Kowalewski, M., 2010. Non-avian theropod dinosaurs from the early  
22 Late Cretaceous of Central Europe. *Cretaceous Research* 31, 304-320.
- 23  
24 Ösi, A., Butler, R.J., Weishampel, D.B., 2010. A Late Cretaceous ceratopsian dinosaur from  
25 Europe with Asian affinities. *Nature* 465, 466-468.
- 26  
27 Ösi, A., Clark, J.M., Weishampel, D.B., 2007. First report on a new eusuchian crocodyliform  
28 with multicusped teeth from the Upper Cretaceous (Santonian) of Hungary. *Neues*  
29 *Jahrbuch für Geologie und Paläontologie Abhandlungen* 243, 169-177.
- 30  
31 Ösi, A., Makádi, L., 2009. New remains of *Hungarosaurus tormai* (Ankylosauria,  
32 Dinosauria) from the Upper Cretaceous of Hungary: skeletal reconstruction and body  
33 mass estimation. *Paläontologische Zeitschrift* 83, 227-245.
- 34  
35 Ösi, A., Mindszenty, A., 2009. Iharkút, dinosaur-bearing alluvial complex of the Csehbánya  
36 Formation, in: Babinszky, E. (Ed.), *Cretaceous sediments of the Transdanubian Range*.  
37 Hungarian Geological Society, Budapest, pp. 51-63.
- 38  
39 Ösi, A., Prondvai, E., Butler, R.J., Weishampel, D.B., 2012. Phylogeny, histology and  
40 inferred body size evolution in a new rhabdodontid dinosaur from the Late Cretaceous of  
41 Hungary. *PLoS ONE* 7, e44318. doi:10.1371/journal.pone.0044318
- 42  
43 Ösi, A., Rabi, M., Makádi, L., Szentesi, Z., Botfalvai, G., Gulyás, P., 2012. The Late  
44 Cretaceous continental vertebrate fauna from Iharkút (Western Hungary): a review, in:  
45 Godefroit, P. (Ed.), *Bernissart Dinosaurs and Early Cretaceous Terrestrial Ecosystems*.  
46 Indiana University Press, Bloomington, pp. 532-569.
- 47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

- 1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65
- Ósi, A., Weishampel, D.B., Jianu, C.M., 2005. First evidence of azhdarchid pterosaurs from the Late Cretaceous of Hungary. *Acta Palaeontologica Polonica* 50, 777-787.
- Pereda-Suberbiola, X., 2009. Biogeographical affinities of Late Cretaceous continental tetrapods of Europe: a review. *Bulletin de la Société Géologique de France* 180, 57-71.
- Rabi, M., Tong, H., Botfalvai, G., 2012. A new species of the side-necked turtle *Foxemys* (Pelomedusoides: Bothremydidae) from the Late Cretaceous of Hungary and the historical biogeography of the Bothremydini. *Geological Magazine* 149, 662-674.
- Rage, J.-C., 1999. Squamates (Reptilia) from the Upper Cretaceous of Laño (Basque Country, Spain). *Estudios del Museo de Ciencias Naturales de Alava* 14, 121-133.
- Scotese, C.R., 2004. Cenozoic and Mesozoic paleogeography: changing terrestrial biogeographic pathways, in Lomolino, M.V., Heaney, L.R. (Eds.), *Frontiers of Biogeography*. Sinauer Associates, Sunderland, pp. 9-26.
- Seeley, H.G., 1881. The Reptile Fauna of the Gosau Formation preserved in the Geological Museum of the University of Vienna. *Quarterly Journal of the Geological Society* 37, 620-707.
- Smith, J.B., Dodson, P., 2003. A proposal for a standard terminology of anatomical notation and orientation in fossil vertebrate dentitions. *Journal of Vertebrate Paleontology* 23, 1-12.
- Stampfli, G.M., Borel, G.D., Marchant, R., Mosar, J., 2002. Western Alps geological constraints on western Tethyan reconstructions, in: Rosenbaum, G. and Lister, G.S. (Eds.), *Reconstruction of the evolution of the Alpine-Himalayan Orogen*. *Journal of the Virtual Explorer* 7, 75-104.
- Sulimski, A., 1975. Macrocephalosauridae and Polyglyphanodontidae (Sauria) from the Late Cretaceous of Mongolia. *Palaeontologia Polonica* 33, 25-102.
- Szalai, E., 2005 (Unpublished results). Paleomagnetic studies in Iharkút [in Hungarian: Paleomágneses vizsgálatok Iharkúton]. Manuscript, Eötvös Loránd University Department of Environmental Geology, Budapest.
- Szentesi, Z., Venczel, M., 2010. An advanced anuran from the Late Cretaceous (Santonian) of Hungary. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 256, 291-302.
- Szentesi, Z., Venczel, M., 2012. A new discoglossid frog from the Upper Cretaceous (Santonian) of Hungary. *Cretaceous Research* 34, 327-333.
- Tabuce, R., Vianey-Liaud, M., Garcia, G., 2004. A eutherian mammal in the latest Cretaceous of Vitrolles, southern France. *Acta Palaeontologica Polonica* 49, 347-356.
- Tuba, Gy., Kiss, P., Pósfai, M., Mindszenty, A., 2006. Preliminary data on the diagenesis of Cretaceous dinosaur bones from the Bakony Mts, Hungary [in Hungarian: Diagenesis-



történeti vizsgálatok a bakonyi felső-kréta dinoszaurusz lelőhely csontanyagán]. Földtani  
Közlöny 136, 1-24.

Vasile, Ș., Csiki, Z., 2010. Comparative paleoecological analysis of some microvertebrate  
fossil assemblages from the Hațeg Basin, Romania. Oltenia. Studii și comunicări. Științele  
Naturii 26, 315-322.

Vasile, Ș., Csiki, Z., 2011. New Maastrichtian microvertebrates from the Ruscă Montana  
basin (Romania). Oltenia. Studii și comunicări. Științele Naturii 27, 221-230.

Venczel, M., Csiki, Z., 2003. New frogs from the latest Cretaceous of Hațeg Basin, Romania.  
Acta Palaeontologica Polonica 48, 609-616.

Vullo, R., Néraudeau, D., 2008. Cenomanian vertebrate assemblages from southwestern  
France: a new insight into the European mid-Cretaceous continental fauna. Cretaceous  
Research 29, 930-935.

Vullo, R., Rage, J.-C., Néraudeau, D., 2011. Anuran and squamate remains from the  
Cenomanian (Late Cretaceous) of Charentes, western France. Journal of Vertebrate  
Paleontology 31, 279-291.

Weishampel, D.B., Csiki, Z., Benton, M.J., Grigorescu, D., Codrea, V., 2010.  
Palaeobiogeographic relationships of the Hațeg biota – Between isolation and innovation.  
Palaeogeography, Palaeoclimatology, Palaeoecology 293, 419-437.

## Figure legends

**Fig. 1.** Geographical and geological setting. Geographical position (A) and schematic  
geological section of the Iharkút vertebrate locality (B) and the most important SZ-6 site (C).  
Q: Quaternary deposits, ICF: Iharkút Conglomerate Formation, CsF: Csehbánya Formation,  
NBF: Nagytárkány Bauxite Formation, MDF: Main Dolomite Formation.

**Fig. 2.** MTM PAL2012.31.1. holotype maxilla of *Distortodon rhomboideus* n. g. n. sp.  
Maxilla in lateral (A), medial (B, D) and dorsal (C) views, dentition in occlusal view (E).  
Numbers indicate preserved tooth positions. A– C are photographs, D and E are ESEM  
micrographs. Scale bar equals 1 mm. Note that the specimen has been further prepared  
between taking photographs and ESEM micrographs.

**Fig. 3.** MTM PAL2012.32.1. right dentary of *Distortodon rhomboideus* n. g. n. sp. in lateral  
(A), medial (B, D), and occlusal (C, E) views. Numbers indicate preserved tooth positions.

1  
2 A– C are photographs, D and E are ESEM micrographs. Scale bar equals 1 mm. Note that the  
3 specimen has been further prepared between taking photographs and ESEM micrographs.  
4

5 **Fig. 4.** MTM PAL2012.33.1. partial left dentary of *Distortodon rhomboideus* n. g. n. sp.  
6  
7 Dentary in lateral (A), medial (B, D), and occlusal (C) views, and its distal dentition in  
8 occlusal (E) view. Numbers indicate preserved tooth positions. A– C are photographs, D and  
9 E are ESEM micrographs. Scale bar equals 1 mm. Note that the specimen has been further  
10 prepared between taking photographs and ESEM micrographs.  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

Figure 1

[Click here to download high resolution image](#)

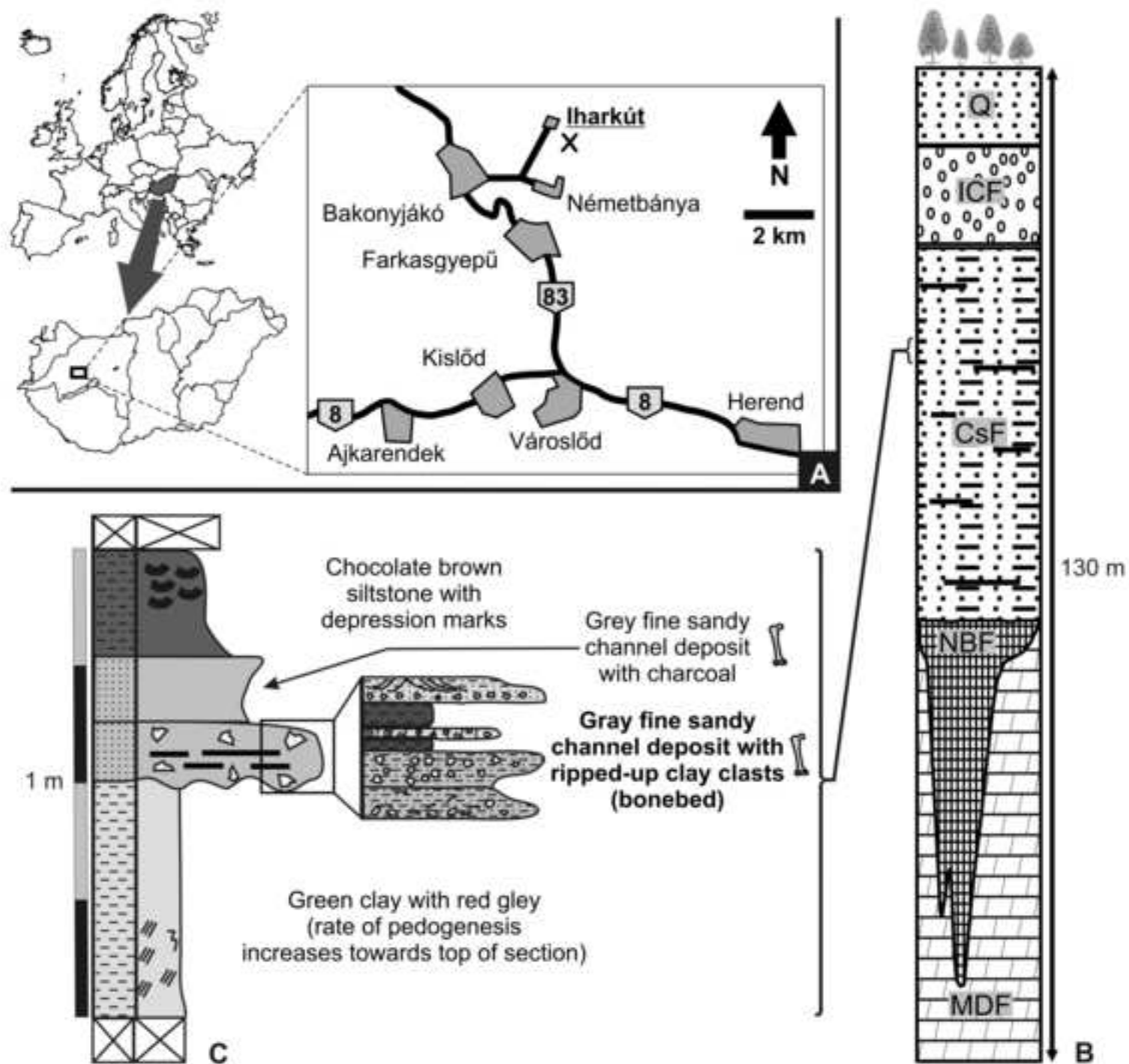


Figure2  
[Click here to download high resolution image](#)

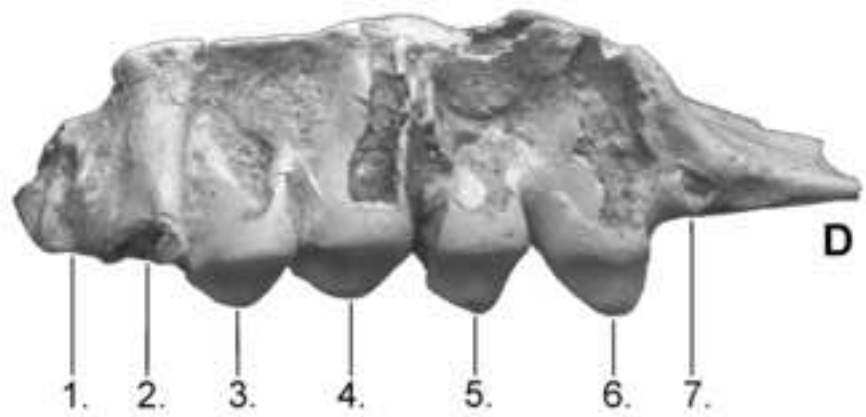


Figure 3  
[Click here to download high resolution image](#)

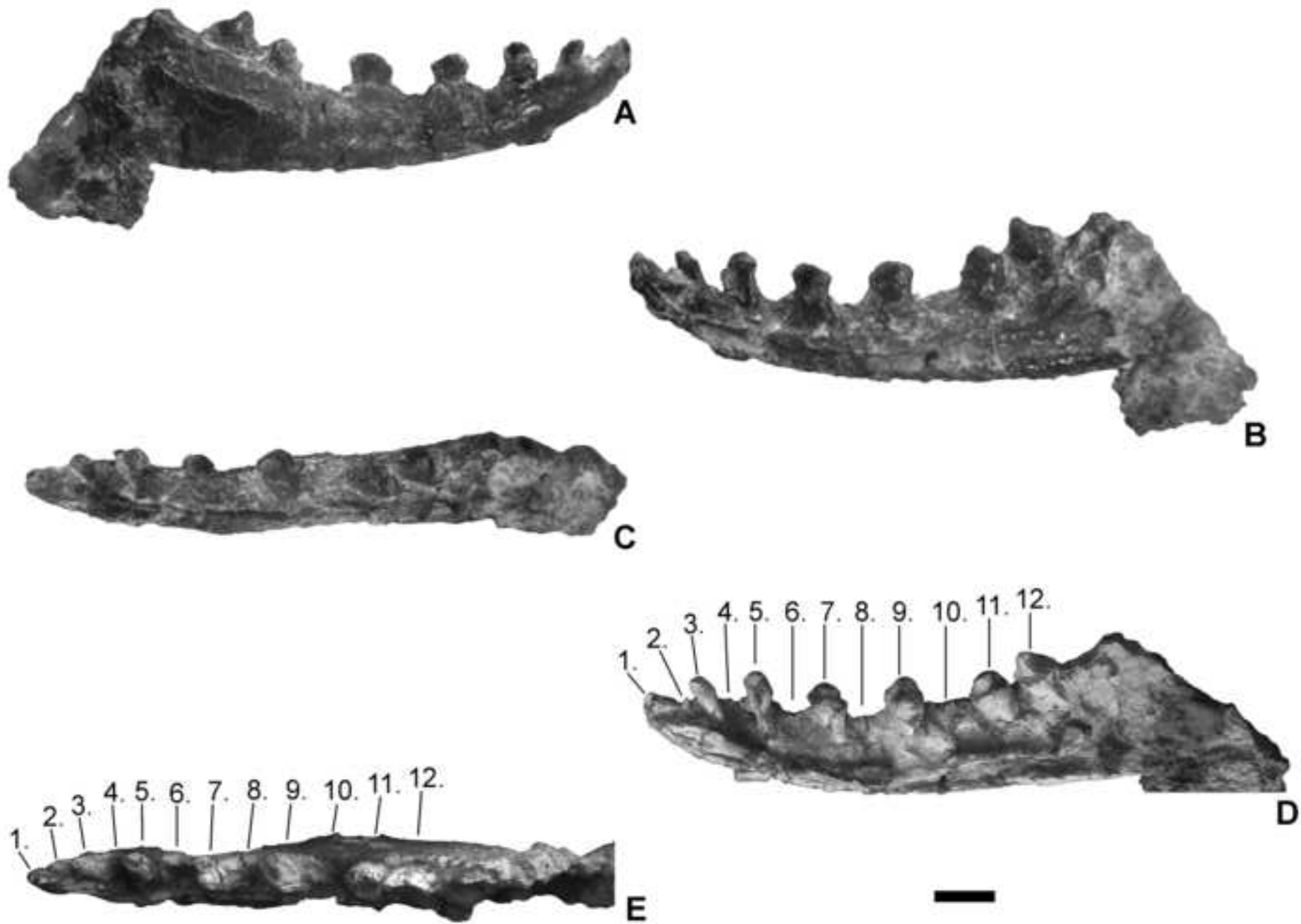


Figure 4  
[Click here to download high resolution image](#)

