A NEW ZALAMBDALESTID (EUTHERIA) FROM THE LATE CRETACEOUS OF MONGOLIA AND ITS IMPLICATIONS FOR THE ORIGIN OF GLIRES

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Fostowicz-Frelik, Ł. 2016. A new zalambdalestid (Eutheria) from the Late Cretaceous of Mongolia and its implications for the origin of Glires. *Palaeontologia Polonica* **67**, 127–136. LSID urn:lsid:zoobank.org:pub:DC3BF9B8-6689-46FD-AF5C-116A5195F68A

Barunlestes butleri Kielan-Jaworowska, 1975 from the Late Cretaceous of Mongolia was erected as a second genus of Zalambdalestidae, a specialized family of Asiatic Cretaceous eutherian mammals. Since the beginning, the peculiarities of one specimen (MgM-I/135), which could not be attributed to individual variation, led to questioning not only its generic but even family status. Among the differences the most notable are: more enlarged lower incisor (i1), which reaches the end of the tooth row, enamel cover on the i1 only ventral, deeper mandible body, the ultimate lower premolar with more strongly developed trigonid having large metaconid, a well-shaped high paraconid, and the metaconid transversely aligned with the protoconid. Thus, this specimen is herein assigned to *Zofialestes longidens* gen. et sp. n. It is definitely a zalambdalestid, although the most derived of all genera currently known. On the other hand, a combination of morphological characters shared also with some basal Glires suggests paraphyletic status of Zalambdalestidae and their plausibly ancestral position to the entire Euarchontoglires clade.

Key words: Crown placentals, Anagalida, Zalambdalestidae, *Barunlestes*, Mongolia, Late Cretaceous.

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Received 27 November 2015, accepted 25 January 2016.

http://dx.doi.org/10.4202/pp.2016.67_127

INTRODUCTION

Zalambdalestidae constitute a family of specialized Eutheria restricted to the Late Cretaceous of Asia (Kielan-Jaworowska *et al*. 2004). The nominal genus *Zalambdalestes* was originally described by Gregory and Simpson (1926) on the basis of three specimens. Kielan-Jaworowska (1975) recognized a second monotypic genus *Barunlestes* and included it into Zalambdalestidae. Apart from the fragmentary holotype skull with both mandibles in association (cataloged under ZPAL MgM-I/77), the preliminary description of the material mentioned three damaged skulls and two isolated mandibles, not figured in that paper. Kielan-Jaworowska and Trofimov (1980) provided a detailed account of the cranial morphology of *Barunlestes butleri* together with all specimen numbers and descriptions. Specifically, under ZPAL MgM-I/135 they listed: "incomplete lower jaw with alveoli for P_1–P_2 and P_3–M_3", figured in Jaworowska and Trofimov (1980: pl. 7: 2a–c). They noted that the specimen shows the best-preserved molars among *Barunlestes* specimens, but otherwise the teeth do not differ from those of *Zalambdalestes* (Kielan-Jaworowska and Trofimov 1980, p. 178). The first to formally recognize the morphological incompatibility of this specimen with other mandibles of *Barunlestes* were Li and Ting (1985). They proposed that MgM-I/135 represents a new genus and may be related to Paleocene eurymylids (Mammalia, Glires) on the basis of a greatly enlarged lower incisor and mesiodistally compressed lower molar trigonids. Subsequently, Li *et al*. (1987) included this single individual into a new family named "MgMidae" assigned to the order Mimotonida and hypothesized it as the most basal clade of Glires (Li *et al*. 1987, p. 105, fig. 2). McKenna (1994, p. 57) almost certainly referred to that specimen when commenting on "outer U-shaped band of single-layered enamel" on i1 of *Barunlestes* (but see Wible 2004, p. 30). Finally, Fostowicz-Frelik and Kielan-Jaworowska (2002) accepted that MgM-I/135 belongs to a new genus but did not name it, while pointing to the invalid status of "MgMidae" by virtue of being indicative only.

Currently Zalambdalestidae include five genera: *Alymlestes* Averianov *et* Nessov, 1995, *Barunlestes* Kielan-Jaworowska, 1975, *Kulbeckia* Nessov, 1993, *Zalambdalestes* Gregory *et* Simpson, 1926, and *Zhangolestes* Zan *et al*., 2006; all are monospecific (but see Wible *et al*. 2004 for *Zalambdalestes*). While *Zalambdalestes* is among the most completely known Late Cretaceous mammals from the standpoint of cranial and postcranial morphology (*e.g*., Kielan-Jaworowska 1978, 1984; Wible *et al*. 2004), *Alymlestes* is represented only by the crown of left m1 (Averianov and Nessov 1995).

In the present paper I reexamine the specimen MgM-I/135 and formally recognize it as a representative of a new genus and species within Zalambdalestidae. Further, some anatomical characters in *Barunlestes* are clarified; thirdly, I discuss the issue of zalambdalestid paraphyly and their suggested affinities with Glires, a crown clade of placental mammals.

Institutional abbreviations. — AMNH, American Museum of Natural History, New York, NY, USA; PIN, Paleontological Institute, Russian Academy of Sciences, Moscow, Russia; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

Acknowledgements. — This work was initiated over ten years ago at the suggestion of Zofia Kielan-Jaworowska and has had a rather prolonged incubation. I would like to thank Peter Bartsch (Museum für Naturkunde Berlin, Germany) for X-ray images of MgM-I/135 and comparative specimen of *Zalambdalestes*, Magdalena Groszkowska (Museum and Institute of Zoology, Polish Academy of Sciences, Warsaw, Poland) for the photographs shown in Fig. 1, and Morgan Hill (AMNH), Katarzyna Janiszewska and Jarosław Stolarski (both Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland) for help with micro-CT scanning. Andrés Giallombardo (formerly AMNH) kindly shared his expertise on zalambdalestid dental structure. Aleksandra Hołda-Michalska (Institute of Paleobiology, Polish Academy of Sciences) helped with Fig. 2. The author appreciates careful reviews by Rich Cifelli (University of Oklahoma, Norman, OK, USA) and Jin Meng (AMNH). This project was partly supported by a SYNTHESYS grant (project DE-TAF 291), a KOLUMB-supporting grant from the Foundation for Polish Science, AMNH Roosevelt Research Fellowship, and by the European Union within the European Regional Development Fund, through the Innovative Economy Operational Programme NanoFun POIG.02.02.00-00-025/09.

MATERIAL AND METHODS

Initially, the specimens ZPAL MgM-I/135, *Barunlestes butleri* (ZPAL MgM-I/90), and *Zalambdalestes lechei* ZPAL MgM-I/43 were studied with DIMA Soft P41 (Feinfocus, Garbsen, Germany) central focus

X-ray system at 25 and 29 kV (exposure *ca*. 7 s for all) at the Museum für Naturkunde Berlin, Germany. MgM-I/135 was CT-scanned with Phoenix v|tome|x L 240 scanner (GE Measurement & Control Solutions) (voxel size 0.020 mm, voltage 120 kV at the AMNH), while the holotype specimen of *Barunlestes butleri* (ZPAL MgM-I/77) was studied with a micro-CT scanner Zeiss XRadia MicroXCT-200 (Laboratory of Microtomography, Institute of Paleobiology Polish Academy of Science); the images of this specimen are accessible as the SOM (Supplementary Online Material available at http://www.palaeontologia.pan.pl/SOM/pp67-Fostowicz-Frelik_SOM.mpg). The photographs were taken with a Leica microscope with photo-stacking software (at the Museum and Institute of Zoology, Polish Academy of Sciences, Warsaw) and DinoLite PRO digital microscope. All measurements were taken with a Sylvac electronic caliper with the accuracy of 0.1 mm for mandible fragments and 0.01 mm for teeth.

The dental nomenclature follows Kielan-Jaworowska *et al.* (2004). Premolar counting is after Archibald and Averianov (2003), recently advocated by O'Leary *et al.* (2013). According to this convention five premolar loci in eutherians are consecutively marked as p/P1 through p/P5. On the other hand, Cifelli (2000) proposed to count the premolars consistently as p/P1 through p/P4 for the eutherians having four premolars, and in the genera displaying five premolars mark the teeth as p/P1–2, p/Px, and p/P3–4, where "p/Px" is the tooth of uncertain position. Although teeth counting consecutively from p/P1 through p/P5 is straightforward for basal eutherians (see Archibald and Averianov 2003; Zan *et al.* 2006), the matter gets complicated when referring to more derived eutherian taxa and dental homologies within large clades, *e.g.*, Glires, which have premolars traditionally numbered as p/P1 through p/P4. Mimotonids, eurymylids and lagomorphs of modern aspect lost the anterior premolars and retain only three upper and two lower premolars (marked usually as P2, p/P3, and p/P4). It is obvious that in basal Glires the ultimate premolar was never lost and the two retained lower premolars should be actually marked as p4 and p5 *sensu* O'Leary *et al.* (2013); however, the traditional counting method for this group allows us to avoid potential confusion, especially when discussing homologies with extant placentals. The lower and upper dental loci are indicated by lowercase and uppercase letters, respectively.

I recognize Anagalida Szalay *et* McKenna, 1971 (*sensu* McKenna and Bell 1997) in a restricted sense; that is, to the exclusion of Macroscelidea Butler, 1956. The Linnean classification provided below follows Kielan-Jaworowska *et al.* (2004). This paper and nomenclatural acts contained herein have been registered in ZooBank, the Official Register of the International Commission on Zoological Nomenclature (ICZN) and can be accessed at http://zoobank.org using LSID identifiers.

SYSTEMATIC PALEONTOLOGY

Infraclass **Eutheria** Gill, 1872 (*sensu* Huxley, 1880)

Magnorder **Epitheria** McKenna, 1975

Grandorder **Anagalida** Szalay *et* McKenna, 1971

Family **Zalambdalestidae** Simpson *et* Gregory, 1926

Genus ***Zofialestes*** gen. n.

LSID urn:lsid:zoobank.org:act:64D6D19E-E4BC-4922-9EDE-1BDC8787C4E3

Type species: *Zofialestes longidens* sp. n., monotypic.

Etymology: *Zofia*-, after the given name of the late Professor Kielan-Jaworowska, my demanding but always generous-to-teach mentor; and *-lestes* from Greek: robber or thief, a common suffix for small mammals of suggested predatory behavior.

Distribution. — As for the type and only species.

Diagnosis. — As for the type and only species.

Zofialestes longidens sp. n.

(Figs 1, 2)

LSID urn:lsid:zoobank.org:act:98D3AE0D-045E-4A7E-88F5-C173BD2B90D7

Barunlestes butleri: Kielan-Jaworowska and Trofimov 1980, pp. 169, 177, 178, pl. 7: 2 [in part].

Barunlestes butleri: Martin 2004: pp. 411, 417, 418, 421, fig. 2B [in part].

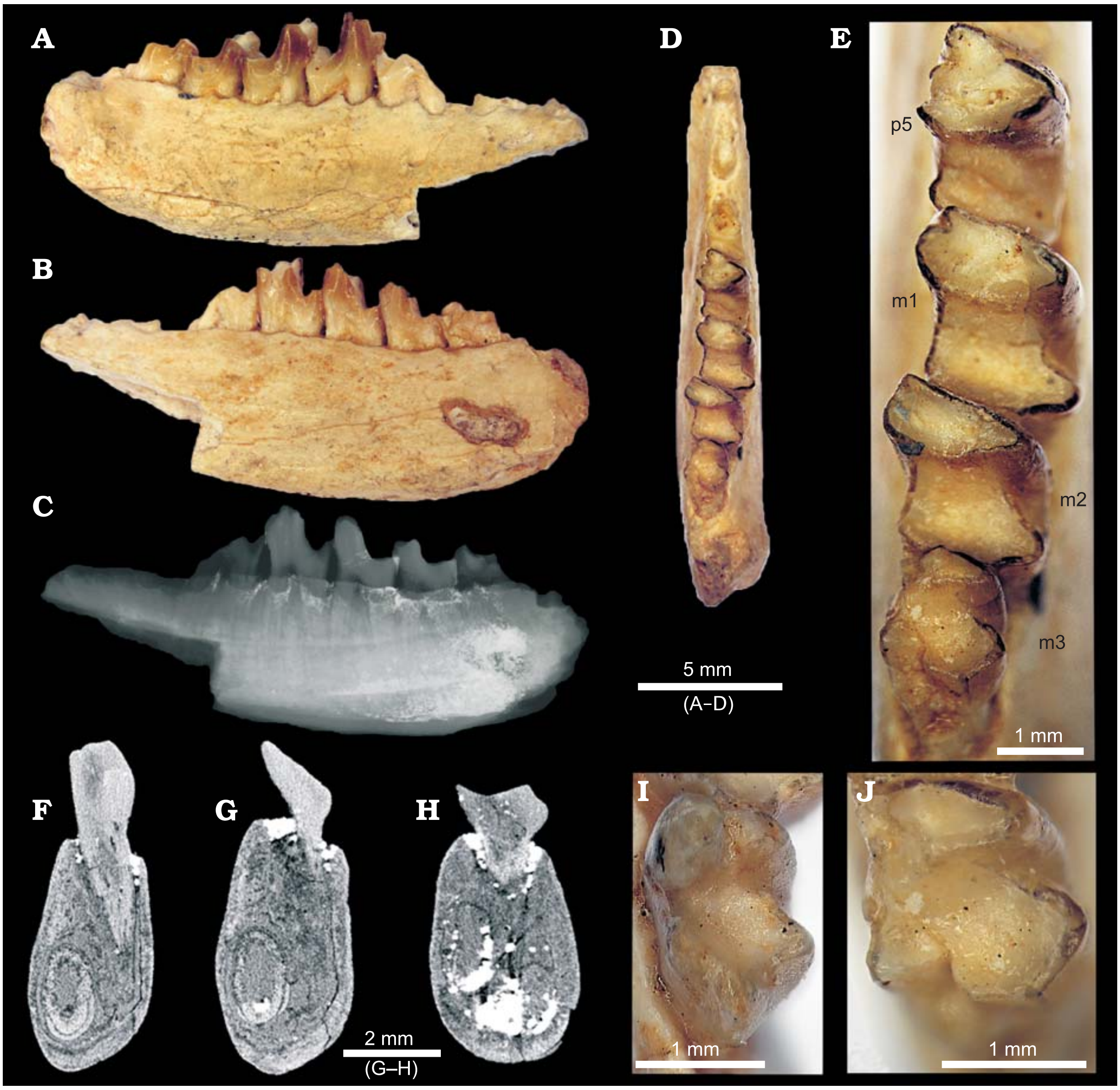

Fig. 1. *Zofialestes longidens* gen. et sp. n., right mandible (ZPAL MgM-I/135) with p4–m3 and roots of p1 and c; Baruungoyot Formation, Nemegt, Eastern Sayr (**A**–**H**, **J**); and *Barunlestes butleri* holotype (ZPAL MgM-I/77) (**I**). **A**. Buccal view. **B**. Lingual view. **C**. An X-ray image. **D**. Occlusal view of the whole mandible fragment. **E**. Occlusal view of p5–m3. **F**. Cross-section of the mandible at the level of p4/p5 transition (note the thick enamel layer). **G**. Cross-section at the level of m1. **H**. Cross-section at the level of distal m2 (note the lack of a distinct enamel layer at the distal end of the incisor). **I**. Structure of m3 in *Barunlestes butleri*. **J**. Structure of m3 in *Zofialestes longidens* gen. et sp. n.

Holotype: ZPAL MgM-I/135, fragmentary right mandible body with partially preserved lower incisor i1, root portions of c and p1, and p3–m3 *in situ*.

Etymology: From Latin “*longus*”, long and “*dens*” tooth; refers to a notably elongated lower incisor.

Type locality and horizon: Nemegt, Eastern Sayr, Nemegt Basin, Gobi Desert, Mongolia; Baruungoyot Formation, Late Cretaceous (?late Campanian) (see Gradziński *et al*. 1977, fig. 4).

Diagnosis. — Differs from *Barunlestes*, *Kulbeckia*, *Zalambdalestes*, and *Zhangolestes* in more enlarged lower incisor (i1), which reaches the end of the tooth row, in being slightly larger with a deeper mandible body, and in lacking hypoconulids on p5–m2. From *Kulbeckia*, *Zhangolestes*, and *Zalambdalestes* it differs in having only three premolars. *Zofialestes* differs from all four aforementioned genera in having enamel covering only the ventral half of i1, in a more molarized ultimate lower premolar that has a stronger developed trigonid with a large metaconid, well-shaped high paraconid, and metaconid aligned with protoconid. Further, it differs from *Barunlestes* in having two mental foramina on the lateral surface of the dentary, larger and wider m3 (with wider talonid) and from *Kulbeckia* in having a one-rooted canine.

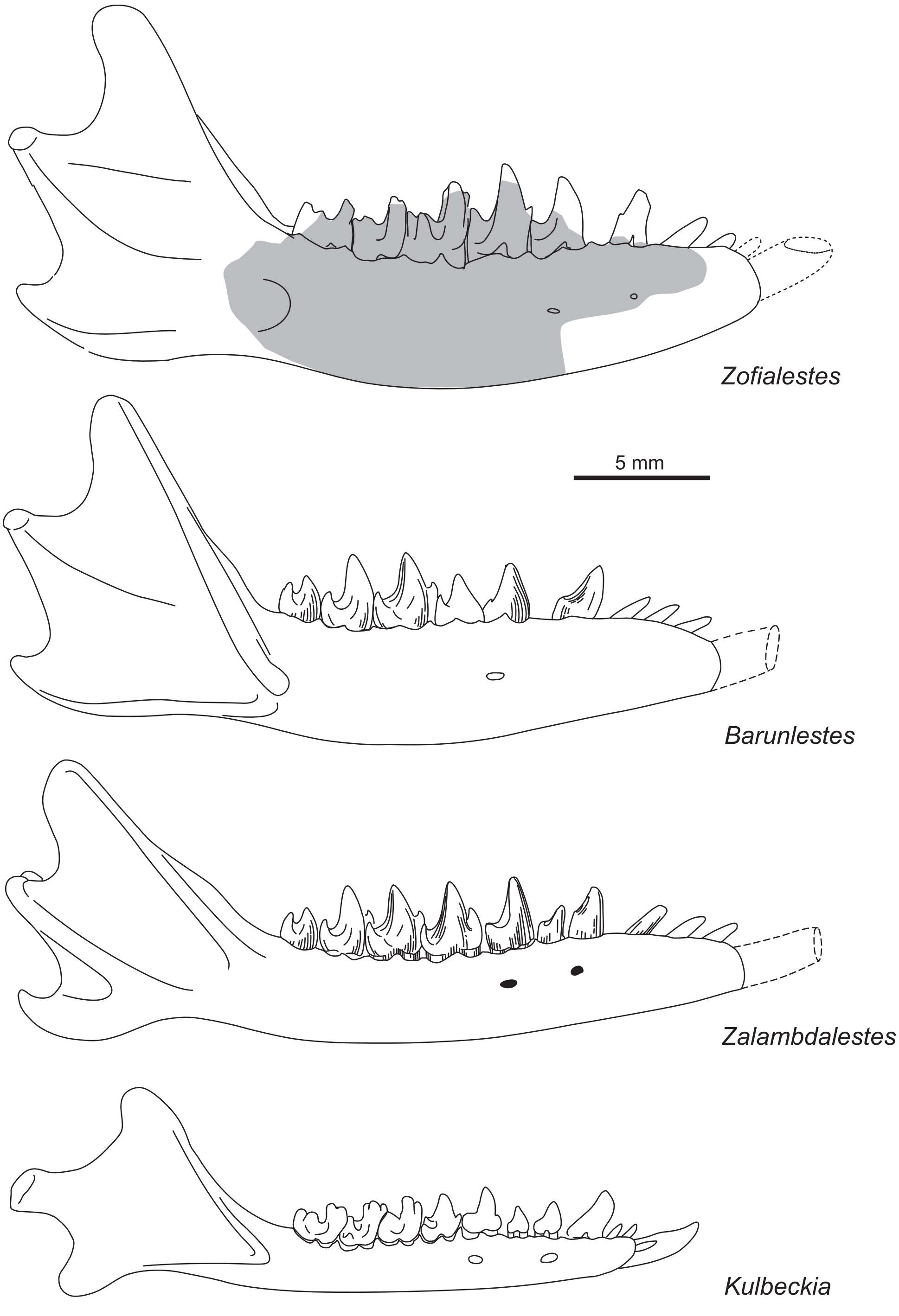

Fig. 2. Reconstructions of the right lower jaw in Zalambdalestidae. *Barunlestes butleri* and *Zalambdalestes lechei* redrawn from Kielan-Jaworowska (1975), *Kulbeckia kulbecke* redrawn from Archibald and Averianov (2003).

Comparative description. — The present external appearance of the specimen MgM-I/135 differs from that shown in Kielan-Jaworowska and Trofimov (1980, pl. 7: fig. 2) by the absence of the ventral part of the mandible body in the premolar portion, which was removed in order to study the incisor cross-section (by the late M.C. McKenna, AMNH).

The mandible is slightly more massive and relatively higher (Fig. 2; see Table 1) than in other zalambdalestids, including *Barunlestes*, which was previously cited as the species with the highest mandible body among zalambdalestids (Kielan-Jaworowska and Trofimov 1980). The molars are slightly wider than those of *Barunlestes* and *Zalambdalestes*, although the strong wear of most *Barunlestes* and *Zalambdalestes* specimens housed at the ZPAL collection makes the metrical comparisons not very informative. The ven-

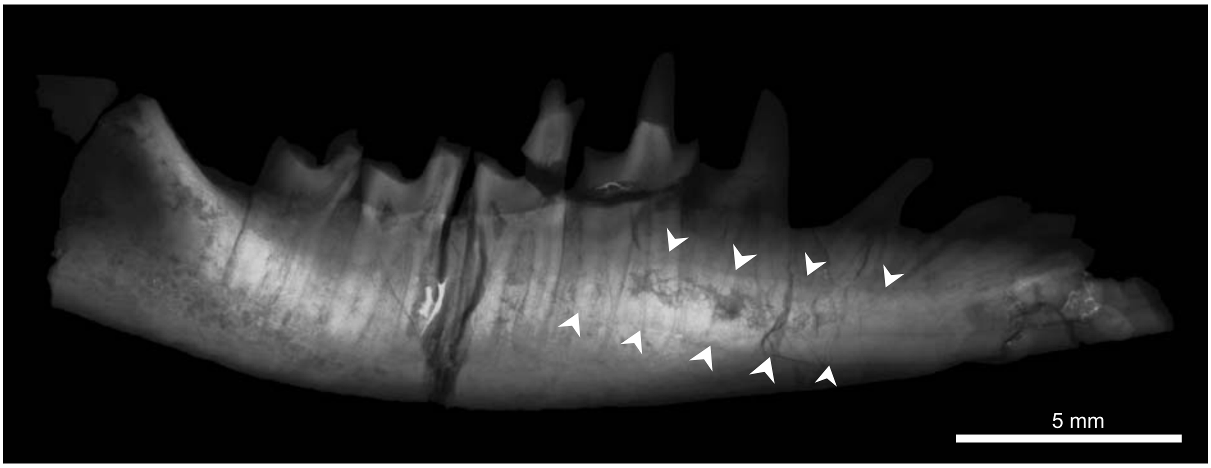

Fig. 3. X-ray image of the right mandible of *Zalambdalestes lechei* (ZPAL MgM-I/43) from Bayn Dzak locality, showing position and course of the i1 (white arrowheads).

tral margin of the mandible body is gently convex and is deeper than in *Barunlestes* (Fig. 2). In *Zofialestes* the curvature of the ventral margin of the mandibular body reaches its maximum under p4, and visibly decreases distally starting from the talonid of m1. The molar portion of the mandibular body is somewhat swollen and much thicker linguobuccally than in *Barunlestes* and other Zalambdalestidae, which have more delicate and slender mandibles (Figs 2, 3). Two mental foramina appear below p1 and p3, respectively, the same as in *Kulbeckia* and *Zalambdalestes* (in *Zhangolestes* the posterior mental foramen is visible under a p3 [p4 of Zan *et al*. 2006] alveolus). The masseteric tubercle is round and quite large, although it does not protrude as sharply as in *Barunlestes* (ZPAL MgM-I/104) but is rather blunt. It occurs below the distal part of the m3 talonid, slightly more anteriorly than in *Barunlestes*, where it occurs distal to the tooth row.

The tooth row is generally straight, with teeth erect (apart from m3, which is slightly slanted anteriorly), thus the occlusal surface of the entire tooth row is level.

The most characteristic feature of *Zofialestes* is a greatly elongated i1, which extends along the entire lower tooth row (at the lingual side of the roots, Fig. 1F–H) and ends at the distal margin of the m3 talonid (Fig. 1C), much farther distally than in *Kulbeckia* (see Archibald and Averianov 2003), *Zalambdalestes* (Fig. 3), and *Barunlestes* (see SOM); where it ends either under the ultimate premolar or the first molar (Fostowicz-Frelik and Kielan-Jaworowska 2002). Compared to *Zalambdalestes*, i1 of *Zofialestes* does not rise dorsally at its distal end (as in *Zalambdalestes*, Fig. 3), but is subparallel to the convex ventral margin of the mandible (Fig. 1C). The i1 of *Zofialestes* is massive, compressed buccolingually (oval in cross-section, with gently rounded ventral and dorsal sides) and open-rooted as in other zalambdalestids (see Fostowicz-Frelik and Kielan-Jaworowska 2002; Archibald and Averianov 2003; Zan *et al*. 2006). The enamel layer does not cover all the circumference of the tooth but is mostly restricted to the ventrobuccal side of the tooth; it encroaches on the ventrolingual side but does not reach this side as dorsally as it reaches buccally (*ca*. half of the tooth height; Fig. 1F, G). Compared to *Kulbeckia* and *Zhangolestes* the enamel layer is more restricted ventrally, forming, in cross-section, a U-shaped structure different from the C- or D-shaped band in *Kulbeckia* or *Zhangolestes*, respectively (Archibald and Averianov 2003; Zan *et al*. 2006). The enamel layer is thicker than in *Barunlestes* and *Zalambdalestes*, and its thickness is uniform along the circumference of the tooth; although the enamel layer gradually becomes thin distally, along the tooth length.

Table 1. Mandible parameters of chosen Zalambdalestidae taxa (measurements in mm). Abbreviations: MH, mandible height at p5; N, number of specimens; OR, observed range.

Species	m1–m3 L	MH	MH/m1–m3 ratio
Zofialestes longidens N = 1	5.8	5.2	0.89
Barunlestes butleri N = 8	5.9±0.42 OR 5.2–6.6	4.4±0.58 OR 3.2–5.0	0.75± 0.11 OR 0.58–0.87
Zalambdalestes lechei N = 2	6.4 OR 6.2–6.5	4.4	0.69 OR 0.68–0.70

The holotype of *Zofialestes longidens* has preserved the root portions of the canine and p1. Distal to p1 there is a small diastema marking the lack of p2 (absent also in *Barunlestes*), but present in *Zalambdalestes* and *Kulbeckia* (Kielan-Jaworowska and Trofimov 1980; Archibald and Averianov 2003). The canine was single-rooted and most probably was peg-like and semi-procumbent, similar to the condition in *Barunlestes* (Kielan-Jaworowska and Trofimov 1980). The gap between the canine and the root portion of p1 is narrower than in *Barunlestes* (about twice as narrow), the same applies to the diastema between p1 and p4 (p3 *sensu* Kielan-Jaworowska and Trofimov 1980). The p1 has two roots and their structure indicates that the tooth morphology may have been similar to that of *Barunlestes*, forming a sharp blade, slightly inclined anteriorly, and supported by a weaker anterior root and stronger distal one.

The p4 has a broken trigonid cusp, thus its structure cannot be fully ascertained. Nevertheless, judging from its remains, the tooth was structured as in other Zalambdalestidae, with a prominent spiky trigonid and a small heel-like talonid, sloping sharply in the lateral direction. However, the p4 of *Zofialestes* is slightly wider than in *Barunleste*s and *Zalambdaleste*s and gives the impression of being more massive than in any of the other genera. The distolateral margin of the trigonid is sharp and adjoins the similar structure created by the distolateral margin of the talonid. Both edges meet laterally at the base of the crown, forming an acute angle, which is lacking in *Zalambdalestes* and more weakly expressed in *Barunlestes* (best visible in MgM-I/104). The talonid is a relatively small triangle-shaped groove, rapidly tapering laterally and inclined in that direction. The distal part of the talonid rises up and conforms to the trigonid of p5 (p4 *sensu* Kielan-Jaworowska and Trofimov 1980), as in *Barunlestes*. The distal margin of the talonid shows two nascent folds or cusps, which may or may not be homologous with the entoconid and hypoconulid. Such cusps are absent in *Zalambdalestes*, while in *Barunlestes* only the hypoconulid-like fold is displayed in the adult specimen MgM-I/104. The talonid of p4 in *Zofialestes* is slightly larger and better defined than in *Zalambdalestes*; on the other hand, while it is very similar to that of *Barunlestes*, it is also shorter (compressed mesiodistally) and wider, with its sharp lateral edge forming a small but distinct projection.

The p5 is the longest tooth in the lower tooth row (Table 2). Its occlusal surface almost equals that of m1, but the tooth seems more strongly built in lateral view. The occlusal surface is slightly crumbled and partly worn, but the general shape and location of all cusps can be recognized. The trigonid of p5 is larger and more robust than in *Zalambdalestes*. It has an outline close to a right triangle, formed by an eminent protoconid and well-developed paraconid and metaconid. The presence of a well distinguished and large paraconid differentiates *Zofialestes* from other zalambdalestids and suggests that p5 displays more advanced molarization. The p5 paraconids of *Zalambdalestes* and *Kulbeckia* are relatively small cusps located anteriorly and relatively low at the tooth crown (Kielan-Jaworowska 1975; Archibald and Averianov 2003). Kielan-Jaworowska and Trofimov (1980) stated that in *Barunlestes* p5 (p4 in their paper) lacks the anterior basal cusp (= paraconid) entirely (but see PIN 3142-701, *ibidem* pl. 4, 1b, d). Moreover, in a relatively young specimen, ZPAL MgM-I/72, a freshly erupted p5 displays a similar small basal anterior cusp. The p5 paraconid in *Zalambdalestes* and *Kulbeckia* is placed more centrally (almost in the parasagittal plane of the tooth) than in *Barunlestes* where it is slightly linguad. In *Zofialestes* the p5 paraconid has its base higher on the crown and is larger than in other zalambdalestids; it is also located much more lingually, almost aligned with the metaconid, which protrudes slightly more lingually (Fig. 1D, E). The p5 metaconid in *Zofialestes* was larger and much longer than in *Barunlestes* judging from its preserved lingual margin. The protoconid was most probably the largest and highest of the cusps (as in *Zalambdalestes* and *Barunlestes*). The talonid of p5 is less inclined laterally than in *Barunlestes* and *Zalambdalestes*, creating a slightly larger and more horizontal occlusal surface. Compared to *Barunlestes* the occlusal surface of the p5 talonid in *Zofialestes* is of similar size, but wider in relation to the trigonid, and more basined. Moreover, it has a distinct large entoconid, protruding lingually. The distal margin of the talonid is flat and lacks any traces of the hypoconulid.

The molars show moderate tooth wear but all dental structures are visible. The m1 is largest of the molars and has the greatest occlusal surface of all teeth in the row. The trigonid of m1 is somewhat triangular in outline with a small paraconid and larger metaconid at the lingual side, and a large protoconid. The metaconid is slightly higher than the protoconid at this stage of wear, as in *Zalambdalestes* (also in a less worn specimen ZPAL MgM-I/51). The well-defined paraconid differentiates *Zofialestes* from *Barunlestes*, in which this cusp is

Table 2. Dental measurements (in mm) of *Zofialestes longidens* holotype (ZPAL MgM-I/135). Abbreviations: L, tooth length; Wtal, talonid width; Wtri, trigonid width.

Tooth	L	Wtri	Wtal
p5	2.46	1.76	1.48
m1	2.43	1.95	1.93
m2	2.11	1.91	1.85
m3	–	1.49	1.50

very weakly developed (observed only in a young specimen, ZPAL MgM-I/72). The talonid of m1 is large and basined with a large hypoconid projecting buccally and a smaller entoconid. There is no trace of a hypoconulid on m1.

The m2 is smaller than m1, with the trigonid more compressed mesiodistally. The paraconid is more reduced than in m1 but it is still recognizable. The talonid is similar to that of m1 with a well-developed hypoconid, also slightly protruding buccally. The entoconid is slightly damaged and smaller than the hypoconid; no trace of the hypoconulid is observed.

The m3 differs somewhat in structure from m1–2. The medial side of the trigonid is damaged; thus, the exact shape of the paraconid and metaconid cannot be ascertained (Fig. 1E, J). I presume that both cusps were present as in *Zalambdalestes* because the lingual part of the tooth is relatively long, compared to *Barunlestes*, which has no paraconid on m3 (see ZPAL MgM-I/107; Fig. 1I). The talonid of m3 in *Zofialestes* is also partly damaged but the presence of a relatively large hypoconulid is certain, judging from the extended distal root portion (Fig. 1E), unlike in *Barunlestes* and *Zalambdalestes* where it tends to be spiky in younger specimens and small and insignificant in mature, more worn individuals. The hypoconid (Fig. 1J) is larger and more round than in *Barunlestes* and *Zalambdalestes*. However, the hypoconulid in *Zofialestes* was most probably shorter and more compressed anterodistally than in *Barunlestes* and *Zalambdalestes*.

DISCUSSION

According to Li *et al*. (1987, p. 104), the dubious status of MgM-I/135 as a zalambdalestid stems from the following characters shared with all Glires: "(3) I1/1 and I2/2 (permanent) lost, (4) dI2/2 retained, enlarged and ever-growing, with di2 extending back to below m2 or m3 (extrapolation from living rodents and lagomorphs; see Luckett, 1985), and (5) molar trigonids compressed." Of these characters only the last is valid, but it is a plesiomorphy for Glires, and is listed as typical of Zalambdalestidae (Kielan-Jaworowska *et al*. 2004).

The total count of the lower incisors is unknown in *Zofialestes longidens*; the other genera of Zalambdalestidae have retained three to four lower incisors, with the largest being identified as i1 (Kielan-Jaworowska 1975; Archibald and Averianov 2003; Zan *et al*. 2006); thus, I assume that *Zofialestes* did not differ significantly in this respect. However, the homologies of zalambdalestid incisors with the incisors of Lagomorpha are uncertain (Fostowicz-Frelik and Kielan-Jaworowska 2002); in particular it is unclear whether the enlarged and procumbent lower incisors in Zalambdalestidae are deciduous teeth and whether they represent the second pair of the incisors; in Lagomorpha the enlarged anteriormost incisors are identified as DI2/di2.

A variously procumbent and enlarged lower incisor is not unusual in Euarchonta, as it is known for Paleogene *Plesiadapis* and living *Daubentonia* (see Szalay and Delson 1979, figs 32 and 73, respectively); also some Anagalidae express definitely procumbent, although less enlarged incisors (*e.g.*, *Anagale*, Simpson 1931, fig. 2; *Qipania*, Hu 1993, fig. 6). In fact, the lower incisors of the earliest duplicidentate *Mimotona* are more bladelike than those of any lagomorphs (see Li and Ting 1993, figs 11.3, 11.4C, D) and they have the occlusal surfaces shaped very similar to those of plesiadapids, although in a more gentle way. Thus, the shape of the incisors is variable within Glires (and Euarchontoglires; see Meng *et al*. 2003, pp. 118–119, character 11, for more data on incisor morphology in Glires).

Another question is the extent of restricted enamel on the incisor; in *Zofialestes* the enamel layer covers only the ventral half of the tooth (Fig. 1F, G), which is suggestive of and parallels the enamel formation in lower incisors of Glires, including the basal representatives (see *e.g.*, *Tribosphenomys*, Meng and Wyss 2001, fig. 4A); while in *Barunlestes* and *Zalambdalestes* enamel covers also the lingual and most of the buccal side of the tooth, and in *Kulbeckia* and *Zhangolestes* it covers most of the incisor circumference and is only lacking on the lingual side of the tooth, creating in cross-section either a C- or D-shaped pattern of distribution (see Archibald *et al*. 2001, fig. 5B; Zan *et al*. 2006, fig. 4).

The available morphological evidence indicates that *Zofialestes longidens* should be included in Zalambdalestidae, and it is definitely not a member of Glires. However, inclusion in Zalambdalestidae does not necessarily preclude *Zofialestes* from belonging to the lineage which eventually gave rise to Glires or the Glires+Anagalidae clade, as previously suggested (Archibald *et al*. 2001, fig. 3b; Archibald and Averianov 2003; see also Meng 2004 for more discussion). Taking into account the enlarged i1 reaching the end of the tooth row, the presence of only three premolars, a higher mandibular body and more advanced molarization of premolars and development of molar talonids, *Zofialestes* is undoubtedly the most derived of zalambdalestids. Further, *Zofialestes* shows some characters which may be interpreted as antecedent to Glires: a distinct paraconid on p5 (marked in Glires as "p4"), shifted lingually and present in a slightly reduced form in the permanent dentition of some basal Glires (*e.g.*, *Rhombomylus*, see Meng *et al*. 2003, figs 8D, E, 13, 14F, larger in Dp4 of eurymylids; *ibidem*, fig. 14A–C; Dashzeveg *et al*. 1987), slight enlargement of m3 in relation to m2 (a noticeable trend for increasing m3 size is known for eurymylids, mimotonids and rodents), and slight inclination of the m3 in the anterior direction as an incipient stage towards formation of a slightly concave occlusal surface of the entire tooth row (also typical of Glires). Additionally, the alignment of the metaconid and protoconid in ultimate premolar and molars is characteristic of some basal Glires (*e.g.*, *Rhombomylus*, Meng *et al*. 2003 and *Eurymylus*, Sych 1971). As for Glires these characters are mostly plesiomorphic; nevertheless they indicate overall evolutionary trends and may become synapomorphic for a more inclusive clade. The evolutionary morphology of Glires is well known to demonstrate a very high level of convergence and parallelism in dental and osteological characters (*e.g.*, Lazzari *et al*. 2008; Cox *et al*. 2012, fig. 2; Fostowicz-Frelik and Meng 2013), thus obscuring phylogenetic relationships by frequent homoplasies.

Phylogenetic analyses involving the three best-studied zalambdalestids (*Barunlestes*, *Kulbeckia*, and *Zalambdalestes*) returned this group as a monophyletic clade (Archibald *et al*. 2001, fig. 3a; Meng *et al*. 2003; Asher *et al*. 2005) close to Asioryctitheria. In the analysis of Archibald *et al*. (2001, fig. 3b) with the inclusion of the basal Glires taxa *Tribosphenomys* and *Mimotona*, Zalambdalestidae tend to be paraphyletic and group at the base of the clade joining them with Glires. However, this analysis did not include anagalids, Scandentia and Dermoptera, which may have placed Zalambdalestidae immediately outside the entire Euarchontoglires clade (see Meng *et al*. 2003; fig. 74 and Meng 2004 for a broader discussion). To evaluate the broad concept of Anagalida that would include also some Cretaceous placental taxa (see McKenna 1975) and thus, actually may extend crown placental mammals below the K-Pg boundary (unsupported by O'Leary *et al*. 2013), an increased coverage (both taxonomical and morphological) of Glires, Anagalidae and Pseudictopidae is needed for further phylogenetic analysis. In particular, the primitive state for characters should be meticulously analyzed and all characters scrutinized against homoplasies.

Concluding, the scarcity of material precludes a definitive placement of *Zofialestes* within the crown placentals. However, it currently appears to be the Cretaceous placental morphologically closest to Glires, to which it may be related.

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