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Lower incisor in zalambdalestid mammals (Eutheria) and its phylogenetic implications

ŁUCJA FOSTOWICZ-FRELIK and ZOFIA KIELAN-JAWOROWSKA

Relationships of the specialized eutherian family Zalambdalestidae (Late Cretaceous, Asia) have long been debated. Beginning with suggestion of Van Valen (1964) and including the recent phylogenetic analysis of Archibald et al. (2001), a possible close relationship of Zalambdalestidae to Glires (Lagomorpha + Rodentia) has been repeatedly suggested (but see Meng and Wyss 2001). One of the characteristics of Glires is the structure of the lower incisor, which is enlarged and open-rooted. An open-rooted incisor has been documented in the oldest known zalambdalestid, *Kulbeckia*, but structure of this tooth has remained unknown for the Mongolian representatives of this family, *Zalambdalestes* and *Barunlestes*. Here we present evidence on the presence of an open-rooted first lower incisor in *Zalambdalestes lechei* and *Barunlestes butleri*; we argue, however, that structure of this incisor does not necessarily indicate relationship of Zalambdalestidae to Glires.

Introduction.—Zalambdalestidae Gregory and Simpson, 1926 are a group of small, ricochetal mammals that inhabited Central Asia during the Late Cretaceous (Kielan-Jaworowska 1978, 1984, and references therein). Four genera are currently known: *Zalambdalestes* Gregory and Simpson, 1926, *Barunlestes* Kielan-Jaworowska, 1975, *Kulbeckia* Nessov, 1993, and *Alymlestes* Averianov and Nessov, 1995. The phylogenetic relationships of the Zalambdalestidae are somewhat obscure. Kielan-Jaworowska (1978) stated that the mosaic of derived and plesiomorphic characters observed in Zalambdalestidae did not suggest a particular relationship to any other known group of mammals. However, a different point of view, suggesting a close relationship either to Lagomorpha or Glires has been supported, among others, by Van Valen (1964), McKenna (1975), Li et al. (1987), McKenna and Bell (1997), and Archibald et al. (2001). Zalambdalestidae were placed among the Anagalida, an order originally erected by Szalay and McKenna (1971) to include four extinct, Asiatic families (Zalambdalestidae, Pseudictopidae, Anagalidae, Eurymylidae), in turn hypothesized by these authors to be proximal relatives of Lagomorpha. Subsequently, McKenna (1975) enlarged the scope of Anagalida, giving it grandorder rank and including in it living Macroscelidea as well as Lagomorpha. The classification of McKenna and Bell (1997) is similar, with one important change: the addition of order Rodentia to grandorder Anagalida. On the other hand, Meng and Wyss (2001) excluded Zalambdalestidae from Glires.

The first lower incisor of Zalambdalestidae is notably large and procumbent, oval in cross-section, with enamel apparently restricted, or at least thicker on the ventro-lateral side (see Archibald et al. 2001: fig. 2c), but how far back it extends has been questionable. Kielan-Jaworowska (1975) and Kielan-Jaworowska and Trofimov (1980) suggested that it reached the level of p3 in *Zalambdalestes*, but Meng and Wyss (2001), based on informal comments of McKenna (1994, personal communication), suggested that it extended back to the level of the anterior molars. However, Meng and Wyss (2001) referred to ZPAL MgM-I/135, which belongs to another genus (see below).

Li and Ting (1985) and Li et al. (1987) suggested that *Barunlestes* had an open-rooted lower incisor, basing on ZPAL MgM-I/135. MgM-I/135 differs from other specimens in ZPAL collection formally referred to *Barunlestes butleri*. Li and Ting (1985) suggested that it might belong to a new genus, related to eurymylids. We agree that ZPAL MgM-I/135 is not congeneric with the holotype of *Barunlestes butleri* and consider it to represent a new, as yet unnamed genus.[1]

Results.—We examined all dentaries of *Zalambdalestes* and *Barunlestes* (see lists in Kielan-Jaworowska and Trofimov 1980, and Kielan-Jaworowska 1984) housed at the Institute of Paleobiology, Polish Academy of Sciences, Warsaw (abbreviated ZPAL), and we photographed the first lower incisor in three of them.

The best results were obtained from the right dentary of *Barunlestes butleri* (ZPAL MgM-I/90, not figured previously) from Khermeen Tsav. In this dentary (Fig. 1), apart from the conspicuously procumbent lower incisor, three molars, part of p4 (subsequently damaged), and the roots of p3, p1, canine, i3, and i2 are preserved (Kielan-Jaworowska and Trofimov 1980). The molars are very strongly worn, which suggests an advanced ontogenetic age for this individual. In this specimen we removed a large part of the labial wall of the dentary to expose the whole extent of the incisor root. The root ends below the posterior part of m1, and its apex is open.

In Fig. 2 we present SEM micrographs of the anterior part of the left dentary in another specimen of *Barunlestes butleri* (ZPAL MgM-I/72, not figured previously). This specimen was not listed by Kielan-Jaworowska and Trofimov (1980), as it was still unprepared at the time that paper was published. This dentary has been broken between m1 and m2, and the posterior part is missing. We removed a tiny part of the lingual wall of the dentary below m1. Because of the extreme fragility of this specimen, in which the root of i1 is filled with weakly consolidated, fine-grained sediment, we were unable to expose the entire root. The pulp cavity is large and surrounded by extremely thin root walls; dimensions of the visible elliptical root section are similar to those of the anterior part (crown) of the tooth. Both conditions are characteristic also for lagomorphs

[1] Li et al. (1987) named for ZPAL MgM-I/135 the family "MgMidae", assigned to the order Mimotonida (see also Li and Chow 1994). According to International Commission on Zoological Nomenclature (1999: Article 13. Names published after 1930) the name "MgMidae", as proposed only by indication, is not available.

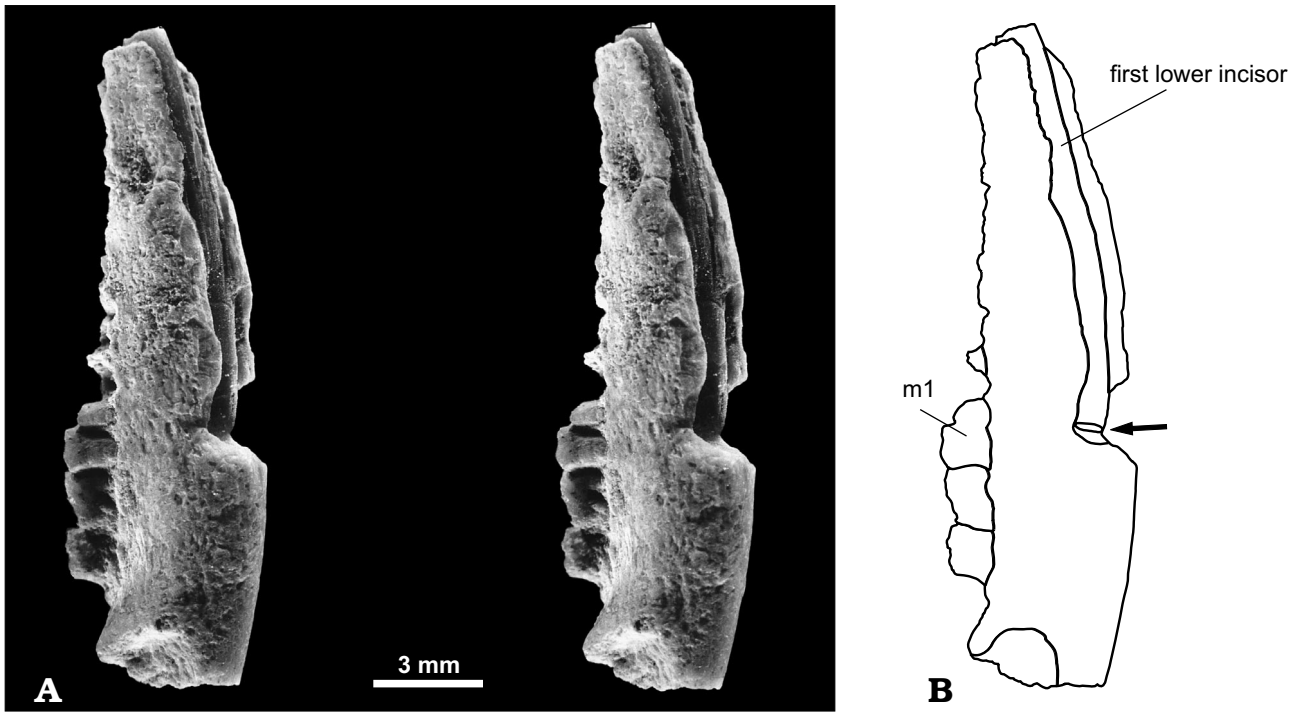

Fig. 1. Right dentary of *Barunlestes butleri*, ZPAL MgM-I/90. Stereophotograph showing the exposed root of i1, in labial view (**A**), and explanatory drawing for the same (**B**). The arrow points at the end of i1.

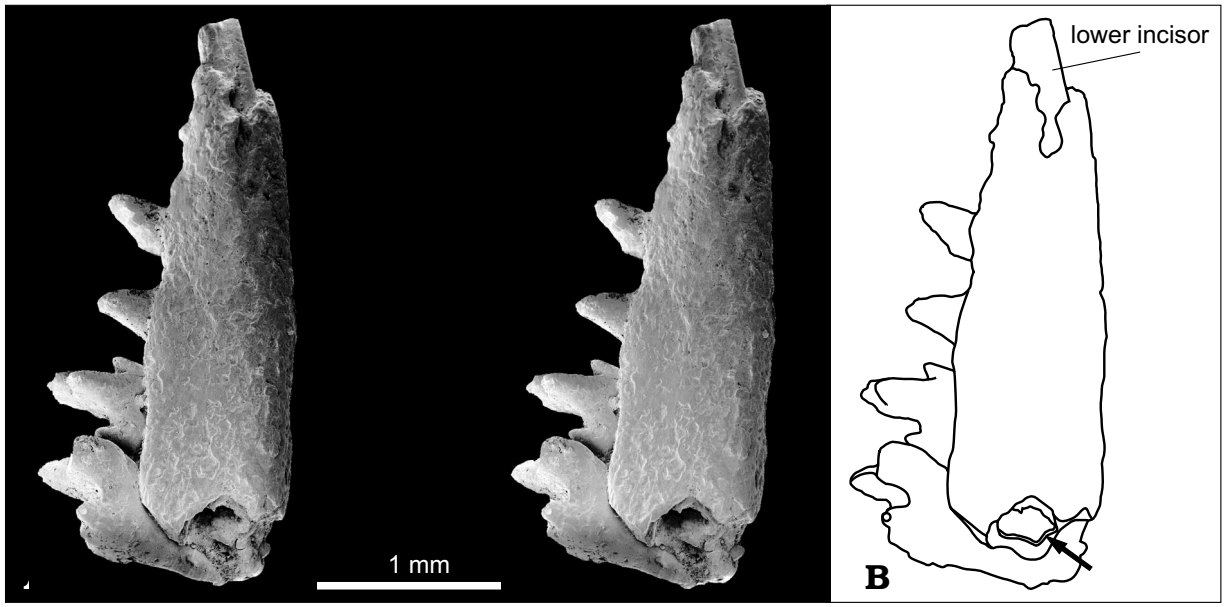

Fig. 2. Left dentary of *Barunlestes butleri*, ZPAL MgM-I/72. SEM stereo-micrograph of the anterior part of the dentary broken at the level of m1, in lingual view (**A**), and explanatory drawing for the same (**B**). The arrow points at the end of i1.

and rodents. Although we cannot be certain given the preservation, the exposed portion below m1 (Fig. 2) is probably at or near the apical end of the root.

Among specimens of *Zalambdalestes lechei* deposited at ZPAL, we studied the right and left dentaries (ZPAL MgM-I/51 and ZPAL MgM-I/43, respectively) from the Djadokhta Formation, at Bayan Zag (formerly Bayn Dzak, see Benton 2000), Gobi Desert. Specimen ZPAL MgM-I/51 was figured previously by Kielan-Jaworowska and Trofimov (1981: pl. 2: 2), and ZPAL MgM-I/43 by Kielan-Jaworowska (1984: pl. 15: 1a–c). Specimen ZPAL MgM-I/51 belonged to a relatively young individual. It is fairly complete, containing the entire lower tooth row: i3 c1 p4 m3 (Kielan-Jaworowska 1969, 1984; Kielan-Jaworowska and Trofimow 1981). The dentary had been broken between p4 and m1 and subsequently repaired. We dissolved the glue and exposed a tiny part of the lower incisor root wall from the lingual side. The incisor is not filled with sediment, so

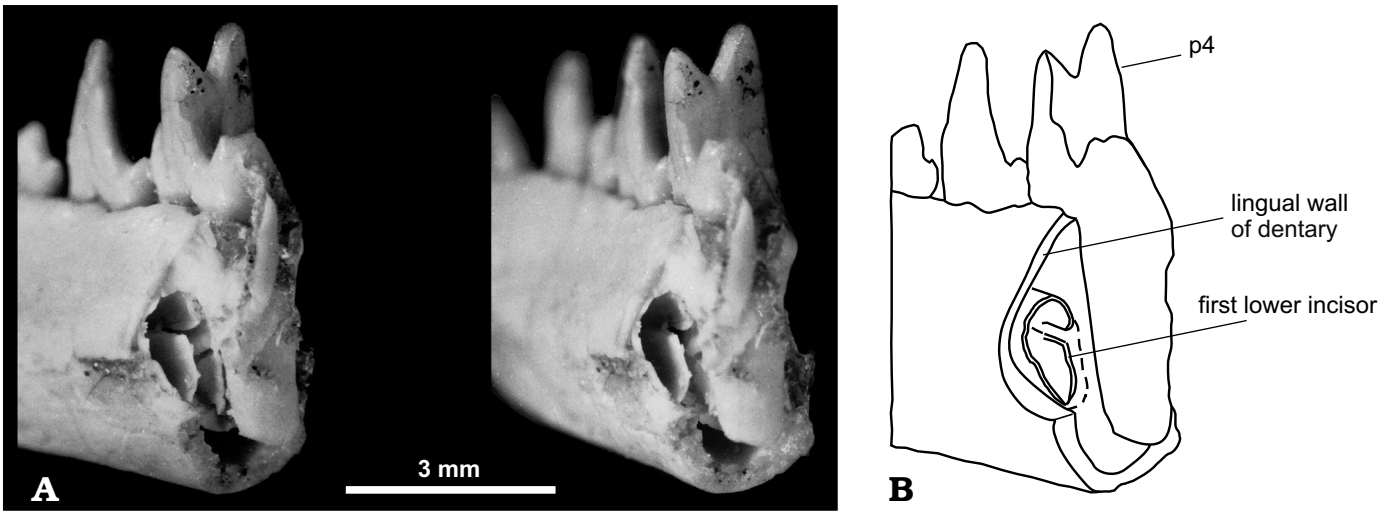

Fig. 3. Right dentary of *Zalambdalestes lechei*, ZPAL MgM-I/51. Stereophotograph of the anterior part of the dentary broken between p4 and m1, in disto-lingual view (**A**), and explanatory drawing for the same (**B**).

that the root can be easily seen to be open. On the other hand, lack of a stabilizing, interior matrix has resulted in some cracking and shifting of the labial parts of the root walls (Fig. 3), which prevented further exposure and investigation. In the same way, we examined specimen ZPAL MgM-I/43, which had been similarly broken and repaired, in this case, between p4–m1 and m1–2. The large open root of i1 was well visible below p4 and the anterior part of m1. Moreover, below m2 and further backward the posterior part of the dentary does not contain any trace of the root of i1.

Discussion.—The question arises as to whether the open-rooted zalambdalestid lower incisor speaks for a phylogenetic relationship between the Zalambdalestidae and Glires. There is no consensus as to whether the first lower incisor of zalambdalestids is homologous to those of lagomorphs and rodents (Meng and Wyss 2001). For instance, Li et al. (1987) stated that Glires have lost I1/1 and I2/2, but retained (enlarged) dI2/2; while it is probable that the enlarged lower incisor in Zalambdalestidae is i1 (Kielan-Jaworowska 1975; McKenna 1975; Kielan-Jaworowska and Trofimov 1980; Archibald et al. 2001). On the other hand, McKenna (1975) stated that the incisor formula ancestral for lagomorphs is: i1 I2 I3. Thus the issue of homology and synapomorphy remains open.

The condition of the open-rooted lower incisor in Zalambdalestidae is apomorphic in comparison with other Cretaceous epitherian mammals (e.g., *Asioryctes*, *Kennalestes*), but it differs from those in Glires in several characters. It is straight and procumbent, rather than being strongly bent upwards as in Glires. It shares with Glires restricted enamel band, albeit the enamel boundary in Zalambdalestidae is less sharp than in Glires, and one cannot be sure whether a thin layer of enamel still remains on the lingual side of the tooth. Further differences between the two taxa concern the upper incisors. The three or two (Kielan-Jaworowska 1969, 1984) upper incisors in Zalambdalestidae are not notably enlarged, and do not function as a self-sharpening cutting mechanism with the lower ones, contrary to the strongly enlarged upper incisors in Glires. Hence, the series of evolutional events leading to the transformation of, presumably, ancestral state of incisor character observed in Zalambdalestidae into that of Glires seems rather intricate. More probably it may be presented as simultaneous evolution of both upper and lower incisorrs. The uncertainty concerning the homology of the lower incisor in Zalambdalestidae and Glires, discussed in the preceding paragraph, and the above-cited differences (albeit some of these characters are plesiomorphies) cast doubt on a close relationship between Zalambdalestidae and Glires. However, one can argue that the curvature of lower incisors in lagomorphs varies and is less strongly expressed than in rodents, where it could be related to the hypsodonty of lower molars. It cannot be excluded that the Zalambdalestidae represent an incipient stage from which (or from related forms) the advanced incisors of lagomorphs and rodents originated. As long as the intermediate forms between the discussed groups are not known, the hypothesis of a relationship between Zalambdalestidae and Glires (supported by the analyses of Archibald et al. 2001, but not by those of Meng and Wyss 2001) must be viewed with caution.

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Łucja Fostowicz-Frelik [lfost@twarda.pan.pl] and Zofia Kielan-Jaworowska [zkielan@twarda.pan.pl], Instytut Paleobiologii PAN, ul. Twarda 51/55, PL-00-818 Warszawa, Poland.