

# Petrosal bones of placental mammals from the Late Cretaceous of Uzbekistan

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Petrosal bones representing “Zhelestidae” and *Kulbeckia* (“Zalambdalestidae”) were recovered from the Late Cretaceous of Uzbekistan and are formally described. The “zhelestid” petrosal retains several characters ancestral to eutherians (if not more basally in the mammalian phylogeny), including a prootic canal, a lateral flange, and a less elliptical fenestra vestibuli. The only other eutherian taxon to retain these structures is the Early Cretaceous *Prokennalestes*. No characters unique to “zhelestids” and ungulates were found in the “zhelestid” petrosal. The petrosal of *Kulbeckia* shares several characters in common with other “zalambdalestids” (such as *Zalambdalestes* and *Barunlestes*), as well as *Asioryctes* and *Kennalestes*, including a curved ridge connecting the crista interfenestralis to the caudal tympanic process, and presence of a “tympanic process” at the posterior aspect of the petrosal.

Key words: Mammalia, “Zhelestidae”, “Zalambdalestidae”, *Kulbeckia*, petrosal, Late Cretaceous, Uzbekistan.

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## Introduction

Mammalian petrosal bones recovered from upper Turonian–Coniacian deposits in the Bissekty Formation, Dzharakuduk, Kyzylkum Desert, Uzbekistan have been assigned to two Late Cretaceous eutherian mammal taxa: “Zhelestidae” and the “zalambdalestid” *Kulbeckia kulbecke*. These petrosal bones, which house the structures of the inner ear of these taxa are significant because they add to our body of knowledge of eutherian and early placental mammal evolution.

“Zhelestidae” was first described by Nessov (1985), and although it is best known from Dzharakuduk, members of this group have been found in Europe as well as North America (Nessov et al. 1998). Archibald (1996) argued that “Zhelestidae” has strong affinities with modern ungulates, and a “zhelestid”-ungulate relationship has been supported by several later studies, including Nessov et al. (1998), Archibald et al. (2001), and Ji et al. (2002). The results of Archibald et al.’s (2001) analyses, which included “zhelestids” and “zalambdalestids”, as well as archaic ungulates (*Protungulatum* and *Oxyprimus*) and glires (*Mimotona* and *Tribosphenomys*), nest the archaic ungulates within the “zhelestid” clade, rendering “Zhelestidae” paraphyletic (hence the quotation marks around the name). “Zalambdalestidae” is also rendered paraphyletic by these results, as modern Glires nests within it.

Characters uniting “Zhelestidae” with Ungulata have been taken exclusively from the dentition of these animals because

until recently (Archibald et al. 2001) only dental material had been known for “Zhelestidae”. Dental characters that unite “Zhelestidae” with Ungulata include two parastylar cuspsules, slight antero-posterior expansion of the protocone, trapezoidal molar crown in occlusal view, metaconid on the ultimate premolar significantly smaller than the protoconid, and a lowering of the trigonid (see Archibald et al. 2001 for further discussion of these characters).

*Kulbeckia kulbecke* was named and described by Nessov (1993), and its possible relationship to other “zalambdalestids” was first suggested several years later (Nessov 1997). A strong relationship between *Kulbeckia* and other “zalambdalestids” has been supported in subsequent studies, including Archibald et al. (2001). A relationship between “Zalambdalestidae” and Glires is more controversial, however. Such a relationship was supported by Van Valen (1964), McKenna (1975), McKenna and Bell (1997), and Archibald et al. (2001), but it was not supported by the phylogenetic analyses of Meng and Wyss (2001), and Fostowicz-Frelik and Kielan-Jaworowska (2002) suggested that a “Zalambdalestidae”-Glires relationship be approached with caution.

Nonetheless, several characters support a relationship between “Zalambdalestidae” and Glires, including a markedly enlarged procumbent lower medial incisor with enamel restricted to the more labial aspect of the tooth, posterior exten-

sion of the root of the lower medial incisor below p1, large apical opening in the root of the lower medial incisor, anteroposterior constriction of the trigonid at the midpoint of the para- and protocristid on m1–3, and a marked narrowing of the snout anterior to the posterior premolars (see Archibald et al. 2001 for further discussion of these and other characters).

The petrosal bones of “Zhelestidae” and *Kulbeckia* have not been described, although a brief preliminary description of the bones has been published (Ekdale et al. 2001). A formal identification and full description of the structure of the petrosals for both taxa are given here, as is a reconstruction of the soft tissues associated with the ear regions of these mammals. A discussion is provided of the characters taken from the basicranium of these animals that were used in the phylogenetic analyses performed by Archibald et al. (2001).

*Institutional and locality abbreviations.*—AMNH, American Museum of Natural History, New York, NY; CBI, Central Kyzylykum, Bissekty Formation; PSS-MAE, Collections of Joint Paleontological and Stratigraphic Section of the Geological Institute, Mongolian Academy of Sciences, Ulaanbaatar-American Museum of Natural History, New York, NY; SDSU, San Diego State University, San Diego, CA; URBAC, Uzbekistan/ Russian/ British/ American/ Canadian joint paleontological expedition, Kyzylykum Desert, Uzbekistan, specimens in the Institute of Zoology, Tashkent and currently at San Diego State University, San Diego, CA; ZIN C., Systematic Collections, Zoological Institute, Russian Academy of Sciences, Saint Petersburg, Russia.

## Materials and methods

Twenty isolated petrosal bones recovered from the Late Cretaceous of Uzbekistan could be identified as “Zhelestidae” and *Kulbeckia kulbecke* (see below for a discussion of specimen identifications). Nine petrosals initially identified as type I represent “Zhelestidae”: URBAC 99-02 (CBI-14, left isolated petrosal), 99-41 (CBI-14, right isolated petrosal), 99-73 (CBI-14, right isolated petrosal), 00-06 (CBI-4e, left isolated petrosal), 00-26 (CBI-14, left isolated petrosal), ZIN C. 82587 (CBI-14, left isolated petrosal), 85511 (CBI-?, right isolated petrosal), 85512 (CBI-4b, left isolated petrosal), and 85514 (CBI-14, left isolated petrosal). Eleven petrosals initially identified as type II represent *Kulbeckia kulbecke*: URBAC 98-113 (CBI-14, right isolated petrosal), 00-02 (CBI-14, right isolated petrosal), 00-16 (CBI-14, left isolated petrosal), 02-14 (CBI-4e, right isolated petrosal), 02-56 (CBI-4e, right isolated petrosal), 02-84 (CBI-4e, left isolated petrosal), 02-92 (CBI-4e, left isolated petrosal), 02-113 (CBI-4e, left isolated petrosal), ZIN C. 85045 (CBI-117, left isolated petrosal), 85513 (CBI-5a, right isolated petrosal), and 85516 (CBI 4b, left isolated petrosal). The petrosals of “zhelestids” and *Kulbeckia* were compared to the petrosal referred to *Prokennalestes* (PSS-MAE 136) from the Early Cretaceous of

Mongolia, and to the petrosal of recent *Didelphis virginiana* (SDSU S-221). The specimen from CBI-117 (ZIN C. 85045, *K. kulbecke*) is from the Aitym Formation (?Santonian), and all other Uzbekistan petrosals are from the Bissekty Formation (Turonian/Coniacian).

Many of the petrosal structures that were examined could easily be seen by the naked eye, but the use of a dissecting microscope was necessary for detailed observations. Petrosal measurements were taken using a calibrated scale bar within the dissecting microscope. Terminology used follows McDowell (1958), MacIntyre (1972), Cifelli (1982), and Wible et al. (2001).

## Identification of specimens

Table 1 lists mammalian taxa recovered from the localities in the Upper Cretaceous Bissekty Formation, Kyzylykum Desert, Uzbekistan. The taxonomic assignments based on the dentition represent a work in progress; nonetheless, they are helpful in referring isolated petrosals to taxa based on dental remains. Only one species, which we here refer to as *Daulestes kulbeckensis* (includes *D. nessovi* and probably *Taslestes inobservabilis*, *Kumlestes olzha*, and *Kennalestes* (?) *uzbekistanensis*), has a petrosal associated with dental remains (described by McKenna et al. 2000). The other petrosals described and discussed here are all isolated elements. These petrosals were initially designated type I and type II (Ekdale et al. 2001) as they clearly represented two forms. Within these two morphs, small size differences could be detected (Table 2) and as discussed later, may represent multiple closely related species.

There are several approaches applicable to referring these isolated petrosals to taxa known previously only from dentitions, such as, comparative anatomy, relative abundances, and size. Morphology eliminates several of the taxa in the fauna that these petrosals might represent. The two petrosal types are most likely therian, as neither type possesses a lateral flange that parallels the length of the promontorium forming a lateral trough as is observed in non-therian mammals (Wible et al. 2001). Based upon a broken specimen (ZIN C. 85514), type I petrosals possess cochleae coiled nearly 360° further suggesting that this form belongs to a therian taxon. Although type II is probably similar in the coiling of the cochleae, this has not yet been established with certainty. The two petrosal types are more likely eutherian than metatherian, because they possess an ascending canal for the superior ramus of the stapedia artery that is absent in metatherians. Additionally, the anterolateral position of the sulcus for the anterior distributor of the transverse sinus relative to the subarcuate fossa differs in the type I petrosal from the posterolateral position in metatherians (Wible et al. 2001; see below for further discussion of these characters). Among the eutherian taxa recovered from the fauna, *Daulestes* can be eliminated as a possible identity of the two petrosal morphs based on anatomy, because the petrosal of *Daulestes* pos-

Table 1. Preliminary list of mammaliaforms from the Bissekty Formation, Dzaharakuduk\*.

Taxon	No. of specimens	Range of m3 area (n)**	Avg. m3 area in mm <sup>2</sup>	Range of estimated m3 area***
Symmetrodonta				
Spalacotheriidae				
<i>Shalbaatar bakht</i>	1			
Allotheria				
Cimolodonta				
<i>Uzbekbaatar kizylkumensis</i>	1			
Metatheria				
Deltatheroidea				
<i>Sulestes karakshi</i>	5			
<i>Deltatherus kizylkumensis</i>	2			
Asiadelphia				
<i>Marsasia aenigma</i> and <i>Marsasia</i> sp.	3			
Eutheria				
Asioryctitheria				
<b><i>Daulestes</i> (all species combined)</b>	26	<b>0.6–1.3 (5)</b>	0.9	
<i>Daulestes kulbeckensis</i>	8	0.9 (1)	0.9	
<i>Daulestes</i> cf. <i>D. kulbeckensis</i>	2	0.6–0.8 (2)	0.7	
<i>Daulestes</i> sp. nov.	16	1.3 (2)	1.3	
<i>Bulaklestes kezbe</i>	2	unknown	unknown	
Placentalia				
Gliriformes				
<b>“Zalambdalestidae”</b>	47	<b>2.2–3.4 (9)</b>	2.7	<b>2.2–3.3</b>
<i>Kulbeckia kulbecke</i>	46	2.4–3.4 (8)	2.8	
<i>Kulbeckia</i> new smaller sp.	1	2.2 (1)	2.2	
Ungulatomorpha				
<b>“Zhelestidae”</b>	<b>79</b>	<b>2.6–6.1 (6)</b>	<b>4.3</b>	2.8–4.4
<i>Aspanlestes aptap</i>	28	2.6–2.7 (2)	2.6	2.8
<i>Parazhelestes minor</i> (11), <i>Zhelestes temirkazyk</i> (2), and <i>Sorlestes budan</i> (25) (incls. <i>Kumsuperus avus</i> )	38	4.5 (1)	4.5	3.2–3.5
<i>Eoungulatum kudukensis</i> (8) and <i>Parazhelestes robustus</i> (5)	13	5.9–6.1 (2)	6.0	3.8–4.4
Eutheria <i>incertae sedis</i>				
<i>Paranyctoides aralensis</i>	9	1.9 (1)	1.9	

\* This includes all specimens identified to the species level through the 2000 field season, except for some of the very smallest taxa that are yet to be recovered from the finest concentrate, and the specimen of “*Kulbeckia* new smaller sp.” that was recovered in 2002. *Daulestes* values were made by the second author, “Zalambdalestidae” values are mostly from Archibald and Averianov (2003a), and “Zhelestidae” values are from Nessov et al. (1998). Units for all areas are in mm<sup>2</sup>.

\*\* Area estimates are computed using greatest length *versus* greatest width of m3.

\*\*\* Based on promontorium area (see text). Range for “Zalambdalestidae” based on only the five largest type II petrosals.

sesses a sulcus on the promontorium for the internal carotid artery (McKenna et al. 2000), a structure that is not present on either of the petrosal types described here. It is reasonable to assume that the dental specimens referred to all species of *Daulestes* and the closely related and possibly congeneric *Bulaklestes* had petrosals of a similar structure and thus are unlikely candidates for the two known petrosal types.

Using anatomy alone, the petrosals most likely belong to “zhelestids”, “zalambdalestids”, or *Paranyctoides*. *Paranyctoides* cannot be assigned with certainty to a higher taxon (Archibald and Averianov 2001), but various phylogenetic analyses indicate close affinities to “zhelestids” (e.g., Archibald et al. 2001). We have not, however, included it with “zhelestids” in this analysis.

A second approach is to compare numbers of petrosals of each type *versus* numbers of dental remains per taxon. Between “zhelestids” and “zalambdalestids”, the most common taxon is “Zhelestidae” with some 79 dental remains, followed by “Zalambdalestidae” with 47 specimens (Table 1). “Zhelestids” represent roughly 63% of the dental specimens of “Zhelestidae” and *Kulbeckia* combined; therefore, using the relative abundance of these two taxa, one would expect roughly 63% of the isolated petrosals (13 out of 20) to be “zhelestids”, and the remaining 37% to be “zalambdalestids”, however this pattern is not observed in the isolated petrosal sample (11 type II petrosals versus 9 type I petrosals). By numbers alone, the isolated petrosal types cannot be assigned to either “Zhelestidae” or *Kulbeckia*.

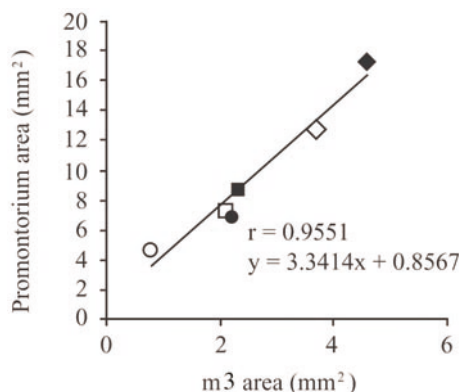


Fig. 1. Promontorium area versus lower m3 area for taxa with associated petrosal and dental remains. Open circle, *Daulestes kulbeckensis*; closed circle, *Kennalestes gobiensis*; open square, *Prokennalestes trofimovi*; closed square, *Asioryctes nemegetensis*; open diamond, *Barunlestes butleri*; closed diamond, *Deltatheridium pretrituberculare*.

A third method for assigning petrosals and dental remains to the same taxon is by comparing the sizes of the isolated type I and II petrosals to dentally based taxa. To make such comparisons, m3 and promontorium areas were calculated for Cretaceous therian mammals from Asia for which both dental and petrosal remains are known: *Asioryctes nemegetensis*, *Barunlestes butleri*, *Daulestes kulbeckensis*, *Deltatheridium pretrituberculare*, *Kennalestes gobiensis*, and *Prokennalestes trofimovi* (measurements are presented in Table 2). Although m3 is often more variable than m1 or m2, it was chosen because it is the tooth position known for most of the taxa being studied.

The promontorium and m3 areas were plotted on a graph to investigate the correlation between promontorium and ultimate molar areas for these taxa (Fig. 1). The r-value of the regression line for these data when they were plotted was 0.9551 suggesting a strong relationship between promontorium and m3 areas for these taxa. The equation of the line is  $y = 3.3414x + 0.8567$ , where y = promontorium area and x = m3 area. This equation was used to estimate m3 area for the type I and type II petrosal specimens (Table 2).

The estimated m3 areas of the type I petrosals (range = 2.8–4.4 mm<sup>2</sup>) fall within the range of “zhelestid” ultimate molar areas (range = 2.6–6.1 mm<sup>2</sup>, see Table 1). The estimated ultimate molar areas (range = 2.2–3.3 mm<sup>2</sup>) for the five largest of the type II petrosals (Table 2) fall within the range of ultimate molar areas of *Kulbeckia* (range = 2.2–3.4 mm<sup>2</sup>, see “Zalambdalestidae” in Table 1). The estimated ultimate molar areas (range = 0.8–1.7 mm<sup>2</sup>) for the four smallest type II petrosals fall below the range of *Kulbeckia* ultimate molar areas (range = 2.2–3.4 mm<sup>2</sup>, see “Zalambdalestidae” in Table 1).

Using comparative anatomy and the size comparisons described above, the type I and the larger type II petrosals can be assigned to taxa known previously from dentition alone. Not only do the expected ultimate molar areas of the larger type II petrosals fall within the range of *Kulbeckia*, the struc-

Table 2. Promontorium and ultimate molar areas for Late Cretaceous taxa.

Taxon (petrosal type)	Prom. area*	m3 area**
type I – small (URBAC 00-26)	10.2	2.8
type I – medium (URBAC 99-41)	12.5	3.5
type I – medium (ZIN C. 82587)	11.6	3.2
type I – large (URBAC 99-02)	15.6	4.4
type I – large (URBAC 99-73)	14.8	4.2
type I – large (URBAC 00-06)	13.9	3.9
type I – large (ZIN C. 85511)	13.7	3.8
type I – large (ZIN C. 85512)	14.7	4.1
type I – ? (ZIN C. 85514)	–	–
type II – small (URBAC 98-113)	3.6	0.8
type II – medium (URBAC 00-02)	6.7	1.7
type II – medium (ZIN C. 85045)	6.0	1.5
type II – medium (ZIN C. 85516)	6.0	1.5
type II – large (URBAC 02-14)	9.3	2.5
type II – large (URBAC 02-92)	8.3	2.2
type II – large (URBAC 02-113)	8.8	2.4
type II – large (ZIN C. 85513)	9.4	2.6
type II – very large (URBAC 00-16)	11.1	3.1
type II – very large (URBAC 02-56)	12.0	3.3
type II – ? (URBAC 02-84)	–	–
<i>Asioryctes nemegetensis</i>	8.8	2.3
<i>Barunlestes butleri</i>	12.7	3.7
<i>Daulestes kulbeckensis</i>	4.7	0.8
<i>Deltatheridium trituberculare</i>	17.2	4.6
<i>Kennalestes gobiensis</i>	6.9	2.2
<i>Prokennalestes trofimovi</i>	7.3	2.1

\* Values for the type I and type II petrosals were measured from specimens. ZIN C. 85514 (type I) and URBAC 02-84 (type II) are broken specimens and their promontorium areas could not be calculated. The areas for the remaining taxa were measured from figures in published literature: *Asioryctes nemegetensis* (Kielan-Jaworowska 1981: fig. 8 and pl. 16), *Barunlestes butleri* (Kielan-Jaworowska and Trofimov 1980: pl. 2), *Daulestes kulbeckensis* (McKenna et al. 2000: fig. 8), *Deltatheridium trituberculare* (Rougier et al. 1998: fig. 3), *Kennalestes gobiensis* (Kielan-Jaworowska 1981: fig. 3 and pl. 4), *Prokennalestes trofimovi* (Wible et al. 2001: fig. 1). Units are in mm<sup>2</sup>.

\*\* m3 areas based on the type I and type II petrosals are estimates calculated by using the equation of the regression line presented in Fig. 1. The m3 area of *Daulestes kulbeckensis* was measured by the second author. The areas for the remaining taxa were measured from figures in published literature: *Asioryctes nemegetensis* (Kielan-Jaworowska et al. 1979: fig. 12-3), *Barunlestes butleri* (Kielan-Jaworowska and Trofimov 1980: pl. 4), *Deltatheridium trituberculare* (m3 measured from Kielan-Jaworowska 1975: fig. 5), *Kennalestes gobiensis* (estimated from Kielan-Jaworowska 1981: table 1), *Prokennalestes trofimovi* (estimated from Kielan-Jaworowska and Dashzeveg 1989: table 1). Units are in mm<sup>2</sup>.

ture of the type II petrosal is very similar in morphology to that of the “zalambdalestid” *Zalambdalestes* (as scored by Rougier et al. 1998). The smaller type II petrosals do not differ morphologically from the larger type II petrosals, so it is

reasonable to believe that all of the type II petrosals are from “zalambdalestids” if not *Kulbeckia*, the only “zalambdalestid” genus recovered from the fauna thus far. A dentary of *Kulbeckia* (URBAC 02-17, *Kulbeckia* new smaller sp. in Table 1) was recovered during the 2002 field season that is only 65–75% the size of most other specimens referred to *K. kulbecke* (Archibald and Averianov 2003). Although this specimen groups with the larger specimens based on the isolated petrosals, it demonstrates that the full taxonomic and size range of “zalambdalestids” has yet to be recovered or recognized at Dzharakuduk.

As noted under materials, one petrosal, ZIN C. 85045, was recovered from locality CBI-117 in the Aitym Formation. Based on the morphology of this specimen and the fact that dental remains of *Kulbeckia* sp. also have been recovered from locality CBI-117 (Averianov and Archibald 2003), there is little doubt that this petrosal is referable to *Kulbeckia*.

Based on the criteria discussed above coupled with the identification of the type II petrosal as *Kulbeckia*, the type I petrosals most likely belong to “zhelestids”. Assigning the type I petrosal to species within “Zhelestidae” is more speculative. The five “zhelestid” taxa from the Late Cretaceous of Uzbekistan recognized by Nessov et al. (1998) based on upper dentitions can be divided into three size classes based on dental material (ranging from smallest to largest): (1) *Aspanlestes aptap*, (2) *Parazhelestes minor* and *Zhelestes temirkazyk*, and (3) *Parazhelestes robustus* and *Eoungulatum kudukensis* (Nessov et al. 1998). Ongoing research by the second and third authors suggests that *Eoungulatum kudukensis* may be a junior synonym for *Parazhelestes robustus*. *Parazhelestes minor* and *Zhelestes temirkazyk* are similar in size but have morphological differences suggesting that each is a valid taxon. The petrosals that are referred to “Zhelestidae” can also be separated into three general size classes (see Table 2): small (URBAC 00-26), medium (URBAC 99-41 and ZIN C. 82587), and large (URBAC 99-02, 99-73, 00-06, ZIN C. 85511 and 85512). The estimated ultimate molar area of the small “zhelestid” petrosal (2.8 mm<sup>2</sup>, see Table 2) is close to the average ultimate molar area of *Aspanlestes aptap* (2.6 mm<sup>2</sup>, see Table 1), suggesting that the petrosal represents this taxon. Species identifications cannot be made for the type I petrosals of medium and large sizes, as the estimated ultimate molar areas do not fall within the ranges for the medium and large “zhelestid” size classes, but rather between the small and medium dental size classes (see Table 1).

Caution must be taken before formally assigning any of the petrosal specimens to individual “zhelestid” and *Kulbeckia* taxa. Although size ranges can be recognized for both dentition and petrosals, unless the petrosals are associated with teeth, accurate species identifications cannot be made. Because of this, petrosals were not assigned to individual taxa by Archibald et al. (2001). When scoring their character matrix, all “zhelestid” taxa were scored identically for the petrosal characters.

## “Zhelestidae” (type I)

The majority of the “zhelestid” material that has been recovered from the Late Cretaceous consists of teeth. Isolated petrosal bones were assigned to “Zhelestidae” based on size and morphology (see above). Although aspects of the “zhelestid” petrosal were used in earlier phylogenetic analyses (Archibald et al. 2001), a detailed description of the structure of the “zhelestid” petrosal has not been published.

**Cerebellar surface.**—The cerebellar or dorsal (endocranial) surface of the petrosal is marked by two large, distinct openings (Fig. 2A). The anteromedial of the two openings, the ovoid internal auditory meatus, is clearly divided by the crista transversa into the foramen acusticum inferius medially and the foramen acusticum superius laterally. The subarcuate fossa is the second distinct opening. In “zhelestids”, this depression is circular in shape and quite deep.

Medial to the subarcuate fossa is the aquaeductus vestibuli. This small opening is directed posterodorsally, and it is followed by a small sulcus traveling towards the caudal border of the petrosal bone. The opening for the aquaeductus is best preserved in ZIN C. 85511, and it appears as a small and circular hole, unlike the slit-like opening observed in other eutherians including archaic ungulates, but rather like the aquaeductus vestibuli in *Prokennalestes* (PSS-MAE 136; Wible et al. 2001).

Two additional conspicuous openings are found lateral to the internal auditory meatus and anterolateral to the subarcuate fossa in “Zhelestidae”. The anterior of the two openings is an anteriorly directed circular opening known as the fenestra semilunaris. It can be observed in ZIN C. 82587 (as well as in URBAC 99-41, ZIN C. 855111, and 85512 to a lesser extent) that a very small foramen exists on the anterior wall of the fenestra semilunaris. This foramen appears to be the endocranial opening of the aquaeductus Fallopii. The aquaeductus Fallopii of “Zhelestidae” is a small, anteriorly directed canal that ultimately opens into the tympanic cavity via the hiatus Fallopii (see Fig. 2C).

The second of the two openings found on the lateral edge of the cerebellar surface of the petrosal is immediately posterior to the fenestra semilunaris (Fig. 2A). It is significantly larger than the fenestra semilunaris, and it opens posterodorsally. This structure is positioned similarly to and appears very much like the endocranial opening of the prootic canal in the Late Cretaceous eutherian *Prokennalestes* (PSS-MAE 136; Wible et al. 2001). The canal is termed the prootic canal in “Zhelestidae” following Wible and Hopson (1995) because the canal most likely transmitted the prootic sinus in life (see vascular reconstructions below for further discussion of this matter). Endocranially, a very broad and distinct sulcus for the prootic sinus can be seen running into the opening of the canal at its posteromedial aspect. The prootic sinus was the anterior distributor of the transverse sinus in “Zhelestidae”, and it is found anterolateral to the subarcuate fossa, as it is in eutherians including *Prokennalestes*, rather than posterolateral

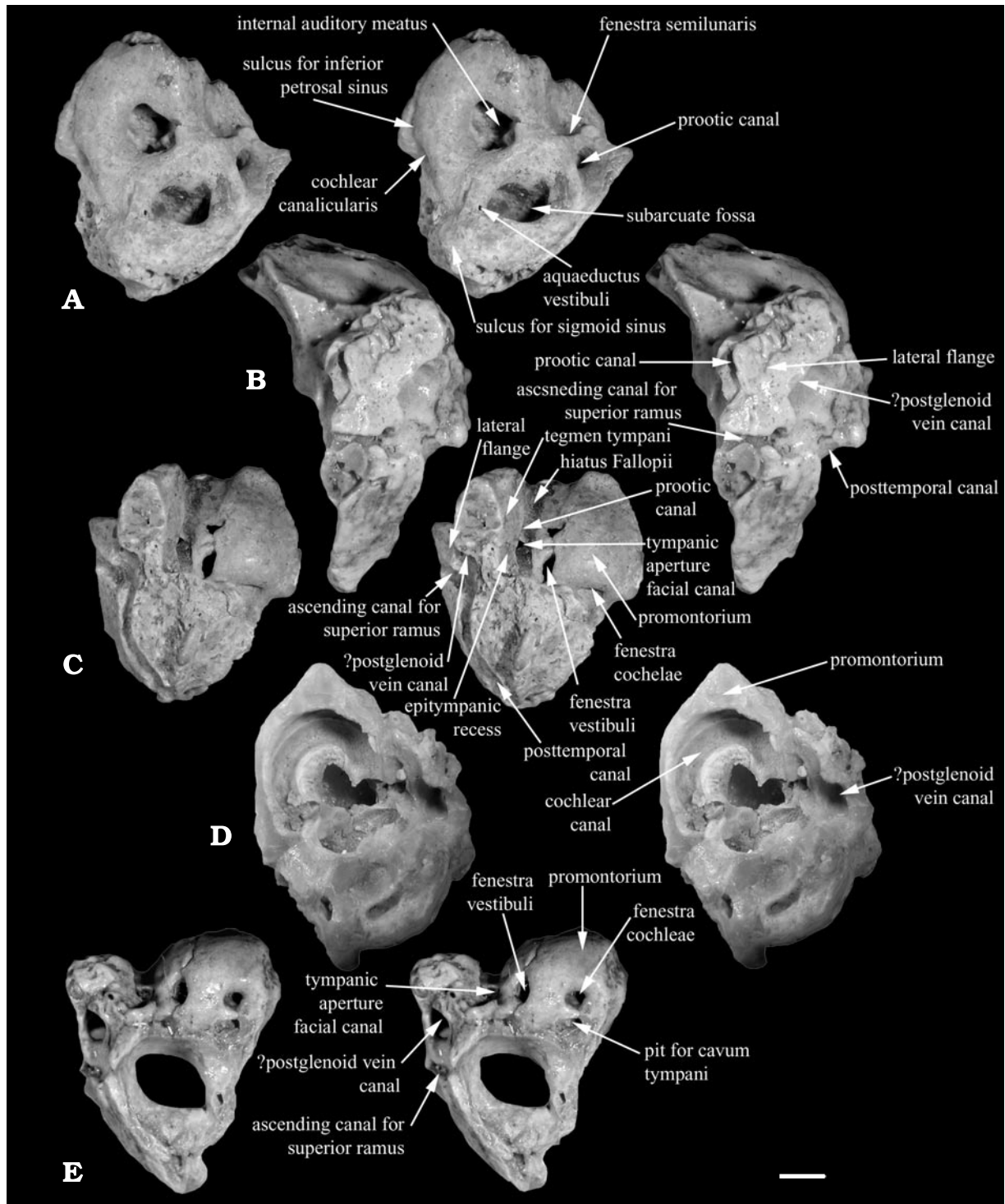


Fig. 2. Stereophotographs of the petrosal of "Zhelestidae". **A.** Cerebellar view of URBAC 99-41. **B.** Squamosal view of URBAC 99-41. **C.** Tympanic view of URBAC 99-41. **D.** Tympanic view of ZIN C. 85514 with internal structures exposed. **E.** Lambdoidal view of URBAC 99-73. Scale bar 1 mm. Anterior towards the top in A-D; tympanic towards top in E.

to the fossa, as it is in metatherians such as *Deltatheridium* and *Didelphis* (Rougier et al 1998; Wible et al. 2001).

A sulcus for the inferior petrosal sinus can be seen traversing the medial edge of the cerebellar side of the petrosal bone (Fig. 2A). The sulcus runs posteriorly from the rostral apex of the petrosal to a position posterior to the internal au-

ditory meatus. Immediately posterior to the posterior terminus of the sulcus for the inferior petrosal sinus is a small, circular, medially oriented opening for the cochlear canalicularis.

In URBAC 99-41, a sulcus can be seen skirting the posteromedial and posterior borders of the subarcuate fossa.

This sulcus is not continuous with the sulcus for the inferior petrosal sinus, and it courses towards, but does not join with, the sulcus for the prootic sinus. At its medial aspect, it comes in contact with the posterior lacerate foramen. This is most likely the sulcus for the sigmoid sinus.

**Squamosal surface.**—The tegmen tympani, a sheet of bone that separates the middle ear cavity from the cranial cavity at the anterolateral aspect of the petrosal bone (Fig. 2C), is not inflated in “Zhelestidae” as it is in many ungulates, but the “zhelestid” petrosal does possess a distinct flange of bone at the posterolateral corner of the bone (Fig. 2B, C). Given the proximity of a similar flange in *Prokennalestes* (Wible et al. 2001), this process is termed the lateral flange for “zhelestids”.

A large opening leading to a canal is found at the anterior aspect of the lateral flange. This structure is best preserved in URBAC 99-41, but it can be seen in the other “zhelestid” specimens to a lesser extent. Just inside this opening, on the medial wall of the canal, is a small foramen leading to a medially oriented duct. This short and horizontal duct, which opens into the tympanic cavity (see Figs. 2C, 4A, B), is the ventral aspect of the prootic canal, and it is homologous to the prootic canal in metatherians, including the American opossum, *Didelphis virginiana*. Dorsal to this horizontal duct is the dorsal aspect of the prootic canal, which opens on the cerebellar surface of the petrosal (Fig. 2A). The dorsal aspect of the prootic canal appears homologous to the prootic canal of earlier mammals, including *Prokennalestes* (Wible et al. 2001). The canal extending posteroventrally from the dorsal and ventral aspects of the prootic canal (eventually opening on the squamosal surface of the petrosal bone) is termed the ?postglenoid vein canal (Fig. 2) after the vessel that occupied it (see venous reconstructions below).

A deep and distinct sulcus can be seen traveling posteriorly from the opening of the ?postglenoid vein canal on the squamosal surface of the petrosal (Fig. 2B, C). When the squamosal and petrosal bones were articulated, this sulcus formed the medial wall of a canal known as the posttemporal canal. The petrosal contribution to the posttemporal canal can be seen curving medially along the lateral surface of the petrosal, and onto the lambdoidal (posterior) surface of the bone, ending near the posterior lacerate foramen.

Just posterior to the squamosal opening of the ?postglenoid vein canal is a second groove running dorsally perpendicular to the posttemporal canal (Fig. 2B). It would form a short bony tube where the petrosal and squamosal bones articulate. The location of this groove is similar to the ascending canal for the superior ramus of the stapedial artery seen in *Prokennalestes* and other eutherian mammals (Rougier et al. 1992; Wible et al. 2001), and this sulcus is most likely the petrosal contribution of the ascending canal for the superior ramus of the stapedial artery in “Zhelestidae” as well. The ventralmost end of this sulcus is confluent with the posttemporal canal traveling posteriorly from the ?postglenoid vein canal.

**Tympanic surface.**—The tympanic (ventral) surface of the petrosal is marked anteriorly by the semiovoid bulge of the promontorium (Fig. 2C). The mammalian promontorium houses the cochlea, which includes the organ of hearing. In “Zhelestidae”, the promontorium is round and rather bulbous. It is almond shaped, and the rostral apex appears to be pointed. Lateral to the promontorium is the tegmen tympani, which roofs the middle ear cavity.

In one poorly preserved “zhelestid” specimen (ZIN C. 85514; identified as “Zhelestidae” based on the presence of the prootic canal), the ventral aspect of the promontorium has been broken away, conveniently revealing the internal structure of the petrosal (Fig. 2D). It is clear that the cochlea of “Zhelestidae” was coiled at least 270°, and although this is the extent of the coiling that is visible, the cochlear canal is broken along its path in this specimen, and it most likely completed nearly one full 360° turn.

The promontorium is penetrated by two distinct openings along its posterolateral and posteromedial aspects (Fig. 2C). On the posteromedial aspect of the promontorium is the fenestra cochleae, which is also known as the round window given its round shape in most mammals. In some “zhelestid” specimens, especially in URBAC 00-26, it appears as though there is a sulcus traveling up the medial edge of the promontorium from the fenestra cochleae. It is unlikely that this is an actual sulcus, however. Rather, the petrosal expands along its medial border creating a flattened area of bone. This “groove” appears to be associated with the flattening of this petrosal expansion.

In several of the specimens, including URBAC 99-73, ZIN C. 82587 and 85512, there is an anteriorly directed pit just posterodorsal to the fenestra cochleae (Fig. 2E). This excavation most likely accommodated the cavum tympani, an air-filled sac that filled the middle ear space in life. The pit is poorly developed (but nonetheless present) in ZIN C. 82587, but it is very well developed in both URBAC 99-73 and ZIN C. 85512. This excavation for the cavum tympani is obscured from view by the posterior wall of the petrosal in ZIN C. 85512, but the lambdoidal surface of URBAC 99-73 is broken giving a clear view of both the fenestra cochleae and the excavation for the cavum tympani. In this specimen, it appears that this excavation is in fact a foramen, but this is almost certainly caused by damage to the bone. Whether the excavation is a pit or a foramen is indeterminable in ZIN C. 85512, but it is clearly an anteriorly directed pit, and not a foramen, in ZIN C. 82587.

The second opening on the promontorium is the fenestra vestibuli or oval window given its oval shape in most eutherian mammals. It is found on the posterolateral aspect of the promontorium (Fig. 2C), and it accommodates the footplate of the stapes. It does not appear that a sulcus for the stapedial branch of the internal carotid artery is present in “Zhelestidae”, as neither side of the fenestra vestibuli is notched in any of the specimens. The fenestra vestibuli is oval in most of the “zhelestid” specimens (especially URBAC 02-14), but it appears to be rounded in URBAC

99-73, and even more so in ZIN C. 85511. The average stapedial ratio for “Zhelestidae” is 1.6 (the range being 1.2–2.0 and the standard deviation is 0.3). Lateral to the fenestra vestibuli, and ventral to the tegmen tympani, is an area known as the epitympanic recess (Fig. 2C). In life, the auditory ossicles articulate within this region of the middle ear.

A distinct and broad sulcus for the inferior ramus of the stapedial artery can be seen running anteriorly just lateral to the promontorium. There is no indication of a transpromontorial sulcus for the internal carotid artery in any of the “zhelestid” petrosals.

Anterolateral to the fenestra vestibuli is the tympanic aperture of the facial canal (Fig. 2C). The facial canal itself runs ventrolaterally from its cerebellar entrance (the foramen acusticum superius) to the fenestra semilunaris before opening in a posterior direction on the tympanic surface of the petrosal. The position of the hiatus Fallopii is not clear in all of the “zhelestid” petrosals, and there may be some variation. In some specimens, including URBAC 99-41, ZIN C. 85511, and 82587, the hiatus can clearly be seen opening anterior to the facial canal on the tympanic surface of the petrosal, rather than the lateral edge. A faint sulcus can be seen traveling anteriorly, especially in ZIN C. 85511. The bony sheet flooring the facial canal is damaged in URBAC 99-02, 00-26, and ZIN C. 85512 obscuring the position of the hiatus. In URBAC 99-73, it almost appears as if the hiatus Fallopii is incomplete within the petrosal (only a notch that opens laterally is preserved). The foramen may be completed in a fully articulated skull (as is most likely the case with *Prokennalestes*; Wible et al. 2001), or this may simply be the result of damage and not the true nature of the structure.

Near the tympanic aperture of the facial canal is the tympanic opening of the prootic canal. The exact position of the tympanic opening of the prootic canal in relation to the tympanic aperture of the facial canal may be variable in “Zhelestidae”. In most of the petrosal specimens preserving this opening (URBAC 00-26 and ZIN C. 85512 are too damaged to determine the position of the opening), including URBAC 99-41, 99-73, and ZIN C. 82587, the prootic canal opens anterior and ventral to the lateralmost aspect of the tympanic aperture of the facial canal. The canal appears to open posterior to the facial canal in URBAC 99-02 and ZIN C. 85511. URBAC 99-02 is damaged along its lateral edge exposing the paths of the prootic and ?postglenoid vein canals, however, so an exact determination of the position of the prootic canal opening cannot be made, but in ZIN C. 85511, there is a distinct opening just posterior to the lateral aspect of the facial canal. This may not be the opening to the prootic canal, however, as the same specimen possesses a small foramen anterior to the tympanic aperture of the facial canal in the same location as the tympanic opening of the prootic canal in the other “zhelestid” specimens. The purpose of this foramen posterolateral to the facial canal, if a real foramen at all, is unclear.

## *Kulbeckia* (type II)

Ear regions from the Late Cretaceous of Uzbekistan were assigned to the genus *Kulbeckia* based on similarity to the petrosal structure of other “zalambdalestid” taxa, including *Zalambdalestes* and *Barunlestes* (Kielan-Jaworowska and Trofimov 1980; Kielan-Jaworowska 1984; Rougier et al. 1998) and other criteria discussed earlier. The overall structure of the *Kulbeckia* petrosal is described below.

**Cerebellar surface.**—Two conspicuous openings are found on the cerebellar surface of the petrosal of *Kulbeckia*: the internal auditory meatus anteriorly, and the subarcuate fossa posteriorly (Fig. 3A). The ovoid internal auditory meatus is subdivided by the crista transversa into the foramen acusticum inferius (medial) and the foramen acusticum superius (lateral). The foramen acusticum inferius is oval in shape and opens dorsolaterally, whereas the foramen acusticum superius is smaller, rounder, and opens dorsally and anteromedially.

The subarcuate fossa sits posterolateral to the internal auditory meatus. Unfortunately, none of the *Kulbeckia* specimens preserve a complete subarcuate fossa. The best preserved fossa can be seen on URBAC 00-16. Although the borders of the fossa on this specimen have been damaged, it can be determined that the fossa is indeed present in the *Kulbeckia* petrosal, and it forms a deep and circular pit with smooth and thin walls. In addition, because of the damaged borders, portions of the paths of the semicircular canals are exposed.

Traveling in an anterior-posterior direction along the medial edge of the petrosal bone is the sulcus for the inferior petrosal sinus. The sulcus skirts the medial rim of the cerebellar surface from the rostral apex (where the sulcus is quite broad, but narrows as it extends posteriorly) to a level at the posteriormost aspect of the internal auditory meatus (Fig. 3A).

Immediately posterior to the posterior terminus of the sulcus for the inferior petrosal sinus is the small and circular opening of the cochlear canaliculus. It opens medially and slightly posteriorly. A short sulcus can be seen traveling posteriorly from this small opening.

Posterior to the cochlear canaliculus is a jagged piece of bone that is marked by several sulci and pits. The area is best preserved in URBAC 00-16, but this region of the petrosal bone can be observed in the other *Kulbeckia* specimens to a lesser extent. This surface of the petrosal forms the lateral wall of the posterior lacerate foramen. Because the only basicranial elements known for *Kulbeckia* are isolated petrosal bones, the ultimate shape and size of the posterior lacerate foramen cannot be determined for this taxon at this time.

**Squamosal surface.**—In *Kulbeckia*, the tegmen tympani is thin and uninflated. At the posterior aspect of the squamosal surface of the petrosal bone run two broad sulci, which are almost parallel to each other, divided by a distinct crest (Fig. 3B). The anterior of the two sulci is the petrosal contribution to the ascending canal for the superior ramus of the stapedial artery (the other portion would be contributed by the squa-



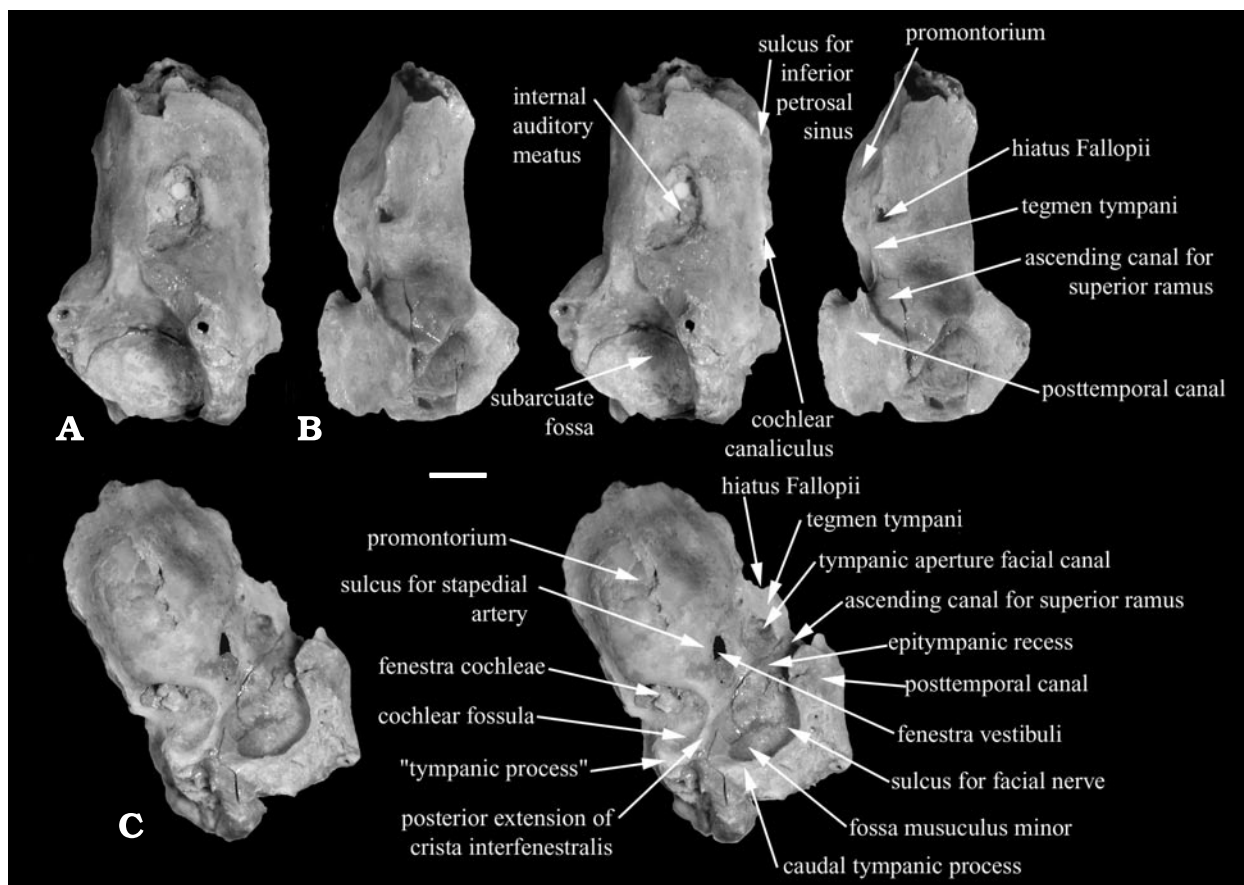


Fig. 3. Stereophotographs of the petrosal of *Kulbeckia kulbecke* (URBAC 00-16) in cerebellar (A), squamosal (B), and tympanic views. Scale bar 1 mm. Anterior towards the top in all views.

mosal in an articulated skull). This canal runs from a position just posterolateral to the anterior border of the subarcuate fossa to an anteroventral position on the tympanic surface of the bone. The posterior sulcus runs in a more anterior-posterior direction ventral to the first sulcus mentioned. The second sulcus, which is the petrosal contribution of the posttemporal canal, is shallower than the first, and it widens as it extends posteriorly.

**Tympanic surface.**—The tympanic surface of the *Kulbeckia* petrosal is marked by the semi-ovoid bulge of the promontorium (Fig. 3C). Although the internal structure of the *Kulbeckia* ear has yet to be determined, given the overall similarity of the external petrosal structure to that of other “zalambdalestids”, it is safe to assume that the cochlea completes at least one full 360° coil, as is the case with all therian mammals (Wible et al. 2001). The promontorium is tear-drop in shape, and the surface is fairly smooth, although it does possess a few dimples.

The fenestra cochleae is found along the posteromedial aspect of the promontorium, just ventral to the cochlear canaliculus. The fenestra is round, it opens posterodorsally, and it is subequal in size to the fenestra vestibuli sitting at the posteroventral aspect of the promontorium. The fenestra vestibuli opens dorsolaterally, and it has an average stapedial

ratio of 1.9 (the range being 1.4–2.8 and the standard deviation is 0.4). The wide range of variation in the stapedial ratios does not appear to be a result of damage, and without associated skeletal elements, it cannot be determined whether the variation is taxonomic (i.e., these petrosals represent more than one taxon) or not. There is not a correlation between stapedial ratio and promontorium area, so it is unlikely that the variation is a result of body size.

Traversing the fenestra vestibuli in a medial to lateral direction is a distinct sulcus for the stapedial branch of the internal carotid artery. This groove can be seen clearly on all of the specimens extending from a position just lateral to the fenestra cochleae and across the fenestra vestibuli. Its position lies in line with the anterior sulcus found on the squamosal side of the petrosal as discussed above. On ZIN C. 85045, the sulcus notches the fenestra vestibuli on its medial aspect, but no other *Kulbeckia* petrosal specimens display this notch.

Anterior to the fenestra vestibuli on all *Kulbeckia* specimens is a slight depression, giving the promontorium a dimpled appearance. The depression is in the same location as the sulcus for a promontorial branch of the internal carotid artery in other mammals, but upon closer inspection, it is doubtful that this depression carried a blood vessel in life, as it is merely a depression and not a sulcus.

Posterior to the promontorium are two depressions separated by a thick, curved crest. These two depressions are best preserved in URBAC 00-02 and 00-16. The medialmost depression, which sits posteriorly adjacent to the fenestra cochleae, is the cochlear fossula. This rounded and shallow depression accommodated the cavum tympani in life. The fossa is bordered anteriorly by the posterior lip of the fenestra cochleae, medially by the posterior lacerate foramen, posteriorly by a distinct wall of bone running the width of the petrosal known as the caudal tympanic process, and laterally by a posterior extension of the crista interfenestralis which, by connecting to the caudal tympanic process of the petrosal, divides the cochlear fossula from the second depression posterior to the promontorium. The crista interfenestralis is the bridge of bone separating the fenestrae vestibuli and cochleae.

On the portion of the caudal tympanic process bordering the cochlear fossula posteriorly is a “tympanic process”, as originally described for *Asioryctes* and *Kennalestes* by Kielan-Jaworowska (1981) and scored as present for *Zalambdalestes* by Rougier et al. (1998). The “tympanic process” is incomplete in all of the *Kulbeckia* petrosals studied here. A reason for this is that the process is composed of both petrosal and exoccipital in other taxa, and the same may be true for *Kulbeckia*, for which no exoccipital is known. Nonetheless, a portion of the process can be seen in URBAC 00-16. The crista interfenestralis extends posteriorly to contact the “tympanic process”, and in so doing, divides the two depressions posterior to the promontorium.

The depression lateral to the posterior extension of the crista interfenestralis lies immediately posterior to the fenestra vestibuli. It is significantly larger and deeper than the cochlear fossula, and it is ovoid in shape. The medial portion of this depression is the fossa musculus minor, and the lateral aspect is the sulcus for the facial nerve. Posterolaterally, this depression is formed by a large and distinct paroccipital process of the petrosal bone, as is best preserved in URBAC 00-16, as well as the lateral portion of the caudal tympanic process of the petrosal. Unfortunately, because all of the *Kulbeckia* specimens are damaged posteriorly, none of them possess a complete paroccipital process.

At the anterior end of the facial sulcus and anterolateral to the fenestra vestibuli is the tympanic aperture of the facial canal. In *Kulbeckia*, this opening is oriented posteriorly and slightly dorsally (Fig. 3C). The opening is rounded anteriorly.

Laterally adjacent to the fenestra vestibuli, and ventral to the tegmen tympani, is a small, flat, and uniformly concave epitympanic recess for the articulation of the auditory ossicles (Fig. 3C). Lateral to the epitympanic recess is the ventral terminus of the sulcus for the superior ramus of the stapedial artery. Traveling anteriorly from this sulcus on the ventral surface of the petrosal is a groove for the inferior ramus of the stapedial artery (Fig. 3C). The sulcus can be seen parallel to the promontorium along the ventral bony flooring of the facial canal. This sulcus is best observed in URBAC 00-16, but can be seen in the other specimens to a lesser extent.

Anterior to the tympanic aperture of the facial canal in URBAC 00-16 and 00-02 is the anteriorly directed hiatus Fallopii. In URBAC 00-16, the hiatus is positioned at the anterior edge of the tegmen tympani, but in URBAC 00-02, the hiatus appears to open on the tympanic surface of the bone followed by a short sulcus. The hiatus is not preserved in all *Kulbeckia* specimens, however. The area around the tympanic aperture of the facial canal is too damaged to determine the presence/absence or orientation of the hiatus in URBAC 98-117, but it appears to be absent in ZIN C. 85513 and 85045. In these specimens that appear to lack a hiatus, a small sulcus can be seen leading anteriorly from the tympanic aperture of the facial canal, but this is most likely the sulcus for the inferior ramus of the stapedial artery and the ventral flooring of the aquaeductus Fallopii is broken.

## Soft tissue reconstructions

Living organisms are composed of more than just a skeleton, and many evolutionary questions require an accurate reconstruction of soft tissues that are not preserved in the fossil record. The reconstructions of blood vessels that are made in the present study follow reconstructions made for Late Cretaceous mammals in the current literature (including Kielan-Jaworowska et al. 1986; Rougier et al. 1992; Wible and Hopson 1995; Wible and Rougier 2000; Wible et al. 2001).

**Nervous reconstruction.**—The internal auditory meatus functions as the major conduit for nerves through the ear region in all extant mammals. Entering the petrosal bone of both “Zhelestidae” and *Kulbeckia* via the foramen acusticum inferius was the cochlear branch of the vestibulocochlear nerve (cranial nerve VIII). The vestibular branch of the vestibulocochlear nerve entered the petrosal bone via the posterior aspect of the foramen acusticum superius. These two nerve branches innervated the cochlea and the vestibule respectively.

The facial nerve (cranial nerve VII) entered the petrosal bone via the anterior aspect of the foramen acusticum superius (in front of the vestibular branch of the vestibulocochlear nerve). The facial nerve traveled ventrally within a short facial canal to an open area known as the cavum supracochleare. This open area accommodated the geniculate ganglion of the facial nerve in life. The geniculate ganglion sent off two branches of the facial nerve in opposite directions. Anteriorly, the greater petrosal branch of the facial nerve traveled to and entered the fenestra semilunaris in “Zhelestidae”, and the small nerve branch continued its anterior course within the aquaeductus Fallopii, ultimately exiting via the hiatus Fallopii in both “zhelestids” and *Kulbeckia* (see Fig. 4B, G, H).

Traveling posteriorly from the geniculate ganglion was the hyomandibular branch of the facial nerve. This branch exited the cavum supracochleare via the tympanic aperture of the facial canal, and it continued its course posteriorly

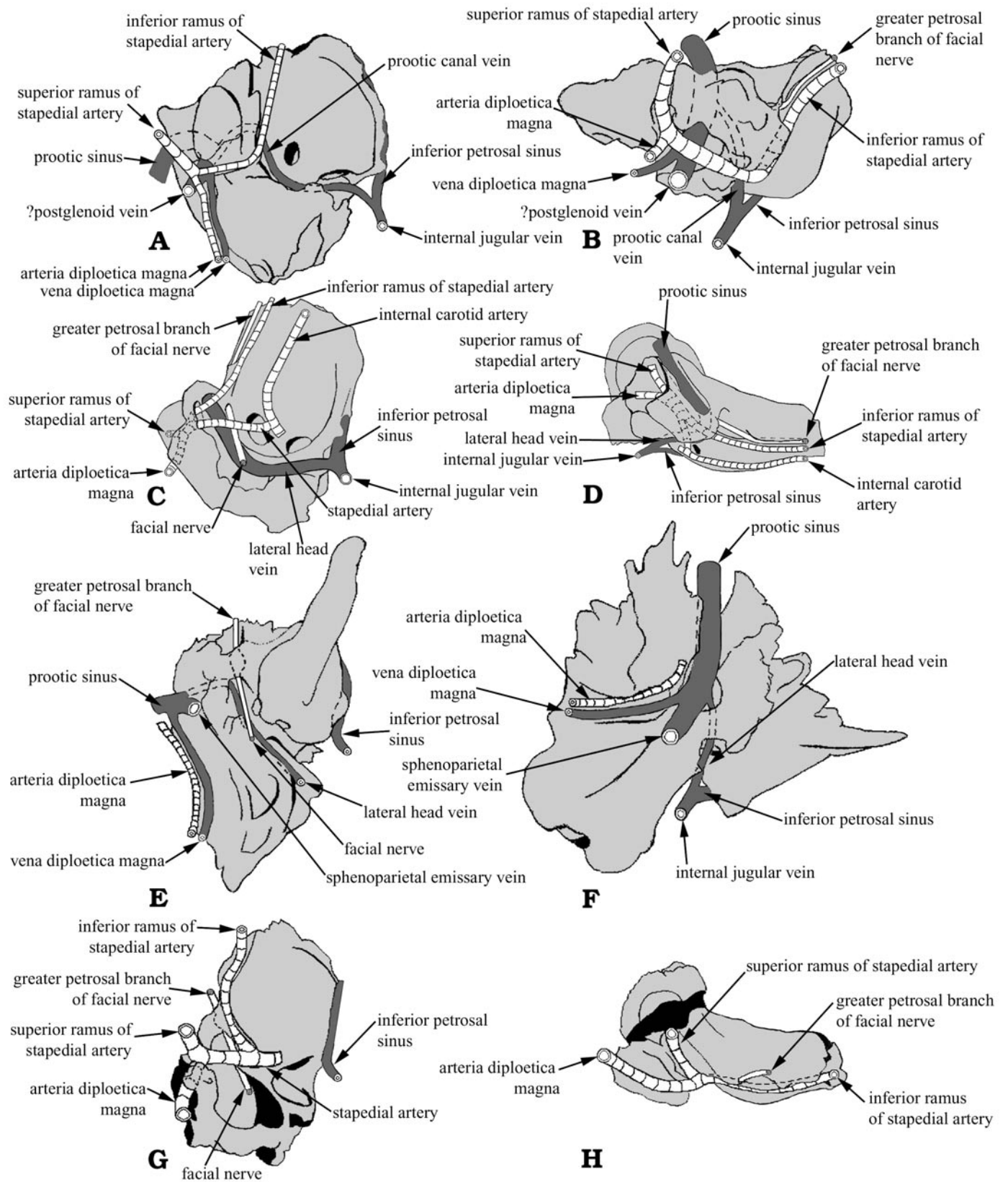


Fig. 4. Soft tissue reconstructions. **A.** Tympanic view of “Zhelestidae”. **B.** Squamosal view of “Zhelestidae”. **C.** Tympanic view of *Prokennalestes* (modified from Wible et al. 2001). **D.** Squamosal view of *Prokennalestes* (modified from Wible et al. 2001). **E.** Tympanic view of *Didelphis virginiana* (modified from Wible 1990). **F.** Squamosal view of *Didelphis virginiana* (modified from Wible 1990). **G.** Tympanic view of *Kulbeckia kulbecke*. **H.** Squamosal view of *Kulbeckia kulbecke*. Anterior towards the top in A, C, E, and G. Anterior towards the right in B, D, F, and H.

along the lateral aspect of the promontorium before exiting the auditory region. If the hiatus Fallopii is in fact absent in the *Kulbeckia* specimens ZIN C. 85513 and 85045 (rather than being an artifact of preservation), then the greater petrosal nerve would share an egress with the facial nerve. The greater petrosal branch would travel anteriorly, while the facial nerve would continue posteriorly.

Posterior to the internal auditory meatus is the subarcuate fossa. This pit supported the paraflocculus of the cerebellum in mammals possessing the structure, including “Zhelestidae” and *Kulbeckia*.

**Venous reconstructions.**—Running along the medial aspect of the cerebellar surface of the petrosal bone in both “Zhelestidae” and *Kulbeckia*, within its own sulcus, was the inferior petrosal sinus (Fig. 4). This vessel receives blood from the inner ear, as well as veins surrounding the medulla, pons, and inferior surface of the cerebellum in humans (Pick and Howden 1977). Because an endocast is not known for either “Zhelestidae” or *Kulbeckia*, the exact drainage pattern for the two taxa cannot be determined. In extant eutherians, the sinus travels posteriorly where it joins with the sigmoid sinus extracranially to form the internal jugular vein, one of the major vessels draining venous blood from the head.

The vessel that traveled through the prootic canal ventrally in “Zhelestidae” was the prootic sinus (Fig. 4A, B). From its origin off the transverse sinus, the prootic sinus traveled anteriorly inside the cranial cavity and entered the endocranial opening of the prootic canal. Near the opening of the ?postglenoid vein canal on the squamosal side of the petrosal, but within the canal itself, the prootic canal continues medially as a small duct, transmitting an extension of the prootic sinus. This vessel may be homologous with the lateral head vein of other mammals, but without developmental data, the exact identity of the vessel cannot be determined. Because of this, the vessel is termed the prootic canal vein here. The prootic canal opens anterolateral and ventral to the tympanic aperture of the facial canal. The prootic canal vein curved posteriorly and exited the cranium below the posterior lacerate foramen before joining with the inferior petrosal sinus to form the internal jugular vein (as seen in *Prokennalestes*, Fig. 4C, D; Wible et al. 2001).

Branching off from the prootic sinus before the prootic canal vein was a vessel that exited the ?postglenoid vein canal on the squamosal side of the petrosal bone. After exiting the ?postglenoid vein canal, the vessel divided into the ?postglenoid vein and the vena diploetica magna, the latter of which ran posteriorly along with its arterial counterpart (the anterior diploetica magna) in the distinct groove that is the petrosal contribution of the posttemporal canal. The ?postglenoid vein most likely exited the skull via the postglenoid foramen, or some morphological equivalent, given its similarity to the sphenoparietal emissary vein in metatherians and the postglenoid vein in eutherians. Because the only basicranial elements known for “Zhelestidae” are isolated petrosal bones, any definitive information concerning the exit of

the ?postglenoid vein in “zhelestids” is simply an assumption based on extant correlates. Although the ?postglenoid vein of “zhelestids” appears similar to the emissary vessels in metatherians and eutherians, without developmental data, one cannot be sure if the “zhelestid” ?postglenoid vein is homologous to the metatherian sphenoparietal emissary vein, the eutherian postglenoid vein, or a neomorphic vessel that is homologous to neither (Wible personal communication 2002). Because of this, the vessel is given the name ?postglenoid vein.

This reconstruction of the venous blood flow through the ear region of “Zhelestidae” is very similar to that seen in metatherians, including the extant marsupial *Didelphis virginiana* (Fig. 4E, F; Wible 1990; Wible and Hopson 1995). “Zhelestids” and *Didelphis virginiana* differ, however, in that the dorsal portion of the prootic canal (opening endocranially) runs within the suture between the petrosal and squamosal bones in *Didelphis*, but it is completely enclosed within the petrosal in “zhelestids” (as is seen in *Prokennalestes*; Fig. 4C, D; Wible et al. 2001).

**Arterial reconstructions.**—The major arteries that supply blood to the head in mammals are the external and internal carotid arteries, as well as the vertebral arteries. In all recent mammals, the internal carotid artery, at the level of the auditory region where the vessel enters the cranial cavity, is a single vessel that is derived from the dorsal aorta; this vessel remains homologous throughout all recent mammalian taxa (Presley 1979).

The internal carotid artery can take one of three courses in living eutherian mammals (Wible 1986): transpromontorial (across the ventral face of the promontorium within the tympanic cavity), perbullar (through the wall of the tympanic cavity), or extrabullar (outside of the tympanic cavity). A transpromontorial groove for the internal carotid artery is not observed in any of the *Kulbeckia* specimens, and thus it is doubtful that the vessel took a transpromontorial course in this taxon. Because an osseous tympanic bulla is not known to exist for *Kulbeckia*, whether or not the internal carotid artery traveled inside or outside the bulla cannot be determined at this time. Because there is no transpromontorial groove for the internal carotid artery in “Zhelestidae”, the vessel may have taken a course medial to the promontorium, or perhaps a perbullar course (as in several eutherians, including some extant primates and rodents; Wible 1986). As with *Kulbeckia*, only isolated petrosals are known of the “zhelestid” basicranium, so the exact course of the internal carotid artery cannot be determined for this taxon either.

The inferior ramus of the stapedial artery ran anteriorly in the broad sulcus lateral to the promontorium of “Zhelestidae” (Fig. 4A). After separating from the arteria diploetica magna, the superior ramus of the stapedial artery traveled within the ascending canal just posterior to the squamosal opening of the prootic canal (Fig. 4B). The arteria diploetica magna was transmitted posteriorly via the posttemporal canal.

Both *Kulbeckia* and “Zhelestidae” appear to have an ascending canal for the superior ramus of the stapedia artery, but between these two taxa, only *Kulbeckia* possesses a transpromontorial sulcus for the stapedia artery crossing the fenestra vestibuli. Although a sulcus for the stapedia artery is not found in any “zhelestid” specimen, the vessel may have been present to feed the superior and inferior rami of the stapedia artery. A more likely scenario is that these two vessels received blood from the arteria diploetica magna, and the stapedia artery was simply absent in the taxon. In *Kulbeckia*, the stapedia branch of the internal carotid artery crossed over the fenestra vestibuli in a medial to lateral direction before it split into two vessels lateral to the fenestra vestibuli (Fig. 4G). One of these branches was the inferior ramus of the stapedia artery that occupied the sulcus lateral to the promontorium and ventral to the facial canal. The second branch extended laterally before bifurcating into the superior ramus of the stapedia artery and the arteria diploetica magna. The superior ramus traveled dorsally into the cranial cavity within the anterior of the two sulci found on the posterior aspect of the squamosal surface of the petrosal (Fig. 4H). The arteria diploetica magna continued posteroventrally within the posttemporal canal which is preserved as the posterior of the two sulci.

## Basicranial characters and character states

The phylogenetic analyses performed by Archibald et al. (2001) were the only analyses to incorporate data from the basicranium of “zhelestids” and *Kulbeckia* at the time the paper was published. The taxa used in their analyses included several better known Cretaceous eutherian taxa, including the five “zhelestid” taxa from Uzbekistan and the “zalambdalestids” *Kulbeckia kulbecke*, *Zalambdalestes lechei*, and *Barunlestes butleri*, as well as Paleogene eutherian taxa, including Glires (*Mimotona* sp. and *Tribosphenomys* sp.) and archaic ungulates (*Protungulatum* and *Oxyprimus*). The results of the phylogenetic analyses supported a strong relationship between “Zalambdalestidae” and Glires, as well as a relationship between “Zhelestidae” and ungulates.

The taxa were scored for 70 osteological characters (mostly dental), and nine of these characters were taken from the basicranium (Archibald et al. 2001). Because the authors did not feel comfortable referring petrosals to specific “zhelestid” species, they coded all five of the “zhelestid” taxa equally for the basicranial characters. Below is a description of the basicranial characters used in their analyses, as well as a discussion of the coding for “Zhelestidae” and *Kulbeckia*. The wording of each character follows that of the supplementary information of Archibald et al. (2001).

**Stapedial ratio.**—Rounded, less than 1.8 (0), elliptical, more than 1.8 (1) (Rougier et al. 1998). The stapedial ratio

quantifies the shape of the stapedial footplate by dividing the length of the footplate by its width (Segall 1970). The stapes fits tightly within the fenestra vestibuli, so if a stapes is not preserved, the stapedial ratio can be determined by using the fenestra vestibuli as a proxy. Segall (1970) calculated the stapedial ratios for several monotreme, marsupial, and placental mammals, and he concluded that monotremes and marsupials generally tend to have slightly elliptical fenestrae vestibuli, with ratios less than 1.8, whereas placentals tend to have more elliptical fenestrae vestibuli, with ratios greater than 1.8. Segall (1970) did note, however, a couple of exceptions as the marsupials *Dromiciops* and *Macropus* each have stapedial ratios around 2.1. Rougier et al. (1998) calculated the stapedial ratios of many therian taxa. By their calculations, *Dromiciops* was unique among metatherians in having a stapedial ratio greater than 1.8 (they did not consider *Macropus* in their analyses), and *Prokennalestes* was unique among eutherians in having a stapedial ratio less than 1.8. *Kulbeckia* ratios averaged 1.9, but the “zhelestid” ratios averaged below the 1.8 mark at 1.6, which is less than any other eutherian, including *Prokennalestes* (which has a ratio of 1.71 as reported by Wible et al. 2001).

**Sulcus for stapedia artery.**—Present (0), absent (1) (Rougier et al. 1998). Rougier et al. (1998) argue that the absence of the stapedia artery is an unambiguous synapomorphy for metatherians, as no metatherian preserving a petrosal bone has this structure. A distinct sulcus for the stapedia artery is observed in all of the specimens confidently identified as *Kulbeckia*. Other “zalambdalestids”, including *Zalambdalestes* and *Barunlestes* (Rougier et al. 1998) possess this sulcus as well. Archibald et al. (2001) coded “Zhelestidae” as absent for the sulcus given that no sulcus is found in the vicinity of the fenestra vestibuli. Besides “Zalambdalestidae”, other eutherian taxa coded as having this sulcus by Archibald et al. (2001) include *Asioryctes*, *Daullestes*, *Kennalestes*, *Prokennalestes*, and *Protungulatum*.

**Prootic canal.**—Present (0), absent (1) (modified after Rougier et al. 1998). Rougier et al. (1998) recognized four states for this character by identifying three separate states when the canal is present (long and vertical, short and vertical, and short and horizontal). Because Archibald et al. (2001) used a more limited set of taxa than Rougier et al. (1998), only presence or absence of the structure applied. Out of the taxa considered by Archibald et al. (2001), only the petrosals of *Prokennalestes* and “Zhelestidae” possess prootic canals. No other eutherians, including *Kulbeckia*, are known to possess this structure. Although both *Prokennalestes* and “Zhelestidae” possess prootic canals anterolateral to the subarcuate fossa (unlike the canals posterolateral to the subarcuate fossa in metatherians), the morphology of the canals differs between the taxa. The “zhelestid” canal is much smaller than the *Prokennalestes* canal, and the canal is short and horizontal in “Zhelestidae” as it is in metatherians, rather than short and vertical as it is in *Prokennalestes*. Furthermore, the prootic canal in *Prokennalestes* is solitary through the petrosal in that it is not associated with any other canal,

such as the prootic canal and ?postglenoid vein canal that are associated in “Zhelestidae”.

**Crista interfenestralis and caudal tympanic process of petrosal connected by curved ridge.**—Absent (0), present (1) (Rougier et al. 1998). This structure is the posterior extension of the crista interfenestralis, and it divides the cochlear fossula from the fossa musculus minor posterior to the promontorium of *Kulbeckia*. Among the taxa considered by Archibald et al. (2001), such a ridge is only found in “zalambdalestids”, *Asioryctes*, and *Kennalestes*. This structure is absent in all “zhelestid” specimens studied here, as well as all other taxa considered by Archibald et al. (2001).

**Transpromontorial sulcus for the internal carotid artery.**—Present (0), absent (1) (Rougier et al. 1998). In extant mammals, the internal carotid artery can travel an extrabullar, perbullar, or transpromontorial course (Wible 1986). If the vessel takes a transpromontorial (within the tympanic cavity) course, then it often leaves a trace as a sulcus extending across the ventral face of the promontorium from the fenestra cochleae to the rostral apex of the bone. No specimens of “Zhelestidae” or *Kulbeckia* that preserve the petrosal possess this groove. The only taxa that Archibald et al. (2001) coded as possessing this sulcus were *Daulestes*, *Prokennalestes*, and *Protungulatum*.

**Tympanic aperture of hiatus Fallopii.**—In roof through petrosal (0), in roof through petrosal or at anterior edge (1), at anterior edge (2) (modified from Rougier et al. 1998). The hiatus was present in all of the taxa considered by Archibald et al. (2001). Rougier et al. (1998) did not code this character for *Zalambdalestes*, but Wible et al. (2001) subsequently observed that the hiatus is at the anterior edge of the petrosal for this taxon. The coding of this character for *Kulbeckia* is problematic, because the hiatus appears to open at the anterior edge of the petrosal in URBAC 00-16, but in URBAC 00-02 the hiatus appears to open in the roof through the petrosal (tympanically). The other *Kulbeckia* specimens are not well enough preserved for an accurate determination. Because of this, Archibald et al. (2001) coded this character as intermediate (state 1) for *Kulbeckia*. The hiatus opens in the roof through the petrosal in *Asioryctes*, *Prokennalestes*, “Zhelestidae”, and even in *Protungulatum*, despite the anterior opening of the hiatus in most archaic ungulates (Cifelli 1982).

**Lateral flange.**—Restricted to posterolateral corner (0), or greatly reduced or absent (1) (modified from Rougier et al. 1998). In non-therian mammals, the promontorium is bordered laterally by a broad lateral trough, the lateral edge of which is formed by a lateral flange. In therian mammals, the lateral flange is either greatly reduced or absent (Wible et al. 1995). Rougier et al. (1998) coded *Prokennalestes* as having a lateral flange restricted to the posterolateral corner of the petrosal, and Archibald et al. (2001) coded “Zhelestidae” the same way. The lateral flange is absent in *Kulbeckia* and all other taxa considered by Archibald et al. (2001).

**Coiling of the cochlea.**—Less than 360° (0), more than 360° (1) (Rougier et al. 1998). The cochlear duct is developed as a straight tube in non-therian mammals, including modern monotremes (Graybeal et al. 1989), but no extant therian mammal possesses a cochlea that is coiled less than 360° in a clockwise direction (Meng and Fox 1995; Wible et al. 2001). McKenna et al. (2000) observed that the cochlea of *Daulestes* is coiled beyond the cochleae of monotremes and the therian *Vincelestes*, but it is coiled to a lesser degree than the cochleae of all other therian mammals. Archibald et al. (2001) coded *Daulestes* alone as having a cochlea coiled less than 360° for this reason. It is evident from a broken specimen (ZIN C. 85514) that “Zhelestidae” does in fact possess a cochlea that is coiled at least 270°, but it most likely was coiled 360° as in all other taxa considered by Archibald et al. (2001).

**“Tympanic process”.**—Absent (0), present (1) (Rougier et al. 1998). This structure, on the posterior aspect of the petrosal, was coded as present for *Asioryctes*, *Kennalestes*, and *Zalambdalestes*. Out of the eleven petrosals assigned to *Kulbeckia*, only one preserves part of the area in question. In this specimen, there is a thickened and anteriorly pointing flange of bone that appears to be the lateral half of this “tympanic process”. This process is absent in “Zhelestidae” and all other taxa considered by Archibald et al. (2001).

## Phylogenetic implications

Neither *Mimotona* nor *Tribosphenomys* were coded for any of the above petrosal characters by Archibald et al. (2001), so the relationship between Glires and “Zalambdalestidae” can not be discussed based on basicranial material. Basicranial data do support a relationship between *Kulbeckia* and other “zalambdalestids”; however, there is no support for a “zalambdalestid” clade to the exclusion of all other taxa considered by Archibald et al. (2001). *Zalambdalestes*, *Kulbeckia*, and *Asioryctes* were coded nearly identically for all nine of the basicranial characters discussed above (*Barunlestes* and *Kennalestes* were coded similarly to these taxa as well, but both taxa are missing data for certain characters). *Zalambdalestes* and *Asioryctes* differ by only one character, character 67 (tympanic opening of hiatus Fallopii). Archibald et al. (2001) coded the hiatus opening in the roof through the petrosal bone (state 0) for *Asioryctes* and the hiatus opening anteriorly (state 2) in *Zalambdalestes* (and *Barunlestes*). As discussed above, *Kulbeckia* was coded as intermediate for this character (1); therefore, it cannot be determined, based on basicranial data alone, whether *Kulbeckia* is more closely related to *Zalambdalestes* or *Asioryctes*.

The basicranium of archaic ungulates is fairly well known (Cifelli 1982; Thewissen 1990; Luo and Gingerich 1999), and a discussion of the relationship between “Zhelestidae” and Ungulata based on basicranial material can be made. Of the two ungulate taxa studied by Archibald et al. (2001), only *Protungulatum* was coded for basicranial

characters (well preserved basicrania are not known for *Oxyprimus*). Out of the nine basicranial characters used by Archibald et al. (2001), *Protungulatum* and “zhelestids” were only coded identically for four of them (characters 65, 67, 69, and 70), and none of these characters are unique to *Protungulatum* and “Zhelestidae”. More similarity is found between “Zhelestidae” and *Prokennalestes*, which were coded identically for seven out of the nine characters (characters 62, 64, 65, 67, 68, 69, and 70). Of these seven characters, the states of characters 62 (stapedial ratio), 64 (prootic canal), and 68 (lateral flange) are plesiomorphic retentions found in both “Zhelestidae” and *Prokennalestes*, and no other taxon considered by Archibald et al. (2001) possessed these states. The stapedial ratios of both “Zhelestidae” and *Prokennalestes* are less than 1.8, and they both possess prootic canals (despite the differences in morphology) as well as lateral flanges restricted to the posterolateral corner of the petrosal. Among eutherians, these characters are only seen in *Prokennalestes* and “Zhelestidae”.

## Conclusions

In order to determine the relationships between modern mammals, whether they be marsupials, placentals, or monotremes, fossil taxa must be taken into consideration. There has been much attention directed toward the origin of extant eutherian mammals at and around the Cretaceous–Tertiary boundary. As more and more eutherian fossils are recovered from the Late Cretaceous, a clearer picture of extant mammal origins and relationships emerges.

Many, if not most, past studies incorporating mammalian taxa from the Late Cretaceous focus heavily on teeth, the reason being that in most cases, Late Cretaceous mammals are only known from teeth. Other skeletal elements, including basicranial and postcranial material are useful in determining relationships between these mammals, and they are used whenever they are available.

The major goal of this paper is to provide descriptions of the petrosal bones for the Late Cretaceous mammals “Zhelestidae” and *Kulbeckia* so that this information can be used in further phylogenetic studies. Although the basicranial data presented here may or may not support certain relationships by themselves, such as an ungulate–“zhelestid” clade, the characters described above come from a very limited region of the mammalian anatomy, the petrosal bone, and results from analyses incorporating characters from several different regions of the mammalian anatomy (such as Rougier et al. 1998; Archibald et al. 2001) are stronger in their interpretations of mammalian relationships.

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