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THE LATE CRETACEOUS PLACENTAL MAMMAL *KULBECKIA*

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ABSTRACT—*Kulbeckia*, a placental mammal from the late Turonian–Coniacian (Late Cretaceous) of Uzbekistan, was originally placed in the monotypic Kulbeckiidae. Important new material indicates that *Kulbeckia* is the basal most memberof ''Zalambdalestidae'', which also includes *Zalambdalestes*, *Barunlestes*, and the poorly known *Alymlestes*, all from the Late Cretaceous of Asia. *Kulbeckia* shares with other zalambdalestids: a narrow, somewhat elongated snout; procumbent, enlarged, and open-rooted medial lower incisor with enamel restricted to the more ventrolabial surface; and anteroposteriorly compressed and centrally pinched molar trigonids. Commensurate with its 10-million-year earlier age relative to other zalambdalestids, it is notable in its smaller size, probable retention of four lower incisors, bifurcated or two-rooted lower canine, relatively smaller or absent diastemata between anterior teeth, more lingually placed cristid obliqua, less reduced M3 and m3, and more dorsal and posterior placement of the angular process in adults. *Kulbeckia kansaica* (Tadjikistan) and *Kulbeckia rara* (Uzbekistan) are regarded as synonyms of *Kulbeckia kulbecke*, the only recognized species of *Kulbeckia*.

INTRODUCTION

Here we describe and discuss material almost exclusively from the Bissekty Formation (Upper Cretaceous, upper Turonian–Coniacian), Dzharakuduk, Uzbekistan, with one specimen from the Yalovach Formation (Upper Cretaceous, lower Santonian), Kansai, Tadjikistan that we refer to ''Zalambdalestidae''. We compare these fossils with previously described taxa of Cretaceous eutherians.

The paleoecology, geology, and biostratigraphy of the Bissekty Formation (including its correlation with the Yalovach Formation) was described in detail in Nessov et al. (1998) and Archibald et al. (1998). Here we only provide a brief summary and present new information. The 200+ m escarpment at Dzharakuduk in the central Kyzylkum Desert, Uzbekistan consists (from bottom to top) of the Uchkuduk (brackish and marine), Dzheirantuj (marine), Kenyktjube (marginal marine), Bissekty (fluvial), and Aitym (marginal marine) formations. The Bissekty Formation has produced a rich vertebrate fauna of about 100 species (Nessov, 1997). Localities in the overlying Aitym Formation produced extensive marine invertebrates. In 1999, Chris King and Noel Morris discovered fossils of marine invertebrates at the base of the section in what was interpreted as the Uchkuduk Formation. The invertebrate and marine faunas are still under study (King, Morris, and Ward, pers. comm., 1999), but one preliminary assessment suggests the Bissekty Formation is of post-Cenomanian age and may be part of a thick lower Turonian succession (i.e., it is lower or middle Turonian). Alternatively, it is younger than at least some lower Turonian units, but older than the earliest Santonian (i.e., it is Coniacian). Whichever hypothesis is correct, the Bissekty fauna will be among the most tightly correlated Late Cretaceous faunas in the world because of the presence of good marine faunas below and above in the same section. For now, we treat the Bissekty fauna as upper Turonian through Coniacian in age, the same assessment originally suggested by Nessov (see Nessov et al., 1998). The lowest locality, CDZH-17a, is considered to be upper Turonian in age and the others are considered to be Coniacian, although there is no clear basis for placing the Turonian/Coniacian boundary. These sites are about 10 million years older than the better-known vertebrate faunas of the Gobi Desert (Kielan-Jaworowska et al., 2000).

Methods—We use the dental terminology of Nessov et al. (1998:fig. 1) with two additions. We define the area bounded by the preparaconular and postparaconular cristae, and the lingual margin of the paracone as the paraconular basin. We define the area bounded by the premetaconular and postmetaconular cristae, and lingual margin of the metacone as the metaconular basin. Measurements were taken according to the method illustrated by Archibald (1982:fig. 1). At least three methods of naming eutherian premolars have been proposed. In order to maintain the traditional identification of premolars 1 through 4 in eutherians, Clemens (1973) suggested that the premolar occasionally found in the third position in *Gypsonictops* spp. be called ''c.'' While maintaining the traditional 1 through 4 premolar count, using the third letter of the alphabet has the advantage of recognizing that this tooth is in the third position. More recently, Cifelli (2000) suggested that this tooth should be designated by an ''x.'' Unfortunately, this offers no suggestion as to the position of this tooth and thus we feel that of these two schemes, the one proposed by Clemens (1973) is preferable. In recent years it has become clear that a total of five premolars is very common in a variety of Cretaceous eutherians, and that the third premolar has been repeatedly lost. Thus, while it requires some relearning of nomenclature we feel that its is best to refer to the premolars as 1, 2, 3, 4, and 5 when there is sufficient reason to actually name the premolar sites. Thus, for the purposes of this paper, when four premolars are present, they are identified as upper or lower 1, 2, 4, and 5, based on information that position 3 is lost in early eutherians (Novacek, 1986; Archibald, 1996; Archibald and Averianov, 1997, 1998; Nessov et al., 1998). Premolars 4 and 5 correspond to numbers 3 and 4 in most other traditional descriptions. Teeth were projected on a computer screen using a video camera mounted on a binocular microscope and measured to the nearest 0.1 mm using NIH Image 1.61 software. Unless otherwise indicated, the figures and photographs are by the authors. Photographs were taken with a Nikon CoolPix 990 digital camera.

Abbreviations—**Institutional**: **BMNH**, British Museum of Natural History; **CCMGE**, Chernyshev's Central Museum of Geological Exploration, Saint Petersburg; **IZANUz**, Institute of Zoology Academy Nauk Uzbekistan, Tashkent; **MAE**, Mongolian Academy of Sciences—American Museum of Natural

3; URBAC 98-10, R edentulous dentary with partial alveoli for i1, i4(?), and complete alveoli for c, p1–m1, partial alveoli for m2; ZIN C.82567, L edentulous dentary with alveoli for m2–m3; ZIN C.82568, L edentulous dentary with alveoli or roots for m1–m3.

Localities—All referred specimens except those listed below are from locality CBI-14, middle part of Bissekty Formation, Upper Cretaceous (Coniacian), Dzharakuduk, western Uzbekistan. CCMGE 52/12455 (the type), 53/12455, 54/12455, 60/12455, 102/12455 and ZIN C.82567 are from locality CBI-5a. CCMGE 5/12176 is from locality CDZH-17a, lower part Bissekty Formation, Upper Cretaceous (upper Turonian), Dzharakuduk, western Uzbekistan. The locality of ZIN C.82565 is uncertain but is most likely from CDZH-17a, CBI-14, or CBI-5a. CCMGE 9/12455 and CCMGE 73/12455 are from locality FKA-7a, lower part of Yalovach Formation, Upper Cretaceous (lower Santonian), Kansai, northern Tadjikistan (Nessov et al., 1998).

Revised Diagnosis—Relative to other zalambdalestids, characters labeled with a plus (+) are apomorphic, those labeled with a minus (−) are plesiomorphic, and those labeled with a question mark (?) are of uncertain polarity. Compared to other zalambdalestids, notably *Zalambdalestes lechei*: tooth size ranges from 62 to 85 percent of *Zalambdalestes lechei* (−); upper incisor, canine, and anterior premolar diastemata smaller, especially between I2 and C (−); four upper premolars rather than three or four (−); conules, especially paraconule, placed lingually (except labial M3 metaconule, which is similar to condition in other zalambdalestids) rather than more labially (this is problematic as *Zalambdalestes* is argued to have more labially placed conules, but it may be similar to *Kulbeckia* as the conules are quite worn in *Zalambdalestes*), with internal cristae distinct and low rather than being winglike (again this is problematic as *Zalambdalestes* is quite worn in this area); para- and metaconular basins each form distinct depression rather than being flat or convex (again this is problematic as *Zalambdalestes* is quite worn in this area); upper molar protocones usually with a small vertical crenulation or small cuspule on antero- and posterolingual margins to small but well-developed cingula, rather than lacking such features (+); M3 and m3 are not as small relative to other molars (−); four lower incisors rather than three (−); lower canine two-rooted or possibly with a single bifurcated root rather than single-rooted (−); lower canine and premolars with almost no diastemata (−); trigonids not as anteroposteriorly shortened (−); cristid obliqua contacts posterior of trigonid at protocristid notch rather below protoconid (−); angular process more posteriorly placed relative to end of tooth row and more dorsally placed relative to ventral margin of dentary at least in adults (−).

DESCRIPTION OF *KULBECKIA KULBECKE*

Cranium—All information regarding skull morphology is based on URBAC 99-53, which preserves the left side of skull from near the anterior end of the rostrum to the middle of the orbit. The medial side of the specimen follows the sagittal plane very closely (Fig. 1).

On the lateral side of URBAC 99-53, the nasal bone is crushed and distorted so that the maxilla has overridden the nasal dorsally for several millimeters. Preservation is sufficient, however, so the dorsal/ventral proportions of the skull can confidently be restored (Fig. 2). What appears to be the facial exposure of the lacrimal is distorted somewhat ventrally (Fig. 1A), but can be restored to its original position along with the nasals (Fig. 2C). Enough of the sutures are preserved to strongly suggest that the nasal is laterally expanded dorsal to the infraorbital foramen, makes considerable contact with the lacrimal, and extends posteriorly at least over the anterior margin of the orbit (Fig. 2C). The lacrimal has considerable facial exposure. A canal runs from the orbital exposure of this bone on to the facial portion (Fig. 2C). Wible (written comm., 2002) has identified this canal in *Zalambdalestes* and named it the translacrimal canal, which he believes is unique to *Zalambdalestes* and *Kulbeckia*. The maxilla has an orbital component, but sutures cannot be discerned between this bone, the lacrimal, or any other bones within the orbital wall posterior and medial to the lacrimal. The arc of the preserved anterior portion of the orbit is quite large. A slight bulge near the anterolateral end of the frontal appears to be a weak postorbital process. Sculpting posteriorly on the posterolateral margin of the frontal suggests the sutural contact with the parietal. A foramen is present in the anterodorsal aspect of the orbital wall, probably in the frontal (Fig. 2C). Its identity is uncertain but it may be the frontal diploic foramen that may have transmitted the frontal diploic vein or another vein (Thewissen, 1989; Wible and Rougier, 2000). Wible (written comm., 2002) indicates that it does not have a counterpart in *Zalambdalestes*. The suture between the frontal and nasal, and less certainly between the frontal and lacrimal can be discerned with some confidence. A large infraorbital foramen is dorsal to the penultimate premolar. There are four very small foramina just anterior to the infraorbital foramen (Figs. 1A, 2C). The rostrum becomes constricted just anterior to the infraorbital foramen (and above the penultimate premolar), so that anteriorly the snout is noticeably narrow relative to the rest of the facial (and palatal) region (Figs. 1B, 2E). A sulcus along the posterior margin of the maxilla and ventral margin of the lacrimal almost certainly received the anterior edge of the jugal (Figs. 1A, 2C). Although the course of the premaxilla-maxilla suture is not discernible throughout its entire length, a crack appears to approximate its course quite well. At its ventral margin, the suture appears to bisect I2 (Figs. 1A, 2C). This suture is not vertically oriented, but contacts the nasal more posteriorly above the canine.

Medially, the skull is preserved along the sagittal plane (Fig. 1C). Various bony ridges indicate the areas of attachment for the maxillo- and ethmoturbinals. It cannot be determined if any portions of the ethmoid or vomer are preserved. A large concavity in the posterodorsal aspect of the medial side was for the olfactory bulb of the brain. Except for a small area anterodorsal to the concavity of the olfactory bulb where the nasal overlaps the frontal, sutures are not discernible on the medial side.

In palatal view, there is no indication of an incisive foramen (Figs. 1B, 2E). Also premaxillae do not contact along the midline. These observations suggest that the most anterior portion of the specimen is absent. None, one (as shown in Fig. 2E), or possibly two incisors could have been present in this missing portion of the premaxilla. The premaxilla-maxilla suture is discernible medial to the first preserved incisor. Of the three incisors, the most anterior is completely within the premaxilla, the second appears to be on the border between the premaxilla and maxilla, and the much smaller third incisor may be completely within the maxilla (Figs. 1B, 2E). The palatine–maxilla suture is identifiable at the posterior end of the palate just lingual to a very small tubercle (Fig. 1B); however anteriorly the placement of this suture is more conjectural (Fig. 2E). This appears to be the finished posterolateral margin of the palatine. What appears to be an at least partially complete medioposterior palatine margin may have bordered a posterior palatine foramen (not indicated in Fig. 2E). Anteriorly, the course of the palatine-maxillary suture is less certain, but very likely it turns medially at a 90-degree angle between M1 and M2, following a transverse course to the midline. As noted above, just anterior to the penultimate premolar, the rostrum is noticeably constricted, showing that the snout from there anteriorly was constricted. There is a slight bulge lateral to the roots of the two-rooted or

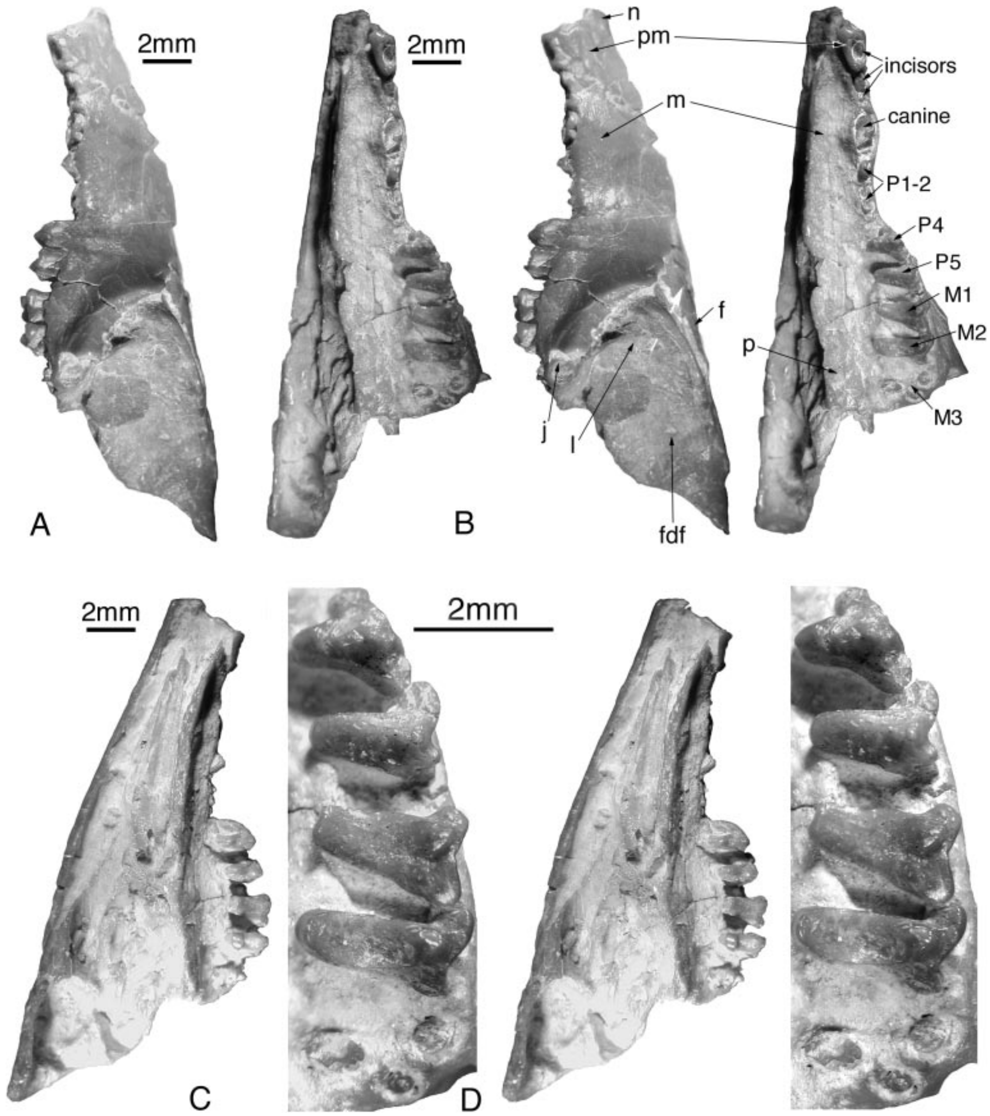

FIGURE 1. *Kulbeckia kulbecke*, stereophotographs of left anterior skull fragment, URBAC 99-53. **A**, lateral view; **B**, palatal view; **C**, medial view; and **D**, occlusal view of P4–M2, M3 roots (all somewhat damaged, M1 and M2 heavily worn, P5 and M2 missing metastylar region). **Abbreviations**: **f**, frontal; **fdf**, frontal diploic foramen; **j**, sulcus on maxilla for reception of jugal; **l**, lacrimal; **m**, maxilla; **n**, nasal; **pm**, premaxilla; **p**, palatine. White arrow shows course of translacrimal foramen.

bifurcate-rooted canine. The labial edges of P4–P5 and M1–M3 (only roots of M3) form a slight convex arch with the lingual edges of the teeth forming a subtle concave arch. There is slight dorsal arching throughout the anteroposterior axis of the palate. There are distinct embrasure pits between each of the posterior premolars and molars. Both the dorsal arching and embrasure pits may be exaggerated by some distortion of the palate.

Upper Dentition—None of the teeth in URBAC 99-53 are well preserved, damaged by both dental wear and postmortem breakage (Fig. 1D). Fresh breaks on the roots of P2 and M3 suggest these teeth were lost during collection of the specimen. The teeth or evidence of teeth in URBAC 99-53 are as follows: roots for three incisors, roots for a double-rooted or bifurcate-rooted C, worn double-rooted P1, roots for double-rooted P2, worn three-rooted P4, worn three-rooted P5 missing metasylar lobe, worn M1, worn M2 missing metasylar lobe, and three roots for M3. As we cannot determine if there were any incisors anterior to the roots of the three preserved incisors, we refer to these three as the anteromost, penultimate, and ultimate upper incisors. There are small diastemata posterior to all teeth from anteromost incisor through P1. A slightly larger diastema occurs between P2 and P4. There is no indication of a P3, although this does appear to be an old individual and thus an earlier loss of this tooth with subsequent bone remodeling cannot be ruled out. Although numbers of upper and lower premolars or other tooth positions do vary in mammals, it is of interest to note that an edentulous dentary referred to *Kulbeckia kulbecke* described below has alveoli for only four premolars, as seems to be the case for URBAC 99-53. Even with damage to some teeth and loss of M3, it can be determined in URBAC 99-53 that P4–P5 and M1–M3 were in close approximation with their neighbors. Although the more complete teeth are described next, some aspects of tooth size and shape, and crown morphology can be discerned from URBAC 99-53.

The roots of the anteromost and penultimate incisor are of similar size, although the latter is more laterally compressed (Fig. 1B). The round root of the ultimate incisor is about one-

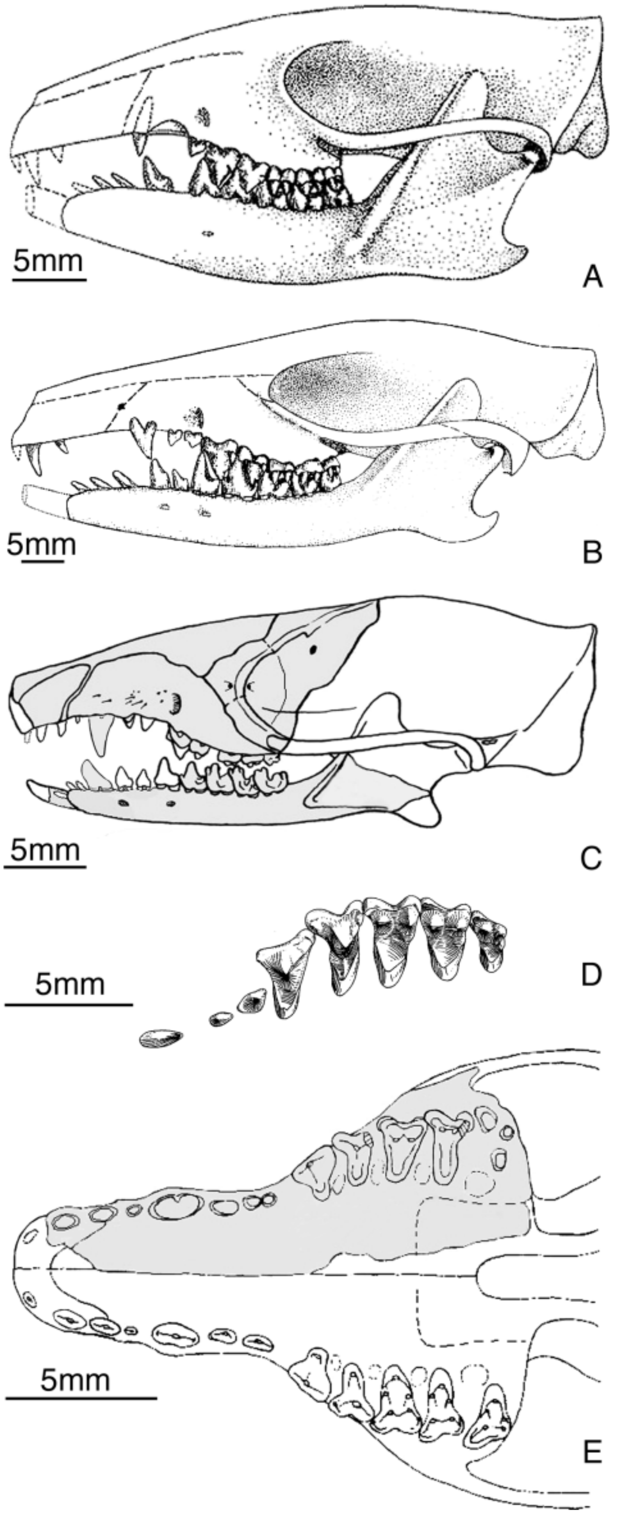

FIGURE 2. Reconstructions of **A**, *Barunlestes butleri*; **B**, **D**, *Zalambdalestes lechei*; and **C**, **E**, *Kulbeckia kulbecke* in lateral (**A**, **B**, and **C**) and occlusal views (**D**, **E**). *Barunlestes* and *Zalambdalestes* are after Kielan-Jaworowska (1975); *Kulbeckia* modified from Archibald et al. (2001). Shaded areas of *Kulbeckia* are those portions represented by specimens.

third the size of the other two. All the incisors are vertically implanted. The root(s), or possibly the very base of the crown of the canine together are about twice the size of either of the roots of the anteromost and penultimate incisors. The lateral side definitely indicates the partial bifurcation of a single root if not the presence of two roots (Fig. 1A, B). The latter is probably the case as an isolated upper canine described below has two roots. The premolars increase in size posteriorly with P1 about the length of anteromost and penultimate incisors (Figs. 1B, 2E). From what can be discerned of the crown of the two-rooted P1, it is a ventrally directed triangle, probably formed from a single, somewhat laterally compressed cusp. The posterior part of the tooth is slightly wider. Only the two-roots of the slightly larger P2 remain. Both P4 and P5 are three-rooted, have well-developed para- and metastylar lobes (the latter is missing but obviously was present on P5), at least a paracone, and a protocone. Because of wear nothing can be determined regarding the presence or position of a metacone or conules. The protocone on P5 is larger than on P4, and in this sense is more reminiscent of M1 and M2 (Fig. 1D). In both P4 and P5, the protocone is aligned perpendicular to the anteroposterior axis of the skull. The labial margins of these teeth approximate the bony margin of the palate. Because the rostrum narrows markedly at the P4, the labial margin of the tooth bends sharply inward; thus, creating an oblique angle with the protocone. The occlusal surfaces of M1 and M2 are obliterated by dental wear and M3 is missing (Fig. 1D). Moderately well-developed parastylar and metasylar lobes are present on M1. M2 has a moderately well-developed parastylar lobe. The metastylar lobe of M2 is missing, but was almost certainly present. The bases of the paracone and metacone are closely approximated but show no indication of fusion. The protocone is well developed and lingually extended on M1 and M2.

ZIN C.82566 (Fig. 3A–C) is an upper right canine with a well-preserved crown and the bases of two, nearly equally sized, round roots. The crown is vertically oriented but curves slightly posteriorly. There is some lateral compression. The labial surface is slightly more convex than the lingual surface. There is a small swelling at the base of the posterior side of the crown. The roots indicate that it is about the size of the canine that is missing in URBAC 99-53 although these specimens are clearly not from the same individual. The tip of the crown has a ventromedially facing wear facet, presumably for the lower canine.

URBAC 98-102 is a right P5 that preserves more of the crown than that in URBAC 99-53, although it either lacks most of the enamel on the crown or the enamel has been deeply etched (Fig. 3L). It is similar in proportions to that in URBAC 99-53 although it is somewhat larger. The labial margin of the tooth is slanted anteriorly about 70 degrees to the axis of the protocone. The parastylar lobe is larger than the metasylar lobe and has a distinct parastyle. The paracone is tall and situated near the labial margin of the tooth. There is no indication of a metaconal swelling on the postparacrista or of conules, but this may be the result of damage to the crown. The protocone is anteroposteriorly narrow, lower than the paracone, and supported by a robust lingual root. What appears to be a faint cingulum extending from the anterior to the posterior side of the protocone, may well be the edge of damage on the crown.

Fourteen complete or partial upper molars (six M1s, six M2s, and two M3s) are referred to *Kulbeckia kulbecke*. The most distinctive features separating upper molars are the relative sizes of the para- and metastylar lobes. In M1, these lobes are of similar size, but the parastylar lobe projects anterolabially while the metastylar lobe projects (and extends) more labially. This is clear seen in the holotype, CCMGE 52/12455, a left M1 as well as in other M1s (Fig. 3D, I, M). Another character distinguishing first and second upper molars is the extent of meta-

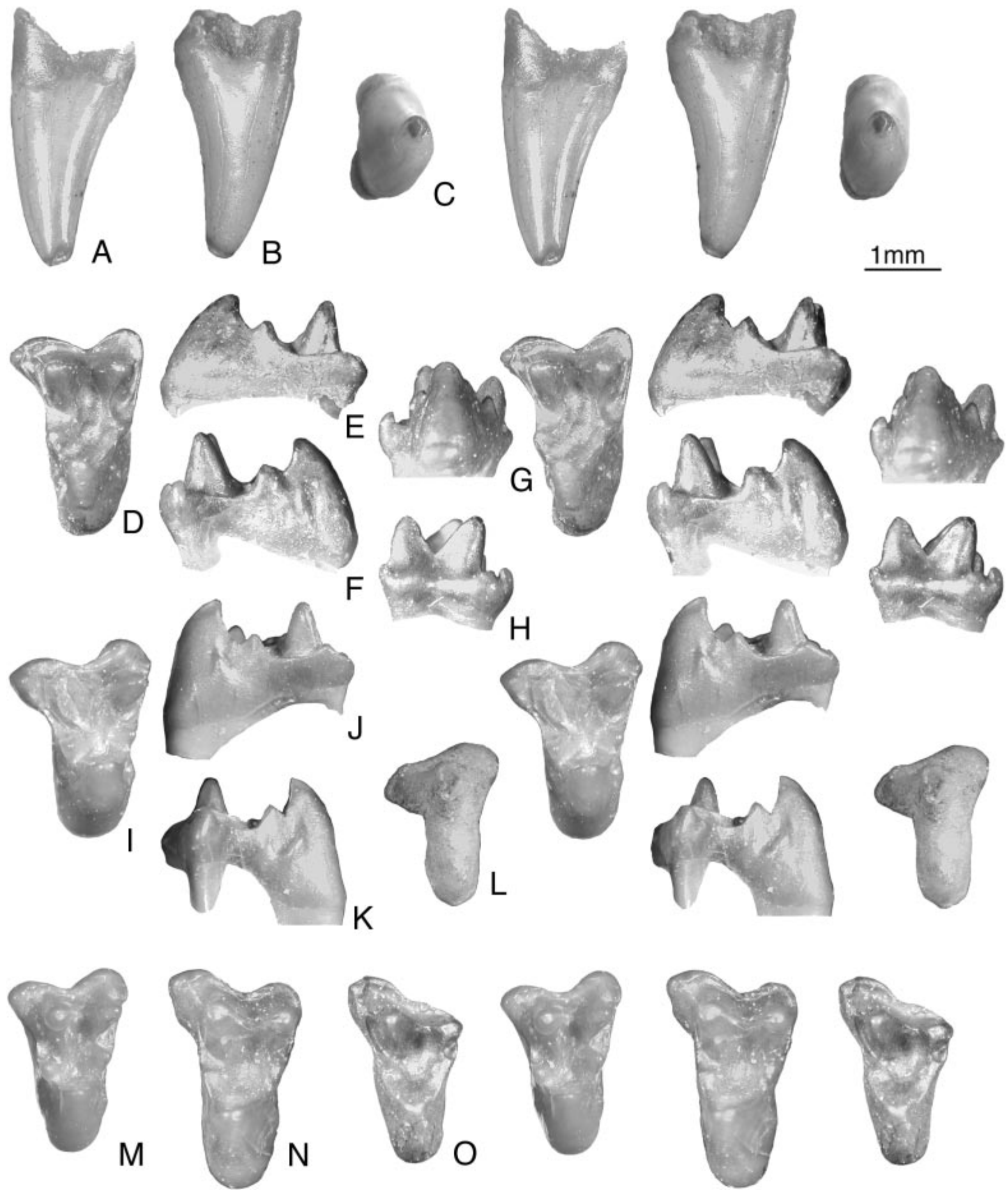

FIGURE 3. *Kulbeckia kulbecke*, stereophotographs of isolated upper teeth. **A**, lingual; **B**, labial; **C**, occlusal views, ZIN C.82566, right upper canine; **D**, occlusal; **E**, posterior; **F**, anterior; **G**, lingual; **H**, labial views, CCMGE 52/12455, left M1 (holotype of *K. kulbecke*); **I**, occlusal; **J**, anterior; **K**, posterior views, URBAC 98-134, right M1 (reversed, paracone missing); **L**, URBAC 98-102, right P5 (reversed, heavily chemically weathered); **M**, occlusal view, URBAC 98-100, right M1 (reversed); **N**, occlusal view, ZIN C.82565, left M2; **O**, occlusal view, CCMGE 54/12455, right M3 (reversed).

cingulum development. The metacingulum on M1s is continuous posterior to the base of the metacone and the postmetacrista, while on all M2s except ZIN C.82565, the metacinglum terminates or is very faint posterior to the base of the metacone. The metacingulum on ZIN C.82565 is better developed than on other M2s but is weaker than on M1s (compare Fig. 3D and N). The weaker metacingulum on M2s may relate to the adjacent, well-developed parastylar lobe of M3.

The overall shape of the stylar shelf of the M1 in *Kulbeckia kulbecke* in occlusal view is not unlike that in the M2 of some other Late Cretaceous therians, and hence the questionable identification of CCMGE 52/12455 as an M2 by Nessov (1993). The parastylar lobe is missing on five isolated M2s (CCMGE 5/12176, CCMGE 9/12455, URBAC 98-101 (or M1), URBAC 98-103, and URBAC 97-1), but is present on a sixth isolated M2 (ZIN C.82565) (Fig. 3N) and on the M2 in the skull fragment URBAC 99-53. Based on ZIN C.82565 and URBAC 99-53, the M2 is somewhat unusual for a Late Cretaceous eutherian. As in M1, the M2 parastylar lobe projects anterolabially while the metastylar lobe projects labially. Unlike in M1, however, the metastylar lobe is distinctly smaller than and does not project more labially than the parastylar lobe (Fig. 3, compare D, I, and M, with N). This trend is carried on in the M3 where the parastylar lobe is considerably larger than the almost nonexistent metastylar lobe (Fig. 3O, CCMGE 54/12455). This morphology is typical for M3s of Late Cretaceous therians.

There are two size morphs within *Kulbeckia kulbecke*, which may represent sexual dimorphism or even the presence of two species. Within the upper dentition, this size variation is best seen in M1s. The two smallest M1s are between 74 and 82

TABLE 1. Measurements (in mm) of *Kulbeckia kulbecke* upper teeth. Exclamation mark values are estimates; bold values are roots or crown bases; dagger (†) indicates a type specimen. **Abbreviations: L**, length; **W**, width; **AW**, anterior width; **PW**, posterior width, **H**, height.

	I1		I2		I3		C			P1		P2		P4		
Spec. No.	L	W	L	W	L	W	H	L	W	L	W	L	W	L	AW	PW
99-53	**0.6**	**0.5**	**0.7**	**0.4**	**0.3**	**0.3**	—	**1.5**	**1.0**	0.9	0.5	**1.0**	**0.6**	1.5	1.0	1.8
82566	—	—	—	—	—	—	2.5	1.5	1.0	—	—	—	—	—	—	—

	P5			M1				M2				M3		
Spec. No.	L	AW	PW	L	AW	PW	L/PW	L	AW	PW	L/PW	L	AW	PW
99-53	—	1.9	—	1.4	2.2	2.4	0.6	—	2.5	—	—	**1.2**	**2.1**	**1.8**
†52/12455	—	—	—	1.7	2.6	2.7	0.6	—	—	—	—	—	—	—
†9/12455	—	—	—	—	—	3.0	—	—	—	—	—	—	—	—
6/12455	—	—	—	1.9	2.5	2.7	0.7	—	—	—	—	—	—	—
98-100	—	—	—	1.4	2.0	2.1	0.7	—	—	—	—	—	—	—
98-134	—	—	—	1.9	2.5	2.6	0.7	—	—	—	—	—	—	—
97-1	—	—	—	—	—	—	—	—	—	2.5	—	—	—	—
†5/12176	—	—	—	—	—	—	—	—	—	2.6	—	—	—	—
8/12565	—	—	—	—	—	—	—	1.8	2.9	2.8	0.6	—	—	—
54/12455	—	—	—	—	—	—	—	—	—	—	—	1.6	2.5	2.2
98-135	—	—	—	—	—	—	—	—	—	—	—	—	2.4	—
Average	—	—	—	1.7	2.4	2.6	0.7	—	—	2.6	—	—	2.5	—
Standard deviation	—	—	—	0.2	0.2	0.2	—	—	—	0.2	—	—	—	—

percent of the length of the largest specimens (Table 1). Although the small size of the M1 of URBAC 99-53 can be partly attributed to substantial wear, this is not the case with the well-preserved URBAC 98-100, which is overall the smallest M1. Thus the size differences are real, but too few specimens are known to establish bimodality in the sample.

Stylar cusps are common only on the parastylar lobe. On M1s a small, but distinct parastyle and stylocone are found in CCMGE 52/12455 (Fig. 3D–H) and URBAC 98-100 (Fig. 3M), while a parastyle but no stylocone occurs in URBAC 98-105 and 98-134. A short, weak preparacrista is present on only some of the M1s and does not contact any stylar cusps. It may be directed toward the parastyle or between the parastyle and stylocone. The unusual parastylar region in CCMGE 6/12455 has at least two small cuspules within the depression formed by labial rim of the stylar shelf. The tooth, however, shows chemical damage to the surface, so the presence of true cuspules in the indicated areas is suspect. On the only M2 preserving the parastylar lobe, CCMGE 8/12565, all stylar cusps are subdued, but the parastyle is larger than the stylocone (Fig. 3N). The preparacrista is directed toward the parastyle rather than the stylocone, but merges with the crown before reaching it. A very slight swelling lingual to the parastyle on ZIN C.82565 is reminiscent of a preparastyle (Nessov et al., 1998). On the M3s, CCMGE 54/1245 and URBAC 98-135, each has a discernable but small parastyle and stylocone (Fig. 3O). On each, a subdued preparacrista is directed to what looks like a preparastyle. The preparastylar region on M1s and M2s may be slightly swollen but never bears a cusp. The parastylar lobe on URBAC 98-135 is large because of a wider paracingulum.

Although a very low ridge on all molars borders the relatively narrow stylar shelf, there are no other stylar cusps with a few minor exceptions. CCMGE 6/12455 has a swelling in the mesostylar (cusp C) region, but as noted above, this tooth shows some chemical damage and thus we regard this as either pathological or caused by chemical wear. Two M1s (URBAC 98-100, Fig. 3M, and URBAC 98-134, Fig. 3I) and one M2 (CCMGE 9/12455) have a variably developed stylar cusp E on the postmetacrista near the base of the metacone. A small notch can be developed between the cusp E and the postmetacrista.

On all molars, the paracone and metacone are separate at their bases and have a low but distinct centrocrista joining the two cusps. The proportions of the paracone and the metacone vary within and between tooth sites. On CCMGE 52/12455, these cusps are similar in size at their bases, but the metacone is slightly shorter (Fig. 3H). In CCMGE 6/12455, the base and height of the metacone are less than for the paracone. In M2s, the base of the metacone is similar in size to that in the paracone (CCMGE 5/12176, CCMGE 9/12455, and ZIN C.82565) or is slightly smaller (URBAC 97-1), and the metacone is always shorter than the paracone (estimated in CCMGE 9/12455 as the metacone is partly missing). In the only M3 preserving the metacone (CCMGE 54/12455), it is half the girth and height of the paracone.

Both para- and metaconules are well developed on all three molars (Fig. 3D, I, M–O), and cusp-like when unworn. On M1 and M2, the postparaconular crista and, to a lesser extent, the premetaconular crista form moderately long, low crests that are easily obliterated by wear, making it difficult to locate the position of the conules relative to the para- and metacone labially and the protocone lingually. When unworn, these cristae form the internal margins of the para- and metaconular basins, respectively, which are distinctly concave, as is seen on unworn molars (Fig. 3D, M). Based upon five M1s and four M2s, the paraconule is slightly closer to the protocone while the metaconule is intermediate in position between the metacone and protocone, or slightly closer to the metacone (Fig. 3D, I, M, N). On the two M3s, the conules range from worn to slightly worn, but it can be seen that the paraconule is equidistant or just slightly closer to the paracone than to the protocone, and the metaconule is distinctly closer to the metacone than to the protocone (Fig. 3O).

On M1s and M2s that preserve the anterolabial part of the crown, the preparaconular crista forms a continuous, narrow paracingulum that contacts the parastyle. On one M3 (CCMGE 54/12455), the paracingulum is slightly interrupted by a crest from the paracone to the parastyle, presumably the preparacrista (Fig. 3O), while, as noted above, the other M3 (URBAC 98-135) has a better developed paracingulum. None of the molars show much, if any wear in the shallow parastylar groove.

The protocone on M1 and M2 is well developed and slightly expanded anteroposteriorly, but its lingual placement gives the crown a decidedly transversely extended appearance. The height of the protocone reaches or slightly surpasses that of the para- and metacone on unworn and slightly worn specimens (Fig. 3F, K). The lingual margin of the protocone is convexly arched from the lingual base of the cusp to the more labially placed apex. The protocone on M3 is the same as that described above for M1 and M2, except that the crown is less transverse.

Pre- or postcingula are absent on all but one molar, but most M1s and M2s, and one of the M3s have a small crenulated area or even a small cuspule in the position where such cingula would occur. The one exception is URBAC 98-134 (Fig. 3I), which has narrow but distinct cingula that run lingually from a position level with the protocone apex labially to a position level with the para- and metaconule. When viewed either anteriorly or posteriorly (Fig. 3J, K), it can be seen that these cingula are unusual, possibly unique among Late Cretaceous eutherians. Normally pre- and postcingula are more or less at the same dorsoventral level throughout their length. The cingula of URBAC 98-134 are positioned at a very steep angle paralleling the lingual face of the protocone. Viewed anteriorly or posteriorly these cingula are clearly positioned similarly to the anterior and posterior crenulations found on other upper molars (Fig. 3B, F). In URBAC 98-134 they simply are enlarged to form narrow cingula.

The one specimen that we refer to *Kulbeckia kulbecke* that does not come from Dzharakuduk is CCMGE 9/12455, an M2 missing the parastylar lobe, the holotype of *Kulbeckia kansaica* Nessov, 1993. Although it is from a locality hundreds of kilometers to the southeast of Dzharakuduk and is possibly slightly younger, we cannot discern any consistent differences with the material from Dzharakuduk, except its slightly larger size. A second specimen, CCMGE 73/12455, was reported from FKA-7a (Nessov, 1997), but was not available for study. Based on the relatively few specimens we have, we cannot confidently assess whether more than one taxon is present. For now we feel it best to refer all specimens to *Kulbeckia kulbecke*.

Dentary—The following description of the dentary and lower dentition of *Kulbeckia kulbecke* is based on 30 specimens. In addition to two isolated canines and 13 isolated molars (three m1s, six m2s, four m3s), the sample includes 10 dentaries preserving teeth and five edentulous dentaries that are referred to *K. kulbecke* based on the size, proportions, and numbers of alveoli, jaw depth, and positions of mental foramina.

All adult dentaries are similar in depth, ranging from about 2.7 to 3.1 mm deep. Depth is quite uniform throughout the corpus of the dentary, decreasing only gradually anteriorly. It appears that dentary depth may have increased slightly after the adult dentition was acquired, as one of the oldest individuals based on molar attrition (URBAC 00-9) has the deepest dentary at 3.1 mm. Dentaries with one or more unerupted or erupting teeth are shallower than adult dentaries. Anteriorly the dentary is slightly thickened linguolabially from about the juncture of p2 and p4 forward, delineating the mandibular symphysis. None of the dentaries preserve a complete coronoid process, mandibular condyle, or angular process. What is known of the angular process suggests no angular inflection, but the more distal portion is not preserved and thus we cannot be sure there was not some inflection. In what we interpret as adult dentaries (e.g., URBAC 98-4), the area where the angular process merges with the corpus of the dentary is positioned distinctly posterior to the end of the tooth row and distinctly dorsal to the ventral margin of dentary (Fig. 2C). In what we believe are subadults (m3 not yet erupted, such as ZIN C.82571), the juncture between the angular process and corpus of the dentary is placed more ventrally and anteriorly, just ventral and posterior to the unerupted m3. We regard this as the juvenile or subadult condition. The masseteric fossa is of moderate depth (Fig. 4A). Ventrally it gradually merges into the corpus of the dentary. The anterior edge of the coronoid process is markedly thickened forming a distinct boundary with the masseteric fossa. A mandibular foramen is located on the lingual surface of the dentary 4 mm posterior to the M3 (Fig. 4D). A mental foramen occurs below the anterior or posterior root of p4 (Fig. 4A). Another small mental foramen occurs below p2 (URBAC 98-3) or p1 (98-4) (Figs. 4C, 5E). Unlike in the upper dentition where there are diastemata between more anterior teeth, only a small diastema sometimes occurs between the lower canine and p1.

Lower Dentition—Four specimens in particular (URBAC 98-3, URBAC 98-4, URBAC 98-10, and URBAC 00-52) provide information concerning the anterior dentition, especially anterior to the two-rooted canine. URBAC 98-4 and 98-10 are edentulous dentaries, probably of adults. Each preserves varying portions of a large alveolus that extends to below p2. URBAC 98-10 is more complete in this region. The large alveolus is linguolabially compressed, probably for a procumbent medial incisor with a root extending to below p2. This alveolus is followed by a partial large alveolus that may have held one or more incisors. Next posteriorly in URBAC 98-10 are complete double alveoli for c, p1, p2, p4, p5, m1, and partial alveoli for m2. Size of alveoli and positions of the mental foramina below what are interpreted as p1 and p4 support these identifications. The canine was doubled-rooted with the anterior root larger. Alveoli for the canine and p1 are similar in size; those for p2 are uncharacteristically small for *Kulbeckia*. This description applies almost equally well for URBAC 98-4, which preserves complete alveoli from the canine through m3 (Fig. 4C). The two exceptions for URBAC 98-4 are the canine alveoli, which are not completely divided, and the p2, which is the smallest premolar based on alveoli, but not as small as in URBAC 98-10.

The other two dentaries preserving part of the anterior dentition are subadults as some teeth are not erupted (URBAC 98-3) or a dp5 is still present (URBAC 00-52). URBAC 98-3 is rather poorly preserved. It preserves much of a laterally compressed, elongated incisor with the tip missing. There was a fragment of a small tooth at the labioposterior margin where the larger incisor emerged from the dentary, which was removed to better expose the larger incisor (Fig. 5D, E). This was followed posterolabially by two small alveoli that were also mostly removed (Fig. 5E). Just posteriorly, and still preserved, appears to be a permanent canine that is just beginning to erupt (Fig. 5E, F). As the base is not visible, we cannot determine the number of roots. This is followed by two roots for p1 (or dp1) and portions of two alveoli from which is erupting what we believe is the tip of p2 (Fig. 5E, F).

We cannot be certain of incisor homologies. For the sake of convenience we label the incisors consecutively, with the greatly enlarged incisor being i1 and followed by three very small teeth, i2–i4. Although URBAC 98-3 has been excavated around i1 and is not well preserved, the other sub-adult, URBAC 00-52 helps to verify the above identifications. URBAC 00-52 also preserves much (the tip is missing) of a laterally compressed, elongated incisor (Fig. 5A). In this specimen just laterally and slightly posteriorly are three very small alveoli that increase slightly posteriorly, which we identify as alveoli for i2–i4, again simply for the sake of convenience (Fig. 5A). Just lingual to the alveolus for i4 in URBAC 00-52 are partial alveoli that we interpret as alveoli for a two-rooted canine (deciduous?), followed by three or possibly four slightly larger partial alveoli that probably housed the dp1 and dp2 (or p1 and p2). These are followed by a similarly sized alveolus and talonid that almost certainly belong to dp4, and a complete dp5 and m1 (Fig. 6D–H).

The much larger, laterally compressed i1 is decidedly procumbent. In URBAC 98-3, the height to width ratio is 2.0, while it is 1.8 in URBAC 00-52. In both specimens the cross-section of the tooth is preserved (Fig. 5A, B). In cross-section, the enamel is distinctly thickened on all but the dorsolingual part of the tooth, where the enamel is either very thin or absent. The laterally compressed tooth is slightly convex labially and more flattened lingually, except where the exposed dentine or

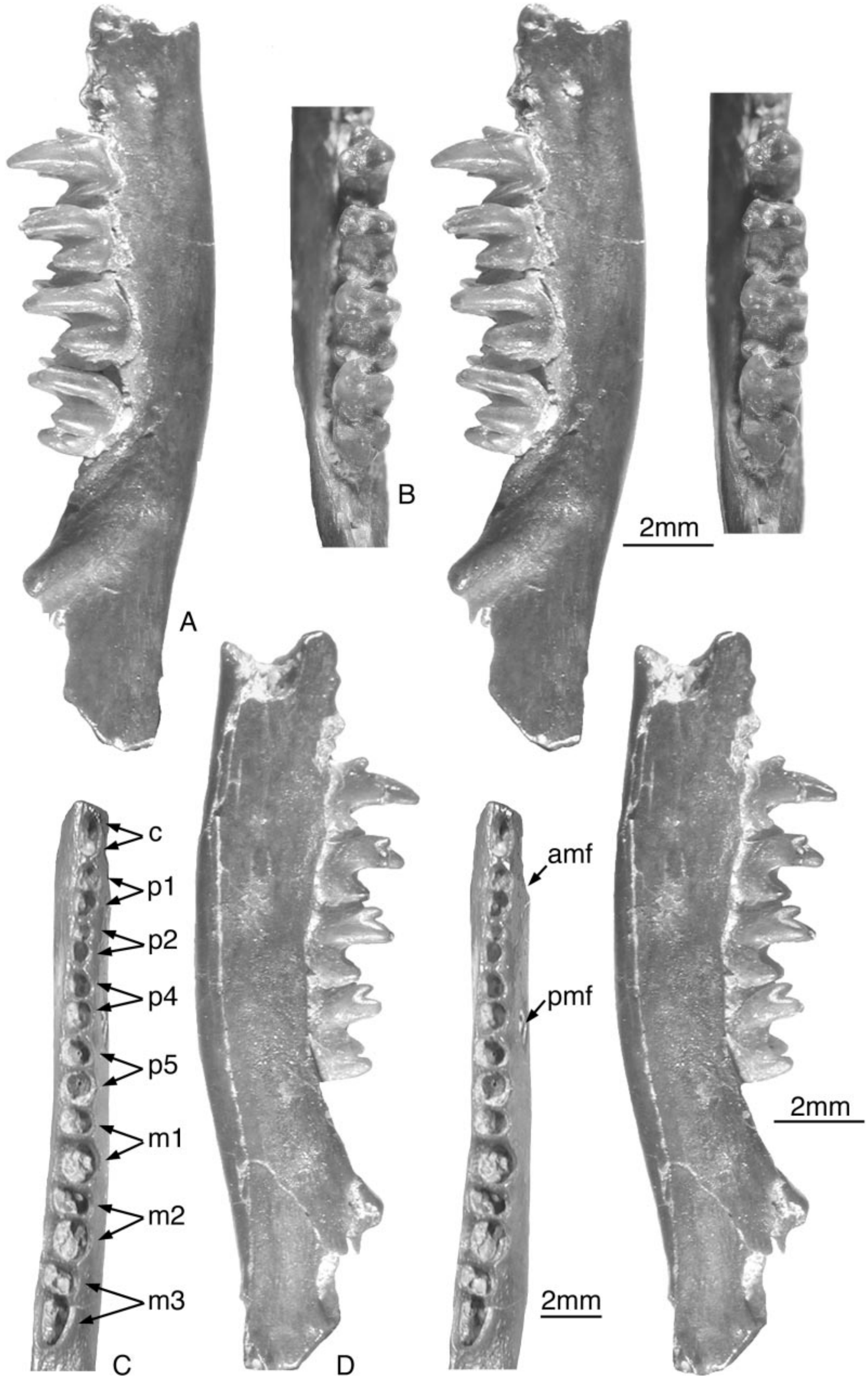

FIGURE 4. *Kulbeckia kulbecke*, stereophotographs of dentary and lower dentition. **A**, **B**, and **D**, URBAC 98-2, right dentary with p3 alveoli, p4 roots, p5, m1–3, **A**, labial, **B**, occlusal, and **D**, lingual views; **C**, URBAC 98-4, right edentulous dentary with partial alveoli for i1, i4(?), and complete alveoli for c, p1, 2, 4, 5, m1–3. **Abbreviations**: **amf**, anterior mental foramen; **pmf**, posterior mental foramen.

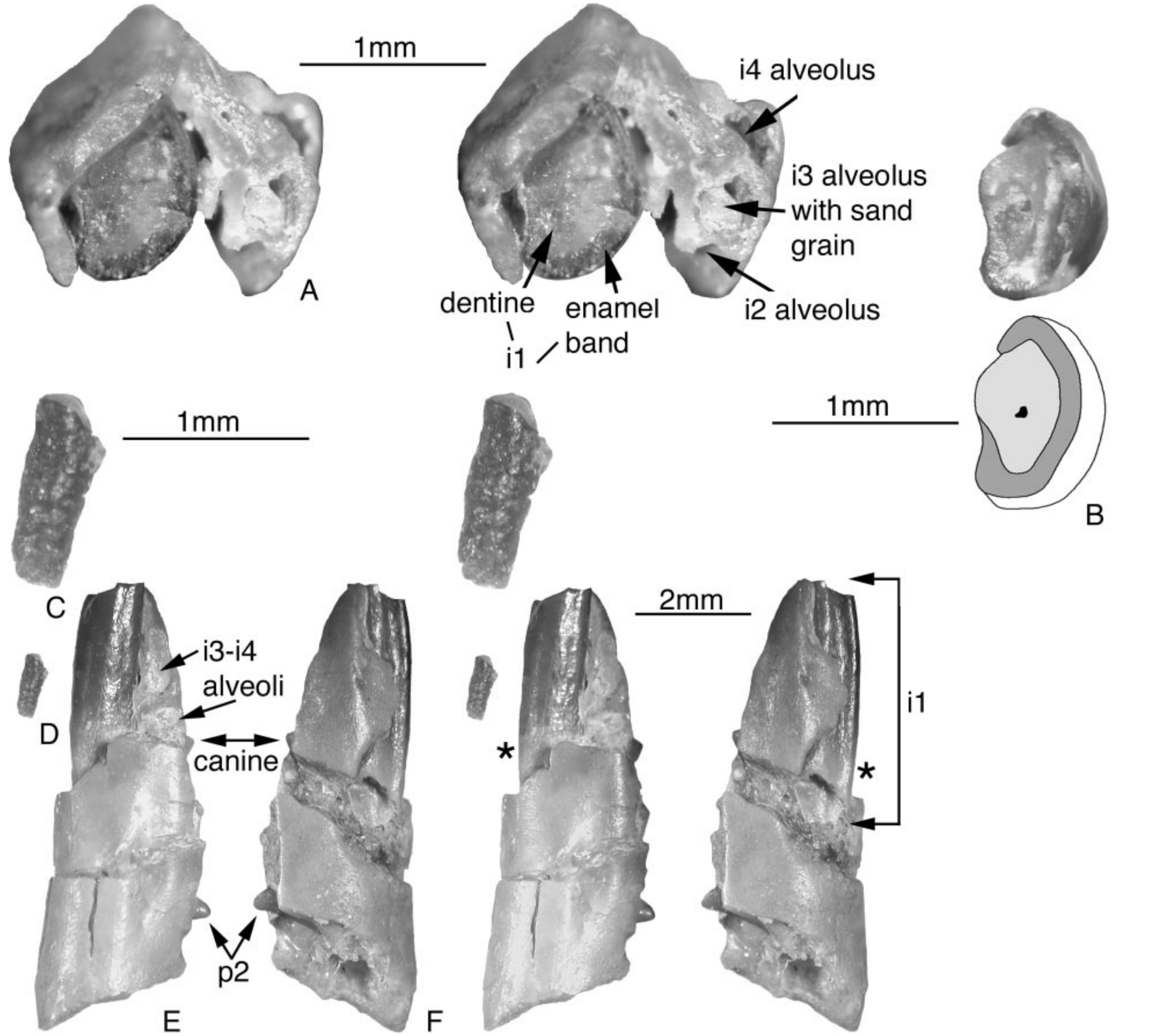

FIGURE 5. *Kulbeckia kulbecke*, stereophotographs of anterior lower dentition. **A**, URBAC 00-52, anterior view of dentary showing broken i1, alveoli for i2–4; **B**–**D**, URBAC 98-3, left dentary with broken i1, i2, partial alveoli for i3 and 4, erupting canine, four alveoli or partial alveoli for p1–2, erupting protoconid of p4. **B**, photograph and drawing of anterior view of i1 showing dentine and restricted enamel; **C**, labial view, i2; D, labial view i2 at same magnification as **E** and **F**; **E**, labial and **F**, lingual views, i1, (i2 in D is separated from dentary), partial alveoli for i3–4, erupting canine, alveoli for p1 (or dp1, not visaible), erupting p2. Asterisk indicates approximate posterior extension of enamel on i1. Note large apical root opening in F.

very thin enamel bulges slightly. The remainder of the i1 morphology can only be seen in URBAC 98-3. Although it was well exposed on its labial side when found, this specimen almost certainly had lost some bone during fossilization or collection (Fig. 5E). The tooth was probably only beginning to erupt at the time of death, and thus only what was the exposed tip is now missing. As noted, most of the labial side of i1 has been exposed resulting in the removal of the much smaller i2 fragment (Fig. 5C, D). The i1 was already exposed on much of its lingual side when found. The i1 extends posteriorly to below p1 (Fig. 5F), as it also appears to do in URBAC 00-52 (compared to below p2 in the two edentulous adult dentaries URBAC 98-4 and URBAC 98-10). The apical root opening is very large, encompassing most of the height and width of the root (Fig. 5F). Scanning electron micrographs were taken at various positions along the length of the tooth, but the exact posterior extent of the enamel was not detected. On both the ventral and labial surfaces, enamel appears to extend to at least within 1 mm of the apical root opening (Fig. 5E, F). What is preserved is not inconsistent with an ever-growing or gliriform incisor or at least the precursor of such an incisor as found in rodents, lagomorphs, vombatid marsupials, and the primate *Daubentonia*, among others (Koenigswald, 1985). The evidence, however, is not conclusive regarding whether the incisor was truly hypselodont. The large apical root opening might also reflect the young age of the individual because the erupting canine and p2 protoconid may also be open-rooted. As noted above, lateral to the i1 what we interpret as a fragment of a small i2 was present, but has since been removed (Fig. 5C, D).

Part of an erupting canine is known in URBAC 98-3 (Fig. 5E, F). Much of the lingual surface and the apex of the crown are visible. It is about 60 percent the size of the isolated upper

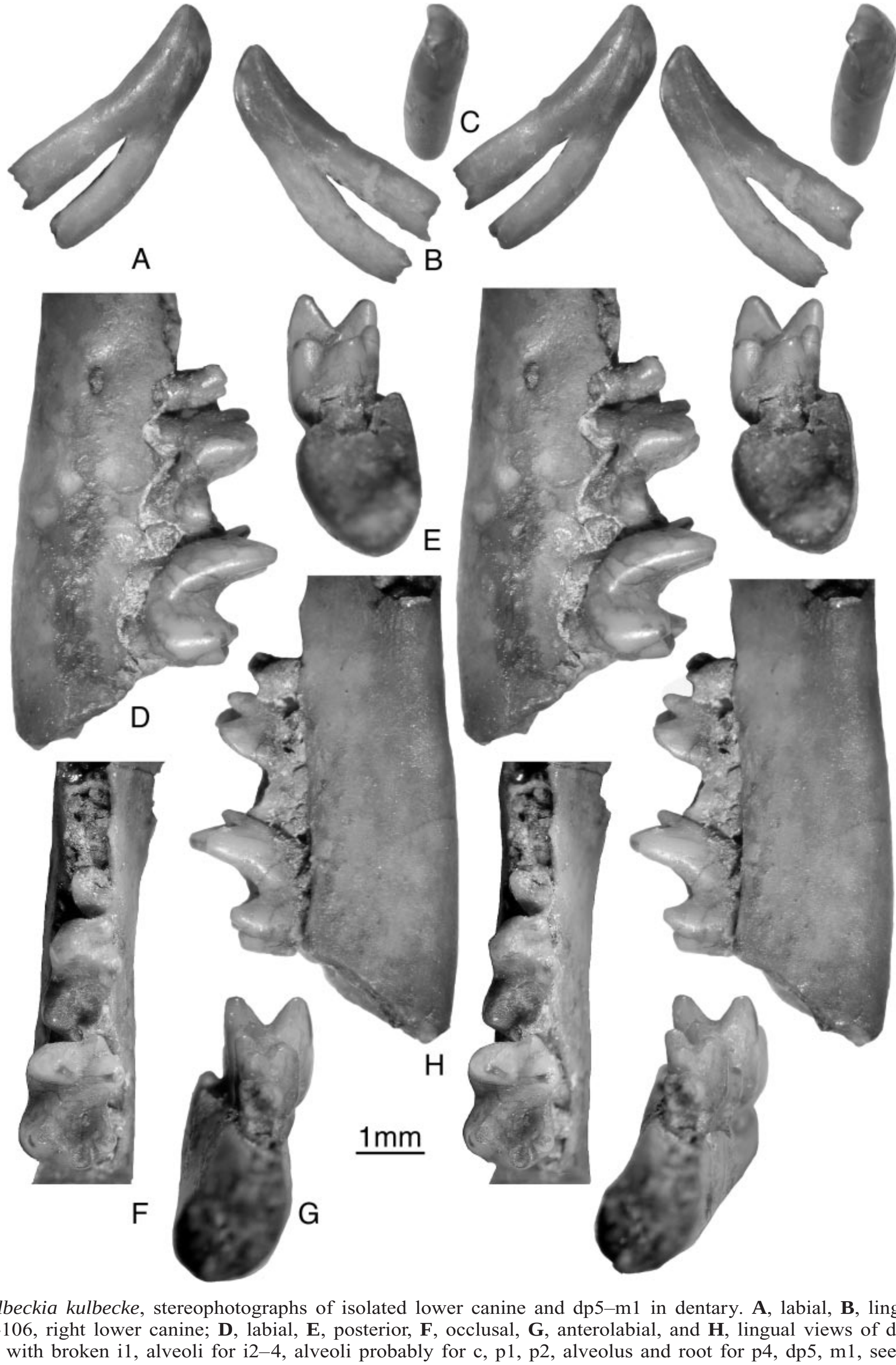

FIGURE 6. *Kulbeckia kulbecke*, stereophotographs of isolated lower canine and dp5–m1 in dentary. **A**, labial, **B**, lingual, and **C**, occlusal views, URBAC 98-106, right lower canine; **D**, labial, **E**, posterior, **F**, occlusal, **G**, anterolabial, and **H**, lingual views of dp5 and m1, URBAC 00-52, (left dentary with broken i1, alveoli for i2–4, alveoli probably for c, p1, p2, alveolus and root for p4, dp5, m1, see Fig. 5A for view of broken i1, alveoli for i2–4).

canine, ZIN C.82566 and probably has one (or more?) large apical root opening(s) and thus possibly may not yet be of full height. There may be some slight lateral compression. The apex curves slightly lingually. Two isolated teeth are identified as lower canines of *Kulbeckia*: URBAC 98-106 (Fig. 6A–C); and ZIN C.82572. They are similar in morphology, but ZIN C.82572 is somewhat smaller. The crown is vertically oriented and slightly laterally compressed. The apex of the crown curves slightly posterolingually. There is a distinct ridge on the posterior edge of the crown with a small but distinct cuspule at the base, which is larger than its counterpart in the upper canine. There is a faint ridge on the anterior margin that follows the margin as it curves lingually midway in its height. This ridge is absent on the upper canine. Although complete roots of upper canines are not known, from what is preserved, it appears that the roots of the lower canine are at a greater angle to the crown.

The posterior root is larger than the anterior root. The tip of URBAC 98-106 has a small, dorsolabially oriented wear facet, presumably from the upper canine.

No p1s, p2s, or p4s are completely preserved in any specimen, although the crown tip of an erupting p2 is present in URBAC 98-3 (Fig. 5E, F) and the poorly preserved heel of dp4 is found in URBAC 00-52 (Fig. 6D, F–H). The erupting p2 in URBAC 98-3 is only represented by a complete protoconid. The remainder of the crown and roots had not formed. The heel of the dp4 in URBAC 00-52 is too poorly preserved to provide useful information.

Descriptions of p5 and lower molars are based on the well-preserved dentary URBAC 98-2 (Fig. 4A, B, D). This represents the only known p5, but information for molars were checked against isolated specimens. The p5 has a well-developed trigonid in which the protoconid is the dominant cusp. The metaconid is about half the girth of the protoconid. Although its tip is missing, the metaconid was probably at least two-thirds the height of the protoconid. The paraconid is about half the girth of the metaconid. It is situated low on the anterior margin of the tooth slightly lingual to the midline. There is a very small, narrow precingulid. The talonid is slightly shorter than but almost as wide as the trigonid. A small entoconid and slightly larger cusp in the hypoconulid position are present. There is no cusp in the hypoconid position; rather, the equivalent of the cristid obliqua leads anteriorly from the hypoconulid nearly along the midline of the talonid. The entocristid, entoconid, postcristid, hypoconulid, and cristid obliqua-equivalent form a small basin in the lingual half of talonid. The p5 is slightly shorter than m1 (Table 2).

URBAC 00-52 preserves the dp5 (Fig. 6D, F–H). Although the crown surface is somewhat chemically abraded, the general morphology is well preserved. The trigonid is fully molariform, with all three cusps of similar proportions to that seen in a molar. Notably, the paraconid is relatively larger compared to that in the p5 of URBAC 98-2. In both, the paraconid is slightly lingual to the midline and the trigonid is not anteroposteriorly compressed. Although abraded, the dp5 appears to have a small precingulid as in p5. The talonid in the dp5 is absolutely and relatively larger than that in the p5. The dp5 talonid is fully developed with the three usual talonid cups found in molars. They are equidistant from each other.

The m1 is slightly shorter than m2 and m3, which are similar in length (Table 2). In width, m2 is greatest while m1 and m3 are similar. The m1 trigonid and talonid are similar in width or the talonid can be slightly wider; the m2 trigonid is usually wider than the talonid but the opposite can be true; the m3 talonid is slightly narrower on most teeth. The protoconid is slightly greater in girth compared to the metaconid on all three molars, but on all three molars the metaconid is distinctly taller or less commonly similar in height to the protoconid on unworn specimens (Figs. 4, 6, 7). On all molars the paraconid is smaller and lower than the other two trigonid cusps but distinct (except in CCMGE 102/12455), and located about halfway between the midline and the lingual margin of the trigonid. The paraconid of CCMGE 102/12455 is very small, almost lacking. In contrast, the paraconids of CCMGE 8/12953 and ZIN C.82573 are well developed and almost as tall as the protoconid. URBAC 98-121 is unique in having a small cusp on the paraconid halfway up its anterolingual margin (Fig. 7K).

Trigonid to talonid length becomes less going from m1 to m3. All molars show some anteroposterior shortening of the trigonid, to the greatest degree on m2. Both the para- and protocristid are present on all three molars and are deeply notched at the midline of the trigonid. Also at the midline of each cristid, the trigonid is slightly but distinctly compressed, giving the impression of an anteroposterior pinching of the trigonid at this point (Fig. 7A, F). The cristid obliqua on all three molars contacts the posterior wall of the trigonid at the protocristid notch, or even more lingually (CCMGE 60/12455). Most m1s have only a hint of a precingulid (almost lacking in CCMGE 102/12455). The precingulid on m2 and m3 is very narrow but runs from below the paraconid to below the protoconid. CCMGE 53/12455, an m3, has a very well-developed precingulid; it is wider and almost twice as long as on other lower molars. A narrow but distinct postcingulid is present on most molars, and is best developed on m2s. The m3 sometimes has a cuspulid on the postcingulid (URBAC 98-2; Fig. 4A).

The talonids on all molars are wide relative to the trigonid with a large entoconid, hypoconulid, and slightly larger hypoconid. Unworn talonid cusps are more or less equidistant to each other or the entoconid and hypoconid are closer to one another (but not twinned). With wear, especially on the lingual side of the hypoconulid, this cusp and the entoconid appear to be slightly closer. When unworn, the hypoconulid and especially the entoconid are distinctly taller than the hypoconid. The talonids are also deep when unworn (e.g., URBAC 98-2) with well-defined cristids joining the three talonid cusps. The m3s of URBAC 98-2 and CCMGE 53/12455 have a distinct cuspulid (entoconulid) on the entocristid, and there is a hint of this on the m2 of URBAC 98-2 and a well-developed cuspulid on the m2 in URBAC 98-116. The hypoconulid of m3s is usually set slightly more posteriorly than on m1 or m2 (Fig. 7F). The talonid of p5 and m1–m3 in labial view is quite high, reaching at least 50 percent if not more of the trigonid height (Figs. 4, 6, 7). URBAC 98-121 is unique (in addition to possessing the preparaconid cusp noted above) in having a small cristid that runs anterolingually from the anterolabial edge of hypoconulid towards the entoconid.

COMPARISONS WITH *ZALAMBDALESTES* AND *BARUNLESTES*

The narrow, somewhat elongated snout, procumbent if not gliriform i1, and anteroposteriorly compressed and centrally pinched molar trigonids are some of the more obvious features of *Kulbeckia* that unmistakably show the hallmarks of ''Zalambdalestidae''. *Kulbeckia* does, however, retain ancestral features commensurate with its 10-million-year earlier age relative to the much better known Mongolian zalambdalestids, notably its smaller size, less of the premaxilla contributing to the elongate snout, probable retention of four lower incisors, bifurcated or two-rooted lower canine, relatively smaller or absent diastemata between anterior teeth, more lingually placed cristid obliqua, little reduction of M3 and m3, and angular process at juncture of corpus more posteriorly placed relative to end of tooth row and more dorsally placed relative to ventral margin of dentary at least in adults.

There are a number of cranial similarities found in *Zalambdalestes lechei*, *Barunlestes butleri*, and *Kulbeckia kulbecke* although information for the third species is limited. In these taxa, the facial exposure of the premaxillary–maxillary suture is oblique and the face is markedly constricted anterior to the penultimate upper premolar forming a very narrow snout (Fig. 2A–C). We regard at least the latter condition as derived for eutherians. The nasals are expanded posteriorly in all three taxa and have considerable contact with the lacrimal, which has a considerable facial exposure. Wible (pers. comm., 2001) regards both of these character states as ancestral at least for eutherians. In at least *Zalambdalestes* and *Kulbeckia* there is a translacrimal foramen piercing the lacrimal (Fig. 2C) (Wible, written comm., 2002). *Kulbeckia* has a foramen, possibly the frontal diploic foramen, in the dorsal aspect of the orbital wall (only in *Kulbeckia* in Fig. 2C). Wible (written comm., 2002) indicates this foramen is absent in *Zalambdalestes*.

Wible (written comm., 2002) indicates that *Zalambdalestes*

TABLE 2. Measurements (in mm) of *Kulbeckia kulbecke* lower dentitions. Exclamation mark values are estimates; dagger (†) indicates a type specimen. **Abbreviations: L**, length; **W**, width; **TRW**, trigonid width; **TAW**, talonid width; **TRL**, trigonid length; **TAL**, talonid length, **H**, height.

	i1			p5 (or dp5)					m1				
Spec. No.	H	L	W	L	TRW	TAW	TRL	TAL	L	TRW	TAW	TRL	TAL
98-3	1.0	!4.1	0.5	—	—	—	—	—	—	—	—	—	—
00-52**	0.9	—	0.5	1.9	1.2	1.2	1.0	0.9	2.1	1.6	1.6	0.9	1.2
98-2*	—	—	—	1.7	1.2	1.1	1.1	0.6	1.8	1.3	1.4	0.8	1.0
00-9	—	—	—	—	—	—	—	—	1.9	1.5	1.7	0.9	1.0
60/12455	—	—	—	—	—	—	—	—	1.7	1.3	1.3	0.8	0.9
102/12455	—	—	—	—	—	—	—	—	1.8	1.3	1.3	0.8	0.9
98-1	—	—	—	—	—	—	—	—	1.9	1.5	1.5	0.9	1.1
99-64	—	—	—	—	—	—	—	—	1.9	1.4	1.5	0.9	1.0
Average	1.0	—	0.5	—	—	—	—	—	1.9	1.4	1.5	0.9	1.0
Standard deviation	—	—	—	—	—	—	—	—	0.1	0.1	0.1	0.1	0.1

98-2* p5–m3 = 7.4 mm.
00-52** dp5, not p5.

lechei has two upper premaxillary incisors, with a very small maxillary incisor variably present. Figure 2A and B show the number and placement of upper incisors as in the older, original reconstruction of Kielan-Jaworowska (1975) indicating two premaxillary incisors and questionably another more anterior premaxillary incisor. Based only on URBAC 99-53, *Kulbeckia kulbecke* has at least three upper incisors with the first and second of similar size, and the third decidedly smaller but not as reduced as in *Zalambdalestes* (Fig. 2C, E). As in *Zalambdalestes*, the larger more anterior incisors are within the premaxilla and the smaller third incisor is in the maxilla. It cannot be determined if more anteriorly *Kulbeckia* had none, one, or two more incisors (Fig. 2C, E show only one extra incisor). The incisor crowns are not preserved in URBAC 99-53. The following comparisons are based upon the preserved roots. Wible (written comm., 2002) indicates that in *Zalambdalestes* the second incisor is more laterally compressed than the first, which is also the case in *Kulbeckia*. Unlike in *Zalambdalestes*, the second incisor is not smaller than the first in *Kulbeckia*. In fact, the second incisor in *Kulbeckia* is slightly anteroposteriorly longer than the first. Wible (pers. comm., 2001) notes that in *Zalambdalestes* the first incisor is vertically implanted while the second slants posteriorly to some degree. In *Kulbeckia*, the roots suggest a vertical orientation for the first and second incisors relative to the palatal plane, but when oriented in life position, these incisors may have both been directed somewhat posteriorly because of the slightly down turned snout.

Based on an isolated tooth, ZIN C.82566, as well as the preserved roots in URBAC 99-53, the upper canine is a double-rooted (or at least a bifurcate-rooted), trenchant tooth as in *Zalambdalestes* (Kielan-Jaworowska, 1975). As described above, the crown of the two-rooted P1 of *Kulbeckia* is a ventrally directed triangle, probably formed from a single, somewhat laterally compressed cusp. The posterior part of the tooth is slightly wider. This is similar to Kielan-Jaworowska's (1969) description for P1 in *Zalambdalestes*. P1 is lacking in some specimens of *Zalambdalestes*, and apparently is also lacking in *Barunlestes* (Kielan-Jaworowska, 1975; Kielan-Jaworowska and Trofimov, 1980) (Fig. 2A). The P2 is not known in *Kulbeckia*, but as in *Zalambdalestes* was two-rooted. In URBAC 99-53, the P4 (P3 in Kielan-Jaworowska, 1969) is complete, but the surface is so heavily weathered that surface details are most likely caused by wear. As in the P4 of *Zalambdalestes*, there are an asymmetrical protocone, as well as parastylar and metastylar lobes (Fig. 2E). There is a dominant paracone near the labial edge, but any other cusps have been obliterated. The P4 protocone in *Kulbeckia* may be slightly broader anteroposteriorly but narrower labiolingually compared to that in *Zalambdalestes*. Kielan-Jaworowska (1969) notes that the P4 protocone is directed obliquely anteromedially. In both *Zalambdalestes* and *Kulbeckia*, the P4 protocone does form an acute angle anteriorly with the labial half of the tooth. We, however, think it more accurate to state that the protocone is nearly transverse to the long axis of the tooth row, as is also the case for P5 and M1–M3. It is the labial edge of P4 that is sharply inclined anteriorly following the line of the snout as it markedly narrows at this point (Fig. 2D, E). As with the P4 in URBAC 99-53, the P5 (P4 in Kielan-Jaworowska, 1969) is heavily worn and the metasylar lobe is broken, although it was clearly well developed as is the case on URBAC 98-102. It can be seen in URBAC 99-53 and in URBAC 98-102 that as in *Zalambdalestes*, the protocone of P5 is well developed in *Kulbeckia*, essentially matching the size of this cusp in the molars. In *Kulbeckia*, the pre- and postparacristae are of similar size, while in *Zalambdalestes* the latter is slightly larger. *Kulbeckia* differs in lacking any metaconal swelling on the postparacrista. Two areas on the worn P5 of URBAC 99-53 are what appear to be para- and metacingula.

The molars in URBAC 99-53 are very heavily worn and damaged; thus, the following comparisons with upper molars of *Zalambdalestes* are based upon the isolated teeth of *Kulbeckia* described earlier. In overall shape and size, the molars of *Kulbeckia* are very similar to those of *Zalambdalestes* except that the M3 of *Kulbeckia* shows little if any reduction. There are several points of surface anatomy and cusp size, however, that require comment. After examining several specimens or casts of upper molars of *Zalambdalestes* (PSS-MAE 130, a BMNH cast of ZPAL MgM-I/43, and a ZIN cast of ZPAL MgM-I/14), and examining various illustrations and accompanying descriptions by various authors, we conclude that all published specimens of this taxon are too worn to show most surface anatomy of the lingual half of the crown and the relative size of the protocone. We do not know but suspect that *Kulbeckia* and *Zalambdalestes* shared the following aspects of molar anatomy that are well preserved in the former taxon. Kielan-Jaworowska (1969) noted that the ''protocone is situated lower than the paracone and metacone'' in *Zalambdalestes*. This is true, but all known teeth are worn. As described above in *Kulbeckia*, in an unworn condition, the height of the protocone reaches or slightly surpasses that of the para- and metacone. The lingual margin of the protocone is convexly arched from the lingual base of the cusp to the more labially placed apex. The only difference between the protocone of these taxa may be that an unworn molar protocone of *Kulbeckia* has vertical crenulations, small cuspules, or very rarely cingula in the pre- and postcingular position. We treat this as an autapomorphy for *Kulbeckia*.

Authors (e.g., Crompton and Kielan-Jaworowska, 1978), while sometimes noting the wear in the conular area of upper

TABLE 2. Extended.

	m2					m3				
Spec. #	L	TRW	TAW	TRL	TAL	L	TRW	TAW	TRL	TAL
98-2*	1.9	1.6	1.5	0.8	1.1	2.0	1.4	1.3	0.8	1.2
!00-9	!12.0	!1.5	!1.7	!1.0	!1.0	!2.1	!1.6	!1.5	!0.9	!1.2
98-1	2.3	1.6	1.5	1.1	1.2					
99-64	2.0	1.6	1.5	0.9	1.1					
93-5	2.0	1.6	1.5	0.9	1.1					
98-136	2.0	1.3	1.4	0.8	1.2					
!82553						!2.0	!1.4	!1.3	!0.8	1.2
!82569						!1.8	!1.4	!1.3	!0.7	1.1
53/12455						2.0	1.2	1.1	0.9	1.1
!82570						!1.9	!1.4	!1.0	!0.8	*1.1*
99-100						2.1	1.3	1.4	0.8	1.2
00-28						2.1	1.3	1.2	0.8	1.3
Average	2.0	1.5	1.5	0.9	1.1	2.0	1.4	1.3	0.8	1.2
Stand. dev.	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1

molars, have suggested that the conules on upper molars of *Zalambdalestes* are situated relatively close to the paracone and metacone (Fig. 2D). Given the worn condition of all upper molars of *Zalambdalestes* known to us, we hesitate to endorse this reconstruction given what is known in *Kulbeckia*. If the condition is as described for *Zalambdalestes*, however, then *Kulbeckia* is considerably different in the morphology of the conules, especially that of the paraconule on M1 and M2. In *Kulbeckia*, the paraconule is closer to the protocone on M1 and M2, and the metaconule is about equidistant between the protocone and metacone on these molars (Figs. 2E, 3). Only in M3 is the paraconule slightly closer to the paracone than to the protocone, and the metaconule is distinctly closer to the metacone than to the protocone. A similar M3 metaconule is evident on a cast of ZPAL MgM-I/43 (Crompton and Kielan-Jaworowska, 1978:fig.10). Crompton and Kielan-Jaworowska (1978) also showed the conules of M2 in *Zalambdalestes* with wing-like internal cristae. Again, if correct, this differs from the low, distinct internal cristae seen in *Kulbeckia*.

As seen in Figure 2, the dentary of *Kulbeckia* is more similar to *Zalambdalestes* than it is to *Barunlestes* (Kielan-Jaworowska, 1975; Kielan-Jaworowska and Trofimov, 1981). In the former two taxa, the dentary is somewhat shallower, and both the ventral margin of the masseteric fossa and the anterior margin of the angular process are positioned more posteriorly. We regard these as ancestral states relative to those of *Barunlestes*. Additionally, in *Kulbeckia*, what is preserved of the ventral margin of the angular process is positioned slightly more dorsally than in *Zalambdalestes*, which we regard as the ancestral condition, probably for eutherians if not earlier. *Kulbeckia* has mental foramina below p1 or p2 and p4 and *Zalambdalestes* has mental foramina below p1 and p4 (Kielan-Jaworowska, 1975; Kielan-Jaworowska and Trofimov, 1981). *Barunlestes* has a single mental foramen below p4 (Kielan-Jaworowska, 1975; Kielan-Jaworowska and Trofimov, 1980; Fig. 2A–C).

As described above, aspects of the lower anterior dentition of *Kulbeckia* are largely known based on four specimens. Although very similar, there are some differences between these specimens and the anterior dentition of *Zalambdalestes lechei* as described by Kielan-Jaworowska (1969). In both taxa there is an enlarged medial incisor that is procumbent and transversely compressed. Although homologies with other eutherians are not clear, for convenience we call this i1. The enamel is markedly thicker on the more labial aspects of the tooth and in fact may be restricted to the more labial surface (Fostowicz-Frelik and Kielan-Jaworowska, 2002). In *Kulbeckia*, i1 is almost certainly followed by three small, single-rooted incisors. Although these incisors for the most part are not preserved for *Kulbeckia*, the alveoli indicate some procumbency especially in the more anterior of these small incisors as in *Zalambdalestes* (Kielan-Jaworowska, 1975; Kielan-Jaworowska and Trofimov, 1981; Fig. 2B, C). As described above, the fragment of a small tooth was found labial of the large i1 in URBAC 98-3. We interpret

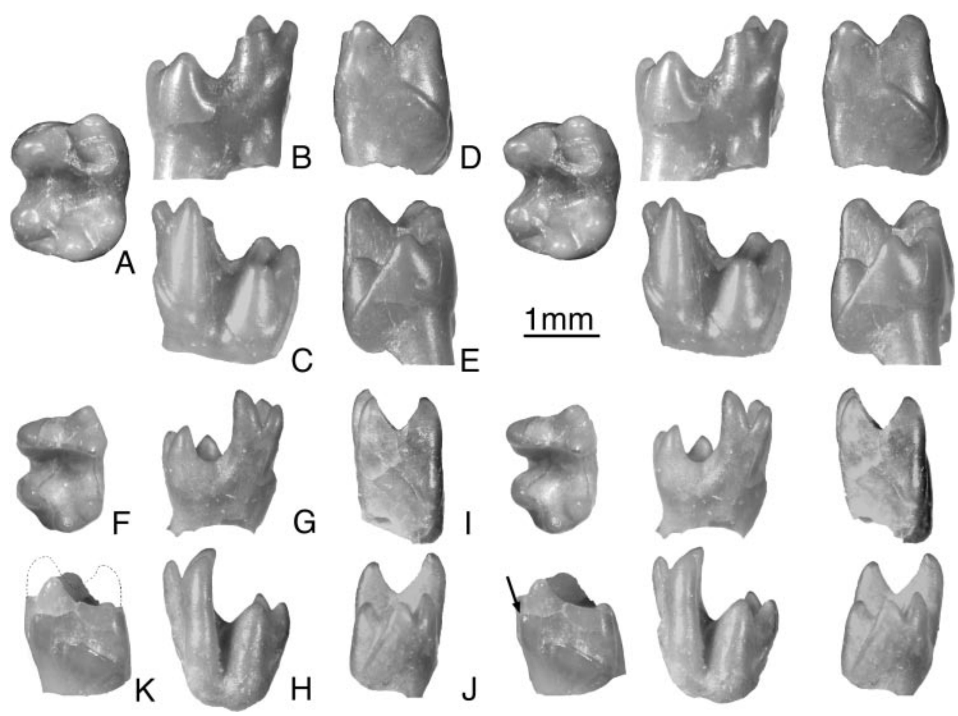

FIGURE 7. *Kulbeckia kulbecke*, stereophotographs of isolated m2 and m3s. **A**, occlusal; **B**, lingual; **C**, labial; **D**, anterior; and **E**, posterior views, CCMGE 8/12953, left m2; **F**, occlusal; **G**, lingual; **H**, labial; **I**, anterior; and **J**, posterior views, ZIN C.82574, left m3; **K**, anterior view, URBAC 98-121, showing preparaconid (arrow), protoconid and metaconid missing (indicated by dotted outline).

this as i2, thus making the partial alveoli that follow for i3 and i4. These are very similar in position to those identified as i2 and i3 in *Zalambdalestes* suggesting that these incisors in *Zalambdalestes* may well be i3 and i4 as in *Kulbeckia*. If this interpretation is correct *Zalambdalestes* does not preserve or has lost i2.

The lower canine of *Zalambdalestes* and *Barunlestes* is single-rooted (Kielan-Jaworowska, 1975). *Kulbeckia* may vary from two roots to a bifurcated root on the lower canine. Unlike *Zalambdalestes* and *Barunlestes*, *Kulbeckia* has little or no diastemata between anterior teeth, except possibly small spaces between i4 and c, and c and p1. Again, based on limited evidence, *Kulbeckia* always has four premolars, which we identify as p1–p2 and p4–p5, while *Zalambdalestes* has three or four lower premolars (Kielan-Jaworowska, 1969) and *Barunlestes* has three (Kielan-Jaworowska, 1975). Although p1 and p2 are not known for *Kulbeckia*, the alveoli in URBAC 98-4 for these teeth suggest that as in *Zalambdalestes* the p1 is slightly larger than p2 (Kielan-Jaworowska, 1975:fig. 2; Kielan-Jaworowska and Trofimov, 1981:fig.2).

For the last lower premolar and molars more information is available for *Kulbeckia*, allowing a better comparison with *Zalambdalestes*. Compared to the lower dentition of *Zalambdalestes* (BMNH cast of ZPAL MgM-I43), the p5 and m1–m3 in *Kulbeckia* (URBAC 98-2) are similar with only a few differences. Tooth length in *Kulbeckia* is about 85 percent that of *Zalambdalestes*. Molar trigonids in *Zalambdalestes* are slightly more anteroposteriorly shortened. The cristid obliqua is more lingually placed in lower molars of *Kulbeckia*. We regard the states of these three characters in *Kulbeckia* as ancestral for ''Zalambdalestidae''. The m3 in *Zalambdalestes* is derived in that it is noticeably reduced relative to its size in *Kulbeckia*. *Kulbeckia* might be more derived in that in some lower molars the height of the metaconid is slightly higher than the protoconid. It is not clear whether any of the usually more worn lower molars of *Zalambdalestes* show this trait, which is unusual for Cretaceous eutherians. It is seen in some Tertiary taxa such as rodents. There appear to be other minor differences, but we feel these are best attributed to the greater wear in the known specimens of *Zalambdalestes*.

CONCLUSIONS

Our understanding of the evolutionary history of Mesozoic mammals is fraught with problems, not the least of which is the quality of the fossil material. The spectacular material from the Late Cretaceous of Mongolia demonstrates, however, that this is not the only and possibly not the greatest obstacle. The lack of evolutionary diversification within clades of Mesozoic mammals may be the greatest impediment. This is almost certainly not an artifact of the fossil record. We believe this lack of diversity will not increase markedly as the record improves, which it is bound to do. There are some exceptions. Arguably the best of these known among Late Cretaceous eutherians are the zalambdalestids, which have remarkable convergences if not actual homologies in skeleton, skull, and teeth with extinct and extant placentals—notably rodents and rabbits. Some have emphasized their possible evolutionary relationships (e.g., McKenna, 1994; McKenna and Bell, 1997). Others, such as Novacek et al (1997) have suggested that zalambdalestids are allied with asioryctitheres. McKenna et al. (2000) described the skull of *Daulestes* from a site in the Kyzylkum from which a specimen of *Kulbeckia* also comes. They noted that in skull design *Daulestes* is similar to *Asioryctes* and tentatively referred *Daulestes* to Asioryctitheria. They also noted (p. 47) that in skull design, *Daulestes* is ''very different from Zalambdalestidae.'' Most recently, Archibald et al. (2001) argued that ''Zalambdalestidae'' (including *Kulbeckia*) and Glires (Duplicidentata and Simplicidentata, Macroscelidea was not included) form a well-supported clade (bootstrap value >70%). The present study was not intended to address this wider question; it does, however, strongly support *Kulbeckia* as the basal-most zalambdalestid, clearly showing the hallmarks of this taxon, but also indicating the transition from other Late Cretaceous eutherians.

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