

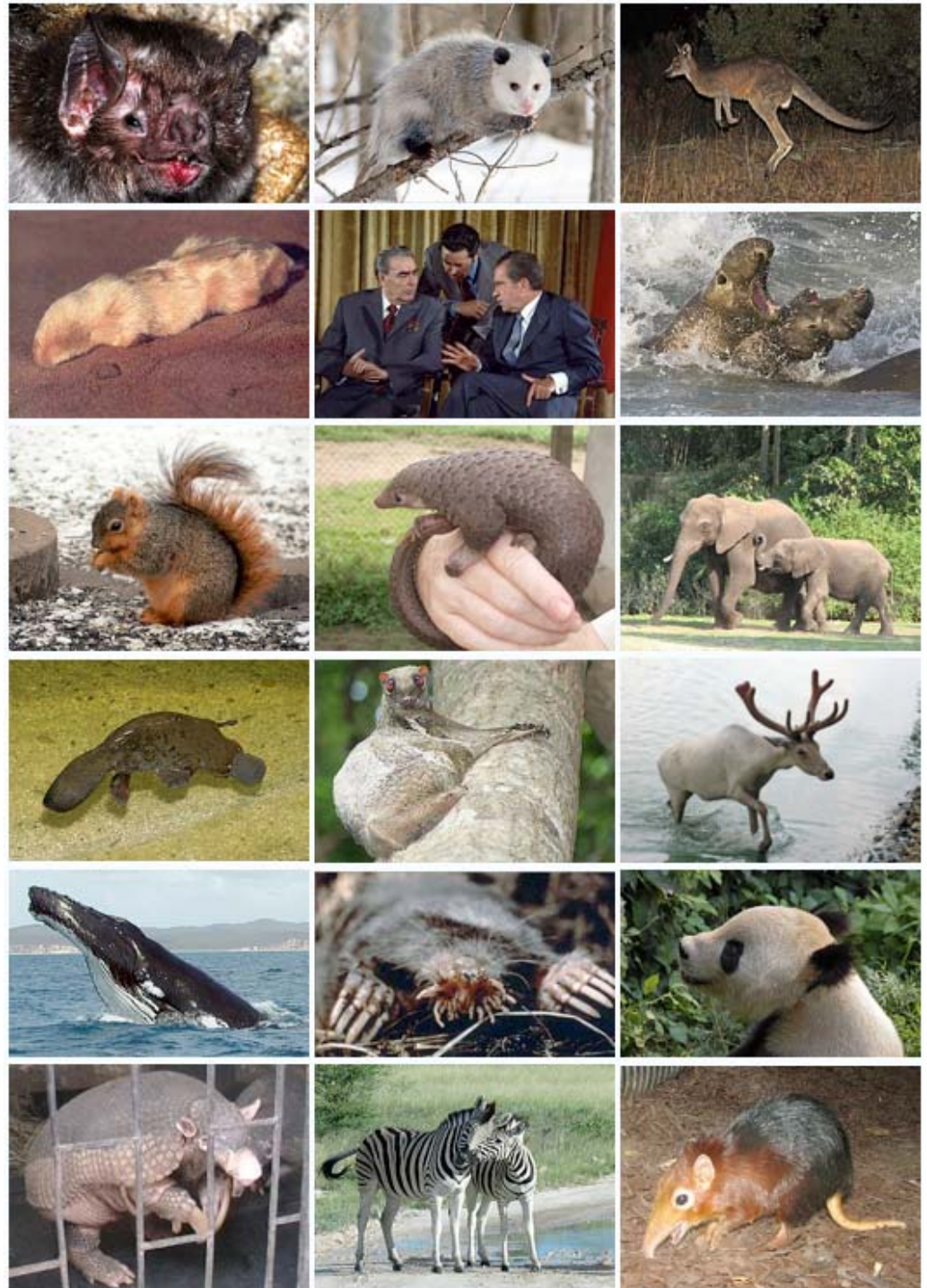
# Происхождение плацентарных млекопитающих

А.О. Аверьянов

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Monotremata:	3	5
Marsupialia:	91	331
Placentalia:	1135	5080
Mammalia:	1229	5416

Wilson & Reeder (2005)



# The Placental Mammal Ancestor and the Post–K-Pg Radiation of Placentals

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To discover interordinal relationships of living and fossil placental mammals and the time of origin of placentals relative to the Cretaceous-Paleogene (K-Pg) boundary, we scored 4541 phenomic characters de novo for 86 fossil and living species. Combining these data with molecular sequences, we obtained a phylogenetic tree that, when calibrated with fossils, shows that crown clade Placentalia and placental orders originated after the K-Pg boundary. Many nodes discovered using molecular data are upheld, but phenomic signals overturn molecular signals to show Sundatheria (Dermoptera + Scandentia) as the sister taxon of Primates, a close link between Proboscidea (elephants) and Sirenia (sea cows), and the monophyly of echolocating Chiroptera (bats). Our tree suggests that Placentalia first split into Xenarthra and Epitheria; extinct New World species are the oldest members of Afrotheria.



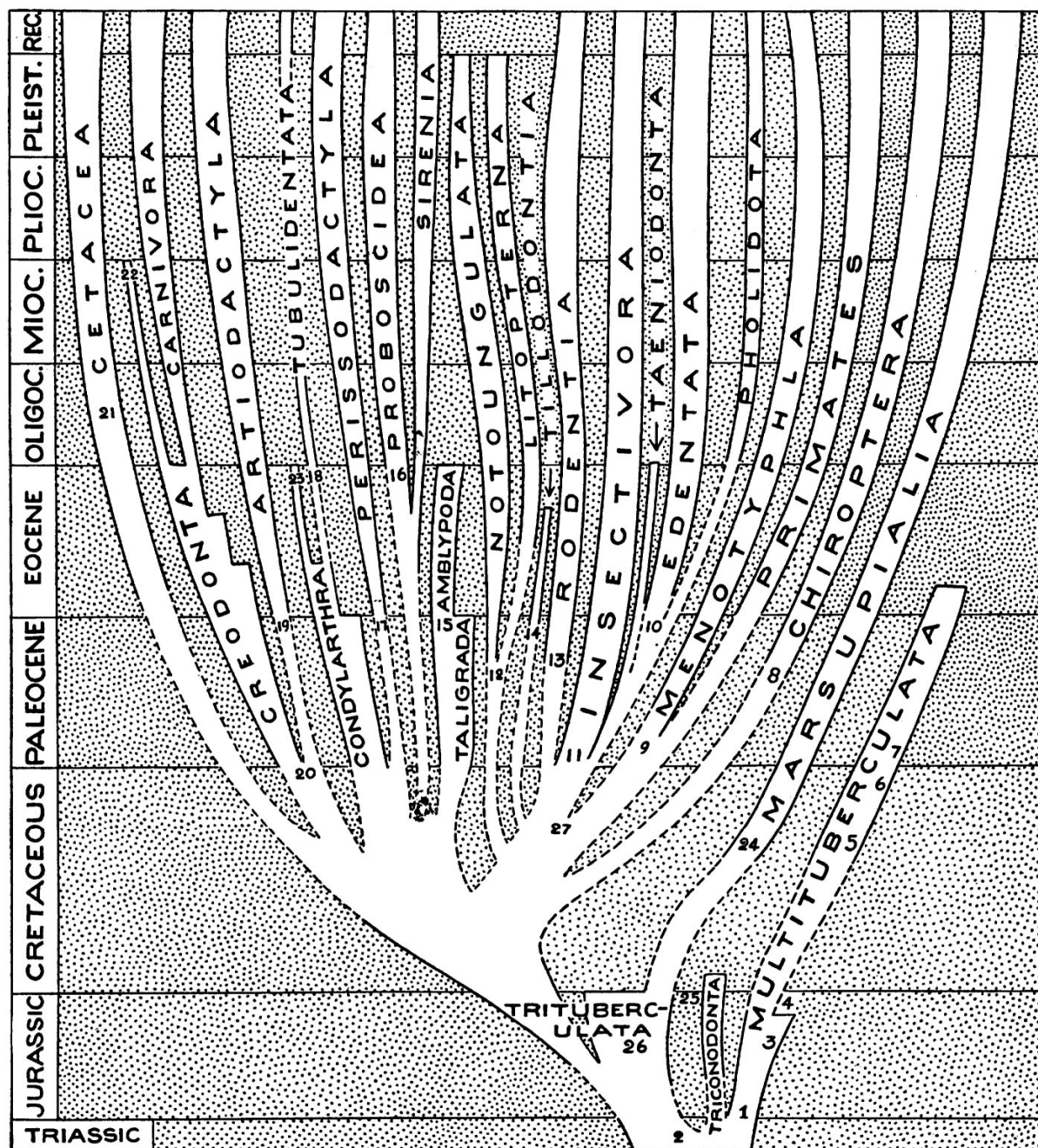
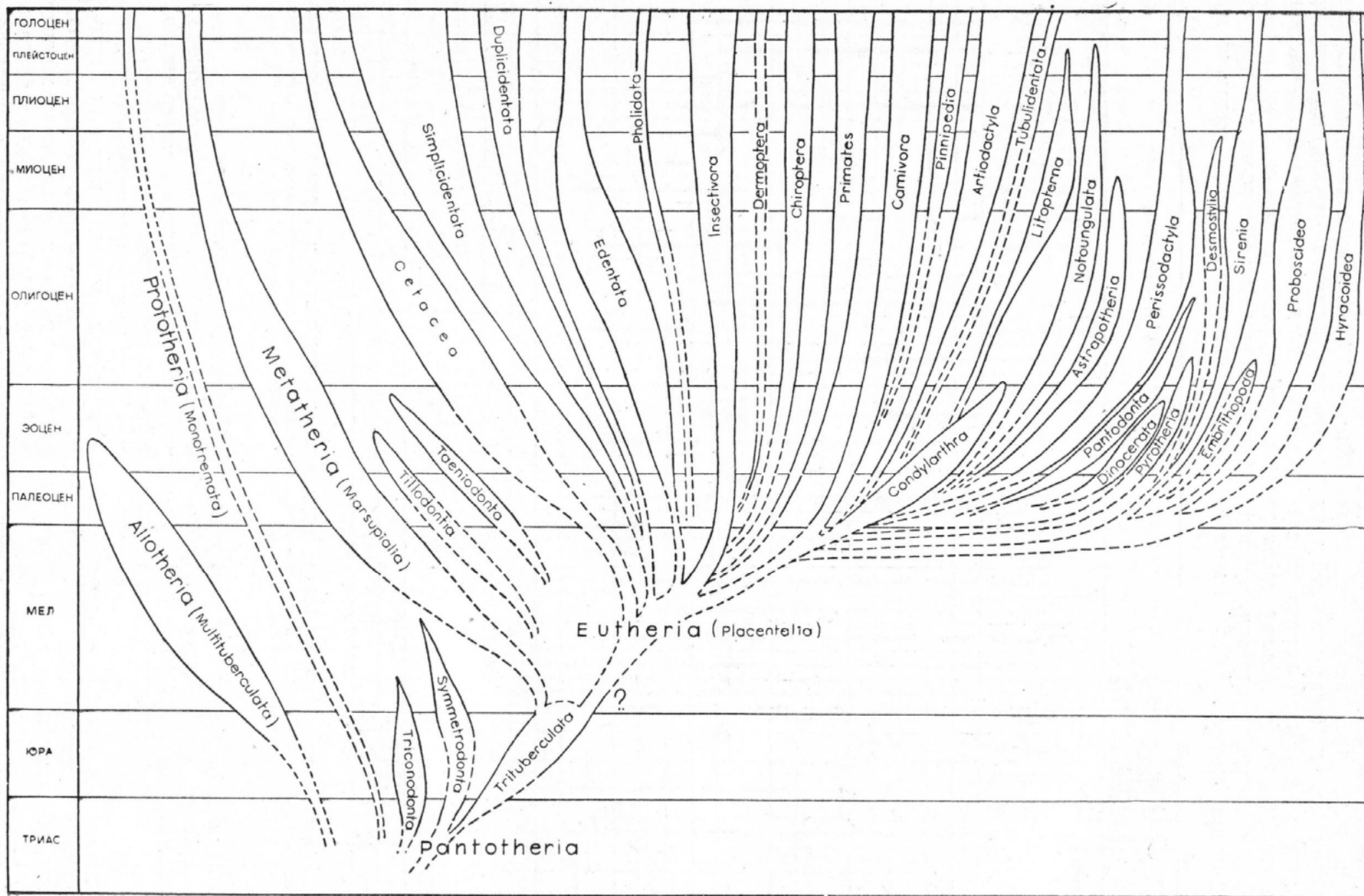


FIG. 1.—Phylogeny of the orders of mammals according to W. D. Matthew's views of about 1925. Numbers on the chart refer to comments in the accompanying text.





Громова, 1962

Рис. 9. Филогения млекопитающих

## Cretaceous Mammal Skulls from Mongolia.

By Dr. WILLIAM K. GREGORY and G. G. SIMPSON.

THE discovery of Cretaceous mammal skulls in Mongolia by the Central Asiatic Expedition of the American Museum of Natural History is an event of exceptional importance in vertebrate paleontology. The Cretaceous forerunners of the varied placental mammals of the Palaeocene and Eocene have hitherto been known only by inference. The studies of Cope, Osborn, Wortman, Matthew, and others upon the dentition and skeleton of Eocene mammals led to the view that the earliest insectivores and creodonts, taken collectively, were descendants of the most primitive group of placentals, for which the name Therioidia was proposed by Gregory in 1910.<sup>1</sup> It was



FIG. 1.—*Deltatheridium pretrituberculare*. Type palate and mandible. Diadockta formation, Mongolia. Twice natural size.

further inferred that the stem placentals of the Cretaceous would be more or less intermediate in character between the Jurassic "Amphitherium" and such early Eocene forms as *Palaeoryctes*, *Didelphodus*, and the *Oxyclaenidae*.<sup>2</sup>

In 1924 and 1925 the third Asiatic Expedition, under the leadership of Roy C. Andrews, explored the Djadockta formation of Mongolia, which yielded the famous dinosaur eggs and the superb series of Protoceratops skulls and skeletons. Here Mr. Walter Granger and his associates, after prolonged search, finally discovered no fewer than seven skulls or parts of skulls, some with associated lower jaws, of Cretaceous mammals. Of these the first specimen discovered in 1924 proved to be an allotherian or multituberculata, and has been described as the type of a new genus

and family of allotherians in the *American Museum Novitates*.<sup>3</sup>

The remaining specimens discovered in 1925 have been very skilfully extricated from the matrix by Mr. Albert Thomson and generously entrusted to us for description by Prof. Osborn and Dr. Matthew. Upon examination the new specimens appear to be quite distinct from all of the hitherto described jaws and teeth of Cretaceous mammals, including those in the Marsh collection of the Peabody Museum, Yale University, in the American Museum of Natural History, in the United States National Museum, and elsewhere.

All the known American Cretaceous mammals, except the allotherians, are marsupials, related rather closely to the existing opossums, so that as the evidence now stands the placental mammals did not invade north-western America until the Palaeocene. All the Mongolian Cretaceous mammals, on the contrary, again excepting the allotherians, so far appear to be placental.

So far back as Morrison (basal Cretaceous) times the pantotherian or trituberculata mammals were differentiated into several families. We are therefore not surprised to find that the Mongolian Cretaceous placentals show considerable diversity among themselves, so that even in the half-dozen specimens now available there are representatives of not less than four genera and two families, all apparently new to science.

The largest of these animals was somewhat bigger than a large house rat. Its skull and dentition were distinctly carnivorous in type, with enlarged laniary canines and sharp-bladed, narrow, triangular molars, approaching in these features the most primitive Eocene creodonts. Three genera are referred to this family, which is named by us the *Deltatheridiidae*.<sup>4</sup> The upper molar teeth are in what may be called a pre-trituberculata stage of evolution, since the para- and meta-cones are connate or not separated from each other and are median in position, in line with the primitive tips of the premolars, while the so-called 'protocones' are internal spurs from the base of the crown. The lower molars are trituberculata, with shearing paraconid-protoconid blades and narrow heels.

In the second family, called *Zalambdalestidae*, the very elongate snout suggests that of *Solenodon*, except that the lateral, not the median, incisors are enlarged. The cheek teeth, much worn in the type, strongly suggest those of zalambdodont insectivores, but a referred specimen indicates that the para- and meta-cones were partly separated and more buccal in position than in modern zalambdodonts, thus supporting Matthew's view<sup>5</sup> that the peculiar zalambdodont molars have been derived from a more normal trituberculata type. The lower molars are tuberculo-sectorial, with fairly broad heels. One pair of the anterior teeth, probably the median incisors, were much enlarged and procumbent, working between the enlarged upper incisors. The canines were small or absent, and

<sup>1</sup> Simpson, G. G., 1925. A Mesozoic Mammal Skull from Mongolia. *American Museum Novitates*, No. 210, Nov. 24, 1925.

<sup>2</sup> *American Museum Novitates*, October 1926. Cretaceous Mammal Skulls from Mongolia, by William K. Gregory and G. G. Simpson.

<sup>3</sup> Matthew, W. D., 1913. A Zalambdodont Insectivore from the Basal Eocene, *Bull. A.M.N.H.*, 32, Art. 27, pp. 307-314.

there were long spaces behind the enlarged front teeth. The skull avoids the specialisations of modern zalambdodonts, the nasals being separate, the zygomatic

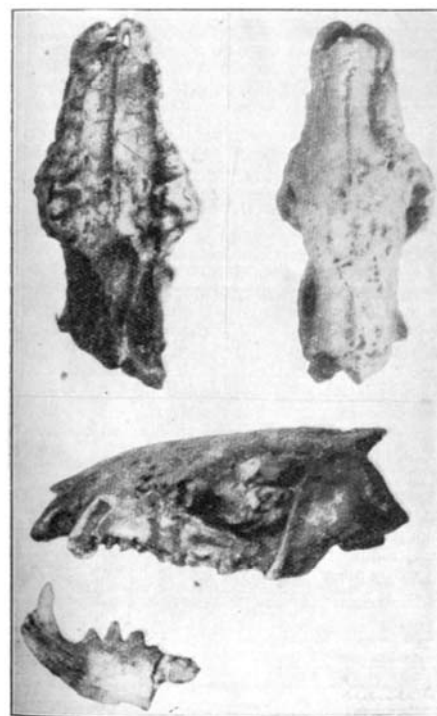


FIG. 2.—*Deltatheridium pretrituberculare*. Referred specimen. Twice natural size.

arches complete and the glenoids not displaced medially; orbital region less reduced, with prominent lacrymal rims; brain-case moderately expanded, not tubular. In these and other important details the *Zalambdalestidae* agreed with the *Deltatheridiidae*, and the characters of one of the new genera named *Hyotheridium* indicate that at that time the two families were still closely related, however much their presumed descendants, the placental carnivores and insectivores, diverged in later times.

Accordingly these specimens afford additional support for the following conclusions, based on much other evidence.

(1) The Palaeocene and Eocene insectivores and oxyclaenid creodonts, taken collectively, represent survivors of an earlier insectivore-creodont stock, examples of which have now been discovered in Mongolia.

(2) The discovery of these earliest of definite placentals in Mongolia furnishes some support to the hypothesis that Central Asia was the homeland of the placental radiation.

(3) The Mongolian Cretaceous mammals stand between the Jurassic pantotherians and the Palaeocene placentals, both in time and in dental structure, but are somewhat nearer to the latter.

(4) The Mongolian Cretaceous mammals favour the view of Wortman and others that the para- and meta-cones collectively of the mammalian trituberculata molar are in line with, and homologous with, the 'reptilian' tip of the premolar crowns, and that the so-called protocones represent internal basal spurs, correlated functionally with the differentiation of a heel or talonid, on the lower molars.

The following is a list of the mammalian fauna now known from the Djadockta formation:

## MULTITUBERULATA.

## Philodontidae.

*Djadochtherium matthewi* Simpson.

## INSECTIVORA.

## Deltatheridiidae.

*Deltatheridium pretrituberculare* G. and S.

*Deltatheroides cretacicus* G. and S.

*Hyotheridium dobsoni* G. and S.

## Zalambdalestidae.

*Zalambdalestes lechei* G. and S.

Of these all are known from at least part of the skull, including the palate, and all but *Deltatheroides* also

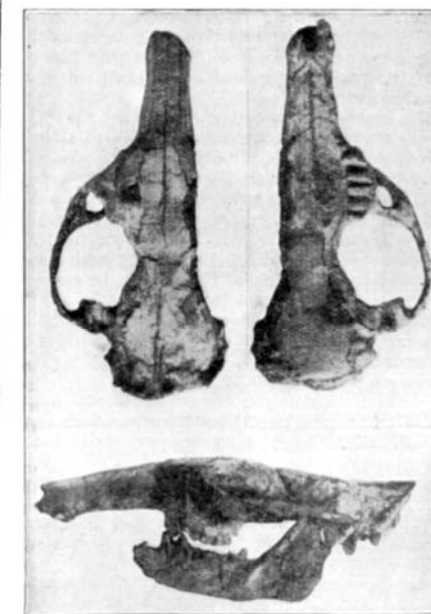


FIG. 3.—*Zalambdalestes lechei*. Type. Twice natural size.

from associated lower jaws. *Zalambdalestes* is incomparably the best known of all Mesozoic mammals, every main part of the skull and jaws being known, although some features are still rather obscure.

<sup>1</sup> The Orders of Mammals, *Bull. A.M.N.H.*, 27, p. 464; see also pp. 304-307, 462, 468.

<sup>2</sup> "The Origin and Evolution of the Human Dentition." Baltimore, 1922, pp. 99-107, 512.



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## CRETACEOUS MAMMAL SKULLS FROM MONGOLIA<sup>1</sup>

BY WILLIAM K. GREGORY AND G. G. SIMPSON

The discovery of Cretaceous mammal skulls in Mongolia by the Central Asiatic Expedition of the American Museum of Natural History is an event of exceptional importance in vertebrate palæontology. The Cretaceous forerunners of the varied placental mammals of the Paleocene and Eocene have hitherto been known only by inference. The studies of Cope, Osborn, Wortman, Matthew and others upon the dentition and skeleton of Eocene mammals led to the view that the earliest insectivores and creodonts, taken collectively, were descendants of the most primitive group of placentals, for which the name Therictioidea was proposed by Gregory in 1910.<sup>2</sup> It was further inferred that the stem placentals of the Cretaceous would be more or less intermediate in character between the Jurassic *Amphitherium* and such early Eocene forms as *Palæoryctes*, *Didelphodus* and the Oxyclænidae.<sup>3</sup>

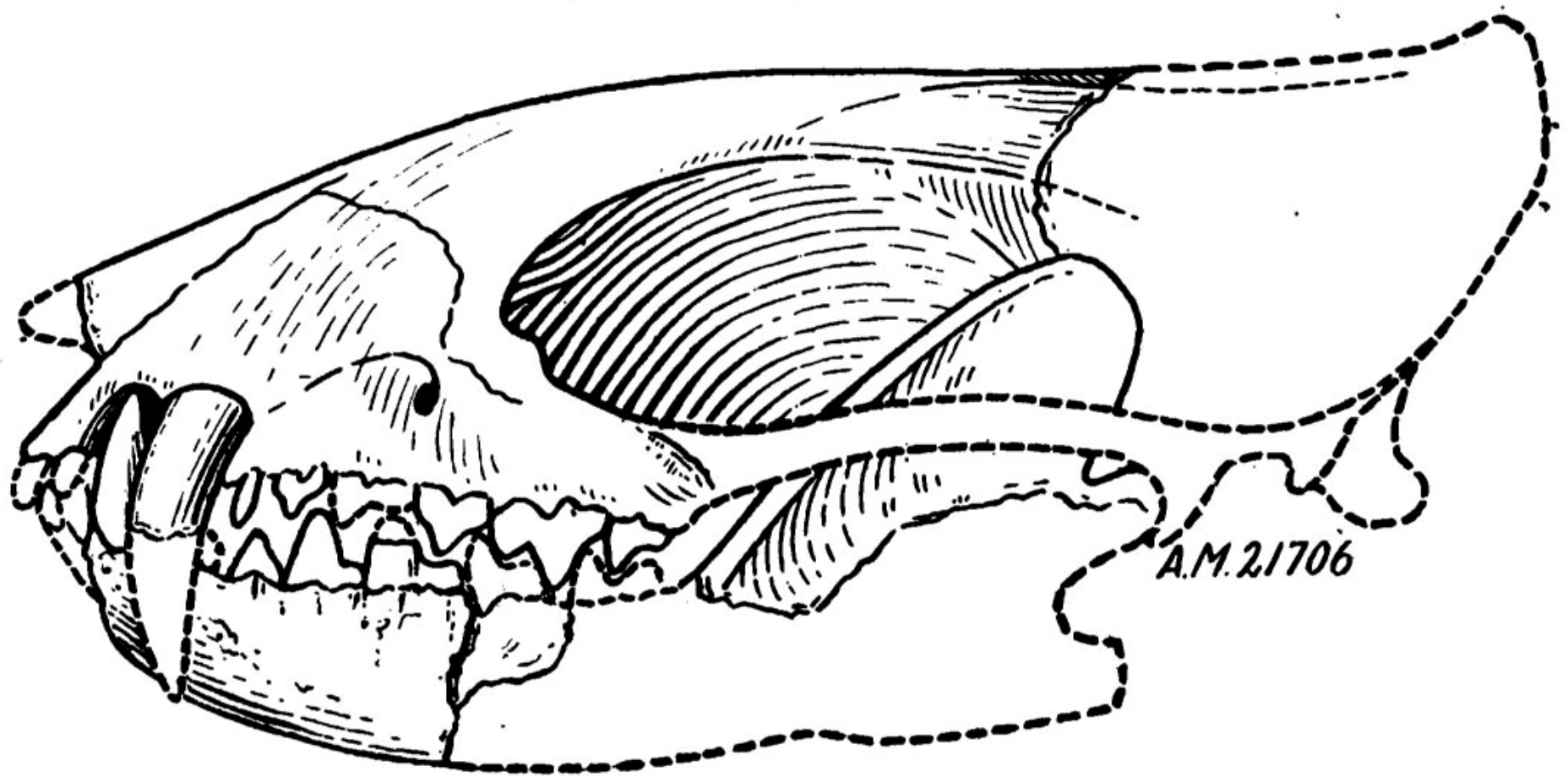


Fig. 8. *Deltatheridium pretrituberculare*. Restoration based on referred skull.  $\times \frac{1}{2}$ .



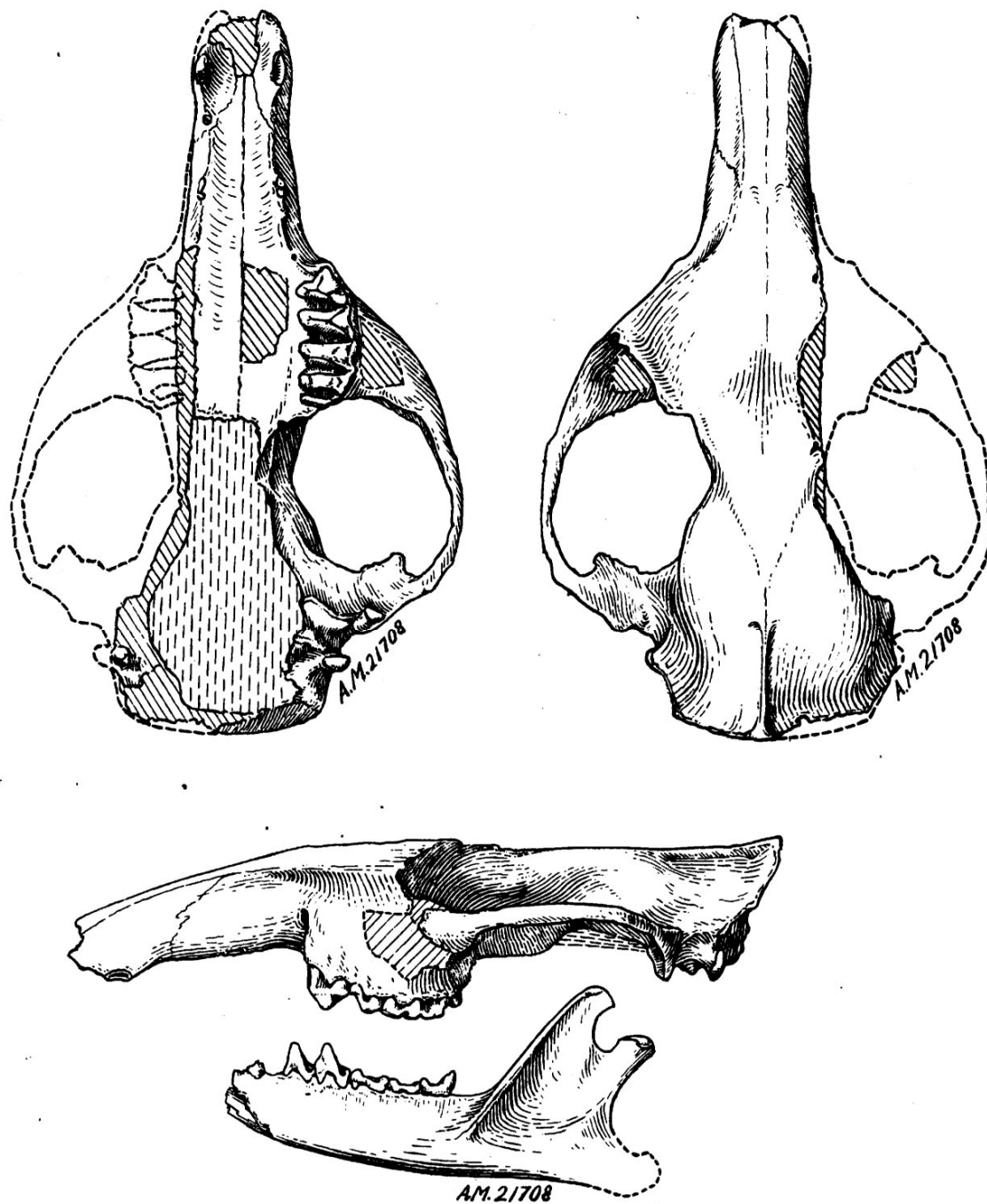


Fig. 14. *Zalambdalestes lechei*. Type.  $\times \frac{2}{1}$ .

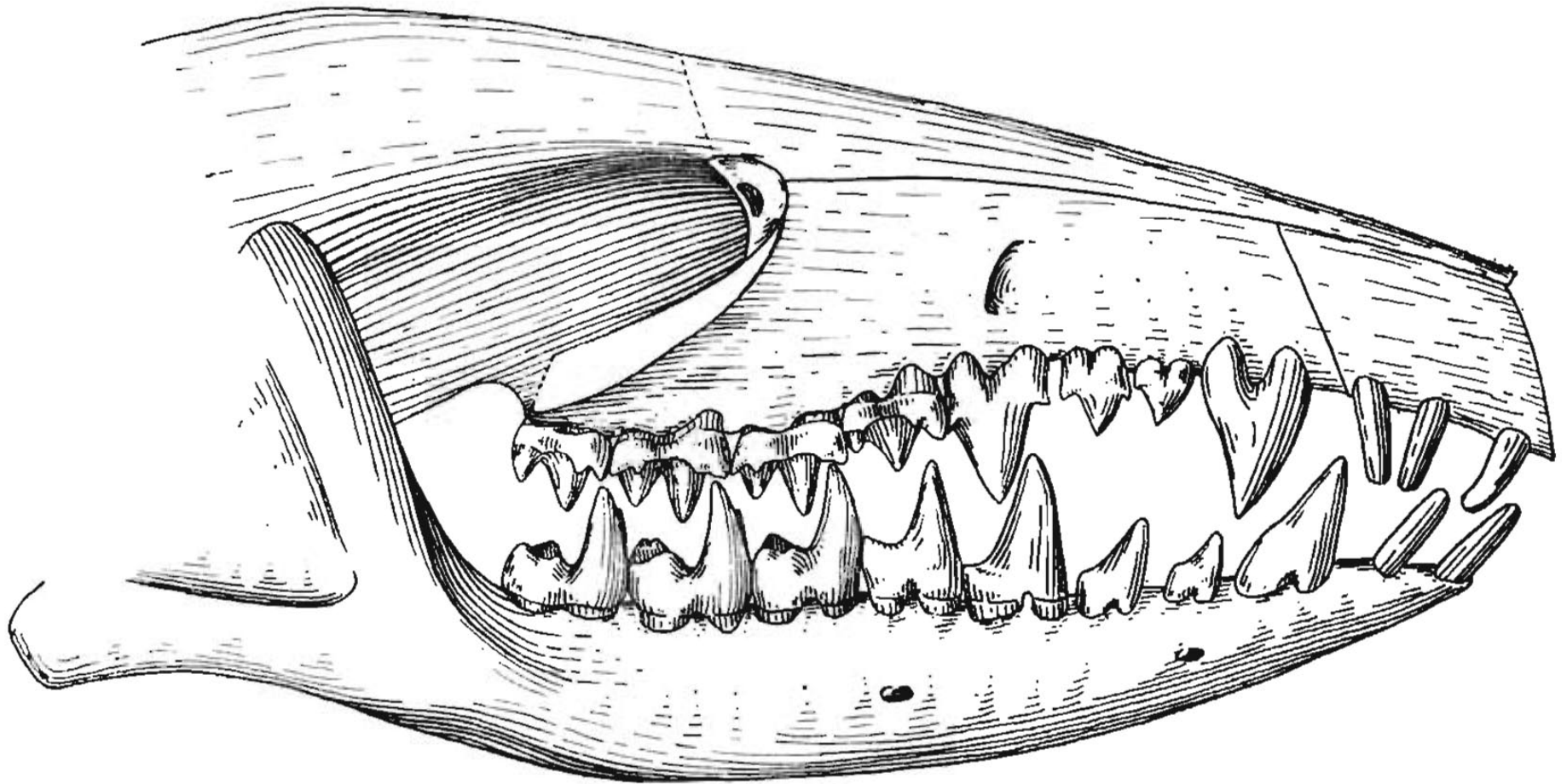


Fig. 3

*Kennalestes gobiensis* n. sp., schematic reconstruction of the anterior part of the skull in lateral view;  $\times 6$ .



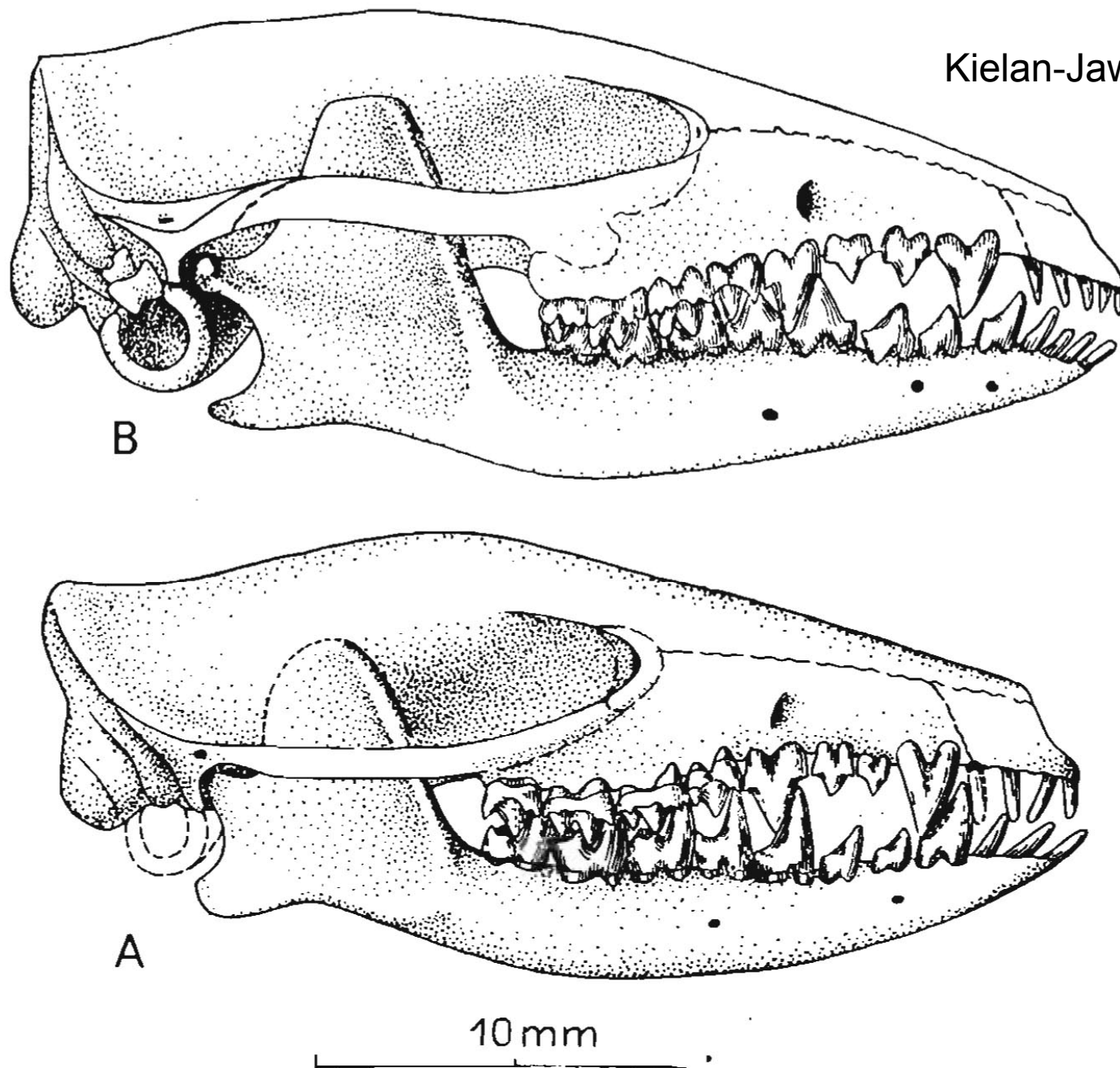


Fig. 1

Skulls of: A — *Kennalestes gobiensis*, B — *Asioryctes nemegetensis*, reconstructed.

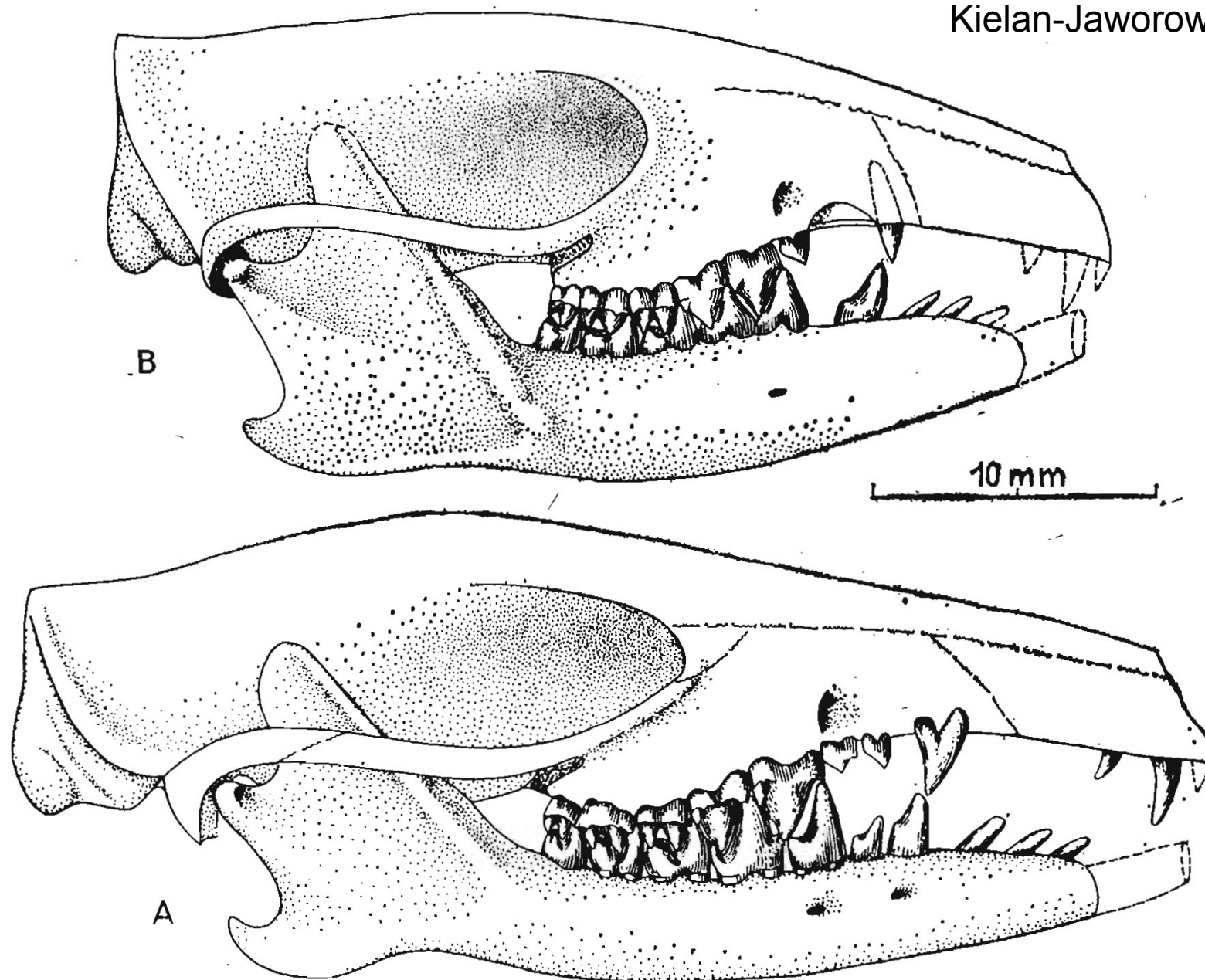
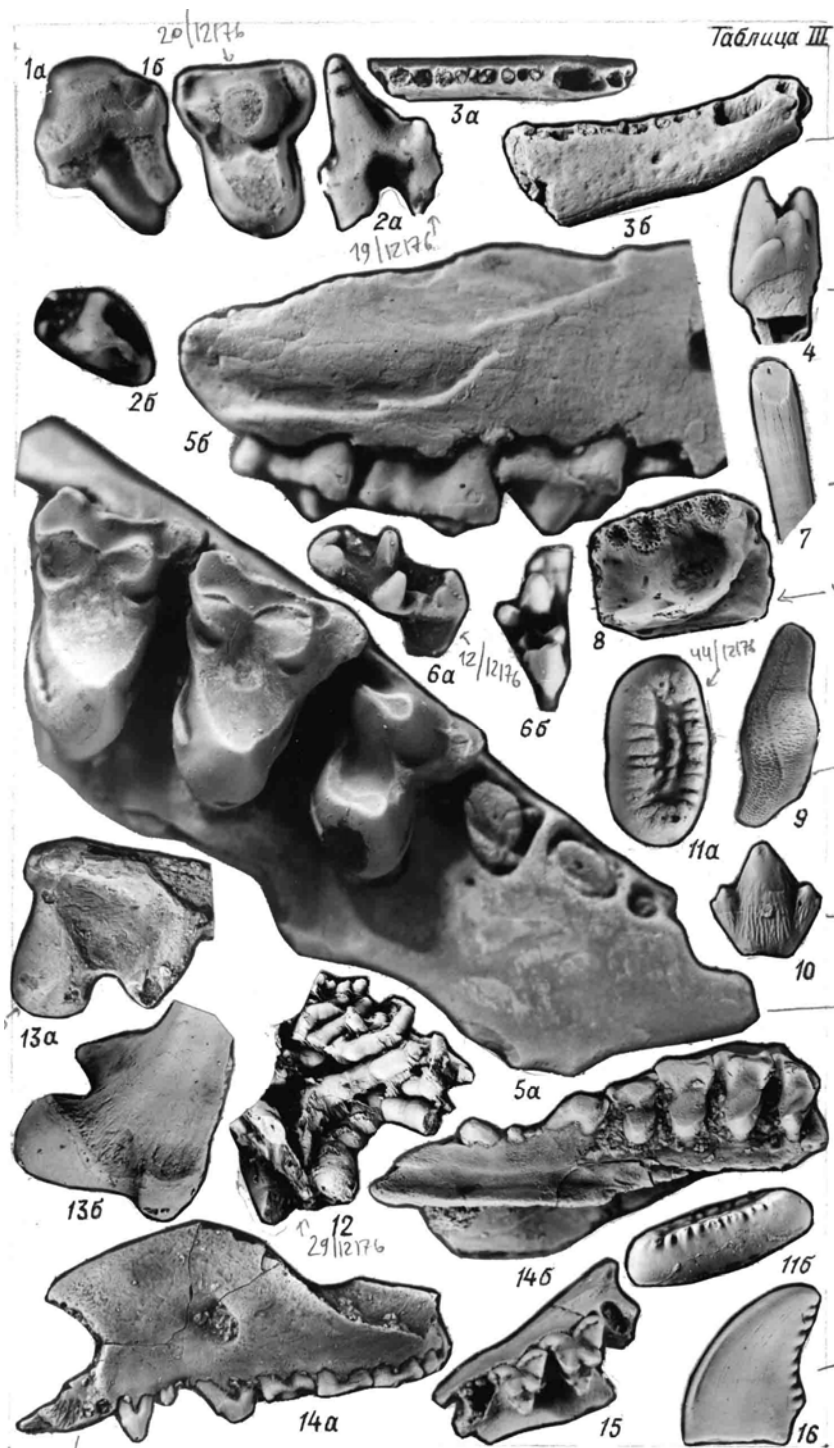
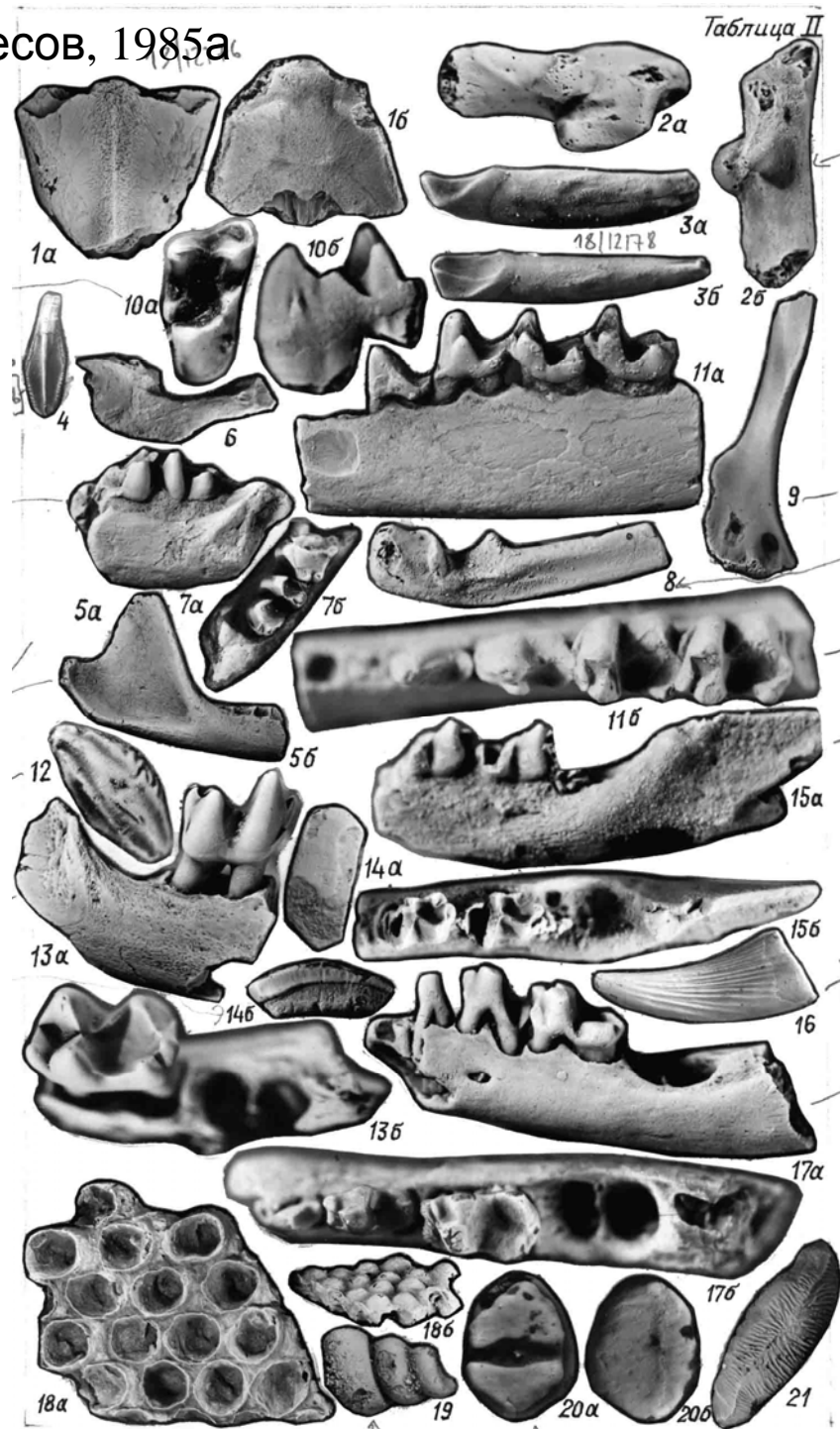
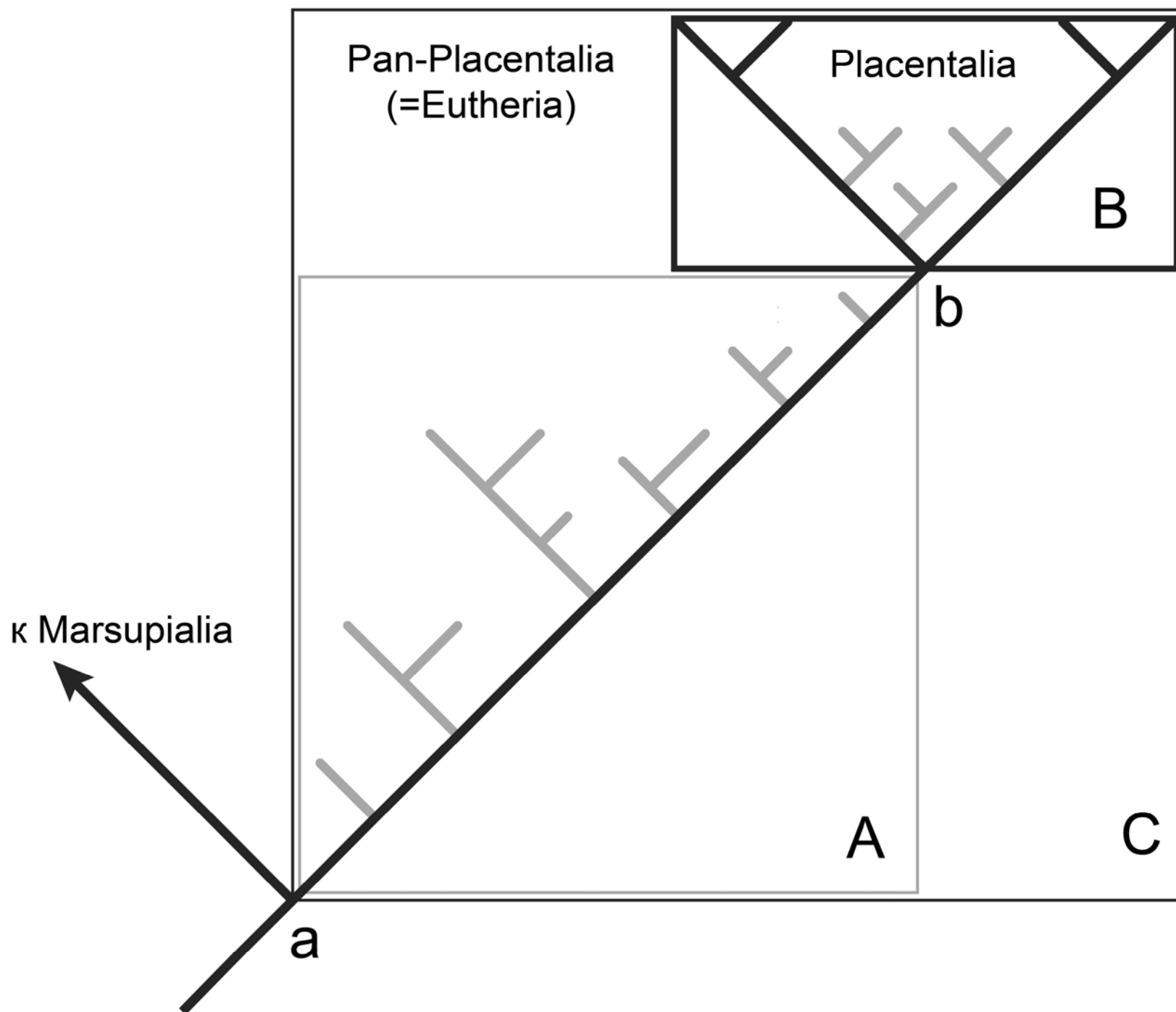


Fig. 2  
Skulls of: A — *Zalambdalestes lechei*, B — *Barunlestes butleri*, reconstructed.



Несов, 1985а.





# Fossil Evidence for a Late Cretaceous Origin of "Hoofed" Mammals

J. David Archibald

Seventeen of eighteen orders of living placental mammals are not known before 65 million years ago. The monophyly of each order is well established, but interrelations have been less certain. A superordinal grouping of up to seven extant orders plus a variety of extinct orders, all included within Ungulata ("hoofed" mammals), can be linked to Late Cretaceous mammals from the 85-million-year-old Bissekty Formation, Uzbekistan (and, less certainly, North America and Europe), thus pushing the origin of this major clade back by 20 million years. Ungulatomorphs are not closely related to primates, rodents, or rabbits.

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Whether they include one (aardvarks) or 1750 (rodents) extant species, orders are the most inclusive groupings for which there is certainty of monophyly within Mammalia. The monophyly of superordinal taxa such as Ungulata has been much less certain (1). The mammalian division Ungulata is usually argued to include archaic ungulates ("Condylarthra") (2), South American native ungulates (3), Desmostylia, and Embrithopoda, and the extant Artiodactyla, Cetacea, Hyracoidea, Perissodactyla, Proboscidea, Sirenia, and questionably Tubulidentata, but it excludes the extinct Pantodonta, Tillodontia, and Dinocerata (4). None of these orders had been known from before the earliest Tertiary [65 million years ago (Ma)] except for questionable Late Cretaceous occurrences in North and South America (5). Fossils recovered from the 85-million-year-old Bissekty Formation, Uzbekistan (6), however, appear to have ungulate affinities (7, 8) on the basis of dental morphology that seems to mark the beginnings of herbivory in placental mammals. These fossils, plus possibly others from North America and Europe, comprise

the family "Zhelestidae" (9). A review of the biostratigraphy of the Bissekty Formation (10) corroborates the ~85-million-year age estimate and also suggests that various of its named and unnamed mammalian species are best referred to "Zhelestidae." In this report, I present the results of a species-level phylogenetic analysis of better known, Late Cretaceous placental mammals, including the "zhelestids," plus Ungulata. Trends in increased herbivory among "zhelestids" compared to other Late Cretaceous placental mammals are also discussed.

The phylogenetic analysis (Fig. 1) of all species of better known Late Cretaceous placental mammals (Table 1) shows that "zhelestids" are monophyletic relative to other Late Cretaceous eutherians. The upper and lower dentitions of the mid-sized Asian "zhelestids" cannot at this time be matched; thus, the study was limited to the better known upper dentition. As shown in Fig. 1, the analysis includes Tertiary Ungulata represented by *Protungulatum* (or *Oxyprimus*) as an exemplar. Because some "zhelestids" have a more recent common ancestry with Ungulata than with other "zhelestids," "Zhelestidae" is paraphyletic (and thus the quotation marks). With Ungulata, however, "Zhelestidae" forms a clade

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relative to all Late Cretaceous mammals that is here named Ungulatomorpha (11). "Zhelestids" are of particular interest because they evolved character states leading toward herbivory, which are even more strongly developed within Ungulata. The only other extant orders of placental mammals that show similar overall tendencies toward herbivory are rodents, rab-

bbits, and primates. Rodents and rabbits are currently thought to belong to a superordinal clade, Anagalida, which also includes elephant shrews and the Late Cretaceous Asian genera *Zalambdalestes* and *Barunlestes*; this superordinal clade is not closely related to ungulates (12). The analysis in Fig. 1 supports the view that the anagalidans *Zalambdalestes* and *Barun-*

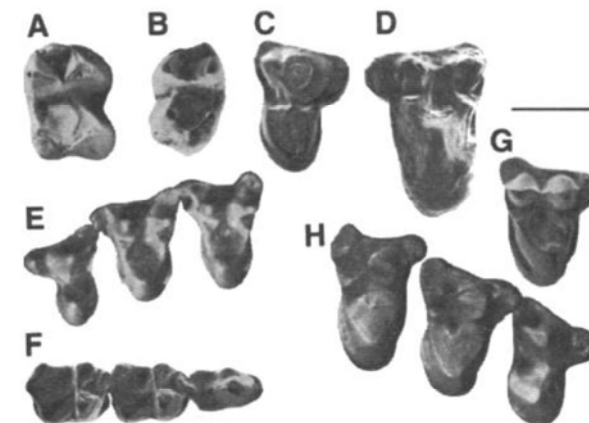
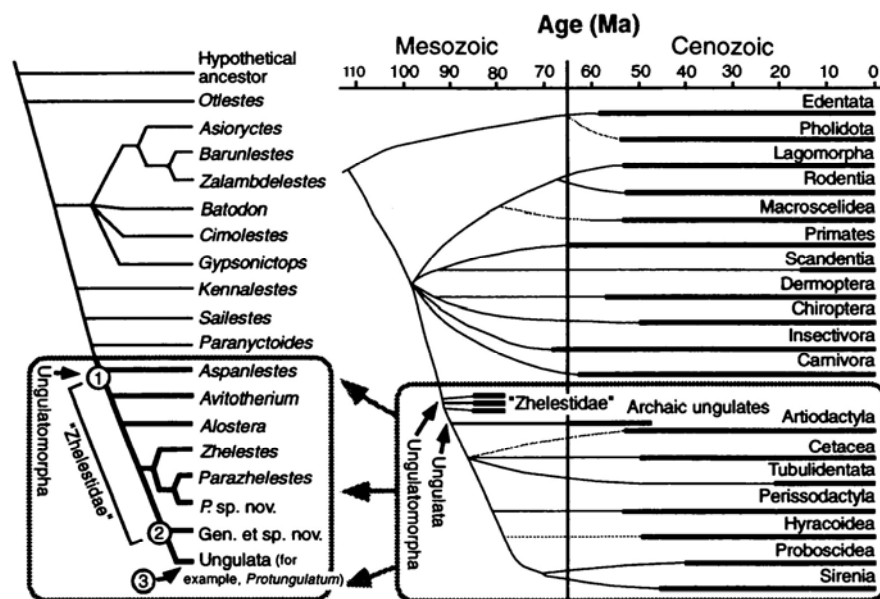
*lestes* are not closely related to ungulates. The earliest known primatomorphs (13) such as *Purgatorius* retain primitive features, especially in their lower dentition (such as less anteroposteriorly compressed trigonid than in "zhelestids"), that argue against membership in Ungulatomorpha.

Some of the 85-million-year-old "zhelestids" resemble the 65-million-year-old archaic ungulates (so-called condylarths). For example, the largest "zhelestid," gen. et sp. nov. (Fig. 2, A through D, and Fig. 3D), at first could be mistaken for an archaic ungu-

**Fig. 1.** Phylogenetic tree

of placental mammals [after (1)] compared to a cladistic analysis (22) of ungulatomorphs ("zhelestids" and Ungulata) including the 10 Late Cretaceous eutherians listed in Table 1. The more important morphological shifts (some of which are found as homoplasies in other taxa) are as follows: Node 1, Ungulatomorpha: stylar shelf narrow, ultimate pre-molar ( $P^5$ ) with metacone or swelling (Fig. 2, C, E, and H), pre- and postcingula reach or extend below conules, and two cus-

pules in the parastylar region. Node 2, Gen. et sp. nov. (Fig. 2, C and D) plus Ungulata: substantial anteroposterior expansion of protocone, substantial labial shift of protocone, and molar crown shape at least subrectangular. Node 3, Ungulata (*Protungulatum donnae* as exemplar): molar conules with little or no internal wings, metaculum formed by postmetaconular crista continuing on to metastylar region, parastylar region reduced with one cusp, four or fewer premolars [sirenians have five premolars (23)], upper molars rectangular in occlusal view, parastylar groove (and lobe) reduced, and conules closer to protocone than to midposition of the crown. Four other Ungulata autapomorphies have been noted (2): more bunodont, lower crowned teeth; molar trigonids anteroposteriorly shortened;  $M_3$  with a large posteriorly projecting hypoconulid; and astragalus with a shorter, robust head. Of these, the first two are in all ungulatomorphs, and the second is hinted at in the  $M_3$  tentatively referred to the new genus and species (Fig. 2B). The fourth was not evaluated.



**Fig. 2.** Occlusal views: cf. gen. et sp. nov. (A) right  $M_2$  (Chernyshev's Central Museum of Geological Exploration of Saint Petersburg or CC-MGE 17/12953), (B) left  $M_3$  (CCMGE 16/12953), (C) right  $P^5$  (CCMGE 35/12176); gen. et sp. nov. (D) left  $M^2$  (CCMGE 2/12455, type); *Aspanlestes aptap* (E) left  $P^5$  and  $M^{1-2}$  (CCMGE 1/12455, cast of type of *Zhelestes bezelgen*), (F) right  $P^5$  and  $M^{1-2}$  (CCMGE 4/12176, type); *Parazhelestes* sp. nov. (G) right  $M^1$  (CCMGE 11/12953, type), (H)  $P^5$  and  $M^{1-2}$  (CCMGE 11/12176, cast). Scale bar, 2 mm.

# 18 признаков

**Table 1.** Matrix of taxon and the characters and states defined in (24), which were used in the phylogenetic analysis in Fig. 1.

Species	Character																	
	a	b	c	d	e	f	g	h	i	j	k	l	m	n	o	p	q	r
Hypothetical ancestor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Late Cretaceous eutherians represented by upper teeth																		
<i>Asioryctes nemegetensis</i>	0	0	1*	0	0	0	1	0	?	1	0	0	0	0	0	0	0	0
<i>Batodon tenuis</i>	0	0	0	0	0	0	1	0	0	1	0	1	1	?	0	0	0	0
<i>Barunlestes butleri</i>	0	0	1	0	1?	0?	0	0	0	1†	0	0	0,1	1	0	0	0	0
<i>Cimolestes</i> spp.	0	0	0	0	0	0	0,1	0	0	1	0	0,1	0,1	0	0	0	0	0
<i>Gypsonictops</i> spp.	0	0	0	0	1	0	1	0?	1	0,1	0	1	0,1	0	0	0	0	0
<i>Kennalestes gobiensis</i>	0	0	0	0	0	1	1	0	0,1	0,1	0	1,2	0	0	0	0	0	0
<i>Paranyctoides maleficus</i>	1,2	0	0	0	0	0	1	1	0	?	1	1,2	0	0	0	1	0	0
<i>Otlestes meiman</i>	0	0	0,1	0	0	0?	0	0	?	0	0	0	0	0?	0	1	0	0
<i>Sailestes quadrans</i>	1	0	0	0	0	1	1	0?	?	?	0	2	1	?	0	1	1	0
<i>Zalambdalestes lechei</i>	0	0	1?	0	0,1	0	0	0	1?	1	0	0	0	1	0	1	0	0
Ungulatomorphs																		
<i>Alostera</i>																		
<i>saskatchewanensis</i>	1	0	0	1	1	0	2	1	1	?	1	2	2	?	1	1	1	0
<i>Avitotherium utahensis</i>	1	0	0	0	1	1	1,2	1	1	?	1	2	0,1	?	0	1	1	0
<i>Aspanlestes aptap</i>	1	0	0	0	1	1	2	1	1	0?	1	2	0,1	0	0	1	0	0
<i>Zhelestes temirkazyk</i>	1	0?	0	0	1	1	2?	1?	1	0	1	3	1	0	0	1?	2?	0
<i>Parazhelestes robustus</i>	2	1	0	0	1	1	2	1	1	0?	1	3	1	1	0	1	2	1
<i>Parazhelestes</i> sp. nov.	1,2	1	0	0	1	1	2	1	0,1	0?	1	2	1	?	0	1	2	0
Gen. et sp. nov.	3	2	0	0	1	1	2	1?	1?	?	2	3	2	?	0	1	2	0
Ungulata (for example, <i>Protungulatum</i> )	3	2	1	1	1	0	2	1	0,1	1**	3	3	1,2	0	1	1	2	1

## UNGULATE-LIKE MAMMALS FROM THE LATE CRETACEOUS OF UZBEKISTAN AND A PHYLOGENETIC ANALYSIS OF UNGULATOMORPHA

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### ABSTRACT

(Supergrandorder) Ungulatomorpha Archibald, 1996b includes (grandorder) Ungulata and (family) "Zhelestidae." "Zhelestidae" Nesson, 1985a is best known from the Upper Cretaceous (upper Turonian–Coniacian) Bissekty Formation, Dzhyrakuduk, Kyzylkum Desert, Uzbekistan. Asian taxa (lower Turonian–Coniacian) include: *Kumsuperus avus* Nesson, 1984b, nomen dubium; *Zhelestes temirkazyk* Nesson, 1985a; *Sorlestes budan* Nesson, 1985a; *Aspanlestes aptap* Nesson, 1985a; *Sorlestes kara* Nesson, 1993; *Parazhelestes robustus* Nesson, 1993; *P. minor*, n. sp.; and *Eoungulatum kudukensis*, n. gen. and sp. North America taxa (mid-Campanian–early Paleocene) include: *Gallolestes pachymandibularis* Lillegraven, 1976; *G. agujaensis* Cifelli, 1994; *Alostera saskatchewanensis* Fox, 1989; and *Avitotherium utahensis* Cifelli, 1990. European taxa (Campanian–Maastrich-

tian) include: *Lainodon orueetxebarriai* Gheerbrant and Astibia, 1994; *Labes quintanillensis* Sigé in Pol et al., 1992; and *Labes garimondi* Sigé in Pol et al., 1992. An  $M_1$  fragment (late Santonian) from Vinton Bluff, Mississippi, U.S.A., is questionably referred to Ungulatomorpha. *Wania chowi* Wang, 1995 is not a zhelestid but may have anagalidan affinities. "Zhelestids" occur at localities in wetter, low coastal plain settings in western Asia and North America, but are absent from contemporaneous Late Cretaceous sites in higher, drier settings in Mongolia. Diverse Asian "zhelestids" with apomorphies foreshadowing much later archaic ungulates suggest that archaic ungulates reached North America near the end of the Cretaceous via Beringia. A phylogenetic analysis (18 characters of the upper dentition) strongly supports monophyly of Ungulatomorpha, which includes "Zhelestidae" and Ungulata, as represented by the exemplar *Protungulatum donnae*. A close relationship among rodents (represented by *Tribosphenomys*), primatomorphs (represented by *Purgatorius*), and ungulatomorphs is possible, but the resemblances are equally attributable to convergence.

<sup>1</sup> Lev A. Nesson died on October 1, 1995, during the final stages of the preparation of the review draft of the manuscript.

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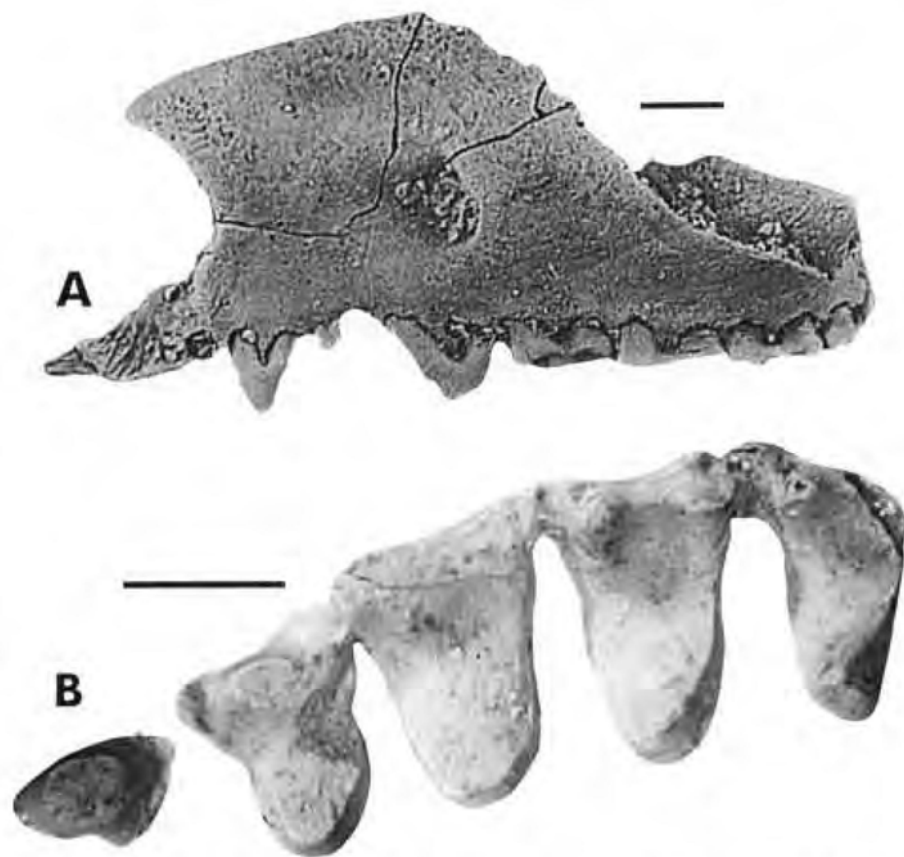


Fig. 9.—*Zhelestes temirkazyk* Nessov, 1985a, CCMGE 10/12176, holotype left maxilla preserving part of alveolus for large, single-rooted  $C^1$ ; alveolus for small, single-rooted  $P^1$ ; crown of  $P^2$ ; roots of small  $P^3$ ; crowns of  $P^4$ – $M^3$  in labial (A) and occlusal (B) views. Scales = 2 mm.

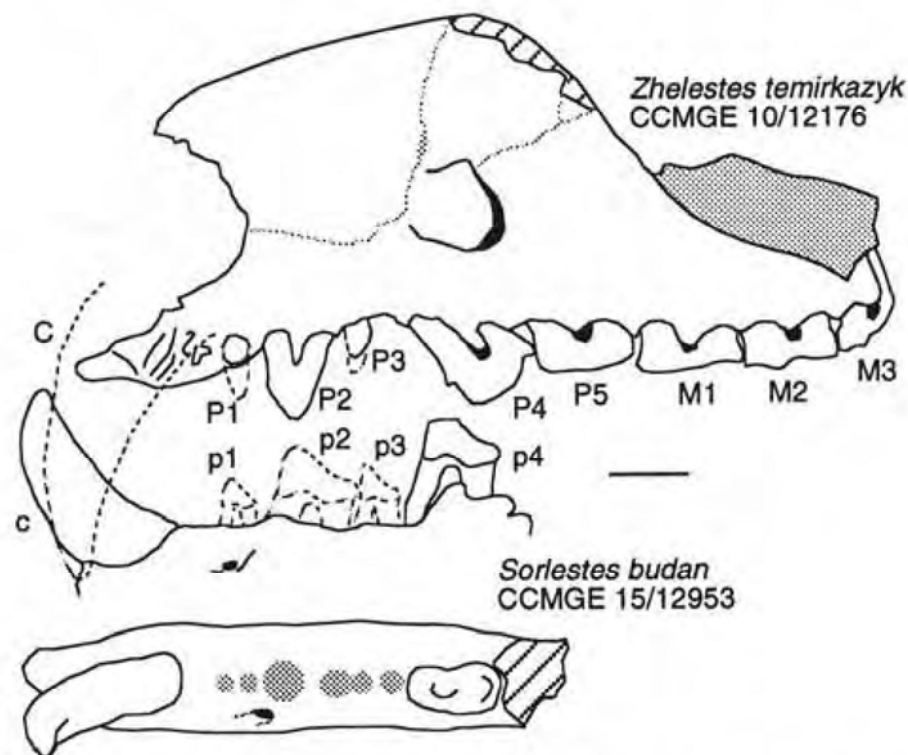
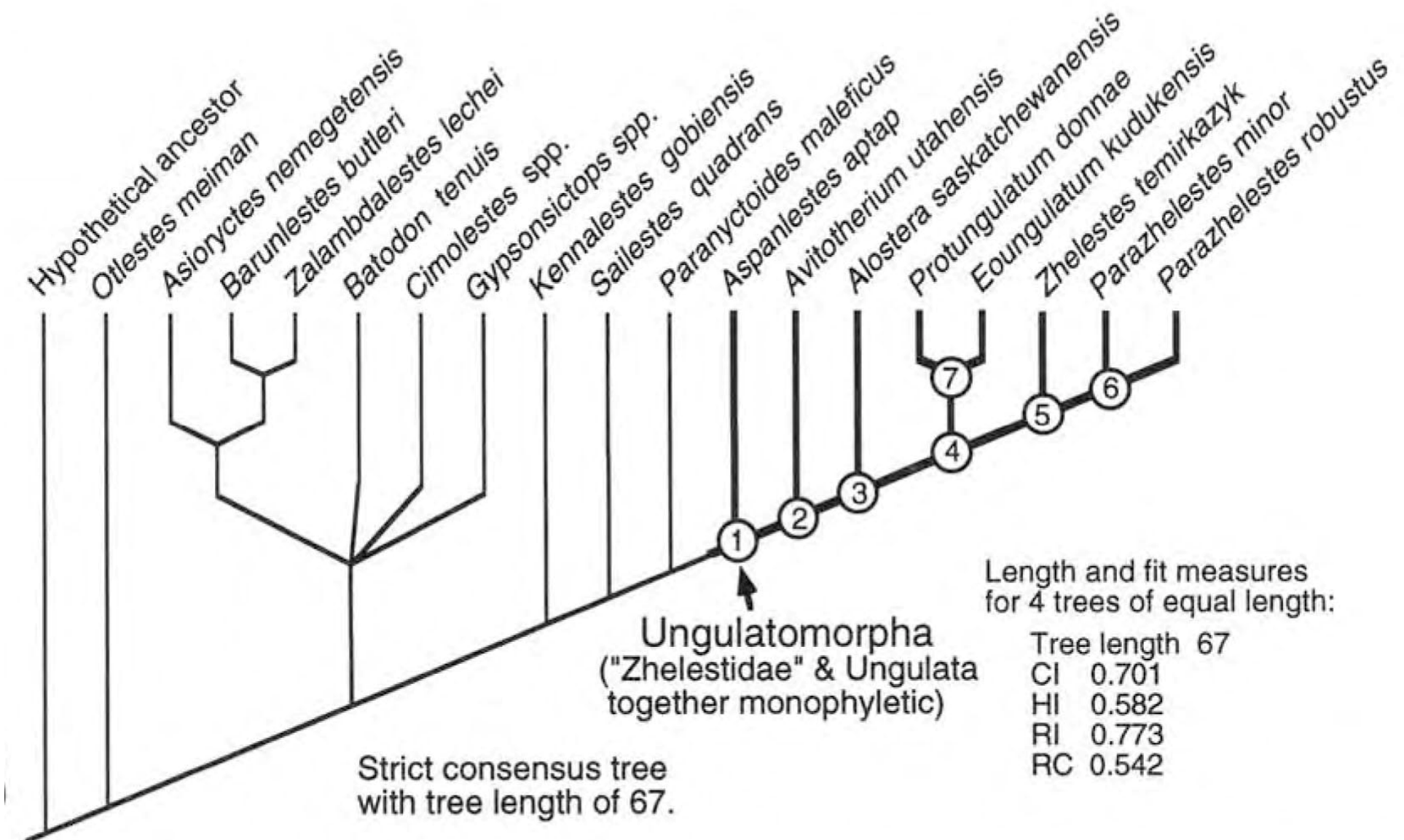


Fig. 10.—Left labial view of maxilla of *Zhelestes temirkazyk* shown in Figure 9 compared to dentary of *Sorlestes budan* shown in Figure 19D–F. Lower view is occlusal view of dentary showing alveoli. Reconstructed teeth are shown by dotted lines. Diagonal lines are broken areas. Stippling on dentary shows alveoli. Stippling on maxilla shows suture with jugal. Note the evidence for five premolars in maxilla, and relative size of premolars,  $P^5 > P^4 > P^2 > P^3 > P^1$ . Scale = 2 mm. See text for discussion.



18 признаков

Table 3.—*Characters and character states of the upper dentition in a hypothetical ancestor, Late Cretaceous eutherians, the primatomorph Purgatorius, the rodent Tribosphenomys, and ungulatormorphs ("zhelestids" plus Ungulata, represented by Protungulatum donnae). Primitive or ancestral state = 0, derived states = 1–3. See Figures 20–23.*

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- 1) Degree of anteroposterior expansion of protocone: none (0); slight (1); moderate (2); substantial (3).
  - 2) Degree of labial shift of protocone: none (0); moderate (1); substantial (2).
  - 3) Postparaconular and premetaconular cristae: strong and wing-like (0); weak or absent (1).
  - 4) Metacingulum: formed only by the postmetaconule crista and terminates dorsal to postmetacrista, which is continuous with the metastylar lobe (0); formed by the postmetaconule crista continuing onto the metastylar lobe (1).
  - 5) Styler shelf: wide (0); narrow (1).
  - 6) Number of cuspsules in parastylar region: one (0); two (1).
  - 7) Pre- and postcingula: absent or poorly developed (0); present but do not reach or extend below the conules (1); present and reach or extend below the conules (2).
  - 8) Height and size of paracone and metacone: paracone higher and larger (0); cusps of similar height and size (1).
  - 9) Metacone or metaconal swelling on P<sup>5</sup> (or ultimate upper premolar): absent (0); present (1).
  - 10) Number of premolars: five (0); four or fewer (1).
  - 11) Shape of molar crown in occlusal view: triangular (0); trapezoidal (1); subrectangular (2); rectangular (3).
  - 12) Constriction of crown through conular region with or without cingula present: no constriction, no cingula (0); marked constriction with cingula (1); slight constriction with cingula (2); no constriction with cingula (3).
  - 13) Ectoflexus: deep (0); shallow (1); none (2).
  - 14) M<sup>3</sup> linguolabial width relative to other molars: not markedly narrowed (0); markedly narrowed (1).
  - 15) Parastylar groove: well developed (0); very reduced or absent (1).
  - 16) Base of paracone and metacone: merged (0); separate (1).
  - 17) Distance between paracone or metacone and protocone relative to total anterior or posterior width, respectively: between 45–55% of crown width (0); more than 55% of crown width (1); less than 45% of crown width (2).
  - 18) Position of conules (especially paraconule) relative to paracone and metacone versus protocone: conules closer to midposition (0); conules closer to protocone than to the midposition (1).
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# Late Cretaceous relatives of rabbits, rodents, and other extant eutherian mammals

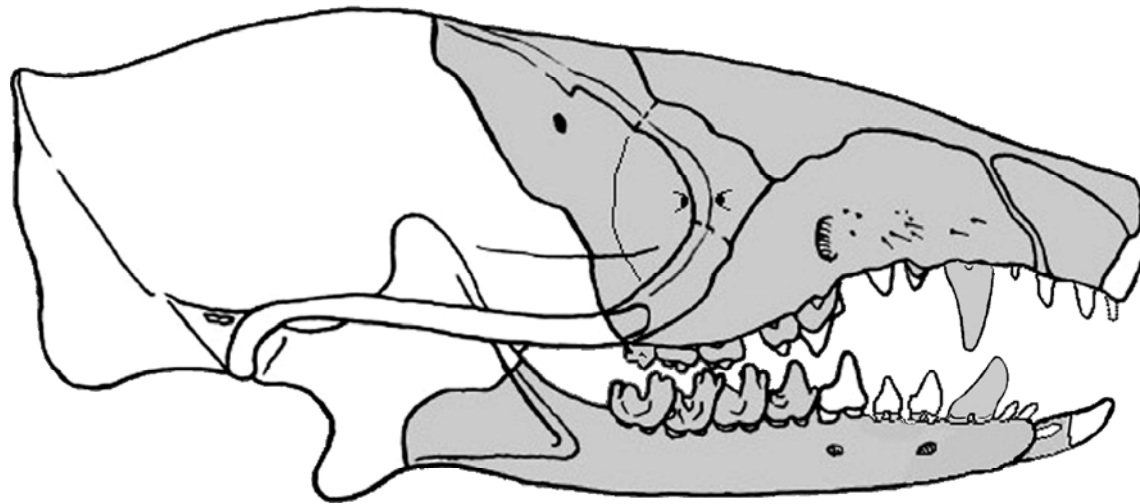
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Extant eutherian mammals and their most recent common ancestor constitute the crown group Placentalia. This taxon, plus all extinct taxa that share a more recent common ancestor with placentals than they do with Metatheria (including marsupials), constitute Eutheria<sup>1</sup>. The oldest well documented eutherian-dominated fauna in the world is Dzharakuduk, Uzbekistan<sup>2</sup>. Among eutherians that it yields is *Kulbeckia*, an 85–90-Myr-old member of Zalambdalestidae (a family of Late Cretaceous Asian eutherians)<sup>3</sup>. This extends Zalambdalestidae back by some 10 million years from sites in the Gobi Desert, Mongolia<sup>4</sup>. A phylogenetic analysis of well described Late Cretaceous eutherians strongly supports Zalambdalestidae, less strongly supports ‘Zhelestidae’ (a Late Cretaceous clade related to Tertiary ungulates), but does not support Asioryctitheria (a group of Late Cretaceous Asian eutherians). A second analysis incorporating placentals from clades that include rodents (*Tribosphenomys*), lagomorphs (*Mimotona*) and archaic ungulates (*Protungulatum* and *Oxyprimus*) strongly supports Zalambdalestidae in a clade with Glires (rabbits, rodents and extinct relatives) and less strongly ‘Zhelestidae’ within a clade that includes archaic ungulates (‘condylarths’). This argues that some Late Cretaceous eutherians belong within the crown group Placentalia. The ages of these taxa are in line with molecularly based estimates of 64–104 Myr ago (median 84 Myr ago) for the superordinal diversification of some placentals<sup>5</sup>, but provide no support for a Late Cretaceous diversification of extant placental orders.

Euarchontoglires?  
Zalambdalestidae  
*Kulbeckia kulbecke*  
(composite)



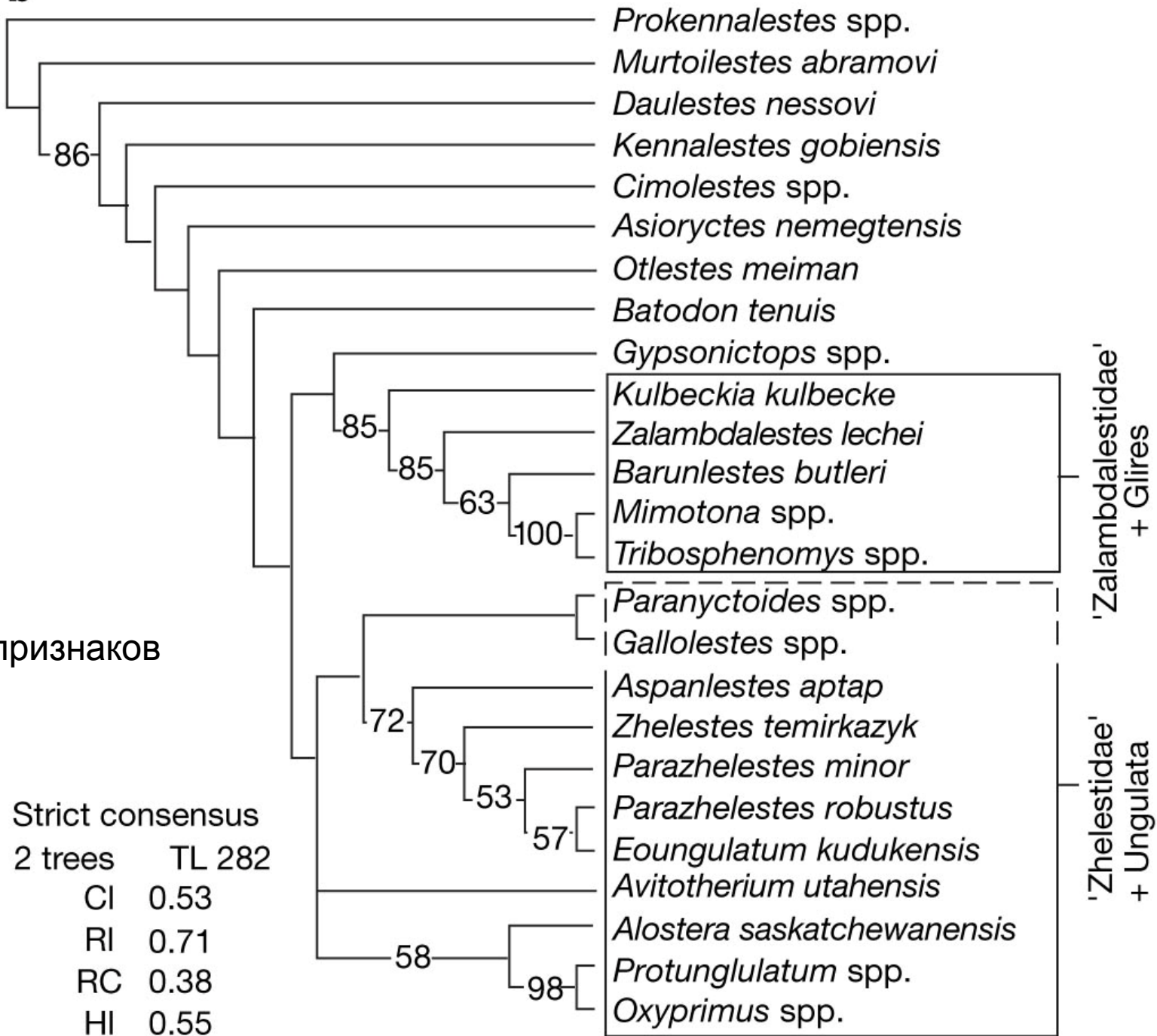
2 mm

Archibald & Averianov 2003

**b**

70 признаков

Strict consensus  
 2 trees TL 282  
 CI 0.53  
 RI 0.71  
 RC 0.38  
 HI 0.55





# **Quantitative Analysis of the Timing of the Origin and Diversification of Extant Placental Orders**

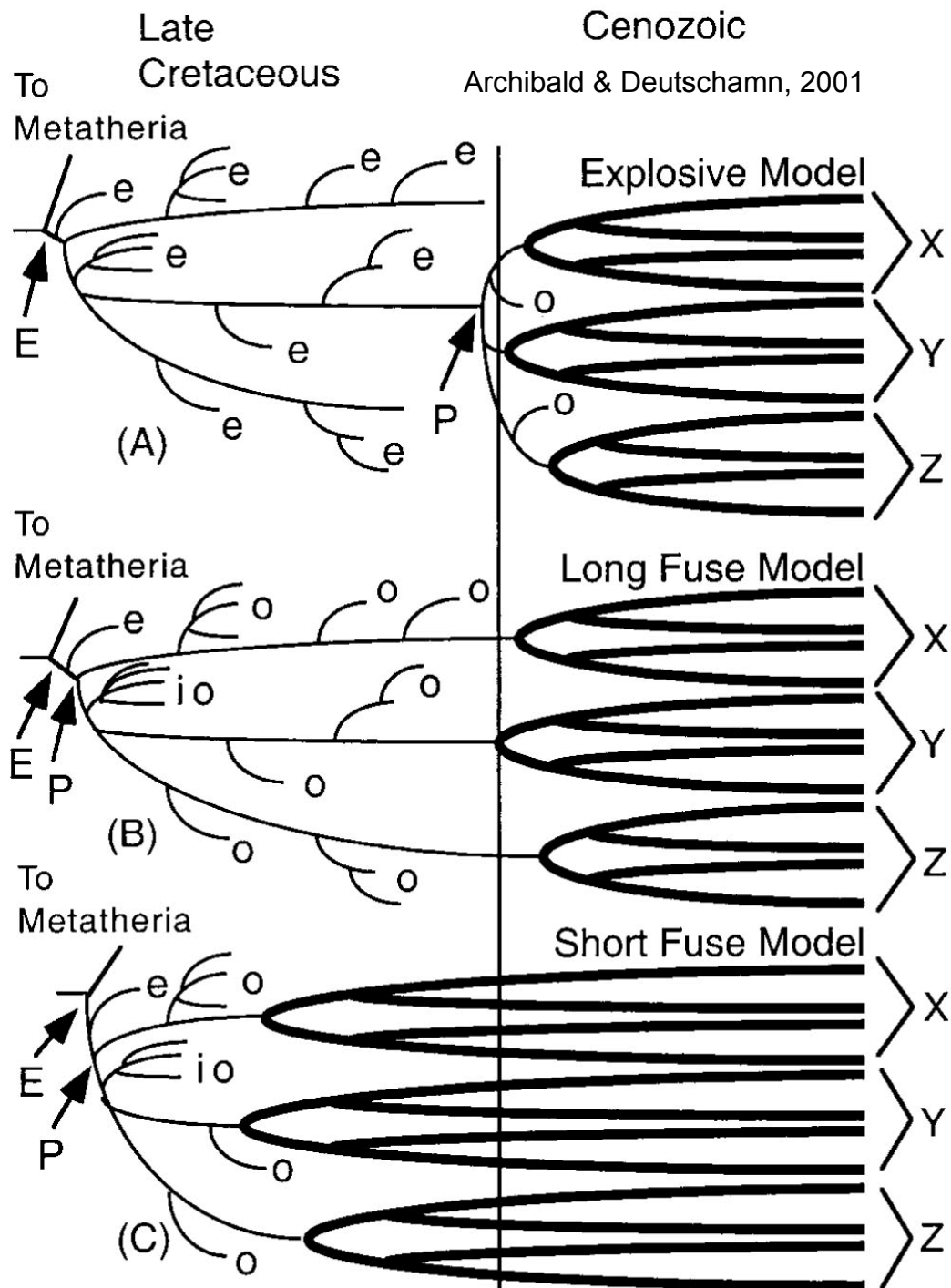
**J. David Archibald<sup>1,2</sup> and Douglas H. Deutschman<sup>1</sup>**

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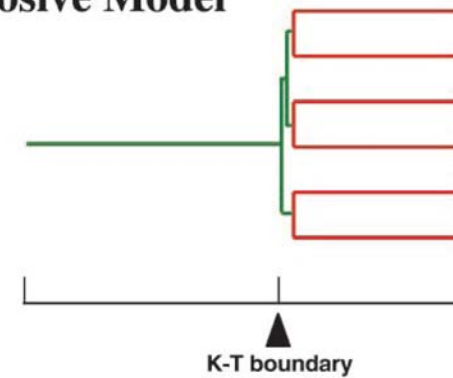
Fossil evidence is consistent with origination and diversification of extant placental orders in the early Tertiary (Explosive Model), and with the possibility of some orders having stem taxa extending into the Cretaceous (Long Fuse Model). Fossil evidence that 15 of 18 extant placental orders appeared and began diversification in the first 16 m.y. of the Cenozoic is, however, at odds with molecular studies arguing some orders diversified up to 40 m.y. earlier in the Early Cretaceous (Short Fuse Model). The quality of the fossil record was assessed by tabulating localities of all mammals in the last 105 m.y. Global locality data (except Africa) for 105 m.y. of eutherian evolution indicate discernible biogeographic patterns by the last 15 m.y. of the Cretaceous. Eutherian genera increase from 11 in latest Cretaceous to 139 in earliest Tertiary, although both are represented by about 50 localities. Yet even in the Late Cretaceous of North America and Asia where eutherians are abundant, none of the 18 extant orders are definitely known. A series of Monte Carlo simulations test whether the rapid appearance of most mammalian orders is statistically significant, and if so, whether it is a radiation event or an artifact of a limited fossil record. Monte Carlo tests affirm that the clustering of appearances in the early Cenozoic is statistically significant. Quantitative analysis of the locality data suggests that the number of genera described is a function of the number of localities sampled. In contrast, the number of orders is not a simple function of localities and thus does not appear to be limited by localities. A second set of Monte Carlo simulations confirms that the increase in orders cannot be explained by the limited number of localities sampled. Even for best-fit simulations, the observed pattern of ordinal appearances is steeper than expected under a variety of null models. These quantitative analyses of the fossil record demonstrate that the rapid ordinal appearances cannot be ascribed to limited Late Cretaceous sample sizes; thus, early Tertiary ordinal diversification is real. Although the fossil record is incomplete, it appears adequate to reject the hypothesis that orders of placentals began to diversify before the K/T boundary.

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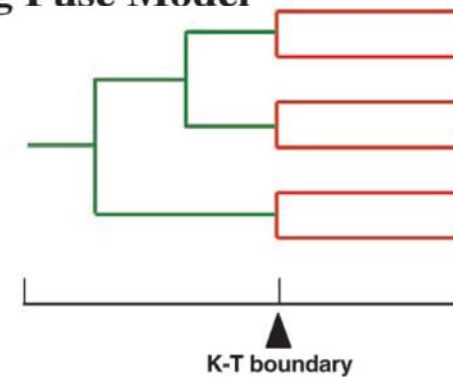
**KEY WORDS:** Eutheria; placental ordinal radiation; evolutionary rates.



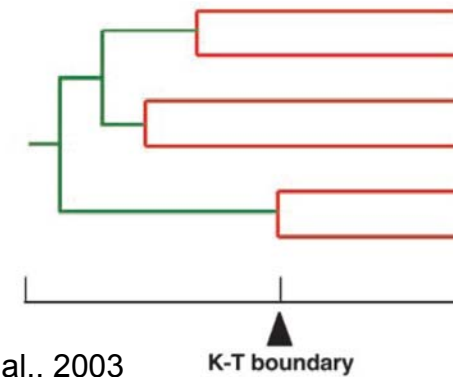
### a Explosive Model



### b Long Fuse Model

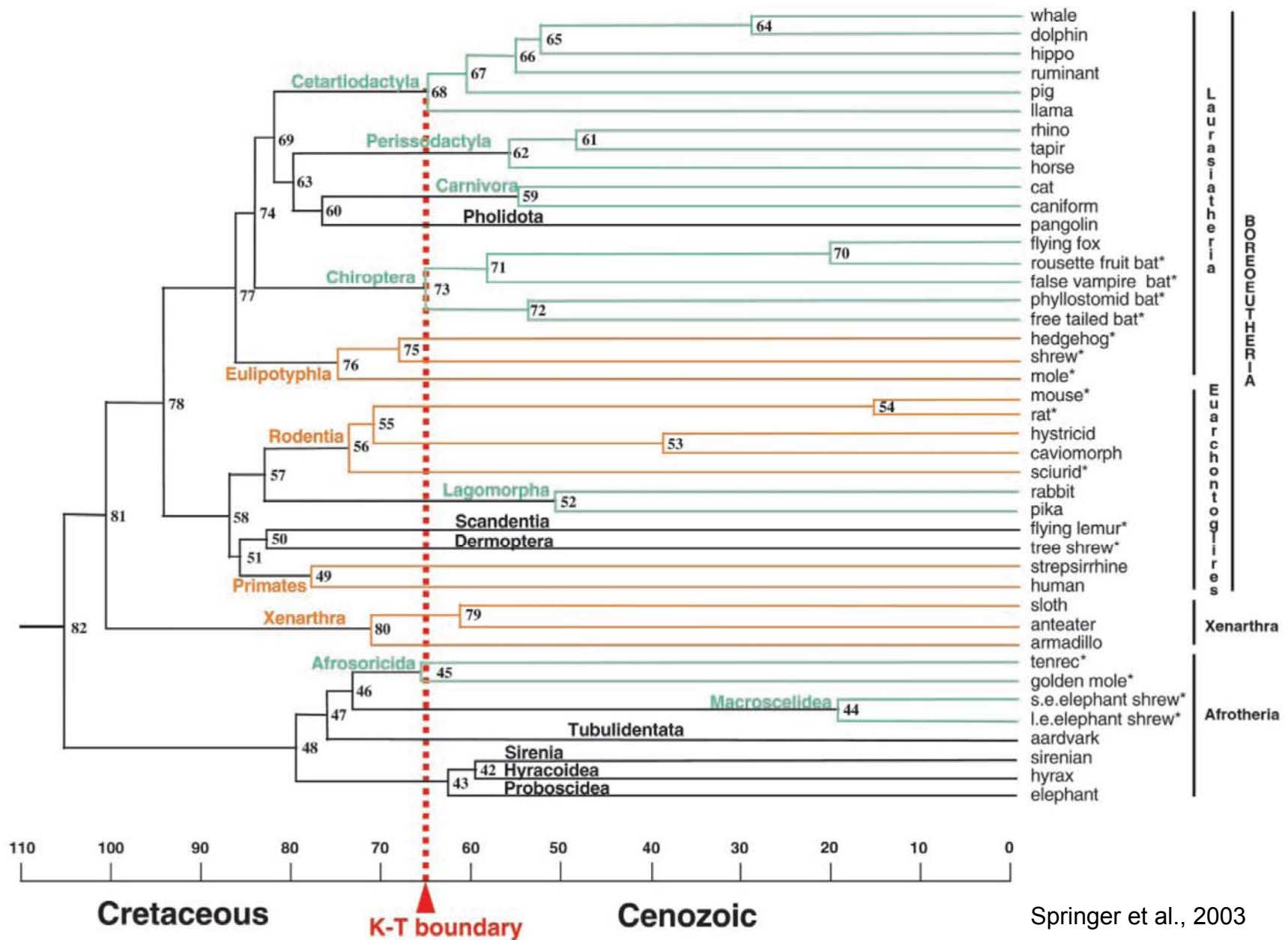


### c Short Fuse Model



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Fig. 1. Simplified versions of three models (1) for the timing and diversification of placental mammals. Red branches indicate intraordinal diversification; green branches indicate interordinal divergences. A simplified time scale is shown below each tree, with an arrow marking the K/T boundary.



Springer et al., 2003

**Fig. 2.** Molecular time scale for the orders of placental mammals based on the 16,397-bp data set and maximum likelihood tree of ref. 14 with an opossum outgroup (data not shown), 13 fossil constraints (*Materials and Methods*), and a mean prior of 105 mya for the placental root. Ordinal designations are listed above the branches. Orange and green lines denote orders with basal diversification before or after the K/T boundary, respectively. Black lines depict orders for which only one taxon was available. Asterisks denote placental taxa included in the "K/T body size" taxon set. The composition of chimeric taxa, including caniform, caviomorph, strepsirrhine, and sirenian, is indicated elsewhere (14). Numbers for internal nodes are cross-referenced in the supporting information.



## Epipubic bones in eutherian mammals from the Late Cretaceous of Mongolia

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An important transformation in the evolution of mammals was the loss of the epipubic bones. These are elements projecting anteriorly from the pelvic girdle into the abdominal region in a variety of Mesozoic mammals, related tritylodonts, marsupials and monotremes but not in living eutherian (placental) mammals<sup>1-3</sup>. Here we describe a new eutherian from the Late Cretaceous period of Mongolia, and report the first record of epipubic bones in two distinct eutherian lineages. The presence of epipubic bones and other primitive features suggests that these groups occupy a basal position in the Eutheria. It has been argued that the epipubic bones support the pouch in living mammals<sup>1,3,4</sup>, but epipubic bones have since been related to locomotion and suspension of the litter mass of several attached, lactating offspring<sup>5</sup>. The loss of the epipubic bones in eutherians can be related to the evolution of prolonged gestation, which would not require prolonged external attachment of altricial young. Thus the occurrence of epipubic bones in two Cretaceous eutherians suggests that the dramatic modifications connected with typical placental reproduction<sup>3,6,7</sup> may have been later events in the evolution of the Eutheria.

lower jaws articulated, missing anterior snout and anterior mandible. PSS-MAE 111, complete skull and lower jaws articulated.

**Diagnosis.** *Ukhaatherium nessovi* bears a close resemblance to the Mongolian Late Cretaceous monotypic eutherians *Asioryctes* and *Kennalestes*, here united in the Asioryctitheria by the following characters: postglenoid vein exit within rather than posterior to postglenoid buttress, which is developed medially into an entoglenoid process; well-developed fusiform auditory bulla; pronounced caudal tympanic process of petromastoid (CTPP), connecting to promontorium by distinct interfenestral ridge; large piriform fenestra in anterior roof of tympanic cavity. *Ukhaatherium* and *Asioryctes* are grouped within Asioryctidae and separated from *Kennalestes* by the following characters<sup>13</sup> P<sup>2</sup> (second upper premolar) smaller than P<sup>1</sup>; upper molars more strongly elongated transversely, lacking pre- and postcingula; lower molars with smaller paraconids and more compressed trigonids, mastoid exposure rectangular in outline with large lower foramen; anterior contact of jugal with maxilla strongly bifurcate. *Ukhaatherium* differs from *Asioryctes* in having: enlarged, single-rooted upper canine (smaller and double-rooted in *Asioryctes*); less robust P<sup>3</sup> with less salient paracone; large diastema between I<sup>5</sup> (fifth upper incisor) and upper canine for occlusion of large lower canine; two mental foramina in lower jaw (between four and six in *Asioryctes*); smaller facial process of lacrimal so that nasal-maxillary contact in facial region is broader; and only one foramen in mastoid.

The asioryctitheres *Ukhaatherium*, *Asioryctes* and *Kennalestes* share features that indicate allocation to the Eutheria (Fig. 1) with close similarities to lipotyphlan insectivorans<sup>14,15</sup>, including: a large maxilla component in the orbital wall and, probably, the concomitant early eruption of the cheek teeth<sup>16</sup>; an entoglenoid process<sup>14-16</sup>; the features of the CTPP noted above; and a piriform fenestra.

These features notwithstanding, *Ukhaatherium* and its relatives *Kennalestes* and *Asioryctes* also have several primitive (plesiomorphic) skull and dental traits (for example, five upper incisors, posteriorly expansive nasals, facial process of the lacrimal, well-developed and posteriorly extensive jugal in the zygoma) radically



Since 1990, joint expeditions of the Mongolian Academy of Sciences and the American Museum of Natural History (MAE) have surveyed and collected the Cretaceous and Lower Tertiary sequences exposed in the Gobi Desert of Mongolia<sup>8,9</sup>. In 1993 MAE discovered an extremely fossiliferous locality, Ukhaa Tolgod, noted for its Late Cretaceous assemblage of abundant and exquisitely preserved dinosaur skeletons, eggs and embryos, birds, lizards and mammals<sup>8-11</sup>. More than 500 mammal skulls, many with well-preserved skeletons, have been collected at Ukhaa Tolgod. Skeletons of two eutherian taxa preserve epipubic bones: a zalambdalestid (cf. *Zalambdalestes*<sup>12</sup>), and a new taxon of insectivore-like eutherian closely related to the previously described *Asioryctes*<sup>13</sup>. The new taxon, *Ukhaatherium nessovi*, and its inclusive groups are here diagnosed:

Mammalia Linneaus, 1758

Theria Parker and Haswell, 1897

Eutheria incertae sedis Gill, 1872

Asioryctitheria, new

Asioryctidae Kielan-Jaworowska, 1981

*Ukhaatherium nessovi* new genus and species; Figs 1, 2.

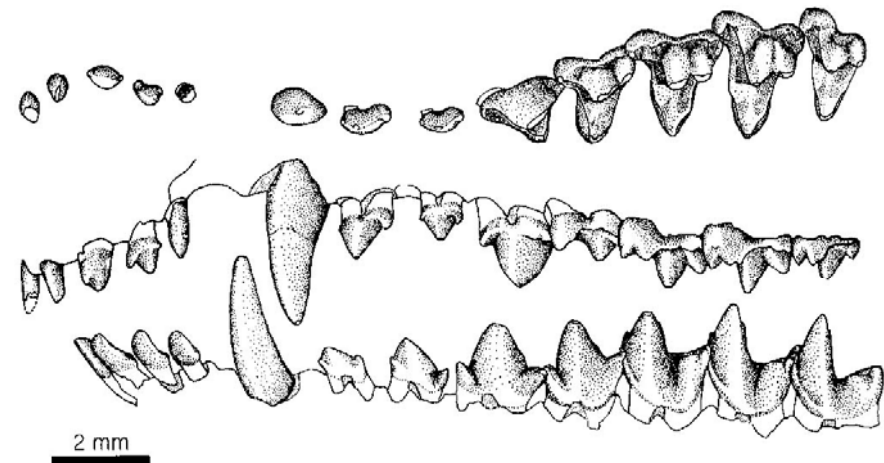
**Etymology.** Ukhaa (Mongolian), brown; theria (Latin), beast; nessovi, named after the late Lev Nessov for his pioneering work on Mesozoic mammals from Kazakhstan and Uzbekistan.

**Age and locality.** Late Cretaceous. Djadokhta? Formation, Ukhaa Tolgod, Mongolia.

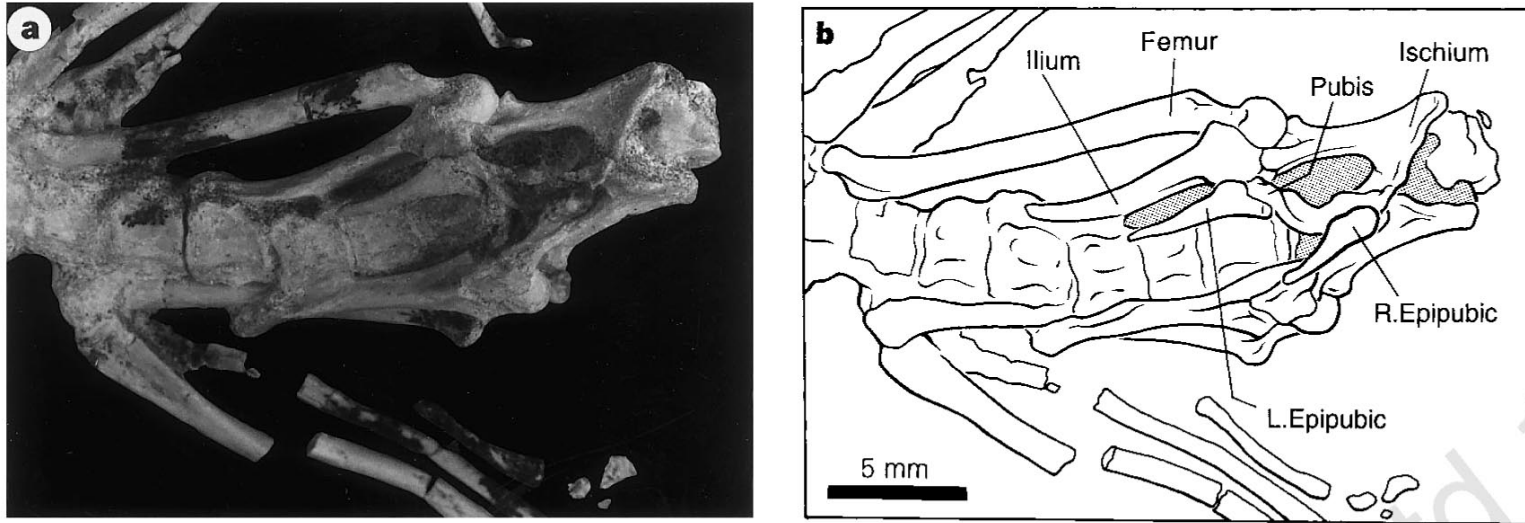
**Type and only species.** *Ukhaatherium nessovi*.

**Type specimen.** PSS-MAE 102, skull with nearly complete skeleton.

**Referred specimens.** PSS-MAE 103–106, skulls and skeletons found in association with the type. PSS-MAE 110, skull with

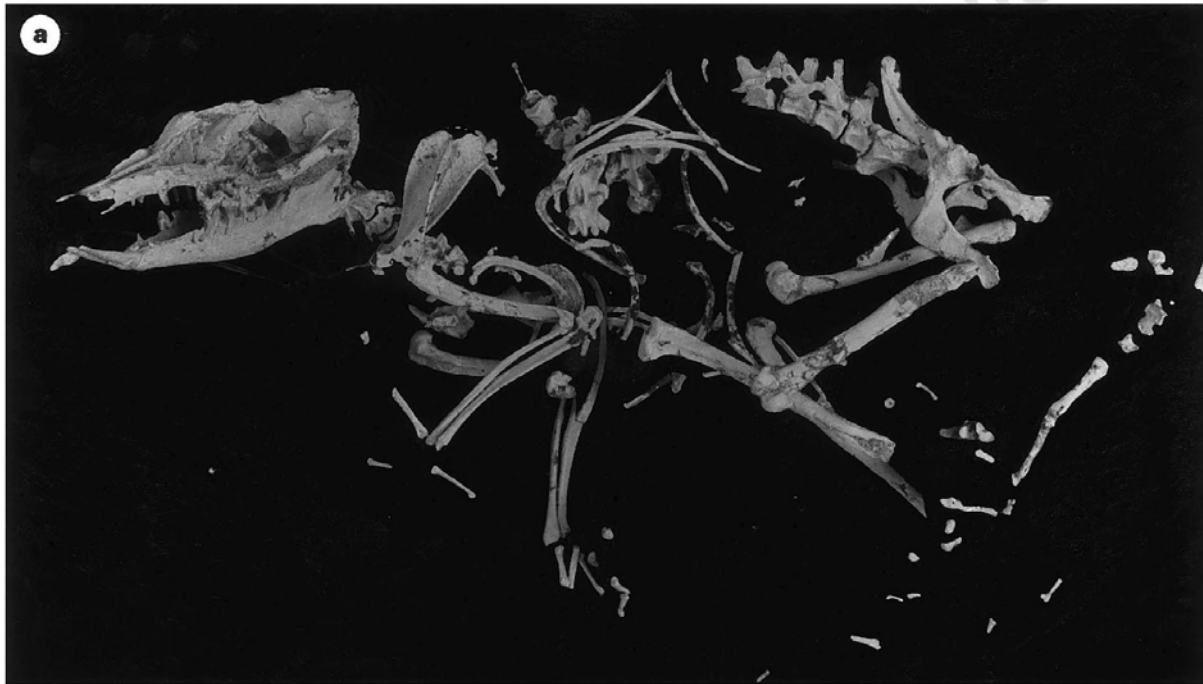


**Figure 1** Dentition of the type specimen (PSS-MAE 102) of *Ukhaatherium nessovi*. Occlusal (top) and labial (middle) views of the left upper dentition: I<sup>1-5</sup>, C, P<sup>1-4</sup>, M<sup>1-3</sup>. Labial view of lower dentition (bottom): I<sub>1-4</sub>, C, P<sub>1-4</sub>, M<sub>1-3</sub>. Lower dentition is a composite of the right I<sub>1-3</sub> and C, and the left I<sub>4</sub>, P<sub>1-4</sub> and M<sub>1-3</sub>. The dentition of *U. nessovi* shows several derived traits shared with Placentalia (here defined as the clade composed of the most recent common ancestor of living eutherians and its descendants): three molars, reduced styler shelf, small paraconid, compressed trigonid, complex posterior premolars, and other putative distinctive features, such as paracone larger than metacone and absence of styler cusp C. Other cranial diagnostic features include the presence of an optic foramen, a small facial process of the lacrimal, a slender zygomatic arch, presence of ectopterygoid flanges of the alisphenoid, and a well-developed crista interfenestralis connecting the promontorium with the paroccipital process. Primitive features absent among placentals, but present in *U. nessovi* and closely allied forms, suggest these Late Cretaceous forms from Mongolia are basal members of Eutheria (mammals more closely related to Placentalia than to Metatheria).



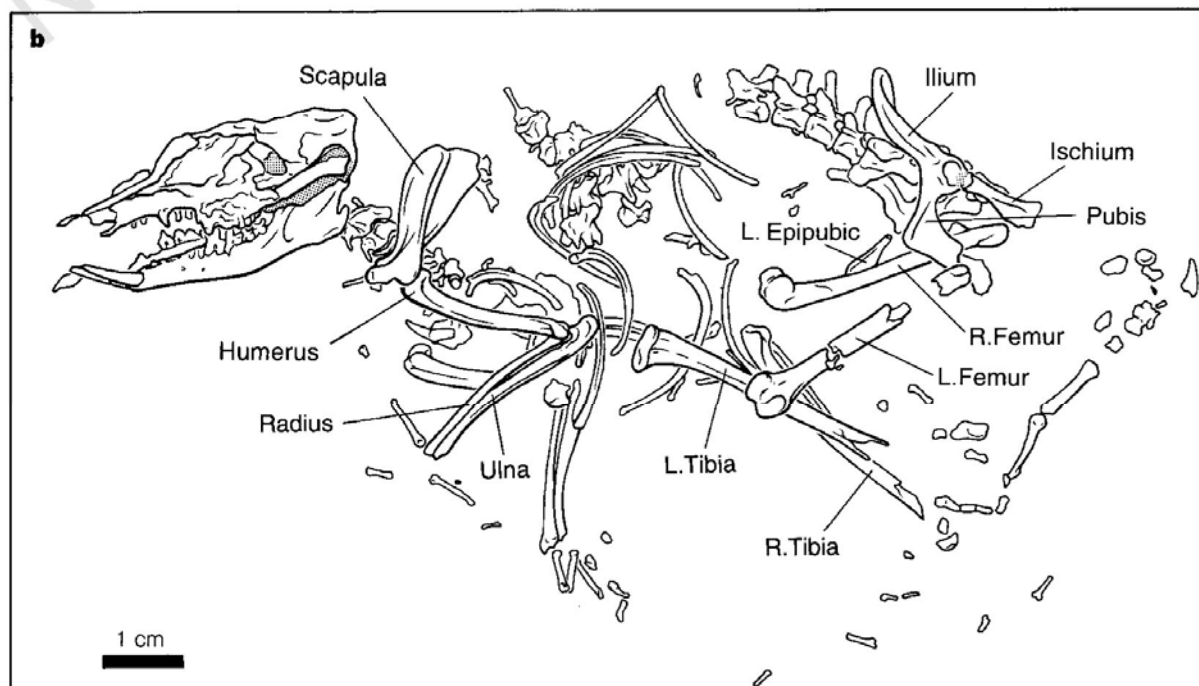
**Figure 2** Detail of the skeleton (PSS-MAE 105) of *Ukhaatherium nessovi* showing the pelvic girdle and epipubic elements. Ventral view. **a**, Photograph; **b**, labelled sketch. The epipubics are posteriorly expanded and plate-like near the point of articulation with the pubis. They taper anteriorly in a splint-like process with a

slight concave upward curvature. A roughened ridge on the anterolateral corner of the pubis indicates the point of contact with the epipubics. Epipubic bones are not as well preserved in the type specimen PSS-MAE 102, but they are very similar in proportion and shape to those of the skeleton PSS-MAE 105. L., left; R., right.



**Figure 3** Lateral view of the skeleton (PSS-MAE 131) of cf. *Zalambdalestes*. **a**, Photograph; **b**, labelled sketch. L., left; R., right.

Novacek et al., 1997



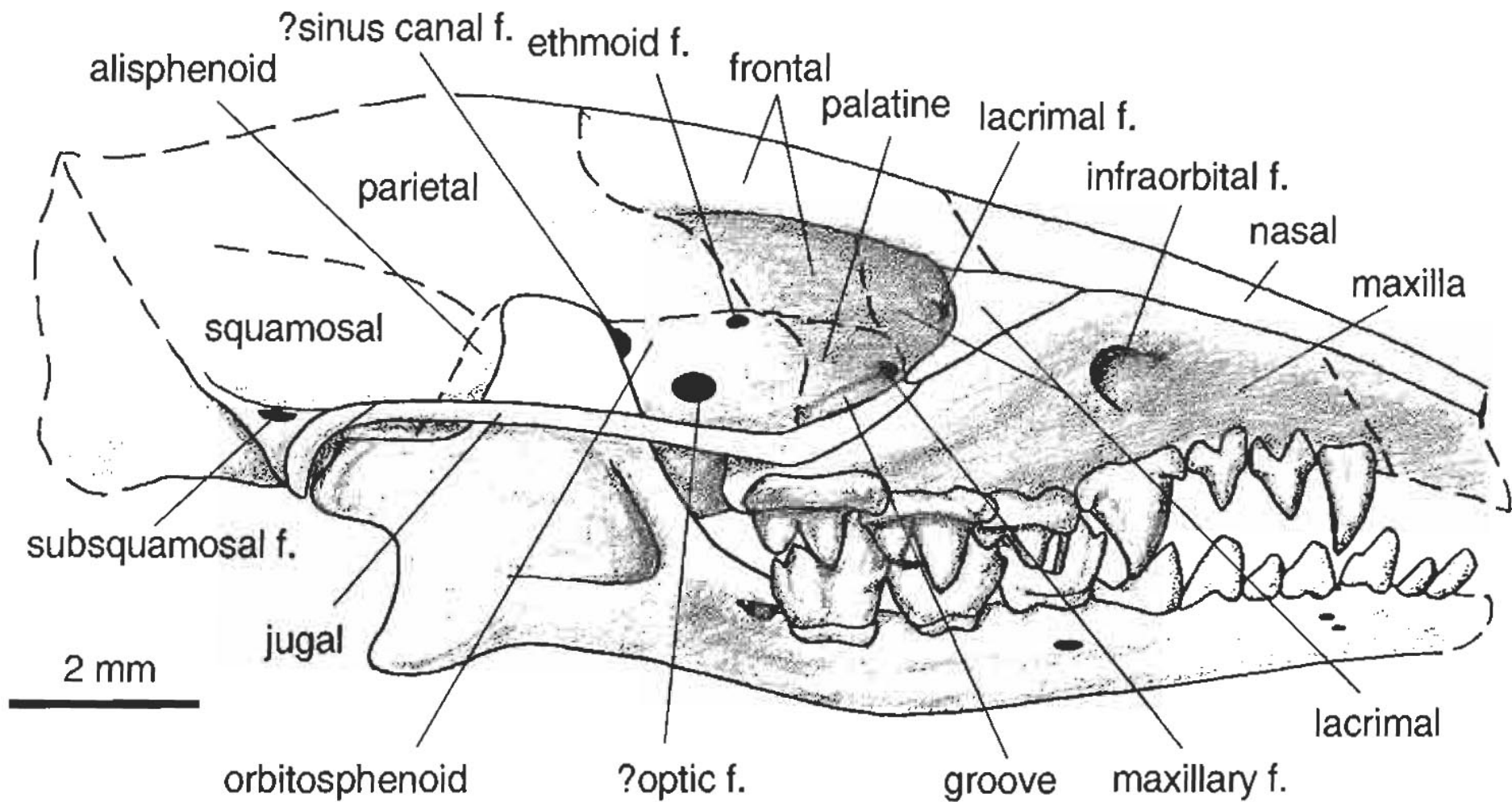


Fig. 7. Tentative reconstruction of the skull of *Daulestes nessovi* sp. n. (ZIN C. 79066) in lateral view.



# Late Cretaceous asioryctitherian eutherian mammals from Uzbekistan and phylogenetic analysis of Asioryctitheria

J. DAVID ARCHIBALD and ALEXANDER O. AVERIANOV



Archibald, J.D. and Averianov, A.O. 2006. Late Cretaceous asioryctitherian eutherian mammals from Uzbekistan and phylogenetic analysis of Asioryctitheria. *Acta Palaeontologica Polonica* 51 (2): 351–376.

Four small asioryctitheres at Dzharakuduk (Turonian), Uzbekistan are *Daulestes kulbeckensis* (= *Kumlestes olzha*), *D. inobservabilis* (= *Kennalestes? uzbekistanensis*), *Uchkudukodon* (gen. nov.) *nessovi* and *Bulaklestes kezbe*. *Uchkudukodon nessovi* is one of the smallest therians (molars about 1 mm long). Lower canine is two-rooted in *Uchkudukodon* gen. nov. and *Bulaklestes* (uncertain in *Daulestes*). All lower premolars in all four species are double-rooted. Teeth identified as dp1, p2 and dp2 in holotype of *Uchkudukodon nessovi* (McKenna et al. 2000) are here identified c, p1, and p2. A phylogenetic analysis weakly supported Asioryctitheria by four synapomorphies: conular basins become distinct, the number of roots reverts to two on the lower canine, the p5 becomes longer than p4, and the metaconid on p5 is reduced and lost. Other characters diagnostic of asioryctitheres are four upper and lower premolars (arguably five upper premolars in juvenile *Kennalestes*), P4 has a protocone swelling or protocone, some asymmetry of the styler shelf on M1–2, the paraconule on M1–3 is distinctly closer to the protocone than is the metaconule, protocone is of moderate height on M1–3 (70–80% of paracone or metacone height), Meckel's groove is absent, and the mandibular foramen opens into a smaller depression on lingual side of mandibular ascending ramus. *Asioryctes* and *Ukhaatherium* are placed in Asioryctinae and along with *Kennalestes* are placed in Asioryctidae. Kennalestidae Kielan-Jaworowska, 1981 is a junior subjective synonym for Asioryctidae Kielan-Jaworowska, 1981. Because of uncertainties in the analysis, the positions of *Daulestes*, *Uchkudukodon* gen. nov., and *Bulaklestes* cannot be determined beyond referral to Asioryctitheria.

Key words: Mammalia, Eutheria, Asioryctitheria, *Daulestes*, *Bulaklestes*, *Uchkudukodon*, Cretaceous, Dharakuduk, Uzbekistan.

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Alexander O. Averianov [sasha@AA1923.spb.edu], Zoological Institute, Russian Academy of Sciences, Universitetskaya nab. 1, Saint Petersburg 199034, Russia.

## LETTERS

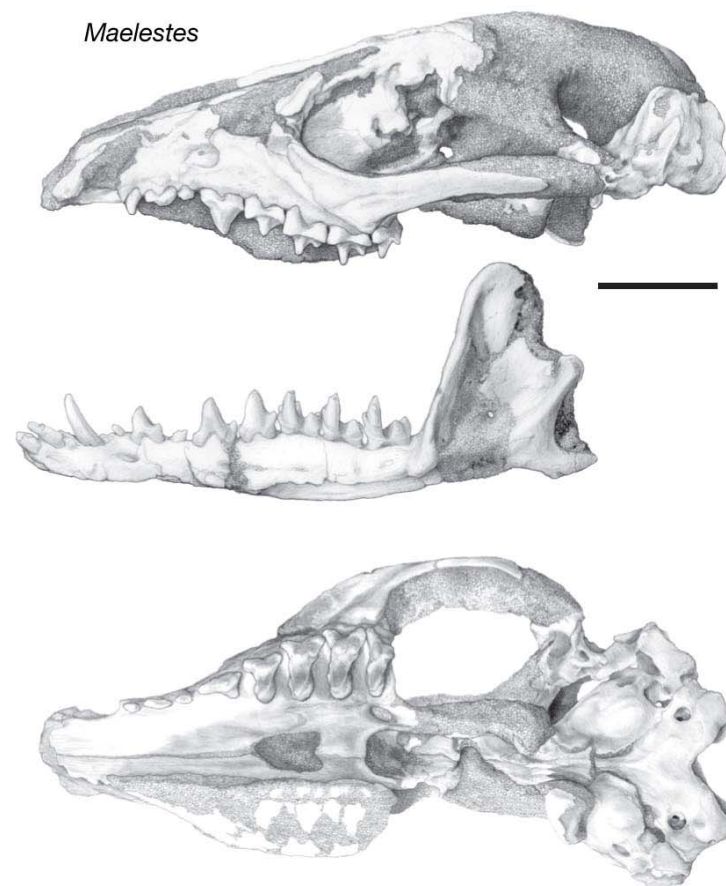
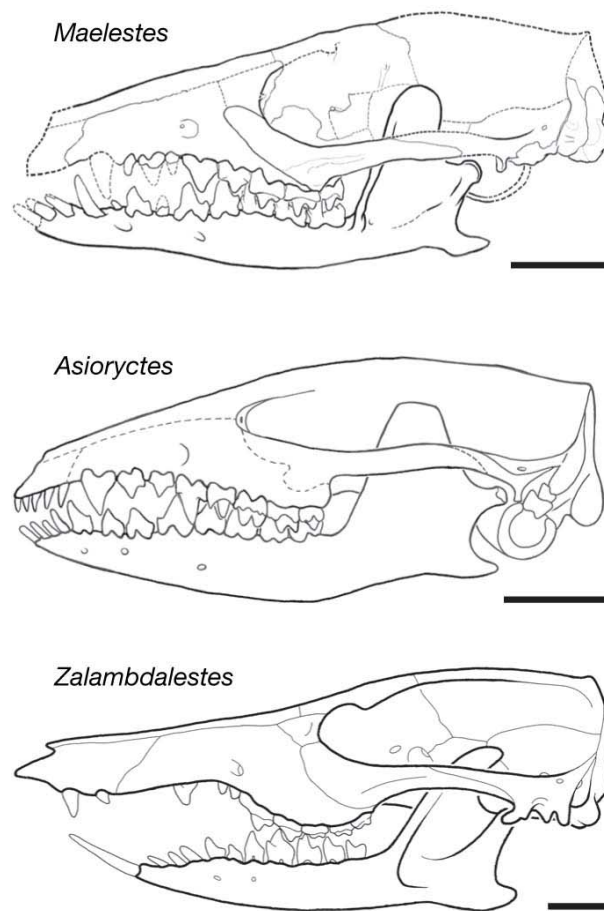
# Cretaceous eutherians and Laurasian origin for placental mammals near the K/T boundary

J. R. Wible<sup>1</sup>, G. W. Rougier<sup>2</sup>, M. J. Novacek<sup>3</sup> & R. J. Asher<sup>4</sup>

Estimates of the time of origin for placental mammals from DNA studies span nearly the duration of the Cretaceous period (145 to 65 million years ago), with a maximum of 129 million years ago<sup>1</sup> and a minimum of 78 million years ago<sup>2</sup>. Palaeontologists too are divided on the timing. Some<sup>3–5</sup> support a deep Cretaceous origin by allying certain middle Cretaceous fossils (97–90 million years old) from Uzbekistan with modern placental lineages, whereas others<sup>6,7</sup> support the origin of crown group Placentalia near the close of the Cretaceous. This controversy has yet to be addressed by a comprehensive phylogenetic analysis that includes all well-known Cretaceous fossils and a wide sample of morphology among Tertiary and recent placentals<sup>6</sup>. Here we report the discovery of a new well-preserved mammal from the Late Cretaceous of Mongolia and a broad-scale phylogenetic analysis. Our results exclude Cretaceous fossils from Placentalia, place the origin of Placentalia near the Cretaceous/Tertiary (K/T) boundary in Laurasia rather than much earlier within the Cretaceous in the Southern Hemisphere<sup>8,9</sup>, and place afrotherians and xenarthrans in a nested rather than a basal position<sup>8,9</sup> within Placentalia.

**Age and locality.** Late Cretaceous Djadokhta Formation, Ukhaa Tolgod (between Camel Humps and Sugar Mountain), Mongolia. Recent age estimates of Djadokhta Formation are 75–71 million years<sup>12</sup>.

**Diagnosis.** Upper dentition: I<sup>2</sup>, C<sup>1</sup>, P<sup>5</sup>, M<sup>3</sup>. Lower dentition: I<sub>3</sub>, C<sub>1</sub>, P<sub>5</sub>, M<sub>3</sub> (Figs 1 and 2). Differs from other Mongolian Djadokhta Formation eutherians (asioryctitheres *Kennalestes*, *Asioryctes*<sup>13</sup> and *Ukhaatherium*<sup>14</sup>, and zalambdalestids *Zalambdalestes* and *Barunlestes*<sup>15</sup>) in having five upper and lower premolars, three subequal procumbent lower incisors, palatal vacuity between maxilla and palatine, postglenoid foramen behind postglenoid process, transpromontorial internal carotid artery, and small prootic canal. Resembles *Kennalestes* and *Asioryctes*<sup>13</sup> in having hypoglossal foramen housed in an opening larger than jugular foramen and petrosal roof for external acoustic meatus. Differs from Central Asian Late Cretaceous asioryctitheres *Bulaklestes*, *Daulestes* and *Uchkudukodon*<sup>16</sup> in having five upper and lower premolars, single-rooted lower canine, penultimate upper premolar with three roots, upper molars much wider than long with narrower styral shelves, and lower molars with protoconid subequal to metaconid. Differs from Central Asian Late Cretaceous

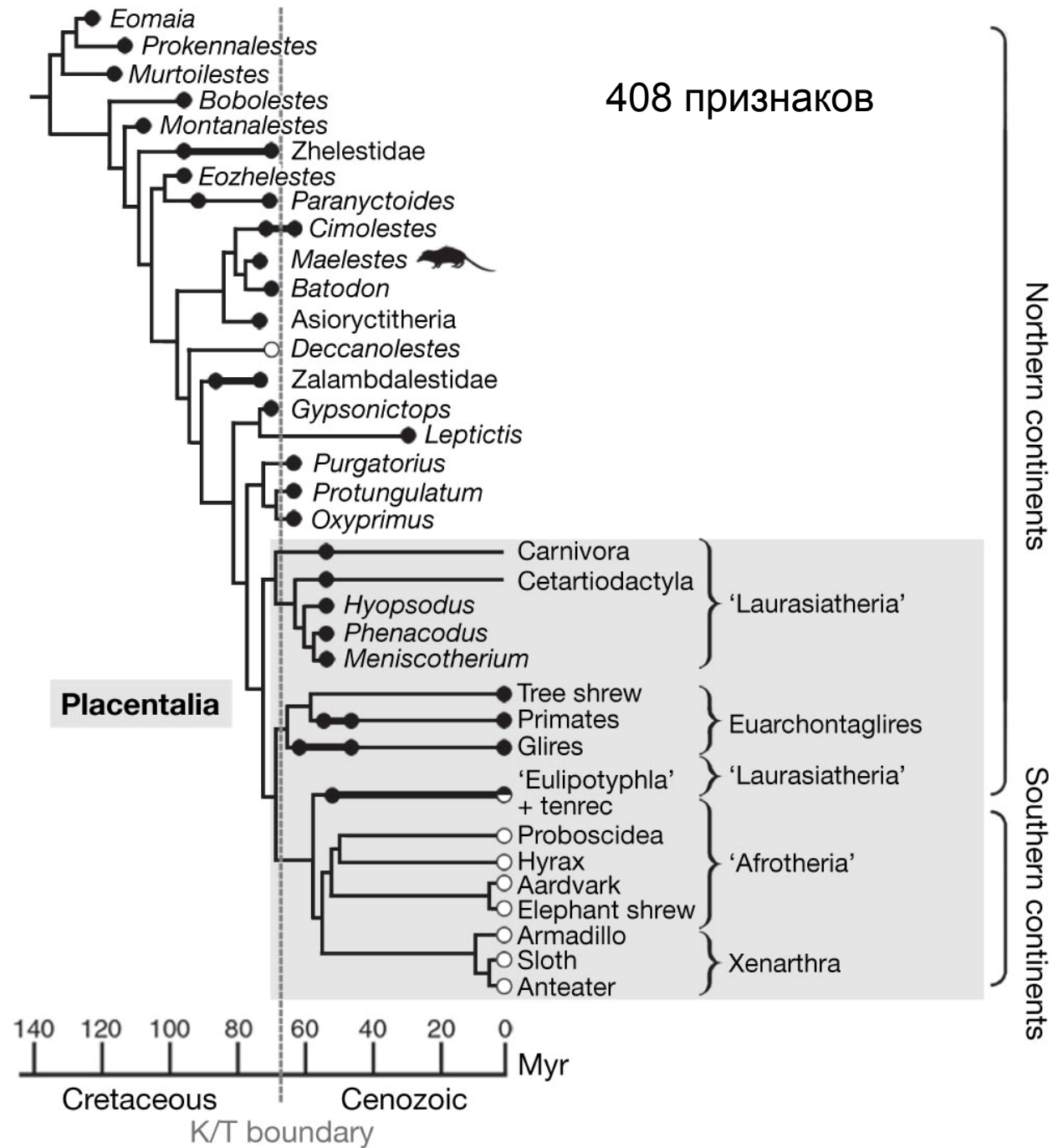


**Figure 1 | *Maelestes gobiensis* gen. et sp. nov. (holotype, PSS-MAE 607) skull and mandible in comparison to other Djadokhta eutherians.** Left panel: reconstructions of *Maelestes*, *Asioryctes* and *Zalambdalestes*, the last two of which are redrawn from ref. 15. Right panel: incomplete *Maelestes* skull in left lateral (top) and ventral (bottom) views, and left *Maelestes*

mandible in lateral view (middle). The large opening in the palate between the palatines and maxillae is a palatal vacuity. *Maelestes* probably had some upper incisors, but only a small non-tooth-bearing fragment of the premaxilla is preserved. Scale bars, 5 mm.

# Eutheria

408 признаков





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

ERIC G. EKDALE, J. DAVID ARCHIBALD, and ALEXANDER O. AVERIANOV



Ekdale, E.G., Archibald, J.D., and Averianov, A.O. 2004. Petrosal bones of placental mammals from the Late Cretaceous of Uzbekistan. *Acta Palaeontologica Polonica* 49 (1): 161–176.

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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## Phylogenetic analysis, taxonomic revision, and dental ontogeny of the Cretaceous Zhelestidae (Mammalia: Eutheria)

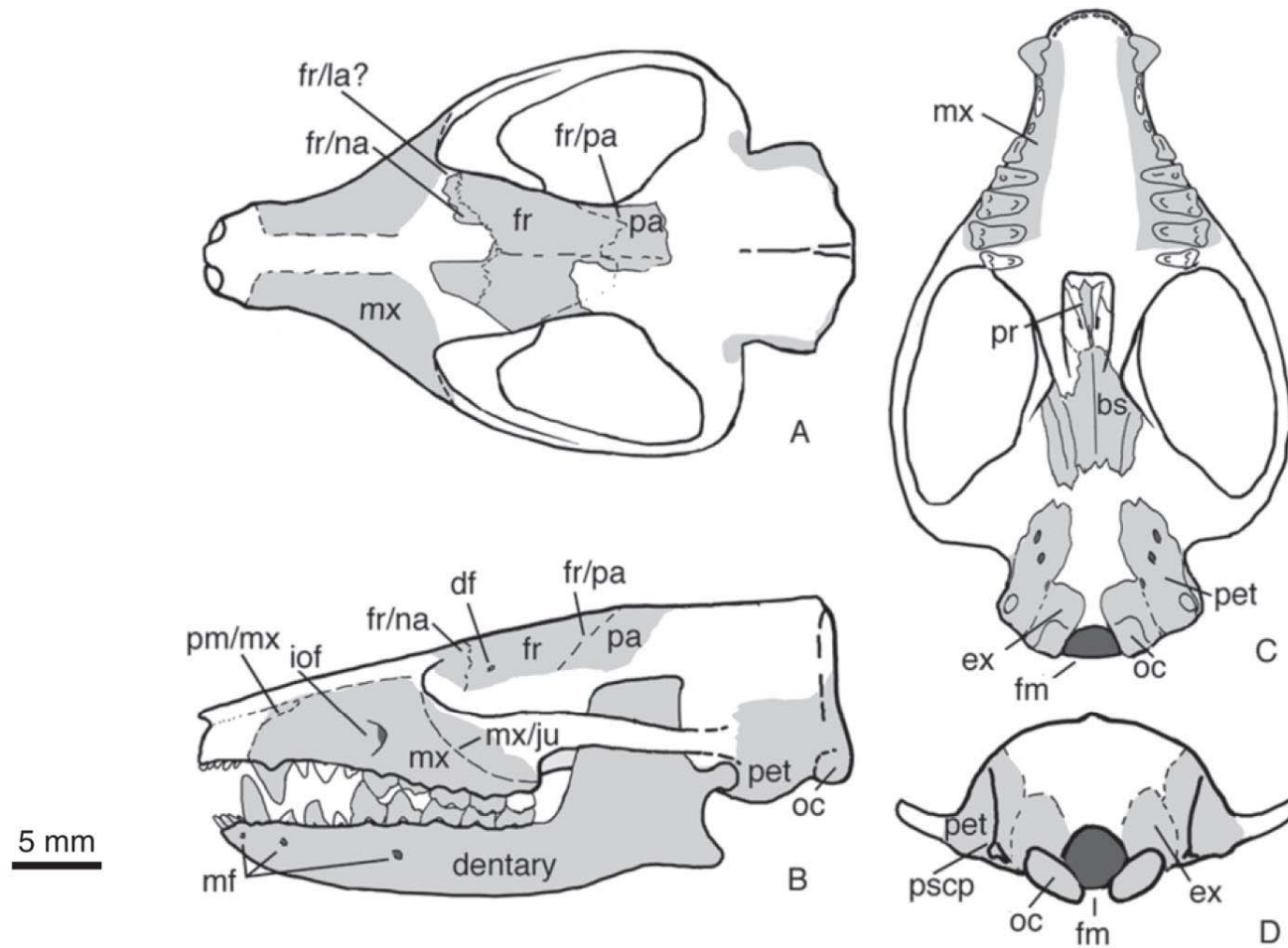
J. DAVID ARCHIBALD<sup>1\*</sup> and ALEXANDER AVERIANOV<sup>2</sup>

<sup>1</sup>*Department of Biology, San Diego State University, San Diego, CA 92182-4614, USA*

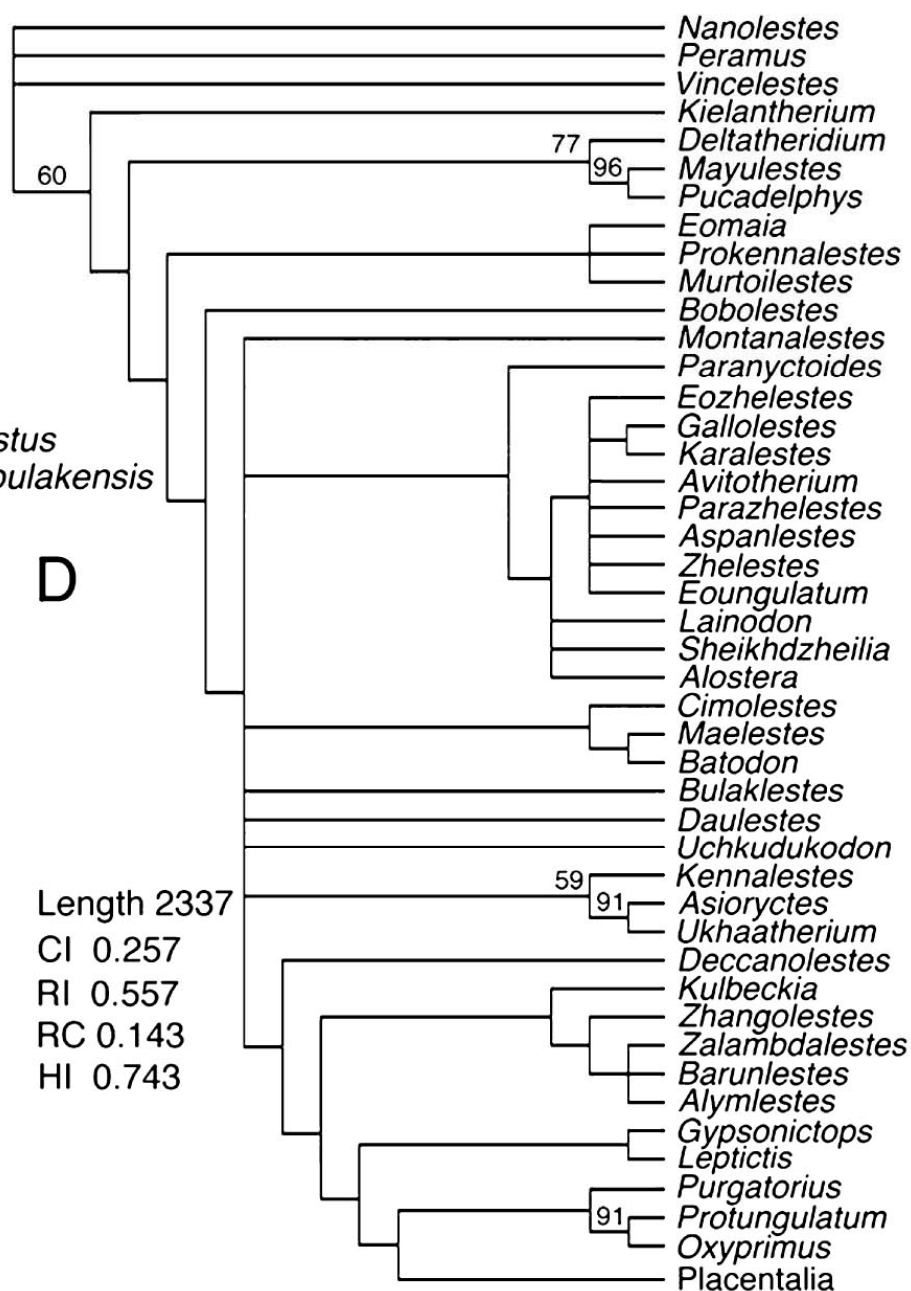
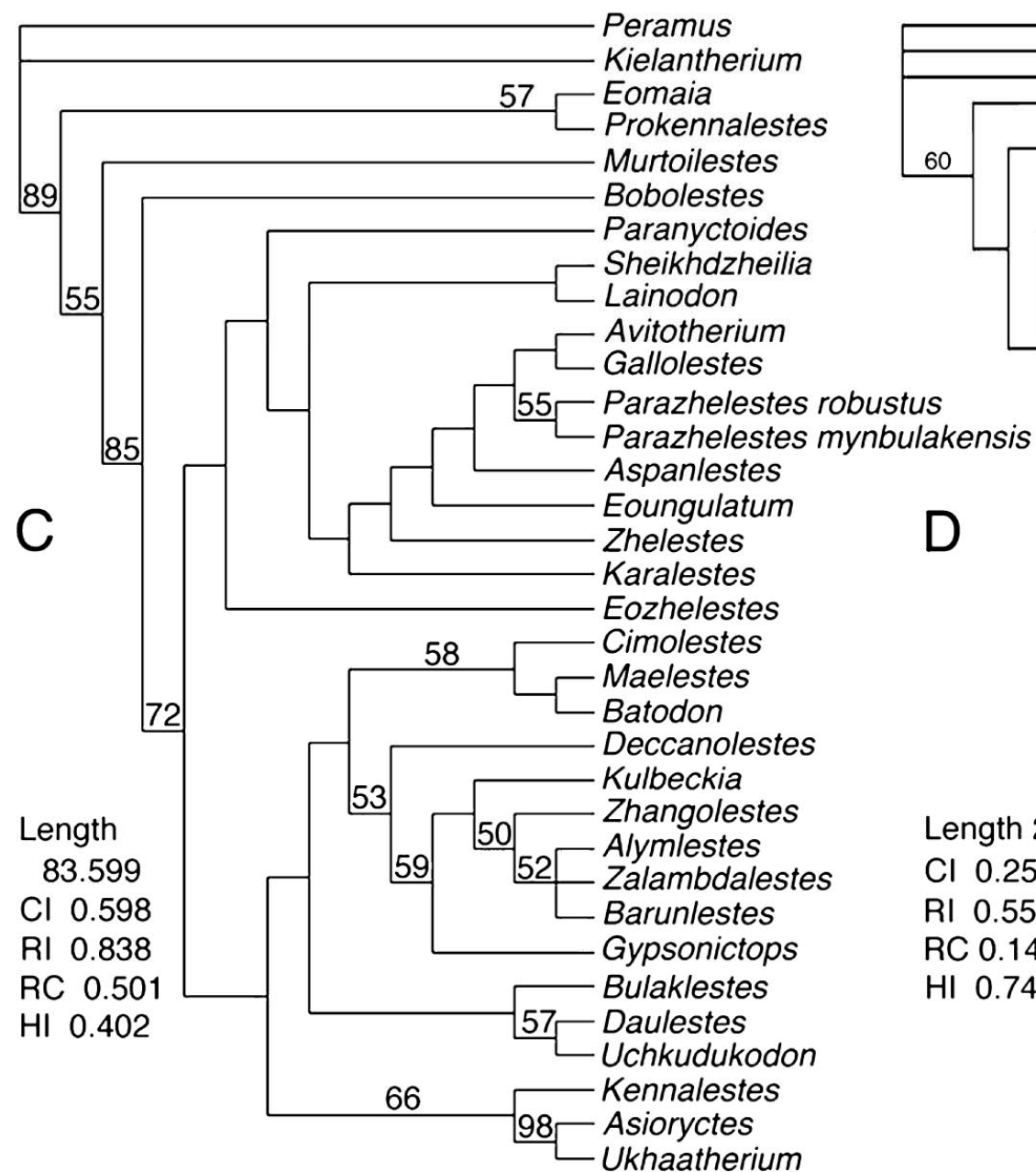
<sup>2</sup>*Zoological Institute, Russian Academy of Sciences, Universitetskaya nab. 1, 199034, Saint Petersburg, Russia*

*Received 25 October 2010; revised 11 May 2011; accepted for publication 5 July 2011*

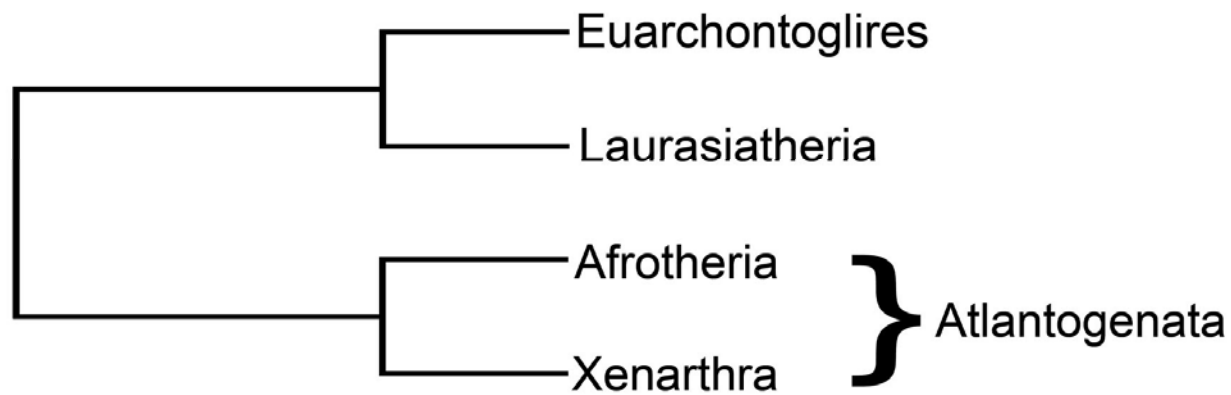
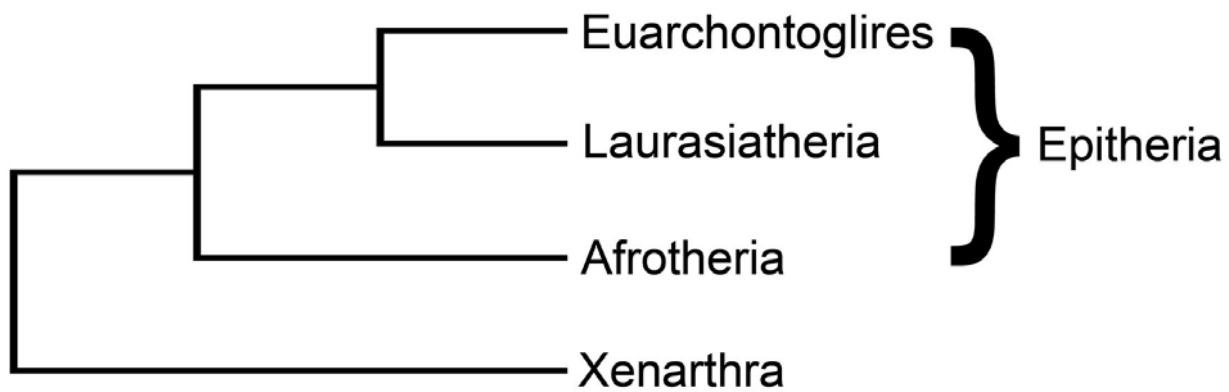
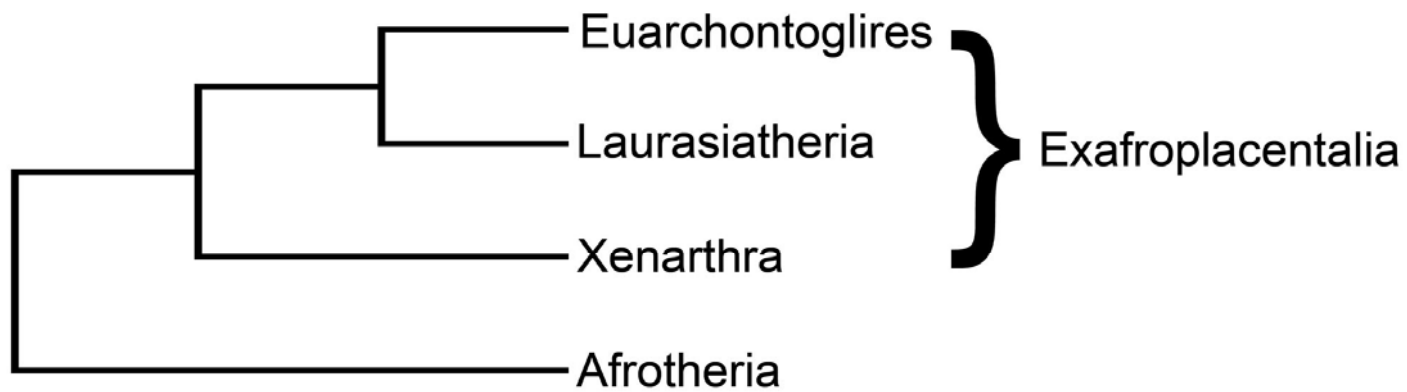
The eutherian, family-level clade Zhelestidae is consistently although weakly supported in five phylogenetic analyses that we performed on all Cretaceous eutherians. Additionally in the fifth analysis, which included some placentals, Zhelestidae is placed as a stem eutherian clade rather than grouping within the crown clade Placentalia as argued in some previous studies but not others. The subfamily Zhelestinae, Dzharakuduk (Turonian –?Coniacian ages), Kyzylkum Desert, Uzbekistan includes *Zhelestes temirkayzk*, *Aspanlestes aptap*, *Parazhelestes mynbulakensis* (= *Sorlestes budan*), *Parazhelestes robustus*, *Eoungulatum kudukensis*. Additional taxa for the time being recognized as Zhelestidae *incertae sedis* are: *Sheikhdzheilia rezvyii* (Cenomanian, Uzbekistan), ***Borisodon kara* gen. nov.** (= ‘*Sorlestes*’ *kara*) (Turonian, Kazakhstan), *Lainodon orueetxebarriai* (Campanian or Maastrichtian, Spain), *Labes quintanillensis* (Maastrichtian, Spain), *Labes garimondi* (Campanian, France), *Gallolestes pachymandibularis* (Campanian, Mexico), *Gallolestes agujaensis* (Campanian, USA), and *Avitotherium utahensis* (Campanian, USA). *Eozhelestes mangit* (Cenomanian, Uzbekistan) is a questionable zhelestid (?Zhelestidae), possibly stem to Zhelestidae. *Paranyctoides* (Asia and North America) is often linked to Zhelestidae. *Alostera*, previously referred to Zhelestidae, is a eutherian of unknown affinities. Associated skull fragments permitted the first reconstruction of a zhelestid (*Aspanlestes*) skull. Abundant dentulous and edentulous dentaries allowed examination of dental replacement from the canine posteriorly in Dzharakuduk zhelestids as follows: [dc, p1, dp2, p3, dp4, dp5] → m1 → p2 → c, p4, m2 → p5 → m3.

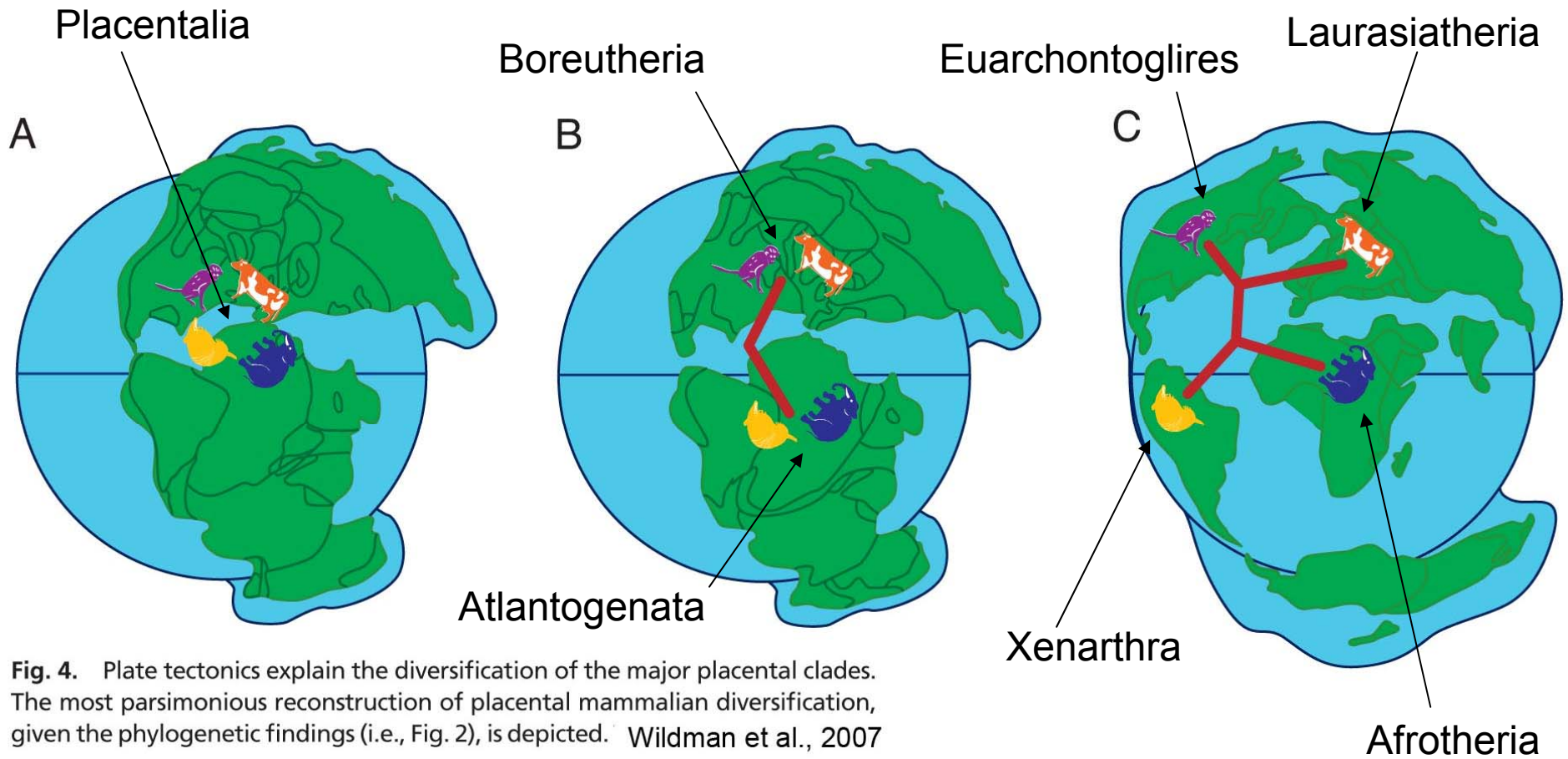


**Figure 1.** *Aspanlestes aptap*, reconstruction of the skull and dentary based on URBAC 03–93 and 02–45 as well as various dentary and dental remains referred to this species. A, dorsal; B, lateral; C, ventral; D, posterior views. Light grey areas represent known parts or mirror images of known parts. Scale bar = 5 mm. See Appendix 1 for abbreviations.









we name this clade the Atlanto-genata. The name is derived from “Atlanto”, referring to the *Atlantic* ocean (and also the lost mythical land to the west of the pillars of Hercules), and “genata” for *generated* by (i.e., the vicariant divergence generated by the Atlantic ocean).

Waddell et al., 1999: 134

# The Placental Mammal Ancestor and the Post–K-Pg Radiation of Placentals

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To discover interordinal relationships of living and fossil placental mammals and the time of origin of placentals relative to the Cretaceous-Paleogene (K-Pg) boundary, we scored 4541 phenomic characters *de novo* for 86 fossil and living species. Combining these data with molecular sequences, we obtained a phylogenetic tree that, when calibrated with fossils, shows that crown clade Placentalia and placental orders originated after the K-Pg boundary. Many nodes discovered using molecular data are upheld, but phenomic signals overturn molecular signals to show Sundatheria (Dermoptera + Scandentia) as the sister taxon of Primates, a close link between Proboscidea (elephants) and Sirenia (sea cows), and the monophyly of echolocating Chiroptera (bats). Our tree suggests that Placentalia first split into Xenarthra and Epitheria; extinct New World species are the oldest members of Afrotheria.



The ~5100 living placental species collectively exhibit extreme size ranges (1.5-g bumblebee bat to 190,000-kg blue whale); dramatic locomotor diversity (e.g., running, flying, and swimming); and diverse degrees of encephalization (4). Moreover, extinct species in the placental fossil record are even more numerous and exhibit a broader range of adaptations (5). Given this diversity, it is of interest to determine the phenotype of the ancestral placental mammal.

Determining placental origins and relationships has met with the practical challenge of codifying phenomic data on a scale comparable to that for genomic data to produce a maximally informed phylogenetic tree. We built a phenomic character matrix (4541 characters; 403 constant and 482 parsimony uninformative) using MorphoBank (12). The matrix contains newly scored characters for 86 species representing all living placental orders plus 40 fossil species, with more than 12,000 annotated images supporting the phenomic homologies. These data were examined with molecular sequences compiled from 27 nuclear genes from GenBank (table S1).



[www.sciencemag.org/cgi/content/full/339/6120/662/DC1](http://www.sciencemag.org/cgi/content/full/339/6120/662/DC1)

132 pp.

## Supplementary Materials for

### **The Placental Mammal Ancestor and the Post–K-Pg Radiation of Placentals**

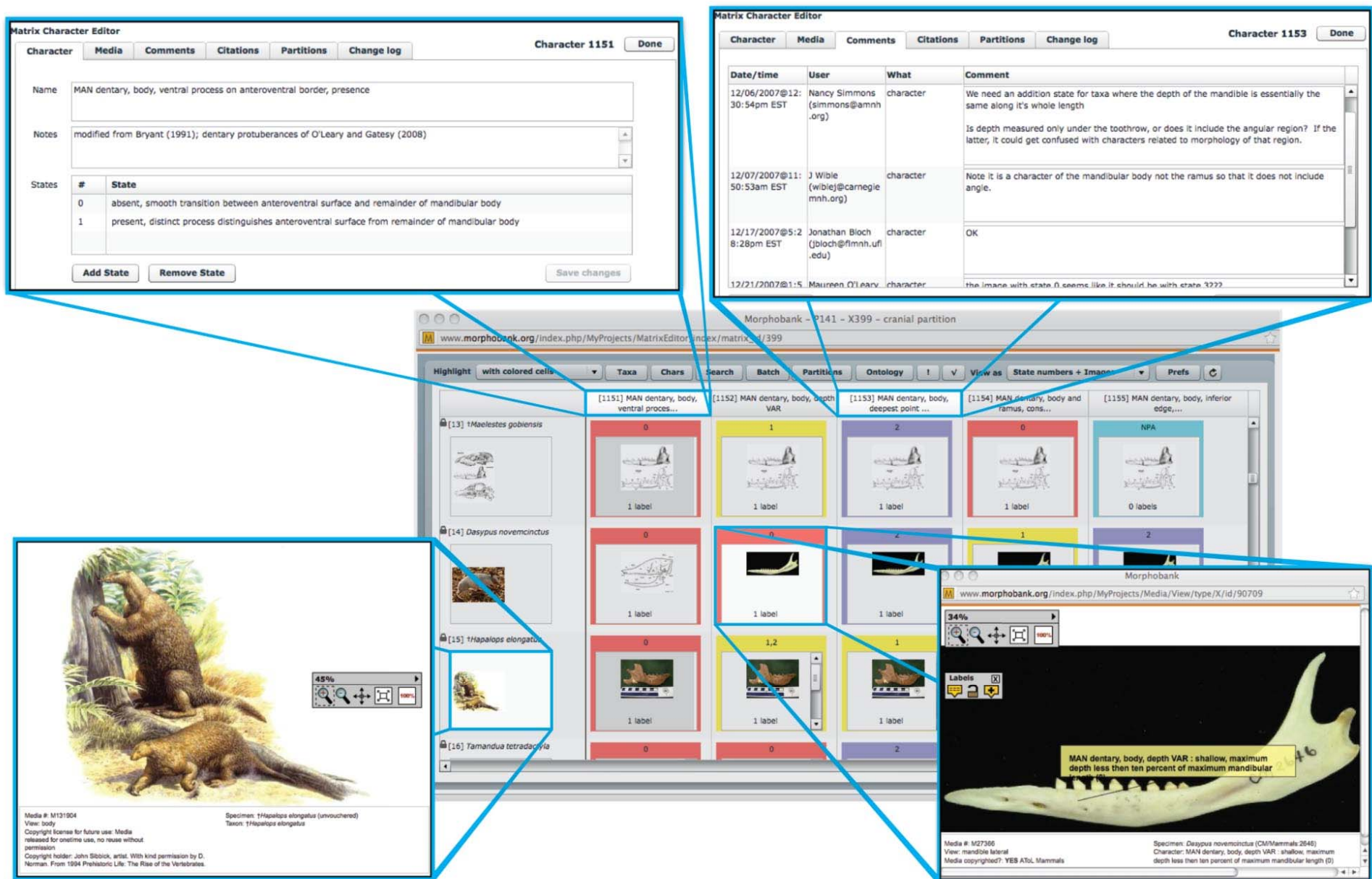
Maureen A. O’Leary,\* Jonathan I. Bloch, John J. Flynn, Timothy J. Gaudin, Andres Giallombardo, Norberto P. Giannini, Suzann L. Goldberg Brian P. Kraatz Zhe-Xi Luo Jin Meng Xijun Ni Michael J. Novacek Fernando A. Perini Zachary S. Randall Guillermo W. Rougier Eric J. Sargis Mary T. Silcox Nancy B. Simmons Michelle Spaulding Paúl M. Velazco Marcelo Weksler John R. Wible Andrea L. Cirranello

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DOI: 10.1126/science.1229237





**Fig. S1.** Screenshots of the phenomic matrix constructed in MorphoBank ([www.morphobank.org](http://www.morphobank.org)) demonstrating the deep data documentation, including images describing character scoring and discussion threads about homology.





# MORPHOBANK

HOMOLOGY OF PHENOTYPES OVER THE WEB

## **v3.0 Quickstart Guide** 20 pp.

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**Last Updated:** March 2012

**Produced by the MorphoBank team:**

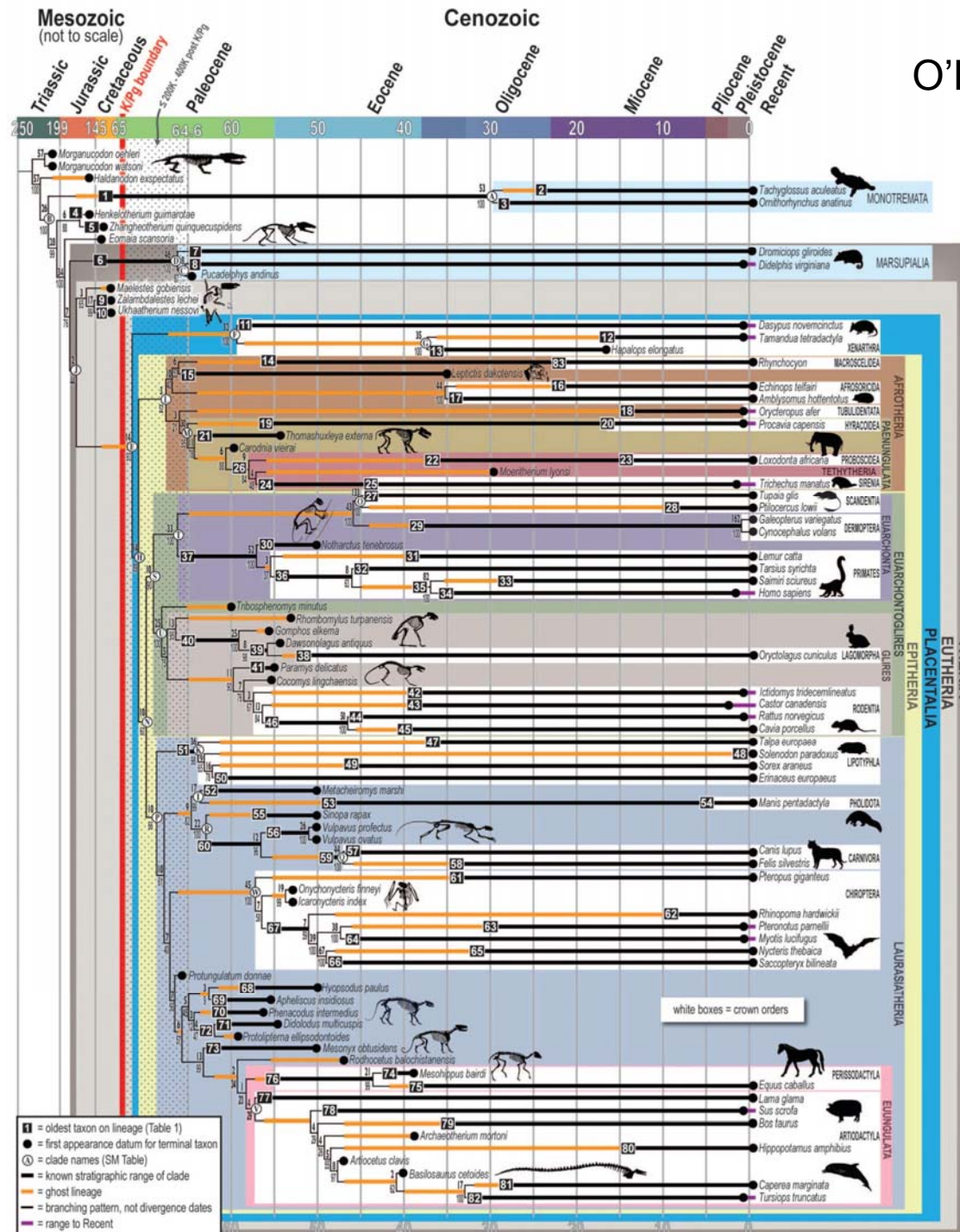
**Executive Committee:** Peter Crane, Gonzalo Giribet, Michael Novacek, Nancy Simmons, Dennis Stevenson, Marvalee Wake

**Project Director:** Maureen O'Leary

With support from the National Science Foundation, Divisions of Environmental Biology and Geosciences, NESCENT and NOAA

Results support the monophyly of most traditional orders originally identified on the basis of phenotypes, as well as interordinal groupings discovered using molecular sequence data (Fig. 1 and Table 1). Twenty nodes (over 40%) are congruent in partitioned molecular and phenomic analyses (fig. S2).

O'Leary et al., 2013: 662





When time-calibrated, this tree indicates that none of the six, very complete Mesozoic fossil species (e.g., *Ukhaatherium*, *Maelestes*, and *Zalambdalestes*) sampled falls within crown clade Placentalia. Instead, these Mesozoic fossils emerge as nonplacental members of Eutheria or at lower nodes. This tree suggests that interordinal and ordinal diversification occurred within the first few hundred thousand years after the K-Pg event, and the first members of modern placental orders began appearing 2 to 3 million years (My) later during the Paleocene.



We recognize *Protungulatum donnae* as the oldest undisputed species within crown Placentalia (Fig. 1), and this species dates to the earliest Paleocene (13) within an interval extending from the K-Pg boundary to ~200,000 to ~400,000 years later (16, 17). Integration of fossils as primary data in the phylogeny indicates that ~10 interordinal speciation events might have occurred in as little as 200,000 years.

System	Series	Stage	Age (Ma)
Neogene	Miocene	Aquitanian	younger
Paleogene	Oligocene	Chattian	23.03–28.1
		Rupelian	28.1–33.9
	Eocene	Priabonian	33.9–38.0
		Bartonian	38.0–41.3
		Lutetian	41.3–47.8
		Ypresian	47.8–56.0
	Paleocene	Thanetian	56.0–59.2
		Selandian	59.2–61.6
		Danian	61.6–66.0
Cretaceous	Upper	Maastrichtian	older

Subdivision of the Paleogene Period according to the [ICS](#), as of January 2013. <sup>[1]</sup>

62-63 млн. лет: формирование современных отрядов Placentalia

65 млн. лет: формирование надотрядов Placentalia

66 млн. лет: появление Placentalia

# *Protungulatum*, Confirmed Cretaceous Occurrence of an Otherwise Paleocene Eutherian (Placental?) Mammal

J. David Archibald · Yue Zhang · Tony Harper · Richard L. Cifelli

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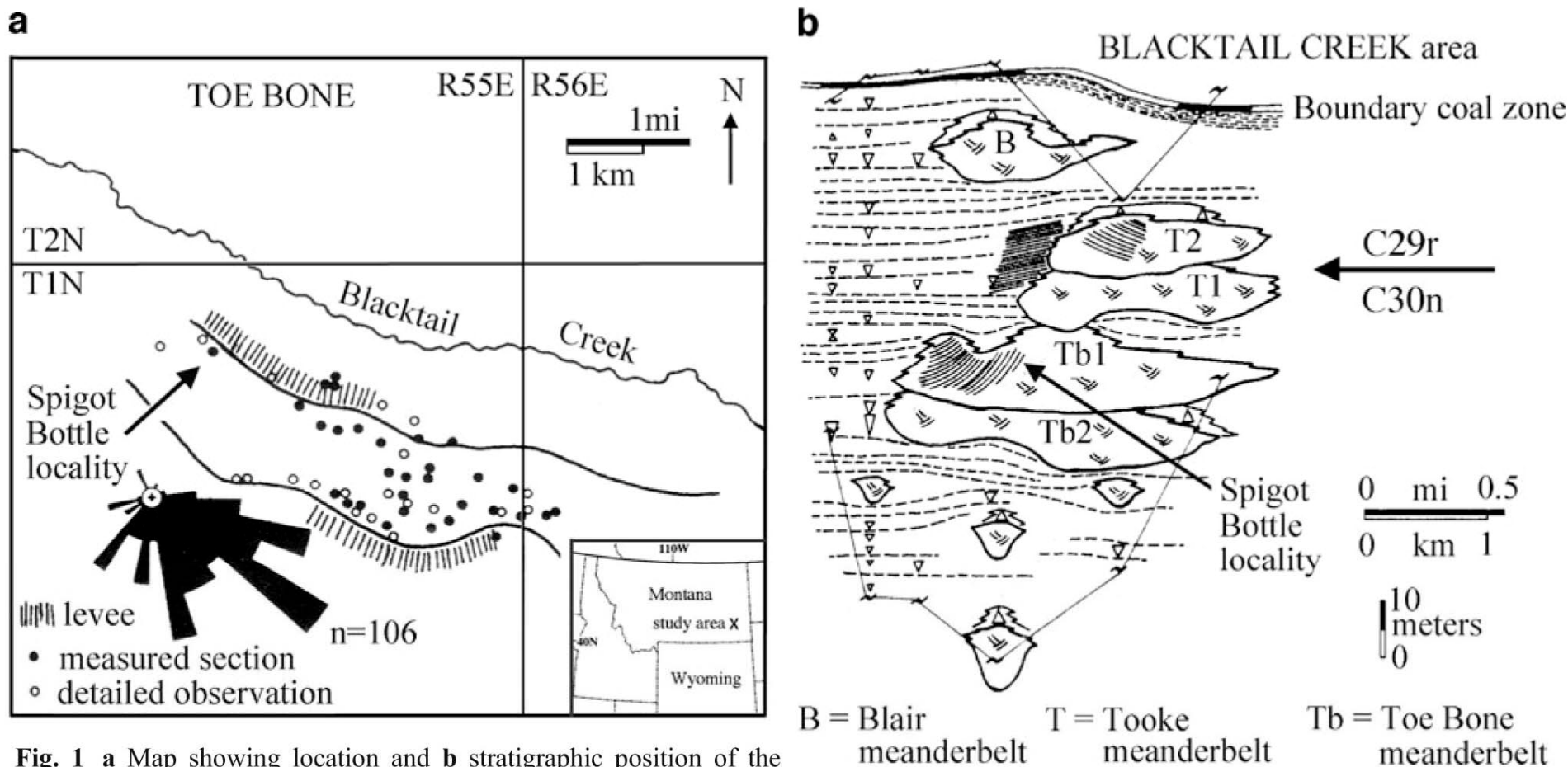
**Abstract** Neither pre-Cenozoic crown eutherian mammals (placentals) nor archaic ungulates (“condylarths”) are known with certainty based on the fossil record. Herein we report a new species of the Paleocene archaic ungulate (“condylarth”) *Protungulatum* from undisputed Late Cretaceous aged rocks in Montana USA based on an isolated last upper premolar, indicating rare representatives of these common early Tertiary mammals appeared in North America a minimum of 300 k years before the extinction of non-avian dinosaurs. The other 1200 mammal specimens from the locality are characteristic Late Cretaceous taxa. This discovery overturns the current hypothesis that archaic ungulates did not appear in North America until after the Cretaceous/Tertiary (K/T) boundary and also suggests that other reports of North American Late Cretaceous archaic ungulates may be correct. Recent studies, including ours, cannot determine whether *Protungulatum* does or does not belong to the crown clade Placentalia.

**Keywords** Eutheria · Placentalia · Archaic ungulate · *Protungulatum* · Late Cretaceous · Hell Creek Formation

## Introduction

The archaic ungulate or “condylarth” *Protungulatum donnae* was described from Bug Creek Anthills in northeastern Montana, U. S. A. (Sloan and Van Valen 1965). The sequence including Bug Creek Anthills and several other localities was thought to be Late Cretaceous in age, arguing for a gradual appearance of mammals otherwise known only from the Paleocene, and a gradual disappearance of typical Late Cretaceous mammals and dinosaurs (Sloan et al. 1986). This work argued that there were gradual rather than catastrophic extinctions at the Cretaceous/Tertiary (K/T) or Cretaceous/Paleogene (K/Pg) boundary. Although common co-occurrences of dinosaurs and Late Cretaceous mammals at Bug Creek Anthills argued for a Late Cretaceous age, subsequent work indicated the sites are Paleocene (Smit and Van der Kaars 1984) and fossils were reworked from Cretaceous sediments (Lofgren 1995). Thus, no archaic ungulates were known from Late Cretaceous localities.

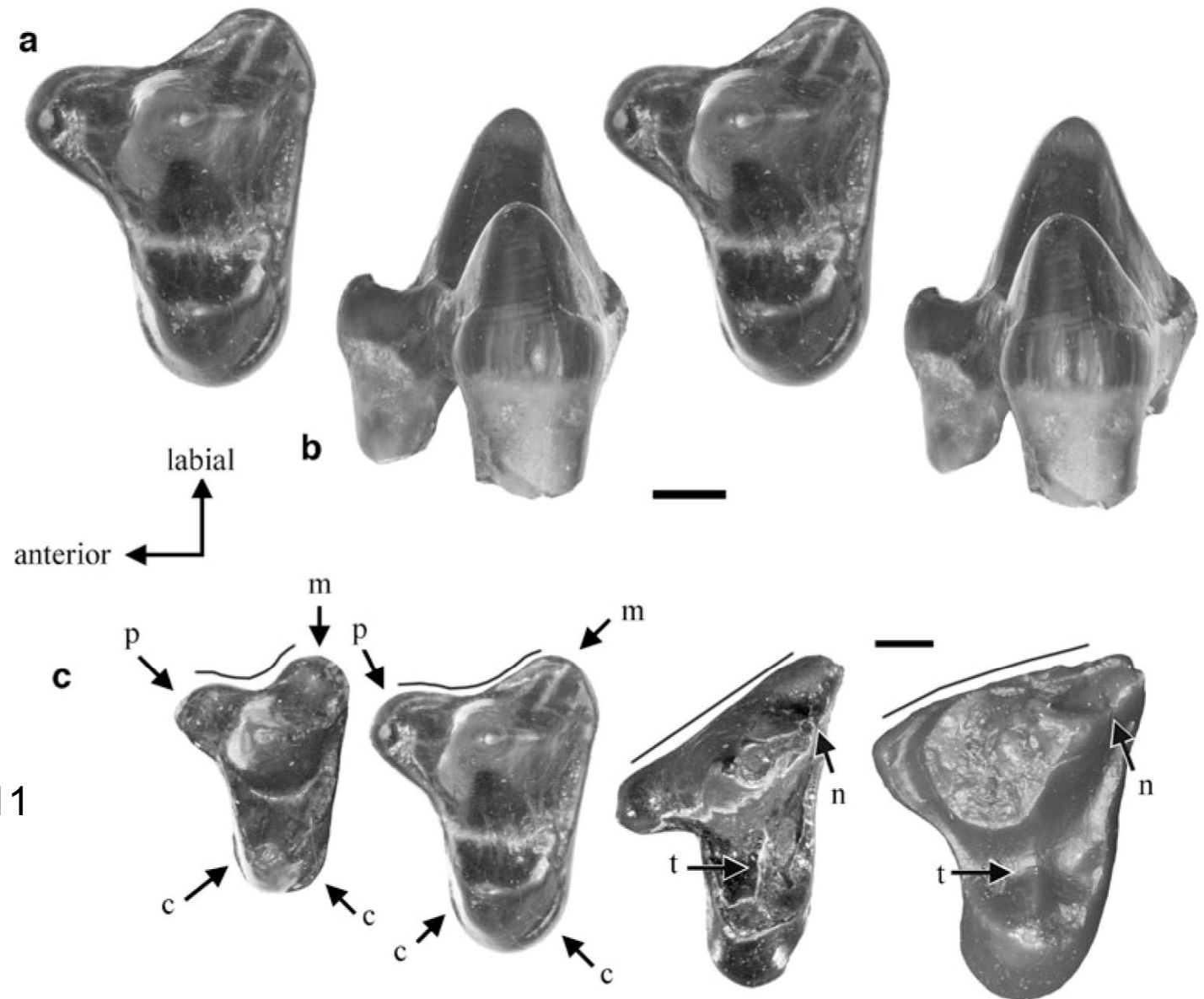
Two Canadian Late Cretaceous sites were argued to



**Fig. 1** **a** Map showing location and **b** stratigraphic position of the Spigot-Bottle locality within the Toe Bone Channelbelt, southeastern Montana (modified after Belt et al. 1997)

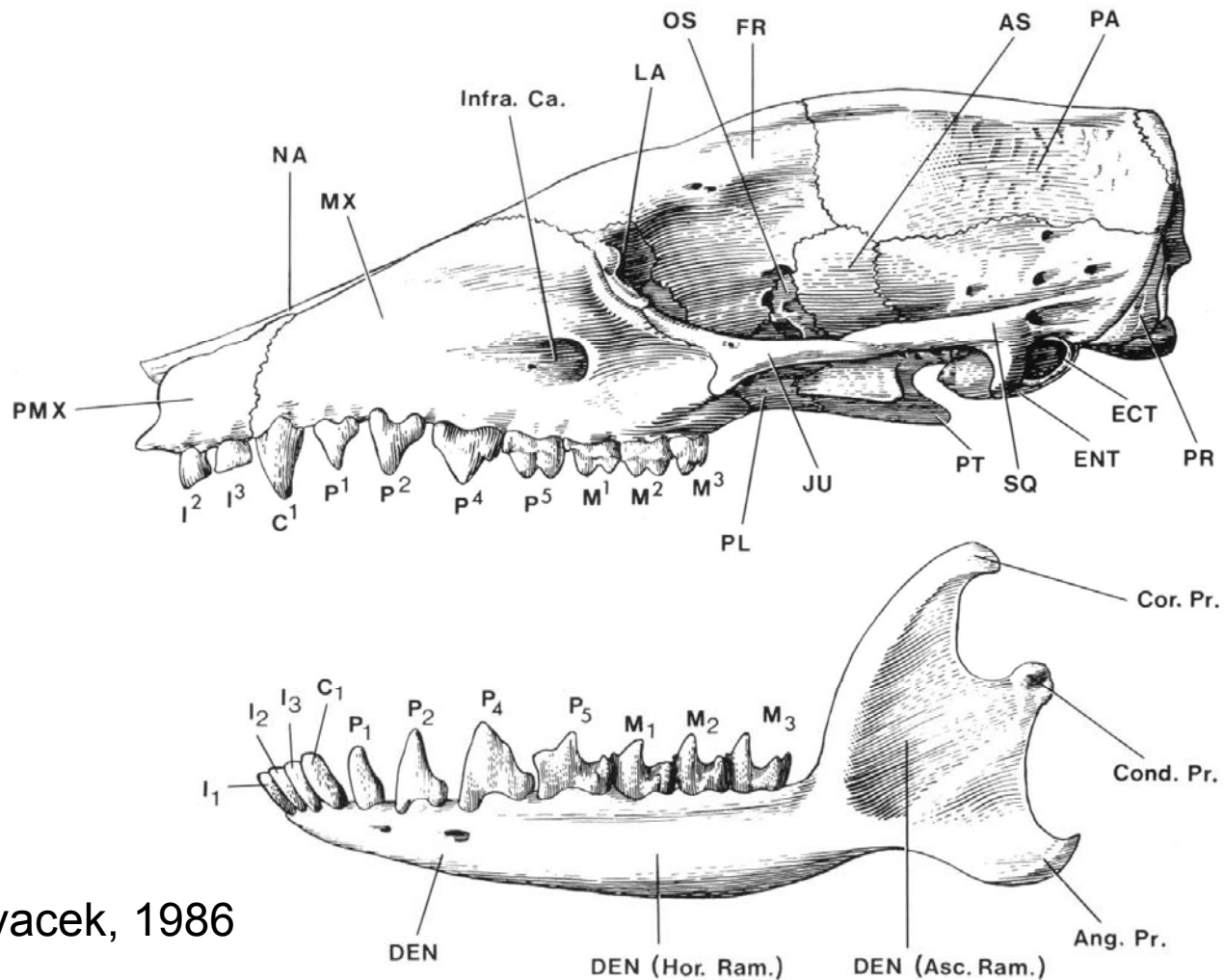
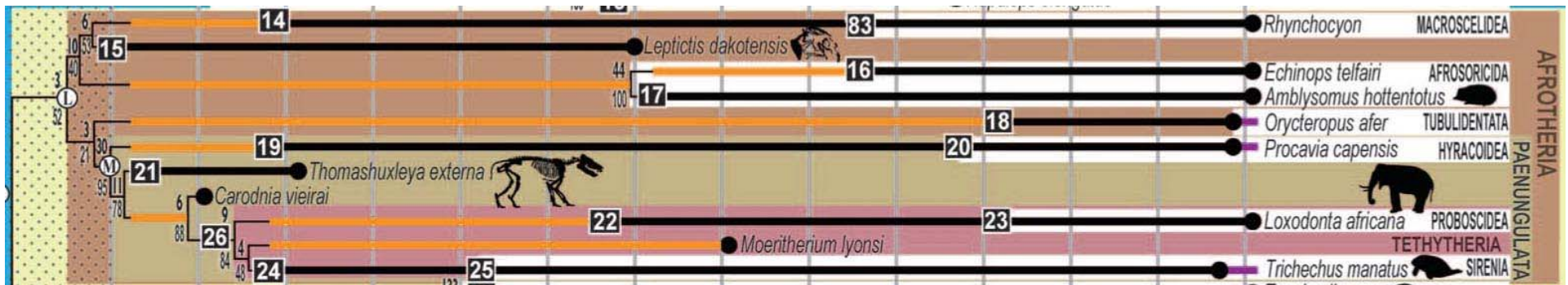


**Fig. 2** Photographs of last upper premolars: **a** occlusal and **b** lingual views (stereo pairs) of OMNH 64985, holotype of *Protungulatum coombsi*. **c** From left to right, occlusal views of *Protungulatum donnae*, UCMP 125961 (in maxilla, view reversed); *Protungulatum coombsi*, OMNH 64985; *Cimolestes stirtoni*, UCMP 52189; and cast of *Cimolestes magnus*, UCMP 107743 (in maxilla, view reversed). Scales equal one millimeter. c, cingula; m, metastylar region; n, carnassial notch; p, parastylar region; t, central crista



Archibald et al., 2011

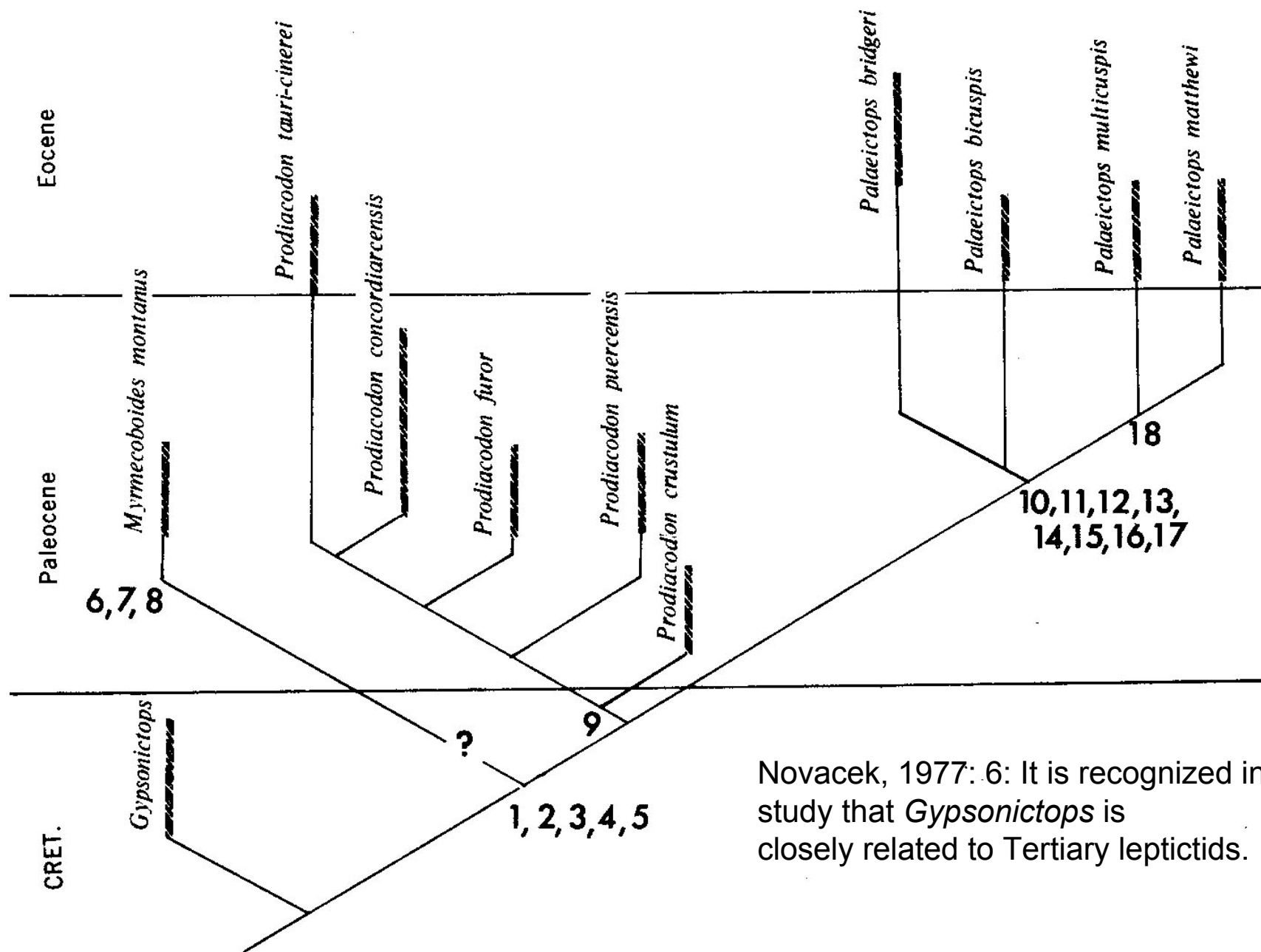
*Protungulatum donnae* was explicitly included in our analysis and falls within Placentalia contra (11, 51). *Protungulatum* has an age range restricted to the Paleocene with the exception of a proposed new species, *P. coombsi*, based on a single upper premolar from the Late Cretaceous Hell Creek Formation (122). We agree that there are general points of similarity (but not necessarily synapomorphy) between the single known tooth of *P. coombsi* and the tooth with the presumed equivalent locus in the species *P. donnae*. The extremely limited data for *P. coombsi* preserved in a single tooth is not sufficiently diagnostic for placement of this species among taxa considered in our study. Robust phylogenetic investigation of the placement of *P. coombsi* would require direct integration into the supermatrix of numerous other Mesozoic fossil species with diverse dentitions, including *Prokennalestes*, *Murtoilestes*, cimolestids, zhelestids, zalambdalestids, asioryctitheres and at least all taxa scored in (11, 51). If such a test showed that *P. coombsi* was a member of Placentalia this result would mean that interordinal but not ordinal diversification of placentals would extend to the very latest Mesozoic, a slightly older date than reported here but one that is still significantly younger than diversification dates found using molecular clocks (7, 8, 88, 123). This result would also conform to the explosive model of interordinal and ordinal diversification (3). At present *P. coombsi* has only ambiguous bearing on the timing of origin of placentals.



Novacek, 1986

FIG. 1. Lateral view of *Leptictis dakotensis* skull and jaws. For abbreviations see pp. 5–7.

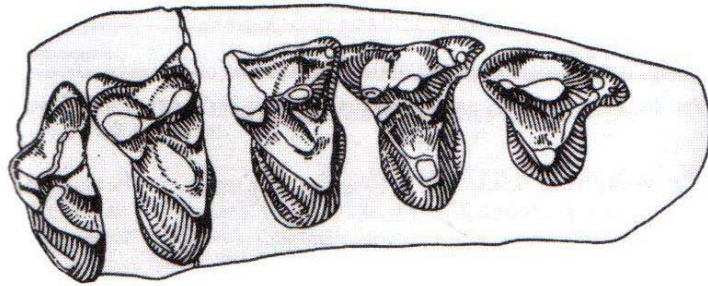




Novacek, 1977: 6: It is recognized in this study that *Gypsonictops* is closely related to Tertiary leptictids.

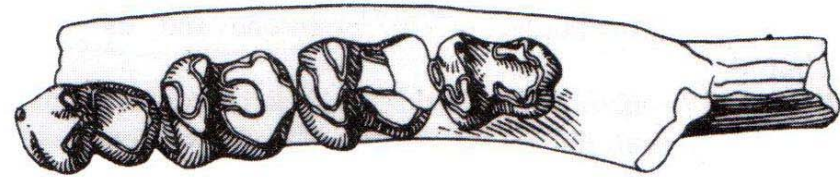
FIG. 14. Postulated phylogenetic relationships of the North American Paleocene and Eocene Leptictidae.



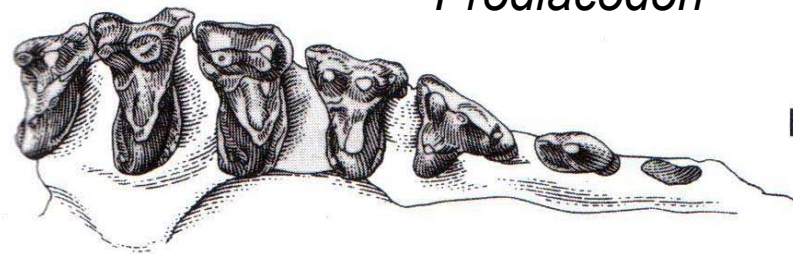


*Gypsonictops*

A

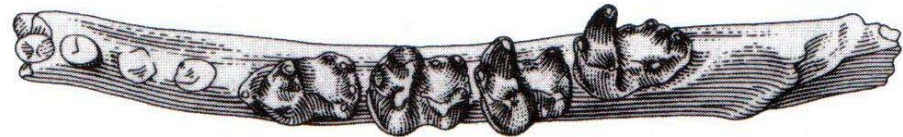


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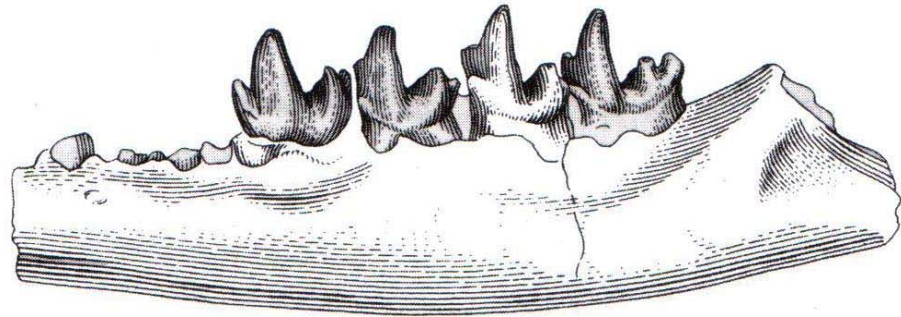
*Prodiacodon*

B



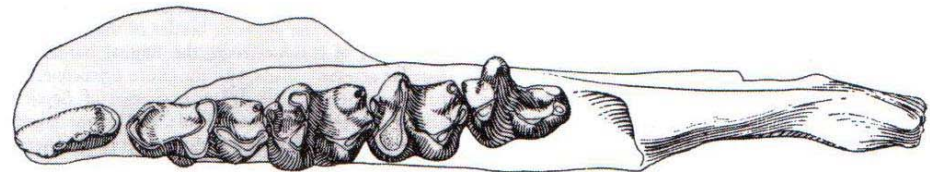
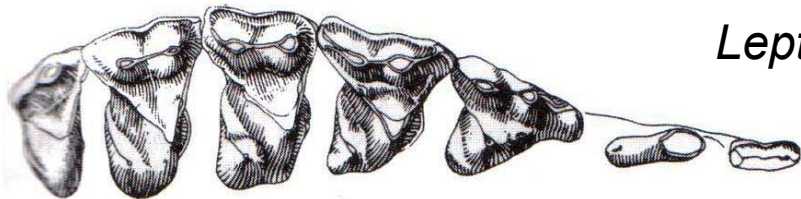
4 mm

Rose K.D. 2006. The Beginning of the Age of Mammals. Baltimore, John Hopkins University Press. XV+428.



*Leptictis*

C



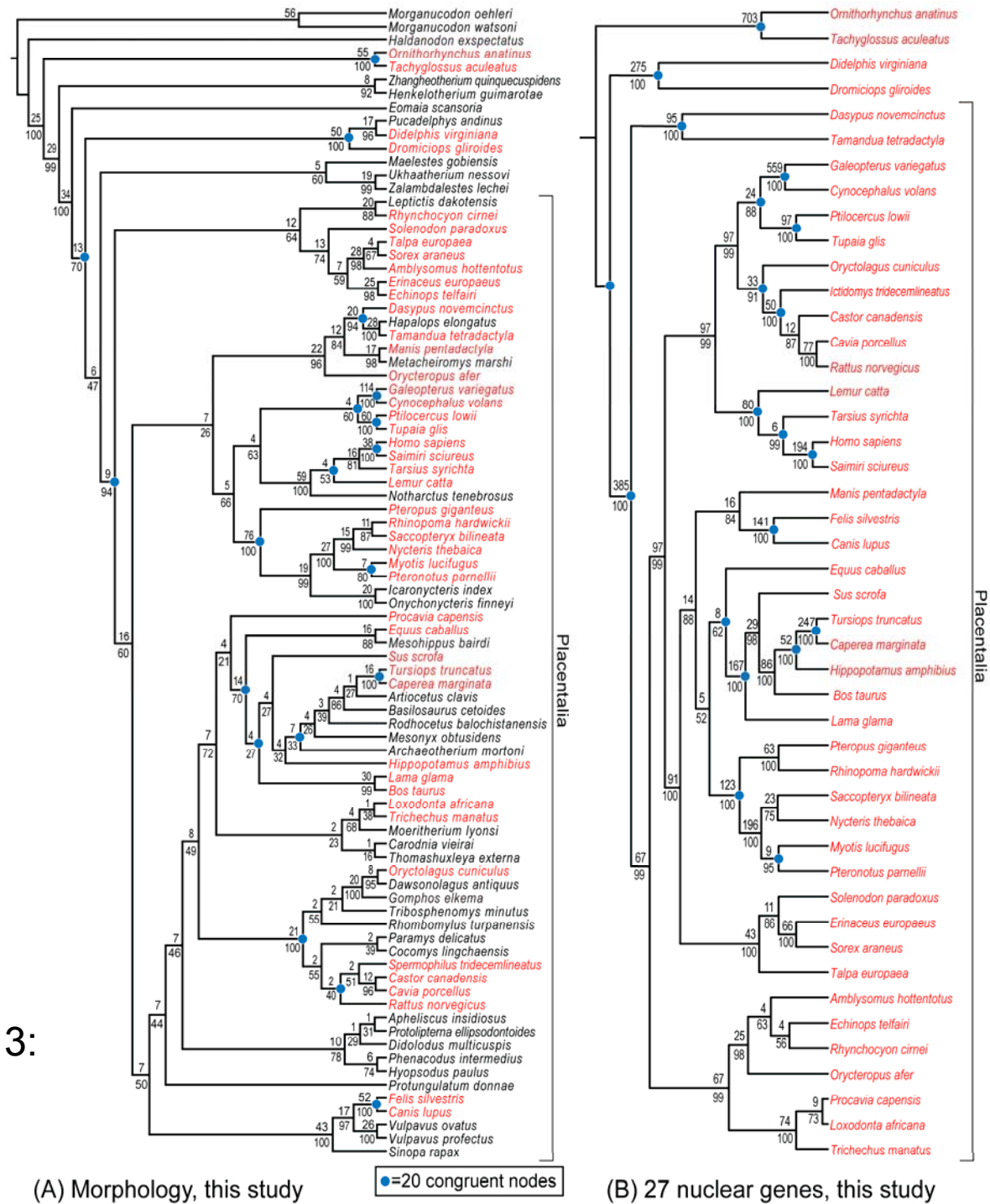
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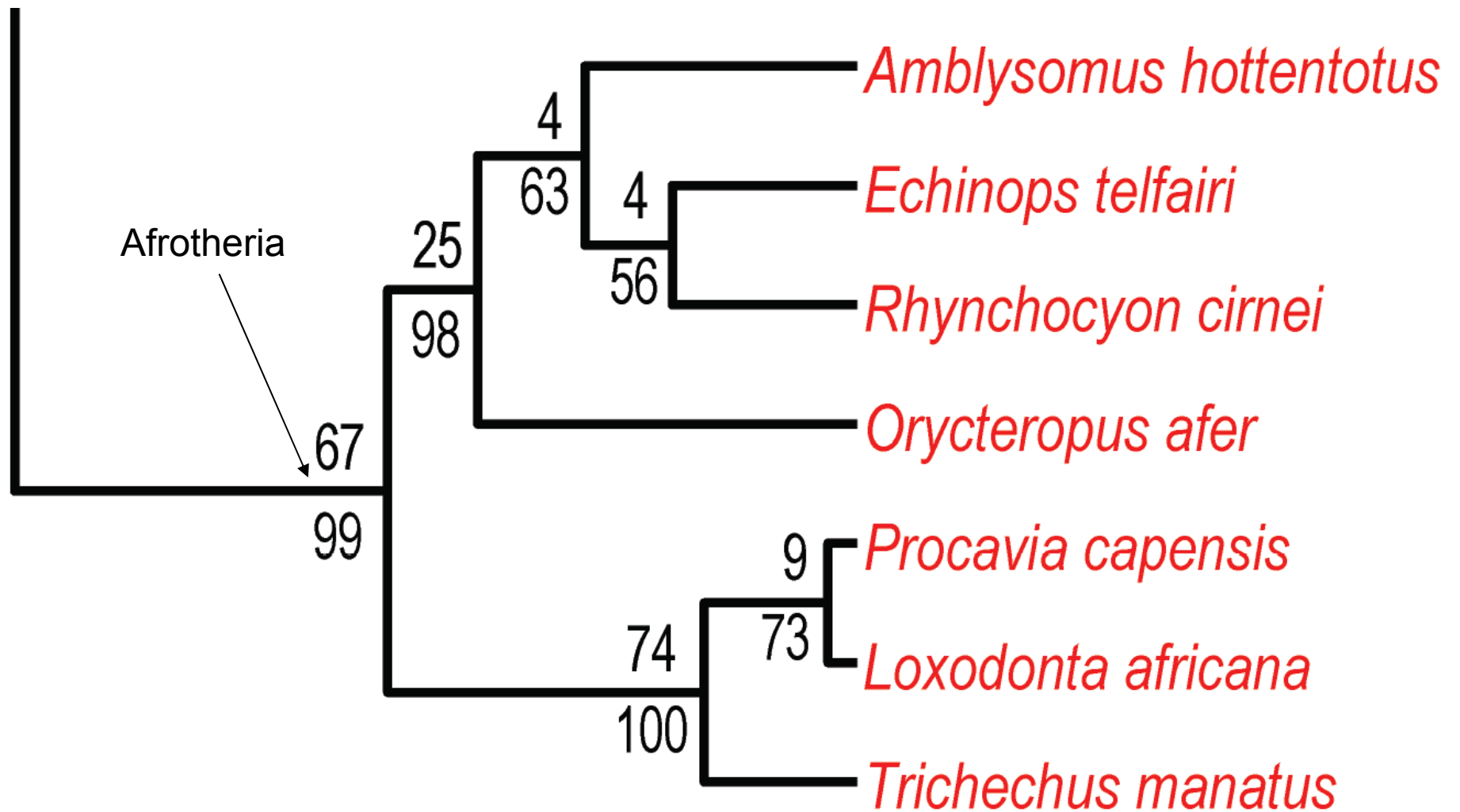
**Fig. 9.2.** Leptictidan dentitions, right upper teeth (left column), left lower teeth (right): (A) Late Cretaceous *Gypsonictops*; (B) Paleocene *Prodiacodon*; (C) late Eocene–early Oligocene *Leptictis*. (A, C from Lillegraven, 1969; B from Novacek, 1977.)

We have further comments on the choice of taxa selected to date minimum divergence times using ghost lineages (Fig. 1). One incompletely represented Late Cretaceous taxon, *Gypsonictops*, has been previously allied with leptictids (11, 33, 51, 120). Leptictids are represented in this paper by *Leptictis*, which falls within Placentalia in the combined data tree (Fig. 1). If a close relationship between *Gypsonictops* and *Leptictis* were upheld, it would extend the time of origin of crown placentals into the Mesozoic a few million years prior to the K-Pg event and would also expand the membership of Placentalia to include a taxon that has five premolars (33). The most comprehensive recent review of Mesozoic eutherians (11, 51) grouped *Gypsonictops* with *Leptictis* but placed this entire clade outside crown Placentalia. *Gypsonictops* is represented solely by partial dentitions, mandibles, and maxillae. This genus is known from at least four named species and perhaps several more currently left in open nomenclature (121), and a thorough taxonomic review of both published and unpublished material has yet to be accomplished. Any consideration of this taxon's affinities would require a more comprehensive comparative study with large numbers of Cretaceous and early Paleocene taxa, many of which are represented primarily by dental material. Pending such studies, the extensive dental and cranio-skeletal data represented by the Cretaceous taxa *Zalambdalestes*, *Maelestes*, and *Ukhaatherium* considered here seem the most effective basis for distinguishing stem from crown placentals and for estimating the time of origin of the latter clade.



O'Leary et al., 2013:  
fig. S2

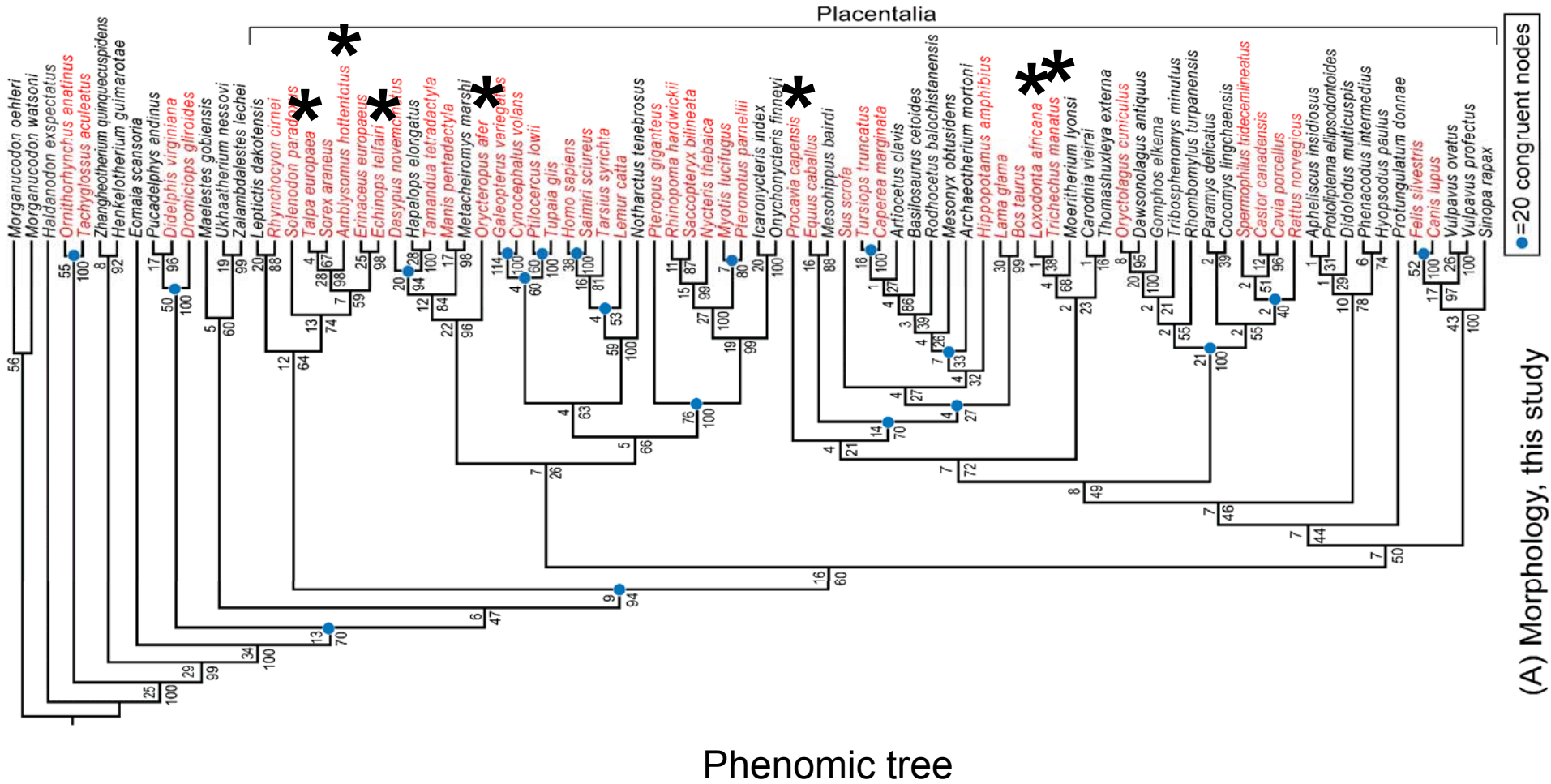


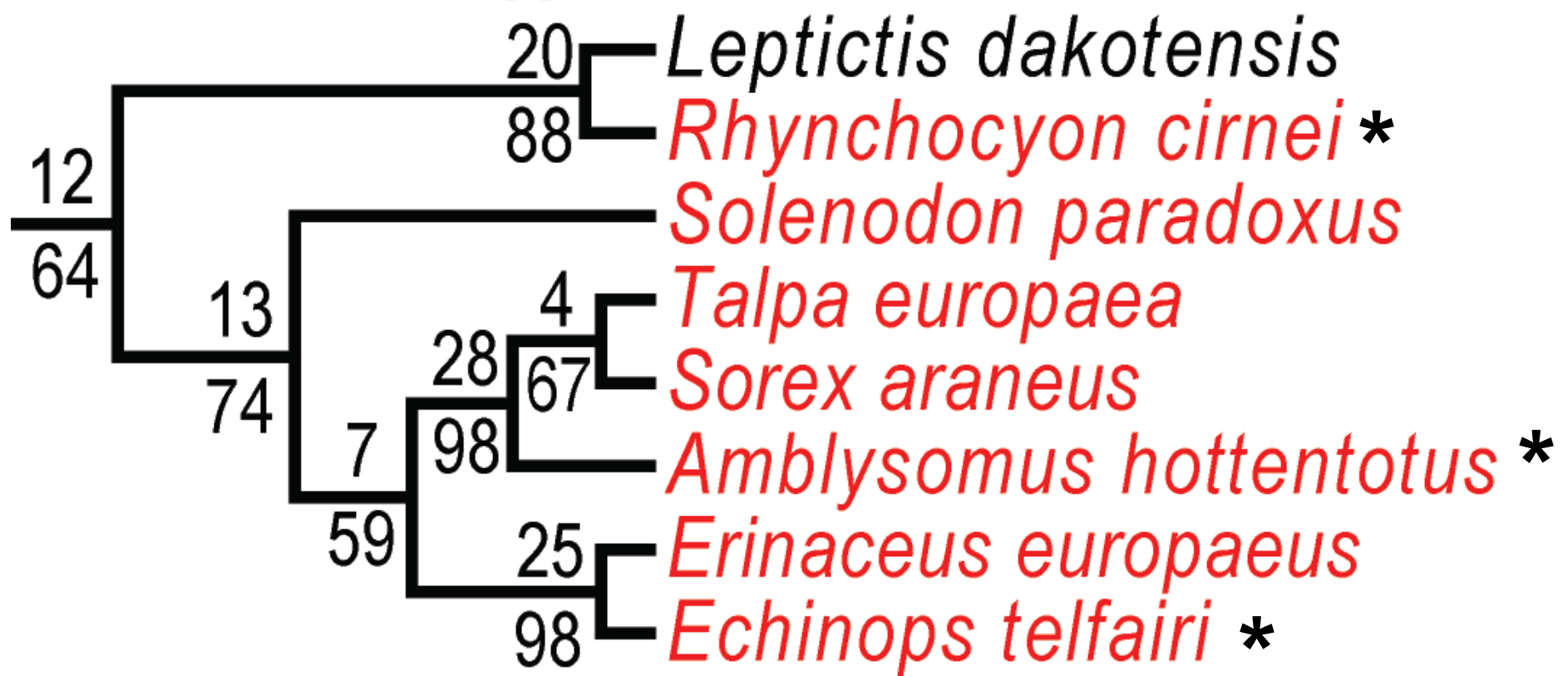


Genomic tree



# \* - “Afrotheria”





## Checkered elephant shrew<sup>[1]</sup>



### Conservation status



Near Threatened (IUCN 3.1)<sup>[2]</sup>

### Scientific classification

Kingdom: [Animalia](#)  
 Phylum: [Chordata](#)  
 Class: [Mammalia](#)  
 Order: [Macroscelidea](#)  
 Family: [Macroscelididae](#)  
 Genus: [Rhynchocyon](#)  
 Species: ***R. cirnei***

### Binomial name

***Rhynchocyon cirnei***

Peters, 1847



### Leptictis

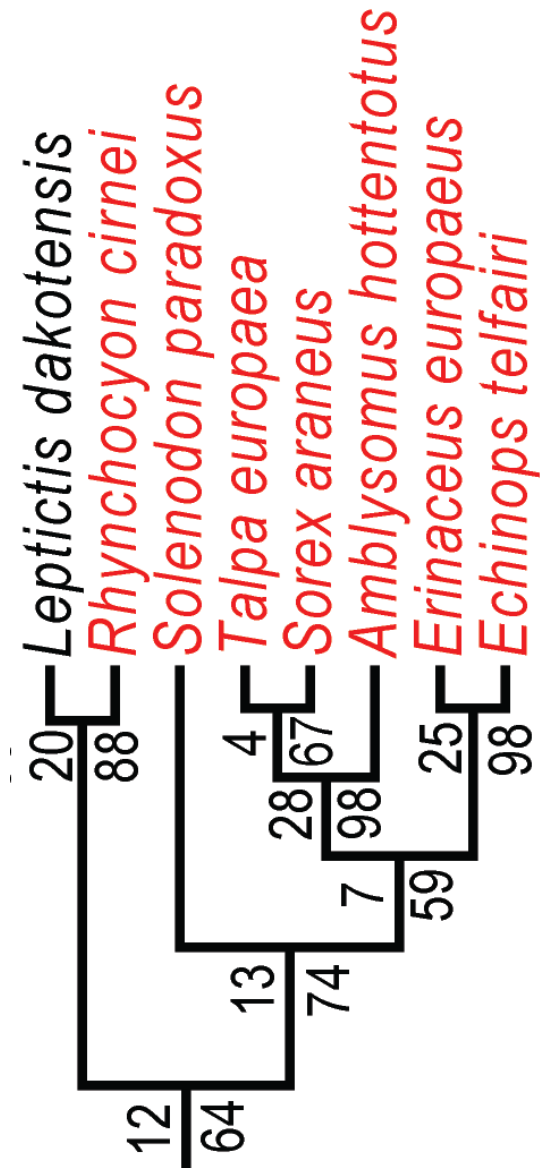
Temporal range: late [Eocene](#) to late [Oligocene](#)



*Leptictis acutidens*

### Scientific classification

Kingdom: [Animalia](#)  
 Phylum: [Chordata](#)  
 Class: [Mammalia](#)  
 Order: †[Leptictida](#)  
 Family: †[Leptictidae](#)  
 Genus: †[Leptictis](#)  
 Leidy, 1868

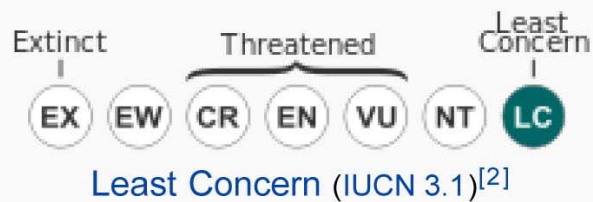




## European mole<sup>[1]</sup>



### Conservation status



### Scientific classification

Kingdom: Animalia  
 Phylum: Chordata  
 Class: Mammalia  
 Order: Soricomorpha  
 Family: Talpidae  
 Genus: *Talpa*  
 Species: *T. europaea*

### Binomial name

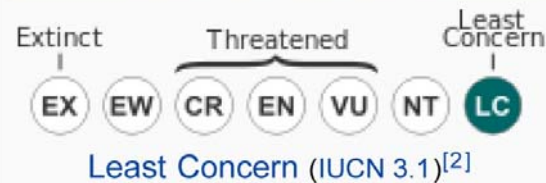
*Talpa europaea*

Linnaeus, 1758



## Hottentot golden mole<sup>[1]</sup>

### Conservation status



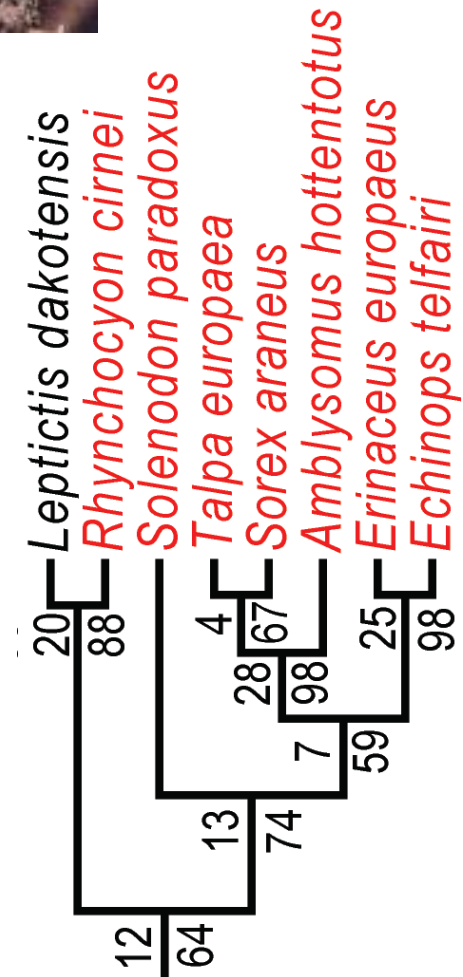
### Scientific classification

Kingdom: Animalia  
 Phylum: Chordata  
 Class: Mammalia  
 Order: Afrosoricida  
 Family: Chrysochloridae  
 Genus: *Amblysomus*  
 Species: *A. hottentotus*

### Binomial name

*Amblysomus hottentotus*

(A. Smith, 1829)

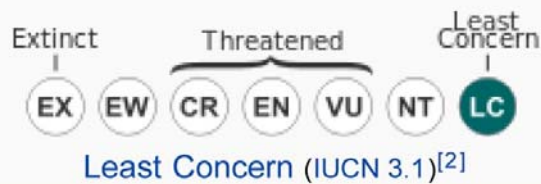




## European hedgehog<sup>[1]</sup>



### Conservation status



### Scientific classification

Kingdom: Animalia  
 Phylum: Chordata  
 Class: Mammalia  
 Order: Erinaceomorpha  
 Family: Erinaceidae  
 Subfamily: Erinaceinae  
 Genus: *Erinaceus*  
 Species: *E. europaeus*

### Binomial name

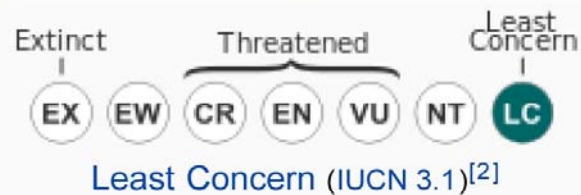
*Erinaceus europaeus*

Linnaeus, 1758

## Lesser hedgehog tenrec<sup>[1]</sup>



### Conservation status



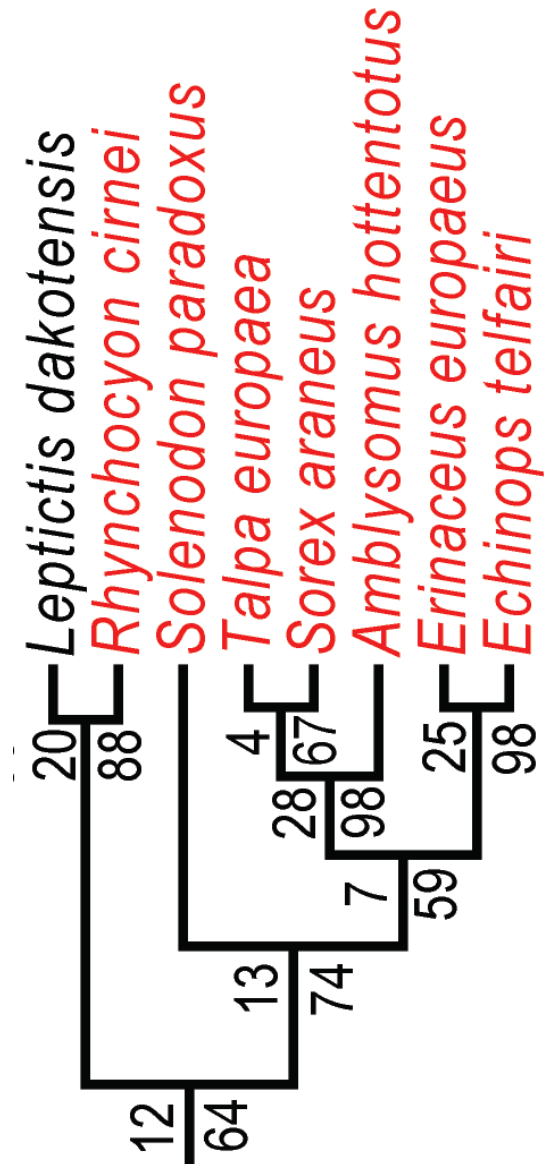
### Scientific classification

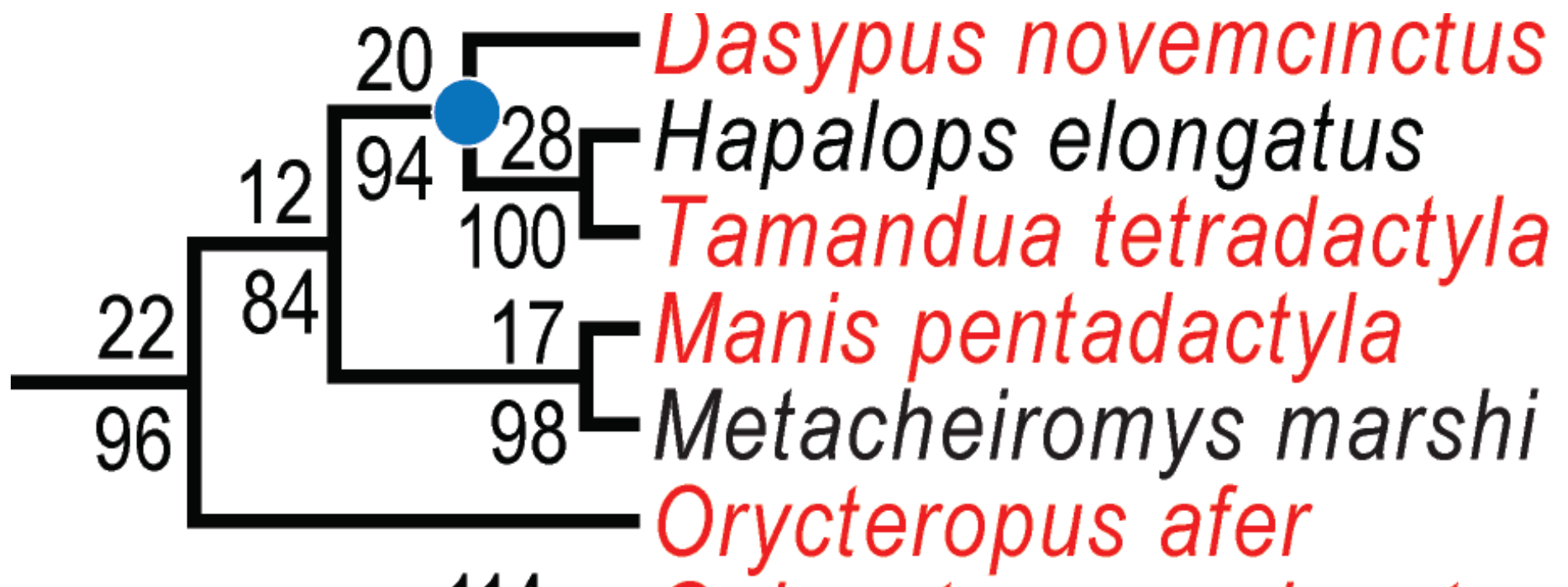
Kingdom: Animalia  
 Phylum: Chordata  
 Class: Mammalia  
 Order: Afrosoricida  
 Family: Tenrecidae  
 Genus: *Echinops*  
 Martin, 1838  
 Species: *E. telfairi*

### Binomial name

*Echinops telfairi*

Martin, 1838







Order **EDENTATA.**

Suborder **PILOSA.**

Bradypodidæ.  
Myrmecophagidæ.

Suborder **LORICATA.**

Dasypodidæ.

Suborder **SQUAMATA.**

Manidæ.

Suborder **TUBULIDENTATA.**

Orycteropodidæ.

Flower W.H. 1883. On the arrangement of the orders and families of existing Mammalia. Proceedings of the Zoological Society of London: 178-186.



**Metatheria common ancestor:** (7 postcanine teeth, 3 premolars, 4 molars, passed on to Marsupialia)

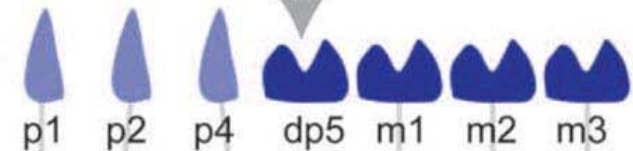
**Marsupialia**

*non-marsupial  
metatherians*

**METATHERIA**

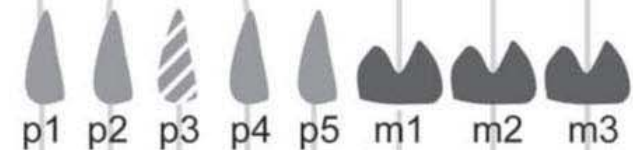
## Adult Postcanine Dental Formulae

*in matrix adult tooth is directly compared to deciduous teeth of non-metatherian taxa*



**Theria common ancestor:**  
(7 postcanine teeth with  
some variation to 8,  
4-5 premolars, 3 molars)

**THERIA**



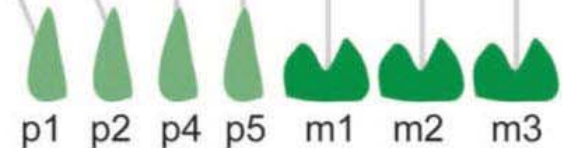
**Eutheria common ancestor:**  
(7-8 postcanine teeth, 4-5 premolars, 3 molars)

**EUTHERIA**

*non-placental  
eutherians*

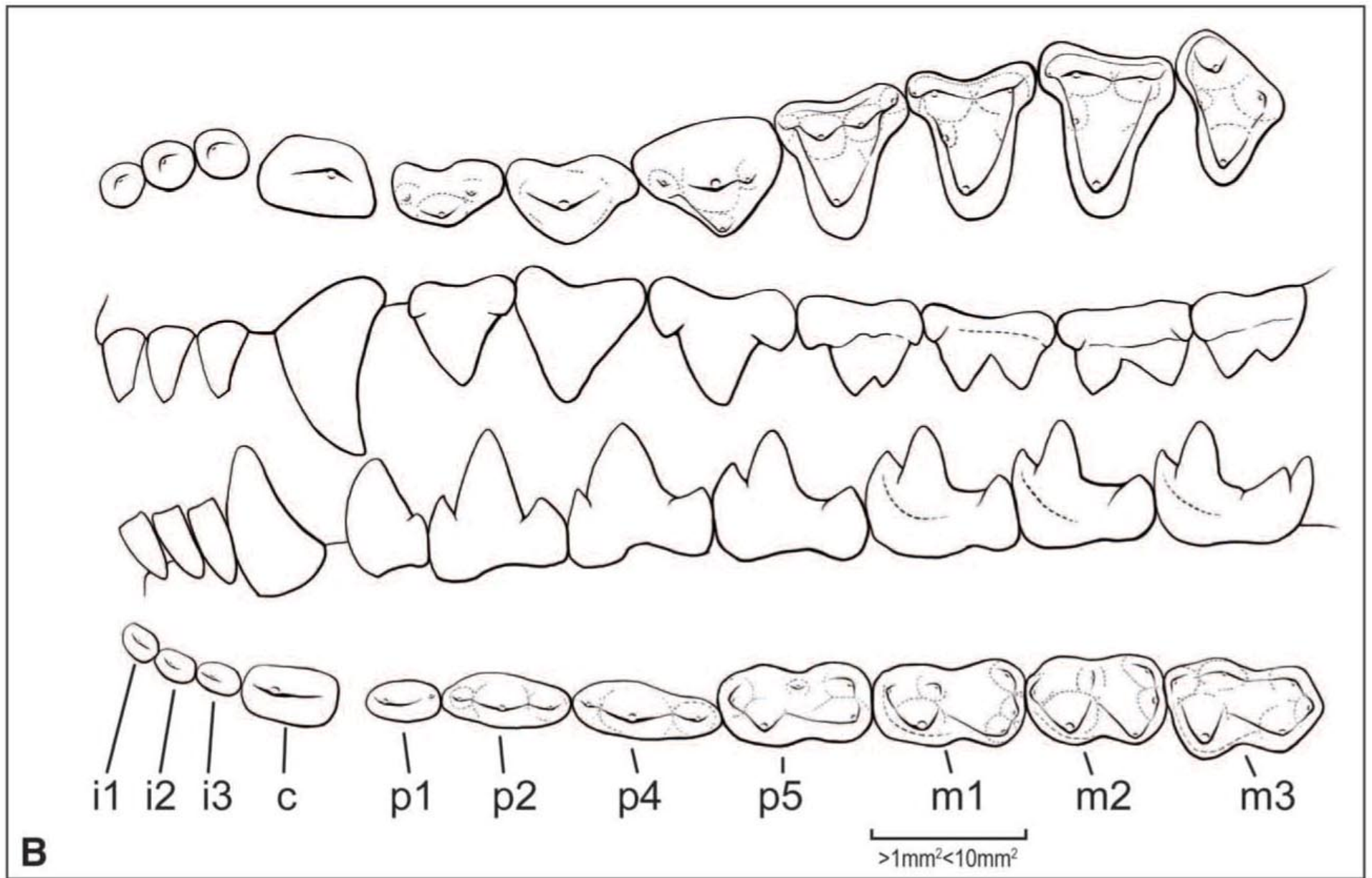
**Placentalia**

**Placentalia common ancestor:**  
(7 postcanine teeth: 4 premolars, 3 molars)

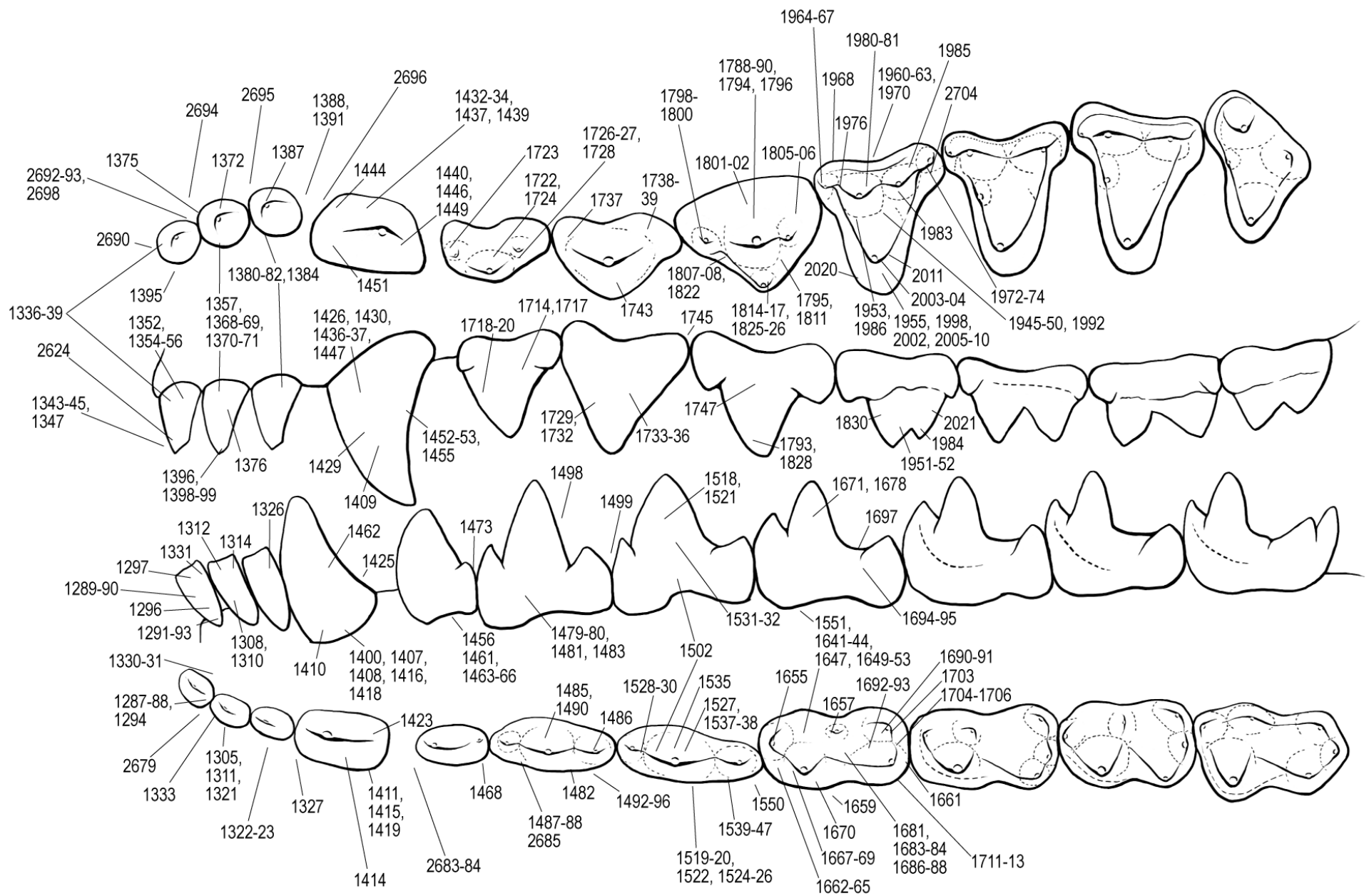


**A**



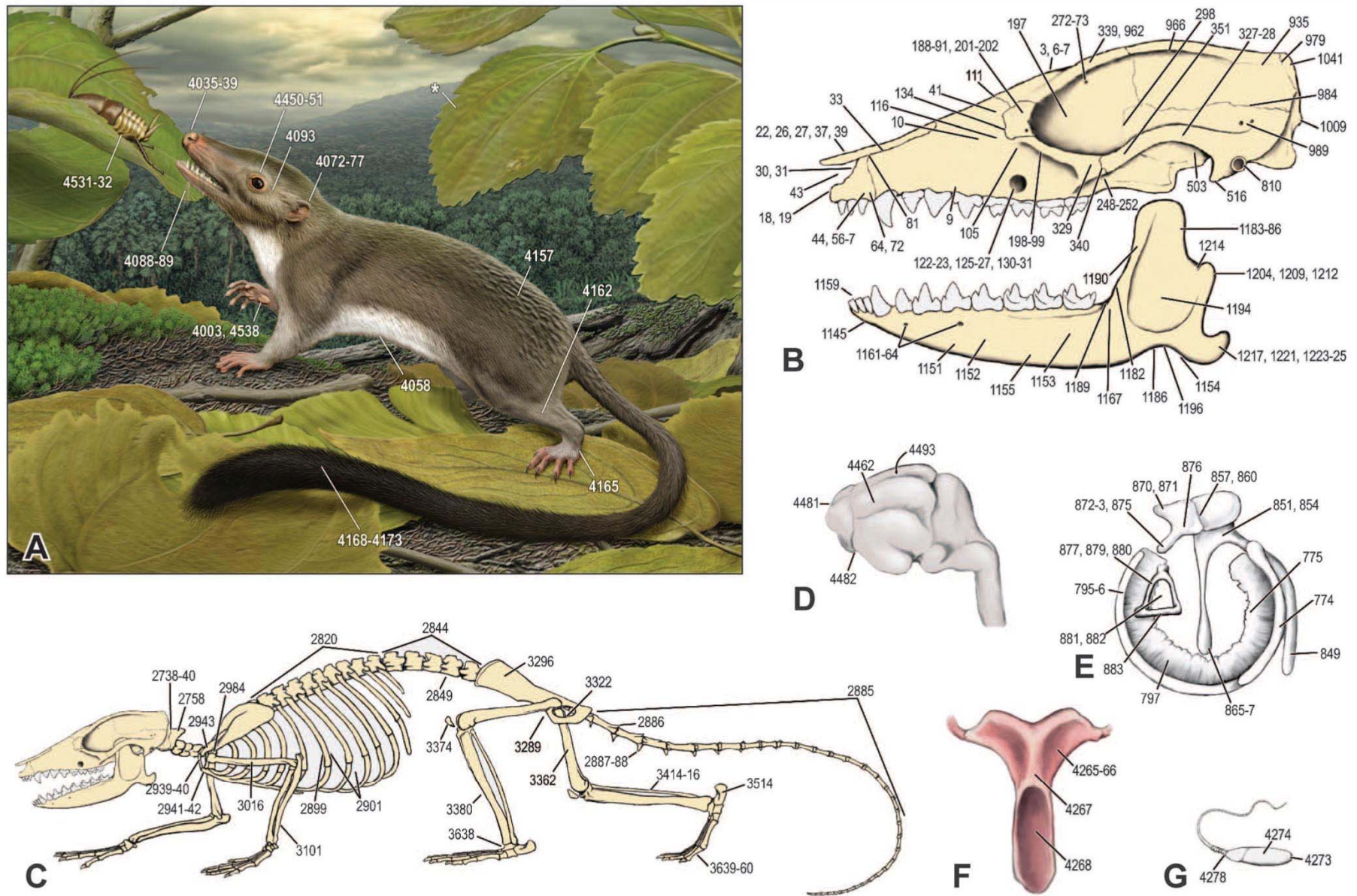


O'Leary et al., 2013: fig. 3B



**Fig. S11.** Characters used to reconstruct the incisors, canines, and premolars of the ancestral placental. Teeth shown from the left side. From top to bottom views are: occlusal and buccal I1-M3, and buccal and occlusal i1-m3.

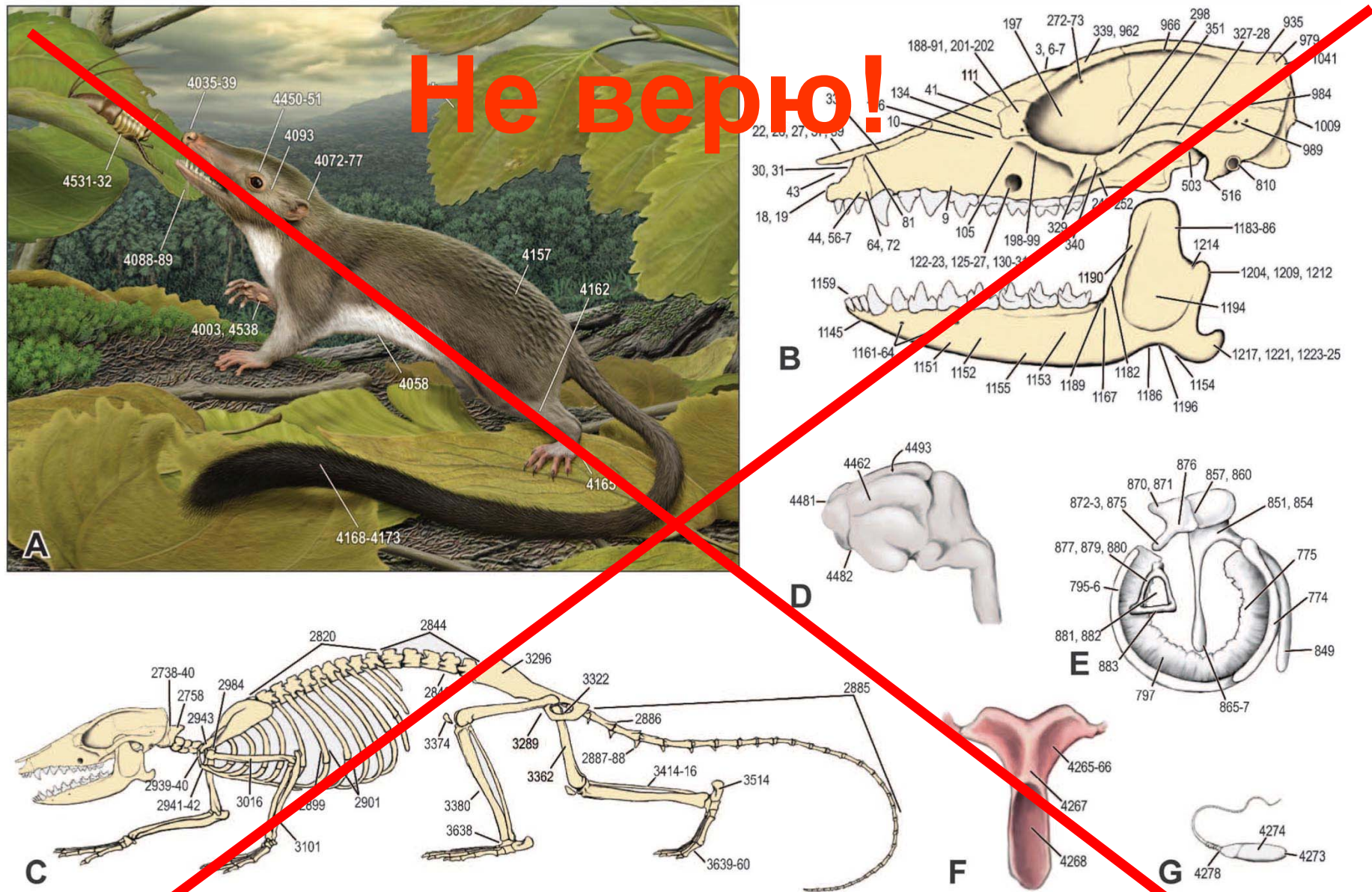




**Fig. 2.** Reconstructions of the phenotype of the hypothetical placental ancestor derived from the combined data matrix optimized onto the tree in Fig. 1. The mammal is shown in an early Paleocene ecosystem. (A) External body, posture, and diet of insectivory; asterisk depicts the plant *Paranymphea*

*crassifolia* of the early Paleocene. (B) Cranium and dentary bone, (C) skeleton, (D) brain in left lateral view, (E) ear ossicles and ectotympanic bone, (F) uterus, and (G) sperm cell. Numbers designate a subset of the numerous phenomic characters used to build these reconstructions (appendix S1).





**Fig. 2.** Reconstructions of the phenotype of the hypothetical placental ancestor derived from the combined data matrix optimized onto the tree in Fig. 1. The mammal is shown in an early Paleocene ecosystem. (A) External body posture, and diet of insectivory; asterisk depicts the plant *Paranymphea*

*crassifolia* of the early Paleocene. (B) Cranium and dentary bone, (C) skeleton, (D) brain in left lateral view, (E) ear ossicles and ectotympanic bone, (F) uterus, and (G) sperm cell. Numbers designate a subset of the numerous phenomic characters used to build these reconstructions (appendix S1).