

A New Species of *Arfia* (Hyaenodontidae, Creodonta) from the Basal Eocene of Mongolia

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Abstract—A lower jaw fragment of the creodont *Arfia langebadrae* sp. nov. (Hyaenodontidae, Proviverrinae) from the Lower Eocene Bumban Member of the Naran Bulak Formation of the Tsagan-Khushu locality (Mongolia) is described. This is the first record of this genus in Asia, which suggests a pan-Holarctic range of *Arfia* in the Early Eocene. The new species is similar to *A. zeke* Gingerich et Deutsch and is more specialized than *A. junnei* Gingerich and *A. gingerichi* Smith et Smith. A rapid migration of *Arfia* from Asia through North America to Europe at the Paleocene–Eocene transition is reconstructed. In addition to *A. langebadrae*, the Bumbanian Faunal Assemblage from Tsagan-Khushu includes the creodont *?Prototomus* sp.

Key words: *Arfia*, Proviverrinae, Hyaenodontidae, Creodonta, basal Eocene, Mongolia.

INTRODUCTION

Arfia belongs to the subfamily Proviverrinae of the creodont family Hyaenodontidae, which is typical for the Early Eocene of North America and Europe. The genus was originally established by Van Valen (1965) and included two North American species, *Sinopa opisthotoma* Matthew, 1901 (type species) and *S. shoshoniensis* Matthew, 1915. Subsequently, three more species were established, i.e., *Arfia junnei* Gingerich, 1989 and *A. zeke* Gingerich et Deutsch, 1989 from the Lower Wasatchian of North America and *A. gingerichi* Smith et Smith, 2001 from the basal Eocene of Europe (Gingerich, 1989; Gingerich and Deutsch, 1989; Smith and Smith, 2001).

Arfia is characterized by the following: the paracone and the metacone of M^1 and M^2 are nonfused; the metastyle (postmetacrista) of the upper molars (especially that of M^2) has a well-developed and long blade; the enamel of the cheek teeth is clearly rugose; and M_1 – M_3 have wide talonids and wide, round, and closed basins (Gingerich, 1989). The horizontal ramus of the lower jaw is massive and slightly narrows anteriorly (in contrast to that of *Prototomus* and *Tritemnodon*). The premolars are conical, labiolingually compressed, and have well-developed shearing edges on both the posterior and anterior sides of the main cone (similar to the premolars of Apterodontini). The upper canine (*A. opisthotoma*) is high-crowned (long), has a pointed apex, and lacks clear shearing edges (especially on the anterior side); P^1 is double-rooted, while P_1 is single-rooted. The cingula and cingulids are well-developed on the upper and lower premolars, except for P^1 (*A. opisthotoma*) and P_1 (*A. shoshoniensis*). P^4 has a

large protocone projection, while P^3 lacks this projection.

The earliest finds of North American *Arfia* come from the basal Wasatchian (Sandcouleean, Wa0) of the Clarks Fork Basin (Wyoming). This is the most frequently registered member of the Hyaenodontidae, which survived in North America to the Middle Wasatchian (Early Graybullian, Wa3). *Arfia* is considered to be one of the best index taxa of the Early Eocene of North America (Gingerich, 1989).

The European species *A. gingerichi* is known from the basal Eocene (Zone MP7) of Belgium (Dormaal), France (Marne: Erquelinnes, Try), and Great Britain (Suffolk: Kyson).

The first *Arfia* discovered in Asia is described below. This specimen comes from the base of the red gravelstone beds of the Bumban Member of the Tsagan-Khushu locality in Mongolia. It was found by the South Gobi Party of the Joint Soviet–Mongolian Paleontological Expedition headed by V.Yu. Reshetov in 1980.

The teeth are described on the basis of the standard terminology (Lange-Badre, 1979; Smith and Smith, 2001) proposed by Van Valen (1966; see also Kay and Hiimae, 1974). Some original terms are introduced as well. The paracristid is considered to be only the blade of the paraconid (which is located anterior to the carnassial notch); the anterior crest of the protoconid is termed the protoconid blade, or the preprotocristid; a supplementary cuspule of the talonid that is located anterior to the entoconid is designated as the ectoconulid; and the cuspule in the middle of the cristid oblique is designated as the mesoconid (Fig. 1). In the upper molars, the crests that are separated from one

another by the carnassial notch are designated as the postmetacrista and metastylar blade (the latter is located anterolabial to the carnassial notch).

The measurements were performed according to the scheme proposed by Gingerich and Deutsch (1989). The labial length of the talonid was measured from the anterior end of the cristid oblique in the point of its contact with the posterior wall of the trigonid to the posterior border of the hypoconulid. The lingual length of the talonid was measured from the base of the posterior side of the metaconid to the posterior border of the hypoconulid. The heights of the paracone and metacone were measured from the ventral surface of the cingulum to the cone apex. The metastylar length was measured along the longitudinal axis from the carnassial notch to the posterior border of the tooth crown. The lower jaw robustness index was calculated as the ratio of the lower jaw depth under M_1 to the length of the row of the lower cheek teeth.

The following abbreviations are used in this study: (DPC) Duke Primate Center, Durham, North Carolina, United States; (IVPP) Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Science, People's Republic of China; (PIN) Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia; (UM) Museum of Paleontology, University of Michigan, Ann Arbor, Michigan, United States; (L) length; (W) width; (TAW) talonid width; (TRL) trigonid length; (TRW) trigonid width; (n) sample size; (h) depth of the horizontal ramus of the lower jaw at the middle of M_1 ; (LP_1-M_3) length of the lower cheek teeth; and (Kmlj) lower jaw robustness index, $Kmlj = h : LP_1-M_3$.

SYSTEMATIC PALEONTOLOGY

Order Creodonta Cope, 1875

Family Hyaenodontidae Leidy, 1869

Subfamily Proviverrinae Schlosser, 1886

Genus *Arfia* Van Valen, 1965

Arfia langebadrae Lavrov et Lopatin, sp. nov.

Plate 9, figs. 1–4

E t y m o l o g y. In honor of Brigitte Lange-Badre, a well-known French paleotheriologist and expert on creodonts.

H o l o t y p e. PIN, no. 3104/785, left dentary fragment with DP_4-M_1 ; southern Mongolia, Tsagan-Khusu locality; basal Eocene, Naran Bulak Formation, Bumban Member.

D e s c r i p t i o n (Fig. 2). The lower jaw fragment belongs to a young animal. Its DP_4 is slightly worn, while M_1 has almost completely erupted. The horizontal ramus of the lower jaw is low. The teeth are medium-sized compared to those in other members of the genus.

DP_4 and M_1 are tuberculate sectorial and low-crowned. The enamel surface is rugose. The rugose

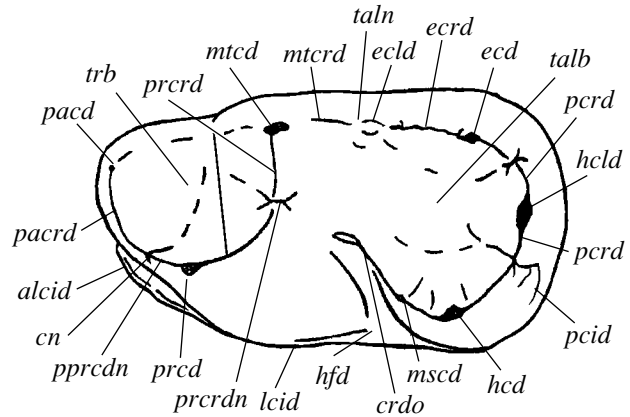
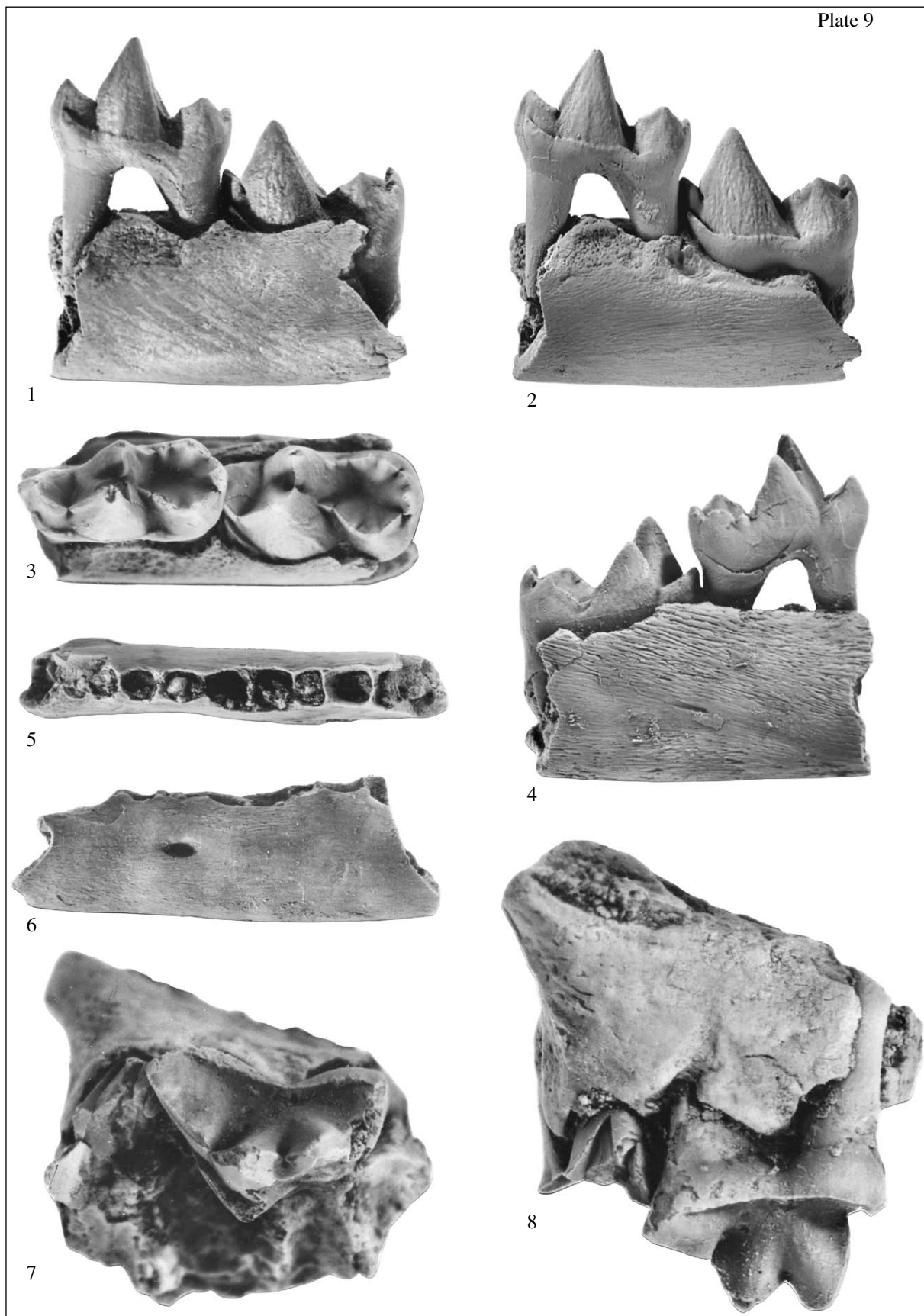


Fig. 1. Terminology for structural elements of the occlusal surface of the lower molars of the Proviverrinae illustrated by the example of M_1 of *Arfia*. Designations: (alcid) anterolabial cingulid, (cn) carnassial notch, (crdo) cristid oblique, (ecd) entoconid, (eald) entoconulid, (ecrd) entocristid, (hcd) hypoconid, (hald) hypoconulid, (hfd) hypoflexid, (lcid) labial cingulid, (mscd) mesoconid, (mtcd) metaconid, (mtrcd) metacristid, (pacd) paraconid, (pacrd) paracristid, (pcid) postcingulid, (pprcrd) preprotocristid, (prcd) protoconid, (prcrd) protocristid, (prcrdn) protocristid notch, (talb) talonid basin, (taln) talonid notch, and (trb) trigonid basin.

structure is especially well-pronounced on the labial side of M_1 .

DP_4 is molariform and has well-developed cones of the talonid and trigonid, including the metaconid. The trigonid basin is narrow and shallow. The anterolabial cingulid is well-developed and extends from the base of the anterolabial wall of the paraconid to the line of the carnassial notch, under which it is connected to the narrow and weak labial cingulid. The labial cingulid is thickened in the area of the hypoflexid and terminates in line with the middle of the cristid oblique. The paraconid is large and conical. In an occlusal view, its anterolingual edge tapers (Pl. 9, fig. 3; Fig. 2b). The anterior surface of the paraconid is clearly convex; the posterior surface, which is formed by the paracristid, is slightly concave (Fig. 2a). The paraconid blade (paracristid) is less than half the length of the protoconid blade (preprotocristid). The protoconid blade is straight (Fig. 2a). The horizontal angle between the paracristid and preprotocristid is approximately 145° , and the vertical angle is 80° . The carnassial and protocristid notches are relatively shallow, but clearly pronounced. The protoconid is high, conical, symmetrical, and almost twice as high as the paraconid. The metaconid portion of the protocristid is straight, while the protoconid portion is absent, because the lingual wall of the protoconid is broken off. The metaconid is slightly lower than the protoconid and is somewhat displaced posteriorly. On the lingual edge of the posterior side,



the metaconid has a well-pronounced and sharp crest, the metacristid.

The talonid is slightly wider than the trigonid and slightly less than half as long as the tooth. The talonid basin is round and relatively wide (Fig. 2b). The talonid notch is well-pronounced. The anterior edge of the cristid oblique is displaced lingually, closely approaches the line of the protocristid notch, and ascends on the posterior wall of the trigonid to its midheight. The talonid is relatively high and has a large hypoconid and a well-pronounced cristid oblique. The latter has a small additional cuspule, the mesoconid. The hypoconulid expands labiolingually. The entoconid is small compared to the other two talonid cusps and extends antero-posteriorly. Its anterior projection forms a short and high entocristid. The small conical entoconulid is located between the entocristid and the metacristid. The posterocristid has a distinct notch between the hypoconulid and the entoconid. The hypoconid and hypoconulid are isolated from each other by a narrow fold.

The anterior root of DP₄, which is exposed in a broken site of the jaw, has an unclosed root canal. The crown is raised above the alveolar margin of the lower jaw.

M₁ is slightly longer and substantially wider than DP₄. The trigonid and talonid are equal in width. The anterolabial cingulid is prominent at the base of the paraconid and extends posteriorly to the line of the middle of the protoconid blade. The narrow labial cingulid extends from the middle of the labial wall base of the protoconid to the posterior region of the hypoflexid. The posterior end of the anterolabial cingulid is located a small distance from the anterior edge of the labial cingulid (approximately 0.4 mm apart, while the tooth is 6.4 mm long).

The carnassial notch is deep. The trigonid basin is narrow (Fig. 2b). The paraconid is relatively small, substantially lower than the metaconid. The apex of the paraconid is far displaced lingually (Fig. 2b). The paraconid blade is less than half as long as the protoconid blade, the paracristid and preprotocristid are straight, and the horizontal angle between them is approximately 135°, while the vertical angle is approximately 90°. The protoconid is high, massive, and slightly inclined anteriorly; its labial surface is convex. The protocristid has a clear shearing edge and a deep notch. The metaconid is substantially lower than the protoconid, and its apex is slightly displaced posteriorly with reference to the

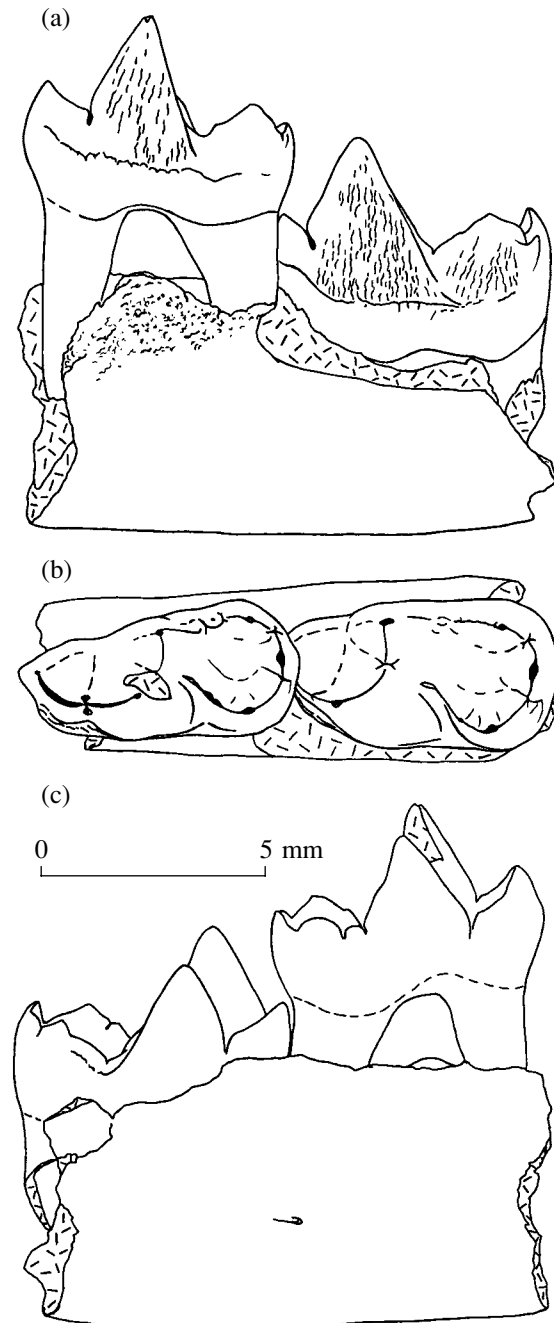


Fig. 2. *Arfia langebadrae* sp. nov., holotype PIN, no. 3104/785, left dentary fragment with DP₄ and M₁: (a) labial, (b) occlusal, and (c) lingual views.

Explanation of Plate 9

All specimens come from the Bumban Member of the Naran Bulak Formation, basal Eocene; Tsagan-Khusu locality, southern Mongolia.

Figs. 1–4. *Arfia langebadrae* sp. nov., holotype PIN, no. 3104/785, fragmentary left dentary with DP₄ and M₁, ×6: (1) labial view; (2) labial view, the upper part of the labial wall of the bone removed at M₁; (3) occlusal view; and (4) lingual view.

Figs. 5–8. ?*Prototomus* sp.: (5, 6) specimen PIN, no. 3104/787, fragmentary left dentary with fragmentary roots and alveoli of P₂–M₂, ×4.5: (5) occlusal and (6) labial views; (7, 8) specimen PIN, no. 3104/786, fragmentary right maxilla with partially preserved M² and the base of M³, ×10: (7) occlusal and (8) labial views.

Table 1. Measurements of DP₄ and M₁ in different species of *Arfia* (for earlier known species, after Gingerich, 1989; Gingerich and Deutsch, 1989; Smith and Smith, 2001): (*) original measurements, cast of the holotype of *A. zeke*, UM, no. 69372; mean values are in parentheses; the ratios L/W M₁ are estimated on the basis of mean values, except for *A. junnei*, *A. zeke* (UM, no. 69372), and *A. langebadreae* sp. nov.

Species	DP ₄				M ₁				
	L	W	TRW	TAW	L	W	TRW	TAW	L/W M ₁
<i>A. junnei</i>					5.6	3.2			1.750
<i>A. opisthotoma</i>					6.7–8.4 (7.55)	4.2–5.0 (4.61)			1.638
<i>A. zeke</i>					6.1–6.8 (6.54)	3.5–4.2 (3.87)			1.690
<i>A. zeke</i> (UM 69372)					6.2	3.6	3.6*	3.5*	1.722
<i>A. shoshoniensis</i>					6.6–8.5 (7.32)	4.2–4.9 (4.53)			1.616
<i>A. gingerichi</i>	5.5	2.5			5.6–6.0 (5.89)	4.2–4.9 (4.53)			1.893
<i>A. langebadreae</i> sp. nov.	6.25	3.0	2.8	3.0	6.4	3.5	3.5	3.5	1.829

protoconid. The metacristid is subvertical, only weakly developed, and lacks a shearing edge.

The talonid is half as long as the tooth crown. The talonid notch is clearly pronounced. The cristid oblique is stout, more massive and higher than that of DP₄. The anterior edge of the cristid oblique is displaced lingually close to the line of the protocristid notch and ascends on the posterior wall of the trigonid in a way similar to the arrangement of these elements in DP₄. The talonid is high. The talonid basin is large and deep. The hypoconid is stout. A small mesoconid is present. The hypoconulid is slightly higher than the hypoconid. The entoconid is relatively small; the entocristid reaches the posterior base of the metaconid; and the entoconulid is well-pronounced, confined to the entocristid, and positioned close to the entoconid. The hypoconulid is transversely widened and isolated from the hypoconid and entoconid by well-pronounced notches. The postcingulid is rudimentary and looks like a tiny, smooth ridge located posterior to the notch between the hypoconid and hypoconulid.

Measurements, mm. Holotype: DP₄: total length, 6.25; labial length of the talonid, 2.6; lingual length of the talonid, 2.2; trigonid width, 2.8; talonid width, 3.0; and labial height on the protoconid, 4.2; M₁: total length, 6.4; labial length of the talonid, 3.0; lingual length of the talonid, 2.6; trigonid width, 3.5; talonid width, 3.5; and labial height along the protoconid, 4.2. Labial depth of the horizontal ramus of the lower jaw between DP₄ and M₁, 5.7. The length to width ratio of M₁ (L/W M₁), 1.829 (Table 1).

Comparison. *A. langebadreae* sp. nov. differs from *A. zeke* Gingerich et Deutsch, *A. junnei* Gingerich, *A. opisthotoma* (Matthew), and *A. shoshoniensis* (Matthew) in the rudimentary postcingulid of M₁. The talonid of M₁ of *A. langebadreae* is longer than that of *A. zeke* (on the labial side, they are 3.0 and 2.4 mm long, respectively) and is relatively lower than that of *A. shoshoniensis*, *A. opisthotoma*, and *A. zeke*. The new species differs from *A. gingerichi* Smith et Smith in the presence of the anterolabial cingulid, the rugose enamel on the crown and the rounder outline of the talonid of

DP₄ (in occlusal view), and the preservation of a rudimentary postcingulid on M₁.

In regard to the dimensions of M₁, *A. langebadreae* is substantially larger than *A. junnei* and *A. gingerichi* (Smith and Smith, 2001, table 3), smaller than *A. opisthotoma* and *A. shoshoniensis*, and similar to *A. zeke* (Table 1). The index L/W M₁ (1.829) is the same as in the small species *A. gingerichi* and *A. junnei* (about 1.75–1.89, i.e., the tooth is similarly elongated), and is higher than that of *A. zeke* (1.62–1.74; the mean is 1.69). The lowest index (i.e., the most massive M₁) is characteristic of the largest species, such as *A. shoshoniensis* and *A. opisthotoma* (1.616 and 1.638, respectively).

Remarks. *Arfia woutersi* Lange-Badre et Godinot from the basal Eocene of Europe (Lange-Badre and Godinot, 1982) is currently assigned to the family Oxyaenidae (genus *Oxyaena*) (Smith and Smith, 2001).

Arfia is characterized by relatively massive jaws and a deep horizontal ramus of the lower jaw. The low horizontal ramus of the specimen described above is accounted for by its young individual age, since the eruption of molars has not been accomplished (Pl. 9, figs. 1, 2). As the permanent dentition developed at subsequent ontogenetic stages, the stoutness of the jaws increased.

Material. Holotype.

DISCUSSION

Arfia langebadreae displays a number of plesiomorphic characters in the structure of M₁, including the high stoutness of the tooth, the elongated talonid, and the preservation of the anterolabial cingulid.

The new species is similar in the stoutness of M₁ to *A. zeke* (the most massive M₁ has been registered in *A. gingerichi*). It is distinguished from all North American taxa by an almost completely reduced postcingulid of M₁. This suggests the assignment of *A. langebadreae* to the same lineage as the European *A. gingerichi*, which also has a reduced postcingulid of M₁. The preservation of the postcingulids of M₁–M₃ in all North American species is probably a characteristic feature of

this lineage of the genus *Arfia*. The affinity between *A. gingerichi* and *A. langebadreae* is additionally supported by the similarly developed labial cingulid of M_1 .

A. langebadreae is larger than *A. junnei* and *A. gingerichi*, which indicates a high degree of specialization of this species. It may be inferred that, in a number of characters, *A. langebadreae* is more advanced than *A. junnei* and *A. gingerichi*. In degree of specialization, *A. langebadreae* is similar to the Early Wasatchian (Wa1) *A. zele*.

Proceeding from the hypothesis of the Asiatic origin of creodonts and penetration of the Hyaenodontidae in North America at the Paleocene–Eocene boundary (Gingerich, 1989), it is conceivable that primitive species of *Arfia* that were closely related to *A. junnei*, occupied North America at the onset of the Wasatchian and simultaneously entered Europe through the North Atlantic bridge.

A. langebadreae is a descendant of the Asiatic lineage of this genus that evolved from a primitive species (that was morphologically similar to *A. junnei*) to a specialized form resembling *A. zele*. However, the similarity between *A. zele* and *A. langebadreae* (in particular, in their measurements) is the result of parallel evolutionary development. The species differentiation within the genus *Arfia* is schematically shown in Fig. 3.

The main evolutionary trends displayed by the genus *Arfia* involve growth of the body size, an increase in the depth and stoutness of the lower jaw, the development of the sectorial pattern of molars, and the elongation of M_3 relative to M_2 .

The largest members of the genus *Arfia* are *A. shoshoniensis* and *A. opisthotoma* from the Early Graybulian (Wa3) of North America. Their M_3 is 9.0–11.5 mm long, the molar row is 24–30 mm long, the row of the lower cheek teeth is about 60–70 mm long, the lower jaw of *A. shoshoniensis* is up to 133 mm long, the horizontal ramus of the lower jaw is 17.8 mm in depth ($n = 28$), and the jaw with the coronoid process is 62 mm in depth (UM, no. 69474). *A. zele* is 13% smaller than *A. shoshoniensis* and *A. opisthotoma* (Gingerich and Deutsch, 1989): its M_3 is 8.0–9.5 mm long, the molar row is 21–25 mm long, and the row of the lower cheek teeth is about 55 mm long. Judging from the measurements of M_1 , *A. langebadreae* was similar in size to *A. zele*. *A. junnei* was 13% smaller than *A. zele* (Gingerich, 1989): M_3 is 7.3–7.5 mm long, the molar row is 19.5–20.5 mm long, and the row of the lower cheek teeth is approximately 38–40 mm long. Judging from the tooth measurements (see Smith and Smith, 2001, table 3), *A. gingerichi* only slightly differed in size from *A. junnei*. M_3 of *A. gingerichi* is 6.3–7.4 mm long, and the M_1 – M_3 row (original reconstruction) is 19–20 mm long.

Large species differ from small forms in the substantially greater depth and robustness of the lower jaw. The lowest and most gracile horizontal ramus of the lower jaw is characteristic of *A. junnei*. The horizontal ramus of *A. zele* and *A. shoshoniensis* is more massive.

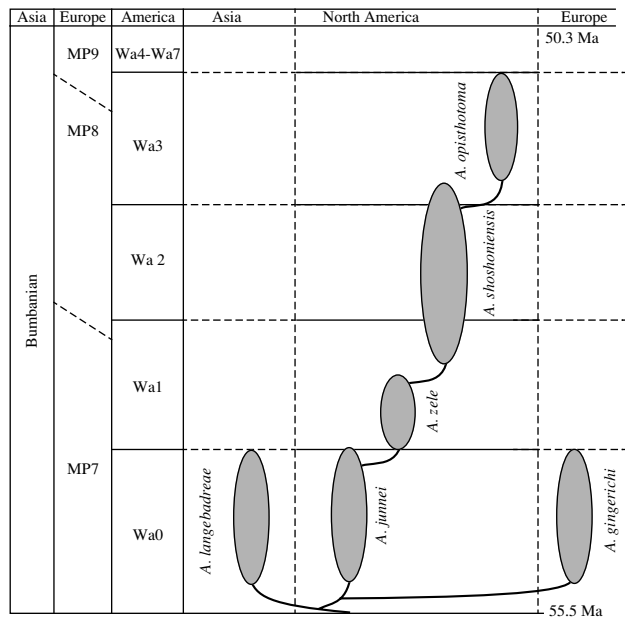


Fig. 3. Differentiation of species within the genus *Arfia*.

In *A. opisthotoma* (Wa3; $h = 16.1$ – 22.6 mm; $n = 12$), which is similar in size to *A. shoshoniensis* (Wa1–Wa2 to the beginning of Wa3; $h = 13.8$ – 22.0 mm; $n = 28$), the horizontal ramus is substantially deeper than in *A. zele* (Wa0–Wa1; $h = 13.8$ – 15.8 ; $n = 4$; Gingerich and Deutsch, 1989). The values of K_{mlj} (lower jaw robustness index) in *A. opisthotoma*, *A. shoshoniensis*, and *A. zele* are 0.352, 0.239, and 0.288, respectively. For comparison, we calculated this index in *Meles meles* (mean $K_{mlj} = 0.417$, ranging from 0.353 to 0.523; $n = 23$) and *Vulpes vulpes* (mean $K_{mlj} = 0.246$, ranging from 0.226 to 0.265; $n = 27$).

In the early half of the Wasatchian Age, North American species displayed progressive morphological changes in the structure of the lower molars. The cutting function of the teeth developed. From *A. junnei* to *A. opisthotoma*, the trigonid of M_3 became narrower and longer (Gingerich, 1989; Gingerich and Deutsch, 1989), and its length-to-width ratio ($TRL/TRW M_3$) increased. In the early half of the Wasatchian (Wa0–Wa3), the crowns of the lower molars became longer (the ratio $TRL/TRW M_3$ changed from 0.95–1.0 in *A. zele* to 1.10–1.15 in *A. opisthotoma*; see Gingerich and Deutsch, 1989), because the trigonid increased in length. In small species, the talonid and trigonid of M_1 and M_2 are approximately equal in length, whereas, in *A. shoshoniensis* and *A. opisthotoma*, the trigonid of M_3 is substantially longer than the talonid, which is indirectly associated with the index TRL/TRW .

Beginning with the evolutionary level of *A. zele* (Wa0–Wa1), M_3 became longer than M_2 (in *A. junnei*, $LM_2 = LM_3$). In *A. gingerichi* (only isolated teeth are available), M_2 (6.9 mm long, $n = 1$) is most likely similar in length to M_3 (6.4–7.4 mm long, $n = 4$; Smith and

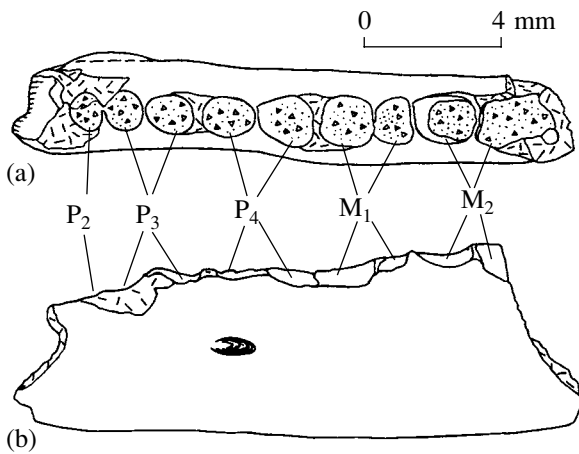


Fig. 4. *?Prototomus* sp. from the basal Eocene of Mongolia, specimen PIN, no. 3104/787, fragmentary left dentary with fragmentary roots and alveoli of P₂–M₂: (a) occlusal and (b) labial views; Tsagan-Khusu locality, Bumban Member, Naran Bulak Formation.

Smith, 2001). Thus, small species of the genus *Arfia* are plesiomorphic in the approximately equal lengths of M₂ and M₃.

In the lower jaw of all species, the premolar row is somewhat longer than the molar row (e.g., in *A. zele*, LP₁–P₄ : LM₁–M₃ = 1.21), which is evidence of the stable proportions of the slightly elongated facial region of the skull in the evolution of this genus.

The reconstructed body weight of *A. opisthotoma* and *A. shoshoniensis* is 5–7 kg (Gingerich and Deutsch, 1989), which fits with that of the fox *Vulpes vulpes* (5–10 kg, see Geptner *et al.*, 1967). Based on the proportions of the lower jaw and teeth, *A. zele* and *A. langebadreae* are considered similar in body size to the yellow-throated marten (*Martes flavigula*). *A. gingerichi* and *A. junnei* are similar in the measurements of the lower jaw and skull to the African marsh mongoose *Atilax plaudinosus*.

An important morphological feature of the jaw apparatus of *Arfia* is a high degree of sectorial specialization of dentition (the long metastylar blade of M¹ and M² and well-developed shearing blades of premolars) combined with retention and development of wide talonids with basins, a complete set of talonid cusps, and labiolingually extended talons of M¹ and M². The rugose enamel is indicative of the that the enamel

microstructure has been rearranged in such a way that it has become resistant to a high load. *Arfia* demonstrates the highest sectorial specialization compared to all the known genera of the earliest Hyaenodontidae; consequently, it was well-adapted for feeding on relatively large prey (macrophagy).

Thus, the genus *Arfia* evolved toward the sectorial specialization of cheek teeth, improvement of adaptations for breaking hard food objects (bones, firm ligaments, etc.), and preservation of the crushing function of the molars (wide and large talonids of M₁–M₃). *Arfia* was probably a harmoniously specialized predator that consumed both animals and plants, similar to the majority of extant members of the families Canidae and Procyonidae and dissimilar to the Felidae. Judging from the extent to which the talonids and talons are developed, *Arfia* was better adapted for grinding and feeding on plants than the genera *Canis* and *Vulpes* were.

Arfia persisted in North America from the onset to the middle of the Wasatchian, i.e., about 2.5 Ma (note that the Wasatchian lasted for about 5 Ma (McKenna and Bell, 1997)). During this period, members of this genus evolved from small forms with a gracile jaw apparatus to medium-sized predators with massive jaws and highly specialized sectorial teeth. The genus presumably appeared in Asia at the Paleocene–Eocene boundary, since the earliest *Arfia* comes from the basal Eocene of Mongolia.

The jaw fragment of *Arfia langebadreae* was found together with jaw fragments of other small carnivorous mammals. It is impossible to identify some specimens more accurately than to the order to which they belong; however, two fragments certainly belong to the Creodonta.

A fragment of the left horizontal ramus of the lower jaw (PIN, no. 3104/787, Pl. 9, figs. 5, 6; Fig. 4) is determined as *?Prototomus* sp. Fragmentary roots and alveoli from the posterior root of P₂ to the anterior root of M₂ are preserved. This specimen resembles in its proportions and measurements the European *Prototomus minimus* (see Smith and Smith, 2001, fig. 3) and differs from it in the absence of a diastema between P₂ and P₃. The measurements of the alveoli of the lower tooth row of the Asian *Prototomus* are similar to those of European species (Table 2).

Judging from the preserved fragment, the lower jaw was low, long, and somewhat increased in depth posteriorly from M₁ to M₃. The lower edge of the jaw is

Table 2. Dental measurements of *Prototomus minimus* from the basal Eocene of Belgium (after Smith and Smith, 2001) and *?Prototomus* sp. from the basal Eocene of Mongolia; (*) measurement along alveoli and (**) reconstructed measurement

Species	Measurement	P ₃	P ₄	M ₁	L/W M ₁	M ₂
<i>Prototomus minimus</i>	L	3.1	3.45–3.8	3.35–3.9	2.0–2.03	3.65
	W	1.25	1.3–1.45	1.65–1.95		4.95
<i>?Prototomus</i> sp. (PIN, no. 3104/787)	L	3.2*	3.4*	3.3*	1.65*	4.2
	W	1.2*	1.7*	2.0*		4.8**

straight under P_2 – M_1 ; under P_3 , it slightly curves dorsally, while, posterior to M_1 , it curves ventrally. The alveolar edge of the jaw is straight in the premolar region and slightly curves dorsally in the molar region. The symphysis is syndesmotomic. Its posterior end reaches the posterior edge of the anterior root of P_3 . The symphyseal axis is subhorizontal, which follows from the fact that the end of the alveolus of the canine lies under the root of P_2 . The anterior mental foramen is located on the broken anterior side of the specimen. The posterior mental foramen is under the posterior root of P_2 . The alveoli of P_2 – P_4 are densely spaced, without diastemata.

The second specimen (PIN, no. 3104/786) is a fragmentary right maxilla of *?Prototomus* sp. with the base of the zygomatic process, partially preserved M^2 , and the base of M^3 (Pl. 9, figs. 7, 8; Fig. 5). This specimen is similar in its measurements to the lower jaw of *?Prototomus* sp., specimen PIN, no. 3104/787. The labial length of M^2 is 4.2 mm.

The labial surface of M^2 is clearly concave (the ectoflexus is well-developed). The structure of the labial lobe is similar to that of M^2 of *Prototomus? minor* (see Lange-Badre, 1979). The anterior and labial cingula are well-pronounced. The labial cingulum is wide, while the anterior cingulum is narrow. The labial cingulum is well-developed anteriorly and extends to the line of the metacone apex. The parastylar lobe is large. The parastyle is shaped like a cone that isolates the anterior and labial cingula from one another. The paracone and metacone are partially fused to form a high, labiolingually compressed, and bilobate amphicone. The paracone is high, slightly higher than the metacone, as opposed to that of *Prototomus phobos* (in which the metacone is substantially higher than the paracone). The blades of the preparacrista and postparacrista are well-pronounced. The notch between the paracone and metacone is approximately one-third as deep as the paracone height (the paracone measured from the ventral edge of the labial cingulum to the apex is 1.8 mm high).

The metacone is similar in height, width, and length to the paracone. The premetacrista and postmetacrista have well-pronounced shearing edges. The carnassial notch is deep. On the labial surface, it is continued by a well-pronounced valley that isolates the metastylar lobe from the metacone. The metastylar blade is straight in the horizontal and parasagittal planes; caudally, its edge is slightly inclined dorsally. The metastyle is long and has a shearing edge (2.1 mm long, i.e., half the length of the tooth). The index of metastyle elongation (Kmtst) is 0.5. The angle between the longitudinal axis of the amphicone and the metastylar blade (angle QM^2) is 110° – 112° (in *P. minimus*, it is 98° – 100°).

The labial portion the postmetaconule crest extends along the posterior border of the tooth and is especially well-pronounced posterolingually to the metacone. The

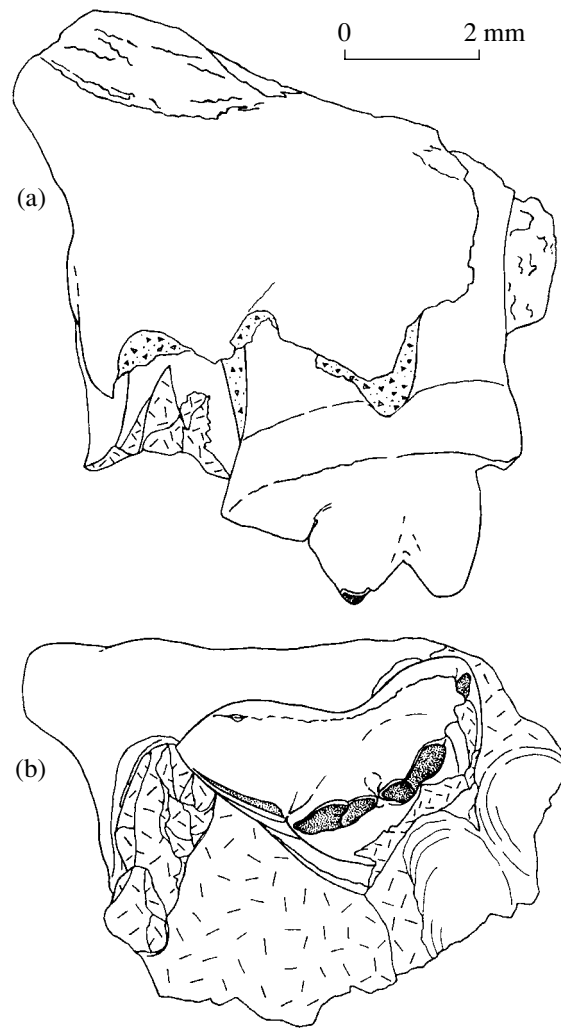


Fig. 5. *?Prototomus* sp. from the basal Eocene of Mongolia, specimen PIN, no. 3104/786, fragmentary right maxilla with partially preserved M^2 and the base of M^3 : (a) labial and (b) occlusal views; Tsagan-Khusu locality; Bumban Member, Naran Bulak Formation.

lingual surface of the amphicone has clear wear facets formed by the trigonid of M_3 as a result of occlusion.

The protocone has been broken off; however, judging from the position of the preserved labial wall of the lingual root, it substantially projected lingually and the tooth crown was at least 4.5–5.0 mm wide. The posterior edge of the protocone projection was most likely located in the same transverse line as the posterior border of the metacone.

M^3 is transversely extended and single-rooted. Its crown and lingual part of the root are broken off. The visible dimensions of the alveolus (length \times width) are 1.8×4.7 mm, while the reconstructed dimensions of the tooth are 1.8×5.0 mm.

The diagnosis of the genus *Prototomus* Cope, 1874 includes the following characters (developed to a variable extent) (Gingerich and Deutsch, 1989): (1) the

anterior (premolar) part of the cheek tooth row is elongated and has diastemata between P_1 – P_2 and P_2 – P_3 (which distinguishes this genus from the majority of other Proviverrinae); (2) the talonid of M_1 – M_3 is narrow, more sectorial than that of *Proviverra*, and has a cristid oblique that deviates from the metaconid instead of the protoconid; and (3) the trigonid of M_1 – M_3 is short, wide, and longitudinally compressed (Gingerich and Deutsch, 1989, p. 345) (distinction from *Tritemnodon*). In addition, *Prototomus* has a single-rooted P_1 , and its M_3 is smaller than, or equal to, M_2 .

The genus comprises seven North American and two European species (*P. minimus* and *P. girardoti*). In addition, certain species, i.e., the North American *Prototomus? vulpeculus* (Matthew, 1915) and the European *Prototomus? bulbosus* Lange-Badre, 1979 and *Prototomus? minor* Lange-Badre, 1979, are tentatively placed in this genus.

The absence of a diastema between P_2 and P_3 in the Asian *Prototomus* and the more massive M_1 than in *P. minimus* (Table 2, L/W) are plesiomorphic characters. This suggests that the Asian *Prototomus* is primitive and close to the basal state of the genus.

At the same time, specimen PIN no. 3104/786 displays a number of apomorphic characters: (1) the metastyle is half as long as M^2 (Kmtst = 0.5), i.e., longer than that of *P. phobos* and similar to that of the European *P. minimus*; (2) the amphicone of M^2 is fused to a greater extent than in *P. minimus* and *P. phobos*; (3) the QM^2 angle is slightly larger than in *P. minimus*; and (4) M^3 is extremely compressed longitudinally (L/W is lower than this ratio in other species). The metacone and paracone were most likely completely fused, as in *Prototomus? minor* and *P. minimus* (in *Prototomus? vulpeculus*, *Prototomus? bulbosus*, and *P. phobos*, the metacone and paracone of M^3 are separate).

These three characters of M^2 are indicative of a higher sectorial specialization (and higher cutting ability of the tooth) of the Bumbanian form. This form is characterized by sectorial molars combined with the retention of the moderately elongated rostral region of the cheek tooth row (there is no diastema between P_2 and P_3) and relatively massive lower molars (due to the stout protoconid).

The earliest creodonts of Asia are known from the Upper Paleocene of China: *Prolimnocyon chowi* Meng *et al.*, 1998 (Limnocyoninae, Hyaenodontidae) and *Creodonta* fam. indet. (see Meng *et al.*, 1998), which is represented by two M_1 of unusual shape (specimens IVPP, nos. V-11140.1 and V-11140.2). The researchers noticed a certain similarity in the talonid structure to the teeth of both *Prolimnocyon* and *Viverravidae* (Carnivora) and indicated that it was not inconceivable that they were dealing with a deciduous tooth of *Prolimnocyon*.

Prolimnocyon chowi is represented by a lower jaw fragment with M_2 , M_3 , and roots of P_4 and M_1 . The identification of this specimen is beyond question. In addition, two isolated upper molars from the same

locality were identified as M^1 of *P. chowi* (specimens IVPP, nos. V-11139.1 and V-11139.2).

Specimen IVPP, no. V-11139.2 resembles M^2 of *?Prototomus* sp. (specimen PIN no. 3104/787) in its dimensions (each specimen is slightly more than 4 mm long), the amphicone structure, and the extent to which the metastyle is elongated. The main difference is the presence of a well-pronounced ectoflexus in M^2 of *?Prototomus* sp. It is worth noting that the same character distinguishes the two molars of "*Prolimnocyon*" (IVPP, nos. V-11139.1 and V-11139.2) from *P. atavus* (which is similar to *P. chowi* in the structure of the cheek tooth row), i.e., they lack an ectoflexus on the labial side. The presence of the ectoflexus is a plesiomorphic character. Therefore, the well-developed ectoflexus in the Eocene *P. atavus* and the absence of this element in the Paleocene *P. chowi* are surprising. At the same time, specimen IVPP, no. V-11139.1 is similar to *P. atavus* (DPC, no. 5364) in the measurements of the parastyle, the extent to which the amphicone is fused, the angle Q (113°–115°), and the development of the metastyle (Kmtst values are 0.392 and 0.396, respectively).

The fragmentary preserved molar (IVPP, no. V-11139.2) substantially differs from specimen IVPP, no. V-11139.1 in the following: (1) the parastyle is less developed, and (2) the metastyle is substantially longer, Kmtst M^1 = 0.527 and 0.392, respectively (the latter is similar to the value calculated for *Prolimnocyon atavus*, Kmtst = 0.396). It is possible to explain these differences by only a higher sectorial specialization of molar IVPP, no. V-11139.2. In creodonts, M^2 is more specialized than M^1 . Thus, both the identification of these specimens as M^1 and the assignment to *Prolimnocyon* are questionable. They may have belonged to certain other genera of the Hyaenodontidae.

In addition, Dashzeveg (1982, 1988) noticed the presence of *Oxyaena* sp. and *Sinopa* sp. in the Upper Paleocene Naran Member of the Naran Bulak Formation of the Naran Bulak locality in Mongolia. These specimens have not been depicted, and it is impossible for us to examine them. However, the presence of the genus *Sinopa*, which is characteristic of the Middle Eocene of North America, in the Upper Paleocene of Asia is highly improbable.

Specimens PIN, nos. 3104/787 and 3104/786 are only tentatively assigned to the genus *Prototomus*, because they are rather fragmentary. However, they represent the second taxon of the subfamily Proviverrinae (and *Creodonta* as a whole) from the basal Eocene of Asia.

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