

A Zalambdodont Insectivore of the Family Apternodontidae (Insectivora, Mammalia) from the Middle Eocene of Mongolia

A. V. Lopatin

Paleontological Institute, Russian Academy of Sciences, Profsoyuznaya ul. 123, Moscow, 117997 Russia

e-mail: alopata@paleo.ru

Received December 4, 2001

Abstract—A new Asian zalambdodont insectivore of the family Apternodontidae, *Asiapternodus mackennai* gen. et sp. nov., from the Middle Eocene of Mongolia (Khaychin Formation, Khaychin-Ula 2 locality) is described. In *Asiapternodus*, P⁴ is nonmolariform and the protocone on the upper molars is very large, clearly distinguishing the new genus from *Oligoryctes* and *Apternodus* found in the Eocene–Oligocene of North America. Regarding the structure of the lower molars, *Asiapternodus* is most similar to *Parapternodus* from the Lower Eocene of North America. The dental structure, relatively large zygomatic process of the maxilla, and the structure of the ascending ramus of the lower jaw suggest that *Asiapternodus* is more primitive than the previously described North American apternodontids.

Key words: Zalambdodont insectivores, Apternodontidae, Middle Eocene, Mongolia, Asia.

INTRODUCTION

The Apternodontidae are an extinct family of zalambdodont soricomorph insectivores widespread in North America beginning with the Late Paleocene to the Early Oligocene. To date, three apternodontid genera have been described, i.e., Early Eocene *Parapternodus*, Middle–Late Eocene *Oligoryctes*, and Middle Eocene–Early Oligocene *Apternodus* (Matthew, 1903; Hough, 1956; Bown and Schankler, 1982; Stucky, 1992; McKenna and Bell, 1997). In addition, various Apternodontidae indet. were found in the Upper Paleocene (Edinger, 1964; Sloan, 1969; Rose, 1981; Savage and Russell, 1983; McKenna and Bell, 1997; Wood *et al.*, 2000) and Eocene (McKenna *et al.*, 1962; Jepsen and Woodburne, 1969; West and Atkins, 1970; Galbreath, 1979; Emry, 1990; McKenna and Bell, 1997).

The genus *Apternodus* was rather thoroughly investigated; in particular, a number of well-preserved skulls were examined (Schlaikjer, 1933, 1934; Scott and Jepsen, 1936). Five species were described from the Chadronian of the United States: *A. mediaevus* Matthew, 1903 from Montana (Matthew, 1903) and South Dakota (Clark *et al.*, 1967); *A. gregoryi* Schlaikjer, 1933 and *A. brevisrostris* Schlaikjer, 1934 from Wyoming (Matthew, 1910; Schlaikjer, 1933, 1934; Scott and Jepsen, 1936; Emry, 1992); *A. altitalonidus* Clark, 1937 from South Dakota (Clark, 1937; Clark *et al.*, 1967) and Wyoming (Emry, 1992); and *A. iliffensis* from Colorado (Galbreath, 1953). "*Apternodus*" *bicuspis* from the Whitneyan of South Dakota (Macdonald, 1951) actually belongs to the Erinaceidae of the genus *Proterix* (Gawn, 1968). Members of two other North American genera of the Apternodontidae, Chadronian *Oligoryctes cameronensis* Hough, 1956 and Early

Wasatchian *Parapternodus antiquus* Bown et Schankler, 1982 were described from Wyoming (Hough, 1956; Bown and Schankler, 1982). The data on a wider stratigraphic and geographical distribution of *Apternodus* and *Oligoryctes* are based on the specimens that were not identified to species from the Uintan, Duchesnean, and Orellan of the United States and the Uintan of Canada (Black and Dawson, 1966; Krishtalka and Setoguchi, 1977; McKenna, 1980; Storer, 1984, 1995; Stucky, 1992).

The zalambdodont teeth of apternodontids are very similar to those of tenrecs and solenodons; therefore, this group is usually referred to as a subfamily of the family Tenrecidae (Matthew, 1910; Van Valen, 1967) or Solenodontidae (Schlaikjer, 1933, 1934; Winge, 1941; Simpson, 1945; Macdonald, 1951; Galbreath, 1953; Saban, 1958; Paula Couto, 1979) or ranked as a special family of the Tenrecoidea (Osborn, 1910; Simpson, 1931; Scott and Jepsen, 1936; Clark, 1937; Hough, 1956; McKenna, 1975; Galbreath, 1979; etc.). At present, the Apternodontidae along with the Solenodontidae are assigned to the Soricoidea (Romer, 1966; McKenna and Bell, 1997) or Solenodontoidea (Paula Couto, 1979) and considered to be only distantly related to the Tenrecoidea. According to available molecular data (Stanhope *et al.*, 1998; Waddell *et al.*, 1999; Madsen *et al.*, 2001; Murphy *et al.*, 2001), tenrecs are even more distant; together with golden moles (Chrysochloridae), they are referred to as a special order, Afrosoricida, of the clade Afrotheria comprising endemic African placentals.

A close relationship between the Apternodontidae and the Solenodontidae is corroborated not only by dental morphology but also by cranial structure (Mat-

thew, 1910; Schlaikjer, 1933, 1934; Scott and Jepsen, 1936; McKenna, 1975). McDowell (1958) excluded *Apternodus* from the Soricomorpha and even from the Lipotyphla (placing it relatively close to the Creodonta) on the basis of studying a poorly preserved skull of *A. brevirostris* (McKenna, 1975). McKenna (1975, p. 38) indicated that, judging from the cranial morphology, apternodontids undoubtedly belonged to the Soricomorpha and noted that, among other things, the teeth of *Apternodus* were pigmented, similar to those of *Solenodon* and the Soricidae.

The Apternodontidae were previously registered in the Paleogene of Asia (Russell and Zhai, 1987; McKenna and Bell, 1997; Tong, 1997). The first data were based on a zalambdodont insectivore found in the Eocene Formation Khaychin of the Khaychin-Ula 2 locality in Mongolia (collected by the South Gobi Team of the Joint Soviet–Mongolian Paleontological Expedition headed by V.Yu. Reshetov in 1973). As follows from a label written by M.C. McKenna (American Museum of Natural History), the researcher assigned this insectivore to the Apternodontinae and Tenrecoidea; B.A. Trofimov [Paleontological Institute of the Russian Academy of Sciences (PIN), personal communication] indicated that McKenna saw this specimen in 1973 in Ulaanbaator. Subsequently, this specimen was mentioned as Tenrecoidea gen. et sp. nov. (Badamgarav and Reshetov, 1985) or Apternodontidae indet. (Russell and Zhai, 1987). McKenna and Bell (1997, p. 285) noted that, in addition to the Paleogene of North America, apternodontids existed in the Middle Eocene of Asia; as was marked in a footnote, this statement was based on an undescribed specimen found in the Khaychin-Ula locality and stored at the PIN (Moscow). This specimen is an upper jaw fragment described in the present study as the holotype of *Asiapternodus mackennai* gen. et sp. nov. In addition, an isolated M_3 and a lower jaw fragment containing broken molars found among the specimens from Khaychin-Ula 2 are assigned to *A. mackennai*.

The Khaychin-Ula 2 locality is dated as the Middle Eocene (Badamgarav and Reshetov, 1985; Russell and Zhai, 1987; Averianov and Godinot, 1998) or the end of the Middle—the beginning of the Late Eocene (Devyatkin, 1981, 1994). I hold the first point of view. The fauna from Khaychin-Ula 2 belongs to the Irindmanhan Asian Land Mammal Age correlated with the Early–Middle Uintan of North America (McKenna and Bell, 1997) and, consequently, should be dated to the middle of the Middle Eocene.

Recently, Tong (1997) described zalambdodont insectivores determined as cf. *Apternodus* sp. (Apternodontidae), *Iconapternodus qii* Tong, 1997, cf. *Iconapternodus* sp. I, and cf. *Iconapternodus* sp. II (?Apternodontidae) from the Middle Eocene of China. In my opinion, the structure of P_4 – M_3 of *Iconapternodus* (Tong, 1997, text-fig. 12, pl. II, figs. 1–4) suggests that this genus belongs to the Palaeoryctidae rather than to the Apternodontidae.

A new form of the Apternodontidae from the Eocene of Mongolia is described below. The main difference between the variants of terminology for the structural elements of zalambdodont molars consists in the designation of the main cusp (zalambdocone, after McDowell, 1958); it is named the protocone (Osborn, 1907; Gregory, 1910; McDowell, 1958), paracone (Matthew, 1913; Butler, 1937, 1939, 1941; Hough, 1956, p. 534; Van Valen, 1966, 1967; Morgan and Ottenwalder, 1993; etc.), metacone (Allen, 1918), a cusp of the para-metacone (Schlaikjer, 1933), amphicone (Galbreath, 1953; Hough, 1956, p. 540), or eocone (Hershkovitz, 1971). Following the hypothesis of the formation of the zalambdodont molars on the basis of a primitive dilambdodont pattern (Matthew, 1913; Butler, 1941, 1996), I regard this cusp as the paracone. The other elements of the dental structure are designated according to the standard nomenclature (see Szalay, 1969). The upper teeth are measured according to the technique proposed by Galbreath (1953, fig. 12), i.e., (length) the distance from the anterior edge of the parastyle to the posterior edge of the metastyle along a straight line extending parallel to the longitudinal axis of the tooth row and (width) the greatest distance from the labial edge of the parastylar lobe to the lingual edge of the protocone base along a straight line.

The following abbreviations are used in the present study: (AMNH) American Museum of Natural History, New York; (PIN) Paleontological Institute of the Russian Academy of Sciences, Moscow.

SYSTEMATIC PALEONTOLOGY

Family Apternodontidae Matthew, 1910

Genus *Asiapternodus* Lopatin, gen. nov.

Etymology. From Asia and the generic name *Apternodus*.

Type species. *Asiapternodus mackennai* sp. nov.

Diagnosis. Small-sized apternodontids. Zygomatic process of maxilla projecting posteriorly beyond M^3 . Anterior foramen of the infraorbital canal located above P^4 and posterior foramen located above M^1 . P^3 small. P^4 nonmolariform: narrow, with small lingual projection, and lacking trigon basin. Molars very wide, width decreasing in series $M^3 > M^2 > M^1$. Protocone of M^1 – M^3 well-developed, large, and strongly extended transversely; hypocone absent; precingulum and postcingulum weak. Ectoflexus of M^2 very deep. M^3 nonreduced. Articular condyles of lower jaw moderately wide. Talonid of M_1 unicuspid; talonid of M_2 expanded transversely, strongly projecting ventrolabially, and possessing relatively large lingual cusplule and weak supplementary posterolabial cusplule. Postvallid of M_2 positioned subtransversely. M_3 nonreduced and having long talonid.

Species composition. Type species.

Comparison. The new genus differs from *Apternodus* Matthew, 1903 and *Oligoryctes* Hough,

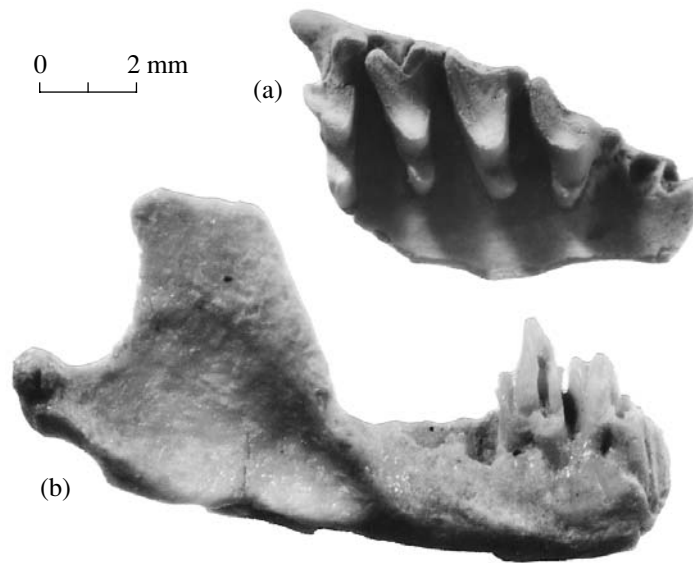


Fig. 1. *Asiapternodus mackennai* sp. nov.: (a) holotype PIN, no. 3107/400, fragment of the right maxilla with P⁴–M³; (b) specimen PIN, no. 3107/399, fragment of the right dentary with M₁ and M₂.

1956 by nonmolariform P⁴, relatively wider upper molars of different width ratios of M¹–M³ (in *Apternodus*, M¹ > M² > M³ or M¹ < M² > M³; in *Oligoryctes*, M¹ > M² > M³, stronger developed protocone on M¹–M³, nonreduced M³, and by the structure of the talonid of M₂. In addition, it differs from *Apternodus* by a less reduced zygomatic process of the maxilla, a more posterior position of the infraorbital foramen, a narrower articular condyle of the lower jaw, the absence of the hypocone and smaller cingula of M¹ and M², and a deeper ectoflexus of M². Additional distinction from *Oligoryctes* is a substantially smaller P³. *Asiapternodus* is distinguished from *Parapternodus* Bown et Schanler, 1982 (only M₂ and M₃ have been found) by a greater transverse expansion of the talonid of M₂, the presence of supplementary posterolabial talonid cuspule on M₂, and nonreduced M₃.

Asiapternodus mackennai Lopatin, sp. nov.

Etymology. The species is named in honor of the paleontologist Malcolm C. McKenna.

Holotype. PIN, no. 3107/400, incomplete right maxilla containing P⁴–M³; Mongolia, Khaychin-Ula 2 locality; Middle Eocene, Khaychin Formation.

Description (Figs. 1–4). The infraorbital canal is short, large, and narrowed transversely. The anterior foramen of the infraorbital canal is oval, its height is almost three times greater than the width (in the holotype, 2.0 × 0.7 mm), and located directly above the middle of P⁴. Anterior to the infraorbital foramen, the lateral side of the maxilla contains a small foramen facing posterolaterally and open into the nasal cavity. The posterior foramen of the infraorbital canal is semicircular, has a straight medial wall, and lies above the central

part of M¹. The internal surface of the medial wall of the infraorbital canal has a small crest marking the division of the canal into two unequal parts, the ventral part is larger and the dorsal part is smaller; this is evidence that the infraorbital nerve and blood vessels passing through the canal were located one under the other. The canal passes between the labial and lingual roots of P⁴ and M¹. In the ventral region of the canal, the lateral walls are pierced by small foramina most likely leading into the cavities in the roots of the cheek teeth. The largest foramen opens in the medial wall of the canal on a level with the apex of the lingual root of M¹, faces posteriorly, and is connected to a distinct groove extending along the bottom of the canal to the exit. Immediately posterior to the exit of the infraorbital canal, the orbital floor has a large depression; short grooves deviate laterally and medially from the depression and terminate in very small foramina apparently leading into the roots of M². The orbital floor is short and its surface is rough and pitted; in the posterior part, it is pierced by the roots of M³. The thick lateral wall of the infraorbital canal extends posteriorly and merges into a massive zygomatic process of the maxilla.

The zygomatic arch is reduced. The zygomatic process of the maxilla is relatively well developed, directed posteriorly and slightly laterally, and projects posteriorly beyond M³. The slightly raised dorsolateral end of the process has a well-pronounced flat area delimited ventrally by a well-developed crest fusing anteriorly with a small tubercle. This area most likely served as the attachment of the ventral portion of the dilatator nasi muscle, as is observed in living tenrecs and solenodons (Gambaryan, 1989). A large area on the lateral side of the base of the zygomatic process above M¹–M³

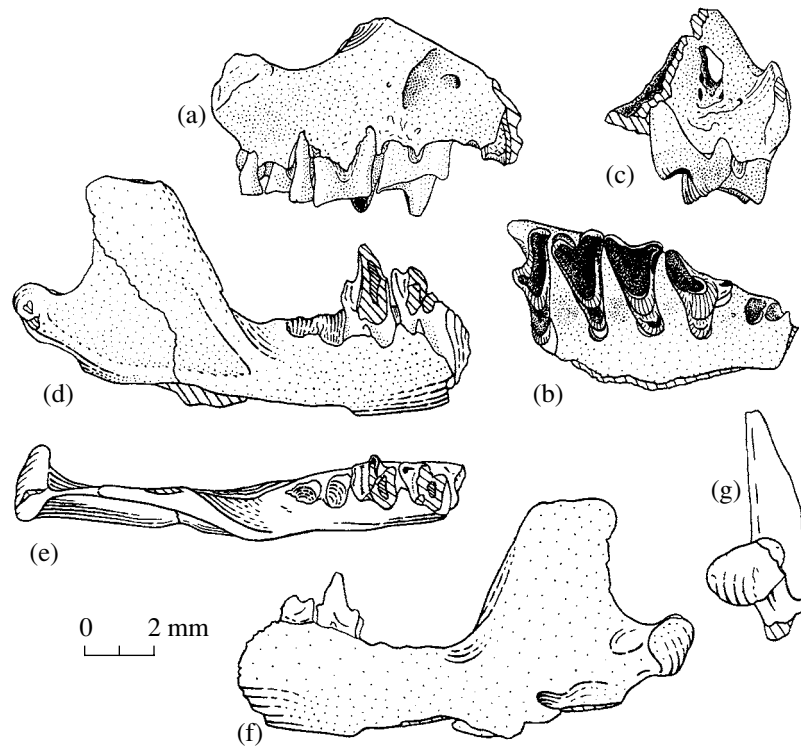


Fig. 2. *Asiapternodus mackennai* sp. nov.: (a–c) holotype PIN, no. 3107/400, fragment of the right maxilla with P^4 – M^3 : (a) labial view, (b) occlusal view, and (c) rear view; (d–g) specimen PIN, no. 3107/399, fragment of the right dentary with M_1 and M_2 : (d) labial view, (e) occlusal view, (f) lingual view, and (g) rear view.

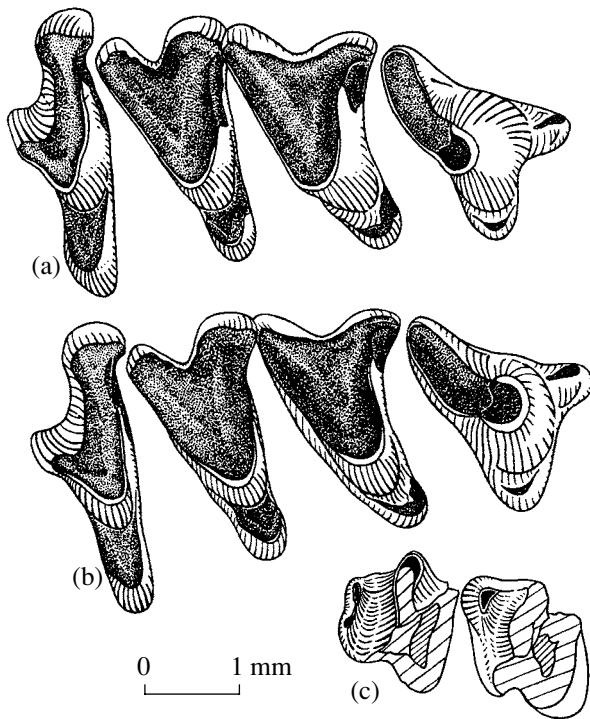


Fig. 3. Teeth of *Asiapternodus mackennai* sp. nov.: (a) holotype PIN, no. 3107/400, right P^4 – M^3 , occlusal surface; (b) the same, slightly inclined anteriorly; and (c) specimen PIN, no. 3107/399, right M_1 and M_2 , occlusal surface.

has a rough and slightly concave surface interpreted as the attachment area for the maxillonasalis muscle.

Anterior to P^4 , the jaw fragment contains three alveoli. The anterior alveolus is identified by a small fragment of the posteromedial wall. The second looks like a small round foramen slightly extended posteromedially. The third is the largest; it expands transversely and, in the middle part, is slightly compressed longitudinally. Its anterior wall has a distinct projection, indicating that the alveolus contained two partially fused roots. The anterior alveolus preserved in the specimen most likely contained the posterior root of P^2 , the second contained the anterior labial root of P^3 , and the third contained partially fused posterior labial and lingual roots of P^3 . Judging by the sizes of two posterior alveoli, P^3 was relatively small and had a weakly developed lingual projection.

P^4 – M^3 are three-rooted. P^4 has a long labial lobe and a relatively small lingual projection. The parastylar lobe is large and markedly projects anteriorly. The cuspsule of the parastyle is low. The paracone is high, massive, and conical. The stout postparacrista descends from the apex of the paracone to the metastyle. The metastylar lobe is long and the metastyle is low. The protocone is small and low, with a poorly pronounced apex and small crests of the preprotocrista and postprotocrista.

The molars are narrow triangular, short, and wide; they decrease in length and increase in width from M^1 to M^3 . M^1 has a relatively shallow ectoflexus and anteriorly oblique lingual lobe. The metastylar lobe is larger than the parastylar lobe. A small cusplule of the parastyle is located at the anterior edge of the parastylar lobe and isolated from the labial end of the preparacrista by an extensive depression. A weak ectocingulum having a small eminence in the posterolabial part of the parastylar lobe, i.e., a reduced stylocone, extends from the parastyle to the metastyle. A small crest of the precingulum is connected to the parastyle and borders the anterolingual side of the parastylar lobe. The metastylar lobe is posterolabially extended. The paracone is stout and triangular. The preparacrista terminates in the lingual part of the occlusal surface of the parastylar lobe. The postparacrista connects the apex of the paracone to the metastyle. The protocone is relatively large, its conical apex is strongly displaced anteriorly with reference to the apex of the paracone and positioned on the same transverse line as the parastyle. A small crest of the postprotocrista is present. The precingulum is very narrow and weak, especially in the middle part. The postcingulum is poorly pronounced and discontinuous, only its lingual portion bordering the posterolingual wall of the paracone base is relatively prominent; the traces of other projections of the postcingulum appear as two extended wear facets on the posterior side of the paracone base.

M^2 expands transversely and has a very deep ectoflexus. The parastylar lobe is markedly larger than the metastylar lobe. The labial edge of the parastylar lobe is straight. As the tooth is worn, the parastyle becomes fused with the labial part of the precingulum. The stylocone is relatively large. The ectocingulum is weak. The cusplule of the metastyle is small. The paracone is smaller than that on M^1 . As the tooth is worn, the labial part of the preparacrista becomes fused with the wear facet of the parastyle and precingulum and the postparacrista connects the apex of the paracone to the metastyle. The apex of the protocone is located on the same transverse line as the apex of the paracone. The precingulum is better pronounced than on M^1 and extends along the entire anterior side of the paracone. The postcingulum is discontinuous, and looks like slightly convex enamel segments at the base of the posterior (located similar to the side wear facets on M^1) and posterolingual sides of the paracone.

M^3 has a stout parastylar lobe located on the same transverse line as the apices of the paracone and the protocone. The metastylar lobe is reduced and projects somewhat posteriorly, the metastyle is prominent. The common wear facet of the parastyle and precingulum is isolated from the preparacrista. The crest of the preparacrista is stout and long and reaches the stylocone. The crest of the postprotocrista is short and joins with the metastyle. The lingual lobe is very broad, substantially broader than that of M^1 and M^2 . The proto-

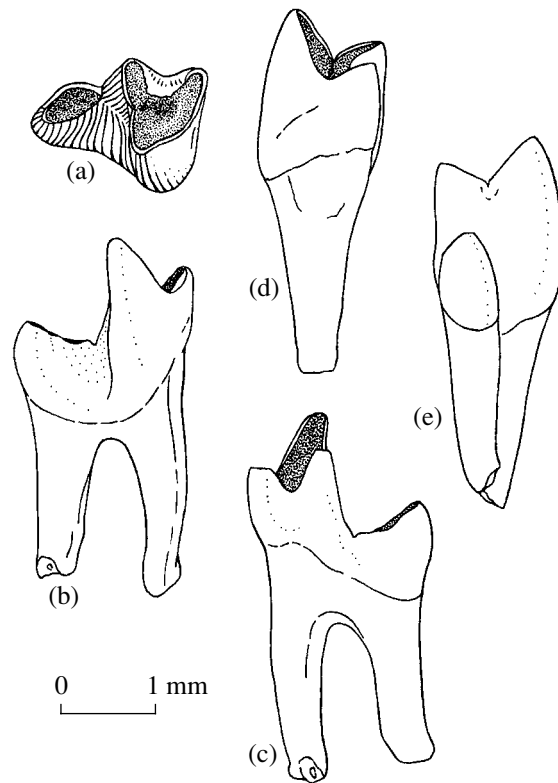


Fig. 4. *Asiapternodus mackennai* sp. nov., specimen PIN, no. 3107/398, isolated right M_3 : (a) occlusal surface and (b) labial, (c) lingual, (d) frontal, and (e) rear views.

cone is low. The precingulum is developed to the same extent as that of M^2 . The postcingulum is absent.

It is worth noting that certain elements on the occlusal surface (styles, stylocone, ectocingulum, and the crests of the protocone) of M^1 – M^3 of the holotype are markedly smoothed by wear; however, their initial shape, arrangement, and size are discovered because the dentin of the united wear facets bears clear rough traces.

The spaces between the central parts of cheek teeth on the maxilla contain deep oval vascularized fossae (located opposite the high trigonids of P_4 – M_3) increasing in depth posteriorly (from P^3/P^4 to M^2/M^3). The anterior side of M^1 – M^3 displays distinct wear facets (Fig. 3a) showing a close contact with the posterior edge of the trigonids of M_1 – M_3 when the jaws are closed.

The lower jaw is characterized by a specific shape of the coronoid region, similar to that of other apternodontids (Matthew, 1903, text-fig. 2; Schlaikjer, 1934; Scott and Jepsen, 1936; Hough, 1956), i.e., the ascending ramus is substantially displaced laterally with reference to the horizontal ramus and notably deviates medially with reference to the longitudinal axis of the tooth row and the articular condyle is widened and inclined anteromedially and ventromedially.

The horizontal ramus of the lower jaw is relatively massive. The lingual wall of the alveolar margin is substantially higher than the labial wall. The ascending and horizontal rami are positioned at an angle of approximately 110°. The coronoid process is high and thin. The masseteric fossa is superficial but clearly outlined anteriorly. The stout condylar crest extending to the lateral side of the articular condyle borders the masseteric fossa ventrally. The incisure between the coronoid and the articular process is broad but superficial. The condyle is large, massive, relatively short, and wide and located on a level with the base of the molar crowns. The transverse axis of the condyle is only slightly inclined anteromedially and posterolaterally. The articular surface covers a sector of about 180°. The majority of the articular surface faces posteroventrally. The neck of the condyle is short, straight, and has a small depression on the medial side (the upper pterygoid fossa for the attachment of a portion of the pterygoideus externus muscle) and a sharp dorsal crest.

The mandibular foramen is large and oval and located on a level with the middle of the coronoid process; posterior to the foramen, there is a large and deep depression. The incisure between the articular and angular processes is relatively small.

The preserved fragments of the lower molars show that M_1 and M_2 are approximately equal in length. The size of the M_3 alveolus suggests that the tooth was longer than M_2 and had a well-developed talonid. The structure of M_1 and M_2 is typical of apternodontids: the roots are stout; the crowns are compressed longitudinally; the trigonids are high and their posterior walls are vertical; and the talonids are short and low, i.e., reduced. The talonid of M_1 has an oblique labial edge and a single massive cusp in the posterolingual corner. The talonid of M_2 is widened; at the base, it substantially projects posterolabially and has a weak supplementary posterolabial cusp that is smaller and lower than the lingual cusp. The cusps of the talonid are connected to each other by a prominent subtransverse posterior crest. Isolated M_3 (PIN, no. 3107/398; Fig. 4) has a large paraconid, a high protoconid, and a relatively low metaconid. The talonid is long and narrow, with a longitudinally oriented wear facet and a small cusp at the posterior edge.

Measurements, mm. Holotype: length of P^4 – M^3 along the crowns is 6.6; teeth (length \times width): P^4 , 2.25×1.8 ; M^1 , 1.75×3.1 ; M^2 , 1.6×3.2 ; and M^3 , 1.15×3.6 .

Specimen PIN, no. 3107/399: length of M_1 – M_3 along the alveoli, ca. 4.6; length of M_1 , ca. 1.5; talonid length, 0.5; and talonid width, 0.5. Length of M_2 , 1.5; talonid length, 0.55; talonid width, 0.8; and metaconid height, 1.5. Length of the M_3 alveolus, 1.6. Lingual depth of the horizontal ramus at M_1/M_2 , 3.2; thickness at M_3 , 1.35; distances from the posterior edge of the articular condyle to the posterior alveolus of M_3 , 7.0, and to the anterior base of the coronoid process, 6.0;

thickness of the articular condyle, 1.5; width of the articular head, 2.4; and the dorsal length of the neck and the head, 2.0 (1.0 + 1.0).

M_3 (PIN, no. 3107/398): total length, 2.1; talonid length, 1.05; trigonid width, 1.65; talonid width, 0.75; protoconid height, 2.0; and metaconid height, 1.5.

Material. In addition to the holotype, PIN, no. 3107/399, a fragment of the right dentary with broken M_1 and M_2 and the M_3 alveolus and a fragmentary ascending ramus with the articular process, and PIN, no. 3107/398, isolated M_3 , from the type locality.

DISCUSSION

The zalambdodonty is a special type of upper molar structure characterized by the following: the trigon is formed by a large paracone located lingually, V-shaped in plan paracrista, and style; the metacone and protocone are strongly reduced or absent; and the conules are undeveloped (Butler, 1939, 1941; Hershkovitz, 1971). The zalambdodonty means that, in the lower molars, the trigonid is excessively developed, the paracristid oblique and a very high and wide transverse protocristid are formed, and the talonid is reduced. A primitive zalambdodont type is characterized by the presence of a rudimentary metacone (included in the postparacrista); a relatively large protocone and, correspondingly, a lesser degree of excessive development of the trigonids and a lesser reduction of the talonids (Butler, 1941). Hershkovitz (1971) designated the true zalambdodont teeth of insectivores as the complex zalambdomorphic type and primitive zalambdodont pattern as the zalambdomorphic–dilambdomorphic type.

The terms Zalambdodonta and Dilambdodonta were introduced by Gill (1885, p. 136) in 1885 as the taxonomic names for the following sections of Recent insectivores (Gill, 1875, 1885; Gregory, 1910) proposed by him in 1875: the Zalambdodonta included the Centetoidea, comprising tenrecs, solenodons, and otter shrews, and the Chrysochloroidea; and the Dilambdodonta included the Erinaceoidea, Soricoidea, and Tupaioida. Later, these terms were only used in the morphological sense to designate the teeth of appropriate types.

Living zalambdodont insectivores include tenrecs from Madagascar, otter shrews and golden moles from Africa, and solenodons from the Greater Antilles. The Tenrecidae and Chrysochloridae appear in the fossil record in the Early Miocene of Africa (McKenna and Bell, 1997); however, according to molecular data, the order comprising them and named the Afrosoricida should appear about 70 Ma, whereas tenrecs and golden moles should diverge about 50–57 Ma (Stanhope *et al.*, 1998). Extinct solenodontids are known from the Pleistocene and Holocene of the West Indies only (Morgan and Ottenwalder, 1993).

Among extinct forms, the primitive zalambdodont type of tooth structure (where a rudimentary metacone

is preserved, a large protocone is present, and the talonid is relatively weakly reduced) is characteristic of certain Paleocene–Eocene Palaeoryctidae, in particular, *Palaeoryctes* and *Eoryctes* (Matthew, 1913; Butler, 1941; Thewissen and Gingerich, 1989); however, among extinct insectivores, only members of the family Apternodontidae can be referred to as true zalambdodonts.

In North America, the earliest Apternodontidae indet. (fragmentary skull without teeth) comes from the Tiffanian of Wyoming (Edinger, 1964; McKenna and Bell, 1997; Wood *et al.*, 2000). The earliest genus and species is *Parapternodus antiquus* found in the Lower Wasatchian (beginning of the Eocene, about 55 Ma) and represented by only a lower jaw fragment containing M_2 and M_3 (Bown and Schankler, 1982, p. 68, pl. 9, figs. 3, 4). M_2 of *Parapternodus* has a posterolabial projection at the base of the talonid and a subtransversely positioned postvallid, similar to that of *Asiapternodus*; these are primitive features distinguishing *Asiapternodus* and *Parapternodus* from *Apternodus* and *Oligoryctes*.

A very small Early Eocene Apternodontidae indet. was determined in the Upper Bridgerian of Wyoming and the Lower Bridgerian of Utah (McKenna *et al.*, 1962; West and Atkins, 1970) and Nevada (Emry, 1990). The form from the Bridgerian of Wyoming [including a lower jaw fragment of “?Soricidae gen. et sp. indet.” described by G. Simpson (see McGrew *et al.*, 1959, p. 151, text-fig. 7)] and Utah is known as “*Eoryctes*” nomen nudum (not to be confused with the above mentioned valid genus *Eoryctes* Thewissen et Gingerich, 1989 belonging to the Palaeoryctidae), since Romer (1966, p. 381), Novacek (1976, p. 34), and Bown and Schankler (1982, pp. 67–69) mentioned it under this name proposed by McKenna in his manuscript (Bown and Schankler, 1982; McKenna and Bell, 1997, p. 211).

According to the morphological characteristics of the lower molars of “*Eoryctes*” proposed by Bown and Schankler (1982), i.e., relatively low crowns and weak longitudinal compression of trigonids on M_2 and M_3 , the presence of the posterolabial projection at the base of the talonid of M_2 , and anterolingually–posterolabially positioned postvallid on M_2 , this apternodontid substantially differs from *Asiapternodus*. Simpson (McGrew *et al.*, 1958, p. 152) and Bown and Schankler (1982, p. 69) noted the similarities between this form and the Soricidae in the structure of the ascending ramus of the lower jaw (a superficial masseteric fossa and a sharp medial crest extending from the posterior end of the alveolar margin above the mandibular foramen and supposedly showing the initial stage of the formation of the internal temporal fossa). The soricid-like structural features of the lower jaw (a shallow masseteric fossa, a deep triangular posteromedial fossa, a large angular process, the position and shape of the articular condyle, and a deep lower pterygoid fossa) are also observed in *Oligoryctes* (Bown and Schankler, 1982). In *Asiapternodus*, these features are not

observed; on the contrary, the masseteric fossa is relatively deep, the condylar crest is clearly developed and stout, the medial side of the coronoid process lacks a crest, and the condyle is low and massive. One can propose that the above characters of “*Eoryctes*” and *Oligoryctes* are associated with the very small sizes of these animals; Simpson (McGrew *et al.*, 1959) believed that the form from the Bridgerian was at most as large as *Suncus etruscus* (Savi, 1822). The massive lower jaw of *Apternodus*, which has a high coronoid process and very strongly expanded condyles, especially in *A. gregoryi* (Scott and Jepsen, 1936, pl. I, fig. 1d), shows a profound specialization of this genus. Thus, the above characters of the lower jaw of *Asiapternodus* are probably plesiomorphic to the family.

Regarding the extent to which the zygomatic process of the maxilla is reduced, *Asiapternodus* is substantially inferior to *Apternodus* and *Oligoryctes* (Matthew, 1910; Schlaikjer, 1934; Hough, 1956). Among living zalambdodont insectivores, a similar shape of the zygomatic process is characteristic of *Tenrec*, *Oryzoryctes*, and *Microgale*, whereas in *Potamogale* and *Solenodon*, the zygomatic processes are longer and widely spaced (Hough, 1956; Morgan and Ottenwalder, 1993). The incompletely reduced zygomatic arch shows that *Asiapternodus* is more primitive than apternodontids existing at approximately the same geological time and later; *Oligoryctes* and *Apternodus* are known from the Early Uintan and Early Duchesnean, respectively (McKenna, 1980; Stucky, 1992).

Specialized characters of *Asiapternodus* include the presence of strongly shortened infraorbital canal located on the same vertical as P^4-M^1 (in *Apternodus* and *Oligoryctes*, it is above P^3-M^1). The large size of the infraorbital canal suggests that *Asiapternodus* most likely had a sensitive proboscis (Thewissen and Gingerich, 1989).

Primitive structural characters of the upper teeth of *Asiapternodus* are nonmolariform P^4 , a large protocone on M^1-M^3 , and nonreduced M^3 . As the structure of the upper molars of various apternodontids and living zalambdodont insectivores are compared, *Apternodus* is most similar to *Solenodon*, while *Oligoryctes* closely resembles the tenrecs *Oryzoryctes* and *Microgale*. *Asiapternodus* and the Recent otter shrew *Potamogale* and Paleocene *Palaeoryctes* share the markedly transversely extended protocone of the upper molars (Matthew, 1913; Butler, 1939, 1941). The upper molars of *Potamogale* and *Palaeoryctes* are considered to be a transitional type between the zalambdodonty and dilambdodonty (Butler, 1939, 1941; Hershkovitz, 1971). Thus, the structure of the upper teeth of *Asiapternodus* agrees with the hypothesis of the origin of zalambdodont molars from the primitive dilambdodont type by a reduction of the metacone and progressive diminution of the protocone (Butler, 1941, text-fig. 8; 1996, text-fig. 1).

Phylogenetic relationships between the genera of the Apternodontidae remain uncertain. The structure of

the lower molars of *Asiapternodus* and *Parapternodus* shows common plesiomorphic features; however, currently, it is impossible to prove or reject conclusively their close relationship, since the data on the upper teeth of *Parapternodus* are not available. *Oligoryctes* and *Apternodus* are strongly specialized and undoubtedly belong to separate lineages deviating from the common stock not later than the terminal Early Eocene or the basal Middle Eocene. In Asian "cf. *Apternodus* sp." from the upper part of the Middle Eocene of China (Tong, 1997, text-fig. 11, pl. I, figs. 14, 15), the lower molars are more specialized in structure than in *Asiapternodus*; this agrees with its later geological age (Sharamuronian Land Mammal Age).

ACKNOWLEDGMENTS

I am grateful to A.K. Agadjanian (PIN) and A.O. Averianov (Zoological Institute of the Russian Academy of Sciences) for useful discussion on the morphology and evolution of certain groups of zalambodont insectivores.

This study was supported by the Russian Foundation for Basic Research, project nos. 99-04-48636, 00-15-97754, 01-05-65448, and 01-04-06241.

REFERENCES

- Allen, G.M., Fossil Mammals from Cuba, *Bull. Mus. Comp. Zool.*, 1918, vol. 62, pp. 133–148.
- Averianov, A. and Godinot, M., A Report on the Eocene Andarak Mammal Fauna of Kirgizstan, *Bull. Carnegie Mus. Nat. Hist.*, 1998, no. 34, pp. 210–219.
- Badamgarav, D. and Reshetov, V.Yu., *Paleontologiya i stratigrafiya paleogena Zaaltaiskoi Gobi* (Paleontology and Stratigraphy of the Paleogene of the Transaltai Gobi), Moscow: Nauka, 1985.
- Black, C.C. and Dawson, M.R., Paleontology and Geology of the Badwater Creek Area, Central Wyoming: 1. History of Field Work and Geological Setting, *Ann. Carnegie Mus.*, 1966, vol. 38, art. 13, pp. 297–307.
- Bown, T.M. and Schankler, D.M., A Review of the Proteutheria and Insectivora of the Willwood Formation (Lower Eocene), Bighorn Basin, Wyoming, *Bull. US Geol. Surv.*, 1982, no. 1523, pp. 1–79.
- Butler, P.M., Studies of the Mammalian Dentition: 1. The Teeth of *Centetes ecaudatus* and Its Allies, *Proc. Zool. Soc. London, Ser. B*, 1937, vol. 107, part 1, pp. 103–132.
- Butler, P.M., Studies of the Mammalian Dentition: Differentiation of the Postcanine Dentition, *Proc. Zool. Soc. London, Ser. B*, 1939, vol. 109, part 1, pp. 1–36.
- Butler, P.M., A Theory of the Evolution of Mammalian Molar Teeth, *Am. J. Sci.*, 1941, vol. 239, no. 6, pp. 421–450.
- Butler, P.M., Dilambodont Molars: A Functional Interpretation of Their Evolution, *Palaeovertebrata*, 1996, vol. 25, no. 2–4, pp. 205–213.
- Clark, J., The Stratigraphy and Paleontology of the Chadron Formation in the Big Badlands of South Dakota, *Ann. Carnegie Mus.*, 1937, vol. 25, art. 21, pp. 261–351.
- Clark, J., Beerbower, J.R., and Kietzke, K.K., Oligocene Sedimentation, Stratigraphy, Paleogeology and Paleoclimatology in the Big Badlands of South Dakota, *Fieldiana Geol. Mem.*, 1967, vol. 5, pp. 1–158.
- Devyatkin, E.V., *Kainozoi vnutrennei Azii (stratigrafiya, geokhronologiya, korrelyatsiya)* (The Cenozoic of Inner Asia: Stratigraphy, Geochronology, and Correlation), Moscow: Nauka, 1981.
- Devyatkin, E.V., The Magnitostatigraphic Scheme of the Cenozoic of Mongolia, *Stratigr. Geol. Korrelyatsiya*, 1994, vol. 2, no. 2, pp. 35–45.
- Edinger, T., Midbrain Exposure and Overlap in Mammalia, *Am. Zoologist*, 1964, vol. 4, pp. 5–19.
- Emry, R.J., Mammals of the Bridgerian (Middle Eocene) Elderberry Canyon Local Fauna of Eastern Nevada, *Geol. Soc. Am. Spec. Pap.*, 1990, no. 243, pp. 187–210.
- Emry, R.J., Mammalian Range Zones in the Chadronian White River Formation at Flagstaff Rim, Wyoming, in *Eocene–Oligocene Climatic and Biotic Evolution*, Prothero, D.R. and Berggren, W.A., Eds., Princeton: Princeton Univ. Press, 1992, pp. 106–115.
- Galbreath, E.C., A Contribution to the Tertiary Geology and Paleontology of Northeastern Colorado, *Univ. Kansas Paleontol. Contrib.*, 1953, vol. 4, pp. 1–120.
- Galbreath, E.C., An Apternodontid (Insectivora) from the Chadronian Oligocene of Northeastern Colorado, *Trans. Kansas Acad. Sci.*, 1979, vol. 81, no. 4, pp. 297–302.
- Gambaryan, P.P., *Evolutsiya litsevoi muskulatury mlekoopitayushchikh* (Evolution of the Facial Muscles in Mammals), Leningrad: Nauka, 1989.
- Gawn, C.F., The Genus *Proterix* (Insectivora, Erinaceidae) of the Upper Oligocene of North America, *Am. Mus. Novit.*, 1968, no. 2315, pp. 1–26.
- Gill, T.N., Synopsis of Insectivorous Mammals, *Bull. US Geol. Geogr. Surv. Terr., Ser. 2*, 1875, no. 2, pp. 91–120.
- Gill, T.N., Insectivora, in *The Standard Natural History*, vol. 5: *Mammals*, Boston, 1885, pp. 134–158.
- Gregory, W.K., The Orders of Mammals, *Bull. Am. Mus. Nat. Hist.*, 1910, vol. 27, pp. 1–524.
- Hershkovitz, P., Basic Crown Patterns and Cusp Homologies of Mammalian Teeth, in *Dental Morphology and Evolution*, Dahlberg, A.A., Ed., Chicago–London: Univ. Chicago Press, 1971, pp. 95–150.
- Hough, J., A New Insectivore from the Oligocene of the Wind River Basin, Wyoming, with Notes on the Taxonomy of the Oligocene Tenrecoidea, *J. Paleontol.*, 1956, vol. 30, no. 3, pp. 531–541.
- Jepsen, G.L. and Woodburne, M.O., Paleocene Hyracothere from Polecat Bench Formation, Wyoming, *Science*, 1969, vol. 164, pp. 543–547.
- Krishtalka, L. and Setoguchi, T., Paleontology and Geology of the Badwater Creek Area, Central Wyoming: Part 13. The Late Eocene Insectivora and Dermoptera, *Ann. Carnegie Mus.*, 1977, vol. 46, pp. 71–99.
- Macdonald, J.R., Additions to the Whitneyan Fauna of South Dakota, *J. Paleontol.*, 1951, vol. 25, no. 3, pp. 257–265.
- Madsen, O., Scally, M., Douady, C.J., et al., Parallel Adaptive Radiations in Two Major Clades of Placental Mammals, *Nature*, 2001, vol. 409, pp. 610–614.

- Matthew, W.D., The Fauna of *Titanotherium* Beds of Pipestone Springs, Montana, *Bull. Am. Mus. Nat. Hist.*, 1903, vol. 19, art. 6, pp. 197–226.
- Matthew, W.D., On the Skull of *Apternodus* and the Skeleton of a New Artiodactyl, *Bull. Am. Mus. Nat. Hist.*, 1910, vol. 28, art. 5, pp. 33–42.
- Matthew, W.D., A Zalambodont Insectivore from the Basal Eocene, *Bull. Am. Mus. Nat. Hist.*, 1913, vol. 32, art. 17, pp. 307–314.
- McDowell, S.B., The Greater Antillean Insectivores, *Bull. Am. Mus. Nat. Hist.*, 1958, vol. 115, art. 3, pp. 113–214.
- McGrew, P.O., Berman, J.E., Hecht, M.C., *et al.*, The Geology and Paleontology of the Elk Mountain and Tabernacle Butte Area, Wyoming, *Bull. Am. Mus. Nat. Hist.*, 1959, vol. 117, art. 3, pp. 117–176.
- McKenna, M.C., Toward a Phylogenetic Classification of the Mammalia, in *Phylogeny of the Primates: A Multidisciplinary Approach*, Luckett, W.P. and Szalay, F.S., Eds., New York: Plenum Press, 1975, pp. 21–46.
- McKenna, M.C., Late Cretaceous and Early Tertiary Vertebrate Paleontological Reconnaissance, Togwotee Pass Area, Northwestern Wyoming, in *Aspects of Vertebrate History: Essays in Honor of E.H. Colbert*, Jacobs, L.L., Ed., Flagstaff: Mus. N. Arizona Press, 1980, pp. 321–343.
- McKenna, M.C. and Bell, S.K., *Classification of Mammals above the Species Level*, New York: Columbia Univ. Press, 1997.
- McKenna, M.C., Robinson, P., and Taylor, D.W., Notes on Eocene Mammalia and Mollusca from Tabernacle Butte, Wyoming, *Am. Mus. Novit.*, 1962, no. 2102, pp. 1–33.
- Morgan, G.S. and Ottenwalder, J.A., A New Extinct Species of *Solenodon* (Mammalia: Insectivora: Solenodontidae) from the Late Quaternary of Cuba, *Ann. Carnegie Mus.*, 1993, vol. 62, no. 2, pp. 151–164.
- Murphy, W.J., Eizirik, E., Johnson, W.E., *et al.*, Molecular Phylogenetics and the Origins of Placental Mammals, *Nature*, 2001, vol. 409, pp. 614–618.
- Novacek, M.J., Insectivora and Proteutheria of the Later Eocene (Uintan) of San Diego County, California, *Contrib. Sci. Los Angeles County Nat. Hist. Mus.*, 1976, no. 283, pp. 1–52.
- Osborn, H.F., *Evolution of Mammalian Molar Teeth to and from the Triangular Type*, New York: Macmillan Co., 1907.
- Osborn, H.F., *The Age of Mammals in Europe, Asia and North America*, New York: Macmillan Co., 1910.
- Paula Couto, C. de, *Tratado de paleomastozoologia*, Rio de Janeiro: Acad. Brazil., 1979.
- Romer, A.S., *Vertebrate Paleontology*, Chicago: Univ. Chicago Press, 1966.
- Rose, K.D., The Clarkforkian Land Mammal Age and Mammalian Faunal Composition across the Paleocene–Eocene Boundary, *Pap. Paleontol. Univ. Michigan*, 1981, no. 26, pp. 1–196.
- Russell, D.E. and Zhai, R.-J., The Paleogene of Asia: Mammals and Stratigraphy, *Mém. Mus. Nat. Hist. Nat. Paris, Ser. C*, 1987, vol. 52, pp. 1–488.
- Saban, R., Insectivora, in *Traité de paléontologie: T. 6*, Paris: Masson et Cie, 1958, vol. 2, pp. 822–909.
- Savage, D.E. and Russell, D.E., *Mammalian Paleofaunas of the World*, London: Addison–Wesley Pub. Co., 1983.
- Schlaikjer, E.M., Contributions to the Stratigraphy and Paleontology of the Goshen Hole Area, Wyoming: I. A Detailed Study of the Structure and Relationships of a New Zalambodont Insectivore from the Middle Oligocene, *Bull. Mus. Comp. Zool. Harvard*, 1933, vol. 76, no. 1, pp. 1–28.
- Schlaikjer, E.M., A New Fossil Zalambodont Insectivore, *Am. Mus. Novit.*, 1934, no. 698, pp. 1–8.
- Scott, W.B. and Jepsen, G.L., The Mammalian Fauna of the White River Oligocene: 1. Insectivora and Carnivora, *Trans. Am. Phil. Soc., Nov. Ser.*, 1936, vol. 28, part 1, pp. 1–153.
- Simpson, G.G., A New Classification of Mammals, *Bull. Am. Mus. Nat. Hist.*, 1931, vol. 59, pp. 259–293.
- Simpson, G.G., The Principles of Classification and Classification of Mammals, *Bull. Am. Mus. Nat. Hist.*, 1945, vol. 85, pp. 1–350.
- Sloan, R.E., Cretaceous and Paleocene Terrestrial Communities of Western North America, *Proc. N. Am. Paleontol. Conv.*, 1969, part E (Evolution of Communities), pp. 427–453.
- Stanhope, M.J., Waddell, V.G., Madsen, O., *et al.*, Molecular Evidence for Multiple Origins of Insectivora and for a New Order of Endemic African Insectivore Mammals, *Proc. Nat. Acad. Sci. USA*, 1998, vol. 95, no. 17, pp. 9967–9972.
- Storer, J.E., Mammals of the Swift Current Creek Local Fauna (Eocene: Uintan, Saskatchewan), *Contrib. Saskatchewan Mus. Nat. Hist.*, 1984, no. 7, pp. 1–158.
- Storer, J.E., Small Mammals of the Lac Pelletier Lower Fauna, Duchesnean of Saskatchewan, Canada: Insectivores and Insectivore-like Groups, a Plagemoenid, a Microsypoid and Chiroptera, in *Vertebrate Fossils and the Evolution of Scientific Concepts*, Sarjeant, W.A.S., Ed., Saskatoon: Gordon and Breach Pub., 1995, pp. 595–615.
- Stucky, R.K., Mammalian Faunas in North America of Bridgerian to Early Arikarean “Ages” (Eocene and Oligocene), in *Eocene–Oligocene Climatic and Biotic Evolution*, Princeton: Princeton Univ. Press, 1992, pp. 464–493.
- Szalay, F.S., Mixodectidae, Microsypoidae, and the Insectivore–Primate Transition, *Bull. Am. Mus. Nat. Hist.*, 1969, vol. 140, no. 4, pp. 193–330.
- Thewissen, J.G.M. and Gingerich, P.D., Skull and Endocranial Cast of *Eoryctes melanus*, a New Palaeoryctid (Mammalia: Insectivora) from the Early Eocene of Western North America, *J. Vertebr. Paleontol.*, 1989, vol. 9, no. 4, pp. 459–470.
- Tong, Y.S., Middle Eocene Small Mammals from Liguangqiao Basin of Henan Province and Yuanqu Basin of Shanxi Province, Central China, *Palaeontol. Sin., Nov. Ser. C*, 1997, no. 26, pp. 1–256.
- Van Valen, L., Deltatheridia, a New Order of Mammals, *Bull. Am. Mus. Nat. Hist.*, 1966, vol. 132, no. 1, pp. 1–126.
- Van Valen, L., New Paleocene Insectivores and Insectivore Classification, *Bull. Am. Mus. Nat. Hist.*, 1967, vol. 135, no. 5, pp. 217–284.
- Waddell, R.J., Okada, N., and Hasegawa, M., Towards Resolving the Interordinal Relationships of Placental Mammals, *Syst. Biol.*, 1999, vol. 48, pp. 1–5.
- West, R.M. and Atkins, E.G., Additional Middle Eocene (Bridgerian) Mammals from Tabernacle Butte, Sublette County, Wyoming, *Am. Mus. Novit.*, 1970, no. 2404, pp. 1–26.
- Winge, H., *The Interrelationships of the Mammalian Genera*, Copenhagen: C.A. Reitzels Forlag, 1941, vol. 1.
- Wood, C.B., McKenna, M.C., and Bosko, D., An Old Specimen of a New Undescribed Late Paleocene *Apternodus*-like Insectivore, *J. Vertebr. Paleontol.*, 2000, vol. 20, suppl. no. 3, p. 80A.