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A Leptictid Mammal from the Hsanda Gol Formation (Oligocene), Central Mongolia, with Comments on Some Palaeoryctidae¹

ALEXANDER W. A. KELLNER² AND MALCOLM C. MCKENNA³

ABSTRACT

Recent fieldwork in the Tertiary of Mongolia has produced a wealth of new early Oligocene specimens representing both known and previously unknown taxa. As part of our efforts to make this material known, we describe here a new leptictid mammal, *Ongghonia dashzevegi*, from the Oligocene Hsanda Gol Formation of Central Mongolia. This is the first bona fide leptictid to be reported from Asia. Assignment of *Ongghonia* to the Leptictidae is due to the particular molarization of the last premolar. Although the ingroup relationships of leptictids have yet to be established, the dental features of *Ongghonia* suggest that this species occupies a primitive position among Leptictidae and is closely related to *Diphyodectes* and *Prodiacodon*. Thus, the presence of leptictids in both Asia and North America in

the early Oligocene is not necessarily an indication of leptictid dispersion at that time. Observations on some early placental mammals lead us to new interpretations. We reassign *Xenacodon*, based on the molariform condition of the last premolar, and *Leptonysson*, based on the penultimate premolar, to the Leptictidae, as proposed in their original descriptions. *Pararyctes pattersoni* has well-developed precingula and postcingula on the upper molars. We therefore exclude it from the Palaeoryctidae and place it in Eutheria, incertae sedis. We transfer *Thelysia artemia* to the Pantolestidae from its current position in the Palaeoryctidae because it exhibits a well-developed mental foramen under the first molar, a condition that we regard as a synapomorphic character of pantolestids.

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² Department of Vertebrate Paleontology, American Museum of Natural History and Department of Geological Sciences, Lamont-Doherty Geological Observatory, Columbia University; Fellow, Conselho Nacional de Desenvolvimento Científico e Tecnológico—CNPq (Brazil).

³ Frick Curator, Department of Vertebrate Paleontology, American Museum of Natural History, and Professor of Geology, Columbia University.

INTRODUCTION

Currently the American Museum of Natural History and the Mongolian Academy of Sciences are conducting joint expeditions to the Cretaceous and Tertiary rocks of Mongolia. Many undescribed taxa and excellently preserved specimens of formerly poorly known taxa have been found. Part of the work concerns the stratigraphy and biostratigraphy of the Hsanda Gol Formation (Berkey and Granger, 1923), at and near the Hsanda Gol Fm. stratotype. This area is near Camp Loh (45°25'22"N; 101°47'40"E) along Shand Gol in Mongolia's Valley of Lakes. Although a badland area south-southwest of Camp Loh in the stratotype is richly fossiliferous, another area in and around Tatal Gol (about 13 km west of the stratotype) is even more productive and over the years has yielded many skulls, jaws, postcranial bones, and teeth of numerous taxa. For this reason, many expeditions have explored the exposures at Tatal Gol. Two main faunal levels can be discerned in the Hsanda Gol Fm. The lower fauna brackets an interbedded lava. The sediments below the level of a lava interbedded in the Hsanda Gol Fm. have yielded most of the specimens in the Tatal Gol area. The lower part of the Hsanda Gol Fm. is very rich in rodents and lagomorphs (Matthew and Granger, 1923a, 1923b), creodonts and carnivores (Matthew and Granger, 1924a), and lipotyphlan insectivorans (Matthew and Granger, 1924b); but it also contains perisodactyls and artiodactyls (Matthew and Granger, 1924b). Additional taxa are present in collections made recently, one of which we describe here as part of a series of papers on newly found Mongolian fossil mammals. Both the physical stratigraphy and the biostratigraphy of the Hsanda Gol Fm. are under review (McKenna et al., ms). The faunal sequence of Mongolia's Hsanda Gol Fm. continues to serve as a valuable standard with which other Asian Oligocene faunas can be compared.

The Mongolian Academy of Sciences—American Museum of Natural History Expedition of 1991 collected fossils from the Hsanda Gol Fm., both above and below the level of an intercalated lava. The lava has been dated as 31.5–32.2 Ma (Evernden et al.,

1964; here corrected according to Steiger and Jäger, 1977). Among the specimens found recently below the level of the lava, in what we regard as early Oligocene sediments, are a fragment of a right maxilla with the last premolar and the first molar and a fragment of a left mandibular ramus with the three lower molars. These specimens do not belong to a previously recognized Hsanda Gol taxon, nor do they represent a single individual, but they are appropriate in both size and morphology for representatives of a single taxon. Although there is always a small chance that the specimens actually belong to two new taxa, we believe that they represent upper and lower teeth of a single species, the first leptictid to be reported from the Hsanda Gol fauna. The taxon was evidently a very rare element in the lower Hsanda Gol faunal assemblage. Despite repeated prospecting attempts since 1991 in these and correlated deposits of the Hsanda Gol Fm., no new specimens similar to these have been recovered.

ABBREVIATIONS

Nomenclature for molars follows Van Valen (1966), with the modifications suggested by Szalay (1969). We introduce two new descriptive terms: *metastyle basin*, defined as the part of the styler shelf between the metastyle and the posterolabial base of the metacone; and *parastyle basin*, defined as the surface between the parastyle and the basal part of the paracone. The parastyle basin corresponds approximately to the area called "groove for the protoconid" by Crompton and Kielan-Jaworowska (1978: fig. 1). The dental formula for leptictids follows McKenna (1975), who considered the last premolar to be the fifth.

Measurements

APL	Anteroposterior length
AW	Anterior width
PW	Posterior width
TRH	Height of trigon from base of enamel to protocone
TRDH	Height of trigonid (labially) from base of enamel to apex of protoconid
TALH	Height of talonid (labially) from base of the enamel to hypoconulid

LIDD	Depth of dentary at lingual side, between m2 and m3
LADD	Depth of dentary at labial side, between m2 and m3
MSL	Mean sea level

The measurements were based on the criteria described by Lillegraven et al. (1981). Heights of the trigon, trigonid, and talonid were measured (table 1). All measurements were taken by a digital optical micrometer (Shopscope and Microcode II).

Institutions

AMNH	American Museum of Natural History
SMM	Science Museum of Minnesota, Minneapolis
UA	University of Alberta, Edmonton
UM	University of Michigan Museum of Paleontology, Ann Arbor
UW	University of Wyoming, Laramie

ACKNOWLEDGMENTS

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GEOLOGICAL SETTING

The type Hsanda Gol Formation occurs in the Tsagan Nor Basin (Central Mongolia) and was first described by Berkey and Granger (1923). Further information was provided later by Berkey and Morris (1927) and by various Russian, Polish, and Mongolian authors. This rock unit consists mainly of reddish to buff clays and silts (Goroshko and Kurochkin, 1979). The Hsanda Gol Fm. crops out in many places along the north side of the Tsagan Nor Basin, where it overlies white ?Eocene sediments of the Elegen Fm. and earlier rocks. The Hsanda Gol Fm. is in turn overlain by Miocene rocks of the Loh Formation (Osborn, 1924; Berkey and Morris, 1927: 365). Most of the described 1922 collections were made from Oligocene outcrops along Shand Gol (current Mongolian transliterated spelling), where the Hsanda Gol Fm. stratotype is located. Shand Gol is a prominent local sayr (Mongolian word for “dry wash” in western American parlance). The name of this sayr is spoken and spelled “Shand Gol” by modern Mongols but “officially” misspelled “Hsanda Gol” in the literature generated by the Central Asiatic Expeditions and by later writers (Berkey and Morris, 1927: pl. 29; Russell and Zhai, 1987: fig. 170). Although the formation’s name is a misspelling, it should not now be changed. In addition to the stratotype, the Hsanda Gol Fm. is especially fossiliferous in the drainage of Tatal Gol, a badland area about 13 km west of the stratotype. In 1925, the Central Asiatic Expedition made extensive collections at and near Tatal Gol, also earlier briefly called “Grand Canyon” by members of that expedition on the basis of reconnaissance in 1922 (Matthew and Granger, 1924b: 3). Since the 1920s, many expeditions have collected in and around Tatal Gol because of the richly fossiliferous sediments, especially near lat. 45°17′50″N; long. 101°37′16″E; elevation 4540 ft, mean sea level (average of 20 satellite fixes, WGS84 ellipsoid) where several expeditions have camped at the foot of a low series of fossiliferous ridges just west of the main drainage.

A mafic lava flow dated by the whole-rock K/Ar method at 31.5 and 32.2 Ma (average = 31.85 Ma) by Evernden et al. (1964: 193, corrected according to Steiger and Jäger, 1977)

occurs within the Hsanda Gol Fm. section at Tatal Gol and is exposed discontinuously over a large area between Tatal Gol and Shand Gol but not immediately to the west of Tatal Gol except in a small area. Two small outcrops were mapped by Berkey and Morris (1927: pls. 28, 29) in the type section itself, close to the water well in Shand Gol (lat. $45^{\circ}16'56''\text{N}$; long. $101^{\circ}47'40''\text{E}$) that lies east of Camp Loh. More recent dating of samples of the flow, using the same K/Ar method (Devyatkin and Smelov, 1979) achieved similar results. Currently, efforts are under way to date various outcrops of lava in the area by the $^{40}\text{Ar}/^{39}\text{Ar}$ method, but results are being presented elsewhere. Provided that it is a single unit, the flow provides a convenient datum for determining the stratigraphic position of fossils in areas where outcrops of sediments are available and whose relationships to the lava are determinable; however, for several kilometers west of the course of Tatal Gol there are extensive but low exposures without evidence of the lava intercalation. Outcrops there must be correlated by other means to the areas where relationships with the flow are clear. Lava crops out again to the north and northwest of Tatal Gol near a volcanic edifice named Black Peak on Berkey and Morris's map (1927: pl. 29), but we are not completely sure that the subsurface continuity shown in section A-B on Berkey and Morris's map margin is demonstrable.

Fossils have been found both above and below the level of the dated flow, notably near Tatal Gol. Specimens collected in the reddish sediments below the level of the flow and for a few meters above it are now thought to be early Oligocene in age (*sensu* Swisher and Prothero, 1990). In these rocks, species of *Tsaganomys* and *Cricetops* are the dominant taxa, but after the faunal change that occurs in the sediments above the level of the lava, species of *Tachyoryctoides* and ?*Yindirtemys* are abundant. The environment during deposition has been interpreted as semiarid (Mellett, 1968).

PREPARATION OF THE SPECIMENS

Preservation of both specimens is rather poor. Although there is no major compression, parts of the surfaces of the bones and teeth (especially m3) are not preserved. The

two specimens were found embedded in a reddish siltstone, cemented with carbonate minerals. Preparation was carried out by immersing these specimens in a 3 to 5% formic acid solution, following the procedure of Kellner (1991). After removal of most of the matrix, we observed a white mineral (possibly gypsum) in some parts of the specimens. This proved to be insoluble in formic acid, and was removed mechanically.

SYSTEMATICS

CLASS MAMMALIA LINNAEUS, 1758

COHORT EPITHERIA MCKENNA, 1975

SUPERORDER LEPTICTIDA MCKENNA,
1975

FAMILY LEPTICTIDAE GILL, 1892

Ongghonia, new genus

TYPE SPECIES: *Ongghonia dashzevegi*, new species.

LOCALITY, ASSOCIATED FAUNA, AGE, AND DISTRIBUTION: As for the type species.

ETYMOLOGY: Name derived from Ongghon, which in the Mongolian culture are images of ancestors that protect the living.

DIAGNOSIS: As for the species.

Ongghonia dashzevegi, new species

Figures 1-3; table 1

TYPE SPECIMEN: Fragmentary right maxilla with the last premolar (P5) and the first molar (M1). Original: Mongolian/American Museum of Natural History collections, Mongolian Academy of Sciences, Hsanda Gol Number 1991-104; cast: AMNH 129417.

REFERRED SPECIMEN: Fragment of left dentary with molars (m1-m3), same collection as the holotype: Mongolian/American Museum of Natural History collections, Mongolian Academy of Sciences, Hsanda Gol Number 1991-237; cast: AMNH 129418.

LOCALITY: Tatal Gol, Mongolia (Tatal Gol Camp: lat. $45^{\circ}17'50''\text{N}$; long. $101^{\circ}37'16''\text{E}$).

ASSOCIATED FAUNA: Lower Hsanda Gol fauna, from beneath the level of the lava intercalated in the Hsanda Gol Fm.

AGE: Early Oligocene, *sensu* Swisher and Prothero (1990).

DISTRIBUTION: Type locality only.

ETYMOLOGY: Species name in honor of Ac-

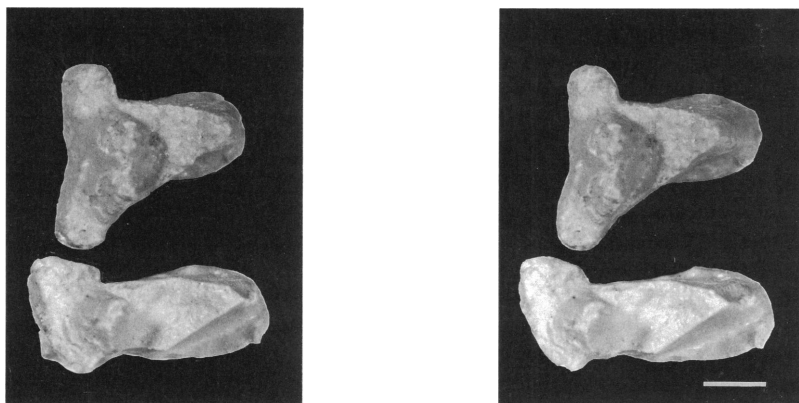


Fig. 1. *Ongghonia dashzevegi*, stereopair of the holotype (cast of AMNH 129417), showing the occlusal view of right maxilla with last upper premolar and first upper molar. Scale = 1 mm.

ademician Demberlyin Dashzeveg, participant in the Mongolian—American Museum of Natural History expeditions.

DIAGNOSIS: Leptictid smaller than *Prodiacodon puercensis* and slightly larger than *Prodiacodon tauricinerei*. Last upper premolar (P5) molariform, with paracone and metacone more connate at their base than in *Leptictis*; metastyle basin larger than in *Prodiacodon puercensis*. Upper first molar (M1) precingulum and postcingulum smaller than in *Prodiacodon puercensis* and limited at the basal part of the crown; hypocone comparatively small. Lower molars (m1–m3) with

trigonid high with respect to the talonid and straighter than in other leptictids (e.g., *Prodiacodon* and *Leptictis*); paraconid bladelike as in some palaeoryctids (e.g., *Aaptoryctes ivyi*) and in the leptictid *Diaphyodectes prolatus*; precingulid comparatively well developed, larger than in other leptictids (e.g., *Prodiacodon puercensis*).

DESCRIPTION

Only the right last premolar (P5) and the first molar (M1) are preserved in the type upper dentition. These teeth are connected

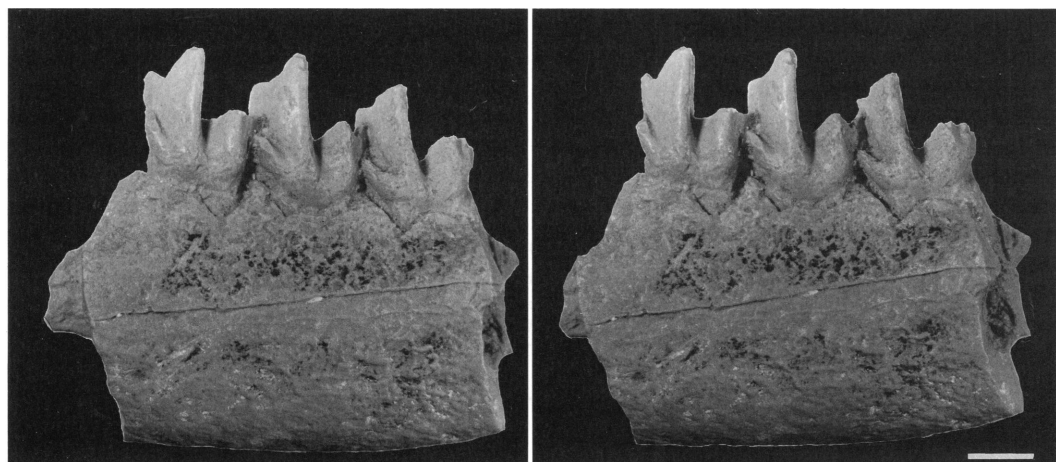


Fig. 2. *Ongghonia dashzevegi*, stereopair of referred specimen (cast of AMNH 129418), showing labial view of left mandibular ramus with lower molars. Scale = 1 mm.

1977: 31). The postcingulum is well developed, although it is smaller than in *Prodiacodon puericensis*. At the base of the crown the postcingulum forms the posterolingual margin, where a small hypocone is present.

The lower dentition (referred specimen) is represented by all three left molars in the dentary (table 1). This material suggests that *Ongghonia* had the posterior part of the mandible almost straight, somewhat deeper than in *Prodiacodon*, and teeth very close to one another.

The pattern of the lower molars is uniform, with m3 the longest anteroposteriorly and m2 the largest tooth (figs. 2, 3; table 1). Trigonids and talonids are similar in relative height to those of *Prodiacodon*. Buccal and lingual margins are nearly straight and the trigonid is not curved lingually as in *Prodiacodon* and *Leptictis*. The protoconid and metaconid are subequal in size and are larger than the paraconid. On m3 the metaconid is broken. The shape of the protocristid in posterior view is similar to an asymmetric V, displaced to the protoconid side. On m1 the protocristid is less sharp compared with the protocristid of m2. The paraconid is bladelike and closer to the metaconid than to the protoconid. On m1 the paraconid is more isolated and larger than on the other molars. The trigonid basin of m1 is slightly inclined in comparison to m2 and m3, where it is more rounded and concave. A precingulid showing wear facets is well developed at the anterobuccal margin of the base of the trigonid in all molars.

The molar talonids have distinguishable hypoconids, hypoconulids, and entoconids (figs. 2, 3). Of those, the entoconid is the smallest. The presence of extra cusps could not be determined other than a small entoconulid on m2. The cristid obliqua is pronounced and joins the base of the trigonid in the midline between the protoconid and metaconid. The cristid obliqua on m2 and m3 is more curved and displaced buccally to the protoconid side than on m1. The hypoflexid is similar in all molars. In *Ongghonia dashzevegi* the hypoflexid is slightly less excavated than in the species of *Prodiacodon* (e.g., *P. puericensis* and *P. tauricinerei*). The m2 entocristid is poorly preserved. It is low and has a tiny entoconulid. The m3 talonid is narrower but more elongated than those of m2 and m1.

DISCUSSION

The most distinguishing features of the leptictid dentition are the molariform last premolars (Butler, 1956; McKenna, 1975; Novacek, 1986). Although molarization of the last premolars is a tendency observed in some other mammal groups, the condition in Leptictidae is distinct, supporting leptictid monophyly. The last upper premolar is transverse, has a triangular shape with precingulum (reduced or absent) and postcingulum, is compressed anteroposteriorly, and bears a well-developed independent protocone, metacone, and paracone. The last lower premolar has a tricuspid trigonid with protoconid and metaconid subequal in size, and a developed talonid, with two or more cusps. Since the upper last premolar of *Ongghonia dashzevegi* is molariform and conforms to the above conditions (no lower premolar of this species is currently known), we classify this new taxon in the Leptictidae.

This species differs from other leptictids such as *Prodiacodon* and *Leptictis* by some discrete dental features. In the upper dentition of *Ongghonia* the paracone and metacone are comparatively more connate at the basal part of the crown, the hypocone on M1 is comparatively smaller, and the metastyle basin is larger. As far as can be observed on the present material, the upper dentition of *Ongghonia* is more similar to that of *Prodiacodon* than to that of other leptictid genera, with a more developed parastyle basin of the last premolar and first molar, reduced lingual cingula, and smaller hypocone.

The lower molars of *Ongghonia dashzevegi* share some common features with the European leptictid *Diaphyodectes prolatus* Russell, 1964. Although no complete mandible of the latter is known, the lower molars attributed to it have an almost bladelike paraconid, which is similar to that of *Ongghonia* (Russell, 1964: pl. 4, fig. 1a, b). In *Prodiacodon* and *Leptictis* the paraconid tends to be more isolated, forming a well-defined cusp.

A bladelike paraconid is also present in some palaeoryctoids, markedly in Palaeoryctinae, sensu Van Valen (1966). But in them the paraconid is positioned close to the metaconid, giving a more constricted appearance to the trigonid (see comments on Palaeoryctidae below).

In comparing relative sizes of the trigonid versus the talonid, there is no clear distinction between leptictids, palaeoryctids, and some other eutherian mammals as they are currently diagnosed. The relative heights of the trigonid in *Aptoryctes* (Palaeoryctidae) and *Prodiacodon* (Leptictidae), for example, are very similar. *Ongghonia dashzevegi* approaches both, equally, in this feature.

We also support leptictid affinities of two additional taxa, both known only from their holotypes: *Xenacodon mutilatus* Matthew and Granger, 1921, and *Leptonysson basiliscus* Van Valen, 1967. The first, *Xenacodon mutilatus*, was found at Mason pocket, Tiffany beds (Paleocene), Colorado (Simpson, 1935). It consists of a right mandibular ramus, with p5 (traditional p4) still partially inserted in the dentary, m2 and m3 (AMNH 17407). Matthew and Granger (1921) classified *Xenacodon* in the Leptictidae. Simpson (1935) suggested that this assignment was uncertain, although probable. Some years later Simpson (1945) regarded *Xenacodon* as a member of Leptictidae, incertae sedis, without presenting further discussion. Butler (1948) considered the dentition of *Xenacodon* to approach that of the Erinaceidae, where he reassigned it. Van Valen (1967) considered *Xenacodon* to be a species of the family Adapisoricidae (subfamily Creotarsinae).

The last lower premolar of the type and only specimen of *Xenacodon mutilatus* was just starting to erupt at death. However, it is evident that the trigonid has a very well-developed metaconid, subequal in size to the protoconid. The paraconid is smaller but positioned equidistantly from the other trigonid cusps. The talonid is much smaller, but most of it is still out of sight inside the dentary. Nevertheless, the presence of at least two distinct cusps can be observed.

Although the paraconid is small, the trigonid of the last lower premolar of *Xenacodon mutilatus* is definitely molariform. This suggests that *X. mutilatus* is a leptictid. The talonid of this tooth, however, is not identical to the condition of most leptictids, being proportionally smaller. Even so, we consider that the classification of this species in the Leptictidae, based on the complete molariform trigonid of the last lower premolar, is better supported than other suggestions (e.g., Butler, 1948; Van Valen, 1967).

The second taxon for which we claim leptictid affinities is *Leptonysson basiliscus* Van Valen, 1967, from Gidley Quarry, Lebo Formation (middle Paleocene), Crazy Mountain Field, Montana. The holotype of *L. basiliscus* consists of a left mandibular ramus with p2, p4 (traditional p3), and m1 to m3 (AMNH 35295). This species was placed by Van Valen (1967) in the Leptictidae. Subsequently, Clemens (1973) reassigned it to Palaeoryctidae, based on the overall trenchant morphology of the lower premolar crowns. Novacek (1977) also excluded this taxon from Leptictidae, following the arguments presented by Clemens (1973).

Although the last lower premolar is not preserved, *L. basiliscus* has a penultimate lower premolar p4 (leptictid dental formula of McKenna, 1975) with three independent trigonid cusps. Of these, the protoconid is the largest. Lingually there is a clearly distinguishable metaconid, separated from the protoconid. The paraconid is well developed and larger than the metaconid. This "semimolariform" structure of the trigonid strongly suggests that the next premolar (p5) was molariform, and therefore indicates leptictid affinity. We agree with Clemens (1973: 29) that the teeth present in this species were not deciduous.

Moreover, the penultimate lower premolar of palaeoryctids (e.g., *Palaeoryctes puercensis* and *Aptoryctes ivyi*) presents only two cusps, the protoconid and one accessory cusp on its posterior basal portion. In leptictids, the penultimate lower premolar can have as many as five cusps (Novacek, 1986: 15). Because *L. basiliscus* (with four cusps in the penultimate lower premolar) also better approaches the leptictid condition for this feature, we reassign *L. basiliscus* to the Leptictidae. It is important to note that the cusps of the penultimate lower premolar in *L. basiliscus*, especially the metaconid and paraconid, are more developed than in other leptictids.

PALEOGEOGRAPHIC DISTRIBUTION OF THE LEPTICTIDAE

The leptictids were a primitive group of placental mammals. Many authors have attributed a central position to leptictids in the evolution and diversification of placentals (see Novacek, 1986, for a review). At the very

least, the family Leptictidae includes the genera *Prodiacodon*, *Leptictis*, *Palaeictops*, *Myrmecoboides*, and *Diaphyodectes*. Here we return *Xenacodon* and *Leptonysson* to the Leptictidae, where both were placed in the original descriptions, and we add the new genus *Onghghonia*.

Most of the known leptictid species are found in early Tertiary mammalian faunas from North America and belong to the subfamily Leptictinae. The earliest record of this group is *Prodiacodon crustulum* Novacek, 1977, from the early Paleocene (Puercan) of Montana. Other species of *Prodiacodon* occur in middle Paleocene (Torrejonian) to early Eocene (Wasatchian) sediments (Novacek, 1977; Bown and Schankler, 1982). Additional North American leptictid genera such as the monospecific *Myrmecoboides*, *Leptonysson*, and *Xenacodon* were found only in Paleocene formations, and the various species of *Palaeictops* occur in early to middle (Wasatchian to Uintan) Eocene rocks (Novacek, 1977). In the late Eocene (Chadronian) and early Oligocene (Orellan), the Leptictidae of North America are represented by the genus *Leptictis*, with several species (Novacek, 1976, 1986), restricted to North America.

The only bona fide member of Leptictinae in Europe is the monospecific genus *Diaphyodectes*, found in Paleocene sediments in a fissure fill near Walbeck, Germany. There is also a complete skeleton of a leptictid, found in Paleocene sediments of the Menat Basin, France, described by Guth (1962). It has molariform last premolars, which led Guth (1962: 9) to assign the specimen to the genus *Ictops* (junior synonym of *Leptictis*).

Another European taxon originally classified in the Leptictidae is *Leptictidium auderiense* Tobien, 1962, found in the middle Eocene of Messel, Germany. The last premolars are clearly molariform (Tobien, 1962). Sigé (1974, 1975) pointed out that this species is similar to *Pseudorhynchocyon cayluxi* Filhol, 1892, found in middle Eocene to lower Oligocene sediments of Quercy, France, in having a very elongated snout. Sigé (1974, 1975) placed both taxa in a new subfamily of the Leptictidae, *Pseudorhynchocyoninae*.

The only known occurrence of Leptictidae in Asia is *Onghghonia*. *Ictopidium*, from the Oligocene of Mongolia and China, once

thought to be a leptictid (Zdansky, 1930), is now regarded as an erinaceoid insectivoran (Butler, 1988: 123).

Although the monophyly of Leptictidae is supported by cranial (Novacek, 1986) and dental (leptictid molariform last premolar) characters, the relationships among the different taxa have yet to be established. However, some general observations about leptictid phylogeny can be made. The most primitive leptictid taxa are *Prodiacodon*, *Onghghonia*, and *Diaphyodectes*, based on the high trigonids versus talonids and the comparatively large piercing cusps. *Leptonysson* and *Xenacodon* may also be considered part of the primitive leptictids. A close relationship among the several species of *Prodiacodon* was proposed by Novacek (1977) on the basis of the presence of a double paraconule in the upper molars. Conceivably *Onghghonia* and *Diaphyodectes* are more closely related to each other than to other leptictids by possessing a well-developed bladeliike paraconid in the lower molars. Possibly the most derived group is represented by *Palaeictops* and *Leptictis*, characterized by comparatively smaller trigonids, upper molars and premolars less compressed anteroposteriorly, larger postcingulum, and larger hypocone.

Although it is represented by only one species, the genus *Myrmecoboides* is clearly set apart from the rest of the Leptictidae by possessing closely appressed metaconids and paraconids, anteroposteriorly elongated talonids, and widely spaced anterior premolars (Novacek, 1977). Also forming an independent lineage within Leptictidae are the *Pseudorhynchocyoninae* (*Pseudorhynchocyon* and *Leptictidium*), which have an elongated snout. Nevertheless, according to figures of the upper molars presented by Sigé (1975), this group has an upper dentition similar to that of *Prodiacodon*, especially with respect to the postcingulum and the hypocone, which are small compared to derived forms such as *Leptictis* and *Palaeictops*.

COMMENTS ON PALAEORYCTIDAE

The Palaeoryctidae constitute a poorly understood family of early placental mammals. The stratigraphic range of the group, depending on author and assigned taxa, varies between Campanian and Eocene, or is re-

stricted to early Tertiary (Paleocene-Eocene). The systematic position of this group is still controversial. Some authors refer it to the lipotyphlan insectivorans (Matthew, 1913; Simpson, 1931, 1945; Clemens, 1973). Others have suggested that it is not directly related to insectivorans (e.g., McDowell, 1958; Van Valen, 1966, 1967; Lillegraven, 1969; Szalay, 1977; Butler, 1988).

The Palaeoryctidae sensu stricto (= Palaeoryctinae of Van Valen, 1966) currently comprises the species *Palaeoryctes puercensis* Matthew, 1913; *Palaeoryctes punctatus* Van Valen, 1966; *Palaeoryctes cruoris* Gunnell, 1994; *Pararyctes pattersoni* Van Valen, 1966; *Aptoryctes ivyi* Gingerich, 1982; and *Eoryctes melanus* Thewissen and Gingerich, 1989. To those, Gingerich (1982) added *Thelysia artemia*, considering it to belong to Palaeoryctidae, incertae sedis. The unity of this group was postulated on characteristics of the upper and lower molars by Van Valen (1966), who was followed by other authors (Gingerich, 1982; Thewissen and Gingerich, 1989). Typical palaeoryctid upper molars are characterized by having piercing cusps, transverse orientation, very wide stylar shelves, and paracone and metacone connate. Van Valen (1966) also proposed that some palaeoryctids had developed precingula and postcingula in the upper molars.

The upper molars of *Palaeoryctes puercensis*, however, are very compressed anteroposteriorly and lack lingual cingula. *Palaeoryctes cruoris*, *Eoryctes melanus*, and *Aptoryctes ivyi* also show this basic (though less compressed) upper molar pattern, and also lack lingual cingula. Therefore, we regard the absence of lingual cingula as characteristic of Palaeoryctidae sensu stricto (contra Van Valen, 1966). The upper molar that is the holotype (UW no. 2002) of *Pararyctes pattersoni*, found in late Paleocene sediments of Wyoming, differs markedly in possessing a well-developed precingulum and postcingulum (Van Valen, 1966: 58, 59), and should not be classified in the Palaeoryctidae. Among other specimens attributed to this species by Van Valen (1966) is a fragment of a maxilla, bearing two teeth, identified as the left P4 and M1 (Van Valen, 1966: pl. 7, fig. 3). The fragmentary nature of this specimen, especially of the M1, makes its assignment to this species unsure.

Krishtalka (1973) attributed fragments of molars and premolars, found in Paleocene strata of Alberta, to *Pararyctes* sp. Although this material is very fragmentary, Krishtalka (1973: 42) observed the precingulum and postcingulum on the upper premolars and molars. Holtzman (1978) referred an incomplete upper premolar and some molars to *Pararyctes pattersoni*. These were found in late Paleocene sediments of the Tongue River Formation, North Dakota. The figured molar (Holtzman, 1978: 68–69, fig. 5.11, SMM P77.8.66) clearly presents a precingulum and a well-developed postcingulum.

The best preserved specimen attributed to *Pararyctes* sp. was discussed by Fox (1983). It consists of a partial skull and mandible (UA 16268), with almost the complete dentition preserved. Unfortunately, no detailed description or figures showing the morphology of the teeth of this specimen, especially of the premolars, are available yet. Therefore, we assign *Pararyctes pattersoni* to Eutheria, incertae sedis.

The last taxon classified as a member of Palaeoryctidae that we discuss is *Thelysia artemia*. Gingerich (1982) doubtfully assigned this species, known only from its type material (UM 68281, cast AMNH 128989) to this family, basically because of dental resemblances to *Leptonysson basiliscus*, which was also regarded by Clemens (1973) as a member of the Palaeoryctidae. However, Gingerich (1982: 46) pointed out that there is no particular resemblance among *Thelysia*, *Leptonysson*, and *Palaeoryctes*. He also emphasized that discovery of new material could lead to the reassignment of *Thelysia* to the pantolestids or leptictids.

As far as we could observe in the original material (both mandibular rami with only the lower molars), there is no particular characteristic that would support a leptictid or palaeoryctid classification of *Thelysia artemia*. On the other hand, the position of a mental foramen under m1 observed in *Thelysia* indicates a closer relationship to the pantolestids. Since this character is consistent within this group and can be observed in different genera such as *Pantolestes* and *Propalaeosinopa*, it is here considered a synapomorphy of Pantolestidae. Therefore, in our opinion, the classification of *Thelysia artemia* in the Pantolestidae is supported.

FINAL CONSIDERATIONS

The relationships of many early eutherian taxa are very difficult to establish. Most species are based on fragmentary material, usually teeth, whose condition and interpretation have led to many disagreements. The potential for parallelism, individual variations, and questions of homology in such incomplete fossils is very high. Leptictids are no exception; most leptictid taxa are known by very few poorly preserved specimens.

In terms of dental characters, the condition of the last premolars seems taxonomically important, and evolved in different ways in several mammal lineages (Butler, 1956; Novacek, 1986). However, the particular "leptictid" way of molarization of the last premolars is the best dental character found so

far that unites and distinguishes Leptictidae from all other early eutherian mammals.

Ongghonia dashzevegi is the first bona fide leptictid to be found in Asia. Although *Ongghonia* is early Oligocene in age, its closest probable relatives are Paleocene taxa: *Prodiacodon* from the Puercan and Torrejonian of North America and *Diaphyodectes* from the Cernaysian of Europe. The time of the last possible common ancestor of the Asian and Euramerican leptictids is unknown, but we hypothesize that it may have been in the latest Paleocene or early Eocene, when many faunal elements were shared among the northern continents. The long gap between the time of occurrence of *Ongghonia* and its probable time of origin suggests that our understanding of leptictid evolution is still very incomplete.

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