ARTIODACTYLA FROM THE EARLY EOCENE OF KYRGYZSTAN

by

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CONTENTS

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ABSTRACT

Isolated upper cheek teeth of the primitive artiodactyl *Diacodexis* sp., upper molars of *Eolantianius russelli* gen. et sp. nov. (Diacodexeidae), two lower molars tentatively referred to *Eolantianius russelli* gen. et sp. nov., and astragali of Diacodexeidae indet. are described from the early Eocene (late Ypresian) of locality Andarak 2 in Kyrgyzstan.

RESUME

De la localité Andarak 2 au Kirghizstan (Eocène inférieur, Yprésien supérieur) sont décrites des dents isolées d'artiodactyles primitifs, dents jugales supérieures de *Diacodexis* sp., molaires supérieures d'*Eolantianus russelli* n. gen. n. sp. (Diacodexeidae), deux molaires inférieures attribuées provisoirement à *Eolantianus russelli* n. gen. n. sp., et deux astragales de Diacodexeidae indet.

INTRODUCTION

Artiodactyla from the beginning of the Eocene are rare in Asia. In Central Asia, Dashzeveg (1982) reported Artiodactyla indet. from the Bumban Member of the Naran Bulak Svita at Tsagan-Khushu, Mongolia. Elsewhere, the Chakpaktas Svita and Lower Obayla Subsvita in the Zaissan Depression, eastern Kazakhstan, has yielded Dichobunidae n. gen. n. sp.; *Aksyiria oligostus* GABUNIA, 1973; *Paraphenacodus solivagus* GABUNIA, 1971; and Dichobunidae indet. (Gabunia 1971, 1973, 1977, 1984), which may also be early Eocene in age (Gabunia 1984).

Abundant remains of Artiodactyla have been reported only from the Indian subcontinent: the diacodexeid *Diacodexis pakistanensis* THEWISSEN, RUSSELL, GINGERICH & HUSSAIN, 1983 from the lower part of the Kuldana Formation (Ypresian) at Barbora Banda, Pakistan (Thewissen *et al.* 1983), and the raoellid *Khirtharia dayi* PILGRIM, 1940 from the Kuldana Formation in Pakistan and Subathu Formation at Subathu, India (Russell & Zhai 1987). Remains of *D. pakistanensis* were reported from the upper part of the Subathu Formation of Kalakot, India (Kumar & Jolly 1986), which may be of early Eocene age (Sudre, pers. comm.) although Kumar & Sahni (1985), Kumar & Jolly (1986), and Russell & Zhai (1987) considered the age of the upper part of the Subathu Formation to be middle Eocene.

In the early-to-middle Eocene of Indo-Pakistan, artiodactyls are much more abundant and diverse than those known from Central Asia. Six families are represented: Dichobunidae (endemic genera *Chorlakkia* and *Dulcidon* from the Indian subcontinent (which may be synonymous, Thewissen *et al.* 1987); Entelodontidae, Leptomerycidae, Raoellidae (endemic family for Indian subcontinent), Helohyidae, and Anthracotheriidae (Russell & Zhai 1987). The last two widely-distributed families seem to have had an Asiatic origin (Coombs & Coombs 1977a, 1977b, Suteethorn *et al.*

1988). Thus explosive radiation of Asiatic artiodactyls in the early-to-middle Eocene suggests a long and complex evolution of the order in the early Eocene of Asia.

Another central Asiatic locality with relatively abundant remains of Artiodactyla is the locality Andarak 2 in Kyrgyzstan. The age of Andarak 2 was considered previously as middle Eocene (Lutetian; Russell & Zhai 1987, and references therein), but after recent study of its extremely rich elasmobranch fauna it has been redated as early Eocene (late Ypresian; Averianov & Udovichenko 1993). Previously, only Dichobunidae indet. was cited but not described from Andarak 2 (Reshetov *et al.* 1978). Here remains of diacodexeids *Diacodexis* sp., *Eolantianius russelli* n. gen. n. sp., and Diacodexeidae indet. are described from this locality.

Abbreviations

dex - dexter (right)
sin - sinister (left)
Wtr - width of the trigonid
L - length
W - width
Wtl - width of the talonid
ZIN - Zoological Institute, Russian Academy of Sciences, Saint Petersburg

All measurements are in mm.

SYSTEMATIC PALEONTOLOGY

Order **ARTIODACTYLA** OWEN, 1848
Artiodactyla *incertae subordines*
Family **DIACODEXEIDAE** GAZIN, 1955
Genus ***DIACODEXIS*** COPE, 1882

Diacodexis sp.
(Pl. 1a-b)

Referred specimens: ZIN 34351 dex P^4 (fragmental), ZIN 34352 sin M^1.

Locality: Andarak 2, Kyrgyzstan. Early Eocene (Ypresian).

Description

Labial part of the known P^4 is broken off (Pl. 1a). This tooth seems to be rectangular in shape. The protocone is relatively high and there is a strong preprotocrista which continues as a distinct ridge connecting the protocone and the base of the paracone. There is a weak, indistinct postprotocrista. Around the base of the tooth there is a weak but distinct cingulum.

M^1 is triangular in shape and has three main cusps (Pl. 1b). The paracone and the metacone are subequal in size and height and are compressed labiolingually. The protocone is as high as the labial cusps and slopes lingually. The metaconule is well developed, whereas the paraconule is virtually absent. The preprotocrista and the

postprotocrista are distinct ridges. The postmetaconule crista extends to the posterolingual base of the metacone and contacts the labial cingulum. The metaconule is connected to the base of the metacone by a sharp ridge. A straight centrocrista is confluent posteriorly with a postmetacrista as far as the cingulum. There is no metastyle. The labial cingulum is interrupted at the ectoflexus opposite the junction of the metacone and paracone. There is a strong and high posterior cingulum, but it does not form a hypocone. The anterior margin lacks a cingulum as far as it is preserved on the described specimen. A lingual cingulum is also completely absent.

Measurements

		L	W
ZIN 34351	P^4	ca. 2.4	-
ZIN 34352	M^1	ca. 3.0	3.8

Comparisons

Diacodexis sp. from Andarak 2 differs from *D. pakistanensis* from the early Eocene Kuldana Formation of Pakistan (Thewissen *et al.* 1983), from *D. gazini* GODINOT, 1978 from the early Eocene (early Ypresian) of Rians, France (Godinot 1981), from *D. varleti* SUDRE, RUSSELL, LOUIS & SAVAGE, 1983 from the Ypresian of Condé-en-Brie, Mutigny, Avenay and Pourcy, France, and from *Diacodexis* sp. from the early Ypresian of Dormaal, Belgium (Sudre *et al.* 1983) in the smaller dimensions of M^1, in the interrupted labial cingulum on M^1, and in the relatively shorter P^4. It differs from *Diacodexis* sp. from the late Ypresian of Prémontré, France, in the same features and in the more triangular shape of M^1, which is less rounded at the base of the lingual cusps, and it differs in having a complete lingual cingulum on P^4. It differs from the Spanish late Ypresian *Diacodexis* sp. (Sudre *et al.* 1983) in the same features and also in its considerably smaller size.

The Andarak *Diacodexis* sp. is close in the size of its M^1 to *D. antunesi* ESTRAVÍS & RUSSELL, 1989 from the earliest Ypresian of Silveirinha, Portugal, which is apparently the oldest and most primitive member of the genus (Estravís & Russell 1989). It differs from the latter species by absence of a precingulum and weakly defined paraconule on M^1.

The Andarak *Diacodexis* sp. differs from most of the early-middle Eocene North American species of *Diacodexis* (Krishtalka & Stucky 1985) in its considerably smaller size, absence of a precingulum and a paraconule, and in the less inflated base of the labial cusps on M^1. The oldest North American *Diacodexis*, *D. ilicis* GINGERICH, 1989 from the basal Wasatchian of Wyoming (Gingerich 1989), is approximately the same size as *Diacodexis* sp. from Andarak. However, the former species is known from the lower dentition, whereas the latter species is represented by the upper one only, precluding the possibility of comparison.

Discussion

Diacodexis is predominantly an early Eocene North American, European and Asiatic genus that is characteristized by rather primitive (secondarily simplified?) and

generalized dental morphology, even in comparison with most condylarths. However, it has a surprisingly derived postcranial skeleton (Rose 1985). The early Eocene Asiatic *D. pakistanensis* is one of the most primitive species of the genus. It differs from most of the American species in being smaller. It differs from these and from the European early Eocene *D. gazini* GODINOT, 1978 in its lingual narrowness of M^1 and M^2, and in the weakly developed posterolingual cingulum of these teeth (Thewissen *et al.* 1983). The earliest Eocene European *Diacodexis* sp. from Dormaal (Sudre *et al.* 1983) and *D. antunesi* from Silveirinha (Estravís & Russell 1989) are smaller than the Pakistan species and may be more primitive. *Diacodexis* sp. from Andarak 2 is apparently more primitive than *D. pakistanensis* and *D. antunesi* in lacking a precingulum, in having a relatively short P^4, and being smaller. However, it is more derived than both species in lacking a distinct paraconule on M^1. This mosaic of dental characteristics in the Andarak species may indicate a more complex evolution of early artiodactyls in Asia than was evident before.

According to Gentry & Hooker (1988), the genus *Diacodexis* is paraphyletic, different species being related to different subordinal groups of Selenodontia, which precludes it from being the stem artiodactyl. I think that this conclusion may be an artefact caused by lack of information, combined with the parsimony technique (and ideology) used. *Diacodexis metsiacus* COPE, 1882 [= *D. secans* COPE, 1881] is united by these authors with Leptochoeridae on the cladogram 1 (Gentry & Hooker 1988, Fig. 9.7, node 24) by synapomorphies 42A (P_3 length greater than 120% of M_1 length) and 99 (tibia and fibula fused distally). But the state of character 99 is unknown for *D. varleti* and *D. pakistanensis*, and state 42 is unknown for *D. varleti* (Gentry & Hooker 1988, Fig. 9.6, data matrix 1). "Autapomorphies" for *D. metsiacus* (node 73, characters 89A, 93, 107) are all postcranial characters whose states are not known for *D. varleti* and *D. pakistanensis* (Gentry & Hooker 1988, data matrix 1). *D. pakistanensis* really differs from *D. metsiacus* in characters 34, 42, 59 and 64, and *D. varleti* differs from *D. metsiacus* only in character 34. All these characters are dental features which are too liable to homoplasy (especially, reduction of canines) to be used for the reconstruction of a phylogeny. So, I think that the conclusion about the paraphyletic nature of *Diacodexis* is rather doubtful or, at least, premature.

Genus *EOLANTIANIUS* gen. nov.

Etymology: From Greek *Eos*, dawn, and genus *Lantianius* CHOW, 1964.

Type species: *Eolantianius russelli*, sp. nov.

Known distribution: Early Eocene (Ypresian), Kyrgyzstan.

Diagnosis: Relatively derived diacodexeine with subquadrate low-crowned upper molars having a complete robust lingual cingulum and a well developed hypocone. The paraconule and the postparaconule crista on M^{1-3} are virtually absent.

Comparisons

The new genus is most similar to the late Eocene *Lantianius* CHOW, 1964 from China (Chow 1964, Gingerich 1976) in having a complete lingual cingulum with a large

hypocone (a possible synapomorphy between both genera). From this genus it differs in the more subquadrate upper molars, nearly straight centrocrista and more labially placed paracone and metacone on M^{1-2}, and more rounded labial cusps on M^{1-3}. The new genus differs from *Diacodexis* COPE, 1882, *Wasatchia* SINCLAIR, 1914, *Bunophorus* SINCLAIR, 1914, *Simpsonodus* KRISHTALKA & STUCKY, 1986, *Protodichobune* LEMOINE, 1891, *Buxobune* SUDRE, 1978 and *Aumelasia* SUDRE, 1980 in its complete lingual cingulum and well developed hypocone on the upper molars. It differs from *Wasatchia* and *Bunophorus* also in having less bunodont molars, and from *Aumelasia* in lacking a mesostyle on M^2.

The new genus can be distinguished from *Aksyiria* GABUNIA, 1973 by its complete lingual cingulum, weaker premetaconule crista, and absence of a postparaconule crista on the upper molars.

Eolantianius russelli sp. nov.

(Pl. 1d-h)

Etymology: Named in honor of Dr. D.E. Russell, to recognize his contribution to understanding mammalian evolution in the Paleogene of Asia.

Holotype: ZIN 34357, dex M^1 (Pl. 1e).

Referred specimens: ZIN 34358, dex M^2; 34359, sin M^3; 34032, sin DP^4; and 34033, sin DP^4.

Locality: Andarak 2, Kyrgyzstan. Early Eocene (Ypresian).

Description

Upper molars are nearly subquadrate, low-crowned bunodont teeth. The paracone and the metacone on M^{1-3} are equal in size and shifted to the labial side. The centrocrista is straight on M^{1-2} and curved on M^3. The ectocingulum is well developed, sometimes with a number of minute cuspules (ZIN 34358, M^2). The preparacrista is weak on all the upper molars. The preparaconule crista is strong and attached to the parastyle, which varies in size. The lingual cingulum is robust and the hypocone is well developed, arising from this cingulum. The preprotocrista is a robust ridge usually without a paraconule. There is a weak paraconule on DP^4 (ZIN 34032). The postprotocrista is weaker and shorter, but bears a metaconule. This crista is better developed on M^3. The premetaconule crista stops short of the metacone on M^{1-2} but reaches it on M^3, dividing the talon basin on this tooth into two parts. The labial side of M^3 (ZIN 34359) is greatly inclined in a posterolingual direction.

Two relatively worn M^1-like teeth, ZIN 34032 and 34033 are recognized to be DP^4 because they have completely eroded roots and somewhat thinner enamel. Together with the noted wearing of these teeth, this indicate that both of them were shed during tooth replacement. Both DP^4s have wide and narrow crowns, nearly identical in morphology to M^1.

Measurements

		L	W	L	W	L	W	L	W
ZIN 34032	DP^4	ca 3.4	–						
ZIN 34033	DP^4	3.6	4.8						
ZIN 34357	M^1			4.1	4.8				
ZIN 34358	M^2					4.1	5.1		
ZIN 34359	M^3							3.7	4.5

?Eolantianius russelli

(Pl. 1c)

Material: ZIN 34355, dex M_2; and 34356, sin M_3 with a fragment of mandible.

Locality: Andarak 2, Kyrgyzstan. Early Eocene (Ypresian).

Description

On M_2 the talonid is wider than the trigonid. On the trigonid the metaconid is the highest cusp. There is a greatly reduced ridge-like paraconid and a distinct precingulid. The entoconid is the highest among the talonid cusps. It is connected to the hypoconid by a transverse ridge (hypolophid) crossing the talonid basin. The hypoconulid is a short transverse ridge, connected by a small crista (postcristid) to the hypolophid. The cristid obliqua is short but distinct.

On M_3 the trigonid is as wide as the talonid. There is a long precingulid and there is no trace of a paraconid. The tips of the labial cusps (the protoconid and the hypoconid) are considerably worn. The metaconid and the entoconid are much higher than the labial cusps and have their tips unworn. The hypoconid and the entoconid are connected by a weak hypolophid. The cristid obliqua is long. The talonid basin opens lingually through a wide talonid notch. The hypoconulid is a large robust cusp forming the third column of the tooth.

Measurements

		L	Wtr	Wtl	L	Wtr	Wtl
ZIN 34355	M_2	4.1	2.5	2.8			
ZIN 34356	M_3				5.6	3.2	3.0

Discussion

The M_2 is basically similar to that of *Diacodexis* and other Diacodexeidae, but the presence of a hypolophid and a postcristid shows a departure from the condylarth-like molar morphotype which is characteristic for this genus. *Diacodexis* species also usually have a shorter hypoconulid on M_2 than is seen in the present specimen.

The second lower molar of *Chorlakkia hassani* from the middle Eocene of Pakistan differs from ZIN 34355 in lacking a hypolophid and in having a twinned entoconid and hypoconulid. The Andarak M_2 is somewhat similar to those of the

contemporaneous *Protodichobune oweni* from Monthelon, late Ypresian (Cuisian) (Sudre *et al.* 1983 and pers. obs.) in the stage of paraconid reduction and in having a hypolophid which appears continuous on moderately worn teeth. The third lower molar from Andarak has the typical morphology of primitive artiodactyls, including Diacodexeidae. It differs from most Diacodexeidae by its sharper, non-bunodont main cusps. In this feature the Andarak M_3 more closely resembles molars of some rodents than artiodactyls. It differs from most species of *Diacodexis* and other Diacodexeidae also in completely lacking a paraconid, and in having a noticeably higher trigonid relative to the talonid. Therefore, this derived feature (absence of paraconid) is combined here with a distinctly plesiomorphic non-bunodont structure of the molar cusps and a difference in height between the trigonid and the talonid. It differs from M_3 of *Chorlakkia hassani* also in having a more isolated hypoconulid, and a more separated trigonid and talonid.

Undoubtedly both molars described here belong to a member of Diacodexeidae. According to size and morphology, which is somewhat distinct from the condition of *Diacodexis*, it is preferable to tentatively assign these molars to *Eolantianius russelli* n. gen. n. sp. rather than to the Andarak *Diacodexis* sp. described above. However for a final assignment it is necessary to obtain more complete material of *Eolantianius*.

Diacodexeidae indet.

(Pl. 1 i-l)

Material: ZIN 34353 and 34354, both sin astragali.

Locality: Andarak 2, Kyrgyzstan. Early Eocene (Ypresian).

Description

Both astragali are nearly identical and show the "double pulley" morphology with a well-developed trochlea at both ends, which is typical for all artiodactyls (Schaeffer 1947), even for the oldest known (Rose 1985). The completely preserved specimen, ZIN 34353, is slightly larger than the other, ZIN 34354, which lacks the dorsal part of the distal trochlea. The tibial trochlea is deep and well defined. The cuboid facet on the distal trochlea is much narrower than the navicular facet and it is separated by a definite keel. The calcaneoastragalar facet is very small, while the sustentacular facet is large and oval in outline.

Discussion

These astragali are basically similar to those of *Diacodexis* (Schaeffer 1947, Rose 1985; *Diacodexis* sp. from Prémontré, pers. obs.), as well as to other Diacodexeidae (Guthrie 1968). It is possible that both bones belong to the above described species of *Diacodexis* or to *Eolantianius russelli* n. gen. n. sp. In their dimensions they are closer to the astragalus of *D. gazini* from the early Eocene of Rians (Godinot 1981).

Measurements: Length of the astragali (between the deepest points of each trochlea) 8.6 (ZIN 34353) and ca. 8.2 (ZIN 34354).

GENERAL DISCUSSION

The Andarak Artiodactyla comprise two taxa: a rather primitive *Diacodexis* sp., a member of the Holarctic-wide genus, and a relatively derived *Eolantianius russelli* n. gen. n. sp., possibly a close relative of late Eocene *Lantianius xichuensis* from China. Together with the possibly early Eocene problematic primitive artiodactyl *Aksyiria oligostus* (Diacodexeidae?) and *Paraphenacodus solivagus* (Dichobunidae?) from the Zaissan Depression, Kazakhstan, the Andarak artiodactyls show a substantial diversity of the order in the early Eocene in central Asia. This diversity suggests that this part of Asia is an appropriate region to search for the most ancient Artiodactyla, including ancestors of the main families.

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LEGEND OF THE PLATE

PLATE 1

Cheek teeth in occlusal view (**a-h**) and astragali (**i-l**) of Artiodactyla from the Andarak 2 locality in Kyrgyzstan. Figures **a** to **h** are scanning electron micrographs of casts; **i** to **l** are photographs of original specimens. The two scale bars are 2 mm (above for the teeth, below for the astragali).

a-b, *Diacodexis* sp., P^4 ZIN 34351 (**a**), M^1 ZIN 34352 (**b**);

c, ?*Eolantianus russelli* n. gen. n. sp., M_2 ZIN 34355 (**c**);

d-h, *Eolantianus russelli* n. gen. n. sp., M^3 ZIN 34359 (**d**), M^1 ZIN 34357, holotype (**e**), DP^4 ZIN 34032 (**f**) and DP^4 ZIN 34033 (**g**), M^2 ZIN 34358 (**h**);

i-l, astragali, ZIN 34354 (**i**, **j**) and ZIN 34353 (**k**, **l**).

PLATE 1