Ceratomorphs (Mammalia, Perissodactyla) from the early Eocene Andarak 2 locality in Kyrgyzstan

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ABSTRACT

KEY WORDS
Mammalia,
Perissodactyla,
Ceratomorpha,
Lophialetidae,
Deperetellidae,
Rhodopagidae,
Amynodontidae,
Eocene,
Andarak,
Kyrgyzstan,
new species.

Four taxa of ceratomorph perissodactyls are identified from the lower Alay beds (latest early Eocene, Ypresian) at the Andarak 2 locality in Kyrgyzstan: the deperetellid *Teleolophus medius* Matthew & Granger, 1925 (= *Deperetella ferganica* Belyaeva, 1962), the rhodopagid *Pataecops minutissimus* (Reshetov, 1979) n. comb. (= *Pataecops microdon* Reshetov, 1979), the amynodontid *Sharamynodon kirghisensis* (Belyaeva, 1971), and the lophialetid *Eoletes tianshanicus* n. sp.; this new species is characterized by its small size, a low and anteriorly situated infraorbital foramen, a low zygomatic root, a long bony palate and a two-rooted P1.

RÉSUMÉ

MOTS CLÉS
Mammalia,
Perissodactyla,
Ceratomorpha,
Lophialetidae,
Deperetellidae,
Rhodopagidae,
Amynodontidae,
Éocène,
Andarak,
Kirghizstan,
nouvelle espèce.

Les cératomorphes (Mammalia, Perissodactyla) du gisement éocène inférieur d'Andarak 2 au Kirghizstan.
Quatre taxons de périssodactyles cératomorphes sont identifiés dans le gisement d'Andarak 2, au Kirghizstan, qui est situé dans les couches inférieures d'Alay (fin de l'Éocène inférieur, Yprésien) : le depérétellidé *Teleolophus medius* Matthew & Granger, 1925 (= *Deperetella ferganica* Belyaeva, 1962), le rhodopagidé *Pataecops minutissimus* (Reshetov, 1979) n. comb. (= *Pataecops microdon* Reshetov, 1979), l'amynodontidé *Sharamynodon kirghisensis* (Belyaeva, 1971) et le lophialétidé *Eoletes tianshanicus* n. sp. ; cette nouvelle espèce est caractérisée par sa petite taille, son foramen infraorbitaire en position basse et antérieure, la racine zygomatique basse, un long palais osseux et une P1 à deux racines.

INTRODUCTION

Paleogene perissodactyls from Kyrgyzstan are poorly known. The first record of this group there, which also was the first Eocene mammal record from the former Soviet Middle Asia, was an isolated upper premolar from the marine Alay beds at Andarak 1 locality in the Fergana Depression (southwestern Kyrgyzstan; Fig. 1). It was referred to a new species, *Deperetella ferganica*, by Belyaeva (1962). Subsequent expeditions by the Paleontological Institute, USSR Academy of Sciences, added some new information about Kyrgyzstan Eocene perissodactyls. The new amynodontid species *Lushiamynodon? kirghisensis* was described from the Andarak 1 locality based on a maxillary fragment with M2-3 and some other isolated upper teeth (Belyaeva 1971). From the newly discovered near shore marine locality Andarak 2 two new rhodopagid species were described (Reshetov 1979): *Rhodopagus minutissimus*, known from the holotype only (maxillary fragment with upper D4 M1-2) and *Pataecops parvus*, known from four isolated upper molars. Remains of *Forstercooperia?* sp. and Chalicotheriidae indet. were also cited for this fauna (Reshetov *et al.* 1978) but never described. The determination of the latter taxon is doubtful as Chalicotheriidae are not known before the Oligocene, and Eocene Chalicotheroidea were represented by Eomoropidae. Other perissodactyl material has been recovered in a series of expeditions since 1964 by the Moscow Paleontological Institute in the Chonkurchak Svita at the Toru-Ajgyr locality in the Issyk-Kul Depression, Northern Kyrgyzstan (Russell & Zhai 1987 and references therein; Kondrashov *et al.* 1997; Agadjanian & Kondrashov 1999). In 1997-1998 additional excavations at Toru-Ajgyr were made by the Halle Martin Luther University, which produced some new perissodactyl material (Erfurt *et al.* 1999); this material will be described elsewhere.

In this paper we describe the perissodactyl material collected by the first author since 1988 and by both authors in 1995 at Andarak 2, and discuss the reliability of these fossils for biostratigraphy.

For the geological setting of the locality and a recent faunal list see Averianov & Godinot (1998).

ABBREVIATIONS

AMNH American Museum of Natural History, New York;
KAN Laboratory of Paleozoology, Institute of Zoology, Academy of Sciences of the Republic of Kazakhstan, Alma-Ata;
PIN Paleontological Institute, Russian Academy of Sciences, Moscow;
PSS Paleontologo-stratigraphic section of the Geological Institute, Mongolian Academy of Sciences, Ulan-Bator;
ZIN Zoological Institute, Russian Academy of Sciences, Saint Petersburg.

Measurements
L length;
W width;
WTR width of the trigonid;
WTL width of the talonid.
All measurements are in mm.
The dental terminology is the same as in Dashzeveg & Hooker (1997: fig. 24A-C), with the exception of the metalophid of these authors, that we prefer to call cristid obliqua. In the classification of the ceratomorph perissodactyls we follow Holbrook (1999: table 6). Upper and lower case letters, I/i (incisor), C/c (canine), P/p (premolar), M/m (molar) and D/d (deciduous tooth) refer to upper and lower teeth, respectively.

SYSTEMATICS

Order PERISSODACTYLA Owen, 1848
Suborder TAPIROMORPHA Haeckel, 1866
Infraorder CERATOMORPHA Wood, 1937
Superfamily TAPIROIDEA Gray, 1825
Family LOPHIALETIDAE Matthew & Granger, 1925
Genus *Eoletes* Biryukov, 1974

***Eoletes tianshanicus* n. sp.**
(Fig. 2A-I)

Eomoropus sp. – Averianov & Udovichenko 1993: 141.

Schlosseria magister – Averianov & Udovichenko 1993: 141.

Eoletes sp. – Averianov & Godinot 1998: 212.

Eomoropus? sp. or ?cf. *Propachynolophus* sp. – Averianov & Godinot 1998: 212.
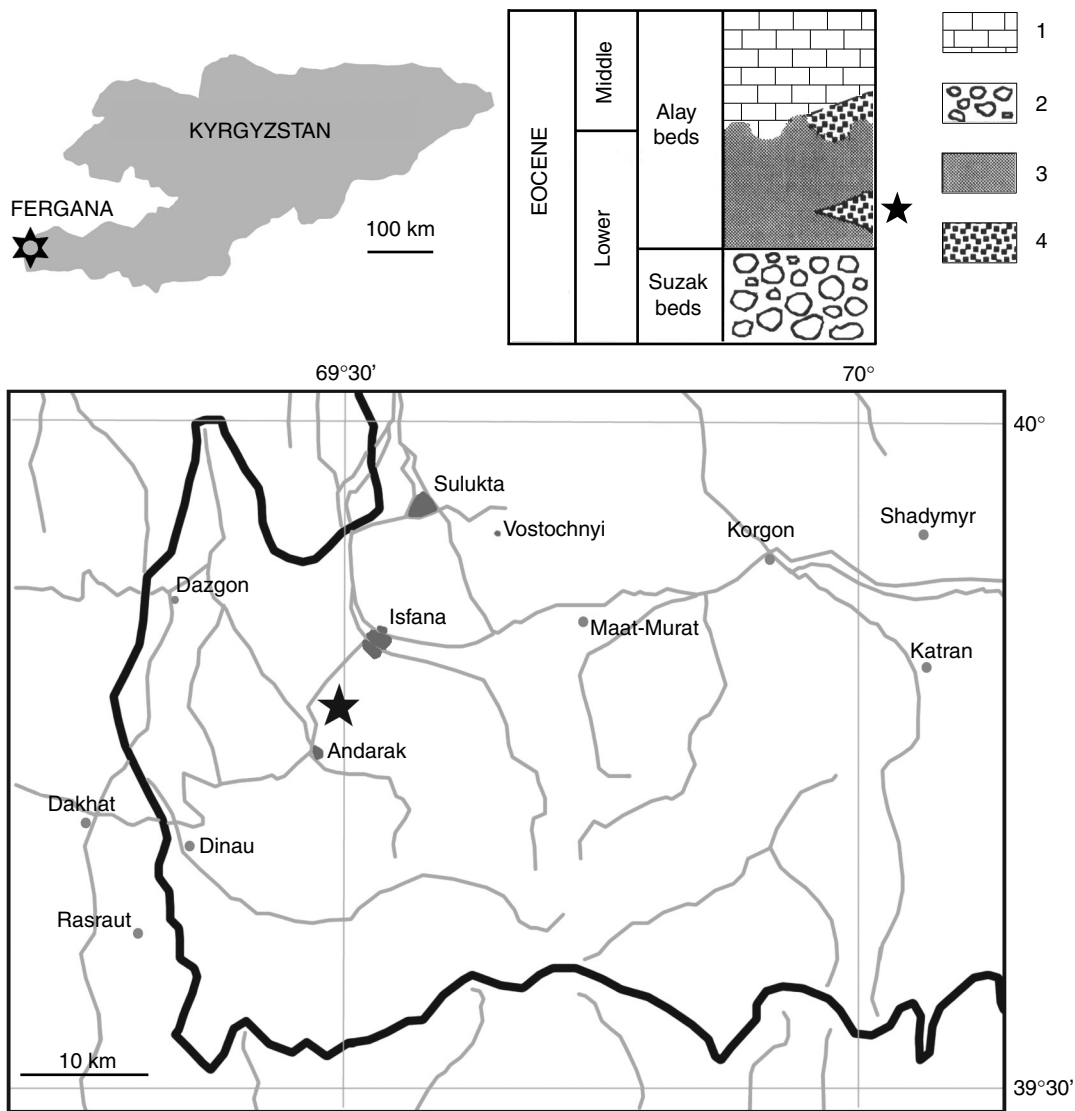
FIG. 1. — Geographical and stratigraphic (top right) position of Andarak locality (★) in south Fergana valley of Kyrgyzstan (top left), close to Andarak settlement in foothills of Turkistan Range (bottom). **1**, limestone; **2**, pebble beds and conglomerate; **3**, sand and sandstone; **4**, gravel and sand.

HOLOTYPE. — ZIN 32754, left maxillary fragment with P2-M2 and alveolus of P1. Andarak 2 locality, Osh Province, Kyrgyzstan. Lower Alay beds, latest early Eocene (Ypresian).

ETYMOLOGY. — After the Tian Shan mountains in Middle Asia.

REFERRED MATERIAL. — ZIN 35282, right maxillary fragment with P1 and the alveoli of P2; ZIN 35283, left M2; ZIN 34023, right M2; ZIN 32760, posterior portion of left M2; ZIN 35284, incomplete left M3; ZIN 32758, right m1 or m2; ZIN 32755, left astragalus; ZIN 34024, right astragalus; ZIN 34025, right astragalus of juvenile animal. Locality as for the holotype.

DIFFERENTIAL DIAGNOSIS. — *Eoletes tianshanicus* n. sp. differs from the type species, *E. gracilis* Biryukov, 1974 from the middle Eocene of Kazakhstan (Biryukov 1974;
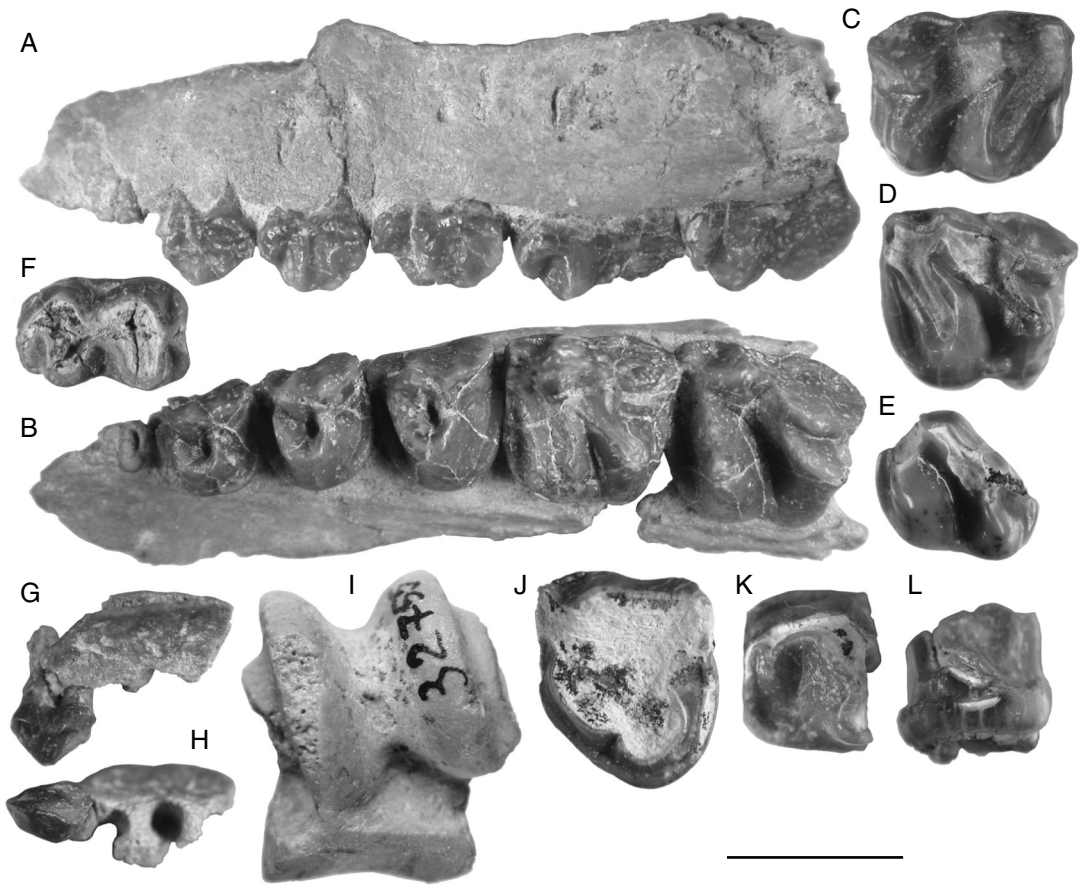
Fig. 2. — **A**-**I**, *Eoletes tianshanicus* n. sp.; **J**-**L**, *Teleolophus medius* Matthew & Granger, 1925; in labial (**A**, **G**), anterior (**I**, **L**) and occlusal (**B**-**F**, **H**, **J**, **K**) views; Andarak 2, Kyrgyzstan, Alay beds, Irdinmanhan; **A**, **B**, ZIN 32754, holotype, left maxillary fragment with P2-M2 and alveolus of P1; **C**, ZIN 34023, right M1 or 2; **D**, ZIN 35283, left M2; **E**, ZIN 35284, left M3; **F**, ZIN 32758, right m1 or 2; **G**, **H**, ZIN 35282, right maxillary fragment with P1; **I**, ZIN 32755, left astragalus; **J**, ZIN 35285, left P2; **K**, **L**, ZIN 32756, right p3 trigonid. Scale bar: 1 cm.

Lucas *et al.* 1997) by its smaller size (Table 1), its lower and anteriorly situated infraorbital foramen (above P3 instead of above the anterior part of P4 in *E. gracilis*), a two-rooted P1 (three-rooted in *E. gracilis*), and an interrupted lingual cingulum on P3-4. From *E. xianensis* (Zhang & Qi, 1981) from the middle(?) Eocene of China (Zhang & Qi 1981; Lucas *et al.* 1997), *Eoletes tianshanicus* n. sp. differs by its smaller size, lower placed anterior zygomatic root and infraorbital foramen, a longer bony palate, extending behind M2 (between M1 and M2 in *E. xianensis*), and the presence of a P1.

REMARKS
Lucas *et al.* (2001) referred the so-called hyrachyid *Subhyrachyus tshakpaktasensis* Gabunia,

1999 from the Arshantan Chakpaktas Svita in the Zaisan Basin, eastern Kazakhstan (Gabunia 1999) to the lophialetid genus *Eoletes*. However, this taxon clearly differs from *Eoletes* and other lophialetids by the presence of a crista on the ectoloph of the upper molars and premolars. Whether or not this taxon belongs to *Eoletes*, it differs from *Eoletes tianshanicus* n. sp. by this character and its noticeably larger size.

DESCRIPTION
The palatal portion of the maxilla (ZIN 32754) appears to be very narrow. The intermaxillar

TABLE 1. — Measurements (in mm) of upper cheek teeth in *Eoletes*. **L**, length; **W**, width; *, after Lucas *et al*. 1997.

Specimens	P1		P2		P3		P4		M1		M2		M3	
	L	W	L	W	L	W	L	W	L	W	L	W	L	W
***E. tianshanicus* n. sp., Andarak 2**														
ZIN 32754, holotype	–	–	6.0	6.1	6.1	7.5	7.1	8.5	9.5	10.0	11.1	10.5	–	–
ZIN 35282	4.8	3.4												
ZIN 34023											11.8	10.3		
ZIN 35283											11.2	10.7		
ZIN 35284													9.7	–
E. gracilis*, Shinzhaly														
KAN 5088/69, holotype	6.1	5.5	7.4	8.3	8.6	10.5	9.2	11.8	13.3	12.3	13.9	13.2	13.7	12.5
KAN 5088/69	5.3	4.9	7.1	7.8	8.3	9.4	8.8	10.5	12.3	11.6	12.4	12.5	14.6	11.7

suture is preserved in the region of P1-2. At the level of M1-2 there is a thick maxillary-palatine suture, which indicates that the end of the bony palate was probably far more posteriorly. The infraorbital foramen is located relatively low and anteriorly, 8.7 mm above the anterior half of P3. The anterior root of the zygomatic arch begins above M2 and relatively low, only slightly above the tooth row.

The P1 is a two-rooted tooth, as can be seen from both the alveoli on the holotype and the tooth on the maxillary fragment ZIN 35282. The tooth is relatively small, its width being less than half of the width of P2. The crown is dominated by one cusp (paracone), without traces of a metacone. There is a very small protocone which is placed lingually and posteriorly to the paracone center and above the posterior tooth root.

The P2-4 are quite uniform in morphology. They differ mainly by a slight posterior increase in size. These premolars are non-molariform (*sensu* Radinsky 1967). They have a relatively straight to slightly sinuous ectoloph, and the pro-toloph-metaloph loop characteristic of the Lophialetidae. The parastyle is relatively well separated. On P2 the paracone is noticeably larger than the metacone; on P3-4 both cusps are of equal size. The anterior and posterior cingula are well developed on P2-4, but a lingual cingulum is present only on P2. The ectoflexus is very shallow on P2-3 and almost absent on P4.

The M1-2 are similar in morphology, differing mostly in proportions (M1 is squarish, M2 is more trapezoid, antero-posteriorly elongated).

The parastyle is relatively large, but about two times lower than the paracone. The paracone is higher than the metacone, but on M2 the latter has a longer base. On both teeth the metacone is considerably deflected lingually. The metastyle is almost indistinct. In occlusal view, the ectoloph runs antero-posteriorly above the paracone, then makes an almost right angle and runs parallel to the metaloph until the summit of the metacone, and posteriorly it is bent postero-labially. It is more confluent with the metaloph on M2 than on M1. The protoloph connects the parastyle. The metaloph connects nearly the paracone on M1 and midway between paracone and metacone on M2. The hypocone is higher than the proto-cone. There is a strong anterior cingulum and a weaker posterior cingulum. A very small lingual cingulum is present only on ZIN 35283 (Fig. 2D), confined to an embrasure between the bases of the protocone and hypocone.

ZIN 35284 is an M3 with a broken off parastylar region and most of the lophs. It was possibly not fully erupted as the preserved parts of the pro-toloph and metaloph are unworn and the roots apparently were not developed. The metacone is deflected lingually and the postmetacrista is relatively short. The protocone is higher than the hypocone. There are remnants of anterior and posterior cingula; the enamel is lacking on the lingual side.

The crown of m1-2 is rectangular in outline, with a somewhat rounded anterior side. The para-lophid is relatively long but low. The trigonid basin is very narrow and short. The protolophid

and the hypolophid are almost perpendicular to the crown longitudinal axis. The hypolophid is distinctly lower than the protolophid. The cristid obliqua is well developed, joining the protolophid at the center. The hypoconulid is a distinct, transversely wide ridge, connected to the hypolophid by a short posthypocristid. There is a faint anterior cingulid below the paralophid and a very short labial cingulid, between the bases of protoconid and hypoconid.

The astragalus is typical of ceratomorph perissodactyls, having a well developed trochlea, a short neck, and a saddle-shaped astragalar head (navicular facet). The sustentacular and distal calcaneal facets are not confluent. The adult astragali are slightly smaller than those of *Lophialetes expeditus* (Radinsky 1965; Reshetov 1979) and similar in size with those of *Eoletes gracilis* (Biryukov 1974; Lucas *et al.* 1997).

Measurements

For upper dentition see Table 1. m1-2 (ZIN 32758): L = 10.1; WTR = 5.7; WTL = 5.8. Astragali (ZIN 32755, 34025): proximodistal height = 18.3, 17.1; distal width = 12.0, -.

DISCUSSION

Eoletes tianshanicus n. sp., with its two-rooted P1, is intermediate in the state of reduction of P1 between *E. gracilis* (three-rooted P1) and *E. xianensis* (P1 is totally lacking).

Family DEPERETELLIDAE Radinsky, 1965
Genus *Teleolophus* Matthew & Granger, 1925

Teleolophus medius Matthew & Granger, 1925
(Fig. 2J-L)

Teleolophus medius Matthew & Granger, 1925: 3, figs 4, 5. — Xu & Chiu 1962: 316, pl. 1, fig. 7. — Radinsky 1965: 218, fig. 12B. — Reshetov 1975: 39, fig. 14, pl. 1, fig. 7; 1979: 33, pl. 1, fig. 7. — Lucas *et al.* 1997: 242, fig. 7A.

Deperetella ferganica Belyaeva, 1962: 144, fig. 1. — Reshetov 1979: 38, fig. 6-3.

Teleolophus medius? – Radinsky 1965: 219, fig. 12A, pl. 3, fig. 1.

Teleolophus cf. *Teleolophus medius* – Radinsky 1965: 220, fig. 12C.

Teleolophus? *ferganicus* – Radinsky 1965: 221.

Teleolophus beliajevi Biryukov, 1974: 78, figs 1, 2. — Reshetov 1979: 37, fig. 6-2.

?*Teleolophus magnus* Reshetov, 1975: 39, figs 15, 16, pl. 1, figs 5, 6.

?*Teleolophus magnus*? – Reshetov 1979: 35, pl. 1, figs 5, 6.

REFERRED MATERIAL. — ZIN 35285, left P2; ZIN 32756, right p3 trigonid.

DESCRIPTION

There are no traces of cement on the teeth. P2 is a submolariform tooth. The crown is heavily worn, trapezoidal in outline, with an oblique anterior side. The parastyle and the paracone are prominent cusps, the former being somewhat smaller and lower. Posterior to the paracone the ectoloph is straight. The metacone is completely eliminated by wear; this indicates that it was smaller than the paracone. The preprotocrista is shorter than the prehypocrista and bent along the anterior margin of the crown. The prehypocrista goes to the ectoloph at an angle of about 45°. The hypocone was relatively large. The strong cingulum borders nearly all the crown, being most developed along the lingual side. It is interrupted around the metastyle and between the paracone and the metacone on the labial side. The tooth had two roots. The posterior one is more than two times larger than the anterior one, and lies under the postero-lingual part of the crown.

The p3 trigonid (ZIN 32756) bears a long paracristid which goes through a relatively large paraconid to the antero-lingual corner of the tooth. There is a short but distinct accessory crest running from the paraconid lingually and parallel to the paracristid (Fig. 2K). The trigonid basin is shallow and small, completely closed ventrally by the cingulid. The protocristid is oblique to the antero-posterior tooth axis and bent near the metaconid. There is a well developed cingulid on the preserved fragment, which is interrupted only under the metaconid.

TABLE 2. — Measurements (in mm) of upper premolars in *Teleolophus* and *Deperetella*. **L**, length; **W**, width; *, after Belyaeva 1962; **, after Lucas *et al.* 1997; ***, after Radinsky 1965; ****, after Reshetov 1979; *****, calculated after Radinsky 1965: pl. 3, fig. 2.

Specimens	P2		P3	
	L	W	L	W
Teleolophus medius				
ZIN 35285, Andarak 2	10.4	12.1		
PIN 1996-1, Andarak 1, holotype of *D. ferganica**			16.0	16.4
KAN 48471/68-4, Shinzhaly, holotype of *T. beliajevae***	10.4	11.8	11.5	15.2
AMNH without No., Irdin Manha***	9.9	11.0		
AMNH 26286, Ulan Shireh [North Mesa]***	10.4	11.0	11.1	13.5
Teleolophus medius*?, Khaychin Ula II*				
PIN 3107-34	13.3	16.0	13.9	18.7
***Teleolophus magnus*, Ulan Gochu**				
AMNH 26063, holotype*****			16.1	20.0
Deperetella cristata*, Shara Murun				
AMNH 20290, holotype***	19.9	21.8		
AMNH 20293			18.7	24.4

Measurements
P2 (ZIN 35285): see Table 2. p3 (ZIN 32756): TRW = 9.0.

DISCUSSION
The only previously described specimen of deperetellid from the Andarak fauna was an unworn upper premolar (PIN 1996-1) from the Andarak 1 site, that has been considered as a P2 (Belyaeva 1962: fig. 1; Radinsky 1965: 221; Reshetov 1979: fig. 6-3). This tooth, the holotype of *Deperetella ferganica* Belyaeva, 1962, appears to be generally very similar with ZIN 35285. It differs from the latter mostly by its larger size (Table 2) and its complete labial cingulum. The size difference between PIN 1996-1 and ZIN 35285 cannot be attributed to sexual dimorphism, because they differ also in the presence of the labial cingulum. Thus we consider here ZIN 35285 as a P2 and PIN 1996-1 as a P3. Moreover, in PIN 1996-1 the metaloph is meeting the ectoloph at an almost right angle, which also suggests that this tooth is a P3 rather than a P2. Such an assignment precludes the attribution of this taxon to the genus *Deperetella*, because the latter has a fully molariform P3 with strong parallel protoloph and metaloph.

ZIN 32756 (right p3 trigonid) is considered here as belonging to a deperetellid because it has a long paracristid, a shallow trigonid basin and a strong cingulid. Most important, a paraconid accessory crest is present on ZIN 32756, a feature recently found to be diagnostic of *Teleolophus* (Dashzeveg & Hooker 1997: 116). This makes the attribution of the Andarak's deperetellid to the latter genus quite reasonable.

We tentatively assign Andarak's upper premolars to *T. medius* because they are closer in size to those of this species than to those of *T. magnus* Radinsky, 1965 (Table 2). The latter species is known only from the holotype (maxilla with lower jaws from the "Ulan Gochu", late Eocene of Inner Mongolia, China; Radinsky 1965) and referred teeth from the late Eocene (Ergilian) localities Khoer-Dzan and Dzhavkhalan-Ula in Mongolia (Reshetov 1979). Both *Teleolophus* species differ mostly in size, *T. magnus* being about 35% larger (Radinsky 1965). *T. medius* from the Eocene Schinzhaly locality in Kazakhstan is about 10% larger than the topotypic sample of the species from Inner Mongolia (Lucas *et al.* 1997). In the middle Eocene Mongolian locality Khaychin Ula 2 together with *T. medius* of typical size were found remains of *Teleolophus* approximating in size *T. magnus*, which were subsequently attributed to *T. magnus* (Reshetov 1975: 39) and to *T. magnus*? (Reshetov 1979: 35). This difference may be caused by sexual dimorphism, so the limits of interspecific variation for *Teleolophus* are still unknown. In

size ZIN 32756 is closer to a p3 of *T. medius* from Irdin Manha (W = 7.6; Radinsky 1965) than to a p3 of *T. magnus* from Dzhavkhalan-Ula (W = 12.8; Reshetov 1979).

Teleolophus(?) *shandongensis* Chow & Qi, 1982 (? = *Teleolophus* sp. from the same locality), known from a few teeth from the Guanzhuang Formation in Shandong, China (Chow & Qi 1982), could belong to the primitive deperetellid *Irdinolophus* Dashzeveg & Hooker, 1997, which is known from the Irdin Manha and possibly the Kholboldzhi faunas (Dashzeveg & Hooker 1997: 115). *Teleolophus primarius* Qi, 1987 from the Arshanto Formation in Inner Mongolia, China (Qi 1987: fig. 41a, b) also could be attributable to *Irdinolophus* (Dashzeveg & Hooker 1997: 116). *Teleolophus xiangshanensis* Zong, Chen, Huang & Xu, 1996 is known by a dentary fragment with d4 and m1-2, and an isolated m2 (Zong *et al*. 1996: fig. 2-3, pl. 32, fig. 3) from the middle-late Eocene of Xiangshan in the Hengduan Mountains, Qinghai-Tibetan Plateau, China. It is characterized by a relatively small size and low crowned molars and also could belong to *Irdinolophus*. A dentary fragment with m2-3 from the same locality (Zong *et al*. 1996: pl. 32, fig. 3), referred to "*Diplolophodon similis*" Zdansky, 1930, has a similar morphology but slightly larger molars, with a tiny hypoconulid on m3. It may also belong to *Irdinolophus*.

Superfamily RHINOCEROTOIDEA Owen, 1845
?Family RHODOPAGIDAE Reshetov, 1975
Genus *Pataecops* Radinsky, 1966

Pataecops minutissimus (Reshetov, 1979) n. comb.
(Fig. 3)

Rhodopagus minutissimus [*nomen nudum*] Reshetov, Shevyreva, Trofimov & Chkhikvadze, 1978: 151.

Pataecops microdon [*nomen nudum*] Reshetov, Shevyreva, Trofimov & Chkhikvadze, 1978: 151.

Rhodopagus minutissimus Reshetov, 1979: 29, fig. 5-1. — Gabunia & Kukhaleishvili 1991: 111.

Pataecops microdon Reshetov, 1979: 31, fig. 5-3.

"*Pataecops*" *microdon* – Dashzeveg 1991: 36.

REFERRED MATERIAL. — ZIN 35286, right D3?; ZIN 34030, left D4; ZIN 35287, left maxillary fragment with P4 (broken) and M1; ZIN 34029, right maxillary fragment with M1-2; ZIN 35288, left maxillary fragment with P3-M3 and alveolus of P2; ZIN 35289, right maxillary fragment with M3 and partially preserved M1-2; ZIN 35290, left maxillary fragment with D4 M1-2; ZIN 35291, right maxillary fragment with M2-3; ZIN 35293, left maxillary fragment with M1; ZIN 34031, right M1; ZIN 35292, left M2; ZIN 35296, right M2; ZIN 35295, left M3; ZIN 35294 and 35297, right M3; ZIN 34028, right dentary fragment with d3-4 and alveoli of d2 and m1, and fragments of m2 in the alveolus; ZIN 35298, dentary symphysis fragment with alveoli of i3, c1 and p2.

DESCRIPTION

The infraorbital foramen (seen only in ZIN 35288, Fig. 3A) is relatively small and placed above P2. The anterior zygomatic process of the maxilla begins above M1 and terminates at the posterior end of M3. The zygomatic arch is placed relatively low on the maxilla, close to the tooth row. The bony palate terminates approximately between M2 and M3.

No P1 is present in our material. This tooth is most probably lacking in *Pataecops parvus* (Radinsky, 1965) and *Rhodopagus pygmaeus* Radinsky, 1965: a two-rooted alveolus in front of P2 in these species (e.g., Radinsky 1965: 212, fig. 8) may actually belong to a D1, which persisted late enough to leave unresorbed alveoli present with the definitive upper cheek dentition, and which was never replaced by a P1. This situation would be symmetrical to that on the lower jaw, where d1 was present but not replaced by p1 (see below).

P2 was two-rooted, as can be judged from its alveolus (ZIN 35288), with a large rounded and labiolingually elongated posterior root and a much smaller anterior root.

The P3-4 are non-molariform teeth, subtriangular (P3) to subrectangular (P4) in crown outline. The parastyle is smaller than the paracone. The ectoloph is straight (P3) or slightly convex labially (P4). On P3 the metaloph is a short ridge well separated from the protocone by a narrow valley. In P4 this feature is obliterated by wear. The anterior and posterior cingula are well developed. The lingual and labial cingula are completely lacking on P3-4.
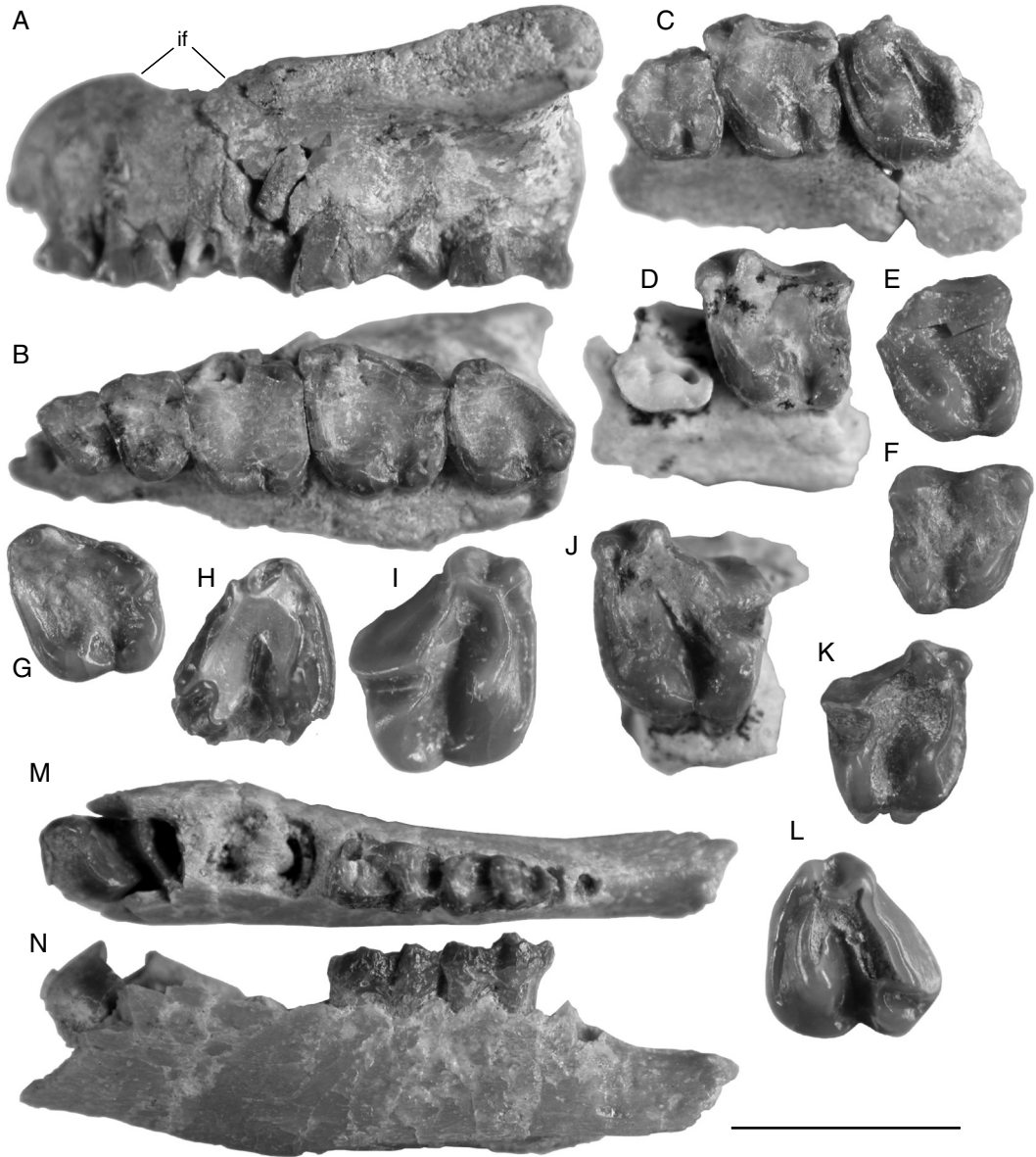
FIG. 3. — *Pataecops minutissimus* (Reshetov, 1979) n. comb. in labial (**A**, **N**) and occlusal (**B-M**) views; Andarak 2, Kyrgyzstan, Alay beds, Irdinmanhan; **A**, **B**, ZIN 35288, left maxillary fragment with P3-M3 and alveolus of P2; **C**, ZIN 35290, left maxillary fragment with D4 M1-2; **D**, ZIN 35287, left maxillary fragment with M1 and root of P4; **E**, ZIN 34030, left D4; **F**, ZIN 35286, right D3(?); **G**, ZIN 35292, left M2; **H**, ZIN 35294, right M3; **I**, ZIN 35296, right M2; **J**, ZIN 35293, left maxillary fragment with M1; **K**, ZIN 34031, right M1; **L**, ZIN 35295, left M3; **M**, **N**, ZIN 34028, right dentary fragment with d3-4, alveoli of d2, m1, and with partial m2 crown in crypt. Abbreviation: **if**, infraorbital foramen. Scale bar: 1 cm.

TABLE 3. — Measurements (in mm) of upper cheek teeth in *Pataecops*. **L**, length; **W**, width; *****, after Reshetov 1979; ******, after Radinsky 1965; *******, after Dashzeveg 1991.

Specimens	D3		D4		P2		P3		P4		M1		M2		M3	
	L	W	L	W	L	W	L	W	L	W	L	W	L	W	L	W
***Pataecops minutissimus*, Andarak 2**																
ZIN 35286	4.3	4.5														
PIN 3486-1, holotype of			5.0	5.8							5.9	6.8	7.0	7.5		
Rhodopagus minutissimus*																
ZIN 35290			3.1	4.1							5.6	5.4	5.9	–		
ZIN 34030			–	5.4												
ZIN 35288					3.0	3.6	3.3	3.7			5.1	6.1	5.9	6.6	5.7	5.7
ZIN 34029											5.7	5.5	5.9	5.5		
PIN 3486-4*											5.7	6.5				
ZIN 34031											5.2	6.0				
ZIN 35287											5.0	5.4				
ZIN 35293											5.7	6.4				
PIN 3486-5*													5.7	6.2		
ZIN 35291													6.4	–		
ZIN 35292													6.1	6.8		
ZIN 35296													6.0	7.1		
PIN 3486-2, holotype of *Pataecops microdon**													5.2	6.2		
ZIN 35289															5.4	5.5
ZIN 35294															5.2	6.0
ZIN 35295															5.3	5.9
ZIN 35297															5.4	5.8
Pataecops parvus*, Kholbolchi*																
AMNH 21747, holotype			4.2	4.4	5.3	6.5	5.6	8.0	–	–			8.3	8.9	7.2	8.6
AMNH 21746					5.1	5.9	6.0	7.1			7.3	9.0	7.8	9.6	7.2	9.0
Pataecops parvus*, Menkhen Teg*																
PSS 14-1			4.0	4.0	5.0	5.5	5.5	7.2	7.0	8.2			7.8	9.3	7.0	8.2

The D3? and D4 are fully molariform. They differ from M1 only by their smaller size and straighter ectoloph.

The M1 and the M2 differ from one another in size and proportions: M2 is larger and more elongated antero-posteriorly, M1 is more squarish. On M2 the ectoloph is slightly more deflected lingually. The parastyle is well developed, but lower than the paracone and columnar. Posteriorly to the paracone, the ectoloph is bent, concave or convex labially. The protoloph and the metaloph are oblique crests. The protoloph joins the ectoloph between the parastyle and the paracone. The metaloph runs to the metacone ("premetaconule crista" of Hooker 1989). There is a relatively strong anterior cingulum and a weaker posterior cingulum. The labial cingulum is absent. The lingual cingulum is better developed on smaller teeth; on larger teeth it is interrupted at the protocone and hypocone bases. On all available M2s the postmetacrista is bent labially and not confluent with the metaloph.

The M3s vary significantly in size (Table 3) and crown shape. The crown has a generally triangular outline. The parastyle is relatively large, but much lower than the paracone and columnar. The ectoloph is much deflected lingually and nearly parallel to the protoloph. The metaloph is half the length of the protoloph. The postmetacrista is usually shorter than the metaloph and confluent with the latter. There is only an anterior cingulum, which is well developed. Sometimes at the base of the protocone there is a remnant of lingual cingulum.

The specimens ZIN 35288, 35290, and 35293 give some information about the roots of the upper cheek teeth. On ZIN 35288 the roots of P3-4 are extremely long and gradually tapering towards their free ends. The same can be seen on ZIN 35290, a juvenile specimen, for D4 and M1. However, the

molars of ZIN 35288 and ZIN 35293, much older individuals, have bulbous (swollen) roots and sometimes curved at their free ends. Swollen roots is probably an age correlated character, which is apparently more variable than was thought by Radinsky (1965), who used it for distinguishing *Rhodopagus pygmaeus* from *Pataecops parvus*. At least in one specimen of *P. parvus* (Dashzeveg 1991: fig. 16) the upper molars appear to have lingual roots inflated distally, like in *R. pygmaeus*.

The dentary symphysis is completely fused, relatively short (11.5 mm, ZIN 35298) and terminates at the level of p2 (first cheek tooth). The alveolus for c1 is relatively large. The length of the lower diastema is 6.9 mm. There is a small mental foramen between c1 and p2.

There was no d1, judging from absence of its alveolus in ZIN 34028. Apparently, it was not replaced by p1, because this tooth is lacking in *P. parvus* and *Rhodopagus*.

The d2 was two-rooted, distinctly smaller than the d3.

The d3 and the d4 have broadly similar morphologies, differing mostly in size and proportions. The trigonid and talonid basins are widely open lingually. The labial part of the paralophid and the crista obliqua are almost parallel to the labial side of the crown. The protolophid and the hypolophid are oblique crests. d3 has a relatively longer and more open trigonid with a distinct paraconid. On d4 the antero-lingual portion of the paralophid goes parallel to the protolophid.

The m2 is preserved only on ZIN 34028 (Fig. 3M, N), where it is slightly incomplete and not fully erupted. The protolophid and hypolophid are obliquely oriented to the longitudinal axis of the tooth. The hypolophid is higher than the protolophid. The cristid obliqua is relatively unreduced, high, relatively long, and arcuate, meeting the protolophid rather lingually. The posterior cingulid is rather short, limited to the lingual portion of the crown.

Measurements
For upper dentition: see Table 3. ZIN 34028: d3: L = 4.5, WTR = 2.2, WTL = 2.5; d4: L = 5.4, WTR = 3.0, WTL = 3.1.

DISCUSSION

As was pointed out by Gabunia & Kukhaleishvili (1991: 111), the holotype of *R. minutissimus* (PIN 3486-1) sharply differs from the other specimens of *Rhodopagus* and other lophialetids except *Pataecops* by a much more considerable lingual displacement of the elongated ectoloph on M1 and M2. They also noted some differences in the ectoloph structure between the molars of *R. minutissimus* and those of *Pataecops*. Indeed, the ectoloph in the *R. minutissimus* holotype is concave labially and the metaloph seems to be slightly less reduced than in *Pataecops parvus* from the middle Eocene of Mongolia (Radinsky 1965; Dashzeveg 1991). Our specimens show, however, that these characters are quite variable. Among five M1-2 at our disposal, three have a concave ectoloph and two a convex one. Moreover, the degree of metaloph reduction on M1-2 is greatly variable. Crucial for our taxonomic conclusion is the association of an M2 with a labially concave ectoloph and a relatively long metaloph and an M3 of typical *Pataecops* pattern (ZIN 35288; Fig. 3B) (the holotype and only known specimen of *R. minutissimus* lacks M3). This fact lumps together specific characters of *R. minutissimus* and *Pataecops microdon*, which was known previously from four isolated upper molars from the same locality, Andarak 2. Thus we conclude that there is only one species of small archaic rhinoceratoids ("rhodopagids") in the Andarak 2 locality. We consider *Pataecops microdon* Reshetov, 1979 (p. 31) as a junior synonym of *Rhodopagus minutissimus* Reshetov, 1979 (p. 29) by page priority, and we refer this species to the genus *Pataecops* as *P. minutissimus* (Reshetov, 1979) n. comb. The names *Pataecops microdon* and *Rhodopagus minutissimus* were used in an earlier publication, in an abstract by Reshetov *et al.* (1978) which provided a preliminary faunal list for the Andarak locality. However, in that publication these names clearly appeared as nomina nuda as they were not accompanied by any description, nor by a holotype designation.

Dashzeveg (1991: 36, tabl. 8) considered "*Pataecops*" *microdon* as belonging neither to

Pataecops nor to *Rhodopagus*, because of its small size and the shape of its crown, with a lingually shifted and short ectoloph parallel to the protoloph. However, the holotype of *P. microdon* (PIN 3486-2) represents the extreme case of M3 variation in Andarak's sample. Among four M3 at our disposal, three (ZIN 35288, 35294, 35295; Fig. 3B, H, L) approximate the condition of PIN 3486-2 in having a reduced metaloph parallel to the ectoloph as well as other small differences in crown shape, and one specimen (ZIN 35297) approximates the condition of Mongolian *P. parvus* with a relatively longer metaloph not parallel to the ectoloph. *P. minutissimus* n. comb. is further similar with *P. parvus* in having a small infraorbital foramen placed above P2 (in *R. pygmaeus* this foramen is larger and placed above P1; Radinsky 1965: 208). All this allows us the placement of Andarak's species in the genus *Pataecops*.

The Andarak species clearly differs from the Mongolian middle Eocene *P. parvus* by its smaller size, the lack of a labial cingulum on P3-4, more variable M1-2 some of which have a concave ectoloph and more variable M3 which in some cases are more derived than those of the Mongolian species in having a more reduced metaloph parallel to the ectoloph. The upper molars in all known specimens of *P. parvus* from the Kholbolzdhi Formation at the Valley of Lakes, Mongolia (Radinsky 1965; Dashzeveg 1991) have a convex ectoloph.

The genera *Rhodopagus* and *Pataecops* were originally placed by Radinsky (1965) in the family Lophialetidae with a question mark. He noted an evolution of these genera toward a functionally bilophodont dentition (by the lingual depression of the metacone), while the typical lophialetids show the development of a rhinocerotoid-like molar occlusion. However, he also noted later (Radinsky 1969) some similarities of these genera with rhinocerotoids in the wear facet pattern. Reshetov (1975) united *Rhodopagus* and *Pataecops* into a new subfamily Rhodopaginae provisionally placed within the Lophialetidae. Subsequently, Lucas & Schoch (1981) transferred both genera to the Hyracodontidae Cope,

1879 and cited eight shared characters which they considered synapomorphies for this family. Prothero *et al.* (1986) placed "rhodopagids" in a trichotomy with Hyracodontidae and Rhinocerotidae Gray, 1821. They considered *Rhodopagus* and *Pataecops* as primitive sister taxa of either hyracodontids, or possibly the sister-group of the rhinocerotids plus hyracodontids. Attribution of "rhodopagids" to Hyracodontidae was upheld by Hopson (1989) and Dashzeveg (1991), but was not supported by the cladistic analysis of Hooker (1989), who suggested that Rhodopaginae may be the sister group of Deperetellidae. Prothero *et al.* (1986: 361) cited as an additional "hyracodont feature" of *Rhodopagus* the reduced c1 in *R. minimus* (AMNH 26112; this character may be seen also in *R. zdanskyi* Lucas & Schoch, 1981: fig. 4f). In ZIN 35298, a symphysis fragment of *P. minutissimus* n. comb., the alveolus for c1 is nearly two times larger than the alveolus for the preceding incisor, so the lower canine in this species was not reduced (unknown for *P. parvus*).

Gabunia & Kukhaleishvili (1991) reviewed the characters listed by Lucas & Schoch (1981) as synapomorphies between *Rhodopagus* and Hyracodontidae, based on the discovery of the oldest *Rhodopagus* species, *R. radinskyi* from the early Eocene Chakpaktas Svita in Zaisan Basin, eastern Kazakhstan. They came to the conclusion that *Rhodopagus* is closer to the tapiroids (Lophialetidae) than to the rhinocerotoids (Hyracodontidae). Dashzeveg & Hooker (1997) found that this conclusion was based on plesiomorphic or wider distributed characters. They found also that "*Rhodopagus*" *radinskyi* should be placed "in a new rhodopagid genus" (Dashzeveg & Hooker 1997: 128). According to these authors, *Veragromovia desmatotheroides* Gabunia, 1961, known by one isolated M3 from the middle Eocene Obayla Svita of the Zaisan Basin, Kazakhstan and originally described as a helaletid, should be transferred to the Rhodopagidae. The lower crowned Rhodopagidae do not show special relationships with other rhinocerotoid families, but two characters advocate for their inclusion into the

Rhinocerotoidea (Dashzeveg & Hooker 1997: 128): 1) a distinct break between the metaloph and the protocone, which is characteristic of non-molariform teeth of hyrachyids, hyracodontids, amynodontids, and rhinocerotids, and well marked in *Pataecops* and "*Rhodopagus*" *radinskyi*, although less obvious in *Rhodopagus*; and 2) the lack of any sign of the major narial incision which typifies all tapiroids except *Heptodon*. The latter character among rhodopagids is known only for "*Rhodopagus*" *radinskyi*, a more or less complete skull of which is known (Gabunia & Kukhaleishvili 1991: fig. 1a, b). A relatively anterior position of the infraorbital foramen in *R. pygmaeus*, *P. parvus*, and *P. minutissimus* n. comb. may suggest the lack or the incipient stage of a narial incision, although these features are not unequivocally related (Antoine 2002). However, this character may not be so important because in the primitive lophialetid *Eoletes gracilis* the narial incision is also poorly developed (Lucas *et al.* 1997: fig. 6). Only the presence of a distinct break between the metaloph and the protocone on the upper premolars, found also in Andarak's *P. minutissimus* n. comb. (ZIN 35288, see above), remains a good character indicating rhinocerotoid affinities of the Rhodopagidae. We subsequently classify this family as Rhinocerotoidea *incertae sedis*.

Interestingly, the upper cheek teeth of *Pataecops* look more rhinocerotoid-like (more advanced) than those of *Rhodopagus*: on the premolars the metaloph is more distinctly separated from the protocone, P4 may bear a short crista (Dashzeveg 1991: fig. 16); the parastyles on M1-3 are more columnar, M3 is essentially more rhinocerotoid-like in its triangular shape, lingually displaced metacone, and greater reduction of the postmetacrista. Moreover, *Rhodopagus* has simpler upper premolars with a less evident break between metaloph and protocone (approximating the lophoid loop of lophialetids), relatively larger scale-like parastyles (another "tapiroid" feature) and more trapezoid M3 with less reduced metacone and postmetacrista (which is typical for "tapiroids", but also found in some early hyracodontids, e.g., *Triplopus* Cope, 1880). However,

Rhodopagus and *Pataecops* still share some derived traits (Hooker 1989; Holbrook 1999): loss of p1, lingually displaced metacone on upper molars, loss of m3 hypoconulid (for *P. parvus* see Dashzeveg 1991: 36).

Pataecops minutissimus n. comb. is the smallest known ceratomorph ever found: length of M1-3 is 17.1 (ZIN 35288) and 17.5 (ZIN 35289). This length is 19.2 in the previously known smallest ceratomorph *Fouchia elegans* Emry, 1989 from the middle Eocene of North America (Emry 1989).

Family AMYNODONTIDAE Scott & Osborn, 1883
Genus *Sharamynodon* Kretzoi, 1942

Sharamynodon kirghisensis (Belyaeva, 1971)
(Fig. 4)

Lushiamynodon(?) *kirghisensis* Belyaeva, 1971: 40, fig. 1.

Lushiamynodon? *kirghisiensis* [sic] – Russell & Zhai 1987: 185.

Lushiamynodon? sp. – Russell & Zhai 1987: 188.

Andarakodon kirghisiensis [sic] – Averianov & Potapova 1996: 1062, figs 1, 2A.

Sharamynodon kirghisensis – Lucas & Emry 2001: 522, fig. 5A.

REFERRED MATERIAL. — ZIN 34313, left and right maxillary fragments with P4-M3; ZIN 35299, left(?) upper(?) incisor; ZIN 34021, lingual part of left P3; ZIN 35300, left p4; ZIN 35301, left lower molar trigonid.

DESCRIPTION
For description and measurements of the upper cheek teeth see Belyaeva (1971: 40-42) and Averianov & Potapova (1996: 1062-1063).
The supposed upper incisor (Fig. 4D, E) is spatulate with a slightly asymmetrical crown and a heel-like cingulum projection.
The p4 is a molariform tooth with a relatively high (unilaterally hypsodont) crown somewhat compressed antero-posteriorly. The trigonid is only slightly smaller than the talonid. The protocristid and hypolophid are slightly oblique
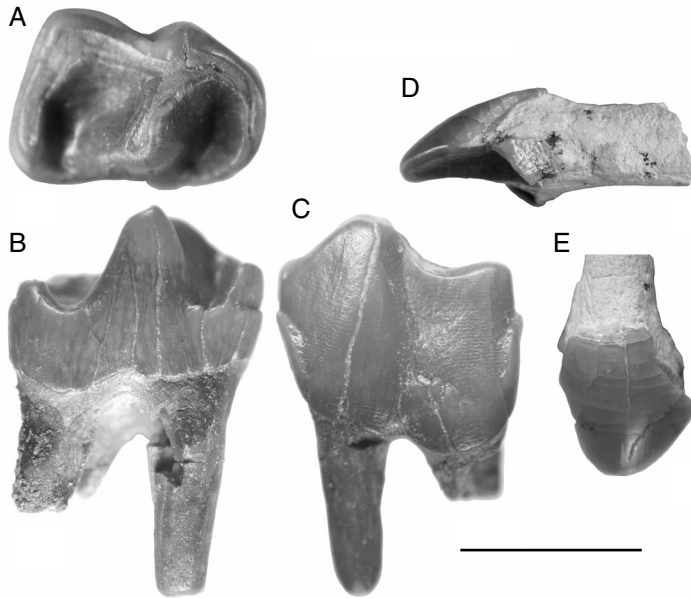
Fɪɢ. 4. — *Sharamynodon kirghisensis* (Belyaeva, 1971); **A-C**, ZIN 35300, left p4; **D**, **E**, ZIN 35299, left(?) upper(?) incisor; in occlusal (**A**), lingual (**B**), labial (**C**), profile (**D**), and anterior (**E**) views; Andarak 2, Kyrgyzstan, Alay beds, Irdinmanhan. Scale bar: 1 cm.

crests. The paracristid is very long. It markedly decreases in height toward the antero-lingual corner of the trigonid. Its anterior branch is nearly parallel to the protocristid. The metaconid is higher than the protoconid. The cristid obliqua is nearly perpendicular to the protocristid and joins it near its labial end. The hypoconid is higher than the entoconid, which is completely merged into the hypolophid. The narrow trigonid and talonid basins are open lingually. There are weak anterior and posterior cingulids, and there is a very weak and short labial cingulid between the bases of the protoconid and hypoconid. The tooth has two relatively small roots.

Measurements
ZIN 35300, p4: L = 14.2, WTR = 9.9, WTL = 10.6. ZIN 35301 (lower molar): WTR = 10.2.

Dɪsᴄᴜssɪᴏɴ
The p4 ZIN 35300 is referred here to the Amynodontidae because of its relatively shortened and hypsodont crown, its very weak labial cingulid, and the entoconid not distinct from the

hypolophid. By these characters this specimen differs from the p4s in the Asiatic Eocene hyracodontids *Triplopus*, *Prohyracodon* Koch, 1897, *Forstercooperia* Wood, 1939, and *Juxia* Chow & Chiu, 1964 (data from Radinsky 1967; Gabunia 1977; Lucas *et al.* 1981, 1997; Lucas & Sobus 1989; Dashzeveg 1991). It fits well in size with the teeth of *S. kirghisensis* (Belyaeva 1971; Averianov & Potapova 1996) from the same locality. The WTL/L ratio in ZIN 35300 is 0.75, which is essentially the same as for the p4 of *Zaisanamynodon borisovi* from Kazakhstan (Belyaeva 1971), or near this ratio in the Chinese specimens of *Z. borisovi* (0.62-0.68; Lucas *et al.* 1996).

AGE OF THE ANDARAK 2 LOCALITY

Three currently recognized Land Mammal Ages (LMA) encompass early-middle Eocene of Asia: Bumbanian, Arshantan, and Irdinmanhan (Russell & Zhai 1987; Tong *et al.* 1995). Lucas & Emry (2001) also included part of the

Nongshanian LMA in the early Eocene, however this controversial view seems refuted by more recent work which located the base of the Bumbanian very close to the Paleocene-Eocene boundary (Bowen *et al.* 2002). The distinction between Arshantan and Irdinmanhan by Lucas (2001) is based on several FAD (First Appearance Data), including those of the brontothere *Protitan*, *Teleolophus*, Amynodontidae, and *Gobiohyus*. By this defintion, the Andarak fauna is Irdinmanhan, despite it lacks brontotheres, *Gobiohyus*, anthracotheres, etc. It also lacks *Gobiatherium*, index taxon of the Arshantan LMA according to Lucas (2001).

The lack of large mammals in the Andarak fauna could be due to a taphonomic bias against large fossils, or to ecological reasons concerning these taxa (e.g., *Gobiatherium* is a very peculiar mammal), or to some palaeogeographical reason. In fact, a possible insularity for Andarak mammals is suggested on the detailed palaeogeographical map of Alay age in the Fergana (Gekker *et al.* 1962). It might explain the presence in the fauna of only small mammals, the largest being the amynodontid, which in turn is the smallest representative of its family. However, this hypothesis should be tested through further analysis of the entire fauna.

Because the Andarak mammalian fauna is found within a marine section, it has been possible to suggest for it a latest Early Eocene (late Ypresian) age, based on a large selachian fauna and other geological evidence (Averianov & Udovichenko 1993; Averianov & Godinot 1998). Correlation with western European selachians is questioned by Lucas & Emry (2001), however it is still a serious possibility, which deserves further scrutiny. Placing the Andarak localities securely within a marine stage would be important. This fauna gives a unique point of correlation between the Asiatic continental land mammal ages and the marine geological stages. The proposed correlation would imply that the Irdinmanhan begins during the late Ypresian, whereas the more common opinion, which places the Irdinmanhan in the Lutetian (Lucas & Emry 2001), does this through a very indirect and distant correlation

with the Bridgerian, a North American land mammal age not directly correlated to the marine scale. Such a distant correlation is broadly valid but does not allow the precise correlation of limits, especially to a marine boundary. The Andarak correlation point is thus very important, and to give it its full value, it will be necessary to scrutinize how its mammalian fauna fits within a possible succession of Irdinmanhan faunas. Furthermore, there are no micromammals in the list of typical Irdinmanhan taxa provided by Lucas (2001), and this absence precludes a good use of nine species of Glires found in Andarak (Averianov & Godinot 1998). Clearly, more needs to be done on Andarak and other Irdinmanhan mammalian faunas.

Acknowledgements

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