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New Palaeoryctidae (Mammalia) from the Eocene of Kyrgyzstan and Mongolia

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Abstract—Two new palaeoryctids from the Eocene Asiatic genus *Nuryctes* are described. *N. alayensis* sp. nov. (terminal Lower Eocene, Alai Beds, Andarak 2 locality, Kyrgyzstan) is more primitive in the extent of premolar reduction than the type species *N. qinlingensis* (Tong, 1997) from the Middle Eocene of China. *N. gobiensis* sp. nov. (Middle Eocene, Khaychin Formation, Khaychin-Ula 2, Mongolia) is more advanced in the structure of cheek teeth than the other two species.

Key words: Palaeoryctidae, *Nuryctes*, Lower–Middle Eocene, Kyrgyzstan, Mongolia.

INTRODUCTION

The family Palaeoryctidae comprises small primitive Early Paleogene eutherians of uncertain taxonomic position that have been referred to as Insectivora (Matthew, 1913; Gingerich, 1982; Thewissen and Gingerich, 1989; Tong, 1997), Deltatheridia (Van Valen, 1966, 1967), Kennalestida (McKenna, 1975), Leptictimorpha (Szalay, 1977), Proteutheria (Kielan-Jaworowska, 1981; Bown and Schankler, 1982), Soricomorpha (McKenna et al., 1984), and Cimolesta (McKenna and Bell, 1997).

Initially, the Palaeoryctidae were usually assigned to zalambdodont insectivores (Matthew, 1913). Subsequent to the exclusion of Palaeoryctidae from the Soricomorpha, Lipotyphla, and Zalambdodonta (McDowell, 1958; Butler, 1988), they were placed in the superorder Insectivora (sensu Novacek, 1986) beyond the orders Lipotyphla and Leptictida (Thewissen and Gingerich, 1989; MacPhee and Novacek, 1993). Butler (1988) was the first to indicate a marked similarity in dentition between *Palaeoryctes* and *Cimolestes*, and, currently, palaeoryctids are assigned to Cimolesta subord. indet. Thus, they are included in the same order as the Didelphodonta, Apatotheria, Taeniodonta, Tillodonta, Pantodonta, and Pantolesta, which are ranked as suborders (McKenna, 1975; McKenna and Bell, 1997).

Earlier, the Deltatheridiinae, Didelphodontinae, Micropternodontinae (Van Valen, 1966, 1967), and Asioryctinae (Kielan-Jaworowska, 1981) were placed in the Palaeoryctidae; however, for various reasons, they were subsequently excluded from this family (Butler, 1972; Butler and Kielan-Jaworowska, 1973; Wilson, 1985; Thewissen and Gingerich, 1989; MacPhee and Novacek, 1993; McKenna and Bell, 1997). According to the recent concept, palaeoryctids (Palaeoryctinae sensu McKenna, 1975; Thewissen and Gingerich, 1989; Palaeoryctidae sensu McKenna and Bell, 1997) comprise only four genera: *Palaeoryctes* (Early Paleocene–Early Eocene of North America and Late Paleocene–Early Eocene of North Africa), *Aaptoryctes* (Late Paleocene of North America), *Eoryctes* (Early Eocene of North America), and *Nuryctes* (Middle Eocene of Asia).

In some North American palaeoryctids, such as *Palaeoryctes puercensis* Matthew, 1913, *P. punctatus* Van Valen, 1966, *Aaptoryctes ivyi* Gingerich, 1982, and *Eoryctes melanus* Thewissen et Gingerich, 1989, the skull structure is at least partially known. The humerus of *P. punctatus*, found in association with the skull, and a number of cranial characters of *Palaeoryctes* and *Eoryctes* provide evidence for a fossorial mode of life of palaeoryctids (Van Valen, 1966; Thewissen and Gingerich, 1989).

The Asian *Nuryctes qinlingensis* (Tong, 1997) was described on the basis of mandibular fragments and isolated lower teeth from the Middle Eocene of China. The list of specimens also included an upper molar and an upper premolar (Tong, 1997, p. 194); however, they were neither figured nor described.

The American palaeoryctids *Palaeoryctes* and *Aaptoryctes* (in *Eoryctes*, the structure of anterior teeth is unknown) are characterized by the presence of three procumbent incisors in the lower jaw, including a strongly reduced I_3; a relatively large canine; absence of P_1; a small single-rooted P_2; relatively large and nonmolariform P_3 and P_4 (of a crushing type, as in *Aapto-*

ryctes); and specialized M_1–M_3, which have high and wide trigonids and low and narrow talonids with reduced cusps and without an entocristid (these characters of cheek teeth are also typical for *Eoryctes*). The molars of palaeoryctids display the so-called primitive zalambdodont structural pattern, i.e., have a rudimentary metacone in the postparacrista, a relatively large protocone, and, hence, less developed trigonids and less reduced talonids than in the true zalambdodont pattern (Butler, 1941).

Tong (1997) proposed that the Asian palaeoryctid *"Neoryctes" qinlingensis* is similar in dental formula to American palaeoryctids and interpreted its P_2 and P_3 as single-rooted and peglike teeth. However, in our opinion, this researcher mistook root fragments of a double-rooted P_3 for these teeth. Thus, *"Neoryctes" qinlingensis* differs from American palaeoryctids in the absence of P_2. The same feature is apparently characteristic of the new species from the Early Eocene of Kyrgyzstan.

The generic name *Neoryctes* Tong, 1997 is preoccupied by *Neoryctes* Arrow, 1908 (Insecta, Coleoptera, Scarabaeidae) (Arrow, 1908, p. 342) and has recently been replaced by the name *Nuryctes* (Tong, 2003). In the present study, two new Eocene species of the genus *Nuryctes* are described: *N. alayensis* sp. nov. from Kyrgyzstan (Andarak 2 locality; collected by N.S. Shevyreva and V.Yu. Reshetov in 1975 and by A.O. Averianov from 1988 to 1995) and *N. gobiensis* sp. nov. from Mongolia (Khaychin-Ula 2 locality; collected by V.Yu. Reshetov in 1971 to 1973).

The Khaychin-Ula 2 locality is dated as the Middle Eocene (Badamgarav and Reshetov, 1985; Russell and Zhai, 1987; Averianov and Godinot, 1998) or the end of the Middle–the beginning of the Late Eocene (Devyatkin, 1981, 1994). We adhere to the first point of view. The fauna from Khaychin-Ula 2 belongs to the Irdinmanhan Asian Land Mammal Age, which correlates with the Early–Middle Uintan of North America (McKenna and Bell, 1997).

The Andarak Fauna is dated as the Middle Eocene (Russell and Zhai, 1987; Shevyreva, 1995) or the end of the Early Eocene (Late Ypresian) (Averianov and Godinot, 1998).

The following abbreviations are used in the present study: (PIN) Paleontological Institute of the Russian Academy of Sciences, Moscow; and (ZIN) Zoological Institute of the Russian Academy of Sciences, St. Petersburg.

SYSTEMATIC PALEONTOLOGY

Family Palaeoryctidae Winge, 1917

Genus *Nuryctes* Tong, 2003

Neoryctes (non Arrow, 1908): Tong, 1997, p. 29.

Nuryctes: Tong, 2003, p. 88.

Type species. *Neoryctes qinlingensis* Tong, 1997, Middle Eocene of China.

Diagnosis. Anterior and posterior foramina of infraorbital canal located above P^3 and above P^4, respectively. Upper molars of zalambdodont type and having rudimentary metacone, considerably lingually displaced paracone, and small protocone. P_2 absent. P_3 double-rooted and relatively large. P_4 nonmolariform, lacking paraconid, and having well-developed unicuspid talonid. Trigonid of lower molars moderately high. M_1–M_3 without entoconid. Talonid of M_1 and M_2 short, with small hypoconid and hypoconulid, while talonid of M_3 lengthened, with moderately developed hypoconid and high terminal hypoconulid.

Species composition. *N. qinlingensis* (Tong, 1997), Middle Eocene (Irdinmanhan) of China; *N. alayensis* sp. nov., uppermost Lower Eocene (Irdinmanhan) of Kyrgyzstan; and *N. gobiensis* sp. nov., Middle Eocene (Irdinmanhan) of Mongolia.

Comparison. This genus differs from *Palaeoryctes* Matthew, 1913, *Aaptoryctes* Gingerich, 1982, and *Eoryctes* Thewissen et Gingerich, 1989 in the considerably lingually displaced paracone, small protocone, and rudimentary metacone of the upper molars, the absence of P_2, and in the lower crowns and the absence of entoconids on M_1–M_3. In addition, it differs from *Palaeoryctes* in the lengthened talonid of M_3, from *Aaptoryctes* in the structure of the talonid of P_4, and from *Eoryctes* in the absence of a paraconid and the better developed talonid of P_4.

Nuryctes alayensis Lopatin et Averianov, sp. nov.

Etymology. From the Alai Mountains.

Holotype. ZIN, no. 86145, fragmentary right dentary with I_3, P_4, and M_1 and alveoli of I_1, I_2, C_1, and P_3; Kyrgyzstan, Andarak 2 locality; uppermost Lower Eocene, Alai Beds.

Description (Figs. 1a, 1b, 2–4). The infraorbital canal extends from the level of the posterior labial root of P^3 to the level of the posterior root of P^4. The anterior foramen of the infraorbital canal is round (1.0×0.8 mm). The foramen of the posterior labial root of P^3 opens in the anterior region of the infraorbital canal. The posterior foramen of the infraorbital canal is in the shape of a laterally compressed oval (Fig. 2c). It is visible in the rear view that the posterior part of the medial wall of the infraorbital canal has a thickening that divides the canal longitudinally into two parts.

The zygomatic arch is absent, i.e., at the level of the anterior labial root of M^2, the lateral wall of the anterior part of the orbital rim abruptly slopes (the alveolus of the posterior labial root of M^2 is located much more lingually within the palatine process of the maxilla). In this region, the dorsal side of the maxilla has a relatively sharp crest that passes posteriorly into a stout thickening. On a level with M^1, the lateral surface of the bone contains a small and round area that was probably the origin for the maxillonasal muscle.

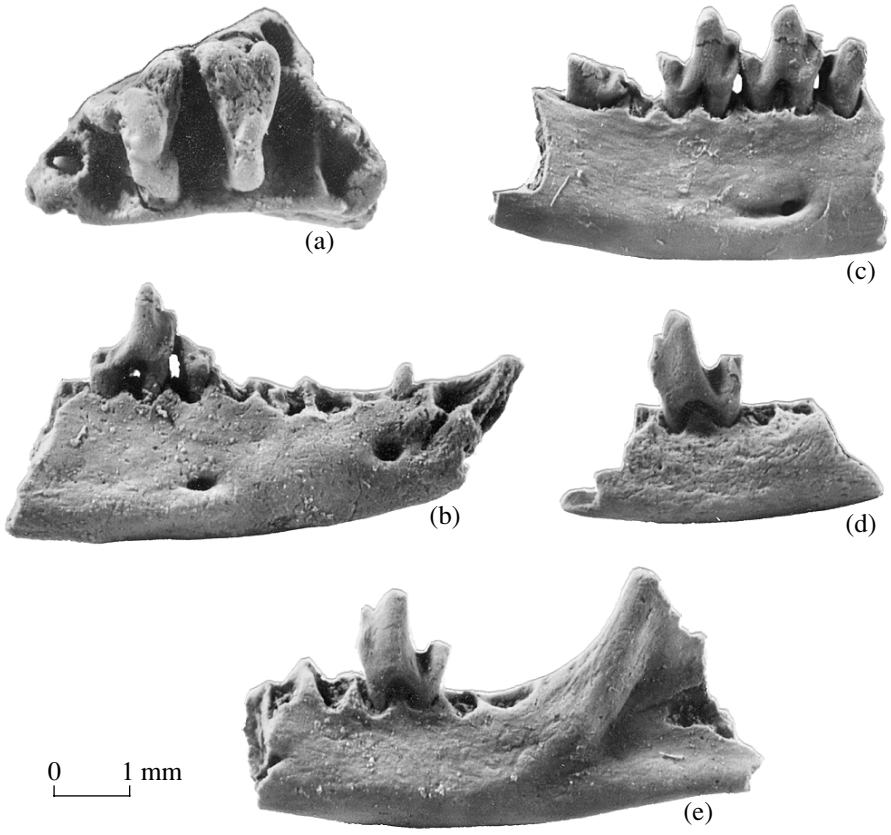

Fig. 1. New species of *Nuryctes* from the Eocene of Asia: (a, b) *N. alayensis* sp. nov.: (a) specimen PIN, no. 3486/110, fragmentary left maxilla with P^4 and M^1; (b) holotype ZIN, no. 86145, fragmentary right dentary with I_3, P_4, and M_1; Kyrgyzstan, Andarak 2 locality, uppermost Lower Eocene, Alai Beds; (c–e) *N. gobiensis* sp. nov.: (c) holotype PIN, no. 3107/414, fragmentary right dentary with P_4–M_3; (d) specimen PIN, no. 3107/415, fragmentary left dentary with M_2; and (e) specimen PIN, no. 3107/416, fragmentary left dentary with M_2; Mongolia, Khaychin-Ula 2, Middle Eocene, Khaychin Formation.

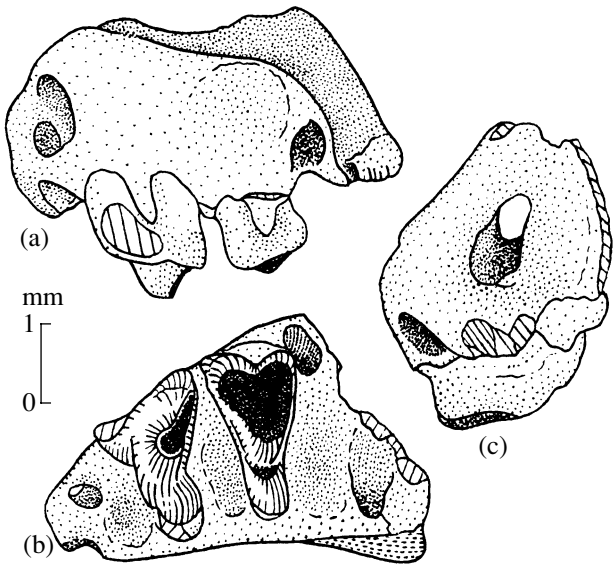

Fig. 2. *Nuryctes alayensis* sp. nov., specimen PIN, no. 3486/110, fragmentary left maxilla with P^4 and M^1: (a) labial, (b) occlusal, and (c) rear views.

P^4 is relatively wide and has a large lingual projection. The parastylar lobe is relatively small and projects anteriorly, while the metastylar lobe is large and strongly projects posterolabially. The ectocingulum is weak. The massive paracone and small metastyle are connected by a stout postcrista. The postcingulum is well-developed at the level of the paracone and postcrista. The protocone is relatively large but low.

M^1 is a symmetrical narrow triangle in outline and has a deep ectoflexus. The parastylar lobe is better developed than the metastylar lobe. The parastyle looks like a small cingular cuspule on the anterolabial end of the parastylar lobe; lingually and posteriorly, it is connected to the preprotocrista and the base of the stylocone, respectively (Fig. 3). Most of the parastylar lobe is occupied by a relatively large and massive stylocone, which is lingually connected to the preparacrista. The anterior projection of the stylocone, which is shaped like a small cuspule, is connected to the lingually oriented and short additional crest adjoining the preprotocrista. The ectocingulum is weak. The metastylar lobe extends posterolabially. The stylar shelf is large.

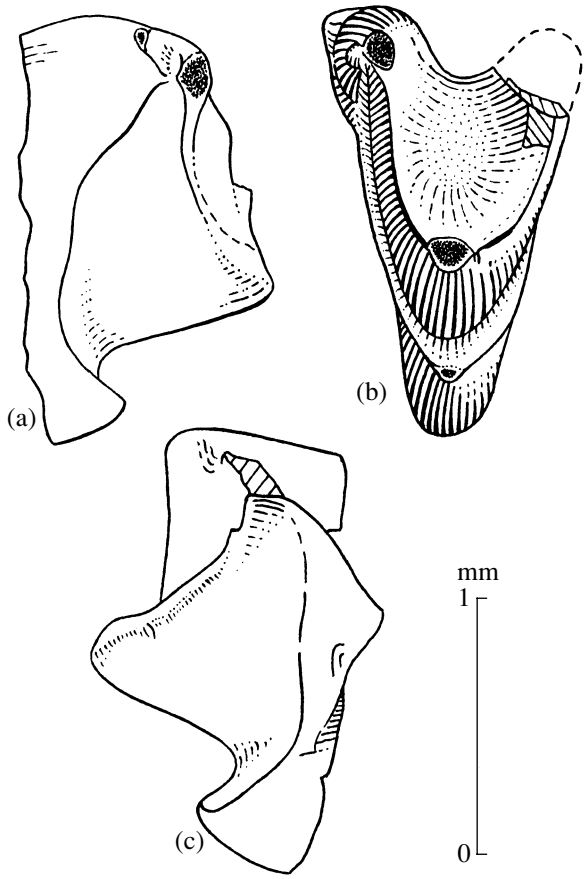

Fig. 3. *Nuryctes alayensis* sp. nov., specimen PIN, no. 3486/207, left M^1: (a) frontal, (b) occlusal, and (c) rear views.

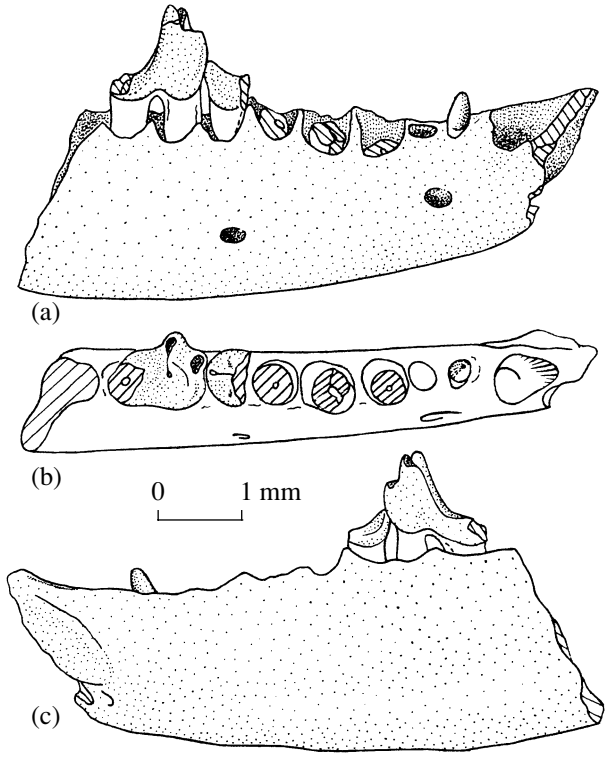

Fig. 4. *Nuryctes alayensis* sp. nov., holotype ZIN, no. 86145, fragmentary right dentary with I_3, P_4, and M_1: (a) labial, (b) occlusal, and (c) lingual views.

The crests of the preparacrista and postmetacrista are sharp. The paracone is stout, has a conical apex, and occupies the center of the tooth crown. Immediately posterolabial to the paracone apex, the premetacrista and postmetacrista have a clear small thickening that is apparently a rudimentary metacone. The protocone is relatively small and low (in a slightly worn tooth, it is half as high as the paracone) and has a conical apex on a level with the paracone apex. The crests of the preprotocrista and postprotocrista are relatively long and extend labially to the parastyle and metastyle, respectively.

Judging from the alveoli, M^2 was substantially wider than M^1. M^3 and its alveoli are not preserved. The spaces between the maxillary teeth contain deep, oval vascular fossae.

The horizontal ramus of the lower jaw is relatively high and thin (Fig. 4), and its lingual side is higher than the labial side. The mental foramina are large. The anterior foramen is located under the space between I_3 and C_1 at the midheight of the horizontal ramus, while the posterior foramen is located closer to the ventral edge of the jaw under the talonid of P_4. The symphysis extends posteriorly to the space between I_2 and I_3.

$I_3 < C_1 < I_1 < I_2$. The alveoli of I_1 and I_2 are large (especially that of I_2) and longitudinally extended. I_3 is substantially reduced, very small, and peglike. The canine is a little larger than I_3. Judging from the alveoli, P_3 was double-rooted, relatively large, and approximately as long as P_4. P_4 is relatively large, double-rooted, and has a low and moderately developed talonid with a small terminal cusp and a short longitudinal crest. In M_1, the precingulid is weak, while the paraconid is relatively large and stout. The protoconid and metaconid are high, thin, and strongly inclined anteriorly; the protocristid has a clear deep notch. The talonid is narrow (its posterior part is broken off, so that structural details remain uncertain).

Measurements, mm. Holotype: length of the alveolus of I_2, ca. 0.85; I_3: length, 0.27; width, 0.25; alveolus of C_1: length, 0.35; width, 0.35; length of P_3 along alveoli, 1.2; length of P_4, ca. 1.15; total length of M_1, ca. 1.1; talonid length, ca. 0.5; trigonid width, 0.75; talonid width, 0.65; trigonid height along the protoconid, 1.1; and the dentary depth at M_1/M_2 on the lingual side, 2.1, the same on the labial side, 2.0.

Specimen PIN, no. 3486/110: length from the anterior root of P^4 to the posterior wall of the alveolus of the lingual root of M^2, 3.6; length × width: P^4, 1.4 × 1.6; M^1, 1.15 × 2.05; width of M^2 along the alveoli of the anterior labial and lingual roots, 2.3.

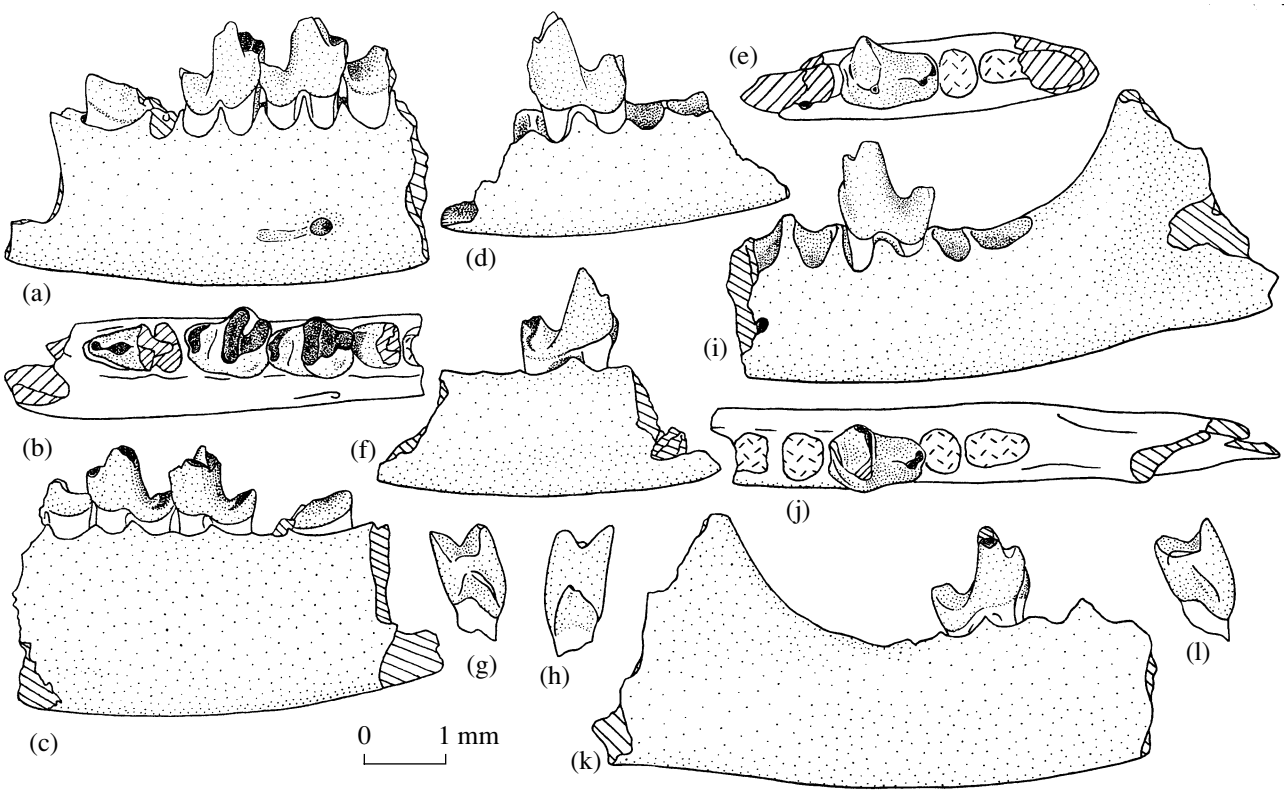

Fig. 5. *Nuryctes gobiensis* sp. nov.: (a–c) holotype PIN, no. 3107/414, fragmentary right dentary with P_4–M_3: (a) labial, (b) occlusal, and (c) lingual views; (d–h) specimen PIN, no. 3107/415, fragmentary left dentary with M_2: (d) labial, (e) occlusal, and (f) lingual views; (g) M_2, frontal view; and (h) M_2, rear view; and (i–l) specimen PIN, no. 3107/416, fragmentary left dentary with M_2: (i) labial, (j) occlusal, and (k) lingual views; and (l) M_2, frontal view.

Specimen PIN, no. 3486/207, M^1: length, more than 1.05; width, 1.8; height (posteriorly): paracone, 1.1; protocone, 0.55.

Comparison. *N. alayensis* sp. nov. is distinguished from *N. qinlingensis* by a less reduced P_3, which is approximately as long as P_4 (while in the latter species, P_3 is almost two times shorter than P_4); a weak precingulid of M_1; and a more anterior position of the posterior mental foramen (under P_4 instead of under M_1).

Material. In addition to the holotype, a fragmentary maxilla with heavily worn P^4 and M^1 and alveoli of P^3 and M^2 (PIN, no. 3486/110) and an isolated slightly worn M^1 (PIN, no. 3486/207) from the type locality.

Nuryctes gobiensis Lopatin et Averianov, sp. nov.

Etymology. From the Gobi Desert.

Holotype. PIN, no. 3107/414, fragmentary right dentary with P_4–M_3; Mongolia, Khaychin-Ula 2 locality; Middle Eocene, Khaychin Formation.

Description (Figs. 1c–1e, 5). The horizontal ramus of the lower jaw is low in young individuals (with unworn molars, Figs. 1d, 1e, 5d–5f) and relatively high in older animals (Figs. 1c, 5a–5c). The lingual side is substantially higher than the labial side. The posterior mental foramen is relatively small and positioned near the ventral edge of the jaw on a level with the anterior root of M_1 (sometimes, it is located in a short groove: Fig. 5a). In P_4, the talonid is short and low, the longitudinal crest is weak, and the posterior terminal cusp is undeveloped.

M_1 and M_2 are similar in size and structure. M_1 is distinguished by its narrower trigonid, which is open lingually to a greater extent. The precingulid is distinct but small and only projects slightly. The anterior side of the tooth crown has a vertical reentrant fold that is formed by the precingulid and the anterolingual projection of the crown and contains the posterior projection of the talonid of the anteriorly adjoining tooth. The paraconid is small, ridgelike, and raised high above the level of the precingulid. The paracristid is positioned at an angle of approximately 45° to the long axis of the jaw. The protoconid and metaconid are approximately equal in height and massive at the base. The protocristid is positioned transversely and has a deep and wide notch. The trigonid basin is shallow. The talonid is relatively narrow. The oblique cristid is weak and positioned longitudinally. The hypoconid and hypoconulid are very small and closely adjoin each other. In an unworn or slightly worn tooth, the hypoconid is slightly higher than the hypoconulid. The entoconid is absent. In a considerably worn tooth, the trigonid basin disap-

pears, and two large facets appear; the first is on the paraconid and the anterior walls of the protoconid and metaconid, and the second is in the region of the protocristid. The wear facet on the talonid unites the hypoconid and hypoconulid and descends along the posterolingual wall.

M_3 is longer than other molars. Its talonid is low, very narrow, and clearly elongated; its hypoconid and hypoconulid are located in the same longitudinal line. The hypoconulid is terminal and raised above the hypoconid. The entoconid is absent.

Measurements, mm. Holotype: length of M_1–M_3, 3.5; M_1: total length, 1.1; talonid length, 0.4; trigonid width, 0.7; talonid width, 0.6; M_2: total length, 1.15, talonid length, 0.45; trigonid width, 0.85; talonid width, 0.65; length of M_3 along the alveoli, 1.25; depth of the horizontal ramus at M_1/M_2 on the lingual side, 2.25; and the same on the labial side, 2.0.

Specimen PIN, no. 3107/415: total length of M_2, 1.2; talonid length, 0.6; trigonid width, 0.9; talonid width, 0.6; height of the trigonid along the protoconid, 1.2; height of the talonid along the hypoconid, 0.7; depth of the horizontal ramus at M_1/M_2 on the lingual side, 1.5; and the same on the labial side, 1.45.

Specimen PIN, no. 3107/416: length of the alveoli of M_1, 1.1; total length of M_2, 1.2; talonid length, 0.5; trigonid width, 0.8; talonid width, 0.5; height of the trigonid along the protoconid, 1.25; height of the talonid along the hypoconid, 0.7; length of the alveoli of M_3, 1.25; depth of the horizontal ramus at M_1/M_2 on the lingual side, 2.0; and the same on the labial side, 1.75.

Comparison. *N. gobiensis* sp. nov. is distinguished from *N. alayensis* by the more reduced talonid of P_4, more massive cusps of the trigonid and better developed precingulid of M_1, and the more posterior position of the posterior mental foramen (under M_1 instead of P_4). It differs from *N. qinlingensis* in the more reduced talonid of P_4 and the relatively smaller paraconid and precingulid of M_2.

Material. In addition to the holotype, two fragmentary dentaries: one with M_2 and alveoli of M_1 and M_3 (PIN, no. 3107/415) and one with M_2, alveoli of M_1 and M_3, and the basal part of the ascending ramus (PIN, no. 3107/416) from the type locality.

DISCUSSION

The dental structure of *Nuryctes* differs from that of other known palaeoryctids in the better pronounced zalambdodont pattern of the upper molars, the absence of P_2, absence of an entoconid on M_1–M_3, and elongated talonid of M_3. These characters display the evolutionary trend that developed in the family during the Paleocene and Early Eocene, while their advanced states agree with the relatively young geological age of the genus.

The discovery of new *Nuryctes* species enables us to recognize evolutionary changes within this genus during the Middle Eocene. Thus, in the earlier species *N. alayensis*, P_3 is substantially larger than in *N. qinlingensis*, and the posterior mental foramen occupies a more anterior position than in *N. qinlingensis* and *N. gobiensis.* In *N. gobiensis*, the talonid of P_4 and the paraconid of M_2 are reduced to a greater extent than in *N. alayensis* and *N. qinlingensis.* Thus, morphological characteristics of the lower jaw and teeth of *Nuryctes* display the following evolutionary trends: (1) the posterior mental foramen is displaced from the level of P_4 to the level of M_1, (2) P_3 is consecutively reduced, (3) the talonid of P_4 decreases in size, and (4) the paraconid of M_2 is reduced.

The shortening of the talonid of P_4 and paraconid of molars is likely a manifestation of an increase in specialization of the zalambdodont dentition. Based on the tooth wear pattern, Butler (1972) proposed that, in the course of food treatment, palaeoryctids mainly applied the primitive vertical shearing movements, as opposed to the zalambdodont Lipotyphla, which treated food mainly by transverse grinding movements. In *Nuryctes*, the main shearing effect was probably produced by the interaction of the long, high subtransverse crests of the preparacrista, postprotocrista, and protocristid (double prevallum/postvallid shearing, see Fox, 1975). The paracristid interacted with the postmetacrista and postprotocrista, while the talonid interacted with the protocone. Thus, the longitudinal shortening of the paraconid is associated with a more transverse orientation of the paracristid, which is connected functionally with the modification of the postmetacrista that is caused by the reduction of the metacone and progressive expansion of molars. The reduction of the talonid is associated with a decrease in size of the protocone, which is also intended for an increase in the shearing function of the main crests. The exception is the elongated crest of the talonid of M_3, which apparently interacted with the long and posteriorly inclined postmetacrista of M^3.

The foregoing suggests that *N. gobiensis* is more advanced than *N. qinlingensis* and, consequently, the Shipigou locality (Xichuan County, Henan Province, China) may be older than the Khaychin-Ula 2 locality (within the Irdinmanhan and, hence, Middle Eocene). Thus, Eocene faunas containing *Nuryctes* should be put in the following sequence (from earlier to later): Andarak 2–Shipigou–Khaychin-Ula 2.

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The specimen illustrations are by A.V. Lopatin.

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