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New Brachyericinae (Erinaceidae, Insectivora, Mammalia) from the Oligocene and Miocene of Asia

A. V. Lopatin* and V. S. Zazhigin**
**Paleontological Institute, Russian Academy of Sciences, Profsoyuznaya ul. 123, Moscow, 117997 Russia*
e-mail: alopat@paleo.ru
***Geological Institute, Russian Academy of Sciences, Pyzhevskii per. 7, Moscow, 109017 Russia*
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Abstract—Four new taxa of the subfamily Brachyericinae, *Exallerix manahan* sp. nov. (Lower Oligocene of Mongolia), *Synexallerix otus* gen. et sp. nov. (Lower Miocene of eastern Kazakhstan), *Postexallerix securis* gen. et sp. nov. (Lower Miocene of Mongolia), and *P. mustelidens* sp. nov. (Middle Miocene of Mongolia) are described. *E. manahan* is similar in size and dental structure to Late Oligocene *Metexallerix gaolanshanensis* Qiu et Gu, 1988 from China; therefore, the latter species is transferred to the genus *Exallerix*, and *Metexallerix* is regarded as a junior synonym of *Exallerix*. *“Metexallerix” junggarensis* Bi, 1999 from the Lower Miocene of China is considered to be the type species of *Synexallerix*. The genus *Synexallerix* is proposed to be very similar to the ancestor of Miocene North American *Brachyerix* and *Metechinus*. The genus *Postexallerix* comprises the latest and most specialized Asian Brachyericinae characterized by a very narrow and long trigonid of M_1 and by a strongly reduced M_2. Phylogenetic relationships and adaptations of the Brachyericinae are discussed.

INTRODUCTION

Short-faced hedgehogs (Brachyericinae) compose an extinct subfamily characterized by a short facial region of the skull, certain distinctive structural features of the auditory region, and reduced number of cheek teeth ($P^2/_{1-2}M^2/_2$). To date, four genera of the Brachyericinae have been described, i.e., *Brachyerix* and *Metechinus* from the Miocene of North America and *Exallerix* and *Metexallerix* from the Oligocene and Miocene of Asia (Matthew, 1929; Matthew and Mook, 1933; McKenna and Holton, 1967; Rich and Rich, 1971; Rich, 1981; Qiu and Gu, 1988; Gould, 1995; Lopatin, 1996; Bi, 1999).

The North American Brachyericinae include four species (Rich, 1981): *Brachyerix macrotis* Matthew, 1933 from the Early Miocene, Hemingfordian; *B. incertis* (Matthew, 1924) from the Early–Middle Miocene, Hemingfordian and Barstovian; *Metechinus amplior* Rich, 1981 from the Middle–Late Miocene, Barstovian and Clarendonian; and *M. nevadensis* Matthew, 1929 from the Late Miocene, Clarendonian. The cranial structure, skull base, and auditory region of these forms were examined in detail (Matthew, 1929; Matthew and Mook, 1933; Rich and Rich, 1971; Rich, 1981; Gould, 1995).

The Asian Brachyericinae were found in Mongolia, China, and Kazakhstan (McKenna and Holton, 1967; Qiu and Gu, 1988; Lopatin, 1996; Bi, 1999). Early Oligocene *Exallerix hsandagolensis* McKenna et Holton, 1967 from Mongolia has two lower premolars, P_3 and P_4 (McKenna and Holton, 1967); this distinguishes it from the other Brachyericinae characterized by the presence of only one lower premolar, P_4. Early Miocene *E. efialtes* Lopatin, 1996 from Kazakhstan probably has P_3, the presence of which is evidenced by the size and shape of the alveolus located anterior to P_4 (Lopatin, 1996). Either species is represented by fragmentary lower jaws. M_1 is extended, P_4 and M_2 are substantially reduced, and the base of the labial surface of the lower teeth is covered by small enamel tubercles.

The type species of the genus *Metexallerix*, *M. gaolanshanensis* Qiu et Gu, 1988 from the Late Oligocene Lanzhou Fauna (China), was described on the basis of a skull and a mandible (Qiu and Gu, 1988). Regarding the structure of the lower jaw and teeth, *M. gaolanshanensis* is closely similar to *Exallerix*; however, it is distinguished by its large size and the absence of P_3 and enamel ornament on P_4–M_2. It should be noted that the differences in size and the extent to which enamel tubercles are developed should not be taken as characters of generic rank; at the same time, the reduction of P_3 shows the evolutionary advantage of Late Oligocene *M. gaolanshanensis* as compared to Early Oligocene *E. hsandagolensis*. Therefore, the generic rank of *Metexallerix* is in doubt and we propose to assign *M. gaolanshanensis* to the genus *Exallerix*.

“Metexallerix” junggarensis Bi, 1999 recently described on the basis of an incomplete skull and fragmentary jaws from the Lower Miocene of China (Bi, 1999) was referred to as the genus *Metexallerix* because of the absence of P_3. In our opinion, this form from the Junggar Basin should be assigned to a new genus on the basis of the structure of P^3–M^2, M_1, and M_2.

In the present study, the Brachyericinae from the Lower Miocene of eastern Kazakhstan and Lower Oligocene and Lower–Middle Miocene of Mongolia are described. The specimen from Kazakhstan was found in the Ayaguz locality (collected by N.S. Shevyreva and V.M. Chkhikvadze in 1980), the fauna of which was earlier dated as MN3/MN4 (Zazhigin and Lopatin, 2000). The material from the Lower Oligocene of Mongolia was collected in the Shand-Gol Formation of Tatal-Gol (collected by the Mongolian Expedition of the PIN headed by I.A. Efremov in 1948 and 1949) and Elste-Turamne-Ar (or Els-Turamny-Ar, a locality recently discovered in the Valley of Lakes, collected by E.K. Sytchevskaya and E.L. Dmitrieva in 1995). The specimens from the Miocene of Mongolia were found in the Lower Miocene Loo Formation of the Ulan-Tologoi locality (Valley of Lakes, collected by V.S. Zazhigin and V.I. Zhegallo in 1972) and in the Middle Miocene Lower Oshin Subformation of Naran-Bulak (Depression of the Large Lakes, collected by Zhegallo in 1979) and Sharga 2 (Shargain Gobi, collected by Zazhigin in 1978). The Ulan-Tologoi Fauna is dated as MN4 and the Naran-Bulak and Sharga 2 faunas are dated as MN7+8 (Zazhigin and Lopatin, 2000).

We also used for comparison the Brachyericinae housed at the PIN, i.e., *E. hsandagolensis* (Mongolia, Tatal-Gol locality; Lower Oligocene, Shand-Gol Formation; collected by of the Mongolian Expedition of the PIN in 1948 and 1949) and *E. efialtes* (Kazakhstan, Altynshokysu locality; Lower Miocene, Aral Formation, collected by A.V. Lopatin in 1992).

We used the terminology and the technique for tooth measurements proposed by Rich (1981). Rich designated the lower incisors of the Brachyericinae as I_1 and I_2. The lower premolar between the canine and P_4 of *Exallerix* is usually identified as P_3 (McKenna and Holton, 1967; Rich, 1981; Gould, 1995). Bi (1999) designated the lower antemolars of the Brachyericinae as I_2, I_3, C_1, P_2, and P_4 by analogy with the Recent Erinaceinae (Frost *et al.*, 1991). We adhere to the modification proposed by Gould (1995), i.e., I_2, I_3, C_1, P_3, and P_4.

The following abbreviations are used in the present study: (GIN) Geological Institute of the Russian Academy of Sciences and (PIN) Paleontological Institute of the Russian Academy of Sciences.

SYSTEMATIC PALEONTOLOGY

Family Erinaceidae Fischer, 1817

Subfamily Brachyericinae Butler, 1948

Genus *Exallerix* McKenna et Holton, 1967

Exallerix: McKenna and Holton, 1967, p. 3.

Metexallerix: Qiu and Gu, 1988, p. 199.

Type species. *E. hsandagolensis* McKenna et Holton, 1967; Lower Oligocene of Mongolia.

Diagnosis. Medium-sized and large Brachyericinae with dental formula $I^3/_2C^1/_1P^2/_{2-1}M^2/_2$. Ventrally, lateral edges of the skull base almost parallel; mastoid and paroccipital processes large; tympanic bullae relatively small and widely spaced; and jugular and stylomastoid foramina isolated from each other by high crest. Posterior and lateral surfaces of zygomatic process of squamosal outlined by ridge. Ventral ends of interparietal projecting anteriorly between parietals and mastoids. Protocone of P^3 weak. P^4 and M^1 lacking parastyle. M^2 lacking metastyle [characters of skull and upper teeth given on basis of *E. gaolanshanensis*, see Qiu and Gu (1988)]. Paraconid of P_4 rudimentary or absent, metaconid absent. On labial surface of lower teeth, sculpturing composed of enamel tubercles developed to variable degree. Ratio of length to width of trigonid on M_1 approximately 125–145%. Talonid of M_1 equal in width to, or slightly narrower than trigonid and approximately half (43–58%) as long as trigonid. Talonid basin deep and closed lingually. Entoconid relatively high and conical. Hypoconid and entoconid connected by postcristid. M_2 reduced (about 50% as long as M_1) and has short double-cuspid talonid. Masseteric crest of lower jaw extremely stout. Angular process large and finlike.

Composition. *E. hsandagolensis* McKenna et Holton, 1967; *E. manahan* sp. nov., Lower Oligocene of Mongolia; *E. gaolanshanensis* (Qiu et Gu, 1988), Upper Oligocene of northern China; and *E. efialtes* Lopatin, 1996, Lower Miocene of western Kazakhstan.

Comparison. *Exallerix* differs from *Brachyerix* Matthew, 1933 and *Metechinus* Matthew, 1929 by the presence of P_3 (in certain species), smaller P_4 and M_2, a longer and narrower trigonid of M_1, the absence of parastyle on M^1, a more massive masseteric crest, and a large finlike angular process of the lower jaw. In the cranial structure, it differs from *Brachyerix* by less flattened and widely spaced tympanic bullae and by the presence of a high crest isolating the jugular and stylomastoid foramina; it differs from *Metechinus* by the shape of the skull base and the structure of the posterior region of the zygomatic arch and the ventral projections of the interparietal.

Exallerix manahan Lopatin et Zazhigin, sp. nov.

Etymology. From the Mongolian *Manakhan* (name of a mythological giant, deity of hunting).

Holotype. PIN, no. 475/3029, fragment of right dentary with M_1–M_2, and alveoli of I_2 and P_4; Mongolia, Tatal-Gol locality; Lower Oligocene, Shand-Gol Formation.

Description (Figs. 1e–1h, 2c, 2d). The largest form of the Brachyericinae. The horizontal ramus of the lower jaw is massive, short, and high. The symphysis extends posteriorly to the anterior part of M_1 and forms a small posteroventral projection, the mental tubercle. The mental foramen is large, funnel-shaped, and located on a level with the anterior root of M_1. A stout lower masseteric crest crosses the labial surface of the horizontal ramus and ascends to the mental foramen. It bounds a very deep and relatively large depression

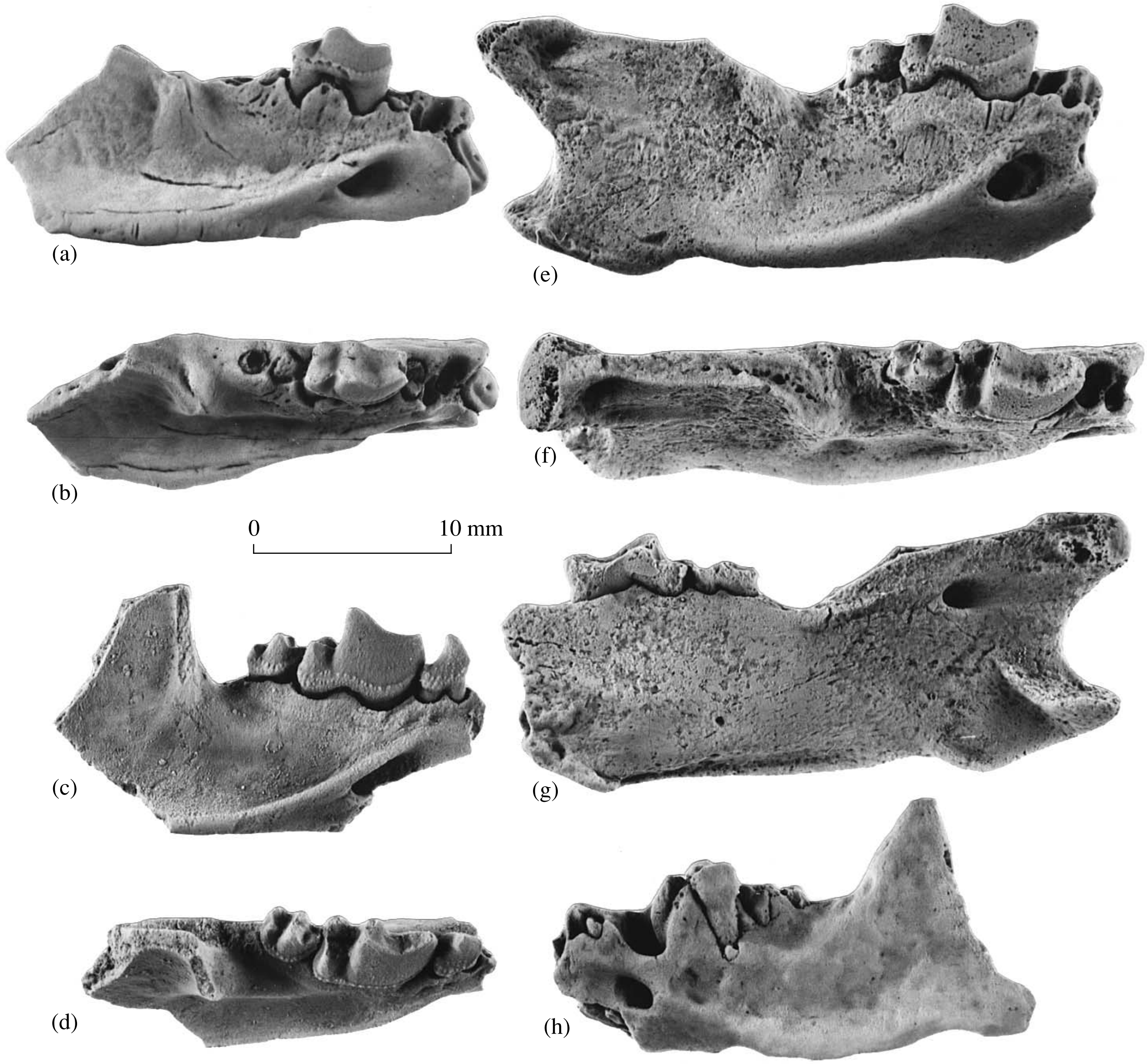

Fig. 1. Lower jaws of *Exallerix*: (a, b) *E. hsandagolensis* McKenna et Holton, 1967, specimen PIN, no. 475/3037, fragment of right dentary with M_1: (a) labial and (b) occlusal views; Mongolia, Tatal-Gol locality; Lower Oligocene, Shand-Gol Formation; (c, d) *E. efialtes* Lopatin, 1996, holotype PIN, no. 4516/1, fragment of right dentary with P_4–M_2: (c) labial and (d) occlusal views; Kazakhstan, North Aral Region, Altynshokysu locality; Lower Miocene, Aral Formation; (e–h) *E. manahan* sp. nov.: (e–g) holotype PIN, no. 475/3029, fragment of right dentary with M_1 and M_2: (e) labial, (f) occlusal, and (g) lingual views; Mongolia, Tatal-Gol locality; Lower Oligocene, Shand-Gol Formation; (h) specimen PIN, no. 4597/16, fragment of left dentary with damaged M_1 and M_2 and alveoli of P_3 and P_4, labial view; Mongolia, Elste-Turamne-Ar locality; Lower Oligocene, Shand-Gol Formation.

providing the attachment area for the portion of the masticatory muscle that is displaced far anteriorly (musculus masseter). A clearly outlined area for the anterior belly of the digastric muscle extends along the lingual side of the lower edge of the dentary from the mental tubercle to the base of the angular process.

The ascending ramus is relatively long. The anterior edge of the coronoid process is positioned at an angle of about 120° to the horizontal ramus. The distance between the base of the coronoid process and the posterior edge of M_2 is equal to the length of this tooth. At the base of the coronoid process, the medial crest (for the attachment of a portion of the temporal muscle) is weak. The masseteric fossa is relatively shallow. The mandibular foramen is large and located in the middle of the ascending ramus on a level with the tooth row.

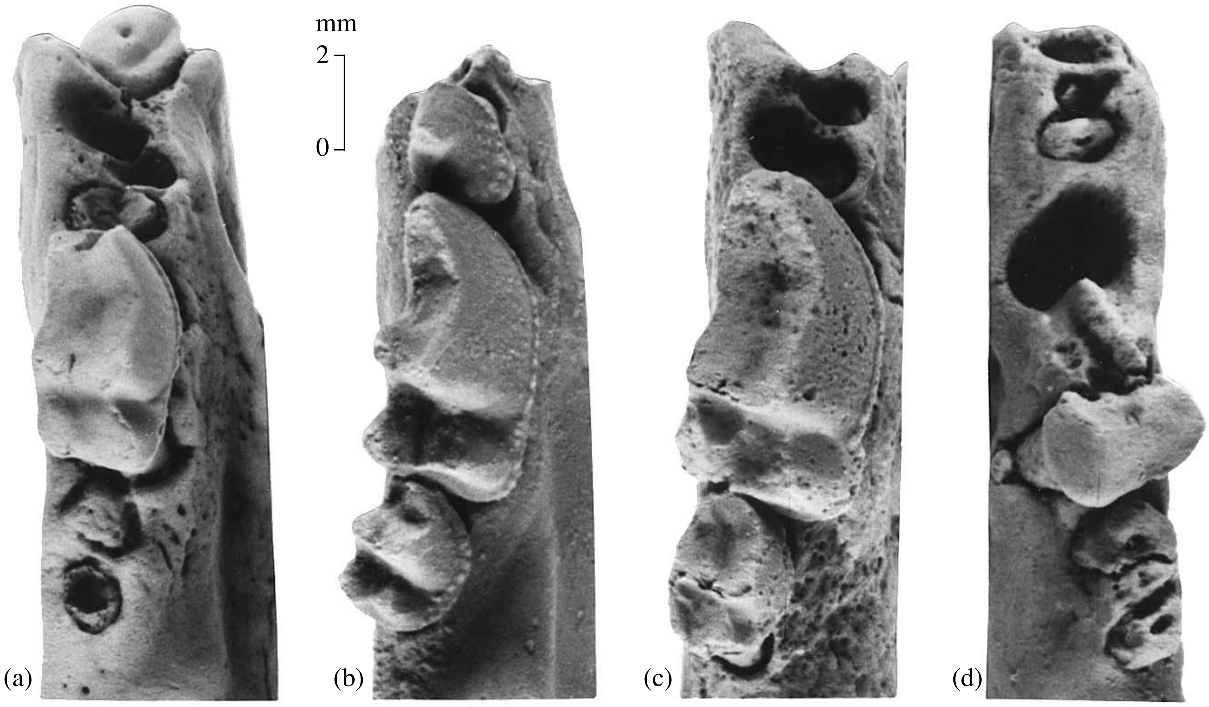

Fig. 2. Tooth rows of *Exallerix*: (a) *E. hsandagolensis* McKenna et Holton, 1967, specimen PIN, no. 475/3037, fragmentary I_2, M_1, and alveoli of P_3, P_4, and M_2; Mongolia, Tatal-Gol locality; Lower Oligocene, Shand-Gol Formation; (b) *E. efialtes* Lopatin, 1996, holotype PIN, no. 4516/1, P_4–M_2 and alveolus of P_3; Kazakhstan, North Aral Region, Altynshokysu locality; Lower Miocene, Aral Formation; (c, d) *E. manahan* sp. nov.: (c) holotype PIN, no. 475/3029, M_1, M_2, and alveoli of P_4; Mongolia, Tatal-Gol locality; Lower Oligocene, Shand-Gol Formation; (d) specimen PIN, no. 4597/16, damaged M_1 and M_2 and alveoli of P_3 and P_4; Mongolia, Elste-Turamne-Ar locality; Lower Oligocene, Shand-Gol Formation.

The articular process is short; on the labial side, there is a well-pronounced fossa for the attachment of a portion of the masseter. The condyle is broad and located on a level with the occlusal surface of the lower molars. The head of the condyle is only partially detached, the articular surface covers a sector of about 180°. The notch between the articular and angular processes is deep. The angular process is large and finlike; anteriorly and posteriorly, its lingual surface is limited by high and sharp crests forming the edges of a deep fossa for the attachment of the internal pterygoid muscle. The posterior surface of the angular process is divided into two parts by a weak median crest.

Anterior to the molars, the holotype retains two alveoli containing fragmentary roots of P_4; the anterior alveolus is displaced labially and half as large as the posterior alveolus. In specimen PIN, no. 4597/16, there is no normally developed alveolus for single-rooted P_3 anterior to the alveoli of P_4; however, this position is occupied by a small fossa (Figs. 1h, 2d). This fossa is deepened in the labial part occupied by a small foramen that is probably connected to the mandibular canal. Thus, one can propose that P_3 was substantially reduced and had a very short root.

M_1 is large and massive. The trigonid is twice as long as the talonid. The paraconid is low and strongly projects anteriorly. As the tooth is worn, an extensive weakly concave area is formed on the trigonid; it is bounded labially by the paralophid and, posteriorly, by the protoconid and metaconid fused at the base. The protoconid is substantially more massive and higher than the metaconid. The posterior wall of the trigonid is almost vertical and flat. The talonid basin is closed lingually, since the anterior projection of the entoconid is connected to the posterolingual corner of the metaconid base. The hypoconid strongly projects posterolabially. The cristid oblique is poorly pronounced and connected to the middle of the base of the posterior wall of the protoconid. The entoconid is massive and somewhat extended longitudinally. There is a weak labial cingulid formed by a longitudinal row of small fused enamel tubercles.

M_2 is reduced (approximately half as long as M_1), short, low, and oval. The paraconid is broad and semicircular. The paralophid is weakly curved and short. The trigonid basin is extensive, shallow, and widely open lingually. The protoconid and metaconid fused. The protoconid is somewhat higher and more massive than the metaconid. The protocristid is short. The talonid is substantially shorter than the trigonid. The talonid basin is shallow; lingually, it is closed by a very small and low ridgelike entoconid. The hypoconid is massive. The cristid oblique is short.

Measurements, mm. Holotype: length of M_1–M_2, 9.7; total length of M_1, 6.9; trigonid length, 4.6; lingual length of talonid, 1.6; labial length of talonid, 2.3; trigonid width, 3.6; and talonid width, 3.6; total length of M_2, 3.4; trigonid length, 2.2; talonid length, 1.2; trigonid width, 2.4; and talonid width, 2.1; labial depth of the lower jaw under M_1, 9.0, and under M_2, 8.8.

Specimen PIN, no. 4597/16: length of M_1–M_2 along the alveoli, 10.0; length of M_1 along the alveoli, ca. 6.5; talonid width, 3.1; length of M_2 along the base, ca. 3.3; labial depth of the lower jaw under M_1, 8.3, and under M_2, 7.5.

Comparison. The new species is substantially larger than *E. hsandagolensis* and *E. efialtes* (Figs. 1, 2) and a little larger than *E. gaolanshanensis*. In addition, it differs from *E. hsandagolensis* by a more reduced P_3, weaker enamel relief on the labial surface of M_1 and M_2, and shorter M_2; it differs from *E. gaolanshanensis* by the presence of enamel relief on the lower molars and from *E. efialtes* by a wider trigonid and relatively larger talonid of M_1, more reduced M_2 (Tables 1, 2), more gently sloping anterior edge of the coronoid process of the lower jaw, and a weaker medial crest at the base of this process.

Material. In addition to the holotype, a fragmentary left dentary with damaged M_1 and M_2, the base of the anterior incisor, and the alveoli of P_4 from the Elste-Turamne-Ar locality.

Genus *Synexallerix* Lopatin et Zazhigin, gen. nov.

Etymology. From the Greek *syn* (together) and the generic name *Exallerix*.

Type species. *Metexallerix junggarensis* Bi, 1999; Lower Miocene of China.

Diagnosis. Medium-sized Brachyericinae with dental formula: $I^3/_2C^1/_1P^2/_1M^2/_2$. P^3 with clear protocone. P^4 and M^1 with parastyle. M^2 with metastyle (characters of upper teeth given on basis of only type species, see Bi, 1999). Paraconid of P_4 rudimentary or absent, metaconid absent. Base of labial surface of crowns of P_4, M_1, and M_2 with longitudinal row of enamel tubercles occasionally fused to form continuous cingulid. Ratio of length to width of trigonid of M_1 about 120–150%. Talonid of M_1 greater than or equal to trigonid in width and more than half (50–75%) as long as trigonid. Talonid basin deep and closed lingually. Entoconid relatively high, conical, and extended. Hypoconid and entoconid connected by postcristid. M_2 weakly reduced (about 65% as long as M_1) and having well-developed talonid with two cusps. Masseteric crest of lower jaw relatively weak.

Composition. *S. junggarensis* (Bi, 1999), Lower Miocene of China; *S. otus* sp. nov., Lower Miocene of eastern Kazakhstan.

Comparison. The new genus differs from *Exallerix* by a better developed protocone of P^3, the presence of the parastyle on P^4 and M^1 and the metastyle on M^2, the ratio of measurements of the trigonid and talonid of M_1, extended entoconid of M_1, relatively large M_2 with a well-developed large talonid, and by a weaker masseteric crest of the lower jaw. The differences from *Brachyerix* and *Metechinus* consist in the presence of a well-developed protocone on P^3, parastyle on P^4 and M^1, and metastyle on M^2; stronger reduced P_4; the presence of enamel tubercles on P_4–M_2; and in a better developed masseteric crest. In addition, *Synexallerix* differs from *Metechinus* by a relatively longer and narrower trigonid of M_1.

Remarks. Bi (1999) indicated that, in *"Metexallerix" junggarensis*, M^1 is larger than P^4, whereas in *"M". gaolanshanensis*, P^4 is larger than M^1. In actual fact, M^1 is more massive than P^4 in all Brachyericinae; however, the first is shorter than the second, as measured along the labial side. Therefore, we excluded this character from the distinctive features of *Synexallerix* and *Exallerix*.

We believe that two large M_1 described by Ziegler (1990, p. 31, pl. 5, figs. 3, 5) as *"?Plesiosorex* n. sp." and P^4 and "M^2" (in actual fact, M^1) referred to as *"?Amphechinus"* sp. 1 and sp. 2 (Ziegler, 1990, p. 25, pl. 3, figs. 9, 11) from the Early Miocene Petersbuch 2 locality (Germany, MN4a) should be assigned to the Brachyericinae and most likely belong to *Synexallerix* sp. Judging from the figures of M_1, the form from Petersbuch 2 is similar to *S. junggarensis* and *S. otus* in the ratio of the trigonid to talonid, measurements, almost identical structure, and even a weak enamel ornament on the labial surface; however, it differs by the completely closed talonid basin (Ziegler, 1990, pl. 5, fig. 3). In the structure of P^4 and M^1, *Synexallerix* sp. from Germany closely resembles *S. junggarensis* (Bi, 1999). Thus, the Early Miocene range of the genus *Synexallerix* included Europe.

To date, *Synexallerix* sp. from Petersbuch 2 is the only evidence of the existence of short-faced hedgehogs in Europe. Earlier, some researchers (McKenna and Holton, 1967; Rich and Rich, 1971; Gureev, 1979) assigned Early Miocene *Dimylechinus bernoullii* Hürzeler, 1944 from France to the Brachyericinae on the basis of the absence of $M^3/_3$. However, the structure of the upper and lower cheek teeth and the lower jaw indicate that the genus *Dimylechinus* belongs to the tribe Amphechinini of the subfamily Erinaceinae (Hürzeler, 1944; Rich, 1981; Gould, 1995).

Synexallerix otus Lopatin et Zazhigin, sp. nov.

Etymology. From the Greek *Otus* (name of a mythological giant).

Holotype. PIN, no. 4051/150, fragment of right dentary with M_1; eastern Kazakhstan, Semipalatinsk Region, Ayaguz locality; Lower Miocene, green sandy clays.

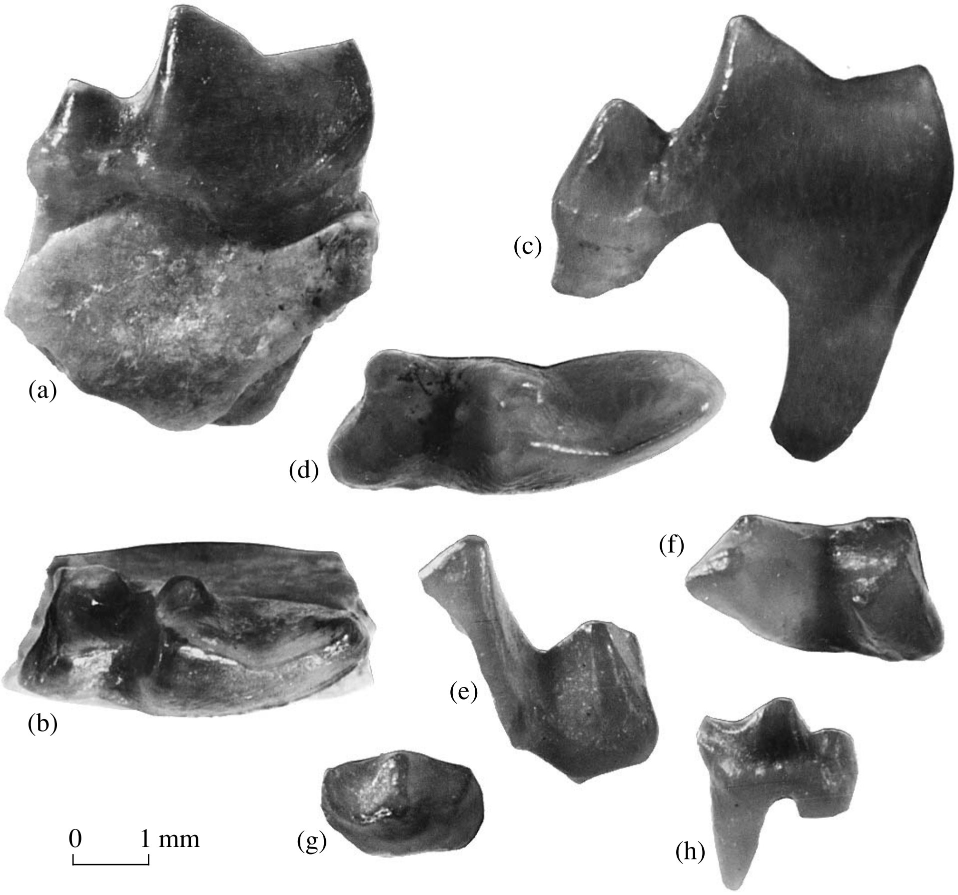

Fig. 3. New Miocene Brachyericinae: (a, b) *Synexallerix otus* sp. nov., holotype PIN, no. 4051/150, fragment of right dentary with M_1: (a) labial and (b) occlusal views; eastern Kazakhstan, Ayaguz locality, Lower Miocene; (c, d) *Postexallerix securis* sp. nov., holotype GIN, no. 960/28, right M_1: (c) labial and (d) occlusal views; Mongolia, Ulan-Tologoi locality, Lower Miocene; (e–h) *P. mustelidens* sp. nov.: (e, f) holotype GIN, no. 1105/9, left M_1: (e) labial and (f) occlusal views; and (g, h) GIN, no. 1105/10, left M_2: (g) occlusal and (h) labial views; Mongolia, Naran-Bulak locality, Middle Miocene.

Description (Figs. 3a, 3b, 4). M_1 is relatively narrow and almost straight, with a long trigonid and relatively short talonid, the talonid is approximately half as long as the trigonid. The paraconid strongly projects anteriorly, the paralophid is stout, bladelike, and weakly curved labially. The blade of the paraconid is somewhat longer than the blade of the protoconid; in the vertical plane, they are positioned at an angle of about 115°–120°. The trigonid basin is reduced and looks like a small fold between the metaconid and the protoconid. The protoconid is somewhat higher than the paraconid. The metaconid is relatively massive, substantially lower than the protoconid, slightly displaced posteriorly with reference to the protoconid, and fused with the latter for two-thirds of the height. The apices of the metaconid and protoconid are separated from each other by a weak notch. The posterior wall of the trigonid is almost vertical and flat.

The talonid basin is closed; however, a deep talonid notch is present. The hypoconid strongly projects posterolabially. The cristid oblique is connected to the middle of the base of the posterior wall of the protoconid, and its anterior part encroaches somewhat on the protoconid. The entoconid is massive and longitudinally extended. The entocristid looks like a thin crest on the anterior slope of the entoconid. In the region of the talonid notch, the entocristid is connected to a very small metastylid crest. The postcristid is connected to the posterior base of the entoconid; in the central part, it has a weak expansion. No clear postcingulid is observed; however, the posterolabial side of the crown has a weak eminence resembling this element in a similarly extended outline. The labial cingulid is complete and well developed; at the level of the paralophid and talonid, it is wide. Its surface is rough; at the level of the protoconid and hypoflexid, the relief is composed of small and closely spaced tubercles. On the labial surface of the trigonid, the enamel is weakly wrinkled.

Measurements, mm. Holotype: total length, 4.55; trigonid length, 3.0; labial length of the talonid, 1.55; lingual length of the talonid, 1.4; trigonid width, 2.1; talonid width, 2.0; paraconid height, 2.5; proto-

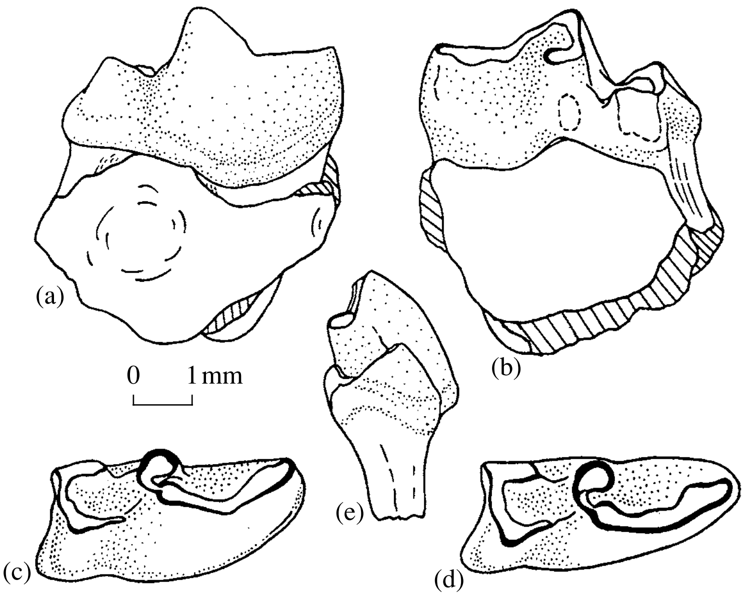

Fig. 4. *Synexallerix otus* sp. nov., holotype PIN, no. 4051/150, fragment of right dentary with M_1: (a) labial, (b) lingual, (c) occlusal, (d) dorsolingual, and (e) rear views.

conid height, 2.8 (from the apex to the base of the labial side of the trigonid); and hypoconid height, 1.5. The ratio of length to height of the trigonid, 107%.

Comparison. The new species is substantially smaller than *S. junggarensis* from China and differs from the latter by a narrower M_1, approximately equal width of the trigonid and talonid of M_1, and the presence of a continuous labial cingulid. *S. otus* differs from *Synexallerix* sp. from Germany by smaller measurements, only partially closed talonid basin, and the presence of a clear labial cingulid on M_1.

Material. Holotype.

Genus *Postexallerix* Lopatin et Zazhigin, gen. nov.

Etymology. From the Latin *post* (after) and the generic name *Exallerix*.

Type species. *P. securis* sp. nov.

Diagnosis. Medium-sized Brachyericinae with tentative dental formula $I^{3?}/_{2}C^{1}/_{1}P^{2?}/_{1?}M^{2}/_{2}$. Protocone of M^1 compressed longitudinally and strongly projecting lingually, hypocone very small, and precingulid well developed and stout. Sculpture composed of enamel tubercles on labial surface of lower teeth reduced. M_1 with very narrow and long trigonid (ratio of length to width more than 190%). Metaconid strongly reduced. Talonid somewhat wider than trigonid and less than half as long as trigonid (approximately 45%). Talonid basin small and open lingually. Entoconid low and ridgelike. Hypoconid and entoconid isolated from each other by well-pronounced posterior fold. Posterior arm of hypoconid lacking contact with entoconid. M_2 strongly reduced (approximately 40% as long as M_1), with very short unicuspid talonid. Masseteric crest of lower jaw weak.

Composition. *P. securis* sp. nov., Lower Miocene of Mongolia; *P. mustelidens* sp. nov., Middle Miocene of Mongolia.

Comparison. The new genus differs from the other genera of the Brachyericinae by a substantially narrower and longer trigonid of M_1 with reduced metaconid, a strongly reduced M_2 with unicuspid talonid, and by the unique structure of the talonid of M_1 and the lingual part of M^1.

Remarks. The degree to which the trigonid is elongated and narrowed and the talonid is shortened on M_1 of the Brachyericinae is estimated by the indices given in Table 1. The ratios between the lengths of M_1 and M_2 are given in Table 2.

Postexallerix securis Lopatin et Zazhigin, sp. nov.

Etymology. From the Latin *securis* (ax, poleax).

Holotype. GIN, no. 960/28, isolated right M_1; Mongolia, Ulan-Tologoi locality; Lower Miocene, Loo Formation.

Description (Figs. 3c, 3d, 5). M^1 is represented by the lingual part only. The paracone is in a more labial position than the metacone. The apices of the protocone and hypocone fall into almost the same longitudinal line; however, the base of the protocone substantially projects lingually. The anterolingual and posterolingual walls of the protocone are straight; therefore, the lingual projection of the protocone is acute-angled in section. The anterolabial corner of the protocone is connected to the anterolingual side of the base

Table 1. The main parameters of M_1 in the Brachyericinae: (L) total length, (L_{TL}) talonid length, (L_{TR}) trigonid length, and (W_{TR}) trigonid width

Species	Data	L_{TR}/L	L/W_{TR}	L_{TR}/W_{TR}	L_{TL}/L_{TR}
Exallerix hsandagolensis	McKenna and Holton, 1967	–	1.92	1.26	0.58
Exallerix efialtes	PIN, no. 4516/1	0.7	2.04	1.43	0.425
Exallerix manahan	PIN, no. 475/3029	0.67	1.92	1.28	0.5
Exallerix gaolanshanensis	Qiu and Gu, 1988	–	1.94	1.36	0.52
Synexallerix junggarensis	Bi, 1999	–	2.05	1.19–1.33	0.57–0.74
Synexallerix otus	PIN, no. 4051/150	0.66	2.17	1.43	0.52
Synexallerix sp.	Ziegler, 1990	0.625	1.96–2.42	1.22–1.51	0.60–0.63
Postexallerix securis	GIN, no. 960/28	0.69	2.83	1.94	0.46
	GIN, no. 960/32	~0.7	~2.84	2.0	~0.42
Brachyerix macrotis	Rich and Rich, 1971	0.58–0.62	1.79–2.12	1.05–1.28	0.61–0.73
	Rich, 1981	0.59–0.64	1.95–2.29	1.16–1.47	0.56–0.68
Brachyerix incertis	Rich and Rich, 1971	0.64	2.07	1.33	0.55
	Rich, 1981	0.55–0.64	1.94–2.64	1.23–1.45	0.55–0.81
Metechinus amplior	Rich, 1981	0.53–0.62	1.66–2.0	0.87–1.23	0.62–0.9
Metechinus nevadensis	Rich, 1981	0.51–0.52	1.72–1.82	0.9–0.93	0.92–0.96

Table 2. The ratios of lengths of P_4, M_1, and M_2 in the Brachyericinae (L_{P4}, L_{M1}, and L_{M2}, respectively)

Species	Data	L_{P4}/L_{M1}	L_{M2}/L_{M1}
Exallerix hsandagolensis	McKenna and Holton, 1967	0.5	–
Exallerix efialtes	PIN, no. 4516/1	0.44	0.53
Exallerix manahan	PIN, no. 475/3029	–	0.49
Exallerix gaolanshanensis	Qiu and Gu, 1988	0.38	0.54
Synexallerix junggarensis	Bi, 1999	0.37–0.41	0.64–0.68
Postexallerix mustelidens	GIN, nos. 1105/9 and 10	–	~0.45 (?)
Brachyerix macrotis	Rich and Rich, 1971; Rich, 1981	0.375–0.53	0.59–0.71
Brachyerix incertis	Rich and Rich, 1971; Rich, 1981	0.48	0.64–0.69
Metechinus amplior	Rich, 1981	0.39–0.43	0.67–0.75
Metechinus nevadensis	Rich, 1981	0.4	0.72

of the paracone by a well-developed preprotocrista and a stout and high preparaconule crest. The postprotocrista extends posterolabially; at the middle of the tooth, it bifurcates; the posterolingual arm is connected to the hypocone, and the higher labial arm terminates at the anterolingual corner of the base of the metacone. The metaconule is undeveloped. The base of the anterior wall of the crown is bordered by a well-developed precingulum extending from the level of the preparaconule crest to the level of the center of the protocone. The tooth has one large lingual root with a clear groove on the lingual side, which marks the boundary between the fused anterior and posterior roots; the anterior segment is twice as large as the posterior segment.

The horizontal ramus of the lower jaw is relatively low. The base of the anterior edge of the coronoid process is inclined at an angle of approximately 125° to the horizontal ramus. Posterior to the alveoli of M_2, the medial projection of the bone has a distinctly outlined triangular area for the attachment of a large portion of the temporal muscle. The masseteric fossa is deep and clearly outlined. The masseteric crest is poorly pronounced, weak, and extends anteriorly to the level of the anterior root of M_2. The mandibular foramen is large and located only slightly below the level of the alveolar edge of the horizontal ramus.

The lower teeth are represented by I_3, C_1, and M_1. The incisor and canine are extended and similar in shape, the occlusal surface is rounded triangular. The incisor is somewhat more massive than the canine and has a higher crown. The posterior edge of the I_3 crown is straight. A relatively sharp crest extends from the main cusp to the posterior edge of the occlusal surface. The crest slightly deviates from the midline and weakly

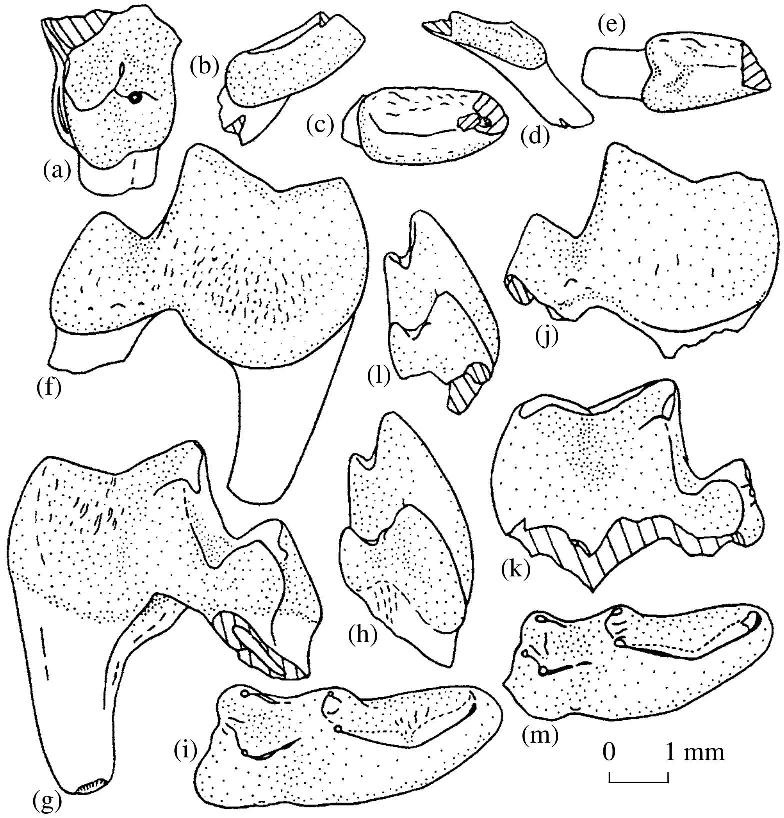

Fig. 5. *Postexallerix securis* sp. nov.: (a) GIN, no. 960/29, fragment of left M^1; (b, c) GIN, no. 960/30, right I_3: (b) labial and (c) occlusal view; (d, e) GIN, no. 960/31, left C_1: (d) labial and (e) occlusal views; (f–i) holotype GIN, no. 960/28, right M_1: (f) labial, (g) lingual, (h) rear, and (i) occlusal views; (j–m) GIN, no. 960/32, right M_1: (j) labial, (k) lingual, (l) rear, and (m) occlusal views.

curves labially. The enamel on the lingual and labial sides of I_3 is strongly wrinkled. The posterior edge of the canine crown has a small groove. The longitudinal crest is weak and displaced labially; at the posterior edge, it bifurcates. The enamel is wrinkled to a lesser extent than that of I_3.

M_1 is very narrow, with a strongly extended trigonid and a short and reduced talonid. The paralophid is stout, bladelike, and weakly curved labially. The blades of the paraconid and protoconid are equal in length; in the vertical plane, they are positioned at an angle of approximately 130° to each other. The trigonid basin is reduced; as a result, it is a very small valley between the metaconid and the protoconid. The protoconid and paraconid are almost equal in height. The metaconid is small, low, and fused with the protoconid along almost the entire height; however, it has a separate conical apex isolated from the apex of the protoconid by the above valley and a relatively deep notch in the posterior wall of the trigonid. The posterior wall of the trigonid is almost vertical. The talonid basin is open lingually (the entocristid is weak and terminates short of reaching the wall of the trigonid) and posteriorly (there is a deep posterior fold isolating the entoconid and the hypoconid from each other). The hypoconid strongly projects posterolabially. The cristid oblique is connected to the middle of the base of the posterior wall of the protoconid and encroaches somewhat on the protoconid. The entoconid is low, ridgelike, and weakly extended longitudinally in the anterior part. The talonid notch and the metastylid crest are absent. The posterior arm of the hypoconid is positioned posterolingually; it reaches the posterior edge of the occlusal surface somewhat labial to the exit from the posterior fold; at the end, it forms a small and low cuspule located below the surface of the talonid basin. Postcingulid and labial cingulid are absent. The enamel on the labial surface of the crown is only slightly wrinkled, enamel tubercles are not numerous (two or three) and present only on a level with the hypoflexid. In the upper part of the lingual surface of the paralophid, the enamel is strongly wrinkled.

Judging from the measurements of the M_2 alveoli, this tooth was less than half as long as M_1.

Measurements, mm. Holotype: total length, 5.1; trigonid length, 3.5; labial length of the talonid, 1.6; lingual length of the talonid, 1.25; trigonid width, 1.8; talonid width, 1.95; paraconid height, 3.0; protoconid height, 3.5; and hypoconid height, 2.0. The ratio of length to height of the trigonid, 100%.

M_1, specimen GIN, no. 960/32: total length, ca. 4.55; trigonid length, 3.2; labial length of the talonid, ca. 1.35;

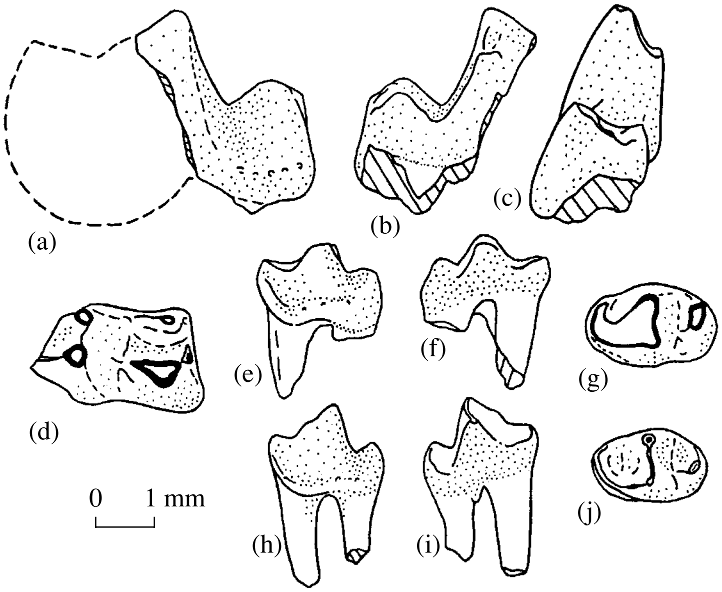

Fig. 6. *Postexallerix mustelidens* sp. nov. from the Middle Miocene of Mongolia: (a–d) holotype GIN, no. 1105/9, left M_1 from the Naran-Bulak locality: (a) labial, (b) lingual, (c) rear, and (d) occlusal views; (e–g) GIN, no. 1105/10, left M_2 from the Sharga 2 locality: (e) labial, (f) lingual, and (g) occlusal views; (h–j) GIN, no. 959/1138, left M_2: (h) labial, (i) lingual, and (j) occlusal views.

lingual length of the talonid, 1.1; trigonid width, 1.6; talonid width, 1.65; paraconid height, 2.6; and protoconid height, 3.1. The ratio of length to height of the trigonid, 103%.

Length of the lingual part of M^1 (specimen GIN, no. 960/29), 2.05. Width of I_3 (specimen GIN, no. 960/30), 1.3; and C_1 (specimen GIN, no. 960/31), 1.3. Length of M_2 along the alveoli (specimen GIN, no. 960/33), 2.2. Dentary depth under M_2 (specimen GIN, no. 960/33), 3.3.

Remarks. It is impossible to homologize a small cusp located on the talonid of M_1 posterolingual to the hypoconid with the hypoconulid, since it is nonconical (looks like a thickening on the posterior arm of the hypoconid) and is most likely formed by rudimentary postcristid and postcingulid.

Material. In addition to the holotype, fragmentary M^1, I_3, and C_1; almost complete M_1; and a fragment of the lower jaw without teeth from the type locality.

Postexallerix mustelidens Lopatin et Zazhigin, sp. nov.

Etymology. From the generic name *Mustela* and the Latin *dens* (tooth).

Holotype. GIN, no. 1105/9, isolated left M_1; Mongolia, Naran-Bulak locality; Middle Miocene, Oshin Formation, Lower Subformation.

Description (Figs. 3e–3h, 6). M_1 is narrow and has a short talonid. The paralophid is high. The trigonid is very narrow. The trigonid basin is entirely reduced, even the valley between the metaconid and the protoconid is extremely poorly pronounced. The metaconid is very small, low, and fused with the protoconid; the apex is weakly detached. The posterior wall of the trigonid is almost vertical. The talonid basin is open lingually, because the entocristid is strongly developed but terminates short of reaching the posterior wall of the metaconid; a broad talonid notch is present. Posteriorly, the talonid basin is open, the fold between the entoconid and the posterior arm of the hypoconid is relatively narrow. The hypoconid is high and strongly projects posterolabially. The posterior arm of the hypoconid has a thickening at the end. The cristid oblique is connected to the middle of the base of the posterior wall of the protoconid and ascends along the protoconid for approximately one-third of its height. The metastylid crest is weak. The entoconid is low, ridgelike, and strongly extended longitudinally in the anterior part to form the entocristid. A small supplementary cuspule adjoins the posterior base of the entoconid. The enamel tubercles are very small, scarcely visible, and widely spaced at the hypoconid level (three cusps are distinguishable). The enamel is almost smooth and lacks clear wrinkles.

M_2 is very small, low, and oval. The paraconid is wide, low, and semicircular in plan. The paralophid is short and weakly curved. The trigonid basin is extensive, shallow, and widely open lingually. The protoconid and metaconid have fused, only their apices remain free. The protoconid is somewhat higher and more massive than the metaconid. The protocristid is short. The talonid is substantially shorter than the trigonid and has only one cusp, the hypoconid. In the anterior part, the talonid is somewhat narrower than the trigonid; however, it is strongly narrowed posteriorly. The talonid basin is shallow and widely open lingually. The hypoconid is massive, conical, and connected to the base of the posterior wall of the protoconid by a short cristid oblique. A thin crest descending along the posterolingual wall of the hypoconid frames the posterolingual corner of the talonid basin. Under the paralophid, there is a weak precingulid. Small and widely spaced enamel tubercles (ranging in number from one to four) are located at the base of the protoconid and (or) under the hypoflexid.

Measurements, mm. Holotype: labial length of the talonid, 1.5; lingual length of the talonid, 1.3; trigonid width, 1.7; talonid width, 1.75; and hypoconid height, 2.0.

M_2, specimen GIN, no. 1105/10: total length, 2.15; trigonid length, 1.45; talonid length, 0.7; trigonid width, 1.2; talonid width, 1.1; paraconid height, 1.0; protoconid height, 1.4; and hypoconid height, 1.0.

M_2, specimen GIN, no. 959/1138: total length, 1.95; trigonid length, 1.3; talonid length, 0.65; trigonid width, 1.2; talonid width, 1.1; paraconid height, 1.0; protoconid height, 1.5; and hypoconid height, 0.9.

Comparison. *P. mustelidens* differs from *P. securis* by a more reduced metaconid and a better developed entocristid of M_1.

Remarks. M_1 is incompletely preserved; therefore, it is impossible to calculate exactly the ratio of the lengths of M_2 and M_1. On the assumption that the paralophid of M_1 of *P. mustelidens* is at least as long as that of *P. securis*, it may be thought that M_2 is approximately 45% as long as M_1.

Material. In addition to the holotype, M_2 from the type locality and M_2 from the Sharga 2 locality.

PHYLOGENETIC RELATIONSHIPS OF THE BRACHYERICINAE

The genus *Exallerix*, some members of which retain P_3, is the most primitive among the currently known Brachyericinae. The Chinese researchers Qiu and Gu (1988) and Bi (1999) believed that *Exallerix* was a direct ancestor of *"Metexallerix." "M." gaolanshanensis* was derived directly from *E. hsandagolensis* (Qiu and Gu, 1988) or through "the intermediate form," *"M". junggarensis* (Bi, 1999). The lower specialization of *"M". junggarensis* compared to *"M". gaolanshanensis* was interpreted as evidence of an earlier geological age (Bi, 1999; Qiu *et al.*, 1999); however, the composition of mammalian assemblages (Qiu and Gu, 1988; Bi, 2000; Ye *et al.*, 2000) indicated that the opposite situation occurred; i.e., *Exallerix gaolanshanensis* was a Late Oligocene form, whereas *Synexallerix junggarensis* existed in the Early Miocene. The North American genera were considered to descend from *"Metexallerix"* or from a common ancestor of *"Metexallerix"* and *Exallerix* (Bi, 1999).

New data show that phylogenetic relationships within the Brachyericinae are much more complex. The evolution of the genus *Exallerix* was not unidirectional. Early Miocene *E. efialtes*, which apparently retains P_3, compares well with Late Oligocene *E. gaolanshanensis* in the extent to which P_4 is reduced and is superior to the latter species in the specialization of M_1 (long paralophid and reduced metaconid) (Lopatin, 1999). This lineage probably evolved independently of the *E. gaolanshanensis* lineage. In Early Oligocene *E. manahan*, P_3 is rudimentary; the talonid of M_1 is short (Table 1); M_2 is strongly reduced (Table 2); and enamel tubercles on the labial surface of M_1 and M_2 are flat, weakly individualized, and form an extremely weak cingulid. On the basis of the above characters (and measurements), this form can be considered to be an early member of the *E. gaolanshanensis* lineage. Thus, two phyletic lineages, *E. hsandagolensis–E. efialtes* and *Exallerix manahan–E. gaolanshanensis*, should be distinguished in the genus *Exallerix*.

In the Early–Middle Miocene genus *Postexallerix*, the trend characteristic of *Exallerix* toward the specialization of the trigonid of M_1 reached the most advanced state (Table 1). In addition, M_2 and enamel sculpturing of the lower molars of *Postexallerix* are strongly reduced. This genus is probably a direct descendant of the genus *Exallerix*.

None of the *Exallerix* species could be an ancestor of *Synexallerix*, since, in *E. gaolanshanensis*, the protocone of P^3, the parastyle of P^4 and M^1, the metastyle of M^2, and the paraconid of P_4 are reduced and the enamel relief is absent; in *E. hsandagolensis* and *E. efialtes*, the metastylid on M_1 is absent and the metaconid is reduced; in the three species, M_2 is strongly reduced (Table 2). Thus, a special brachyericine lineage that gave rise to Early Miocene *Synexallerix* should exist in the Oligocene.

Among the Asian Brachyericinae, *Synexallerix* is most similar to North American *Brachyerix* and *Metechinus* in the structure of the upper and lower teeth, parameters of M_1 (Table 1), and the relations of P_4, M_1, and M_2 (Table 2). This allows one to consider this genus as the ancestor of the North American Brachyericinae. P_4 of *S. junggarensis* is relatively strongly reduced (in *Brachyerix*, P_4 has a well-pronounced paraconid and a rudimentary metaconid); therefore, it is believed that *Brachyerix* originates from a relatively primitive member of *Synexallerix*. Most likely, *Brachyerix* and *Synexallerix* are connected by a more remote relationship, i.e., originate from a common Oligocene ancestor that developed independently of the *Exallerix* and *Postexallerix* lineage.

A distinctive feature of the Asian Brachyericinae is the presence of surface sculpturing composed of small enamel tubercles at the base of the labial side of the lower teeth. M_1 of the holotype of *Exallerix hsandagolensis* has two longitudinal rows of such tubercles (McKenna and Holton, 1967, text-fig. 2). One row of tubercles is present on M_1 and M_2 of *E. efialtes* (Lopatin, 1996, pl. I, fig. 6, text-fig. 3) and *Synexallerix junggarensis* (Bi, 1999, pl. I, fig. 1a); however, the latter species has a smaller number of tubercles and they are relatively widely spaced. In *Exallerix manahan* and *Synexallerix otus*, the tubercles fused to form the labial cingulid; however, in the first, the cingulid is weak and rudimentary; in the second, it is well developed. In *Exallerix gaolanshanensis* and *Postexallerix*, the enamel tubercles are partially or completely reduced.

From the above, it might be assumed that the evolutionary changes of brachyericine enamel sculpturing followed two main trends, i.e., (1) a longitudinal row (or several rows) of closely spaced tubercles—a row of densely packed tubercles—continuous cingulid—reduction or expansion of the cingulid and (2) a longitudinal row of closely spaced tubercles—row of widely spaced tubercles—isolated tubercles—entirely reduced tubercles. Thus, the extent of the development of sculpturing can be used for the determination of relationships between species of a particular phyletic lineage.

ADAPTATIONS OF THE BRACHYERICINAE

Asian short-faced hedgehogs show a specialized dental system, which has no parallel in extinct and extant Erinaceidae. They are characterized by a strongly enlarged and extended anterior lower incisor, short lower jaw, strongly reduced teeth between the anterior incisor and M_1, extended M_1 with a sharp bladelike paralophid, reduced M_2, and well-developed and snout masticatory muscles displaced far anterior along the jaw. McKenna and Holton (1967, p. 9) were the first to describe these features of *Exallerix hsandagolensis* and proposed that, during a bite, the teeth pressed strongly but slowly, according to the so-called nutcracker type which is adapted to feeding on hard-shelled prey. The efficiency of cutting interaction of P^4/M_1 is intensified by the lingually open trigonid and extended paralophid of M_1.

Gureev (1979, p. 76) believed that the teeth of the Brachyericinae were adapted for "treating mainly the food that was rough with reference to mechanical structure." This researcher proposed that short-faced hedgehogs predominantly fed on "slow-moving animals" (Gureev, 1979, p. 98), which were captured with the use of the enlarged anterior incisors, and vegetable food (Gureev, 1979, p. 140). Apparently, by "slow-moving animals with hard cover" were meant bivalves and gastropods.

In the *E. hsandagolensis–E. efialtes* lineage, M_1 increased in relation to P_4 and M_2; its trigonid lengthened and narrowed; the metaconid reduced; and the masseteric crest became more massive (Lopatin, 1996, 1999). This is considered to be a directional adaptation of the *Exallerix* species to predation. New data show that similar changes of M_1 were characteristic of the *Synexallerix junggarensis–S. otus* lineage and achieved the maximum in *Postexallerix securis* and *P. mustelidens.* The lower teeth of Miocene Asian brachyericines acquired obvious features of convergent similarity to the teeth of small carnivores of the family Mustelidae, i.e., an excessively developed anterior incisor functioning as a carnivoral canine; reduced teeth anterior and posterior to M_1; and a very long and high paralophid, a reduced metaconid, and a short talonid on M_1 (thus, M_1 became a carnassial of a sort). Shortened lower jaws and the short facial region of the skull, a high and massive horizontal ramus of the lower jaw, and a relatively low coronoid process are also characteristic of small mustelines (e.g., *Mustela*). In the latest member of the Asian Brachyericinae, Middle Miocene *Postexallerix mustelidens*, not only the size but also the structure of the talonid of M_2 is reduced; such reduction is atypical of insectivores and characteristic of some carnivores, including the Mustelidae.

The efficiency of cutting interaction between the paralophid of M_1 and the metacrista of P^4 in Asian short-faced hedgehogs was provided by the high and sharp cutting edges of these crests. Probably, the sharp carnassial-like teeth and well-developed masticatory muscles of brachyericines were not only helpful in cutting muscles and tendons of prey, but also allowed these animals to crack and crush bones. This is an adaptive feature of true predators and scavengers, distinguishing them from carnivorous–insectivorous forms. The presence of strong masticatory muscles and large caniniform anterior incisors enabled them to kill relatively large animals, comparable to them in size. Probably, the main prey of short-faced hedgehogs were small terrestrial vertebrates (rodents, lagomorphs, insectivores, lizards, and frogs).

A similar predatory specialization in the structure of M_1 and P^4 is observed in *Deinogalerix* Freudenthal, 1972, an endemic genus of the Galericinae from the Late Miocene insular Gargano Fauna (Italy), including giant *D. koenigswaldi* (Freudenthal, 1972, pls. 1–3) and smaller *D. intermedius, D. brevirostris, D. freudenthali*, and *D. minor* (Butler, 1980, text-figs. 1, 2, pls. 1–3). M_1 and P^4 increased in comparison with other cheek teeth of these gymnures and had high and long blades of the paralophid and the metacrista, respectively; in addition, M_1 became closely similar in proportions and structure to M_1 of the Brachyericinae. Consequently, *Deinogalerix* could cut muscular tissue and crack bones, as brachyericines did. *Deinogalerix* is characterized by a strongly extended rostral region of the skull, a long and low mandible, increased I^1 and C_1, and other characters of the skeletal structure commonly interpreted as adaptation to predation accompanied by specialization to capturing mobile medium-sized prey, such as fish, amphibians, and crustaceans (Butler, 1980). Butler (1980, p. 54) believed that large P^4 and P_4 and stout trigonid of M_1 of *Deinogalerix* were effective in crushing bones of vertebrates and the armor of crustaceans. Thus, although the Brachyericinae and *Deinogalerix* followed different paths in the development of predatory specialization, the formation of a strong cutting and crushing apparatus caused similar modifications of P^4 and M_1.

The changes in the masticatory apparatus of *Exallerix* are associated with certain structural features of the skull and lower jaw. The well-developed postorbital processes and frontal crests, a relatively high anterior part of the sagittal crest (Qiu and Gu, 1988, text-fig. 2), and a distinct medial crest at the base of the coronoid process (Fig. 1d) indicate the presence of a stout anterior portion of the temporal muscle providing for effective crushing interaction between the metacrista of P^4 and the paralophid of M_1. The unique (among insectivores) structure of the lower masseteric crest is associated with the excessively developed anterior portion of the medial masticatory muscle (musculus masseter medialis) functioning as a very strong adductor (Fig. 1). A large finlike angular process with a deep depression is evidence of the strong development of the internal pterygoid muscle contributing to transverse masticatory movements. The development of a stout digastric muscle (reconstructed on the basis of the presence of its insertional area on the horizontal ramus of the lower jaw, Fig. 1g) is most likely attributable to a great force lowering the mandible, which is required for fast and wide opening the mouth in order to grasp prey.

Probably, the predatory mode of life is associated with the relatively large sizes of Asian brachyericines, as compared to the other Erinaceidae. It should be pointed out that each species of the Asian Brachyericinae coexisted with true hedgehogs (from the subfamily Erinaceinae) of approximately the same size, which showed insectivorous and euryphagous feeding adaptation. For example, in addition to *Exallerix hsandagolensis* and *E. manahan*, the Shand-Gol Fauna includes four species of the genus *Amphechinus*, in particular, large-sized *A. rectus* (Matthew et Granger, 1924) and *A. gigas* Lopatin, 2002 (Matthew and Granger, 1924; Trofimov, 1960; Sulimski, 1970; Huang, 1984; Lopatin, 2002). In addition to *Exallerix efialtes*, the Erinaceidae from the Early Miocene Aral Fauna are represented by three species of *Amphechinus*, including relatively large *A. akespensis* Lopatin, 1999 (Lopatin, 1999). *Synexallerix junggarensis* coexisted with at least two species of the genus *Amphechinus* (Bi, 2000). *Postexallerix securis* from the Ulan-Tologoi Fauna and *P. mustelidens* from the Oshin Formation co-occurred with *Mioechinus* spp. (collection of GIN). Apparently, this shows the absence of significant competition for food between the Brachyericinae and the Erinaceinae.

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