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A New Genus of the Galericinae (Erinaceidae, Insectivora, Mammalia) from the Middle Eocene of Mongolia

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Abstract—The earliest member of the subfamily Galericinae, *Eogalericius butleri* gen. et sp. nov., from the Middle Eocene Khaychin Formation of the Khaychin-Ula 2 locality is described. *Eogalericius* displays plesiomorphic similarity to *Eochenus* from the Middle Eocene of China. It is primitive in the following characters: P^4–M^2 are short, wide, and have small hypocones; the stylar lobes of M^1 and M^2 and the parastyle of P^4 are large and clearly project; P_2 and P_3 are nonreduced; P_4 is relatively small with a well-developed metaconid and paraconid; in M_1, the trigonid is short and the paracristid is subtransversely oriented; M_3 has a hypoconulid; and two mental foramina are present.

Key words: Galericinae, Erinaceidae, Middle Eocene, Mongolia.

INTRODUCTION

Hedgehogs of the subfamily Galericinae (shrew-hedgehogs or hairy hedgehogs) are presently restricted to southeastern Asia. However, they were a rather diverse and widespread Holarctic group in the Paleogene and Neogene. From the Late Eocene to the Early Pliocene, the Galericinae inhabited Europe; in the Oligocene and Miocene, they lived in North America; and in the Miocene, they occurred in the north of Africa (McKenna and Bell, 1997). In Asia, they are known beginning with the Middle Eocene (Wang and Li, 1990; McKenna and Bell, 1997).

Only four shrew-hedgehogs have been discovered in the Paleogene of Asia: the Middle Eocene *Eochenus sinensis* Wang et Li, 1990 from northeastern China; the Early Oligocene *Pseudoneurogymnurus*[1] *schevyrevae* Gureev, 1979 and *P. zhchikvadzei* Gureev, 1979 from eastern Kazakhstan; and the Early Oligocene *Neurogymnurus indricotherii* Lopatin, 1999 from western Kazakhstan (Gureev, 1979; Wang and Li, 1990; Lopatin, 1999). It is not inconceivable that "*Tupaiodon*" *huadianensis* Wang et Li, 1990 from the Middle Eocene of China also belongs to the Galericinae. In addition, Galericinae indet. have been registered in several Upper Eocene–Lower Oligocene stratigraphic levels of different ages that were studied in the Zaisan Depression of eastern Kazakhstan (Gureev, 1979; Gabunia and Gabunia, 1987; Gabounia and Chkhikvadze, 1997).

It may well be that the erinaceids determined as "Erinaceidae gen. et sp. nov. cf. *Litolestes*" (Tong and Wang, 1998, text-fig. 3C) from the Early Eocene Wutu Fauna (China, Shandong) and certain Erinaceoidea from the Upper Eocene Caijiachong Formation (China, Yunnan), which were identified as Erinaceidae gen. et sp. indet. and "Dormaaliidae or Erinaceidae" (Rich *et al.*, 1983, text-figs. 4A, 4B, 4G, 4H; 6A–6C) also belong to the Galericinae.

The collection of the Paleontological Institute of the Russian Academy of Sciences (PIN) contains certain Galericinae specimens from the Paleogene and Neogene of Kazakhstan and Mongolia that have not been described. The earliest member of the subfamily Galericinae from the Middle Eocene of Mongolia is described below. The material comes from the Khaychin Formation of the Khaychin-Ula 2 locality (collected by the Southern Gobi Team of the Joint Soviet–Mongolian Paleontological Expedition headed by V.Yu. Reshetov in 1971–1973). The Khaychin Fauna belongs to the Irdinmanhan Land Mammal Age of Asia, which is dated as the Middle Eocene (Badamgarav and Reshetov, 1985; Russell and Zhai, 1987) or the beginning of the Middle Eocene (Averianov and Godinot, 1998).

SYSTEMATIC PALEONTOLOGY

Family Erinaceidae Fischer, 1817

Subfamily Galericinae Pomel, 1848

Genus *Eogalericius* Lopatin, gen. nov.

E t y m o l o g y. From the Greek *eos* (dawn), the Greek *gale* (small predator), and the Latin *ericius* (hedgehog).

T y p e s p e c i e s. *Eogalericius butleri* sp. nov.

[1] Some researchers transfer the genus *Pseudoneurogymnurus* from the Erinaceidae to the Plesiosoricidae (McKenna and Bell, 1997). However, the structure of the upper molars in *P. schevyrevae* and *P. zhchikvadzei* (Gureev, 1979, text-fig. 61) strongly suggests that they belong to the Erinaceidae. The status of *Pseudoneurogymnurus* is subject to additional analysis.

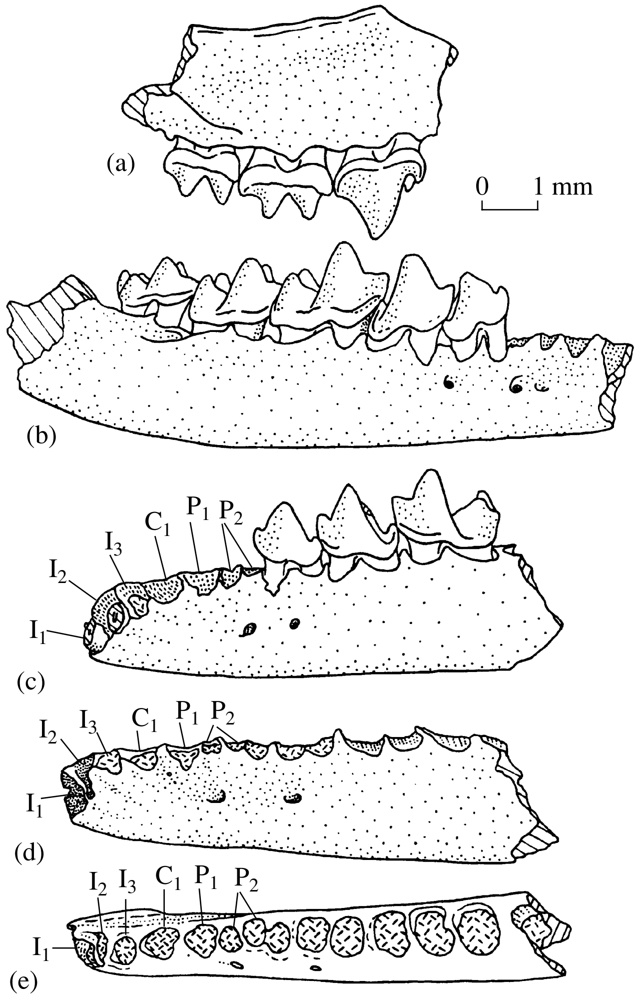


Fig. 1. *Eogalericius butleri* sp. nov.: (a) holotype PIN, no. 3107/420, fragmentary right maxilla with P^4–M^2, labial view; (b) specimen PIN, no. 3107/422, fragmentary right dentary with P_3–M_3 and alveoli of C_1–P_2, labial view; (c) specimen PIN, no. 3107/425, fragmentary left dentary with P_3–M_1, fragmentary I_1 and I_2, and alveoli of I_3–P_2, labial view; and (d, e) specimen PIN, no. 3107/440, fragmentary left dentary with alveoli of I_1–M_1: (d), labial and (e) occlusal views.

D i a g n o s i s. Dental formula: $I^3/_3C^1/_1P^4/_4M^3/_3$. P^4–M^2 short and broad with small hypocones. Parastyle of P^4 large. Stylar lobes of M^1 and M^2 large and strongly projecting. Hypocone of M^1 and M^2 isolated from protocone. Postmetaconule crest long and connected to postcingulum. M^3 short. C_1 small. P_2 and P_3 slightly reduced. P_4 relatively small (at most as high as M_1 and at most 75–80% of its length) and having a well-developed paraconid and metaconid. M_2 somewhat shorter than M_1 (about 85–95%), M_3 substantially shorter than M_2 (75–85%). Trigonid of M_1 short, its paracristid subtransverse. Hypoconulid of M_3 positioned close to, or fused with, entoconid. Paracristid of M_3 long. Two mental foramina present under P_2 and P_3.

S p e c i e s c o m p o s i t i o n. Type species.

C o m p a r i s o n. The new genus differs from all known genera of the subfamily Galericinae, except for *Eochenus* Wang et Li, 1990, in the relatively small hypocones of P^4–M^2, large parastyle of P^4, strongly projecting stylar lobes of M^1 and M^2, relatively small P_4, short trigonid and subtransverse paracristid of M_1, presence of the hypoconulid on M_3, and obligatory presence of two mental foramina. It differs from *Eochenus* in the long postmetaconule crest and detached hypocone of M^2, small C_1, larger P_2 and P_3, less massive and lower P_4 (in *Eochenus*, P_4 is 86–94% of the M_1 length, see Wang and Li, 1990, table 1), better developed metaconid of P_4, ratio between the lengths of the lower molars (in *Eochenus*, M_2 is relatively smaller, only 80–85% as long as M_1, whereas M_3 is almost equal to M_2, 90–100%), and in the longer paracristid of M_3.

Eogalericius butleri Lopatin, sp. nov.

Plate 11, figs. 1–10

E t y m o l o g y. Named in honor of the English paleotheriologist P. Butler.

H o l o t y p e. PIN, no. 3107/420, fragmentary right maxilla with P^4–M^2; Mongolia, Khaychin-Ula 2 locality; Middle Eocene, Khaychin Formation.

D e s c r i p t i o n (Figs. 1, 2). A small-sized hedgehog. The base of the zygomatic process of the maxilla is located in line with the posterior labial root of M^1. The upper margin of the zygomatic process is thin and ridgelike. The base of the zygomatic arch and adjacent area on the lateral side of the maxilla above M^1 and M^2 form an extensive depression for the maxillonasalis muscle. The infraorbital foramen is small and located in line with P^3. The posterior foramen of the infraorbital canal is directly above the space between P^4 and M^1. The infraorbital canal is narrow.

P^4–M^3 are three-rooted, including one lingual root. P^4 has a high paracone, a stout metacrista, and a well-developed lingual lobe. The parastyle is relatively large and projects anteriorly. The ectocingulum is narrow. The protocone is somewhat compressed longitudinally, and the preprotocrista is long and connected to the crest, which extends along the anterior margin of the occlusal surface to the parastyle. The hypocone is conical and small, approximately half as high as the protocone, and markedly projects lingually. The postcingulum is stout.

The occlusal surface of M^1 and M^2 is trapezoid, and the lingual lobe is slightly shorter than the labial lobe. The stylar lobes are large; in the middle region (in line with the conules), the anterior and posterior edges of the crown are noticeably concave. The ectoflexus is weak. The stylar shelf is narrow. The ectocingulum is thin but distinct and continuous. The precingulum is well-pronounced but short, and it extends at the base of the anterior side of the crown in line with the paraconule and preprotocrista. The parastylar and metasty-

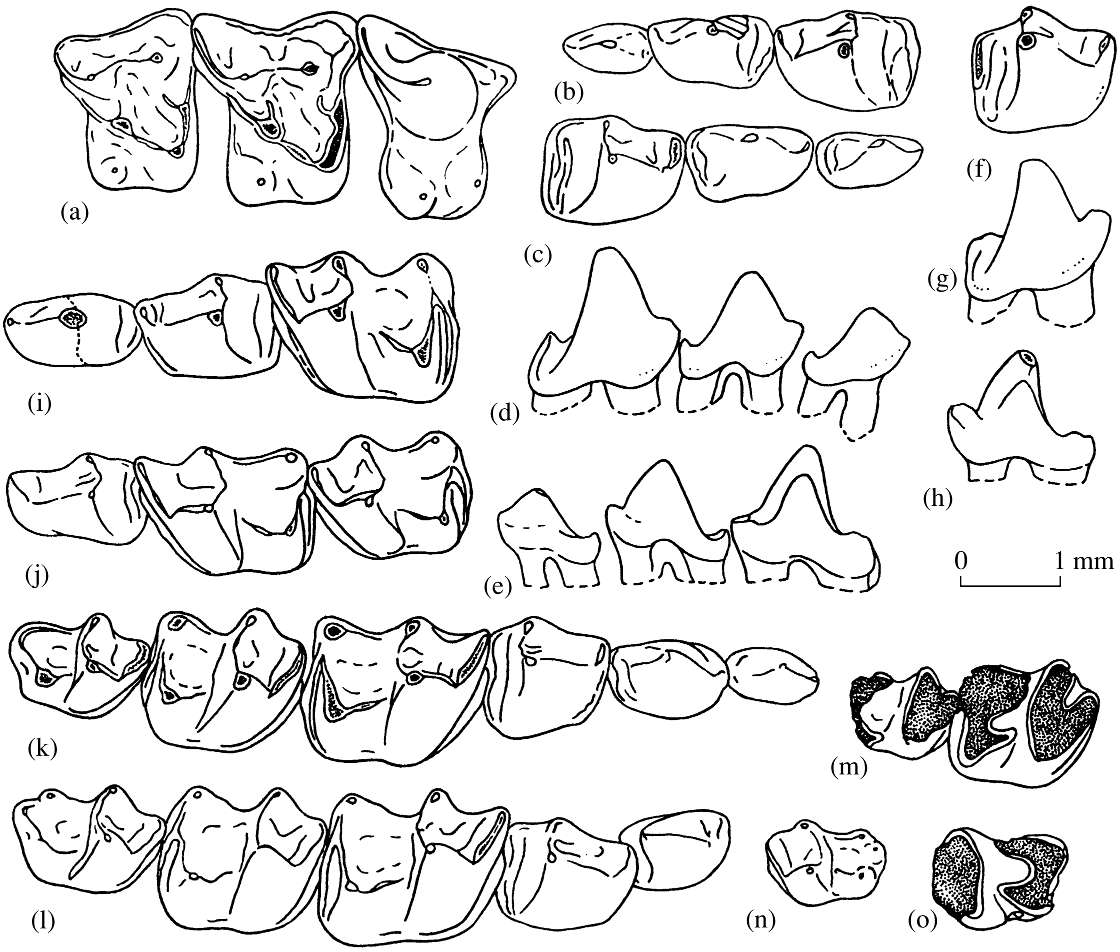


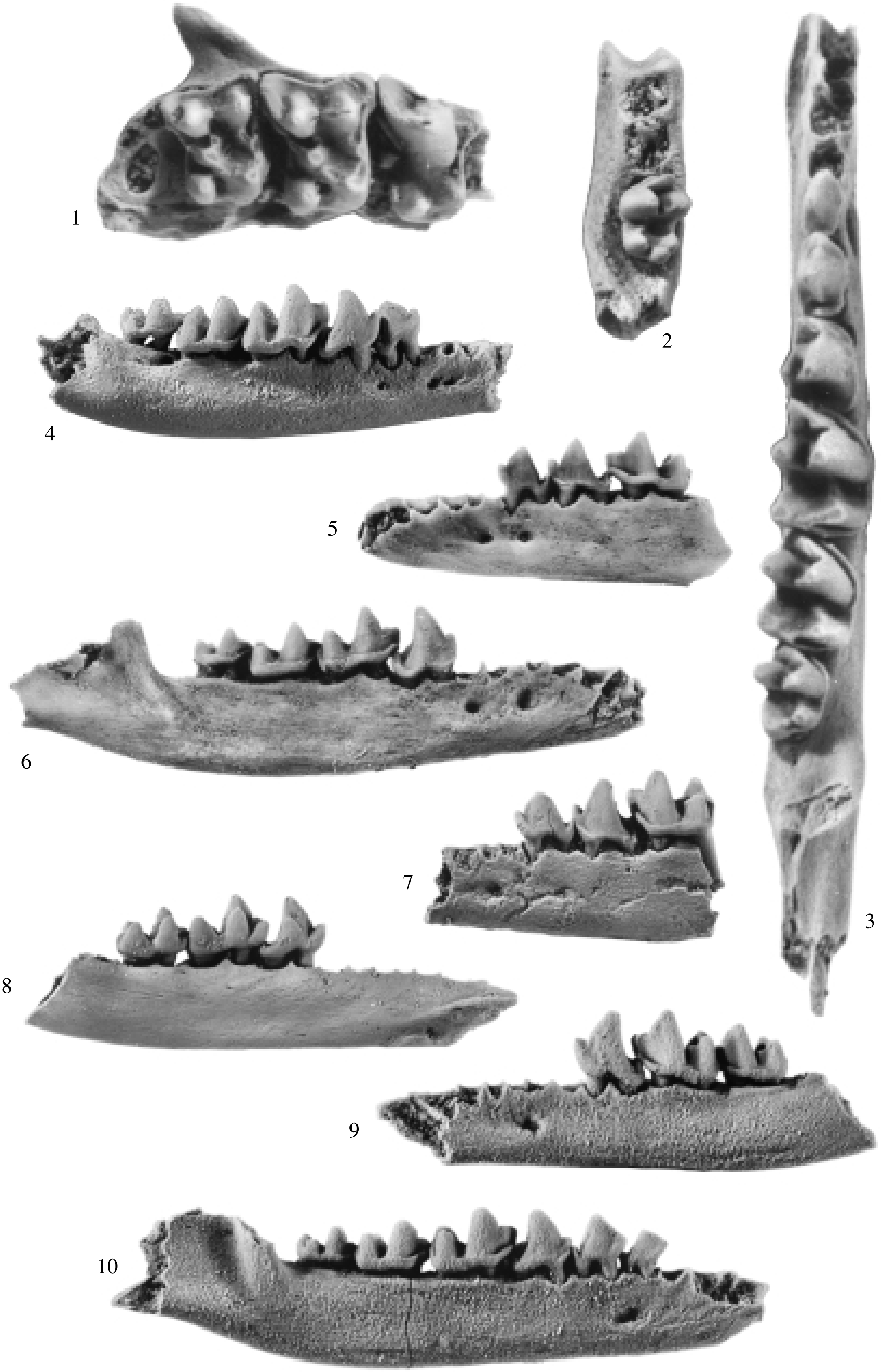
Fig. 2. Teeth of *Eogalericius butleri* sp. nov.: (a) holotype PIN, no. 3107/420, right P^4–M^2; (b) specimen PIN, no. 3107/424, left P_2–P_4; (c–e) specimen PIN, no. 3107/431, right P_2–P_4: (c) occlusal (d), labial, and (e) lingual views; (f–h) specimen PIN, no. 3107/433, right P_4: (f) occlusal, (g) labial, and (h) lingual views; (i) specimen PIN, no. 3107/426, left P_3–M_1; (j) specimen PIN, no. 3107/427, left P_4–M_2; (k) specimen PIN, no. 3107/430, right P_2–M_3; (l) specimen PIN, no. 3107/422, right P_3–M_3; (m) specimen PIN, no. 3107/436, heavily worn right M_2 and M_3; (n) specimen PIN 3107/429, left M_3; and (o) specimen PIN, no. 3107/437, heavily worn left M_3.

lar lobes strongly project anterolabially and posterolabially, respectively. The parastylar crest is weak; the metacrista is well-developed and is especially long and stout in M^1. The paracone and metacone are widely spaced and approximately equal in height and stoutness, with their apices being pointed. In M^2, the labial cusps are more widely spaced and the centrocrista is weaker than in M^1. The protocone is large and massive. The preprotocrista and postprotocrista are short and connected to conules. The transversely extended paraconule is substantially smaller than the metaconule. The preparaconule crest is stout and extends to the parastylar lobe. The postparaconule crest is short and thin and terminates at the base of the lingual wall of the paracone. The metaconule is relatively massive. The premetaconule crest is short, weak, and connected to the base of the lingual wall of the metacone. The postmetaconule crest is long, stout, extends posterolabially, and joins with the labial portion of the postcingulum. The lingual portion of the postcingulum is well-pronounced at the level of the metaconule and postprotocrista posterolabial to the hypocone apex. The hypocone is relatively small and conical; its apex is completely isolated from the trigon (there is no crest connected to the postprotocrista). M^2 is slightly shorter and substantially narrower than M^1.

Judging from the alveoli, M^3 was substantially smaller than M^2 in both length and width and was shaped like a narrow triangle. This last character means that M^3 lacks a hypoconal shelf and is distinguished by the noticeably reduced area of the metacone and metastyle.

The horizontal ramus of the lower jaw is relatively narrow and low. The symphyseal region extends posteriorly to the midlength, or the posterior root, of P_2. Its posteroventral part contains a small symphyseal foramen. Two mental foramina are usually present under P_2

Plate 11



and P_3 (Pl. 11, figs. 5–7; Figs. 1c–1e); rarely, there are three foramina: under the anterior and posterior roots of P_2 and under P_3 (Pl. 11, fig. 4; Fig. 1b); and occasionally, two small foramina are fused in one large and deep fossa located under the posterior root of P_2 and the anterior root of P_3 (Pl. 11, figs. 9, 10).

The anterior edge of the base of the coronoid process is straight. The ascending and horizontal rami are positioned at an angle of approximately 105°. The masseteric crest is stout, while the masseteric fossa is superficial. The mandibular foramen is located at the level of the molar crowns above the alveolar edge of the horizontal ramus. There is a relatively weak medial crest at the base of the coronoid process. The lower edge of the coronoid region forms a typical dorsal curvature.

The incisors, canines, and P_1 are single-rooted, while the other teeth are double-rooted. Judging from the preserved tooth fragments and alveoli, the single-rooted antemolars are arranged in size in the following order: $C_1 > P_1 > I_2 = I_1 > I_3$ (Figs. 1c–1e). P_2 is small and compressed laterally, and it has a tiny paraconid and a low and short talonid. The paraconid is elevated and connected by a short and bladelike crest to the apex of the main cusp. P_3 is substantially longer, wider, and higher than P_2; however, it is similar to this tooth in its general proportions and structures and differs in the more massive main cusp, better detached paraconid, and distinct talonid. The postcingulid is well-developed. The precingulids of P_2 and P_3 are absent.

P_4 is semimolariform and has a well-differentiated trigonid and a very short talonid. The paraconid is relatively high, conical or more or less ridgelike, and separated from the protoconid by a clear notch. The protoconid is massive and high, the metaconid is substantially smaller and approximately half as high as the protoconid. The crest on the anterior side of the protoconid is weakly or moderately developed. The apices of the protoconid and metaconid are positioned within the same transverse line. The protocristid has a deep notch. The precingulid is usually weak, narrow, and confined to a small area under the paracristid; occasionally, it is completely lost. The talonid has one low cuspule, which is located in the central or lingual region of the transverse postcingulid crest; however, it never occupies the extreme posterolingual corner of the talonid. The talonid basin is small and closed lingually by a narrow metastylid crest, which descends along the posterolingual edge of the metaconid and adjoins the postcingulid crest. The postcingulid crest descends ventrolabially and usually terminates in the posterolabial corner of the crown; in some cases (where it is transformed into the postcingulid), it extends along the labial side to the level of the anterior part of the posterior root.

The lower molars are low and transversely expanded, $M_1 > M_2 \geqslant M_3$. In M_1, the talonid is slightly wider than the trigonid. The trigonid basin is open. The paraconid is raised, ridgelike, and anterolingually oriented. The shearing paracristid has a well-developed carnassial notch. The protoconid and metaconid are widely spaced. The protocristid has a deep notch. The apex of the metaconid is located somewhat anterior to the apex of the protoconid. The precingulid and ectocingulid are fused into an integrated labial cingulid, which terminates anterior to the base of the hypoconid. The hypoflexid is shallow. The talonid basin is closed. The hypoconid and entoconid are positioned opposite to each other, with the latter being much higher. The entocristid is high and reaches the base of the metaconid. The cristid oblique is low and connected to the middle of the base of the posterior wall of the protoconid. The lingual region of the postcristid (which ascends onto the entoconid) is poorly pronounced and narrow; occasionally, it is absent (Fig. 2j). The postcingulid is stout and connected to the postcristid at the posterolabial corner of the base of the entoconid; from this point, the postcingulid descends ventrolabially to the base of the hypoconid.

M_2 is similar in structure to M_1; however, its trigonid is relatively shorter, while the paracristid is lower, shorter, and transversely positioned. The talonid is equal in width to the trigonid, or slightly narrower.

M_3 is similar in trigonid structure to M_2; however, its talonid is narrower. The entocristid is complete, while the postcingulid is absent. In contrast to M_1 and M_2, M_3 has a well-developed hypoconulid that is positioned close to the entoconid and fused with it at the base. The apical notch between the hypoconulid and the entoconid ranges from deep to superficial (Pl. 11, fig. 2; Figs. 2l, 2n); occasionally, the two cusps are completely fused (Pl. 11, fig. 3; Fig. 2k).

M e a s u r e m e n t s in mm. Holotype: length of P^4–M^2 along the crowns, 4.7; length of P^4–M^3 along the alveoli, 5.25.

Explanation of Plate 11

Figs. 1–10. *Eogalericius butleri* sp. nov.: (1) holotype PIN, no. 3107/420, fragmentary right maxilla with P^4–M^2 and alveoli of M^3, occlusal view, ×11; (2) specimen PIN, no. 3107/429, fragmentary left dentary with M_3 and alveoli of M_2, occlusal view, ×11; (3, 10) specimen PIN, no. 3107/430, fragmentary right dentary with P_2–M_3 and alveoli of I_2–P_1: (3) occlusal view, ×11, (10) labial view, ×7; (4) specimen PIN, no. 3107/422, fragmentary right dentary with P_3–M_3 and alveoli of C_1–P_2, labial view, ×7; (5) specimen PIN, no. 3107/425, fragmentary left dentary with P_3–M_1, fragmentary I_1–I_2 and alveoli of I_3–P_2, labial view, ×7; (6) specimen PIN, no. 3107/421, fragmentary right dentary with P_4–M_3, fragmentary I_1–I_2, and alveoli of I_3–P_3, labial view, ×7; (7) specimen PIN, no. 3107/426, fragmentary left dentary with P_3–M_1 and alveoli of P_1–P_2, labial view, ×7; (8, 9) specimen PIN, no. 3107/427, fragmentary left dentary with P_4–M_2 and alveoli of I_2–P_3 and M_3, ×7: (8) lingual and (9) labial views.

Measurements of the upper teeth in the holotype:

Tooth	length		width	
	labial	lingual	parastyle–protocone	metastyle–hypocone
P^4	1.7	1.05	1.7	2.0
M^1	1.7	1.3	2.0	2.15
M^2	1.4	1.25	1.9	1.65

Length of I_1–M_3 along the alveoli: 10.3 (PIN, no. 3107/421). Tooth rows: P_2–M_3, 8.2 (no. 3107/430); P_3–M_3, 7.1 (no. 3107/422) and 7.25 (no. 3107/430); P_4–M_3, 6.0 (no. 3107/421) and 6.05 (no. 3107/430); P_2–P_4, 3.45 (no. 3107/430), 3.6 (no. 3107/424), and 3.8 (no. 3107/431); P_2–P_3, 2.1 (no. 3107/430) and 2.15 (no. 3107/424); P_3–P_4, 2.3–2.8 (nos. 3107/422, 424–426, 430); P_3–M_1, 4.2–4.55 (nos. 3107/422, 425, 426, 430); P_4–M_2, 4.55–4.95 (nos. 3107/421–423, 427, 430, 435); P_4–M_1, 3.0–3.3 (nos. 3107/421–423, 425–428, 430, 435); M_1–M_3, 4.7–4.95 (nos. 3107/421, 422, 430); M_1–M_2, 3.25–3.5 (nos. 3107/421-423, 430, 434); and M_2–M_3, 2.55 (no. 3107/436), 2.9 (no. 3107/421), 3.0 (no. 3107/430), and 3.15 (no. 3107/422).

Measurements of the lower teeth (in I_1 and I_2, root diameters; in I_3–P_1, dimensions of alveoli):

Tooth	length (in M_1–M_3, total/trigonid)			width(in M_1–M_3, trigonid/talonid)		
	n	limits	mean	*n*	limits	mean
I_1	1	0.4	–	1	0.6	–
I_2	2	0.4	–	2	0.5–0.6	0.55
I_3	4	0.25–0.35	0.3	3	0.5–0.6	0.57
C_1	5	0.7–0.9	0.74	5	0.6–0.7	0.63
P_1	10	0.55–0.7	0.61	10	0.45–0.6	0.56
P_2	3	0.95–1.05	1.0	3	0.5–0.55	0.53
P_3	7	1.1–1.4	1.22	6	0.7–0.77	0.73
P_4	12	1.35–1.5	1.44	12	0.95–1.1	1.03
M_1	10	1.8–1.9/0.9–1.0	1.85/1.0	10	1.3–1.4/1.3–1.45	1.34/1.36
M_2	8	1.45–1.7/0.75–0.9	1.61/0.79	8	1.3–1.35/1.2–1.35	1.32/1.28
M_3	6	1.1–1.5/0.6–0.75	1.32/0.67	6	0.9–1.0/0.7–0.9	0.98/0.82

Depth of the horizontal ramus: under P_2, 1.75–2.0; under P_3, 1.65–2.2; under P_4, 2.0–2.4; under M_1, 2.05–2.5; under M_2, 2.05-2.5; and under M_3, 2.0–2.5. In a young individual (specimen PIN, no. 3107/429), depth of the horizontal ramus under M_2, 1.8; under M_3, 1.5.

M a t e r i a l. In addition to the holotype, 19 fragmentary dentaries from the type locality (PIN, nos. 3107/421–438, 440): one with P_2–M_3, one with P_3–M_3, two with P_2–P_4, two with P_3–M_1, one with P_3–P_4, one with P_4–M_3, three with P_4–M_2, one with P_4–M_1, one with P_4, one with M_1–M_2, two with M_2–M_3, one with M_3, and two without teeth (one with alveoli of I_1–M_1, another with alveoli of M_2–M_3).

DISCUSSION

At first sight, *Eogalericius butleri* displays a certain similarity to the Tupaiodontinae, especially to *Zaraalestes russelli* Storch et Dashzeveg, 1997 of approximately the same geological age, i.e., discovered in the Middle Eocene of Mongolia (Storch and Dashzeveg, 1997). This similarity is visible in the shapes of P^4–M^2 (which are transversely expanded and have a clear longitudinal constriction in the middle, large stylar lobes, and small hypocones), the structure of M_1–M_3, and the presence of the hypoconulid in M_3. However, the occlusal surface of P^4–M^2 of *Eogalericius* is less expanded, and its hypocone is much better developed than in *Zaraalestes*. In contrast to all tupaiodontines, M^1 and M^2 of *Eogalericius* have a postparaconule crest, a well-developed paraconule, and a conical rather than ridgelike metaconule; its I_1 is not enlarged; C_1 is only slightly reduced; P_2 is double-rooted; the main cusp of P_3 is low and laterally compressed; P_4 is relatively larger and lacks a paracristid shearing blade, the metaconid is reduced, and the cuspule of the talonid occupies a more central position; and the trigonids of the lower molars are lower, the cusps and crests are less sharp, the paracristid of M_1 is shorter, and the hypoconulid of M_3 is partially fused with the entoconid.

The dental formula and the structure of the upper and lower teeth strongly suggest that *Eogalericius* belongs to the Galericinae. The presence of two mental foramina is a primitive character typical of the Amphilemuridae and archaic Erinaceidae, such as *Litolestes*, *Leipsanolestes*, and *Litocherus* (Novacek *et al.*, 1985). The double mental foramen is occasionally observed as a variation in later Galericinae, for example, in *Eochenus* (Wang and Li, 1990, p. 193), *Neurogymnurus* (Viret, 1947, text-fig. 4), *Galerix* (Butler, 1948, pp. 465, 468), and *Lantanotherium* (Baudelot, 1972, text-fig. 69).

The short trigonid and only slightly anteriorly inclined (subtransverse) paracristid of M_1 are functionally associated plesiomorphic characters, which are typical for *Eogalericius, Eochenus,* and primitive Erinaceidae from the Late Paleocene–Early Eocene of North America (Novacek *et al.*, 1985). In *Eogalericius* and *Eochenus,* the paracristid is inclined anteriorly to a greater extent than in primitive Erinaceidae.

Within the subfamily Galericinae, only *Eogalericius* and *Eochenus* have a hypoconulid on M_3; however, this is characteristic of the Tupaiodontinae (Butler, 1988; Storch and Dashzeveg, 1997) and primitive Erinaceidae (Novacek *et al.*, 1985); in the latter, the hypoconulid is present on each lower molar. Thus, this is also a plesiomorphic character. In *Eogalericius*, the hypoconulid and entoconid are partially or, occasionally, completely fused. In the latter case (Pl. 11, fig. 3; Fig. 2k), the lingual region of the talonid forms a relatively large posterior projection resembling that of M_3 in the Galericini (see Engesser, 1972, text-fig. 2; 1980, text-figs. 3, 14; Novacek *et al.*, 1985, text-fig. 4A; Mein and Martín-Suarez, 1993, text-fig. 3, pl. 1, fig. 6) and *Neurogymnurus* (Viret, 1947, text-fig. 3).

The phylogenetic relationships of shrew-hedgehogs are poorly understood. The majority of the genera of the subfamily Galericinae are usually placed in the tribe Galericini (Gould, 1995; McKenna and Bell, 1997); the genera *Neurogymnurus* and *Proterix*, which are assigned to monotypic tribes, are exceptions. Hoek Ostende (2001) believes that the tribe Galericini includes only four genera: *Galerix* (= *Tetracus*; = *Pseudogalerix*), *Parasorex*, *Schizogalerix*, and *Deinogalerix*. The concept of Galericini sensu stricto goes back to the system proposed by Butler (1948), in which Galericini are opposed to Echinosoricini (*Lantanotherium*, *Echinosorex, Hylomys*, and *Podogymnura*). The diagnostic features of Galericini sensu stricto include the following (Hoek Ostende, 2001): in M^1 and M^2, the width substantially exceeds the length; the metaconule of M^1 and M^2 has a posterior arm (postmetaconule crest); P^3 has a well-developed inner projection, which bears at least a well-developed protocone; and M^3 is simplified and usually lacks a metastylar crest (metacrista). With the exception of the unknown structure of P^3, *Eogalericius* fits into the diagnosis of Galericini sensu stricto. At the same time, as was shown above, it markedly differs from most of the Galericinae in the shape and structure of P^4–M^2 and P_4–M_3.

Within the subfamily Galericinae, *Eogalericius* is most similar to *Eochenus* from the Middle Eocene of China (Huadian Fauna). However, all the common features of these genera (wide and short P^4–M^3 and M_1–M_2, relatively short trigonid and subtransverse paracristid of M_1, and presence of the hypoconulid on M_3) should be regarded as plesiomorphic characters. Therefore, it is unreasonable to combine them in any special taxon of supergeneric rank.

Eogalericius is more primitive than *Eochenus* in a number of characters: its P_2 and P_3 are reduced to a much lesser extent, P_4 is smaller, the paraconid and metaconid of P_4 are better developed, and the foramen of the mental canal is double. This concurs well with the earlier age of the Khaychin Fauna than the Huadian Fauna (Wang and Li, 1990).

Thus, among currently known genera, *Eogalericius* is considered to be most similar morphologically and phylogenetically to the ancestor of all Galericinae.

It should be noted that the form described by Wang and Li (1990) as *"Tupaiodon" huadianensis* from the Middle Eocene Huadian Fauna in actuality does not belong to the genus *Tupaiodon* (Storch and Dashzeveg, 1997). It apparently belongs to the Galericinae rather than to the Tupaiodontinae (Tong, 1997). This form is distinguished from all tupaiodontines by a very large P_4, the paracristid of P_4 lacking a shearing blade, lower trigonids of M_1 and M_3, and a greater anterior inclination of the paracristid of M_1. This animal is similar in size to *Eogalericius butleri* and differs in its larger P_4, with a better developed metaconid, and in the presence of only two alveoli between C_1 and P_3.

Thus, at the beginning of the Middle Eocene, two hedgehog subfamilies, the Tupaiodontinae and Galericinae, co-occurred in Asia. Apparently, they diverged even earlier; this is evident from the discovery of Erinaceidae in the Lower Eocene Wutu Formation in China. "Erinaceidae gen. et sp. nov. cf. *Litolestes*" resembles the Galericinae (Tong and Wang, 1998), while *Changlelestes dissetiformis* and "Changlelestidae gen. et sp. nov." (Tong and Wang, 1993, 1998) are considered to be the earliest members of the subfamily Tupaiodontinae (McKenna and Bell, 1997) or a closely related group (Changlelestinae: Tong, 1997). It may be suggested that the earliest adaptive radiation of erinaceids in Asia occurred during the Pan-Holarctic faunal exchange at the Paleocene–Eocene boundary.

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