

The First Find of Geolabididae (Soricomorpha, Mammalia) in Asia (Upper Paleocene of Mongolia)

A. V. Lopatin

Paleontological Institute, Russian Academy of Sciences, Profsoyuznaya ul. 123, Moscow, 117997 Russia

e-mail: alop@paleo.ru

Received September 10, 2003

Abstract—*Gobigeolabis verigranum* gen. et sp. nov. is described based on jaw fragments from the Upper Paleocene Zhigden Member of the Naran Bulak Formation of the Tsagan-Khushu locality (Mongolia). This is the first Asian member of the Geolabididae, a soricomorph family that has previously been recorded from the Upper Cretaceous–Lower Miocene of North America. *G. verigranum* was an extremely small mammal; the dimensions of its M_1 suggest this animal was approximately 2.25 g in body weight (i.e., similar in size to the smallest extant shrews).

Key words: Geolabididae, Soricomorpha, body weight of extinct mammals, Late Paleocene, Mongolia.

INTRODUCTION

The Geolabididae is a family of soricomorph insectivores, which was widespread in the Paleogene of North America. This group was originally established as a subfamily of the Erinaceidae and included three genera: *Geolabis* (= *Metacodon*), *Myolestes*, and *Hypacodon* (McKenna, 1960). Somewhat later, *Hypacodon* was reduced to a junior synonym of *Centetodon* (McKenna *et al.*, 1962). Subsequently, *Geolabis* was also synonymized with *Centetodon* (Setoguchi, 1978; Lillegraven *et al.*, 1981), while the name *Myolestes* Matthew, 1909 (a junior homonym for *Myolestes* Brèthes, 1905, Insecta) was replaced by *Marsholestes* (McKenna and Haase, 1992). At present, the family Geolabididae is usually considered to include the North American genera *Batodon* (Late Cretaceous), *Centetodon* (Early Eocene–Early Miocene, Wasatchian–Arikarean), *Marsholestes* (Middle Eocene, Bridgerian), and *Batodonoides* (Early–Middle Eocene, Wasatchian–Uintan) (McKenna and Bell, 1997; Bloch *et al.*, 1998).

Until it was recognized that *Centetodon*, *Geolabis*, and *Metacodon* were congeneric, they were placed in different groups of Insectivora. *Centetodon* was usually assigned to the Nyctitheriidae (Simpson, 1945), *Metacodon* was placed in the Erinaceidae (Patterson and McGrew, 1937; Galbreath, 1953; Clark, 1966) or a special family, the Metacodontidae (along with *Plesiosorex* and *Meterix*; Butler, 1948), while *Geolabis* was referred to as Insectivora incertae sedis (Simpson, 1945; Saban, 1958). Saban (1958) believed that *Geolabis* could have belonged to the Soricoidae. Since the subfamily Geolabidinae was established, it was for some time commonly assigned to the Erinaceidae (McKenna, 1960; Russell, 1960; Clark, 1966). Van Valen

(1967) considered the subfamily Geolabidinae to belong to the Adapisoricidae (Erinaceoidea), Robinson (1968) placed it in the Nyctitheriidae, and Gureev (1979) indicated that it is similar to the Tenrecidae. Butler (1972) was the first to assign with certainty this group to Soricomorpha and ranked it as a family; subsequently, this point of view was accepted by other researchers (McKenna, 1975; Novacek, 1976; Sigé, 1976). Butler believed that the Geolabididae belonged to a soricomorph insectivoran lineage that gave rise to the Nesophontidae and Solenodontidae (Butler, 1972, 1988; see also Seiffert and Simons, 2000; Whidden and Asher, 2001).

The Geolabididae were as small as living shrews. This family includes the smallest known mammal *Batodonoides vanhouteni* Bloch, Rose et Gingerich, 1998 from the Lower Eocene of Wyoming (Bloch *et al.*, 1998).

The Geolabididae are characterized by an elongate facial region of the skull, the presence of the zygomatic arches (Butler, 1988), complete dental formula, an increased first pair of the upper incisors, nonmolariform P^4 lacking a metacone (a rudimentary metacone is present in *Batodon*) but possessing a very high paracone. The upper molars are widened, with well-developed styles, closely positioned paracone and metacone, reduced conules, and well-developed postcingulum (the hypocone shelf). They displayed a trend toward bifurcation of the lingual root of the upper molars. The lower premolars are double-rooted (except for P_1 of *Batodon tenuis* and *Batodonoides vanhouteni*), and P_3 is reduced. P_4 is semimolariform and has a conical paraconid, large protoconid and metaconid, and a simplified shearing talonid with a small lingual basin. The lower molars have high and closely positioned cusps of

the trigonid and low cusps of the talonid, and the hypoconulid is often fused with the entoconid.

The Maastrichtian *Batodon tenuis* Marsh, 1892 is presumably the earliest member of the Geolabididae and of the Lipotyphla as a whole (Benton, 1999). This form was considered to belong to the Palaeoryctidae (Van Valen, 1967; Kielan-Jaworowska *et al.*, 1979; Butler, 1988; Storer, 1991) or Cimolestidae (Clemens, 1973). Szalay and Decker (1974) proposed that it is related to the Nyctitheriidae. McKenna was the first to propose in personal communication in 1974 that *Batodon* could have belonged to the Geolabididae (Novacek, 1976; Bown and Schankler, 1982). However, the Late Cretaceous *Batodon* is separated by a considerable time gap from the earliest North American Geolabididae (Paleogene), the Early Eocene *Centetodon patratius* and *C. neashami* from Wyoming (Bown and Schankler, 1982; Butler, 1988). Taking into account the differences in dentition between *Batodon* and the Paleogene Geolabididae, this genus is sometimes referred to as Placentalia incertae sedis (Wood and Clemens, 2001).

Russell and Dashzeveg (1986) described Early Eocene insectivores (and also the so-called proteutherians, i.e., cimolestids and pantolestids) from the Bumban Member of the Naran Bulak Formation of the Tsagan-Khushu locality (Mongolia) and indicated that *Tsaganianus ambiguus* Russell et Dashzeveg, 1986 is similar to *Batodon tenuis* (which was assigned by these researchers to the Palaeoryctidae). They placed *Tsaganianus* in the subfamily Didelphodontinae (Palaeoryctidae) and proposed that the ancestor of *Tsaganianus* was similar to *Batodon*; however, no intermediate Paleocene forms were known (Russell and Dashzeveg, 1986, p. 286). *Tsaganianus* differs from the Geolabididae in its large P₃, crestlike paraconid of P₄ (the presence of the paracristid), better differentiated metaconid and protoconid of P₄-M₃, shorter talonid of M₁ and M₂, and better developed hypoconulid of M₁-M₃. Currently, this genus is usually assigned to the Cimolestidae (Didelphodonta, Cimolesta) (McKenna and Bell, 1997).

It was also proposed that a fragmentary maxilla with molars from the Bumban Member of Tsagan-Khushu that was identified as Lipotyphla indet. (Russell and Dashzeveg, 1986, text-fig. 6) belonged to the Geolabididae.

The present paper describes the first unquestionable representative of the Geolabididae from Asia. The specimens under study come from the Zhigden Member of the Naran Bulak Formation of the Tsagan-Khushu locality (collected by the Southern Gobi Party of the Joint Soviet-Mongolian Paleontological Expedition headed by V. Yu. Reshetov in 1987). The Zhigden Member has been dated terminal Late Paleocene, and its fauna is assigned to the Gashatan Asian Land Mammal Age (Badamgarav and Reshetov, 1985; Ting, 1998; Wang *et al.*, 1998). Extinct soricomorph insectivores assigned to the Nyctitheriidae and Micropternodon-

tidae were previously discovered in the Gashatan faunas of Mongolia and China (Matthew and Granger, 1925; Matthew *et al.*, 1929; Szalay and McKenna, 1971; Meng *et al.*, 1998; Lopatin *et al.*, 2001; Kondrashov *et al.*, 2004; Lopatin and Kondrashov, 2004).

SYSTEMATIC PALEONTOLOGY

Family Geolabididae McKenna, 1960

Genus *Gobigeolabis* Lopatin, gen. nov.

Etymology. From the Gobi Desert and the generic name *Geolabis*.

Type species. *G. verigranum* sp. nov.

Diagnosis. P³-M² short and broad, with strongly projecting lingual lobe. Postcingulum of M¹ and M² narrow, lacking hypocone shelf and additional lingual root; conules substantially reduced. Styler shelf of M² relatively narrow, parastylar wing small, additional styler cuspules absent, and ectoflexus small. Metaconid of P₄ well-developed; talonid elongated, narrow, and unicuspid; and lingual talonid basin very small. Trigonid of M₁ and M₂ short, protoconid and metaconid equal in height, entoconid small and low, hypoconulid completely fused with entoconid, and entocristid and ectocingulid absent.

Species composition. Type species.

Comparison. The new genus is distinguished from *Centetodon* Marsh, 1872 (= *Embassis* Cope, 1873; *Geolabis* Cope, 1884; *Proctictops* Peterson, 1934; *Metacodon* Clark, 1936; *Hypacodon* McKenna, 1960) by all the characters of the upper teeth and talonids of the lower molars that are listed in the diagnosis and by the talonid structure of P₄. It is distinguished from *Batodon* Marsh, 1892 by the more strongly developed lingual lobe of P³ and P⁴, the absence of the metacone on P⁴, the narrower styler shelf of the upper molars, the large metaconid of P₄, equal height of the protoconid and metaconid of M₁ and M₂, and by the reduced hypoconulid of M₁ and M₂. It is distinguished from *Batodonoides* Novacek, 1976 by the better developed lingual lobe of P³ and P⁴, the presence of the metaconule, the reduced paraconule, the narrow styler shelves, the absence of additional styler cuspules and preparaconule and postparaconule crests, the cingula of the upper molars that is only slightly developed, the small parastylar wing and the superficial ectoflexus of M², and the absence of an ectocingulid and the shorter trigonids of M₁ and M₂. It is distinguished from *Marsholestes* McKenna et Haase, 1992 by the reduced entoconid and hypoconulid and the absence of an entocristid on M₁ and M₂.

Gobigeolabis verigranum Lopatin, sp. nov.

Etymology. From the Latin *verus* (true) and *granum* (granule, grain).

Holotype. PIN, no. 3104/776, right dentary fragment with P₄-M₂; Mongolia, Tsagan-Khushu locality;



Fig. 1. *Gobigeolabis verigranum* sp. nov., holotype PIN, no. 3104/776, fragmentary right dentary with P₄–M₂, labial view.

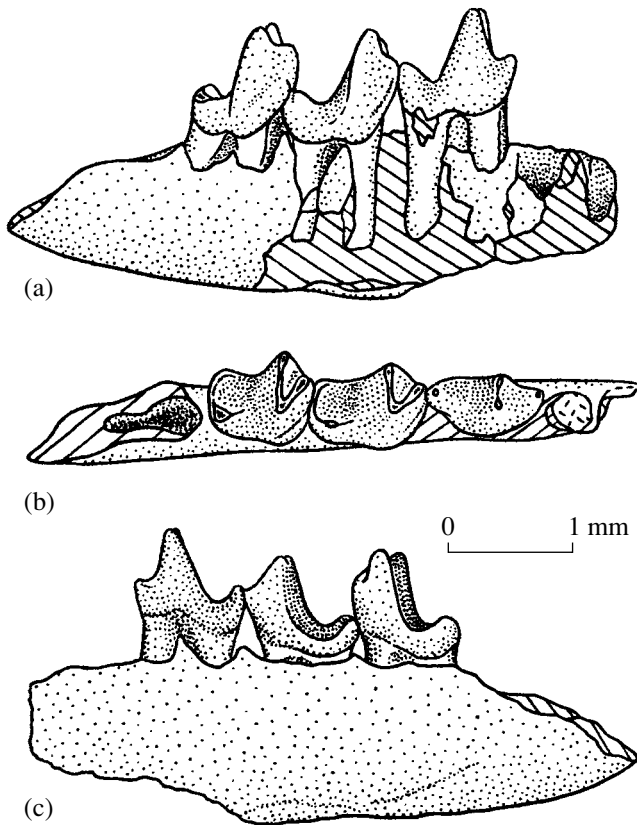


Fig. 2. *Gobigeolabis verigranum* sp. nov., holotype PIN, no. 3104/776, fragmentary right dentary with P₄–M₂: (a) labial, (b) occlusal, and (c) lingual views.

Upper Paleocene, Naran Bulak Formation, Zhigden Member.

Description (Figs. 1–3). An extremely small insectivore, similar in size to the smallest members of the Soricidae.

P³ is small, three-rooted. Its parastyle is small, low, and rounded. The paracone is thick and relatively high. The metastylar crest is short and sharp. The metastyle is poorly developed. The ectocingulum is only slightly

differentiated and only present at the level of the metastylar crest. The protocone strongly projects lingually and is oblique anteriorly. The protocone cusp is low and pointed. The precingulum is absent, while the postcingulum is very narrow, extending along the posterior side of the crown from the protocone to the metastyle.

P⁴ is relatively large, three-rooted. The parastyle is well-developed, conical, has a pointed apex, and strongly projects anteriorly. A short but well-pronounced crest of the preparacrista is present and connects the parastyle with the anterior base of the paracone. The paracone is very high, massive at the base, and narrow at the apex. The metastylar crest is stout and bladelike. The metastyle is small and slightly differentiated. The ectocingulum is poorly pronounced. The protocone is large, wide, and strongly projects lingually but is relatively short. The protocone apex is substantially raised, and the preprotocrista is positioned at a very acute angle to the postprotocrista. The precingulum is absent. The postcingulum is relatively broad and has a distinct projection (without an eminence) in the region of the hypocone.

The upper molars are three-rooted. M¹ and M² strongly expand transversely. M¹ is damaged, only its lingual lobe is preserved. The conules are weak. The protocone is larger than that of P⁴, and the preprotocrista is positioned at a larger angle to the postprotocrista. The cingula are well-developed both anterior and posterior to the protocone; the precingulum is narrow, while the postcingulum is wider and has a weak eminence in place of the hypocone.

M² has a large conical parastyle, which substantially projects anterolabially. The preparacrista is short and relatively high. The paracone is broken. The metacone is relatively high, conical, and somewhat inclined posteriorly. The postmetacrista is thick and high. The metastylar lobe is large and projects posterolabially. The metastyle is small. The ectocingulum is narrow but distinct, being especially well-developed on the metastylar lobe. The paraconule and metaconule are weak and ridgelike. The protocone is more massive than that of M¹, the preprotocrista and postprotocrista are more widely spaced, and the trigon basin is larger. The precingulum is narrow but distinct. The postcingulum is a little weaker than in M¹ but has a clear expansion and eminence in place of the hypocone. M³ is not preserved.

The horizontal ramus of the lower jaw is thin and low, and its lower edge is gently rounded under P₄–M₂. Judging from the alveoli, P₃ was relatively large, only slightly shorter in longitudinal direction than P₄.

P₄ is semimolariform, extended, relatively large, and high, slightly higher than the molars. The paraconid is well-pronounced, high, conical, and occupies a central position on the anterior side of the crown. The paracristid is absent. The protoconid and metaconid are approximately equal in height and stoutness and are tightly fused almost to their apices. The protocristid is transversely positioned and short. The precingulid is

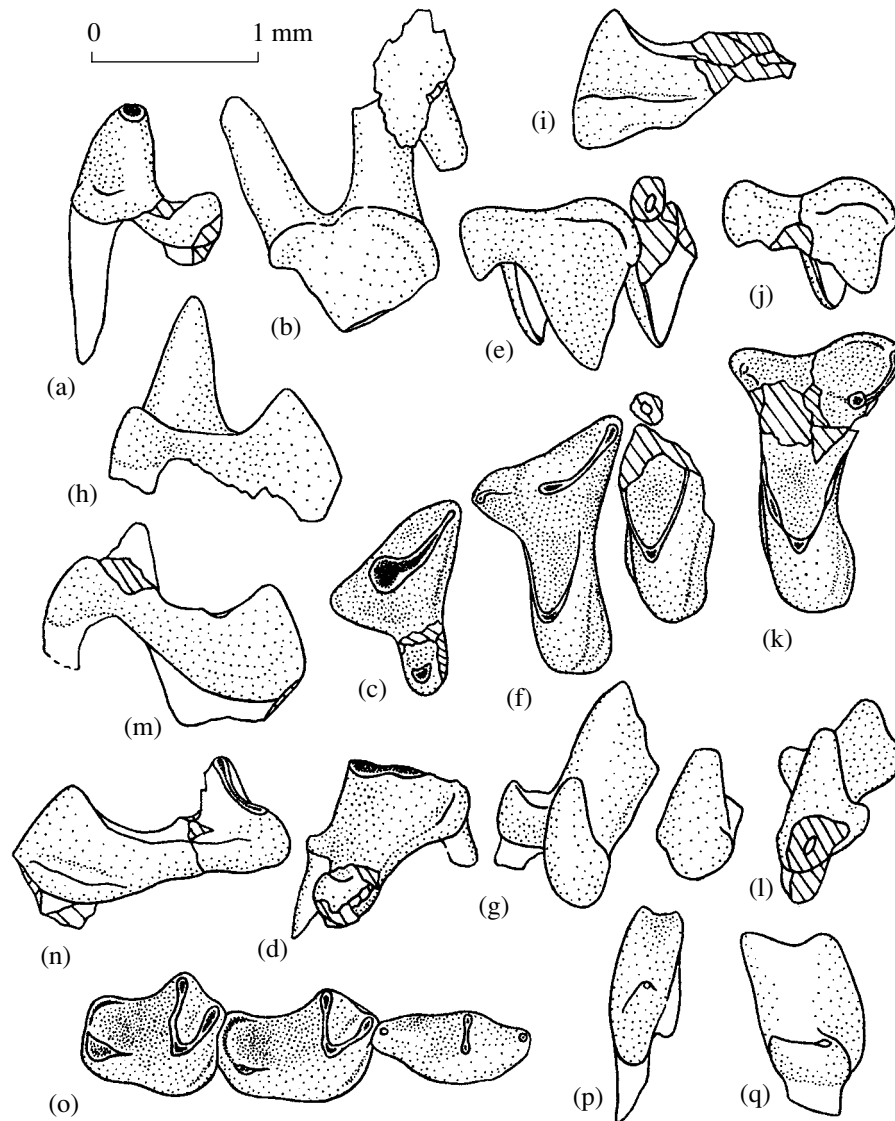


Fig. 3. Teeth of *Gobigeolabis verigranum* sp. nov.: (a–n) specimen PIN, no. 3104/800, left P³–M²: (a–d) P³, (e–g) P⁴ and fragmentary M¹, (h) P⁴, (i) fragmentary M¹, and (j–n) M²; (a, h, m) anterior, (b, e, j) labial, (c, f, k) occlusal, (d, g, l) lingual, and (i, n) rear views; (o–q) holotype PIN, no. 3104/776, right P₄–M₂: (o) P₄–M₂, occlusal view; (p) P₄, anterior view; and (q) M₂ rear view.

absent. The talonid is relatively long and narrow. The longitudinal crest of the talonid (cristid oblique) is very weak. A very small basin is present on the lingual side. The labial side of the talonid is slightly concave. The terminal cuspule of the hypoconid is somewhat displaced lingually and raised to the level of the paraconid apex of M₁.

M₁ and M₂ are similar in structure but differ in shape; M₂ is substantially shorter, has a wider trigonid and a shorter talonid, and its paraconid and metaconid are positioned closer to one another. The trigonid of M₁ and M₂ is longitudinally compressed. The paraconid is small and highly raised. The protoconid and metaconid are fused at the base, equally high, turned slightly

anterolingually with reference to the axis of the tooth row (therefore, the protocristid is subtransverse), and are anterolingually inclined. The precingulid is well-developed at the base of the anterolabial wall of the protoconid (on M₂ it is more prominent than on M₁). The hypoflexid is relatively superficial. The talonid basin is large, shallow, and open lingually. The cusps of the talonid are low. The hypoconid is located in the posterolabial corner of the talonid. The cristid oblique is low and connected to the posterior wall of the trigonid behind the protoconid apex. The entoconid is ridgelike and extends along the posterolingual angle of the occlusal surface from the hypoconid to the midlength of the lingual side of the talonid. The hypoconulid is indiscernible, probably completely fused with the entoconid. In

Table 1. Tooth dimensions (maximum length \times maximum width, mm) and estimated body weight (Y_{m1} , g) in some extremely small Paleogene insectivoran mammals

Species	P ⁴	M ²	P ₄	M ₁	M ₂	Y _{m1}
<i>Gobigeolabis verigranum</i> (Geolabidae), Upper Paleocene of Mongolia: original data	1.10 \times 1.35	1.10 \times 1.65	1.00 \times 0.45	0.95 \times 0.60	0.90 \times 0.65	2.25
<i>Batodonoides vanhouteni</i> (Geolabidae), Lower Eocene of the United States: Bloch <i>et al.</i> , 1998, tables 1 and 2	0.89 \times ?	0.63 \times 1.09	0.76 \times 0.44	0.75 \times 0.54	0.70 \times 0.56	1.3
<i>Bayanulanius tenuis</i> (Nyctitheriidae), Upper Paleocene of China: Meng <i>et al.</i> , 1998, p. 158	–	1.00 \times 1.65	–	–	1.00 \times 0.62	?
<i>Tsaganium ambiguus</i> (Didelphodontidae), Lower Eocene of Mongolia: Russell and Dashzeveg, 1986, p. 286	–	–	0.95 \times 0.60	1.00 \times 0.70	0.90 \times 0.65 0.95 \times 0.73	3.14
<i>Soricolestes soricavus</i> (Soricidae), Middle Eocene of Mongolia: Lopatin, 2002, p. 82	–	–	1.00 \times 0.60 1.05 \times 0.60	1.38 \times 0.95 1.35 \times 1.00	1.33 \times 0.85 1.30 \times 0.95	8.73 9.15

M₁, the boundary between the hypoconid and the entoconid–hypoconulid complex is marked by a small posterolabial fold.

Judging from the alveoli preserved in the specimen, M₃ was somewhat shorter than M₂.

Measurements, mm. P³: tooth length, 1.05; protocone length, 0.3; width (parastyle–protocone), 0.9; paracone height, 0.7; protocone height, 0.4; P⁴: tooth length, 1.1; protocone length, 0.45; width, 1.35; paracone height, 1.05; protocone height, 0.8; M¹: protocone length, 0.55; protocone height, 0.85; M²: tooth length, 1.1; protocone length, 0.6; width, 1.65 (specimen PIN, no. 3104/800).

Length of P₄–M₂, 2.75; length of two alveoli of P₃, ca. 0.8; P₄: tooth length, 1.0; trigonid width, 0.45; talonid width, 0.35; M₁: tooth length, 0.95; trigonid width, 0.6; talonid width, 0.5; M₂: tooth length, 0.9; trigonid width, 0.65; talonid width, 0.5; height of P₄, M₁, and M₂ at the protoconid: 0.9, 0.85, and 0.8, respectively; and lingual depth of the horizontal ramus at M₂, 1.25 (holotype).

Material. In addition to the holotype, specimen PIN, no. 3107/800 from the type locality: P³, P⁴–M¹, and M² from a damaged left maxilla.

DISCUSSION

Gobigeolabis verigranum is assigned to the Geolabidae because it is closely similar to *Centetodon* and *Batodonoides* in the structure of the upper and lower cheek teeth. P₄–M₂ and P⁴ of *Gobigeolabis* are rather similar in shape to those of *Centetodon* (see McKenna, 1960; Setoguchi, 1978, text-fig. 10a; Lillegraven and Tabrum, 1983, text-figs. 3–5) but differ in the wider P³–M². The poorly developed postcingulum (not forming the hypocone shelf) and the nondoubled lingual root of the upper molars, which are also characteristic of the Wasatchian *Batodonoides vanhouteni* (Bloch *et al.*, 1998), are primitive characters for the Geolabidae. The upper molars of the Early Eocene *Centetodon patratius* and *C. neashami* are unknown. In the Middle Eocene *C. pulcher* and *C. bembicophagus*, the lingual

root is not doubled or only slightly bifurcates, in contrast to the later members of this genus (Storer, 1984, 1995; Russell and Dashzeveg, 1986).

Gobigeolabis displays a number of advanced characters (as compared to *Batodonoides*): the large lingual lobes of P³ and P⁴, a narrow stylar shelf and reduced conules of M¹ and M², a shallow ectoflexus and small parastylar wing of M², a long talonid of P₄, and relatively shorter trigonids of M₁ and M₂.

The strongly transversely extended upper molars of *G. verigranum* with their weak postcingula are similar in shape and structure to M¹ and M² of *Batodon tenuis* (Lillegraven, 1969; Storer, 1991, text-fig. 10K), being distinguished by their smaller stylar lobes and smaller conules. With regard to the upper molar structure, *Batodon* is more similar to *Gobigeolabis* than to *Batodonoides* and *Centetodon*. This is not to say that *Gobigeolabis* is an intermediate linking unit between *Batodon* and the Eocene North American Geolabidae; however, this supports the hypothesis that *Batodon* belongs to Soricomorpha.

Thus, *Gobigeolabis verigranum* is the earliest Paleogene member of the family. The fact that it occurs in the Upper Paleocene of Mongolia suggests that the Geolabidae could have emerged in Asia, if *Batodon* did not belong to this family (see Butler, 1988; Wood and Clemens, 2001). Alternatively, the Geolabidae persisted in Asia throughout the Paleocene, i.e., over the time when they were absent from North America. If this is the case, the Early Eocene North American Geolabidae could have descended from immigrants from Asia. Judging from the structure of the upper cheek teeth, *Gobigeolabis* is too highly specialized to be ancestral to the genera *Centetodon* and *Batodonoides*. It probably represents a result of an earlier adaptive radiation of the Geolabidae in Asia.

Gobigeolabis verigranum is one of the smallest Paleogene insectivores (Table 1). Its body weight was estimated using the formula $Y = 1.628X + 1.726$, where Y is the natural logarithm of the body weight (g), and X is the natural logarithm of the product of L (M₁ length

in mm) by W (M_1 width in mm) (Bloch *et al.*, 1998). The value obtained is 2.25 g.

The smallest known mammal is the Early Eocene geolabidid *Batodonoides vanhouteni* (United States, Wyoming, dated as ca. 53 Ma). Based on the dimensions of M_1 , its body weight was estimated as 1.3–2.04 g (Bloch *et al.*, 1998). The body weight of the Early Jurassic *Hadrocodium wui* from China was estimated on the basis of its skull size (12 mm long) as approximately 2 g (Luo *et al.*, 2001).

The smallest living mammals are shrews. The mean weight of *Suncus etruscus* is 2.0–2.5 g (ranging from 1.2 to 2.7 g, its body is 35–53 mm long), *Sorex minutissimus* weighs 1.5–4.0 g, and *Microsorex hoyi* weighs 2–4 g (Nowak, 1991; Fons *et al.*, 1997). The bumblebee bat *Craseonycteris thonglongyai* from Thailand weighs approximately 1.5–3.0 g (adults weigh on average 2 g), and its body is 29–33 mm (*Grzimek's Encyclopedia...*, 1990; Nowak, 1991). Its skull is shorter than that of *Suncus etruscus* (11 and 13 mm long, respectively); however, the relative skull length of bats is shorter than that of shrews. Thus, in terms of the body weight, the smallest animal is *Suncus etruscus*.

It is appropriate at this point to consider the question of how small a mammal can be. It is well known that the smaller a warm-blooded animal is, the greater difficulties it faces in the balance of heat production and heat emission. Below a certain size limit, it can maintain its body temperature only by increased heat production. Therefore, it is generally accepted that the minimum mammal size is directly associated with the limiting parameters of the thermoregulation system and also depends on the ambient temperature (see Strel'nikov, 1970; Bloch *et al.*, 1998). This suggests that, during the geological epochs with relatively warm climate, the smallest mammals could have been smaller than at the present time. However, the lower size limit of warm-blooded vertebrates is not determined by the possibility of retaining heat (the example of insects that warm themselves before flight shows that functionally warm-blooded animals can be much smaller than the smallest birds and mammals), but is restricted by the arrangement of systems that supply tissues with oxygen and the heart as a blood pump (Schmidt-Nielsen, 1984). Apparently, extant warm-blooded vertebrates that follow the path of general miniaturization have already exhausted all possibilities of functional optimization of the blood system. Thus, the minimum body weight of mammals of any geological epoch could not be lower than in the smallest living shrews, i.e., on the average, 1.2–1.5 g in young animals and 2.0–2.5 g in adults.

Small size is a characteristic of the Lipotyphla (especially Soricomorpha) throughout their historical development. Bloch *et al.* (1998) have shown that, at the Paleocene–Eocene boundary, North American members of the Lipotyphla (1.3–53 g of body weight) were the smallest insectivoran placentals and conceded the ecological niches of larger insectivorous mammals

to numerous proteutherians. To date, data on the Early Paleogene of Asia are extremely scarce; however, the occurrence of *Bayanulanius tenuis* (Meng *et al.*, 1998) and *Gobigeolabis verigranum* (Table 1) suggests that, in the Late Paleocene of Asia, the smallest mammals were represented by soricomorph insectivores.

ACKNOWLEDGMENTS

This study was supported by the Russian Foundation for Basic Research (project nos. 01-05-65448, 02-04-48458, 03-04-06798, and 04-05-64805), the Board of the President of the Russian Federation (project nos. MK-726.2004.04 and NSh-1840.2003.4).

REFERENCES

1. D. Badamgarav and V. Yu. Reshetov, *Paleontology and Stratigraphy of the Paleogene of the Transaltai Gobi* (Nauka, Moscow, 1985) [in Russian].
2. M. J. Benton, "Early Origins of Modern Birds and Mammals: Molecules vs. Morphology," *BioEssays* **21** (12), 1043–1051 (1999).
3. J. I. Bloch, K. D. Rose, and P. D. Gingerich, "New Species of *Batodonoides* (Lipotyphla, Geolabididae) from the Early Eocene of Wyoming: Smallest Known Mammal?," *J. Mammal.* **79** (3), 804–827 (1998).
4. T. M. Bown and D. M. Schankler, "A Review of the Proteutheria and Insectivora of the Willwood Formation (Lower Eocene), Bighorn Basin, Wyoming," *Bull. US Geol. Surv.*, No. 1523, 1–79 (1982).
5. P. M. Butler, "On the Evolution of the Skull and Teeth in the Erinaceidae, with Special Reference to Fossil Material in the British Museum," *Proc. Zool. Soc. London, Ser. B* **118**, 446–500 (1948).
6. P. M. Butler, "The Problem of Insectivore Classification," in *Studies of Vertebrate Evolution*, Ed. by K. A. Joysey and T. S. Kemp (Oliver and Boyd, Edinburgh, 1972), pp. 253–265.
7. P. M. Butler, "Phylogeny of the Insectivores," in *The Phylogeny and Classification of the Tetrapods*, Vol. 2: *Mammals*, Ed. by M. J. Benton (Clarendon, Oxford, 1988), pp. 117–141.
8. J. Clark, "Status of the Generic Names *Metacodon* and *Geolabis* (Insectivore)," *J. Paleontol.* **40** (5), 1248–1251 (1966).
9. W. A. Clemens, "Fossil Mammals of the Type Lance Formation, Wyoming: Part 3. Eutheria and Summery," *Univ. California Publ. Geol. Sci.* **94**, 1–102 (1973).
10. R. Fons, S. Sender, T. Peters, and K.-D. Jurgens, "Rates of Rewarming, Heart and Respiratory Rates and Their Significance for Oxygen Transport During Arousal from Torpor in the Smallest Mammal, the Etruscan Shrew *Suncus etruscus*," *J. Experim. Biol.* **200**, 1451–1458 (1997).
11. E. C. Galbreath, "A contribution to the Tertiary Geology and Paleontology of Northeastern Colorado," *Paleontol. Contrib. Univ. Kansas*, No. 13, Part 4, 1–120 (1953).
12. *Grzimek's Encyclopedia of Mammals* (McGraw-Hill, New York, 1990).

13. A. A. Gureev, "Insectivores (Mammalia, Insectivora): Hedgehogs, Moles, and Shrews (Erinaceidae, Talpidae, Soricidae)," *Fauna of the USSR: Mammals* (Nauka: Leningrad, 1979), Vol. 4, No. 2 [in Russian].
14. Z. Kielan-Jaworowska, T. M. Bown, and J. A. Lillegraven, "Eutheria," in *Mesozoic Mammals: The First Two-Thirds of Mammalian History*, Ed. by J. A. Lillegraven, Z. Kielan-Jaworowska, and W. A. Clemens (Univ. California Press, Berkeley, 1979), pp. 221–258.
15. P. E. Kondrashov, A. V. Lopatin, and S. G. Lucas, "Late Paleocene (Gashatan) Nyctitheriidae (Mammalia, Lipotyphla) from Mongolia," *Bull. New Mexico Mus. Natur. Hist. Sci.*, No. 26, 185–193 (2004).
16. J. A. Lillegraven, "Latest Cretaceous Mammals of Upper Part of Edmonton Formation of Alberta, Canada, and Review of Marsupial–Placental Dichotomy in Mammalian Evolution," *Paleontol. Contrib. Univ. Kansas*, No. 50, 1–122 (1969).
17. J. A. Lillegraven, M. C. McKenna, and L. Krishtalka, "Evolutionary Relationships of Middle Eocene and Younger Species of *Centetodon* (Mammalia, Insectivora, Geolabididae) with a Description of the Dentition of *Ankyledon* (Adapisoricidae)," *Univ. Wyoming Publ.*, No. 45, 1–115 (1981).
18. J. A. Lillegraven and A. R. Tabrum, "A New Species of *Centetodon* (Mammalia, Insectivora, Geolabididae) from Southwestern Montana and Its Biogeographical Implications," *Contrib. Geol. Univ. Wyoming* **22** (1), 57–73 (1983).
19. A. V. Lopatin, "The Earliest Shrew (Soricidae, Mammalia) from the Middle Eocene of Mongolia," *Paleontol. Zh.*, No. 6, 78–87 (2002) [*Paleontol. J.*, No. 6, 650–659 (2002)].
20. A. V. Lopatin and P. E. Kondrashov, "Sarcodontinae, a New Subfamily of Micropternodontid Insectivores from the Early Paleocene–Middle Eocene of Asia," *Bull. New Mexico Mus. Natur. Hist. Sci.*, No. 26, pp. 177–184 (2004).
21. A. V. Lopatin, P. E. Kondrashov, and S. G. Lucas, "Late Paleocene (Gashatan) Mammal Fauna from the Tsagan Khushu Locality (Mongolia)," *J. Vertebr. Paleontol.* **21** (3, Suppl.), 74A (2001).
22. Z. X. Luo, A. W. Crompton, and A. L. Sun, "New Mammaliaform from the Early Jurassic and Evolution of Mammalian Characteristic," *Science* **292** (5521), 1535–1540 (2001).
23. W. D. Matthew and W. Granger, "Fauna and Correlation of the Gashato Formation of Mongolia," *Am. Mus. Novit.*, No. 189, 1–12 (1925).
24. W. D. Matthew, W. Granger, and G. G. Simpson, "Additions to the Fauna of the Gashato Formation of Mongolia," *Am. Mus. Novit.*, No. 376, 1–12 (1929).
25. M. C. McKenna, "The Geolabidinae, a New Subfamily of Early Cenozoic Erinaceoid Insectivores," *Univ. California Publ. Geol. Sci.* **37** (2), 131–164 (1960).
26. M. C. McKenna, "Toward a Phylogenetic Classification of the Mammalia," in *Phylogeny of the Primates: A Multidisciplinary Approach*, Ed. by W. P. Luckett and F. S. Szalay (Plenum Press, New York, 1975), pp. 21–46.
27. M. C. McKenna and S. K. Bell, *Classification of Mammals above the Species Level* (Columbia Univ. Press, New York, 1997).
28. M. C. McKenna and F. Haase, "*Marsholestes*, a New Name for the Eocene Insectivoran *Myolestes* Matthew, 1909, not *Myolestes* Brèthes, 1904," *J. Vertebr. Paleontol.* **12** (2), 256 (1992).
29. M. C. McKenna, P. Robinson, and D. W. Taylor, "Notes on Eocene Mammalia and Mollusca from Tabernacle Butte, Wyoming," *Am. Mus. Novit.*, No. 2102, 1–33 (1962).
30. J. Meng, R. Zhai, and A. R. Wyss, "The Late Paleocene Bayan Ulan Fauna of Inner Mongolia, China," *Bull. Carnegie Mus. Natur. Hist.*, No. 34, 148–185 (1998).
31. M. J. Novacek, "Insectivora and Proteutheria of the Later Eocene (Uintan) of San Diego County, California," *Contrib. Sci. Los Angeles County Natur. Hist. Mus.*, No. 283, 1–52 (1976).
32. R. M. Nowak, *Walker's Mammals of the World* (Johns Hopkins Univ. Press, Baltimore, 1991), Vol. 1.
33. B. Patterson and P. O. McGrew, "A Soricid and Two Erinaceids from the White River Oligocene," *Field Mus. Natur. Hist., Geol. Ser.* **6**, 245–272 (1937).
34. P. Robinson, "Nyctitheriidae (Mammalia, Insectivora) from the Bridger Formation of Wyoming," *Contrib. Geol. Univ. Wyoming* **7** (2), 129–138 (1968).
35. D. A. Russell, "A Review of the Oligocene Insectivore *Micropternodus borealis*," *J. Paleontol.* **34** (5), 940–949 (1960).
36. D. E. Russell and D. Dashzeveg, "Early Eocene Insectivores (Mammalia) from the People's Republic of Mongolia," *Palaeontology* **29** (2), 269–291 (1986).
37. R. Saban, "Insectivora," in *Traité de paléontologie, T. 6* (Masson et Cie, Paris, 1958), Vol. 2, pp. 822–909.
38. K. Schmidt-Nielsen, *Scaling: Why Is Animal Size So Important?* (Cambridge Univ. Press, Cambridge, 1984).
39. E. R. Seiffert and E. L. Simons, "Widanelfarasia, a diminutive placental from the late Eocene of Egypt," *Proc. Nat. Acad. Sci. USA* **97** (6), 2646–2651 (2000).
40. T. Setoguchi, "Paleontology and Geology of the Badwater Creek Area, Central Wyoming: Part 16. The Cedar Ridge Local Fauna (Late Oligocene)," *Bull. Carnegie Mus. Natur. Hist.*, No. 9, 1–61 (1978).
41. B. Sigé, "Insectivores primitifs de l'éocène supérieur et Oligocène inférieur d'Europe occidentale: Nyctithériidés," *Mém. Mus. Nat. Hist. Natur., Sér. C* **34**, 1–140 (1976).
42. G. G. Simpson, "The Principles of Classification and Classification of Mammals," *Bull. Am. Mus. Natur. Hist.* **85**, 1–350 (1945).
43. J. E. Storer, "Mammals of the Swift Current Creek Local Fauna (Eocene: Uintan, Saskatchewan)," *Contrib. Saskatchewan Mus. Natur. Hist.*, No. 7, 1–158 (1984).
44. J. E. Storer, "The Mammals of the Gryde Local Fauna, Frenchman Formation (Maastrichtian: Lancian), Saskatchewan," *J. Vertebr. Paleontol.* **11** (3), 350–369 (1991).
45. J. E. Storer, "Small Mammals of the Lac Pelletier Lower Fauna, Duchesnean of Saskatchewan, Canada: Insectivores and Insectivore-like Groups, a Plagemenid, a Microsypid and Chiroptera," in *Vertebrate Fossils and the Evolution of Scientific Concepts*, Ed. by W. A. S. Sargeant (Gordon and Breach Publ., Saskatoon, 1995), pp. 595–615.

46. I. D. Strel'nikov, *Anatomical and Physiological Foundations of Speciation in Vertebrates* (Nauka: Leningrad, 1970) [in Russian].
47. F. S. Szalay and R. L. Decker, "Origins, Evolution, and Function of the Tarsus in the Late Cretaceous Eutheria and Paleocene Primates," in *Primate Locomotion*, Ed. by F. A. Jenkins. N.Y.: Academic, New York, 1974, pp. 223–259.
48. F. S. Szalay and M. C. McKenna, "Beginning of the Age of Mammals in Asia: The Late Paleocene Gashato Fauna, Mongolia," *Bull. Am. Mus. Natur. Hist.* **144**, 269–318 (1971).
49. S. Ting, "Paleocene and Early Eocene Land Mammal Ages of Asia," *Bull. Carnegie Mus. Natur. Hist.*, No. 34, 124–147 (1998).
50. L. Van Valen, "New Paleocene Insectivores and Insectivore Classification," *Bull. Am. Mus. Natur. Hist.* **135** (5), 217–284 (1967).
51. Y. Wang, Y. Hu, M. Chow, and Ch. Li, "Chinese Paleocene Mammal Faunas and Their Correlation," *Bull. Carnegie Mus. Natur. Hist.*, No. 34, 89–123 (1998).
52. H. P. Whidden and R. J. Asher, "The Origin of the Greater Antillean Insectivorans," in *Biogeography of the West Indies, Patterns and Perspectives*, Ed. by C. A. Woods and F. Sergile (CRC Press, Boca Raton, 2001), pp. 237–252.
53. C. B. Wood and W. A. Clemens, "A New Specimen and a Functional Re-association of the Molar Dentition of *Batodon tenuis* (Placentalia, incertae sedis), Latest Cretaceous (Lancian), North America," *Bull. Mus. Compar. Zool.* **156** (1), 99–118 (2001).