

The Largest Asiatic *Amphechinus* (Erinaceidae, Insectivora, Mammalia) from the Oligocene of Mongolia

A. V. Lopatin

Paleontological Institute, Russian Academy of Sciences, Profsoyuznaya ul. 123, Moscow, 117997 Russia
e-mail: alop@paleo.ru

Received October 26, 2000

Abstract—A lower jaw fragment of a new hedgehog species, *Amphechinus gigas* sp. nov., from the Oligocene Shand-Gol Formation of Mongolia is described. This species is substantially larger than *A. rectus*, *A. akespensis*, and other known *Amphechinus* species from Asia and comparable in size to the European species *A. robustus*, *A. ginsburgi*, and *A. intermedius*. Regarding the length of the lower cheek tooth row, *A. gigas* is comparable to Recent *Erinaceus europaeus*; however, the much deeper and more massive horizontal ramus of the dentary shows that *A. gigas* is larger than the latter.

INTRODUCTION

Amphechinus belongs to the earliest genera of the subfamily Erinaceinae. This genus was widespread in the Oligocene and Miocene of Eurasia and occurred in the Miocene of North America and Africa (Gureev, 1979; Gould, 1995). The following six species were described from Asia: Oligocene *A. rectus* (Matthew et Granger, 1924), *A. kansuensis* (Bohlin, 1942), and *A. minimus* (Bohlin, 1942) from China and Mongolia; Early Miocene *A. akespensis* Lopatin, 1999 and *A. microdus* Lopatin, 1999 from Kazakhstan; and Early Miocene *A. bohlini* Bi, 2000 from China (Matthew and Granger, 1924; Bohlin, 1942; Trofimov, 1960; Mellett, 1968; Sulimski, 1970; Huang, 1984; Lopatin, 1999; Bi, 2000). *A. minimus* and *A. microdus* are small, i.e., comparable in size to living *Sorex araneus* L. *A. kansuensis* and *A. bohlini* are somewhat larger. *A. rectus* and *A. akespensis* are only slightly smaller than *Erinaceus europaeus* L. Late Oligocene *A. arvernensis* (Blainville, 1839) and Early Miocene *A. edwardsi* (Filhol, 1879) from Europe are of approximately the same size. Certain European species of *Amphechinus*, i.e., Oligocene *A. robustus* (Lavocat, 1951); Middle Miocene *A. ginsburgi* Baudelot, 1972; and *A. intermedius* (Gailard, 1899) are as large as Recent *Erinaceus europaeus*. *Postpalerinaceus vireti* (Crusafont Pairo et Villalta, 1947) from the Pliocene of Spain is larger than all the above-listed species. Crusafont Pairo and Villalta (1947) and Gould (1995) assigned *P. vireti* to the genus *Amphechinus* (= *Palaeoerinaceus*, *Palerinaceus*), whereas Gureev (1979) assigned it to a particular subgenus of the genus *Erinaceus*.

The present study describes a new species of the genus *Amphechinus* from the Lower Oligocene of Mongolia. Regarding the tooth measurements, the new species is comparable to *A. robustus*, *A. ginsburgi*, *A. intermedius*, *Postpalerinaceus vireti*, and *Erinaceus*

europaeus; at the same time, its lower jaw is substantially larger and more massive than those of the listed species. The fragmentary lower jaw of the new species was found together with *A. rectus* and *A. cf. kansuensis*.

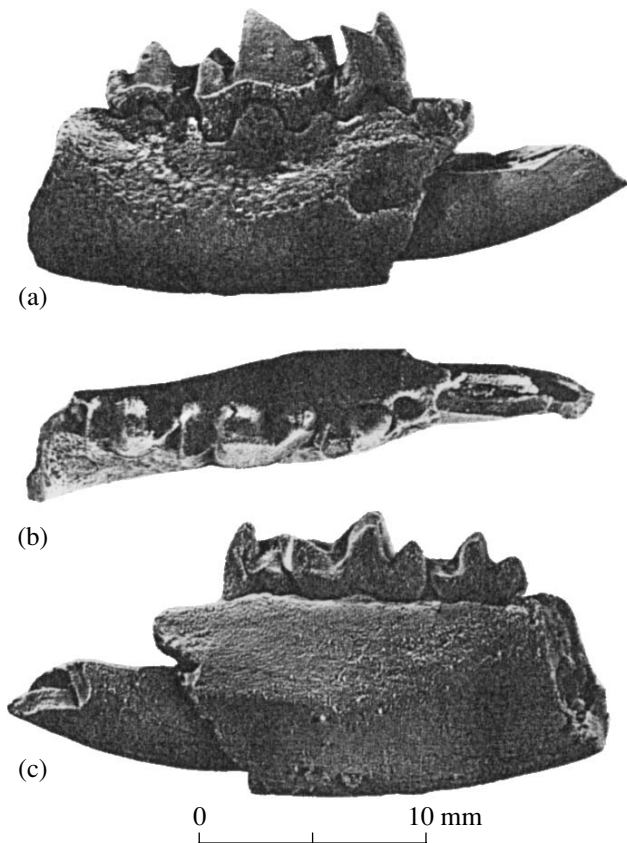


Fig. 1. *Amphechinus gigas* sp. nov., holotype PIN, no. 4567/14, fragmentary right dentary containing P₄–M₂: (a) labial, (b) occlusal, and (c) lingual views.

The material comes from the Shand-Gol Formation. The specimens were found in a bed located 10–15 m above a basalt layer in the eastern slope of the Khunuk Valley, opposite to the Menkhen-Teg locality in the Valley of Lakes (collected by E.V. Devyatkin and I.G. Liskun, 1972). The material on *A. rectus* from several Shand-Gol localities (Ulan-Khurekh 1, collected by V.Yu. Reshetov in 1979; Tsagan-Obo 3 and Elste-Turamne-Ar, collected by E.K. Sytchevskaya in 1993 and 1995) and specimen PIN, no. 475/1200 from the Tatal-Gol locality, described by Trofimov (1960), were used for comparison.

The following abbreviations are used in this paper: (PIN) Paleontological Institute of the Russian Academy of Sciences, Moscow, and (IVPP) Institute of Vertebrate Paleontology and Paleoanthropology, Beijing.

SYSTEMATIC PALEONTOLOGY

Family Erinaceidae Fischer, 1817

Subfamily Erinaceinae Fischer, 1817

Tribe Amphechinini Gureev, 1979

Genus *Amphechinus* Aymard, 1850

Amphechinus gigas Lopatin, sp. nov.

Amphechinus cf. *rectus*: Huang, 1984, p. 308, pl. I, fig. 12.

E t y m o l o g y. From the Greek *gigas* (giant).

H o l o t y p e. PIN, no. 4567/14, fragmentary right dentary containing P_4 – M_2 ; Mongolia, Khunuk locality; Lower Oligocene, Shand-Gol Formation.

D e s c r i p t i o n (Figs. 1, 2, and 3a). A large hedgehog, P_4 – M_3 is approximately 15 mm long, and M_1 – M_3 is approximately 12 mm long. The horizontal ramus of the lower jaw is deep and massive. The large mental foramen is on a level with the posterior root of P_4 . The I_2 is stout. Judging by the preserved alveoli, the canine was larger than the anterior premolar.

P_4 has a weakly developed posterior cingulid. The paraconid is somewhat higher than the protoconid. The protoconid is noticeably posteriorly inclined. Metaconid is absent, the lingual wall of the protoconid is almost straight, flat, and only slightly inflated at the base. The talonid is very short but broad, broader than the trigonid.

M_1 is large and long, the trigonid is more than two-thirds as long as the entire M_1 . The labial cingulid is well developed and broad, the postcingulid is extremely weak. The paraconid is large and massive. The paralophid is long and has a weak notch. The protoconid is substantially more massive and higher than the metaconid. The metalophid notch looks like a small depression between the apices of the protoconid and the metaconid. The metastylid is undeveloped. The talonid is substantially shorter than the trigonid, but it is of the same width. The entoconid is higher than the hypoconid, strongly longitudinally compressed, and extends anteriorly to form a relatively high and straight entocristid, which encloses lingually the talonid basin. The

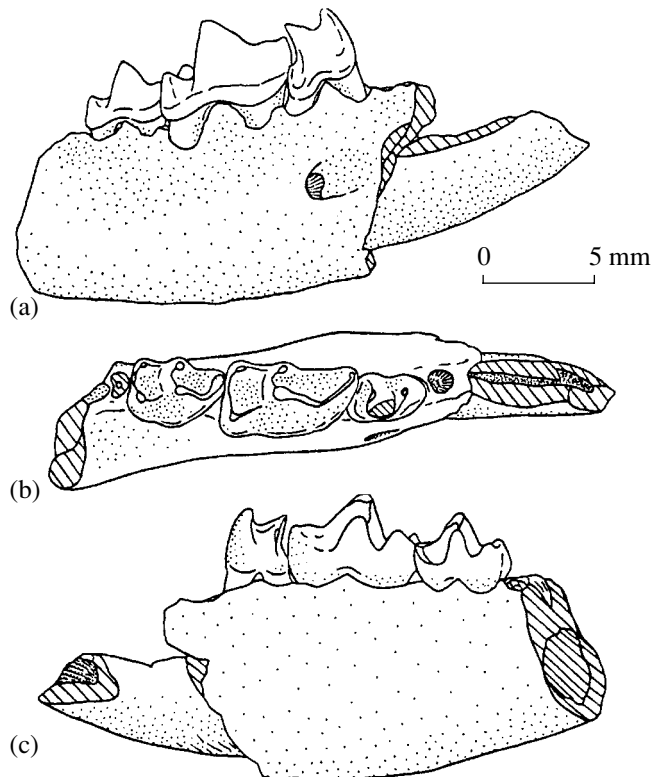


Fig. 2. *Amphechinus gigas* sp. nov., holotype PIN, no. 4567/14, fragmentary right dentary containing P_4 – M_2 : (a) labial, (b) occlusal, and (c) lingual views.

cristid oblique connects the hypoconid to the middle of the posterior base of the protoconid. The metalophid and the posterolophid curve posteriorly; the entocristid and the cristid oblique extend almost in parallel to the longitudinal tooth axis.

M_2 is almost 1.5 times shorter than M_1 . The trigonid is slightly broader and 1.7 times longer than the talonid. M_2 is similar to M_1 in structural pattern, but differs in certain features, i.e., the paralophid is shortened, the metaconid is reduced to a lesser extent, and the metastylid looks like a weak projection.

M_3 is represented by the anterior root located in the alveolus and by the anterior wall of the alveolus of the posterior root. Judging from the arrangement and measurements of these structures, M_3 was at most half as long as M_2 .

M e a s u r e m e n t s, mm. Holotype: length of P_4 – M_2 is 12.6; length of M_1 – M_2 , 9.7; length \times width: (P_4) 3.2×2.1 ; (M_1) 5.8×3.1 (trigonid, 4.0×3.1 ; talonid, 1.8×3.1); and (M_2) 4.0×2.75 (trigonid, 2.5×2.75 ; talonid, 1.5×2.45); dentary depth at P_4 and M_1 , 8.0; at M_2 , 8.2; and at M_3 , 7.7; dentary thickness at P_4 , 4.9; at M_1 , 4.3; and at M_2 , 4.2.

C o m p a r i s o n. *A. gigas* sp. nov. differs from all known species of the genus by very large measurements (table) and extremely massive lower jaw. In

Measurements of teeth and lower jaws of large-sized hedgehog species (*Ampechinus*, *Postpalerinaceus*, and *Erinaceus*)

Species	Reference	P ₄ -M ₃	P ₄ -M ₂	M ₁ -M ₃	M ₁ -M ₂	P ₄	M ₁	M ₂	M ₂ /M ₁	Jaw depth under P ₄ -M ₁
<i>A. rectus</i>	Huang, 1984	–	–	7.5–8.1	–	1.4–2.5	3.7–4.4	2.4–3.2	0.62–0.74	3.9–5.1
	PIN, no. 475/1200	11.5	9.9	9.0	7.3	2.6	4.4	3.3	0.75	6.6
	PIN, no. 4567/12	about 12.0	about 10.0	9.7	7.5	–	4.7	3.3	0.70	6.6
<i>A. akespensis</i>	Lopatin, 1999	–	10.5	–	–	2.8	4.7–4.8	3.5	0.73	6.5
<i>A. arvernensis</i>	Baudelot, 1972	11.2	–	9.0	–	2.4	4.4	3.4	0.79	6.03
	Ziegler, 1998	–	–	–	–	2.62–2.98	3.93–4.38	2.9–3.54	0.74–0.81	4.05–5.25
<i>A. edwardsi</i>	Baudelot, 1972	11.2	–	9.0	–	2.8	4.4	3.2	0.75	5.7–6.0
	Ziegler, 1990	–	–	–	–	2.6–3.15	4.01–5.0	3.32–3.61	–	–
<i>A. gigas</i>	holotype	about 15.0	12.6	about 12.0	9.7	3.2	5.8	4.0	0.69	8.0
<i>A. robustus</i>	Huang, 1984	–	–	–	–	–	5.9	–	–	–
	Lavocat, 1951	–	12.0	10.0–11.0	9.0	2.7	4.95	3.9	0.79	6.1
	Ziegler, 1990	–	–	–	–	2.75	–	3.53	–	–
	Ziegler, 1998	–	–	–	–	4.11–4.35	5.4–6.2	4.17–4.8	0.77	6.0–6.9
<i>A. ginsburgi</i>	Baudelot, 1972	14.6–14.9	–	11.3–11.5	–	3.2–3.47	5.2–5.34	4.38	0.82	6.2–7.0
<i>A. intermedius</i>	Baudelot, 1972	15.0	–	11.5	–	3.8	5.5	4.5	0.86	7.0
<i>P. vireti</i>	Baudelot, 1972	–	–	–	–	3.52–3.84	5.52–6.04	4.6–5.3	0.85	7.2
<i>E. europaeus</i>	collection PIN	15.0–15.3	12.7–13.5	12.3–12.4	10.0–10.3	3.5	5.5–5.9	4.5–4.9	0.81–0.83	5.4–5.9

addition, it differs from the majority of species by the structure of P₄ (in which the paraconid is higher than the protoconid and metaconid is absent) and by the presence of double-rooted M₃. The new species differs from the most similar species from Asia (*A. rectus* and *A. akespensis*) by the absence of metaconid on P₄ and certain structural details of the lower molars, in particular, weak postcingulids of M₁ and M₂ and the absence of metastylid on M₁.

Remarks. Judging from the measurements (5.9 mm long and 3.3 mm wide) and structure, the large M₁ (specimen IVPP, no. V7340) from the Ulan-tatal locality of China, which was initially determined as *A. cf. rectus* (Huang, 1984), actually belongs to *A. gigas*.

Occurrence. Lower Oligocene of Mongolia and China.

Material. Holotype.

DISCUSSION

The Recent Erinaceidae are divisible into three groups by measurements: small, in which the body is 10–15 cm long and the skull is 30–40 mm long;

medium-sized, the body is 15–30 cm long, the skull is 41–63 mm long; and large forms, the body is 31–45 cm long and the skull is 60–87 mm long. The first group comprises the shrew-hedgehogs *Hylomys* (including *Neotetracus* and *Neohylomys*) and *Podogymnura*, the second comprises the true hedgehogs *Hemiechinus*, *Paraechinus*, and *Erinaceus* (including *Aterix* and *Mesechinus*), and the third includes the gymnura *Echinorex gymnurus*. The largest member of true hedgehogs (Erinaceinae) is the European hedgehog *Erinaceus europaeus* (Gureev, 1979), the body of which is 19.5–30 cm long, and the skull is 43–63 mm long.

Extinct hedgehogs include certain giant insectivores. In particular, the skull of *Deinogalerix koenigswaldi* Freudenthal, 1972 from the Late Miocene of Italy (Gargano) is 210–223 mm long (Freudenthal, 1972). Judging from the reconstructed skeleton, the body of this shrew-hedgehog was approximately 60–70 cm long. Quite apparently, this is an exception accounted for by the insular gigantism (Guérin, 1997); in general, extinct hedgehogs that are comparable in size to *Erinaceus europaeus* should be regarded as large erinaceids. Only a small number of such forms occurred in the Oligocene and Miocene of Eurasia; these were mainly the

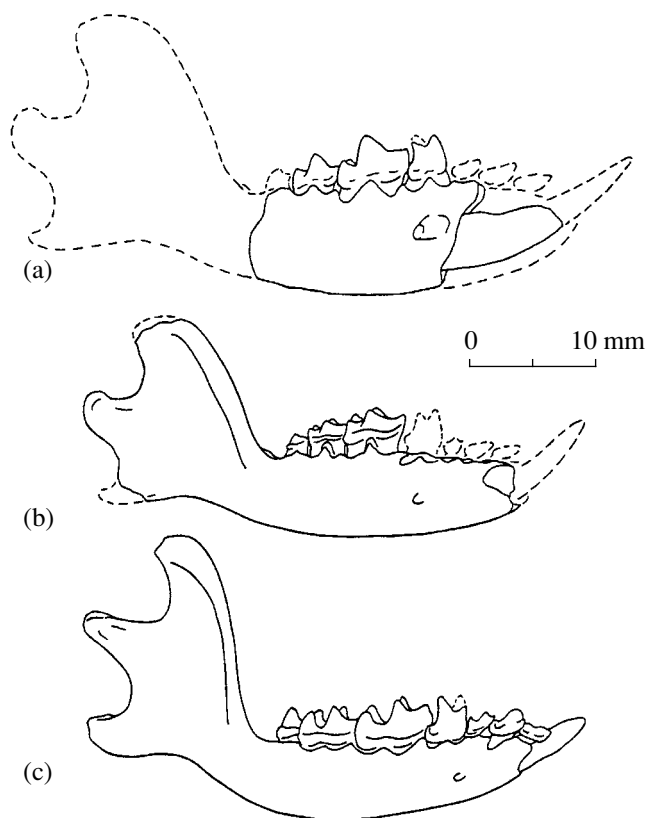


Fig. 3. Comparison of lower jaw measurements of the Erinaceidae: (a) *Amphechinus gigas* sp. nov., reconstructed based on holotype PIN, no. 4567/14; (b) *A. rectus* (Matthew et Granger), reconstructed based on specimen PIN, no. 4567/12, right dentary with M_1 – M_3 ; Mongolia, Khunuk locality; Lower Oligocene, Shand-Gol Formation; and (c) *Erinaceus europaeus* L., specimen PIN, no. 2/473, right dentary; Russia, Recent.

above-mentioned species of the genus *Amphechinus*. Certain members of the Brachyericinae also reach relatively large sizes; in particular, the skull of Late Oligocene *Metexallerix gaolanshanensis* Qiu et Gu, 1988 from China is approximately 50 mm long (Qiu and Gu, 1988).

The table shows the tooth measurements of large-sized species of *Amphechinus* and proper hedgehogs. The teeth of *Amphechinus* are relatively small and the horizontal ramus of the lower jaw is relatively deeper and more massive than those of *Erinaceus* (Fig. 3); therefore, it is impossible to perform direct comparisons of sizes between the members of these genera. Based on the ratios between the lengths of the lower tooth row (table), lower jaw, and skull in certain European species of the genus *Amphechinus* (the skulls of *A. arvernensis* and *A. edwardsi* are approximately 35 mm long), it is possible to estimate the measurements of the species from Asia as follows: the skulls of *A. minimus* and *A. microdus* are approximately 20 mm long, those of *A. kansuensis* and *A. bohlini* are about

25 mm long, those of *A. rectus* and *A. akespensis* are about 30–45 mm long, and those of *A. gigas* are about 55–60 mm long.

To date, the following species of the family Erinaceidae have been found in the Shand-Gol Fauna of Mongolia and northern China: *Tupaiodon morrissi* and *Zaraalestes minutus* (Tupaiodontinae); *Exallerix hsandagolensis* (Brachyericinae); and *Palaeosceptor acridens*, *Amphechinus rectus*, and *A. cf. minimus* (Erinaceinae) (Matthew and Granger, 1924; Trofimov, 1960; McKenna and Holton, 1967; Mellett, 1968; Sulimski, 1970; Huang, 1984). Taking into account the preliminary study of the Oligocene Erinaceidae from Mongolia stored at the PIN, the number of *Amphechinus* species recorded in the Shand-Gol Fauna increases by four; these are *A. cf. minimus*, *A. cf. kansuensis*, *A. rectus*, and *A. gigas*. These species are well distinguished from each other not only by the dental structure but also by the measurements. This fact is evidence of adaptive radiation of Oligocene *Amphechinus* and explains the presence of a large number of sympatric species of the same genus in Central Asia. As far as is known (Bohlin, 1942; Bendukidze, 1993; Lopatin, 1999; Meng *et al.*, 1999; Bi, 2000), the differentiation in size of the *Amphechinus* species remained in Asia at the end of the Late Oligocene (*A. minimus*, *A. kansuensis*, and *A. cf. rectus*) and early in the Miocene (*A. microdus*, *A. bohlini*, and *A. akespensis*); however, the species comparable in size to *A. gigas* have not been recorded in the deposits of this age.

ACKNOWLEDGMENTS

This study was supported by the Russian Foundation for Basic Research, project nos. 98-04-49089, 99-04-48636, and 00-15-97754.

REFERENCES

- Baudelot, S., Étude des chiroptères, insectivores et rongeurs du Miocène de Sansan (Gers), *These Univ. Toulouse*, 1972, no. 496.
- Bendukidze, O.G., *Melkie mlekopitayushchie miotsena Yugo-Zapadnogo Kazakhstana i Turgaya* (Small Mammals from the Miocene of Southwestern Kazakhstan and Turgay), Tbilisi: Metsniereba, 1993.
- Bi, Sh.-D., Erinaceidae from the Early Miocene of North Junggar Basin, Xinjiang Uygur Autonomous Region, China, *Vertebr. Palasiat*, 2000, vol. 38, no. 1, pp. 43–51.
- Bohlin, B., The Fossil Mammals from the Tertiary Deposits of Taben-Buluk, Western Kansu. Part 1: Insectivora and Lagomorpha, *Palaeontol. Sin., Nov. Ser. C*, 1942, no. 8a, pp. 40–99.
- Crusafont Pairo, M. and Villalta, J.F., Sur un nouveau *Palerinaeus* du Pontien d'Espagne, *Ecol. Geol. Helv.*, 1947, vol. 40, no. 2, pp. 320–333.
- Freudenthal, M., *Deinogalerix koenigswaldi* nov. gen., nov. spec., a Giant Insectivore from the Neogene of Italy, *Scr. Geol.*, 1972, no. 14, pp. 1–19.

- Gould, G.C., Hedgehog Phylogeny (Mammalia, Erinaceidae)—the Reciprocal Illumination of the Quick and the Dead, *Am. Mus. Novit.*, 1995, no. 3131, pp. 1–45.
- Guérin, C., Le nanisme insulaire au Quaternaire, *Bull. Mens. Soc. Linn. Lyon*, 1997, vol. 66, no. 3, pp. 69–80.
- Gureev, A.A., Insectivores (Mammalia, Insectivora): Hedgehogs, Moles, and Shrews (Erinaceidae, Talpidae, Soricidae), *Fauna SSSR. Mlekopitayushchie* (Fauna of the USSR: Mammals), Leningrad: Nauka, 1979, vol. 4, no. 2.
- Huang, X., Fossil Erinaceidae (Insectivora, Mammalia) from the Middle Oligocene of Ulanatal, Alxa Zouqi, Nei Mongol, *Vertebr. Palasiat.*, 1984, vol. 22, no. 4, pp. 305–309.
- Lavocat, R., *Révision de la faune des mammifères oligocènes d'Auvergne et du Velay*, Paris: Sci. et Avenir, 1951.
- Lopatin, A.V., The Stratigraphy and Small Mammals from the Aral Formation of the Altynshokysu (North Aral Region), *Stratigr. Geol. Korrelyatsiya* (Moscow), 1996, vol. 4, no. 2, pp. 65–79.
- Lopatin, A.V., Oligocene and Early Miocene Insectivores (Insectivora, Mammalia) from Western Kazakhstan, *Paleontol. Zh.*, 1999, no. 2, pp. 66–75.
- Matthew, W.D. and Granger, W., New Insectivores and Ruminants from the Tertiary of Mongolia, with Remarks on the Correlation, *Am. Mus. Novit.*, 1924, no. 105, pp. 1–7.
- McKenna, M.C. and Holton, C.P., A New Insectivore from the Oligocene of Mongolia and a New Subfamily of Hedgehogs, *Am. Mus. Novit.*, 1967, no. 2311, pp. 1–11.
- Mellett, J.S., The Oligocene Hsanda Gol Formation, Mongolia: A Revised Faunal List, *Am. Mus. Novit.*, 1968, no. 2318, pp. 1–16.
- Meng, J., Ye, J., Wu, W.-Y., and Bi, Sh.-D., The Petrosal Morphology of the Late Oligocene Erinaceid from North Junggar Basin, *Vertebr. Palasiat.*, 1999, vol. 37, no. 4, pp. 300–308.
- Qiu, Z.X. and Gu, Z.G., A New Locality Yielding Mid-Tertiary Mammals near Lanzhou, Gansu, *Vertebr. Palasiat.*, 1988, vol. 26, no. 3, pp. 198–213.
- Sulimski, A., On Some Oligocene Insectivore Remains from Mongolia, *Palaeontol. Pol.*, 1970, no. 21, pp. 53–70.
- Trofimov, B.A., Insectivores of the Genus *Palaeoscaptor* from the Oligocene of Asia, *Tr. Paleontol. Inst. Akad. Nauk SSSR* (Moscow), 1960, vol. 77, no. 4, pp. 35–40.
- Ziegler, R., Didelphidae, Erinaceidae, Metacodontidae und Dimylidae (Mammalia) aus dem Oberoligozän und Unteroligozän Süddeutschlands, *Stuttgart. Beitr. Naturk., Ser. B*, 1990, no. 158, pp. 1–99.
- Ziegler, R., Marsupialia und Insectivora (Mammalia) aus den oberoligozänen Spaltenfüllungen Herrlingen 8 und Herrlingen 9 bei Ulm (Baden-Württemberg), *Senckenberg Lethaea.*, 1998, vol. 77, nos. 1–2, pp. 101–143.