

New Late Miocene murids from China (Mammalia, Rodentia) Nouveaux muridés (Mammifères, Rongeurs) du Miocène supérieur de Chine

Gerhard Storch ^{a,*}, Xijun Ni ^b

^aForschungsinstitut Senckenberg, Senckenberg-Anlage 25, 60325 Frankfurt am Main, Germany

^bInstitute of vertebrate paleontology and paleoanthropology (IVPP), Chinese Academy of Sciences, P.O. Box 643, Beijing, China

Received 10 December 2001; accepted 11 February 2002

Abstract

New murids of Late Miocene (medial Baodean Chinese Mammal Unit) age from Inner Mongolia, northern China, and from Yunnan Province, southern China, are described. *Hansdebruijnia perpusilla* nov. sp. represents the earliest known and morphologically most primitive species of the genus, which is known from the latest Miocene of Europe and western Asia. The new species suggests an eastern Palaearctic origin of *Hansdebruijnia*. “*Progonomys*” *yunnanensis* QIU and STORCH, 1990 from Lufeng, Yunnan Province, is referred to *Linomys* nov. gen. New samples from Leilao, Yuanmou County, Yunnan Province, are included in this species, although this population is somewhat more primitive than that from Lufeng. *Leilaomys zhudingi* nov. gen. and sp. from Leilao shows a unique combination of apomorphic and plesiomorphic characters, which suggest an early divergence from the murid stem. The new findings indicate that our knowledge of the early radiation of murids in southeast Asia is still in its infancy. © 2002 Éditions scientifiques et médicales Elsevier SAS. All rights reserved.

Résumé

De nouveaux muridés du Miocène supérieur (unité mammalienne chinoise Baodéen moyen) de Mongolie intérieure, Chine du Nord sont décrits. *Hansdebruijnia perpusilla* nov. sp. représente la plus ancienne espèce du genre connue et la plus primitive morphologiquement. Elle est connue à partir du Miocène terminal de l'Europe et de l'Asie de l'Ouest. La nouvelle espèce suggère une origine orientale paléoarctique du genre *Hansdebruijnia*. “*Progonomys*” *yunnanensis* QIU and STORCH, 1990 de Lufeng, Province du Yunnan, ont rapportée à *Linomys* nov. gen. De nouveaux spécimens provenant de Leilao, région de Yuanmou, Province du Yunnan sont inclus dans cette espèce bien que cette population soit un peu plus primitive que celle de Lufeng. *Leilaomys zhudingi* nov. gen. et sp. de Leilao montre une combinaison unique de caractères apomorphiques et plésiomorphiques ce qui suggère une divergence précoce à partir du groupe-souche muridé. Les nouvelles découvertes indiquent que notre connaissance de la radiation précoce des muridés en Asie du Sud n'en est encore qu'à ses débuts. © 2002 Éditions scientifiques et médicales Elsevier SAS. Tous droits réservés.

Keywords: Murinae; Late Miocene; China; New taxa

Mots clés: Murinés; Miocène supérieur; Chine; Taxons nouveaux

1. Introduction

We describe new murids of Late Miocene (= medial Baodean Chinese Mammal Unit) age from Inner Mongolia

in northern China and from Yunnan Province in the south of China. Our knowledge of murids from these regions was previously based on the local faunas of Ertemte and Harr Obo in Inner Mongolia (Storch, 1987) and Shihuiiba near Lufeng, Yunnan (Qiu and Storch, 1990).

Since the 1980s, the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP) systematically organized

* Corresponding author.

E-mail address: gstorch@sng.uni-frankfurt.de (G. Storch).



Fig. 1. Map showing the location of the fossil localities mentioned in this paper.

Fig. 1. Carte montrant les localités fossilifères mentionnées dans cet article.

screen-washing operations in Inner Mongolia, most of these were initiated and carried out by Professor Qiu Zhuding. Around a dozen of Neogene micromammalian faunas have been reported (Qiu and Wang, 1999). In the summer of 2000, excavations at the Baogedawula site near the town of Abaga produced several teeth of a new murid species, the oldest one known from eastern Inner Mongolia (Fig. 1). Biochronologically, Baogedawula takes an intermediate position between the eastern Inner Mongolian faunas of Shala near Sonid Youqi (without murids) and Ertemte (with diverse murine fauna) (Qiu and Wang, 1999).

Excavations at the Leilao locality near Yuanmou, Yunnan, were carried out by the IVPP and the Yunnan Provincial Institute of Archeology, Kunming, in 1999 and 2000. More than 10 tons of sediment processed yielded several hundreds of teeth. They include the remains of a new murid genus that will be described below. Leilao, located in the Yuanmou Basin on the northern Yunnan-Guizhou Plateau, is famous for its *Lufengpithecus* remains (Zheng and Zhang, 1997). Based on an analysis of micromammals, Leilao is considered somewhat older than the hominoid locality Lufeng, but both are of Middle Baodean age (Ni and Qiu, 2002).

In addition to the description of newly discovered murid remains, we refer *Progonomys yunnanensis* QIU and

STORCH, 1990 to a new genus and briefly comment on the exclusion of *Karnimata hipparionum* (SCHLOSSER, 1924) from Ertemte from the genus *Karnimata* JACOBS, 1978.

2. Systematic paleontology

Family Muridae ILLIGER, 1811

Subfamily Murinae ILLIGER, 1811

Hansdebruijnina STORCH and DAHLMANN, 1995

Type species: *Occitanomys neutrum* DE BRUIJN, 1976

Diagnosis: (after Storch and Dahlmann, 1995; originally described as subgenus of *Occitanomys*): M1/ with distinct tma. M1/ and M2/ with t12; t12 distinctly ridge-like. M1/ usually without or with poorly developed t1bis. Stephanodonty poorly developed; t1–t5 and t3–t5 connections on M1/ mostly absent and if present, weak and low. Small-sized.

Species included: *Hansdebruijnina pusilla* (SCHAUB, 1938), *H. neutrum* (DE BRUIJN, 1976), and *H. perpusilla* nov. sp.

Distribution: Medial Baodean (≈ Early Turolian) to Early Yushean (≈ Early Ruscinian) of China (Storch, 1987; Zheng and Zhang, 2001), Late Turolian (MN13) of Asia Minor (Ünay et al., 2001), Middle to Late Turolian of Europe (de Bruijn, 1976, 1989; Storch and Dahlmann, 1995).

Remarks: Re-examination of the rich sample of *Occitanomys pusillus* from Ertemte, Inner Mongolia (Storch, 1987) did not corroborate the arguments of Storch and Dahlmann (1995) about its exclusion from *Hansdebruijnina*. The species fits the generic diagnosis of *Hansdebruijnina*. The sample of *H. pusilla* from Harr Obo, Inner Mongolia (Storch, 1987), appears to exhibit a few slightly advanced features as compared to Ertemte specimens, e.g., a somewhat enlarged t1 on M1/.

H. neutrum is distinct from *H. pusilla* in having:

- an asymmetrical anteroconid complex of M1/ (the lingual anteroconid protruding more anteriorly than the labial anteroconid),
- the tma of M1/ isolated from the paired anteroconid,
- the medial ridge between the protoconid–metaconid and hypoconid–entoconid chevrons less developed, and
- the more frequent connections between t1 and t5 on M1/.

Hansdebruijnina perpusilla nov. sp.

Fig. 2(1–4); Table 1

Holotype: IVPP V13075.1, right first upper molar (Fig. 2(1)).

Type locality: Baogedawula Sumu, Abaga Qi (County), Inner Mongolia, China.

Stratum Typicum: Late Miocene (Medial Baodean ≈ Early Turolian), Baogedawula Formation.

Paratypes: IVPP V13075.2–4; 1 M1/, 1 M1/ fragment, 2 M2/, 1 M2/, 2 M2/ fragments.

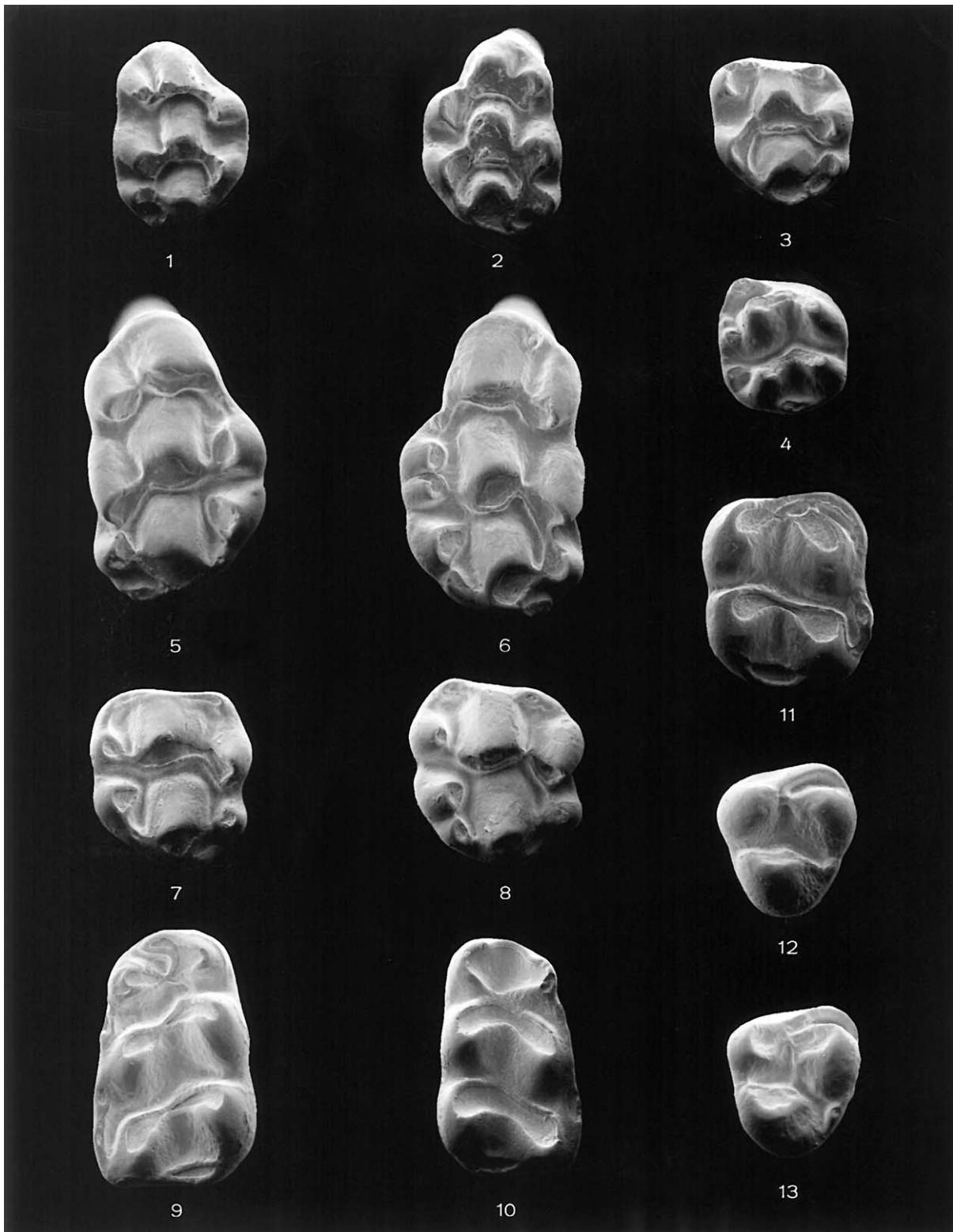


Fig. 2. 1–13. Isolated molars of murids from the Late Miocene of China in occlusal view. *Hansdebrujinia perpusilla* nov. sp.: 1, R M1/ (holotype, IVPP V13075.1); 2, L M1/ (IVPP V13075.2); 3, L M2/ (IVPP V13075.3); 4, L M2/ (IVPP V13075.4). *Leilaomys zhudingi* nov. gen. et sp.: 5, R M1/ (holotype, IVPP V13119.1); 6, L M1/ (IVPP V13119.2); 7, L M2/ (IVPP V13119.7); 8, L M2/ (IVPP V13119.8); 9, L M1/ (IVPP V13119.3); 10, R M1/ (IVPP V13119.9); 11, R M2/ (IVPP V13119.4); 12, R M3/ (IVPP V13119.5); 13, R M3/ (IVPP V13119.6).

Fig. 2. 1–13. Molaires isolées de muridés du Miocène supérieur de Chine en vue occlusale. *Hansdebrujinia perpusilla* nov. sp. : 1, R M1/ (holotype, IVPP V13075.1); 2, L M1/ (IVPP V13075.2); 3, L M2/ (IVPP V13075.3); 4, L M2/ (IVPP V13075.4). *Leilaomys zhudingi* nov. gen. et sp. : 5, R M1/ (holotype, IVPP V13119.1); 6, L M1/ (IVPP V13119.2); 7, L M2/ (IVPP V13119.7); 8, L M2/ (IVPP V13119.8); 9, L M1/ (IVPP V13119.3); 10, R M1/ (IVPP V13119.9); 11, R M2/ (IVPP V13119.4); 12, R M3/ (IVPP V13119.5); 13, R M3/ (IVPP V13119.6).

Table 1

Measurements (in mm) of molars of *Hansdebruijnia perpusilla* nov. sp., *Leilaomys zhudingi* nov. gen. et sp., and *Linomys yunnanensis* Qiu and Storch, 1990

		Length				Width			
		<i>n</i>	Mean	Min	Max	<i>n</i>	Mean	Min	Max
<i>Hansdebruijnia perpusilla</i>	M1/	2	1.52	1.48	1.56	2	1.06	1.04	1.08
	M2/	1	1.12	–	–	1	1.08	–	–
	M2	1	1.08	–	–	1	1.00	–	–
<i>Leilaomys zhudingi</i>	M1/	5	2.24	2.16	2.40	5	1.38	1.32	1.44
	M2/	4	1.47	1.40	1.56	4	1.38	1.24	1.56
	M1	6	2.03	1.92	2.12	6	1.21	1.12	1.28
	M2	6	1.50	1.44	1.56	6	1.22	1.12	1.28
<i>Linomys yunnanensis</i> (Leilao)	M3	5	1.18	1.12	1.24	5	1.04	0.96	1.08
	M1/	10	1.76	1.64	1.88	10	1.11	1.04	1.20
	M2/	10	1.15	1.12	1.20	10	1.09	1.04	1.16
	M3/	5	0.78	0.76	0.84	5	0.84	0.80	0.88
	M1	10	1.59	1.48	1.72	10	0.96	0.88	1.00
	M2	10	1.13	1.08	1.20	10	1.00	0.92	1.04
	M3	9	0.95	0.92	1.00	9	0.85	0.84	0.88

Diagnosis: Smaller than *H. pusilla* and *H. neutrum*, with more delicate cusps and ridges. No connection between t6 and t9 of M1/ and M2/, except when heavily worn; in *pusilla* and *neutrum*, t6 and t9 always connected, even in unworn teeth.

Etymology: *per* (Latin) = very, and *pusilla* (Latin) = tiny, in allusion to dental size.

Description: M1/: slender cusps and thin ridges; t1 well connected with t2, not connected with t5; t1 and t4 displaced posteriorly to t3 and t6, respectively; no t1bis; t3 with short and low posterior spur; t4 connected with t8 by low ridge; t6 separated from t9, only connected when heavily worn; t12 well developed and distinctly ridge-like; deep fold between t12 and t9; 3-rooted, with central rootlet.

M2/: cusp t3 much smaller than t1; t1 not connected with t5; no t1bis; t4 connected with t8 by low and thin ridge; t6 isolated from t9; t12 well developed and ridge-like; t4 displaced posteriorly to t6; 3-rooted.

M2/: rather sharp cusps; labial anteroconid well developed and connected to protoconid–metaconid chevron by a thin ridge; the valley separating labial anteroconid and protoconid wide and deep; no medial ridge; postcingulid crest-like; lateral cingulid low and thin, with small c1 and c2.

Remarks: *H. perpusilla* nov. sp. is the smallest, morphologically most primitive, and earliest known species of the genus and thus suggests an eastern Palearctic origin for *Hansdebruijnia*. Although based on a rather limited sample, it can be easily distinguished from *H. pusilla* and *H. neutrum*.

Qiu and Wang (1999) considered the fauna of Baogedawula to be essentially of the same age as that of Shala in Inner Mongolia, that means of medial Baodean age and roughly comparable to the European MN11–12 zones (see also Qiu and Li, in press). The murid remains described were discovered during the field work of 2000 and represent the only murid species from this locality. The presence of *H. perpusilla* in Baogedawula does not alter the previous biostratigraphical assignment of this fauna.

Linomys nov. gen.

Type species: *Progonomys yunnanensis* QIU and STORCH, 1990.

Etymology: Lin = Chinese for forest, in allusion to its supposed paleoenvironment.

Diagnosis: *Linomys* differs from *Progonomys* SCHAUB, 1938, in having a stronger connection between t4 and t8 on M1/, and usually a well developed tma on M1/. It differs from *Apodemus* KAUP, 1829/*Parapodemus* SCHAUB, 1938 in having t6 and t9 of M1/ and M2/ separated. It differs from *Yunomys* QIU and STORCH, 1990 in having less voluminous cusps. Moreover, the t7 of M1/ is absent or only incipiently developed, and the occlusal outline of M1/ and M2/ is narrower.

Species included: Type species only.

Distribution: Late Miocene (Medial Baodean ≈ Early Turolian) of Yunnan Province, China.

Remarks: The Siwalik taxa “*Progonomys*” *debruijnia* JACOBS, 1978 and “*Progonomys*” *hussaini* CHEEMA et al., 2000, in our opinion cannot be referred to the genus *Linomys*. *P. debruijnia* is distinct in having a crest-like t1 on M1/, more or less twinned t8 and t9, and a weaker connection of t4 and t8. *P. hussaini* is distinct in having twinned t8 and t9 on M1/, less posteriorly inclined cusps, and a variable t1.

Linomys yunnanensis was previously known only from its type locality Shihuiba, Lufeng County of Yunnan Province (Qiu and Storch, 1990). Rather rich new samples were collected by screen washing by the IVPP at Leilao, Yuanmou County of Yunnan Province (Ni and Qiu, 2002) in recent years.

The Leilao population (Fig. 3(1–12); Table 1) is slightly less derived than that from Shihuiba (Fig. 3(13–18)) in such characters as the total lack of t7 on M1/ and M2/, a wider separation of t6 and t9 on M1/, and the absence or only faint development of an anterior spur on the hypoconid–entoconid chevron of M1/. Most probably these populations represent an evolutionary lineage. For the time being we assign both assemblages to the same species.

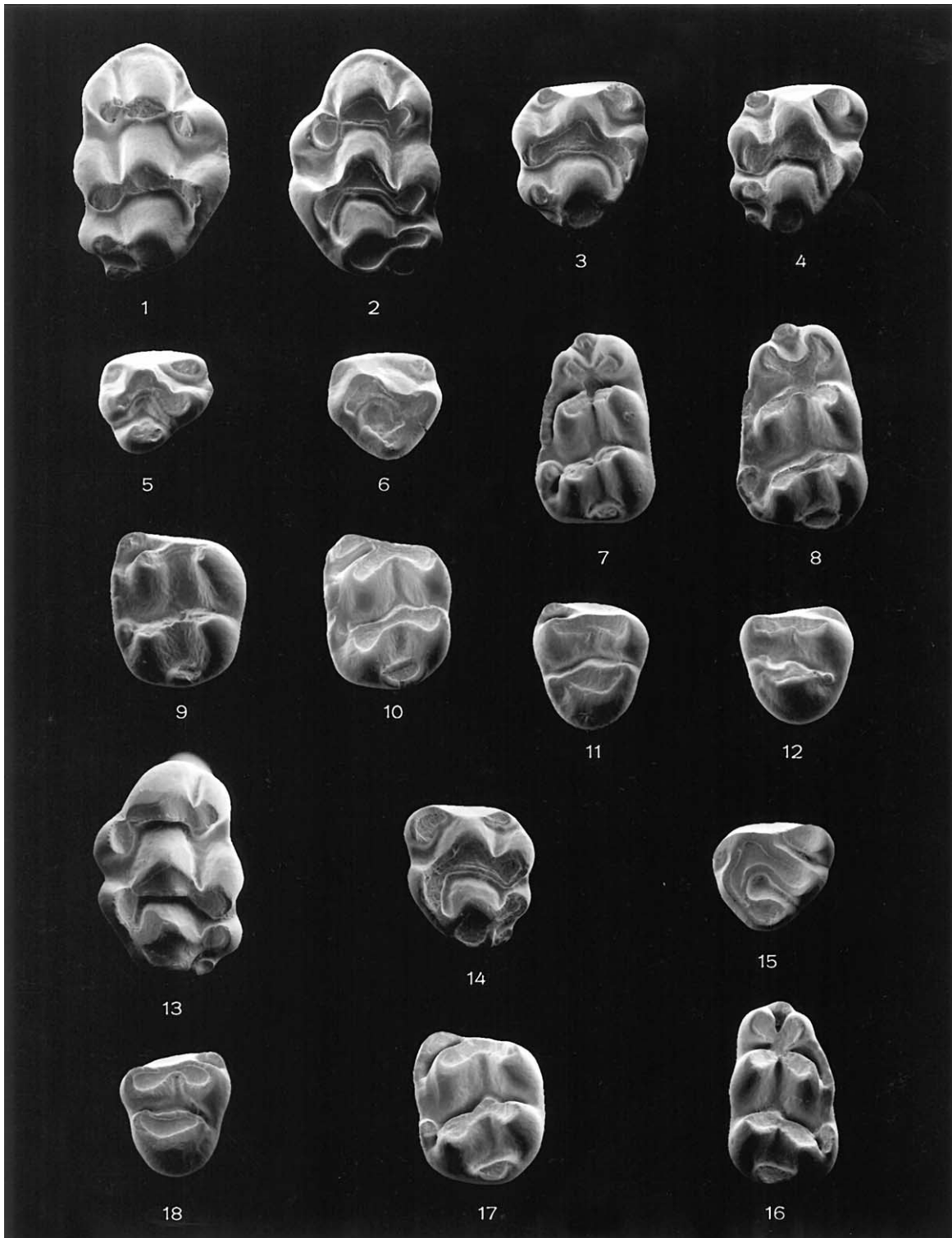


Fig. 3. 1–18. Isolated molars of murids from the Late Miocene of China in occlusal view. *Linomys yunnanensis* QIU and STORCH, 1990: Yuanmou population: 1, R M1/ (VPP V13120.1); 2, L M1/ (IVPP V13120.6); 3, R M2/ (IVPP V13120.3); 4, R M2/ (IVPP V13120.8); 5, R M3/ (IVPP V13120.9); 6, R M3/ (IVPP V13120.10); 7, L M1/ (IVPP V13120.11); 8, L M1/ (IVPP V13120.12); 9, L M2/ (IVPP V13120.14); 10, L M2/ (IVPP V13120.15); 11, L M3/ (IVPP V13120.17); 12, R M3/ (IVPP V13120.5). Lufeng population: 13, L M1/ (holotype, IVPP V9493); 14, L M2/ (IVPP V9494.26); 15, R M3/ (IVPP, V9494.234); 16, R M1/ (IVPP, V9494.236); 17, L M2/ (IVPP, V9494.94); 18, R M3/ (IVPP, V9494.260).

Fig. 3. 1–18. Molaires isolées de muridés du Miocène supérieur de Chine en vue occlusale. *Linomys yunnanensis* QIU and STORCH, 1990: population du Yuanmou : 1, R M1/ (VPP V13120.1) ; 2, L M1/ (IVPP V13120.6) ; 3, R M2/ (IVPP V13120.3) ; 4, R M2/ (IVPP V13120.8) ; 5, R M3/ (IVPP V13120.9) ; 6, R M3/ (IVPP V13120.10) ; 7, L M1/ (IVPP V13120.11) ; 8, L M1/ (IVPP V13120.12) ; 9, L M2/ (IVPP V13120.14) ; 10, L M2/ (IVPP V13120.15) ; 11, L M3/ (IVPP V13120.17) ; 12, R M3/ (IVPP V13120.5). Lufeng population : 13, L M1/ (holotype, IVPP V9493) ; 14, L M2/ (IVPP V9494.26) ; 15, R M3/ (IVPP, V9494.234) ; 16, R M1/ (IVPP, V9494.236) ; 17, L M2/ (IVPP, V9494.94) ; 18, R M3/ (IVPP, V9494.260).

It seems that *Yunomys* and *Linomys* represent endemic Southeast Asian clades.

Leilaomys nov. gen.

Type species: *Leilaomys zhudingi* nov. sp.

Etymology: Named after the village of Leilao, where the type locality is located.

Diagnosis: Cusps weakly connected. M1/: t1 markedly displaced posteriorly and connected by a long cingulum-like ridge with t2; connecting ridge always bearing a t1bis-like cuspule (enteroconule of [Jacobs, 1978](#)). t4 isolated from t5 and connected with t8 by a high crest. t6 and t9 usually connected. t3 and t6 strongly inclined posteriorly. t12 well developed, cingulum-like. M1/: paired cusps individualized, with low connections. Paired anteroconid not connected with protoconid–metaconid. Transverse valleys between cusp pairs wide and straight. Tma present. Labial cingulid narrow, usually without well differentiated cuspules. M/2 and M/3: labial anteroconid evenly bowed and crest like.

Species included: Type species only.

Distribution: Late Miocene (Medial Baodean ≈ Early Turolian) of Yunnan Province, China.

Leilaomys zhudingi nov. sp.

[Fig. 2\(5–13\)](#); [Table 1](#)

Holotype: IVPP V13119.1, right first upper molar ([Fig. 2\(5\)](#)).

Type locality: Leilao village, Yuanmou County, Yunnan Province, China.

Stratum Typicum: Late Miocene (Medial Baodean ≈ Early Turolian), Xiaohe Formation.

Paratypes: IVPP V13119.2–25; 3 M1/, 8 M1/ fragments, 4 M2/, 2 M2/ fragments, 7 M/1, 1 M/1 fragment, 5 M/2, 1 M/2 fragment, 5 M/3.

Diagnosis: As for genus.

Etymology: Dedicated to Professor Qiu Zhuding, in recognition of his outstanding work on Neogene Chinese micromammals.

Description: M1/: Brachyodont. Occlusal outline almond-shaped. Central longitudinal cusp row predominant in size, wear facets of central cusps directed slightly labially. Some specimens with very weak anterior cingulum on anterior face of t2. Connecting crest between t4 and t8 slightly inflated in the position of the t7 in most specimens. t1 and t5 sometimes very weakly connected. Three-rooted, occasionally with additional central rootlet.

M2/: t1 conspicuously displaced posteriorly and connected with anterior face of t5 by a well developed bowed ridge; sometimes with cuspule on this ridge. t3 usually small and ridge-like. t4 not connected with t5, but connected with t8 by a strong crest. One specimen with a well developed t7. t6 and t9 connected. t5 and t8 predominate in size. t12 well developed, cingulum-like. Three-rooted.

M1/: Tma hardly protruding mesially beyond the lingual anteroconid and transversely connected to anteroconid

cusps. There is no trace of any medial spur. Postcingulid is well developed. Labial cingulid narrow and ledge-like, occasionally with weak c1 being separated from hypoconid.

M/2: The arched labial anteroconid is continuous with labial cingulid and metaconid. Labial cingulid very weak and without cuspules.

M/3: Labial anteroconid as on M/2. Sometimes presence of a vestigial hypoconid. The strong entoconid is centered rather lingually, on some specimens meeting the metaconid on lingual margin of the crown. Protoconid–hypoconid connection very thin.

Remarks: *Leilaomys* shares with *Antemus* [JACOBS, 1978](#), some plesiomorphous characters such as the presence of a long connecting ridge between t1 and t2 of M1/, bearing an enteroconule; t4 isolated from t5 on M1/ and M2/; wide transverse valleys between paired cusps on M/1 and M/2; and protoconid–metaconid and hypoconid–entoconid, respectively, of M/1 and M/2 weakly connected and not forming chevrons. Apomorphic features of *Leilaomys* occur in *Progonomys* or *Apodemus*. These include the presence of t6–t9 connection and predominance of central cusp row on M1/ and M2/; the tendency to develop t7 on M1/ and M2/; and the presence of tma on M/1. Striking characters of *Leilaomys* such as the extreme backward position of t1 and the connection of t1 with t5 on M1/ are also found in *Orientalomys* ([DE BRUIJN and VAN DER MEULEN, 1975](#)) and *Chardinomys* ([JACOBS and LI, 1982](#)). However, we consider these corresponding features to be the result of parallel evolution.

3. Comments on “*Karnimata*” *hipparionum* from Ertemte, Inner Mongolia

[Storch \(1987\)](#) referred *Mus hipparionum* [SCHLOSSER, 1924](#) to the genus *Karnimata* [JACOBS, 1978](#). He emended the original diagnosis of *Karnimata* to include incipient stephanodonty, in order to house the species *hipparionum*. Re-examination of the rather rich material from Ertemte showed that the previous assessment of specimens without t6–t9 connection was essentially based on unworn molars and “*K.*” *hipparionum* can be actually considered stephanodont. Thus, *hipparionum* departs from the morphology seen in taxa referred to *Karnimata* and is herewith excluded from this genus. At this point, we refrain from any generic assignment of *hipparionum*.

We do not consider the type species of *Karnimata*, *K. darwini* [JACOBS, 1978](#), a junior synonym of *Progonomys woelferi* [BACHMAYER and WILSON, 1970](#). [Jacobs \(1978\)](#) already suggested that *Karnimata* represents a different clade from that of *Progonomys*. *K. darwini* differs from *P. woelferi* in having t4 on M1/ in a more anterior, symmetrical position relative to t6, and t1 more closely approaching t2. We think that these different morphologies reflect an early divergence of two separate clades.

4. Discussion

The oldest murids known from China are *Progonomys* from the Bahe Formation, Lantian County, Shaanxi Province (Qiu et al., 2002), *Hansdebruijnia perpusilla* from Baogedawula, Inner Mongolia (this paper), *Linomys yunnanensis*, *Yunomys wui*, and *Leilaomys zhudingi* from Yunnan Province (this paper and Qiu and Storch, 1990). Their age is Late Miocene, corresponding to the early to middle Baodean Chinese Mammal Unit, which can be roughly correlated to the Late Vallesian to Early Turolian of Europe (Qiu and Wang, 1999; Qiu et al., 2002). Thus, the fossil record of murids commences in China considerably later than on the Indian subcontinent. The Yunnan murids appear to be restricted to the south of China while the early murids from northern China, *Progonomys* and *Hansdebruijnia*, show a wide Eurasian distribution and offer a good future chance for biochronological long distance correlations. Obviously, since Late Miocene time particular subtropical–tropical forest habitats and the uplift of the Tibetan Plateau contributed to the local evolution of a variety of murid taxa restricted to this area or segments thereof.

Yunomys was originally considered to be closely related to the *Saidomys-Parapelomys-Karnimata* complex of SE Asian murids (Qiu and Storch, 1990). We now prefer the view of close relationship of *Yunomys* with *Linomys*. The *Linomys* population from Lufeng is slightly more advanced than that from Yuanmou because there is a tendency to develop a stronger t4–t8 connection and an incipient t7, evolutionary trends seen in several murid lineages. *Yunomys* presents an even more derived character state in showing a small, but distinct, cusp-like t7.

The origin and relationships of *Leilaomys* are currently not understood. It shows a unique combination of apomorphic and plesiomorphic characters, which suggest an early divergence from the main murid stem. This indicates that our knowledge of the SE Asian early radiations of murids is still in its infancy.

Acknowledgements

We thank Professor Qiu Zhuding of IVPP for discussions of the subject and helpful comments. We extend our gratitude to Dr. Hans de Bruijn and Dr. Burkart Engesser for providing helpful comments on an earlier version of this paper. We thank Angelika Helfricht and Dr. Thomas Dahlmann of Senckenberg Research Institute for preparing casts and the SEM plates. The CAS-KZCX 2-103, the NSFC-J9930095, the Pandeng Project (95-special) (Xijun Ni) and Max-Planck-Society, Munich (Gerhard Storch) provided financial support.

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