



PLATACANTHOMYIDS (RODENTIA, MAMMALIA) FROM THE LATE MIOCENE YUANMOU HOMINOID LOCALITY OF YUNNAN, CHINA

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Abstract: Remains of platacanthomyids from Leilao, a late Miocene hominoid locality in Yuanmou, Yunnan, China are described. Five species in three genera are recognized: *Neocometes* sp., *Platacanthomys dianensis* QIU, 1989, *Typhlomys* aff. *T. primitivus* QIU, 1989, *T. hipparionum* QIU, 1989 and *T. storchi* n. sp. Leilao is the only locality that produces fossils of all three known genera of the family Platacanthomyidae. The new species *T. storchi* is characterized by its huge dimensions and continuous endoloph(id)s and ectoloph(id)s incorporated with the anteroloph(id)s and posteroloph(id)s to encircle the occlusal surface. That the genus *Neocometes* from southeastern Asia shows a tendency of forming an ectoloph on the upper molars and an endolophid on the lower molars indicates that the South China species probably represents an evolutionary lineage independent from that of European *Neocometes*. Both *P. dianensis* and *T. aff. T. primitivus* exhibit more derived dental morphology than the related species from Shihuiba of Lufeng, suggesting a younger age of the Leilao Fauna, which is incompatible with the conclusion drawn from the studies of other groups of small mammals.

Key words: Platacanthomyidae, Rodentia, Mammalia, Yuanmou hominoid locality, late Miocene

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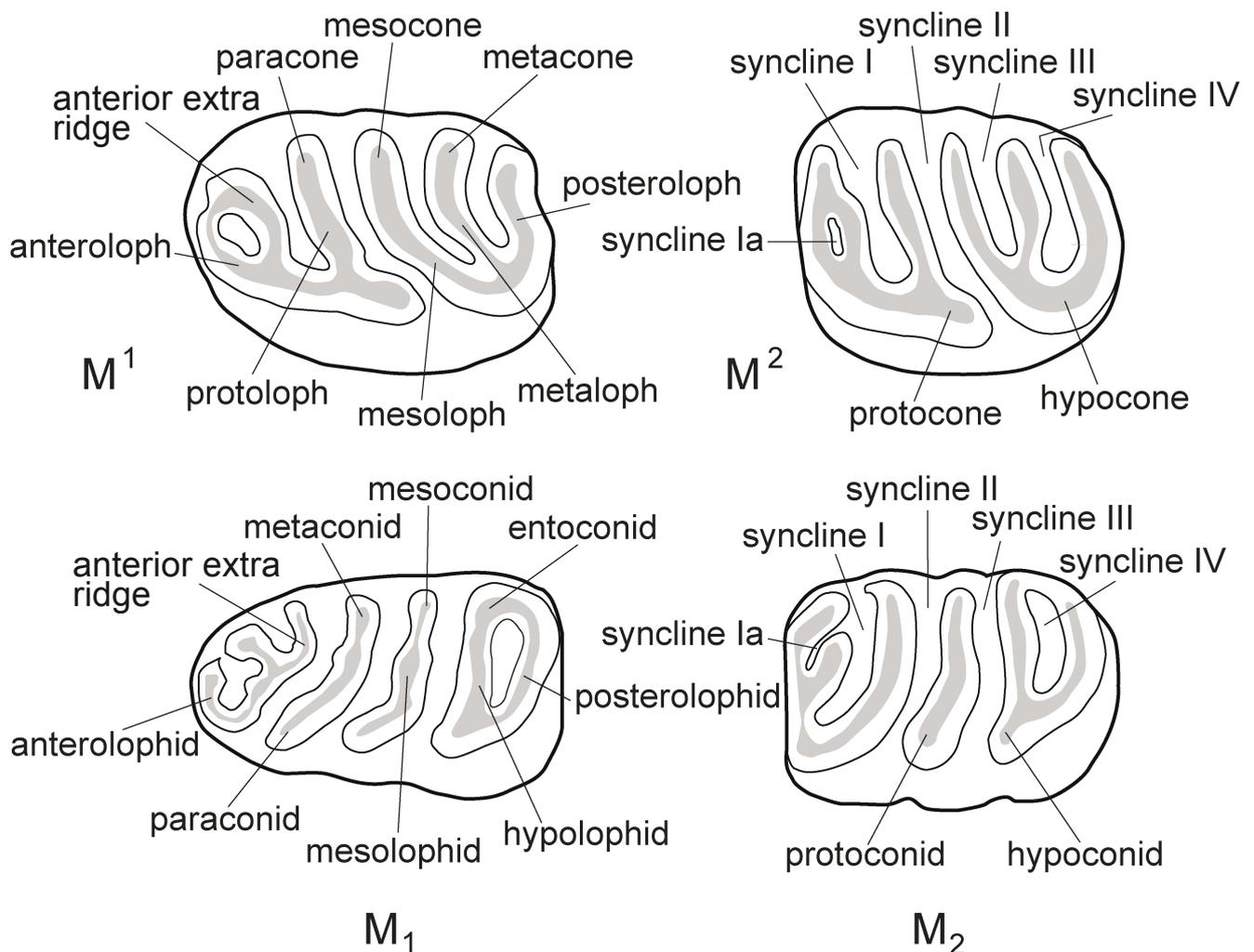
Introduction

Platacanthomyids are aberrant muroid rodents, but a useful group, because of their wide palaeogeographic distribution and relatively low diversity (Fejfar and Kalthoff 1999). The family comprises three genera, one fossil genus *Neocometes* recorded in the Miocene of Eurasia, and two living genera, *Platacanthomys* and *Typhlomys*, locally in the Oriental Region, with their first occurrences in the late Miocene of Yunnan, China (Qiu 1989). In China their occurrence is limited to only a few scattered spots in the southern part of the country.

The Yuanmou Basin in Yunnan Province lies on the northern edge of the Yunnan-Guizhou Plateau. Following the discovery of *Lufengpithecus* in the basin in 1986 (Zheng and Zhang 1997), a series of excavations was conducted at the sites of the basin. So far, a cranial fragment, several pieces of jaws, and more than one thousand isolated teeth of hominoids have been recovered, besides numerous other mammal remains (Qi and Ni 2006). Excavations and screen-washing operations were carried out at Leilao, one of the hominoid localities in the basin during the 1999 – 2000 field seasons. In these

campaigns, the locality has yielded rich fossils, including those of *Lufengpithecus* and other medium to larger mammals, as well as 41 small mammals (Ni and Qiu 2002, Qi and Zhang 2006). Ni and Qiu (2002) correlated the micromammalian fauna with the Shihuiba Fauna of Lufeng, another hominoid locality in Yunnan, and considered the Leilao Fauna somewhat older than the Shihuiba Fauna, estimating an age of about 9 Ma for the Yuanmou fauna (Qi et al. (2006) gave a palaeomag estimate of the age range for the section of the fossil-bearing Xiaohe Formation of about 7.2 to 8.2 Ma).

After a report on field works and preliminary results by Ni and Qiu in 2002, several groups of the small mammals have been described in detail (Tupaiaidae by Ni and Qiu 2012, Sciuridae by Qiu and Ni 2006, Eomyidae by Qiu 2006, 2017, Muridae by Storch and Ni 2002), which has greatly improved the record of fossil micromammal groups. This paper deals with Platacanthomyidae collected from Leilao. Interestingly, specimens found include all three genera of this family, although they are isolated teeth only. The described specimens are deposited in the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Chinese Academy of Sciences, Beijing.



Text-fig. 1. Terminology of molar morphology for Platacanthomyidae (modified after Fahlbusch 1966 and Fejfar 1999).

The Leilao assemblage was produced from ~30–150 cm thick grayish-yellow bands of sandstone from the Xiaohu Formation. For the geological background of the localities, the reader is referred to Ni and Qiu (2002). The dental terminology of molars of platacanthomyids is given in Text-fig. 1.

We are pleased to dedicate this paper to our close friend Gerhard Storch, whose works in China have stimulated advancements in the field of palaeontology, especially for Neogene micromammalian research in this country.

Systematic palaeontology

Family Platacanthomyidae ALSTON, 1876

Genus *Neocometes* SCHAUB et ZAPFE, 1953

Neocometes sp.

Text-fig. 2

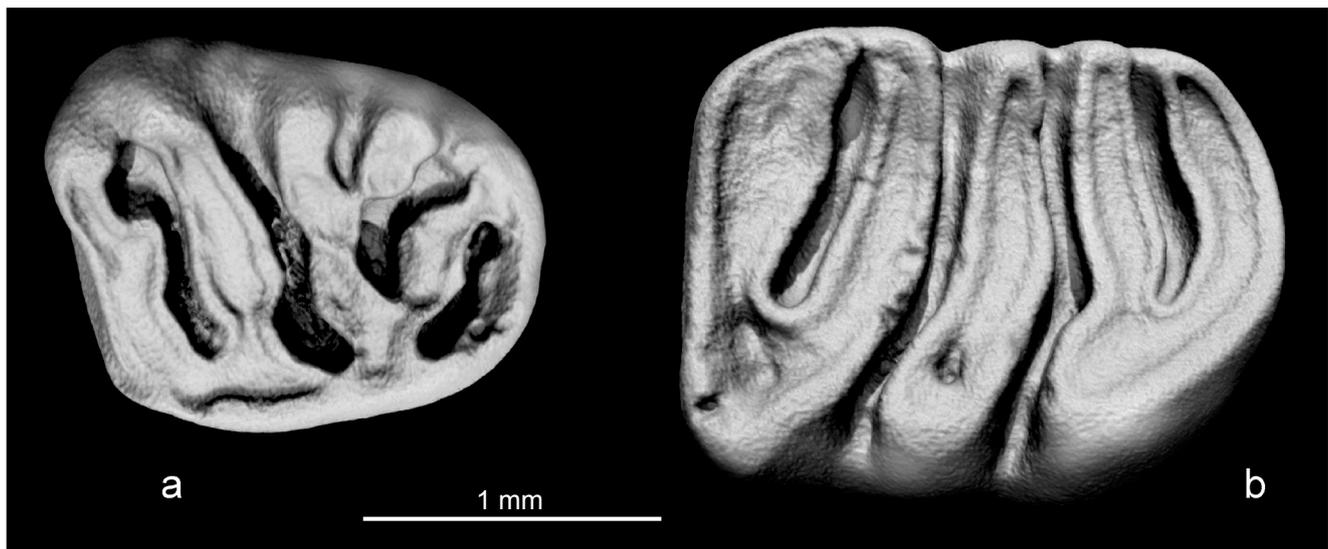
Referred material. One right M^3 and one left M_2 (IVPP V 25882.1–2) from Loc. 9905, Leilao, Yuanmou.

Measurements. M^3 : 1.65 × 1.40 mm; M_2 : 2.05 × 1.55 mm (length × width).

Description. The M^3 is subrectangular in occlusal view, with longitudinally concave grinding surface. It

is unilaterally hypsodont, with the lingual crown height distinctly higher than the buccal one. The anteroloph is connected with the endoloph lingually and separated from the paracone by a notch buccally. The anterior extra ridge is fused with the anteroloph to form a thick lingual portion of the ridge. The protoloph is pronounced, but distinctly constricted at the contact with protocone. Its mesial angle to the longitudinal axis is about 70°. The buccally free mesoloph is almost as thick as, and roughly parallel to the protoloph. The metaloph is interrupted into two cusp-like parts, with the lingual one connecting with the hypocone and the posteroloph, and the buccal one with the mesoloph and the metacone. The posteroloph is thin and curved backwards, originating from the hypocone and extending to the base of metacone. The endoloph is continuous, but indicative of a weaker connection between the protocone and hypocone in early stages of wear. Syncline Ia is absent. Syncline I is narrow and shallow, lingually closed and buccally opened. Syncline II is the longest syncline of the tooth, widely opened buccally. The buccally open syncline III and the distinct syncline IV are interrupted by the incomplete metaloph. The M^3 has two smaller anterior roots and a larger posterior one.

The M_2 is longer than wide and rectangular in occlusal view, with straight anterior margin, curved posterior margin and nearly parallel lateral margins. The grinding surface is



Text-fig. 2. *Neocometes* sp. from Leilao, Yuanmou. a) right M³ (IVPP V 25882.1, reversed), b) left M₂ (IVPP V 25882.2).

longitudinally concave, consisting of five thick diagonal/transversal ridges and four synclines. The anterolophid is nearly transverse, extending from the paraconid to the anterolingual corner of the tooth. The anterior extra ridge is completely confluent with the anterolophid to thicken the lingual portion of the ridge. The paraconid-metaconid connection is thick and slightly curved posterobuccally. The laterally free mesolophid is as strong as, and roughly parallel to the paraconid-metaconid connection, with a ~70° mesial angle to the longitudinal axis. The lingually free hypolophid is oriented nearly transversely, and slightly constricted at the contact with the hypoconid buccally. The posteriorly curved posterolophid is also prominent, extending from the hypoconid to the posterolingual corner of the tooth. The endolophid is not continuous. Syncline Ia is obliterated. Syncline I is a closed furrow obliquely situated. Syncline II and syncline III are longer, laterally opened, and similar in orientation. The lingually opened syncline IV is like syncline I in length, but more transversely directed. The M₂ has two roots.

Discussion. The two teeth exhibit characters that are highly diagnostic for the genus *Neocometes* SCHAUB et ZAPFE, 1953: the concave grinding surface, the distinctly inclined mid-ridges/synclines, the opening of the mid-buccal synclines on M³, and the laterally open synclines II and III on M₂. By these features, they can be easily distinguished from *Platacanthomys* and *Typhlomys* in the family Platacanthomyidae. Moreover, the two teeth show consistency in: the relatively large size with strong and crowded ridges, the fused anterior extra ridge with the anteroloph(id), and the early obliteration of syncline Ia.

Neocometes similis, *Neocometes* cf. *N. similis* and *N. brunonis* from Europe, and five species from Asia, *N. orientalis*, *Neocometes* cf. *N. orientalis* (Thailand), *N. sinensis*, *N. magna* (China) and *Neocometes* aff. *N. similis* (South Korea) are documented in the early or middle Miocene (Schaub and Zapfe 1953, Fahlbusch 1966, Fejfar 1974, 1999, Mein et al. 1990, Mein and Ginsburg 1997, Fejfar and Kalthoff 1999, Chaimanee et al. 2007, Lee and Jacobs 2010, Qiu and Jin 2017). Remains of these taxa are usually scarce, especially those from Asia. This scarcity hinders

attempts to effectively compare the two teeth from Yuanmou with other species, because corresponding teeth, either M³ or M₂ are absent in most samples from Asia. As far as dimension is concerned, the two teeth are larger than those of any previously described sample other than *N. magna*. In addition, the Yuanmou specimens are characterized by their strong and crowded ridges, and confluence of anterior extra ridge with the anteroloph(id). By these characters they can be distinguished from most other known taxa. The M₂ differs from the corresponding tooth of *N. orientalis* and *N. cf. N. orientalis* in having a lingually opened syncline III. There is a possibility that the specimens described may be referred to *N. sinensis*, because of the closeness in size and the presence of similar ridges, but no corresponding teeth are available for comparison. The scarcity of the material renders it impossible to give a more definitive identification below the generic rank.

The indeterminate species represented by the two teeth from the late Miocene deposits of Yuanmou is considered the latest occurrence of the genus. Its dental characters and late occurrence deserve further attention. Whether it can be assigned to a new species of *Neocometes* must await more material.

Genus *Platacanthomys* BLYTH, 1859

Platacanthomys dianensis QIU, 1989

Text-figs 3, 4

Holotype. Left M¹ (IVPP V 8816).

Type locality. Shihuiba, Lufeng, Yunnan Province, China.

Referred material. Yuanmou: 2 M³, 1 M₂, 1 M₃ (IVPP V 25883.1–4) from Loc. 9903; 1 M³, 1 M₃ (IVPP V 25883.5–6) from Loc. 9904; 2 M¹, 3 M², 2 M³, 2 M₁ (IVPP V 25883.7–15) from Loc. 9905; 10 M¹, 6 M², 9 M³, 16 M₁, 5 M₂, 10 M₃ (IVPP V 25883.16–71) from Loc. 9906.

Measurements. See Tab. 1.

Description. These teeth are unilaterally hypsodont and typically lophodont, with flat grinding surface, but with

Table 1. Measurements of *Platacanthomys dianensis* from Yuanmou (in mm). N = number of specimens.

Tooth	Length			Width		
	N	Mean	Range	N	Mean	Range
M ¹	11	2.02	1.80–2.20	11	1.39	1.20–1.50
M ²	9	1.63	1.45–1.70	9	1.43	1.35–1.50
M ³	12	1.30	1.20–1.45	12	1.29	1.15–1.40
M ₁	15	2.05	1.95–2.20	15	1.28	1.20–1.40
M ₂	6	1.72	1.65–1.80	6	1.43	1.35–1.65
M ₃	11	1.48	1.45–1.55	12	1.27	1.20–1.35

neither an anterior extra ridge nor a syncline Ia on the upper molars. The mid-ridges/synclines are distinctly inclined (with a mesial angle to the longitudinal axis being generally 55° to 70° on the upper molars and 45° to 60° on the lower molars). Synclines I, II and III on the upper molars, and synclines II, III and IV on the lower molars are buccally open. The endoloph is developed, but is interrupted by syncline II, while the endolophid is continuous. The upper molars have 3 roots each, and the lower molars are two-rooted.

The M¹ is longer than wide, with nearly parallel lateral margins. The anteroloph is slightly anteriorly curved, strong, but short. The protoloph and mesoloph are long, prominent and parallel in arrangement, being oblique lingually, and then turning transversely at the midline of the tooth. The metaloph is connected to the anterior part of hypocone. The straight posteroloph is relatively transverse, connecting with the metacone to enclose syncline IV in 4 of 9 specimens. Syncline I is the longest and deepest syncline of the tooth. Two out of 12 specimens show a connection between the protocone and hypocone, with completely lingually enclosed syncline II in one specimen.

The M² is similar to M¹ in outline and structure, but the anteroloph is long and straight. Syncline I is usually closed buccally in early stages of wear. Syncline II is lingually closed in one of 9 specimens. In 2 from 8 M²s, syncline IV is buccally closed in little-worn specimens.

The M³ is subtriangular, with relatively transverse ridges and synclines. The posterior part of the tooth is reduced, showing narrow ridges and synclines, or incomplete ridges and synclines in some specimens. The endoloph is generally continuous, and syncline I is usually closed buccally. Among the 14 M³s, 6 have a weakly developed longitudinal connection between the ridges.

The M₁ is distinctly longer than wide, with the lateral margins being slightly convergent anteriorly. The anterolophid is short, weakly developed and anteriorly curved. The anterior extra ridge is the shortest diagonal ridge of the tooth, joining the anterolophid to enclose syncline Ia. The paraconid-metaconid connection, mesolophid and hypolophid are marked, and oriented roughly parallel to the anterior extra ridge, only slightly increasing the mesial angle from the anterior extra ridge to the hypolophid. The posterolophid is transverse, connecting with the entoconid to enclose syncline IV lingually. Syncline Ia is small, oval-shaped, usually with a stylid or a crest attached to the anterolophid, and consequently the syncline is separated by a short ridge when the tooth is in an advanced stage of wear. Syncline I is laterally closed in all

specimens. The endolophid is developed, usually with a notch between the metaconid and mesoconid, and between the mesoconid and entoconid in a fresh tooth, but continuous in the early stages of wear. A low longitudinal connection buccal to the midline of the tooth is sometimes present in synclines II, III and IV, on 9 out of 17 specimens.

The M₂ is similar to M₁ in structure, but distinctly shorter, and with straight anterior margin. The anterior extra ridge is very short, joining the endolophid and the anterolophid to enclose a small and oval-shaped syncline Ia situated in the anterolingual corner of the tooth. The endolophid is complete and continuous. Of 6 M₂s, 5 exhibit variably developed longitudinal connections, usually present in syncline II or III.

The M₃ is similar to M₂ in morphology, except for its somewhat reduced posterior part and more curved posterior margin. A small syncline Ia is present or discernible in 9 out of 10 identifiable specimens. The hypolophid and syncline 4 are relatively short, but still prominent and complete. Some M₃s show a tendency to develop the longitudinal connections.

Discussion. The Leilao specimens are characterized by relatively large size, the flat grinding surface, rather oblique mid-ridges/synclines, upper molars lacking anterior extra ridge and syncline Ia, but having buccally opened synclines I, II and III, the lower molars possessing buccally opened synclines II, III, IV and developed endolophid, and the less reduced M³ and M₃, which fit the diagnosis of the genus *Platacanthomys*. The form represented by these specimens closely matches, both in morphology and dimensions, *P. dianensis*, the only fossil species of the genus, from type locality Shihuiba of Lufeng (Text-fig. 4). Minor differences are the less developed longitudinal connections between the ridges buccally to the midline of the lower molars. The weak development of longitudinal connections seems to be suggestive of more advanced status of *Platacanthomys*, because of the frequent presence of the connections on M₁ and M₂ in the late Miocene *P. dianensis* of Lufeng, Yunnan, but absence in the specimens of extant *P. lasiurus* housed in the Natural History Museum, London (also see Fejfar and Kalthoff 1999: 195). These differences would imply that the Leilao population is younger than the Shihuiba one.

Genus *Typhlomys* MILNE-EDWARDS, 1877

***Typhlomys* aff. *T. primitivus* QIU, 1989**

Text-figs 5, 6

Holotype of *T. primitivus*. Left M1 (IVPP V 8818).

Type locality of *T. primitivus*. Shihuiba, Lufeng, Yunnan Province, China.

Referred material. Yuanmou: 1 M¹, 3 M₂, 1 M₃ (IVPP V 25884.1–5) from Loc. 9903; 1 M¹, 1 M³, 4 M₁, 2 M₂ (IVPP V 25884.6–13) from Loc. 9904; 10 M¹, 11 M², 2 M³, 6 M₁, 9 M₂, 1 M₃ (IVPP V 25884.14–52) from Loc. 9905; 14 M¹, 19 M², 7 M³, 24 M₁, 14 M₂, 5 M₃ (IVPP V 25884.53–135) from Loc. 9906.

Measurements. See Tab. 2.

Description. Molars are lophodont, with concave grinding surface, and unilateral hypsodonty of the upper

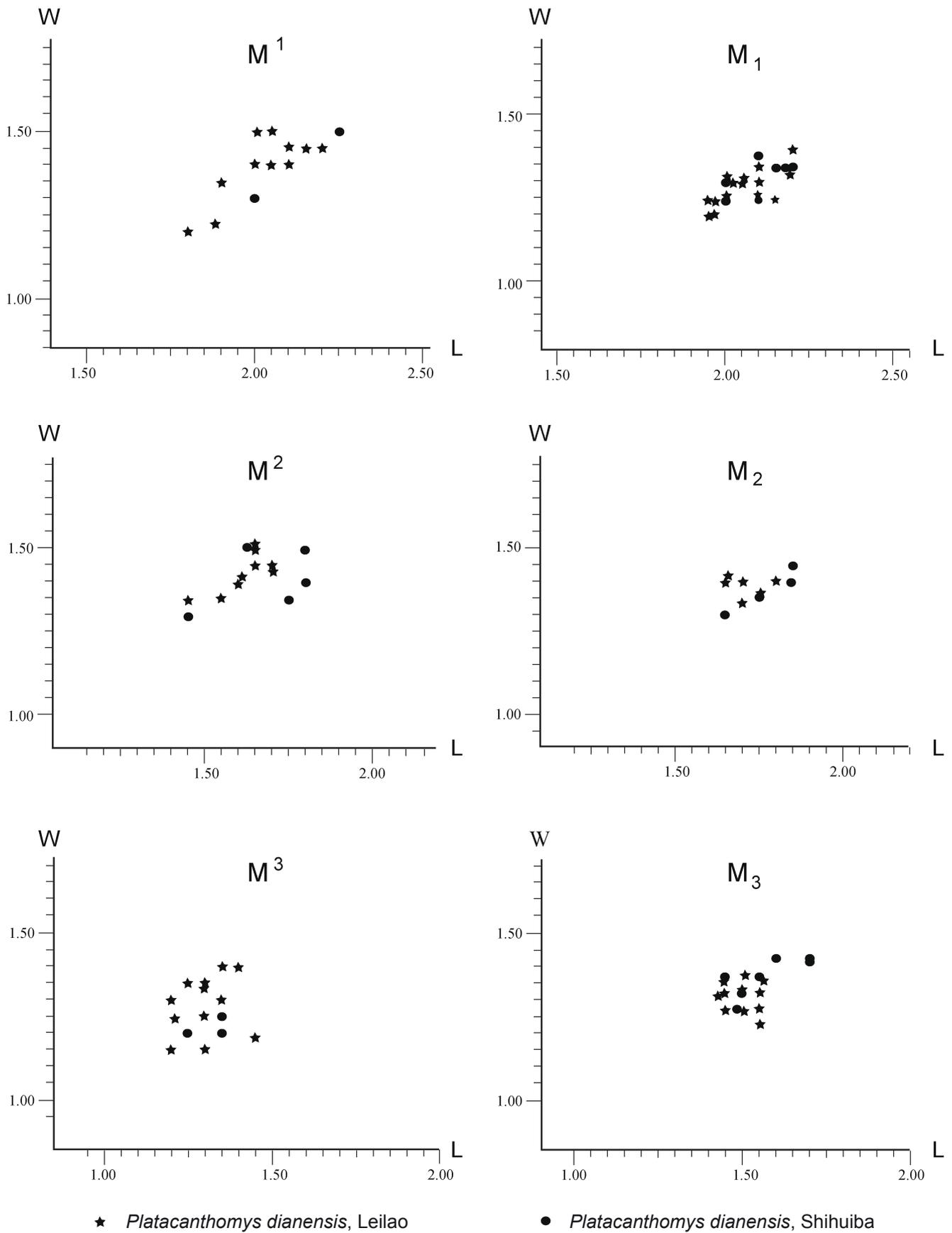
molars. The first and second molars usually consist of six diagonal/transversal ridges and five synclines. The mid-ridges/synclines have a mesial angle to the longitudinal axis of generally 45° to 55° on the upper molars and 25° to 45° on the lower molars. Synclines II on the upper molars are open both buccally and lingually in little-worn specimens, and synclines II and III on the lower molars are buccally open. The endoloph and the endolophid are well-developed,

but the endoloph is interrupted at syncline II in the early stages of wear. The upper molars have 3 roots, and the lower molars are two-rooted.

The M^1 is long and narrow, with the lateral margins being slightly convergent anteriorly. The anteroloph is short and slightly anteriorly curved. The anterior extra ridge is present in all M^1 , enclosing a small syncline Ia with the anterolophid. The protoloph and mesoloph are prominent and



Text-fig. 3. *Platacanthomys dianensis* Qiu, 1989 from Leilao, Yuanmou. a) left M^1 (IVPP V 25883.16), b) right M^1 (IVPP V 25882.17), c) left M^2 (IVPP V 25883.18), d) right M^2 (IVPP V 25883.7), e) left M^3 (IVPP V 25883.19), f) right M^3 (IVPP V 25883.20), g) left M_1 (IVPP V 25883.21), h) right M_1 (IVPP V 25883.8), i) left M_2 (IVPP V 25883.1), j) right M_2 (IVPP V 25883.22), k) left M_3 (IVPP V 25883.23), l) right M_2 (IVPP V 25883.2).



Text-fig. 4. Scatter diagrams (length and width) of *Platanthomys dianensis* measurements from Leilao, Yuanmou in comparison with those of the species from Shihuiba, Lufeng.

parallel in arrangement, and mostly free buccally in little-worn specimens. The metaloph is short, but longer than the

anterior extra loph. The posteroloph is relatively thin and nearly transverse. Syncline Ia is present in all specimens, but

Table 2. Measurements of *Typhlomys* aff. *T. primitivus* from Yuanmou (in mm). N = number of specimens.

Tooth	Length			Width		
	N	Mean	Range	N	Mean	Range
M ¹	22	1.59	1.40–1.76	23	0.93	0.80–1.10
M ²	29	1.32	1.15–1.45	29	0.94	0.75–1.16
M ³	9	0.98	0.90–1.03	9	0.85	0.70–1.00
M ₁	28	1.66	1.60–1.80	32	0.94	0.70–1.08
M ₂	24	1.34	1.18–1.45	26	0.94	0.84–1.10
M ₃	5	1.03	1.00–1.05	7	0.84	0.75–0.90

variably developed. Synclines I and II are shallowly open buccally in most specimens. Syncline II is lingually closed in 8 out of 25 teeth. Syncline IV is small, open buccally in 2 M¹s.

The M² is subrectangular in outline. It is similar to M¹ in structure, but the anteroloph is straight, and longer than the posteroloph. A continuous endoloph develops in early stages of wear, and an ectoloph forms with advanced wear of the tooth. Syncline Ia is variably developed, in 8 of 21 M²s it is distinct, in 4 specimens present as a discernible trace, in 9 completely absent.

The M³ is subtriangular, with relatively transverse ridges and reduced posterior part. The protoloph, endoloph and ectoloph are complete and continuous. The mesoloph is present in most of the specimens. Among the 10 M³s, 1 has a small syncline Ia, and in 2 a trace of the syncline is discernible. In 3 from 8 M³s the metaloph is very short or incomplete, and in 4 it is absent. Syncline IV is absent in 5 out of 9 specimens.

The M₁ is distinctly longer than wide, with the lateral margins being slightly convergent anteriorly. The anterolophid is anteriorly curved. The anterior extra ridge is prominent and roughly anterobuccal-posterolingually oriented, frequently joining the anterolophid to enclose syncline Ia. The paraconid-metaconid connection is the longest diagonal/transversal ridge in the tooth, joining the anterolophid and endolophid to enclose long syncline I. The mesolophid is marked and free buccally. The hypolophid is nearly transverse and shorter than the mesolophid. The posterolophid is relatively thin, connecting to the hypoconid and entoconid to enclose a small syncline IV. Syncline I is laterally closed, while synclines II and III are buccally open. The endolophid is continuous, even in fresh teeth.

The M₂ is subrectangular, with a constricted posterobuccal corner. It has the same ridges and synclines as in M₁, but synclines Ia and IV are relatively small and shallow, and disappear in rather early stages of wear.

The M₃ is subtriangular, with reduced and curved posterior part. The paraconid-metaconid connection and the mesolophid are present in all 7 M₃s. In the 6 specimens identified, a small syncline Ia is present or a trace of it is discernible. None of the M₃ shows a hypolophid or syncline IV.

Discussion. The platanthomyid represented by the described specimens exhibits the following suite of dental characters: small molars with concave grinding surface; presence of anterior extra ridge and syncline Ia; less inclined mid-ridges/synclines; a tendency toward the development of endoloph and ectoloph on the upper molars, presence of a continuous endolophid on the lower molars,

and the relative reduction of the third molars. These features agree with the diagnosis of *Typhlomys* given by Milne-Edwards (1877) and emended by Qiu (1989).

Typhlomys is a monospecific living genus distributed in the Oriental Region. Six fossil species of the genus, *T. primitivus*, *T. hipparionum*, *T. intermedius*, *T. macrourus*, *T. cinereus* and *T. anhuiensis*, have been documented from the late Cenozoic deposits in China (Qiu 1989, Zheng 1993, Jin et al. 2009). The dental pattern of *Typhlomys* seems to be quite stable. The changes that took place between late Miocene *T. primitivus* and Recent *T. cinereus* are rather slight. Definition of these taxa is mainly based on size differences, and species distinction is subtle. For example, the Pleistocene species *T. intermedius*, *T. cinereus* and *T. anhuiensis* show close resemblance in size and morphology, and it is difficult to distinguish them when material is inadequate.

In morphology and dimensions, the platanthomyid from Yuanmou matches *Typhlomys primitivus* from Lufeng. In general size, the molars of *T. primitivus* of the former fall within the range of the latter, but at the lower end (Text-fig. 6). In morphology, minor differences of the Leilao taxon from the Shihuiba form are the presence of anterior extra ridge and syncline Ia in all M¹s, in having syncline Ia in a few M³s, the absence of syncline IV in M₃. In spite of these differences, the Yuanmou platanthomyid seems to have its closest affinities with *T. primitivus* from Lufeng. The slightly larger size, the presence of anterior extra ridge and syncline Ia in all M¹s and in a few M³s, and the absence of syncline IV in M₃, may be interpreted as derived features for the Yuanmou taxon, which is treated as *Typhlomys* aff. *T. primitivus* here.

Typhlomys aff. *T. primitivus* is smaller than *T. hipparionum* from Lufeng. It is also smaller than *Typhlomys cinereus* and *T. macrourus* (Zheng 1993). In addition, it differs from the two Pleistocene species in lacking or having weakly developed syncline Ia in some M²s.

***Typhlomys hipparionum* QIU, 1989**

Text-figs 6, 7

Holotype. Right M¹ (IVPP V 8820).

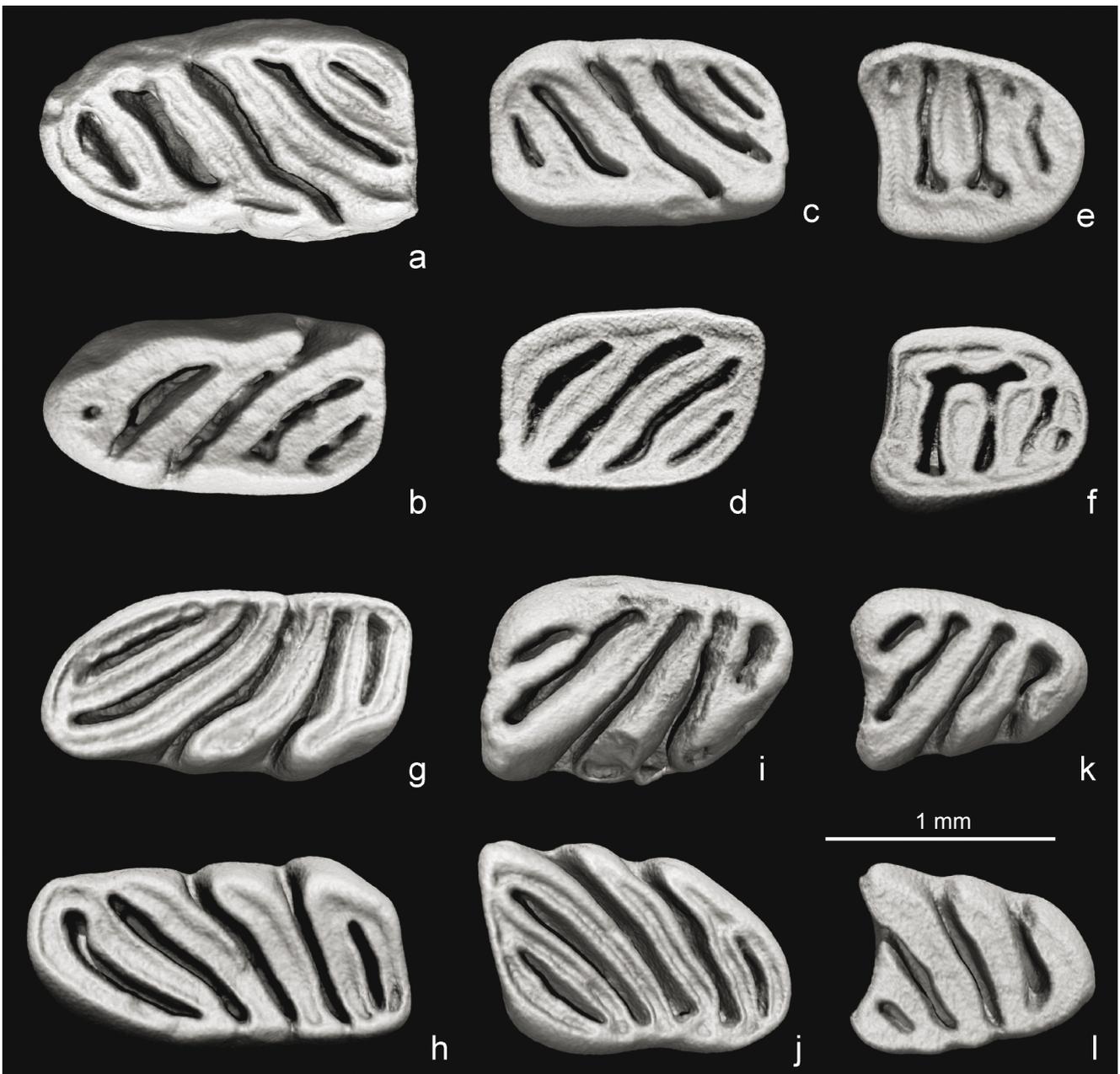
Type locality. Shihuiba, Lufeng, Yunnan Province, China.

Referred material. Yuanmou: 1 M², 1 M³, 1 M₃ (IVPP V 25885.1–3) from Loc. 9904; 1 M¹ (IVPP V 25885.4) from Loc. 9905; 3 M¹, 2 M², 2 M³, 4 M₁, 4 M₂, 2 M₃ (IVPP V 25885.5–21) from Loc. 9906.

Measurements. M¹: 1.75–1.90 × 1.15–1.30 mm; M²: 1.60–1.65 × 1.00–1.10 mm; M³: 1.15–1.25 × 0.90–1.00 mm; M₁: 1.90–2.10 × 1.00–1.10 mm; M₂: 1.50–1.55 × 1.05–1.10 mm; M₃: 1.20–1.35 × 0.88–1.00 mm (length × width).

Description. *Typhlomys hipparionum* from Leilao is larger than *T. aff. T. primitivus* in size, but closely matches in morphology and dimensions *T. hipparionum* from Shihuiba of Lufeng (Text-fig. 6), the type locality of this species. However, minor differences between the two forms can be observed, which should not be overemphasized in view of the rather limited amount of material from the two sites.

All 4 M¹s from Yuanmou are relatively wide and short in comparison with the holotype. Syncline Ia is slightly smaller than or equal to syncline IV, rather than slightly larger than



Text-fig. 5. *Typhlomys* aff. *T. primitivus* Qiu, 1989 from Leilao, Yuanmou. a) left M¹ (IVPP V 25884.53), b) right M¹ (IVPP V 25884.54), c) left M² (IVPP V 25884.55), d) right M² (IVPP V 25884.14), e) left M³ (IVPP V 25884.56), f) right M³ (IVPP V 25884.57), g) left M₁ (IVPP V 25884.15), h) right M₁ (IVPP V 25884.58), i) left M₂ (IVPP V 25884.59), j) right M₂ (IVPP V 25884.60), k) left M₃ (IVPP V 25884.61), l) right M₂ (IVPP V 25884.62).

syncline IV, as in the holotype. All 3 M²s show distinctly and laterally closed synclines Ia and IV, and continuous endoloph and ectoloph in this stage of wear. All 3 M³s have a distinct mesoloph and show a smaller syncline Ia at the anterobuccal corner of the tooth and a longer syncline IV at the posterobuccal corner.

The M₁ has a continuous endolophid, even in the fresh specimens. As in *Typhlomys hipparionum* from Lufeng and other species of the genus, the mesial angle of diagonal ridge/synclines to the longitudinal axis gradually increases toward the back. In 1 of 2 identifiable M₁s, syncline Ia is long and narrow, and the other is short and separated by a crest. All 4 M₂s have small and shallow synclines Ia and IV. All 3 M₃s show discernable synclines Ia, but no hypolophid and synclines IV.

Typhlomys storchi n. sp.

Text-figs 6, 8

Holotype. Right M₁ (IVPP V 25886); dimensions: 2.75 × 1.30 mm (length × width).

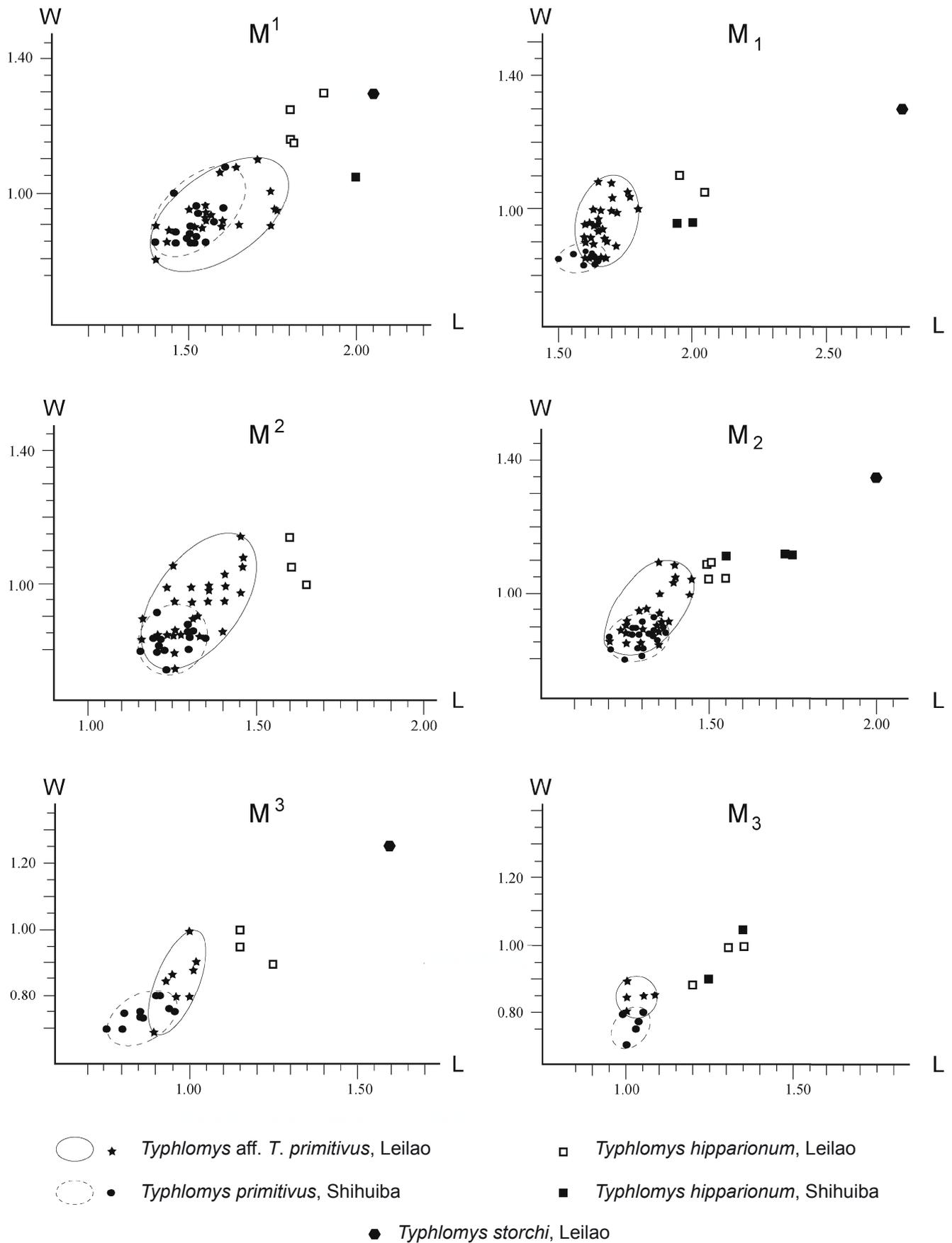
Etymology. This new species is dedicated to Gerhard Storch.

Type locality. Loc. 9905, Leilao, Yuanmou, Yunnan Province, China.

Type stratum. 30–150 cm grayish bands of pebbly sandstone, Xiaohe Formation.

Age. Late Miocene.

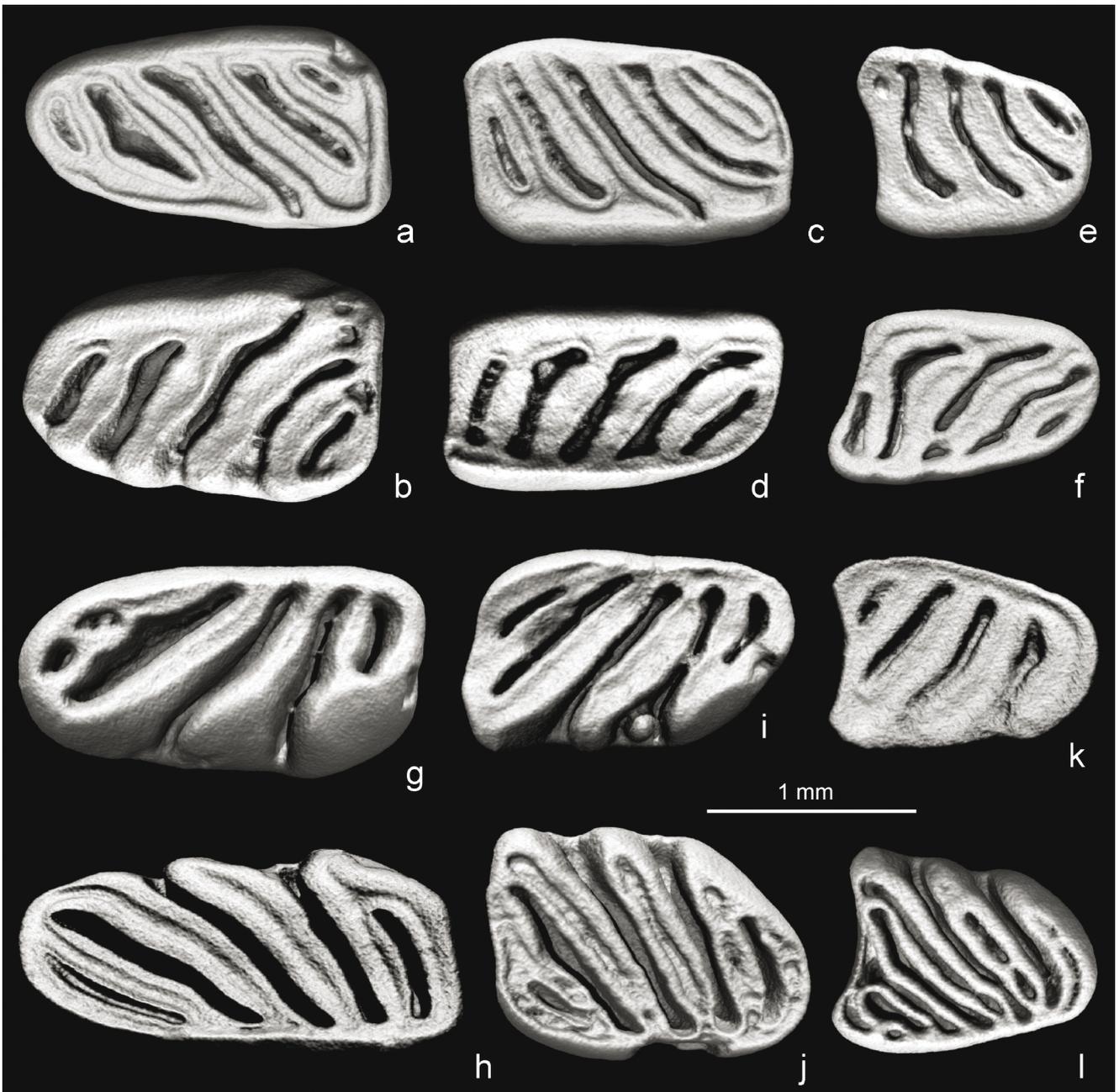
Paratype. 1 left M¹ (IVPP V 25887.1) from Loc. 9905; dimensions: 2.05 × 1.30 mm (length × width).



Text-fig. 6. Scatter diagrams (length and width) of *Typhlomys* aff. *T. primitivus* measurements from Leilao, Yuanmou in comparison with those of *T. hipparionum* and *T. storchi* from Leilao, and of *T. primitivus* and *T. hipparionum* from Shihuiba, Lufeng.

Referred material. 2 isolated teeth (1 M^3 from Loc. 9906, 1 M_2 from Loc. 9903; IVPP V 25887.2–3).

Measurements for referred material. M^3 : 1.60 × 1.25 mm; M_2 : 2.00 × 1.35 mm (length × width).



Text-fig. 7. *Typhlomys hipparionum* Qiu, 1989 from Leilao, Yuanmou. a) left M¹ (IVPP V 25885.4), b) right M¹ (IVPP V 25885.5), c) left M² (IVPP V 25885.6), d) left M² (IVPP V 25885.7, reversed), e) left M³ (IVPP V 25885.8), f) right M³ (IVPP V 25885.9), g) left M₁ (IVPP V 25885.10), h) right M₁ (IVPP V 25885.11), i) left M₂ (IVPP V 25885.12), j) right M₂ (IVPP V 25885.13), k) left M₃ (IVPP V 25885.1), l) left M₃ (IVPP V 25885.14, reversed).

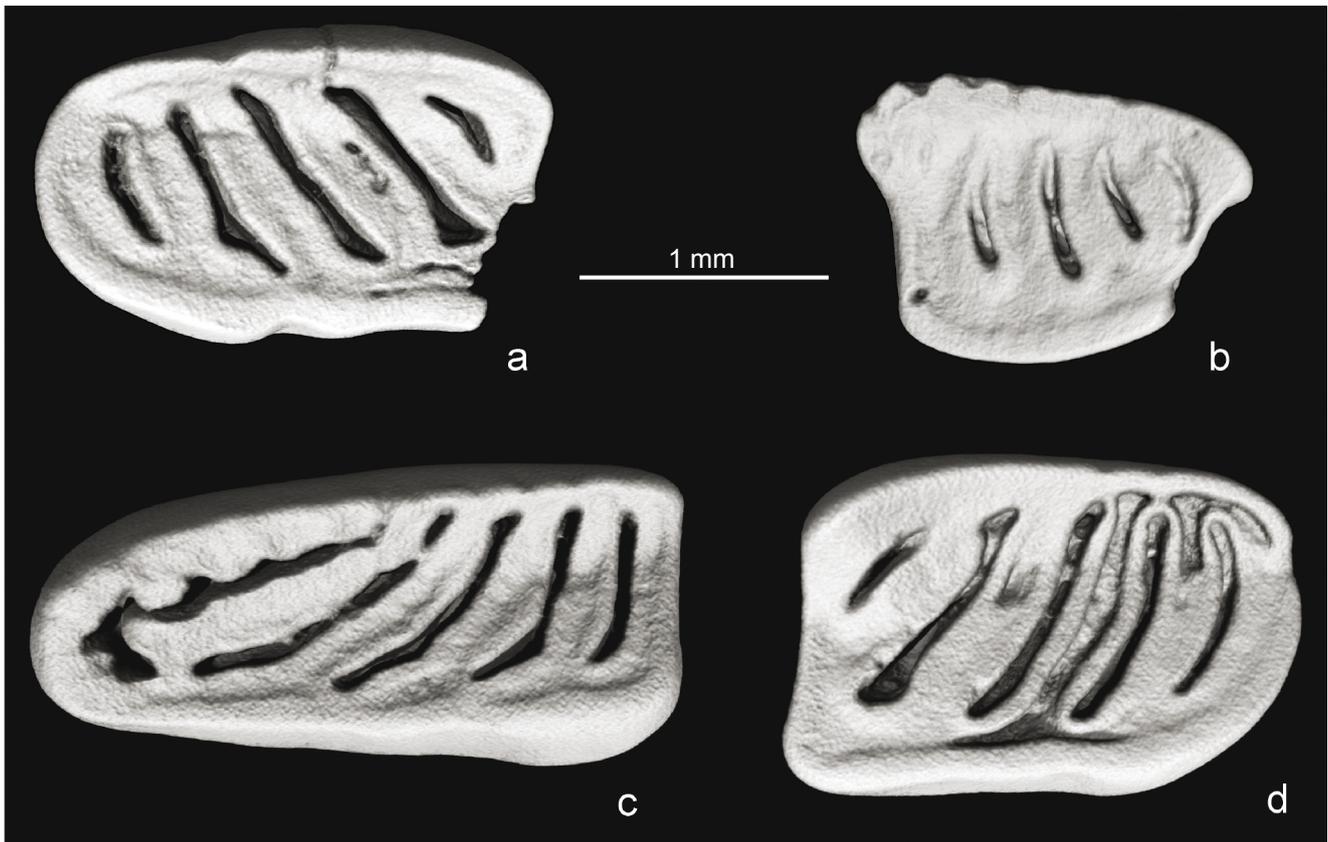
Diagnosis. Large-sized species of *Typhlomys*. Molars with concave grinding surface, six inclined diagonal ridges separated by five synclines, continuous endoloph(id)s and ectoloph(id)s incorporated with the anteroloph(id)s and posteroloph(id)s to circle the occlusal surface without buccal opening of synclines II and III. Anterior portion of M₁ distinctly extending forward.

Stratigraphic range. *Typhlomys storchi* n. sp. is known so far only from Leilao, the type locality.

Description. The available molars (M¹, M³, M₁, M₂) are lophodont, with concave grinding surface, slight unilateral hypsodonty of the upper molars, and have six diagonal/transversal ridges separated by five synclines. The

endoloph and the endolophid are rather developed, and the synclines are laterally closed in all stages of wear.

The M¹ is subrectangular in occlusal view, with nearly parallel lateral margins. The anteroloph is pronounced and anteriorly curved. The anterior extra ridge is prominent, enclosing a crescent syncline Ia with the anterolophid. The protoloph and mesoloph are long and strong, roughly parallel to the anterior extra ridge in direction. The mesoloph has a mesial angle to the longitudinal axis of 53°. The metaloph is short, but longer than the anterior extra ridge. The posteroloph is nearly transverse. Synclines II and III are marked, and in parallel arrangement; there is no trace of a buccal opening of the synclines. Syncline IV is close to syncline Ia in size.



Text-fig. 8. *Typhlomys storchi* n. sp. from Leilao, Yuanmou. a) left M¹ (IVPP V 25887.1, paratype), b) right M³ (IVPP V 25887.2, reversed), c) right M₁ (IVPP V 25886, holotype, reversed), d) right M₂ (IVPP V 25887.3, reversed).

The M³ is an elongated-triangle in occlusal view, with the lateral margins being slightly convergent posteriorly. It has a reduced posterior part and relatively transverse ridges. The anterior extra ridge is fused with the thick anteroloph lingually. The protoloph and mesoloph are conspicuous and nearly transverse in direction. The metaloph is short and slightly curved backward. A trace of syncline Ia is discernible at the anterobuccal corner of the tooth. Syncline II is the longest furrow on the tooth. Syncline IV is more distinct than syncline Ia. The M³ has 3 roots.

The M₁ is much longer than wide, with the lateral margins converging and distinctly extended anteriorly. The tooth is in very early wear, but shows continuous endolophid and ectolophid. No deep buccal opening of synclines II and III is visible as seen in other *Typhlomys*. The anterior extra ridge is long and pronounced, but does not touch the anterolophid in this stage of wear. The paraconid-metaconid connection is the longest diagonal/transverse ridge on the tooth, with a mesial angle to the longitudinal axis of about 40°. The mesolophid is nearly transverse in the lingual area, and then turns anterobuccally at the middle of the tooth width. The hypolophid is short and transverse, joining with the posterolophid to form a continuous loop posteriorly. Syncline Ia is long but narrow, due to the thickening of the endolophid anteriorly. Syncline I is the longest syncline on the tooth. Synclines II and III are similar in shape and parallel in arrangement, but the former is longer than the latter. Syncline IV is short and transverse. M₁ has two roots.

The M₂ is subrectangular in occlusal outline, with a straight anterior margin and slightly curved posterior margin.

The tooth is in early wear, and shows continuous endolophid and ectolophid, which are incorporated with the anterolophid and posterolophid to circle the occlusal surface. As in the M₁, there is no trace of a buccal opening of synclines II and III. The anterior extra ridge is short, joining the endolophid and the anterolophid to enclose an elongated oval syncline Ia. The paraconid-metaconid connection, the mesolophid and the hypolophid are roughly parallel in arrangement, but successively reduced in length. The mesolophid has a ~60° mesial angle to the longitudinal axis. Synclines I, II and III are similar in shape and orientation. Syncline IV is short, but longer than syncline Ia, slightly curved backward. M₂ has two roots.

Discussion. The described specimens are referred to the genus *Typhlomys*, due to the lophodont molars with concave grinding surface, six diagonal/transverse ridges and five synclines, mid-ridges/synclines less inclined to the longitudinal axis, developed endoloph in the upper molars and continuous endolophid in the lower molars. In these characters, they resemble *Typhlomys*, but differ from *Neocometes* and *Platacanthomys*.

The huge dimensions (Text-fig. 6) of these specimens are striking, even larger than those of *Typhlomys macrourus*, the currently largest known form of the genus from Longgupo of Wushan, Chongqing (Zheng 1993). The relative anterior extension of M₁ is also unique in *Typhlomys*. In addition, the specimens possess morphological features different from all known species of *Typhlomys*, for example, the presence of continuous endoloph(id)s and ectoloph(id)s, and the lack

of buccal opening of synclines II and III. The four molars from Leilao obviously represent a new platacanthomyid. Therefore, it is assigned to a new species of *Typhlomys*, although the material is rather scarce.

A possibility of the species described here belonging to a new genus of the Platacanthomyidae cannot be precluded, due to the huge size, the presence of continuous endoloph(id)s and ectoloph(id)s, the distinct extension of anterior portion on M_1 , and the lack of buccal opening of synclines II and I in molars. Nevertheless, it is considered inadvisable to create a new genus in view of the inadequate material.

Relationships of platacanthomyids from Europe and Asia

Among Platacanthomyidae, only the genus *Neocometes* is recorded in Asia and Europe (both continents). Therefore, the relationships of Eurasian platacanthomyids involve only *Neocometes*.

Of the eight known *Neocometes* found in Eurasia, *N. sinensis* and *N. magna* from China resemble *N. orientalis* and *N. cf. orientalis* from Thailand, in having prominent anteroloph(id) and anterior extra ridge on the first molars, presence of buccally closed syncline IV on M^1 , and a tendency toward the closing of the lingual synclines on M_1 , but they differ in larger size and in having stronger and crowded ridges. The different features of the Chinese taxa from the Thailand forms may imply that the former is more derived than the latter. It is worth noting that the features they share, i.e. the tendency to form an ectoloph on the upper molars and an endolophid on the lower molars, can be seen in the extant genus *Typhlomys* or *Platacanthomys*, but are never encountered among European species of *Neocometes*. On the basis of the characters shown in *N. orientalis* and *N. cf. orientalis*, Chaimanee et al. (2007) considered that the Thailand specimens may preclude their attribution to *Neocometes*, but need to be referred to a new genus that is closely related to *Typhlomys*. This also implies that *N. sinensis* and *N. magna* from China should be excluded from the genus *Neocometes*.

Although the Asian species of *Neocometes*, other than *N. aff. similis* from South Korea, including the indeterminate species described above, show some dental characters different from the European species of *Neocometes*, it would be better to retain provisionally their attribution to the genus *Neocometes*, until sufficient information on morphology is known. So far as the dental morphology is concerned, the Asian taxa demonstrate more similarities to *Neocometes* than to *Typhlomys*, because they have distinctly steeper mid-ridges/synclines than in *Typhlomys*, and possess deeply buccal opening of syncline I, II, III on M^1 , and lingually opened synclines II, or/and syncline III on M_1 and M_2 , as in *Neocometes*. A complete endolophid as in *Typhlomys* is lacking in these specimens. Using these features for generic biological definition, these characters seem sufficient to differentiate *Neocometes* from *Typhlomys* and *Platacanthomys*. The morphological differences of Asian and European *Neocometes* species, mainly the molars showing a tendency toward forming ectoloph on the upper molars and endolophid on the lower molars in the Asian

forms, are considered indicative of different specific status, and probably represent two independent evolutionary lineages with different trends in the genus (Qiu and Jin 2017). The European lineage, starting with *N. similis* (from MN 4), can be followed via *N. cf. similis* (from MN 5) to *N. brunonis* (from MN 6–8), and undergoes very little morphological changes, but with gradual increase in size and crown height during the Miocene. The Asian line, however, seems to have evolved independently in strengthening the diagonal/transversal ridges, developing ectolophs on the upper molars and endolophids on the lower molars, as well as the increased size.

Neocometes aff. *N. similis* represented by an $M1$ from the Miocene Bukpyeong Formation, South Korea, with inclined ridges/synclines and distinctly lingually opened synclines I–IV, is more similar, both in size and morphology, to *N. similis* than *N. orientalis* and *N. cf. N. orientalis* from Thailand and *N. sinensis* and *N. magna* from southern China. The occurrence of *Neocometes* aff. *N. similis* in South Korea has confirmed that the genus has a wide palaeogeographic distribution, and that there was continuous gene flow between the *Neocometes* populations of eastern Asia and western Europe. Nevertheless, we do not know where or when *Neocometes* evolved.

Biostratigraphic age of the Leilao Fauna

The Leilao Fauna of Yuanmou shares 22 taxa (accounting for 53.7 %) with the late Miocene Shihuiba Fauna of Lufeng. The two faunas have the following genera or species in common: *Prodendrogale*, *Hylomys* aff. *suillus*, *Yunosaptor scalprum*, *Heterosorex wangi*, *Blarinella*, *Sorex*, *Sciurotamias wangi*, *Tamiops atavus*, *Callosciurus*, *Dremomys primitivus*, *Miopetaurista asiatica*, *Hylopetodon dianense*, *Yunopterus jiangi*, *Steneofiber?*, *Platacanthomys dianensis*, *Typhlomys*, *Plesieomys mirabilis*, *Heteroeomys yunnanensis*, *Yuneomys*, *Miorhizomys tetracharax*, *Kowalskia hanae*, *Linomys yunnanensis* (Ni and Qiu 2002, 2012, Storch and Ni 2002, Qiu 2006, Qiu and Ni 2006, this paper). The Yuanmou fauna, however, contains some other genera that are absent in the Lufeng fauna, such as *Tupaia*, *Ratufa*, *Pliopetaurista*, *Neocometes*, *Leilaomys*, and lacks some genera that are present in the Lufeng fauna, for example, *Lanthanotherium*, *Yunomys*, *Nesolagus*. These differences might indicate a time gap between the two faunas. In spite of the difference, there seems to be little doubt that the two faunas are close, and reasonably attributed to late Miocene.

Based on the preliminary observation of rhizomyids, cricetids and murids, Ni and Qiu (2002) assigned the Leilao Fauna to the late Miocene, and considered the Yuanmou fauna (at about 9 Ma) to be older than the Shihuiba fauna. This conclusion appears to have been supported by subsequent studies of the Tupaiidae, Sciuridae, Eomyidae, Cricetidae and Muridae (Storch and Ni 2002, Qiu 2006, Qiu and Ni 2006, Ni and Qiu 2012). On the basis of our current understanding of the small mammals from Yunnan, we still consider both Lufeng and Yuanmou faunas a late Miocene age or early Baodean in the Chinese land mammal stage/age system (equivalent to MN 12 of the European land mammal

zonation), however, the study of Platacanthomyidae does not give a consistent conclusion that the Leilao Fauna is older than the Shihuiba Fauna. This discrepancy is highlighted by the morphological distinctions of *Platacanthomys* and *Typhlomys* between the two faunas. Judging from the general evolutionary trend in *Platacanthomys*, there exists a reduction of the longitudinal connection in lower molars, and in *Typhlomys* a development of the anterior extra ridge in M¹. The weak development of the longitudinal connection of *Platacanthomys* and the presence of anterior extra ridge on all M¹s of *Typhlomys* in the Leilao sample are morphologically intermediate between the Shihuiba species and the extant species. This seems to imply that the Lufeng fauna is older than the Yuanmou Fauna. This result is in sharp contrast to conclusions drawn for the other groups. This discrepancy indicates that our understanding of geologic age of the Yunnan mammal faunas is still in its infancy. Whether a reversible morphological trend has happened in the evolution of platacanthomyids remains a question as well.

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