

Myospalacines (Cricetidae, Rodentia) from the Miocene-Pliocene red clay section near Dongwan Village, Qin'an, Gansu, China and the classification of Myospalacinae

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Summary

A new classification scheme of the Myospalacinae on the generic level is proposed mainly based on the interparietal existed or absent, the occiput flat, convex or concave, and the molar rooted or rootless.

The classification keys of the Myospalacinae:

- I. Interparietal existed; occiput convex; molars rooted.....Tribe Prosiphneini Leroy, 1940
 - Ia. Interparietal is quadrilateral and locates posterior to the lambdoid crest. On m1, the bra2 is opposite to the Ira3, and parameters a, b, c, d and e are 0.0-0.5, 0.0-1.8, 0.3-1.6, 0.0-1.4 and 0.0-1.0 respectively.....Genus *Prosiphneus* Teilhard de Chardin, 1926
 - Ib. Interparietal is fusiform and locates between two wings of the lambdoid crest. On m1, the bra2 is opposite to the Ira3, and parameters a, b, c, d and e are 0.0-0.3, 0.5-3.2, 0.7-3.3, 1.3-5.5 and 0.0-4.5 respectively.....Genus *Pliosiphneus* Zheng, 1994
 - Ic. Interparietal is semicircle-shaped and locates anterior to the lambdoid crest. On m1, the bra2 located posterior to the Ira3, and parameters a, b, c, d and e are 0.0-0.5, 1.8-4.0, 1.4-3.2, 1.6-5.2 and 0.7-4.9 respectively.....Genus *Chardina* Zheng, 1994
- II. Interparietal disappeared; occiput convex, flat or concave; molars rooted or rootless
.....Tribe Myospalacini Miller & Gidley, 1918
 - II-I. Upper occiput locates posterior to the lambdoid crest, molars rootless, anterior enamel absent on m1 and the Ira3 very shallow (convex occiput)
 - II-Ia. Lingual reentrant (salient) angles on upper and buccal reentrant (salient) angles on lower molars are strong. The Ira4 absent on m1Genus *Eospalax* Allen, 1938
 - II-Ib. Lingual reentrant (salient) angles on upper and buccal reentrant (salient) angles on lower

- molars are weak. The *lra4* exists on *m1* Genus *Allosiphneus* Kretzoi, 1961
- II-II. Upper occiput locates anterior to the lambdoid crest (concave occiput)
- II-IIa. Molars rooted. The *bra 2* on *m1* locates posterior to the *lra3* and parameters *a*, *b*, *c*, *d*, and *e* are 0.4-7.2, >1.8-8.0, 2.1-7.5, 1.7-7.9 and 1.1-8.0 respectively
..... Genus *Mesosiphneus* Kretzoi, 1961
- II-IIb. Molars rootless. The anterior enamel band on *m1* exists and the *bra2* is opposite or posterior to the *lra3* Genus *Yangia* (=Youngia) Zheng, 1997
- II-III. Upper occiput locates at the same position with lambdoid crest (flat occiput)
- II-IIIa. Molars rooted. The *lra 3* on *m1* is shallower than the *bra2* and parameters *a*, *b*, *c*, *d*, and *e* are 0.3->3.6, >3.7->6.8, >4.2->7.7, >3.3->8.2 and >3.9->7.6 respectively
..... Genus *Episiphneus* Kretzoi, 1961
- II-IIIb. Molars rootless. The lingual reentrant angles on *m1* is very shallow and an anterior enamel exists Genus *Myospalax* Laxmann, 1769

Myospalacines (including 10 species) from the Upper Miocene-Lower Pliocene red clay section (consisting of 12 layers) near the Dongwan Village consist approximately one fourth of the known mammal forms listed by Liu et al. in 2011. Because Myospalacines occurred in a single section with precise stratigraphic or chronological data (~7.2–3.5 Ma), they are extremely significant to understand the phylogeny and evolutionary history of the subfamily in this period.

Order Rodentia Bowdich, 1821

Family Cricetidae Rochebrune, 1883

Subfamily Myospalacinae Lilljeborg, 1866

Genus *Prosiphneus* Teilhard de Chardin, 1926

Revised diagnosis Small myospalacines with convex occiput and square interparietal. The interparietal locates behind the joined lambdoid crests. Interorbit is narrow and squamosal is not present on occiput. *M1* has two or three roots. The *ac* of *m1* locates centrally or slightly buccally. Parameter *A* on *M1* and parameters *a* and *e* on *m1* are near zero.

Type species *Prosiphneus licenti* Teilhard de Chardin, 1926.

Included species *P. qinanensis* Zheng et al., 2004; *P. qiui* Zheng et al., 2004; *P. haoi* Zheng et al., 2004; *P. murinus* Teilhard de Chardin, 1942; *P. tianzuensis* (Zheng & Li, 1982); *P. eriksoni* (Schlosser, 1924).

Prosiphneus licenti Teilhard de Chardin, 1926

Revised diagnosis *M1* has three roots that fuse together at their bases. The lowest points of buccal enamel curves of *M1* are slightly lower than upper ends of *BRA1* and *BRA2*, and parameters *A*, *B*, *C* and *D* on *M1* are 0–0.1, 0.3–0.8, 0.3–0.8 and 0.0–0.7 respectively. The *ac* of *m1* locates buccally. The highest points of lingual enamel curves of *m1* are slightly higher than the lowest points of *lra1* and *lra2*, and parameters *a*, *b*, *c*, *d* and *e* on *m1* are 0.0–0.1,

0.0–0.8, 0.3–0.7, 0.0–0.5 and 0.0–0.2 respectively.

***Prosiphneus tianzuensis* (Zheng & Li, 1982)**

Revised diagnosis M1 has two base-fused roots. The ac of m1 locates slightly buccally, parameters a, b, c, d and e on m1 are 0.0–0.1, 0.5–0.9, 0.6–1.0, 0.4–1.0 and 0.0–0.3 respectively. Parameters A, B, C and D on M1 are 0.1–0.2, 0.3–1.4, 0.5–1.9 and 0.0–0.8 respectively.

Remarks This species was originally named as a subspecies of *P. licenti* Teilhard de Chardin, 1926 (Zheng and Li, 1982) based on having an enamel ring between the third and fourth triangles on M3. Later on, more materials indicate that the enamel ring is not a stable character on the teeth. But we still think it is a valid species distinguishing from *P. liceni* by its larger size, two rather than three roots on M1, larger parameter values, and more inclined bra1 on lower molars and BRA2 on upper molars (Zheng, 1994). *P. tianzuensis* is closed to *P. eriksoni* in size, but roots of M1 are shorter, parameter values of b, c and e on m1, and parameter A on M1 are smaller. Therefore, *P. tianzuensis* is an intermedium species between *P. licenti* and *P. eriksoni*.

***Prosiphneus eriksoni* (Schlosser, 1924)**

Revised diagnosis M1 has two base-fused roots. The ac of m1 locates centrally, parameters a, b, c, d and e on m1 are 0.0–0.5, 0.2–1.7, 0.4–1.5, 0.0–1.0 and 0.0–1.0 respectively, parameters A, B, C and D on M1 are 0.0–0.7, 0.0–1.3, 0.5–1.5 and 0.0–1.0 respectively.

Remarks *P. eriksoni* (Schlosser, 1924) is the first named species of molars-rooted myospalax. Since then many molar-rooted materials from different localities were assigned to this species. However, the materials of “*P. eriksoni*” from Houshan (Hoshan)(Loc. 5), Baode, Shanxi (Teilhard de Chardin and Young, 1931) and from Bainiuyu, Longxian (Peiniuyu, Lunghsien), Shaanxi (Mi, 1943) were reassigned to *Mesosiphneus intermedius* and *Chardina truncatus* respectively (Zheng, 1997). The “*P. cf. eriksoni*” from Bilike, Huade, Nei Mongol (Qiu and Storch, 2000) is more closed to *P. lyratus* by its much larger enamel parameter values (see Table 1). The “*P. ex. gr. eriksoni*” from the Middle Baikal region (Mats et al., 1982) may be synonymous with *P. eriksoni* by its occusal pattern and lingual enamel waves of m1. The presence of “*Prosiphneus eriksoni*” in Yushe basin (Flynn et al., 1991; Tedford et al., 1991) is not supported by recent study (Zheng, in preparation)

Genus *Pliosiphneus* Zheng, 1994

Revised diagnosis Medium to large size, the squamosal on occiput is triangular. The fusiform interparietal locates between two lambdoid crests. The two interorbital crests separate well each other in more progressive forms. The sagittal area is broad and lyriform. Both temporal and lambdoid crests are well developed. M1 has a single root. The ac of m1 locates centrally. Parameters A, B, C, D and a, b, c, d, e are larger than those in the genus *Prosiphneus*.

Type species *Prosiphneus lyratus* Teilhard de Chardin, 1942.

***Pliosiphneus* cf. *Pl. lyratus* (Teilhard de Chardin, 1942)**

Remarks The type of this species (H. H. P. H. M. 31.076) is a male skull probably from Zone II of Yushe basin (Teilhard de Chardin, 1942: figs. 36 and 36a). The molars are too worn to be described. After restudying the materials from Yushe basin, we assign three more materials to *P. lyratus*. These materials include an anterior part of a skull with left and right M1–M2 (H. H. P. H. M. 31.077), a skull without molars once assigned as <murinus group> (Teilhard de Chardin, 1942: fig. 34B) and a skull with left and right M1–M3 used to be *Yangia omegodon*. They are identical with the type of *P. lyratus* in having occiput posterior to lambdoid crests, fusiform interparietal between the lambdoid crests, concave and lyric sagittal area, wide inter-orbit constriction, and well separating supra-orbital ridges. The relatively weak temporal (or sagittal) crests and supra-orbital crests on these skulls can be considered as female individuals. Such a result provides possibility to compare skull with isolated molar. Based on corresponding relationship between upper and lower molars on enamel parameters, the mandible with m1–m3 from Huabaogou of the Nihewan Basin was assigned to this species (Zheng, 1994, 1997). The parameters A, B, C and D of M1 from the Yushe basin are 1.4–2.4, 2.0–2.7, 1.5–2.5 and 1.0–2.3 respectively, while parameters a, b, c, d and e from Nihewan basin are 0.0, 1.9, 1.7, >4.6 and >3.6 respectively.

Both corresponding parameters of M1 from Dongwan are 1.0, 1.9, 1.6, and 1.3, and m1 are 0.0, 1.0–2.5, 1.5–3.2, 3.6 and 2.7, the values are too small to compare with *Pl. lyratus*. They are similar to those materials of “*Prosiphneus* cf. *eriksoni*” from Bilike of Nei Mongol (Qiu and Storch, 2000). So the materials from Dongwan and Bilike and that of “*Prosiphneus paretengi*” from Baikal (Mats et al., 1982) together can be considered as a comparable species which is more primitive than *P. lyratus*.

Genus *Chardina* Zheng, 1994

Revised diagnosis Semi-circled interparietal is anterior to lambdoid crests. Convex occiput slightly protrudes outside lambdoid crest, supraoccipital process is weak. Squamosal in the occiput is triangular. Breadth of posterior sagittal region is about 1.8 times of that of the interorbital region. Molars are rooted and relatively brachydont. Roots of M1 fused together. Parameter a value of m1 is near zero.

Type species *Prosiphneus truncatus* Teilhard de Chardin, 1942.

Included species *C. sinensis* (Teilhard de Chardin & Young, 1931); *C. gansuensis* sp. nov.

***Chardina sinensis* (Teilhard de Chardin & Young, 1931)**

Revised diagnosis Molars are relatively brachydont. Parameters a, b, c, d, e of m1 are 0.0–0.4, 1.8–2.2, 1.4–3.0, 1.6–2.6, 0.7–1.6 respectively and parameters A, B, C, D of M1 are 0.9–1.9, 1.8–2.1, 1.8–2.8, 1.3–1.5 respectively.

Remarks The type of *C. sinensis* is an anterior part of skull with left and right M1–M2 (Cat. C. L. G. S. C. No. c/21) from Hequ, Shanxi (Loc. 7). An individual with upper and lower molars from Yushe basin shows the enamel parameter values of M1 is bigger than that of m1.

Therefore, the right mandible with m1–m3 (No. c/22) from Shenmu, Shaanxi (Loc. 12) can not be assigned to this species because its enamel parameter values of m1 are larger than those of M1 from Hequ. The mandible represents a more advanced species (Zheng, 1997).

***Chardina gansuensis* sp. nov.**

Holotype IVPP V 18598, a right mandible with m1.

Etymology The specific name is derived from Gansu, the province of the type locality of the species.

Horizon Layer 14 and 15, lower Pliocene.

Diagnosis Crown height is intermediate between *C. sinensis* and *C. truncatus*. Parameters a, b, c, d and e of m1 are 0.0–0.4, 2.1–2.4, 2.1–3.2, 2.6–3.6 and 1.6–2.8 respectively.

Comparison and discussion Although the materials from the Dongwan section are limited, we still can do some comparison. The enamel parameter values of both m1 and m2 are comparable to those from Shenmu (Teilhard de Chardin and Young, 1931), but larger than *C. sinensis* (see Table 2). It indicates that the materials from the two above localities should be considered as a new species, which intermediates between *C. sinensis* and *C. truncatus* in evolution.

The “*Prosiphneus eriksoni*” from Bainiuyu, Shaanxi (Mi, 1943) has larger parameter values of b, c and d on m1, it should be assigned to *C. gansuensis* as well.

***Chardina truncatus* (Teilhard de Chardin, 1942)**

Revised diagnosis Relatively hypsodont. Parameters a, b, c, d and e of m1 are 0.0–0.5, 2.0–4.0, 2.0–3.2, 3.6–5.2 and 3.5–4.9 respectively. Parameters A, B, C and D of M1 are 1.6–>3.8, 2.5–>4.5, 3.0–4.8 and 1.5–4.9 respectively.

Remarks Type specimen of this species is an extremely old skull (RV 4005) from Yushe (Teilhard de Chardin, 1942), and is difficult to compare with other tooth materials. Fortunately, an adult skull with mandible (V 756) was collected from Jinnangou, Yushe in 1958 and provides a good understanding of teeth. Comparing the m1 from the Dongwan section with that from Jinnangou, they match each other on size, characters of the anterior cap of molar, and enamel parameter values (see Table 2). *C. truncatus* has been documented from Nihewan Basin (Li et al., 2008), Yushe basin (Teilhard de Chardin, 1942), and the Loess Plateau (Zheng and Zhang, 2001) and is a typical Middle-Late Pliocene taxon.

Genus *Mesosiphneus* Kretzoi, 1961

Revised diagnosis Medium to large size. Interparietal absent, supraoccipital process strong. The breadth of the posterior sagittal is 2–2.3 times of that of the interorbit. The concaved upper occiput locates anterior to the lambdoid crests. The squamosal on the occiput is narrow. The rooted molars are hypsodont. Parameter a of m1 is larger than zero.

Type species *Prosiphneus praetingi* Teilhard de Chardin, 1942.

Included species *M. primitivus* sp. nov.; *M. teilhardi* Zhang, 1999; *M. intermedius* (Teilhard de Chardin & Young, 1931) = *M. paratingi* (Teilhard de Chardin, 1942).

***Mesosiphneus primitivus* sp. nov.**

Holotype A right mandible with m1–m3 (IVPP V 18601).

Etymology The specific name refers to Latin word *primitivus*, means primitive.

Horizon Layer 15 and 16, lower Pliocene.

Diagnosis Molars brachyodont. Parameters a, b, c, d and e of m1 are 0.4–0.7, 1.9–2.9, 2.1–2.5, 1.7–5.2 and 1.1–4.6 respectively.

Description The ascending ramus of the mandible is not well preserved and its coronoid process is broken. The posterior mandible symphysis is just under m1. The diastema is about 6 mm. There are two distinct and strong projections on the developed masseteric crest. The ac of m1 deviates lingually, anterior fold is absent or very shallow, and bra2 locates distinctly posterior to ira3. The parameter value a is larger than zero, while parameter d is more than two times of the parameter b. Both m2 and m3 have deeper buccal reentrants and a narrower posterior lobe.

Comparison and discussion Comparing to *M. praetingi* (Teilhard de Chardin, 1942), parameter values of *M. primitivus* are smaller, especially the parameter a of m1. It is different from *M. teilhardi* Zhang, 1999 by smaller parameter values of b, c, d and e, from *M. intermedius* (Teilhard de Chardin & Young, 1931) by the half values of dental parameters.

***Mesosiphneus praetingi* (Teilhard de Chardin, 1942)**

Revised diagnosis Parameters a, b, c, d and e of m1 are 1.1–2.9, >1.8–4.3, >2.3–4.4, >2.0–>5.0 and >1.6–>5.0 respectively; parameters A, B, C and D of M1 are >1.3–>4.5, >1.7–>4.1, >1.6–4.2 and >1.4–5.4 respectively.

Remarks The type specimen (No. 19.903) is an extremely old skull from Gaozhuang Formation or Zone II of Yushe Basin (Teilhard de Chardin, 1942), while an individual with maxilla and mandible (No. 29.483) provide well preserved molars.

M. praetingi is also reported from the Pliocene of Nihewan Basin (Li et al., 2008), Yushe Basin (Teilhard de Chardin, 1942) and Loess Plateau (Zheng and Zhang, 2001).

***Mesosiphneus intermedius* (Teilhard de Chardin & Young, 1931)**

Revised diagnosis Molars hypsodont. Parameters a, b, c, d, and e of m1 are 2.1–7.2, >3.2–8.0, >3.0–7.5, >2.6–7.9, >4.4–8.0 respectively.

Remarks The specimens from the Dongwan section are similar to that of *M. paratingi* from Yushe Basin in size and molar shape. Because the dental parameter values (see Table 3) are similar and the same geologic age, we believe *M. paratingi* is a synonym of *M. intermedius*.

The materials from Jiashiashan, Tangshan (Chiachiashan, Tongshan)(Pei, 1930) and Cap of Zhoukou dian (Choukoutien)(Pei, 1939), were assigned to this species by Teilhard de Chardin and Leroy in 1942, but we intend to shift them to *Episiphneus youngi* considering of their geographical distribution.

Kretzoi (1961) reassigned “*P. intermedius*” to genus *Episiphneus*, however the species is more similar to the genus *Mesosiphneus* because the ira3 locates anterior to bra2 on m1 (Zheng, 1994, 1997).

The parameter values of a, b, c, d and e of each species of *Mesosiphneus* separate well, for example, the parameter a is 0.4–0.7 in *M. primitivus*, 1.1–1.5 in *M. praetingi* and 4.3–5.5 in *M. intermedius* (see Table 3). We suggest *M. primitivus*, *M. praetingi* and *M. intermedius* (= *M. paratingi*) belong to one evolutionary lineage, the lineage shows an evolutionary trend from brachyodont to hypsodont.

Discussion and conclusion The stratigraphic distributions of 10 described myospalacines from Dongwan section are shown in Fig. 5, with detailed paleomagnetic (Hao and Guo, 2004) and biostratigraphic information (Liu et al., 2011). Three distinct evolutionary lineages are recognized: *Prosiphneus licenti*→*P. tianzuensis*→*P. eriksoni*, *Chardina sinensis*→*C. gansuensis*→*C. truncatus*, and *Mesosiphneus primitivus*→*M. praetingi*→*M. intermedius*.

Fig. 5 shows that each derived species and its direct ancestor coexist for some time. For example, *C. gansuensis* evolved from *C. sinensis* and coexisted with it in layer 14; both *C. truncatus* and *M. primitivus* evolved from *C. gansuensis* and coexisted with it in layer 16; *M. intermedius* coexisted with its ancestor *M. praetingi* in layer 19. The ten species are recorded from 71.2 m section and span a time interval from 3.596 to 7.212 Ma. The turnover of each species needs 0.362 Ma in average. Such quick turnover of species reflects strong and frequent climatic changes during Late Miocene-Early Pliocene. In late Late Miocene, the convex occiput forms are dominant, and in the Early Pliocene, the concave occiput forms became dominant. Such a change can be also found in the Nihewan Basin (Li et al., 2008), Yushe Basin (Flynn et al., 1997), and Lingtai sections (Zheng and Zhang, 2000, 2001). During the late Late Miocene (7.21–5.33 Ma), 3 species evolved, *Pr. tianzuensis*, *Pr. eriksoni*, *Pliosiphneus* cf. *Pl. lyrtus*, but during the Early Pliocene (5.47–4.19 Ma), 6 species evolved, *Chardina sinensis*, *C. gansuensis*, *C. truncatus*, *Mesosiphneus primitivus* sp. nov., *M. praetingi*, *M. intermedius*. In other word, the average turnover rate of a species in the Late Miocene (0.627 Ma) was slower than that in Early Pliocene (0.213 Ma). This indicates the climatic change was more frequent and stronger in Early Pliocene than in Late Miocene.

甘肃秦安晚中新世-早上新世的化石鼯鼠 (Myospalacinae, Cricetidae, Rodentia)兼论鼯鼠亚科 的分类

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摘要: 根据头骨上间顶骨存在与否、枕盾形状和位置、臼齿带牙根与否以及带牙根臼齿的高冠程度等, 将Myospalacinae分成2族9属。记述了甘肃秦安董湾剖面中的3种原鼯鼠: *Prosiphneus licenti* Teilhard de Chardin, 1926, *P. tianzuensis* (Zheng & Li, 1982)和*P. eriksoni*

(Schlosser, 1924); 1种上新鼯鼠: *Pliosiphneus* cf. *Pl. lyratus* (Teilhard de Chardin, 1942); 3种日进鼯鼠: *Chardina sinensis* (Teilhard de Chardin & Young, 1931), *C. gansuensis* n. sp. 和 *C. truncatus* (Teilhard de Chardin, 1942); 3种中鼯鼠: *Mesosiphneus primitivus* sp. nov., *M. praetingi* (Teilhard de Chardin, 1942) 和 *M. intermedius* (Teilhard de Chardin & Young, 1931)。修订了原鼯鼠属(*Prosiphneus*)、上新鼯鼠属(*Pliosiphneus*)、日进鼯鼠属(*Chardina*)和中鼯鼠属(*Mesosiphneus*)的属征。根据古地磁年代记录, 探讨了 *Pr. eriksoni*→*Pliosiphneus* cf. *Pl. lyratus*, *Pr. eriksoni*→*C. sinensis*, *C. gansuensis*→*M. primitivus* 之间的进化关系。

关键词: 甘肃董湾, 晚中新世-早上新世, 鼯鼠, 分类, 演化

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1 研究历史

鼯鼠(myospalacine)是亚洲特有的一类啮齿动物, 其化石分布范围与现生类群大体一致(Zheng, 1994)。化石鼯鼠种类多, 进化速率快, 是中国北方晚新生代最重要的化石门类之一。最早的化石鼯鼠是秦安原鼯鼠(*Prosiphneus qinanensis* Zheng et al., 2004), 它出现于秦安-I (QA-I)剖面82.2 m深度, 古地磁年龄约11.7 Ma (Guo et al., 2002), 可能起源于中中新世末的近古仓鼠(*Pleisiodipus* Young, 1927)(邱铸鼎等, 1981; 李传夔、计宏祥, 1981; 邱铸鼎, 1996; 郑绍华等, 2004)。

目前有关鼯鼠在高阶元上的分类大致有4种观点: 1) 不考虑臼齿有根与否和头骨形态, 鼯鼠各种都归入*Myospalax*属(Lawrence, 1991), 并置于鼠科(Muridae)下的鼯鼠亚科(Myospalacinae); 2) 将臼齿有根的种类归入*Prosiphneus*属, 将臼齿无根的种类归入*Myospalax*属, 仍为鼠科之下的鼯鼠亚科(McKenna and Bell, 1997); 3) 鼯鼠亚科仍只包含*Prosiphneus*和*Myospalax*两个属, 但归属于鼯形鼠科(Spalacidae)(Musser and Carleton, 2005); 4) 独立为鼯鼠科(Siphneidae或Myospalacidae), 其下分为平枕型的鼯鼠亚科(Myospalacinae)、凸枕型的原鼯鼠亚科(Prosiphneinae)和凹枕型的中鼯鼠亚科(Mesosiphneinae)(Zheng, 1994, 1997; Zheng et al., 2004)。目前, 鼯鼠类作为一个亚科的观点占优势, 独立成科的观点应做降级调整, 考虑到鼯鼠亚科起源于仓鼠科的*Pleisiodipus*属, 因此我们将它作为仓鼠科中一个亚科对待。

鼯鼠的属一级分类的主要分歧集中在横向还是纵向划分。主张横向划分者将臼齿有根者归为*Prosiphneus*属, 将臼齿无根者归为*Myospalax* (= *Siphneus*)属(Teilhard de Chardin and Young, 1931; Leroy, 1940; Teilhard de Chardin, 1942; Teilhard de Chardin and Leory, 1942; McKenna and Bell, 1997); 主张纵向分类者将头骨形态放在首位, 先将鼯鼠分成平枕、凸枕和凹枕3个大类, 然后按臼齿有根与否及有根臼齿的高冠程度分成不同的属(Kretzoi, 1961; Zheng, 1994, 1997)。本文作者基本支持先依据头骨特征、再根据臼齿有根与否及进步程度进行纵向划分的思路。但所谓的平枕、凸枕和凹枕的形成是在进化过程中完全丢失间顶骨之后, 因此我们以间顶骨存在与否作为首要的分类依据, 存在者为*Prosiphneini*族, 消失者为*Myospalacini*族。有间顶骨存在的类型都具有凸枕、牙齿有根等原始性状, *Prosiphneini*族包括*Prosiphneus*, *Pliosiphneus*和*Chardina*三个属; 而无间顶骨存在的类型包括凹枕的、臼齿有根的*Mesosiphneus*属和臼齿无根的*Yangia*属, 平

枕的、臼齿有根的*Episiphneus*属和臼齿无根的*Myospalax*属, 凸枕的臼齿无根的*Eospalax*和*Allosiphneus*属。这个分类方案不仅反映出鼯鼠类从有间顶骨到无间顶骨、从凸枕到凹枕(或平枕)、从臼齿有根到无根的进化过程, 也更好地解决了一些分类问题的困惑, 例如将头骨具有凸枕性状而臼齿具有凹枕性状的*Chardina*属归入凹枕类还是凸枕类。但是这个方案仍然需要今后随着新的头骨材料发现不断补充、验证和改进, 例如原始的平枕型鼯鼠是否有间顶骨? 较进步的、臼齿有根的凸枕型鼯鼠是否失去了间顶骨?

鼯鼠亚科在属及以上水平的分类检索方案如下:

- I. 间顶骨存在, 枕盾面上部突出于人字脊两翼之后(凸枕型), 臼齿具牙根
 族*Prosiphneini* Leroy, 1940
- Ia. 间顶骨方形, 位于人字脊两翼连线之后, m1颊侧第2褶沟(bra2)与舌侧第3褶沟(lra3)相对, m1舌侧珐琅质参数a, b, c, d, e值分别为0.0~0.5, 0.0~1.8, 0.3~1.6, 0.0~1.4, 0.0~1.0..... 属*Prosiphneus* Teilhard de Chrdin, 1926
- Ib. 间顶骨梭形, 位于人字脊两翼之间, m1颊侧第2褶沟(bra2)与舌侧第3褶沟(lra3)相对, m1舌侧珐琅质参数a, b, c, d, e值分别为0.0~0.3, 0.5~3.2, 0.7~3.3, 1.3~5.5, 0.0~4.5
 *Pliosiphneus* Zheng, 1994
- Ic. 间顶骨半圆形, 位于人字脊两翼之前, m1颊侧第2褶沟(bra2)位于舌侧第3褶沟(lra3)之后, m1舌侧珐琅质参数a, b, c, d, e值分别为0.0~0.5, 1.8~4.0, 1.4~3.2, 1.6~5.2, 0.7~4.9..... 属*Chardina* Zheng, 1994
- II. 间顶骨消失, 枕盾凸、平、凹, 臼齿具或不具牙根
 族*Myospalacini* Miller & Gidley, 1918
- II-I. 枕盾面上部突出于人字脊两翼之后(凸枕), 臼齿无牙根, m1前端无珐琅质层, 舌侧第3褶沟很浅
- II-Ia. 上臼齿舌侧、下臼齿颊侧褶沟(或褶角)发育, m1舌侧缺失第4褶沟
 属*Eospalax* Allen, 1938
- II-Ib. 上臼齿舌侧、下臼齿颊侧褶沟(或褶角)极不发育, m1舌侧存在第4褶沟
 属*Allosiphneus* Kretzoi, 1961
- II-II. 枕盾面上部凹入人字脊两翼之前(凹枕)
- II-IIa. 臼齿具牙根, m1颊侧第2褶沟(bra2)显著位于舌侧第3褶沟(lra3)之后, m1舌侧珐琅质参数a, b, c, d, e值分别为0.4~7.2, >1.8~8.0, 2.1~7.5, 1.7~7.9, 1.1~8.0
 属*Mesosiphneus* Kretzoi, 1961
- II-IIb. 臼齿无牙根, m1前端有珐琅质层且颊侧第2褶沟相对于或后于舌侧第3褶沟
 属*Yangia* (= *Youngia*) Zheng, 1997
- II-III. 枕盾面上部与人字脊后缘持平(平枕)
- II-IIIa. 臼齿具牙根, m1舌侧第3褶沟较颊侧第2褶沟浅, m1舌侧珐琅质参数a, b, c, d, e值分别为0.3~>3.6, >3.7~>6.8, >4.2~>7.7, >3.3~>8.2, >3.9~>7.6
 属*Episiphneus* Kretzoi, 1961
- II-IIIb. 臼齿无牙根, m1舌侧第3褶沟极浅, m1前端有珐琅质层
 属*Myospalax* Laxmann, 1769

本文将采用上述分类记述董湾剖面中的鼯鼠材料, 仅涉及 *Prosiphneus*, *Pliosiphneus*, *Chardina* 和 *Mesosiphneus* 四个属。虽然材料多为单个牙齿, 但在修订属的特征时, 综合了我们以前对头骨及其与上、下臼齿相关特征的了解。

甘肃秦安董湾剖面是一个基本连续沉积的、厚74.8 m的风成红粘土剖面, 包含了从C3Br.1n (7.258 Ma)至C2An.3n (3.596 Ma)的所有古地磁正、负极性事件(Hao and Guo, 2004; 刘丽萍等, 2011)。因此, 该剖面涵盖了中新统/上新统的界线, 也就是高庄阶的底界。此外, 该剖面多个层位中还发现了相当数量小哺乳动物化石, 这在中国北方, 特别是红粘土分布地区是很难见到的。经过郝青振于2001年及刘丽萍等于2007, 2009和2010年的野外采集, 该剖面共产出30多种化石小哺乳动物, 其中鼯鼠类的比重最大(刘丽萍等, 2011)。详细研究该剖面的鼯鼠化石有助于完善这一时段鼯鼠类的进化历史并提供一些环境变化的新证据。

文中除了2001年所采标本保存在中国科学院地质与地球物理研究所外(文中无编号), 其余标本均保存在中国科学院古脊椎动物与古人类研究所(IVPP V编号或保留原编号)。

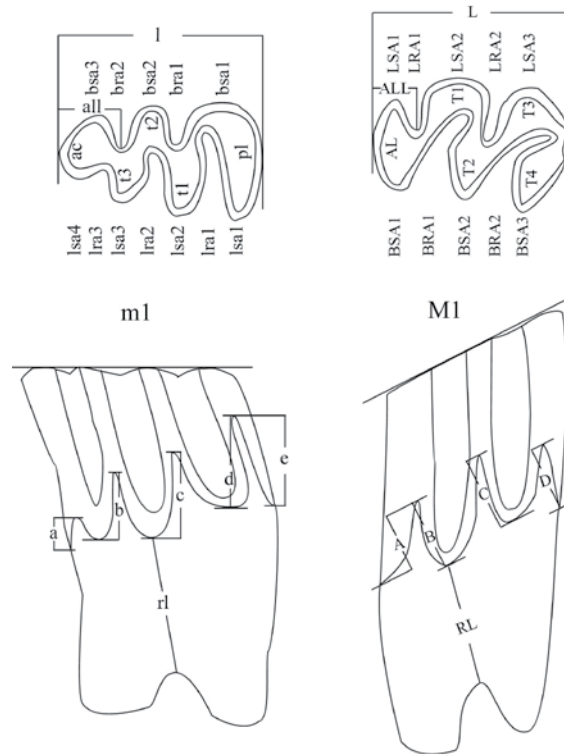


图1 鼯鼠臼齿术语及测量方法

Fig. 1 Terminologies of teeth and explanation of measurements

简字说明Abbreviations: ac. anterior cap 前帽; acl. length of anterior cap 前帽长; AL. anterior lobe 前环; ALL. length of anterior lobe 前环长; bra (BRA). buccal reentrant angle 颊侧褶沟; bsa (BSA). buccal salient angle 颊侧褶角; lra (LRA). lingual reentrant angle 舌侧褶沟; lsa (LSA). lingual salient angle 舌侧褶角; pl. posterior lobe 后环; rl (RL). root length 牙根长; t (T). triangle 三角; a, b, c, d, e. lower molar enamel parameters 下臼齿舌侧珐琅质参数; A, B, C, D. upper molar enamel parameters 上臼齿颊侧珐琅质参数

文中所用上、下臼齿术语及测量方法见图1, 测量用Wild-7显微镜, 精确到0.1 mm。

2 系统描述

啮齿目 Order Rodentia Bowdich, 1821

鼠形亚目 Suborder Myomorpha Brandt, 1855

仓鼠科 Family Cricetidae Rochebrune, 1883

鼯鼠亚科 Subfamily Myospalacinae Lilljeborg, 1866

原鼯鼠族 Prosiphneini Leroy, 1940

原鼯鼠属 *Prosiphneus* Teilhard de Chardin, 1926 (= *Myotalpavus* Miller, 1927)

特征(修订) 小型。间顶骨方形, 位于人字脊两翼连线之后。枕盾面显著突出于人字脊之后(凸枕)。头骨眶间区相对狭窄。枕区无鳞骨。M1具2~3个齿根。m1的ac偏向颊侧或居中, bra2位置与lra3相对; M1的珐琅质参数A和m1的珐琅质参数a和e值接近于零。

属型种 *Prosiphneus licenti* Teilhard de Chardin, 1926。

包括种 *P. qinanensis* Zheng et al., 2004; *P. qiui* Zheng et al., 2004; *P. haoi* Zheng et al., 2004; *P. murinus* Teilhard de Chardin, 1942; *P. tianzuensis* (Zheng & Li, 1982); *P. eriksoni* (Schlosser, 1924)。

桑氏原鼯鼠 *Prosiphneus licenti* Teilhard de Chardin, 1926

层位及材料 董湾剖面(下同)第1层: 1右m1(IVPP V 18593.1), 1前环破损的右m1(V 18593.2), 1破损的右m2(V 18593.3), 2左M1(V 18593.4, V 18593.5); 第3层: 1左m1(V 18593.6), 1破损的左m2(V 18593.7), 1左、3右M1(V 18593.8-11), 1右M2(V 18593.12); F30(=第4层): 1右m1。

特征(修订) M1具3齿根, 齿根在基部愈合。m1的ac偏向颊侧, 舌侧珐琅质曲线最高点轻微高于其后褶沟(lra1和lra2)的终端, 其参数a, b, c, d, e值分别为0.0~0.1, 0.0~0.8, 0.3~0.7, 0.0~0.5, 0.0~0.2。M1颊侧珐琅质曲线最低点轻微低于其后褶沟(BRA1和BRA2)的终端点, 其参数A, B, C, D值分别为0~0.1, 0.3~0.8, 0.3~0.8, 0.0~0.7。

测量 见表1。

描述 m1的ac椭圆, 偏向颊侧; 深的bra2与浅的lra3相对; t2和t3间齿质空间宽敞、汇通; lra1-3从后向前逐渐变浅; bra1-2的深度相当, 但不及lra1和lra2; lra1和bra1分别较lra2和bra2深; lra3向下开沟深度小于lra2之半; 舌侧珐琅质参数a和e值为零, 而b和c值稍大(图2A)。

M1的AL较窄; LRA1-2横向深入齿冠直达牙纵轴附近, BRA1-2向后内深入齿冠程度均超过牙纵轴; 牙根3个, 在基部愈合; 牙齿高4.4~5.8 mm (图3A)。

比较与讨论 在秦安材料发现之前, *P. licenti*仅发现于典型地点——甘肃庆阳教子川赵家沟。与典型地点的材料比较, 秦安m1的各项测量数据均在典型地点标本的变异范围内, 两地M1的咬面长度虽然相当, 但牙齿高度的变异范围以及M1的颊侧珐琅质参数B, C, D值的变异范围均比典型地点略偏大(见表1)。这些微小的差异, 我们认为并不

超出种间差异的正常范围，可以视为同一个种。

表1 原鼯鼠和上新鼯鼠各种的臼齿测量

Table 1 The tooth measurements of *Prosiphneus* and *Pliosiphneus* (mm)

		<i>Pr. licenti</i>	<i>Pr. tianzuensis</i>	<i>Pr. eriksoni</i>	<i>Pl. cf. Pl. lyratus</i>
m1	Occlusal length	2.7-3.0(2.8, 3)*	3.0*	2.7-4.3(3.36, 9)*	3.3-4.0(3.7, 3)*
		2.4-3.1(2.79, 12) [#]	3.0-3.5(3.33, 6)*	2.6-3.6(3.12, 16) [☆]	3.2-3.9(3.53, 18) [◇]
	Lingular length of anterior cap	0.5-0.6(0.53, 3)*	1.0*	0.7-1.1(0.92, 10)*	0.9-1.1(0.97, 3)*
		0.4-0.7(0.58, 10) [#]	0.7-0.9(0.82, 6)*	0.6-0.9(0.74, 16) [☆]	0.8-1.1(0.93, 18) [◇]
	Buccal length of anterior cap	0.5-0.7(0.63, 3)*	1.0*	0.7-1.2(1.04, 10)*	1.0-1.1(1.07, 3)*
		0.6-0.9(0.75, 12) [#]	0.8-1.2(0.98, 6)*	0.7-1.0(0.83, 16) [☆]	0.8-1.1(0.91, 18) [◇]
	Height	4.0-5.3(4.6, 3)*	6.0*	4.5-6.5(5.84, 9)*	6.0-6.9(6.45, 2)*
		4.2-5.0(4.7, 4) [#]	6.0-6.5(6.27, 3)*	4.7-6.6(5.72, 16) [☆]	5.9-7.6(6.68, 18) [◇]
	a	0.0-0.0(0.0, 3)*	0.0*	0.0-0.1(0.02, 6)*	0.0-0.0(0.0, 3)*
		0.0-0.1(0.09, 9) [#]	0.0-0.1(0.05, 6)*	0.0-0.5(0.05, 15) [☆]	0.0-0.3(0.03, 18) [◇]
b	0.2-0.3(0.23, 3)*	0.7*	0.6-1.5(1.16, 6)*	1.0-2.5(1.93, 3)*	
	0.0-0.8(0.46, 9) [#]	0.5-0.9(0.73, 6)*	0.9-1.7(1.21, 15) [☆]	0.9-2.2(1.48, 18) [◇]	
c	0.4-0.7(0.5, 3)*	1.0*	0.6-1.0(0.83, 6)*	1.5-3.2(2.37, 3)*	
	0.3-0.7(0.48, 9) [#]	0.6-0.8(0.72, 6)*	0.7-1.5(1.07, 15) [☆]	1.0-2.0(1.51, 18) [◇]	
d	0.0-0.2(0.1, 3)*	1.0*	0.0-1.4(0.97, 4)*	3.6*	
	0.1-0.5(0.24, 8) [#]	0.4-0.6(0.5, 6)*	0.1-1.0(0.51, 15) [☆]	1.6-4.1(2.72, 18) [◇]	
e	0.0-0.2(0.07, 3)*	0.3*	0.1-0.9(0.55, 4)*	2.7-2.7(2.7, 2)*	
	0.0-0.2(0.1, 8) [#]	0.0-0.3(0.12, 6)*	0.0-1.0(0.4, 15) [☆]	1.1-3.1(2.21, 18) [◇]	
m2	Occlusal length	2.5*	2.7*	2.3-3.0(2.84, 7)*	3.1-3.6(3.35, 2)*
		2.5-2.9(2.65, 15) [#]	3.0-3.2(3.08, 5)*	2.4-3.3(2.71, 16) [☆]	2.6-3.2(2.97, 18) [◇]
	Height	4.5*	5.8*	4.6-5.6(5.35, 6)*	7.0*
		3.5-4.8(4.2, 6) [#]	5.5-6.4(5.95, 2)*	4.6-6.1(5.39, 16) [☆]	5.4-7.4(6.22, 18) [◇]
	b	0.2-0.6(0.38, 9) [#]	0.5*	0.1-0.6(0.38, 3)*	2.0*
			0.1-0.3(0.2, 4)*	0.5-1.3(0.78, 16) [☆]	0.4-1.6(1.05, 18) [◇]
c	0.2-0.7(0.46, 9) [#]	0.9*	0.5-0.8(0.63, 3)*	2.1-3.3(2.7, 2)*	
		0.5-0.9(0.63, 4)*	0.4-1.0(0.64, 16) [☆]	0.9-2.3(1.37, 18) [◇]	
d	0.2-0.5(0.34, 9) [#]	1.1*	0.6-1.4(1.0, 2)*	>2.8*	
		0.1-0.6(0.38, 4)*	0.3-0.5(0.39, 16) [☆]	0.0-4.0(2.45, 18) [◇]	
e	0.0-0.1(0.01, 9) [#]	0.4*	0.2-1.0(0.6, 2)*	>2.4*	
		0.0-0.4(0.2, 4)*	0.0-0.4(0.19, 16) [☆]	0.0-3.2(1.75, 18) [◇]	
m3	Occlusal length	1.9-2.1(2.0, 6) [#]	2.2-2.8(2.5, 2)*	2.0-2.8(2.19, 5)*	3.0*
				1.9-2.5(2.14, 16) [☆]	1.9-2.7(2.24, 10) [◇]
	Height	2.8-3.4(3.1, 2) [#]		3.3-4.3(3.07, 4)*	6.8*
				3.1-4.5(3.75, 16) [☆]	3.5-4.5(4.13, 10) [◇]
b	0.0-0.3(0.13, 3) [#]	0.1*	0.3-1.1(0.65, 3)*	2.6*	
			0.3-0.8(0.57, 16) [☆]	0.4-1.2(0.7, 10) [◇]	
c	0.1-0.3(0.23, 3) [#]	0.4*	0.7-1.0(0.68, 3)*	2.2*	
			0.3-0.7(0.48, 16) [☆]	0.4-1.3(0.93, 10) [◇]	

续表

		<i>Pr. licenti</i>	<i>Pr. tianzuensis</i>	<i>Pr. eriksoni</i>	<i>Pl. cf. Pl. lyratus</i>
m3	d	0.0-0.2(0.1, 3) [#]	0.1 [*]	0.4-1.1(0.58, 3) [*] 0.0-0.4(0.18, 16) [☆]	3.7 [*] 0.0-1.2(0.64, 10) [◇]
	e	0.0-0.2(0.07, 3) [#]	0.0 [*]	0.2-0.4(0.3, 3) [*] 0.0-0.2(0.05, 16) [☆]	3.5 [*] 0.0-0.7(0.2, 10) [◇]
	Length of m1-m3	7.2-7.9(7.58, 4) [#]	8.5 [*]	7.9-8.6(8.25, 2) [*] 9.5 [☆]	
M1	Occlusal length	2.5-3.0(2.7, 7) [*] 2.5-3.0(2.68, 11) [#]	2.9-3.1(3.0, 3) [*] 2.8-3.6(3.32, 5) [*]	3.2-3.5(3.3, 3) [*] 2.7-3.3(2.97, 16) [☆]	3.5-3.7(3.57, 3) [*] 2.7-3.7(3.3, 20) [◇]
	Length of anterior lobe	0.4-0.6(0.54, 7) [*] 0.4-0.7(0.55, 10) [#]	0.6-0.9(0.73, 3) [*] 0.5-0.7(0.64, 5) [*]	0.7-0.7(0.7, 2) [*] 0.5-0.7(0.66, 16) [☆]	0.6-0.8(0.7, 3) [*] 0.6-0.8(0.72, 20) [◇]
	Height	4.4-5.8(4.74, 7) [*] 4.0-4.8(4.4, 4) [#]	4.7-5.0(4.83, 3) [*] 5.0-5.9(5.38, 4) [*]	5.3-6.2(5.58, 4) [*] 4.7-6.5(5.64, 16) [☆]	6.5 [*] 5.2-7.9(6.85, 20) [◇]
	A	0.0-0.1(0.09, 7) [*] 0.0-0.1(0.07, 9) [#]	0.2-0.2(0.2, 3) [*] 0.1-0.2(0.18, 5) [*]	0.2 [*] 0.0-0.7(0.28, 16) [☆]	1.0 [*] 0.1-2.6(1.16, 20) [◇]
	B	0.4-0.8(0.59, 7) [*] 0.3-0.6(0.5, 9) [#]	0.3-1.4(0.73, 3) [*] 0.8-1.4(1.02, 5) [*]	1.3 [*] 0.5-1.3(1.03, 16) [☆]	1.9 [*] 0.7-2.9(1.99, 20) [◇]
	C	0.4-0.8(0.59, 7) [*] 0.3-0.7(0.56, 8) [#]	0.5-1.9(1.03, 3) [*] 0.7-1.1(0.88, 5) [*]	1.4-1.4(1.4, 2) [*] 0.9-1.5(1.17, 16) [☆]	1.6 [*] 1.0-3.0(1.86, 20) [◇]
	D	0.4-0.7(0.47, 7) [*] 0.0-0.4(0.16, 8) [#]	0.2-0.8(0.43, 3) [*] 0.0-0.0(0.0, 5) [*]	1.0-1.0(1.0, 2) [*] 0.0-0.8(0.32, 16) [☆]	1.3 [*] 0.7-2.2(1.59, 20) [◇]
M2	Occlusal length	2.1-2.5(2.26, 11) [#]	2.5 [*] 2.7 [*]	2.3-2.5(2.4, 4) [*] 2.1-2.6(2.32, 16) [☆]	2.6-2.6(2.6, 2) [*] 2.2-3.1(2.87, 20) [◇]
	Height	4.0-5.2(4.46, 7) [#]	6.3 [*]	4.8-5.9(5.38, 4) [*] 4.1-6.0(5.28, 16) [☆]	6.0 [*] 5.6-7.5(6.5, 20) [◇]
	A	0.0-0.2(0.07, 9) [#]	0.0 [*] 0.1 [*]	0.1-0.6(0.3, 3) [*] 0.0-0.5(0.18, 16) [☆]	0.5 [*] 0.6-1.7(1.05, 20) [◇]
	B	0.0-0.2(0.12, 9) [#]	0.0 [*] 0.3 [*]	0.4-0.5(0.43, 3) [*] 0.0-0.8(0.24, 16) [☆]	0.2 [*] 0.3-1.5(0.71, 20) [◇]
	C	0.2-0.6(0.33, 8) [#]	0.5 [*] 0.5 [*]	0.7-1.1(0.83, 3) [*] 0.5-1.0(0.85, 16) [☆]	1.4 [*] 0.9-1.9(1.38, 20) [◇]
	D	0.0-0.3(0.14, 8) [#]	0.3 [*] 0.0 [*]	0.6-0.8(0.7, 3) [*] 0.1-0.9(0.44, 16) [☆]	1.0 [*] 0.6-3.0(1.29, 20) [◇]
M3	Occlusal length	1.6-2.1(1.9, 7) [#]	1.5-2.2(1.85, 2) [*] 2.1-2.3(2.2, 2) [*]	1.8-2.4(2.18, 4) [*] 1.8-2.3(2.01, 16) [☆]	2.0-2.6(2.37, 3) [*] 1.7-2.5(2.24, 14) [◇]
	Height	3.0-3.9(3.53, 6) [#]	2.7-4.2(3.45, 2) [*] 4.0-4.9(4.45, 2) [*]	3.7-5.1(4.43, 4) [*] 3.4-4.5(4.0, 16) [☆]	4.0-5.0(4.6, 3) [*] 3.7-5.6(4.63, 14) [◇]
	A	0.0-0.2(0.09, 7) [#]	0.0-0.2(0.1, 2) [*] 0.3-0.3(0.3, 2) [*]	0.5-1.0(0.9, 3) [*] 0.0-0.4(0.08, 16) [☆]	1.9-2.0(1.95, 2) [*] 0.2-1.0(0.47, 14) [◇]
	B	0.0-0.2(0.07, 7) [#]	0.0-0.0(0.0, 2) [*] 0.1-0.1(0.1, 2) [*]	0.0-0.2(0.1, 3) [*] 0.0-0.2(0.04, 16) [☆]	0.3-2.0(1.15, 2) [*] 0.0-0.6(0.15, 14) [◇]

续表

		<i>Pr. licenti</i>	<i>Pr. tianzuensis</i>	<i>Pr. eriksoni</i>	<i>Pl. cf. Pl. lyratus</i>
M3	C	0.0-0.3(0.19, 7) [#]	0.1-0.3(0.2, 2)* 0.3-0.3(0.3, 2)*	0.5-0.7(0.6, 3)* 0.1-0.6(0.3, 16) [☆]	1.0-1.2(1.1, 2)* 0.4-0.9(0.72, 14) [◇]
	D	0.0-0.1(0.07, 7) [#]	0.0-0.1(0.05, 2)* 0.2-0.2(0.2, 2)*	0.1-0.8(0.53, 3)* 0.0-0.5(0.14, 16) [☆]	0.9* 0.1-0.8(0.49, 14) [◇]

注: 1) 牙齿高度(height of teeth)=齿冠高度(height of crown)+齿根高度(height of root);

2) 符号代表化石产地地点(the symbols after the measurements show the fossil localities): * 秦安董湾(Dongwan, Qin' an), # 庆阳教子川(Jiaozichuan, Qingyang), * 天祝松山(Songshan, Tianzhu), ☆ 化德二登图(Ertmet, Huade), ◇ 化德比例克(Bilike, Huade);

3) 括弧内第一数值为平均值, 第二数值为标本数目(values in parentheses is average and specimens number).

*P. licenti*的正型标本是1破损头骨连着下颌骨(RV 26010)。为了保护标本的完整性, 至今也未将头骨和下颌骨拆分开, 因而其臼齿的形态并不清楚。Teilhard de Chardin (1926)当初只是着重描述了头骨特征, 后来在与正型标本同一层位的红粘土岩块中发现了更多的材料, 他(1942)又对该种的臼齿特征作了补充记述, 指出该种下臼齿的后外谷(褶沟)有一恒定的基部尖; 上臼齿外谷(颊侧褶沟)较内谷(舌侧褶沟)长, 下臼齿内谷(舌侧褶沟)较外谷(颊侧褶沟)长, 而且越是进步的种越长; M1的前内谷向下开沟短, 磨蚀到一定程度就会消失, 像*P. murinus*和*Episiphneus youngi*一样, 变成 ω 型; 极年轻个体的M2牙根虽未长出, 仍可辨认出2个外谷和一个内谷; m1具前褶沟, 但后外谷基部缺失附尖。我们观察其他种类时发现, 除了反映上、下臼齿单面高冠的内、外谷长度是比较稳定的特征外, 其余性状均属个体变异。

在上下臼齿齿列长度、咬面长度、牙齿整体高度和齿冠高度等方面, *P. licenti*与*P. murinus*均十分接近, 只是后者的几乎所有数据范围和平均值都略大, 例如它的两件

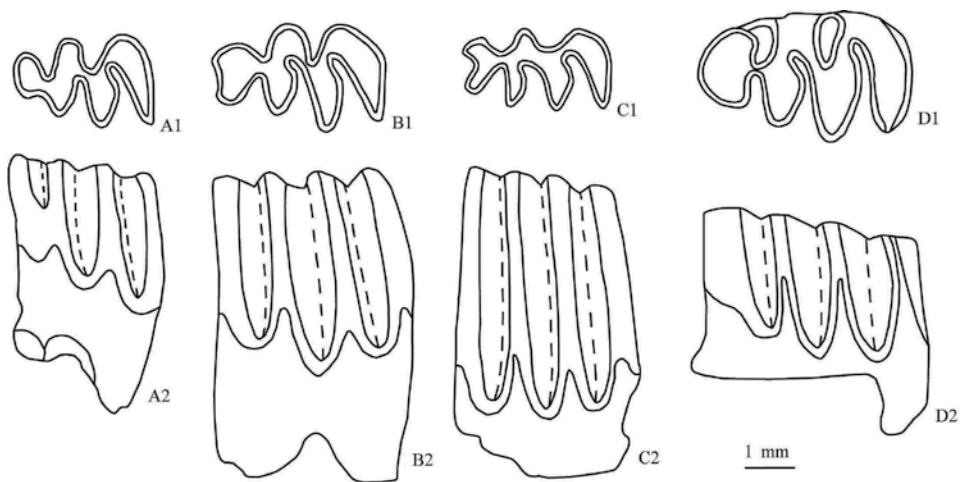


图2 桑氏原鼯鼠(A)、天祝原鼯鼠(B)、艾氏原鼯鼠(C)和琴颊上新鼯鼠(相似种)(D)的m1咬面(1)及舌侧面(2)

Fig. 2 Occlusal (1) and lingual (2) views of m1 of *Prosiphneus licenti* (A), *P. tianzuensis* (B), *P. eriksoni* (C) and *Pliosiphneus cf. Pl. lyratus* (D)

m1-m3长8.3~8.5 mm, 一件M1-M3长8.2 mm, 比前者相应的7.2~7.9 mm (4件)和6.9~7.5 mm (3件)都长, 因而显得更为进步。此外, 在头骨上的显著差别是前者的眶上脊较后者分开更明显。

P. licenti, *P. qinanensis*和*P. qiui* (Zheng et al., 2004)的M1都有3个牙根, 但前者基部愈合, 后二者不愈合; *P. licenti*也不同于M1只有2牙根且基部愈合的较进步种类*P. tianzuensis* (Zheng and Li, 1982)和*P. eriksoni* (Schlosser, 1924)(Zheng, 1994)。同样, 在上臼齿颊侧和下臼齿舌侧珐琅质曲线起伏程度方面, *P. licenti*也介于前两种和后两种之间。*P. haoi* Zheng et al., 2004仅有下臼齿, 其下臼齿舌侧珐琅质曲线起伏明显较弱。在牙根数为3且基部愈合的形态特征上, *P. licenti*与*P. murinus* Teilhard de Chardin, 1942相似, 但后者上下臼齿的珐琅质参数值较大(Zheng, in preparation)。

天祝原鼯鼠 *Prosiphneus tianzuensis* (Zheng & Li, 1982)

层位及材料 第7层: 1段左上颌带M1-M2(IVPP V 18594.1), 1右m1(V 18594.2), 1右m2(V 18594.3), 2右M1(V 18594.4-5), 2右M3(V 18594.6-7)。

特征(修订) 上臼齿具2个基部愈合的齿根。m1的ac略偏颊侧, 珐琅质参数a, b, c, d, e值分别为0.0~0.1, 0.5~0.9, 0.6~1.0, 0.4~1.0, 0.0~0.3; M1珐琅质参数A, B, C, D值分别为0.1~0.2, 0.3~1.4, 0.5~1.9, 0.0~0.8。

测量 见表1。

描述 个体较*P. licenti*明显大。m1的ac椭圆, 居中。lra3与bra2相对。lra1和lra2向前外方向伸展并超过牙纵轴与bra1相错。舌侧珐琅质曲线的最高点均超过其相邻褶沟的终端; 颊侧珐琅质曲线的最高点与其相邻褶沟终端几乎在同一水平(图2B)。成年个体舌侧齿冠高度大于颊侧齿冠高度。

m2的基本形态和m1前帽以后的部分类似, 但bra1-2较浅, 而lra1-2较深。

M1前叶相对较宽, LRA1与牙纵轴垂直; LRA2较深, 前外向伸展。BRA1-2向后内伸展程度相当, 且与LRA2相交错。在老年个体(图3B), BRA2的舌侧端向后折曲。颊侧珐琅质曲线的最低点低于其前、后褶沟的下端。具两个基部愈合的宽扁牙根。

M2的基本形态和M1前叶之后的部分一致。

M3的形态如M2, 具2齿根, 但明显退化; 牙齿明显向前弯曲。

比较与讨论 *P. tianzuensis*最初被视为*P. licenti*的亚种(郑绍华、李毅, 1982), 主要依据是其M3的T3和T4间有一附加珐琅质环。在对比了更多标本后发现, 此环是一极不稳定的性状。但是考虑到以下几个方面, 我们认为*P. tianzuensis*依然应该视为独立的种: 1) 个体明显较*P. licenti*大; 2) M1牙根数为2而不是3; 3) 上、下臼齿舌、颊侧珐琅质曲线起伏较大, m1珐琅质参数a, b, c, d, e值和M1珐琅质参数A, B, C, D值较*P. licenti*的大; 4) m1-m2的bra1及M1-M2的BRA2更向前内倾斜。

秦安的材料与典型地点甘肃天祝松山第二地点的材料相比, m1咬面长度、牙齿高度、珐琅质参数a, b, e值, m2的牙齿高度和c值, M1的咬面长度、牙齿高度、A, B, C值, 以及M3的咬面长度、牙齿高度、C值等均在天祝材料的变异范围或部分重叠, 只是m1的c, d值、m2的b, d值、M1的D值略大于天祝标本(见表1)。

*P. tianzuensis*个体大小与*P. eriksoni*接近, 但不同点在于: 1) m1, m2和m3的咬面长度和M3的牙齿高度均较大; 2) m1的b, c, e值、M1的咬面长度及A值均较小(见表1)。

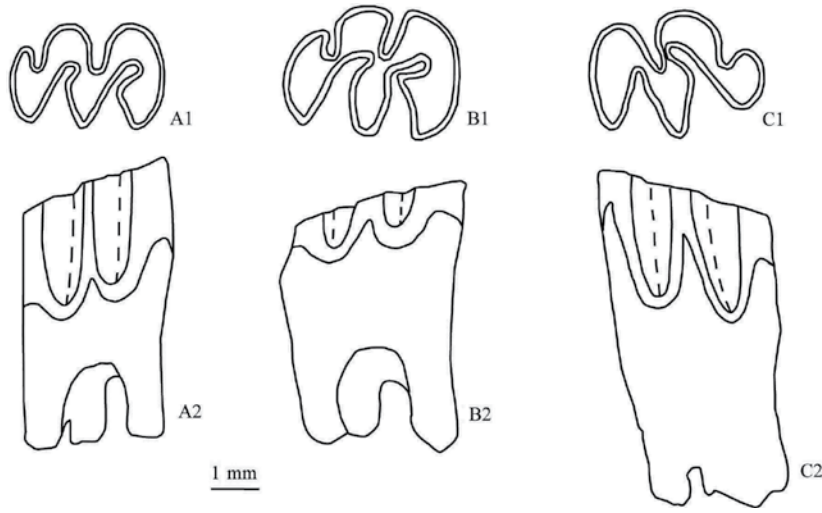


图3 桑氏原鼯鼠(A)、天祝原鼯鼠(B)和艾氏原鼯鼠(C)的M1咬面(1)及颊侧视(2)

Fig. 3 Occlusal (1) and buccal (2) views of M1s of *Prosiphneus licenti* (A), *P. tianzuensis* (B) and *P. eriksoni* (C)

*P. tianzuensis*上下臼齿的珐琅质曲线参数介于*P. licenti*和*P. eriksoni*之间，因此在进化谱系上，*P. tianzuensis*可视为*P. licenti*和*P. eriksoni*之间一个短暂生存的种类。

*P. tianzuensis*和*P. eriksoni*曾被一起归入*Myotalpavus*属(Zheng, 1994)。后来我们认识到*Prosiphneus* Teilhard de Chardin, 1926与*Myotalpavus* Miller, 1927为同物异名，又将它们重新置于*Prosiphneus*属(郑绍华等, 2004)。

艾氏原鼯鼠 *Prosiphneus eriksoni* (Schlosser, 1924)

层位及材料 第8层：2右m1(IVPP V 18595.1-2), 1右m2(V 18595.3); 第9层：1左m2(V 18595.4); 第10层：1较完整右下颌带m1-m3(V 18595.5), 1左、2右m1(V 18595.6-8), 1左m2(V 18595.9), 1左m3(V 18595.10), 1左M1(V 18595.11); 第11层：1段左下颌带m1-m3(V 18595.12), 4左、3右m1(V 18595.13-19), 2左、2右m2(V 18595.20-23), 2左m3(V 18595.24-25), 2左、2右M1(V 18595.26-29), 3左、3右M2(V 18595.30-35), 3左、2右M3(V 18595.36-40); 第12层：1右M1(V 18595.41)。

特征(修订) 上臼齿各具两个基部更加愈合的齿根。m1的ac居中，其珐琅质参数a, b, c, d, e值分别为0.0~0.5, 0.2~1.7, 0.4~1.5, 0.0~1.0, 0.0~1.0; M1珐琅质参数A, B, C, D值分别为0.0~0.7, 0.0~1.3, 0.5~1.5, 0.0~1.0。

测量 见表1。

描述 目前归入该种的材料虽较多，但多数为老年个体或破碎标本。年轻个体中，m1的ac居中，前端有一宽浅纵沟；bra1-2深入齿冠浅，舌侧褶沟深入齿冠较深；齿冠很高，齿根未发育完全(图2C)。成年个体，ac明显偏向颊侧，前端纵沟消失；颊侧褶沟深入齿冠较深，随着年龄增长，颊侧褶角外端珐琅质层中断，从而变成珐琅质环；老年个体齿冠逐渐变低，齿根逐渐加长。无论年轻或成年个体，颊、舌侧珐琅质曲线参数值都基本稳定在一定范围内。

m2和m3基本形态与m1前帽之后的部分相似。但m3显著退化，后叶收缩变窄。

M1为老年个体，其前叶相当窄，近乎椭圆。BRA1后内向伸至LRA2前壁。齿冠高

度不及齿根长度的一半。颊、舌侧珐琅质曲线起伏大。牙根分叉晚, 仅2根(图3C)。

M2和M3形态相似, 颊、舌侧珐琅质曲线起伏程度从M1到M3逐渐减小。M3的BRA2深入齿冠较深, 在一些标本上, 其终端可形成珐琅质环。

比较与讨论 秦安标本数量虽然较少, 但其各项测量数据均在*P. eriksoni*典型地点——内蒙古化德二登图标本的变异范围内(见表1)。

P. eriksoni (Schlosser, 1924)是发现最早的白齿带根的鼯鼠。从那以后, 一些地点白齿带根的材料都被归入此种或其相似种(Teilhard de Chardin and Young, 1931; Mi, 1943; Mats et al., 1982; Flynn et al., 1991; Tedford et al., 1991; Qiu and Storch, 2000)。

根据m1的性状, 山西保德火山的“*P. eriksoni*” (Teilhard de Chardin and Young, 1931)应是同一地点*Mesosiphneus intermedius*的同物异名; 陕西陇县白牛峪一带m1的右下颌(Mi, 1943; Young et al., 1943)应是下述*Chardina gansuensis* sp. nov.的较老年个体。内蒙古化德比例克的“*Prosiphneus cf. eriksoni*” (Qiu and Storch, 2000)虽然具有白齿带根凸枕型鼯鼠的特征(郑绍华, 1997), 但其个体、上白齿颊侧和下白齿舌侧珐琅质参数值均显著较*P. eriksoni*大, 更接近榆社的*Pliosiphneus lyratus* (见表1)。榆社盆地的“*Prosiphneus eriksoni*” (Flynn et al., 1991; Tedford et al., 1991)的鉴定可能有误, 因为后来对这批材料的详细研究未发现有该种存在(Zheng, in preparation)。

根据m1的咬面形态及其舌侧珐琅质曲线判断, 中贝加尔的“*Prosiphneus ex. gr. eriksoni*” (Mats et al., 1982)应与*P. eriksoni*一致。

*P. eriksoni*最初被置于*Siphneus*属(Schlosser, 1924), 后被归入*Myotalpavus*属(Miller, 1927; Zheng, 1994)。但是*Myotalpavus*属被认定为*Prosiphneus*属(Teilhard de Chardin, 1926)的同物异名后(郑绍华等, 2004), 目前普遍将其置于*Prosiphneus*属内。

上新鼯鼠属 *Pliosiphneus* Zheng, 1994

特征(修订) 中型。间顶骨呈梭形镶嵌于两侧人字脊两翼之间。枕盾面突出于人字脊之后。原始种眶上脊彼此靠近, 眶间区较窄; 进步种眶上脊彼此不靠近, 眶间区较宽。枕区鳞骨呈三角形。矢状区宽, 呈竖琴状。颞脊和人字脊发育。白齿具牙根。M1齿根愈合合成单根; m1的ac居中; 上白齿颊侧、下白齿舌侧的各项珐琅质参数值均显著大于最进步的*Prosiphneus*种。

属型种 *Prosiphneus lyratus* Teilhard de Chardin, 1942。

琴颊上新鼯鼠(相似种) *Pliosiphneus cf. Pl. lyratus* (Teilhard de Chardin, 1942)

层位及材料 第13层: 1左下颌带m1-m2(IVPP V 18596.1), 1破左m1(V 18596.2), 1左、1右m2(V 18596.3-4), 1右上颌带M1-M3(V 18596.5), 1左、1右M3(V 18596.6-7); F19(=14层): 1右m1, 1左M1; F20(=14层): 1右M1, 1左M2; F22(=13层): 1残破左m2。

测量 见表1。

描述 m1均为成年个体, ac居中, 前端呈弧形; bra2与lra3相对, 褶沟前壁均较直使得ac成半圆形; 颊侧褶沟较舌侧褶沟浅, 随着磨蚀加深, 形成珐琅质环; 颊侧珐琅质曲线起伏程度较舌侧大, 前后向下延伸长; 舌侧珐琅质曲线形成三个峰, 前后向下延伸短(图2D)。

m2的形态与m1前帽以后的部分相当, 成年个体的颊侧褶沟形成珐琅质环, 舌侧珐琅质曲线的起伏程度较m1的稍小。m3为年轻个体, 基本形态如m2, 但牙齿齿根向颊侧

弯曲显著；颊侧褶沟较浅；后叶明显较狭窄。

上颌臼齿咬面已磨蚀到齿冠基部，是一极端老年个体，齿列长9.45 mm。M3后叶退化，其上无珐琅质环；颊、舌侧齿冠高度相当，珐琅质曲线形成两个波峰。

比较与讨论 *Pl. lyratus*的正型标本(H. H. P. H. M. 31.076)可能是来自榆社盆地II带(具体地点和层位不详)的雄性老年个体头骨(Teilhard de Chardin, 1942: figs. 36, 36a)。由于标本年龄太大，不能确定其臼齿性状。近年来对榆社标本重新研究时发现，H. H. P. H. M. 31.077(=RV 42040)号头骨(带左右M1-M2)、被归入“*murinus group*”的头骨(不带臼齿)(Teilhard de Chardin, 1942: figs. 28, 34B)以及混杂在*Yangia omegodon*中的头骨前部(带左右M1-M3)等3件标本与*Pl. lyratus*具有相同的性状：枕盾面突出于人字脊之后，间顶骨呈梭形位于两侧人字脊之间，矢状区中心凹陷呈竖琴状，眶间收缩区宽，眶上脊彼此强烈分开等。这些标本的颞脊较正型标本弱的性状可视为性别差异，可能属于雌性个体。这样，*Pl. lyratus*就有了与头骨相对应的臼齿性状。根据上、下臼齿珐琅质参数值的对应关系，产自泥河湾盆地花豹沟1段带m1-m3的成年个体的下颌(V 15474)被归入此种(Zheng, 1994)。榆社盆地M1的珐琅质参数A, B, C, D值分别为1.4~2.4, 2.0~2.7, 1.5~2.5和1.0~2.3，而花豹沟的m1珐琅质参数a, b, c, d, e值分别为0.0, 1.9, 1.7, >4.6, >3.6。

董湾标本的上述参数值M1分别为1.0, 1.9, 1.6和1.3, m1分别为0.0, 1.0~2.5, 1.5~3.2, 3.6, 2.7, 都显著较*Pl. lyratus*小，因此归入此种(刘丽萍等, 2011)可能并不合适。这些数据十分接近内蒙古化德比例克地点的“*Prosiphneus cf. eriksoni*” (Qiu and Storch, 2000)的变异范围(见表1)。因此，董湾的这些材料以及内蒙比例克的材料可能是*Pliosiphneus*属中较为原始的种类。这些材料齿冠高度显著大于*Pr. eriksoni*而较为接近*Pl. lyratus*。就臼齿形状和齿冠高度而言，中贝加尔的“*Prosiphneus praetingi*” (Mats et al. 1982)似应与董湾标本属于同一类型。

日进鼯鼠属 *Chardina* Zheng, 1994

特征(修订) 间顶骨半圆形，位于人字脊之前；头骨枕盾面轻微突出于人字脊之后；枕上突弱；枕区鳞骨呈三角形；矢状区后部下凹，其宽度约为眶间宽度的1.8倍。臼齿具牙根，相对低冠；M1的齿根愈合成单齿根；m1的珐琅质参数a值接近于零。

属型种 *Prosiphneus truncatus* Teilhard de Chardin, 1942。

归入种 *C. sinensis* (Teilhard de Chardin & Young, 1931); *C. gansuensis* sp. nov., *C. teilhardi* (Zhang, 1999)。

中华日进鼯鼠 *Chardina sinensis* (Teilhard de Chardin & Young, 1931)

材料及层位 第13层：1段右下颌带m1(IVPP V 18597.1), 1残破左m1(V 18597.2), 1左m2前部(V 18597.3), 1左M3(V 18597.4); 第14层：1段左下颌带m1-m2(V 18597.5), 1段右下颌带m1-m2(V 18597.6), 1右 m1(V 18597.7), 2左m2(V 18597.8-9), 1左、1右m3(V 18597.10-11), 1左M1(V 18597.12), 1左M2(V 18597.13)。

特征(修订) 臼齿相对低冠。m1的珐琅质参数a, b, c, d, e值分别为0.0~0.4, 1.8~2.2, 1.4~3.0, 1.6~2.6, 0.7~1.6。M1珐琅质参数A, B, C, D值分别为0.9~1.9, 1.8~2.1, 1.8~2.8, 1.3~1.5。

测量 见表2。

表2 日进鼯鼠各种的臼齿测量

Table 2 Tooth measurements of species of *Chardina*

(mm)

		<i>C. sinensis</i>	<i>C. gansuensis</i>	<i>C. truncatus</i>
m1	Occlusal length	3.4-4.2(3.72, 6)*	3.8-4.1(3.93, 2)* 3.7 [◇]	3.7* 4.1(cotype)* 3.1-4.4(4.03, 7) [☆]
	Lingual length of ac	0.9-1.2(1.03, 4)*	1.0-1.1(1.05, 2)* 0.9 [◇]	0.9-0.9(0.9, 2)* 0.9* 0.9-1.4(1.04, 11) [☆]
	Labial length of ac	1.4-1.5(1.45, 4)*	1.4-1.6(1.5, 2)* 1.2 [◇]	1.2-1.4(1.3, 2)* 1.4* 1.1-1.8(1.43, 11) [☆]
	Height	6.2-7.4(6.92, 5)*	8.0* >5.5 [◇]	6.2* 6.1-8.7(7.49, 10) [☆]
	a	0.0-0.2(0.05, 4)*	0.0-0.2(0.1, 2)* 0.4 [◇]	0.1* 0.0* 0.0-0.5(0.16, 11) [☆]
	b	1.8-2.2(2.0, 2)*	2.2-2.4(2.3, 2)* 2.1 [◇]	2.8* 3.3* 2.0-4.0(2.6, 12) [☆]
	c	1.4-1.9(1.7, 2)*	2.1-3.2(2.65, 2)* 3.0 [◇]	3.2* 2.0* 2.0-3.2(2.52, 11) [☆]
	d	1.6-1.6(1.6, 2)*	2.8-3.6(3.2, 2)* 2.6 [◇]	>4.1* >4.7* 3.5-5.2(4.22, 6) [☆]
	e	0.7-0.9(0.8, 2)*	2.1-2.8(2.45, 2)* 1.6 [◇]	>3.6* >4.4* 2.5-4.7(3.92, 6) [☆]
m2	Occlusal length	2.5-3.1(2.8, 4)*	3.2* 3.2 [◇]	2.9-3.3(3.07, 3)* 3.1* 2.8-3.7(3.32, 9) [☆]
	Height	5.6-7.5(6.58, 4)*	7.0* 6.0 [◇]	5.1-6.5(5.87, 3)* 5.5-8.9(7.73, 8) [☆]
	b	2.0*	2.0* 2.0 [◇]	2.6* 2.3* 1.9-3.2(2.51, 9) [☆]
	c	2.1*	2.1* 2.6 [◇]	3.9* 2.1* 2.1-3.5(2.56, 9) [☆]
	d	3.4*	2.6* 2.9 [◇]	3.6* >4.5* 2.0-4.2(3.12, 9) [☆]

续表

		<i>C. sinensis</i>	<i>C. gansuensis</i>	<i>C. truncatus</i>
m2	e	2.1*	1.9*	2.7*
			1.8 [◇]	>4.1*
m3	Occlusal length	2.4-2.4(2.4, 2)*	2.4*	2.4*
			2.5 [◇]	2.7*
	Height	4.4-4.5(4.45, 2)*	4.4*	4.4*
			3.7 [◇]	3.9-6.8(5.74, 5) [☆]
	b	0.6-1.0(0.8, 2)*	1.2*	1.9*
			1.1 [◇]	1.7*
	c	1.6-1.9(1.75, 2)*		2.1*
			1.2 [◇]	2.0*
	d	1.1-1.1(1.1, 2)*		1.1-2.1(1.56, 5) [☆]
			0.5 [◇]	1.6*
e	0.7-0.7(0.7, 2)*		1.9*	
		0.2 [◇]	0.9-2.7(1.57, 6) [☆]	
M1	Occlusal length	3.9*	3.8*	0.8*
		3.2 [#] (type)		1.3*
	Length of AL	0.8*	0.8*	0.4-1.7(0.83, 6) [☆]
		0.6 [#]		9.9*
	Height	7.5*	6.3*	10.1 [☆]
		6.0 [#]		
	A	1.8*		3.9-4.2(4.03, 3)*
		0.9 [#]		3.6-4.2(4.03, 10) [☆]
	B	2.1*		0.8-0.8 (0.8, 2)*
		1.8 [#]		0.7-0.9(0.81, 10) [☆]
C	2.8*		7.6-7.7(7.65, 2)*	
	1.8 [#]		6.5-9.0(8.12, 10) [☆]	
D	1.3*		>3.5->3.8(>3.65, 2)*	
	1.5 [#]		1.6-4.4(3.36, 7) [☆]	
M2	Occlusal length	2.9*		>3.9->4.5(>4.2, 2)*
		2.4 [#]		2.5-4.2(3.57, 7) [☆]
	Height	7.0*		4.0-4.0(4.0, 2)*
		5.3 [#]		3.0-4.8(3.55, 8) [☆]
A	2.0*		4.8-4.9(4.85, 2)*	
	0.7 [#]		2.5-4.8(3.19, 8) [☆]	

续表

		<i>C. sinensis</i>	<i>C. gansuensis</i>	<i>C. truncatus</i>
M2	B	2.2*		3.1*
		0.5 [#]		0.3-1.8(1.25, 6) [☆]
	C	2.9*		3.3*
1.2 [#]			2.2-4.1(2.83, 6) [☆]	
D	1.0*		23.3*	
	0.7 [#]		2.0-3.0(2.58, 6) [☆]	
M3	Occlusal length	2.8*	2.5*	2.3-2.4(2.35, 2)*
		2.2 [#]		2.2-2.7(2.53, 3) [☆]
	Height	5.2*	5.1*	5.2*
		3.9 [#]		5.4-6.0(5.7, 3) [☆]
	A	1.1*		1.1*
		0.6 [#]		0.7-1.0(0.9, 3) [☆]
	B	0.2*		1.0*
		0.2 [#]		0.2-1.0(0.52, 3) [☆]
	C	>0.9*		1.8*
		1.2 [#]		0.7-1.5(1.23, 3) [☆]
D	0.4*		1.9*	
	0.4 [#]		0.7-1.5(1.03, 3) [☆]	

注: 1) 牙齿高度(height of teeth)=齿冠高度(height of crown)+齿根高度(height of root);

2) 符号分别代表化石产地(the symbols after the measurements show the fossil localities): * 秦安董湾(Dongwan, Qin'an), * 榆社V 756 (Yushe V 756), # 河曲(Hequ), ☆ 灵台雷家河(Leijiahe, Lingtai), ◇ 神木(Shenmu);

3) 括弧内第一数值为平均值, 第二数值为标本数(values in parentheses is average and specimens number).

描述 m1的ac前端在年轻个体多向后凹, 颊侧褶沟较舌侧褶沟宽浅; 在成年个体, ac前端变圆, 颊侧褶沟深。但无论年轻或成年个体, ac总是偏向舌侧, bra2总是位于Ira3之后并彼此交错排列。珐琅质参数a值接近于零; e值小于1.0; b, c, d值不大于2.2 (图4A)。m2和m3颊、舌侧各具2褶沟, 基本形态像m1的ac之后部分, 只是后叶逐渐变窄。

上臼齿的颊侧较舌侧高冠。M1的褶沟深入齿冠深, 舌侧两个褶沟分别前于颊侧两个褶沟; 颊侧褶沟珐琅质曲线形成3个几乎等高的、约为齿冠高度一半的波峰。M2的中叶宽度明显大于前、后叶处的宽度, 珐琅质参数A、B值小于同一个体M1的相应参数, 但C和D值与M1的相当。M3前、中叶的宽度大于后叶处的宽度, 珐琅质参数A, B, C, D值较M2的小。从所观测的标本看, 每一上臼齿都是单一的齿根。

比较与讨论 *C. sinensis*的正型标本是产自山西河曲巡检司(Loc. 7)的1件带左右M1-M2的头骨前部材料(Cat. C. L. G. S. C. No. c/21), 归入标本是产自陕西府谷镇羌堡西(Loc. 11)的1件左M3 (No. c/23)和产自陕西神木城东山(Loc. 12)的1件带m1-m3的右下颌(No. c/22)。根据产自榆社高庄的同一个体*C. truncatus* (V 756) M1珐琅质参数值大于m1的对应关系, 河曲的M1与神木的m1在这个特征上并不匹配(M1的参数值小于m1), 因而后者可能是一较进步的种(郑绍华, 1997)。也就是说, 最初被视为该种的头骨前部材料为*C. sinensis*, 而下颌材料则为较近步或较高冠的种类。

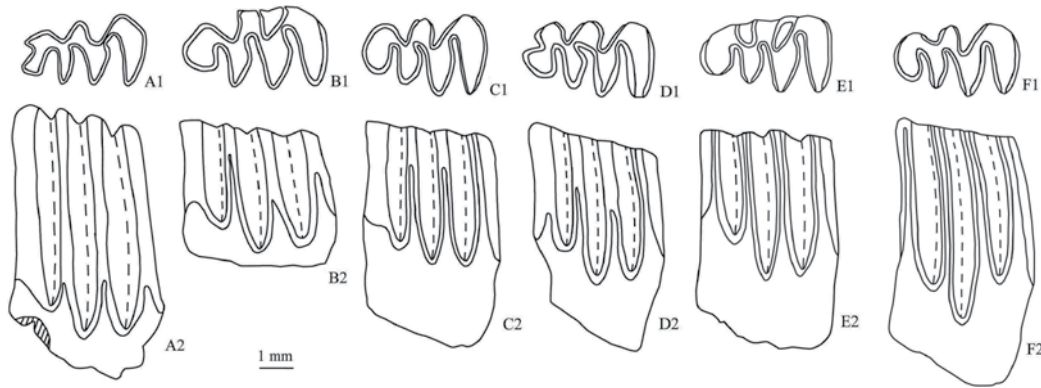


图4 中华日进鼯鼠(A)、甘肃日进鼯鼠(新种)(B)、峭枕日进鼯鼠(C)、原始中鼯鼠(新种)(D)、先丁氏中鼯鼠(E)和中间中鼯鼠(F)的m1咬面(1)及舌侧面(2)

Fig. 4 Occlusal (1) and lingual (2) views of *Chardina sinensis* (A), *C. gansuensis* sp. nov. (B), *C. truncatus* (C), *Mesosiphneus primitivus* sp. nov. (D), *M. praetingi* (E) and *M. intermedius* (F)

董湾的下臼齿，特别是m1的珐琅质参数值小于神木城东山标本，而上臼齿，特别是M1珐琅质参数值则与*C. sinensis*的相近或相同(见表2)。因此，董湾的上、下臼齿无疑可以归入*C. sinensis*。

甘肃日进鼯鼠(新种) *Chardina gansuensis* sp. nov.

1931 *Prosiphneus sinensis* Teilhard de Chardin and Young, 1931, p. 14; Pl. IV, fig. 1; Pl. V, fig. 5

1943 *Prosiphneus eriksoni* Young et al., p. 29

1943 *Prosiphneus eriksoni* Mi, p. 158; Pl. I, figs. 2a-d

2011 *Chardina sinensis* Liu et al., part

模式标本及层位 1段右下颌带m1(IVPP V 18598), 第15层。

归入标本及层位 第14层: 1左m1(V 18599.1), 1残破左M2(V 18599.2); 第15层: 1右m2(V 18599.3), 1右m3(V 18599.4), 1左M1(V 18599.5), 1左M3(V 18599.6)。

特征 臼齿齿冠高度介于*C. sinensis*和*C. truncatus*之间。m1珐琅质参数a, b, c, d, e值分别为0.0~0.4, 2.1~2.4, 2.1~3.2, 2.6~3.6, 1.6~2.8。

词源 以甘肃的汉语拼音Gansu命名。

测量 见表2。

描述 m1的ac偏向舌侧; bra明显位于lra3之后; 颊侧褶沟沟端与舌侧褶沟沟端彼此交错; 舌侧珐琅质曲线起伏较大, 在lra1-3上形成3个高度不等的波峰(图4B)。m2为成年个体, 齿根偏向颊侧; 基本形态如m1的ac之后部分; 齿根分叉晚。m3为老个体, 冠面形态极不清楚。

M1和M3均为十分破损的老年个体, 冠面颊、舌侧珐琅质均中断; 牙齿均愈合成本单根。

比较与讨论 董湾的归入材料虽少, 但其m1和m2的舌侧珐琅质参数a, b, c, d, e值与神木城东山标本(Teilhard de Chardin and Young, 1931)非常接近(表2)。因此两地的材料可视为同种。由于该种m1和m2的珐琅质参数值大于*C. sinensis*, 而小于*C. truncatus*, 因此代

表C. *sinensis*和C. *truncatus*之间的过渡类型。

陕西陇县白牛峪的“*Prosiphneus eriksoni*” (Mi, 1943: Pl. I, figs. 2a-d)因其m1的ac偏向舌侧、bra2位置后于lra3和珐琅质参数a值等于零, 应属日进鼯鼠属(*Chardina*); 因其珐琅质参数b, c, d值(分别为2.3, 1.9, >2.3)在新种甘肃日进鼯鼠(*C. gansuensis* sp. nov.)的范围内, 可归入该新种。

峭枕日进鼯鼠 *Chardina truncatus* (Teilhard de Chardin, 1942)

层位及材料 第16层: 2左m1(IVPP V 18600.1-2), 1右m1前部(V 18600.3), 3左m2(V 18600.4-6), 1左m3(V 18600.7); F16(=16层): 1右m1; F10(=19层): 1左m1。

特征(修订) 相对高冠。m1的a, b, c, d, e值分别为0.0~0.5, 2.0~4.0, 2.0~3.2, 3.6~5.2, 3.5~4.9。M1的A, B, C, D值分别为1.6~>3.8, 2.5~>4.5, 3.0~4.8, 1.5~4.9。

测量 见表2。

描述 m1为成年-老年个体。ac偏向舌侧, 前端椭圆; bra2位于lra3之后; 颊侧褶沟深入齿冠较深, 其内端超过舌侧褶沟外端, 彼此交错排列; 舌侧珐琅质曲线起伏大, 在lra1-3上形成3个陡峭的波峰, 其中第1褶角上的波峰最高(图4C); 珐琅质参数a值接近于零。m2的咬面形态相似于m1前帽之后的部分, 颊侧两个褶沟略向前内倾斜, 舌侧两个褶沟几与牙纵轴垂直, 彼此相错排列; 珐琅质参数c值比m1的稍大。m3为老年个体, 形态如m2, 但后叶更窄。

比较与讨论 该种的正型标本是发现于山西榆社盆地II带的一极端老年个体头骨(IVPP RV 4005)(Teilhard de Chardin, 1942), 臼齿磨蚀极深, 其他地点的臼齿材料无法与之对比。幸运的是, 1958年中国地质科学院地质研究所的胡承志等组成的一个野外队从榆社高庄乡的井南沟采集到1件连着下颌的头骨(V 756), 与正型标本的特征一致。由于该标本相对年轻并带有全部臼齿, 这就为确定该种的上、下臼齿特征提供了条件, 并为单个臼齿的对比提供了可能(Zheng, in preparation)。董湾的m1与V 756号标本相比, 在个体大小、前帽性状、珐琅质参数值(表2)等方面是一致的。其臼齿珐琅质参数值大于上述C. *sinensis*和C. *gansuensis* sp. nov.。按照*Chardina*属的修订特征, 甘肃宁县的“*Mesosiphneus*” *teilhardi* Zhang, 1999应归入该属, 因为其m1的珐琅质参数a值接近于零。除了个体较小、m1和m2的d和e值较小外, C. *teilhardi*和C. *truncatus*的区别是微小的。目前暂保留该种, 以待更多材料及后续研究。

C. *truncatus*分布较广, 泥河湾盆地(李强等, 2008)、榆社盆地(Teilhard de Chardin, 1942)和黄土高原(郑绍华、张兆群, 2000, 2001)都有报道, 是中晚上新世一个有标志意义的化石鼯鼠种类。

中鼯鼠属 *Mesosiphneus* Kretzoi, 1961

特征(修订) 间顶骨缺失; 头骨枕盾上部明显凹入人字脊之前(凹枕); 枕上突粗壮; 枕区鳞骨成狭条状; 顶骨-鳞骨缝线与颞脊在顶骨中部相交; 矢状区后部宽度为眶间宽的2~2.3倍; 臼齿具牙根, 高冠。m1的珐琅质参数a值大于零。

属型种 *Prosiphneus praetingi* (Teilhard de Chardin, 1942)。

包括种 *M. primitivus* sp. nov.; *M. intermedius* (Teilhard de Chardin and Young, 1931)。

原始中鼯鼠(新种) *Mesosiphneus primitivus* sp. nov.

2011 *Mesosiphneus* sp. Liu et al., part

正型标本及层位 第15层: 1右下颌带m1-m3 (IVPP V 18601)。

归入标本 第15层: 1右m1(V 18602.1), 1右m1前部(V 18602.2), 2左m3前部(V 18602.3-4), 1左M3(V 18602.5); 第16层: 1段左下颌带m1-m2(V 18602.6), 1左m3前部(V 18602.7), 1左M3(V 18602.8)。

特征 臼齿相对低冠。m1珐琅质参数a, b, c, d, e值分别为0.4~0.7, 1.9~2.9, 2.1~2.5, 1.7~5.2, 1.1~4.6。

词源 以拉丁词primitivus (原始的)命名, 意即该属中最原始的种。

测量 见表3。

表3 中鼯鼠各种的臼齿测量

Table 3 Teeth measurements of species of <i>Mesosiphneus</i>		(mm)		
		<i>M. primitivus</i>	<i>M. praetingi</i>	<i>M. intermedius</i>
m1	Occlusal length	3.7-4.1(3.87, 3)*	3.8-3.9(3.83, 3)* 4.1 [#]	3.6* 3.4 [☆]
	Lingual length of ac	0.9-1.1(1.05, 4)*	0.8-1.0(0.9, 3)* 1.1 [#]	0.8* 0.8 [☆]
	Labial length of ac	1.2-1.5(1.38, 4)*	1.4-1.5(1.43, 3)* 1.5 [#]	1.2* 1.2 [☆]
	Height	7.0-7.5(7.33, 3)*	5.8-6.5(6.1, 3)* 8.5 [#]	7.4* 7.7 [☆]
	a	0.4-0.7(0.5, 4)*	1.1-1.2(1.15, 2)* 1.5 [#]	4.3* 5.5 [☆]
	b	1.9-2.9(2.4, 4)*	>1.8-2.3(2.05, 2)* 4.3 [#]	4.4* 6.8 [☆]
	c	2.1-2.5(2.3, 3)*	>2.3-2.8(2.55, 2)* 4.4 [#]	>5.6* 6.9 [☆]
	d	1.7-5.2(3.45, 2)*	>2.0->4.2(>3.1, 2)* >5.0 [#]	>4.5* 7.3 [☆]
	e	1.1-4.6(2.85, 2)*	>1.6->3.5(>2.55, 2)* >5.0 [#]	>4.6* 7.0 [☆]
m2	Occlusal length	2.4-3.0(2.73, 3)*	2.9-3.0(2.97, 3)* 3.1 [#]	3.0*
	Height	5.5-5.6(5.55, 2)*	5.5-6.5(6.0, 3)* 6.2 [#]	7.0*
	b	1.0-1.3(1.1, 3)*	1.9* 3.7 [#]	5.0*
	c	1.5-2.7(1.93, 3)*	1.6* 3.4 [#]	>5.0*
	d	1.7-1.9(1.8, 2)*	3.9* 3.5 [#]	>4.8*

续表

		<i>M. primitivus</i>	<i>M. praetingi</i>	<i>M. intermedius</i>
m2	e	1.1-1.2(1.15, 2)*	3.9* 3.8 [#]	>5.1*
m3	Occlusal length	2.4*	2.5* 2.3 [#]	
	Height		4.2* 3.7 [#]	
	b		1.6* 2.0 [#]	
	c	1.2*	2.5* 1.9 [#]	
	d	1.6*	2.0* 1.1 [#]	
	e	1.1*	1.7* 1.0 [#]	
	Length of m1-m3	9.9*	9.7 [#]	3.8*
M1	Occlusal length		3.7* 3.9 [#]	
	Length of AL		0.7* 0.8 [#]	0.7*
	Height		5.7* 7.8 [#]	5.8*
	A		>1.3* >4.5 [#]	
	B		>1.7* >4.1 [#]	
	C		>1.6* 4.2 [#]	
	D		>1.4* 5.4 [#]	
M2	Occlusal length		2.6 [#]	
	Height		7.6 [#]	
	A		4.1 [#]	
	B		2.5 [#]	
	C		3.3 [#]	
M3	Occlusal length	2.3-2.3(2.3, 2)*	2.3* 2.4 [#]	2.5-2.5 (2.5, 2)*
	Height	5.6-6.0(5.8, 2)*	4.7* 5.8 [#]	4.9-4.9 (4.9, 2)*
	A	0.9-1.5(1.2, 2)*	1.7* 2.6 [#]	

续表

		<i>M. primitivus</i>	<i>M. praetingi</i>	<i>M. intermedius</i>
M3	B	0.3-0.3(0.3, 2)*	0.3* 1.3 [#]	
	C	0.8-1.4(1.1, 2)*	1.7* 1.3 [#]	
	D	0.4-0.7(0.55, 2)*	1.8* 1.5 [#]	
	Length of M1-M3		9.0 [#]	

注: 1) 牙齿整体高度(height of teeth)=齿冠高度(height of crown)+齿根高度(height of root);

2) 符号分别代表化石产地(the symbols after the measurements show the fossil localities): * 秦安董湾(Dongwan, Qin'an), [#] 榆社No. 29.483 (Yushe No. 29.483), ☆ 保德的模式标本c/23 (Baode No.c/23);

3) 括弧内第一数值为平均值, 第二数值为标本数目(values in parentheses is average and specimens number).

描述 下颌冠状突部分破损。联合部后端位于m1之下; 齿缺长约6 mm; 咬肌脊明显, 其上有m2和m3的根端隆突。m1的ac偏向舌侧, 其前端褶沟无或很浅; bra2后于lra3; 颊侧褶沟向前内方向深入, 随着年龄增加深度也逐渐增加, 并与舌侧褶沟交错; 舌侧珐琅质曲线起伏较低, 并在lsa1-4上形成4个从前向后高度逐渐增加的波峰, 其中最显著的特点是珐琅质参数a值大于零, 而d值通常大于b值(图4D)。m2和m3的形态相似于m1前帽之后部分, bra2都相对较深, 舌侧珐琅质曲线起伏较小; 但m3后叶显著变窄。

M3为成年个体。牙齿明显向后弯曲; 舌侧有一深的、与bra2相对的附加褶沟; 颊侧珐琅质曲线形成的2个波峰较舌侧的2个波峰陡峭。

比较与讨论 新种与榆社盆地的*M. praetingi* (Teilhard de Chardin, 1942)相比, 个体大小相当, 但m1珐琅质参数值, 尤其是a值较小; 与榆社(Teilhard de Chardin, 1942)和山西保德的*M. intermedius* (Teilhard de Chardin and Young, 1931)相比, 其珐琅质参数值不及后者的一半。因此, 建立一个新种较为合适。

先丁氏中鼯鼠 *Mesosiphneus praetingi* (Teilhard de Chardin, 1942)

层位及材料 第18层: 1左下颌带m1-m2(IVPP V 18603.1), 2右m1(V 18603.2-3), 2右m2(V 18603.4-5), 1左m3(V 18603.6), 1左M1(V 18603.7), 1右M3(V 18603.8); F1(=20层): 1左m1, F5(=20层): 1右M3。

特征(修订) 白齿较高冠。m1珐琅质参数a, b, c, d, e值分别为1.1~2.9, >1.8~4.3, >2.3~4.4, >2.0~>5.0, >1.6~>5.0; M1珐琅质参数A, B, C, D值分别为>1.3~>4.5, >1.7~>4.1, >1.6~4.2, >1.4~5.4。

测量 见表3。

描述 标本多为老年个体。白齿相当高冠。m1的ac偏向舌侧, 其前端圆; bra2在年轻个体较浅, 在成年个体深, 但都显著位于lra3之后; 两个颊侧褶沟内端与两个舌侧褶沟外端彼此交错; 颊侧珐琅质曲线在bsa1-3上形成的3个波峰即使在年轻个体均已贯穿咀嚼面; 舌侧珐琅质曲线起伏很大, 在lsa1-3上的3个波峰几乎接近或穿透牙冠, 而在lsa4上则较低(图4E)。m2和m3形态相似, 牙根均明显向颊侧弯曲; 均有两个较深

的颊、舌侧褶沟, 根端均向颊侧弯曲, 但m3的后叶显著退化, 舌侧珐琅质曲线起伏较小。

M1均为老年个体。一个相对年轻个体显示前叶短宽; 舌侧褶沟横向深入齿冠程度几与颊侧褶沟后内向深入齿冠程度相当; 颊侧齿质已贯穿齿冠; 颊侧前后端珐琅质层终止于同侧褶沟上端水平; 牙根愈合成一个。2个M3中一个为成年个体, LRA2深入齿冠深, 与近乎横向深入齿冠的BRA1和BRA2交错; 后叶轻微变窄, 其上无附加褶沟; 颊侧珐琅质波峰在BSA2上较在BSA3和后叶上的低; 牙齿前后两端珐琅质层向上延伸较同侧褶沟顶端高出很多; 牙根愈合成前后延伸的单根。

比较与讨论 *M. praetingi*的正型标本是产自榆社II带或高庄组的一老年个体头骨(Teilhard de Chardin, 1942: no. 19.903), 被归入该种的两件头骨(no. 19.904和no. 19.905)虽是成年个体, 但不带下颌。尽管德日进带着疑问将同一个体的上下颌齿列(no. 29.483)归入此种, 但他强调其M3后端有一个随磨蚀加深而消失的后褶沟。根据对这些标本的观察对比, 这种归属是合理的。这就为其他地方产出的单个牙齿的对比提供了可能。董湾剖面产出的下颊齿形态与no. 29.483号标本基本一致, 但珐琅质参数值略微偏小(表3)。

*M. praetingi*广泛分布于泥河湾盆地(李强等, 2008)、榆社盆地(Teilhard de Chardin, 1942)和黄土高原(郑绍华、张兆群, 2000, 2001)。

中间中鼯鼠 *Mesosiphneus intermedius* (Teilhard de Chardin & Young, 1931)

1942 *M. paratingi* Teilhard de Chardin, p. 54, figs. 40-41

层位及材料 第19层: 2左m1(IVPP V 18604.1-2), 1左m2(V 18604.3), 1左m3(V 18604.4), 1左M1(V 18604.5), 1左、1右M3(V 18604.6-7)。

特征(修订) 臼齿高冠。m1珐琅质参数a, b, c, d, e值分别为2.1~7.2, >3.2~8.0, >3.0~7.5, >2.6~7.9, >4.4~8.0。

测量 见表3。

描述和比较 董湾标本在个体大小和臼齿形态上与*M. praetingi*基本相同, 但m1和m2珐琅质参数值显著较大, 因而显得更高冠(图4F)。从个体大小和齿冠高度(见表3)判断, *M. intermedius*与榆社盆地的*M. paratingi*十分接近, 两者的地史分布也基本相同(均为晚上新世), 只不过前者分布于西部黄土高原, 后者分布于东部山间盆地。因此我们认为两者为同物异名。

Teilhard de Chardin and Leroy (1942)将唐山贾家山(Pei, 1930)和周口店顶盖砾石层(Pei, 1939)中的零星材料(已丢失)归入此种。从地理分布和地史分布判断, 它们更有可能属于*Episiphneus youngi*。

Kretzoi (1961)曾经将*P. intermedius*置于*Episiphneus*属, 但并没有说明理由。从*P. intermedius*的m1的前环结构判断(即m1的Ira3前于bra2), 无疑应属*Mesosiphneus*属(Zheng, 1994, 1997)。

M. primitivus sp. nov., *M. praetingi*和*M. intermedius* (= *M. paratingi*)三个不同种的m1珐琅质参数值a, b, c, d, e各有自己一定的变异范围, 但并不重叠, 例如3个种的a值变异范围分别为0.4~0.7, 1.1~1.5和4.3~5.5(表3), 这表明它们之间的区别明显, 也表明鼯鼠臼齿从相对低冠逐渐向更加高冠的进化趋势。

3 晚中新世-早上新世期间鼯鼠类的进化关系

由于没有头骨发现, 本文区分凸枕与凹枕型鼯鼠的主要依据是m1前帽的形状、位置及Ira3与bra2的相对位置(郑绍华, 1997): 前帽椭圆、偏向颊侧或居中、Ira3与bra2正向或斜向相对者为凸枕型(如图2所示); 前帽扁宽、偏向舌侧、Ira3显著前于bra2者为过渡型和凹枕型(如图4所示)。董湾剖面中最原始的从凸枕型向凹枕型过渡的中华日进鼯鼠*Chardina sinensis* (图4A)与较进步的凸枕型鼯鼠*Prosiphneus eriksoni* (图2C)相比, 其个体及各项参数值大体相当, 因而最早的*Chardina*鼯鼠最有可能源于*Pr. eriksoni*, 而非*Pliosiphneus* cf. *Pl. lyratus* (图2D), 因为其个体及各项参数值均小于后者。

根据古地磁测年(Hao and Guo, 2004)和地层划分(刘丽萍等, 2011), 董湾剖面中各种鼯鼠的产出层位和时代分布如图5所示。这表明: 1) 10种鼯鼠分布的地层厚度为71.2 m (从C2An.3n正极性事件底的3.596 Ma至C3Bn正极性事件底的7.212 Ma), 代表了3.616 Ma的地质历史。换言之, 这一时期每一种鼯鼠的平均演替速率是0.362 Ma。这样快的速率反映出当时当地气候环境有由相对湿润向相对干燥的频繁而剧烈的波动。2) 晚中新世时期凸枕型鼯鼠(包含*Prosiphneus*和*Pliosiphneus*属)占据了绝对优势, 而早上新世则演变成以凹枕型鼯鼠(*Chardina*和*Mesosiphneus*属)占优势。这种现象在泥河湾盆地上新统剖面(李强等, 2008)、榆社盆地上中新统-上新统剖面(Flynn et al., 1997)以及灵台上中新统-下更新统剖面(郑绍华、张兆群, 2000, 2001)也得到了印证。3) 在晚中新世晚期(7.21~5.33 Ma), 完成了从*Prosiphneus licenti*→*Pr. tianzuensis*→*Pr. eriksoni*→*Pliosiphneus lyratus*种的进化过程; 而上新世早期(含极短暂的晚中新世晚期)(5.47~4.19 Ma)则完成了从*Pr. eriksoni*→*Chardina sinensis*→*C. gansuensis* sp. nov.→*C. truncatus*→*M. primitivus* sp. nov.→*M. praetingi*→*M. intermedius*种的进化。也就是说, 晚中新世晚期完成了3次种的转换, 其转换速率约0.627 Ma; 而上新世早期完成了6次, 其速率约为0.213 Ma。这种情况反映出, 上新世初的气候波动比晚中新世更加剧烈。4) 同一层位祖、裔共存的情形清晰可见。例如, *C. gansuensis*起源于*C. sinensis*并在第14层处于共生状态; *C. truncatus*和*M. primitivus*起源于*C. gansuensis*并在第16层处于共生状态; *M. intermedius*起源于*M. praetingi*且在第19层处于共生状态。5) 祖、裔属种臼齿高冠程度十分接近, 例如, *C. gansuensis*臼齿齿冠高度虽然增加了, 但还是和其直接祖先*C. sinensis*接近; 又如*Pliosiphneus* cf. *Pl. lyratus*的齿冠高度明显大于*C. sinensis*。

董湾剖面记录了鼯鼠进化过程中较明显的4个属种更替阶段:

1) 晚中新世晚期原鼯鼠属内从桑氏原鼯鼠(*Prosiphneus licenti*)演化出天祝原鼯鼠(*P. tianzuensis*), 进而演化为艾氏原鼯鼠(*P. eriksoni*)阶段。

2) 晚中新世晚期-上新世初期可能为从艾氏原鼯鼠(*P. eriksoni*)→琴颊上新鼯鼠(*Pliosiphneus* cf. *Pl. lyratus*)阶段。

3) 最晚中新世-上新世早期为从凸枕型的艾氏原鼯鼠(*P. eriksoni*)演化出头骨仍然具有凸枕型但臼齿已进化成凹枕型的中华日进鼯鼠(*Chardina sinensis*)→甘肃日进鼯鼠(*C. gansuensis*)→峭枕日进鼯鼠(*C. truncatus*)阶段。

4) 上新世早期从中华日进鼯鼠(*C. sinensis*)→甘肃日进鼯鼠(*C. gansuensis*)→原始中

鼯鼠(*Mesosiphneus primitivus*)→先丁氏中鼯鼠(*M. praetingi*)→中间中鼯鼠(*M. intermedius*)阶段代表了白齿有根凹枕型鼯鼠几乎全部的演替过程。

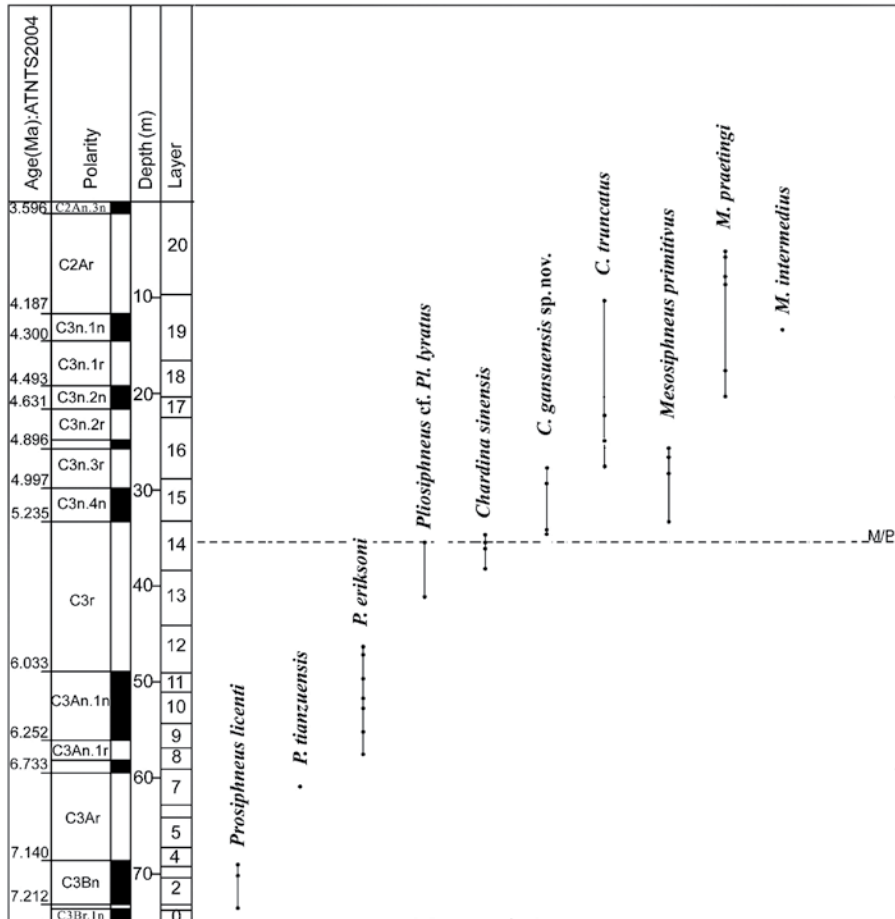


图5 董湾剖面中各种鼯鼠的时代分布

Fig. 5 Stratigraphic distributions of all described myospalacines from Dongwan section

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