山西保德第 30 地点的跳鼠化石
及其环境意义[1]

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摘要：山西保德第 30 地点发现了两种跳鼠化石，主要是三趾跳鼠 *Dipus fraudator*，还有少量的五趾跳鼠 *Paralactaga* cf. *P. suni*。这个跳鼠组合虽然种类不如内蒙古二登图动物群中的丰富，但其优势类群和组成比例都与后者非常相似。而与陕西蓝田灞河组发现的跳鼠组合相比，两者相差很大，后者以 *Protalactaga* 为主，虽然可能有一颗颊齿属于 *Paralactaga*，但其明显比所有已知的种类原始。保德的跳鼠虽然只是该地区首批详细研究的小哺乳动物化石，但已经表明保德动物群和灞河动物群在小哺乳动物组成上也差异显著，进一步证实了灞河期和保德期动物群的截然不同，支持了灞河期的有效性。分析表明，跳鼠从 10 Ma 以后都是与高冠食草动物伴生，显示出其耐旱性。因此，保德第 30 地点和相关层位应该是开阔草原环境，这与之前根据大哺乳动物组合及牙齿稳定同位素分析所恢复的生态环境一致。由于缺乏有效的地理隔离，保德地区第 30 地点和第 49 地点的生态差异显然不是空间上的，而是时间上的。

关键词：山西保德，晚中新世保德期，跳鼠，环境

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THE DIPODIDAE (JERBOAS) FROM LOC. 30 OF BAODE AND
THEIR ENVIRONMENTAL SIGNIFICANCE

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Abstract　　Two types of jerboa are found from Loc. 30 of Baode, Shanxi Province. The three-toed jerboa *Dipus fraudator* is the dominant taxon, accompanied with few teeth of the five-toed jerboa *Paralactaga* cf. *P. suni*. Although the diversity of this jerboa assemblage is not as high as that from Ertemte fauna, the two assemblages are fairly similar to each other. The jerboa assemblage from Baode is quite different to that from the Bahe Formation, where the dominant member is *Protalactaga*. The Lantian assemblage also contains one tooth assigned to *Paralactaga* sp., but it is much primitive than any known species. The Baode jerboa assemblage then has no shared taxa with that of Lantian. Although the small mammals from Baode have not been fully studied, the difference between

the Bahean and Baodean small mammals is already evident. Jerboas are associated with high large mammal hypsodonty values from 10 Ma onwards and can be regarded as a proxy for relatively arid environments since the Late Miocene. The steppe environment suggested by these jerboas for Loc. 30 is consistent with the early analyses of the large mammals and the stable isotopes from ungulate teeth. The two different biomes traditionally recognized in the Baode area are separated temporally other than spatially.

Key words   Baode, Shanxi; Baodean, Late Miocene; Dipodidae; environment

1   Introduction

Li et al. (1984) recognized two land mammalian ages (Bahean, Baodean) for the Chinese Late Miocene. Later workers (Qiu, 1990; Tong et al., 1995) considered that the Bahean fauna was indistinct from that of the Baodean, and extended Baodean to refer the whole Late Miocene.

Our recent work in Lantian found that the large mammalian assemblage from the Bahe Formation is sharply distinct from that of the Lantian Formation, which is contemporary with the classical Baode *Hipparion* faunas (Zhang et al., 2002). We (Zhang et al., 2002; Zhang and Liu, 2005) therefore resurrected the two-part subdivision of the Late Miocene (Li et al., 1984).

Although tons of complete skulls and post-cranial specimens of large mammals were collected from the Baode area, small mammals, which need more professional experience to be searched, were neglected by the former collectors. Are small mammals from the Baode Formation also distinct to those from the Bahe Formation?

In the autumn of 2003 and 2005, we worked two field seasons in the Baode area, mainly focused on establishing a stratigraphic sequence for the large mammal localities and searching for small mammals. The local "dragon-bone" collection was still active and the fossil localities were perfectly exposed by the tunnels. Fortunately, we were able to relocate most of Zdansky's localities such as Loc. 30, Loc. 43, Loc. 49, Loc. 108, and Loc. 109. From Loc. 30, we got some small mammals by screen washing. There are mainly murids, gerbillids, cricetids, and dipodids. The washing of sediments from Loc. 49 and other localities was less productive. Here we present the dipodids from Loc. 30 and discuss their paleoecological interpretation.

The measurements are given in millimeters. The length of the tooth is its maximum length along the longitudinal axis; the width is the maximum width at the right angle to the longitudinal axis. The nomenclatures for the dentition follow Qiu (2003), and Li and Qiu (2005).

2   Systematic paleontology

<div align="center">

Order Rodentia Bowdich, 1821
Family Dipodidae Fischer von Waldheim, 1817
Genus *Dipus* Zimmermann, 1780
***Dipus fraudator* (Schlosser, 1924)**
(Fig. 1)

</div>

1924 *Sminthoides fraudator* Schlosser, p. 34
1976 *Sminthoides fraudator* Zheng, p. 114
1983 *Sminthoides fraudator* Fahlbusch et al., p. 215
2003 *Sminthoides fraudator* Qiu, p. 135

Material   4 P4 (V 15526.33–36), 5 M1 (V 15526.1–5), 7 M2 (V 15526.6–12), 2 M3 (V 15526.13–14), 7 m1 (V 15526.15–21), 7 m2 (V 15526.22–28), 4 m3 (V 15526.29–32)

Locality and horizon Loc. 30, Daijiagou, Baode County, Shanxi Province; Baode Formation, the late Late Miocene.

Measurement (See Table 1)

Table 1 Tooth measurements of *Dipus fraudator* from Baode and the comparison with other
D. fraudator (from Ertemte, Harr Obo, Heshui and Khirgis-Nur 2), and with
D. qiui (from Geotege), *Dipus* sp. nov. (from Shala)   (mm)

	m1		m2		m3		M1		M2		M3	
	L	W	L	W	L	W	L	W	L	W	L	W
	2.07	1.73	2.0	1.73	1.6	1.2	2.2	1.87	1.73	1.57	1.33	1.33
	2.13	1.67	2.0	1.87	1.67	1.33	2.07	1.8	1.8	1.63	1.33	1.33
	2.27	1.9	1.93	1.8	1.4	1.33	2.2	1.8	1.93	1.6		
Baode	2.07	1.67	2.07	1.8	1.47	1.33	2.27	1.87	1.8	1.67		
		1.8	2.2	1.87			2.0	1.87	2.0	1.73		
	2.2	1.67	2.2	1.87					1.87	1.67		
	1.93	1.67	1.87	1.8					1.8	1.73		
Mean	2.11	1.73	2.04	1.82	1.54	1.3	2.15	1.84	1.85	1.66	1.33	1.33
Ertemte[1]	2.36	1.84	2.08	1.86	1.6	1.33	2.23	1.86	1.93	1.69	1.32	1.31
Harr Obo[1]	2.31	1.77	2.14	1.83	1.5	1.32			2.1	1.75		
Heshui[2]							2.18	1.95	1.96	1.76		
Khirgis-Nur 2[3]	2.3	2.0	2.15	1.95	1.65	1.5	2.2	2.0				
Gaotege[2]	2.03	1.62	1.76	1.65	1.29	1.14	1.81	1.61	1.62	1.51	1.29	1.20
Shala[2]							1.51	1.35				

Data sources: 1) Qiu (2003); 2) Li (2006); 3) Zazhigin and Lopatin (2001).

Description P4 is rather simple, with single root and a large conical cusp.

M1 is subrectangular and slightly narrower anteriorly, with the anterior cusps being slightly smaller than or nearly equal to the posterior ones. The lingual cusps are located slightly anterior than the labial cusps. Anteroloph is present but only extends to the labial base of protocone. Paracone separates well from metacone. Mesocone and mesoloph are not present. Protoloph and metaloph are short, directed transversely. A strong entoloph connects the hypocone and protoloph. Posteroloph is short, connecting the hypocone with the metaloph. Parasinus is narrow and flexed posteriorly, while mesosinus is wider and flexed posterolingually. Posterosinus is lacking. The tooth has four roots.

M2 is similar to M1 but smaller in size, slightly narrower posteriorly. Its anterior cusps are larger than posterior ones, and anteroloph is more pronounced. Parasinus and metasinus are more transversely directed and extend less posteriorly.

M3 is similar to M2, but more reduced posteriorly. Metacone fuses with hypocone to build a broad posteromedial loph. Entoloph is weak.

The m1 is subrectangular, narrower anteriorly. Metaconid and hypoconid are conical, while protoconid and entoconid are compressed anteroposteriorly. The main cusps are arranged alternately with the lingual cusps anterior to the labial ones. Hypoconulid is distinct, and locates posterolingually to the hypoconid. A short and narrow metalophid connects the protoconid with the metaconid. Hypolophid is very short and narrow. Ectolophid is always present, connecting the protoconid and entoconid. There is no any connection between the metaconid and entoconid. Posterolophid is strong but low, usually joins to the entoconid. Anterosinusid is narrow and shallow, extending posterolingually. Mesosinusid is deep, and wider than the posterosinusid. There are two roots.

The m2 is subrectangular, slightly narrower posteriorly. A minute, transversely oriented

anteroconid in front of protoconid joins metalophid and metaconid to form a short anterior oblique lophid. The protoconid joins the entoconid by an ectolophid to form a long median oblique lophid. Hypoconid is weakly fused with hypoconulid to form a short posterior oblique lophid. As in the m1, the mesoconid, mesolophid and ectomesolophid are absent. Protosinusid is narrow and shallow, directed transversely. Two roots are present.

The m3 is subtriangular, much smaller than the anterior teeth. Anteroconid is absent and anterolophid is very weak. Protoconid is connected with an indistinct entoconid. Hypoconid merges with posterolophid to form a small transversely oriented cusp at the posterior part of the tooth. Protosinusid is very shallow, and posterosinusid is absent, only mesosinusid is deep. There are two roots.
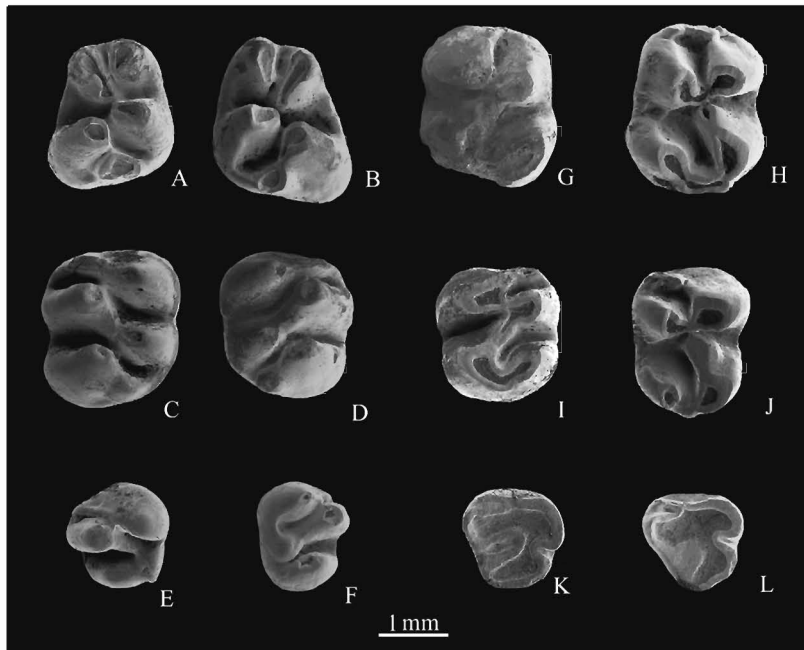

Fig. 1 *Dipus fraudator* from Loc. 30 of Baode, occlusal view

A. V 15526. 15, left m1; B. V 15526. 16, right m1; C. V 15526. 22, left m2; D. V 15526. 23, right m2;
E. V 15526. 29, left m3; F. V 15526. 30, right m3; G. V 15526. 1, left M1; H. V 15526. 2, right M1;
I. V 15526. 6, left M2; J. V 15526. 7, right M2; K. V 15526. 13, left M3; L. V 15526. 14, right M3

Remarks The described materials fall into Dipodidae by the arrangement of cusps, and the absence of anterocone (M1) and anteroconid (m1). By the large size and the absence of mesocone (id) and mesoloph (id), those specimens are further referred to Dipodinae. In China, the fossil three-toed jerboas were usually assigned to *Sminthoides* Schlosser, 1924. Zazhigin and Lopatin (2001) synonymed *Sminthoides* with *Dipus* based on the massive metacone on M1 and M2, which is a diagnosis character of *Dipus*. Hence, there are only two fossil genera in Dipodinae, *Dipus* Zimmermann, 1780 and *Scirtodipus* Savinov, 1970. *Scirtodipus* differs from *Dipus* by a more reduced P4, and more lophodont cheek teeth. The Baode material clearly belongs to *Dipus* by the less lophodont molars and large P4.

The known species of *Dipus* include *D. sagitta*, *D. fraudator*, *D. qiui*, *D. conditor*, *D. essedum*, and *D. singularis* (Qiu, 2003; Li and Qiu, 2005; Li, 2006). The earliest record of the genus is *Dipus* sp. nov. from Shala, Nei Mongol (Qiu and Wang, 1999; Qiu et al., 2006). The only M1 is much smaller and more brachydont than any known species. Comparing

with this unnamed new form, the Baode form is clearly larger and more hyposodont (Fig. 2).
The weak lophodont and less reduced anterolophid molars also distinguish the Baode form from
the type species *D. sagitta*. *D. qiui* differs from the Baode form by its smaller size, and well
developed lophids between the cusps on lower molars. Zazhigin and Lopatin (2001) described
four species of *Dipus* from Mongolia and Kazakhstan as *D. fraudator*, *D. conditor*, *D. essedum*
and *D. singularis*. The Baode materials neither have a spur on paracone as *D. essedum* nor an
obvious anterocone within *D. singularis*. The protoconid of Baode materials is not so separated
with entoconid as the situation in *D. conditor*. By the size and occlusal morphology, the Baode
form is very close to *D. fraudator*. Comparing with the other specimens assigned to *D. frauda-
tor*, the Baode material is further similar to those from Ertemte, Harr Obo and Heshui, the ma-
terial from Khirgis-Nur 2 seems relatively wider than all Chinese specimens (Table 1; Fig. 2).
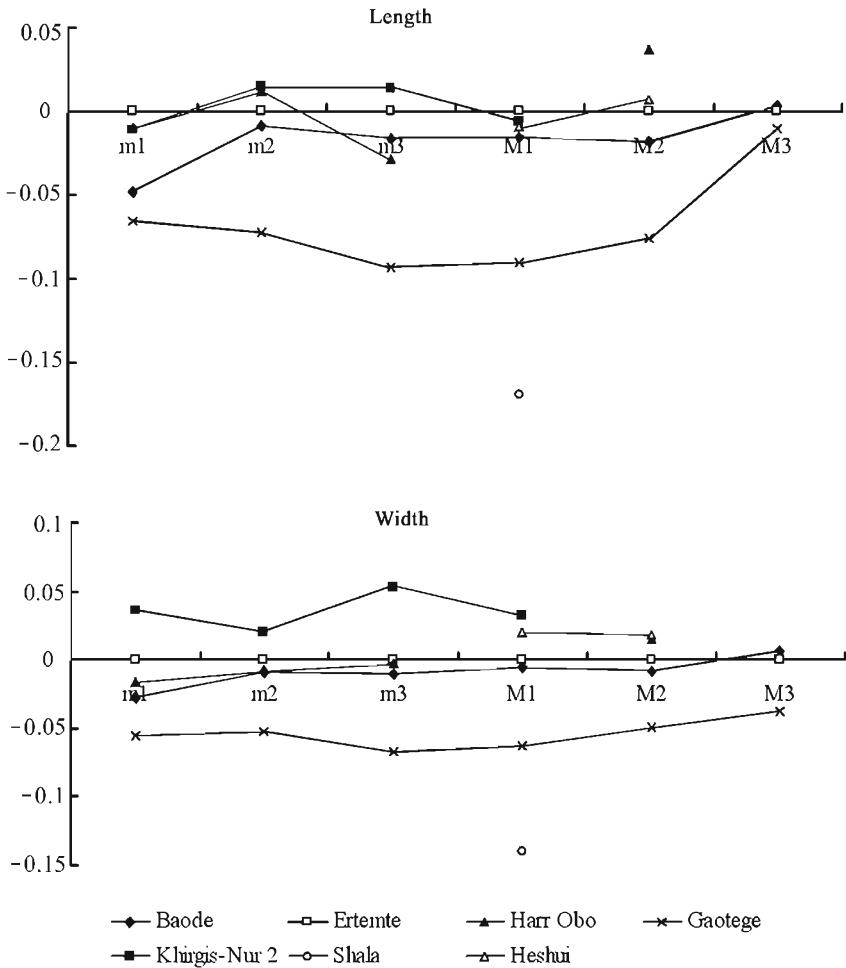

Fig. 2　Logarithmic ratio diagram of dental proportions of *D. fraudator*, *D. qiui* and *D.* sp. nov. (Shala)
Standard: *Dipus fraudator* from Ertemte; data sources same as in Table 1

Genus *Paralactaga* Young, 1927
Paralactaga cf. *P. suni* Teilhard & Young, 1931
(Fig. 3)

Material　A broken m2 (V 15527. 1), and one m3 (V 15527. 2).

Locality and horizon　Loc. 30, Daijiagou, Baode County, Shanxi Province; Baode Formation, the late Late Miocene.

Description　The m2 preserves only the anterior portion, lacking the posterior part from entosinusid. Anteroconid is not very large and connects to metaconid by a transverse metalophid. The mesolophid is weak and extends posteroexternally. There is no parasinusid.

The m3 is similar in occlusal pattern to the anterior portion of m2 with a more reduced anteroconid. Hypoconid is distinct. Entoconid is fused with mesolophid and posterolophid to form a robust posterolingual ridge of the tooth. Mesosinusid is almost as developed as in m2, parasinusid is narrow and shallow.

Although it is broken, the m2 clearly bears the mesolophid, a typical character of the Allactaginae jerboa. The mesolophid extending to the base of entoconid posteroexternally is concordant with those of *Paralactaga*.

Remarks　The type species *Paralactaga anderssoni* was erected by Young (1927) based on the material from Wayaopu, Jingchuan County, Gansu Province. Two other species of *Paralactaga* have been reported from North China and Kazakhstan: one is *P. suni* from Shenmu (Teilhard and Young, 1931), Ertemte and Harr Obo (Qiu, 2003), Bilike (Qiu and Storch, 2000), Gaotege (Li, 2006), Ningxian (Zhang, 1999), and Lingtai (Zheng and Zhang, 2001); the other is *Paralactaga varians* from the Pliocene Pavlodar Formation of Kazakhstan (Savinov, 1970; Shenbrot, 1984).

Fig. 3　*Paralactaga* cf. *P. suni* from Loc. 30 of Baode, occlusal view
A. V 15527. 1, left m2;
B. V 15527. 2, left m3

Paralactaga varians differs from the Chinese species by its less reduced M(m)3, wider lower molars and more developed ectomesolophid, these characters exclude Baode material out of the same species. The two Chinese species are rather close to each other, *P. anderssoni* is only distinguished from *P. suni* by slightly smaller size, three rooted M1 and M2, and less developed cusps on the molars. The poor Baode material has no possibility to check the roots and whole cusps, thus it is very difficult to make a strong appointment for the species assignment. But the molars are more comparable to those of *P. suni* from Ertemte in size, we therefore refer the two teeth as *Paralactaga* cf. *P. suni* (Table 2).
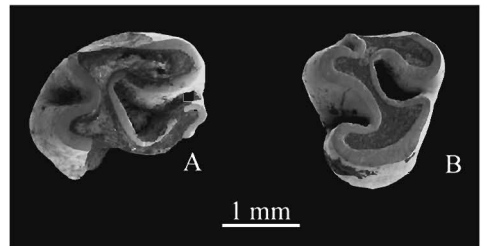
Table 2　The measurements of *Paralactaga* cf. *P. suni* from Baode and comparison with *P. anderssoni* from Wayaopu and *P. suni* from Gaotege and Ertemte　　(mm)

	m2		m3	
	L	W	L	W
Baode		2. 1	1. 9	1. 65
Wayaopu[1]	2. 8	2. 0	2. 2	1. 6
Ertemte[2]	3. 0 ~ 3. 5	2. 25 ~ 2. 5	1. 90 ~ 2. 15	1. 60 ~ 1. 95
Gaotege[3]	3. 15 ~ 3. 35	2. 35 ~ 2. 5	1. 95 ~ 2. 05	1. 85 ~ 1. 95

Note: 1) Young (1927); 2) Qiu (2003); 3) Li (2006).

3　Discussion

3.1　Biochronology of Loc. 30, Baode

Although the small mammals from Baode have not been fully studied, the dipodids already show a clear difference from those of the Bahean. The dipodid assemblage from Lantian is dominated by *Protalactaga*, the most primitive allactaginae, together with a few *Salpingotus* and *Cardiocranius*, and one tooth of an uncertain *Paralactaga* (Li and Zheng, 2005). The Baode dipodids are dominated by *Dipus fraudator*, together with *Paralactaga* cf. *P. suni*, but without *Protalactaga*. The Baode dipodids are rather accordant with those from Ertemte, which is dominated by *Dipus fraudator* (2 maxilla and 133 isolated teeth), accompanied by *Paralactaga suni* (58 isolated teeth) and a few *Brachyscirtetes wimani* (17 teeth). The significant difference between the Bahean and Baodean dipodids thus supports our earlier division of Late Miocene (Zhang et al., 2002; Zhang and Liu, 2005).

3.2　Ecology of Loc. 30, Baode

The dipodids documented here are all found from Loc. 30, a standard "dorcadoides" locality according to Kurtén (1952). That is, the large mammalian assemblage was classified as a high-crowned gazelle fauna and thought to represent a steppe environment. Dipodids make up about 20% of the small mammal fauna of Loc. 30, with similar proportions of murids and cricetids. Today, the family Dipodidae is restricted to the arid areas of the Palearctic Region (Ma et al., 1987; Wang, 2003), and the fossil dipodids are generally considered to indicate a steppe biotope. Conventional criteria thus agree to suggest that the environment from which the Loc. 30 material was drawn as a relatively arid one.

We have previously shown (Fortelius et al., 2002, 2006) that the mean hypsodonty of herbivorous large mammals is a robust proxy for the paleoprecipitation. Here we use hypsodonty analysis to investigate the precipitation context of fossil dipodidae. We used public data NOW database downloaded on November 9, 2007 (Fortelius, 2007; http://www. helsinki. fi/science/ now), restricted to the Late Cenozoic Asia. Localities were grouped as "dipodid" (with at least one dipodid record), "murid" (with at least one murid but without dipodids), and "neither" (without murids and dipodids). We calculate the mean hypsodonty based on an ordination of brachydont = 1, mesodont = 2, hypsodont = 3, of large mammal herbivores, for all localities with at least three taxa with a hypsodonty value present, for time units corresponding to MN-units for each of these groups (see Fortelius et al., 2002 for methodological details). All groups show an increase value over time, with the murid group consistently, and especially after about 10 Ma, showing relatively low values, suggesting a persistent humid occurrence context. The dipodid group does not suggest an arid occurrence context before 10 Ma, but sharply shifts to distinctly more arid context than other groups in the Late Miocene (Fig. 4). This analysis supports the conventional interpretation of Loc. 30 as representing a relatively arid environment.

An interesting extension of this discussion is the environmental interpretation for "mixed fauna" from Loc. 49. This fauna of intermediate hypsodonty was interpreted as representing a more humid or forested environment than Loc. 30 (Kurtén, 1952). Analysis of carbon isotope ratios (Passey et al., 2007) also indicated that the hipparionine horses and *Gazella dorcadoides* consume less C_4 vegetation in Loc. 49 than in Loc. 30. The lower amount of C_4 vegetation also suggests a more humid environment for Loc. 49.

Early workers considered the mammal localities from Baode to be roughly contemporaneous (Zdansky, 1923; Kurtén, 1952). Kurtén (1952) concluded that the two different assemblage types represented geographic position relative to an ecological boundary. While his explanation is plausible for the majority of localities, it cannot be applied within the small Baode area,

where the main localities of Baode (include Loc. 30 and Loc. 49) are situated on either Daijiagou gully or Jijiagou gully. The two gullies are very close to each other (less than 2 km), the highest elevation of the plateau between them is less than 1300 m. On his topographic map, Zdansky (1923) clearly marked localities at different levels within the Red Clay, for example Loc. 49 sites at the bottom of the Red Clay, and Loc. 30 very close to the top. In the field we were able to confirm his observations (unpublished data).

If the model of a spatial boundary between biomes cannot be applied, the biomes must be temporally separated, with the difference in environment representing either sustained, directional change or different phases of cyclic change. Work in preparation by our team will address this question and other details of the stratigraphy and environmental change at Baode.
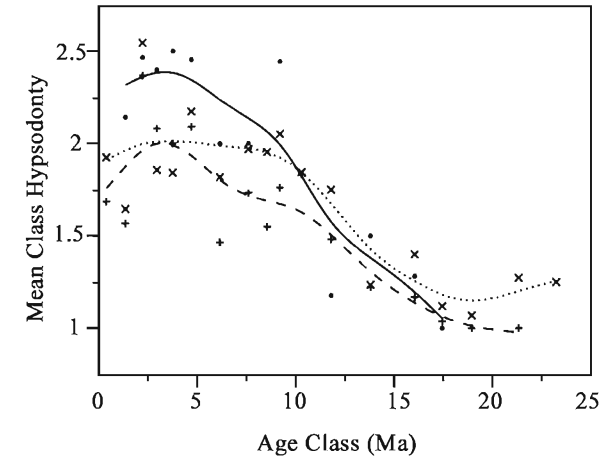

Fig. 4   Comparison of mean large mammal hypsodonty calculated by age class between localities defined by presence of Dipodidae (dot, continuous line), Muridae (cross, hatched line) or neither (×, dotted line) Localities with both dipodids and murids were assigned to the dipodid localities

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