

云南禄丰古猿地点的松鼠类化石¹⁾

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摘要 记述了云南禄丰晚中新世石灰坝古猿地点发现的松鼠科化石。禄丰石灰坝动物群的松鼠动物共有7属7种:地松鼠 *Sciurotamias wangi* sp. nov., 树松鼠 *Tamiops* sp., *Callosciurus* sp., *Dremomys primitivus* sp. nov. 和飞松鼠 *Miopetaurista asiatica* sp. nov., *Hylopetodon dianense* gen. et sp. nov., *Pteromyinae* gen. et sp. indet.。该动物群松鼠类动物的组成以树松鼠和飞松鼠为主,反映了较为湿润的热带—亚热带森林环境。在动物地理上,其成员几乎局限于东南亚分布,具有浓厚的现代东洋界色彩。

关键词 云南禄丰,晚中新世,石灰坝组,松鼠科

中图法分类号 Q915.873

云南禄丰石灰坝晚中新世古猿地点发现的小哺乳动物群于1985年有过简单的报道(Qiu et al., 1985)。此后,有关该动物群的树鼯类、食虫类、猪尾鼠类、竹鼠类、仓鼠类、鼠形类和兔形类的详细描述已先后发表(Qi, 1986; Qiu, 1986, 1989, 1995; Qiu and Han, 1986; Qiu and Storch, 1990; Storch and Qiu, 1990)。本文记述该动物群的松鼠科化石(详见英文部分)。在石灰坝发现的7属7种松鼠动物中,包括1个新属和3个新种。新属和新种的特征如下:

岩松鼠属 *Sciurotamias* Miller, 1901

王氏岩松鼠(新种) *Sciurotamias wangi* sp. nov.

(增订) 中等大小的普通松鼠,齿尖和齿脊粗壮。M1-2的原脊完整,后脊在靠近原尖处收缩或断开;原脊和后脊近于汇聚原尖;无原小尖,但可能有模糊的后小尖。m1-2的下内尖中等发育;下内尖角弧形;外谷窄;外脊直而弱;下中尖小;无下中附尖,下后尖和下内尖间为一宽的凹缺分开;前脊与下原尖连接。m3往后扩伸。

种的种征 齿脊和齿尖相对较弱;M1-2可能有中附尖,但无后小尖;p4向后扩伸。

长吻松鼠属 *Dremomys* Heude, 1898

原始长吻松鼠(新种) *Dremomys primitivus* sp. nov.

属的特征(增订) 中等大小的普通松鼠,齿尖相对比齿脊更为显著。M1-2的原尖较为前位;后尖明显比前尖向唇侧凸出;前尖和后尖的舌侧壁甚为陡峭;原脊连续,后脊在靠近原尖处收缩或断开;无原小尖,但可能会有很弱的后小尖;原脊和后脊近于平行排列;

1) 国家重点基础研究发展规划项目(编号:G2000777000)和中科院院长基金项目(编号:9912)资助。

后边脊在与原尖连接处明显膨大。m1-2 常有清楚的下内尖和小的下中附尖;外谷窄;外脊斜而弱;无下中尖。m3 往后扩伸。

种的特征 齿脊和齿尖相对较弱;M1-2 无后小尖;m1-2 下内尖很醒目,下内尖角角状。

亚洲中新鼯鼠(新种) *Miopetaurista asiatica* sp. nov.

特征 *Miopetaurista* 属中中等大小的一种。P4 与 M1 长度近等,但后者稍宽。P4-M2 的次尖相对明显;M1-2 的次小尖显著,但在 P4 上较弱。上颊齿无中附尖。下颊齿的下中和下中附尖小。齿凹无明显的附属脊,釉质不甚褶皱。

林飞齿鼠(新属) *Hylopetodon* gen. nov.

滇林飞齿鼠(新属、新种) *Hylopetodon dianense* gen. et sp. nov.

属的特征 个体较大的飞松鼠。P4 与 M1 近等长。P4-M2 具弱的次尖而无中附尖;原脊和后脊汇聚于原尖;后小尖在 P4 上强大,在 M1-2 上分为双尖。M3 无后脊。p4-m2 的下中尖和下中附尖明显,后者与下后尖连接;下内尖发育,以一深沟与下中尖分开;无前边尖,也无前唇侧的齿带和谷。颊齿齿凹釉质褶皱,并具不规则的附属脊。

鉴别特征 新属 P4-M2 的原脊和后脊汇聚于原尖,与新近纪以来的飞松鼠属 *Aliveria* De Bruijn et al. 1980、*Albanensia* Daxner-Hock and Mein 1975、*Pliopetaurista* Kretzoi 1962、*Forsythia* Mein 1970、*Shuanggouia* Qiu and Lin 1986 和 *Hylopetes* Thomas 1908 的特征相似,但牙齿的尺寸和其他的一些形态,特别是 M1-2 具双后小尖,使其与上述属有所不同。它以个体较大、M1-2 具双后小尖、M3 无后脊、p4-m2 无前边尖和孤立的下中附尖、齿凹釉质强烈褶皱而不同于 *Aliveria*;以 P4 相对于 M1 较小、M3 无后脊而异于 *Albanensia*;以 P4 相对于 M1 较小、m3 无下次脊和齿凹釉质较褶皱而易于与 *Pliopetaurista* 区分。新属比 *Forsythia* 大很多,欧洲这一属的原尖和次尖很收缩,M3 有后脊,下颊齿具唇侧前谷。它与 *Shuanggouia* 的不同在于后者个体较小,P4 相对于 M1 较大,M3 有后脊。其牙齿构造与 *Hylopetes* 的比较接近,但新属的尺寸远比这一现生属的大,M1-2 具双后小尖,齿凹釉质较褶皱。

种的特征 同属的特征。

石灰坝古猿动物群是华南新近纪堆积物中发现松鼠类化石种类较多的一个动物群。由于松鼠类的演化速度相对较慢,目前对这些松鼠属种的系统发育关系又知之甚少,所以还难以根据这些化石的种类去确定动物群的时代。但由于松鼠类对环境的选择相当严格,使它们在分析动物群的生态环境中具有特殊的意义。该动物群中的 *Tamiops*、*Callosciurus* 和 *Dremomys* 都为现生的树松鼠属,分布于东南亚的森林地区,栖息于阔叶林或阔叶与针叶混交林带(Walker et al., 1968)。飞松鼠为树栖型动物,一般要求有高大的乔木。因此,这一动物群似乎指示了湿润、热带或亚热带的森林环境,这种环境多少与现代禄丰地区的情况有所不同,气候似乎相对更为湿热,林木也许会繁茂些。

在华北地区一些地点的新近纪堆积物中,相同习性类型的松鼠类同样有所发现,如中新世的通古尔、二登图和早上新世的比例克(Qiu, 1991, 1995; Qiu and Storch, 2000)。但北方的这些动物群的成员以反映温带干旱、草原环境的地松鼠(*Atlantoxerus*、*Prosperophilus* 和 *Sino-*

tamias) 和花栗鼠 (*Eutamias*) 为主, 树松鼠为 *Sciurus* 属, 飞松鼠属为 *Pliopetaurista* 和 *Petinomys*, 这些属都未在石灰坝的褐煤堆积物中被发现。欧洲这一时期的松鼠类相当丰富, 尤其是飞松鼠相对更为常见, 但除了 *Miopetaurista* 外, 欧洲的属、种也未在禄丰动物群中出现。因此, 禄丰石灰坝动物群的成员几乎局限于东南亚分布, 并具浓厚现代东洋界的特色。

SCIURIDS FROM THE LATE MIOCENE LUFENG HOMINOID LOCALITY, YUNNAN

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Abstract The Sciuridae from Shihuiba, a late Miocene hominoid locality at Lufeng, Yunnan Province are described. The fauna contains seven species of Sciuridae, including one new genus and four new species. One of the sciurids is a ground squirrel: *Sciurotamias wangi* sp. nov.; three are tree squirrels: *Tamiops* sp., *Callosciurus* sp. and *Dremomys primitivus* sp. nov.; and three are flying squirrels: *Miopetaurista asiatica* sp. nov., *Hylopetodon dianense* gen. et sp. nov. and *Pteromyinae* gen. et sp. indet. The sciurid fauna is characterized by its dominance of tree and flying squirrels, and reflects a rather humid and forested environment. Biogeographically, the fauna is endemic to southeastern Asia, and is obviously Oriental in character.

Key words Lufeng, Yunnan, late Miocene, Sciuridae

1 Introduction

The micromammalian assemblage from Shihuiba, a Neogene locality that produced rich remains of hominoids in Lufeng County, Yunnan was reported by Qiu and others in 1985. Detailed descriptions of some taxa of the Shihuiba Fauna — tupaiids, insectivores, platanthomyids, rhizomyids, cricetids, murids, and leporids, have been published (Qi, 1986; Qiu, 1986, 1989, 1995; Qiu and Han, 1986; Qiu and Storch, 1990; Storch and Qiu, 1990). In this paper the sciurid material is described. It represents a rather diverse Neogene sciurid fauna from South China.

The micromammalian fauna has been collected from the upper part of the Shihuiba Formation (Badgley et al., 1988). The fossiliferous sediments are swamp deposits and mainly consist of lignite and carbonaceous silty sand. On the basis of small mammals, the fossil-bearing beds have been generally assigned to the late Miocene (= Baodean Chinese Land Mammal Age), or an equivalence of upper MN11 or lower MN12 (= early Turolian European Land Mammal Age) (Qiu and Storch, 1990; Qiu and Qiu, 1995; Qiu, 1995). Correlation to the biostratigraphic sequence of rhizomyids from Siwalik faunas of Pakistan suggested an age of about 8 Ma for the Shihuiba Fauna (Flynn and Qi, 1982). Subsequent revision of the magnetic polarity time scale adjusted this estimate to about 9 Ma (Flynn et al., 1998).

2 Systematics

Sciuridae Gray, 1821

Sciurinae Baird, 1857

Sciurotamias Miller, 1901

Type species *Sciurus davidianus* Milne-Edwards, 1867; Recent.

Diagnosis(emended) Mid-sized sciurid rodents with heavily built cusps and crests. On M1-2 the proto-loph is complete and bears no protoconule; meta-loph is constricted at or fails to reach the protocone and probably bears an indistinct metaconule; the two lophs converge towards the protocone rather than having parallel orientation. On m1-2 the entoconid is moderately developed; entoconid

corner is curved; a narrow buccal valley is dammed by a straight, but weak ectolophid and mesoconid; mesostylid is absent; a wide notch is present between the metaconid and entoconid; anterolophid is connected with the protoconid. m3 is expanded posteriorly.

Remarks *Sciurotamias* is similar to *Spermophilinus* from the Neogene of Europe in size and in some characters of the teeth, but different from the latter in that the protoloph and metaloph are more converged toward the protocone on the M1-2, in lower molars the anterolophid is connected with the protoconid, and the m3 is distinctly expanded posteriorly.

Sciurotamias wangi sp. nov.

(Fig. 1)

Synonymy *Sciurotamias* sp. Qiu et al., 1985.

Etymology Named in honour of the outstanding zoologist and my friend Prof. Wang Yingxiang from the Kunming Institute of Zoology, Chinese Academy of Sciences, who helped me a great deal in the study of the Shihuibai sciurid fauna.

Holotype A right fragmentary mandible with p4+m2 from L. II (p4: 1.90 ×1.65mm; m1: 2.25 ×2.20mm; m2: 2.65 ×2.25mm; p4+m2: 6.70mm); IVPP V 13141.

Paratypes L. I: 1 damaged m3; L. II: 1 dp4 (1.55 ×1.40mm), 1 p4 (1.60 ×1.50mm), 1 m1/2 (2.10 ×2.20mm); L. V: 1 P4 (1.95 ×2.30mm), 1 M1/2 (2.10 ×2.70mm), 1 dp4 (1.70 ×1.30mm), 2 m1/2 (2.10 ×2.25mm, 2.05 ×2.00mm); V 13142.1~9.

Diagnosis Cusps and crests relatively slender built; on M1/2 metaconule absent, mesostyle probably present; on p4 posterior portion expanded and rounded.



Fig. 1 *Sciurotamias wangi* sp. nov., occlusal view

1. m1-3 on a damaged right mandible, Holotype (V 13141); 2. P4 (V 13142.7); 3. M1/2 (V 13142.8);
4. dp4 (V 13142.9); 5. m1/2 (V 13142.1); 6. m1/2 (V 13142.5);

fig. 1 is figured as right, ×12, and figs. 2~6 as left, ×16; figs. 2, 4 are reversed

Description P4 is U-shaped with a weak parastyle and heavily built principal cusps and strong crests. The protocone is prominent. The protoloph and metaloph are low, and slightly converge toward the protocone. The metaloph is constricted before reaching the protocone. There is neither a protoconule nor a distinct metaconule. A tiny mesostyle is present, connecting to the paracone. M1/2 are distinctly wider than long with a rather expanded protocone. The protoloph and metaloph converge toward the protocone, with the metaloph failing to reach the protocone. The anteroloph and posteroloph are complete, but low and narrow. A protoconule is absent. A small mesostyle is present, joining the paracone.

The protoconid and metaconid of dp4 are close. The entoconid is completely incorporated into the posterointernal crest joining the metaconid to the hypoconid. The buccal valley is very shallow. The p4 is larger than dp4, with protoconid and metaconid less close, and with an obscure entoconid. The m1/2 are trapezoid shape with a large entoconid merged in the posterointernal crest. There is a distinct notch between the entoconid and the metaconid. The entoconid corners are curved. The strong anterolophid, bearing no anteroconid, joins the protoconid and with the metalophid closes the narrow trigonid basin. The buccal valley is wide and shallow. A low and longitudinal ectolophid is present, bearing a small mesoconid. The m3 is expanded posteriorly.

Comparison and discussion The specimens are referred to *Sciurotamias* due to possession of the following characters: mid-sized squirrel with quite heavily built cusps and crests; protoloph and metaloph slightly converged towards protocone, and bearing neither protoconule nor distinct metaconule on M1/2; m1/2 having moderate developed entoconid, curved entoconid corner, weak ectolophid and mesoconid, no mesostylid but a wide notch between the metaconid and entoconid, anterolophid joining the protoconid.

Sciurotamias is an extant genus confined to China and includes two living species, *S. davidianus* and *S. forresti*. *S. davidianus* is characterized by its slight larger size with heavier build of dentition and a swollen metaloph at the position of metaconule, without any trace of a mesostyle on M1/2, and more pronounced entoconid on m1/2. The Shihuiba taxon is more similar to *S. forresti* than to *S. davidianus* in size and structure (less heavily built dentition, very weak metaconule and a tiny mesostyle on M1/2, less pronounced entoconid on m1/2), but differs from *S. forresti* in cusps and crests being weaker, more prominent mesostyle on M1/2, less expansion of anteroloph on P4, and more expanded posterior portion of p4.

Teilhard (1940) described a Pleistocene species of *Sciurotamias*, *S. praecox* from Loc. 18 of Zhoukoudian. It differs from the Lufeng squirrel in having a better developed metaconule on M1/2, a larger mesoconid and lower trigonid basin on m1/2.

Zheng (1993) described two species, *S. davidianus* and *S. teilhardi* from the Pleistocene of Guizhou and Sichuan provinces. The Lufeng species is similar to *S. teilhardi* in dental pattern, but can be distinguishable from it by having lower height of crown with less robust cusps and lophes.

Tamiops Allen, 1906

Tamiops sp.

(Fig. 2, 1~3)

Material Layer I: 1 m1/2 (1.40 × 1.45mm), 1 m3 (2.05 × 1.80mm); L. V: 2 M1/2 (1.50 × 1.70mm, 1.55 × 1.80mm), 1 m1/2 (1.45 × 1.50mm); V 13143.1~5.

Description M1/2 are subquadrate with the protocone moderately expanded anteroposteriorly. The protoloph and metaloph are low and converge more or less toward the protocone, with the metaloph slightly constricted before reaching the protocone. There is neither a distinct protoconule nor a metaconule, but a swelling at the position of the protoconule and metaconule is present. m1/2 are slightly elongated with a delimited and conspicuous entoconid. The entoconid corner is angular. The anterolophid bears a weak anteroconid and closes a high but small trigonid basin with the metalophid. The buccal valley is narrow and directed slightly anteriorly. An ectolophid and

mesoconid are absent, but a mesostylid can be seen connected to the metaconid. The m3 is moderately expanded posteriorly, with the entoconid incorporated into the posterolophid.

Remarks This taxon is the smallest squirrel in this association and can be referred to the extant Asiatic striped squirrel on the basis of its small dimensions and dental morphology. It is characterized by m1/2 having a distinct entoconid and a narrow buccal valley, plus no ectolophid and mesoconid, which ties this squirrel to the genus *Tamiops* rather than *Eutamias*. The squirrel is comparable in size and shape to the extant *T. swinhoi* that inhabits the Yunnan area, but the material is not large enough for specific determination.

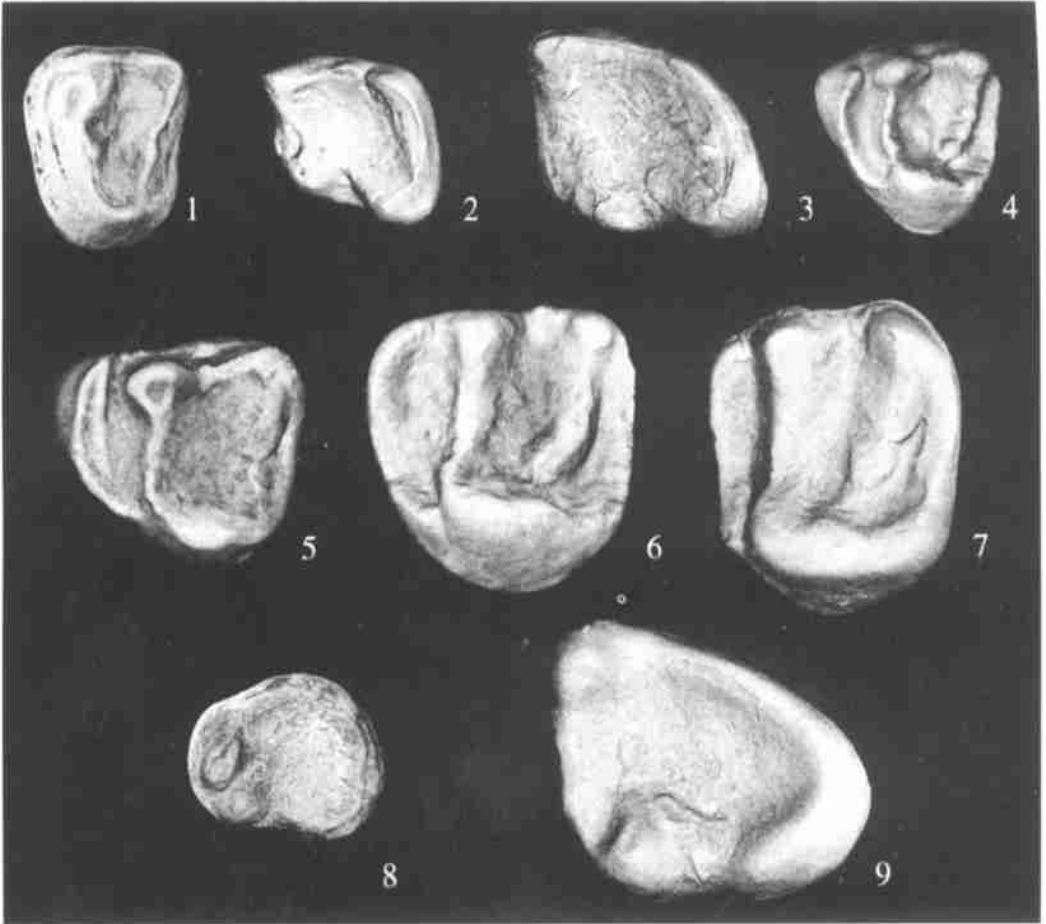


Fig. 2 *Tamiops* sp. 1. M1/2 (V 13143.3) ; 2. m1/2 (V 13143.5) ; 3. m3(V 13143.2)
Callosciurus sp. 4. DP4 (V 13144. 1) ; 5. P4 (V 13144. 3) ; 6. M1/2 (V 13144.4) ; 7. M1/2 (V 13144. 5) ;
 8. dp4(V 13144. 6) ; 9. m3 (V 13144.2)

All occlusal view and figured as left, $\times 16$; figs. 2, 3, 5, 6, 7, 9 are reversed

Callosciurus Gray, 1867

Callosciurus sp.

(Fig. 2, 4~9)

Material L. I: 1 DP4 (1.55 \times 1.50mm) , 1 m3 (2.80 \times 2.25mm) ; L. II: 1 P4 (2.20 \times 1.90mm) , 2 M1/2 (2.20 \times 2.20mm , 2.15 \times 2.50mm) ; L. V: 1 dp4 (1.70 \times 1.90mm) ; V 13144. 1 ~ 6.

Description DP4 has a moderately developed parastyle and expanded anteroloph. The protocone is slight compressed and located anteriorly to the midline. The protoloph and metaloph are prominent and nearly parallel in arrangement. There is neither a protoconule nor a metaconule. The anteroloph connects to the protocone at a very low position. The posteroloph is low, but is conspicuously swollen at the protocone. P4 is trapezoid shape with a very large and expanded anteroloph. The protocone is compressed lingual-buccally and less prominent than the metacone. The protoloph and metaloph are weak and nearly parallel in orientation. M1/2 are subquadrate with the protocone expanded anteroposteriorly. The protoloph and metaloph are thick, but low, and sub-parallel in orientation. The protoloph is complete, while the metaloph fails to reach the protocone. A protoconule and distinct metaconule are absent. A minute mesostyle is present in one of the two teeth. The anteroloph joins the protocone in a very low position. The parastyle on M1 is expanded anteriorly, so that the anterior valley is broad.

The protoconid and metaconid of dp4 are closely appressed. Both the anteroconid and mesoconid are absent. The entoconid is sub-merged in the posteroloph which joins the hypoconid to the metaconid. The m3 is greatly expanded posteriorly. The trigonid basin is low and the metalophid in this tooth fails to reach the metaconid.

Remarks This taxon is larger than the above *Tamias* sp. It is close to *Sciurotamias* in size, but differs in M1/2 being not wider than long, with a more expanded anteroloph, and lower connection of the anteroloph with the protocone.

The squirrel is characterized by having the protocone compressed lingual-labially, the moderately developed protoloph and metaloph nearly parallel, the protoloph turning forward at the protocone, the metaloph failing to reach the protocone, the low connection of the anteroloph with the protocone, and the distinct expansion of anterior valley. It is most similar to the extant genus *Callosciurus* in size and dental morphology, but more precise assignment should await more complete evidence.

Dremomys Heude, 1898

Type species *Sciurus pernyi* Milne-Edwards, 1867; Recent.

Diagnosis (emended) Mid-sized sciurid rodents with robust and blunt cusps. On M1/2 the protocone is located distinctly anteriorly; metacone protruding labially more than the paracone; lingual walls of the paracone and metacone precipitous; weakly developed protoloph and metaloph sub-parallel in orientation; protoloph continual and bearing no protoconule; metaloph constricted at or failing to reach the protocone; protocone-posteroloph union conspicuously expanded. On m1/2 a prominent entoconid and small mesostylid are present; narrow buccal valley is dammed by a weak and oblique ectolophid; the mesoconid is absent. The m3 is expanded posteriorly.

Dremomys primitivus sp. nov.

(Fig. 3)

Synonymy cf. *Dremomys* sp. Qiu et al., 1985.

Etymology Named in allusion to its more primitive features in comparison with the living species.

Holotype A right M1/2 from L. V (1.90 × 2.30mm); V 13145.

Paratypes L. I: 3 M1/2; L. II: 1 DP4, 1 M3, 1 dp4, 1 m3; L. III: a fragmentary mandible with m1/2; L. V: 3 P4, 1 M1/2, 2 M3, 1 m1/2; L. VI: 2 M1/2, 1 p4, 1 m1/2; V 13146. 1 ~ 19.

Diagnosis Cusps and crests of relatively slender built; lacking a metaconule on M1/2; entoconid prominent and entoconid corner distinctly angular on m1/2.

Measurements (Table 1)

mesoconid are absent, but a mesostylid can be seen connected to the metaconid. The m3 is moderately expanded posteriorly, with the entoconid incorporated into the posterolophid.

Remarks This taxon is the smallest squirrel in this association and can be referred to the extant Asiatic striped squirrel on the basis of its small dimensions and dental morphology. It is characterized by m1/2 having a distinct entoconid and a narrow buccal valley, plus no ectolophid and mesoconid, which ties this squirrel to the genus *Tamiops* rather than *Eutamias*. The squirrel is comparable in size and shape to the extant *T. swinhoei* that inhabits the Yunnan area, but the material is not large enough for specific determination.

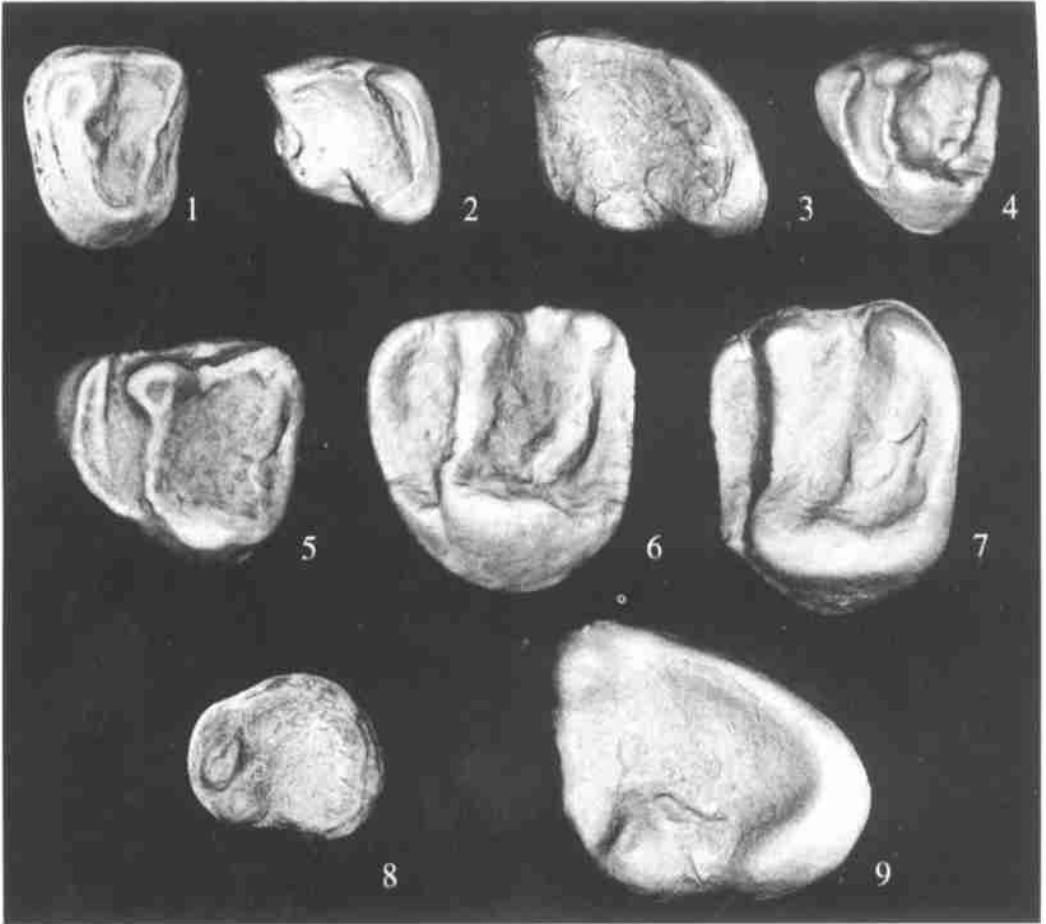


Fig. 2 *Tamiops* sp. 1. M1/2 (V 13143.3) ; 2. m1/2 (V 13143.5) ; 3. m3(V 13143.2)
Callosciurus sp. 4. DP4 (V 13144. 1) ; 5. P4 (V 13144. 3) ; 6. M1/2 (V 13144.4) ; 7. M1/2 (V 13144. 5) ;
 8. dp4(V 13144. 6) ; 9. m3 (V 13144.2)

All occlusal view and figured as left, $\times 16$; figs. 2, 3, 5, 6, 7, 9 are reversed

Callosciurus Gray, 1867

Callosciurus sp.

(Fig. 2, 4~9)

Material L. I: 1 DP4 (1.55 \times 1.50mm) , 1 m3 (2.80 \times 2.25mm) ; L. II: 1 P4 (2.20 \times 1.90mm) , 2 M1/2 (2.20 \times 2.20mm , 2.15 \times 2.50mm) ; L. V: 1 dp4 (1.70 \times 1.90mm) ; V 13144. 1~6.

low, weak, and parallel, with the former constricted at the protocone and the latter failing to reach the protocone. There is neither a distinct protoconule nor a metaconule. The anteroloph is long in one tooth and short in the other three. DP4 is smaller than P4 with weaker cusps and crests. The M1/2 are subquadrate with a moderately developed protocone located distinctly anterior. The metacone is displaced slightly posterolabially. The protoloph and metaloph are low and weakly developed, so that the lingual walls of the paracone and metacone are markedly precipitous. The two lophs are sub-parallel in orientation, with the metaloph failing to reach the protocone. A protoconule and metaconule are absent. There is no indication of a mesostyle, but a low connection between the paracone and metacone is developed in all the teeth. The union of protocone-posteroloph are distinctly thick and expanded. The M3 is little expanded posteriorly and lack a distinct metaloph.

The protoconid and metaconid of p4 are closely situated. There is an indistinct anteroconid and a low entoconid that is submerged in the narrow and compressed posterolophid and separated from the metaconid by a notch. An ectolophid and a mesostylid are absent. The dp4 is similar to p4 in structure, but smaller and lacking an anteroconid. The m1/2 are trapezoid shape with a well delimited entoconid and a small mesostylid connected with the metaconid. A narrow notch between the entoconid and the mesostylid is present. The entoconid corners are angular. The strong anterolophid, bearing no anteroconid, joins the protoconid in a low position and closes the narrow trigonid basin labially. The buccal valley is narrow and oriented slightly obliquely. The ectolophid is weak and low. A mesoconid is absent. The m3 is greatly expanded posteriorly. A narrow, relatively high and open trigonid basin, and a notch separated the entoconid from the mesostylid is still seen in this tooth after moderate wear.

Comparison and discussion The teeth of these squirrels are close in size to those of *Sciurotamias* and *Callomomys* mentioned above, but differ from them in dental morphology. They can be distinguished from the former by having a narrower M1/2 with less heavily built cusps and crests, a more anterior location of the protocone, with distinct precipitous lingual walls of the paracone and metacone, plus well developed union of the protocone-posteroloph, and by m1/2 with a distinct entoconid, angular entoconid corner, narrower buccal valley, and prominent mesostylid. They differ from *Callomomys* sp. in M1/2 having a more anteriorly located protocone, conspicuously developed protocone-posteroloph union, weaker protoloph and metaloph, higher connection of the anteroloph with the protocone, more precipitous lingual walls of the paracone and metacone, and in m3 with a higher trigonid and lacking a notch separating the entoconid from the mesostylid. The size and morphology of these teeth prevent assignment of the taxon to any genus other than the extant *Dremomys*.

Living *Dremomys* are montane forest dwellers distributed on southern Asia. Four species of the genus, *D. lokriah*, *D. gularis*, *D. pemyi* and *D. rufigenis* are found in the Yunnan area. The Lufeng specimens are comparable to those of living species in size and morphology, especially *D. gularis*. Minor differences are less heavily built cusps and crests of the fossil form, which may be interpreted as a retained primitive feature.

The new species from Shihuiba represents the oldest record of this genus. Fossil material of *Dremomys* cf. *D. pemyi* is reported from the Pleistocene of Sichuan and Guizhou provinces (Zheng, 1993). It differs from the new species in having somewhat more heavily built cusps and crests, obscure mesostyle on M1/2, and posteriorly directed buccal valleys on some of the m1/2.

Pteromyinae Brandt, 1855

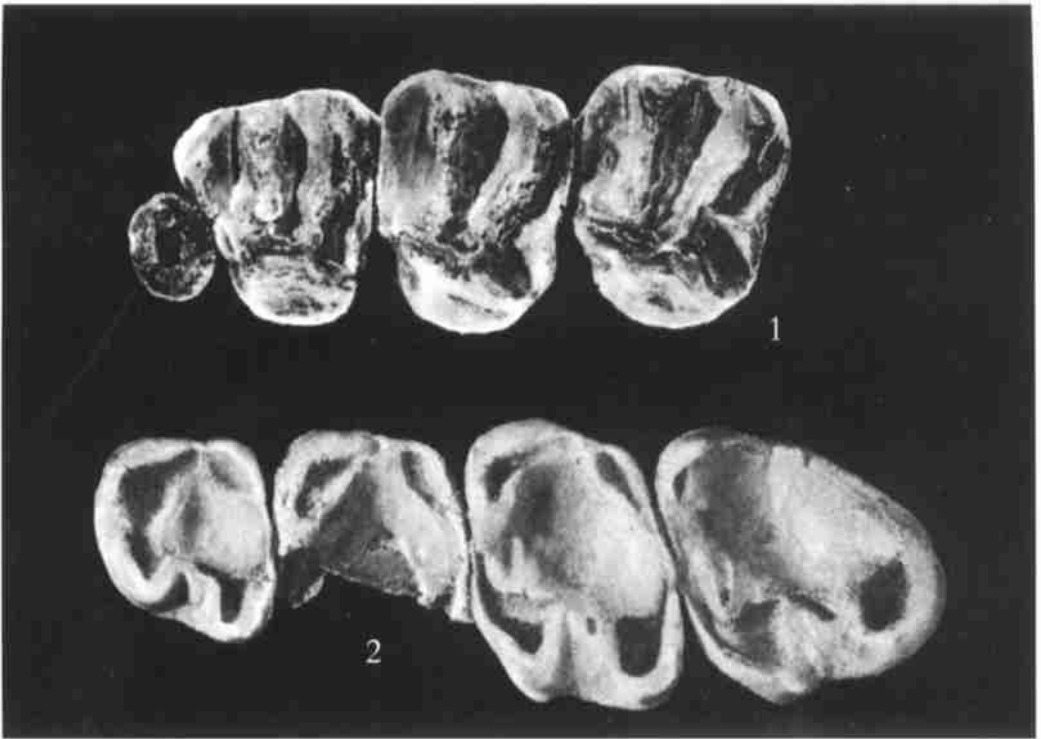
Miopetaurista Kretzoi, 1962

Type species *Sciurus gibberosus* Hofmann, 1893.

Diagnosis See the emended diagnosis by Daxner-Hock and Mein (1975).

Miopetaurista asiatica sp. nov.

(Fig. 4)

Synonymy ?*Forsythia* sp. Qiu et al. , 1985.**Etymology** Named in allusion to its first discovery in Asia.**Holotype** A very damaged left upper jaw with root of P3 and P4-M2 from L. III (P4-M2 : 10.10mm; P4:3.30 ×3.40mm; M1 : 3.25 ×3.85mm; M2 : 3.50 ×3.85mm) ; V 13147.**Paratypes** L. III: 1 damaged mandible with I and p4-m3 (m1 damaged; p4-m1 : 14.30mm; p4: 3.25 ×3.00mm; m1 : 3.15 × - mm; m2: 3.90 ×4.00mm; m3: 5.10 ×4.10mm) ; L. V: 1 M2 (3.50 ×4.15mm) ; V 13148. 1~2.**Diagnosis** Mid-sized *Miopetaurista* species. The P4 nearly equal to M1 in length, but narrower width. Hypocone relatively delimited on P4-M2; hypoconule prominent on M1-2, but weak on P4; mesostyle absent on upper cheek teeth. Mesoconid and mesostylid small. Enamel in basins seldom rugoes.**Description** The mandible preserved part of the horizontal ramus. The diastema is broad width and short (about 12 mm long). The mental foramen is large, round and placed midway in the bend of the diastema. The horizontal ramus measures 11mm below p4. The symphysis is broad.Fig. 4 *Miopetaurista asiatica* sp. nov. , occlusal view, ×8

1. Root of P3 and P4-M2 on a damaged right upper jaw, Holotype (V 13147) ;

2. p4-m3 on a broken left mandible (V 13148. 1)

The P3 is single-rooted. The occlusal outline of the P4 is trapezoid shape due to the expansion and development of the parastyle. The protocone is moderately developed and the hypocone is indistinct. The protoloph and the metaloph are approximately parallel, constricted at the protocone. The metaconule is much larger than the protoconule. The anteroloph and the posteroloph are low and weak, with the latter bearing a bulge near the indistinct hypocone. The mesostyle is absent. The

lingual wall is slight concave. The M1/2 are subquadrate with a weakly developed protocone located relatively anteriorly and a more or less delimited hypocone situated close to the protocone. The protoloph and metaloph are pronounced and nearly parallel, with the former bearing a small protoconule and constricted just labial of the protocone. A metaconule is absent. There is no indication of a mesostyle. The anteroloph and the posteroloph are low and weak, with the latter bearing a marked hypoconule, which joins to the metaloph on the M2 of the type specimen. The enamel of the ridges is rarely crenulated except for a short accessory lophule extending anteriorly from the protoconule. The surface of the basins is not rugose either. On the lingual wall two inflections are present between the anteroloph and the protocone, and the protocone and hypocone.

The cheek teeth on the mandible are very worn. The p4 is transversely narrower anteriorly than posteriorly. The protoconid and metaconid are closely situated. The entoconid is set off from the metaconid and incorporated in a narrow posterointernal crest. The presence of a mesostylid close to the metaconid is indicated by wear. On m1 an evident mesostylid is present, connected with the metaconid in late stages of wear. The entoconid is distinct, and separated from the mesostylid by a notch in late wear. The m2 is rhomboid shape with the same structure seen on the lingual portion of the m1. A small mesoconid is present. The buccal valley is narrow and directed slightly anteriorly. The posterolophid is narrow. The talonid basin is smooth. The m3 is subtriangular and moderately expanded posteriorly. The entoconid is submerged in the strong posterointernal crest. The mesoconid is larger than the mesostylid. The surface of the talonid basin is smooth.

Comparison and discussion This squirrel is assigned to *Miopetaurista* based on size of cheek teeth, approximately parallel protoloph and metaloph on P4-M2, weak or absent conules on M1-2, rhomb shape of m1-2 occlusal surface with delimited entoconid and less sculptured enamel in the basins. It differs from *Aliveria* (De Bruijn et al., 1980), *Forsythia* (Mein, 1970), *Pliopetaurista* (Kretzoi, 1962), *Albanensia* (Daxner-Hock and Mein, 1975), *Hylotropes* (Thomas, 1908), *Blackia* (Mein, 1970), *Meinia* (Qiu, 1981), *Parapetaurista* (Qiu and Lin, 1986) and *Shuanggouia* (Qiu and Lin, 1986) from the Neogene of Eurasia in the above dental features.

Miopetaurista, including six species, is a large-sized flying squirrel previously known from the lower Miocene to lower Pliocene of Europe (De Bruijn, 1999). The new species *M. asiatica* is close to *M. gibberosa*, *M. lappi* and *M. gaillardi* in size, but differs from the former in having a relative wider lower cheek teeth, and from the latter two in the presence of a delimited hypocone and a well developed hypoconule on upper molars, plus the absence of a hypolophid on lower molars. In addition, the mesoconid and the mesostylid in the new species are less prominent. The Asian species seems to have a smaller size and has less complicated dental pattern than *M. neogrivensis*, i. e. P4 without mesostyle and with only one accessory lophule between the metaloph and the posteroloph, plus m3 lacking a hypolophid. It is readily distinguished from *M. crusafonti* by a simple dental pattern of P4 and lower molars. The former is larger than *M. dehmi* and different from the latter in having a hypoconule and missing an accessory lophule between the protoloph and the metaloph on M1-2, plus the mesoconid and mesostylid on p4-m3 are less developed. *M. asiatica* resembles *M. thaleri* in some features, e. g. the presence of an anterior accessory lophule of the protoconule and a hypoconule on M1-2, and the weak mesostylid connected with the metaconid on m1-2; but the former is distinctly smaller than the latter and has an anterior lophule of the hypoconule on M1-2 and lacks a hypolophid on the lower molars.

Compared with the European *Miopetaurista*, in general, the Chinese species shows greater similarity in dental character with the later species (e. g., *M. crusafonti* and *M. thaleri*) than the early species. These characters are the more delimited protocone, the more distinct bulge of the posteroloph (hypoconule) and the less developed mesoconid and mesostylid. However, teeth of the new species show less development of crests in the basin, a characteristic that may occur in early species of the genus in Europe.

Neogene flying squirrels known from North America are "*Sciuropterus*" from the Miocene

(James, 1963; Lindsay, 1972), which was transferred to *Petauristodon* by Engesser (1979) and assigned to *Miopetaurista* by De Bruijn and others (1980). Although the American flying squirrels are smaller than *Miopetaurista* of Eurasia and show minor differences, such as the better developed protoconule and metaconule on M1-2, they display a very close resemblance to the latter in dental morphology. It is an unsolved problem to explain the similarities and the phylogenetic relationships of these squirrels from the two continents. Analysis of faunal composition and sedimentary environment demonstrate that *Miopetaurista* inhabited tropical or subtropical forest areas. Cold climate and rigorous ecologic environment would be a barrier to dispersal of these animals. Therefore, I concur with Engesser's assignment, at least until the assumption of interchange of *Miopetaurista* is firmly established.

Hylopetodon **gen. nov.**

Etymology *Hylopetodon*-*Hylopetes* tooth-like. Referring to its close resemblance to the extant genus *Hylopetes* in dental pattern.

Type species *Hylopetodon dianensis* sp. nov.

Diagnosis Flying squirrel with rather large-sized cheek teeth. P4 nearly equal to M1 in length. P4-M2 with weak hypocone and without mesostyle; protoloph and metaloph converging toward the protocone. Metaconule pronounced on P4, double on M1-2. Metaloph absent on M3. Mesoconid and mesostylid prominent, with the latter connecting to the metaconid. Entoconid prominent and separated from the mesostylid by a deep notch. The anteroconid, anterlabial cingulum and valley are absent. Cheek teeth with irregular low crests and rugose enamel in the basins.

Differential diagnosis *Hylopetodon* is similar to *Aliveria*, *Albanensia*, *Pliopetaurista*, *Forsythia*, *Shuanggouia* and *Hylopetes* in having the protoloph and metaloph of P4-M2 converging toward the protocone, but its dental pattern does not fit the diagnosis for any of them. It differs from *Aliveria* in larger size and having a double metaconule on M1-2, in the absence of metaloph on M3, in lacking an anteroconid and free mesostylid on p4-m2, and in enamel strongly crenulated. The new genus resembles to *Albanensia* in the mesostylid connected with the metaconid on lower molars, and in the absence of the labial branch of the anterolophid and the "anterosinuside", but it is distinguished from the latter by its smaller P4 relative to M1, and in M3 lacking a metaloph. It is larger than *Pliopetaurista*, and differs in having a smaller P4 relative to M1, no trace of a hypolophid on m3 and enamel more crenulated on the basins. The new form is much larger than *Forsythia* in size. In addition, its protocone and hypocone are not as compressed as in the European genus, and there is no metaloph on M3 nor an "anterosinuside" on m3. It differs from *Shuanggouia* in larger size, smaller P4 relative to M1, and M3 lacking a metaloph. *Hylopetodon* shows a surprisingly close resemblance to the extant *Hylopetes* in dental pattern, such as the occlusal outline of the cheek teeth, the nearly equal size of P4 and M1, the converging protoloph and metaloph on P4-M2, the absence of a metaloph on M3, the mesostylid connected with the metaconid on the lower molars, and the distinct posteriorly expanded m3. Nevertheless, the new form can be easily distinguished by its much larger size, presence of a double metaconule on M1-2, absence of an "anterosinuside" on lower molars, and more crenulated enamel on the basins.

Hylopetodon dianense **sp. nov.**

(Fig. 5)

Synonymy cf. *Hylopetes* sp. Qiu et al., 1985.

Etymology Dian—abbreviated form of Yunnan Province, after the name of type locality.

Holotype A crushed skull with all the teeth, but left P3 from L. II (P3-M3: 14.10mm; P3: 1.65 × 1.70mm; P4: 3.70 × 3.75mm; M1: 3.55 × 4.50mm; M2: 3.55 × 4.50mm; M3: 4.00 × 4.10); V13149.

Paratypes L. I: 1 very worn m2; L. II: 2 ml (4.25 × 4.60, 4.25 × 4.10mm), 1 m3

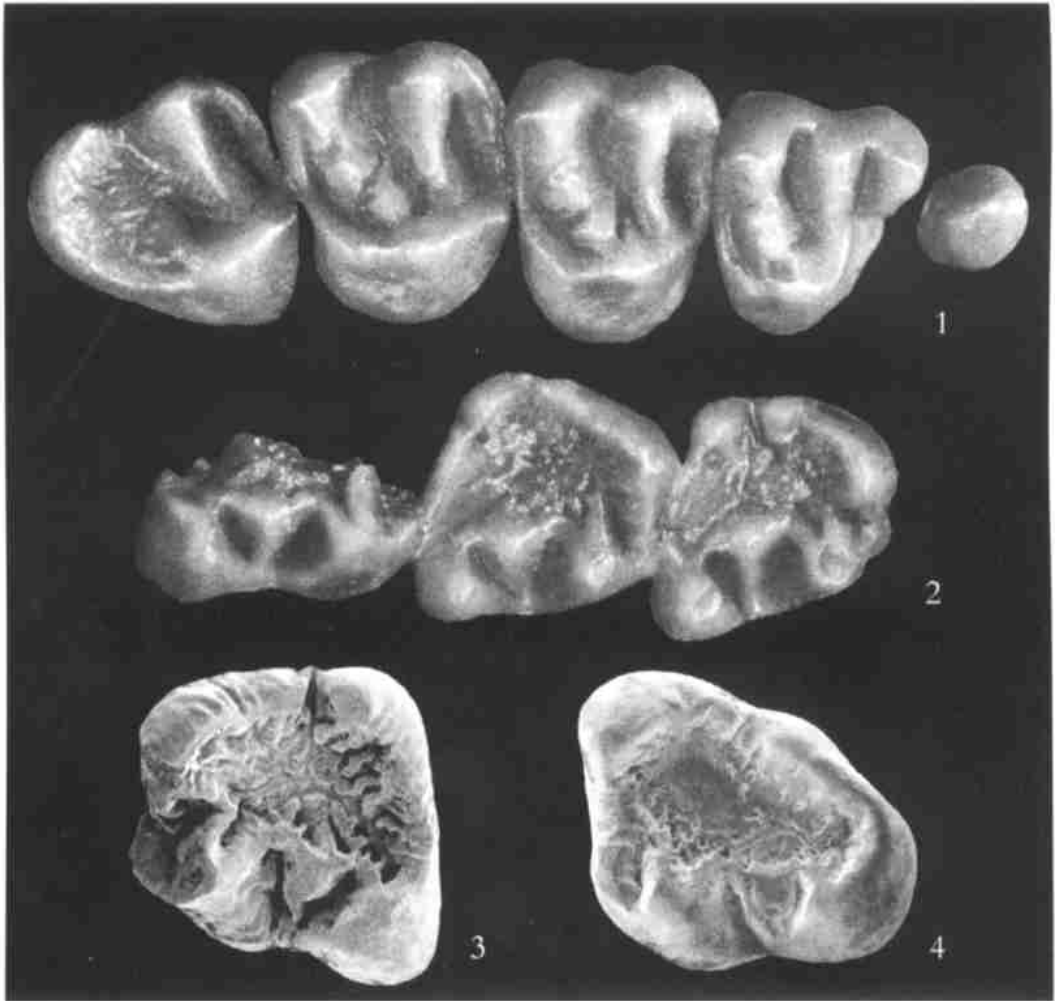


Fig.5 *Hylopetodon dianense* gen. et sp. nov. , occlusal view

1. Right P3-M3 on a crushed skull , Holotype (V 13149) , $\times 10$; 2. p4-m2 on a broken right mandible (V 13150.7) , $\times 10$; 3. m1 (V 13150.3) , $\times 14$; 4. m3(V 13150.5) , $\times 14$

(4.75 \times 4.40mm) ; L. III: 1 m3 (4.40 \times 4.15 mm) ; L. V: 1 M1/2 (3.50 \times 4.50 mm) , 1 damaged mandible with p4 (3.80 \times 3.70mm) , m1 (4.00 \times 4.00mm) , and damaged m2 (4.35 \times - mm) and m3; L. VI: 1 M 1/2 (3.30 \times 4.30 mm) , 1 m3 (5.10 \times 4.40 mm) ; L. mix: 1 dp4(2.90 \times 2.25 mm) ; V13150.1 ~ 10.

Diagnosis As for the genus.

Description The skull and the mandible were poorly preserved and can provide hardly any information except for the distance between the two upper molar rows (about 9.6 mm at M1) , and between the upper incisor and P3 (about 17 mm long) .

P3 is a single cusp and is single-rooted. The occlusal outline of the P4 is subtriangular due to the expansion and prominence of the parastyle. The protocone is well developed and the hypocone is weak. The protoloph and the metaloph converge toward the protocone , and are constricted at the protocone. A protoconule is absent , but the metaconule is strongly developed. The anteroloph and the posteroloph are low and weak. The mesostyle is indistinct. An accessory lophule from the posterolabial side of the protocone and the posterolingual side of the metacone join the metaconule ,

respectively. The lingual wall is slight rugose. M1/2 are subquadrate with a relatively small hypocone located at the posterointernal corner of the teeth. The protoloph and metaloph converge toward the protocone and are constricted just labial of the protocone, with the former bearing a dim protoconule and the latter bearing a double unequal metaconule. The anteroloph and the posteroloph are low and weak. The mesostyle is minute, or is replaced by a small crest from the paracone. The teeth have irregular low crests on the basin and rugose enamel also occurs on the lingual wall. A distinct accessory lophule from the protocone is present between the protoloph and the metaloph. M3 is not very expanded posteriorly. The hypocone, metacone and metaloph are absent. The protoloph bears no protoconule. A tiny mesostyle is present.

The dp4 is similar to p4 in dental features, but is relatively longer with weaker cusps and loph. The p4 is narrower anteriorly than posteriorly. The protoconid and metaconid are closely situated and are separated by a high and anterior open trigonid basin. The entoconid is delimited. A small anteroconid is present. The mesoconid is pronounced. The mesostylid is distinct, which is connected to the metaconid and separated from the entoconid by a very deep notch. The posterolophid is thin, but bears a prominent hypoconulid. The buccal valley is wide. There are irregular low crests on the talonid basin. The m1 is similar to p4 in morphology, but less narrow anteriorly and the narrow trigonid basin is closed by the metalophid and the strong anterolophid. There is no labial branch of the anterolophid nor an "anterosinuside" on this tooth. The m2 is rhomb shape in outline and similar to m1 in structure. The m3 is subtriangular with the talonid basin expanded posteriorly. The entoconid is submerged in the posterointernal crest. The notch between the metaconid and the mesostylid is deeper than on m1. Enamel on the talonid basin is crenulated.

Discussion The similarities of the new genus to *Hylopetes* in dental pattern might suggest that the two genera were closely allied. Nevertheless, the gigantic teeth with a double metaconule on M1-2 and absence of an anterolabial valley on lower cheek teeth would exclude *Hylopetodon* from direct ancestry of *Hylopetes*.

Pteromyinae gen. et sp. indet.

(Fig. 6)

Material and measurement L. II: 1 M3 (4.40 × 4.60 mm); L. III: 1 m1/2 (5.00 × 4.20 mm), 1 mandible fragment with m3 (5.70 × 4.30 mm); L. V: 1 damaged m1/2 (4.00 × - mm); L. VI: 1 dp4 (4.10 × 3.10 mm), 1 m3 (5.30 × 4.50 mm); V 13151. 1~6.

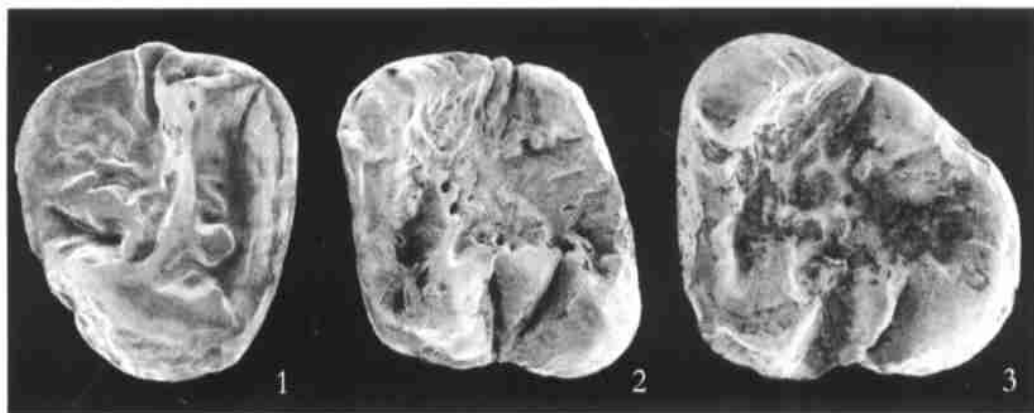


Fig. 6 Pteromyinae gen. et sp. indet., occlusal view, in reverse, ×14
1. M3 (V 13151.1); 2. m1/2 (V 13151.3); 3. m3 (V 13151.6)

Description The M3 is slightly expanded posteriorly. The metacone and hypocone are absent. The protoloph bears no protoconule, but extra lophules occur in front of and behind the

protoloph. The metaloph extending from the protocone and is flexed posteriorly short of the protocone to meet the posteroloph. There is a tiny and isolated mesostyle, and a very short mesoloph directed lingually from the mesostyle. Extra crests on the talon basin are distinct.

The dp4 is slightly damaged. It is narrower anteriorly than posteriorly due to the close position of the protoconid and metaconid. The mesoconid and the hypoconulid are pronounced, but the mesostylid is low and small. Enamel in the basin is well crenulated. The occlusal surface of m1/2 is rhomb shape with a very low trigonid basin. The entoconid and the mesoconid are well developed. The mesostylid is low and double, with the larger one connected to the metaconid and the small lophulate one separated from the metaconid by a narrow and deep notch. The posterolophid is strong. The buccal valley is wide. The trigonid basin is very low and enclosed by a complete metalophid and a low anterolophid. There are irregular low crests on the talonid basin. An anterolabial cingulum from the labial branch of anterolophid joins the labial wall of the protoconid, an "anterosinuside" like valley is present. The m3 is subtriangular with the talonid basin expanded posteriorly. The entoconid is submerged in the posterointernal crest. The notch between the metaconid and the doubled mesostylid is narrow and distinct. The labial branch of the anterolophid is present and the "anterosinuside" like valley is distinct. Enamel on the talonid basin is crenulated.

Remarks The specimens described were originally referred to *Albanensia* sp. (Qiu et al., 1985). It is true that the teeth are similar to *Albanensia* in size, in having a metaloph on M3, mesostylid connected with metaconid on the lower molar, and with distinct crenulated enamel on the basins. Nevertheless, the specimens do not correspond to the diagnosis of *Albanensia* as given by Daxner-Hock and Mein (1975) in having a labial anterolophid and "anterosinuside".

The taxon is characterized by a large size, having a low double mesostylid, a labial anterolophid and an anterolabial valley. It differs from *Hylopetodon* and *Pliopetaurista* in having a metaloph on M3, a low double mesostylid, and a labial anterolophid and "anterosinuside" on the lower molar. It is different from *Miopetaurista* in having a double mesostylid joined to the metaconid. Therefore, the precise determination of this taxon must wait until more material is recovered.

3 Conclusion

The Shihuiba sciurid fauna is composed of seven genera and species, representing two subfamilies; it is a relatively diverse sciurid fauna from the Neogene deposits of East Asia. Among the seven forms, *Tamiops*, *Callosciurus*, *Dremomys* and *Sciurotamias* are extant genera, and one genus (*Hylopetodon*) and four species (*D. primitivus*, *S. wangi*, *M. asiatica* and *H. dianense*) are described as new.

Except for *Miopetaurista*, present in the Neogene of Europe and western Asia, and for *Sciurotamias* in the Pleistocene of northern China, all the other taxa of the Shihuiba Fauna are known only from southeastern Asia. High endemism of the fauna and poor knowledge of phylogenetic relations for these animals make it difficult to determine precisely the age of the fauna. However, the high diversity of the fauna and the habitat preferences of sciurids are conducive to understand the paleoecology of the Lufeng hominoid fauna.

The fauna includes three adaptive types of squirrels. *Sciurotamias* represents a ground squirrel, which mainly inhabits rocky and mountain cliffs. *Tamiops*, *Callosciurus* and *Dremomys* are tree squirrels distributed in forested areas throughout most of the Orient today. They live either in a forest of broadleaf trees or in a mixed forest of coniferous trees and broadleaf trees. Judging from the dental characteristics, *Miopetaurista*, *Hylopetodon* and Pteromyinae gen. indet. belong to the flying squirrels. All of the living flying squirrels are arboreal and usually require some high trees. It is likely that the Lufeng sciurid fauna indicates a rather humid and forested environment of a tropic/subtropical area, which might be warmer and moister during the late Miocene than this area is during

the present day. This seems corroborated by the lignite deposits that produced the remains of squirrels, and by faunal, floral and chemical analysis (Sun and Wu, 1980; Qiu et al., 1985; Badgley et al., 1988).

Different adaptive types of squirrels are also known from the Neogene of North China, such as the ground squirrels *Atlantoxerus*, *Prospermophilus* and *Sinotamias*, the chipmunk *Eutamias*, the tree squirrel *Sciurus*, and the flying squirrel *Pliopetaurista* from the late Miocene and early Pliocene of Ertemte and Bilike faunas (Qiu, 1991; Qiu and Storch, 2000). The ground squirrels and chipmunks, representing taxa of temperate arid steppe, are commonly known from other localities in that area (Qiu, 1996; Qiu and Wang, 1999). However, none of these taxa (at the genus level) occur in the Shihuiba Fauna. Sciurids are well recorded in the Neogene of Europe and usually are important elements in the faunas. Remains of flying squirrels, in particular, are also found frequently in lignite deposits, but none of them shows affinities with the Shihuiba Fauna except *Miopetaurista*. It seems that this sciurid fauna demonstrates no close affinities with either the northeastern Asian or the European faunas. This is also true for the middle Siwaliks sciurid fauna of the Indian subcontinent. It is clear that the Shihuiba sciurid fauna is endemic to southeastern Asia, and is obviously Oriental in character.

Acknowledgements The author gratefully acknowledges Dr. E. Lindsay from Arizona University, Tucson, for critiquing the manuscript and English content. He wishes to thank Zhang Wending from the IVPP for taking the photographs.

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