

云南曲靖晚始新世的梳趾鼠类化石¹⁾

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摘要 根据新材料修订了 *Dianomys* 属及其两个种 (*D. obscuratus* 和 *D. qujingensis*) 的鉴定特征。原定为 *D. obscuratus* 的 P4 应为 dP4, 原定的 M1/2 和 m1/2 分别被确认为 M1 和 m2, 原属 *D. obscuratus* 的 p4, 实属 *D. qujingensis*。 *D. qujingensis* 与 *D. obscuratus* 的区别除个体较大外, 还在于其上颊齿具分叉的后脊, m1 具下中脊和 p4 具较发育的附加刺。另建立了一新属 (杨氏鼠 *Youngomys*), 包括二新种 (云南杨氏鼠 *Y. yunnanensis*、小杨氏鼠 *Y. pisinnus*) 和一未定种 (*Youngomys?* sp.)。 *Youngomys* 的主要特征为: 颊齿比例上较窄长, 齿冠较低, 主尖钝, 脊较细而低; 上臼齿长大于宽, 后脊向原尖斜伸, 内脊较低; 下臼齿下原尖后臂较向后伸, 无明显的舌部, 下内尖臂很弱, 横向, 不与下外脊连等。 *Y. pisinnus* 与 *Y. yunnanensis* 的区别在于个体较小, 齿冠较低, 脊更细弱, 较显丘形, 上臼齿次尖位置向舌侧移, 具较明显的后小尖, 和后脊不与原尖连等。

用 PAUP 3.1.1 对亚洲古近纪的梳齿鼠类进行了系统分析, 表明第四前臼齿的臼齿化和非臼齿化是比较复杂的过程, 而且可能是多次平行演化的结果。认为 *Youngomys* 与 *Mergenomys* 同属一支。进一步确认 *Dianomys* 为梳趾鼠类, 很可能是 *Ctenodactylidae* 加上 *Mergenomys* + *Youngomys* 等属的姐妹群。

关键词 云南曲靖, 晚始新世, 梳趾鼠超科

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LATE EOCENE CTENODACTYLOIDS (RODENTIA, MAMMALIA) FROM QUJING, YUNNAN, CHINA

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Abstract The diagnoses of *Dianomys*, *D. obscuratus* and *D. qujingensis* are revised

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based on new material. The tooth originally described as P4 of *D. obscuratus* is actually dP4, M1 / 2 and m1 / 2 are M1 and m2 respectively, and the p4 referred to *D. obscuratus* is transferred to *D. qujingensis*. *D. qujingensis* differs from *D. obscuratus* not only by larger size, but also in having forked metaloph on upper cheek teeth, mesolophid on m1, and more developed accessory crests in the mesosinusid on p4. A new genus, *Youngomys*, is erected to include two new species (*Y. yunnanensis* and *Y. pisinnus*) and *Youngomys?* sp. The main characters of *Youngomys* include: cheek teeth being long and low crowned, having obtuse main cusps and slender loph; upper molar being longer than wide, having metaloph oblique to protocone and low entoloph; on lower molar rather posteriorly extended posterior arm of protoconid lacking lingual part, and arm of entoconid weak. *Y. pisinnus* differs from *Y. yunnanensis* in smaller size, cheek teeth being lower crowned and more bunodont, upper molar having more lingually positioned hypocone relative to protocone, distinct metaconule and metaloph separated from protocone.

The phylogenetic relationships of the Paleogene Ctenodactyloidea are analyzed based on the dental features using PAUP 3.1.1. It seems that the evolutionary process of the molariform or non-molariform of the fourth premolars is complex and may have occurred parallel in different lineages. *Youngomys* has close relationship with *Mergenomys*. *Dianomys* is a ctenodactyloid and may be a sister group to *Mergenomys* + *Youngomys* group plus the Ctenodactylidae.

Key words Qujing of Yunnan, late Eocene, Ctenodactyloidea

The ctenodactyloids have long been reported from Qujing (Wang, 1984). However, their characters and classification remain obscure because the material then described is very poor. In 1982, 1983 and 1985, the field teams of IVPP collected large number of vertebrate fossils, mainly by screen washing, from the Caijiachong Formation in Caijiachong area, Qujing, Yunnan. Besides a variety of other fossil mammals, abundant ctenodactyloid fossils, including a well preserved lower jaw, were collected. They were collected at six localities (IVPP Locs. 80020, 80021, 80022, 80026, 85001 and 85003) from two layers of the Caijiachong Formation. Locs. 80020, 80026, 85001 and 85003 are in the fourth layer and Locs. 80021 and 80022 are in the sixth layer. The new collection provides more information about the ctenodactyloids of Qujing.

The term used in this paper mainly follows Wang (1997). In the description the frequency of a character variant is expressed as a fraction, with the numerator indicating the number of the variant and the denominator the total number of the specimens observed.

Abbreviations: IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, the Chinese Academy of Sciences; IVPP Loc., locality of IVPP; the IVPP V, catalogue number of the vertebrate fossils of IVPP.

1 Systematics

Ctenodactyloidea Gervais, 1853***Dianomys* Wang, 1984**

Type species *Dianomys obscuratus* Wang, 1984.

Referred species *Dianomys qujingensis* Wang, 1984.

Geographic distribution and geological range South China; late Eocene.

Emended diagnosis Small- and medium-sized ctenodactyloids. Dentition formula 1023 / 1013. Cheek teeth brachydont, four transverse lophs nearly equally developed. On upper cheek teeth protoloph complete, metaloph usually complete, single or forked; anterior cingulum low and not joining with protocone on dP4, P4 and M1 or absent on P4, and high and joining with protocone on M2~3; anterosinus small and shallow or absent on dP4, P4 and M1, and larger and deeper on M2~3. Entoloph usually complete on P4~M2 and varied on M3. P4 / p4 molariformed. On P4 metacone higher than paracone and located posterobuccally, metaloph higher than protoloph. On M1~2 hypocone subequal to protocone and located posteriorly, and sinus transverse. On lower cheek teeth well-developed posterior arm of protoconid extending to lingual border of the tooth, complete and straight ectolophid extending anterobuccally and located buccally to the middle longitudinal line. On lower molar trigonid basin usually closed and increases from m1 to m3, sinusid extending posterolingually. Metalophid I incomplete or absent on P4. Upper cheek teeth and lower molars with three roots and p4 and dp4 with two roots.

***Dianomys obscuratus* Wang, 1984**

(pl. I)

Dianomys obscuratus (partim) Wang, 1984, 38~42, figs. 1~3, 5~8

Specimens 16 dP4 (IVPP V 12388.2, V 12390.1~4, V 12392.1~11), 12 P4 (V 12388.1, V12390.5~6, V 12392.12~20), 19 M1 (V 12388.3~5, V 12390.7~10, V 12392.21~32), 27 M2 (V 12387, V 12388.6~9, V 12390.11~16, V 12391.1~2, V 12392.33~46), 13 M3 (V 12388.10~12, V 12389.1, V 12390.17~20, V 12392.47~51), 6 dp4 (V 12392.52~57), 6 p4 (V 12390.21~23, V 12392.58~60), 19 m1 (V 12388.13~15, V 12390.24~27, V 12392.61~72), 30 m2 (V 12388.16~19, V 12389.2~3, V 12390.28~33, V 12392.73~90), and 13 m3 (V 12388.20, V 12390.34, V 12391.3, V 12392.91~100).

Localities and horizons IVPP Locs. 80020, 80021, 80022, 80026, 85001 and 85003, Caijiachong, Qujing, Yunnan; late Eocene, the 4th and 6th layers of the Caijiachong Formation.

Emended diagnosis Small-sized *Dianomys*; cheek teeth with distinct main cusps; on upper cheek teeth metaloph single, metaconule distinct or indistinct; on P4 anterior

cingulum and anterosinus present, metaloph usually incomplete and hypocone small; entoloph well developed on P4~M2 and usually complete on M3; metaloph usually complete on upper molar; metastylid well developed on lower cheek teeth; on p4 trigonid basin closed lingually, accessory crest in mesosinusid weak or absent, arm of entoconid and posterosinusid weak or absent; and mesolophid absent on m1 and dp4.

Remarks The specimens described here are identical with those of *Dianomys obscuratus* described by Wang (1984) in the basal occlusal pattern and size. Based on the new specimens of *D. obscuratus* the original description by Wang (1984) is revised as follows.

The original described P4 (IVPP V 7300) is actually a dP4 (see below in detail). The P4 is oval in the occlusal view. The protocone is larger than other cusps. The well-developed metacone is higher than the paracone and located posterobuccally. The protoloph is complete and without protoconule. The metaloph is higher than the protoloph and oblique posterolingually and usually incomplete (8 / 10). The metaconule is distinct. The small and low hypocone is posterobuccal to the protocone. The entoloph is complete. The posteroloph is more developed than the anterior cingulum. The anterior cingulum is usually short and low (9 / 10), with a free lingual end and without distinct anterocone. A wear facet is present on the anterior side of most P4 (8 / 10), indicating that a P3 is present during the lifetime. The P4 and upper molars have three roots, two buccal small and one lingual large.

The M1 and M2 were originally described as M1 / 2. Now based on the new material M1 and M2 can easily be distinguished. On M1 the anterior cingulum is lower than the protoloph and has two enlarged ends. Its lingual end does not reach to the protocone, but joins with protoloph by a short crest. The anterior groove is distinct. The posteroloph is higher than the anterior cingulum. The anterosinus is short and shallow. The mesosinus is longer and deeper than the posterosinus. The transverse sinus is symmetric. On M2 the hypocone shifts more buccally than in M1, so that the posterior side of M2 is shorter than the anterior one. The anterior cingulum is higher and joins the protocone. The posteroloph is shorter than the anterior cingulum. The sinus is usually broader than in M1. The enlarged anterosinus is subequal to the posterosinus in size. The mesosinus is larger than the antero- and posterosinus. The anterior groove is weak (7 / 25) or absent (18 / 25). Obviously the molars originally described as M1 / 2 are actually M1.

Describing *D. obscuratus*, Wang (1984) thought that the metaloph of the upper cheek teeth was incomplete based on the holotype. The new specimens indicate that the metaloph of the upper molar of *D. obscuratus* is usually complete and reaches to the entoloph on M1 (16 / 19) and M2 (24 / 26). In addition, the hypocone of M1 and M2 is subequal to the protocone in size and located posteriorly to the protocone rather than posterolingually as described before. The metaconule may be distinct (M1:15 / 19,

M2: 13 / 26) or indistinct (M1: 4 / 19, M2: 13 / 26).

The M3 is similar to M2 in the anterior part. But the anterior groove is absent. The posterior part is narrower. The metaloph joins with the anterior arm of the hypocone. The metaconule is usually absent (9 / 11). The hypocone is posterobuccal to the protocone. The entoloph is usually complete (8 / 11). The posteroloph is short. The mesosinus is larger than the antero- and posterosinus and sometimes communicates with sinus.

The dP4 is similar to M1 in basic occlusal pattern. But its anterior cingulum flares more anteriorly on the buccal part and has a free lingual end. The anterosinus is usually open lingually. The hypocone is usually located posterolingually to the protocone. A wear facet is always present on the anterior side of dP4. It shows that dP3 is present.

IVPP V 7305 described as p4 of *D. obscuratus* is actually a p4 of *D. qujingensis*. The p4 of *D. obscuratus* is smaller and has a simpler occlusal pattern. The metaconid extends buccally and does not reach to the protoconid. The metalophid I is incomplete. The metastylid is well developed and joins with the well-developed posterior arm of the protoconid to close the trigonid basin. The ectolophid is straight and complete and located buccally to the middle longitudinal line. The accessory crest in the mesosinusid is weak or absent. The posterolophid (= lingual arm of hypoconulid) is short and transverse. Its lingual end joins with the entoconid. The mesosinusid is wider than the posteriorly oblique sinusid. The posterosinusid is weak or absent. The hypoconulid is weak or absent and the hyposinusid is shallow. The p4 has two roots.

The molars originally described as m1 / 2 are actually m2. On m1 the anterior side is shorter than posterior one. It has a smaller trigonid basin (subequal to both the meso- and posterosinusid in width but shorter) and a longer ectolophid. On m2 the trigonid basin is subequal to the meso- and posterosinusid in length but wider.

The new collection shows that on the m3 the metastylid is, usually present, the posterior arm of the protoconid joins with the metastylid rather than the entoconid, so that the trigonid basin is closed and mesosinusid is open lingually. As in m2, the trigonid basin is wider than the meso- and posterosinusid. But the posterosinusid is longer than the mesosinusid. The lower molars have three roots, two anterior small and one posterior large.

The dp4 is oval in occlusal view. The trigonid is narrow and short. The metaconid is conical. The V-shaped protoconid has a short and low anterior arm reaching (1 / 4) or not reaching to the low anteroconid (3 / 4). Its well-developed posterior arm reaches to the lingual side of the tooth. The lingual end of its posterior arm extends posteriorly into a low longitudinal crest. The trigonid basin is crescent and opens anteriorly and lingually. The talonid is similar to that of m1 / 2. The ectolophid is straight but not so oblique as in m1 / 2. The entoconid is higher than

the hypoconid and opposite to the latter. The arm of the entoconid is slender and long. The posterolophid is short. Both the hypoconulid and buccal posterior cingulum are distinct. The mesosinusid is narrower than the posterosinusid and trigonid basin, and wider than the sinusid. The sinusid is oblique posteriorly and opposite the posterosinusid. The hyposinusid is well developed and deep. There are two roots.

Dimensions See table 1.

Table 1 Measurements of cheek teeth of *Dianomys obscuratus* (mm)

	N	Min	Max	Aver	SD	CV
P4 L	9	1.2	1.67	1.44	0.13	0.09
P4 W	7	1.6	2.1	1.96	0.16	0.08
M1 L	19	1.44	1.88	1.68	0.1	0.06
M1 W	13	1.8	2.1	1.98	0.09	0.05
M2 L	26	1.5	2.1	1.86	0.14	0.07
M2 W	22	1.97	2.57	2.26	0.17	0.07
M3 L	10	1.5	2.1	1.82	0.18	0.1
M3 W	8	1.98	2.7	2.23	0.21	0.1
dP4 L	9	1.3	1.7	1.5	0.11	0.07
dP4 W	9	1.43	2.08	1.71	0.18	0.1
p4 L	6	1.4	1.78	1.56	0.13	0.09
p4 W	6	1.1	1.53	1.3	0.14	0.11
m1 L	15	1.8	2.06	1.93	0.09	0.05
m1 W	17	1.5	2	1.63	0.11	0.07
m2 L	28	1.85	2.4	2.09	0.11	0.05
m2 W	26	1.6	2.1	1.86	0.12	0.07
m3 L	10	2	2.3	2.13	0.1	0.05
m3 W	9	1.6	1.97	1.8	0.1	0.06
dp4 L	5	1.77	1.9	1.82	0.04	0.02
dp4 W	6	1.18	1.38	1.27	0.07	0.05

Abbreviations: L: length; W: width; N: number of specimens; Min: minimum; Max: maximum; Aver: average; SD: standard deviation; CV: coefficient of variation.

Dianomys qujingensis Wang, 1984

(fig. 1; pl. II)

Dianomys qujingensis Wang, 1984, 42~43, fig. 9

Dianomys obscuratus (partim) Wang, 1984, 38~42, fig. 4

Specimens One left mandible with p4~m3 (IVPP V 12393.1), 3 P4 (V 12393.2~3, V 12394), 6 M1 (V 12393.4~9), 6 M2 (V 12393.10~15), 2 M3 (V 12393.16~17), 2 dp4 (V 12393.18~19), 2 p4 (V 12393.20~21), 5 m1 (V 12393.22~26), 5 m2

(V 12393.27~31) and 4 m3 (V 12393.32~35).

Localities and horizons IVPP Locs. 80021 and 80026 in Caijiachong, Qujing, Yunnan; late Eocene, the fourth and sixth layers of the Caijiachong Formation.

Emended diagnosis Larger than *D. obscuratus* in size; cheek teeth slightly high crowned, with well-developed lophs; upper cheek teeth with forked §-shaped metaloph but without metaconule; on P4 anterior cingulum absent, metaloph complete, hypocone subequal to protocone in size; entoloph complete on M1, partly complete on M2 and absent on M3; metastylid of lower cheek teeth usually weak or absent; on p4 metaconid isolated, accessory crests in mesosinusid well developed, and arm of entoconid and posterosinusid distinct; dp4 and m1 with mesolophid.

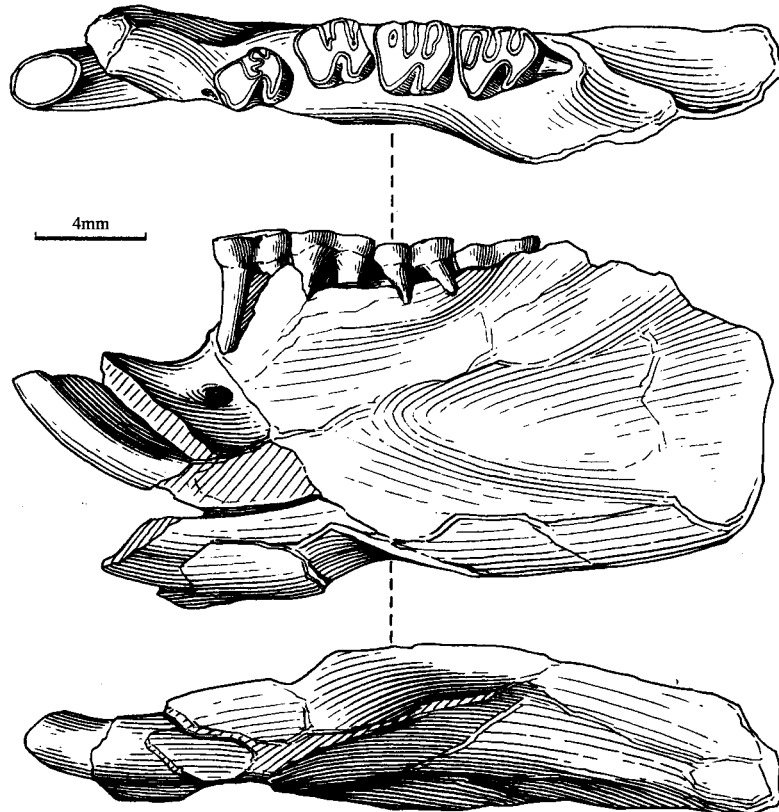


Fig.1 Left lower jaw with i2 and p4~m3 of *Dianomys qujingensis*
Upper: occlusal view; middle: buccal view; lower: ventral view

Remarks *D. qujingensis* was erected based on a single m3. The new material shows more features of *D. qujingensis*.

There is a rather completely preserved left ramus of mandible, of which the horizontal part is slightly fractured (fig.1). The mental foramen is located below the anterior root of p4 near the diastema. The masseteric fossa reaches below anterior side of m2, and has a distinct lower crest, but no distinct upper crest. The angular process

extends below the incisor. The lower jaw of *Dianomys* is sciurognathus.

The cheek teeth are slightly high crowned, with weak cusps and the same number of roots as in *D. obscuratus*.

The P4 is oval in occlusal view, with its anterior side narrower than its posterior one. The protocone, metacone and hypocone are subequal in size. The low and small paracone is anterolingual to the metacone. The protocone is located more buccally than the hypocone. The protoloph is short and complete. One of the particular features is the metaloph. It is composed of lingual and buccal parts. The lingual part forks buccally. Its two buccal branches join with the buccal part to close a small basin. The metaloph is forked §-shaped. The entoloph is present. No distinct anterior cingulum is seen. An anterior wear facet may be present (1 / 3) or absent (2 / 3).

The M1 is generally similar to M1 of *D. obscuratus* in the basic pattern. It mainly differs from that of *D. obscuratus* in the form of the metaloph. As in P4 of *D. qujingensis* the metaloph is §-shaped. But there are some variations: the anterior buccal branch of the lingual part may join with the buccal part (4 / 6) or may be free (2 / 6), and the basin between them may be closed or open buccally. The anterior groove is small. The transverse sinus is compressed longitudinally.

The M2 is trapezoid in occlusal view, with anterior side wider than the posterior one. The anterior part is similar to that of *D. obscuratus*. But the metacone and hypocone are smaller than the two anterior main cusps in size. The metacone shifts slightly lingually. As in M1 of *D. qujingensis* the metaloph is §-shaped. The anterior branch of the lingual part usually joins with the buccal part (5 / 6) and occasionally extends to the buccal side of M2 (1 / 6). The posterior branch of the lingual part occasionally is not developed and does not meet the buccal part. The posteroloph is short. The entoloph is partly complete, the posterior crest from the protocone and the anterior crest from the hypocone are connected at their bases, but separated upwards and form a gap. The mesosinus is larger than the subequal anterosinus and posterosinus and partly communicates with the sinus. No distinct anterosinus is seen.

The M3 is trapezoid in occlusal view and is slightly longer and narrower than the M2. The anterior part is similar to that of M2, but the posterior part is much narrower than the anterior one. The metacone and hypocone are smaller and closer in the position than the two anterior main cusps. The metacone is posterolingual to the paracone and the hypocone is posterobuccal to the protocone. The fork of the metaloph may be distinct or indistinct. No distinct entoloph is seen. The anterosinus is slightly wider than the posterosinus. The mesosinus is the widest and communicates with the sinus to form a posteriorly bend groove.

The lower incisor is triangle in transverse section. The enamel covers the convex labial side, extends lateral border and one-fifth of the medial side, and has weak vein on the surface.

The p4 is trapezoid in occlusal view. Unlike the p4 of *D. obscuratus*, the sharp buccal end of the metaconid may extend buccally or may turn posteriorly, but never reaches to the protoconid. The metalophid I is incomplete or absent. No distinct metastylid is visible. The distinct arm of the entoconid joins with well-developed posterolophid. In the large mesosinusid some distinct accessory crests are present. The posterosinusid is variable from small to developed. The hyposinusid is weak. IVPP V 7305, originally described as p4 of *D. obscuratus* actually belongs to *D. qujingensis* based on its size and occlusal features.

The m1 is rectangular in occlusal view. The trigonid is short. The metaconid and protoconid are subequal in size. The complete metalophid I is lower in the middle part. The metastylid is weak (2 / 4) or absent (2 / 4). The well-developed posterior arm of the protoconid extends to the lingual side. Its slightly enlarged lingual end usually joins with the metaconid or metastylid (3 / 4). The ectolophid is complete and extends posterolingually. One of the particular features is the presence of the mesolophid on m1. The transverse arm of the entoconid reaches to the ectolophid. The posterolophid is well developed and has a distinct hypoconulid. The lingual three sinusids are subequal in width. The trigonid basin is short and usually closed lingually. The mesosinusid is long and deep and open lingually. The sinusid is longer and narrower than the mesosinusid and oblique to the posterosinusid. The hyposinusid is shallow and broad.

The m2 is similar to m1 in occlusal pattern. But the metastylid may be present (3 / 5) or absent (2 / 5). No mesolophid is present. The trigonid basin is wider than the other sinusids. The mesosinusid is deeper than the posterosinusid. The hyposinusid is weak.

The m3 is similar to m3 described by Wang (1984). But sometimes a well-developed metastylid may reach to the posterior arm of the protoconid to close the trigonid basin (2 / 4). No accessory cusp or crest can be seen in the posterosinusid.

The dp4 is similar to dp4 of *D. obscuratus* in the basic features. But the metaconid has a buccal crest reaching to the small anteroconid. The longitudinal crest extending from the lingual end of the posterior arm of the protoconid is more developed and almost reaches to the base of the entoconid. The ectolophid is complete and has short mesolophid. The mesosinusid is longer and narrower than trigonid basin and posterosinusid and wider than slightly oblique posteriorly sinusid. The hyposinusid is distinct. No distinct buccal posterior cingulum is seen.

Dimensions See table 2.

As described above, *D. qujingensis* differs from *D. obscuratus* not only in the size but also in the occlusal pattern. It can be characterized by having forked metaloph on upper cheek teeth, having a complete metaloph, a larger hypocone but lacking anterior cingulum on P4, having a mesolophid on dp4 and m1, having more

Table 2 Measurements of cheek teeth of *Dianomys qujingensis** (mm)

	N	Min	Max	Aver	SD	CV
P4 L	3	1.64	2	1.81	0.15	0.08
P4 W	1			2.56	0	0
M1 L	5	2.06	2.2	2.11	0.05	0.02
M1 W	5	2.4	2.7	2.48	0.11	0.05
M2 L	5	2.2	2.58	2.4	0.13	0.05
M2 W	3	2.6	3.03	2.82	0.18	0.06
M3 L	1			2.48		
M3 W	1			2.93		
p4 L	2	2.3	2.7	2.5	0.2	0.08
p4 W	2	2.1	2.14	2.12	0.02	0.009
m1 L	5	2.4	2.63	2.52	0.08	0.03
m1 W	5	2	2.4	2.19	0.14	0.06
m2 L	5	2.58	2.9	2.67	0.12	0.04
m2 W	6	2.15	2.8	2.38	0.22	0.09
m3 L	3	2.73	3.2	2.94	0.19	0.07
m3 W	3	2.4	2.84	2.58	0.19	0.07
dp4 L	1			2.32		
dp4 W	1			1.58		
p4~m3 L	1			11.8		
m1~3 L	1			9.7		

* Abbreviations see table 1.

developed accessory crests in the mesosinusid and a well-developed posterosinusid on p4 and a more developed longitudinal crest on dp4. Probably *D. qujingensis* represents a more advanced species than *D. obscuratus*.

Youngomys gen. nov.

Type species *Youngomys yunnanensis* sp. nov.

Referred species *Y. pisinnus* sp. nov. and *Youngomys?* sp.

Geographic distribution and geological range South China; late Eocene.

Diagnosis More primitive ctenodactyloid than *Karakoromys*; cheek teeth quite long, brachydont, with obtuse main cusps and low transverse lophs; upper molar longer than wide, metaconule distinct but not swollen, metaloph extending obliquely towards protocone, entoloph complete, transverse sinus broad; on lower molars posterior arm of protoconid extending rather posteriorly and without lingual part, arm of entoconid weak and not reaching to ectolophid, ectolophid located near longitudinal middle line, hypoconulid not swollen and located at middle of posterior side of tooth.

Etymology *Young*, in honor of late Prof. C. C. Young, and the Greek suffix -mys for mouse.

Youngomys yunnanensis sp. nov.

(pl. III, 7~13)

Holotype A left M1 / 2 (IVPP V 12396.1).

Referred specimens 6 M1 / 2 (V 12395.1~4, V 12396.2, V 12397.1), 1 M3 (V 12395.5), 1 dp4 (V 12395.6), 1 p4 (V 12395.7), 5 m1 / 2 (V 12395.8~11, V 12397.2) and 2 m3 (V 12395.12~13).

Localities and horizons IVPP Locs. 80021, 80022 and 85003 in Caijiachong, Qujing, Yunnan; late Eocene, the fourth and sixth layers of the Caijiachong Formation.

Diagnosis Medium-sized *Youngomys*. Upper cheek teeth with relatively well-developed lophs, metaloph usually joins with protocone by a slender crest, metaconule weak or indistinct, hypocone located posteriorly to protocone, anterior cingulum subequal to posteroloph and joins with protocone but not reaching to buccal side.

Etymology *Yunnan* is the province where the ctenodactyls were collected.

Description The cheek teeth are brachydont. The main cusps are obtuse. The M1 / 2 (= M1 or M2) is rectangular in occlusal view, longer than wide. The protocone is subequal to or slightly larger than other main cusps. The hypocone is posterior to the protocone. The protoloph is complete. The metaloph extends towards the protocone and may join with the protocone by a slender crest (5 / 7) or may be free (2 / 7). The metaconule is small. The entoloph is low. The subequal anterior cingulum and posteroloph join with protocone and hypocone respectively but do not reach to the buccal side. The anterocone is distinct (3 / 7) or indistinct (4 / 7). The sinus is broad.

The M3 is trapezoid in occlusal view. The anterior part is similar to that of the M1 / 2, but the posterior part is narrower. The hypocone is smaller than the protocone and located slightly posterobuccally. The metacone is reduced. No distinct metaloph is seen. The metaconule is an isolated flat cusp. The entoloph is weak. The sinus shifts more posteriorly than in M1 / 2.

The p4 is oval in occlusal view. The heavily worn protoconid and metaconid are close in the position, but do not connected by crest. A low and weak crest connects the hypoconid and larger entoconid. The straight and weak ectolophid is located near buccal one-third part. The mesosinusid is wider than the sinusid.

The m1 / 2 (= m1 or m2) is long rectangular in occlusal view. The protoconid is subequal to the metaconid in size. The metalophid I is complete. The posterior arm of the protoconid extends rather posteriorly to meet the ectolophid. Its lingual part is weak or absent. The large trigonid basin is open posteriorly. The ectolophid is located near the longitudinal middle line. The entoconid and hypoconid are opposite in the position. The arm of the entoconid is transverse and weak, and does not reach to the ectolophid. The large hypoconulid is located at the middle of the posterior side. The arm of the hypoconulid reaches to the hypoconid. The posterolophid is short. The three lingual sinusids are communicated. The transverse sinusid is subequal to the

mesosinusid in the width. The hyposinusid is distinct. There are two roots.

The m3 is triangular in occlusal view. The trigonid is similar to that of m1 / 2. The talonid is narrower. The entoconid is located slightly anterolingually to the hypoconid. The small hypoconulid joins with the hypoconid. Sometimes an isolated cusp may be present at the lingual end of the posterolophid (IVPP V 12395.12). The hyposinusid is tiny and indistinct. The other features are similar to those of m1 / 2.

The dp4 is oval in occlusal view. The trigonid is narrow and short. The metaconid is conical. The V-shaped protoconid is smaller than the metaconid and located more posteriorly. Its anterior arm extends to the distinct anteroconid and its posterior arm joins with the ectolophid and has no lingual part. The entoconid is larger than the hypoconid and without distinct arm. The ectolophid is located slightly buccally. The hypoconulid is isolated and located at the middle of the posterior side. The arm of the hypoconulid is weak and does not reach to the hypoconid. The mesosinusid communicates with other lingual sinusids and wider than the transverse sinusid.

Dimensions (L × W, in mm) M1 / 2: 2.27 × 2.1 (holotype), 2.22 × 2.08, 2.2 × 1.98, 2.1 × 1.93; M3: 2.1 × 2; p4: 1.48 × 1.06; m1 / 2: 2.1 × 1.47, 2.05 × 1.6, 1.92 × 1.42, 2 × 1.52; m3: 2.3 × 1.8; dp4: 1.5 × 1.

Comparison The upper molars have four developed transverse lophs, a complete entoloph and a transverse sinus. The p4 is non-molariform. The lower molar has a posteriorly open trigonid basin. The rather posteriorly extending posterior arm of the protoconid lacks the lingual part. The arm of entoconid is transverse. The hypoconulid of m3 is small. All the features are similar to those of *Karakoromys*. They differ from those of *Karakoromys* in cheek teeth being lower crowned, having more distinct main cusps and weak lophs, upper molars being longer than wide and having an oblique metaloph joining with protocone by a slender crest, a lower entoloph, lower molars having a weak and free arm of entoconid. Probably these specimens represent a more primitive genus than *Karakoromys*, named as *Youngomys*.

Among the ctenodactyloids the genera more similar to *Youngomys* also include *Mergenomys*, *Butomys* and *Protataromys*. *Youngomys* differs from *Mergenomys* in cheek teeth being lower crowned, upper molar being longer than wide, having a more developed metaloph joining with protocone by a slender crest, a not swollen metaconule, a complete entoloph, and lower molars having a weak arm of entoconid not reaching to ectolophid and a not swollen hypoconulid; from *Butomys* in having more developed ectolophid, longer and narrower p4 and weak arm of entoconid; from *Protataromys* in cheek teeth being lower crowned, having weakly developed lophs, upper molars having a lower entoloph, and lower molar having a short posterior arm of protoconid without lingual part and a weak arm of entoconid.

Youngomys pisinnus sp. nov.

(pl. III, 1~4)

Holotype A right M1 / 2 (IVPP V 12398.1).**Referred specimens** 2 M1 / 2 (IVPP V 12398.2~3), 2 dP4 (V 12398.4~5) and 3 m1 / 2 (V 12398.6~8).**Locality and horizon** IVPP Loc. 80026 in Caijiachong, Qujing, Yunnan; late Eocene, the fourth layer of the Caijiachong Formation.**Diagnosis** Smaller than *Y. yunnanensis* in size; cheek teeth brachydont, more bunodont, with weak and low transverse crest; upper molars usually with distinct metaconule and incomplete metaloph; on M1 / 2 hypocone located more lingually than protocone, anterior cingulum located buccally, not joining protocone but with a slightly enlarged buccal end.**Etymology** *Pisinnus*, Latin, small, little.**Description and comparison** As in *Y. yunnanensis* the upper molars are longer than wide in occlusal view. The metaloph extends anterolingually. The entoloph is complete. The dP4 is similar to M1 / 2 in the occlusal pattern, but has lower anterior cingulum with a more anteriorly flared buccal part, a distinct anterocone and more lingually shifted hypocone.

On the lower molar the posterior arm of the protoconid extends posterolingually and has no lingual part. The trigonid basin is open posteriorly. The ectolophid is complete and located near middle of the tooth. The arm of the entoconid is weak and does not reach to the ectolophid. The hypoconulid is not swollen and located at the middle of the posterior side.

However, they are smaller than those of *Y. yunnanensis* in size. The cheek teeth are lower crowned. The four main cusps are more distinct and the lophes are more slender and lower. The hypocone is posterolingual to the protocone. The metaloph is incomplete and does not reach to the protocone. The metaconule is usually distinct. The anterior cingulum shifts buccally and does not join with the protocone, but has a more or less enlarged buccal end. All the features are different from those of *Y. yunnanensis*. The specimens described above may represent a more primitive new species than *Y. yunnanensis*, named as *Y. pisinnus*.**Dimensions** (L × W, in mm) dP4: 1.25 × 1.30, 1.37 × 1.3; M1 / 2: 1.6 × 1.5 (holotype), 1.6 × 1.48, 1.46 × 1.3; m1 / 2: 1.69 × 1.28, 1.52 × 1.17, 1.6 × 1.3.*Youngomys?* sp.

(pl. III, 5~6)

One M1 / 2 (IVPP V 12399.1) and three M3 (V 12399.2~4) were collected from the fourth layer of the Caijiachong Formation at IVPP Loc. 80026, Caijiachong, Qujing, Yunnan. The upper molars are similar to *Youngomys yunnanensis* in size and having an oblique metaloph. However, the upper molar is quadrate in occlusal view

and has a complete metaloph reaching to the protocone. On M1 / 2 no entoloph is present, instead the anterior arm of the hypocone extends obliquely to the metaloph. The hypocone of M3 shifts anteriorly to close to the protocone in the position. All these features are different from the known species of *Youngomys*. The specimens mentioned above may represent a new species or even a new genus. Dimensions (L × W, in mm): M1 / 2: 1.8 × 1.79; M3: 1.7 × 1.78, 1.85 × 1.67, 1.80 × 1.80.

2 Discussion

2.1 Biostratigraphy of ctenodactyloids from Qujing

The ctenodactyloids were collected from two layers of the Caijiachong Formation, the fourth and sixth layers, in Caijiachong area, Qujing, Yunnan. Both layers yield almost the same taxa. However, careful analysis shows that there are some differences between the two layers. A large number of specimens of the more primitive *Dianomys obscuratus* were collected from the fourth layer and only a few from the sixth layer. Likewise, all the specimens of the more primitive *Youngomys pisinnus* are known only from the fourth layer. To the contrary, almost all specimens of the more advanced *D. qujingensis* and *Y. yunnanensis* were collected from the sixth layer, whereas only one or two teeth from the fourth layer. It seems that the ctenodactyloids were evolving from more primitive taxa to the advanced ones from the fourth layer to the sixth one.

2.2 Phylogenetic relationships of the Paleogene ctenodactyloids

The phylogenetic relationships of the Ctenodactyloidea have been studied by many paleontologists (Wood, 1977; Dawson et al., 1984; Flynn et al., 1986; Wang, 1994, 1997; Averianov, 1996; Tong, 1997 and Dashzeveg and Meng, 1998). These problems will be discussed here based on the new material from Qujing.

2.2.1 Character analysis

The following analysis of the characters is mainly based on the dentition, which are commonly used in phylogenetic classification of the ctenodactyloids. We follow Dashzeveg and Meng (1998) to use *Tribosphenomys* as the outgroup and the molariform P4 / p4 as primitive. Terminal taxa are genera except the subfamilies of the Ctenodactylidae: Tataromyinae, Karakoromyinae, Distylomyinae and Ctenodactylinae (Wang, 1994, 1997). Some ctenodactyloid taxa are not included in the present analysis because of their poor preservation and uncertainty in taxonomy: such as those described by Dashzeveg (1990), Shevyreva (1989), Tong (1997, in part) and Dashzeveg and Meng (1998, in part). The characters and states suggested by Dashzeveg and Meng (1998) have been revised as follows (See Wang et al. MS in detail).

01. The infraorbital foramen: protrogomorph (0), hystricomorph (1).

02. The posterior zygomatic root: it levels with M1 or more posterior (0), with P4 (1), anterior to P4 (2).

03. The masseteric fossa extending to: below m2 or more posteriorly (0), below m1 (1), below p4 (2).
04. The masseteric crest: both upper and lower crests are present (0), upper crest indistinct, lower crest distinct (1), having only one developed horizontal crest (2).
05. The crown of cheek teeth: brachydont (0), hypsodont (1).
06. Cheek teeth: bunodont (0), more lophodont (1), tri- or bilobate (2).
07. P3: present (0), absent (1).
08. P4 / p4: molariform (0), non-molariform (1).
09. The shape of upper molars: wider than long (0), quadrate (1), longer than wide (2).
10. The metaconule on M1~3: distinct (0), absent (1), inflated (2).
11. The paraconule on M1~3: present (0), absent (1).
12. The metaloph on M1~2: weak, joining or not joining protocone (0), developed but not joining protocone (1), developed and joining protocone (2).
13. The anterior cingulum on M1~3: not developed (0), present but low (1), lower but with broad buccal part (2), high and usually joining protoloph (3).
14. The entoloph on M1~2: weak (0), well developed (1), absent (2).
15. The sinus on M1~2: shallow or deep and transverse (0), oblique posteriorly (1), oblique anteriorly (2).
16. The hypocone of M1~2: small (0), large (1), large and more lingually positioned (2).
17. On p4: metalophid II absent, weak, or low (0), both metalophid I and II developed (1), metalophid I absent and metalophid II extending to the lingual side (2), metalophid I absent and metalophid II V-shaped (3).
18. The metalophid II of m1~3: weak or distinct, extending rather transversely and parallel to the metalophid I (0), developed and extending more posteriorly (1), developed and fusing partly with metalophid I and closing the trigonid (2), reduced or lost (3).
19. The mesoconid on m1~3: present (0), absent (1).
20. The ectolophid on m1~3: weak, incomplete, buccally positioned (0), developed and complete, buccally positioned (1), middle or more lingually positioned (2).
21. The talonid basin on m1~3: complete (0), divided into mesosinusid and posterosinusid (1), mesosinusid narrow (subequal to or narrower than the sinusid) (2).
22. The arm of the entoconid on m1~3: absent (0), weak, complete or incomplete, variously joining ectolophid, hypoconid or hypoconulid (1), bend posteriorly and joining only hypoconulid (2), developed and joins ectolophid before hypoconid or even more anterior element (3).
23. The sinusid on m1~3: shallow (narrower than mesosinusid) and symmetric (0), deep (subequal to or deeper than the mesosinusid) and transverse (1), deep and oblique posteriorly (2).
24. The hypoconulid on m1~3: small (0), large (1), large crescent or anteriorly extended (2).
25. The hyposinusid on m1~2: absent or weak (0), distinct but narrow (1), deep and wide (2), shallow and wide or disappears (3).
26. The incisor enamel: pauciserial (0), multiserial (1).

Table 3 Data Matrix of the Characters of the Paleogene Ctenodactyloidea of Asia
(Question marks indicate missing data)

Taxa	Character																										
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	
<i>Tribosphenomys</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Cocomys</i>	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Bandaomys</i>	?	0	?	?	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	?
<i>Hohomys</i>	1	1	0	0	0	0	0	0	1	0	1	0	1	1	0	0	0	0	0	1	1	1	0	0	0	?	?
<i>Petrokozlovina</i>	1	1	0	0	0	0	0	1	0	1	1	1	1&2	0	1	0	0	1	1	1	1	0	0	0	1	0	1
<i>Tamquammys</i>	1	1	0	0	0	0	0	1	1	0	0	0	1	0	0	1	0	0	0	0	1	1	0	0	1	1	1
<i>Alaymys</i>	1	1	0	0	0	0	0	1	1	0	1	0	1	1	0	0	0	0	0	0	1	1	0	0	0	1	1
<i>Tsinlingomys</i>	1	1	0	0	0	1	0	1	1	0	1	2	2	2	0	0	0	0	1	1	1	2	0	0	1	?	?
<i>Yuomys</i>	1	1	0	0	0	1	0	0	1	0	1	1	3	1	0	2	1	0	1	1	1	3	0	0	0	1	?
<i>Advenimus</i>	1	2	0	0	0	0	0	0	1	0	0	1	1	1	0	2	0	0	0	0	1	1	0	0	1	1	1
<i>Birbalomys</i>	1	2	0	0	0	0	0	0	1	2	0	0	1	1	0	2	0	1	0	1	1	3	0	0	1	0	0
<i>Chapatimys</i>	?	?	?	?	0	0	0	0	1	2	0	0	1	1	0	2	1	1	0	1	1	3	0	0	1	0	0
<i>Stelmomys</i>	?	?	0	1	0	0	0	0	1	0	1	1	1	0	0	1	0	0	1	1	1	1	0	0	1	?	?
<i>Chuankueimys</i>	1	1	0	0	0	1	0	1	1	1	1	2	2	2	0	0	0	0	1	1	1	2	0	0	1	?	?
<i>Protataromys</i>	?	?	?	?	0	1	?	1	1	0	1	1	3	1	0	1	1	1	1	2	2	3	1	2	2	?	?
<i>Mergenomys</i>	?	2	1	1	0	0	?	?	1	2	1	0	3	2	0	1	?	1	1	2	2	3	1	1	1	?	?
<i>Dianomys</i>	?	?	1	1	0	1	0	0	0	0	1	1	1&3	1	0	1	2	1	1	1	1	3	2	1	3	?	?
Tataromyinae	1	1	1	1	0	1	1	1	2	1	1	2	3	2	1	1	3	2	1	2	2	3	1	2	2	1	1
Karakoromyinae	1	2	1	1	0	1	1	1	1	1	1	1	3	1	0	1	3	1	1	2	2	3	1	2	2	1	1
Distylomyinae	?	?	2	1	1	2	?	1	?	?	?	?	?	?	?	?	?	?	3	1	2	2	3	1	2	3	1
Ctenodactylinae	1	2	2	2	1	2	1	1	1	1	1	1	3	1	2	1	3	3	1	2	2	3	2	2	3	1	1
Gen. et sp. nov.*	?	?	?	?	0	0	1	1	1	0	1	0	3	1	0	1	0	1	1	2	2	1	2	1	2	?	?
<i>Youngomys</i>	?	?	?	?	0	0	?	1	2	0	1	0	1&3	0	0	1&2	0	1	1	1	0	1	1	1	2	?	?

* Ctenodactyloidea gen. et sp. nov. (see Wang et al., MS)

2.2.2 Phylogenetic analysis

Table 3 shows the tabulation of the characters of the Paleogene ctenodactyloids from Asia. A total of 23 taxa and 26 characters are involved in the calculation. The data were analyzed using the PAUP 3.1.1 program. Many of the characters have multistates. Valid character-state symbols are coded as 0 1 2 3. All characters are unordered and unweighted. The ACCTRAN optimization was used. Heuristic search yielded three equally most parsimonious trees of 91 steps. The three trees differ in the position of Tataromyinae and Karakoromyinae. Each tree has the following properties: Consistency index (CI) = 0.593, Homoplasy index (HI) = 0.451, CI excluding uninformative characters = 0.559, HI excluding uninformative characters = 0.461, Retention index (RI) = 0.770, and Rescaled consistency index (RC) = 0.457. The strict consensus of the three trees is illustrated in fig.2.

1) Molariform or non-molariform P4 / p4. One of the criteria to find out the

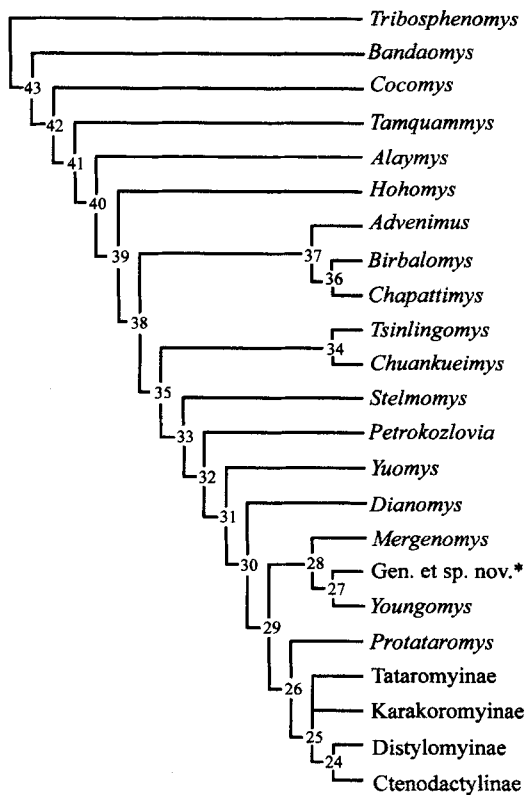


Fig. 2 Diagram of the phylogenetic relationships of the Paleogene Ctenodactyloidea of Asia, showing the position of *Dianomys* and *Youngomys* gen. nov.

* Ctenodactyloidea gen. et sp. nov. (see Wang et al., MS)

relationships of the ctenodactyloids has long been on the form of the fourth premolar: molariform or non-molariform (Dawson et al., 1984; Wang, 1994, 1997; Hu, 1995; Tong and Dawson, 1995; Tong, 1997). In fact the concept of the molariform and non-molariform P4 / p4 are not so clear as expected before. As mentioned by Dashzeveg and Meng (1998), a non-molariform P4 / p4 can be interpreted differently. Likewise, the molariform P4 / p4 has also been differently understood. For example, in *Hohomys* and *Bandaomys* the molariform P4 has a very tiny metacone joining the paracone, while in *Chapattimys* and *Birbalomys* the metacone of P4 is developed and separated from the paracone widely. In *Tamquammys tantillus*, the metacone of P4 varies from distinct to absent. It seems that the limit line separating molariform P4 / p4 from non-molariform

ones is in no way clean-cut. The fig.2 indicates that the lineages of the taxa with the molariform P4 / p4 are also mixed with those with non-molariform P4 / p4.

2) The relationships among the Ctenodactylidae. The Karakoromyinae were considered as the sister group of the Distylomyinae-Ctenodactylinae (Wang, 1994, 1997). Dashzeveg and Meng (1998) argued that the Tataromyinae had closer relationship with the Distylomyinae-Ctenodactylinae than did the Karakoromyinae. The strict consensus of the three trees indicate that the Karakoromyinae and Tataromyinae are equal in phylogenetic position: (1) The Karakoromyinae may have closer relationship with the Distylomyinae-Ctenodactylinae (as suggested by Wang, 1997); (2) the Tataromyinae have more closer relationship with the Distylomyinae-Ctenodactylinae (as suggested by Dashzeveg and Meng, 1998); or (3) the three groups are trichotomy (as shown in fig.2).

The Tataromyidae were suggested by Tong (1997) to include the Tataromyinae, Karakoromyinae and *Protataromys*. As shown in the fig.2, Tong's Tataromyidae are a paraphyletic group. I agree with some paleontologists (Dawson, 1964, 14~15; Black, 1972, 240; Wood, 1977, 122; Wang, 1997, 6~7) that the Tataromyidae are invalid.

But I follow Tong in putting *Protataromys* in the Ctenodactylidae.

3) *Youngomys* has close relationships with *Mergenomys* and Ctenodactyloidea gen. et sp. nov. from Kazakhstan (Wang et al. MS).

4) *Dianomys* was referred to the Yuomyidae (Wang, 1984, Tong, 1997) or the Phiomyidae (de Bruijn, 1986). Obviously *Dianomys* belongs to the Ctenodactyloidea rather than Phiomyidae based on the basic features, such as sciurognathous lower jaw, cheek teeth with four lophs, m3 larger than m2, and deciduous tooth replaced by permanent tooth early. As fig. 2 shows, *Dianomys* is a sister group to the *Mergenomys* + Ctenodactyloidea gen. et sp. (Wang et al. MS) + *Youngomys* plus the Ctenodactylidae in the Ctenodactyloidea.

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Explanations of plates**Plate I**

Occlusal view of cheek teeth of *Dianomys obscuratus* Wang, 1984, scale = 1mm

1. Left dP4 (V 12392.1), 2. left P4 (V 12392.12), 3. right M1 (V 12392.30), 4. left M2 (V 12392.33), 5. left M2 (V 12392.34), 6. left M3 (V 12392.48), 7. left M3 (V 12392.47), 8. right dp4 (V 12392.55), 9. right p4 (V 12392.58), 10. left m1 (V 12392. 62), 11. left m2 (V 12392.74), 12. left m3 (V 12392.91)

Plate II

Occlusal view of cheek teeth of *Dianomys qujingensis* Wang, 1984, scale = 1 mm

1. Left lower jaw with p4~m3 (V 12393.1), 2. right P4 (V 12394), 3. right M1 (V 12393.5), 4. right M2 (V12393.10), 5. right M3 (V 12393.16), 6. right p4 (V 12393.20), 7. right dp4 (V 12393.18), 8. right m1 (V 12393.25), 9. right m2 (V 12393.29), 10. left m3 (V 12393. 32)

Plate III

Occlusal view of cheek teeth of *Youngomys* gen. nov., scale = 1mm

1~4. *Y. pisinnus* sp. nov., 1. right dP4 (V 12398.4), 2. right M1 / 2 (holotype, V 12398.1), 3. left m1 / 2 (V 12398.6), 4. right m1 / 2 (V 12398.8)

5~6. *Youngomys?* sp., 5. right M1 / 2 (V 12399.1), 6. right M3 (V 12399.4)

7~13. *Y. yunnanensis* sp. nov., 7. right dp4 (V 12395.6), 8. right p4 (V 12395.7), 9. left m1 / 2 (V 12395.8), 10. left m1 / 2 (V 12397.2), 11. right m3 (V 12395.12), 12. left M1 / 2 (holotype, V 12396.1), 13. right M3 (V 12395.5)





