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Original article

Aeretes melanopterus (Pteromyinae, Rodentia) from Tianyuan Cave near Zhoukoudian (Choukoutien) in China

Aeretes melanopterus (Pteromyinae, Rodentia) de la grotte de Tianyuan près de Zhoukoudian (Choukoutien) en Chine

Haowen Tong

Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing 100044, China

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Abstract

The materials of *Aeretes melanopterus* from the Tianyuan Cave, a Late Pleistocene site with human fossils recovered recently near Zhoukoudian, are the richest of this species ever reported in North China. *Aeretes melanopterus* is an endemic species of China, its relationship with *Petaurista* and *Trogopterus* is still controversal. Studies based on the dental characters show that *Aeretes melanopterus* resembles *Petaurista* more closely than *Trogopterus*. The earliest fossil record of *Aeretes melanopterus* was found in South China in Middle Pleistocene deposits. The earliest records in the Beijing area are from Upper Cave and Tianyuan Cave at Zhoukoudian are of late-Late Pleistocene age, around 30 kyrs BP. The geographical distributions of this species are very limited. In evolution, *Aeretes melanopterus* experienced both the increase and the decrease in tooth size; but its crown height of cheek teeth was continuously increasing.
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Résumé

Le matériel de *Aeretes melanopterus* de la Grotte Tianyuan, gisement situé près de Zhoukoudian, associé à des fossiles humains du Pléistocène supérieur, est le plus riche jamais trouvé dans le nord de la Chine. *Aeretes melanopterus* est une espèce endémique de Chine, sa relation avec *Trogopterus* est controversée. Les études sur les caractères dentaires démontrent que *Aeretes melanopterus* ressemble plus à *Petaurista* que *Trogopterus*. En Chine du sud, le plus ancien fossile de *Aeretes melanopterus* est d'âge Pléistocène moyen, alors qu'en Chine du nord, il est daté de 30 000 BP environ, dans les gisements de la grotte Tianyuan et la grotte supérieure de Zhoukoudian. La distribution de *Aeretes melanopterus* est très limitée. Au cours de son évolution, *Aeretes melanopterus* connaît une augmentation puis une diminution de la taille des dents, mais le développement de l'hypsodontie est continuel.
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Keywords: *Aeretes melanopterus*; Dental characters; Tianyuan Cave; Zhoukoudian area; Late Pleistocene

Mots clés : *Aeretes melanopterus* ; Caractères dentaires ; Grotte Tianyuan ; Région de Zhoukoudian ; Pléistocène supérieur

1. Introduction

The living *Aeretes melanopterus* is a monotypic genus and species (Thorington et al., 2002) with limited and fragmented distribution in China only, both its fossil and living records are rare. It was established by Milne-Edwards in 1867. More than one century has passed since then, but the knowledge about this species is still limited, and many characters of this species remain unknown. Concerning the relationships with *Trogopterus* and *Petaurista*, it's still controversial. Thorington et al. (2002) grouped *Aeretes* and *Petaurista* together as sister group. Mercer and Roth (2003) held the opposite opinion, they thought *Aeretes* resembles *Trogopterus* more closely than does *Petaurista*. The material from the Tianyuan Cave provides more details, especially on the teeth, and evidence for the understanding of this mystery species in morphological features and phylogenetic relationships with other genus and species. The Tianyuan Cave,

E-mail address: tonghaowen@ivpp.ac.cn.

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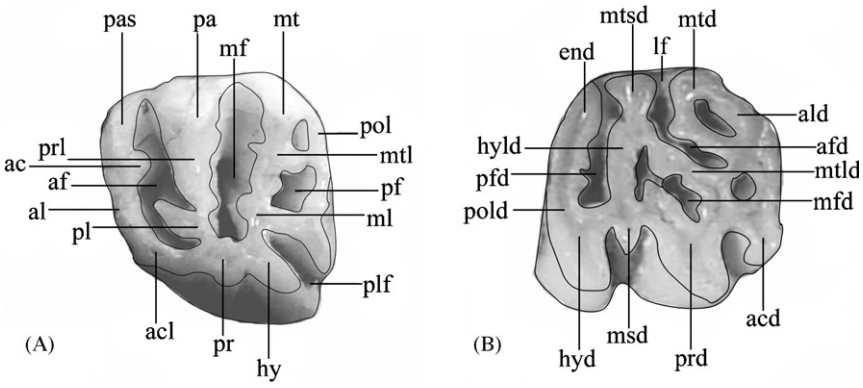

Fig. 1. Dental terminology of *Aeretes melanopterus*. **A**. Left upper M^1; **B**. Right lower M_1. Occlusal view. Abbreviations: see Table 1.
Fig. 1. Terminologie dentaire pour *Aeretes melanopterus*. **A**. M^1 supérieure gauche ; **B**. M_1 inferieure droite. Vue occlusale. Abréviation : voir le Tableau 1.

located about 6 km southwest of the Peking Man Site at Zhoukoudian, is a Late Pleistocene locality bearing *Homo sapiens* fossils (Tong et al., 2004). Not the best, but the richest materials of *Aeretes melanopterus* were recovered there.

Although some researchers once proposed that the tree squirrels and flying squirrels share many similar dental characters, and identifying fossil squirrels solely on dental characteristics is insufficient (Lindsay et al., 2000), this study shows that the dental characters also can be reliable traits in taxonomic identification when the skull and other skeletons are unavailable.

2. Methods and terminology

The dental terminology used in this paper is mainly adapted from James (1963) and Thenius (1989), additionally other author's works were also cited, such as Allen (1940), Mein (1970) and Cuenca Bescós (1988) (Fig. 1 and Table 1).

Measurements: Methods for tooth measuring follow Cuenca Bescós (1988) and Reumer and van den Hoek Ostende (2003), and the upper cheek tooth width was taken at the basal part of each tooth, where the width is the maximum (see Tables 2 and 3).

Institution abbreviations: IVPP, Institute of Vertebrate Paleontology and Paleoanthropology; IOZ, Institute of Zoology (Beijing).

3. Systematic paleontology

Order RODENTIA Bowdich, 1821
Family SCIURIDAE Hemprich, 1820
Subfamily PTEROMYINAE (Brandt, 1855)
Genus ***Aeretes*** (= *Aëretes*) Allen, 1938

Generic diagnosis (emended): Rostrum relatively short and broad; the postorbital processes of both the frontal and the jugal are very large; upper incisors wide and with one longitudinal

Table 1
Terms of dental morphology used in this paper with notes on the equivalents by different authors
Tableau 1
Terminologie dentaire adoptée dans cet article avec les termes équivalents utilisés par d'autres auteurs

Terms used in this paper		Equivalents	Terms used in this paper		Equivalents
Abbrev	Terms		Abbrev	Terms	
ac	anterocone		al	anteroloph	anterior cingulum (James, 1963)
acl	anteroconule		mtl	metaloph	posterior transverse ridge (Allen, 1940)
hy	hypocone		pol	posteroloph	posterior cingulum (James, 1963)
mt	metacone		prl	protoloph	anterior transverse ridge (Allen, 1940)
ml	metaconule		ald	anterolophid	protolophid (James, 1963)
pa	paracone		hyld	hypolophid	
pas	parastyle		mtld	metalophid	
pr	protocone		pold	posterolophid	
pl	protoconule		af	anterofossette	anterior valley (James, 1963)
acd	anteroconulid		mf	medifossette	central valley (James, 1963)
hyd	hypoconid		pf	posterofossette	posterior valley (James, 1963)
end	entoconid		plf	Posterolingual flexus	
msd	mesoconid		afd	anterofossettid	trigonid or anterior valley (James, 1963)
mtd	metaconid	parametaconid (James, 1963)	lf	lingual-flexid	
mld	metaconulid		mfd	medifossettid	
mtsd	metastylid		pfd	posterofossettid	
pad	paraconid				
pasd	parastylid				
prd	protoconid				

Table 2
Dimensions of maxilla and mandible of *Aeretes melanopterus* from Tianyuan Cave, compared with living form (in mm)
Tableau 2
Dimensions des maxillaire et mandibule de *Aeretes melanopterus* de la Grotte Tianyuan, comparée avec l'espèce actuelle (en mm)

Dimensions	*Aeretes melanopterus* Tianyuan Cave				*Aeretes melanopterus szechuanensis* Living form from Sichuan, southwest China			
	Min.	Max.	Mean	Sample number	Min.	Max.	Mean	Sample number
Length of rostrum, infraorb. fm. to ant. end premax			12.5	1	14.6	16.7	15.65	
Width of the zygomatic plate[a]			7.3	1	–	–	–	
Length of the incisive foramen			5.8	1	5.2	5.4	5.3	2
Width of palate between M^1s			7.4	1	6.4	7.2	6.8	2
Width of palate between M^3s			8.7	1	7.6	8.2	7.9	2
Length of upper diastema			18.7	1	12.2	13.2	12.7	2
Upper cheek tooth row length	15.1	17.6	16.57	6	14	14.3	14.15	2
Lower cheek tooth row length	16.8	17.6	17	4	14.7	14.8	14.75	2
Total length of mandible			47.1	1	42.9	45	43.95	2
Length of lower diastema	7.8	7.8	7.8	3	6.8	7.4	7.1	2
Depth of mandible below M_1	12	12	12	4	11.5	11.5	11.5	2
Depth of mandible below M_3	11	11.5	11.3	3	10.4	10.8	10.6	2
Breadth of zygomatic plate			7.2	1	–	–	–	–

[a] Distance between the infraorbital foramen and the posterior edge of the inferior zygomatic root

groove on the labial face; P^3 is atrophy; M^3 is strikingly smaller than other molars. "This flying squirrel differs notably in the characters of the upper incisors from any known species, and merits generic distinction and the excess in length of the nasals over the premaxillaries is unusual" (Allen, 1940) Temporal ridge prominent; infraorbital foramen is very small; jugal process is very large.

Aeretes melanopterus (Milne-Edwards, 1867)

1867. *Pteromys melanopterus* - Milne-Edwards, pp. 375.

1868-1874. *Pteromys melanopterus* Milne-Edwards, plate 15.

1927. *Petaurista sulcatus* - Howell, p. 46.

1940. *Aëretes melanopterus* - Allen, part 2, pp. 745–748.

1940. *Petaurista sulcatus* Howell - Pei, pp. 38–41.

1966. *Aeretes melanopterus szechuanensis* - Wang et al., pp. 87–91.

1993. *Aëretes melanopterus* (Edwards) - Zheng, pp. 53–54.

2002. *Aeretes melanopterus melanopterus* - Chen et al., pp. 176–178.

Species diagnosis (emended): Teeth with slightly rugose enamel. Cheek teeth subhypsodont, and relatively higher-crowned than in other genera and species in this family. On

Table 3
Dimensions of isolated teeth and those attached on the tooth bones (in mm)
Tableau 3
Dimensions de dents isolées et de dents attachées aux mâchoires (en mm)

Measurements		Number	Mean	Range	Standard deviation	Coefficient variation
I^1	Anteropost diam.	9	3.1	2.7–3.2	0.158	5.1
	Transverse diam.	10	3.3	3.0–3.5	0.16	4.9
P^3	Anteropost. diam.	4	1.55	1.48–1.62	0.058	3.7
	Transverse diam.	4	1.72	1.56–1.94	0.178	10.35
P^4	Anteropost. diam.	6	4.44	4.2–4.68	0.152	3.4
	Transverse diam.	6	5.42	5.12–5.78	0.260	4.8
M^1	Anteropost. diam.	7	4.04	3.9–4.3	0.122	3.0
	Transverse diam.	7	5.0	4.7–5.7	0.346	6.9
M^2	Anteropost. diam.	5	3.88	3.62–4.14	0.186	4.8
	Transverse diam.	5	4.67	4.36–5.14	0.381	8.2
M^3	Anteropost. diam	4	3.64	3.36–3.9	0.287	7.9
	Transverse diam.	4	3.74	3.6–3.82	0.115	3.1
I_1	Anteropost.diam.	7	3.9	3.5–4.4	0.315	8.1
	Transverse diam.	7	3.1	3.0–3.3	0.146	4.7
P_4	Anteropost. diam	7	4.48	4.22–4.7	0.176	3.9
	Transverse diam.	7	4.12	3.9–4.36	0.168	4.1
M_1	Anteropost. diam.	7	4.14	3.7–4.5	0.326	7.9
	Transverse diam.	7	4.4	4.04–4.68	0.227	5.2
M_2	Anteropost. diam.	6	4.23	3.74–4.45	0.252	6.0
	Transverse diam.	6	4.62	4.28–4.9	0.226	4.9
M_3	Anteropost. diam	5	4.72	4.24–5.1	0.348	7.4
	Transverse diam.	5	4.36	4.08–4.8	0.327	7.5

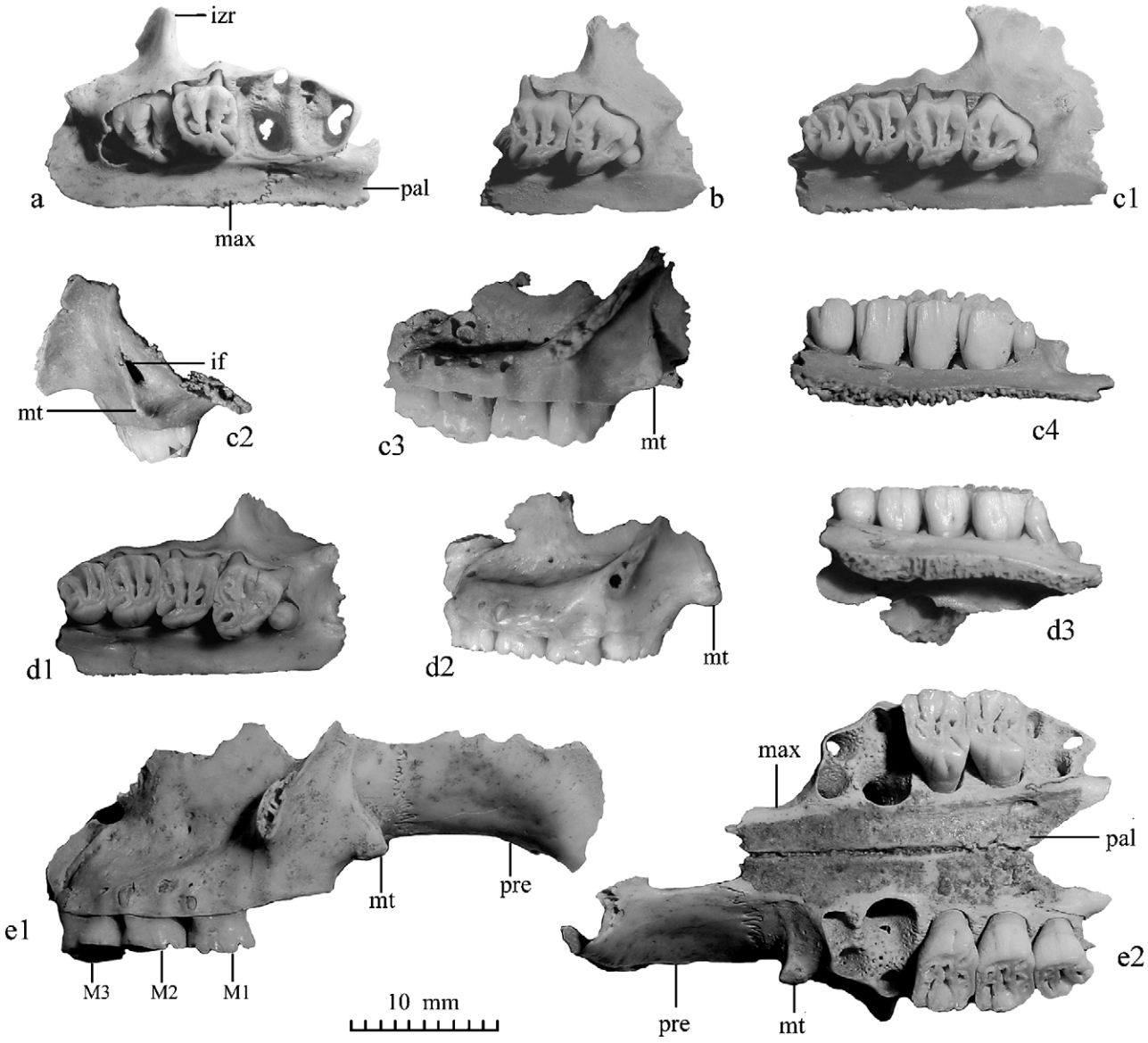

Fig. 2. The fragmented maxillae of *Aeretes melanopterus*. **a**, left maxilla (V 14596.5); **b**, right maxilla (V 14596.2); **c**, right maxilla (V 14596.6); **d**, right maxilla (V 14596.4); **e**, maxilla (V 14596.1). Abbreviations: If = infraorbital foramen; izr = inferior zygomatic root; max = maxilla; mt = masseteric tubercle; pal = palatine; pre = premaxilla (terminology after Voss, 1988).

Fig. 2. Fragments de maxillaire de *Aeretes melanopterus*. **a**, maxillaire gauche (V 14596.5) ; **b**, maxillaire droit (V 14596.2) ; **c**, maxillaire droit (V 14596.6) ; **d**, maxillaire droit (V 14596.4) ; **e**, maxillaire (V 14596.1). Abréviation : If = trou sous-orbitaire ; izr = apophyse zygomatique du maxillaire ; max = maxillaire ; mt = tubercule masséter ; pal = palatin ; pre = intermaxillaire (terminologie d'après Voss, 1988).

upper cheek teeth, the lingual wall is higher than the buccal wall; with well-developed cuspules and lophules; postrolingual flexus is very narrow and deep; the fossettes or valleys in the upper molars are very deep and enclosed on both lingual and buccal sides; the anterior and posterior cingula are very developed and as high as the major transverse ridges.

Material: Broken maxillae (V 14596.1–6); broken mandibles (V 14596.7–12); upper incisors (V 14596.13–22); lower incisors (V 14596.23–24); isolated teeth (V 14596.25–27).

Compared material: IOZ 23272; IOZ 23580.

Locality and horizons: Tianyuan Cave, Zhoukoudian area in the far suburb of Beijing. Late Pleistocene to Holocene.

Premaxilla: On the specimen, only part of one side of the premaxilla was preserved, it shows that the length of the incisive foramen is quite great, but the exact width is not sure. Ventrally the premaxilla-maxilla suture intersects the midline of the palate at the rear edge of the incisive foramens.

Maxilla: Masseteric tubercle is moderate in size, and is situated ventro-laterally to the infraorbital foramen, but not directly ventral to the foramen. The infraorbital foramen is subovate in form, and is very small. The only complete maxilla shows that palate bridge is broad, but it's possible that the specimen was distorted to some extent. Width of palate at M^1 is 7.4 mm. The palatal bridge is very flat, without ridges. The anterior limit of the palatine-maxilla suture is level with the center of M^2. The posterior palatine foramens are within the hard palate, but at the lateral part, it situated exactly on the palatine-maxilla suture. The posterior margin of the hard palate

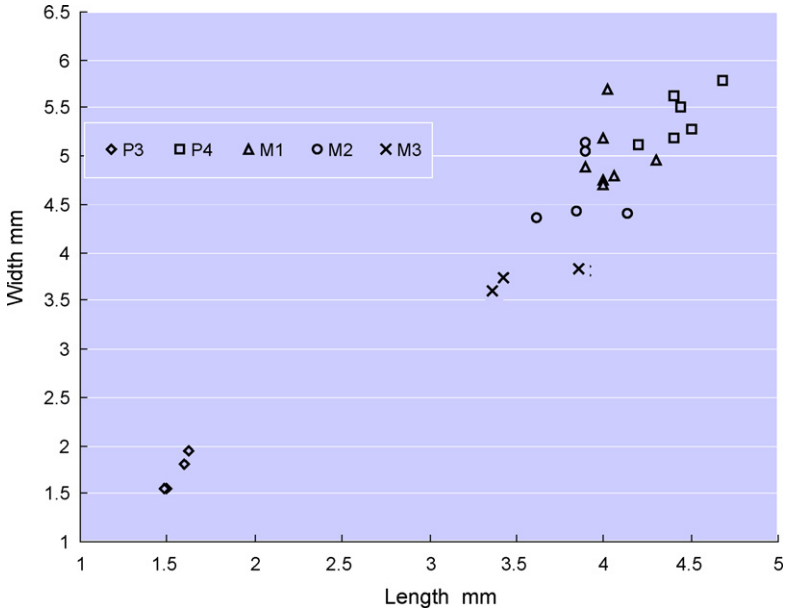

Fig. 3. *Aeretes melanopterus*, scatter graph of length and width of upper cheek teeth (in mm).
Fig. 3. *Aeretes melanopterus*, diagramme de dispersion des longueur et largeur de dents jugales (en mm).

(the anterior limit of the mesopterygoid fossa) is broken, so the form of the rear edge of the palatine is not sure. From the lateral view, no zygomatic notch is observed (Figs. 2 and 3; Table 2).

Mandible: In general, the mandible is short. There is a constriction between the mandibular body and the ascending ramus. The coronoid process is curved in falciform, and tapering. The sigmoid notch between the coronoid and condyloid process is deep. The condyloid process is slender, and the condylar neck is very narrow. The articular surface of condyle is sub-rounded in outline, which is different from the typical rodents in the long-axis orientation of non antero-posterior direction. There is no complete angular process preserved, but the partial angular processes show that it lies approximately in the same plane as the condyloid process. The mental foramen is not stable, in some individuals, only one, in other mandible, there are two small foramens. They are situated approximately at mid-depth of the mandible just anterior to P_4 or slightly away from the level of P_4. Both the masseteric fossa

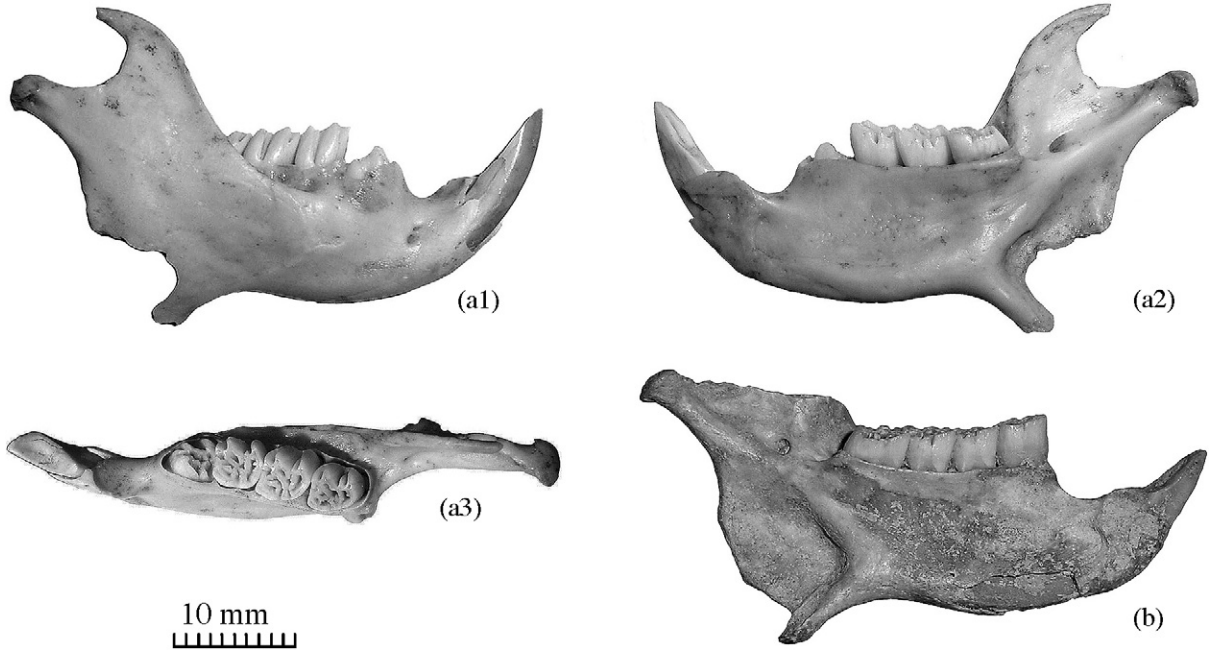

Fig. 4. Mandibles of *Aeretes melanopterus*. **a**, right mandible (V 14596.8); **b**, left mandible (V 14596.7). **a1**, buccal view; **a2, b**, lingual views; **a3**, crown view.
Fig. 4. Mandibules de *Aeretes melanopterus*. **a**, mandibule droite (V 14596.8) ; **b**, mandibule gauche (V 14596.7). **a1**, vue buccale ; **a2, b**, vue linguale ; **a3**, vue occlusale.

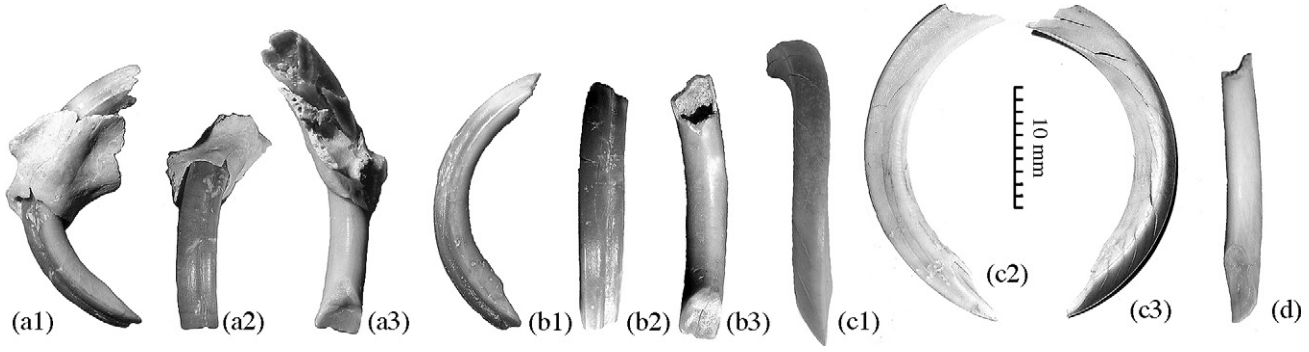

Fig. 5. Upper (**a, b**) and lower (**c, d**) incisors of *Aeretes melanopterus*. **a**, (V 14596.13); **b**, (V 14596.18); **c**, (V 14596.24); **d** (V 14596.23); **a1, b1, c3**, lateral view; **a2, b2, c1**, labial view; **a3, b3, d**, lingual view; **c2**, mesial view.
Fig. 5. Incisives supérieures (**a, b**) et inférieures (**c, d**) de *Aeretes melanopterus*. **a**, (V 14596.13) ; **b**, (V 14596.18) ; **c**, (V 14596.24) ; **d** (V 14596.23) ; **a1, b1, c3**, vue latérale ; **a2, b2, c1**, vue labiale ; **a3, b3, d**, vue linguale ; **c2**, vue mésiale.

and the masseteric ridge are not remarkable; the masseteric fossa of the mandible terminates anteriorly beneath M_1 (Fig. 4; Table 2).

On the lingual side, the inferior pterygoid depression is very deep. There is a ridge separating the superior pterygoid depression from the inferior pterygoid depression. The mandibular foramen is round, and is just above the ridge and at the same level as the margin of the alveolus.

Dental formula: 1.0.2.3/1.0.1.3. = 22. The sequence of cheek teeth eruption is as follows: DP^4, M^1, M^2, M^3, P^4.

Upper incisor: Broader than in any member of *Petaurista* or *Trogopterus*, and with a conspicuous groove on the labial surface, the groove running longitudinally along the outer one-third of the width. The color of the labial surface is changing from light yellow to dark brown with ageing. It has a larger width than length (Fig. 5).

Cheek teeth: This genus and species is higher-crowned than any species in this family. P^3 is the most special one among the upper cheek teeth. P^4 is almost completely molariform, but the anteroloph still doesn't connect with the protocone yet. From P^4 to M^3, the lingual length is increasing, but the reentrant at the antero-internal corner and the groove at about the middle of the lingual side are getting faint. Four transverse ridges are isolated by three depressions or deep valleys. All the upper cheek teeth have very narrow and deep valleys, lacking mesostyle, the lingual wall is much higher than the buccal one, and the transverse diameter is increasing with wearing (Fig. 6). P^3 is single rooted, from P^4 to M^3, each tooth has three roots, one of them on the lingual side, two of them on the buccal side; but the roots on the buccal side are diminished very much (Fig. 7).

P^3 is very small in size and obsolete, peg-like; much lower than other cheek teeth (Fig. 3; Table 3); partially visible in lateral view. The transverse diameter of P^3 has the highest values of coefficient variation among all the teeth.

P^4 is a little larger than M^1; molariform, but triangular in outline, longer buccally than lingually; paracone, metacone, hypocone, protoconule and metaconule are developed, but protocone is small; protocone and hypocone close together. With two conspicuous reentrants, one at the postero-internal corner and the other at the antero-internal corner. Additionally, there exists a remarkable groove at about the middle of the lingual side between protocone and hypocone. The posteroloph, metaloph

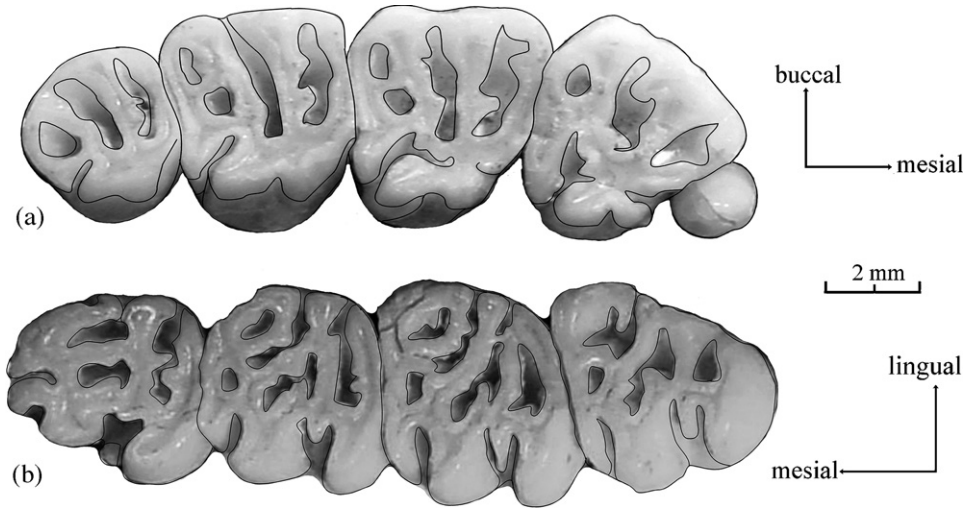

Fig. 6. Upper and lower dentitions of *Aeretes melanopterus*. **a**, right upper dentition (V 14596.3); **b**, right lower dentition (vertically flipped) (V 14596.11). In occlusal view.
Fig. 6. Dentitions de *Aeretes melanopterus*. **a**, dentition supérieure droite (V 14596.3) ; **b**, dentition inférieure droite (inversée) (V 14596.11). Vue occlusale.

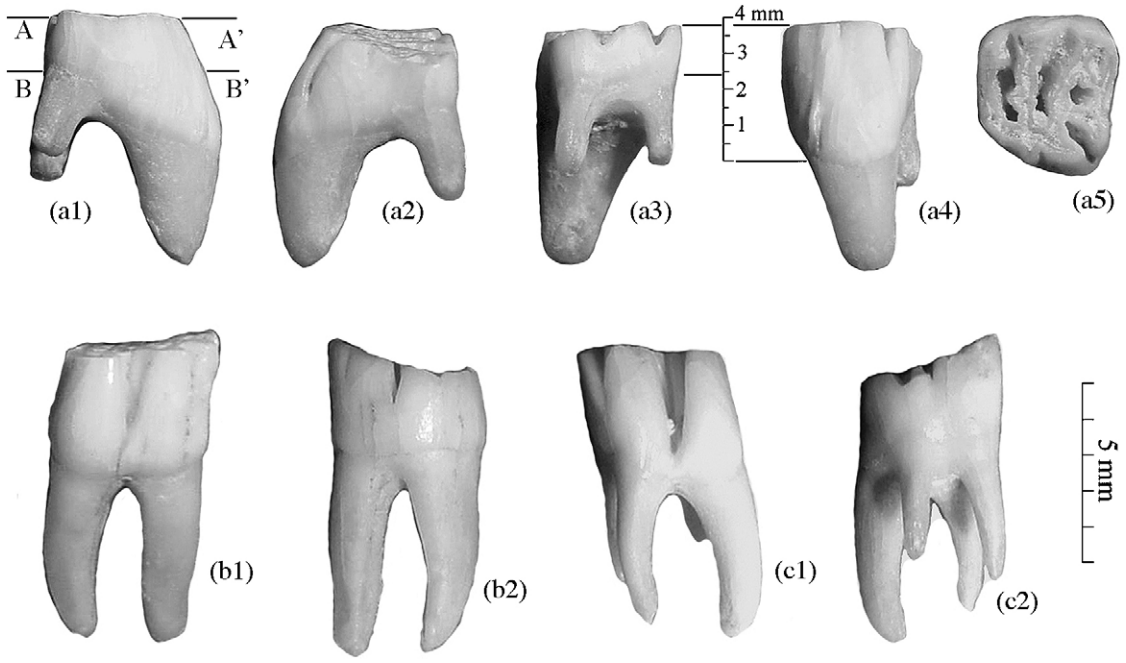

Fig. 7. Upper and lower cheek teeth. **a**, upper M^2 (V 14596.25). **a1**, anterior view; **a2**, posterior view; **a3**, buccal view; **a4**, lingual view; **a5**, occlusal view. **b**, right P_4 (V 14596.26); **b1**, buccal view; **b2**, lingual view. **c**, left M_1 (V 14596.27); **c1**, buccal view; **c2**, lingual view. The transverse diameter is increasing with wearing, BB' is larger than AA' in a1.

Fig. 7. Dents jugales supérieures et inférieures. **a**, M^2 (V 14596.25). **a1**, vue antérieure ; **a2**, vue distale ; **a3**, vue buccale ; **a4**, vue linguale ; **a5**, vue occlusale. **b**, P_4 droite (V 14596.26) ; **b1**, vue buccale ; **b2**, vue linguale. **c**, M_1 gauche (V 14596.27) ; **c1**, vue buccale ; **c2**, vue linguale. Le diamètre transversal augmente avec l'usure, BB' est plus large que AA' en a1.

and protoloph are developed, but the anteroloph is weak, and not connected with the protocone; anteroloph, protoloph and metaloph meet at protoconule. The accessory loph or lophule arising from protocone is diminished. The postero-lingual flexus or postero-internal reentrant extends very deep. Both the anterofossette and the posterofossette are small.

M^1 is almost the same size as M^2. The crown structure is similar to P^4, but different in the following aspects: protocone is more developed, the lophule from metaconule is developed; the anteroloph connects with hypocone, and the reentrant at the antero-internal corner is almost disappeared. The metaloph doesn't connect with the hypocone in the early stage of wear. Length has the lowest value of coefficient variation among all the teeth.

M^2 resembles M^1 very much, but differs in the following aspects: More quadrate, the reentrant at the antero-internal corner is disappeared; the groove at about the middle of the lingual side is faint; metaloph connects with hypocone.

M^3 resembles other molars in general pattern, but is much smaller in size, and looks more rounded in outline; the groove at the middle of the lingual side is almost disappeared.

Mandibles: The mandible is relatively deeper below the molars than in other genera.

Lower incisor: Labio-lingual dimension (= anteroposterior diameter) is larger than the mesio-distal dimension (= transverse diameter); sub-triangular in cross section; the mesial surface is flat; the tip is sharp. The incisor is hollow except the tip part (Fig. 5). The lower incisor goes through the whole mandibular body and just stops underneath M_3; and it makes the mandibular canal very narrow. The lower incisors are of the same color as their upper counterparts.

Lower cheek teeth: The crown structure of the lower cheek teeth is more complicated than that of the upper ones, the transverse ridges are not so regular as in the upper dentition. There is a deep notch on the anterior-external corner and a shallow one on the front edge of each tooth near the middle. The ectolophid is divided by two deep grooves into three perpendicular pillarlike conids: protoconid, mesoconid and hypoconid, it makes the ectolophid look like a deep W-shaped indentation in crown view. The buccal wall is much higher than the lingual wall of the crown. Because of the diminishment of the mesoconid, the W-shaped indentation is not so typical as in *Petaurista*. On the lingual surface, a prominent metastylid is delineated anteriorly and posteriorly by shallow grooves. All of the lower cheek teeth share all these characters mentioned above, but they are different in their outline in crown view. In the lower dentition, P_4 has three roots, two of them on the buccal side, one of them on the lingual side. Sometimes the root on the lingual side is obsolete; from M_1 to M_3, each tooth has four roots, two on the buccal side, other two on the lingual side.

P_4: The anterior part is narrow, with the strongest metastylid and hypoconid. The buccal groove is the broadest among all the lower teeth, and at the entrance of the buccal groove, there is a small tubercle.

M_1: More quadrate in form.

M_2: Rhombus in crown view. Metalophid is well developed.

M_3: Sub-triangular in form. Hypoconid is very developed.

4. Comparisons

4.1. Comparison with Petaurista petaurista (Pallas, 1766) (see Appendix A)

The skull has a well-marked interorbital depression. The most striking difference between *Aeretes* and *Petaurista* is the upper incisor, the upper incisors of the latter lack the longitudinal (or vertical) groove on the labial side; P^3 is more developed; molars sub-equal; without mesostyle; cheek teeth more lower crowned but with thicker enamel layer; enamel has strong wrinkles than that of *Aeretes*; posterolingual flexus is not so narrow and deep as in *Aeretes*; cheek tooth crown structure is more simple; P_4 is prominently smaller than other lower cheek teeth. The upper cheek teeth have lower length/width ratio than *Aeretes* does. The valleys or fossettes are more shallow and open to the buccal side; metastyle is undeveloped; parastyle, paracone, metacone and metastyle are not jointed to each other as in *Aeretes*. In the upper cheek teeth, the posteroloph is not prominent (Fig. 8).

The first upper premolar is small and peg-like. P^4 is molariform and of about the same size as the two succeeding molars in crown area, but the last upper molar is distinctively the smallest of the upper cheek teeth. Each upper molariform teeth has two main transverse enamel ridges, and each of these teeth has two conspicuous reentrant angles, one at the postero-internal corner of the tooth and one near the middle of the posterior border. The former is the deeper, and is clearly visible, even in much worn teeth, while the latter of less vertical extent. Each of the upper molars has a small enamel fold projecting forward from the inner part of the anterior transverse ridge, but it's sometimes lacking in M^3. Sometimes the two anterior molars also have a very shallow vertical groove at about the middle of the lingual side.

The first lower tooth (P_4) is the smallest of the lower cheek teeth, three molars are sub-equal. In the lower molars these reentrants are reversed and there is a deep notch on the antero-external corner and a shallower one on the front edge of each tooth near the middle. Laterally there is a deep W-shaped indentation in the middle of each of the large teeth (Allen, 1940).

Allen grouped *Aeretes* with *Petaurista*. "*Petaurista fulvinus* of Kashmir shows in some specimens evidence of faint grooves on the upper incisors" (Allen, 1940).

Thorington et al. (2002) thought *Aeretes* resembles *Petaurista* more closely than *Trogopterus*. Among the 58 detected characters in *Aeretes*, 50 of which is common with that of *Petaurista*. But the most important character was not mentioned in Thorington et al's paper that is the presence of a groove on the outer surface of the upper incisors of *Aeretes*.

The upper cheek teeth have lower length to width ratio than *Aeretes* does. The valleys or fossettes are more shallow and open to the buccal side; metastyle is undeveloped; parastyle, paracone, metacone and metastyle are not jointed to each other as in *Aeretes*.

4.2. Comparison with Trogopterus xanthipes Milne-Edwards, 1867 (see Appendix A)

Allen (1940) once described *Trogopterus xanthipes* as follows: "The teeth are notable for the enlargement of the posterior upper premolar (pm4) which exceeds in crown area any of the succeeding molar teeth which are themselves nearly sub-equal. The enamel pattern in all these teeth is somewhat complex and irregular, very soon wearing down into a complicated system of enamel islands and infolds. Each of the upper molars has a shallow vertical infold in the middle of the inner face, shallowest in the last molar, and in one specimen not apparent in that tooth. In the middle of the posterior edge of M^1 and M^2, and nearer the postero-internal corner of M^3, is a much deeper reentrant which ends anteriorly in a double lobe."

Ellerman (1940) outlined the characters of this species like this: teeth large and heavy; pattern complex in the extreme; cheek teeth semi-hypsodont. Mandible with angular portion rather sharply pulled inwards; coronoid high, recurved.

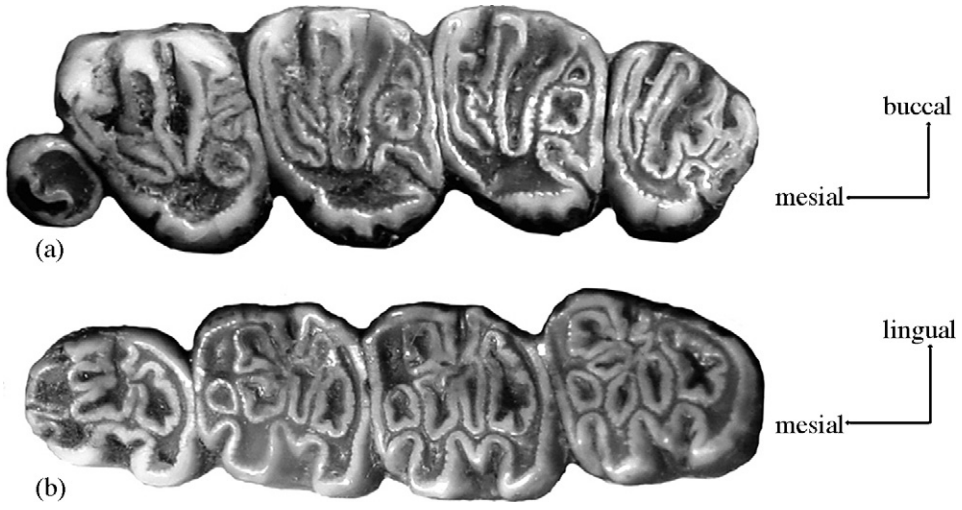

Fig. 8. Upper and lower dentitions of *Petaurista petaurista* (IOZ 24010). **a**, left upper dentition; **b**, left lower dentition. In occlusal view.
Fig. 8. Dentitions supérieure et inférieure de *Petaurista petaurista* (IOZ 24010). **a**, dentition supérieure gauche ; **b**, dentition inférieure gauche. Vue occlusale.

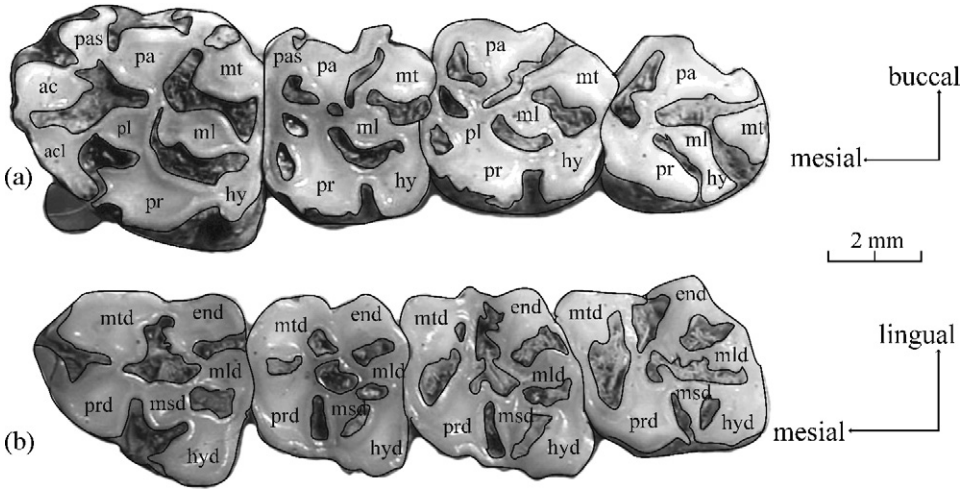

Fig. 9. Tooth rows of *Trogopterus xanthipes*, extant (OV 1296). **a**, left upper tooth row, occlusal view. **b**, left lower tooth row, occlusal view. Abbreviations: see Table 1.
Fig. 9. Dentitions de *Trogopterus xanthipes*, actuel (OV 1296). **a**, dentition supérieure gauche, vue occlusale. **b**, dentition inférieure gauche, vue occlusale. Abréviations : voir Tableau 1.

Based on the observation by the present author, some important differences in skull and dental characters can be summarized as follows: *Trogopterus xanthipes* with very open distal half of the orbit, and the jugal process is very faint; the masseteric tubercle is very developed; and the postorbital process small; the ascending ramus of the mandible is more upright; with larger infraorbital foramen. The upper incisor is narrow and lacking groove. The upper cheek teeth are rhombus shaped in outline and more complicated in crown structure like labyrinth; cheek teeth with developed cusps and intermediate conules, but the lophs and lophids are faint; the transverse ridges or cross lophs are not obvious (Fig. 9). P^3 very minute and not easily detectable; very large P^4 relative to molars, with developed anterocone and anteroconule.

In Thorington et al's paper of 2002, fifty-eight characters of *Aeretes* were taken into consideration in the phylogenetic analysis of flying squirrels (Pteromyinae), only eight of which differ from that of *Petaurista*, but twenty of them are different from that of *Trogopterus*. So it seems that *Aeretes* resembles *Petaurista* more closely than does *Trogopterus*; this paper gets the same conclusion based on the study of dental characters. On the contrary, Mercer and Roth (2003) thought *Aeretes* resembles *Trogopterus* more closely than does *Petaurista*.

Though *Aeretes melanopterus* and *Trogopterus xanthipes* are endemic species of China, the latter distributes more broadly than the former does.

4.3. Comparison with the living forms from Hebei Province near Beijing

The type locality of this species is located in the northeast to Beijing. But it's very difficult to get the living specimen nowadays. So the comparison is based only on the data published by Allen (1940), and the data of another subspecies from Sichuan Province. Through the tooth-row length comparison, it seems that the samples from Tianyuan Cave are much larger in dental size than the living forms.

4.4. Comparison with the fossil forms ever found

Up to now, only few fossil species of *Aeretes* were reported: *Aeretes premelanopterus* Zheng, 1993 and *Aeretes grandidens* Zheng, 1993; both of them from the Early Pleistocene cave deposits in Wushan, Chongqing; *Aeretes* sp. from Luonan, Shaanxi (Xue et al., 1999). The latter has only one M^1, and its tooth's dimension (length × width) is 3.28 × 3.44, which is much smaller than the Tianyuan Cave materials. Most of the dimensions of the two fossil species fall into the ranges of the Tianyuan Cave materials, except few exclusions, some measurements of *Aeretes premelanopterus* are relatively smaller; some dimensions of *Aeretes grandidens* are a little larger, such as P^4. All these species mentioned above have much broader posterolingual flexus and weaker transverse ridges than the living species.

The earliest record of the living species *Aeretes melanopterus* is of Middle Pleistocene age (Zheng, 1993), and the early representatives are markedly smaller than the Tianyuan Cave materials. Among all the measurements of the teeth of the Middle Pleistocene form, only the length of p4, m1 and m2 are longer than their counterparts in the Late Pleistocene forms, and the length of the lower diastema is also shorter.

Upper cave and Tianyuan Cave, the only two Late Pleistocene localities of this species were found in Zhoukoudian area near Beijing. All the fossil forms are similar in size, especially the dimensions are very close for the materials from these two sites, but they are obviously larger than the living forms.

The cheek tooth-row length from Tianyuan Cave is the largest, the living form is the smallest, and the materials from Upper Cave stand between them. It corresponds very well with their geological age. It shows that the body size of *Aeretes melanopterus* is decreasing since Late Pleistocene in Beijing area (Table 4). It's often the case for the mammals of Late Pleistocene have larger body size than their recent representatives (Tong et al., 2004).

Table 4
Tooth-row length comparison between the fossil and living forms of *Aeretes melanopterus* from Beijing area
Tableau 4
Longueur de la dentition de *Aeretes melanopterus* de la région de Pékin. Comparaison entre le fossile et l'actuel

	Aeretes melanopterus Tianyuan Cave	*Aeretes melanopterus* Upper Cave in Zhoukoudian (Pei, 1940)	*Aeretes melanopterus* Living form Allen (1940).	*Aeretes melanopterus szechuanensis*
Chronology	Since 39430 yrs (Tong et al., 2006)	Since 34000 yrs (Chen et al., 1992)	Recent	Recent
P^3–M^3 length	15.1–17.6 (16.57[a])	15.9–16.3[b] (16.1)	12.8–14.4 (13.77)	14–14.3
P_4–M_3 length	16.8–17.6 (17)	16.1–17.45 (16.56)	13.8–14.3 (14.07)	14.7–14.8

[a] Mean
[b] Measured and calculated after the drawings by Pei (1940).

5. Discussions

5.1. Phylogenetic position

Though *Aeretes* is regarded as a monotypic genus (Thorington et al., 2002), it still shares some characters in common with *Petaurista* that is the closest relative of *Aeretes*. If we take the fossil forms into consideration, *Aeretes* is not a real monotypic genus, because other species other than the type species were also established under this genus, such as *Aeretes premelanopterus* Zheng, 1993 and *Aeretes grandidens* Zheng, 1993. The two latter species were erected based only on teeth materials.

5.2. Grooved upper incisor

"Apparently A.B. Howell (1927) was the first to call particular attention to the grooving of the upper incisors in this flying squirrel" Allen (1940). Concerning the broad and grooved incisors, it's really very special, but not unique even among the squirrel group, such as the species *Petaurista fulvinus* of Kashmir mentioned by Allen (1940) shows evidence of faint grooves on the upper incisors in some specimens. The grooved incisors also appear in some other species of other groups of rodents, such as *Heliosciurus* (only in rare individuals), *Syntheosciurus brochus* (Ellerman, 1940), *Cratogeomys castanops*, *Synaptomys cooperi* and species of *Reithrodontomys* with one groove on outer face of upper incisor; the species *Geomys bursarius* has two grooves on each upper incisor. Aside rodents, lagomorphs also have grooved upper incisors. So it's possible that all animals with grooved upper incisors are functional adaptation to some kind of special feeding habits, as proposed by Allen (1940). like this: "Its broad incisors and shortened rostrum may indicate different food habits from other related species."

5.3. Geological and geographical distribution

The earliest record of this genus is from Early Pleistocene, but not many fossil materials were found. The living species originated in Middle Pleistocene in southwest China (Zheng,

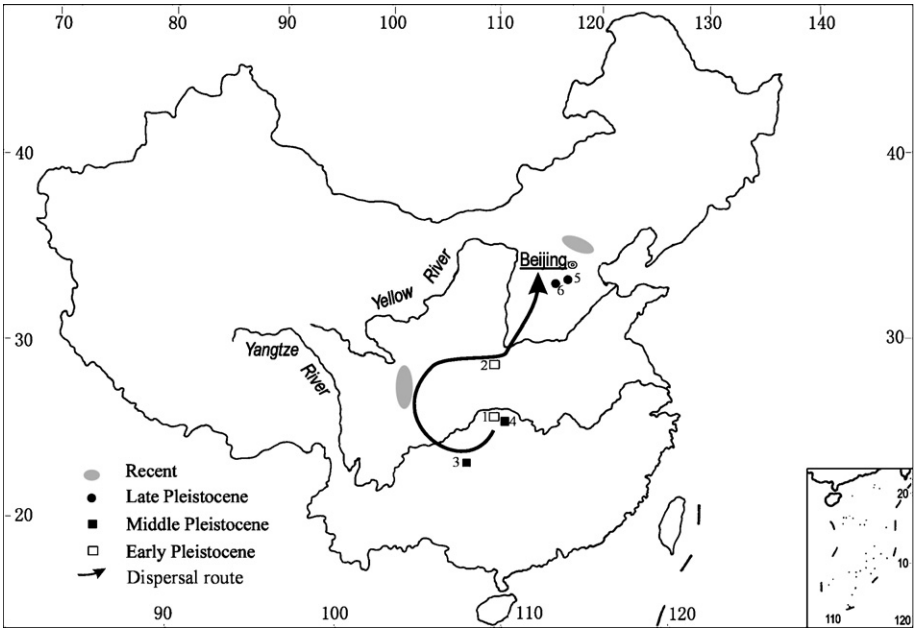

Fig. 10. The geographical distribution of *Aeretes*, both fossil and extant forms. **1**. Longgupo, Chongqing; **2**. Longyadong Cave, Shaanxi; **3**. Yanhui Cave, Guizhou; **4**. Baotansi Cave, Chongqing; **5**. Upper Cave, Zhoukoudian; **6**. Tianyuan Cave; near Zhoukoudian.
Fig. 10. Distribution géographique de *Aeretes*, fossile et actuel. **1**. Longgupo, Chongqing ; **2**. Grotte Longyadong, Shaanxi ; **3**. Grotte Yanhui, Guizhou ; **4**. Grotte Baotansi, Chongqing ; **5**. Grotte supérieure, Zhoukoudian ; **6**. Grotte Tianyuan à côté de Zhoukoudian.

Table 5
Geological distribution of *Aeretes* of both fossil and living forms in China
Tableau 5
Distribution géographique de *Aeretes*, fossile et actuel

Geologic time	*Aeretes melanopterus*	*Aeretes premelanopterus* Zheng, 1993	*Aeretes grandidens* Zheng, 1993	?*Aeretes* sp. Xue et al., 1999
Recent	Hebei, Beijing, Sichuan and Gansu			
Late Pleistocene	Upper Cave and Tianyuan Cave at Zhoukoudian			
Middle Pleistocene	Yanhui Cave in Guizhou, Baotansi Cave in Chongqing			
Early Pleistocene		Units A and B Longgupo in Chongqing	Units A and B Longgupo in Chongqing	Longyadong Cave in Shaanxi

1993), but the late Pleistocene fossil records are only limited to the Zhoukoudian area in North China (Fig. 10; Table 5). In southwest China, all the fossil localities are outside of the distribution of living species. In the later part of Late Pleistocene, *Aeretes melanopterus* dispersed to the north under the accompanying of other oriental mammals, such as *Arctonyx collaris*, *Paguma larvata* and *Capricornis* etc. (Tong et al., 2006). At Zhoukoudian area, the *Aeretes melanopterus* fossil only appears in two localities: Upper Cave and Tianyuan Cave, even though other localities are also very rich in rodent fossils. These two localities are not far from the living forms' distribution area. *Aeretes melanopterus* once coexisted with *Trogopterus xanthipes* in several localities of Middle Pleistocene, such as Yanhui Cave and Baotansi Cave (Zheng, 1993). They also coexist in some areas in Sichuan Province and in vicinity of Beijing nowadays (Chen et al., 2002; Wang and Wang, 1966; Wang and Hu, 1999) (Fig. 10).

6. Conclusion

Aeretes melanopterus can be distinguished from other flying squirrels by the grooved upper incisors, developed transverse ridges in upper molars and the subhypsodont cheek teeth with robust tooth roots. *Aeretes* resembles *Petaurista* more closely than does *Trogopterus* in dental characters. It differs from other genera and species mainly in dental characters. The earliest record of *Aeretes melanopterus* in North China is of later Late Pleistocene age, around 30 kyrs BP, it can be inferred that this species dispersed to North China very late. *Aeretes melanopterus* is a slowly evolved species since its origination in Middle Pleistocene, it has a very limited distribution for both fossil and living forms. In Beijing area, the body size of *Aeretes melanopterus* is decreasing with time since later Late Pleistocene.

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Appendix A

Major characteristics comparisons among *Aeretes*, *Petaurista* and *Trogopterus*

Characters	*Aeretes melanopterus*	*Petaurista petaurista*	*Trogopterus xanthipes*
Upper incisor	Broad and with a longitudinal groove	Narrow and ungrooved	Narrow and ungrooved
Color of incisor	Orange	Orange	Light yellow
P^3 in lateral view	Not hiding behind of P^4	Not hiding behind of P^4	Very diminished and hiding behind P^4
P^4	Slightly larger than M^1	Sub-equal in crown area to M^1 and M^2	Very large, exceeding M^1
M^3	Smaller than other molars	Is the smallest molar	Molars nearly sub-equal
P_4	Usually longer than M_1	The smallest lower cheek tooth	Much larger than molars
M_3	Triangular and slightly longer than other molars	Obviously larger than other molars	The same size as other molars
Transverse ridge on cheek teeth	Developed	Developed	Undeveloped
Occlusal pattern (crenulation)	Simple or with few lophules	Slightly rugose	Complex, excessively wrinkled (Ellerman, 1940)
Enamel layer thickness	Moderate	Thick	Thin
Mesostyle	Absent	Absent	Absent

Appendix A *(Continued)*

Posterointernal reentrant (postero-lingual flexus)	At the postero-internal corner	At the postero-internal corner	In the middle of the inner face
Enamel surface	Smooth	Smooth or slightly crenulated	Folds: lumpy appearance
Crown height	Subhypsodont	Semi-hypsodont (Ellerman, 1940)	Semi-hypsodont (Ellerman, 1940)
P^3–M^3 length	16.6	17.1 (Wang and Hu, 1999)	15.4 (IVPP 1048)
P_4–M_3 length	17	17 (Wang and Hu, 1999)	14.9 (IVPP 1048)
Upper diastema length	18.7	–	16.2 (IVPP 1048)
Lower diastema length	7.8	–	6.4 (IVPP 1048)
Rostrum	Unusually short and broad	Moderate	Moderate
Nasal length/occipito-nasal length	33.55% (measured from the drawing by Pei, 1940) 28.71% (measured from the drawing by Milne-Edwards, 1867)	34.13% (based on data by Huang et al., 1995)	33.46% (IVPP 1048)
Openness of distal half of the orbit	Somewhat open	Mostly open	Mostly open
Masseteric tubercle or knob	Moderate	Moderate	Very developed
Size and shape of postorbital process of frontal	Long	Stout, triangular	Undeveloped
Size of the postorbital process of jugal	Large	Prominent	Faint

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