Swiss J Palaeontol (2012) 131:107–126
DOI 10.1007/s13358-011-0038-z

Tachyoryctoides (Muroidea, Rodentia) fossils from Early Miocene of Lanzhou Basin, Gansu Province, China

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Received: 5 September 2011 / Accepted: 20 December 2011 / Published online: 12 January 2012

Abstract The *Tachyoryctoides* fossils found in the 1990s from the Early Miocene of Lanzhou Basin, China, are described as belonging to three species: *T. engesseri* sp. nov., *T. minor* sp. nov. and *T. kokonorensis*, in addition to some specimens that are indeterminate at the species level. The diagnosis of *Tachyoryctoides* has been reviewed based on all the known species. Detailed character analysis seems to support *Aralomys* as a junior synonym of *Tachyoryctoides*. The discovery of a number of *Tachyoryctoides* species in Lanzhou Basin indicates that *Tachyoryctoides* might have split into at least two groups even since the Late Oligocene. Judging by its cranial morphology and dental characters, *Tachyoryctoides* seems to stand rather apart from Rhizomyidae, Spalacidae and Cricetidae, a fact in favor of defending a separate family, Tachyoryctoididae, for *Tachyoryctoides* and the closely related genera, *Eumysodon* and *Ayakozomys.*

Keywords Tachyoryctoides · Miocene · Lanzhou Basin · China

Abbreviations

GL	Prefix of field locality number of Provincial Museum of Gansu
IVPP	Institute of Vertebrate Paleontology and Paleoanthropology of Chinese Academy of Sciences
IVPP V	Prefix of catalogue number of IVPP vertebrate fossils
PIN	Palaeontological Institute USSR Academy of Sciences
Sh	Prefix of catalogue number of vertebrate fossils from Shargaltein-Tal, Gansu Province
Z. Pal.	Palaeozoological Institute of Polish Academy of Sciences
ИЗ МНВОРК	Institute of Zoology, National Academy of Sciences and Higher Educational Ministry of the Republic of Kazakhstan

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Introduction

Tachyoryctoides is one of the mid-tertiary endemic rodents of eastern and central Asia. The genus was established by Bohlin (1937) based on meager material from Late Oligocene deposits in Shargaltein-Tal of Danhe area, Gansu Province, China, although three species (*T. obrutschewi*, *T. intermedius* and *T. pachygnathus*) were created, each represented by a single lower jaw fragment. Later, materials of this genus were reported from the Late Oligocene of the Taben-buluk area and Lanzhou Basin of Gansu Province (Bohlin 1946; Wang and Qiu 2000), the Early Miocene in Xining Basin of Qinghai Province, China (Li and Qiu 1980), the Late Oligocene in Tsagan Nor Basin of Central Mongolia (Dashzeveg 1971; Kowalski 1974), and the Late Oligocene in the North Aral area of Kazakhstan (Bendukidze 1993, 2009; Lopatin 2004).

Argyropulo (1939) erected a new genus *Aralomys* from Late Oligocene deposits in Agyspe on the northern shore of the Aral Sea of Kazakhstan. Later more material of *Aralomys* was reported from the Late Oligocene in North Aral and Ayaguz areas in Kazakhstan. (Vorontsov 1963; Bendukidze 1993; Tyutkova 2000; Lopatin 2004). Subsequently, the genus *Aralomys* was considered as a junior synonym of *Tachyoryctoides* by some other paleontologists (Mellett 1968; Dashzeveg 1971; Kowalski 1974; Kordikova and de Bruijn 2001; Bendukidze et al. 2009).

Fossils of *Tachyoryctoides* and/or the Tachyoryctoididae were also mentioned in faunal lists of the following localities: Aoerban and Damiao (Early Miocene), and Tairum Nor (Early Middle Miocene) in central Nei Mongol (Wang et al. 2003, 2009; Zhang et al. 2011), Qin'an (Early Miocene) (Guo et al. 2002; Zhan et al. 2011) of Gansu, Ulungur River Region (Late Oligocene-Early Middle Miocene) of Xinjiang, China (Wu et al. 1998; Ye et al. 2000, 2001, 2003), Tsagan Nor Basin (Late Oligocene) of Central Mongolia (Mellett 1968; Daxner-Höck et al. 1997, 2010; Höck et al. 1999), and Aktau Mountain (Early Miocene), Kazakhstan (Kordikova and de Bruijn 2001). Among them some specimens published under the name Tachyoryctoididae [Tachyoryctoididae genus A sp. I reported by Kordikova and de Bruijn 2001 and Tachyoryctoidinae gen. et sp. nov. listed by Ye et al. (2003)] were later suggested to be referable to *Ayakozomys* by Bendukidze et al. (2009).

Of the above-mentioned specimens, the fossils from Qinghai (*T. kokonorensis*) best represent the genus, and include a muzzle part (maxilla with complete sets of upper molars), some mandibles and isolated teeth. Unfortunately, so far practically no skull structure has been discovered for this particular group of rodents, and the characteristic features of the mandible are little known as well.

During the 1990's, the Lanzhou Basin was intensively investigated by a joint paleontological expedition. The expedition comprised geologists and paleontologists from the IVPP, Provincial Museum of Gansu, Institute of Cultural Relics and Archaeology of Gansu, Northwest University of China; American Museum of Natural History, University of Arizona, Northern Arizona University, Peabody Museum of Harvard University of USA; and Naturhistorisches Museum of Basel, Switzerland. As one of the principal investigators, Dr. Engesser actively joined the field work in 1994, 1996, 1997 and 1998. A number of *Tachyoryctoides* specimens, including an incomplete skull in association with its right hemimandible, some mandibles and isolated teeth, were collected from Early Miocene deposits of Lanzhou Basin (Fig. 1; Table 1). So far, this is the best known material of *Tachyoryctoides*. As a result of the present study, two new species are established. The Lanzhou material also sheds new light on the phylogenetic status of *Tachyoryctoides* above the generic level.

The terminology used for molars is presented in Fig. 2. In Table 2, molar length (L) represents the antero-posterior longest distance of crown perpendicular to the posterior wall of the upper molar and anterior wall of lower molar. The molar width (W) represents the largest width of molar crown.

Systematic paleontology

Superfamily Muroidea Illiger, 1811
Family Tachyoryctoididae Schaub, 1958
Genus *Tachyoryctoides* 1937

Type species. *Tachyoryctoides obrutschewi* Bohlin, 1937.

Referred species. *T. intermedius* Bohlin, 1937; *T. pachygnathus*, Bohlin, 1937; *T. gigas* (Argyropulo 1939); *T. glikmani* (Vorontsov 1963); *T. kokonorensis* Li et Qiu, 1980; *T. engesseri* sp. nov., *T. minor* sp. nov. and *Tachyoryctoides* spp.

Geographic distribution and geological age. Eastern and Central Asia [from the easternmost central Nei Mongol (Aoerban area) of China to the westernmost North Aral region of Kazakhstan]; Late Oligocene—Early Miocene.

Emended diagnosis. Large-sized muroids with myomorphous skull and sciurognathous mandible. Lateral masseter muscle attachment area lies within the maxilla; infraorbital foramen large, without ventral slit; glenoid fossa extending backwards to meet occipital crest, situated above and lateral to auditory bulla; and the border of the choana is opposite the middle of M3. The horizontal portion of mandible is thick, with a vertically concave lingual surface; the masseteric fossa extends below m1–m2, with a strong and flaring lower ridge. Molars are moderately high-crowned and lophodont, with transverse lophs(-ids) usually perpendicular to the longitudinal axis, lophs(-ids) are thin with wide and deep reentrants in early wear; three buccal and one lingual reentrants are present on upper molars, three lingual and two buccal reentrants on lower molars; mesoloph(id) are usually very weak or absent; entoloph and ectolophid are extending obliquely; this sinus is extending toward the anterosinus on upper molars, whereas enlarged mesosinusid and sinusid extend toward the small protosinusid and posterosinusid, respectively, on lower molars. On m1, the anterolophid is missing a distinct anteroconid at its extremity, the metaconid is usually linked to the protoconid in its lower part, whereas the metalophid varies from incomplete to complete depending on the wear. The anterolophulid is present on m2-3. The i2 has a flat labial surface and extends posteriorly to below the mandibular notch.

Remarks. Having compared the specimens of *Tachyoryctoides* with *Aralomys*, especially their type species, we find that the molar morphology of *Aralomys* is very close to that of *Tachyoryctoides*. They share common features such as: the lower molars having rather transversely extending metalophid and hypolophid, a long and obliquely oriented ectolophid, enlarged mesosinusid and sinusid obliquely extending toward small protosinusid and

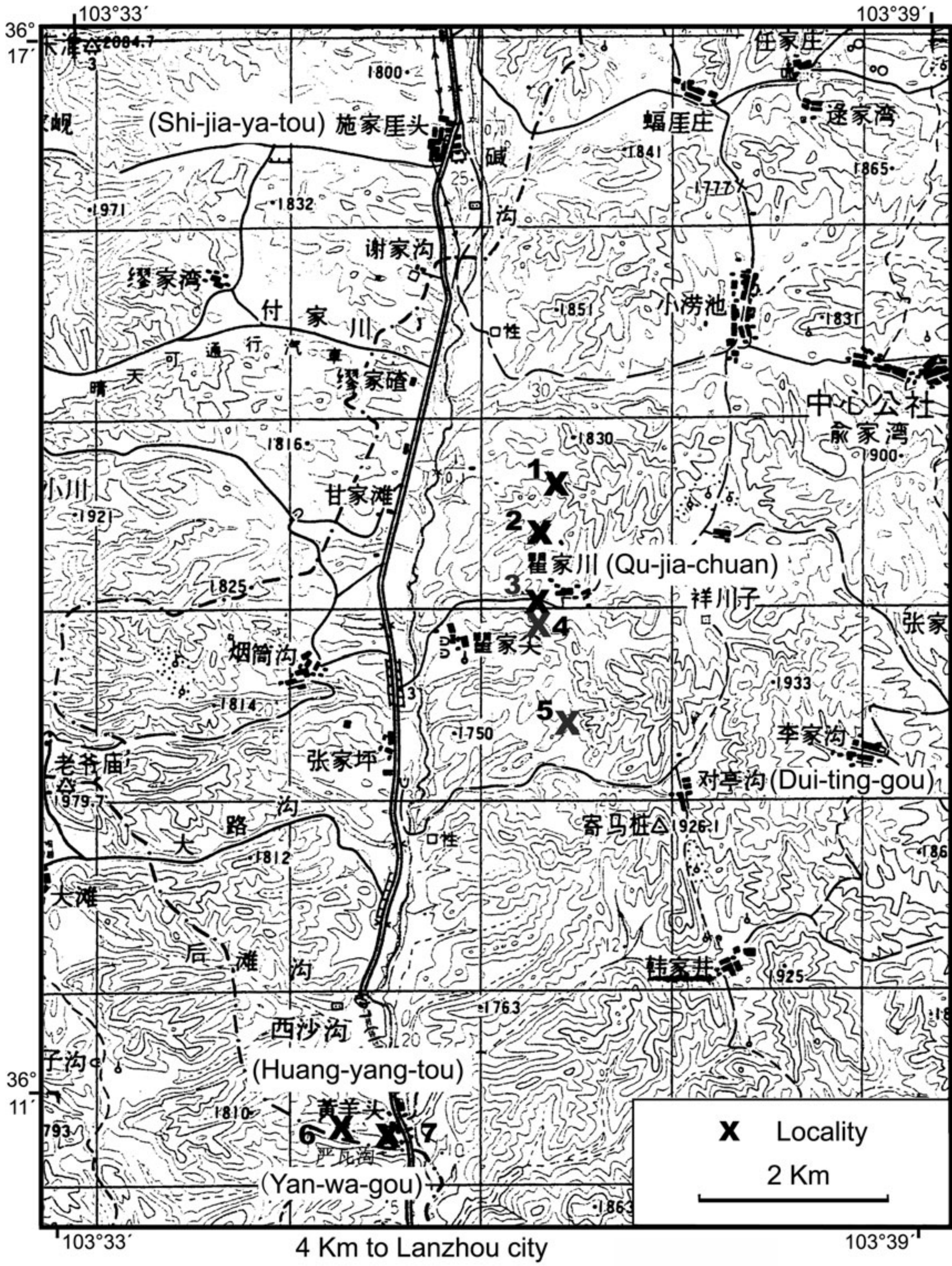

Fig. 1 Localities yielding *Tachyoryctoides* in Lanzhou Basin, Gansu Province. *1* GL 199714, *2* GL 199708, *3* GL 199308, *4* GL 199309, *5* GL 199303, *6* GL 199505, *7* GL 199506 (for their exact localities see Table 1)

posterosinusid, respectively, and m2–m3 having anterolophulid and buccal part of anterolophid, but the mesolophid is short or absent. The main difference between *T. obrutschewi* and *A. gigas* is the presence of the anterolophulid on m1 for the former, whereas it is absent for the latter. However, the anterolophulid is present on the m1 of another *Aralomys* species: *A. glikmani*. Therefore, the presence or absence of anterolophulid on m1 is a variable character within the genus *Aralomys*. Thus, our opinion is that *Aralomys* is a junior synonym of *Tachyoryctoides*.

Table 1 Localities yielding *Tachyoryctoides* in Lanzhou Basin, Gansu Province, China

No. in Fig. 1	Field no.	Locality in Gaolan County	GPS	Horizon	Species
1	GL 199714	North of Qu-jia-chuan	36°14′27.8″N, 103°36′23.4″E	WS I	*Tachyoryctoides* sp.
2	GL 199708	North of Qu-jia-chuan	36°14′10.3″N, 103°36′18.6″E	Between WS II and WS III	*T. engesseri*
3	GL 199308	SW of Qu-jia-chuan	36°13′47.2″N, 103°36′17.6″E	WS I	*T. kokonorensis* *Tachyoryctoides* sp.
4	GL 199309	0.5 km SE of GL 199308	36°13′44.1″N, 103°36′18.6″E	WS III	*Tachyoryctoides* sp. I
5	GL 199303	1.3 km NW of Dui-ting-gou	36°13′05.7″N, 103°36′27.3″E	WS V	*T. minor*
6	GL 199505	Yan-wa-gou	36°10′49.8″N, 103°35′01.0″E	WS I	*Tachyoryctoides* sp.
7	GL 199506	Yan-wa-gou	36°10′46.6″N, 103°35′13.9″E	WS II	*Tachyoryctoides* sp. I

WS white sandstones

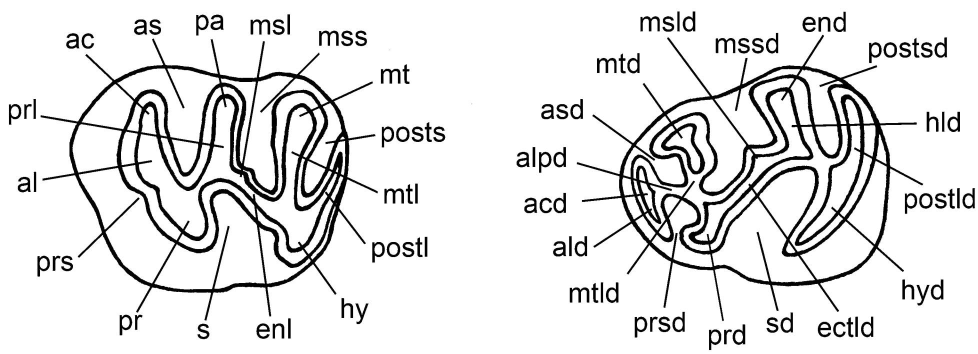

Fig. 2 Terminology of cusps, lophs and reentrants of M1 (*left*) and m1 (*right*) in *Tachyoryctoides.* M1: *ac* anterocone, *al* anteroloph, *as* anterosinus, *enl* entoloph, *hy* hypocone, *msl* mesoloph, *mss* mesosinus, *mt* metacone, *mtl* metaloph, *pa* paracone, *postl* posteroloph, *posts* posterosinus, *pr* protocone, *prl* protoloph, *prs* protosinus, *s* sinus, m1: *acd* anteroconid, *ald* anterolophid, *alpd* anterolophulid, *asd* anterosinusid, *ectld* ectolophid, *end* entoconid, *hld* hypolophid, *hyd* hypoconid, *msld* mesolophid, *mssd* mesosinusid, *mtd* metaconid, *mtld* metalophid, *postld* posterolophid, *postsd* posterosinusid, *prd* protoconid, *prsd* protosinusid, *sd* sinusid

Tyutkova (2000) described a new species of *Aralomys, A. padre*. Judging by the drawing in Fig. 3 of Tyutkova (2000), we agree with Bendukidze et al. (2009) that its holotype (ИЗ МНВОРК, N22/185, Tyutkova 2000, Fig. 3г) "cannot be identified at the genus level" and the referred specimen, m2 (ИЗ МНВОРК, N22/195, Tyutkova 2000, Fig. 3д), may belong to another genus.

Tachyoryctoides engesseri sp. nov.
(Figures 3, 4).

Holotype. Incomplete skull in association with right hemimandible of the same individual (IVPP V 18176.1).

Referred specimens. One LM2 (V 18176.2) and several broken molars.

Locality and geological horizon. GL 199708, Qu-jia-chuan, Gaolan County; red mudstone between White Sandstone II and III of Middle Member of the Xianshuihe Formation, Early Miocene.

Diagnosis. Large-sized *Tachyoryctoides.* The premaxillo-maxillary suture intersects the posterior part of incisive foramen. The m1 has broad antero+protosinusid, closed lingually but open buccally, and lacking the anterolophulid and mesolophid. The m2 and m3 have short lingual parts of the anterolophid and small anterosinusids. The m3 is longer than m1/m2, with a wider protosinusid and a small circular posterosinusid. The posteroloph is much shorter than the metaloph, and posterosinus is small on upper molars. The posterosinus is open on M3.

Differential diagnosis. The new species differs from most species of *Tachyoryctoides* (*T. obrutschewi, T. intermedius, T. gigas, T. glikmani* and *T. kokonorensis*) in being larger in size.

It further differs from *T. obrutschewi* in lacking the anterolophulid and mesolophid on m1, having a shorter lingual part of the anterolophid and a smaller anterosinusid on m2 and m3, having a shorter posteroloph and a smaller posterosinus on upper molars and a more reduced posterior part on M3; from *T. gigas* in having m3 much longer than m1/2 and having a posterosinusid, and m1 lacking the mesolophid; from *T. glikmani* in lacking an anterolophulid and a mesolophid on m1; from *T. kokonorensis* in m1 lacking an anterolophulid and having its antero+protosinusid open

Table 2 Measurements of teeth of *Tachyoryctoides* (in mm)

	T. engesseri			*T. minor*	*T. kokonorensis*			*Tachyoryctoides* sp. I	*Tachyoryctoides* sp.		*T. obrutschewi*		
	V 18176.1		V 18176.2	V 18177	V 6000		V 18178	V 18179	V 18181	V 18182	Sh 499	No. 17-(1)	
	Holotype											Dashzeveg (1971)	Bendukidze et al. (2009)
	Left	Right			Left	Right							
M1-3 L	13.1	13.3			12.4+	12.0+							
M1 L	5.6	5.6			4.9	5.1		5.5					42.0–50.3
M1 W	4.7	4.5			4.7	4.6		4.0					34.7–41.6
M2 L	4.2	4.1	4.3		4.5	4.7							33.4
M2 W	4.8	4.7	4.5		4.5	4.4							34.0
M3 L	3.4	3.3		2.0	3.5	3.5							27.7
M3 W	4.3	4.1		2.4	3.8	3.8							31.5
m1-3 L		15.3			14.2	13.7			14.2[a]	16.7[a]	11.4	12	
m1 L		4.8			4.8	4.7	4.8	5.0	4.3		3.6	4.5	36.6–42.4
m1 W		3.7		2.1+	3.8	3.7	3.6	3.8	3.2+		3.3	3.0	29.7–34.3
m2 L		4.6		2.8	4.2	4.2			3.9		3.2	4.0	37.9–38.2, 38.5
m2 W		4.4		2.4	4.2	4ca.					3.5	3.3	33.7–35.5, 35.8
m3 L		5.7			4.5	4.6					3.5	4.0	33.5, 34
m3 W		4.2		2.4+	3.7	3.7					3.3	3.0	31.2–32.8, 29
i2 H		5ca			5ca				5.8	5.4	2.8		
i2 W		4			4.1				5.7	4.5	2.8		
m1-2		9.1			9.4	9.1			8.5		7.3		

	T. obrutschewi (?)		*T. intermedius*	*T. pachygnathus*	*T. gigas*	*T. glikmani*
	MgM-III/38 Kowalski (1974)	MgM-III/39	Sh 498	Sh 829	PIN 210-7 Argyropulo (1939)	PIN 1978-1 Vorontsov (1963)
M1-3 L						
M1 L						
M1 W						
M2 L						
M2 W						
M3 L						
M3 W						
m1-3 L	13.0			15.4	11.1	
m1 L	3.8	3.9		5.1	3.8	3.6
m1 W	3.4	3.1		3.2	3.0	

Table 2 continued

	T. obrutschewi (?)		*T. intermedius*	*T. pachygnathus*	*T. gigas*	*T. glikmani*
	MgM-III/38 Kowalski (1974)	MgM-III/39	Sh 498	Sh 829	PIN 210-7 Argyropulo (1939)	PIN 1978-1 Vorontsov (1963)
m2 L	4.0	3.5	3.6	4.1	3.8	3.5
m2 W	4.1	3.7	3.8	3.4	3.3	
m3 L	4.2		3.7		3.5	
m3 W	3.8		3.5		3.0	
i2 H				5.7		
i2 W			3.7	4.9		
m1-2			7.6	9.4	7.9[b]	7.2

H vertical distance between labial and lingual sides of incisor, *L* length, *W* width, *ca* circa

[a] Alveolar length of m1-3

[b] After Vorontsov (1963)

buccally, upper molars having a shorter posteroloph and a relatively small posterosinus, M3 having an open posterosinus, and m3 having a posterosinusid and a wider protosinusid; and from *T. pachygnathus* in having a slender mandible and i2, and proportionally wider m1 and m2 [in *T. engesseri* m1 (W/L) is 77% and m2 (W/L) is 96% and in *T. pachygnathus* m1 (W/L) is 63% and m2 (W/L) is 83%].

Etymology. The name of the species is dedicated to Dr. B. Engesser.

Description

Skull (Fig. 3). The skull of the holotype is incomplete, with the anterior part of the rostrum damaged, the right half of the occiput and the ear region broken. Both zygomatic arches are lacking. Most of the bones on dorsal surface are splintered, so that their sutures can hardly be traced with certainty.

In dorsal view, the skull is roughly triangular. The postorbital constriction is strong. The frontal crests converge rapidly to form the sagittal crest near the postorbital constriction. The sagittal crest is very long and joins the occipital crest, forming almost a right angle with the latter.

The rostrum is narrow and decreases forwards in dorsoventral dimension. The incisive foramen (inf) is 8 mm long, about 1/3 the length of the maxillary diastema. The premaxillo-maxillary suture intersects the incisive foramen at its posterior end. Thus, the incisive foramen lies largely within the premaxilla. The infraorbital foramen (iof) is large, with its lateral wall mostly broken away. Judging from its remaining part there seems to be no ventral slit. The zygomatic plate (zp) extends in anterodorsal–posteroventral direction, and the attachment area of *m. masseter lateralis* is situated completely within the maxilla. Its anterior border lies roughly at the same level as the anterior end of the incisive foramen and the most anterior point of its arched posterior border is slightly anterior to the posterior end of the incisive foramen. The attachment area of *m. masseter superficialis* (sc) forms an oval depression at the antero-medial margin of the zygomatic plate. The upper cheek tooth row is much shorter than maxillary diastema in length. The two cheek tooth rows are diverge somewhat posteriorly, with a relatively narrow palate. The palatal bridge is about 15 mm long. Its anterior width is 4.7 mm and the posterior one is 5.7 mm. The sagittal crest of the palate is prominent and protrudes backwards slightly beyond the palate. The palatine sulci (ps) are deep, lying medial to the M1-3. There are three pairs of foramina in the palatine sulci. The anterior two pairs located medially to the M2 are evidently the posterior palatal foramina (ppf). The third pair is located medially to the M3, which may be either the posterior-most palatal foramina or the nutrient foramina. The maxilla–palatine suture can be seen

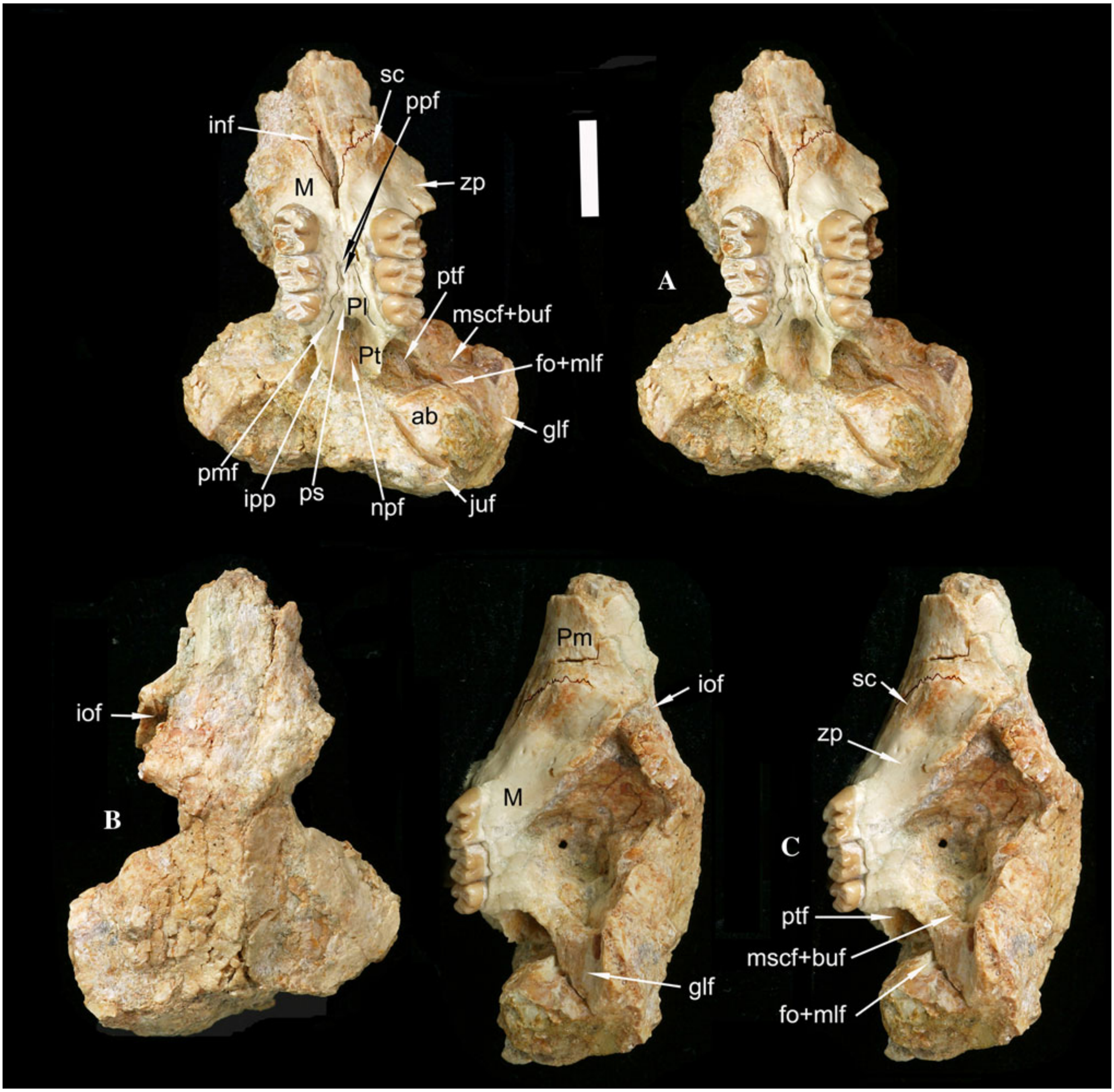

Fig. 3 Skull of V 18176.1 of *Tachyoryctoides engesseri* sp. nov. **A** *ventral view* (in stereo); **B** *dorsal view*; **C** *left lateral view* (in stereo). *M* maxilla, *Pl* palatine, *Pm* premaxilla, *Pt* pterygoid, *ab* auditory bulla, *buf* buccinator foramen, *fo* foramen ovale, *glf* glenoid fossa, *inf* incisive foramen, *iof* infraorbital foramen, *ipp* internal pterygoid process, *juf* jugular foramen, *mlf* middle lacerate foramen, *mscf* masticatory foramen, *npf* nasopharyngeal fossa, *pmf* posterior maxillary foramen, *ppf* posterior palatine foramen, *ps* palatine sulcus, *ptf* pterygoid fossa, *sc* scar of attachment area of m. masseteric superficialis, *zp* zygomatic plate. *Scale bar* 1 cm

extending from the medial or anterior border of the M2 to the posterior maxillary foramen, but its anterior and posterior ends can hardly be traced. The posterior maxillary foramen (pmf) is narrow and long, located medially to the M3. The lower border of the choana is weakly ω-shaped, located medially to the middle of M3. The nasopharyngeal meatus (npf) is relatively wide, subequal or slightly wider than the pterygoid fossa (ptf), which is deep but not penetrated. Its widest part is about 6.2 mm. The internal pterygoid process (ipp) is slightly convergent posteriorly, but slightly slants laterally. The masticatory foramen (mscf) is confluent with the buccinator foramen (buf). The foramen ovale (fo) is also confluent with the middle lacerate foramen (mlf). The glenoid fossa (glf) is long and extends backwards to the occipital crest, situated laterally to the auditory bulla (ab). The outline of the auditory bulla

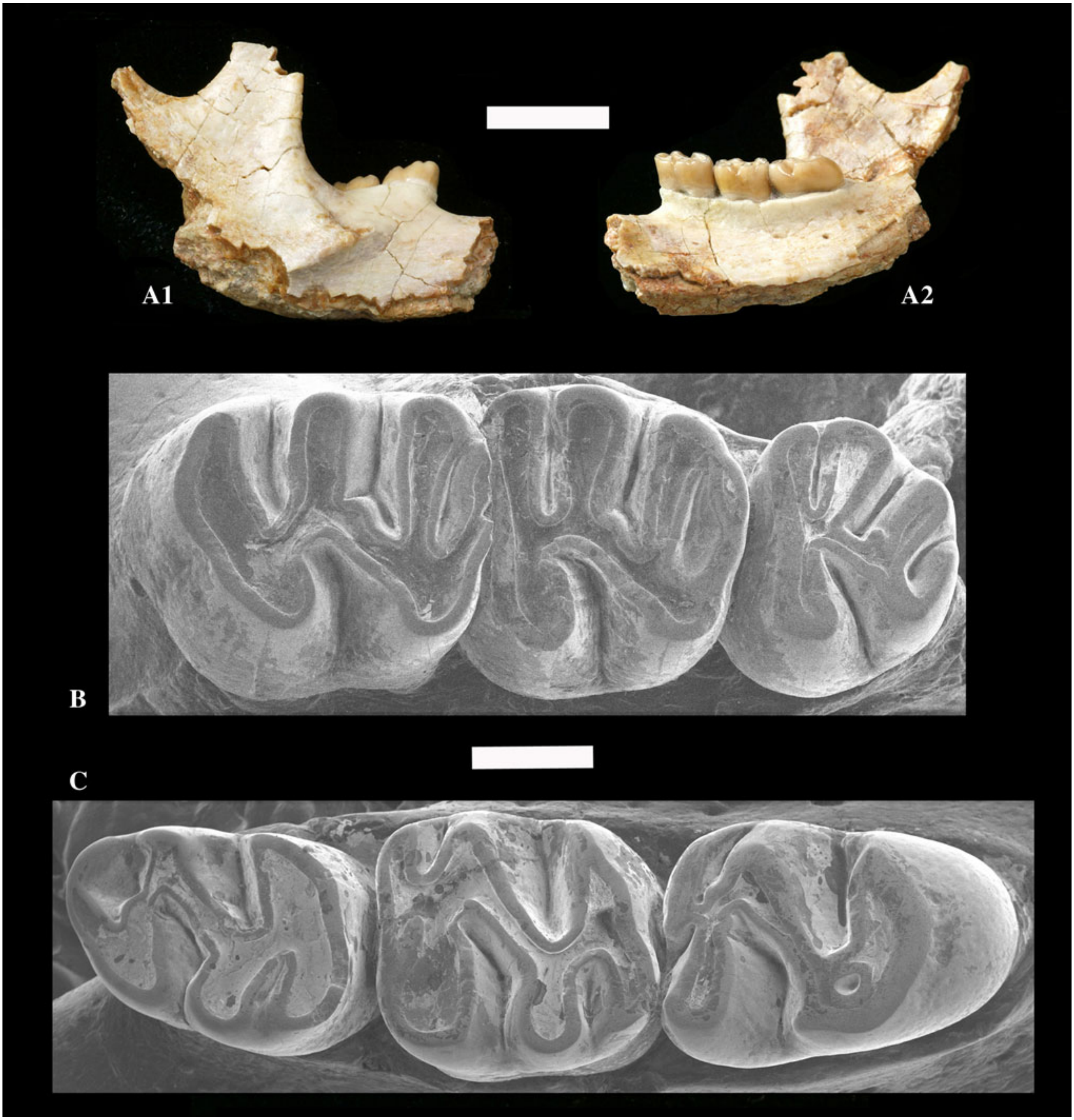

Fig. 4 Mandible and molars of V 18176.1 of *Tachyoryctoides engesseri* sp. nov. **A** right hemimandible: *A1* buccal view, *A2* lingual view; **B** occlusal view of left M1-3; **C** occlusal view of right m1-3. *Scale bars* **A**: 1 cm; **B**–**C**: 2 mm

is moderately inflated and oval, with its major axis extending in anteromedial—posterolateral direction, also with a spine at its antero-medial corner. The jugular foramen (juf) is distinct.

Mandible (Fig. 4A). The right hemimandible of the holotype is damaged, with its symphysial and angular parts and the lower border mostly broken. The horizontal portion is thick, with a vertically concave lingual surface. The masseteric fossa extends below the anterior part of m2, where a masseteric tuberosity is formed. Above the masseteric tuberosity there is a distinct depression, which may serve as the attachment area for the anterior part of *m. masseter medialis*. The lower ridge of the masseteric fossa is more developed than the upper one. The mental foramen is located before the m1, slightly lower than the masseteric tuberosity. The anterior border of the coronoid process slants slightly anteriorly, forming an angle of about 80° with the occlusal surface of the lower molar row, and its lower part takes it origin laterally to the anterior part of m2.

Teeth (Fig. 4B–C). The dental formula is 1003/1003. The crowns of the molars are moderately high. On the upper molars, the lingual sides of the crowns are slightly higher than the buccal ones. The outline of M1 is trapezoid with rounded angles, the buccal side being longer than the lingual side. There are four buccal transverse lophs (anteroloph, protoloph, metaloph and posteroloph), three buccal reentrants (anterosinus, mesosinus and posterosinus) and one lingual reentrant (sinus) on occlusal view. The transverse lophs are usually perpendicular to the longitudinal axis. The mesoloph is reduced to a tiny vestige, and the posteroloph is shorter than the metaloph. The protosinus is reduced to a very shallow groove. All the reentrants are open. The anterosinus is subequal to the mesosinus in length, but slightly narrower transversely. The posterosinus is the shortest and shallowest of the buccal reentrants and has a shallower buccal notch. The entoloph extends antero-buccally from the hypocone to the protoloph, then turns antero-lingually to meet the anteroloph. The sinus extends antero-buccally toward the anterosinus and is deeper than the buccal reentrants. The outline of M2 is trapezoid with a longer anterior side than the posterior one. It is also shorter than the M1. Its occlusal structure is similar to that of M1, but the anterosinus is antero-posteriorly compressed, shorter and shallower than the mesosinus. The mesoloph is weak. M3 is oval in occlusal view, shorter and narrower than M2. Generally, the occlusal structure is similar to that of M2, however, its reentrants, lophs and cusps are more compressed antero-posteriorly. The anterior part of the entoloph extends anteriorly to meet the protoloph and the middle of the anteroloph. The posteroloph is much shorter than the metaloph, and the posterosinus is much smaller than the mesosinus and has a deeply open buccal notch.

The m1 is oval in occlusal view, longer than wide, with a narrower anterior side. No anterolophulid is seen between the anterolophid and metalophid. Thus, the anterosinusid and protosinusid are fused into one reentrant which is called here as antero+protosinusid. The antero+protosinusid is broad and open buccally, but closed lingually, because the anterolophid meets the metaconid. The metaconid is larger than the protoconid. The metalophid is narrow at its middle. It seems possible that the metalophid varied from incomplete to complete with wear. The mesosinusid extends antero-buccally toward the protosinusid and is open lingually. No mesolophid is visible. The sinusid extends postero-lingually toward the posterosinusid. It is subequal to the mesosinusid but wider than the other reentrants, and opens widely on its buccal side. The open posterosinusid is short and narrow, extending slightly postero-buccally. The m2 is rectangular, wider than m1. The posterior part of the m2 displays a similar structure to that of m1. The metalophid and hypolophid are well developed and extends transversely. There is a distinct anterolophulid joining the metalophid with anterolophid to separate the anterosinusid from the protosinusid. The anterolophid is also separated into two parts, the lingual part being much shorter than the buccal one. There are four separated transverse lophids and three reentrants on lingual side. The anterosinusid is much smaller than other reentrants. All of the reentrants of m2 are open. The m3 is of oval shape, longer than wide, with a narrow and convex posterior side. It is similar to m2 in basic structure, but longer. The posterosinusid is reduced into a small circular basin.

The i2 is triangular in cross section, with flat labial side and a round lingual end. Its posterior end extends posteriorly to below the mandibular notch.

Comparison. It is true that V 18176 is similar to that of *Ayakozomys* in some morphological characteristics of the m1, demonstrated in having a lingually open antero+protosinusid, but lacking any anterlophulid and mesolophid. However, V 18176 is different from *Ayakozomys* in some other features of m1: the metalophid extending from lingual end of the protoconid and shorter hypolophid meeting posterolophid more lingually. Besides, V 18176 differs from *Ayakozomys* in the morphology of almost all of the other teeth. In *Ayakozomys,* the sinusid and mesosinusid extend less obliquely, and the sinusid overlaps the posterosinusid on all the lower molars; the anterolophulid is usually absent and anterolophid meets the metaconid to close the anterosinusid buccally on m2 and m3; the protocone is V-shaped with a distinct posterior arm and the sinus is less oblique on M1 and M2. Thus, V 18176 cannot be referred to *Ayakozomys*.

Likewise, V 18176 does not belong to *Eumysodon*, because the lower molars have more transversely oriented mesosinusid and sinusid, and the sinusid overlaps posterosinusid. The m1 has free posterior arm of protoconid in *Eumysodon*.

The referral of V 18176 to the genus *Tachyoryctoides* is based on its possession of a series of features diagnostic of that genus. As in other species of the genus, the horizontal portion of the mandible is thick, with its lingual surface vertically concave, and the masseteric fossa extends to below m2, with a projected anterior end and well developed and flaring lower masseteric ridge; molars are moderately high-crowned and lophodont, loph(id)s usually perpendicular to the longitudinal axis; lower molars with two buccal reentrants, but without mesolophid, m2/3 with anterolophulid, four lingual transverse lophids and three lingual reentrants, and mesosinusid and sinusid extending toward protosinusid and posterosinusid, respectively; the upper molars have four buccal transverse lophs and three buccal reentrants, weak or absent mesoloph, and sinus extending toward the anterosinus. Furthermore, it shares with

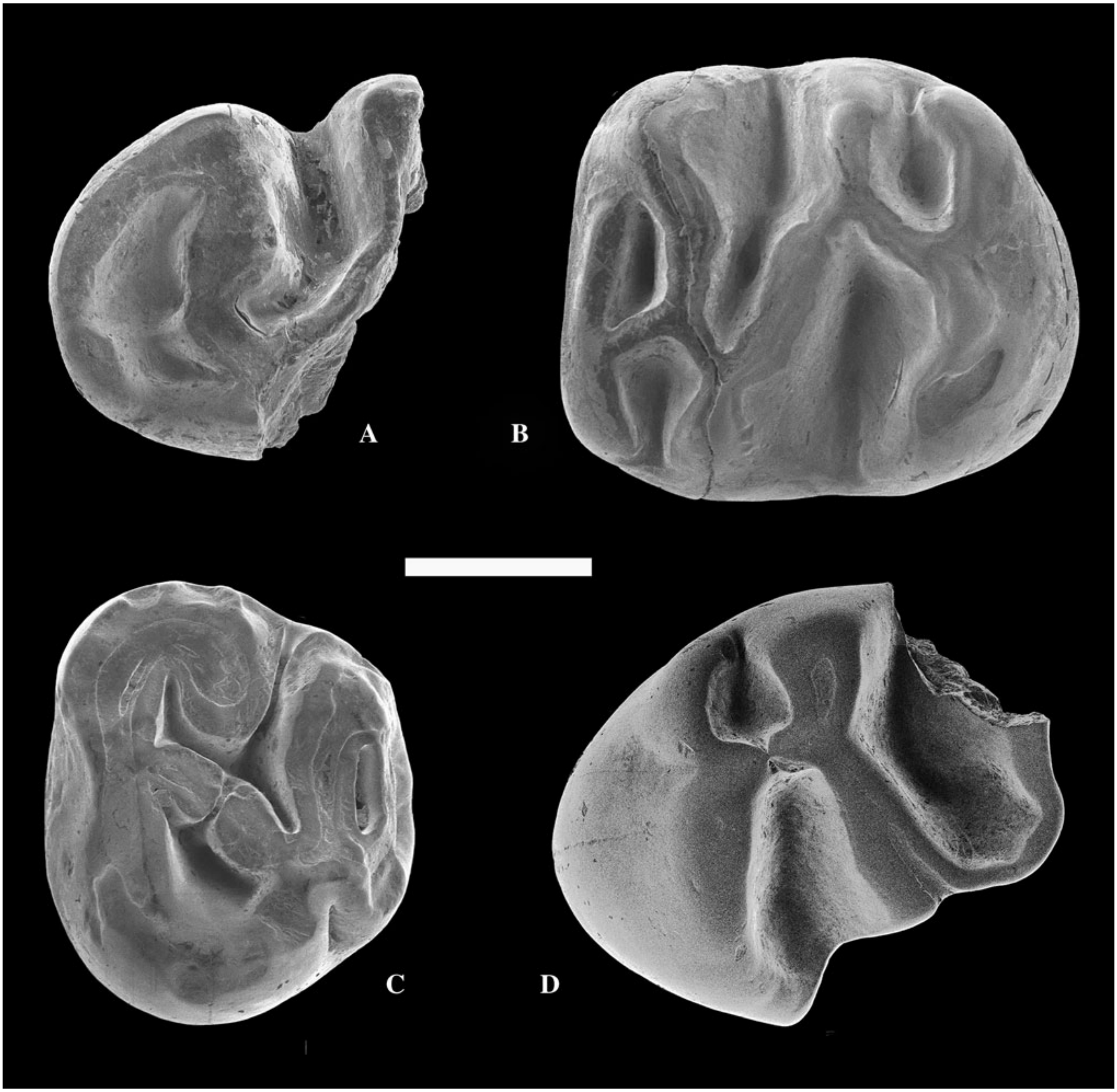

Fig. 5 Occlusal view of V 18177 of *Tachyoryctoides minor* sp. nov. **A** left m1 (V 18177.2), **B** left m2 (V 18177.1), **C** left M3 (V 18177.4), **D** right m3 (V 18177.3). *Scale bar*: 1 mm

T. kokonorensis some features such as the premaxillo-maxillary suture intersecting posterior part of incisive foramen and lower border of choana being opposite to the M3.

Tachyoryctoides minor sp. nov.
(Fig. 5)

Holotype. One left m2 (IVPP V 18177.1).

Referred specimens. Anterior part of one left m1 (IVPP V 18177.2), posterior part of one right m3 (V 18177.3) and one left M3 (V 18177.4).

Locality and geological horizon. GL 199303, 1.3 km NW of Dui-ting-gou, Gaolan County; White Sandstone V of Middle Member of Xianshuihe Formation, Early Miocene.

Diagnosis. Small-sized *Tachyoryctoides*; m1 lacking anterolophulid and mesolophid, but with closed antero+protosinusid; m2 with closed anterosinusid, open protosinusid and posterosinusid; m3 with open posterosinusid; M3 with incomplete protoloph, buccally closed anterosinus, and closed posterosinus and sinus.

Differential diagnosis. It differs from all of the other species of *Tachyoryctoides* in being much smaller (see Table 2).

It further differs from *T. obrutschewi* in m1 lacking the anterolophulid and the mesolophid, and M3 having more complex occlusal structure, more reduced posterior part and a closed posterosinus; from *T. gigas* in m1 lacking the mesolophid, m2 having a larger and closed anterosinusid and an open posterosinusid, and m3 having a posterosinusid; from *T. glikmani* in m1 lacking the anterolophulid and the mesolophid, and m2 having a closed anterosinusid and open protosinusid and posterosinusid; from *T. kokonorensis* in m1 lacking the anterolophulid, m2 having a closed anterosinusid, m3 having a posterosinusid, M3 having a closed anterosinus and sinus, and an incomplete protoloph; and from the new species, *T. engesseri*, in m1 having an antero+protosinusid closed buccally, M3 having closed anterosinus, posterosinus and sinus, and an incomplete protoloph.

Etymology. Minor, Latin, small.

Description

All the molars are moderately high-crowned. Of the m1, only the anterior part is preserved. There is no anterolophulid. The anterosinusid and protosinusid are fused into a single and wide antero+protosinusid closed both lingually and buccally. The metalophid is slightly constricted at the middle. The ectolophid and mesosinusid extend anterobuccally. Neither the mesolophid nor the free posterior arm of protoconid is visible. The m2 is rectangular, longer than wide. Among the three lingual reentrants the mesosinusid is the largest and deepest, extending antero-buccally toward the protosinusid, opening lingually. The anterosinusid and posterosinusid are subequal in width, but the former is slightly shorter and closed lingually and the latter opens lingually. The sinusid is larger than the mesosinusid, extending postero-lingually toward the posterosinusid. The protosinusid is subequal to the posterosinusid in size and opens buccally. The anterolophulid extends antero-buccally to meet the anterolophid, separating the anterolophid into two parts. The ectolophid obliquely extends from the protoconid to the hypolophid, which is much shorter than the metalophid. The mesolophid is absent. Of the m3 only the posterior part is preserved. It is similar to that of m2 in structure, but slightly larger. The M3 is of trapezoid shape, wider than long, also with its anterior side wider than the posterior one. The lingual side of the crown is higher than the buccal one. All three buccal reentrants are compressed longitudinally. Among them, the mesosinus is the widest and opens buccally. Since the protoloph meets the anteroloph buccally but does not meet the entoloph, the anterosinus is closed buccally, but its lingual end links with the mesosinus. The posterosinus forms a short and wide closed basin. The sinus is the largest among the reentrants and subequal to the mesosinus in depth. It is closed lingually but with a tiny notch, because the protocone extends posteriorly to meet the hypocone.

Comparison. These teeth represent a species much smaller than all known species of *Tachyoryctoides*, but close to *Eumysodson* and *Ayakozomys* in size. However, its tooth morphology is closer to that of *Tachyoryctoides* than the latter two. Indeed, the lower molars of V 18177 have enlarged and more oblique mesosinusid and sinusoid, extending toward the small protosinusid and posterosinusid, respectively (in *Eumysodon* and *Ayakozomys*, the mesosinusid and sinusid extend less obliquely and the sinusid overlaps the posterosinusid), an hypolophid much shorter than the metalophid and a smaller posterosinusid (the hypolophid is usually slightly shorter than the metalophid in *Eumysodon* and *Ayakozomys*) and the protoconid lacking the free posterior arm on m1 (it is present in *Eumysodon*). In addition, the M3 of V 18177 is also similar to *Tachyoryctoides* in having three buccal reentrants and one lingual reentrant. Therefore, the species is to be referred to the genus *Tachyoryctoides*.

Tachyoryctoides kokonorensis Li et Qiu, 1980.
(Fig. 6A).

Specimen. One right m1 (IVPP V 18178).

Locality and geological horizon. GL 199308, 0.5 km SW of Qu-jia-chuan, Gaolan County; base of White Sandstone I of Middle Member of Xianshuihe Formation, Early Miocene.

*Remarks***.** V 18178 has an oval outline, with slightly narrow anterior side. The anterolophulid joins the anterolophid to the metalophid to separate the anterosinusid from the protosinusid, both of which are closed. The ectolophid obliquely extends from the protoconid to the hypolophid. No mesolophid is seen. The mesosinusid and sinusid are the largest among the reentrants and are open. The former extends toward the protosinusid and the latter toward the posterosinusid, which extends nearly transverse and opens lingually. All the characters mentioned above are almost identical with those of *T. kokonorensis*. Its size is also subequal to that of *T. kokonorensis*.

Bendukidze et al. (2009) considered that *T. intermedius* and *T. kokonorensis* are junior synonyms of *T. pachygnathus*. It seems difficult for us to say that the three forms have the same molar morphology, since both *T. intermedius* and *T. pachygnathus* are represented by old individuals, molars of which are heavy worn and do not show the occlusal features in detail. However, *T. pachygnathus* does show differences in size and tooth proportion from *T. kokonorensis* and *T. intermedius*. For example, the m1

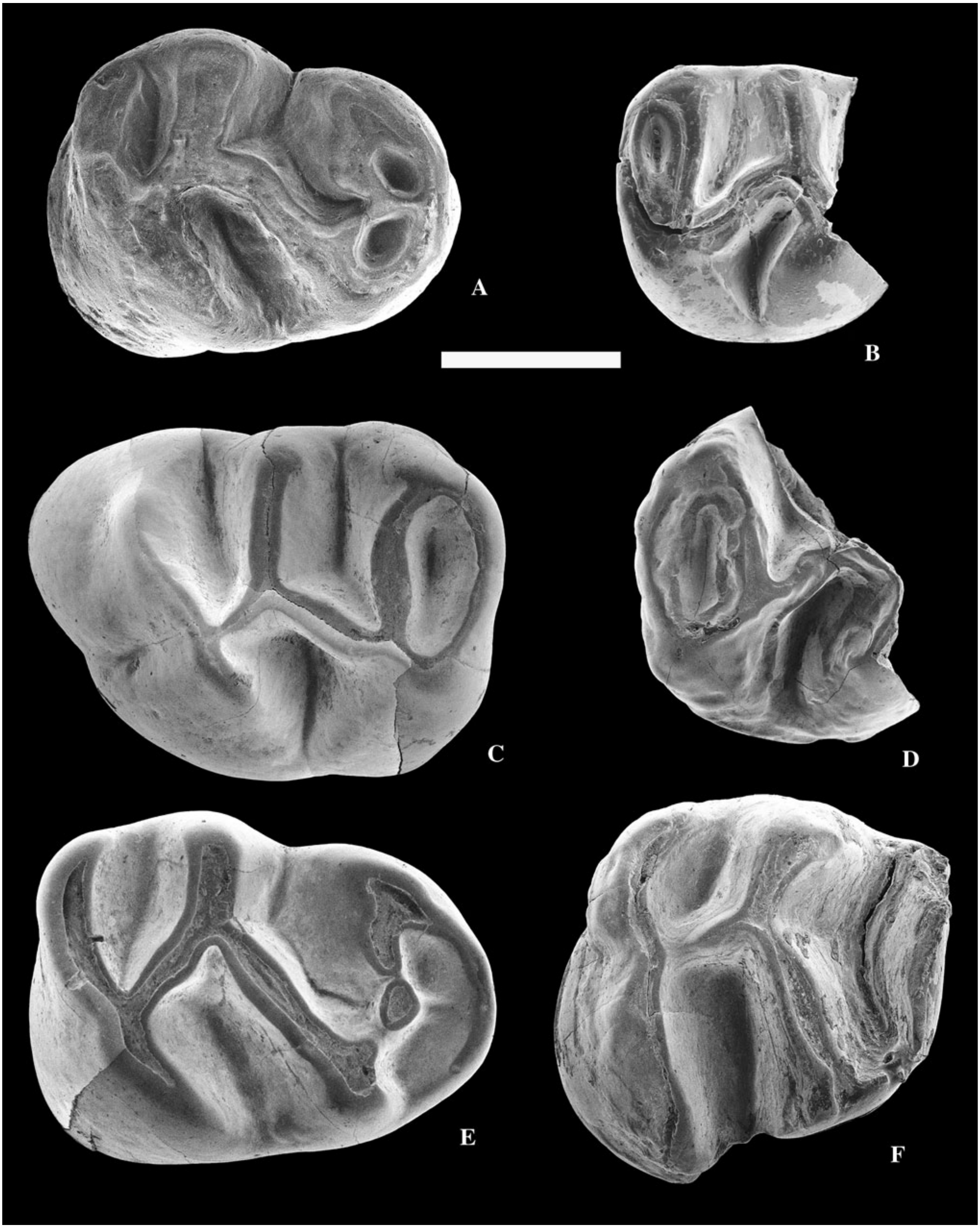

Fig. 6 Occlusal view of molars of *Tachyoryctoides* **A** right m1 (V 18178) of *T. kokonorensis*, **B–F** *Tachyoryctoides* sp. I: **B** right M1/2 (V 18180), **C** left M1 (V 18179.1), **D** right M1/2 (V 18179.2), **E** right m1 (V 18179.3); **F** right m2 (V 18179.4). *Scale bar* 1 mm

and m2 of *T pachygnathus* are longer, but more slender than those of other two species [in *T. kokonorensis* m1 (W/L): 79%, m2 (W/L): 100–105%; in *T. intermedius* m1 (W/L): 106%, m2 (W/L): 95%]. In addition, *T. pachygnathus* has a more robust mandible and larger teeth than those of *T. intermedius*. It seems premature to combine them into one species, *T. pachygnathus,* for the time being.

Kordikova and de Bruijn (2001) doubted whether *T. kokonorensis* belonged to *Tachyoryctoides* at all. Having compared the original specimens of *T. kokonorensis* with those of other species of *Tachyoryctoides*, we are convinced that *T. kokonorensis* is a species of *Tachyoryctoides*. It is close to *T. obrutschewi*, not only in the structures of mandible but also in the tooth morphology, such as the form and anterior extension of the masseteric fossa, the numbers of reentrants of the lower molars (two buccal reentrants and three lingual reentrants on m1 and m2), the enlarged mesosinusid and sinusid extending toward small protosinusid and posterosinusid, respectively. It differs from *T. obrutschewi* only in minor features: the molars are larger, m1 lacks mesolophid, and the posterosinusid of m3 is reduced. In fact, the mesolophid of the m1 is also reduced to a vestige and the posterosinusid of m3 is reduced to a small one on *T. obrutshewi*. All of these differences shown in *T. kokonorensis* seem to be slightly more advanced features. *T. kokonorensis* represents a more advanced species than *T. obrutschewi.*

Tachyoryctoides sp. I
(Fig. 6B–F)

Specimens. One left M1 (IVPP V 18179.1), 2 right M1 or 2 (V 18179.2, V 18180), 1 right m1 (V 18179.3) and 1 right m2 (V 18179.4).

Localities and geological horizons. GL 199506 in Yanwa-gou near Huang-yan-tou (V 18179) and GL 199309, 0.5 km S of GL 199308 (V 18180), Gaolan County; White Sandstone II (GL 199506) and White Sandstone III (GL 199309) of the Middle Member of Xianshuihe Formation, Early Miocene.

Description and comparison. Among the five molars listed above, the left M1 (V 18179.1) and right m1 (V 18179.3) are well preserved, and the others are broken. M1 (Fig. 6C) has well-developed sinus and three buccal reentrants, and a protosinus reduced to a narrow and shallow groove. The posterosinus is closed and the others are open. No mesoloph is visible. V 18179.2 has only its posterior part preserved. It may be M1 or M2. Its occlusal structure is similar to that of V 18179.1. The m1 has three lingual reentrants and two buccal ones, and the large mesosinusid and sinusid extending toward protosinusid and posterosinusid, respectively. All these features are almost identical to those of *Tachyoryctoides*.

Among the species of *Tachyoryctoides,* our specimens are more similar to *T. kokonorensis* and *T. engesseri* than other species due to their larger size and m1 lacking the mesolophid. However, they also differ from the two species mentioned above in M1 having a closed posterosinus and lacking a mesoloph. Furthermore, they are different from *T. engesseri* in m1 having a complete anterolophulid separating the anterosinusid from the protosinusid and M1 having a larger posterosinus; and from *T. kokonorensis* in m1 having a protosinusid open buccally. These molars may represent a new species of *Tachyoryctoides*. However, since the material is scarce, for the moment these molars are referred to *Tachyoryctoides* as species indeterminate.

V 18180 has only its posterior part preserved and may be either a M1 or a M2. It is similar to V 18179.1 and V 18179.2 in occlusal features but smaller (the width of V 18180 is 3.2 mm and those of V 18179.1 and V 18179.2 are 4 mm and 3.9 mm, respectively). V 18180 is temporarily referred to this species, too.

Tachyoryctoides spp. indet.
(Fig. 7)

Specimens. One right hemimandible with m1-2 and i2 (IVPP V 18181), one left hemimandible with i2 (IVPP V 18182), and 1 right m1/2 (IVPP V18183).

Localities and geological horizons. GL 199505, Yanwa-gou near Huang-yan-tou (V 18181), GL 199714, North of Qu-jia-chuang (V 18182), and GL 199308, 0. 5 km SW of Qu-jia-chuan (V 18183), Gaolan County; White Sandstone I of the Middle Member of Xianshuihe Formation, Early Miocene.

Description

The right hemimandible (V 18181) is an old individual. It is well preserved, but its anterior end, condylar process and angular process are broken, and only m1 and m2 are preserved. The horizontal portion is thick, with a slightly convex lower border under the molars and a vertically concave lingual surface. Its height is 11 mm at the mandibular diastema and 12.8 mm below m1 and m2. The symphysis extends antero-superiorly and forms an angle of about 45° with the lower border of the horizontal portion. The masseteric fossa extends anteriorly to below posterior part of m1. The upper masseteric ridge is weak, but the lower masseteric ridge is well developed and flared. The mental foramen is located anterior to m1, at about the same level of the anterior end of the masseteric fossa. The ascending portion is long. The coronoid process is about 8 mm in length measured at the level of the bottom of the mandibular notch. The anterior border of the coronoid process is steep and forms an angle of nearly 90° with the occlusal surface of the m1-2, and its lower part takes its

Fig. 7 Mandibles of *Tachyoryctoides* spp. **A** right hemimandible (V 18181): *A1* lingual view, *A2* occlusal view, *A3* buccal view; **B** left hemimandible (V 18182): *B1* lingual view, *B2* occlusal view, *B3* buccal view. *Scale bar* 1 cm

origin laterally to the m2. The posterior end of the incisor alveolus extends posteriorly to the mandibular notch and forms a distinct bulge on the buccal side.

The two molars are heavily worn. On m1 mesosinusid and sinusid remain only as isolated islets. The mesosinusid is <-shaped and the sinusid becomes a circular basin. On m2 only the sinusid remains as an oval basin. The i2 is robust. Its cross section is triangular, with a flat labial side and rounded lingual apex, nearly rectangular labio-medial angle but rounded labio-lateral angle. Its width is subequal to its height. The enamel is thin and mainly covers the labial side, but only slightly the lateral and medial sides. The labial surface of the enamel is flat and smooth, with two distinct lateral longitudinal ridges, one near the lateral border and the other near the medial border.

V 18181 is similar to *Tachyoryctoides* in the general structure of the mandible and incisor. However, the molars are too worn to show details allowing specific determination. In comparison to *Tachyoryctoides* sp. I represented by V 18179, the molars of V 18181 are much smaller than those of V 18179 (see Table 2). V 18181 could not belong to *Tachyoryctoides* sp. I.

The left hemimandible (V 18182) is toothless. The lower border of the horizontal portion and most parts of lower incisor and ascending portion are lost. The mandibular diastema is about 12 mm long, shorter than the total length of m1-3. As in V 18181, the masseteric fossa extends forwards to below the posterior part of m1, with a well-developed lower ridge. The anterior border of the coronoid process takes its origin laterally to the m2. The incisor is triangular in cross section as in V 18181. Its enamel is also thin and mainly covers the labial side, turns slightly on the lateral and medial sides. The labial surface of the enamel is flat and smooth, with two distinct lateral longitudinal ridges, located near the lateral and medial borders, respectively. The posterior end of the i2 extends backwards to the ascending portion, much posterior to the m3.

The hemimandible of V 18182 is similar to V 18181 in structure. But the cross section of the i2 is higher than the width, thus narrower in proportion than that of V 18181 (see Table 2). It is uncertain whether the two hemimandibles belong to the same species.

V 18183 is a right m1 or m2. Its anterior part is broken. It is similar to *T. gigas* in having weak mesolophid and a closed posterosinusid and in size (the width of the posterior part is 3.3 mm). However, it is too fragmentary to be further identified.

Discussion

Reassessment of some specimens referred to *Tachyoryctoides obrutshewi*

Bendukidze et al. (2009) suggested that *Aralomys gigas* Argyropulo, 1939, and *Aralomys glikmani* Vorontsov, 1963, are junior synonyms of *T. obrutschewi*. Having checked all the described specimens referred to *T. obrutschewi* available to us in comparison with the holotype of the species (Sh 499) we find that the m1 in all the above mentioned specimens has an anterolophulid and a short mesolophid, even if a noticeable variability was observed for these specimens (see Bohlin 1937: Fig. 103; Dashzeveg 1971: figure on 69; Bendukidze et al. 2009, Pl. 7: Fig. 4, 5, and 6). *T. gigas* is different from *T. obrutschewi* in m1 lacking an anterolophulid and *T. glikmani* differs from the holotype (Sh 499) in m1 having a well-developed mesolophid. It is to be noted that no intermediate form has been found among *T. obrutschewi*, *T. gigas* and *T. glikmani*. This inclines us to consider *T. gigas* and *T. glikmani* as valid species.

Bendukidze et al. (2009) further mentioned that the specimen referred to *Ayakozomys sergiopolis* by Tyutkova (2000, ИЗ МНВОРК, N22/269) was also referable to *T. obrutschewi*. Indeed, the drawing of N 22/260 (Tyutkova 2000, Fig. 3a) shows that it is similar to those of *T. obrutschewi* in some occlusal feature of m2/3. However, N22/260 is also similar to *Ayakozomys* in m2/3 having a transversely long and less oblique sinusid. Unfortunately, the N 22/260 is an old individual with heavily worn m2 and m3. It is hence difficult to be sure from the drawing whether the circle pit on the anterior part of m2 represents an anterosinusid or a vestige of the lingual end of the long protosinusid, and whether the posterosinusid is present or not on m2 and m3. Additionally the m1 of N 22/260 is not preserved. We are uncertain whether N22/260 should belong to *T. obrutschewi*.

Kowalski (1974) thought that *Tachyoryctoides tatalgolicus* Dashzeveg, 1971, was a junior synonym of *T. obrutschewi*. We concur with Kowalski in this regard. Although the molars of the holotype [No. 17-(1)] of *T. tatalgolicus* are slightly longer than that of *T. obrutschewi*, the occlusal features of the molars are almost identical to the latter. Kowalski (1974) also referred two specimens (MgM-III/38 and MgM-III/39) from the Late Oligocene of Mongolia to *T. obrutschewi*. MgM-III/39 is different from *T. obrutschewi* in having a well-developed mesolophid, but lacking an anterolophulid on m1. These characters render the ascription of MgM-III/39 to *T. obrutschewi* doubtful. Among the known species of *Tachyoryctoides*, MgM-III/39 is more similar to *T. gigas* and *T. engesseri* in lacking anterolophulid on m1. However, it differs from the above two species in having a well-developed mesolophid and a closed lingual notch of the antero+protosinusid on m1. Furthermore, it differs from *T. gigas* in having a closed buccal notch of the antero+protosinusid on m1 and from *T. engesseri* in being smaller in general size. This specimen may represent a new species of *Tachyoryctoides*. Since MgM-III/38 is an old individual, we are uncertain whether it should be assigned to the species. At present both MgM-III/38 and MgM-III/39 are temporarily listed as *T. obrutschewi* (?) in our Table 2.

Thus, among the species of *Tachyoryctoides* mentioned above only *T. tatalgolicus* Dashzewveg, 1971, is a junior synonym of *T. obrutschewi*, and the species, *T. obrutschewi*, includes only three populations: Sh 499 from Shargaltein-Tal in Gansu, China, No. 17-(1) from Tsagan Nor Basin, Mongolia, and some specimens from Altyn and Sayaken in North Aral area, Kazakhstan, described by Bendukidze et al. (2009) as *T. obrutschewi*.

While describing the holotype (Sh 499) of *T. obrutschewi*, Bohlin 1937, pp. 45) stated that "Der I1 erstreckt sich verhältnismässig wenig nach hinten und kommt nicht an der hinteren Bruchfläche zu Vorschein." Regarding the holotype (Sh 829*) of *T. pachygnathus*, Bohlin (1937, pp. 45) stated again: "Die Inzisiven sind stark, sie ended aber hinten ungefähr an der Bruchfläche der rechten Unterkieferhälfte (Textig. 108)."—[*Bohlin (1937, pp. 45) listed the number of the holotype of *Tachyoryctoides pachygnathus* as "Sh 829" in the Textfigg. 107—108, but as "Sh 629" in the text. Since the number "Sh 829" is written on the specimen and also listed in the Table of Bohlin (1946, pp.71), "Sh 829" is the right number]. In order to know the degree of extension of the i2 in *T. obrutschewi*, a CT scan has been performed for the holotype (Sh 499) (Fig. 8). The scan image of its parasagittal section

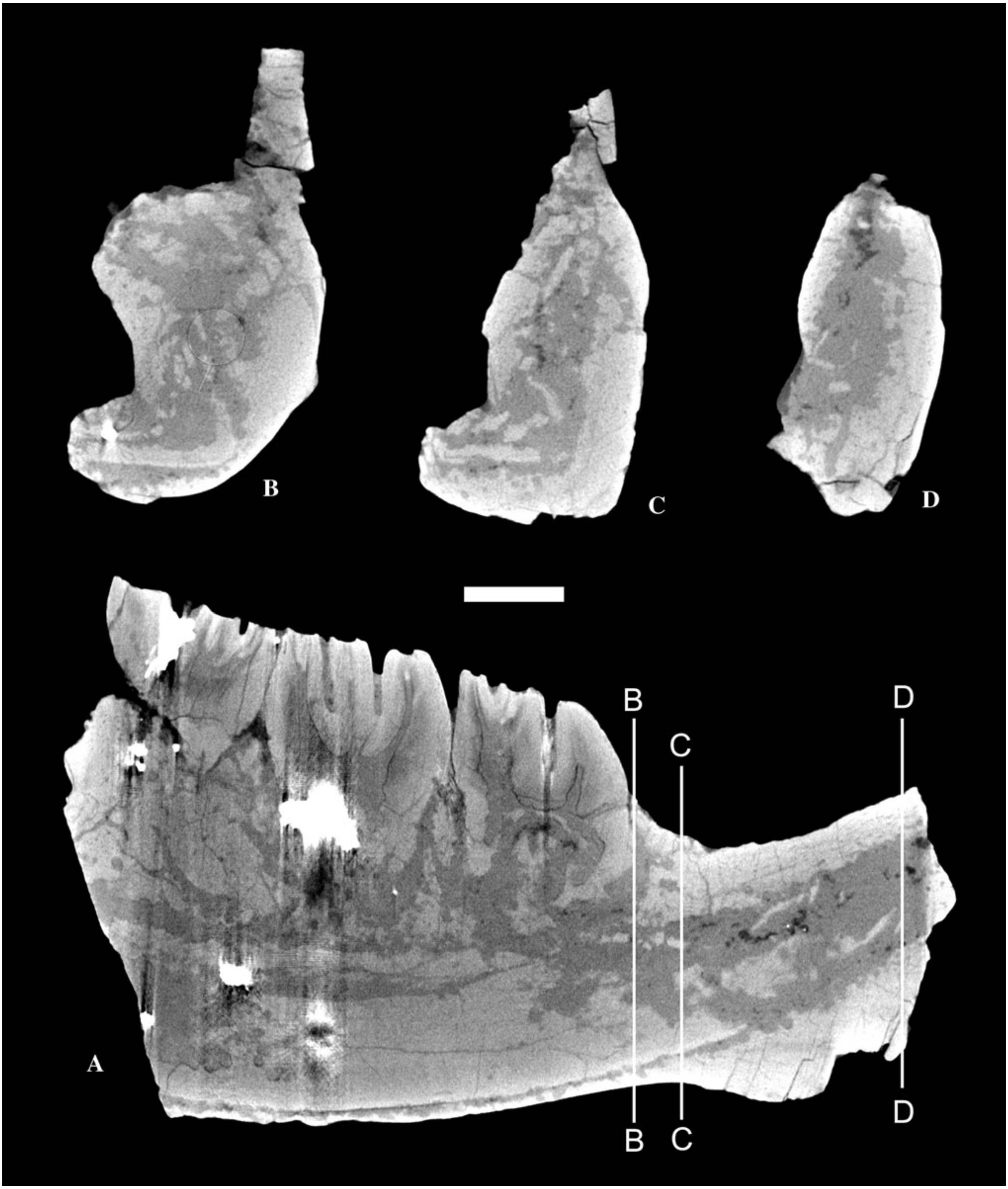

Fig. 8 CT scan images of left hemimandible (Sh 499) (*Tachyoryctoides obrutschewi*). **A** parasagittal section; **B** cross section at line *B–B*; **C** cross section at line *C–C*, **D** cross section at line *D–D*. *Scale bar* 2 mm

(Fig. 8A) shows that the i2 can be seen continuously extending to a point 2.5 mm posterior to m3 and its alveolus can extend to the posterior end of the mandible. On the cross sections, we see that the ventral dentine-enamel band of the i2 is complete at section B–B, just behind the m3 (Fig. 8B), but becomes broken at section C–C, 1.2 mm

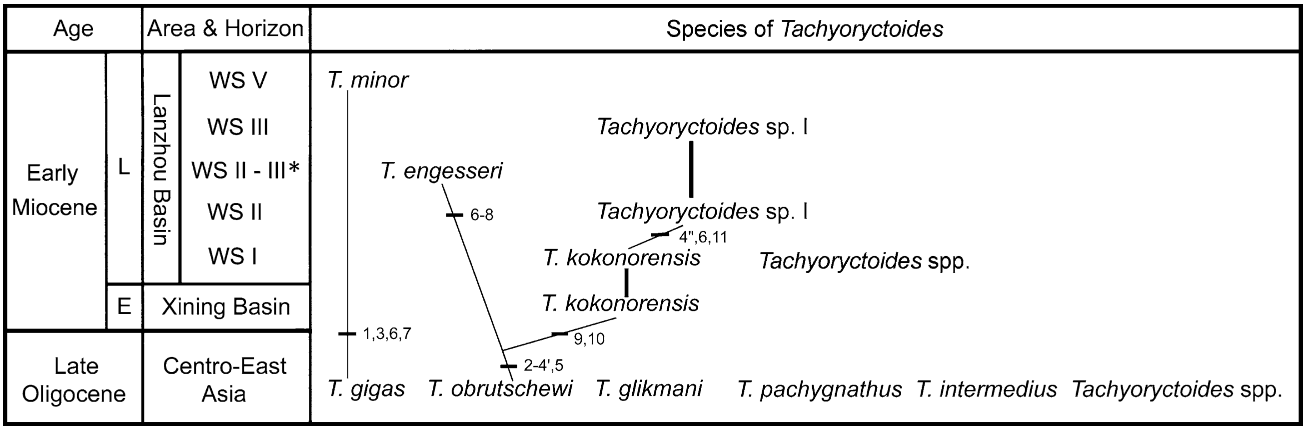

Fig. 9 Evolutionary history of *Tachyoryctoides*. *1* Decrease in size, *2* increase in size, *3* mesolophid of m1 disappears, *4* mesoloph of M1 and M2 tends to be reduced (4′) or absent (4″), *5* lingual part of aneterolophid becomes shorter and anterosinusid becomes smaller on m2 and m3, *6* the anterolophulid of m1 disappears, *7* posterior part of M3 reduced, *8* posterolophs of upper molars become shorter, *9* posterosinusid of m3 disappears, *10* M3 with closed posterosinus, *11* posterosinus of M1 and M2 becomes closed; *WS* white sandstone of middle member of the Xianshuihe Formation; *asterisk* between WS II and WS III

posterior to the m3 (Fig. 8C). Some vestiges of the broken i2 can be followed at section D—D, which is 5.4 mm posterior to the m3 (Fig. 8D). The CT images show clearly that the i2 of *T. obrutschewi* extends much more posteriorly than the m3.

In fact, all the other known mandibles of *Tachyoryctoides* (such as V 18176.1, V 18181, V 18182 and V 6000) show clearly that the posterior ends of the alveoli of i2s extend much more posteriorly than the m3, and V 18181 shows that it forms a bulge on the buccal side of the ascending portion. It seems that this feature of the i2 is also one of the diagnostic features of *Tachyoryctoides*.

Some aspects of evolutionary history of *Tachyoryctoides*

The known stratigraphic range of *Tachyoryctoides* is short, ranging from the Late Oligocene (about 28 Ma) to the Early Miocene (about 20 Ma) (Höck et al. 1999; Qiu et al. 2001). The material of known *Tachyoryctoides* is meager. Consequently, it is difficult to study the systematic relationships among the species of *Tachyoryctoides* in detail.

As shown in Fig. 9, at least five species of *Tachyoryctoides* appeared abruptly in the Late Oligocene. It is interesting to note that *T. obrutschewi* almost simultaneously occurred in the Late Oligocene in the Danghe area of Gansu Province of China, the Tsagan Nor Basin of Mongolia, and the Eastern Aral area of Kazakhstan. This could mean that *Tachyoryctoides* diversified in the Late Oligocene and that *T. obrutschewi* spread widely across eastern and central Asia. This implies that *Tachyoryctoides* may have its root earlier, in the Early Oligocene or even in the Eocene.

The interrelationships between the species can be preliminarily inferred as follows: the known species of *Tachyoryctoides*, other than *T. intermedius, T. pachygnathus* and *Tachyoryctoides* spp., seem to be subdivided into two groups. One group, comprising *T. gigas* and *T. minor*, may represent one evolutionary lineage. In this lineage the animal tends to become smaller in size, with the anterolophulid and the mesolophid of m1 tending to disappear and the posterior part of M3 getting smaller. The second group comprising four or five species, *T. obrutschewi, T. glikmani, T. kokonorensis, T. engesseri* and possibly *T.* sp. I. *T. kokonorensis, T. engesseri* and *T.* sp. I might have derived from some *T. obrutschewi*-like ancestral form and possess commonly shared tendencies (size increase, gradual disappearance of the mesolophid on m1, lingual part of anterolophid becoming shorter and anterosinusid becoming smaller on m2 and m3, and reduction of the mesoloph on M1 and M2). Of the second group, *T. kokonorensis* and *T.* sp. I might form the main sublineage, and *T. engesseri* might form a separate sublineage. In the sublineage of *T. engesseri,* the anterolophulid of m1 disappears, posterolophs of the upper molars become shorter, and the posterior part of M3 is reduced. In the second sublineage, the posterosinus of M3 closes and the posterosinusid of m3 disappears in *T. kokonorensis*, then the mesoloph disappears and the posterosinus closes on M1 and M2 in *Tachyoryctoides* sp I. So far, we are uncertain of the exact relationships between the two groups and relationships of *T. glikmani* to other species of *Tachyoryctoides.*

Systematic status of *Tachyoryctoides* within Rodentia

As to the systematic status of *Tachyoryctoides* within Rodentia, so far opinions are divergent among researchers. While establishing the genus *Tachyoryctoides*, Bohlin (1937, pp. 43) thought that it had close relationship with

Rhizomys. Accordingly, the genus was once referred to family Rhizomyidae (Simpson 1945; Bohlin 1946; Mellett 1968; Kowalski 1974). However, Argyropulo (1939) ascribed his new genus *Aralomys* (a genus normally, but not unanimously, considered synonymous with *Tachyoryctoides*) to the Cricetidae. This point of view was followed by Stehlin and Schaub (1951), Vorontsov (1963) and Dashzeveg (1971). Schaub (1958) created a new subfamily of Cricetidae, Tachyoryctoidinae, to comprise both *Tachyoryctoides* and *Aralomys*. Fejfar, (1972, pp. 190) elevated it to the family rank, Tachyoryctoididae. De Bruijn et al. (1981, pp. 76) also suggested grouping *Tachyoryctoides*, *Aralomys, Eumysodon*, *Argyromys* and one undescribed genus in a separate family, Tachyoryctoididae. Meanwhile, the Tachyoryctoidinae were variously referred to the Rhizomyidae (Chaline et al. 1977), to Spalacidae (Flynn et al. 1985), or to Cricetidae (Kordikova and de Bruijn 2001). Recently, the *Tachyoryctoides* group was considered either as a subfamily (Tachyoryctoidinae) of the family Muridae (McKenna and Bell 1997; Bendukidze et al. 2009) or an isolated family, Tachyoryctoididae (Tyutkova 2000; Lopatin 2004), or a primitive muroid excluded from Spalacidae (Flynn 2009).

Having compared *Tachyoryctoides* with the members of Rhizomyidae, Spalacidae and Cricetidae, we find that *Tachyoryctoides* is quite different from the three above-mentioned families in basic structures of the skull and mandible. *Tachyoryctoides* differs from the Rhizomyidae, Spalacidae and Cricetidae in mandibles having a strong lower masseteric ridge. Furthermore, it differs from Rhizomyidae in having the lateral masseter muscle attachment area confined to the maxilla and the glenoid fossa extending backwards to meet the occipital crest. By courtesy of Prof. Z. D. Qiu, we have observed two unpublished skulls of *Tachyoryctoides* recently collected from Nei Mongol. The skulls show that the external auditory meatus are pushed downwards below the glenoid fossa. In Rhizomyidae, the lateral masseter muscle attachment area extends from the maxilla to the premaxilla, the glenoid fossa does not extend backwards, and the external auditory meatus is located between the glenoid fossa and the occipital crest. *Tachyoryctoides* differs from Spalacidae in having a large and more obliquely positioned zygomatic plate and the pterygoid fossa is not penetrated. *Tachyoryctoides* is different from Cricetidae in having a skull lacking the interparietal. It also has a glenoid fossa extending backwards to meet the occipital crest. The mandible is also robust, with long i2 extending backwards to the ascending portion and forming a bulge on the buccal side.

As far as molars are concerned, a closer comparison is difficult, because the molars of the later, more advanced members of these families usually have a much simplified occlusal structure. However, some of their oldest representatives, such as *Prokanisamys arifi* de Bruijn et al., 1981, of Rhizomyidae, *Debruijnia arpati* Ünay, 1996, and *Heramys eviensis* Klein Hofmeijer and de Bruijn, 1985, of Spalacidae, and Eocene and Oligocene cricetids, show more differences to *Tachyoryctoides* in molar morphology.

Tachyoryctoides differs from *Prokanisamys, Debruijnia, Heramys* and earlier cricetids in molars being simple in occlusal structure, with a mesoloph (id) being much more reduced or even absent and M1 (m1) lacking distinct anterocone (id). Futhermore, it differs from Rhizomyidae in M1/2 having a transverse metaloph linking the entoloph, in m2/3 having a transverse metalophid, and a distinct anterolophulid joining the metalophid to the anterolophid. It differs from Spalacidae in M1/2 having a transverse metaloph meeting the entoloph and in m1/2 lacking a free posterior arm of the hypoconid. It differs from Cricetidae in M1 lacking a distinct anterocone and protosinus and in m1 lacking a distinct anteroconid. In addition, in earlier Cricetidae, the molars are usually brachydont and bunodont with weaker loph(id)s and have a developed mesoloph (id), and lower molars usually have a distinct mesoconid, features quite different from those of *Tachyoryctoides*.

It is necessary to point out that some of the *Tachyoryctoides* features mentioned above show clear apomorphic stages: such as the glenoid fossa extending far backwards and simple molar morphology. However, the first appearance and divergence of *Tachyoryctoides* occurred by the Late Oligocene (about 28 Ma), later than for the Cricetidae, but earlier than for the Rhizomyidae and Spalacidae, of which the oldest representatives found are no earlier than the beginning of the Miocene. *Tachyoryctoides* might be deriving from some cricetid-like ancestral forms in the Early Oligocene or Eocene, earlier than the Rhizomyidae and Spalacidae. Therefore, we agree with de Bruijn et al. (1981) and others (Tyutkova 2000, Lopatin 2004) that Tachyoryctoididae represent a separate family, distinct from Rhizomyidae, Spalacidae and Cricetidae.

While establishing Tachyoryctoidinae, Schaub (1958) listed only two genera, *Tachyoryctoides* and *Aralomys,* and considered his new genus *Argyromys* as Cricetidae *incertae sedis*. Later, the Tachyoryctoididae were suggested to include five genera (*Tachyoryctoides*, *Aralomys, Eumysodon* and *Argyromys* and one undetermined genus, see de Bruijn et al. 1981) or four taxa (*Tachyoryctoides*, *Aralomys, Eumysodon* and *Argyromys*) according to Klein Hofmeijer and Hans de Bruijn (1985). Bendukidze (1993) suggested that *Eumysodon* was a junior synonym of *Tachyoryctoides*. Tyutkova (2000) erected a new genus *Ayakozomys*, and attributed it to this family. Lopatin (2004) moved *Argyromys* to the Spalacidae. RecentlyBendukidze et al. (2009) transferred *Aralocricetodon* Bendukize, 1993, from Cricetidae to this family, so that the Tachyoryctoididae included five genera: *Tachyoryctoides, Aralomys, Eumysodon, Argyromys* and *Aralocricetodon*.

It seems to us that *Aralocricetodon* is more similar to Cricetidae than to Tachyoryctoididae in general occlusal structures of the molar and is also much smaller in size. It is better to keep *Aralocricetodon* in the Cricetidae. The systematic position of *Argyromys* remains unclear. The drawings of *Argyromys* (Argyropulo, 1939: Figure on pp. 207, Ünay, 1999: Fig. 41.2; Lopatin, 2004: Fig. 39) show some similarities with *Debruijnia, Heramys* and *Pliospalax* of the Spalacidae in some features, although they are slightly simpler in molar morphology. On the other hand, *Argyromys* has a number of characters closer to Rhizomyidae than to Tachyoryctoididae: such as the developed mesoloph(id) on molars, the oblique metaloph meeting the posteroloph on M1/2, the oblique metalophid joining the metaconid with the anterolophid on m1-3, etc. Anyway it is better to exclude *Argyromys* from the Tachyoryctoididae. Since *Aralomys* is considered by most micromammalogists as a junior synonym of *Tachyoryctoides*, the Tachyoryctoididae, as currently believed by the present authors, consists of only three genera: *Tachyoryctoides, Eumysodon,* and *Ayakozomys.*

Acknowledgments The authors are greatly indebted to Profs. Li Chuan-Kui, Wu, Wen-Yu and Qiu Zhu-Ding of IVPP for their valuable discussion and to the latter particularly for his kind permission to observe his *Tachyoryctoides* specimens recently collected from Nei Mongol. We owe a great deal to Drs. Hans de Bruijn of Faculty of Geosciences, Utrecht University, Netherlands, and Mary Dawson of Carnegie Museum, USA, for helping in finding some Russian papers unavailable in our institute, and to Dr. Larry Flynn of Harvard University, USA, for the final polishing of the English. Thanks are also given to Mrs. Xie Shu-Hua and Wang Ping of IVPP, late Will Downs of Northern Arizona University, USA, and Daniel Oppliger of Naturhistorisches Museum of Basel, Switzerland, for preparing the fossils; to Mr. Sheng Wen-Long for drawing the figure; to Mrs. Gao Wei and Zhang Wen-Ding for preparing the photos; and to Mr. Zhao Shu-Sen for preparing the CT scan images. Special thanks are extended to the anonymous reviewers, whose invaluable criticism and comments made a major contribution in improvement of our manuscript.

This work was supported by the Knowledge Innovation Program of the Chinese Academy of Sciences (KZCX2-YW-Q09), the National Natural Science Foundation of China (40730210) and the Special Researches Program of Basic Science and Technology of Ministry of Science and Technology (2006FY120400).

References

Argyropulo, A. I. (1939). New Cricetidae (Glires, Mammalia) from the Oligocene of Middle Asia. *Comptes Rendus (Doklady) de l'Académie des Sciences de l'URSS*, *23*(1), 111–114.

Bendukidze, O. G. (1993). *Small mammals from the Miocene of southwestern Kazakhstan and Turgai* (1–144). Tibissi: Menchuereba. [in Russian].

Bendukidze, O. G., de Bruijn, H., & Hoek Ostende, L. W. (2009). A revision of Late Oligocene associations of small mammals from the Aral Formation (Kazakhstan) in the National Museum of Georgie, Tbilissi. *Palaeodiversity, 2*, 343–377.

Bohlin, B. (1937). Oberoligozäne Säugetiere aus-dem Shaergaltein-Tal (Western Kansu). *Palaeontologia Sinica New Series C, 3*, 1–66.

Bohlin, B. (1946). The fossil mammals from the Tertiary deposit of Taben-buluk, Western Kansu. *Palaeontologia Sinica New Series C, 8b*, 1–159.

Chaline, J., Mein, P., & Petter, F. (1977). Les grandes lignes d'une classification évolutive des Muroidea. *Mammalia*, *41*(3), 245–152.

Dashzeveg, D. (1971). A new *Tachyoryctoides* (Mammalia, Rodentia, Cricetidae) from the Oligocene of Mongolia. In *Proceedings of the Joint Soviet–Mongolian Geological Research Expedition,* Vol. *3*, pp. 68–70. [in Russian].

Daxner-Höck, G., Badamgarav, D., & Erbajeva, M. (2010). Oligocene stratigraphy based on a sediment-basalt association in Central Mongolia (Taatsiin Gol and Taatsiin Tsagaan Nuur Area, Valley of Lakes): review of a Mongolian-Austrian project. *Vertebrata PalAsiatica, 48*(4), 348–366.

Daxner-Höck, G., Höck, V., Badamgarav, D., Furtmüller, G., Frank, W., Montag, O., Schmid, H.-P. (1997). Cenozoic stratigraphy based on a sediment-basalt association in Central Mongolia as requirement for correlation across Central Asia. In J. -P. Aguilar, S. Legendre, & Michaux, J. (Eds.), Biochronologie mammalienne du Cénozoique en Europe et domains reliés. Mémoires et Travaux de l'E.P.H.E. Institut de Montpellier, 21, 163–176.

De Bruijn, H., Hussain, S. T., & Leinders, J. J. M. (1981). Fossil rodents from the Murree Formation near Banda Daud Shah, Kohat, Pakistan. In *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen Serie B*, Vol. 81(1), 71–99.

Fejfar, O. (1972). Ein neuer Vertreter der Gattung *Anomalomys* Gaillard, 1990 (Rodentia, Mammalia) aus dem europäischen Miozän (Karpat). *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen, 141*(2), 168–193.

Flynn, L. J. (2009). The antiquity of *Rhizomys* and independent acquisition of fossorial traits in subterranean muroids. *Bulletin of the American Museum of Natural History, 331*, 128–156.

Flynn, L. J., Jacobs, L. L., & Lindsay, E. H. (1985). Problems in muroid phylogeny: relationship to other rodents and origin of major groups. In W. P. Luckett & J. -L. Hartenberges (Eds.), Evolutionary relationships among rodents—a multidisciplinary analysis. NATO ASI series A, (Vol. 92, 589–616).

Guo, Z. T., Ruddiman, W. F., Hao, Q. Z., Wu, H. B., Qiao, Y. S., Zhu, R. X., et al. (2002). Onset of Asian desertification by 22 Myr ago inferred from loess deposits in China. *Nature, 416*, 159–163.

Höck, V., Daxner-Höck, G., Schmid, H. P., Badamgarav, D., Frank, W., Furtmüller, G., et al. (1999). Oligocene-Miocene sediments, fossils and basalts from the valley of Lakes (Central Mongolia)–An integrated study. *Mitteilungen der Österreichischen Geologischen Gesellschaft, 90*, 83–125.

Klein Hofmeijer, G., & Hans de Bruijn (1985). The Mammals from the Lower Miocene of Aliveri (Island of Evia, Greece). Part 4: The Spalacidae and Anomalomyidae. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen Serie B*, *88*, 185–198.

Kordikova, E. G., & de Bruijn, H. (2001). Early Miocene rodents from the Aktau Mountains (South-Eastern Kazakhstan). *Senckenbergiana Lethaea, 81*(2), 391–405.

Kowalski, K. (1974). Middle Oligocene rodents from Mongolia. *Palaeontologia Polonica, 30*, 147–178.

Li, C. K., & Qiu, Z. D. (1980). Early Miocene mammalian fossils of Xining Basin, Qinghai. *Vertebrata PalAsiatica, 18*(3), 198–214. [in Chinese with English summary].

Lopatin, A. V. (2004). Early Miocene small mammals from the North Aral Region (Kazakhstan) with special reference to their biostratigraphic significance. *Paleontological Journal, 38*, 217–323.

McKenna, M. C., & Bell, S. K. (1997). *Classification of mammals above the species level*. New york: Columbia University Press.

Mellett, J. S. (1968). The Oligocene Hsanda Gol Formation, Mongolia: a revised list. *American Museum Novitates, 2318*, 1–16.

Qiu, Z. X., Wang, B. Y., Qiu, Z. D., Heller, F., Yue, L. P., Xie, G. P., et al. (2001). Land mammal geochronology and magnetostratigraphy of mid-Tertiary deposits in the Lanzhou Basin, Gansu province, China. *Eclogae Geologicae Helvetiae, 94*, 373–385.

Schaub, S. (1958). Simplicidentata (=Rodentia). In J. Piveteau (Ed.), *Traité Paléontologie. Tom 6. L'Origine des Mammifères et les Aspects Fondamentaux de leur Évolution* (Vol. 2). Paris: Masson et Ci.

Simpson, G. G. (1945). The principles of classification and a classification of mammals. *Bulletin of the American Museum of Natural History, 85*, 1–350.

Stehlin, H. G., & Schaub, S. (1951). Die Trigonodontie der simplicidentaten Nager. *Schweizerische Paläontologische Abhandlungen, 67*, 1–385.

Tyutkova, L. A. (2000). New Early Miocene Tachyoryctoididae (Rodentia, Mammalian) from the Kazakhstan. *Selevinia, 1–4*, 67–72. [in Russian].

Ünay, E. (1996). On fossil Spalacidae (Rodentia). In R. L. Bernor, V. Fahlbusch, & H. W. Mittman (Eds.), *The evolution of Western Eurasian Neogene mammals faunas* (pp. 246–252). New York: Columbia University.

Vorontsov, N. N. (1963). *Aralomys glikmani*—a new species of Cricetidae. *Paleontologicheskii Zhurnal, 1963*, 151–154. [in Russian].

Wang, B. Y., & Qiu, Z. X. (2000). Micromammal fossils from red mudstone of Lower Member of Xianshuihe Formation in Lanzhou Basin, China. *Vertebrata PalAsiatica, 38*(4), 255–279. [in Chinese with English summary].

Wang, X. M., Qiu, Z. D., Li, Q., Tomida, Y., Kimura, Y., Tseng, Z. J., et al. (2009). A new Early to Late Miocene fossiliferous region in Central Nei Mongol: Lithostratigraphy and biostratigraphy in Aoerban strata. *Vertebrata PalAsiatica, 7*(2), 111–134.

Wang, X. M., Qiu, Z. D., & Opdyke, D. (2003). Litho-, bio-, and magnetostratigraphy and paleoenvironment of tunggur formation (Middle Miocene) in central Inner Mongolia, China. *American Museum Novitates, 3411*, 1–31.

Wu, W. Y., Ye, J., Meng, J., Wang, X. M., Liu, L. P., Bi, S. D., et al. (1998). Progress of the study of tertiary biostratigraphy in north Junggar Basin. *Vertebrata PalAsiatica, 36*(1), 24–31.

Ye, J., Meng, J., & Wu, W. Y. (2003). Oligocene/Miocene beds and faunas from Tieersihabahe in the Northern Junggar Basin of Xinjiang. *Bulletin of the American Museum of Natural History, 249*, 568–585.

Ye, J., Wu, W. Y., & Meng, J. (2001). The age of tertiary strata and mammal faunas in Ulungur River Area of Xinjiang. *Journal of Stratigraphy, 25*(4), 283–287. [in Chinese with English abstract].

Ye, J., Wu, W. Y., Meng, J., Bi, S. D., & Wu, S. Y. (2000). New results in the study of Tertiary biostratigraphy in the Ulungur River region of Xinjiang, China. *Vertebrata PalAsiatica, 38*(3), 192–202.

Zhan, T., Guo, Z. T., Wu, H. B., Ge, J. Y., Zhou, X., Wu, C. L., et al. (2011). Thick Miocene eolian deposits on the Huajialing Mountains: the geomorphic evolution of the western Loess Plateau. *Science China Earth Science, 54*(2), 241–248.

Zhang, Z. Q., Wang, L. H., Kaakinen, A., Liu, L. P., & Fortelius, M. (2011). Miocene mammalian fauna succession from Damiao, central Nei Mongol and the environmental changes. *Quaternary Sciences, 31*(4), 608–613. [in Chinese with English abstract].