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Diversity of Moschidae (Ruminantia, Artiodactyla, Mammalia) in the middle Miocene of China

SHIQI WANG^{1,2}, QINQIN SHI¹, ZHENGCHUANG HUI³, YU LI¹, JUN ZHANG³ AND TINGJIANG PENG³

¹Key Laboratory of Vertebrate Evolution and Human Origins of Chinese Academy of Sciences, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing 100044, China (e-mail: wangshiqi@ivpp.ac.cn)

²CAS Center for Excellence in Tibetan Plateau Earth Sciences, Beijing 100101, China

³Research School of Arid Environment & Climate Change, Key Laboratory of Western China's Environmental Systems (MOE), Lanzhou University, Lanzhou 730000, China

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Abstract. In this paper, we describe newly discovered and previously collected fossil moschid specimens from the middle Miocene of China. Besides the previously reported *Hispanomeryx andrewsi*, we recognize four additional fossil species in two genera of Moschidae in the middle Miocene of China based on dental morphology: *Micromeryx* cf. *flourensianus*, *Micromeryx* sp., *Hispanomeryx* sp. 1, and *Hispanomeryx* sp. 2. The specimens are of Tunggurian age (Neogene Chinese Land Mammal Age), corresponding to European MN6–MN7/8. The records show a diversity of fossil moschids in the middle Miocene of China comparable with the contemporaneous diversity in western European faunas.

Key words: biostratigraphy, Hispanomeryx, Micromeryx, middle Miocene, Moschidae

Introduction

The family Moschidae is a group of small-sized ruminants without cranial appendages and with enlarged saber-like upper canines. The eponymous and only extant genus Moschus Gray, 1821 contains seven species that live as forest dwellers in East and Southeast Asia and the Himalayan area (Groves, 2011; Groves and Grubb, 2011). The phylogenetic position of Moschidae has long been debated. Systematic clustering based on morphological, molecular, and behavioral characters, and 'supertree' methods have been used to recover the phylogenetic relationship of Moschidae. They have been considered to be the sister group of Cervidae, Cervidae + Antilocapridae, Cervidae + Bovidae, Bovidae, or all other pecorans (Janis and Scott, 1987; Hernández-Fernández and Vrba, 2005; Vislobokova and Lavrov, 2009; Prikhod'ko and Zvychainaya, 2011). However, recent studies have confirmed Moschidae as the sister group of Bovidae, based on both morphological and molecular methods (Hassanin and Douzery, 2003; Sánchez et al., 2009, 2010).

The fossil record shows that various hornless pecorans possessing enlarged upper canines were distributed throughout Eurasia and North America from the late Oligocene to the early Miocene (Prothero, 2007). In Mongolia, the most ancient Pecora date from the early Oligocene (Vislobokova, 1997; Vislobokova and Daxner-Höck, 2002). Most of these have been tentatively included in the Moschidae (Prothero, 2007); however, recently these attributions have been debated, many researchers have excluded them from Moschidae (Vislobokova, 2007; Vislobokova and Lavrov, 2009; Sánchez et al., 2010; Costeur, 2011), and only two Miocene genera, Micromervx and Hispanomervx, are generally regarded as belonging to Moschidae. They share cranial, dental, and postcranial synapomorphies with the extant Moschus. In the dental features, p4 of Moschidae is highly modified, with an anterior valley almost enclosed by the anterolingual cristid, and with a posterolingually oblique transverse cristid. The postentocristids of the molars are well developed, and enclose the posterior ends. The m3 has a bicuspidate third lobe with a well developed postentoconulidcristid (Sánchez et al., 2010). Within the family, Hispanomeryx differs from Micromeryx in the reduction of the lower premolar tooth row and in an inclination to hypsodonty, with relatively reduced labial and lingual structures (Sánchez et al., 2010). Therefore, in Hispanomeryx, the labial side of an upper tooth and the lingual side of a lower tooth show more slender ribs and styles or stylids with a columnar

rather than a pyramidal outline (Sánchez *et al.*, 2009). Five species have been established in *Micromeryx: M. flourensianus* Lartet, 1851, *M. styriacus* Thenius, 1950, *M. mirus* Vislobokova, 2007, *M. azanzae* Sánchez and Morales, 2008, and *M. soriae* Sánchez *et al.*, 2009; and *Hispanomeryx* contains four species: *H. duriensis* Morales *et al.*, 1981, *H. aragonensis* Azanza, 1986, *H. daamsi* Sánchez *et al.*, 2010, and *H. andrewsi* Sánchez *et al.*, 2011. In this study, we describe and revise fossil Moschidae from China and integrate these results in the Eurasian context.

In China, members of Moschidae are known from Middle and Late Miocene faunas in both northern and southern China, but have been little studied. Besides Moschus grandaevus described by Schlosser (1924) and by Qiu (1979), Moschus sp. is present in the faunal list of the middle Miocene of the Tongxin area and the Linxia Basin (Guan, 1988; Deng et al., 2013), and the late Miocene of Lufeng and Yuanmou (Dong and Qi, 2013). *Micromeryx* sp. has been reported from the early, middle, and late Miocene Damiao faunas (Zhang et al., 2011), the late Miocene Amuusu Fauna (Qiu, Z-D et al., 2013), the middle Miocene Lengshuigou Fauna (Lee and Wu, 1978), and the middle Miocene Lierbao Fauna (Qiu et al., 1981). However, the descriptions and comparisons of fossil Moschidae from China have been inadequate, until the recent description by Sánchez et al. (2011) of abundant Hispanomeryx and rewsi material from the middle Miocene Tunggur Fauna (Inner Mongolia) stored in the Central Asiatic Expeditions collection of the American Museum of Natural History, New York, USA.

Recently, we found a specimen of a small ruminant in the middle Miocene strata of Nanyu quarry, northern China (Figure 1). It is an incomplete right mandible with dp4 and m1. Compared with other small ruminants, the specimen shows the greatest similarity to *Micromeryx flourensianus*. Furthermore we reexamined the material assigned to *Micromeryx* by Lee and Wu (1978), and Qiu *et al.*, (1981), mentioned above, and were able to distinguish three different species belonging to *Micromeryx* and *Hispanomeryx*.

The nomenclature of the tooth crown elements of ruminants follows Bärmann and Rössner (2011) (Figure 2). Measurements were taken on the crown surface with the anteroposterior orientation as the length and the linguolabial orientation as the width. Crown heights were obtained only from unworn or slightly worn teeth. Crown heights were measured on the labial sides of upper teeth and the lingual sides of lower ones. The hypsodonty index represents the ratio of the crown height to the width of a tooth (Janis, 1988).

Institutional abbreviations.—AMNH, American Museum of Natural History, New York, USA; SNSB-BSPG,



Figure 1. Map showing the locations of quarries in northern China that have yielded fossil Moschidae.

Staatliche Naturwissenschaftliche Sammlungen Bayern, Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; IVPP V, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; LZU, Research School of Arid Environment & Climate Change/Key Laboratory of Western China's Environmental Systems (MOE), Lanzhou University, Lanzhou, China; MNCN, Museo Nacional de Ciencias Naturales-CSIC, Madrid, Spain; MNHN, Muséum National d'Histoire Naturelle, Paris, France; NHMW, Naturhistorisches Museum Wien, Vienna, Austria.

Systematic paleontology

Order Cetartiodactyla Montgelard, Catzeflis and Douzery, 1997 Family Moschidae Gray, 1821 Genus *Micromeryx* Lartet, 1851

Type species.—*Micromeryx flourensianus* Lartet, 1851. The type material is from Sansan, France (Filhol, 1891), MN6. Type specimen has not been assigned (Aiglstorfer *et al.*, 2014).

Micromeryx cf. flourensianus Lartet, 1851

Figure 3; Table 1

Material.—A fragmentary right mandible with dp4 and m1 (LZU 201003).

Locality and age.-Nanyu quarry, Gansu Province



Figure 2. Nomenclature of tooth crown elements, after Bärmann and Rössner (2011). **A**, upper premolar (PM); **B**, upper molar (M); **C**, lower premolar (pm); **D**, lower molar (m); **E**, upper dP3/dP4; and **F**, lower dp4.

(34°40'7.5"N, 104°57'52.2"E) (Figure 1) unnamed formation of the Gansu Group, middle Miocene (Wang, S-Q *et al.*, 2013), Tunggurian (Neogene Chinese Land Mammal Age, see Qiu, Z-X *et al.*, 2013).

Description.—The dp4 (Figure 3A–C) is narrow and long. Selenodonty is well developed. The lobes increase in dimensions from anterior to posterior. The lingual rib

of the anteriolingual conid is less developed than those of the meta- and entoconids. Anteriorly, the tooth is enclosed by the connected anterior cristidae of the anterolingual conid and anterolabial conid. The posterior cristid of the anterolingual conid is fused with the premetacristid, and the posterior cristid of the anterolabial conid with the preprotocristid, respectively, forming

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Figure 3. Right dp4 and m1 of *Micromeryx* cf. *flourensianus* (LZU 201003) from Nanyu quarry. **A**, occlusal view; **B**, lingual view; and **C**, labial view.

two nearly parallel crests that do not contact. Thus, the anterior fossa and mesofossa are connected with each other by a narrow channel. A strong anterior ectostylid is present between the anterolabial conid and the protoconid. The lingual rib of the metaconid is inflated; the postmetacristid and postprotocristid are connected lingually. There is a prominent metastylid. The external postprotocristid (= Palaeomeryx-fold) is pronounced and the external postmetacristid is absent. The preentocristid is short and is connected with the posterior wall of the postprotocristid, and the prehypocristid turns lingually to meet with the preentocristid. The lingual rib of the entoconid is also inflated. The postentocristid and posthypocristid are fused posterolingually. The ectostylid is very large. Cingulidae are only weakly developed on the anterior and labial walls of the tooth.

The m1 (Figure 3A–C) is rectangular. The premetacristid and preprotocristid are connected and enclose the tooth anteriorly. The mesostylid is very weak. The lingual ribs of the metaconid and entoconid are inflated. The prehypocristid extends to touch the posterior wall of the postprotocristid. The postentocristid and posthypocristid are fused. The external postprotocristid and ectostylid are also strong.

Discussion.—As only a dp4 and a m1 are available, taxonomic identification is restricted. The size is small, and the conids are crescent-shaped rather than conical. The postentocristid is well developed and closely linked with the posthypocristid. The ectostylid is high and strong. Cingulidae are weakly developed on the anterior and labial walls. These features indicate that the Nanyu specimen belongs to *Micromeryx* (Moschidae). The distal closing of the teeth and relatively high crowns (Figure 4) exclude the Nanyu specimen from some small pecorans with similar dimensions, such as *Pomelomeryx* and *Lagomeryx* (Sánchez *et al.*, 2010; Rössner, 2010; Rössner and Rummel, 2001).

Within Moschidae, in extant *Moschus* the tooth crowns are higher (Figure 4), external postprotocristids are absent, and there are pronounced external postmetacristids on the lower molars. Therefore, the Nanyu specimen does not belong to *Moschus*. Recently, Sánchez *et al.* (2011) described *H. andrewsi* from the Central Asiatic Expeditions collection, AMNH. Compared with that species and with *Hispanomeryx* from Europe, the Nanyu specimen is considerably smaller (Figure 5), and has strong external postprotocristids that are not present in *Hispanomeryx* in general (Sánchez *et al.*, 2010). Based on these comparisons, the morphology again supports the assignment of the Nanyu specimen to *Micromeryx*.

Within the five species in Micromeryx (M. flourensianus, M. styriacus, M. mirus, M. azanzae, and M. soriae) we can easily distinguish our specimen from *M. azanzae*, because the external postprotocristids are absent in that species (Sánchez and Morales, 2008). We can also exclude it from *M. soriae*, because the external postprotocristids are broader (Sánchez et al., 2009). As the characteristic p4 is missing and there is no complete cheek tooth row retained (the premolar to molar length ratio is an important character in specific identification, see Vislobokova, 2007; Sánchez and Morales, 2008), assigning the specimen to one of the other species (or establishment of a new species) is difficult. That it is *M. mirus* is not very likely, because the crown in the latter is relatively high (Figure 4) and the external postprotocristid is relatively weak. It is difficult to compare the Nanyu specimen with M. styriacus (only known from p4 and m3), which is significantly larger in size (Thenius, 1950). This specimen possesses relatively low crowns and narrow, pronounced external postprotocristids as in M. flourensianus, therefore, we preliminarily attribute our specimen to M. cf. flourensianus, as we cannot observe

Middle Miocene Moschidae from China

taxon	cat. no.	locus	length	width at the 1st lobe	width at the 2nd lobe	width at the 3rd lobe	height at the metaconid	height at the entoconid
M. cf. flourensianus	LZU 201003	r. dp4	8.22	2.44	3.3	3.44	3.09	3.1
	LZU 201003	r. m1	6.54	4	4.26		4.03	4.32
Micromeryx sp.	IVPP V18969	r. p4	6.9	3.67	4.26		3.71	
	IVPP V18969	r. m1	7.82	4.75	5.79		4.42	4.06
	IVPP V18969	r. m2	8.11	5.54	5.88		6.1	7.27
	IVPP V18969	r. m3	11.52	5.48	5.36	4.16	7.28	7.3
Hispanomeryx sp. 1	IVPP V3028.1	l. m1	7.47	4.56	5.02		4.9	5.07
	IVPP V3028.1	l. m2	8.01	5.15	5.38		6.46	7.53
	IVPP V3028.1	l. m3	ca. 12.56	ca. 5.99	5.55	4.16		4.72
Hispanomeryx sp. 2	IVPP V6023	l. p4	6.19	3.54	3.82			
	IVPP V6023	l. m1	7.6	4.97	5.6		4.46	3.37
	IVPP V6023.1	r. m3	11.06	5.24	5.19	3.7	5.45	6.35
	IVPP V6023.2	r. m3	12.56	6.02	5.41	3.85	5.45	6.35

Table 1. Measurements (in mm) of lower cheek teeth examined in this study. r. = right, l. = left.



Figure 4. Hypsodonty indices of m1 in some small pecoran species. The top and bottom edges of each box represent the maximum and minimum values we examined. The mid-lines indicate the mean values, and the numbers represent the sample size. Data sources: Rössner, 2004, 2005, 2006; Kaiser and Rössner, 2007; Vislobokova, 2007; Sánchez and Morales, 2008; Sánchez *et al.*, 2009, 2010, 2011; collections from MNHN and NHMW; and casts from SNSB-BSPG and MNCN.

any anatomical differences from the known material.

Micromeryx sp.

Figure 6; Table 1

Material.—IVPP V18969, a right tooth row with p4–m3 (fragmentary mandible).

Locality and age.—Lengshuigou quarry? Shensi (= Shaanxi) Province (Figure 1), Lengshuigou Formation, middle Miocene, MN6 (Qiu, Z-X *et al.*, 1999, 2013; Wang, X-M *et al.*, 2013).

Description.—p4 (Figure 6B–E): The tooth is moderately worn. Both the anterior conid and the anterior stylid are anterolingually oriented. They are closely positioned. Both mesolabial and posterolabial conids are labially inflated and separated by a shallow labial groove. The mesolingual conid has an anteriorly extending anterolingual cristylid; however, the anterior valley is widely open because of the anterolingually oriented anterior conid. The transverse cristid is connected with the posterolingual cristid posteriorly. The posterior cristid and posterior stylid do not close the posterior valley.

m1 (Figure 6C–E): The tooth is deeply worn. The lingual ribs of the metaconid and the entoconid are not very inflated lingually, but the metaconid and the entoconid themselves are slightly labially inflated. The meso-, meta-, and entostylids are weak. The ectostylid is strong. Weak anterolabial cingulidae are present.



Figure 5. Bivariate plots of cheek tooth dimensions among moschids.

m2 (Figure 6C–E): The tooth is moderately worn. The metaconid and the entoconid are slightly lingually and labially inflated. The meso-, meta-, and entostylids are weak. The anterior and posterior ends are well closed by involved cristidae. The postmetacristid, postprotocristid, and preentocristid are fused in a junction, and the prehypocristid meets this junction posterolabially. The ectostylid is low and the external postprotocristid is absent. Weak anterolabial cingulidae are also present.

m3 (Figure 6A, C–E): The tooth is weakly to moderately worn. The metaconid is more lingually inflated than the entoconid; and both are labially inflated. The entoconulid is weak. The meso- and metastylids are small and the entostylid is almost absent. The ectostylid is low, but the anterior cingulid is very weak. The third lobe is well developed with equally developed hypoconulid and entoconulid. A strong stylid is present on the posterior end of the tooth, but the back fossa is not well enclosed posteriorly, showing a notch. In lingual view, the lingual ribs and stylids have pyramidal rather than columnar outlines.

Discussion.—The tooth row has never been published, but was found in the same box as *Hispanomeryx* sp. 1 from Lengshuigou quarry (described below). Thus, there is a high probability that it comes from the middle Miocene Lengshuigou Formation and was sympatric



Figure 6. Right p4–m3 of *Micromeryx* sp. (IVPP V18969) from the Lengshuigou Fauna of the Lengshuigou Formation. **A**, m3, in occlusal view; **B**, p4, in occlusal view; **C**, the tooth row, in occlusal view; **D**, lingual view; and **E**, labial view.

with Hispanomeryx sp. 1. The cristids are not as developed as those in *Hispanomeryx*; the crowns are not as high (as a result, the anterolabial cingulidae are present); the lingual structures are more pyramid-like; and the m1 and m2 are subequal in size. For these reasons we attribute it to Micromeryx. However, no external postprotocristid (= Palaeomeryx-fold) is present. This feature distinguishes the Lengshuigou specimen from known species of *Micromeryx* with external postprotocristids, such as Micromeryx flourensianus, M. styriacus, M. mirus, and M. soriae. Micromeryx lacking external postprotocristids has also been reported, such as M. azanzae from Spain (Sánchez and Morales, 2008) and Micromeryx sp. from Germany (Aiglstorfer and Costeur, 2013). The Lengshuigou specimen differs from M. azanzae in the not enclosed anterior valley in the p4 and in the not reduced third lobe of the m3. It also differs from *Micromeryx* sp. from Germany in the very open anterior valley in the p4 and in the not deep labial groove between the meso- and posterolabial conids in the p4. Here we refer the specimen to *Micromeryx* sp.

Hispanomeryx Morales, Moyà-Solà and Soria, 1981

Type species.—Hispanomeryx duriensis Morales, Moyà-Solà and Soria, 1981, from El Lugarejo, Spain, MN9 (Sánchez *et al.*, 2010).

Hispanomeryx sp. 1

Figure 7; Tables 1 and 2

Micromeryx sp. Lee and Wu, 1978, p. 131, pl. 17, fig. 1.

Material.—IVPP V3208, an upper right tooth row with P3–M3 (partial palate); IVPP V3208.1, an incomplete left mandible with m1 and m2, and a fragmentary left mandible with m3.

Locality and age.—Lengshuigou quarry, Shensi Province (Figure 1), Lengshuigou Formation, Middle Miocene, MN6, Tunggurian (Qiu, Z-X *et al.*, 1999, 2013; Wang, X-M *et al.*, 2013).

Description.—P3 (Figure 7A, B): The anterolabial and the posterolabial cones are nearly equal in size. They are well separated by a labial groove. The anterior style is prominent and the posterior style is smaller. The anterolingual cone is larger and is more lingually inflated than the posterolingual cone. They are separated by a lingual groove.

P4 (Figure 7A, B): The tooth is triangular. Both anterior style and posterior style are prominent. Only a labial cone is present with an inflated labial rib. The lingual cone is large.

M1 (Figure 7A, B): The tooth is so deeply worn that we can only distinguish a prominent mesostyle and a weak parastyle. The length is equal to the width.

M2 (Figure 7A, B): The length is slightly smaller than the width. The para- and mesostyles are strong, vertical



Figure 7. *Hispanomeryx* sp. 1 from the Lengshuigou Fauna of the Lengshuigou Formation. **A**, right P3–M3 (IVPP V3208), in occlusal view; **B**, the same specimen, in labial view; **C**, left m1 and m2 (IVPP V3208.1), in occlusal view; **D**, the same specimen, in lingual view; **E**, the same specimen, in labial view; and **F**, left m3 (IVPP V3208.1), in occlusal view.

Table 2. Measurements (in mm) of upper cheek teeth examined in this study. r. = right, l. = left.

cat. no.	locus	length	width at the 1st lobe	width at the 2nd lobe	height at the paracone	height at the metacone
IVPP V3028	r. P3	6.44	4.5	4.4	3.5	2.84
IVPP V3028	r. P4	5.45	6.26		3.08	
IVPP V3028	r. M1	7.68	7.2	7.58	3.08	3.68
IVPP V3028	r. M2	8.9	9.1	8.48	4.58	4.13
IVPP V3028	r. M3	10.11	9.81	9.19	4.87	5.25

to the labial wall. The metastyle is smaller than the paraor mesostyle and the labial rib of the metacone is absent. Columnar outlines of labial ribs and styles are observed. The anterior and posterior fossae are almost completely worn.

M3 (Figure 7A, B): This tooth (although it has been deeply worn) is the least worn one. The length is greater

than the width, and the width of the posterior lobe is smaller than that of the anterior one. The labial rib of the paracone is prominent and that of the metacone is absent. Both parastyle and mesostyle are prominent. The metastyle extends posterolabially and is turned anterolabially. There is no entostyle and the columnar outlines of labial ribs and styles are clear.

m1 (Figure 7C–E): The size is much smaller than that of m2. The lingual ribs of the metaconid and entoconid are moderately developed. The mesostylid is small and the entostylid is posteriorly oriented. However, the metastylid is relatively protruding in this specimen. The lingual cuspids (metaconid and entoconid) are flattish. The anterior and posterior ends are well enclosed by cristidae. The external postprotocristid is absent and the ectostylid is moderately developed. The tooth crown is high.

m2 (Figure 7C–E): The morphology is almost identical to that of m1, but this tooth is significantly larger in size. The ectostylid is much stronger than that of m1.

m3 (Figure 7F): The tooth is deeply worn and the anterior lobe is damaged. The third lobe is subequal to the second one. The ectostylid is large. The two conids of the



Figure 8. *Hispanomeryx* sp. 2 from the Lierbao Fauna of the Xianshuihe Formation. **A**, left m1 (IVPP V6023), in occlusal view; **B**, right m3 (IVPP V6023.1), in occlusal view; **C**, the same specimen, in lingual view; **D**, right m3 (IVPP V6023.2), in occlusal view; and **E**, the same specimen, in labial view.

third lobe are well developed with a strong entoconulid as the dominant one. The back fossa is well enclosed by the postentoconulidcristid and the posthypoconulidcristid. No external postprotocristid can be seen (but this may be as a result of the deep wear).

Discussion.—These teeth were attributed to *Micromeryx* sp. by Lee and Wu (1978). The original description is very brief. However, in our observation, the crowns of the lower molars are high; the cristids are well developed; the lingual cuspids of the lower molars are flattish; the m1 is far smaller than the m2; and the upper molars are square-shaped with straight and columnar labial ribs and styles. These features would rather indicate an assignment to *Hispanomeryx* rather than to *Micromeryx* (Sánchez and Morales, 2008; Sánchez *et al.*, 2009, 2010). The dimensions of these teeth fall into the range of *Hispanomeryx*, however, are close to the lower boundaries (Figure 5).

Of the four species of *Hispanomeryx* (*H. duriensis*, *H. aragonensis*, *H. daamsi*, and *H. andrewsi*), the first three were established based on material from Spain, and the latter from material in the Central Asiatic Expeditions collection, AMNH. This material was found in the Moergen Fauna of the Tunggur Formation (Inner Mongolia, China), dated as MN7/8, Middle Miocene, Tunggurian (Qiu, Z.-X. *et al.*, 1999, 2013; Wang, X.-M. *et al.*, 2003, 2013). We distinguish the Lengshuigou material from the European species (i.e., *H. duriensis*, *H. aragonensis*, *H. daamsi*) because of the relatively strong metastylids. The

crown morphology of the Lengshuigou material is similar to that of *H. andrewsi* in the relatively strong metastylids of the lower molars, in the vertically protruding parastyles of the upper molars, and in the labial wall of M1 not being aligned with that of M2. Here we refer to the material as *Hispanomeryx* sp. 1.

Hispanomeryx sp. 2

Figure 8; Table 1

Micromeryx sp. Qiu et al., 1981, p. 166, pl. 2, fig. 5.

Material.—IVPP V6023, left fragmentary mandible with damaged p4 and m1; IVPP V6023.1, right fragmentary mandible with m3; IVPP V6023.2, right fragmentary mandible with m3.

Locality and age.—Lierbao quarry, Qinghai Province (Figure 1), Xianshuihe Formation, middle Miocene, MN6, Tunggurian (Qiu, Z-X *et al.*, 2013; Wang, X-M *et al.*, 2013).

Description.—IVPP V6023 (Figure 8A): The remains of the anteriorly broken tooth crown show an elongated outline of a p4, by which we identify the molar as a m1 (not m2). The metastylid is tiny and posteriorly oriented. The entostylid is small and posteriorly oriented. The ectostylid is strong. Other structures have vanished as a result of wear.

IVPP V6023.1 (Figure 8B, C): The tooth crown of the m3 is high. The mesostylid is small, and the metastylid



Figure 9. Chronostratigraphic comparison of Miocene Moschidae of Europe and northern China. Data sources: Thenius, 1950; Rössner, 2004, 2005, 2006; Kaiser and Rössner, 2007; Vislobokova, 2007; Sánchez and Morales, 2008; Sánchez *et al.*, 2009, 2010, 2011; Zhang *et al.*, 2011; Aiglstorfer and Costeur, 2013; Qiu, Z-X *et al.*, 2013; Wang, X-M *et al.*, 2013; and this study.

and entostylid are very weak. Lingual ribs are very weak or absent. The ectostylid is low and the external postprotocristid is absent. The back fossa is well enclosed by a postentoconulidcristid and a posthypoconulidcristid. The entoconulid is smaller than the hypoconulid. Weak anterolabial cingulidae are present.

IVPP V6023.2 (Figure 8D, E): The morphology of this m3 is similar to IVPP V6023.1 but the size is larger. The third lobe is more developed than that of IVPP V6023.1 with a pronounced entoconulid.

Discussion.—As in IVPP V18969, the significant tooth crown height, the reduced and columnar structure of the lingual stylids and ribs, and the lack of an external postprotocristid are consistent with *Hispanomeryx* and differ from *Micromeryx*. The size of these teeth is relatively small in *Hispanomeryx* (Figure 5). We exclude this

material from *H. andrewsi* because of the very weak metastylids and from *H. aragonensis* because of the well enclosed posterior lobes of m3. It is also not *H. daamsi* because the prehypocristid is not in contact with the preentocristid. The material differs from *Hispanomeryx* sp. 1 in the poor development or absence of metastylids. It is difficult to compare the material with *H. duriensis* because no p4 of the present material was found. In *H. duriensis* the transverse cristid is absent (Morales et al., 1981; Sánchez *et al.*, 2011). Here we refer to this material as *Hispanomeryx* sp. 2.

Biochronological range of Miocene Moschidae in northern China

The well established Asian biochronological framework (Qiu, Z-X et al., 2013; Wang, X-M et al., 2013)

enables us to perform faunal correlation and comparison with both global geochronology (Hilgen et al., 2012) and European biochronology (Steininger, 1999; Mein, 1999). The earliest Moschidae from China were reported by Zhang et al. (2011), who identified early Miocene *Micromeryx* sp. from locality DM 16 of Damiao, Xiejia age (as early as MN1 or MN2). As the identification was based only on very few, fragmentary specimens (Zhang, personal communication), we question whether *Micromeryx* appeared as early as they determined. Besides this finding, the first known occurrence of *Micromeryx* in northern China may be in MN6 (Figure 9). The precise dating of the Nanyu quarry is currently under study (Song, personal communication). In the same quarry, an incomplete mandible of Gomphotherium wimani has been reported (Wang, S-Q et al., 2013). Gomphotherium wimani has previously been found in the Xianshuihe Formation, which is correlated with MN6 (Hopwood, 1935; Wang, X-M et al., 2013). We also found G. wimani in the Shinanu Fauna of the Linxia Basin, MN6 (Deng et al., 2013). Therefore, the Nanyu quarry may be also correlated with MN6, as is Sansan, the type locality of *M. flourensianus*. In Europe, *M.* flourensianus ranged from MN5 to MN7/8 (Rössner, 2004, 2005, 2006; Kaiser and Rössner, 2007). The Lengshuigou Fauna is correlated with MN6 (Qiu et al., 1999; Wang, X-M et al., 2013), and contains Micromeryx sp. Sánchez et al. (2011) reported the occurrence of *Micromeryx* in Tunggur, MN6 (perhaps from the same fauna as H. andrewsi), but this material is still under study. Zhang et al. (2011) reported Micromeryx sp. from localities DM01 and DM02 of Damiao (this taxon has a range from MN 7/8 to MN9). Qiu, Z-D et al. (2013) also reported *Micromeryx* sp. from the Amuwusu Fauna, MN9. These two localities may contain the latest occurrences of Micromeryx so far known in northern China (Figure 9).

The first occurrence of *Hispanomeryx* (*Hispanomeryx* sp. 2) in northern China is in the Lierbao Fauna of the Xianshuihe Formation, which has been correlated with MN6 (Qiu *et al.*, 1981; Wang, X-M *et al.*, 2013). *Hispanomeryx* sp. 1, described herein from the Lengshuigou Fauna, is another *Hispanomeryx* species recorded from MN6 of China. The latter species was discovered in the Moergen Fauna of Tunggur, MN7/8 (Sánchez *et al.*, 2011); this is the latest known occurrence of *Hispanomeryx* in China (Figure 9).

Conclusions

In this study, we report on a new specimen of *Micromeryx*. This genus has been little known and little studied in China until recently. In addition, we reevaluate

previously reported material of the genus. We attribute these materials to four species in two different genera: Micromeryx cf. flourensianus, Micromeryx sp., Hispano*meryx* sp. 1, and *Hispanomeryx* sp. 2. They can be clearly distinguished from each other using various dental features. With the previously reported H. andrewsi (Sánchez et al., 2011), the occurrence of at least five fossil species of Moschidae in China is proven, a diversity comparable to the contemporaneous diversity in European faunas. However, in the Late Miocene the record of Moschidae is very poor, and the group survives not later than MN9 in northern China, in contrast to the still highly diversified Moschidae in Europe. This may have been caused by the aridity of the climate in the Late Miocene of eastern Asia, induced by the rapid uplift of the Tibetan Plateau (Guo et al., 2004). However, further studies of fossil moschids are needed to get a clearer idea.

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