A Late Miocene Huerzelerimys (Rodentia: Muridae) skull from Hezheng, Gansu, China postprint

Authors: WANG Ban-Yue, QIU Zhan-Xiang, Li Lü-Zhou

Date: 2020-03-31T00:00:00+00:00

Abstract

A skull with mandible and several cervicals of a new species of Huerzelerimys, H.asiaticus, collected from the Late Miocene Liushu Formation in Linxia Basin, Gansu Province,is described in this paper. The skull is the first one ever found for the genus Huerzelerimys. Its main characters are: size small; skull broad and short with stout rostrum; interorbital roof narrow;premaxillary laterodorsal crest well developed; frontal crests weak and subparallel; incisive foramina long, with their posterior ends lined up with anterior root of M1; posterior palatal foramina located mesial to M2; caudal border of hard palate lying posterior to M3;interpterygoid foramen absent; alisphenoid canal bony; bulla large and inflated; internal carotid foramen located near the basilar tubercle; mandible having low horizontal ramus and deeply concave diastema; anterior end of masseteric ridge lined up with anterior margin of m1; mental foramen situated slightly anterior to masseteric ridge and anteroventral to m1, near to mandibular diastema; upper incisors orthodont; M1 having slightly anteriorly located t1; in M1 and M2 t6 and t9 connected by distinct crest and t12 crest-like; t1 and t3 of M2 and t1 of M3 connected to t5; M3 having t3 and a large isolated t8; small Acc of m1 connected with both Alc and Abc; m1 and m2 having distinct buccal cingula, larger c2 attached to protoconid, and low crest-like posterior heel; m2 and m3 having isolated Abc; c1 absent in m3. The evolutionary level of the described skull tends to show that the age of the upper part of the Liushu Formation yielding H. asiaticus may belong to late Bahean, corresponding to European upper MN11 or lower MN12.

Full Text

Preamble

A Late Miocene Huerzelerimys (Rodentia: Muridae) skull from Hezheng, Gansu, China

WANG Ban-Yue[1], QIU Zhan-Xiang[1], LI Lü-Zhou[2,3]

[1]Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing 100044, China (wangbanyue@ivpp.ac.cn)
[2]School of Earth and Space Sciences, Peking University, Beijing 100871, China
[3]State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing 210008, China

Abstract

This paper describes a skull with mandible and several cervical vertebrae of a new species of *Huerzelerimys*, *H. asiaticus*, collected from the Late Miocene Liushu Formation in the Linxia Basin, Gansu Province. The skull represents the first ever discovered for the genus *Huerzelerimys*. Its main characters are: small size; broad and short skull with a stout rostrum; narrow interorbital roof; well-developed premaxillary laterodorsal crest; weak, subparallel frontal crests; long incisive foramina with posterior ends aligned with the anterior root of M1; posterior palatal foramina located mesial to M2; caudal border of hard palate lying posterior to M3; interpterygoid foramen absent; alisphenoid canal bony; bulla large and inflated; internal carotid foramen located near the basilar tubercle; mandible with low horizontal ramus and deeply concave diastema; anterior end of masseteric ridge aligned with anterior margin of m1; mental foramen situated slightly anterior to masseteric ridge and anteroventral to m1, near the mandibular diastema; upper incisors orthodont; M1 with slightly anteriorly located t1; in M1 and M2, t6 and t9 connected by distinct crest and t12 crest-like; t1 and t3 of M2 and t1 of M3 connected to t5; M3 with t3 and a large isolated t8; small Acc of m1 connected with both Alc and Abc; m1 and m2 with distinct buccal cingula, larger c2 attached to protoconid, and low crest-like posterior heel; m2 and m3 with isolated Abc; c1 absent in m3. The evolutionary level of the described skull suggests that the age of the upper part of the Liushu Formation yielding *H. asiaticus* may belong to the late Bahean, corresponding to European upper MN11 or lower MN12.

Key words: Hezheng, Gansu; Late Miocene; Liushu Formation; *Huerzelerimys*, Murinae

Citation: Wang B Y, Qiu Z X, Li L Z, in press. A Late Miocene *Huerzelerimys* (Rodentia: Muridae) skull from Hezheng, Gansu, China. *Vertebrata PalAsiatica*. DOI: 10.19615/j.cnki.1000-3118.200319

Huerzelerimys is a genus of Murinae that lived in Eurasia during the Late Miocene. In the past, fossils of *Huerzelerimys* were mainly found in Europe, with only recent discoveries in Asia (Mein et al., 1993; Qiu and Li, 2008). However, most known fossils consist of isolated teeth, with only a few fragmentary jaws. In 2005, a skull with mandible and several cervicals of *Huerzelerimys* were collected from the Late Miocene Liushu Formation in the Linxia Basin, Gansu Province by a field team from the IVPP (Institute of Vertebrate Paleontology

and Paleoanthropology, Chinese Academy of Sciences). This skull is the first ever found among *Huerzelerimys* fossils and provides important new information about this genus.

The skull morphological terminology follows Greene (1935), Yang et al. (1985), and Wang and Qiu (2018), and the molar terminology follows Qiu and Li (2016) (Fig. 1 [Figure 1: see original paper]).

Fig. 1 Nomenclature used for molars of Muridae. Abc: anterobuccal cusp; Acc: anterocentral cusp; Alc: anterolingual cusp; c1 c3: accessory cusps; End: entoconid; Hyd: hypoconid; Ls: longitudinal spur; Med: metaconid; Ph: posterior heel; Prd: protoconid; t1 t12: tubercles; t1bis and t2bis: appendices to t1 and t2 (After Qiu and Li, 2016)

1 Systematic Paleontology

Family Muridae Gray, 1821
Subfamily Murinae Gray, 1821
Genus *Huerzelerimys* Mein et al., 1993

Type species: *Parapodemys vireti* Schaub, 1938.

Diagnosis (adopted from Mein et al., 1993): "Molars smaller than or similar in size to those of extant *Rattus rattus*, with poor development of the longitudinal connection between tubercles. Upper molars without t7, but with t4 and t8 connected by a weak crest. M1 and M2 with a well-developed t9, and with t6 and t9 united in more than 50% of specimens. M3 without t9. The m1 with a reduced tma (= Acc), and with a connection between the two anterior pairs of tubercles; three roots; cingular margin moderately developed. Tendency towards strong size increase in the course of time."

***Huerzelerimys asiaticus* sp. nov.** (Figs. 2 5; Tables 1 2)

Holotype: A complete skull with mandible and 5 cervicals (IVPP V 16288).

Locality and horizon: Niuzhawan, Sanhe Village, Hezheng County (IVPP Loc. LX 200503), Linxia Hui Autonomous Prefecture, Gansu Province, China; upper part of the Liushu Formation, Late Miocene late Bahean ALMA/S (Asian Land Mammal Age/Stage), about 8 Ma.

Diagnosis: Small-sized *Huerzelerimys*. Skull broad and short with short, broad rostrum, narrow interorbital roof, more developed premaxillary laterodorsal crest, weak and subparallel frontal crests; incisive foramen long, terminated posteriorly near the anterior root of M1; paired posterior palatal foramina situated mesial to M2; posterior border of hard palate lying posterior to M3; interpterygoid foramen absent; alisphenoid canal bony; bulla large and inflated; internal carotid foramen located near the basilar tubercle; horizontal ramus of mandible low, having a deeply concave diastema; masseteric ridge extending anteriorly below the anterior margin of m1; mental foramen situated anteroventral to m1, anterior to the masseteric ridge, and near mandibular diastema.

I2 orthodont; M1 with slightly anteriorly located t1; M1 and M2 with t6 and t9 connected by distinct crest and crest-like t12; t1 and t3 of M2 and t1 of M3 connected with t5; M3 with t3 and a large isolated t8; m1 with small Acc connected with both Alc and Abc; m1 and m2 having distinct buccal cingula, larger c2 attached to protoconid, low and crest-like posterior heel; m2 and m3 having isolated Abc; c1 absent in m3.

Etymology: Asia, name of the continent where the fossil was collected.

2.1 Skull

The skull is well preserved, but the zygomatic arches are broken and the posterior part of the skull is damaged. The cranial bone sutures are obscure, especially those on the skull roof (Fig. 2 [Figure 2: see original paper]).

The skull is small-sized among muroid rodents, with a myomorphous zygomasseteric structure. It is relatively short and broad, with a condylobasal length subequal to that of a small-sized *Rattus* (*R. rattus*). The rostral part is rather short and broad relative to the cranial part, and the length of the maxillary diastema is slightly shorter than the height of the middle part of the skull.

Dorsal view: The skull is roughly oval in outline. As in *Rattus*, the rostrum is rather short and broad, with its two lateral sides slightly convergent forwards. The rostral end is nearly as wide as the interorbital part. The nasal (N) is wedge-shaped and, caudally, is lined up with the posterior end of the premaxillo-frontal sutures. The premaxillary laterodorsal crest (pmldc) is well developed, nearly parallel to the naso-premaxillary suture, and separates the premaxilla (Pm) into dorsal and lateral parts. The dorsal part of the premaxilla is narrow and long, forming a strip. The premaxillo-frontal suture is strongly serrated, extending anterolaterally to meet the premaxillo-maxillary and maxillo-frontal sutures. The posterolateral end of the maxillo-frontal suture extends to the lacrimal (L). The lacrimal is situated mainly in the orbit, exposed only a little on the dorsal side, forming a distinct lacrimal tubercle (lt) at the anteromesial corner of the orbit. The coronal suture is convex posteriorly. The dorsal parts of the parietals (P) are slightly convex and much broader than those of the frontals (F). The parietals are displaced about 0.5 mm to the right side relative to the frontals, so that the parietal suture and the frontal suture are not in the same longitudinal line. The interparietal (Ip) is a large bone, elliptic in outline and wider than long.

As in other murines, the frontal crest (fc) extends backwards to the crista supratympanica (cst). The two slightly curved frontal crests are roughly parallel with each other as in *Rattus*, but not as well developed as in the latter. Though broken away, the zygomatic arches must be slender and their anterior roots are situated in front of the posterior ends of the nasal and premaxilla.

Lateral view: The skull roof is convex dorsally. The anterior ends of the nasal and premaxilla are situated almost in the same vertical line. The diastema

is much longer than the length of the upper molar row. The anterior part of the skull (anterior to M1) is shorter and lower than the posterior part of the skull (including M1), only about 1/2 as long as the latter. The lateral part of the premaxilla, bordered anterodorsally by the arched pmldc, is broad and slightly concave. The premaxillo-maxillary suture runs roughly vertically in front of the infraorbital foramen. The infraorbital foramen (iof) lies within the maxilla (M), having an oval upper part and an infraorbital fissure below. The masseteric tubercle (mt) is located below the infraorbital fissure. The insertion of the masseter profundus is confined within the infraorbital foramen. The zygomatic plate is located ventrolateral to the infraorbital foramen and its surface is concave, facing anteroventrally and laterally.

The posterior border of the large orbit is formed by the squamosal (Sq). The distinct temporal crest (tc) extends to the crista supratympanica (cst). The ventral surface of the large auditory bulla (ab) is lower than that of the occipital condyle (occ). The external auditory meatus (eam) is formed by a very short bony tube. The stylomastoid foramen (styf) is located behind the external auditory meatus and above the mastoid process (msp). The nuchal surface is vertical and convex posteriorly. The left petromastoid portion (Pms = os mastoideum) is preserved, nearly round in outline with a convex surface. The mastoid foramen (msf) is situated at the mesosuperior corner of the petromastoid portion.

In the orbital area, several foramina can be observed. The optic foramen (opf) is large and located above M3. The ethmoidal foramen (etf) is small, situated anterosuperior to the optic foramen and above M2. The area below the etf and anteroventral to opf is broken, thus the sphenopalatine foramen cannot be identified. The foramen rotundum (fr) is located ventroposterior to the optic foramen and superoposterior to M3. Differing from *Rattus* but similar to *Apodemys*, the alisphenoid canal (asc, canalis alisphenoidale) is a bony canal penetrating the pterygoid. The anterior foramen of the alisphenoid canal (aasc) opens on the lateral side of the external pterygoid process (epp). The large foramen ovale (fo) penetrates the superoposterior part of the external pterygoid process, confluent with the posterior foramen of the alisphenoid canal (pasc).

Ventral view: The incisive foramen (inf) is very long, about 4/5 as long as the diastema, extending posteriorly to the level of the anterior root of M1. The zigzag premaxillo-maxillary suture intersects the incisive foramen at around the anterior 1/3 of the foramen. The zygomatic plate is broad and concave, extending anterodorsally and facing anteroventrally and laterally. The masseteric tubercle (mt) is located at the anteromesial corner of the zygomatic plate, behind the premaxillo-maxillary suture. The left and right cheek tooth rows are nearly parallel to each other. The posterior palatine foramen (ppf) is situated within the palatine (Pl), lying mesial to M2. The distinct palatine sulcus (ps) extends to the ppf. The posterior border of the hard palate is located behind M3. The mesopterygoid fossa (mptf) is subequal to the pterygoid fossa (ptf) in width. In the pterygoid fossa, no interpterygoid foramen (or sphenopterygoid vacuity) is observed. The middle lacerate foramen (mlf) is located at the mesioposterior

corner of the pterygoid fossa. The glenoid fossa (glf) is formed by the zygomatic process of the squamosal and is transversely concave. The postglenoid foramen (pgf) is long and large, extending along the petro-squamosal suture on the posterior part of the glenoid fossa. The auditory bulla is very large (about 1/5 of the condylobasal length) and strongly inflated. No bony septum is present in the broken bulla. The foramen of the Eustachian canal (eucf) opens anteromesially to the bulla. On the mesial side of the bulla, the internal carotid foramen (icf) is located on the anterior 1/3 of the bulla, nearly at the same transverse level as the basilar tubercle (bt). The jugular foramen (juf) is located between the bulla and occipital. There is a distinct stapedial foramen (stf) at the mesioposterior corner of the bulla as in *Rattus* (Guthrie, 1963). The hypoglossal foramen (hyf) is located anterolateral to the occipital condyle.

Table 1 Measurements of skull and mandible of *Huerzelerimys asiaticus* sp. nov. (IVPP V 16288, holotype)

2.2 Mandible

The left and right hemimandibles are well preserved, with only the tops of the coronoid processes broken away. The mandible is sciurognathous. The horizontal ramus is low, with its diastema deeply concave. As in *Rattus* and *Huerzelerimys exiguus*, the masseteric ridge (mr) extends anteriorly to below the anterior margin of m1. The mental foramen (mtf) is located anteroventral to m1, lying near the diastema and anterior to the masseteric ridge (Fig. 3 [Figure 3: see original paper]).

The ascending ramus of the mandible is long. The anterior border of the coronoid process (crp) rises from the buccal side of the mandible below the anterior part of m2, and its upper part curves slightly posteriorly. The condyloid process (cdp) is slightly lower than the coronoid process. The articular facet of the condyle is narrow-ovoid in shape, much longer than wide.

The mandibular notch (mn) is very shallow. On the buccal side of the ascending ramus, the masseteric fossa (mstf) is broad. The bulge (i2b) formed by the posterior end of the lower incisor alveolus is prominent and situated below the mandibular notch on the buccal side. The angular process (ap) extends posteriorly below the condyloid process. On the lower half of the lingual side of the ascending ramus, the internal pterygoid fovea (iptf) is large and triangular in shape, with its anterior angle reaching below m2 and the large posterior portion deeply concave, which is sharply bordered by curved upper and lower ridges. The slightly concave temporal fovae (tf) is located in the lower part of the coronoid process and posterolateral to m3. The mandibular foramen (mdf) is situated below the mandibular notch, and the external pterygoid fovea (eptf) is slightly concave, lying anteroinferior to the condyloid process.

Fig. 3 Mandible of *Huerzelerimys asiaticus* sp. nov. (IVPP V 16288, holotype) from Hezheng, Gansu. A1–3: left mandible; B1–3: right mandible; A1, B1: occlusal view; A2, B2: buccal view; A3, B3: lingual view

2.3 Teeth

The dental formula is $1 \cdot 0 \cdot 0 \cdot 3/1 \cdot 0 \cdot 0 \cdot 3$. The molars are brachyodont and rooted, and are moderately worn (Fig. 4 [Figure 4: see original paper]). The M1 is oval-shaped (Width/Length = 0.65, 0.67). The t1 is rounded in outline and located slightly anteriorly, with its anterior border nearly opposite the posterior part of t3, and connected with the larger t2 by a crest. The t3 is smaller than t1 and t2. No t1bis is present. The t1 and t3 have no spurs extending to t5. The t5 is connected with t4 and t6 by distinct crests, with the crest between t4 and t5 lower than that between t5 and t6. The t4 and t8 are connected by a low crest. No t7 is present. The t9 is well developed and connected with t6 by a distinct crest, and the t12 is crest-like.

The M2 is round-angled triangular in outline, with three roots. The t1 is rounded. The t3 is much smaller than t1, and both connect with t5. The t9 is slightly larger than t3 but smaller than t6. Other features are similar to M1.

The M3 is more triangular than M2 in outline, also with three roots. The t1 is smaller than t4 and connected to t5. The t3 is present but very reduced. The t8 is large and isolated. The t9 is absent.

The m1 is ovoid in outline. The anterolingual cusp (Alc) and anterobuccal cusp (Abc) are subequal in size and connected with each other, with the Alc extending slightly more anteriorly than the Abc. The small anterocentral cusp (Acc) (= tma, medial anteroconid) is heavily worn and attached to both the Abc and Alc. The Alc is connected with the metaconid. The metaconid and entoconid extend transversely, while the protoconid and hypoconid extend buccoposteriorly. The posterior pair of tubercles (hypoconid and entoconid) is separated from the second pair of tubercles (protoconid and metaconid), without longitudinal crest or longitudinal spur (Ls) connecting the two pairs. The buccal cingulum is developed, with distinct accessory cusps on it. Among them, c1 is the largest, and c2 is larger than c3 and attached to the protoconid. The posterior heel (Ph) (= pc, posterior cingulum) is low and crest-like, joining with the entoconid and hypoconid.

On the m2, the Abc is oval-shaped and isolated. The Alc is absent. There is no longitudinal connection between the two posterior pairs of tubercles. The buccal cingulum is broken off. The c2 is smaller than Abc but larger than c1, and attached to the protoconid. The posterior heel is low and crest-like, joining with the entoconid and hypoconid.

On m3, the Abc is reduced to a small, isolated cusp. The protoconid is connected with the metaconid to form a transverse crest. The c1 is absent.

The I2 is orthodont and bends strongly, with its anterior part extending ventrally. The cross-section of I2 is triangular in outline, longer than wide, with its labial side convex. The enamel layer covers the whole labial side and parts of the mesial and lateral sides. The labial surface is smooth without ridges. No gap is

seen on the lingual side.

The i2 is slightly curved in longitudinal direction, with its anterior portion turning anterodorsally. The i2 originates in the ascending ramus of the mandible, forming a bulge on the buccal side. The cross-section of i2 is narrow-ovoid, with convex labial and lateral sides but a narrow, rounded lingual angle. The enamel covering is similar to that of I2.

Fig. 4 Occlusal view of molars of *Huerzelerimys asiaticus* sp. nov. (IVPP V 16288) from Hezheng, Gansu. A1: right M1 3; A2: left M1 3; B1: left m1 3; B2: right m1 3

Table 2 Measurements of teeth of *Huerzelerimys asiaticus* sp. nov. (IVPP V 16288, holotype) (mm)

2.4 Cervical Vertebrae

The five cervical vertebrae (C3 C7) are in quasi-articulated states and well preserved, except C3 and C7 which are more or less damaged. They are similar to each other in general morphology: the body assumes a flattened cylinder shape; the dorsal part of the vertebral arch is bow-shaped, with the spinous process (sp) low, its pedicle short, the pre- and post-zygapophyses (przy and pzy) originating from the pedicle, and the transverse process (trpr) from the lateral side of the pedicle. In C3 C6, the transverse processes have two roots and a large transverse foramen (trf), while in C7 the transverse process has only one large root and lacks the transverse foramen. The transverse process extends posterolaterally in C3–C5, but transversely in C6 with its enlarged lateral part separated into two laminae [lamina ventral vertebrae cervical VI (lvvc) and lamina dorsal vertebrae cervical VI (ldvc)] (Fig. 5 [Figure 5: see original paper]).

Measurements: Total length of vertebral bodies of C4 C7: 6 mm; vertebral fossa of C7 is 0.8 mm in height and 1.8 mm in width; width of C7 at transverse process: 5 mm; width of C4 at prezygapophysis: 4.6 mm.

Fig. 5 Cervical vertebrae of *Huerzelerimys asiaticus* sp. nov. (IVPP V 16288, holotype) from Hezheng, Gansu. A: dorsal view; B: left lateral view; C: anterior view; D: posterior view

3.1 Skull Morphology Compared with Other Murines

As described above, the skull of IVPP V 16288 has a myomorphous zygomasseteric structure, with the infraorbital foramen specialized into a wide upper portion and a narrow infraorbital fissure. The zygomatic plate is broadened and located ventrolateral to the infraorbital foramen and tilted upward. The frontal crest extends backwards to the crista supratympanica, and the mandible is sciurognathous. The cheek teeth are brachyodont with roots, and the crown

cusps are arranged in three longitudinal rows. All these characters clearly show that V 16288 belongs to the Murinae.

Among murines with known skulls, V 16288 is more similar to *Rattus* than to any other murines such as *Apodemys*, *Micromys*, *Leopoldamys*, *Maxomys*, *Niviventer*, etc., as evidenced by the following characters: relatively broad and short rostrum, moderate interorbital constriction, rather broad braincase, very long incisive foramen extending to the level of the anterior part of M1, posterior part of hard palate extending slightly behind M3, and large, strongly inflated bulla (Ellerman, 1941; Huang et al., 1995; Pan et al., 2007). However, V 16288 also differs from *Rattus* in having a more developed premaxillary laterodorsal crest, weaker frontal crest, bony alisphenoid canal, and lacking an interpterygoid foramen in the pterygoid fossa. In dentition, V 16288 further differs from *Rattus* in having more brachyodont molars, M1 and M2 with crests linking t4 with t8 and t6 with t9 and having t12, and m1 with anterocentral cusp and subequal Alc and Abc. Obviously, V 16288 represents a distinct genus, more primitive than *Rattus*.

3.2 Tooth Features Compared with Murines Known Only by Teeth

Some murine genera are known only from teeth. Compared with those genera, IVPP V 16288 is more similar to *Progonomys* and *Huerzelerimys* than to others in the following characters: molars more brachyodont, upper molars with high connection between t4 and t5 and lacking t7, M1 with more anteriorly located t1 but without t1bis, M1 and M2 with low crest between t4 and t8 and having t12, m1 and m2 without longitudinal connections between the two posterior pairs of tubercles (protoconid-metaconid and hypoconid-entoconid), and reduced Acc of m1.

Furthermore, in V 16288, M1 and M2 have well-developed t9 and distinct connection between t6 and t9, M3 lacks t9, m1 has a distinct Acc, connection between the two anterior pairs of tubercles (anterobuccal-anterolingual cusps and protoconid-metaconid), and moderately developed cingular margin. All these features of V 16288 are similar to those of *Huerzelerimys* rather than *Progonomys*.

In addition, according to Mein et al. (1993:59), the incisive foramen extends only to the level mesial to the anterior root of M1 in *H. minor*, but can extend farther backward beyond the anterior root of M1 in *Progonomys*. In this feature, V 16288 resembles *H. minor* rather than *Progonomys*. Meanwhile, the mandible of V 16288 is also similar to that of *H. exiguus*. Therefore, V 16288 should be referred to the genus *Huerzelerimys*.

3.3 Comparison of IVPP V 16288 with Known Species of *Huerzelerimys*

The genus *Huerzelerimys* is known to include five species: *H. vireti* (Schaub, 1938), *H. turoliensis* (Michaux, 1969), *H. oreopitheci* (Engesser, 1989), *H. minor* (Mein et al., 1993), and *H. exiguus* (Qiu and Li, 2008).

The cheek teeth of V 16288 are much smaller than those of *H. turoliensis* and *H. oreopitheci*, but larger than those of *H. exiguus*, and subequal to those of *H. vireti* and *H. minor* (see Mein et al., 1993:fig. 4; Qiu and Li, 2008:table 4).

Morphologically, V 16288 differs from *H. minor* and *H. vireti* in M1 and M2 having distinct crest connecting t6 with t9 and having a crested t12, m1 having nearly centrally located Acc uniting with both Alc and Abc, m1 and m2 having larger c2 attached to protoconid and having lower, crested Ph, and m3 lacking c1.

V 16288 differs from *H. minor* in M3 having isolated t8, and Abc of m2 and m3 being isolated. V 16288 further differs from *H. vireti* in t1 and t3 of M2 and t1 of M3 being connected to t5. Therefore, V 16288 cannot be attributed to either *H. minor* or *H. vireti*.

V 16288 differs from *H. exiguus* in M1 having slightly anteriorly located t1 and t6 and t9 being distinctly connected; m1 having Acc attached to both Alc and Abc; m1 and m2 having more developed accessory cusps and lower, weaker Ph.

V 16288 differs from *H. turoliensis* in M1 and M2 having more developed t12, m1 having distinct Acc, m1 and m2 having more distinct buccal accessory cusps and having lower, crest-like Ph.

V 16288 differs from *H. oreopitheci* in molars being more brachyodont, M1 and M2 having low t12 and smaller t9, M3 having t3, and m1 having more developed Acc and m1 and m2 having larger c2 attached to protoconid and lower, crest-like Ph.

To sum up, V 16288 represents a new species of *Huerzelerimys*, here named *H. asiaticus*.

3.4 Evolutionary Considerations Regarding *Huerzelerimys asiaticus*

Judging from previously known species of *Huerzelerimys*, the overall evolutionary tendencies of *Huerzelerimys* can be summarized as follows: increase in size (a), increase in crown height (b), forward shifting of t1 in M1 (c), gradual convergence and union of t6 and t9 (d), reduction of t12 in M1 (e), reduction of Acc in m1 (f), and development of accessory cusps in m1 (g) (Mein et al., 1993; Martín Suárez and Freudenthal, 1993; Freudenthal and Martín Suárez, 1999; Qiu and Li, 2008).

As discussed above, *H. asiaticus* differs from *H. exiguus* in having such advanced features as a, c, d, and g, showing that *H. asiaticus* is more advanced than *H. exiguus*. Although subequal to *H. minor* and *H. vireti* in size, *H. asiaticus* has some more advanced features (d and g) than the latter two, suggesting it may represent a slightly more advanced species than *H. minor* and *H. vireti*. Although it has more developed accessory cusps in m1, an apomorphic character in *Huerzelerimys* (g), *H. asiaticus* is less advanced than *H. turoliensis* in features a, e, and f, and differs from *H. oreopitheci* in lacking such advanced features as a, b, e, and f. Obviously, *H. asiaticus* may represent a more primitive species than the latter two.

To sum up, *H. asiaticus* is more advanced than *H. exiguus*, *H. minor*, and *H. vireti*, but more primitive than *H. turoliensis* and *H. oreopitheci*.

Since the age of *H. exiguus* is early Late Miocene, roughly corresponding to upper MN10 or lower MN11 in the European time scale (Qiu and Li, 2008), *H. minor* is known from upper MN10, *H. vireti* from MN11, and *H. turoliensis* from upper MN11 to MN12 (Mein et al., 1993), and *H. oreopitheci* is known from middle Turolian (middle MN12) (Engesser, 1989), the age of the upper part of the Liushu Formation yielding *H. asiaticus* may best be estimated as late Bahean, corresponding to upper MN11 or lower MN12.

Acknowledgments

The authors express gratitude to Profs. Qiu Zhuding and Zheng Shaohua for valuable discussions, and to Profs. Qiu Zhuding and Zhang Zhaoqun for careful review of the manuscript and valuable suggestions to improve the text. Many thanks are also given to Mrs. Zhang Lifen for careful preparation of the fossils and to Mr. Gao Wei for the photographs.

References

Ellerman, J. R. (1941). *The Families and Genera of Living Rodents. Vol II. Family Muridae*. British Museum (Natural History). Norwich: Jarrold and Sons Ltd. 1 690.

Engesser, B. (1989). The Late Tertiary small mammals of the Maremma region (Tuscany, Italy). 2nd part: Muridae and Cricetidae (Rodentia, Mammalia). *Bollettino della Società Paleontologica Italiana*, 28(2-3), 227 252.

Freudenthal, M., & Martín Suárez, E. (1999). Family Muridae. In G. E. Rössner & K. Heissig (Eds.), *The Miocene Land Mammals of Europe* (pp. 401 409). München: Verlag Dr. Friedrich Pfeil.

Greene, E. C. (1935). Anatomy of the rat. *Transactions of the American Philosophical Society*, New Series, 27, 1 370.

Guthrie, D. A. (1963). The carotid circulation in the Rodentia. *Bulletin of the Museum of Comparative Zoology*, 128(10), 455 481.

Huang, W. J., Chen, Y. X., & Wen, Y. X. (1995). *Rodents of China*. Shanghai: Fudan University Press. 1 308.

Martín Suárez, E., & Freudenthal, M. (1993). Muridae (Rodentia) from the Lower Turolian of Crevillente (Alicante, Spain). *Scripta Geologica*, 103, 65 118.

Mein, P., Martín Suárez, E., & Agustí, J. (1993). *Progonomys* Schaub, 1938 and *Huerzelerimys* gen. nov. (Rodentia); their evolution in Western Europe. *Scripta Geologica*, 103, 41 64.

Michaux, J. (1969). Muridae (Rodentia) du Pliocène supérieur d' Espagne et du Midi de la France. *Palaeovertebrata*, 3(1), 1 48.

Pan, Q. H., Wang, Y. X., & Yan, K. (2007). *A Field Guide to the Mammals of China*. Beijing: China Forestry Publishing House. 1 420.

Qiu, Z. D., & Li, Q. (2008). Late Miocene micromammals from the Qaidam Basin in the Qinghai-Xizang Plateau. *Vertebrata PalAsiatica*, 46(4), 284 306.

Qiu, Z. D., & Li, Q. (2016). Neogene rodents from central Nei Mongol, China. *Palaeontologia Sinica*, New Series C, 30, 1 684.

Schaub, S. (1938). Tertiäre und Quatäre Murinae. *Abhandlungen der Schweizerischen Paläontologischen Gesellschaft*, 61, 1 39.

Wang, B. Y., & Qiu, Z. X. (2018). Late Miocene pararhizomyines from Linxia Basin of Gansu, China. *Palaeontologia Sinica*, New Series C, 31, 1 271.

Yang, A. F., Wang, P., et al. (1985). *Anatomy and Histology of Rat*. Beijing: Science Press. 1−241.

Note: Figure translations are in progress. See original paper for figures.