

Large-sized fossil hamsters from the late middle Pleistocene locality 2 of Shanyangzhai, China, and discussion on the validity of *Cricetinus* and *C. varians* (Rodentia: Cricetidae)

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A detailed morphological description and comparative study were carried out on hundreds of large-sized hamster remains collected from the late Middle Pleistocene Locality 2 of Shanyangzhai (Syz 2), Hebei Province, China. The comparisons show that these fossils are highly similar to the extant *Tscherskia triton* in size and morphology (such as degree of alternating of the opposite main cusps on M1-3 very small, M3 with axioloph, the mesolophids of m1-2 present but rarely reaching the lingual margin of teeth), although slight differences between the two are still exist, so all of these fossils have been referred to a chronosubspecies of this extant species—*T. triton varians*. The skull and molar morphology of *C. varians* and *T. triton* were compared in detail to clarify the long-disputed issue of the validity of *Cricetinus* Zdansky, 1928 and *C. varians* Zdansky, 1928. The results showed that the differences between the two are very slight, therefore the *C. varians* can only be treated as a chronosubspecies of *T. triton*, i.e., *T. triton varians*, and the *Cricetinus* should be regarded as junior synonym of *Tscherskia*. Meanwhile, we tentatively suggest that among the seven species once referred to *Cricetinus* in Eurasia, *C. europaeus*, *C. gritzai*, *C. janossyi* and *C. koufosi* should be transferred to *Tscherskia*, while *C. beremendensis* should be transferred to *Allocricetus*, and *C. mesolophidos* to *Neocricetodon*. On present evidence, *Tscherskia* may have originated from *Neocricetodon* during the Early Pliocene in Europe and then spread to Asia, and *T. triton* is its only extant representative which now only inhabits in East Asia.

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Abstract

A detailed morphological description and comparative study were carried out on hundreds of large-sized hamster remains collected from the late Middle Pleistocene Locality 2 of Shanyangzhai (Syz 2), Hebei Province, China. The comparisons show that these fossils are highly similar to the extant *Tscherskia triton* in size and morphology (such as degree of alternating of the opposite main cusps on M1-3 very small, M3 with axioloph, the mesolophids of m1-2 present but rarely reaching the lingual margin of teeth), although slight differences between the two **are still exist**, so all of these fossils ~~have been~~ referred to a chronosubspecies of this extant species—*T. triton varians*. The skull and molar morphology of *C. varians* and *T. triton* were compared in detail to clarify the long-disputed issue of the validity of *Cricetinus* Zdansky, 1928 and *C. varians* Zdansky, 1928. The results showed that the differences between the two are very slight, therefore the ***C. varians* can only be treated as a chronosubspecies of *T. triton*, i.e., *T. triton varians***, and the *Cricetinus* should be regarded as junior synonym of *Tscherskia*. Meanwhile, we tentatively suggest that among the seven species once referred to *Cricetinus* in Eurasia, *C. europaeus*, *C. gritzai*, *C. janossyi* and *C. koufosi* should be transferred to *Tscherskia*, while *C. beremendensis* should be transferred to *Allocricetus*, and *C. mesolophidos* to *Neocricetodon*. **On present evidence**, *Tscherskia* may have originated from *Neocricetodon* during the Early Pliocene in Europe and then spread to Asia, and *T. triton* is its only extant representative which now only inhabits in East Asia.

Introduction

The late Middle Pleistocene Locality 2 of Shanyangzhai (village) has yielded very abundant vertebrate fossils and one of the most common among them are the remains of hamsters—so

far more than 50 skulls, 2500 jaws and very numerous isolated teeth have been discovered. These materials can easily be divided into the large-sized group and the small-sized group. The material of the small-sized group has been described by Xie and Li (2016), with two hamster species *Cricetulus longicaudatus* and *C. barabensis* being recognized. The aim of the present paper is to deal with the remains of the large-sized group, making detailed morphological description and comparative study on them.

The genus *Cricetinus* and its type species *C. varians* were erected by Zdansky (1928) on the basis of fossils from the famous Middle Pleistocene Locality 1 of Zhoukoudian (i.e., the Peking Man Site), Beijing. Since then, hamster remains of several other Pleistocene mammal fossil sites have been continuously referred to *C. varians*, making it one of the most common micromammal species of Pleistocene faunas in northern China (refer to the synonymy of *Tscherskia triton varians* given below). Kretzoi (1959) founded the second species of *Cricetinus*, *C. europaeus*, based on the material from the Pliocene fauna of the Csarnóta 2 in the Villány Mountains, southern Hungary. Since Kretzoi, five other hamster species have been allocated to *Cricetinus* successively (e.g., Hir, 1994; Wu & Flynn, 2017), which makes *Cricetinus* a widely distributed genus, both spatially and temporally. However, the validity of *Cricetinus* and *C. varians* have long been questioned by many researchers since 1930s (e.g., Pei, 1936; Teilhard de Chardin & Pei, 1941; Teilhard de Chardin & Leroy, 1942; Gu, 1978; McKenna & Bell, 1997), and the core of the debate is whether ~~the~~ *Cricetinus* and *C. varians* are the junior synonyms of the *Tscherskia* and *T. triton*, respectively. In present paper, on the basis of a detailed description for material of large-sized hamster from Locality 2 of Shanyangzhai, we discuss in detail the long-disputed issue of the validity of *Cricetinus* and *C. varians* to benefit our understanding of the origin and evolution of living Cricetinae taxa.

It is worth pointing out here that *Tscherskia* has long been regarded as a subgenus of *Cricetulus* since the work of Argyropulo (1933) and a few researchers even tend to hold to this view until recently (e.g., Chen & Gao, 2000; Wang, Wu & Qiu, 2020). However, several molecular phylogenetic studies in recent years have demonstrated that *Cricetulus* in traditional sense (usually including *C. barabensis*, *C. longicaudatus*, *C. migratorius*, *C. kamensis*, *C. triton*) is polyphyletic, and the subgenera *Tscherskia* and *Urocricetus* (the Tibetan hamster) should be treated as two independent genera (e.g., Neumann et al., 2006; Stepan & Schenk, 2017; Lebedev et al., 2018; Ding et al., 2020; Romanenko et al., 2021). Furthermore, *C. migratorius* (the grey hamster) should also represents an independent genus and Lebedev et al. (2018) have coined a new genus name *Nothocricetulus* for it. According to the above researches, compared with *Tscherskia*, *Cricetulus* is usually more closely related to *Nothocricetulus*, *Cricetus* and *Allocricetulus*. Except for the evidence from molecular phylogenetic studies, morphologically, *T. triton* also obviously differs from the members of *Cricetulus* (in traditional sense) (Musser & Carleton, 2005) (Figures S1 to S3). For example, *T. triton* has significantly larger body size than the later: average body length of the former is ca.157 mm, by contrast, the same measurement of the later ranges in ca. 90-100 mm (according to the data provided by Chen & Gao, 2000). For another example, we find that the M3 of *T. triton* bears an axioloph (*sensu* Freudenthal &

Daams, 1988) (see “Discussion” for details), which to the best of our knowledge is unique among all species of the living Cricetinae. The presence of the axioph undoubtedly indicates the uniqueness of *Tscherskia* in Cricetinae, although its taxonomic significance remains to be further studied. For above reasons, we follow the prevailing opinion of researchers over the last two decades and no longer consider the *Tscherskia* as a subgenus of *Cricetulus* but as a separate genus.

Geologic setting

Shanyangzhai Village (119°32'14.00"E, 40°5'17.82"N) is located in the central part of Haigang District, Hebei Province, China, about 20 kilometers from Bohai Bay. The Ordovician limestone of Majiagou Formation south of the village is exposed to many fossil-bearing fissures or cave deposits due to quarrying. To date, four mainly fossiliferous localities have been discovered, which are respectively numbered Localities 1, 2, 3, 4 of Shanyangzhai (Syz 1-4 for short) in order of south to north (Fig.1), and judging from their mammalian components they may have different ages. The fossils from Syz 1 and Syz 3 are mainly macromammal, in contrast Syz 2 and Syz 4 have yielded extensive micromammal fossils (Niu, Zhang & Fa, 2003; Kong, 2009; Wang et al., 2010; Zhang et al., 2010; Li & Zhang, 2011, 2013; Li, Zhang & Ao, 2013; Li, Zhang & Li, 2013; Li, Zhang & Zheng, 2013; Zhang & Li, 2015; Li, Li & Zhang, 2016; Xie & Li, 2016; Chen et al., 2021). Although most parts of the native strata of Syz 2 have been disturbed by activity of quarrying, on the whole, the Syz 2 which yielded the fossils studied in present paper may have an age of late Middle Pleistocene (Zhang et al., 2010). This is mainly for its overall similarity in faunal composition with the Middle Pleistocene fauna of Locality 1 of Zhoukoudian (it is usually accepted that the age of the main fossiliferous deposits, i.e. 1-11 layers, is ca. 0.6-0.2 Ma, Hu, 1985; Zhang, 2004; Chen & Zhou, 2009; Liu et al., 2014), and Jinniushan (ca. 0.31-0.2 Ma, Liu et al., 2014). We took a silty clay sample (field number 09SS1, laboratory number 11695) about 2 m below the fossil-bearing horizon at Syz 2 and dated its absolute age using ESR (electron spin resonance) technique at the State Key Laboratory of Earthquake Dynamics, Institute of Geology of China Earthquake Administration. The result indicates an age of 300 ± 30 ka, so the age of the fossil deposits located above the sampling site should be some later. Kong (2009) dated the fauna at $(1.8 \pm 0.2) \times 10^5$ years to $(2.0 \pm 0.2) \times 10^5$ years ago using TL (thermo-luminescence) technique, but the exact sampling layers of Kong (2009) need further verification. Based on the above results of absolute age dating and faunal comparison, we tentatively date the Syz 2 to the late Middle Pleistocene, ca. 0.2 Ma.

Material, methods and abbreviation

Material

The hamster fossils from Syz 2 studied in the present paper are stored in the Department of Geology, Northwest University (Xi'an, Shaanxi Province, China). For comparison, we observed nearly 50 specimens of skull (including mandible) of extant *Tscherskia triton* (the greater long-tailed hamster) stored in the College of Life Sciences, Northwest University, which are all collected from Shaanxi Province. Judging from the collection sites written on the labels of these specimens, they might belong to the subspecies *T. triton incanus* and *T. triton collinus* (and

perhaps *T. triton triton* and *T. triton fuscipes*) according to the subspecies and their geographical distribution of *T. triton* summarized by Chen & Gao (2000).

Methods

For the description of molar occlusal morphology, we mainly follow Freudenthal & Daams (1988), Freudenthal, Hugueney & Moissenet (1994) and Li et al. (2018). The skull morphological terminology mainly follows that of Wang & Qiu (2018) and Voss (1988). Measurements of skull and mandible mainly follow Yang et al. (2005) and Xia et al. (2006). All measurements were made by ZEISS Smartzoom5 automated digital microscope. Some images have been reversed for convenience of comparison and indicated by an underlined label.

Abbreviation

NWU, Northwest University, Xi'an; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing; Syz 1-4, Locality 1, 2, 3, 4 of Shanyangzhai; ZKD, Zhoukoudian (= Choukoutien); JNS, Jinniushan; RZD, Renzidong; Loc, Locality.

Results

Systematic palaeontology

Mammalia Linnaeus, 1758

Rodentia Bowdich, 1821

Cricetidae Rochebrune, 1883

Cricetinae Fisher, 1817

Tscherskia Ognev, 1914

1928 *Cansumys*, Allen

1928 *Cricetinus*, Zdansky

1929 *Asiocricetus*, Kishida

Type species *Tscherskia albipes* Ognev, 1914 (= *Cricetus* (*Cricetulus*) *triton* de Winton, 1899).

Referred species *T. europaeus* (Kretzoi, 1959); *T. rusa* (Storch, 1974) ?; *T. gritzai* (Topachevski et Skorik, 1992); *T. janossyi* (Hír, 1996); *T. koufosi* (Koliadimou, 1996).

Geographic distribution and geologic age Southeastern Europe, Early Pliocene (MN 15, ca. 5-3.5 Ma) to early Middle Pleistocene (ca. 0.7 Ma); Southwestern Asia, Holocene ?; northern China, transitional region between northern and southern China, except *T. sp.* from Youhe fauna with an age of Late Pliocene (ca. 3.15-2.59 Ma), all other reliable material of *Tscherskia* with an age not earlier than Middle Pleistocene. *→ ref. ???*

Diagnosis medium-sized cricetids usually between *Cricetulus* and *Cricetus*; molars brachyodont; mesolophes of M1-3 usually present, either free or connected to the metacone, but rarely reaching the buccal tooth edge; M3 with an anteroposteriorly directed axioph rather than an anterolaterally extended protolophule II; anteroconid of m1 divided or undivided; mesolophid on m3 almost always present and well-developed; the mesolophid also often present on m1 and m2, but rarely reaching the lingual tooth edge (modified from Xie, Zhang & Li, 2021).

Remarks Hír (1996a, 1997) once proposed the diagnosis of *Cricetinus* (i.e. *Tscherskia*) as follows: "the undivided anteroconid on the m1 molars with a smooth and convex oral surface; the mesolophids missing or short on the m1-m2 molars; M1-M2 crowns characterized by the

missing or weekly developed mesolophes; the posterior metalophule rare on M2.” Our observation demonstrates that the diagnosis proposed by Hír are not comprehensive and worthy of further revision, so the diagnosis of *Tscherskia* is redefined here as above.

Tscherskia triton (de Winton, 1899)

Tscherskia triton varians (Zdansky, 1928) (Figs 2-6, Tables 1-7)

1927 *Cricetulus* cfr. *songarus*, Young, p.24 (part)

1928 *Cricetinus* varians, Zdansky, p.54

1930 *Cricetinus* varians, Schaub, p.37

1931 *Cricetinus* varians, Pei, p.12

1932 *Cricetinus* varians, Young, p.4

1934 *Cricetinus* varians, Schaub, p.30

1934 *Cricetinus* varians, Young, p.58

1936 cf. *Cricetinus* varians, Teilhard de Chardin, p.16 (part)

1936 *Cricetinus* varians, Pei, p.59

1939 *Cricetinus* varians, Pei, p.153

1940 *Cricetinus* (*Cricetulus*) varians, Pei, p.42 (part ?)

1941 *Cricetulus* varians, Teilhard de Chardin & Pei, p.49 (part)

1942 *Cricetulus* (*Cricetinus*) varians, Teilhard de Chardin & Leroy, p.35, p.93 (part)

1977 *Cricetulus* varians, Gai & Wei, p.290

1978 *Cricetulus triton*, Gu, p.164

1980 *Cricetulus* varians, Zhang, Zou & Zhang, p.156

1983 *Cricetulus* varians, Zheng, p.231

1984 *Cricetinus* varians, Zheng, p.185

1985 *Cricetulus* varians, Zhang et al., p.73

1985 *Cricetinus* varians, Zheng et al., p.117

1986 *Cricetulus* varians, Zhang, Wei & Xu, p.36

1990 *Cricetulus triton*, Sun & Jin, p.35

1993 *Cricetinus* varians, Zheng & Han, p.65

1996 *Cricetinus* varians, Cheng et al., p.38 (part ?)

2002 *Cricetinus* varians, Jin, p.95

2004 *Cricetinus* varians, Jin et al., p.284

2004 *Cricetulus triton*, Tong et al., p.855

2009 *Cricetinus* varians, Jin et al., p.177 (?)

2010 *Cricetinus* varians, Zhang et al., p.73

2015 *Tscherskia triton*, Liu et al., p.610

2017 *Tscherskia triton*, Chen et al., p.847

2018 *Cricetulus* varians, Tong et al., p.287

2018 *Cricetinus* varians, Wu et al., p.1396

2020 *Cricetulus* varians, Wang, Wu & Qiu, p.104

2021 *Cricetulus* varians, Huang et al., p.269

2021 *Cricetulus triton*, Huang et al., p.269

Lectotype As already mentioned, Zdansky (1928) coined *Cricetinus* and *Cricetinus varians* based on the large-sized hamster material from Locality 1 of Zhoukoudian, which included 8 maxillary fragments, 9 larger and some smaller mandibular fragments, 1 isolated M1 and 3 isolated m1, but no holotype was designated by him for the new genus and its type species, so all of these specimens should be viewed **as the syntype**, Wang, Wu & Qiu (2020, pp.104-105) selected IVPP RV 340020 (original catalogue number C/C. 1049), an anterior portion of skull with right M1-3 and left M1-2 figured by Young (1934, Text-fig. 19, 1, 1a, 1b; Pl. 5, fig. 9) and Zheng (1984a, Fig.1, C), the lectotype of *C. varians*. However, this designation should be considered invalid according to ICZN (1999, Art. 74.2), because IVPP RV 340020 does not belong to the syntype, although it is also collected from Locality 1, even possible from the same layer as the syntype (Young, 1934, p.63). Therefore, the fragmentary right upper jaw with M1-3 figured by Zdansky (1928, Taf. 5, Fig. 4) is here designated as lectotype for *Tscherskia triton varians* (Lagrelus Collection kept in Museum of Evolution, Uppsala University, Sweden), and other specimens in the type series should be viewed **as the paralectotype**. The paralectotype listed by Wang, Wu & Qiu (2020, p.104) are also invalid for reason same to that discussed for the lectotype and should only be viewed as referred specimens.

Type locality and geologic age Locality 1 of Zhoukoudian, Beijing. The deposits of Locality 1, also known as Zhoukoudian Formation, are about 40 meters in thickness and traditionally divided into 1 to 13 layers from top to bottom, representing a period from ca. 0.78 Ma to 0.2 Ma. This division scheme was published by Jia (1959), who adopted the similar scheme first proposed by Teilhard de Chardin & Young (1929), and has been widely adopted from then. Zdansky (1923, p.86) also published two profiles of deposits of Locality 1 (called Loc. 53 by Zdansky) from which the type specimens of *C. varians* and other fossils studied by Zdansky (1928) were collected. Teilhard de Chardin & Young (1929, p.179, footnote) considered that the sections given by Zdansky (1923, p.86) correspond probably to some part of their layers 5 and 6, although they also stated that a precise correlation with the Zdansky's 1923 profile was rather difficult to establish. If Teilhard de Chardin and Young are right, according to Xu et al. (1997, p.219, Table 1), their layers 5 and 6 should basically correspond to layers 4 to 6 of Jia (1959)'s scheme, which cover a period ca. 0.3 - 0.4 Ma in the Middle Pleistocene (Chen & Zhou, 2009, Table 1).

Geographic distribution and geologic age Northern China, transitional region between northern and southern China, late Early Pleistocene to Late Pleistocene.

Referred specimens from Syz 2 21 incomplete skulls (NWUV 1489.a1-21); 10 maxillae with bilateral tooththrows (NWUV 1489.b1-10); 73 left maxillae (NWUV 1489.c1-73); 74 right maxillae (NWUV 1489.d1-74); 185 left mandibles (NWUV 1489.e1-185); 215 right mandibles (NWUV 1489.f1-215); 3 mandibles with bilateral branches (NWUV 1489.g1-3); 55 left M1s (NWUV 1489.h1-55); 54 right M1s (NWUV 1489.i1-54); 46 left M2s (NWUV 1489.j1-46); 35 right M2s (NWUV 1489.k1-35); 2 left M3s (NWUV 1489.l1-2); 8 right M3s (NWUV 1489.m1-8); 16 left m1s (NWUV 1489.n1-16); 22 right m1s (NWUV 1489.o1-22); 15 left m2s

(NWUV 1489.p1-15); 19 right m2s (NWUV 1489.q1-19); 7 left m3s (NWUV 1489.r1-7); 8 right m3s (NWUV 1489.s1-8).

Measurements see Tables 1-2 and Supplementary datasets 1, 3, 5, 7.

Diagnosis *Tscherskia triton varians* is very similar to living *T. triton* in size and most characters of molars (see “Discussion”), but the former has slightly higher frequencies of mesolophid on m1 and m2 (see Table 7). In most measurements of the skull and mandible, the mean values of the *T. t. varians* may be ~~lightly greater~~ than those of living *T. triton*.

Remarks The small differences between *T. triton varians* and recent *T. triton* can only be noticed when there are statistically abundant specimens. The reason for which we refer all the items listed in synonymy, in most of which the material is scarce, to *T. triton varians* is only on account of the geologic age of them, and so this can only be viewed as a makeshift treatment.

Description

(1) Skull

The description of the skull is mainly based on the relatively well-preserved NWUV 1489.a8, while also referring to other specimens (Fig. 2).

Dorsal view: the nasal is posteriorly narrow and anteriorly wide. It is narrowest at the junction with the frontal and then gradually widens forward, and after reaching the widest size, it is slightly narrower again at the anterior border of the nasal. The anterior-most point of the orbit is at the transverse level slightly in front of the posterior end of the nasal. The skull width of NWUV 1489.a7 is larger than normal due to vertical extrusion, but it preserves the complete interparietal, the shape of which is approximately pentagonal just as in extant *T. triton*. The frontal crest appears more clearly in adults, especially elderly individuals, extending backwards from the upper edge of the orbit, beyond the parietal, and at least to the anterior border of the interparietal.

Lateral view: the upper outline of the skull is gently arched, but this shape is often lost due to extrusion. The alveolus of the upper incisor forms a well-defined semicircular crest on the lateral surfaces of the premaxilla and maxilla. The upper part of the infraorbital foramen is fan-shaped and lower part of it is slit-like. The outer wall of the zygomatic plate is slightly concave; both its anterior and posterior edges are slightly arc-shaped, with the former slightly convex anterodorsally and the latter slightly concave anterodorsally; the two edges are nearly parallel. The anterior root of the zygomatic arch is much weaker and about 2-3 times narrower the width of the zygomatic plate. The supraorbital foramen is small, situated behind the interorbital constriction and just below the supraorbital margin.

Ventral view: the incisive foramen is narrow and long, with a significant distance between its posterior edge and the anterior edge of M1. Premaxillary-maxillary suture traverses the incisive foramen at around the anterior 2/5 of the foramen. The anterior-most point of the zygomatic plate is at about the same transverse level of the middle of the incisive foramen. The masseteric tubercle is located at the base of the zygomatic plate and has a rough surface. Two posterior palatine foramina are almost located on the connection line of the posterior roots of two M2s.

maybe add question marks?

The posterior border of the hard palate slightly exceeds the posterior edge of M3 or is flush with it. The two molar series are not completely parallel but slightly diverge anteriorly.

(2) Mandible

The lower edge of mandible (Fig. 3) extends forward in an arc from the base of angular process. The mental foramen is small and round, located anteroventral to the anterior root of m1. The masseteric ridge is thin but clearly present, ending underneath of m1 and posterodorsal of the mental foramen. The coronoid process is comparatively fine and hook-shaped, extending posterodorsally. There is a noticeable bulge at the base of the condylar process and situated anteroventral to the mandibular notch on the buccal side of the mandible, which is formed by the posterior end of the lower incisor. The angular process extends in posteroventral direction. The mandibular notch extends slightly further than the notch between the condylar process and the angular process in anterior direction, while the latter is slightly wider than the former. The mandibular foramen is oval, situated at the base of the condylar process. The groove between the alveolus of molars and the base of the coronoid process inclines gently to the posteroventral direction, not as steep as that in murines; in the middle of the groove is a small foramen, whose function is not clear. The area on inner side of the mandible and under the molar series usually bears many small foramina.

Measurements of skulls and mandibles are shown in Table 1 and [Supplementary datasets 1, 3.](#)

(3) Teeth

The anterior end of the upper incisor (I2) points ventrally, and its posterior end terminates in an anteroventral position to the infraorbital foramen. The enamel layer covers the whole labial surface, which is smooth without ridge on it, and small part of the lateral surface.

The structures of upper molars are shown in Fig. 4. The M1 is kidney-shaped, with an obtuse anterior edge, a comparatively straight buccal edge, but obviously protruding outward at the metacone, and an arc-shaped lingual edge. The degree of alternating of the opposite main cusps on M1 is very small, as well as on M2 and M3. The anterocone is broad and always splits posteriorly into two equal-sized cusps. The anterocone of some specimens also has a certain degree of separation from mesial surface, and in a few specimens the separation degree is comparatively large. The lingual anterolophule is always present, and the buccal anterolophule is present in most of the specimens with a frequency of 89.1% (41/46). A very small number of specimens have the spur of the anterolophule (3.9%, 6/154), all of which are thin and weak, with five cases reaching the buccal margin of tooth (Fig. 4B). The frequency of protolophule I is 57.4% (27/47). The protolophule II is relatively thin and weak, and even missing in a few specimens. The loph that connects the anterior arm of the hypocone and metacone is very thick. In our opinion this loph should be viewed as the mesoloph, because in most specimens there is an obvious trace of connection between the loph and the metacone, which implies the loph does not derive from the metacone. In a few specimens, however, this loph can be completely fused with the metacone without any trace, so it is difficult to determine whether the metalophule I is involved in the formation of the loph in these specimens. There is no specimen whose mesoloph end is free. The metalophule II is present but weakly developed in most specimens. The

posterosinus is small and shallow, and only vestige of it can be observed on specimens with severe abrasion. The tooth is four-rooted.

The M2 is approximately square. The buccal anteroloph is more developed than the lingual one, with sometimes the latter is nearly absent. The position of the buccal anteroloph is also higher than the lingual one. Protolophule is double. The mesoloph is similar to that of M1, but relatively thicker. It also has either merged with the metacone or has an obvious trace of connection between it and the metacone, but never has a free end. In some specimens, the mesoloph can reach the tooth edge by clinging to the anterior wall of the metacone (Fig. 4 B, F). The metalophule II is always present, but comparatively weak. The posterosinus is also very small. The tooth has four roots.

The posterior portion of M3 is distinctly reduced, with the hypocone and metacone being much smaller than those of M1 and M2, resulting in the occlusal outline of M3 resembling a relatively obtuse equilateral triangle. The buccal anteroloph is also more developed and located higher than the lingual one, while the lingual one is either absent or extremely weak. The protolophule I is always present. The most remarkable feature of M3 is the presence of the axioloph, which departs from the junction of the protolophule I and the anterior arm of the protocone and extends anteroposteriorly, forming a small groove between it and the protocone. Sometimes the central part of the groove is closed due to the proximity or fusion of the axioloph and paracone, so that a small pit is formed in the upper part of the groove (Fig. 4 D, F). The morphology of the mesoloph is similar to that in M1 and M2. The metalophule II and posterosinus are not present. The mid-segment of the posteroloph (or the posterior arm of the hypocone) can sometimes be inflated into a small cusp, sandwiched between the hypocone and metacone (Fig. 4C, G). The tooth has three roots.

In a very few specimens, the upper molars possess morphological variation of some structures. For instance, protolophule II on M2 may occasionally have a form similar to that on M3; and vice versa.

The anterior part of the lower incisor (i2) extends anterodorsally. The posterior end of the lower incisor terminates at the base of the condylar process and forms a noticeable bulge on the buccal side of the mandible. The enamel layer covers the whole labial surface, which is smooth without ridge on it, and nearly half part of the lateral surface.

The structures of the lower molars are shown in Fig. 5. The occlusal outline of m1 is comparatively long and thin, and gradually narrows from back to front. The anteroconid on most of the specimens is bisected into two generally equal-sized cusps (93.0%, 80/86). In these specimens, the vast majority of the anteroconids are posteriorly slightly bifid, and the anteroconids rarely have a comparatively large degree of separation on their posterior side; on its anterior side, the anteroconid is only weakly divided (within young individuals) or undivided (within middle aged and elderly individuals). A small part of the specimens' anteroconids are split into three small cusps (7.0%, 6/86) (Fig. 5E). The undivided anteroconids only appear on heavily worn specimens. In overwhelming majority of specimens the anterolophulid is single (97.6%, 82/84), and it either connects to the buccal anteroconulid (70.7%, 58/82), or connects to

behind the middle of the two anteroconulids (26.8%, 22/82), or connects to the lingual anteroconulid (2.4%, 2/82); in a very few specimens the anterolophulid has two branches (2.4%, 2/84), connecting respectively to two anteroconulids. The bottom of the anteroconid is far higher than the bottom of the protosinusid. With the frequency being 43% (44/103), the mesolophids on all specimens are low, weak and short; they connect to the metaconid (18.2%, 8/44), or have a free end (81.8%, 36/44). In the latter case, the longest mesolophid does not exceed 1/2 of the distance from the base to the lingual tooth edge. In most cases it just appears as a spinous process. The transitional part from the hypoconid to posterolophid is very thin, but then the posterolophid quickly swells into a defined cusp; however, it usually does not close the posterosinusid. Cingula usually exist at the entrances of the protosinusid and sinusid, even sometimes forming a small but defined ectostylid at entrance of the latter. The tooth has two roots.

The occlusal outline of m2 is a rounded square, with tooth width greater than that of m1 and m3. The lingual anterolophid is weakly developed or absent, whereas the buccal one is always well developed. The mesolophid is present in 95.2% (158/166) of specimens, and has various morphologies, which can be generally divided into four types: I. having a free end; II. being connected to the metaconid; III. reaching the lingual tooth edge (10.2%, 16/157) (Fig. 5A); or IV. being connected to the entoconid (2.5%, 4/157). Within these four morphotypes, types I and II are present in most specimens, but the boundaries between these two types are sometimes difficult to distinguish. The length of the mesolophid also varies, but most do not exceed 1/2 of the distance from the base to lingual tooth edge. The morphology of the posterolophid and the development situation of cingulum are similar to those on m1, except that the lingual edge of the mesosinusid of m2 sometimes can also bear the cingulum. The tooth has two roots.

Posterior part of the m3 is usually contracted, but there are also a small number of specimens with no obvious contraction (Fig. 5G). In most cases, the entoconid is significantly reduced compared to that of m1 and m2, whereas the hypoconid is often just slightly reduced. Similar to m2, the lingual anterolophid of m3 is also weakly developed and the buccal one is comparatively more developed; but with a difference that the lingual anterolophid of almost all the m3s is present. All but one of the specimens possess a mesolophid (99.2%, 129/130). The morphology of mesolophid is also varied and can be divided into five types: I. having no branch, being connected to the lingual tooth edge (59.4%, 76/128) (Fig. 5 A, C, E, G); II. having two branches, with one being connected to the lingual tooth edge and the other to the metaconid (35.2%, 45/128) (Fig. 5 B, F); III. having three branches, with they being respectively connected to the lingual tooth edge, the metaconid and the junction of the hypoconid and entoconid (0.8%, 1/128); IV. having no branch, being connected to the metaconid (3.9%, 5/128) (Fig. 5D); or V. having a free end (0.8%, 1/128). The posterolophid is somewhat different from that of m1 and m2, which mainly shows in that it usually merges with the entoconid to close the posterosinusid. The posterolophid also has a certain degree of swelling, and it makes the posterolophid very similar to a cusp when undergoing slight wear, so that on the posterior part of m3 there are three side-by-side cusps. The cingulum usually does not exist at the entrance of the sinusid, but is

often relatively developed at entrance of the mesosinusid and sometimes merges with the end of mesolophid to form a small cusp. The tooth has two roots.

As in the upper molars, there is also a variation in some structures of the lower molars within a small number of specimens. For example, the m3 of NWUV 1489.e169 exhibits the ectomesolophid, and this is the only exception in all lower molars; at the same time, on this specimen, not only the mesolophid on m3 but that on m1 and m2 forks into two branches, and this special morphology is also unique in all specimens. In addition, as described above, some rare morphotypes, such as the anterolophid of m1 has two branches, the mesolophid of m2 being connected to the entoconid, the III and V types in mesolophid morphotypes of m3, can also be regarded as morphological variations, because they are all very unusual.

Measurements of molars are shown in Table 2 and Supplementary datasets 5, 7.

Discussion

Identification of large-sized hamster material from Syz 2

The classification issues of Cricetinae fossils found in Quaternary deposits of China and living taxa of Cricetinae inhabiting China are all very disputable now. Combining our own observations and recent research progress (e.g., Lebedev et al., 2018; Wang, Wu & Qiu, 2020), we preliminarily suggest that the following 12 genera should be included in the Cricetinae found from the beginning of Quaternary to the present in China (sorted by chronological order; in parentheses are the common junior synonyms): *Cricetus* Leske, 1779; *Cricetulus* Milne-Edwards, 1867; *Urocrinetus* Satunin, 1902; *Phodopus* Miller, 1910; *Tscherskia* Ognev, 1914 (= *Cricetinus* Zdansky, 1928, *Cansumys* Allen, 1928); *Allocricetus* Schaub, 1930; *Sinocrinetus* Schaub, 1930; *Allocricetulus* Argyropulo, 1932; *Neocrinetodon* Schaub, 1934 (= *Kowalskia* Fahlbusch, 1969); *Bahomys* Chow et Li, 1965; *Amblycricetus* Zheng, 1993; *Nothocrinetulus* Lebedev, Bannikova, Neumann, Ushakova, Ivanova et Surov, 2018. Of these genera, *Allocricetus*, *Sinocrinetus*, *Neocrinetodon*, *Bahomys* and *Amblycricetus* are extinct, and the rest 7 are living. In living genera, *Allocricetulus* and *Nothocrinetulus* have only very scarce and doubtful fossil records (Cai et al., 2004, 2013), while *Cricetus* and *Urocrinetus* have no fossil records in China at all so far. Except that the relationship between *Tscherskia* and *Cricetinus* will be discussed in detail below, it is obviously beyond the scope of this paper to give the detailed reasons for our above conclusion here, because it involves the discussion of the relationship between many synonyms which needs to be elaborated in a special paper.

Except for *Tscherskia*, the differences between the large-sized hamster material from Syz 2 and other genera listed above are marked. The material of Syz 2 is distinguished from nearly of all these genera by the characters such as the mesolophids of m1-2 present but rarely reaching the lingual margin of teeth, M3 with axioloph, the degree of alternating of the opposite main cusps on M1-3 very small. In addition, unlike *Neocrinetodon* and *Amblycricetus*, whose mesoloph(id)s usually reach the tooth edge, the mesoloph(id)s of larger hamster material from Syz 2 barely reach the tooth edge; unlike *Bahomys* and *Sinocrinetus* with comparatively higher crowns, the crowns of material from Syz 2 are low; the sizes of molar, skull and mandible of material from Syz 2 are significantly larger than those of *Cricetulus* (Figures 2 to 5, S1 to S3),

Phodopus, *Urocricetus*, *Allocricetulus* and *Nothocricetulus*, but significantly smaller than *Cricetus*. Some researchers (Zheng et al., 1985, p.117; Cheng et al., 1996, p.40; Jin et al., 2009, p.178) considered that the lack of the mesolophid on m1-2 of *Allocricetulus* is the main character distinguishing it from *Cricetinus* (i.e. *Tscherskia*), but actually this is the character of *Cricetulus*, not *Allocricetulus*, because although *Allocricetulus* do not bear mesolophid on m1, but can develop mesolophid on m2 of some specimens (Table 7). Some other researchers argued that the most important morphological character of *Cricetinus* (i.e. *Tscherskia*) is the undivided anteroconid of m1 (Kretzoi, 1959; Hír, 1996a, 1997), while those of *Allocricetulus* and *Cricetulus* are almost always well divided (Hír, 1994, 1996a), but the observation on molars of extant *T. triton* shows that the anteroconids of the m1 in many specimens have a certain level of separation that Hír considered *Allocricetulus* to have (Hír, 1994, Fig. 4). In *Cricetulus*, the separation degree of anteroconid of m1 of the type species *C. barabensis* is actually very small, while the *C. longicaudatus* indeed has a well divided anteroconid of m1.

Meanwhile, the great similarity between the large-sized hamster material from Syz 2 and the extant *Tscherskia* (i.e., *T. triton*) is easily recognized (Figures 2 to 5, S1 to S3). The molar measurements of the former are very similar to those of the extant *T. triton*, and some of the measurements are even identical (Table 2). Morphologically, the characters of molars and skulls of the former, such as the degree of alternating of the opposite main cusps on M1-3 very small, the anterocene of M1 posteriorly deeply bifid with nearly equal sized buccal and lingual cones, the mesolophs of M1-3 connected to the metacone rather than free, M3 with axioph, the anteroconid of m1 undivided or weakly divided, the mesolophids of m1-2 present but rarely reaching the lingual margin of teeth, nearly all m3s with well-developed mesolophids, the interparietal pentagonal, also closely resembles the extant *T. triton*. Therefore, we can confidently refer the large-sized hamster remains from Syz 2 to *T. triton*.

In most measurements of the skull and mandible, however, the mean values of material from Syz 2 are lightly greater than that of the extant *T. triton* (Table 1, 2), although the measurements of every single molar of the former and the later are almost identical (Table 2, Fig. 6). As will be shown below, there are also small differences on molar morphology between the material of Syz 2 and the extant species. Therefore, it may be more reasonable to further refer these materials from Syz 2 to a chronosubspecies of *T. triton*, i.e., *T. triton varians* (= *Cricetinus varians*, see below for details) on consideration of these differences. In addition, the mean values of lengths of upper and lower toothrows (M1-3 and m1-3) of material from Syz 2 are also lightly greater than that of the extant *T. triton* (Table 2), but the measurements of single molar imply that this phenomenon and even certain measurements of the skull and mandible may likely result from burial deformation (see discussion in Xie, Zhang & Li, 2021).

It is worth explaining the character “axioph” in a little more detail here. The M3s of *T. triton varians* from Syz 2 and the extant *T. triton* both possess an anteroposteriorly directed axioph, which departs from the junction of the protolophule I and anterior arm of protocone, and forms a groove between it and the protocone (Figures 4, S3). In fact, this structure seems to have been noticed by Zdansky (1928) and Schaub (1930) in syntype of *T. triton varians* from Locality 1 of

Zhoukoudian. The term “axioloph”, along with other several terms, was first introduced by Freudenthal & Daams (1988, p.137) to facilitate descriptions of cricetids M3. They defined the axioloph as “an axial connection between paracone and hypocone, fundamentally composed of the posterior protolophule and the posterior part of the (ancient) entoloph”. Morphologically, axiolophs of M3s of Syz 2 and the extant *T. triton* are obviously distinct from the protolophule IIs of the small-sized hamster from Syz 2, and even of all other living taxa of Cricetinae, whose protolophule IIs depart from the posterior wall of paracone and extend in the anteromedial direction, so not forming a groove between it and the protocone (Figure S3). By contrast, fossil taxa of Cricetinae of Eurasia since late Miocene seems relatively more often to develop an axioloph on M3, especially in genus *Neocricetodon* (= *Kowalskia*), such as *Neocricetodon moldavicus* (see Sinitsa & Delinschi, 2016), *Neocricetodon hanae* (see Qiu, 1995), *Neocricetodon yinanensis* (see Zheng, 1984b), *Neocricetodon lii* (see Zheng, 1993). This seems to demonstrate a close affinity between *Neocricetodon* and *Tscherskia*, although the axioloph is also present in some other genera such as *Nannocricetus primitivus* (Zhang, Zheng & Liu, 2008) and seems more often present in cricetids genera of older geologic age (before late Miocene), such as *Democricetodon*, *Megacricetodon*. The phylogenetic significance of the axioloph will not be better understood until a comprehensive phylogenetic analysis covering the taxa mentioned above is conducted, and the homologous structure of the axioloph itself also needs to be further studied.

Discussion on the validity of *Cricetinus* and *Cricetinus varians*

When Zdansky (1928) erected *Cricetinus* and *Cricetinus varians*, he only had the skull specimens of extant *Cricetus cricetus* and *Cricetulus phaeus* (the latter is now considered a subspecies of *Nothocricetulus migratorius*) for comparison, so he apparently did not have the chance to notice the obvious similarity between the fossils from Locality 1 of Zhoukoudian and extant *T. triton* in molar morphology. Zdansky (1928, p.57) seemed to have realized that his study might have the defect that extant specimens used to directly compare with the fossils were too few, so he stated in the monograph that “maybe later a generic identity with one of these [extant] genera will result.” (translated from German). Sure enough, soon after that, there were doubts about the validity of the genus and species. Schaub (1930, 1934) soon noticed *C. varians* and *T. triton* were very similar in molar morphology, although he still retained the independent status of *C. varians*. Teilhard de Chardin (1940, p.56) concluded that he “failed to detect any difference between a ‘*Cricetinus*’ dentition and the dentition of f.i. *Tscherskia* in North China”. Teilhard de Chardin & Pei (1941) emphasized again that except for the somewhat larger size, the large-sized hamster fossils from Locality 13 of Zhoukoudian (early Middle Pleistocene in age) did not show any appreciable difference from *T. triton* in either skull or teeth morphology, and the main reason for them to keep the specific name of “*variens*” for the Pleistocene form was “mainly a question of geologic convenience”. Zheng & Han (1993) stated that it was very difficult to separate *C. varians* from *T. triton* now living in North China and Northeast China in size and molar morphology. In spite of these queries, however, large numbers of remains of such hamsters found in Pleistocene deposits of China were eventually referred to *C. varians*. In the

meantime, as already mentioned, in the Pliocene and Pleistocene deposits of Eurasia there were constantly new fossil hamster species that had been referred to *Cricetinus* since Kretzoi (1959). Therefore, it is necessary to clarify the issue of validity of *Cricetinus* and *C. varians*. To discuss the validity of *Cricetinus*, the validity of *C. varians*, its type species, must be discussed first. However, not only are the material that Zdansky (1928) used in the establishment of *C. varians* scarce, but also the description for them is simple and the plates are very blurred either. All of these make it difficult to compare them with *T. triton* directly. Fortunately, Zheng (1984a) revised most of the hamster fossils collected from the Zhoukoudian area, including *C. varians* specimens from Locality 1 (type locality) and Localities 3, 9, 13, 15, making it possible to conduct detailed comparisons with these materials. Except for the material from Zhoukoudian, we also compared the material from other fossil sites in China which have yielded abundant *C. varians* fossils. In the following discussion, we will make detailed comparisons of skulls and teeth morphology between *C. varians* and extant *T. triton*.

(1) Comparison of skull morphology of *C. varians* and *T. triton*

When Zheng (1984a) revised the hamster fossils from the Zhoukoudian, he proposed several characters of skull that can be used to differentiate between *C. varians* and extant *T. triton*. However, Xie, Zhang & Li (2021) analyzed these characters proposed by Zheng (1984a) and concluded that these differences between *C. varians* and *T. triton* skulls were very dubious and need further verification, and so it is not necessary to repeat it here again. Topachevski and Skorik (1992, p.181) have also suggested three differences in skull morphology between *Cricetinus* and *Tscherskia*. Judging from the context, these views seem to be only based on the observation of the holotype (a maxillary fragment with M1-3) of *Cricetinus gritzai* rather than the specimens of type species (*C. varians*) of the genus. The first is *Cricetinus* differs from *Tscherskia* in having a wider and more concave masseteric plate (i.e. “zygomatic plate” in present paper). However, Topachevski and Skorik (1992) did not provide any measurements of the zygomatic plates of *Cricetinus* and *Tscherskia* to demonstrate it, although the degree of depression of the surface of the zygomatic plate seems difficult to quantify. Even if this view is true, having a wider and more concave zygomatic plate may only be a feature of the *Cricetinus gritzai* species, not the feature of the whole *Cricetinus* genus, because our observations show that there is no obvious difference in the characteristics of the zygomatic plate between the *Tscherskia triton varians* from Syz 2 and the living *T. triton* (Figures 2, S1). The second is *Cricetinus* develops stronger ridges along the posterior side of the incisive foramina [the rim of area for lateral masseter?] than that of *Tscherskia*. Nevertheless, we also failed to discover any appreciable difference of the ridges between *T. t. varians* from Syz 2 and the living *T. triton* (Figures 2, S1). The third is the position of the masseteric tuberosities in *Cricetinus* is more similar to that in *Cricetus* than in *Tscherskia*. Our observations show that the position of the posterior margin of the masseteric tuberosities in living *Cricetus Cricetus* (closer to the posterior edge of the incisive foramen) appears to be slightly further back than that in living *Tscherskia triton* (closer to the middle of the incisive foramen). The position of the masseteric tuberosities of *T. t. varians* from Syz 2 is more similar to that in living *T. triton* rather than *C. cricetus*.

(Figures 2, S1). In conclusion, since the three distinguishing characters between *Cricetinus* and *Tscherskia* proposed by Topachevski and Skorik (1992) may be based on only one specimen of *C. gritzai* (the holotype), and we failed to detect the above differences between extant *T. triton* and *T. t. varians* from Syz 2, so the validity of the above differences, in our opinion, is questionable.

(2) Comparison of teeth morphology between *C. varians* and *T. triton*

① Comparison of the teeth size

Table 2 and Fig. 6 respectively show the measurements and the scatter diagrams of *C. varians* from Zhoukoudian in Beijing (Zheng, 1984a), Jinniushan in Liaoning Province (Zheng & Han, 1993) and Renzidong in Anhui Province (Jin et al., 2009), and of *T. triton* from Syz 2 and of the extant *T. triton*. It can be seen that, except the material from Renzidong, which are obviously smaller, the averages of molar size of the material from other localities are quite close to each other, and the ranges of these data also considerably overlap. In other words, we cannot distinguish *C. varians* from *T. triton* through their size. As for the material from Renzidong, its obvious smaller size and obviously older geologic age—the age of Renzidong is ca. 2 Ma (Jin, Qiu & Zheng, 2009), while other localities are all Middle Pleistocene—make its identification as *C. varians* very dubious. Perhaps the material from Renzidong represents a new form. By the way, with the hamster material originally identified as *Cricetinus varians* (or *Cricetinus* cf. *variens*, *Cricetulus* (*Cricetinus*) *variens*) from several Early Pleistocene sites in China being assigned to *Allocricetus* (e.g., Localities 12, 18 of Zhoukoudian, Gongwangling of Lantian, Shaanxi) (Zheng, 1984a), East cave of Zhoukoudian is currently the only Early Pleistocene site yielding *C. varians* fossils other than Renzidong in China. However, the length of M1-3 of *Cricetinus varians* from East cave is merely 4.83 mm (Cheng et al., 1996, Table 3-11, p.40), smaller than the lower end of the range of variation of that measurement in “typical” *C. varians* and extant *Tscherskia triton* (Table 2). More importantly, the m1s of *C. varians* from East cave totally lack mesolophid (Cheng et al., 1996, p.40), which is remarkably different from “typical” *C. varians* and extant *T. triton* (Table 3). Therefore, the material identified as *C. varians* from East cave clearly warrants reconsideration of its attribution. Given the above explanations, except the *Tscherskia* sp. from the Late Pliocene Youhe fauna (Xie, Zhang & Li, 2021), there is no reliable material of *Tscherskia* in China earlier than the Middle Pleistocene.

② Comparison of the teeth structure

In a hamster individual, the molars which are symmetrically distribute in the mouth (the left and right M3, for instance) may have minor morphological differences; therefore, the characters of both the left and right teeth of large-sized hamster from Syz 2 and the living *T. triton* were statistically analyzed in the present study. The material of *C. varians* used for comparison here is mainly from Zhoukoudian (Zheng, 1984a) and Jinniushan (Zheng & Han, 1993).

m1 In the extant *T. triton*, the specimens with the mesolophid account for 30% of all specimens (Table 3). The mesolophids of these specimens are all weakly developed and of very short length: the longest mesolophid does not exceed 1/5 of the distance from the base to the edge of

the tooth, and in the majority of cases it only shows up as a tiny bulge. The mesolophid is either connected to the metaconid (9.5%, 2/21) or has a free end (90.5%, 19/21).

The localities in Table 3 from top to bottom are roughly ranked in accordance with the geologic age from oldest to youngest (ZKD Loc.1, ca. 0.6-0.2 Ma; Jinniushan, ca. 0.31-0.2 Ma; ZKD Loc.3, late Middle Pleistocene; Syz 2, ca. 0.2 Ma). Although the frequency of mesolophid of *C. varians* and *T. triton* in different geologic ages is not the same, there is not an obvious interruption between them, and the later the age is, the lower the frequency of the mesolophid will be. From the viewpoint of the similarity of other aspects of teeth characters and the practicality of classification, instead of regarding these different frequencies of mesolophid as the interspecific, even intergeneric differences, it is better to regard them as the evolutionary trend of one species, namely the mesolophid gradually reduces.

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m2 Table 4 presents the frequencies of mesolophids on m2 of *T. triton* and *C. varians*. As the table shows, during geologic history the frequencies of mesolophids on m2 of *T. triton* and *C. varians* were all very high and very close to each other, showing no obviously decreased trend, although in the extant *T. triton* the frequency is slightly lower. Except for the Jinniushan locality, the situation of proportions of morphotype iii of specimens from other localities and extant species is also similar to the situation of frequency of mesolophid. Therefore, the characters of mesolophid of m2 of *T. triton* and *C. varians* further prove the consistency of the two, and it seems more reasonable to explain the difference of the frequencies in the evolutionary trend of one species, namely the reducing of the mesolophid.

m3 Table 5 shows the frequencies of mesolophids on m3 of *T. triton* and *C. varians*. It can be seen from the table that the mesolophid exists in almost all of the specimens. The ratios of "the mesolophid extends to the lingual edge" are all high, but the regularity is not obvious. The comparison of the proportions of more detailed morphological characters is difficult due to the lack of data. But overall, the characters of m3 of *T. triton* and *C. varians* are still quite consistent.

M1 The lingual anterocone and protocone on M1 of *T. triton* and *C. varians* are always connected by a anterolophule, while the other anterolophule behind the buccal anterocone is not always present. Table 6 shows that "the anterolophule behind the buccal anterocone" has a higher frequency in both *T. triton* and *C. varians*, but since the statistical data of *C. varians* is based on a relatively small amount of material, the reliability of comparison is reduced. The frequencies of "the protolophule I" are not stable and seem that there is no regularity.

M2 and M3 There is little difference between M2 and M3 of *T. triton* and *C. varians*.

In summary, *C. varians* and *T. triton* show considerable consistency in the characters of skulls and teeth. Although there are still small differences between teeth morphology of them, these differences all change continuously and can only be noticed when there are statistically abundant materials. Therefore, we consider that *C. varians* can only be treated as a chronosubspecies of *T. triton*, i.e., *T. triton varians*, and *Cricetinus* should be discarded as junior synonym of *Tscherskia*.

Referred species of *Tscherskia*

Except for *Cricetinus varians*, there are other 6 species in Eurasia that have been referred to *Cricetinus*:

Cricetinus europaeus Kretzoi, 1959. The type locality of this species is Csarnóta 2 in Hungary. Most researchers believe that the geologic age of this site is MN 15 (Venczel & Gardner, 2005). The type specimens of *C. europaeus* are only three molars, but an M2 of these three molars was later identified as *C. janossyi* by Hír (1996b). Hír (1994) discovered additional material of this species and described them in detail when he examined the material from the type locality, so the nature of the species is now relatively clear. Although *C. europaeus* is one of the earliest *Cricetinus* species in Europe (Hír, 1994), it seems to have rather advanced characters. For example, the ratios of presence of mesolophid on m1 and m2 are even lower than those of extant *T. triton* (Table 7), but because of the paucity of the material, this observation needs to be tested with more material in the future.

Cricetinus gritzai Topachevski & Skorik, 1992. The type locality of this species is Odessa, Ukraine. The important character of this species is that all m1s and partial m2s have a mesolophid (Koufos et al., 2001). On the one hand, this character illustrates its more primitive nature (in other species of *Cricetinus* or *Tscherskia*, the frequency of mesolophid of m1 is 70% at most). On the other hand, the character itself is also unique, because in cricetids the frequency of mesolophid of m1 is almost always lower than that of m2, but in this species the situation is just the opposite. In addition, other molars of *C. gritzai* are slightly smaller than *T. triton* in size, but only the M3 is significantly larger than that of *T. triton* (Topachevsky & Skorik, 1992). If this is not a statistical error (because there is only one M3), it may also illustrate the primitive nature of *C. gritzai*.

Cricetinus beremendensis Hír, 1994. The type locality of this species is Beremend 15 in Hungary, of an geologic age of 2.7 Ma (Hír, 1994; Pazonyi, 2011). Molar morphology of this species, especially the degree of development of the mesolophid, is far from other species currently classified in *Cricetinus*, but very similar to *Allocricetus ehiki* and *A. bursae* in size and structure (Table 7), so it seems more reasonable to place this form in *Allocricetus* Schaub, 1930.

Cricetinus janossyi Hír, 1996. The type locality of this species is Osztramos 7 in Hungary of an geologic age of about 2.3 Ma (Hír, 1996b; Pazonyi, 2011). The molar structures of this species are very similar to that of *T. triton varians* from Syz 2 (Table 7), but the former is slightly larger than the latter in size, and the ages of the two are far from one another. *C. janossyi* is also one of the earliest species of *Cricetinus* in Europe, first appeared in Csarnóta 2 of Hungary at the same time as *C. europaeus*.

Cricetinus koufosi Koliadimou 1996. The type locality of this species is Ravin Voulgarakis of Mygdonia basin of Greece (Koufos et al., 2001). The age of Ravin Voulgarakis has been dated to Nagyarsanyhegy phase of Biharian (ca. 1.2-0.7 Ma) (Koufos et al., 2001), so the species is the latest among several species of *Cricetinus* in Europe. In addition, this species has also been discovered in Marathoussa of Mygdonia basin, with the age of the locality being dated to Betfia phase of Biharian (ca. 1.5-1.2 Ma) (Koufos et al., 2001). Many molar characters of this species

are still unclear, but the lack of mesolophid on m1 of it may indicate its relatively progressive nature.

Cricetinus mesolophidos Wu & Flynn, 2017. Xie, Zhang & Li (2021) concluded that it was more reasonable to place *C. mesolophidos* in *Neocricetodon* rather than in *Cricetinus* (i.e. *Tscherskia*).

In summary, we suggest that *C. europaeus*, *C. gritzai*, *C. janossyi* and *C. koufosi* should be transferred to *Tscherskia*, while *C. beremendensis* should be transferred to *Allocricetus*, and *C. mesolophidos* to *Neocricetodon*. However, this treatment is provisional, because the characters of some of these species are still unclear. Except the type species *T. triton*, the type locality of other four species of *Tscherskia* are located in a small area covered by several neighboring countries in southeastern Europe, thus there is a huge geographic distance between *T. triton* and other species, which makes the above classification somewhat uncertain (Kretzoi, 1959; Hír, 1994). In addition, Storch (1974) described a species *T. rusa* from the Holocene (dated between 2200–700 B.C.) of northern Iran, whose geographic location and age are highly confusing. Although we have included it in the referred species of *Tscherskia*, the validity of this species and whether it should be referred to *Tscherskia* obviously deserve further examination. Table 7 is a summary of comparisons of frequencies of mesolophids on m1-3 between the species of *Cricetinus*, *Tscherskia* and some related genera (*Cricetulus*, *Nothocricetulus* and *Allocricetus*).

Origin and dispersal of *Tscherskia*

Zheng (1984a, b), Zheng et al. (1985) and Zheng & Han (1993) considered that *Cricetinus* (junior synonym of *Tscherskia*) was very likely to have originated from the genus *Kowalskia* (junior synonym of *Neocricetodon*), the idea that had been tentatively proposed by Fahlbusch (1969). Qiu & Li (2016) remarked that this view was very worthy of further study. We also agree with this opinion, and the reasons for this deduction have already been fully explained by Zheng (1984b) (as discussed above, the presence of axioloph in both genera seems also imply this), so it is not necessary to repeat them here again.

The question now is: when and where (Asia or Europe) did *Tscherskia* originate? According to the current evidence, the earliest appearance of *Tscherskia* in Europe is earlier than that in Asia. The earliest species of *Tscherskia* in Europe are *T. europaeus* and *T. janossyi*, both of which occurred at Csarnóta 2 (MN 15, ca. 5-3.5 Ma) in Hungary (Hír, 1994; Venczel & Gardner, 2005). In Asia, the earliest *Tscherskia* is *T. sp.* (the material is a fragmentary mandible with m2-m3) of Youhe fauna from Linwei District, Shaanxi Province, China (Xie, Zhang & Li, 2021), with an age of Late Pliocene (ca. 3.15-2.59 Ma, Yue & Xue, 1996). However, as has already been stated above, other reliable materials of *Tscherskia* in China (or Asia) are all of the geologic age not earlier than Middle Pleistocene. This nearly blank fossil record of *Tscherskia* in East Asia before Middle Pleistocene is a major challenge to the idea of the East Asian origin of *Tscherskia*, although the species similar in morphology to *Tscherskia triton* (e.g., *Neocricetodon yinanensis*) has been found in Late Pliocene (?) in China. In terms of the diversity of the *Tscherskia* species, Europe also has a significantly higher diversity than Asia. Therefore, on present evidence, *Tscherskia* seems more likely to have originated from *Neocricetodon* during the Early Pliocene

in Europe and then spread to Asia, and maybe there is another dispersal event of same direction taken placed in Early Pleistocene, which can explain the absence of the reliable fossil record of *Tscherskia* during the Early Pleistocene in China. Of course, this view still needs the verification of more material in the future.

Conclusions

The detailed morphological description and comparative study show that hundreds of large-sized hamster remains collected from the late Middle Pleistocene Locality 2 of Shanyangzhai (Syz 2) should be referred to a chronosubspecies of the extant *Tscherskia triton*—*T. triton varians*. *T. triton varians* is very similar to extant *T. triton* in size and most characters of molars, but the former has slightly higher frequencies of mesolophid on m1 and m2. In most measurements of the skull and mandible, the mean values of the former may be lightly greater than those of the later. To clarify the long-disputed issue of the validity of *Cricetinus* Zdansky, 1928 and *C. varians* Zdansky, 1928, we compared in detail the *C. varians* and *T. triton* from the aspects of skull and molar morphology, and the results showed that the differences between the two are very slight, therefore the *C. varians* can only be treated as a chronosubspecies of *T. triton*, i.e., *T. triton varians*, and the *Cricetinus* should be discarded as junior synonym of *Tscherskia*. We tentatively suggest that among the seven species once referred to *Cricetinus* in Eurasia, *C. europaeus*, *C. gritzai*, *C. janossyi* and *C. koufosi* should be transferred to *Tscherskia*, while *C. beremendensis* should be transferred to *Allocricetus*, and *C. mesolophidos* to *Neocricetodon*. On present evidence, *Tscherskia* may have originated from *Neocricetodon* during the Early Pliocene in Europe and then spread to Asia, and *T. triton* is its only extant representative which now only inhabits in East Asia.

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References

- Allen GM. 1928. A new cricetine genus from China. *Journal of Mammalogy* 9:244–246.
- Argyropulo AI. 1933. Die Gattungen und Arten der Hamster (Cricetinae Murray, 1866) der Paläarkt. *Zeitschrift für Säugetierkunde* 8:129–149.

754 Cai BQ, Zhang ZQ, Zheng SH, Qiu ZD, Li Q, Li Q. 2004. New advances in the stratigraphic
755 study on representative sections in the Nihewan Basin, Hebei. In: *Professional Papers of*
756 *Stratigraphy and Palaeontology, Number 28*. Beijing: Geology Press, 267–285.

757 Cai BQ, Zheng SH, Liddicoat JC, Li Q. 2013. Review of the Litho-, Bio-, and Chronostratigraphy
758 in the Nihewan Basin, Hebei, China. In: *Fossil Mammals of Asia: Neogene Biostratigraphy and*
759 *Chronology*. New York: Columbia University Press, 218–242.

760 Chen W, Gao W. 2000. Cricetinae. In: *Luo Z X, Chen W, Gao W (Eds.), Fauna Sinica,*
761 *Mammalia, Vol. 6: Rodentia Part III: Cricetidae*. Beijing: Science Press, 20–90.

762 Chen Y, Li YX, Shi JS, Zhang YX, Xie K. 2021. Pleistocene fossil snakes (Squamata, Reptilia)
763 from Shanyangzhai Cave, Hebei, China. *Historical Biology* 33:699–711.

764 Chen SK, Pei J, Yi J, Wei GB, Pang LB, Wu Y, Hu X. 2017. Preliminary report on the
765 mammalian fauna from Yumidong cave, Wushan, Chongqing, and its chronological analysis.
766 *Quaternary Sciences* 37:845–852.

767 Chen TM, Zhou LP. 2009. Dating of the Peking Man site: A comparison between existing
768 chronology and the $^{26}\text{Al}/^{10}\text{Be}$ burial ages. *Acta Anthropologica Sinica* 28:285–291.

769 Cheng J, Tian MZ, Cao BX, Li LY. 1996. *The new mammalian fossils from Zhoukoudian*
770 *(Choukoutien) Beijing and their environmental explanation*. Wuhan: China University of
771 Geosciences Press.

772 Chow MC, Li CK. 1965. Mammalian fossils in association with the mandible of Lantian Man at
773 Chen-chia-ou, in Lantian, Shensi. *Vertebrata Palasiatica* 9:377–393.

774 Ding L, Zhou Q, Sun Y, Feoktistova NY, Liao J. 2020. Two novel cricetine mitogenomes: Insight
775 into the mitogenomic characteristics and phylogeny in Cricetinae (Rodentia: Cricetidae).
776 *Genomics* 112:1716–1725.

777 Fahlbusch V. 1969. Pliozäne und Pleistozäne Cricetinae (Rodentia, Mammalia) aus Polen. *Acta*
778 *Zoologica Cracoviensis* 14:99–138.

779 Freudenthal M, Daams R. 1988. Cricetidae (Rodentia) from the type-Aragonian; the genera
780 *Democricetodon*, *Fahlbuschia*, *Pseudofahlbuschia* nov. gen., and *Renzimys*. *Scripta Geologica,*
781 *Special Issue* 1:133–252.

782 Freudenthal M, Hugueney M, Moissenet E. 1994. The genus *Pseudocricetodon* (Cricetidae,
783 Mammalia) in the upper Oligocene of the province of Teruel (Spain). *Scripta Geologica* 104:57–
784 114.

785 Gai P, Wei Q. 1977. The discovery of Upper Paleolithic Hutouliang Site. *Vertebrata Palasiatica*
786 15:287–300.

787 Gu YM. 1978. New Cave Men and their living environment. In: *Institute of Vertebrate*
788 *Paleontology and Paleoanthropology, Chinese Academy of Sciences (Ed.). Collected Papers of*
789 *Paleoanthropology*. Beijing: Science Press, 158–174.

790 Hír J. 1993a. *Cricetulus migratorius* (Pallas, 1773) (Rodentia, Mammalia) population from the
791 Toros Mountains (Turkey) (With a special reference to the relation of *Cricetulus* and *Allocricetus*
792 genera). *Folia Historico Naturalia Musei Matraensis* 18:17–34.

793 Hír J. 1993b. *Allocricetus ehiki* Schaub, 1930 (Rodentia, Mammalia) finds from Villány 3 and
794 Eszamos 3 (Hungary). *Fragmenta Mineralogica et Palaeontologica* 16:61–80.

795 Hír J. 1994. *Cricetinus beremendensis* sp. n. (Rodentia, Mammalia) from the Pliocene fauna of
796 Beremend 15. (S Hungary). *Fragmenta Mineralogica et Paleontologica* 17:71–89.

Hír J. 1996a. New results in the study of Hungarian Plio-Pleistocene cricetids. *Acta Zoologica Cracoviensis* 39:213–218.

Hír J. 1996b. *Cricetinus janossyi* sp. n. (Rodentia, Mammalia) from the Pliocene fauna of Osztramos 7. (N Hungary). *Fragmenta Mineralogica et Palaeontologica* 18:79–90.

Hír J. 1997. A short scetch of the evolution and stratigraphy of the Plio-Pleistocene cricetids (Rodentia, Mammalia) in Hungary. *Folia Historico Naturalia Musei Matraensis* 22:43–49.

Hu CK. 1985. History and progress of mammalian fossil research of Locality 1 of Zhoukoudian. In: *Multi-disciplinary study of the Peking Man Site at Zhoukoudian*. Beijing: Science Press.

Huang YP, Fu RY, Li X, Hui ZY. 2021. The study of the animal fossils from Jinniushan. In: *School of Archaeology and Museology, Peking University; Liaoning Provincial Academy of Cultural Relics and Archaeology (Eds.). The Jinniushan Hominin Site*. Beijing: Cultural Relics Press, 168–285.

ICZN. 1999. *International Code of Zoological Nomenclature (4th Edition)*. London: International Trust for Zoological Nomenclature.

Jia LP. 1959. Report on 1958's excavation at Peking Man Site. *Palaeovertebrata et Paleoanthropologia* 1:21–26.

Jin CZ. 2002. Chiroptera and Rodentia. In: *Wu R K, Li X X, Wu X Z, Mu X N (Eds.). Homo erectus from Nanjing*. Nanjing: Jiangsu Science and Technology Publishing House, 91–101.

Jin CZ, Dong W, Gao X, Liu W, Liu JY, Zheng LT, Han LG, Xie XC, Cui N, Zhang YQ. 2004. Preliminary report on the 2002 excavation of Jinpendong site at Wuhu, Anhui Province. *Acta Anthropologica Sinica* 23:281–291.

Jin CZ, Qiu ZX, Zheng JJ. 2009. Chapter 5 The characters of the mammalian fauna from the Renzidong Cave and its zoogeographical significance. In: *Jin C Z, Liu J Y (Eds.). Paleolithic site — the Renzidong cave, Fanchang, Anhui Province*. Beijing: Science Press, 336–346.

Jin CZ, Zhang YQ, Wei GB, Cui N, Wang Y. 2009. Rodentia. In: *Jin C Z, Liu J Y (Eds.). Paleolithic site — the Renzidong cave, Fanchang, Anhui Province*. Beijing: Science Press, 166–220.

Kishida K. 1929. A synopsis of Korean hamsters. *Lansania, Tokyo* 1:1–160.

Koliadimou KK. 1996. Palaeontological and Biostratigraphical study of the Neogene/Quaternary micromammals from Mygdonia basin. *Doct thesis, Univ. Thessaloniki*: 612.

Kong FD. 2009. Research on Shanyangzhai Fauna and Their Living Environment of Qinhuangdao. *Journal of EMCC* 19:1–8.

Koufos GD, Vassiliadou KV, Koliadimou KK, Syrides GE. 2001. Early Pleistocene small mammals from Marathoussa, a new locality in the Mygdonia basin, Macedonia, Greece. *Deinsea* 8:49–102.

Kretzoi M. 1959. Insectivoren, Nagetiere und Lagomorphen der jungstpliozanen Fauna von Csarnota im Villanyer Gebirge (Sudungarn). *Vertebrata Hungarica* 1:237–246.

Lebedev V, Bannikova A, Neumann K, Ushakova M, Ivanova N, Surov A. 2018. Molecular phylogenetics and taxonomy of dwarf hamsters *Cricetulus* Milne-Edwards, 1867 (Cricetidae, Rodentia): description of a new genus and reinstatement of another. *Zootaxa* 4387:331–349.

Li Q, Stidham TA, Ni X, Li L. 2018. Two new Pliocene hamsters (Cricetidae, Rodentia) from southwestern Tibet (China), and their implications for rodent dispersal 'into Tibet.' *Journal of Vertebrate Paleontology* 37: e1403443.

Li YX, Li J, Zhang YX. 2016. Fossil *Scapanulus oweni* (Eulipotyphla, Mammalia) from the Shanyangzhai Cave, Middle Pleistocene, Qinhuangdao, China. *Quaternary International* 392:197–202.

Li YX, Zhang YX. 2011. The *Crociodura* fossils (Insectivora, Mammalia) from cave deposits in the Middle Pleistocene of Shanyangzhai site, Hebei Province, China. *Quaternary Sciences* 31:667–674.

Li YX, Zhang YX. 2013. New *Neomys* fossils (Soricidae, Insectivora) from the Middle Pleistocene of China. *Quaternary international* 286:81–84.

Li YX, Zhang YX, Ao H. 2013. *Sorex* fossils (Soricidae, Insectivora) from the Middle Pleistocene cave site of Shanyangzhai, Hebei Province, China. *Quaternary International* 298:187–195.

Li YX, Zhang YX, Li J. 2013. Distribution of several insectivora and the drying trend since the Pleistocene in North China. *Quaternary international* 313:240–247.

Li YX, Zhang YX, Zheng YH. 2013. *Erinaceus europaeus* fossils (Erinaceidae, Insectivora) from the Middle Pleistocene cave site of Shanyangzhai, Hebei Province, China. *Quaternary International* 286:75–80.

Liu JY, Wagner J, Chen PF, Sheng GL, Chen J, Jiang Zuo QG, Liu SZ. 2015. Mass mortality of a large population of the spotted hyenas (*Crocota ultima*) at the Lingxian-dong cave, Qinhuangdao, Hebei Province: a hyena communal den with its palaeoecological and taphonomical interpretation. *Quaternary Sciences* 35:607–621.

Liu W, Wu XJ, Xing S, Zhang YY. 2014. *Human Fossils in China*. Beijing: Science Press.

McKenna MC, Bell SK. 1997. *Classification of mammals: above the species level*. New York: Columbia University Press.

Musser GG, Carleton MD. 2005. Superfamily Muroidea. In: *Wilson D E, Reeder D M (Eds.). Mammals Species of the World: A Taxonomic and Geographic Reference*. Baltimore: The Johns Hopkins University Press, 894–1531.

Neumann K, Michaux J, Lebedev V, Yigit N, Colak E, Ivanova N, Poltoraus A, Surov A, Markov G, Maak S, others. 2006. Molecular phylogeny of the Cricetinae subfamily based on the mitochondrial cytochrome b and 12S rRNA genes and the nuclear vWF gene. *Molecular phylogenetics and evolution* 39:135–148.

Niu PS, Zhang YJ, Fa L. 2003. Formation period and environment of speleothem in the Liujiang Basin inferred from the Shanyangzhai mammal fossils. *Marine Geology & Quaternary Geology* 23:117–122.

Ognev SI. 1914. Die Säugetiere aus dem Südlichen UssuriGebiete. *Journal de la Section Zoologique de la Société Impériale des Amis des Sciences Naturelles, d'Antropologie et d'Ethnographie* 2:101–134.

Pazonyi P. 2011. Palaeoecology of Late Pliocene and Quaternary mammalian communities in the Carpathian Basin. *Acta Zoologica Cracoviensia-Series A: Vertebrata* 54: 1–32.

Pei WC. 1931. Mammalian remains from Locality 5 at Chouk'outien. *Palaeontologia Sinica, Series C* 7:16.

Pei WC. 1936. On the mammalian remains from Locality 3 at Choukoutien. *Palaeontologia Sinica, Series C* 7:120.

Pei WC. 1939. A Preliminary Study on a New Palæolithic Station known as locality 15 within the Choukoutien Region. *Bulletin of the Geological Society of China* 19:147–187.

- Pei WC. 1940. The Upper Cave fauna from Choukoutien. *Palaeontologia Sinica, New Series C* Number 10:1–84.
- Pradel A. 1981. Biometrical remarks on the hamster *Cricetulus migratorius* (Pallas 1773) (Rodentia, Mammalia) from Krak des Chevaliers (Syria). *Acta Zoologica Cracoviensia* 25:271–292.
- Qiu ZD. 1995. A new cricetid from the Lufeng hominoid locality, late Miocene of China. *Vertebrata Palasiatica* 33:61–73.
- Qiu ZD, Li Q. 2016. *Neogene Rodents from Central Nei Mongol, China*. Beijing: Science Press.
- Romanenko SA, Lebedev VS, Bannikova AA, Pavlova SV, Serdyukova NA, Feoktistova NY, Jiapeng Q, Yuehua S, Surov AV, Graphodatsky AS. 2021. Karyotypic and molecular evidence supports the endemic Tibetan hamsters as a separate divergent lineage of Cricetinae. *Scientific reports* 11:1–9.
- Schaub S. 1930. Quartäre und jungtertiäre Hamster. *Abhandlungen der Schweizerischen Palaeontologischen Gesellschaft* 49:1–49.
- Schaub S. 1934. Über einige fossile Simplicidentaten aus China und der Mongolei. *Abhandlungen der Schweizerischen Palaeontologischen Gesellschaft* 54:1–39.
- Sinitsa MV, Delinschi A. 2016. The earliest member of *Neocricetodon* (Rodentia: Cricetidae): a redescription of *N. moldavicus* from Eastern Europe, and its bearing on the evolution of the genus. *Journal of Paleontology* 90:771–784.
- Steppan SJ, Schenk JJ. 2017. Muroid rodent phylogenetics: 900-species tree reveals increasing diversification rates. *PloS one* 12:e0183070.
- Storch G. 1974. Neue Zwerghamster aus dem Holozan von Aserbeidschan, Iran (Rodentia: Cricetinae). *Senckenbergiana Biologica* 55:21–28.
- Sun YF, Jin CZ. 1990. Micromammal fossils. In: *Gulongshan cave site: a Upper Paleolithic site at Dalian City*. Beijing: Beijing Science and Technology Press, 27–43.
- Teilhard de Chardin P. 1936. Fossil mammals from Locality 9 of Choukoutien. *Palaeontologia Sinica, Series C* 7:61.
- Teilhard de Chardin P. 1940. The fossils from Locality 18 near Peking. *Palaeontologia Sinica, New Series C* Number 9:1–94.
- Teilhard de Chardin P, Leroy P. 1942. Chinese fossil mammals: a complete bibliography analysed, tabulated, annotated and indexed. *Géobiologia* 8:1–142.
- Teilhard de Chardin P, Pei WC. 1941. The fossil mammals from Locality 13 of Choukoutien. *Palaeontologia Sinica, New Series C* Number 11:1–106.
- Teilhard de Chardin P, Young CC. 1929. Preliminary report on the Chou Kou Tien fossiliferous deposits. *Bulletin of the Geological Society of China* 8:173–202.
- Tong HW, Shang H, Zhang SQ, Chen FY. 2004. A preliminary report on the newly found Tianyuan Cave, a Late Pleistocene human fossil site near Zhoukoudian. *Chinese Science Bulletin* 49:853–857.
- Tong HW, Wu XJ, Dong Z, Sheng JC, Jin ZT, Pei SW, Liu W. 2018. Preliminary report on the mammalian fossils from the ancient human site of Hualong Cave in DongZhi, Anhui. *Acta Anthropologica Sinica* 37:284–305.
- Topachevsky VA, Skorik AF. 1992. *Neogenovye i pleystocenovye nizhie khomiakoobraznye yuga Vostochnoy Evropy*. Kiev: Naukova Dumka.

Venczel M, Gardner JD. 2005. The geologically youngest albanerpetontid amphibian, from the lower Pliocene of Hungary. *Palaeontology* 48: 1273–1300.

Voss RS. 1988. Systematics and ecology of ichthyomyine rodents (Muroidea): patterns of morphological evolution in a small adaptive radiation. *Bulletin of the American Museum of Natural History*. 188: 259–493.

WU BL, DENG CL, KONG YF, LIU SZ, SUN L, LI SH, GE JY, WANG Y, JIN CZ, ZHU RX. 2018. Magnetostratigraphy of the fluvio-lacustrine sequence on the Guangongtan section in Longzhong Basin, NW China. *Chinese Journal of Geophysics* 61:1390–1399.

Wang BY, Qiu ZX. 2018. *Late Miocene Pararhizomyines from Linxia Basin of Gansu, China*. Beijing: Science Press.

Wang BY, Wu WY, Qiu ZD. 2020. Cricetidae. In: *Qiu Z D, Li C K, Zheng S H (Eds.), Palaeovertebrata Sinica, Volume III, Basal Synapsida and Mammals, Fascicle 5(2) (Serial no. 18-2): Glires II: Rodentia II*. Beijing: Science Press, 10–152.

Wang W, Zhang YX, Li YX, Gong HJ. 2010. A new species of *Lepus* (Lagomorpha, Mammalia) from the Middle Pleistocene of the Liujiang Basin in Qinhuangdao of Hebei Province, China. *Vertebrata Palasiatica* 48:63–70.

Wu WY, Flynn LJ. 2017. The hamsters of Yushe basin. In: *Flynn L J, Wu W Y (Eds.). Vertebrate Paleobiology and Paleoanthropology Series. Late Cenozoic Yushe basin, Shanxi province, China: Geology and fossil mammals, Volume II: Small Mammal Fossils of Yushe Basin*. Dordrecht: Springer, 123–137.

Xia L, Yang QS, Ma Y, Feng ZJ, Zhou LZ. 2006. A guide to the measurement of mammal skull III: Rodentia and Lagomorpha. *Chinese Journal of Zoology* 41:68–71.

Xie K, Li YX. 2016. Middle Pleistocene dwarf hamster of Shanyangzhai fauna in Qinhuangdao area, China. *Quaternary Sciences* 36:322–331.

Xie K, Zhang YX, Li YX. 2021. Revision to *Kowalskia* from the Houhecun Fauna and a New Discovery of *Tscherskia* (Cricetidae, Rodentia) from the Youhe Fauna of Weinan, Shaanxi Province, China. *Acta Geologica Sinica - English Edition* 95:1073–1079. DOI: 10.1111/1755-6724.14776.

Xu QQ, Jin CZ, Tong HW, Dong W, Liu JY, Cai BX. 1997. Three glacial cycles during Peking Man's time. In: *Tong Y S, Zhang Y Y, Wu W Y et al. (Eds.). Evidence for Evolution—Essays in Honor of Prof. Chungchien Young on the Hundredth Anniversary of His Birth*. Beijing: China Ocean Press, 209–226.

Yang QS, Xia L, Ma Y, Feng ZJ, Quan GQ. 2005. A guide to the measurement of mammal skull I : basic measurement. *Chinese Journal of Zoology* 40:50–56.

Young CC. 1927. Fossile Nagetiere aus Nord-China. *Palaeontologia Sinica, Series C* 5:82.

Young CC. 1932. On the fossil vertebrate remains from Localities 2, 7 and 8 at Choukoutien. *Palaeontologia Sinica, Series C* 7:24.

Young CC. 1934. On the Insectivora, Chiroptera, Rodentia and Primates other than Sinanthropus from Locality 1 at Choukoutien. *Palaeontologia Sinica, Series C* 8:160.

Yue LP, Xue XX. 1996. *Palaeomagnetism of Chinese Loess*. Beijing: Geology Press.

Zdansky O. 1923. Über Ein Säugerknochenlager in Chou-K'ou-Tien, Provinz Chihli. *Bulletin of the Geological Survey of China* 5:83–90.

Zdansky O. 1928. Die Säugetiere der Quartärfauna von Chou-K'ou-Tien. *Palaeontologia Sinica, Series C* 5:146.

970 Zhang SS. 2004. *Beijing Annals, World Cultural Heritage Volume, The Peking Man Ruins*
 971 *Annals*. Beijing: Beijing Press.

972 Zhang ZH, Fu RY, Chen BF, Liu JY, Zhu MY, Wu HK, Huang WW. 1985. A preliminary report
 973 on the excavation of Paleolithic site at Xiaogushan of Haicheng, Liaoning, Province. *Acta*
 974 *Anthropologica Sinica* 4:70–81.

975 Zhang YX, Li YX. 2015. The environment change and the migrate of some insectivora since the
 976 Pleistocene in China. 45:905–912.

977 Zhang YX, Li YX, Wang W, Gong HJ. 2010. Middle Pleistocene mammalian fauna of
 978 Shanyangzhai cave in Qinhuangdao area, China and its zoogeographical significance. *Chinese*
 979 *Science Bulletin* 55:72–76.

980 Zhang ZH, Wei HB, Xu ZH. 1986. Fossils of animal. In: *Miaohoushan: a site of early Paleolithic*
 981 *in Benxi County, Liaoning*. Beijing: Wenwu Press, 35–66.

982 Zhang ZQ, Zheng SH, Liu LP. 2008. Late Miocene cricetids from the Bahe Formation, Lantian,
 983 Shaanxi Province. *Vertebrata Palasiatica* 46:307–316.

984 Zhang ZH, Zou BK, Zhang LK. 1980. The discovery of fossil mammals at Anping, Liaoning.
 985 *Vertebrata Palasiatica* 18:154–162.

986 Zheng SH. 1983. Micromammals from the Hexian Man Locality. *Vertebrata Palasiatica* 21:230–
 987 240.

988 Zheng SH. 1984a. Revised determination of the fossil Cricetine (Rodentia, Mammalia) of
 989 Choukoutien district. *Vertebrata Palasiatica* 22:179–197.

990 Zheng SH. 1984b. A new species of *Kowalskia* (Rodentia, Mammalia) of Yinan, Shandong.
 991 *Vertebrata Palasiatica* 22:251–260.

992 Zheng SH. 1993. *Quaternary rodents of Sichuan-Guizhou area, China*. Beijing: Science Press.

993 Zheng SH, Han DF. 1993. Mammalian fossils. In: *Memoirs of Institute of Vertebrate*
 994 *Palaeontology and Palaeoanthropology, Academia Sinica: Comprehensive study on the*
 995 *Jinniushan paleolithic site*. Beijing: Science Press, 43–128.

996 Zheng SH, Yuan BY, Gao FQ, Sun FQ. 1985. Fossil mammals and their evolution. In: *Loess*
 997 *and the Environment*. Beijing: Science Press, 113–141.

Figure 1

Geographic locations of Syz 1~4. Satellite photo credit: Google Earth.



Figure 2

Skulls of *Tscherskia triton varians* from Syz 2.

(A) NWUV 1489.a8, incomplete skull; (B) NWUV 1489.a21, incomplete skull; (C) NWUV 1489.a6, incomplete skull; (D) NWUV 1489.a7, incomplete skull. (A1), (B1), (C1), (D), dorsal view; (A2), (B2), (C2), lateral view; (A3), (B3), (C3), ventral view ; (A4), anterior view. The underlined label indicates the image has been reversed. Abbreviations: arza, anterior root of the zygomatic arc; aui, alveolus of the upper incisor; F, frontal; fc, frontal crest; inf, incisive foramen; iof, infraorbital foramen; lp, interparietal; M, maxilla; mt, masseteric tubercle; N, nasal; P, parietal; pbhp, posterior border of the hard palate; Pm, premaxilla; ppf, posterior palatine foramen; sof, supraorbital foramen; zp, zygomatic plate .

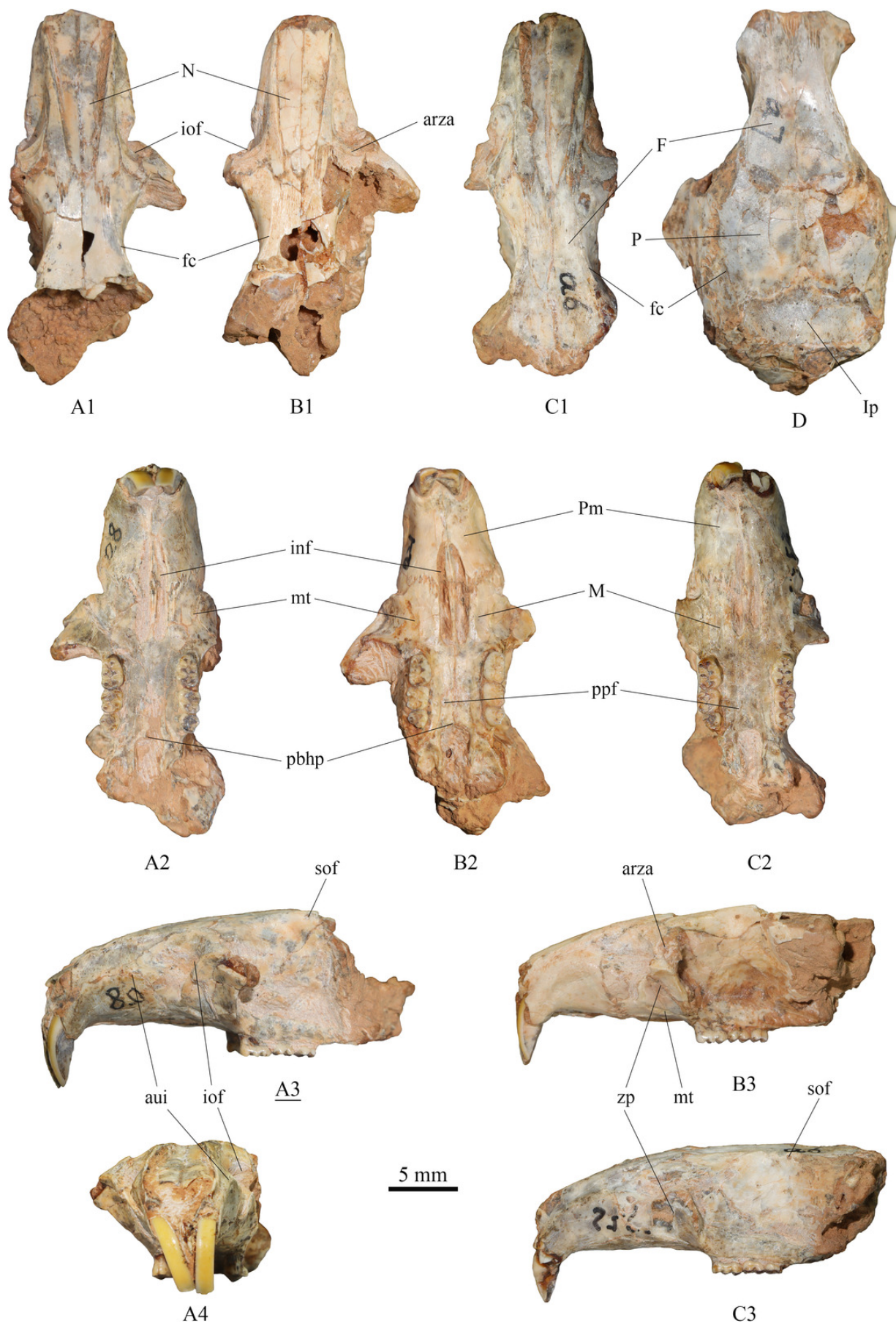


Figure 3

Mandibles of *Tscherskia triton varians* from Syz 2.

(A) NWUV 1489.f206, right mandible; (B) NWUV 1489.f207, right mandible; (C) NWUV 1489.e169, left mandible; (D) NWUV 1489.e164, left mandible. (A1), (B1), (C1), (D1), buccal view; (A2), (B2), (C2), (D2), lingual view; (B3), (C3), occlusal view. Abbreviations: ap, angular process; cdp, condyloid process; crp, coronoid process; fmg, foramen in the middle of the groove (g); g, groove between the alveolus of molars and the base of the coronoid process; i2b, bulge formed by i2; mdf, mandibular foramen; mn, mandibular notch; mr, masseteric ridge; mstf, masseteric fossa; mtf, mental foramen.

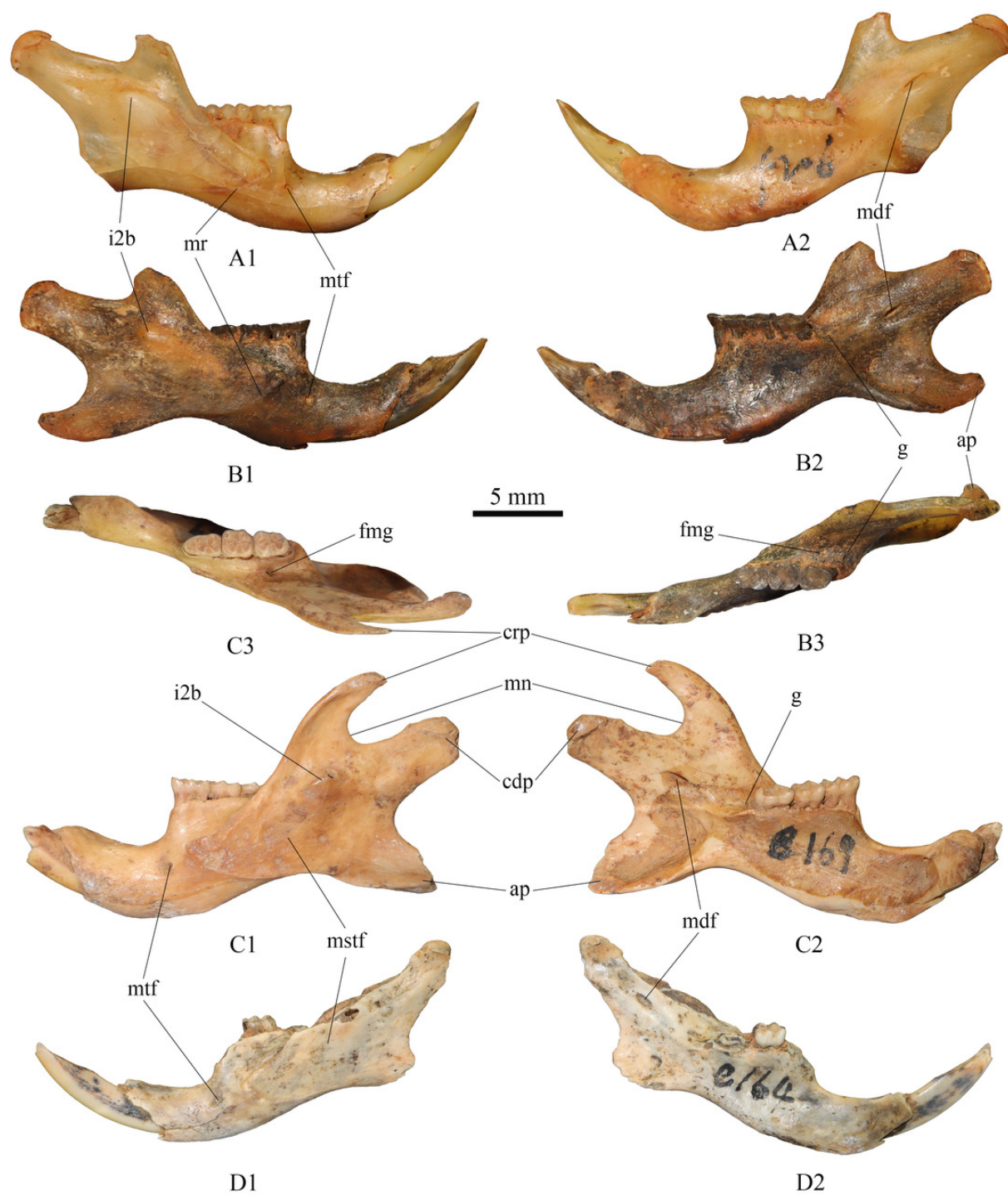


Figure 4

Upper molars of *Tscherskia triton varians* from Syz 2.

(A) NWUV 1489.a5; (B) NWUV 1489.a14; (C) NWUV 1489.a21; (D) NWUV 1489.b1; (E) NWUV 1489.c3; (F) NWUV 1489.c5; (G) NWUV 1489.c16. The arrow indicates the axioloph.



A



B



C



D



E



F



G

1 mm

Figure 5

Lower molars of *Tscherskia triton varians* from Syz 2.

(A) NWUV 1489.f8; (B) NWUV 1489.f13; (C) NWUV 1489.f22; (D) NWUV 1489.f28; (E) NWUV 1489.f31; (F) NWUV 1489.f49; (G) NWUV 1489.f56.



A



B



C



D



E



F

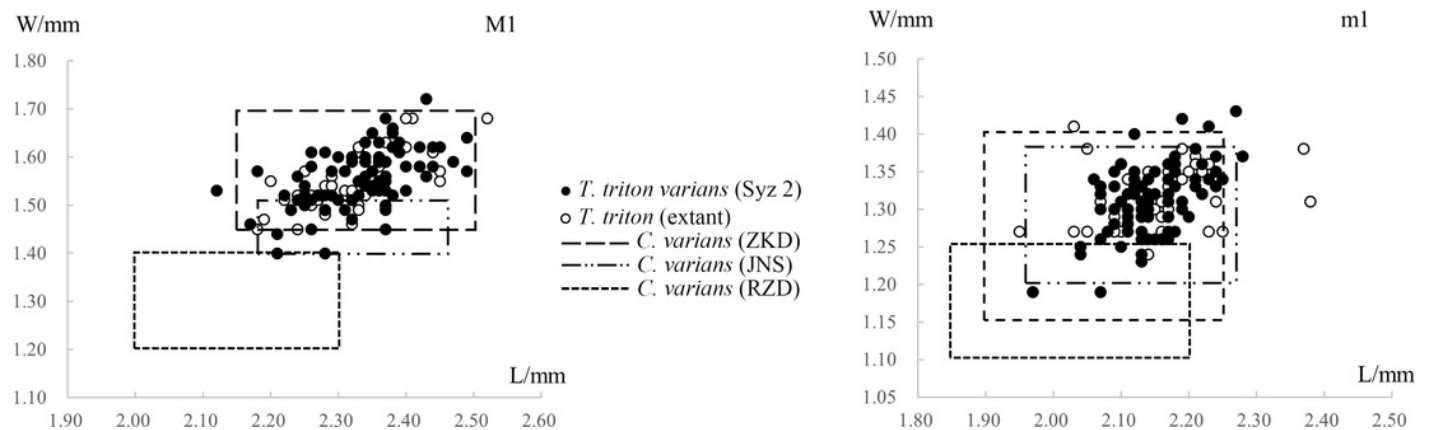


G

1 mm

Figure 6

Scatter diagrams of lengths of M1s and m1s of *Cricetinus varians* and *Tscherskia triton*.



What do the
boxes mean?

Table 1(on next page)

Measurements and comparisons of skulls and mandibles of *Tscherskia triton varians* from Syz 2 and extant *T. triton* (mm)[#]

1

	<i>T. triton</i> variants of Syz 2						extant <i>T. triton</i>					
	N	Min.	Mean	Max.	SD	CV	N	Min.	Mean	Max.	SD	CV
Palatal length	4	16.39	18.01	20.04	1.57	8.7%	40	13.72	17.21	20.13	1.70	9.9%
Upper diastema length	13	9.19	10.83	12.00	0.86	7.9%	46	7.64	9.98	12.31	1.15	11.5%
Length of the incisive foramen	11	6.26	7.11	7.93	0.51	7.2%	46	4.81	6.35	7.66	0.76	12.0%
Anterior palatal breadth	21	3.14	3.60	4.06	0.27	7.4%	44	2.39	3.18	3.78	0.31	9.8%
Posterior palatal breadth	11	3.34	3.78	4.02	0.18	4.7%	39	2.48	3.21	4.02	0.29	9.1%
Width of nasal *	6	1.88	2.18	2.34	0.16	7.4%	45	1.95	2.44	3.31	0.29	12.0%
Frontal suture length	1		9.66				43	8.83	10.68	12.62	0.95	8.9%
Parietal suture length	1		5.78				41	5.33	6.38	7.49	0.51	8.0%
Interparietal length	1		5.83				42	2.70	3.88	6.16	0.58	15.0%
Interparietal width	1		10.79				40	7.70	9.11	10.47	0.68	7.5%
Lower diastema length	21	4.89	5.76	6.70	0.56	9.7%	38	4.77	5.70	6.67	0.46	8.0%
Depth of mandible under anterior edge of alveolus	65	3.54	4.48	6.52	0.50	11.2%	40	3.55	4.56	5.91	0.52	11.4%
Depth of mandible between two roots of m1	78	4.31	5.27	6.63	0.48	9.2%	40	3.60	4.91	6.59	0.71	14.4%
Depth of mandible between two roots of m2	142	3.84	4.80	6.05	0.45	9.4%	40	3.04	4.36	6.05	0.68	15.7%
Depth of mandible between two roots of m3	162	2.83	3.87	4.98	0.44	11.3%	37	2.74	3.57	5.10	0.59	16.4%
Depth of mandible under posterior edge of alveolus	187	2.42	3.33	4.21	0.32	9.6%	40	2.40	3.17	4.44	0.42	13.2%
Length of mandible from the condyle	2	20.38	22.24	24.09	1.86	8.3%	38	16.05	20.30	24.99	2.07	10.2%
Distance from coronion to gonion ventrale	1		13.13				29	7.58	10.23	12.95	1.36	13.3%

See Supplementary datasets 1~4 for raw data.

* "Width of nasal" here refers to the distance between the two junctions of the nasal, premaxilla and frontal.

Table 2 (on next page)

Measurements and comparisons of molars of *Tscherskia triton* and *Cricetinus varians* (mm)[#]

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		M1~3		M1		M2		M3		m1~3		m1		m2		m3	
		L	L	W	L	W	L	W	L	L	W	L	W	L	W	L	W
<i>T. triton</i> varians of Syz 2	N	34	83	84	83	84	47	46	56	89	105	106	107	74	73		
	Min.	5.05	2.12	1.40	1.69	1.44	1.21	1.27	5.40	1.97	1.19	1.65	1.39	1.65	1.27		
	Mean	5.44	2.33	1.56	1.85	1.56	1.43	1.40	5.67	2.14	1.31	1.81	1.54	1.78	1.43		
	Max.	5.69	2.49	1.72	2.00	1.78	1.55	1.48	5.98	2.28	1.43	1.96	1.70	1.93	1.56		
	SD	0.15	0.07	0.06	0.06	0.06	0.07	0.04	0.13	0.06	0.04	0.06	0.05	0.06	0.05		
	CV	2.8%	3.2%	4.0%	3.4%	3.9%	5.2%	3.1%	2.4%	2.6%	3.4%	3.4%	3.2%	3.4%	3.6%		
<i>C. varians</i> of ZKD *	N	12	21	20	18	18	14	14	49	56	56	57	57	51	50		
	Min.	5.25	2.15	1.45	1.65	1.45	1.35	1.25	4.70	1.90	1.15	1.60	1.30	1.60	1.20		
	Mean	5.60	2.32	1.56	1.80	1.59	1.44	1.41	5.52	2.06	1.30	1.72	1.43	1.71	1.36		
	Max.	5.85	2.50	1.70	1.90	1.65	1.50	1.50	5.85	2.25	1.40	1.90	1.55	1.90	1.55		
	SD	0.19	0.10	0.07	0.06	0.07	0.05	0.06	0.20	0.08	0.06	0.09	0.05	0.09	0.06		
	CV	0.4%	4.3%	4.6%	3.5%	4.2%	3.3%	4.1%	3.6%	3.9%	4.5%	5.1%	3.7%	5.0%	4.7%		
<i>C. varians</i> of JNS **	N	5	9	9	9	9	5	5	12	20	20	18	18	12	12		
	Min.	5.28	2.18	1.40	1.77	1.44	1.42	1.30	5.33	1.96	1.20	1.70	1.36	1.67	1.30		
	Mean	5.42	2.34	1.46	1.95	1.52	1.49	1.38	5.59	2.07	1.29	1.73	1.45	1.79	1.35		
	Max.	5.60	2.46	1.51	2.00	1.60	1.57	1.50	6.00	2.27	1.38	2.00	1.60	2.00	1.47		
<i>C. varians</i> of RZD ***	N		35	35	25	25	1	1	2	52	52	50	50	18	2		
	Min.		2.0	1.2	1.5	1.25			4.95	1.85	1.1	1.45	1.15	1.4	1.15		
	Mean		2.15	1.31	1.64	1.32	1.7	1.5	4.98	2.01	1.14	1.59	1.3	1.59	1.26		
	Max.		2.3	1.4	1.8	1.4			5	2.2	1.25	1.65	1.4	1.7	1.3		
extant <i>T. triton</i>	N	42	47	47	47	47	42	42	36	39	38	39	39	36	36		
	Min.	5.01	2.18	1.45	1.64	1.47	1.30	1.26	5.26	1.95	1.24	1.68	1.41	1.66	1.32		
	Mean	5.36	2.32	1.55	1.82	1.59	1.43	1.40	5.58	2.16	1.32	1.81	1.51	1.78	1.40		
	Max.	5.79	2.52	1.68	2.00	1.75	1.67	1.62	5.86	2.38	1.41	1.94	1.63	1.99	1.58		
	SD	0.15	0.07	0.06	0.08	0.05	0.08	0.06	0.15	0.09	0.04	0.06	0.05	0.07	0.06		
	CV	2.7%	3.1%	3.7%	4.2%	3.4%	5.4%	4.1%	2.8%	4.0%	3.1%	3.4%	3.5%	4.0%	4.3%		

2 # See Supplementary datasets 5~8 for raw data.

3 * quoted from Zheng (1984a); ** quoted from Zheng & Han (1993); *** quoted from Jin et al. (2009).

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Table 3 (on next page)

Comparisons of mesolophids of m1s between *Tscherskia triton* and *Cricetinus varians*

Species and locality	frequency of mesolophid on ml
<i>C. varians</i> of ZKD Loc. 1	70% (40/57)
<i>C. varians</i> of JNS	67%
<i>C. varians</i> of ZKD Loc. 3	61% (54/89)
<i>T. triton varians</i> of Syz 2	43% (44/103)
extant <i>T. triton</i>	30% (21/69)

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Table 4(on next page)

Comparisons of mesolophids of m2s between *Tscherskia triton* and *Cricetinus varians*

Species and locality	frequency of mesolophid on m2	proportion of each morphotype of mesolophid on m2		
		I or II*	III*	IV*
<i>C. varians</i> of ZKD Loc. 1	93% (53/57)	—	11.3% (6/53)	—
<i>C. varians</i> of JNS	91% (20/22)	—	0 (0/20)	—
<i>C. varians</i> of ZKD Loc. 3	97% (86/89)	—	14.0% (12/86)	—
<i>T. triton varians</i> of Syz 2	95% (158/166)	87.3% (137/157)	10.2% (16/157)	2.5% (4/157)
extant <i>T. triton</i>	87% (60/69)	96.6% (58/60)	1.7% (1/60)	1.7% (1/60)

* I, having a free end; II, being connected to the metaconid; III, reaching the lingual tooth edge; IV, being connected to the entoconid.

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Table 5 (on next page)

Comparisons of mesolophids of m3s between *Tscherskia triton* and *Cricetinus varians*

Species and locality	frequency of mesolophid on m3	proportion of each morphotype of mesolophid on m3				
		I*	II*	III*	IV*	V*
<i>C. varians</i> of ZKD Loc. 1	100% (57/57)	71%**			—	—
<i>C. varians</i> of JNS	100%	100%**			—	—
<i>C. varians</i> of ZKD Loc. 3	100% (89/89)	91%**			—	—
<i>T. triton varians</i> of Syz 2	99.2% (129/130)	95.3% (122/128) **			3.9% (5/128)	0.8% (1/128)
		59.4% (76/128)	35.2% (45/128)	0.8% (1/128)		
extant <i>T. triton</i>	100% (63/63)	98.4% (62/63) **			1.6% (1/63)	0 (0/63)
		44.4% (28/63)	49.2% (31/63)	4.8% (3/63)		

* I, having no branch, being connected to the lingual tooth edge; II, having two branches, with one being connected to the lingual tooth edge and the other to the metaconid; III, having three branches; IV, having no branch, being connected to the metaconid; V, having a free end. ** being connected to the lingual tooth edge

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Table 6(on next page)

Comparisons of anterolophules and protolophules I of M1s between *Tscherskia triton* and *Cricetinus varians*

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Species and locality	frequency of the anterolophule behind the buccal anterocone	frequency of the protolophule I
<i>C. varians</i> of ZKD Loc. 1, 3	—	76%
<i>C. varians</i> of JNS	100% (9/9)	≥30%
<i>T. triton varians</i> of Syz 2	89.1% (41/46)	57.4% (27/47)
extant <i>T. triton</i>	71.6% (53/74)	37.2% (32/86)

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Table 7 (on next page)

The comparisons of frequencies of mesolophids on m1-3s between the species of *Cricetinus*, *Tscherskia*, *Cricetulus*, *Nothocricetulus* and *Allocricetus*

1

Species		Localities	Geologic age	frequency of mesolophid on m1	frequency of mesolophid on m2	frequency of mesolophid on m3	Sources
present paper	original references						
<i>Tscherskia triton</i> (type species)	/	Shaanxi Province, China	recent	30% (21/69)	87% (60/69)	100% (63/63)	present paper
<i>T. triton varians</i>	/	Syz 2, Hebei Province, China	late Middle Pleistocene	43% (44/103)	95% (162/170)	100% (134/134)	present paper
	<i>Cricetinus varians</i>	ZKD Loc. 3, Beijing, China	late Middle Pleistocene or Late Pleistocene	61% (54/89)	97% (86/89)	100% (89/89)	Zheng, 1984a
		Jinniushan, Liaoning Province, China	late Middle Pleistocene	67%	91% (20/22)	100%	Zheng & Han, 1993
		ZKD Loc. 1 (type locality), Beijing, China	Middle Pleistocene	70% (40/57)	93% (53/57)	100% (57/57)	Zheng, 1984a
<i>T. triton varians</i> ?	<i>Cricetinus varians</i>	Renqidong, Anhui Province, China	early Early Pleistocene	present	present	present	Jin et al., 2009
<i>T. europaeus</i>	<i>Cricetinus europaeus</i>	Csarnóta 2 (type locality), Hungary	Pliocene	33.3% (2/6)	71.4% (5/7)	100% (5/5)	Hír, 1994
<i>T. gritzai</i>	<i>Cricetinus gritzai</i>	Odessa (type locality), Ukraine	Pliocene	present	present	present	Topachevsky & Skorik, 1992
<i>T. janossyi</i>	<i>Cricetinus janossyi</i>	Osztramos 7 (type locality) and Csarnóta 2, Hungary	Pliocene	38.9% (7/18)	95% (19/20)	100% (15/15)	Hír, 1996b
<i>T. koufosi</i>	<i>Cricetinus koufosi</i>	Mygdonia basin (type locality), Greece	Early Pleistocene	0	-	-	Koufos et al., 2001
<i>Neocricetodon mesolophidos</i>	<i>Cricetinus mesolophidos</i>	Yushe basin (type locality), Shanxi Province, China	Pliocene	100%	100%	perhaps 100%	Wu & Flynn, 2017
<i>Cricetulus barabensis</i> (type species)	/	Shaanxi Province, China	recent	0 (0/8)	0 (0/8)	0 (0/8)	present paper
<i>C. longicaudatus</i>	/	Shaanxi Province, China	recent	0 (0/23)	0 (0/23)	26.1% (6/23)	present paper
<i>Nothocricetulus migratorius</i> (type species)	<i>Cricetulus migratorius</i>	Krak des Chevaliers, Syria	recent	0?	0?	very often	Pradel, 1981
		Meydan, Toros Mountains, Turkey	Holocene	0?	10%	81%	Hír, 1993a
<i>Allocricetulus bursae</i> (type species)	/	Tarko Rockshelter 1, Hungary	early Middle Pleistocene	0?	10%	85%	Hír, 1993a
		Tarko Rockshelter 2-10, Hungary		0?	2%	60%	
		Tarko Rockshelter 11-12, Hungary		0?	16%	84%	
		Tarko Rockshelter 13-15, Hungary		0?	28%	100%	
		Tarko Rockshelter 16-18, Hungary		0?	33%	93%	
<i>A. ehiki</i>	/	Villány 3 and Esztramos 3, Hungary	Early Pleistocene	0?	52%	91%	Hír, 1993a, b
		ZKD Loc. 12, 18, Beijing, China	Early Pleistocene	5% or 0?	4%	100% (47/47)	Zheng, 1984a
<i>A. beremendensis</i>	<i>Cricetinus beremendensis</i>	Beremend 15 (type locality) and Csarnóta 4, Hungary	Pliocene	0% (0/72)	14.8% (9/61)	100% (53/53)	Hír, 1994

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