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) (#80883)

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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 chronologic subspecies of this extant species—*T. triton varians*. We compared in detail the *C. varians* and *T. triton* from the aspects of skull and molar morphology 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 chronologic subspecies of *T. triton*, i.e., *T. triton varians*, and the *Cricetinus* should be discarded 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 *Kowalskia*. On present evidence, *Tscherskia* may have originated from *Kowalskia* 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 chronologic subspecies of this extant species—*T. triton varians*. We compared in detail the *C. varians* and *T. triton* from the aspects of skull and molar morphology 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 chronologic subspecies of *T. triton*, i.e., *T. triton varians*, and the *Cricetinus* should be discarded 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 *Kowalskia*. On present evidence, *Tscherskia* may have originated from *Kowalskia* 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 taxa among them is 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 according to their size. 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 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 in the Villány Mountains, southern Hungary. Since Kretzoi, five other hamster species have been allocated to *Cricetinus* successively (e.g., Hír, 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 Syz 2, we discuss in detail the long-disputed issue of the validity of *Cricetinus* and *C. varians* to benefit our understanding of origin and evolution of living taxa in Cricetinae.

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; Steppan & 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). 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 axioloph 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 mainly belong to 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 famous 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 $(2.0\pm0.2) \times 10^5$ 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 detailed collection sites on the labels of these specimens, they might belong to 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) and Freudenthal, Hugueney & Moissenet (1994). Measurements of skull and mandible mainly follow Yang et al. (2005) and Xia et al. (2006). All photography and measurements were made by ZEISS Smartzoom5 automated digital microscope.

Abbreviation

NWUV, Prefix to the catalogue numbers refers to vertebrate fossil specimens stored in the Department of Geology, 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. gritzai* (Topachevski et Skorik, 1992); *T. janossyi* (Hír, 1996); *T. koufosi* (Koliadimou, 1996).

Geographic distribution and geologic age Southeastern Europe, late early Pliocene to early middle Pleistocene (ca. 4 Ma ~ 0.7 Ma); northern China, transition region between northern and southern China, late Pliocene (ca. 3.2 Ma) to present.

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 axioloph rather than an anterior-inwardly 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* (= *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. However, our observation demonstrates that these characters proposed by Hír are not comprehensive, and some of them even differ greatly from the facts. Therefore, the diagnoses of *Tscherskia* are 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
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
2020 *Cricetulus varians*, Wang, Wu & Qiu, p.104

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 Ml-3 figured by Zdansky (1928, Taf. 5, Fig. 4) is here designated as lectotype for Tsc*herskia triton varians* (Lagrelius Collection kept in Museum of Evolution, Uppsala University, Sweden), and other specimens in 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 1~13 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 ~ 6 of Jia (1959)'s scheme, which cover a period ca. 0.3 ~ 0.4 Ma in middle Pleistocene (Chen & Zhou, 2009, Table 1).

Geographic distribution and geologic age Northern China, transition 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 toothrows (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) ;7left m3s (NWUV1489.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, 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 former may be lightly greater than those of the later.

Remarks As will be seen in "Discussion", 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 skull width of NWUV1489.a7 is larger than normal due to vertical extrusion, but it preserves the complete interparietal, the shape of which is approximately pentagonal (Fig.2 D). The posterior border of interparietal is on the same line with crista supratympanica. 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 a very gentle arc, but this shape is often lost due to extrusion. The root part of upper incisor is outward protruding so that the corresponding part on premaxilla and maxilla upheave and form a crest. The lower part of the infraorbital foramen is slit-like, so that its overall shape looks like a stalked ginkgo leaf from the lateral view. The outer wall of lower branch of anterior root of zygomatic arch is slightly concave; both its anterior and posterior edges are arc-shaped, with the former slightly convex anterodorsally and the latter slightly concave anterodorsally; the two edges are nearly parallel. The upper branch of anterior root of zygomatic arch is much weaker than the lower branch, and the width of the former is about 2-3 times the width of the latter.

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 slightly front of middle of the incisive foramen. Two posterior palatine foramina are almost located on the connection line of posterior roots of two M2s. The anterior edge of choana slightly exceeds the posterior edge of M3 or is flush with it. The two molar series are not completely parallel but open outward-forward slightly.

(2) Mandible

The lower edge of mandible (Fig. 3) extends forward in an arc from base of angular process. The mental foramen is small and round, located anteroventral of 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. The angular process extends in posteroventral direction. Mandibular notch extends slightly further than the notch between condylar process and angular process in forward direction, while the latter is slightly wider than the former. The mandibular foramen is oval, situated at the base of condylar process. The groove between the alveolus of molars and the base of coronoid process is gentle, not as steep as that in murines. The area on inner side of mandible and under the molar series usually has many small foramina.

Measurements of skulls and mandibles are shown in Table 1 and Supplementary datasets 1, 3.

(3) Teeth

The upper incisor is almost perpendicular to the maxilla, and its root terminates in an anterior-inferior position to the infraorbital foramen.

The structures of upper molars are shown in Fig. 4. The M1 is kidney-shaped, with an obtuse oral surface, 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 comparatively broad and always split 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 spur of 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 hypocone and metacone is very thick. We think this loph should be 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 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 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 degraded, with 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 axioloph, which departs from the junction of the protolophule I and the anterior arm of 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 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 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. In the case of abundant specimens, the presence of a variety of morphological changes is understandable.

The root of lower incisor terminates at the base of condylar process.

The structures of 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 or 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), respectively connecting to two anteroconulids. The bottom of anteroconid is far higher than the bottom of 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 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 degraded compared to that of m1 and m2, whereas the hypoconid is often just slightly degraded. 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 NWUV1489.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 anterolophulid 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 Quaternay to now in China (sorted by chronological order; in parentheses are the common junior synonyms): *Cricetus* Leske, 1779； *Cricetulus* Milne-Edwards, 1867； *Urocricetus* Satunin, 1902； *Phodopus* Miller, 1910； *Tscherskia* Ognev, 1914（＝*Cricetinus* Zdansky, 1928， *Cansumys* Allen, 1928）； *Allocricetus* Schaub, 1930； *Sinocricetus* Schaub, 1930； *Allocricetulus* Archyropulo, 1932； *Neocricetodon*（＝*Kowalskia* Fahlbusch, 1969） Schaub, 1934； *Bahomys* Chow et Li, 1965； *Amblycricetus* Zheng, 1993； *Nothocricetulus* Lebedev, Bannikova, Neumann, Ushakova, Ivanova et Surov, 2018. Of these genera, *Allocricetus*, *Sinocricetus*, *Neocricetodon*, *Bahomys* and *Amblycricetus* are extinct, and the rest 7 living. In living genera, *Allocricetulus* and *Nothocricetulus* have only very scarce and doubtful fossil records (Cai et al., 2004, 2013), while *Cricetus* and *Urocricetus* 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 *Neocricetodon* 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 *Sinocricetus* 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*, *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 *Allocricetus* is the main character distinguishing it from *Cricetinus* (＝*Tscherskia*), but actually this is the character of *Cricetulus*, not *Allocricetus*, because although *Allocricetus* do not bear mesolophid on m1, but can develop mesolophid on m2 of partial specimens (Table 7). Some other researchers argued that the most important morphological character of *Cricetinus* (= *Tscherskia*) is the undivided anteroconid of m1 (Kretzoi, 1959; Hír, 1996a, 1997), while those of *Allocricetus* 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 *Allocricetus* 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. The molar measurements of the former are very similar to those of the extant *T. triton*, and some of the data 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 axioloph, 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 chronologic subspecies 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 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 “axioloph” 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 axioloph, which departs from the junction of the protolophule I and anterior arm of protocone, and forms a groove between it and the protocone. 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) for the aim 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. 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*, such as *Kowalskia* (=*Neocricetodon*) *moldavicus* (Sinitsa & Delinschi, 2016), *Kowalskia* (=*Neocricetodon*) *hanae* (Qiu, 1995), *Kowalskia* (=*Neocricetodon*) *yinanensis* (Zheng, 1984b), *Chuanocricetus* (=*Neocricetodon*) *lii* (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.” 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. *Tcherskia* 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 keeping the specific name of “*varians*” 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, however, 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.

(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. In the following discussion, we will make a detailed comparison of teeth morphology between *C. varians* and extant *T. triton*.

(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.

② Comparison of the teeth morphology

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 degenerates.

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 degenerative trend, although on 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 degradation 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 the teeth. Although there are still small differences between 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 chronologic subspecies 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 refered to *Cricetinus*:

Cricetinus europaeus Kretzoi, 1959. The type locality of this species is Csartòna 2 in Hungary. 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 (about 4 Ma)(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 (Hír, 1994). 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 (Hír, 1996b). The molar structures of this species are very similar to that of *T. triton* 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, and it first appeared in Csartòna 2 of Hungary around 4 Ma 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 Nagyharsanyhegy 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* (= *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 *Kowalskia*. 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 very confusing, so we tentatively do not include it in *Tscherskia*. 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 *Tscherskia* was very likely to have originated from the genus *Kowalskia* (=*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 apparently earlier than that in Asia. The earliest species of *Tscherskia* in Europe are *T. europaeus* and *T. janossyi*, both of which occurred at the locality Csartòna 2 in Hungary, with an age of approximately 4 Ma (Hír, 1994). *Tscherskia* was relatively common during the Pliocene in southeastern Europe, but it quickly declined after the beginning of the Pleistocene and was then replaced by the rise of genera such as *Allocricetus* and *Cricetus*. In Asia, the earliest *Tscherskia* is *T.* sp. 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). 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 *Kowalskia* 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. 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 chronologic subspecies 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 chronologic subspecies 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 *Kowalskia*. On present evidence, *Tscherskia* may have originated from *Kowalskia* 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.

Acknowledgements

We wish to express our sincere appreciation to Prof. Qiu Zhuding for improving the manuscript, to Prof. Zheng Shaohua for beneficial discussion and to Prof. Wu Wenyu for her warm help (all of them are with the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, China). We thank Li Zhixuan (College of Life Sciences, NWU), Wang Kaifeng and Wang Yan (Shannxi Institute of Zoology, China), Zhang Lixun and Liao Jicheng (School of Life Sciences, Lanzhou University, China), Zhang Yanming (Northwest Institute of Plateau Biology, Chinese Academy of Sciences, China) for their friendly help in the process of observing specimens of extant hamsters. We also thank Prof. Robert F Diffendal, Jr. for his linguistic help.

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Figure 1

Geographic locations of Syz 1~4.

Satellite map after Google Earth.

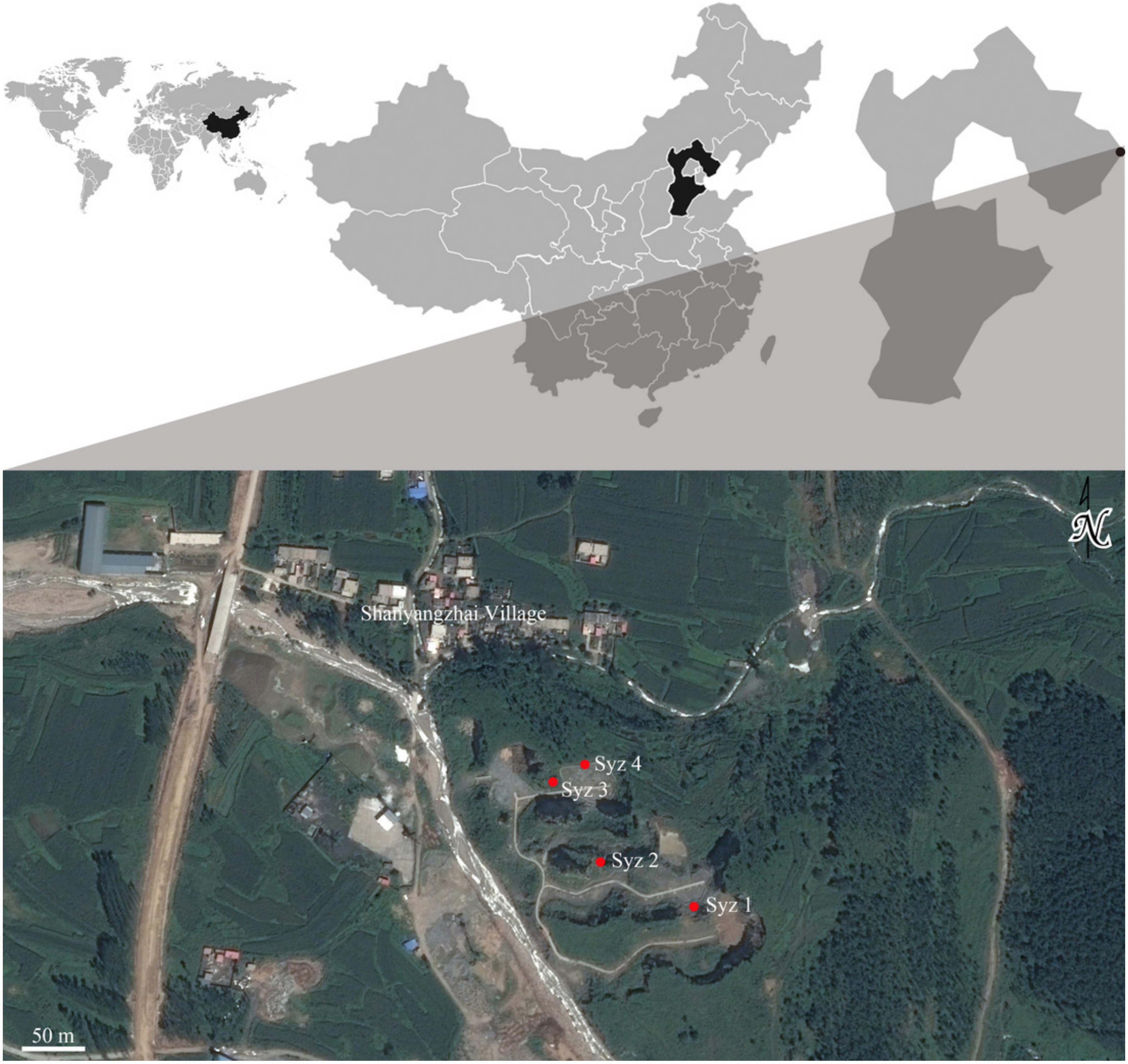

Figure 2

Skulls of *Tscherskia triton varians* from Syz 2.

(A)NWUV1489.a8; (B)NWUV1489.a21; (C) NWUV1489.a6; (D) NWUV1489.a7. **(**A1), (B1), (C1), (D) dorsal view; (A2), (B2), (C2), lateral view; (A3), (B3), ventral view.

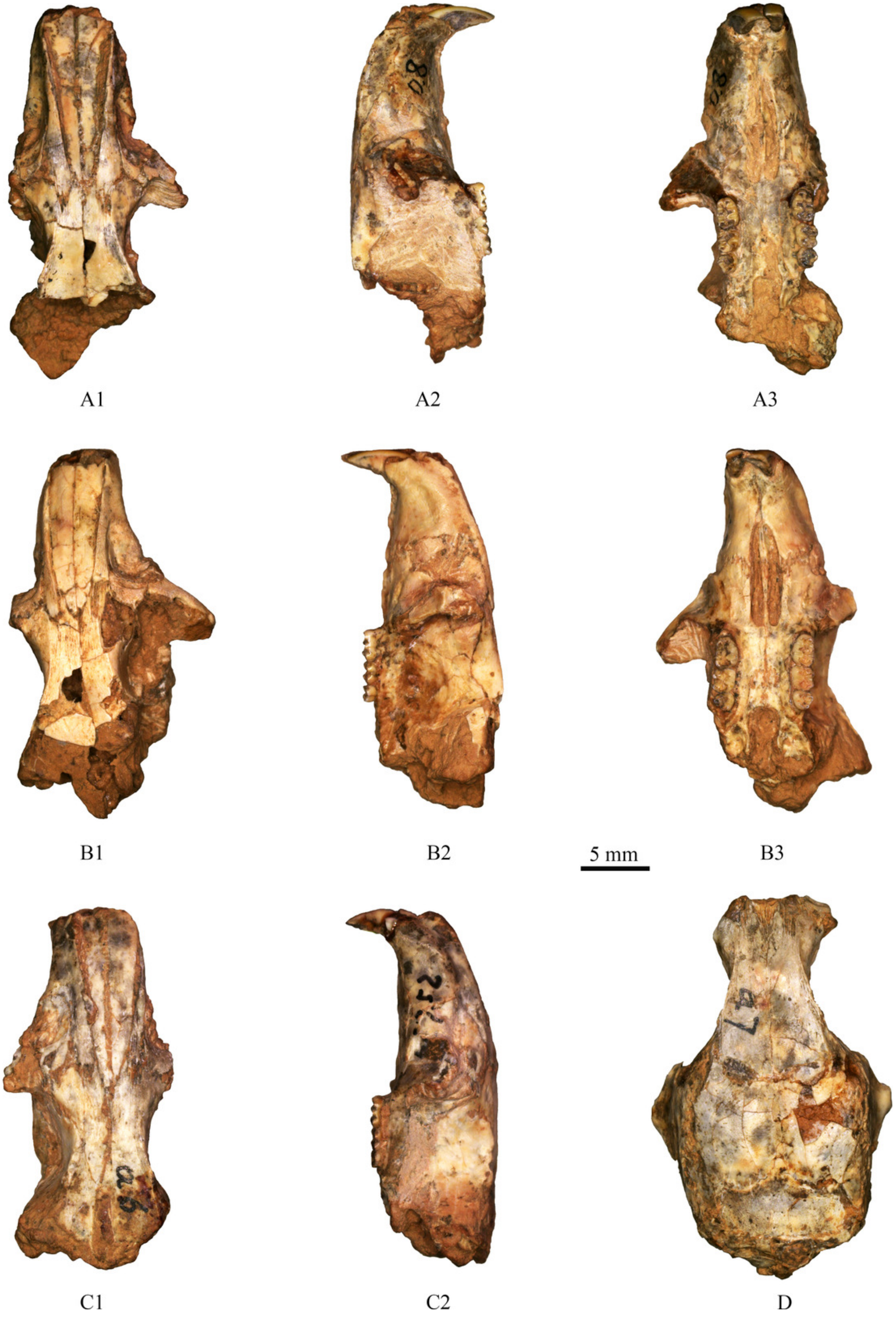
A1
A2
A3
B1
B2
5 mm
B3
C1
C2
D

Figure 3

Mandibles of *Tscherskia triton varians* from Syz 2.

(A) NWUV1489.f50; (B) NWUV1489.f44; (C) NWUV1489.e164; (D) NWUV1489.e169. **(**A1), (B1), (C1), (D1), lingual view; (A2), (B2), (C2), (D2), buccal view.

Figure 4

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

The arrow indicates the axioloph. (A) NWUV1489.a5; (B) NWUV1489.a14; (C) NWUV1489.a21; (D) NWUV1489.b1; (E) NWUV1489.c3; (F) NWUV1489.c5; (G) NWUV1489.c16.

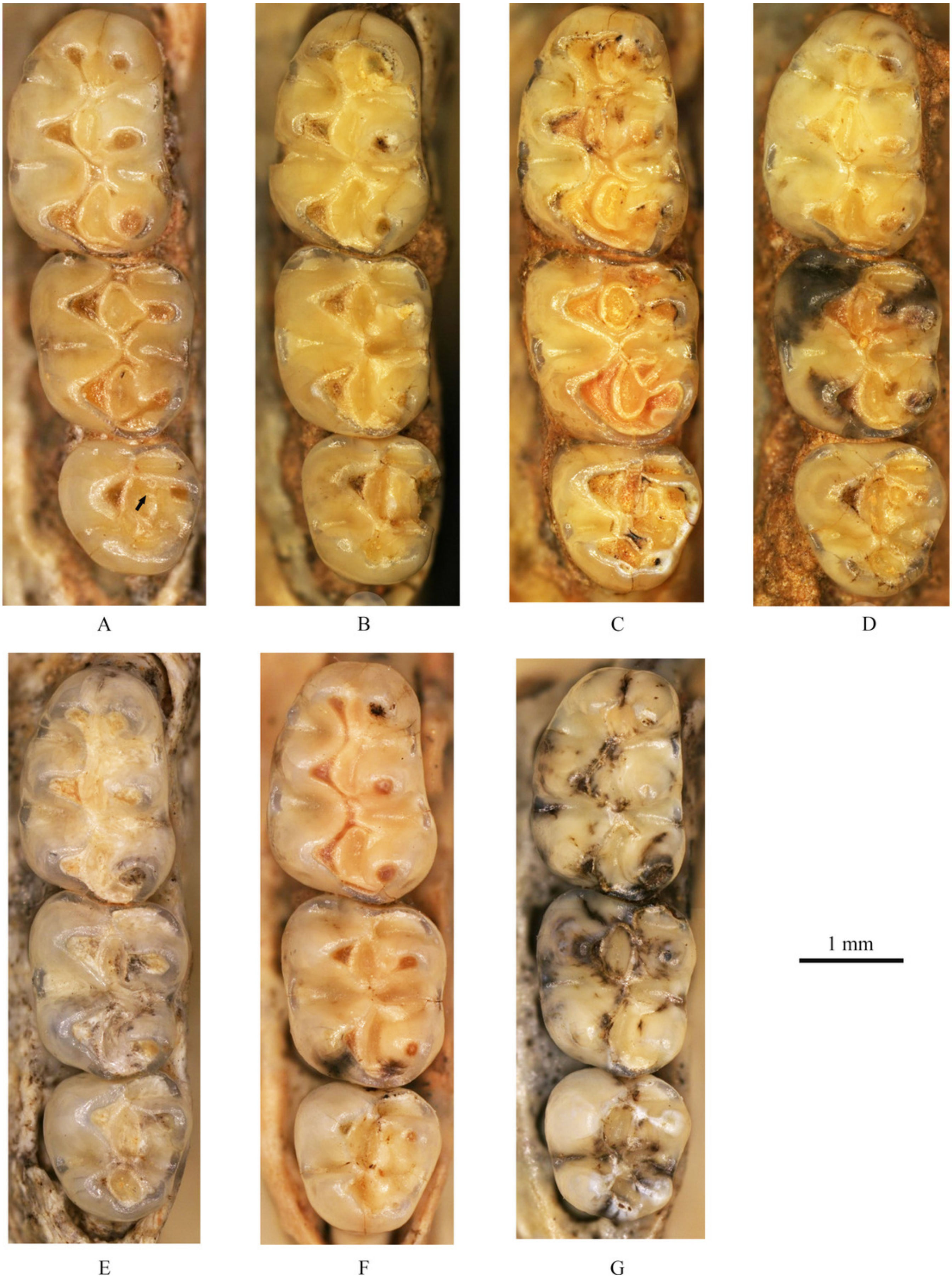
A
B
C
D
E
F
G
1 mm

Figure 5

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

(A) NWUV1489.f8; (B) NWUV1489.f13; (C) NWUV1489.f22; (D) NWUV1489.f28; (E) NWUV1489.f31; (F) NWUV1489.f49; (G) NWUV1489.f56.

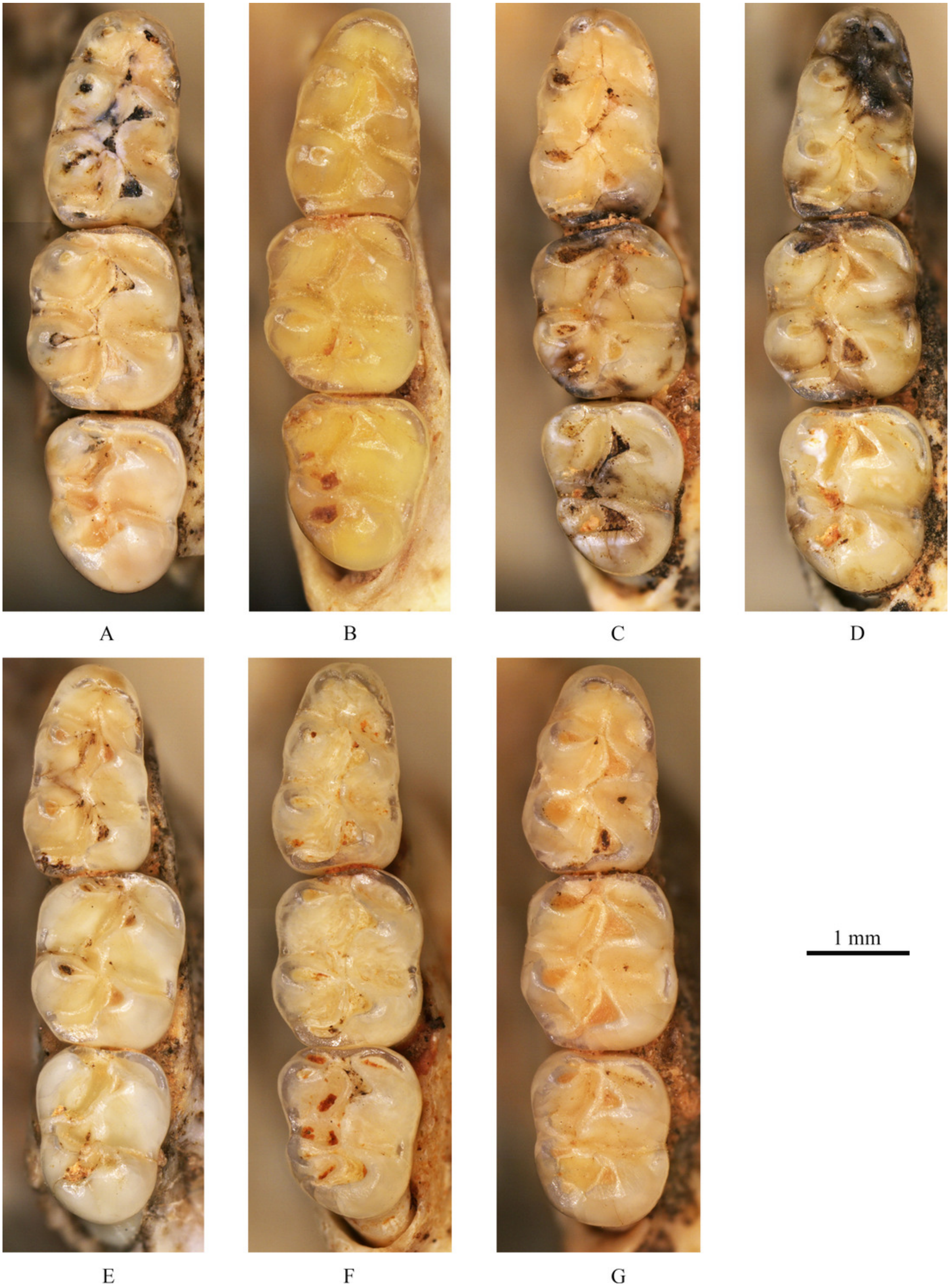
A
B
C
D
E
F
G
1 mm

Figure 6

Scatter diagrams of lengths of M1 and m1 of *Cricetinus varians* and *Tscherskia triton*.

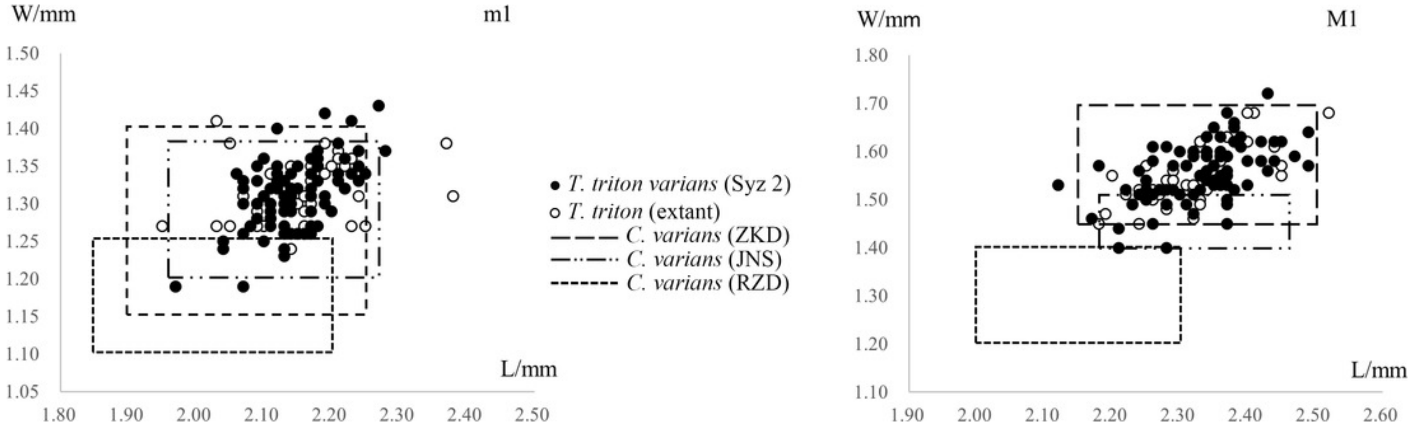

Table 1(on next page)

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

	T. triton varians of Syz 2						the extant *T. triton*					
	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)*

		M1~3	M1		M2		M3		m1~3	m1		m2		m3	
		L	L	W	L	W	L	W	L	L	W	L	W	L	W
T. triton 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%
C. varians 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%
C. varians 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
C. varians 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
the extant *T. triton*	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%

□ See Supplementary datasets 5~8 for raw data.

□□ quoted from Zheng (1984a). □□ quoted from Zheng & Han (1993). □□□ quoted from Jin et al. (2009).

Table 3(on next page)

Comparisons of mesolophids of m1 between *Tscherskia triton* and *Cricetinus varians*

Species and locality	frequency of mesolophid on m1
C. varians of ZKD Loc. 1	70% (40/57)
C. varians of JNS	67%
C. varians of ZKD Loc. 3	61% (54/89)
T. triton varians of Syz 2	43% (44/103)
the extant *T. triton*	30% (21/69)

Table 4(on next page)

Comparisons of mesolophids of m2 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□
C. varians of ZKD Loc. 1	93%（53/57）	——	11.3%（6/53）	——
C. varians of JNS	91%（20/22）	——	0（0/20）	——
C. varians of ZKD Loc. 3	97%（86/89）	——	14.0%（12/86）	——
T. triton varians of Syz 2	95%（158/166）	87.3%（137/157）	10.2%（16/157）	2.5%（4/157）
the extant *T. triton*	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.

Table 5(on next page)

Comparisons of mesolophids of m3 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 □
C. varians of ZKD Loc. 1	100% (57/57)	71%□□			——	——
C. varians of JNS	100%	100%□□			——	——
C. varians of ZKD Loc. 3	100%（89/89）	91%□□			——	——
T. triton varians 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）		
the extant *T. triton*	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; ⅳ, having a free end. □□ being connected to the lingual tooth edge

Table 6(on next page)

Comparisons of anterolophules and protolophules I of M1 between *Tscherskia triton* and *Cricetinus varians*

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

Table 7 (on next page)

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

Species		Localities	Geologic age	frequency of mesolophid on m1	frequency of mesolophid on m2	frequency of mesolophid on m3	Sources
present paper	original references						
Tscherskia triton (type species)	/	Shaanxi Province, China	recent	30% (21/69)	87% (60/69)	100% (63/63)	present paper
T. triton varians	/	Syz 2, Hebei Province, China	late middle Pleistocene	43% (44/103)	95% (162/170)	100% (134/134)	present paper
	Cricetinus varians	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
T. triton varians ?	*Cricetinus varians*	Renzidong, Anhui Province, China	early early Pleistocene	present	present	present	Jin et al., 2009
T. europaeus	*Cricetinus europaeus*	Csartòna 2 (type locality), Hungary	Pliocene	33.3% (2/6)	71.4% (5/7)	100% (5/5)	Hír, 1994
T. gritzai	*Cricetinus gritzai*	Odessa (type locality), Ukraine	Pliocene	present	present	present	Topachevsky & Skorik, 1992
T. janossyi	*Cricetinus janossyi*	Osztramos 7 (type locality) and Csartòna 2, Hungary	Pliocene	38.9% (7/18)	95% (19/20)	100% (15/15)	Hír, 1996b
T. koufosi	*Cricetinus koufosi*	Mygdonia basin (type locality), Greece	early Pleistocene	0	-	-	Koufos et al., 2001
Neocricetodon mesolophidos	*Cricetinus mesolophidos*	Yushe basin (type locality), Shanxi Province, China	Pliocene	100%	100%	perhaps 100%	Wu & Flynn, 2017
Cricetulus barabensis (type species)	/	Shaanxi Province, China	recent	0	0	0 (0/8)	present paper
C. longicaudatus	/	Shaanxi Province, China	recent	0	0	26.1% (6/23)	present paper
Nothocricetulus migratorius (type species)	*Cricetulus migratorius*	Krak des Chevaliers, Syria	recent	0?	0?	very often	Pradel, 1981
		Meydan, Toros Mountains, Turkey	Holocene	0?	10%	81%	Hír, 1993a
Allocricetus bursae (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%	
A. ehiki	/	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
A. beremendensis	*Cricetinus beremendensis*	Beremend 15 (type locality) and Csartòna 4, Hungary	Pliocene	0% (0/72)	14.8% (9/61)	100% (53/53)	Hír, 1994