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 conducted on numerous large-sized hamster remains collected from the late Middle Pleistocene Locality 2 of Shanyangzhai (Syz 2), Hebei Province, China. The comparisons reveal that these fossils are highly similar to the extant *Tscherskia triton* in size and morphology, including the small degree of alternating between the main opposite cusps on M1-3, the presence of axioloph on M3, and mesolophids on m1-2 that are present but seldom reach the lingual margin of the teeth, among other features. However, minor differences between the two still exist. Consequently, all these fossils are designated as a chronosubspecies of the extant species, *T. triton varians* comb. nov. The skull and molar morphologies of *Cricetinus varians* and *T. triton* were meticulously compared to resolve the long-standing debate regarding the validity of *Cricetinus* Zdansky, 1928, and *C. varians* Zdansky, 1928. The findings indicate that the differences between the two are slight; as a result, *C. varians* can only be considered a chronosubspecies of *T. triton*, i.e., *T. triton varians* comb. nov., and *Cricetinus* should be recognized as a junior synonym of *Tscherskia*. We tentatively propose that, among the seven species once referred to *Cricetinus* in Eurasia, *C. europaeus*, *C. gritzai*, *C. janossyi*, and *C. koufosi* should be reassigned to *Tscherskia*, while *C. beremendensis* should be transferred to *Allocricetus*, and *C. mesolophidos* to *Neocricetodon*. Excluding *Tscherskia sp.* from the Late Pliocene Youhe fauna, there are no reliable *Tscherskia* fossils in China earlier than the Middle Pleistocene. Based on the current evidence, *Tscherskia* may have originated from *Neocricetodon* during the Early Pliocene in Europe and subsequently spread to Asia. *T. triton* is its sole surviving representative, which now exclusively inhabits East Asia.

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Abstract

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19   sized hamster remains collected from the late Middle Pleistocene Locality 2 of Shanyangzhai
20   (Syz 2), Hebei Province, China. The comparisons reveal that these fossils are highly similar to
21   the extant *Tscherskia triton* in size and morphology, including the small degree of alternating
22   between the main opposite cusps on M1-3, the presence of axioloph on M3, and mesolophids on
23   m1-2 that are present but seldom reach the lingual margin of the teeth, among other features.
24   However, minor differences between the two still exist. Consequently, all these fossils are
25   designated as a chronosubspecies of the extant species, *T. triton varians* comb. nov. The skull
26   and molar morphologies of *Cricetinus varians* and *T. triton* were meticulously compared to
27   resolve the long-standing debate regarding the validity of *Cricetinus* Zdansky, 1928, and *C.*
28   *varians* Zdansky, 1928. The findings indicate that the differences between the two are slight; as a
29   result, *C. varians* can only be considered a chronosubspecies of *T. triton*, i.e., *T. triton varians*
30   comb. nov., and *Cricetinus* should be recognized as a junior synonym of *Tscherskia*. We
31   tentatively propose that, among the seven species once referred to *Cricetinus* in Eurasia, *C.*
32   *europaeus*, *C. gritzai*, *C. janossyi*, and *C. koufosi* should be reassigned to *Tscherskia*, while *C.*
33   *beremendensis* should be transferred to *Allocricetus*, and *C. mesolophidos* to *Neocricetodon*.
34   Excluding *Tscherskia sp.* from the Late Pliocene Youhe fauna, there are no reliable *Tscherskia*
35   fossils in China earlier than the Middle Pleistocene. Based on the current evidence, *Tscherskia*
36   may have originated from *Neocricetodon* during the Early Pliocene in Europe and subsequently
37   spread to Asia. *T. triton* is its sole surviving representative, which now exclusively inhabits East
38   Asia.

Introduction

The late Middle Pleistocene Locality 2 of Shanyangzhai (village) has yielded 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 be readily divided into two groups based on size. Xie and Li (2016) have described the small-sized group, recognizing two hamster species, *Cricetulus longicaudatus* and *C. barabensis*. The present paper focuses on the remains of the large-sized group, providing a detailed morphological description and comparative study of these specimens.

The genus *Cricetinus* and its type species *C. varians* were erected by Zdansky (1928) on the basis of fossils from the renowned Middle Pleistocene Locality 1 of Zhoukoudian (i.e., the Peking Man Site), Beijing. Since then, hamster remains from 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* below). Kretzoi (1959) founded the second species of *Cricetinus*, *C. europaeus*, based on material from the Pliocene fauna of Csarnóta 2 in the Villány Mountains, southern Hungary. Following Kretzoi, five other hamster species have been successively allocated to *Cricetinus* (e.g., Hír, 1994; Wu & Flynn, 2017), rendering *Cricetinus* a widely distributed genus, both spatially and temporally. However, the validity of *Cricetinus* and *C. varians* has long been questioned by many researchers since the 1930s (e.g., Pei, 1936; Teilhard de Chardin & Pei, 1941; Teilhard de Chardin & Leroy, 1942; Gu, 1978; McKenna & Bell, 1997). The crux of this debate revolves around whether *Cricetinus* and *C. varians* are junior synonyms of *Tscherskia* and *T. triton*, respectively. In the present study, we examine the long-disputed issue of the validity of *Cricetinus* and *C. varians* based on a detailed description of large-sized hamster material from Locality 2 of Shanyangzhai, in order to enhance our understanding of the origin and evolution of extant Cricetinae taxa.

It is worth pointing out that, since Argyropulo (1933)'s work, *Tscherskia* has long been considered a subgenus of *Cricetulus*, with a few researchers maintaining 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 the traditional sense (usually including *C. barabensis*, *C. longicaudatus*, *C. migratorius*, *C. kamensis*, *C. triton*) is polyphyletic. As a result, 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 be recognized as an independent genus, and Lebedev et al. (2018) have proposed a new genus name, *Nothocricetulus*, for it. According to these studies, *Cricetulus* is generally more closely related to *Nothocricetulus*, *Cricetus*, and *Allocricetulus* when compared to *Tscherskia*. In addition to molecular phylogenetic evidence, morphological differences between *T. triton* and members of *Cricetulus* (in the traditional sense) are also apparent (Musser & Carleton, 2005) (Figures S1 to S3). For instance, *T. triton* has a considerably larger body size than the latter: the average body length of the former is approximately 157 mm, while the same

79   measurement for the later ranges approximately from 90-100 mm (based on data provided by
80   Chen & Gao, 2000). Moreover, we find that the M3 of *T. triton* bears an axioloph (*sensu*
81   Freudenthal & Daams, 1988) (see "Discussion" for details), a feature that is, to the best of our
82   knowledge, unique among all living Cricetinae species. The presence of the axioloph
83   undoubtedly highlights the uniqueness of *Tscherskia* within Cricetinae, although its taxonomic
84   significance warrants further investigation. For above reasons, we follow the prevailing opinion
85   of researchers over the last two decades and no longer consider *Tscherskia* as a subgenus of
86   *Cricetulus*, but rather as a distinct genus.

Geologic setting

88   Shanyangzhai Village (119°32′14.00″E, 40°5′17.82″N) is situated in the central part of
89   Haigang District, Hebei Province, China, approximately 20 kilometers from Bohai Bay. The
90   Ordovician limestone of the Majiagou Formation south of the village reveals numerous fossil-
91   bearing fissures or cave deposits due to quarrying activities. To date, four primary fossiliferous
92   localities have been discovered, numbered Localities 1, 2, 3, and 4 of Shanyangzhai (abbreviated
93   as Syz 1-4) in order from south to north (Fig.1). Based on their mammalian components, these
94   localities may have different ages. The fossils from Syz 1 and Syz 3 primarily consist of
95   macromammals, whereas Syz 2 and Syz 4 have yielded an abundance of micromammal fossils
96   (Niu, Zhang & Fa, 2003; Kong, 2009; Wang et al., 2010; Zhang et al., 2010; Li & Zhang, 2011,
97   2013; Li, Zhang & Ao, 2013; Li, Zhang & Li, 2013; Li, Zhang & Zheng, 2013; Zhang & Li,
98   2015; Li, Li & Zhang, 2016; Xie & Li, 2016; Chen et al., 2021). Although the majority of the
99   original strata of Syz 2 site have been disrupted by quarrying activities, the Syz 2, from which
100   the hamster fossils studied in this paper were obtained, is generally considered to date back to the
101   late Middle Pleistocene (Zhang et al., 2010). This estimation mainly results from the overall
102   faunal resemblance between Syz 2 and the Middle Pleistocene fauna of Zhoukoudian Locality 1
103   (where the age of the primary fossiliferous deposits, i.e., layers 1-11, is generally considered to
104   be ca. 0.6-0.2 Ma, Hu, 1985; Zhang, 2004; Chen & Zhou, 2009; Liu et al., 2014) and Jinniushan
105   (ca. 0.31-0.2 Ma, Liu et al., 2014). We obtained a silty clay sample (field number 09SS1,
106   laboratory number 11695) from about 2 meters below the fossil-bearing horizon at Syz 2 and
107   determined its absolute age using the electron spin resonance (ESR) technique at the State Key
108   Laboratory of Earthquake Dynamics, Institute of Geology of China Earthquake Administration.
109   The test result demonstrates an age of 300 ± 30 ka for the sample, implying that the fossil
110   deposits located above the sampling site should be somewhat younger than this age. Kong (2009)
111   dated the fauna between $(1.8 \pm 0.2) \times 10^5$ years and $(2.0 \pm 0.2) \times 10^5$ years ago using the thermo-
112   luminescence (TL) technique, but the precise sampling layers in Kong (2009) require further
113   verification. Based on the aforementioned absolute age dating results and faunal comparisons,
114   we tentatively date Syz 2 to the late Middle Pleistocene, approximately 0.2 Ma.

Material, methods, and abbreviation

Material

117   The hamster fossils from Syz 2 examined in this study are housed in the Department of
118   Geology, Northwest University (Xi'an, Shaanxi Province, China). For comparative purposes, we

119 observed about 50 skull specimens (including mandibles) of extant *Tscherskia triton* (the greater
120 long-tailed hamster) stored in the College of Life Sciences, Northwest University. All of these
121 specimens were collected from Shaanxi Province. Based on the collection sites indicated on the
122 labels of these specimens, they might belong to the subspecies *T. triton incanus* and *T. triton*
123 *collinus* (and possibly *T. triton triton* and *T. triton fuscipes*), following the subspecies
124 classification and geographical distribution of *T. triton* summarized by Chen & Gao (2000).

125 **Methods**

126 The skull morphological terminology primarily follows Wang & Qiu (2018) and Voss (1988).
127 For the description of molar occlusal morphology, we mainly follow Freudenthal & Daams
128 (1988), Freudenthal, Hugueney & Moissenet (1994), and Li et al. (2018). Anatomical
129 abbreviations for upper molars are M1, M2, and M3, while lower molars are represented by m1,
130 m2, and m3. Measurements of the skull and mandible mainly follow the methodology described
131 by Yang et al. (2005) and Xia et al. (2006). For molar measurements, L and W denote the
132 maximum length and width, respectively. All measurements were obtained using a ZEISS
133 Smartzoom5 automated digital microscope. Some images were reversed for ease of comparison
134 and are indicated by an underlined label. Annotations of the synonymy list are in accordance
135 with Matthews (1973). This work and the nomenclatural act it contains have been registered in
136 ZooBank (https://zoobank.org/ urn:lsid:zoobank.org:act:833CA9EC-1051-4C8E-A032-
137 04DF2AC46994).

138 **Abbreviation**

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

142 **Results**

143 **Systematic palaeontology**

144 Mammalia Linnaeus, 1758

145 Rodentia Bowdich, 1821

146 Cricetidae Rochebrune, 1883

147 Cricetinae Fisher, 1817

148 *Tscherskia* Ognev, 1914

149 1928 *Cansumys*, Allen

150 1928 *Cricetinus*, Zdansky

151 1929 *Asiocricetus*, Kishida

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

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

155 **Geographic distribution and geologic age** Southeastern Europe, Early Pliocene (MN 15, ca. 5-
156 3.5 Ma) to early Middle Pleistocene (ca. 0.7 Ma); Southwestern Asia, Holocene ?; northern
157 China, transitional region between northern and southern China, except *T.* sp. from Youhe fauna

158   with an age of Late Pliocene (ca. 3.15-2.59 Ma) (Yue & Xue, 1996; Xie, Zhang & Li, 2021), all

159   other credible material of *Tscherskia* with an age not earlier than Middle Pleistocene.

160   **Diagnosis** Medium-sized cricetids typically between *Cricetulus* and *Cricetus*; molars

161   brachyodont; mesolophes of M1-3 usually present, either free or connected to the metacone, but

162   rarely reaching the buccal tooth edge; M3 with an anteroposteriorly directed axioloph rather than

163   an anterolaterally extended protolophule II; anteroconids of m1 either divided or undivided;

164   mesolophids on m3 almost always present and well-developed; mesolophids also often present

165   on m1 and m2 but rarely reaching the lingual tooth edge (modified from Xie, Zhang & Li, 2021).

166   **Remarks** Hír (1996a, 1997) once proposed the diagnosis of *Cricetinus* (i.e., *Tscherskia*) as

167   follows: "the undivided anteroconid on the m1 molars with a smooth and convex oral surface;

168   the mesolophids missing or short on the m1-m2 molars; M1-M2 crowns characterized by the

169   missing or weekly developed mesolophes; the posterior metalophule rare on M2." Our

170   observation demonstrates that the diagnosis proposed by Hír is not comprehensive and warrants

171   further revision. Therefore, the diagnosis of *Tscherskia* is redefined here as stated above.

172

173   *Tscherskia triton* (de Winton, 1899)

174   *Tscherskia triton varians* comb. nov. (Zdansky, 1928) (Figs 2-6, Tables 1-7)

175   p1927 *Cricetulus* cfr. *songarus* Pallas — Young, p.24

176   *1928 *Cricetinus varians* gen. et sp. nov. — Zdansky, p.54

177   .1930 *Cricetinus varians* Zdansky — Schaub, p.37

178   1931 *Cricetinus varians* Zdansky — Pei, p.12

179   1932 *Cricetinus varians* Zdansky — Young, p.4

180   .1934 *Cricetinus varians* Zdansky — Schaub, p.30

181   1934 *Cricetinus varians* Zdansky — Young, p.58

182   p1936 cf. *Cricetinus varians* Zdansky — Teilhard de Chardin, p.16

183   1936 *Cricetinus varians* Zdansky — Pei, p.59

184   *1939 Cricetinus varians* Zdansky — Pei, p.153

185   p?1940 *Cricetinus* (*Cricetulus*) *varians* Zdansky — Pei, p.42

186   p1941 *Cricetulus varians* (Zdansky) — Teilhard de Chardin & Pei, p.49

187   p1942 *Cricetulus* (*Cricetinus*) *varians* (Zdansky) — Teilhard de Chardin & Leroy, p.35, p.93

188   *1977 Cricetulus varians* (Zdansky) — Gai & Wei, p.290

189   *1978 Cricetulus triton* (Zdansky) — Gu, p.164

190   *1980 Cricetulus varians* (Zdansky) — Zhang, Zou & Zhang, p.156

191   *1983 Cricetulus varians* (Zdansky) — Zheng, p.231

192   1984 *Cricetinus varians* Zdansky — Zheng, p.185

193   *1985 Cricetulus varians* (Zdansky) — Zhang et al., p.73

194   1985 *Cricetinus varians* Zdansky — Zheng et al., p.117

195   *1986 Cricetulus varians* (Zdansky) — Zhang, Wei & Xu, p.36

196   1990 *Cricetulus triton* (de Winton) — Sun & Jin, p.35

197   1993 *Cricetinus varians* Zdansky — Zheng & Han, p.65

198   p?1996 *Cricetinus varians* Zdansky — Cheng et al., p.38
199   2002 *Cricetinus varians* Zdansky — Jin, p.95
200   *2004 Cricetinus varians* Zdansky — Jin et al., p.284
201   *2004 Cricetulus triton* (de Winton) — Tong et al., p.855
202   ?2009 *Cricetinus varians* Zdansky — Jin et al., p.177
203   *2010 Cricetinus varians* Zdansky — Zhang et al., p.73
204   *2015 Tscherskia triton* (de Winton) — Liu et al., p.610
205   *2017 Tscherskia triton* (de Winton) — Chen et al., p.847
206   2018 *Cricetulus varians* (Zdansky) — Tong et al., p.287
207   *2018 Cricetinus varians* Zdansky — Wu et al., p.1396
208   2020 *Cricetulus varians* (Zdansky) — Wang, Wu & Qiu, p.104
209   *2021 Cricetulus varians* (Zdansky) — Huang et al., p.269
210   *2021 Cricetulus triton* (de Winton) — Huang et al., p.269
211   **Lectotype** As previously mentioned, Zdansky (1928) established *Cricetinus* and *Cricetinus*
212   *varians* based on large-sized hamster material from Locality 1 of Zhoukoudian, which included 8
213   maxillary fragments, 9 larger and some smaller mandibular fragments, 1 isolated M1, and 3
214   isolated m1s. However, Zdansky did not designate a holotype for the new genus and its type
215   species, so all these specimens should be considered the syntypes. Wang, Wu & Qiu (2020,
216   pp.104-105) selected IVPP RV 340020 (original catalogue number C/C. 1049), an anterior
217   portion of the skull with right M1-3 and left M1-2 figured by Young (1934, Text-fig. 19, 1, 1a,
218   1b; Pl. 5, fig. 9) and Zheng (1984a, Fig.1, C), as the lectotype of *C. varians*. However, this
219   designation should be considered invalid according to ICZN (1999, Art. 74.2), because IVPP RV
220   340020 does not belong to the syntypes, although it was also collected from Locality 1, possibly
221   even from the same layer as the syntypes (Young, 1934, p.63). Therefore, the fragmentary right
222   upper jaw with M1-3 figured by Zdansky (1928, Taf. 5, Fig. 4) is here designated as the
223   lectotype for *Tscherskia triton varians* (Lagrelius Collection housed in the Museum of
224   Evolution, Uppsala University, Sweden), and other specimens in the type series should be
225   considered the paralectotypes. The paralectotypes listed by Wang, Wu & Qiu (2020, p.104) are
226   also invalid for the same reason discussed for the lectotype and should only be viewed as
227   referred specimens.
228   **Type locality and geologic age** Locality 1 of Zhoukoudian, Beijing. The deposits of Locality 1,
229   also known as Zhoukoudian Formation, are about 40 meters in thickness and traditionally
230   divided into 1 to 13 layers from top to bottom, representing a period from approximately 0.78
231   Ma to 0.2 Ma. This division scheme was published by Jia (1959), who adopted a similar scheme
232   first proposed by Teilhard de Chardin & Young (1929), and has been widely followed since.
233   Zdansky (1923, p.86) also published two profiles of deposits of Locality 1 (called Loc. 53 by
234   Zdansky) from which the type specimens of *C. varians* and other fossils studied by Zdansky
235   (1928) were collected. Teilhard de Chardin & Young (1929, p.179, footnote) considered that the
236   sections given by Zdansky (1923, p.86) correspond probably to some part of their layers 5 and 6,
237   although they also stated that a precise correlation with Zdansky's 1923 profile was rather

238   difficult to establish. If Teilhard de Chardin and Young are correct, according to Xu et al. (1997,
239   p.219, Table 1), their layers 5 and 6 should essentially correspond to layers 4 to 6 of Jia (1959)'s
240   scheme, which cover a period of approximately 0.3 - 0.4 Ma in the Middle Pleistocene (Chen &
241   Zhou, 2009, Table 1).
242   **Geographic distribution and geologic age** Northern China, transitional region between
243   northern and southern China, late Early Pleistocene to Late Pleistocene.
244   **Referred specimens from Syz 2** 21 incomplete skulls (NWUV 1489.a1-21); 10 maxillae with
245   bilateral toothrows (NWUV 1489.b1-10); 73 left maxillae (NWUV 1489.c1-73); 74 right
246   maxillae (NWUV 1489.d1-74); 185 left mandibles (NWUV 1489.e1-185); 215 right mandibles
247   (NWUV 1489.f1-215); 3 mandibles with bilateral branches (NWUV 1489.g1-3); 55 left M1s
248   (NWUV 1489.h1-55); 54 right M1s (NWUV 1489.i1-54); 46 left M2s (NWUV 1489.j1-46); 35
249   right M2s (NWUV 1489.k1-35) ; 2 left M3s (NWUV 1489. l1-2); 8 right M3s (NWUV
250   1489.m1-8); 16 left m1s (NWUV 1489.n1-16); 22 right m1s (NWUV 1489.o1-22);15 left m2s
251   (NWUV 1489.p1-15); 19 right m2s (NWUV 1489.q1-19); 7 left m3s (NWUV 1489.r1-7); 8 right
252   m3s (NWUV 1489.s1-8).
253   **Measurements** Refer to Tables 1-2 and Supplementary datasets 1, 3, 5, 7.
254   **Diagnosis** *Tscherskia triton varians* is highly similar to extant *T. triton* in size and most of the
255   molar characters (see "Discussion"). However, the former exhibits slightly higher frequencies of
256   mesolophids on m1 and m2 (refer to Table 7). In the majority of skull and mandible
257   measurements, the mean values for *T. t. varians* may be slightly larger than those of extant *T.*
258   *triton*.
259   **Remarks** The minor differences between *T. triton varians* and extant *T. triton* can only be
260   observed when a statistically significant number of specimens are available. The reason for
261   referring all items listed in the synonymy, most of which have limited material, to *T. triton*
262   *varians* is solely based on their geologic age. Thus, this should be considered a temporary
263   expedient.
264   **Description**
265   **(1) Skull**
266   The skull description primarily relies on the relatively well-preserved specimen NWUV
267   1489.a8, with reference to other specimens (Fig. 2).
268   **Dorsal view** The nasal exhibits a narrow posterior and a wide anterior aspect. At its junction
269   with the frontal, it is narrowest, then gradually widening anteriorly, and slightly narrowing again
270   at the anterior border. The anterior-most point of the orbit is slightly anterior to the transverse
271   level of the posterior end of the nasal. NWUV 1489.a7 has a larger skull width than normal due
272   to post-mortem deformation, but it retains the complete interparietal, which is approximately
273   pentagonal in shape, resembling that of extant *T. triton*. The frontal crest is more pronounced in
274   adults, particularly in elderly individuals, extending posteriorly from the upper edge of the orbit,
275   beyond the parietal bone, and reaching at least the anterior border of the interparietal bone.
276   **Lateral view** The upper contour of the skull presents a gentle arc, but this shape is often lost
277   due to post-mortem deformation. The alveolus of the upper incisor creates a well-defined

278 semicircular crest on the lateral surfaces of the premaxilla and maxilla. The upper portion of the
279 infraorbital foramen is fan-shaped, while its lower portion is slit-like. The outer wall of the
280 zygomatic plate is slightly concave. Both the anterior and posterior edges of the zygomatic plate
281 exhibit a gentle arc shape; the former is slightly convex anterodorsally, and the latter is slightly
282 concave anterodorsally, with the two edges nearly parallel. The anterior root of the zygomatic
283 arch is weak, measuring about 2-3 times narrower the width of the zygomatic plate. The small
284 supraorbital foramen is situated posterior to the interorbital constriction and just below the
285 supraorbital margin.
286   **Ventral view** The incisive foramen is elongated and narrow, with an obvious distance
287 separating its posterior edge from the anterior edge of M1. The premaxillary-maxillary suture
288 traverses the incisive foramen at about the anterior 2/5 of the foramen. The anterior-most point of
289 the zygomatic plate approximately aligns with the center of the incisive foramen in the
290 mediolateral direction. The masseteric tubercle is positioned at the base of the zygomatic plate,
291 exhibiting a rough surface. Two posterior palatine foramina are almost situated on the connecting
292 line of the posterior roots of the two M2s. The posterior border of the hard palate extends slightly
293 beyond the posterior edge of M3 or is flush with it. The two molar series are not completely
294 parallel, but slightly divergent anteriorly.
295 **(2) Mandible**
296   The lower edge of the mandible (Fig. 3) extends anteriorly in an arc from the base of the
297 angular process. The mental foramen is small and round, located anteroventral to the anterior
298 root of m1. The masseteric ridge is thin yet clearly evident, ending beneath m1 and posterodorsal
299 to the mental foramen. The coronoid process is slender and hook-shaped, extending
300 posterodorsally. A noticeable bulge formed by the posterior end of the lower incisor is present at
301 the base of the condylar process, situated anteroventral to the mandibular notch on the buccal
302 side of the mandible. The angular process extends in a posteroventral direction. The mandibular
303 notch extends slightly further anteriorly than the notch between the condylar process and the
304 angular process, with the latter slightly wider than the former. The mandibular foramen is oval
305 and located at the base of the condylar process. The groove between the alveolus of molars and
306 the base of the coronoid process slopes gently in the posterior direction, not as steep as that of
307 murines; a small foramen of unclear function is situated in the middle of the groove. On the inner
308 side of the mandible, numerous small nutrient foramina are typically found in the area beneath
309 the molar series.
310   Measurements of skulls and mandibles are provided in Table 1 and Supplementary datasets 1,
311 3.
312 **(3) Teeth**
313   **I2** The anterior end of the upper incisor (I2) points ventrally, and its posterior end terminates
314 in an anteroventral position relative to the infraorbital foramen. The enamel layer covers the
315 entire labial surface of I2, which is smooth and devoid of ridges, and also extends to cover a
316 small portion of the lateral surface.

M1 The occlusal morphologies of upper molars are illustrated in Fig. 4. The M1 is kidney-shaped, with an obtuse anterior edge, a comparatively straight buccal edge (but with a noticeable outward protrusion at the metacone), and an arc-shaped lingual edge. The degree of alternating of the opposite main cusps on M1 is small, as is the case for M2 and M3. The anterocone is broad and always splits posteriorly into two equal-sized cusps. In some specimens, the anterocone also exhibits a certain degree of separation from the mesial surface, and in a few cases, this separation is even pronounced. The lingual anterolophule is invariably present, while the buccal anterolophule is observed in 89.1% (41/46) of specimens. A small number of specimens (3.9%, 6/154) exhibit the spur of the anterolophule, which is thin and weak, with five instances extending to the buccal margin of the tooth (Fig. 4B). The presence of the protolophule I is detected in 57.4% (27/47) of specimens. The protolophule II is relatively weak, and even absent in a few specimens. The loph connecting the anterior arm of the hypocone and the metacone, in our opinion, should be viewed as the mesoloph, as in most specimens, there is an obvious contact trace between the loph and the metacone, implying that the loph does not originate from the metacone. In a few specimens, however, this loph can be completely fused with the metacone without any trace, making it difficult to determine whether the metalophule I contributes to the formation of the loph in these cases. No specimens exhibit a mesoloph with a free end. The metalophule II is present but weakly developed in most specimens. The posterosinus is small and shallow, with only a vestige observable in specimens exhibiting severe abrasion. The tooth has four roots.

M2 The M2 is approximately square in shape. The buccal anteroloph is more developed than its lingual counterpart, with the latter occasionally nearly absent. The position of the buccal anteroloph is also elevated compared to the lingual one. The protolophule is double. The mesoloph resembles that of M1 but is relatively thicker. It may either merge with the metacone or display an evident contact trace between them, yet it never has a free end. In some specimens, the mesoloph extends to the tooth edge by adhering to the anterior wall of the metacone (Fig. 4 B, F). The metalophule II is consistently present, albeit comparatively weak. The posterosinus is also small. The tooth is four-rooted.

M3 The posterior portion of M3 is notably reduced, with both the hypocone and metacone significantly smaller than those of M1 and M2. This results in the occlusal outline of M3 resembling a relatively obtuse equilateral triangle. The buccal anteroloph is more developed and positioned higher than the lingual counterpart, which is either absent or extremely weak. The protolophule I is consistently present. The most notable character of M3 is the presence of the axioloph, which originates from the junction of the protolophule I and the anterior arm of the protocone, and extends posteriorly. A small groove forms between the axioloph and paracone. Occasionally, the central part of the groove closes due to the proximity or fusion of the axioloph and paracone, leading to the formation of a small pit in the upper portion of the groove (Fig. 4 D, F). The morphology of the mesoloph is similar to that of M1 and M2. The metalophule II and posterosinus are absent. In some specimens, the mid-segment of the posteroloph (or the posterior

356   arm of the hypocone) inflates into a small cusp, situated between the hypocone and metacone
357   (Fig. 4C, G). The tooth possesses three roots.
358   In a very small number of specimens, the upper molars exhibit morphological variation in
359   certain structures. For example, the protolophule II on M2 occasionally assumes a form similar
360   to that on M3, and vice versa.
361   **i2** The anterior part of the lower incisor (i2) extends anterodorsally, and the posterior end of it
362   terminates at the base of the condylar process, forming a prominent bulge on the buccal side of
363   the mandible. The enamel layer covers the whole labial surface, which is smooth and devoid of
364   ridges, as well as about half of the lateral surface.
365   **m1** The occlusal morphologies of lower molars are shown in Fig. 5. The occlusal outline of
366   m1 is comparatively elongated and gradually narrows from posterior to anterior. The anteroconid
367   is bisected into two approximately equal-sized cusps in most specimens (93.0%, 80/86). In these
368   specimens, the vast majority of anteroconids are slightly bifid posteriorly, although specimens
369   with a more pronounced degree of posterior separation are occasionally observed. From an
370   anterior perspective, the anteroconid is either weakly divided (in young individuals) or undivided
371   (in middle-aged and elderly individuals). A small proportion of specimens (7.0%, 6/86) possess
372   anteroconids split into three small cusps (Fig. 5E). Undivided anteroconids are observed only in
373   heavily worn specimens. In the vast majority of specimens (97.6%, 82/84), the anterolophulid is
374   single and connects either to the buccal anteroconulid (70.7%, 58/82), the midpoint between the
375   two anteroconulids (26.8%, 22/82), or the lingual anteroconulid (2.4%, 2/82). In a very few
376   specimens (2.4%, 2/84), the anterolophulid possesses two branches that connect to the two
377   anteroconulids respectively. The bottom of the anterosinusid is significantly higher than that of
378   the protosinusid. In 43% of the specimens (44/103) (Table 3), a mesolophid is present, which is
379   consistently low, short, and weak. The mesolophid either connects to the metaconid (18.2%,
380   8/44) or has a free end (81.8%, 36/44). In the latter case, the longest free-ended mesolophid does
381   not exceed half the distance from the base to the lingual tooth edge, and in most cases, it only
382   presents as a spine-like projection. The transitional part from the hypoconid to posterolophid is
383   generally slender, but subsequently the posterolophid rapidly swells into a well-defined small
384   cusp. The posterolophid often does not continue anteriorly to connect with the entoconid,
385   resulting in an open posterosinusid in most cases. The cingulum commonly presents at the
386   entrances of the protosinusid and sinusid, occasionally forming a small but distinct ectostylid at
387   the entrance of the latter. The tooth has two roots.
388   **m2** The occlusal outline of m2 exhibits a rounded square shape, with a width greater than that
389   of m1 and m3. The lingual anterolophid is weakly developed or absent, while the buccal
390   anterolophid is always well developed. In 95.2% of specimens (158/166) the mesolophid is
391   present, exhibiting various morphologies that can be essentially categorized into four types
392   (Table 4): I. having a free end; II. connected to the metaconid; III. reaching the lingual tooth
393   edge (10.2%, 16/157) (Fig. 5A); and IV. connected to the entoconid (2.5%, 4/157). Within these
394   morphotypes, I and II are present in most specimens, but the boundaries between the two are
395   sometimes difficult to distinguish. The length of the mesolophid also varies, but most do not

396   exceed 1/2 of the distance from the base to lingual tooth edge. The morphology of the
397   posterolophid and the development of the cingulum are similar to those on m1, except that the
398   lingual edge of the mesosinusid of m2 also occasionally bears the cingulum. The tooth has two
399   roots.
400   **m3** The posterior part of m3 is generally contracted, though a small number of specimens
401   exhibit no obvious contraction (Fig. 5G). In most specimens, the entoconid is significantly
402   reduced compared to that of m1 and m2, while the hypoconid often experiences only slight
403   reduction. Similar to m2, the lingual anterolophid of m3 is also weakly developed and the buccal
404   one is comparatively more pronounced; however, the lingual anterolophid is present in nearly all
405   m3 specimens. The mesolophid is present in all but one specimen (99.2%, 129/130), and its
406   morphology varies, falling into five types (Table 5): I. unbranched (59.4%, 76/128), connected to
407   the lingual tooth edge (Fig. 5 A, C, E, G); II. bifurcated (35.2%, 45/128), with one branch
408   connected to the lingual tooth edge and the other to the metaconid (Fig. 5 B, F); III. trifurcated
409   (0.8%, 1/128), with branches connected to the lingual tooth edge, metaconid, and junction of the
410   hypoconid and entoconid, respectively; IV. unbranched (3.9%, 5/128), connected to the
411   metaconid (Fig. 5D); and V. having a free end (0.8%, 1/128). The posterolophid is somewhat
412   different from that of m1 and m2, primarily in that it usually merges with the entoconid to close
413   the posterosinusid. The posterolophid also exhibits some degree of swelling and appears as a
414   cusp when subjected to slight wear, resulting in three side-by-side cusps on the posterior part of
415   m3. The cingulum is usually absent at the entrance of the sinusid but is often more developed at
416   the entrance of the mesosinusid, occasionally merging with the end of the mesolophid to form a
417   small cusp. The tooth possesses two roots.
418   As observed in upper molars, lower molars also demonstrate variations in some structures
419   among a limited number of specimens. For example, the m3 of NWUV 1489.e169 exhibits an
420   ectomesolophid, the sole exception in all lower molars. Moreover, in this particular specimen,
421   the mesolophids of both m1 and m2, along with m3, bifurcate into two branches, representing a
422   unique morphology not observed in any other specimens. Furthermore, some morphotypes, such
423   as the double-branched anterolophulid on m1, the mesolophid of m2 connected to the entoconid,
424   and the III and V morphotypes of mesolophid of m3, can also be viewed as morphological
425   variations due to their exceptional rarity.
426   Molar measurements are provided in Table 2 and Supplementary datasets 5, 7.

Discussion

Identification of the large-sized hamster material from Syz 2

429   The taxonomies of Cricetinae fossils from Quaternary deposits in China and extant Chinese
430   Cricetinae species remain highly debated. Based on our observations and recent research
431   advancements (e.g., Lebedev et al., 2018; Wang, Wu & Qiu, 2020), we preliminarily suggest that
432   the inclusion of the following 12 genera in the Chinese Cricetinae, ranging from the beginning of
433   the Quaternary to the present (listed in chronological order of naming; in parentheses are the
434   common junior synonyms): *Cricetus* Leske, 1779; *Cricetulus* Milne-Edwards, 1867; *Urocricetus*
435   Satunin, 1902; *Phodopus* Miller, 1910; *Tscherskia* Ognev, 1914 (＝*Cricetinus* Zdansky, 1928,

436   *Cansumys* Allen, 1928); *Allocricetus* Schaub, 1930; *Sinocricetus* Schaub, 1930; *Allocricetulus*
437   Argyropulo, 1932; *Neocricetodon* Schaub, 1934 (＝*Kowalskia* Fahlbusch, 1969); *Bahomys*
438   Chow et Li, 1965; *Amblycricetus* Zheng, 1993; *Nothocricetulus* Lebedev, Bannikova, Neumann,
439   Ushakova, Ivanova et Surov, 2018. Except that the relationship between *Tscherskia* and
440   *Cricetinus* will be discussed in detail below, providing detailed justifications for our conclusions
441   is beyond the scope of this paper. Among the mentioned genera, *Allocricetus*, *Sinocricetus*,
442   *Neocricetodon*, *Bahomys* and *Amblycricetus* are extinct, while the remaining seven are extant.
443   Among the living genera, *Allocricetulus* and *Nothocricetulus* only have very scarce and doubtful
444   fossil records (Cai et al., 2004, 2013), whereas *Cricetus* and *Urocricetus* currently have no
445   known fossil records in China.
446   Aside from *Tscherskia*, the large-sized hamster material from Syz 2 exhibits distinct
447   differences when compared to other genera listed above. The Syz 2 material can be distinguished
448   from nearly all of these genera by characters such as on m1-2 mesolophids being present but
449   rarely reaching the lingual margin of the teeth, M3 possessing an axioloph, the degree of
450   alternating of the opposite main cusps on M1-3 very small, et al. Furthermore, unlike
451   *Neocricetodon* and *Amblycricetus*, which generally have mesoloph(id)s extending to the tooth
452   edge, the mesoloph(id)s of the larger hamster material from Syz 2 scarcely reach the tooth edge.
453   In contrast to *Bahomys* and *Sinocricetus* with comparatively higher crowns, the crowns of
454   remains from Syz 2 are low. The sizes of molars, skulls, and mandibles of the large-sized
455   hamsters from Syz 2 are significantly larger than those of *Cricetulus* (Figures 2 to 5, S1 to S3),
456   *Phodopus*, *Urocricetus*, *Allocricetulus*, and *Nothocricetulus*, but significantly smaller than
457   *Cricetus*. Some researchers (Zheng et al., 1985, p.117; Cheng et al., 1996, p.40; Jin et al., 2009,
458   p.178) considered that the absence of the mesolophid on m1-2 of *Allocricetus* is the key
459   character distinguishing it from *Cricetinus* (i.e., *Tscherskia*). However, this feature actually
460   pertains to *Cricetulus*, not *Allocricetus*, as *Allocricetus* may not bear the mesolophid on m1 but
461   can develop it on m2 in some specimens (Table 7). On the other hand, some researchers argued
462   that the most crucial character of *Cricetinus* (i.e., *Tscherskia*) is the undivided anteroconid of m1
463   (Kretzoi, 1959; Hír, 1996a, 1997), while that of *Allocricetus* and *Cricetulus* is almost always
464   well divided (Hír, 1994, 1996a). However, observations of the extant *T. triton* molars have
465   shown that the degree of separation of the m1 anteroconid in numerous specimens is comparable
466   to that seen in *Allocricetus* according to Hír (1994, Fig. 4). In *Cricetulus*, the separation degree
467   of the anteroconid of m1 in the type species *C. barabensis* is indeed small, while *C.*
468   *longicaudatus* exhibits a well-divided anteroconid of m1 (Figure S3).
469   Meanwhile, the great similarity between the large-sized hamster material from Syz 2 and the
470   extant *Tscherskia* (i.e., *T. triton*) is readily apparent (Figures 2 to 5, S1 to S3). The molar
471   dimensions of the former closely align with those of the extant *T. triton*, with some
472   measurements even being identical (Table 2). Morphologically, the characters of molars and
473   skulls of the former, such as the degree of alternating of the opposite main cusps on M1-3 small,
474   the anterocone of M1 deeply bifid posteriorly with nearly equal-sized buccal and lingual cones,
475   the mesolophs of M1-3 connected to the metacone instead of being free, M3 with the axioloph,

476   the anteroconid of m1 undivided or weakly divided, the mesolophids of m1-2 present but rarely
477   reaching the lingual margin of teeth, nearly all m3s with well-developed mesolophids, and the
478   interparietal pentagonal, also closely resemble those of the extant *T. triton*. Therefore, we can
479   confidently refer the large-sized hamster remains from Syz 2 to *T. triton*.
480   In most skull and mandible measurements, however, the mean values of the material from Syz
481   2 are lightly larger than those of the extant *T. triton* (Table 1, 2), although the measurements of
482   the single upper and lower molar from both the former and the later are nearly identical (Table 2,
483   Fig. 6). As will be demonstrated below, there are also minor differences in molar morphology
484   between the Syz 2 material and the extant species. Therefore, considering these disparities, it
485   may be more reasonable to further classify these materials from Syz 2 as a chronosubspecies of
486   *T. triton*, i.e., *T. triton varians* comb. nov. (=*Cricetinus varians*, see below for details). In
487   addition, the mean values of the lengths of upper and lower toothrows (M1-3 and m1-3) of the
488   Syz 2 material are also lightly greater than those of the extant *T. triton* (Table 2). However, the
489   measurements of the single molar imply that this phenomenon, and even certain skull and
490   mandible measurements, may likely result from the burial deformation (see discussion in Xie,
491   Zhang & Li, 2021).
492   The structure "axioloph" warrants further elaboration here. Both the M3s of *T. triton varians*
493   from Syz 2 and the extant *T. triton* possess an anteroposteriorly directed axioloph, which departs
494   from the junction of the protolophule I and the anterior arm of protocone, and forms a groove
495   between itself and the protocone (Figures 4, S3). In fact, this structure seems to have been
496   noticed by Zdansky (1928) and Schaub (1930) in the syntypes of *T. triton varians* from Locality
497   1 of Zhoukoudian. The term "axioloph," along with several other terms, was first introduced by
498   Freudenthal & Daams (1988, p.137) to facilitate descriptions of M3 of cricetids. They defined
499   the axioloph as "an axial connection between paracone and hypocone, fundamentally composed
500   of the posterior protolophule and the posterior part of the (ancient) entoloph." Morphologically,
501   the axiolophs of M3s of Syz 2 specimens and the extant *T. triton* are obviously distinct from the
502   protolophule IIs of the small-sized hamster remains from Syz 2, and even from all other extant
503   Cricetinae taxa, as their protolophule IIs depart from the posterior wall of the paracone and
504   extend in the anteromedial direction, not forming a groove between itself and the protocone
505   (Figure S3). By contrast, fossil Cricetinae taxa from Eurasia since the Late Miocene appear to
506   more frequently develop an axioloph on M3, especially in the genus *Neocricetodon* (=
507   *Kowalskia*), such as *N. moldavicus* (see Sinitsa & Delinschi, 2016), *N. hanae* (see Qiu, 1995), *N.
508   yinanensis* (see Zheng, 1984b), and *N. lii* (see Zheng, 1993). This seems to imply a close affinity
509   between *Neocricetodon* and *Tscherskia*, although the axioloph is also present in some other
510   genera, such as *Nannocricetus primitivus* (Zhang, Zheng & Liu, 2008), and seems more often
511   present in cricetid genera of older geologic age (before the late Miocene), such as
512   *Democricetodon* and *Megacricetodon*. The phylogenetic significance of the axioloph will not be
513   better understood until a comprehensive phylogenetic analysis covering the taxa mentioned
514   above is conducted, and the homologous structure of the axioloph itself also requires further
515   investigation.

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

When Zdansky (1928) established *Cricetinus* and *Cricetinus varians*, he solely relied on the skull specimens of extant *Cricetus cricetus* and *Cricetulus phaeus* (now considered a subspecies of *Nothocricetulus migratorius*) for comparison. Consequently, he apparently did not have the opportunity to notice the obvious similarity in molar morphology between the fossils from Locality 1 of Zhoukoudian and the extant *T. triton*. Zdansky (1928, p.57) seemed to acknowledge the potential limitation of his study due to the limited number of extant specimens available for direct comparison with the fossils. Thus, he stated in the monograph that "maybe later a generic identity with one of these [extant] genera will result" (translated from German). As expected, doubts about the validity of the genus and species soon emerged. Schaub (1930, 1934) noticed the close resemblance between *C. varians* and *T. triton* in molar morphology, but 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) reiterated that aside from the somewhat larger size, the large-sized hamster fossils from Locality 13 of Zhoukoudian (early Middle Pleistocene in age) showed no appreciable difference from *T. triton* in either skull or tooth morphology, and they maintained the specific name "*varians*" for the Pleistocene form primarily due to "geologic convenience." Zheng & Han (1993) argued that it was challenging to distinguish *C. varians* from extant *T. triton* in North China and Northeast China based on size and molar morphologies. Despite these doubts, a large number of such hamster remains discovered in Pleistocene deposits of China were ultimately assigned to *C. varians*. Meanwhile, as previously mentioned, new fossil hamster species from the Pliocene and Pleistocene deposits of Eurasia have continuously been referred to *Cricetinus* since Kretzoi (1959). Therefore, it is necessary to clarify the issue of validity of *Cricetinus* and *C. varians*.

To address the validity of *Cricetinus*, the validity of its type species, *C. varians*, must be considered first. However, the material Zdansky (1928) utilized for establishing *C. varians* is not only scarce, but also accompanied by a relatively simple description and unclear plates, making direct comparison with *T. triton* difficult. 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, enabling detailed comparisons with these materials. Except for the material from Zhoukoudian, the specimens from other fossil sites in China that have yielded abundant *C. varians* fossils were also compared. In the following discussion, we will conduct a detailed comparison of skull and tooth morphologies between *C. varians* and extant *T. triton*.

(1) Comparisons of the skull morphologies between *C. varians* and *T. triton*

When Zheng (1984a) revisited the hamster fossils from Zhoukoudian, he proposed several distinguishing skull characters to differentiate between *C. varians* and extant *T. triton*. However, Xie, Zhang & Li (2021) assessed these characters proposed by Zheng (1984a) and concluded that these differences between *C. varians* and *T. triton* skulls were questionable and required further verification. Therefore, it is not necessary to reiterate them here.

556   Topachevski and Skorik (1992, p.181) suggested three morphological differences in skull
557   features between *Cricetinus* and *Tscherskia*. Based on the context, these opinions appear to be
558   founded only on the observation of the holotype (a maxillary fragment with M1-3) of *Cricetinus*
559   *gritzai*, rather than the specimens of the type species (*C. varians*) of the genus. Firstly, *Cricetinus*
560   is said to differ from *Tscherskia* by having a wider and more concave masseteric plate (i.e.,
561   "zygomatic plate" in the present paper). However, Topachevski and Skorik (1992) did not
562   provide any measurements of the zygomatic plates of *Cricetinus* and *Tscherskia* to substantiate
563   this claim, even though the degree of depression of the surface of the zygomatic plate seems
564   challenging to quantify. Even if this assertion holds, a wider and more concave zygomatic plate
565   may only be a feature of the *Cricetinus gritzai* species, not the entire *Cricetinus* genus, because
566   our observations show no obvious difference in the characters of the zygomatic plate between
567   *Tscherskia triton varians* from Syz 2 and living *T. triton* (Figures 2, S1). Secondly, *Cricetinus* is
568   said to develop stronger ridges along the posterior side of the incisive foramina [the rim of the
569   area for the lateral masseter?] than *Tscherskia*. However, we likewise failed to discern any
570   appreciable difference in the ridges between *T. t. varians* from Syz 2 and extant *T. triton* (Figures
571   2, S1). Thirdly, the position of the masseteric tuberosity in *Cricetinus* is considered more similar
572   to that in *Cricetus* than in *Tscherskia*. Our observations show that the position of the posterior
573   margin of the masseteric tuberosity in living *Cricetus cricetus* (closer to the posterior edge of the
574   incisive foramen) seems to be slightly further back than that in living *Tscherskia triton* (closer to
575   the middle of the incisive foramen). The position of the masseteric tuberosity of *T. t. varians*
576   from Syz 2 more closely resembles that of extant *T. triton* rather than *C. cricetus* (Figures 2, S1).
577   In conclusion, since the three distinguishing characters between *Cricetinus* and *Tscherskia*
578   proposed by Topachevski and Skorik (1992) seem to be based on just one specimen of *C. gritzai*
579   (the holotype), and we were unable to detect the aforementioned differences between extant *T.*
580   *triton* and *T. t. varians* from Syz 2, the validity of these differences, in our opinion, is
581   questionable.
582   **(2) Comparisons of the teeth morphologies between *C. varians* and *T. triton***
583   ***Comparisons of the teeth size***
584   Table 2 and Fig. 6 show the measurements and scatter diagrams of *C. varians* from
585   Zhoukoudian in Beijing (Zheng, 1984a), Jinniushan in Liaoning Province (Zheng & Han, 1993),
586   and Renzidong in Anhui Province (Jin et al., 2009), as well as *T. triton* from Syz 2 and extant *T.*
587   *triton*. It is evident that, with the exception of the material from Renzidong which is significantly
588   smaller, the average molar sizes from other localities are quite similar, and the data ranges also
589   substantially overlap. In other words, we cannot differentiate *C. varians* from *T. triton* based on
590   their size. As to the material from Renzidong, its significantly smaller size and markedly older
591   geological age—ca. 2 Ma (Jin, Qiu & Zheng, 2009) compared to the Middle Pleistocene age of
592   other localities—cast doubt on its identification as *C. varians*. It is possible that the material
593   from Renzidong represents a new form.
594   Additionally, with the reassignment of hamster material initially identified as *Cricetinus*
595   *varians* (or *Cricetinus* cf. *varians*, *Cricetulus* (*Cricetinus*) *varians*) from several Early

596 Pleistocene sites in China, such as Localities 12, 18 of Zhoukoudian in Beijing, and
597 Gongwangling in Lantian, Shaanxi, being assigned to the genus *Allocricetus* (Zheng, 1984a),
598 East cave of Zhoukoudian has become the only Early Pleistocene site in China, besides
599 Renzidong, yielding *Cricetinus varians* fossils. However, the length of M1-3 of *Cricetinus*
600 *varians* from East cave is merely 4.83 mm (Cheng et al., 1996, Table 3-11, p.40), smaller than
601 the lower limit of the variation range for that measurement in "typical" *C. varians* and extant
602 *Tscherskia triton* (Table 2). More importantly, the m1s of *C. varians* from East cave completely
603 lack the mesolophid (Cheng et al., 1996, p.40), which markedly differs from "typical" *C. varians*
604 and extant *T. triton* (Table 3). Therefore, the material identified as *C. varians* from East cave
605 necessitates reevaluation of its classification. Given the above explanations, except *Tscherskia*
606 sp. from the Late Pliocene Youhe fauna (Xie, Zhang & Li, 2021), there is now no reliable fossil
607 of *Tscherskia* in China predating the Middle Pleistocene.
608 ***Comparisons of the teeth structures***
609 In a hamster individual, the molars symmetrically distributed in the oral cavity (e.g., the left
610 and right M3) may exhibit minor morphological differences; therefore, the morphological
611 structures of both the left and right molars of large-sized hamsters from Syz 2 and living *T. triton*
612 were statistically analyzed in the present study. The material of *C. varians* used for comparison
613 here is mainly from Zhoukoudian (Zheng, 1984a) and Jinniushan (Zheng & Han, 1993).
614 **m1** In extant *T. triton*, about 30% of specimens have a mesolophid (Table 3). The
615 mesolophids are consistently weakly developed and of very short length, with the longest
616 mesolophid not exceeding 1/5 of the distance from the base to the edge of the tooth. In most
617 cases, the mesolophid only appears as a small bulge. It is either connected to the metaconid
618 (9.5%, 2/21) or has a free end (90.5%, 19/21).
619 The localities in Table 3 are listed in descending order, approximately following their
620 geological age from oldest to youngest (ZKD Loc.1, ca. 0.6-0.2 Ma; Jinniushan, ca. 0.31-0.2 Ma;
621 ZKD Loc.3, late Middle Pleistocene; Syz 2, ca. 0.2 Ma). Although the frequencies of
622 mesolophids in *C. varians* and *T. triton* differ across various geological ages, there is no evident
623 discontinuity between them, and as the age advances, the frequency of the mesolophid decreases.
624 Given the similarities in other aspects of tooth morphology and the practicality of classification,
625 it is more appropriate to interpret the differences in mesolophid frequencies as a result of
626 gradualistic evolution within a single species, specifically the progressive reduction of the
627 mesolophid, rather than interspecific or intergeneric differences.
628 **m2** Table 4 presents the frequencies of mesolophids on m2s of *T. triton* and *C. varians*. As
629 shown in the table, throughout their geologic history, the frequencies of mesolophids on m2s in
630 both *T. triton* and *C. varians* were consistently high and similar, although slightly lower in extant
631 *T. triton*. A comparable pattern is also observed in the proportions of morphotype III in *C.*
632 *varians* (excluding Jinniushan specimens) and extant *T. triton*. Therefore, the mesolophid
633 morphology on m2s in *T. triton* and *C. varians* further substantiates the congruence of the "two"
634 species, and it appears more plausible to interpret the minor differences between the two as a

635 gradualistic evolution within a single species, specifically the reduction of the mesolophid,
636 similar to the situation observed in mesolophids on m1.
637   **m3** Table 5 shows the frequencies of mesolophids on m3s of *T. triton* and *C. varians*. As seen
638 from the table, mesolophids are present in nearly all specimens. The proportions of the
639 mesolophids morphotype "connected to the lingual tooth edge " are consistently high, but no
640 clear regularity emerges. Comparing the proportions of more detailed morphological structures is
641 difficult due to insufficient data. But overall, the characters of m3s of *T. triton* and *C. varians* are
642 still quite consistent.
643   **M1** The lingual anterocones and protocones on M1s of *T. triton* and *C. varians* are
644 consistently connected by an anterolophule, whereas the anterolophule behind the buccal
645 anterocone is not always present. Table 6 illustrates that the occurrence frequency of the
646 anterolophule behind the buccal anterocone is high in both *T. triton* and *C. varians*. However, as
647 the statistical data for *C. varians* are based on a relatively small number of specimens, the
648 reliability of the comparison is diminished. The frequencies of "protolophule I" are unstable and
649 appear to lack any discernable regularity.
650   **M2** and **M3** There is practically no morphological difference between M2s and M3s of *T.*
651 *triton* and *C. varians*.
652   In summary, *C. varians* and *T. triton* exhibit substantial consistency in skull and tooth
653 morphologies. Although minor differences in tooth morphology exist between them, these
654 differences exhibit continuous variation and can only be discerned with statistically abundant
655 material. Therefore, we propose that *C. varians* should be considered a chronosubspecies of *T.*
656 *triton*, i.e., *T. triton varians* comb. nov., and *Cricetinus* should be regarded as a junior synonym
657 of *Tscherskia*.
658 **Referred species of *Tscherskia***
659   Apart from *Cricetinus varians*, there are six other species in Eurasia that have been referred to
660 *Cricetinus*:
661   *Cricetinus europaeus* Kretzoi, 1959. The type locality of this species is Csarnóta 2 in Hungary.
662 The majority of researchers believe that the geological age of this site is MN 15 (Venczel &
663 Gardner, 2005). The type specimens of *C. europaeus* consist of only three molars, but one M2
664 among these three molars was later identified as *C. janossyi* by Hír (1996b). Hír (1994)
665 discovered additional materials for this species and described them in detail when examining the
666 materials from the type locality, thus clarifying the nature of the species. Although *C. europaeus*
667 is among the earliest *Cricetinus* species in Europe (Hír, 1994), it appears to exhibit rather
668 advanced morphologies. For instance, the presence ratios of mesolophids on m1 and m2 are even
669 lower than those of extant *T. triton* (Table 7); however, due to the scarcity of material, this
670 observation requires further validation with additional material in the future.
671   *Cricetinus gritzai* Topachevski & Skorik, 1992. The type locality of this species is Odessa,
672 Ukraine. A notable character of this species is that all m1s and partial m2s possess a mesolophid
673 (Koufos et al., 2001). On one hand, this feature indicates a more primitive nature (in other
674 *Cricetinus* or *Tscherskia* species, the mesolophid frequency of m1 reaches a maximum of 70%).

675   On the other hand, the character itself is also unique, because in cricetids, the mesolophid
676   frequency of m1 is almost always lower than that of m2, whereas in this species the situation is
677   reversed. Moreover, other molars of *C. gritzai* are slightly smaller in size than those of *T. triton*,
678   but only M3 is considerably larger than that of *T. triton* (Topachevsky & Skorik, 1992). If this
679   discrepancy is not a statistical error (given that there is only one M3), it may also illustrate the
680   primitive nature of *C. gritzai*.
681   *Cricetinus beremendensis* Hír, 1994. The type locality of this species is Beremend 15 in
682   Hungary, with a geologic age of 2.7 Ma (Hír, 1994; Pazonyi, 2011). The molar morphology of
683   this species, particularly the degree of mesolophid development, is markedly different from other
684   species currently classified in *Cricetinus*, but closely resembles *Allocricetus ehiki* and *A. bursae*
685   in size and morphology (Table 7). Thus, it seems more reasonable to assign this species to
686   *Allocricetus* Schaub, 1930.
687   *Cricetinus janossyi* Hír, 1996. The type locality of this species is Osztramos 7 in Hungary,
688   with a geologic age of approximately 2.3 Ma (Hír, 1996b; Pazonyi, 2011). The molar
689   morphology of this species is very similar to that of *T. triton varians* from Syz 2 (Table 7),
690   although the former is slightly larger in size, and their ages are significantly different. *C. janossyi*
691   is also among the earliest *Cricetinus* species in Europe, first appearing in Csarnóta 2 of Hungary
692   at the same time as *C. europaeus*.
693   *Cricetinus koufosi* Koliadimou 1996. The type locality of this species is Ravin Voulgarakis in
694   Mygdonia basin of Greece (Koufos et al., 2001). The age of Ravin Voulgarakis has been dated to
695   the Nagyharsanyhegy phase of the Biharian (ca. 1.2-0.7 Ma) (Koufos et al., 2001), making this
696   species the latest among several *Cricetinus* species in Europe. Additionally, this species has been
697   discovered in Marathoussa of Mygdonia basin, with the age of the locality dated to the Betfia
698   phase of the Biharian (ca. 1.5-1.2 Ma) (Koufos et al., 2001). Many molar characters of this
699   species remain unclear, but the absence of the mesolophid on m1 may indicate its relatively
700   advanced nature.
701   *Cricetinus mesolophidos* Wu & Flynn, 2017. Xie, Zhang & Li (2021) concluded that it was
702   more reasonable to place *C. mesolophidos* in *Neocricetodon* rather than in *Cricetinus* (i.e.,
703   *Tscherskia*).
704   In summary, we suggest that *C. europaeus*, *C. gritzai*, *C. janossyi*, and *C. koufosi* should be
705   transferred to *Tscherskia*, while *C. beremendensis* should be transferred to *Allocricetus*, and *C.*
706   *mesolophidos* to *Neocricetodon*. However, this treatment is provisional, because the characters of
707   some of these species remain unclear. Except the type species *T. triton*, the type localities of the
708   other four *Tscherskia* species are situated within a small area covered by several neighboring
709   countries in southeastern Europe. This significant geographic distance between *T. triton* and
710   other species introduces a degree of uncertainty to the above classification (Kretzoi, 1959; Hír,
711   1994). In addition, Storch (1974) described a species *T. rusa* from the Holocene (dated between
712   2200–700 B.C.) of northern Iran, whose geographic location and age are highly perplexing.
713   Although we have tentatively placed it in *Tscherskia*, the validity of this species and whether it
714   should be referred to *Tscherskia* clearly warrant further investigation. Table 7 provides a

715 summary of comparisons of frequencies of mesolophids on lower molars among the species of
716 *Cricetinus*, *Tscherskia*, and some related genera (*Cricetulus*, *Nothocricetulus*, and *Allocricetus*).
717 **Origin and dispersal of *Tscherskia***
718 Zheng (1984a, b), Zheng et al. (1985), and Zheng & Han (1993) suggested that *Cricetinus* (a
719 junior synonym of *Tscherskia*) very likely originated from the genus *Kowalskia* (a junior
720 synonym of *Neocricetodon*), an idea tentatively proposed by Fahlbusch (1969). Qiu & Li (2016)
721 remarked that this viewpoint merits further investigation. We also concur with this viewpoint,
722 and the reasons for this deduction have already been fully explained by Zheng (1984b) (as
723 discussed above, the presence of the axioloph on M3 in both genera also appears to support this),
724 so it is not necessary to reiterate these points here.
725 The question that arises now is: when and where (Asia or Europe) did *Tscherskia* originate?
726 Based on current evidence, the earliest appearance of *Tscherskia* in Europe predates that in Asia.
727 The earliest species of *Tscherskia* in Europe, *T. europaeus* and *T. janossyi*, both emerged at
728 Csarnóta 2 (MN 15, ca. 5-3.5 Ma) in Hungary (Hír, 1994; Venczel & Gardner, 2005). In Asia,
729 the earliest known *Tscherskia* is *T.* sp., represented by a fragmentary mandible with m2-m3
730 from the Youhe fauna in Linwei District, Shaanxi Province, China (Xie, Zhang & Li, 2021), with
731 an age of the Late Pliocene (ca. 3.15-2.59 Ma, Yue & Xue, 1996). However, as previously noted,
732 all other credible materials of *Tscherskia* in China (or Asia) are from the Middle Pleistocene or
733 later. This nearly empty fossil record of *Tscherskia* in East Asia before the Middle Pleistocene is
734 a major challenge to the idea of an East Asian origin for *Tscherskia*, although species
735 morphologically similar to *Tscherskia triton* have been found in the Late Pliocene (?) in China
736 (e.g., *Neocricetodon yinanensis*). Furthermore, Europe exhibits a higher diversity of *Tscherskia*
737 species compared to Asia.
738 Therefore, based on the available evidence, it seems more probable that *Tscherskia* originated
739 from *Neocricetodon* during the Early Pliocene in Europe and subsequently spread to Asia. It is
740 possible that another dispersal event in the same direction occurred during the late Early
741 Pleistocene, which could account for the absence of credible *Tscherskia* fossils in China
742 throughout the Early Pleistocene. Meanwhile, the *Tscherskia* that arrived in East Asia during the
743 first dispersal event likely became extinct shortly thereafter and did not survive into the
744 Pleistocene. Of course, this hypothesis still requires verification through the examination of
745 additional material in the future.

Conclusions

747 The detailed morphological description and comparative study of hundreds of large-sized
748 hamster remains collected from the late Middle Pleistocene Locality 2 of Shanyangzhai (Syz 2)
749 indicate that they should be referred to a chronosubspecies of the extant *Tscherskia triton*—*T.*
750 *triton varians* comb. nov. This chronosubspecies is highly similar to extant *T. triton* in size and
751 most molar characters, but exhibits slightly higher frequencies of mesolophids on m1 and m2. In
752 most skull and mandible measurements, the mean values of the former may be lightly greater
753 than those of the later. To resolve the longstanding debate over the validity of *Cricetinus*
754 Zdansky, 1928 and *C. varians* Zdansky, 1928, a detailed comparison of skull and molar

755 morphology was conducted between *C. varians* and *T. triton*. The results demonstrated that the
756 differences between the two are very slight; thus, *C. varians* can only be treated as a
757 chronosubspecies of *T. triton*, i.e., *T. triton varians* comb. nov., and *Cricetinus* should be
758 considered a junior synonym of *Tscherskia*. We tentatively propose that among the seven species
759 once referred to *Cricetinus* in Eurasia, *C. europaeus*, *C. gritzai*, *C. janossyi*, and *C. koufosi*
760 should be transferred to *Tscherskia*, while *C. beremendensis* should be transferred to
761 *Allocricetus*, and *C. mesolophidos* to *Neocricetodon*. Apart from *Tscherskia* sp. from the Late
762 Pliocene Youhe fauna, there are no credible fossils of *Tscherskia* in China earlier than the
763 Middle Pleistocene. Based on the current evidence, *Tscherskia* may have originated from
764 *Neocricetodon* during the Early Pliocene in Europe and subsequently spread to Asia, with *T.*
765 *triton* being its sole extant representative now only inhabiting East Asia.

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778

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Figure 1

Geographic locations of Syz 1~4. Satellite photo credit: Google Earth. © CNES/Airbus.

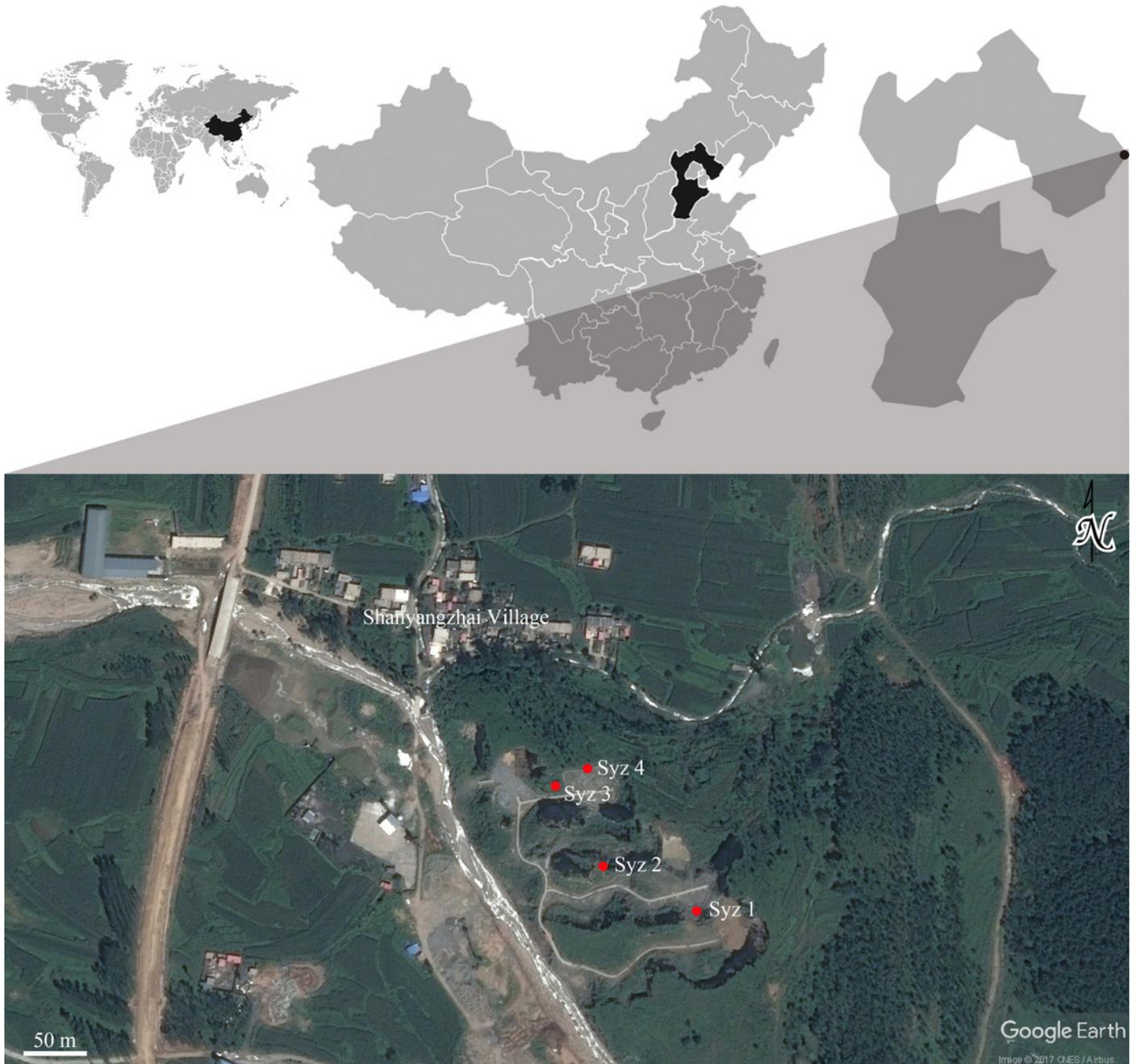



Figure 2

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; Ip, 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 .

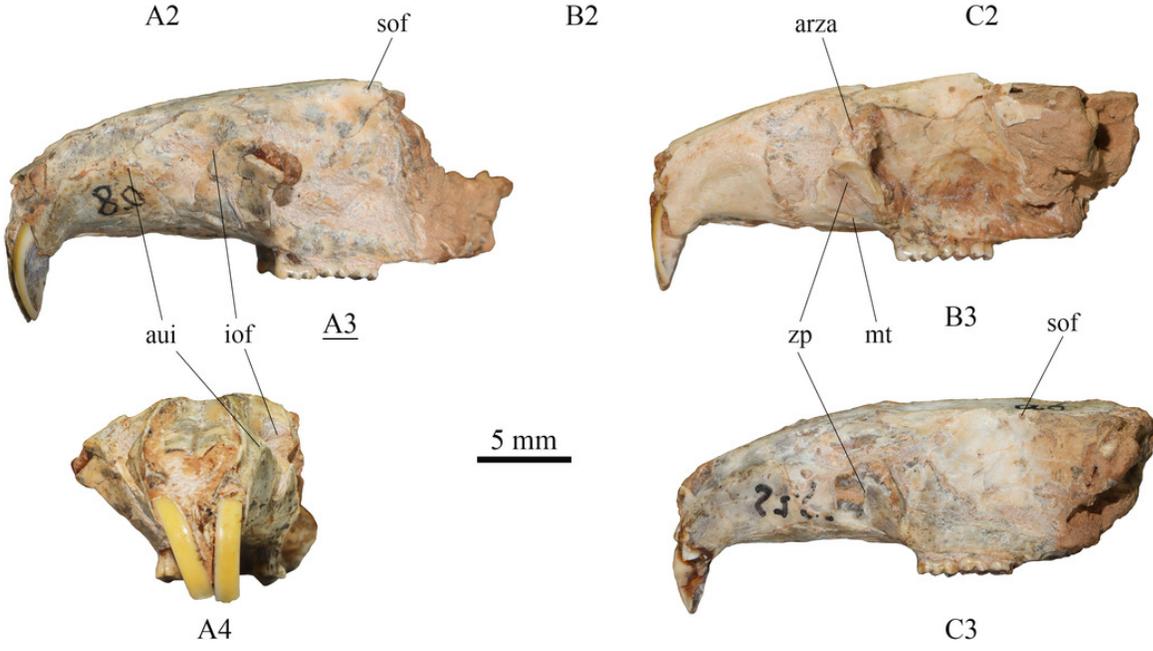
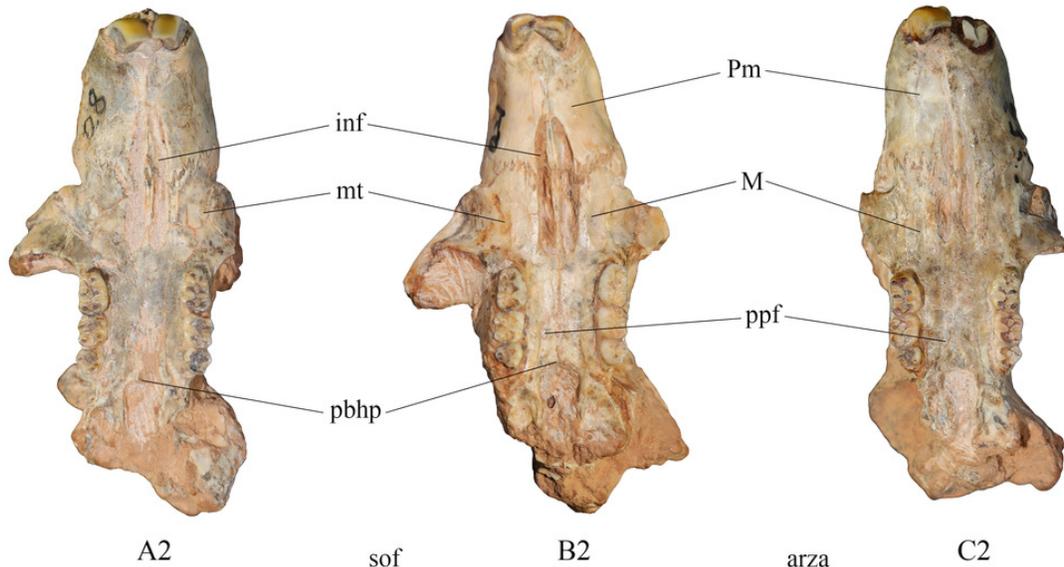
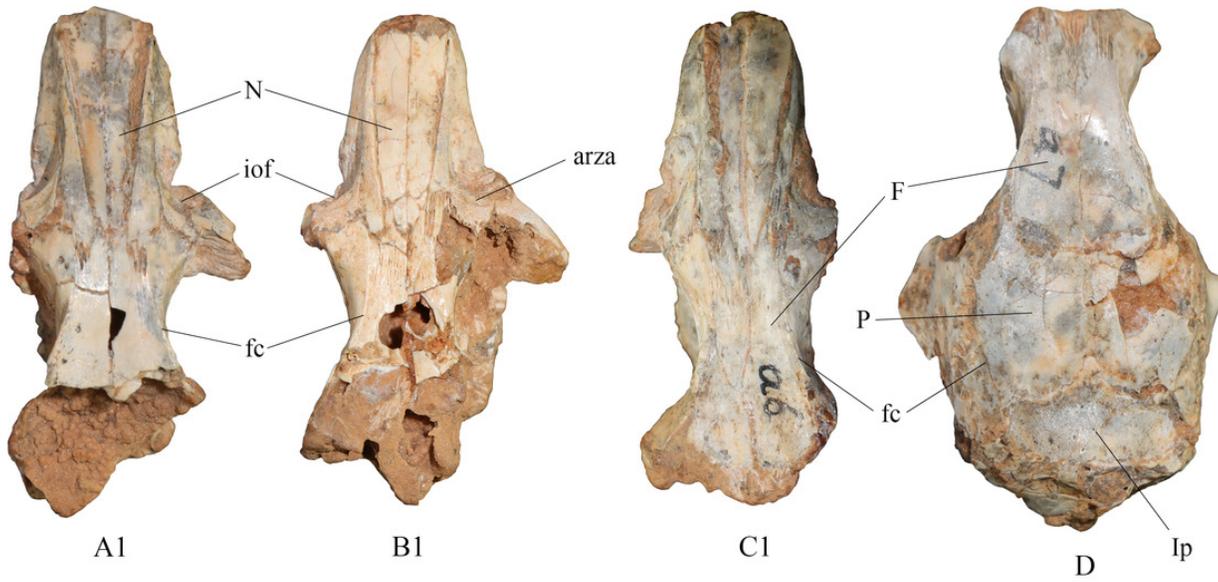



Figure 3

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.

i2b

mr

A1

mtf

A2

mdf

B1

B2

g

ap

5 mm

fmg

fmg

C3

B3

crp

mn

i2b

g

cdp

mstf

mdf

C1

C2

mtf

ap

D1

D2

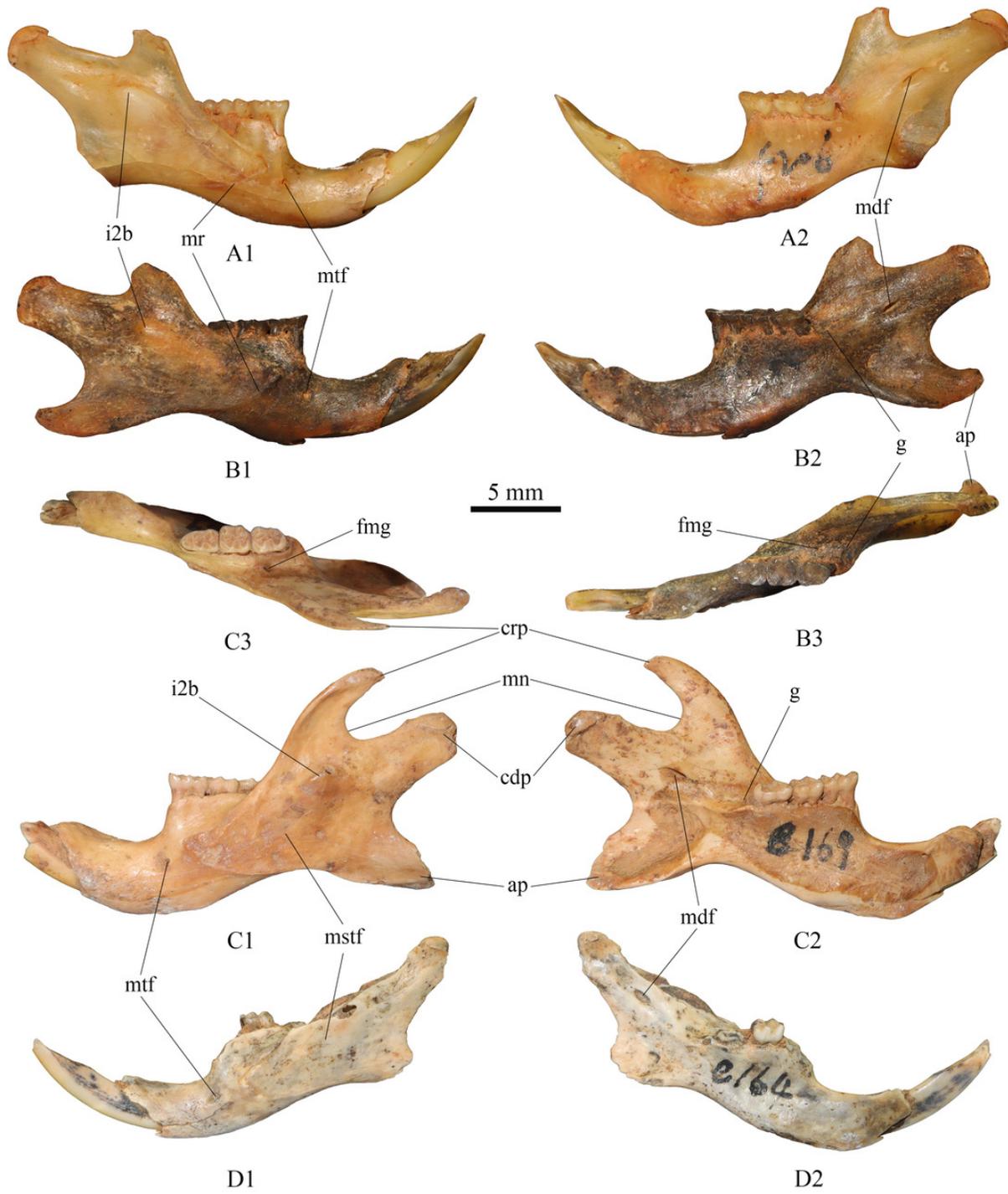



Figure 4

Left 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

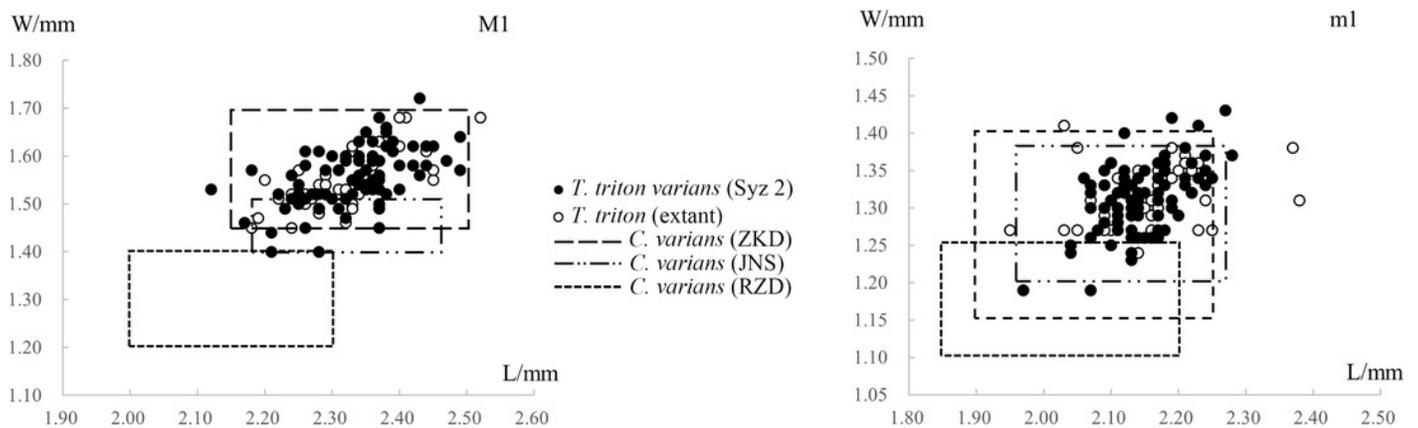
Figure 5

Right 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.

Figure 6

Scatter diagrams of lengths and widths of the first molars of "*Cricetinus*" *varians* and *Tscherskia triton*.

Data source refers to Table 2. The boxes in the figure represent the upper and lower bounds of the length and width values of specimens from specific sites, as the raw data of individual specimen measurements are not available in the original references.

Measurements and comparisons of skulls and mandibles of *Tscherskia triton varians* from 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%

2 # Refer to Supplementary datasets 1-4 for raw data.
3 * "Width of nasal" here indicates the distance between the two junctions of the nasal, premaxilla and frontal.

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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 from 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 from 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 from 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 from 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%

2 # Refer to Supplementary datasets 5-8 for raw data.
3 * quoted from Zheng (1984a); ** quoted from Zheng & Han (1993); *** quoted from Jin et al. (2009).

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

Species and localities	frequencies of mesolophids 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)

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

Species and localities	frequencies of mesolophids on m2	proportions of each morphotype of mesolophids 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)

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

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

Species and localities	frequencies of mesolophids on m3	proportions of each morphotype of mesolophids 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, unbranched, connected to the lingual tooth edge; II, bifurcated, with one branch connected to the lingual tooth edge and the other to the metaconid; III, trifurcated, with branches connected to the lingual tooth edge, metaconid, and junction of the hypoconid and entoconid, respectively; IV, unbranched, connected to the metaconid; V, having a free end. ** connected to the lingual tooth edge.

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

Species and localities	frequencies of anterolophules behind the buccal anterocone	frequencies of protolophule Is
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)

Comparisons of frequencies of mesolophids on lower molars among the species of *Cricetinus*, *Tscherskia*, *Cricetulus*, *Nothocricetulus*, and *Allocricetus*

| Species | | Localities | Geologic age | frequencies of mesolophids on m1s | frequencies of mesolophids on m2s | frequencies of mesolophids on m3s | 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*	Csarnóta 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 Csarnóta 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 (0/8)	0 (0/8)	0 (0/8)	present paper
C. longicaudatus	/	Shaanxi Province, China	recent	0 (0/23)	0 (0/23)	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 Csarnóta 4, Hungary	Pliocene	0% (0/72)	14.8% (9/61)	100% (53/53)	Hír, 1994