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A new fossil marten from Jinyuan Cave, northeastern China reveals the origin of the Holarctic marten group

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Abstract:

Martes is one of the most widely spread genera and has the probably longest evolutionary history among the living Carnivora, yet its fossil record is incomplete, especially those related to the crown group of *Martes*. Here we describe a fossil species, *Martes crassidens* sp. nov. from the Jinyuan Cave, Luotuo Hill, Dalian Puwan Economic Zone, Liaoning Province in northeastern China. The materials were found from the lower deposits belonging to the early-middle Early Pleistocene. Our morphological comparison, morphometric and morphotype analyses suggest the fossil species shows a clear affinity to the Holarctic marten group (here referred to HMG), i.e. *Martes martes*, *Martes zibellina*, *Martes melampus*, *Martes americana*, in having robust dentition, enlarged P4 protocone and M1 inner lobe. It also has unique characters, e.g. relatively large body size, very robust carnassial, high crowned m1 and relatively short talonid, which is different from any living and known fossil species and probably suggests a durophagous dietary behavior. *Martes crassidens* represents so far the earliest record of the HMG, and provides evidence for the chronological framework of the crown marten diversification.

Key Word: *Martes*, Jinyuan Cave, Early Pleistocene, Holarctic marten group

44 1. Introduction

45 *Martes* Pinel, 1792 (Guloninae, Mustelidae) is one of the most widely spread genera in
46 Mustelidae, ranging from Holarctic + Oriental Realm (Proulx et al., 2005). It is also the genus
47 with the longest history in Mustelidae, which appeared since the Early-Middle Miocene
48 (Dehm, 1950; Viret, 1951; Ginsburg, 1961; Peigné, 2012; Valenciano et al., 2020), though
49 whether these early records should be assigned to *Martes* remains to be discussed. There are
50 nowadays seven living species of *Martes*, including Oriental *Martes flavigula* (Boddaert,
51 1785) and *Martes gwatkinsii* Horsfield, 1851, Palearctic *Martes foina* (Erxleben, 1777),
52 *Martes zibellina* (Linnaeus, 1758), *Martes martes* (Linnaeus, 1758), *Martes melampus*
53 (Wagner, 1841) and the Nearctic *Martes americana* (Turton, 1806). Recent molecular
54 phylogeny (Sato et al., 2012; Law et al., 2018) suggested that the Oriental *M. flavigula* (and
55 possibly *M. gwatkinsii*) are the first divergent lineage among the living species (which
56 probably merits a distinct genus *Charronia*), followed by *M. foina*, and the poorly resolved
57 Holarctic marten group (Here referred to HMG) *M. zibellina*, *M. martes*, *M. melampus*, *M.*
58 *americana*. This suggested that the living martens probably originated in the Oriental, and
59 later dispersed to the Holarctic region. Recently, Law et al. (2018) gave a more
60 comprehensive analysis of musteloid with the largest dataset for the group so far (46 genes).
61 Their result shows inconsistency in the relationship of the four species of the HMG using
62 different methods, with the concatenated model supporting the sister group of *M. martes* and
63 *M. zibellina*, and *M. melampus* and *M. americana*, whereas the coalescent model suggests
64 that *M. zibellina* and *M. melampus* are sister group. This inconsistency suggests the presence
65 of incomplete lineage sorting, indicating a rapid diversification of the HMG. Morphological
66 and paleontological evidence is needed to give a better solution to the evolutionary history of
67 the HMG. The molecular phylogeny dated the divergence of living *Martes* species back to the
68 Mio-Pliocene, and several fossil *Martes* species since the Pliocene (Schlosser, 1924; Teilhard
69 de Chardin and Leroy, 1945; Stach, 1959), suggesting that some of these Pliocene *Martes*
70 should be included in the crown group of marten, but few of them have been directly linked
71 to any living species or lineage.

72 In this study, we describe the material of a new Early Pleistocene fossil marten found
73 from Jinyuan Cave, Luotuo Hill in Dalian, Liaoning Province of northeastern Asia. The
74 material is different from any living or known fossil marten, but shows a clear affinity to the
75 living HMG.

76 2. Geological background

77 Jinyuan Cave is located at Luotuo Hill (or Luotuoshan) in Dalian Puwan Economic
78 Zone, Liaoning Province in Northeast China (Fig. 1). It is a large-sized limestone cave with
79 the sedimentary thickness of over 40 m. See the details of the geological setting and faunal

80 list in Jiangzuo et al. (2019) and Jin, Wang et al. (this issue). Total seven layers, including six
81 fossiliferous layers were present, and the new material described in this study was found from
82 the lower part of fourth layer and upper part of fifth layer (L4 and L5), spanning from the
83 early to middle Early Pleistocene (Fig. 1). In the L4, the material was found together with
84 *Ursus etruscus*, whereas in the L5, the material was found together with *Ursus cf. minimus*.
85 *Pachyrocuta brevirostris licenti*, *Canis* sp. and *Megantereon nihowanensis* were found in
86 both layers. The preliminary faunal and paleomagnetic analysis (Jin, Wang et al., this issue;
87 Ge et al., this issue) suggested that the lower part of fourth layer (L4) is comparable to the
88 Xiashagou of Nihewan Basin (1.7–2.0 Ma) (Teilhard de Chardin and Piveteau, 1930; Qiu,
89 2000), whereas the upper part of fifth layer (L5) is comparable to Longdan (2.0–2.2 Ma) (Qiu
90 et al., 2004) in age. Even though the maxilla and mandible described in this study can not be
91 compared directly, they fit each other in size and general morphology, and were regarded as
92 the same species.

93

94 3. Materials and Methods

95 The material described from this study were found in the L4 and L5 of Jinyuan cave in
96 Luotuo Hill, housed in Institute of Vertebrate Paleontology and Paleoanthropology and
97 Dalian Natural History Museum. For comparison, all living species of *Martes*, housed in
98 American Museum of Natural History (AMNH), New York, USA, Smithsonian National
99 Museum of Natural History (USNM), Washington DC, USA, Institute of Zoology, Chinese
100 Academy of Science (IOZ), Beijing, China and Museum of the Institute of Plant and Animal
101 Ecology Ural Branch Russian Academy of Sciences (IPAE), Ekaterinburg, Russia were
102 compared. The fossil *Martes* housed in the Institute of Vertebrate Paleontology and
103 Paleoanthropology, Chinese Academy of Science (IVPP), Beijing, China were compared.

104 We use the dental measurement elements in the way shown in Figure 2.

105 Abbreviation

106 AMNH, American Museum of Natural History, New York, USA

107 IOZ, Institute of Zoology, Chinese Academy of Science, Beijing, China

108 IPAE Institute of Plant and Animal Ecology, Ekaterinburg, Russia

109 IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of
110 Sciences, Beijing, China.

111 USNM Smithsonian National Museum of Natural History, Washington DC, USA

112

113 Published data were used to compare the structure of the new material with modern
114 martens (Miller, 1912; Pavlinin, 1963; Anderson, 1970; Smirnov, 1975; Wolsan et al., 1985;
115 Wolsan, 1988; Wolsan, 1989; Gimranov and Kosintsev, 2015). Unpublished data obtained
116 from the collections of modern *M. martes*, *M. foina* and *M. zibellina* from IPAE were also
117 used. Morphotypes of the P3, P4, M1, p3, p4 and m1, which were not published earlier, were
118 identified. Descriptions of characters of the tooth followed by Hershkovitz (1971) and
119 Wolsan (1989).

120 Morphotypes of P3 are characterized by the buccal convexity or concavity of the crown
121 contour: Morphotypes of m1 are characterized of the structure talonid area: C1 – have a small
122 hypoconid and posterior additional cusp, C2 – double hypoconid, C3 – have a small
123 hypoconid, posterior additional cusp and inner additional cusp close hypoconid, C4 – have a
124 slightly enlarged hypoconid, C5 – have a small hypoconid, posterior additional cusp and
125 inner additional cusp close lingual board of talonid, C6 – have a small hypoconid and inner
126 additional cusp close lingual board of talonid, C7 – have a large hypoconid, C8 – have a large
127 hypoconid and posterior additional cusp.

130 4. Systematic Palaeontology

131 Order **Carnivora** Bowdich, 1821

132 Family **Mustelidae** Fischer [de Waldheim], 1817

133 Subfamily **Guloninae** Gray, 1825

134 *Martes* Pinel, 1792

135 *Martes crassidens* sp. nov.

136 (Fig. 4)

137 **Diagnosis** Relatively large marten with robust dentition. P3 large with weak
138 postero-lingual convexity; P4 very robust, with distinct parastyle and large protocone; M1
139 with slightly enlarged inner lobe; lower premolars robust with postero-lingual convexities, p3
140 with no posterior accessory cuspid and p4 with distinct posterior accessory cuspid; m1 very
141 robust and high-crowned.

142 **Differential diagnosis** Fossil species: differs from *M. zdanskyi* in having more robust
143 dentition, larger P4 protocone, presence of postero-lingual convexity in the premolars,
144 absence of postprotocrista in M1; differs from *M. wenzensis* by smaller size, larger and more
145 robust premolars; differs from *M. vetus* in having a larger size, more robust dentition, larger
146 P4 protocone and higher m1 crown. Living species: differs from *M. martes* in having less
147 robust premolars, generally less enlarged M1 inner lobe and slightly shorter m1 talonid;
148 differs from *Charronia flavigula* in having less robust premolars (mainly p2-p3), premolars
149 without distinct buccal concavity and lingual concavity, more robust carnassial and M1,
150 larger P4 protocone and M1 inner lobe, longer m1 talonid; differs from *M. foina* in having
151 more robust premolars, premolars with lingual concavity located at the posterior side of the
152 teeth, stronger P4 with larger protocone, M1 with enlarged and rounded inner lobe; differs
153 from *M. americana* in having a larger size, more robust dentition, larger P4 protocone, and
154 less reduced m1 metaconid; differs from *M. zibellina* in having a larger size, more robust

155 carnassial, shorter and not widened talonid without additional cusplet; differs from *M.*
156 *melampus* in having more robust carnassial, P4 with larger protocone, p3 lacks posterior
157 accessory cuspid.

158 **Etymology** *crass*, robust, and *dens*, dentition, in referring to its robust teeth.

159 **Holotype** DLJ1408021(field number), a mandible with p2–m1 housed in IVPP.

160 **Description**

161 The maxillary fragment DLJ 1611172 with P3–M1 from the L4. The infraorbital
162 foramen is preserved. The foramen is relatively small, located at the level between the P3 and
163 P4, and is slightly anteriorly inclined.

164 The dentition is robust. The P3 has no accessory cusp. The posterior cingulid forms a
165 short shelf. The buccal contour has indistinct concavity, and the lingual contour is slightly
166 convex. The cusp is located in the anterior part of the tooth. The P4 is very robust. The buccal
167 contour is straight. The parastyle is distinct. The protocone is very large and anteriorly
168 located. A weak ridge links the apexes of paracone and protocone. The lingual cingulum is
169 well developed from the posterior border of the protocone along the lingual border of
170 paracone-metacone blade. The M1 has a paracone larger than the metacone. The buccal shelf
171 along the paracone is much wider than that along the metacone. The protocone ridge is worn,
172 and the protoconule seems to be little differentiated. The inner lobe is enlarged. The lingual
173 border of the M1 is rounded.

174 DLJ1408021 is a partial mandible from the L5. The mandible ramus is moderately high
175 (m1 length/ramus height ratio behind m1 is 1.01) and very robust (width/height ratio of
176 ramus behind m1 is 0.51). The masseteric fossa reaches the level of m1 talonid. There is
177 distinct diastema between the p2 and p3.

178 The lower dentition is robust. The p1 is represented by a single alveolus. The p2–p4 are
179 all double-rooted. The p2 is distinctly asymmetric, and the anterior border is shorter than the
180 posterior border. The degree of asymmetry gets lower down from the p2 to p4. The buccal
181 concavity of the premolars is absent or very weak. The lingual convexity is present in all
182 premolars. This convexity is most distinct in the p4, making the occlusal shape of the p4
183 close to a triangular shape. The m1 is robust and high-crowned. The paraconid is especially
184 wide. There is distinct concavity in the lingual border between the paraconid and metaconid.
185 The talonid is moderately long. The hypoconid is the only cuspid, and the hypoconulid and
186 entoconid are both very weak. The m2 is represented by a single alveolus.

187

188 5. Comparison and Discussion

189 *Martes crassidens* is a large marten, comparable to the large living species of the genus,
190 i.e. *Martes flavigula* and *Martes melampus*. The new species is characteristic by robust
191 dentition, especially carnassial, and several traits connect it with the HMG.

192

193

194 **5.1 Comparison with HMG**

195 The HMG is a unique group of living martens that has parapatric distribution and as a
196 whole, occupies nearly all the Holarctic realm. The group is characterised by having long,
197 relatively narrow skulls, a distinct middle spur of bony choana, a long auditory bulla, a large
198 P4 protocone, an enlarged M1 inner lobe, and a relatively elongated m1 talonid (Anderson,
199 1970; Anderson, 1994).

200 Among the four living species of the HMG, *M. americana* is the most distinct species.
201 *Martes americana* is generally smaller than other species (Anderson, 1994). Its dentition is
202 less robust than that of other species of the HMG. This is mostly reflected by the P3, P4, p2
203 and p3, which are slender compared to those of other species (Fig. 5, 6, 7, 8). The P4
204 protocone is not enlarged as in other HMG species, though the M1 inner lobe is often
205 enlarged. In terms of lower dentition, *M. americana* has special m1 morphology that the
206 metaconid is always very weak, though never absent (Fig. 6). All other species of the HMG,
207 as well as other *Martes*, do not show this trend. The other three species show fewer
208 differences to each other. In general, *M. martes* shows the strongest development of the HMG
209 characteristic traits (Anderson, 1994). The premolars of *M. martes* is the most robust among
210 the HMG. The P4 protocone is similar to two other species, but the M1 inner lobe is the
211 largest. There is considerable variation in M1 shape and size, but it can be distinctly
212 antero-posteriorly elongated than other species. *Martes zibellina* and *M. melampus* are
213 intermediate between *M. martes* and *M. americana* (Anderson, 1994). Both species have
214 moderately robust dentition. *Martes melampus* is distinctly larger than *M. zibellina* and has
215 slightly more robust dentition and rostrum. The P4 protocone of *M. melampus* is slightly
216 larger than that of *M. zibellina*. One peculiarity of *M. melampus* is that the p3 nearly always
217 develops a weak posterior accessory cuspid, which is absent or rare in other species of the
218 HMG. *Martes zibellina* is unique in having an enlarged m1 talonid with accessory cusplet.

219 *Martes crassidens* only preserve dentition. The large P4 protocone and M1 inner lobe of
220 *M. crassidens* all fit with the traits of the HMG. The P4 of *M. crassidens* are more robust than
221 those of any living HMG, and the m1 paraconid is especially wide. In general, *M. crassidens*
222 is the closest to *M. melampus* and to a less extent *M. zibellina*. In terms of carnassial, *M.*
223 *crassidens* slightly exceeds *M. melampus* in robustness and the P4 protocone is larger. The p3
224 however, does not have a posterior accessory cuspid and thus different from that of *M.*
225 *melampus*. The M1 inner lobe is moderately enlarged, similar to that of *M. zibellina* and *M.*
226 *melampus*, but is also overlapped with that of *M. martes* and *M. americana*. The m1 talonid is
227 not widened, unlike that of *M. zibellina*. *Martes crassidens* differs from *M. martes* by having
228 a slightly larger size, less robust premolars without distinct postero-lingual convexity, and
229 more robust carnassial, and M1 inner lobe is not very enlarged. *M. crassidens* differs from *M.*
230 *americana* by having a larger size and distinctly more robust dentition, and the m1 metaconid
231 is not reduced.

232

233 **5.2 Comparison with other living species of *Martes***

234 Three other species are known in *Martes* that do not belong to HMG. *Martes flavigula*
235 and *Martes gwatkinsii* are the first divergent lineage of *Martes* and were sometimes viewed
236 as a distinct genus *Charronia* (Pocock, 1941; Li et al., 2014; Nascimento, 2014). Our
237 observation suggested that this lineage is distinct from other species of *Martes* in morphology.
238 The cranium is very robust, the mandible is deep and the dentition is also peculiar. The
239 premolars of this lineage are robust, having distinct buccal concavity and strong lingual
240 convexity. P4 has a protocone that often has a constriction at its base, making the occlusal
241 view of the protocone more rounded. The M1 is distinctly antero-posteriorly shorter than
242 other *Martes*. The m1 has a very short talonid. These traits combined, as well as the result of
243 molecular phylogeny (that this lineage is the first divergent group among living species of
244 *Martes*), are enough to support a generic distinction of *Charronia*.

245 *Martes foina* is another species that living across the middle latitude of Eurasia. It is
246 intermediate between *Charronia* and the HMG in cranial robustness. The dentition of *M.*
247 *foina* is also very characteristic. The premolars are slender, and the lingual convexity is
248 always located at the level of the main cusp. The latter character is not present in any other
249 species of *Martes*, in which the lingual convexity is always located in the postero-lingual side
250 of the premolars (Gimranov and Kosintsev, 2015). The P4 is slender and has a small
251 protocone. The inner lobe of the M1 is generally not enlarged, and there is often buccal
252 concavity between the paracone and metacone. *M. crassidens* does not possess the
253 above-mentioned traits, and is larger than *M. foina* with distinctly more robust dentition.

254 **5.3 Comparison with Plio-Pleistocene fossil *Martes***

255 *Martes* probably has one of the richest fossil species among Carnivora. This is largely
256 due to the fact that *Martes* has unspecialised dentition, and the primitive forms of different
257 lineages could all be similar to *Martes*. Molecular dating suggested that the crown group of
258 *Martes* originated around the Miocene and Pliocene boundary. Therefore, most Miocene
259 *Martes*, if not all, should be excluded from this genus. In this work, we only concentrated on
260 Plio-Pleistocene *Martes*, as Miocene species are unlikely to be correlated with our new fossil.

261 Two fossil species of *Martes* are known from the Pliocene of China. *Martes anderssoni*
262 were found in Ertemte (Schlosser, 1924), which has the Mio-Pliocene age (Qiu et al., 2006,
263 2013). Anderson (1970) mistakenly viewed that the type of this species was from Baode,
264 Shanxi Province. This species is only represented by a mandibular fragment and several
265 isolated teeth including an M1. The nature of this species is unclear due to poor preservation.
266 *M. crassidens* differs from *M. anderssoni* by having an enlarged M1 inner lobe.

267 Another species, *Martes zdanskyi* Teilhard de Chardin and Leroy (1945), is represented
268 by better material from Taoyang Village, Yushe. The specimen is probably from the upper
269 part of the Gaozhuang Formation and therefore has a late Early Pliocene age (Z. Qiu,
270 personal communication). This species has relatively narrow dentition, and premolars nearly
271 do not have postero-lingual convexity. The P4 has distinct buccal concavity and
272 moderate-sized protocone. The M1 inner lobe is enlarged, similar to that of the HMG, but the

273 presence of postprotocrista is uncommon for HMG (and all living *Martes*). *M. crassidens*
274 differs from *M. zdanskyi* by having a larger size, P4 with larger protocone and the absence of
275 buccal concavity, M1 lacking postprotocrista, more robust lower premolars, and more robust
276 and higher-crowned m1.

277 Two other species have been erected in *Martes* from the Plio-Pleistocene fossil site in
278 China. *Martes pachygnatha* is erected by Teilhard de Chardin and Piveteau (1930) from
279 Nihewan Basin. This species has been assigned to *Pannonictis* (Sotnikova, 1980) or *Eirictis*
280 (Qiu et al., 2004). The two genera are mainly distinguished by upper dentition, especially the
281 P4, but such material is unknown for "*M.* *pachygnatha*". In fact, there is one maxillary
282 fragment with the C–P4 from Nihewan Basin assigned to *?Plesiogulo* sp. nov. (Teilhard de
283 Chardin and Leroy, 1945). The size and morphology are in accordance with those of *Eirictis*
284 from Longdan (Qiu et al., 2004) and Renzidong Cave (Liu and Qiu, 2009). This maxilla is
285 most probably just the upper dentition of "*M.* *pachygnatha*" and this species should be
286 assigned to *Eirictis*. The upper dentition of *Eirictis* is similar to that of *Martes*, as both genera
287 have full premolars and a "Mustelinae" type P4. Nevertheless, our observation suggested that
288 the P4 protocone in *Eirictis* is located at the posterior border of the inner lobe, in contrast to
289 *Martes*, where the protocone is located close to the center of the inner lobe. *M. crassidens* is
290 therefore clearly different from *Eirictis* both in size and morphology. Another species is
291 *Martes crassa* Teilhard de Chardin and Leroy (1945) from Yushe Basin. It is smaller than
292 *Eirictis*, but larger than any Plio-Pleistocene *Martes*. The robust canine with wrinkle, lacking
293 the p1, robust premolars, p4 lacking posterior accessory cuspid, m1 with enlarged talonid
294 basin. These traits are well enough to exclude it from *Martes*. It is most probably also a
295 member of Lyncodontini. *M. crassidens* is different from "*M.* *crassa*" by smaller size, less
296 robust dentition, presence of the p1, and narrower m1 talonid.

297 Numerous species of fossil *Martes* have been named from the Pliocene and Pleistocene
298 deposits in Europe (Anderson, 1970). *Martes wenzensis* Stach (1959) is described from Węże,
299 Poland, MN15. This species has a large size and robust carnassial. *Martes crassidens* differs
300 from *M. wenzensis* in its smaller size, larger and distinctly more robust premolars. The P4 and
301 m1 of *M. wenzensis* are robust, with width/length ratios similar to those of *M. crassidens*, but
302 its premolars are slender, unlike those of any living *Martes*. The P3/P4 length ratio is only
303 0.54, distinctly smaller than that of *M. crassidens* (0.68), but the p4/m1 length ratio is 0.65,
304 which is larger than that of *M. crassidens* (0.61). Unfortunately, Stach (1959) did not give the
305 occlusal view of dentition, which hampers a more detailed comparison. Nevertheless, we can
306 conclude that *M. crassidens* is different from *M. wenzensis* in size and dental proportion.

307 Most Early Pleistocene and many early Middle Pleistocene *Martes* have been assigned
308 to *Martes vetus* (Kurtén, 1968). This species was first described by Heller (1933) from
309 Sackdilling, Germany as *Martes intermedia*. But as this name has already been used as a
310 subspecies of *Martes foina intermedia*, a new name, *Martes vetus* given by Kretzoi (1942)
311 was viewed as the valid name for this species (Anderson, 1970). The type locality Sackdilling
312 is probably the late Early Pleistocene (Wagner et al., 2012), but this species has been found
313 from various localities spanning from the Early to early Middle Pleistocene. This species is
314 therefore more or less contemporary with *M. crassidens* or slightly younger. Ambros et al.
315 (2005) provided a good photo of the type skull of *M. vetus*. In general, this species does not
316 possess specific traits of *M. martes* and *M. foina*, e.g. the premolars are not robust and the M1

317 inner lobe is not enlarged (unlike *M. martes*), and the lingual convexity is located posterior to
318 the apex of the main cusp (unlike *M. foina*). Rabeder (1976) described some *Martes*
319 specimens from Deutsch-Altenburg 2C1 to *Martes* cf. *zibellina*. The age of this locality,
320 according to micromammals and faunal composition, is viewed as 1.2–1.3 Ma (Rabeder et al.,
321 2010). We were able to study this material, and there is one additional partial cranium with
322 nearly complete upper dentition. The upper dentition is generally similar to that of *M. vetus*.
323 As we have not seen many materials of this species, our interpretation of this species will be
324 based on materials from Sackdilling and DA 2C1. We agree with Rabeder (1976)'s original
325 assignment to *Martes* cf. *zibellina*, which implies that this species is most similar to *M.*
326 *zibellina* among the living species. The above-mentioned dental traits mostly represents the
327 primitive traits for the HMG. *Martes zibellina* often has a relatively wide m1 talonid and
328 there are often additional small cusplet in the talonid basin or in entoconid ridge, which is not
329 seen in the DA 2C1 specimen. Notably, the bony choana of the type skull of *M. vetus* is
330 posterior extended, and there is a clear middle spur. Both traits are typical of the HMG
331 species, but never present in *M. foina*. *Martes vetus* probably belongs to the HMG, before the
332 divergent of *M. martes* and *M. zibellina*, or represents the early unspecialised ancestor of *M.*
333 *martes*. *Martes crassidens* is different from *M. vetus* by its larger size, more robust dentition,
334 larger P4 protocone and higher m1 crown.

335 **Morphotype analysis and implication**

336 Due to the intraspecific variation of the morphology, morphotype analyses were carried
337 out to investigate the variation of living species to provide a better background for discussing
338 the evolutionary and taxonomical position of fossil species. Data on the variability characters
339 of the teeth for living species of *Martes* are very scarce (Pavlinin, 1963; Anderson, 1970;
340 Wolsan et al., 1985; Wolsan, 1988; Wolsan, 1989; Gimranov and Kosintsev, 2015), so our
341 comparison and analysis can only be applied to certain living species, as a supplementary
342 work of morphological and morphometric analyses above.

343 **P3** *M. crassidens* has a slightly convex lingual contour (Fig. 4). The *M. martes* (92%)
344 and *M. zibellina* (48%) have the same convexity (Smirnov, 1975). The P3 with a weak
345 convexity belongs to morphotype A2 and is typical for *M. martes* (Wolsan, 1989; Gimranov,
346 Kosintsev, 2015). Note that the buccal contour of *M. crassidens* is nearly straight (A2), which
347 is typical for *M. zibellina*.

348 **P4** *M. crassidens* has a tooth contour (Fig. 4) similar to the morphotype B1. The
349 morphotype B1 is extremely rare and not typical of *M. foina*, *M. martes* and *M. zibellina*
350 (Gimranov and Kosintsev, 2015). The apex of the P4 protocone of *M. crassidens* is located in
351 the center of the inner lobe. This is morphotype D that is peculiar to *M. zibellina* (Gimranov
352 and Kosintsev, 2015). This morphotype is depicted in more detail in Fig. 3.

353 **M1** We cannot describe the morphotypes of the M1 *M. crassidens* due to the worn. The
354 buccal contour between the paracone and metacone of *M. crassidens* is slightly concave (Fig.
355 4). This is morphotype C2 which is often characteristic of *M. zibellina* and *M. americana*
356 (Wolsan, 1989).

357 **p3** *M. crassidens* does not have additional cusps on the posterior crest (Fig. 4). This is
358 morphotype B1 (Wolsan, 1989) or A1 (Gimranov and Kosintsev, 2015). These morphotypes

359 (B1 and A1) significantly dominate the *M. foina*, *M. martes* and *M. zibellina*.

360 **p4** *M. crassidens* has a robust posterior accessory cuspid on the posterior crest (Fig. 4).
361 This is morphotype B4, which is often typical of *M. zibellina* and *M. americana* (Wolsan,
362 1989). However the accessory cuspid of the p4 of *M. crassidens* lies close to the top of the
363 protoconid. It belongs to the morphotype A2, which is typical of *M. zibellina* (Gimranov and
364 Kosintsev, 2015).

365 **m1** *M. crassidens* has a slightly enlarged hypoconid corresponds to C4 morphotype (Fig.
366 3). No other cusps are present on the talonid (Fig. 4). This type of structure was regarded as
367 the morphotype B1 (Gimranov and Kosintsev, 2015). This is morphotype B1 (= C4 of this
368 research), which is extremely rare in *M. foina* and *M. zibellina*. The morphotype B1 is also
369 rare but in a higher frequency in *M. martes* (Gimranov and Kosintsev, 2015).

370 The morphotype comparison with selected living species suggests *M. crassidens* teeth
371 combine the characteristics typical of modern *M. martes* and *M. zibellina* with some of the
372 features typical of *M. foina* and *M. americana*. Therefore, based on morphotype analysis it is
373 not possible to correspond *M. crassidens* with any living species of *Martes*. This confirms the
374 species independence of *M. crassidens*. Nevertheless, the general morphology of *M.*
375 *crassidens* is closer to the morphotype range of *M. martes* and *M. zibellina*, supporting an
376 affinity to the HMG.

377 **Origin of Holarctic marten group**

378 From the morphological aspect, *Martes americana* is a unique member of the HMG. It is
379 not only smaller than other species (Anderson, 1994), but also has slender dentition, smaller
380 P4 protocone, and reduced m1 metaconid. The former two characters are close to those of *M.*
381 *foina* and therefore represent the primitive characters, and the last character is its
382 autapomorphy. Nevertheless, the slightly enlarged M1 inner lobe and the presence of a clear
383 middle spur of bony choana supports its affinity to other species of the HMG. Molecular
384 dating suggested that the living HMG diverged at the Plio-Pleistocene boundary (Sato et al.,
385 2012; Law et al., 2018). Our review and comparison suggested that none of the Pliocene
386 *Martes*, e.g. *M. wenzensis* and *M. zdanskyi*, shows affinity to the HMG. Our new fossil
387 species *M. crassidens* from the early to middle Early Pleistocene coincides with this result
388 and represented the so far earliest known HMG. Our morphology and morphotype analyses
389 support *M. crassidens* is closer to the living Old World HMG (*M. martes*, *M. zibellina* and *M.*
390 *melampus*) than to *M. americana*. If this interpretation is right, the HMG should have
391 appeared during the Pliocene. The younger European species *Martes vetus* also belongs to the
392 HMG and is probably the ancestor of *M. martes*. We hypothesis that the crown marten (here
393 *Martes* + *Charronia*) originated in Asia, as *Charronia* and the early divergent *M. foina* are
394 distributed in this area. The ancestor of the HMG dispersed to the northern part of the Asia, as
395 evidenced by our fossil *M. crassidens*, and then dispersed to the other parts of the Holarctic
396 Realm. This is the most parsimony explanation for marten biogeography, but carnivores are
397 often highly movable, and more fossil materials will be needed to test this hypothesis.

398 **Conclusion**

399 The new Early Pleistocene fossil material of *Martes* from Jinyuan Cave, northeastern
 400 China was distinct from any known fossil and living species of *Martes* and was erected as a
 401 new species *Martes crassidens*. It has enlarged P4 protocone and M1 inner lobe, supporting it
 402 as a member of the Holarctic marten group. The general morphology of *M. crassidens* is
 403 closest to that of *M. melampus*, but it does not possess any traits unique to the latter species
 404 (e.g. presence of p3 posterior accessory cuspid). *M. crassidens* is the earliest known HMG,
 405 and probably closer to the living Old World HMG than to *M. americana*. The new fossil
 406 marten help understand the evolution and diversification of the living species of *Martes*.

407
 408
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423
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516

517 Fig. 1. Geographic and section sequence of Jinyuan Cave. A. Location of Dalian; B.
518 Location of Luotuo Hill in Dalian; C. section sequence and the location of fossils.

519

520

521 Fig. 2. Dental measurement elements. L. length, W. width, BW. blade width, EL.
522 external width, IL. inner lobe width, TrL. trigonid length, AW. anterior (trigonid) width, PW.
523 posterior (talonid) width.

524

525

526 Fig. 3. Morphotype of the P3 and P4 and m1.

527

528 Fig. 4. The material of *Martes crassidens*. A1–2. Maxilla DLJ 1611172, lateral and
529 ventral view; B1–3. DLJ1408021, lateral, medial and dorsal view.

530

531

532 Fig. 5. Comparison of the upper dentation (P3–M1) of fossil and living *Martes*. A. *Martes*
533 *crassidens*, DLJ 1611172; B. *Martes martes*, AMNH M36633; C. *Martes zibellina*, C1.
534 IOZ5222, C2. IOZ5223; D. *Martes melampus*. D1.USNM115684, D2. USNM013832; E.
535 *Martes americana*, E1. USNM057939, E2. USNM148417; F. *Martes foina*, IOZT0314; G.
536 *Charronia flavigula*, AMNH M57046.

537

538

539 Fig. 6. Comparison of the mandible and lower dentition of fossil and living *Martes*. The m1s
540 are enlarged for morphological comparison. A. *Martes crassidens*; B. *Martes martes*, AMNH
541 M36633; C. *Martes zibellina*, C1. IOZ5222, C2. IOZ5231; D. *Martes melampus*.
542 D1.USNM21090, D2. USNM115684; E. *Martes americana*, E1. USNM106897, E2.
543 USNM53361; F. *Martes foina*, IOZT0313; G. *Charronia flavigula*, AMNH M57046. Scale
544 bar for mandible.

545

546 Fig. 7. Dental measurement and ratio of upper dentition. A. P3 length vs P3 width/length
547 ratio; B. P4 length vs P4 width/length ratio; C. P4 length vs P3/P4 length ratio; D M1
548 external length vs external/internal length ratio; E. M1 external length vs width; F. P4 length
549 vs M1 width/P4 length ratio. The 55% confident ellipse is shown.

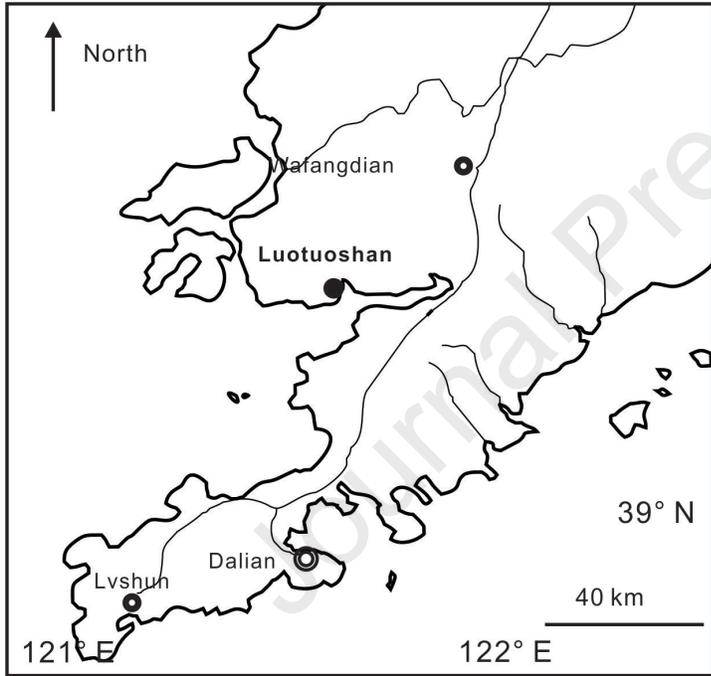
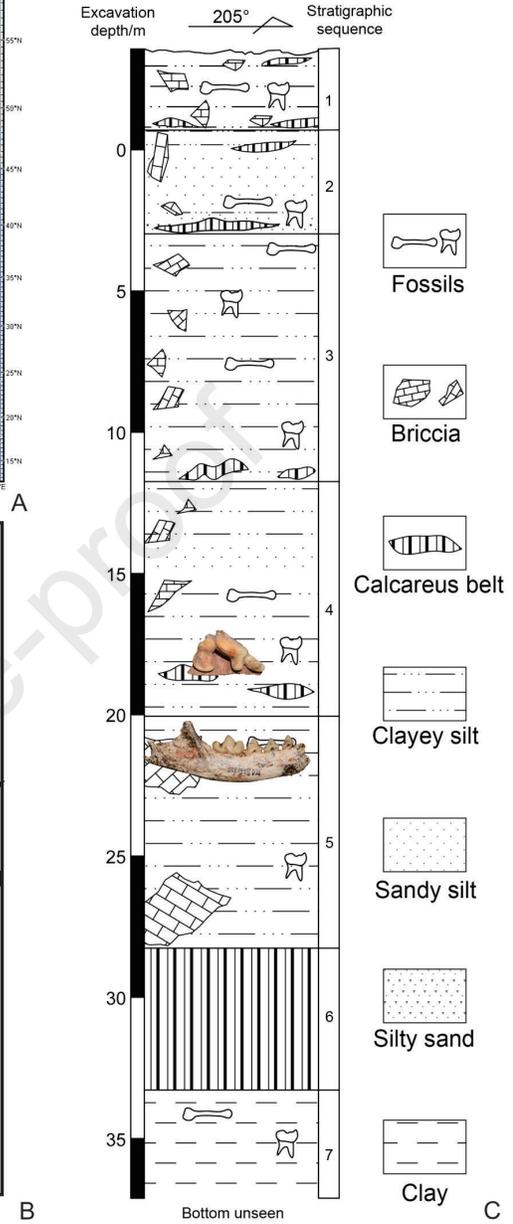
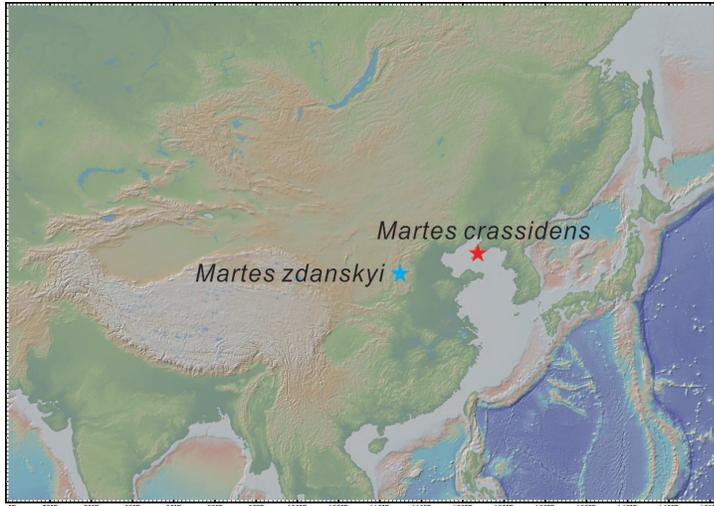
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552 Fig. 8. Dental measurement and ratio of lower dentition. A. p2 length vs p2 width/length
553 ratio; B. p3 length vs p3 width/length ratio; C. p4 length vs p4 width/length ratio; D. m1
554 length vs m1 trigonid width/length ratio; E. m1 length vs m1 trigonid length/length ratio; F.
555 m1 length vs p4/m1 length ratio. The 55% confident ellipse is shown.

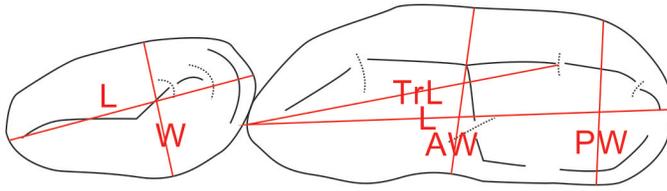
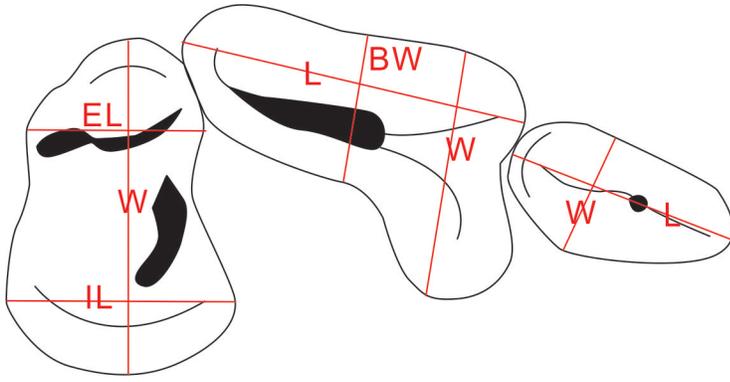
Table 1 Measurements of *Martes crassidens* sp. nov.

Catalogue	P3					P4						
	L	W	H	W/L	W/H	L	W	BW	W/L	BW/L		
	6.92	3.74	4.82	0.54	0.70	10.12	7.22	4.42	0.71	0.44		
Catalogue	M1					M1EL/P4L	M1W/P4L	P3L/P4L	P4-M1 L			
	EL	IL	W	EL/IL	W/EL							
	5.42	6.62	9.64	0.82	1.78	0.78	1.39	0.68	15.94			
Catalogue	p2				p3				p4			
	L	W	H	W/L	L	W	H	W/L	L	W	H	W/L
DLJ1408021	4.22	2.52	3.78	0.60	5.18	2.82	4.02	0.54	6.32	3.64	4.92	0.58
Catalogue	m1											
	L	AW	TrL	PW	AW/L	PW/L	TrL/L					
DLJ1408021	10.42	4.42	7.88	4.42	0.42	0.42	0.76					
Catalogue	Mandible											
	p4L/ m1L	Mandible height p2/p3	Mandible width p2/p3	Mandible height m1/m2	Mandible width m1/m2	m1/Mandible height m1/m2	Mandible width/height m1/m2					
	DLJ1408021	0.61	8.88	4.92	10.32	5.22	1.01	0.51				



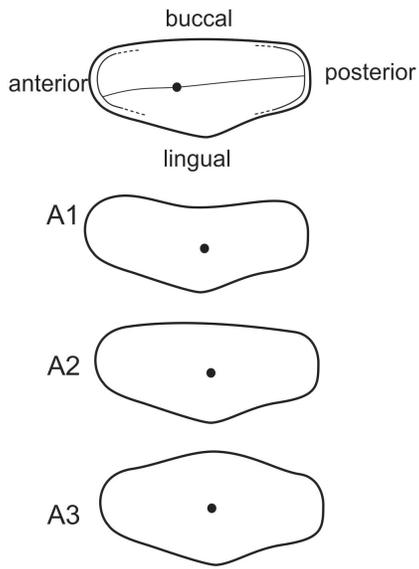
B

C

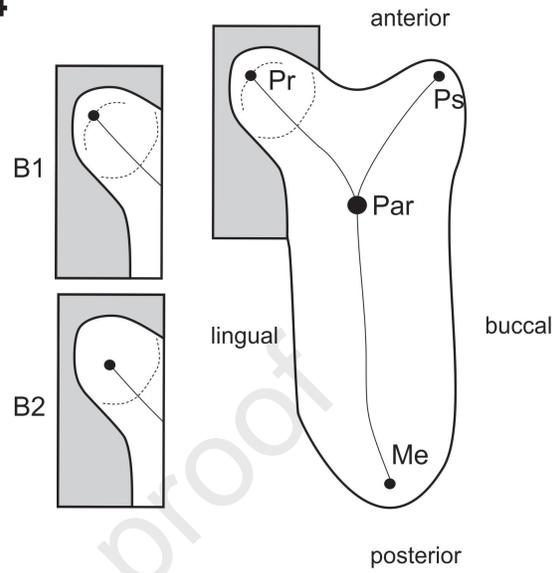


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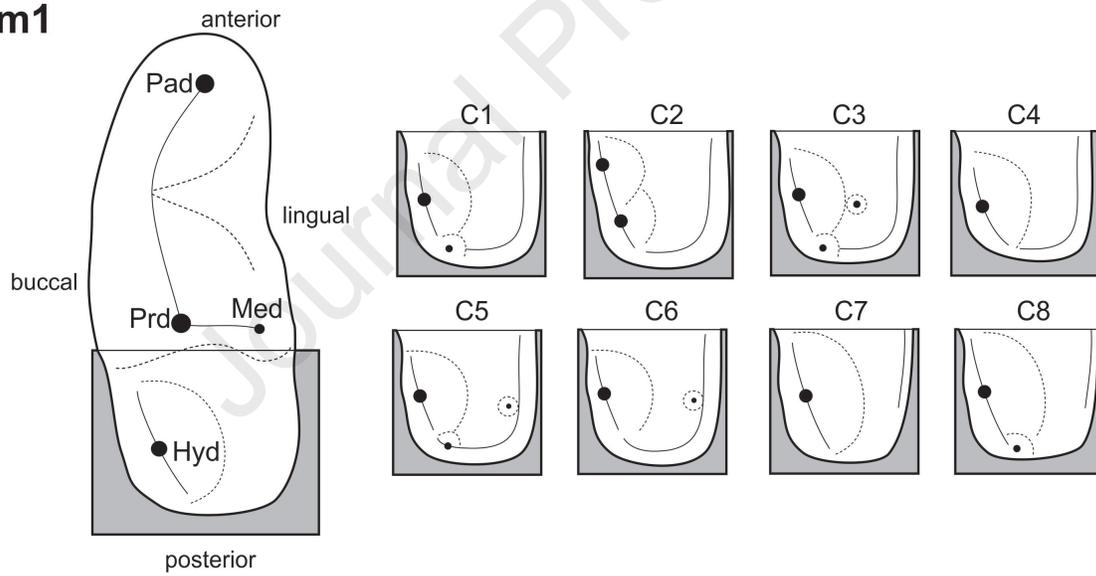
P3

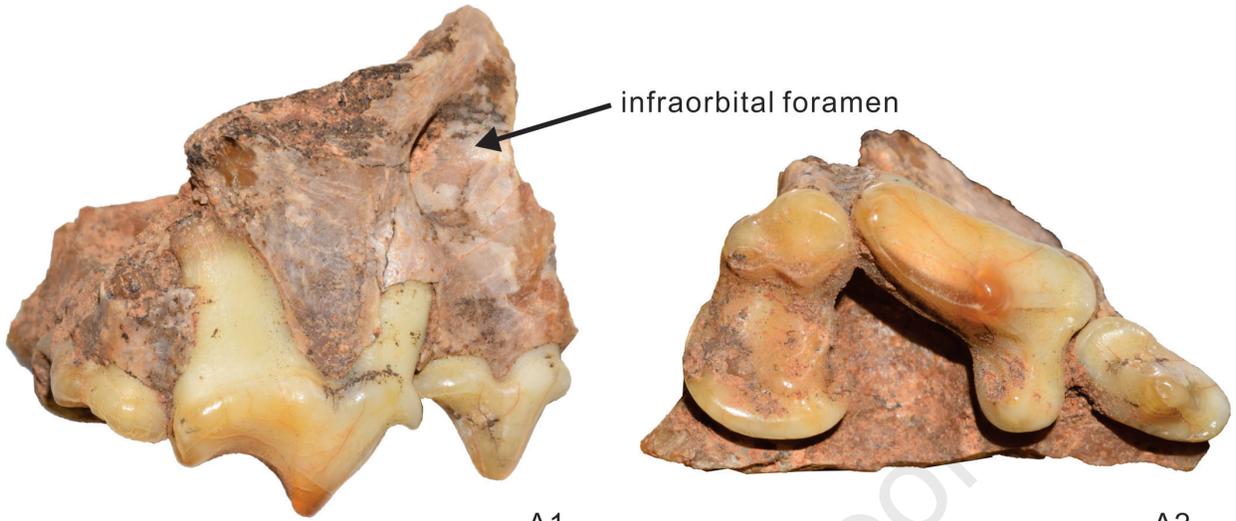


P4



m1



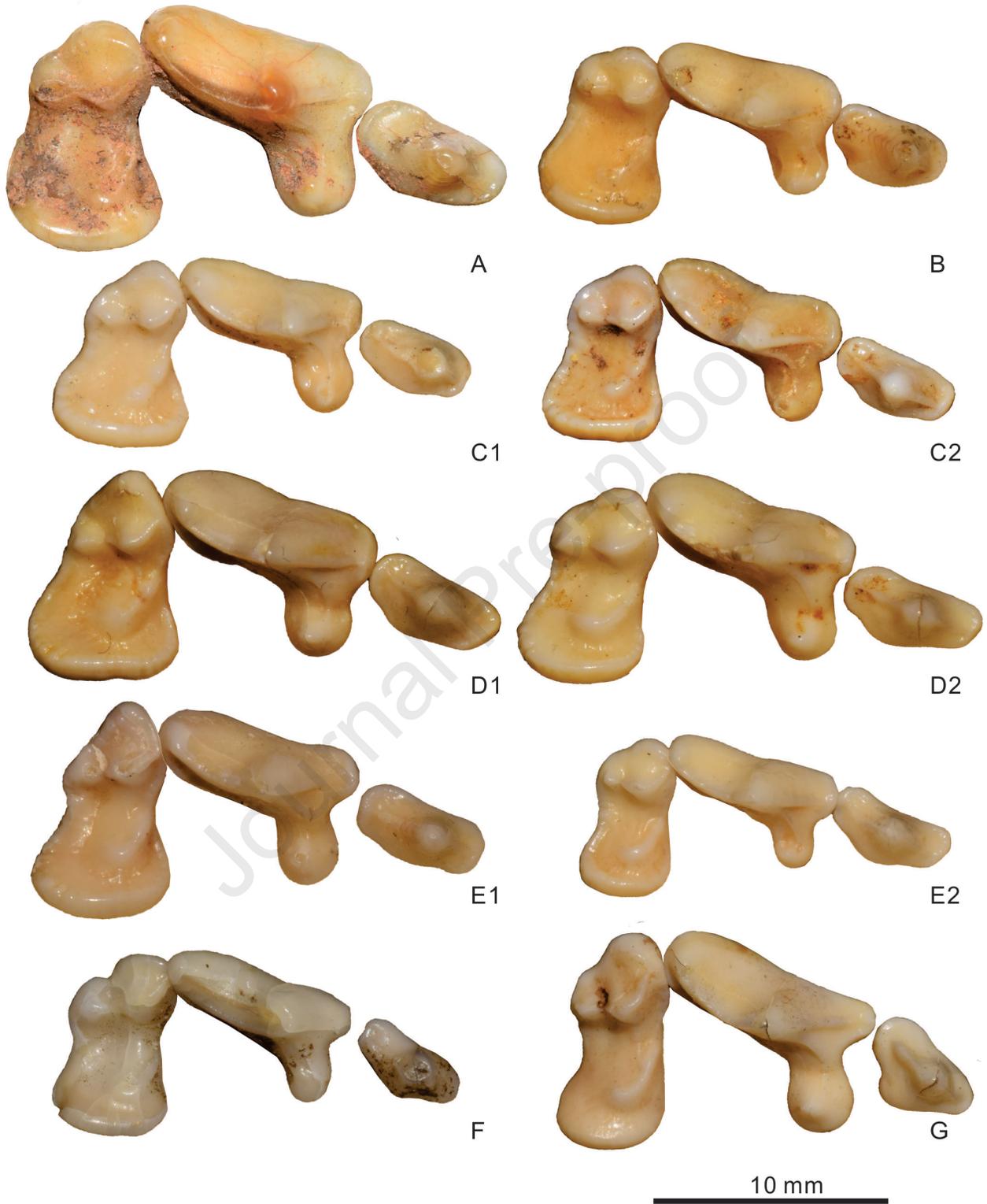


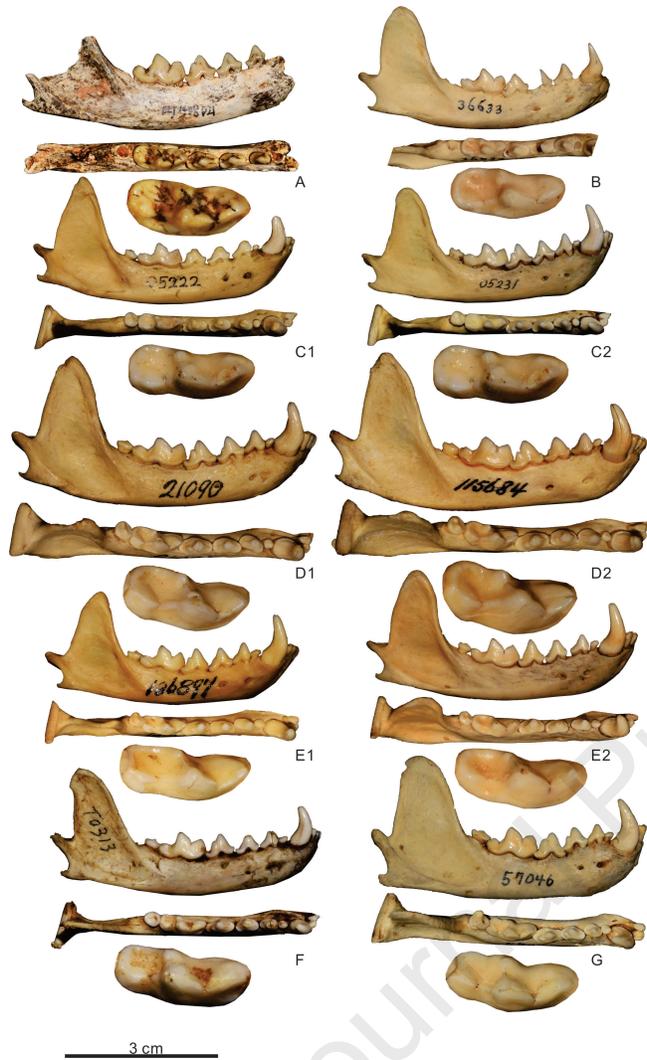
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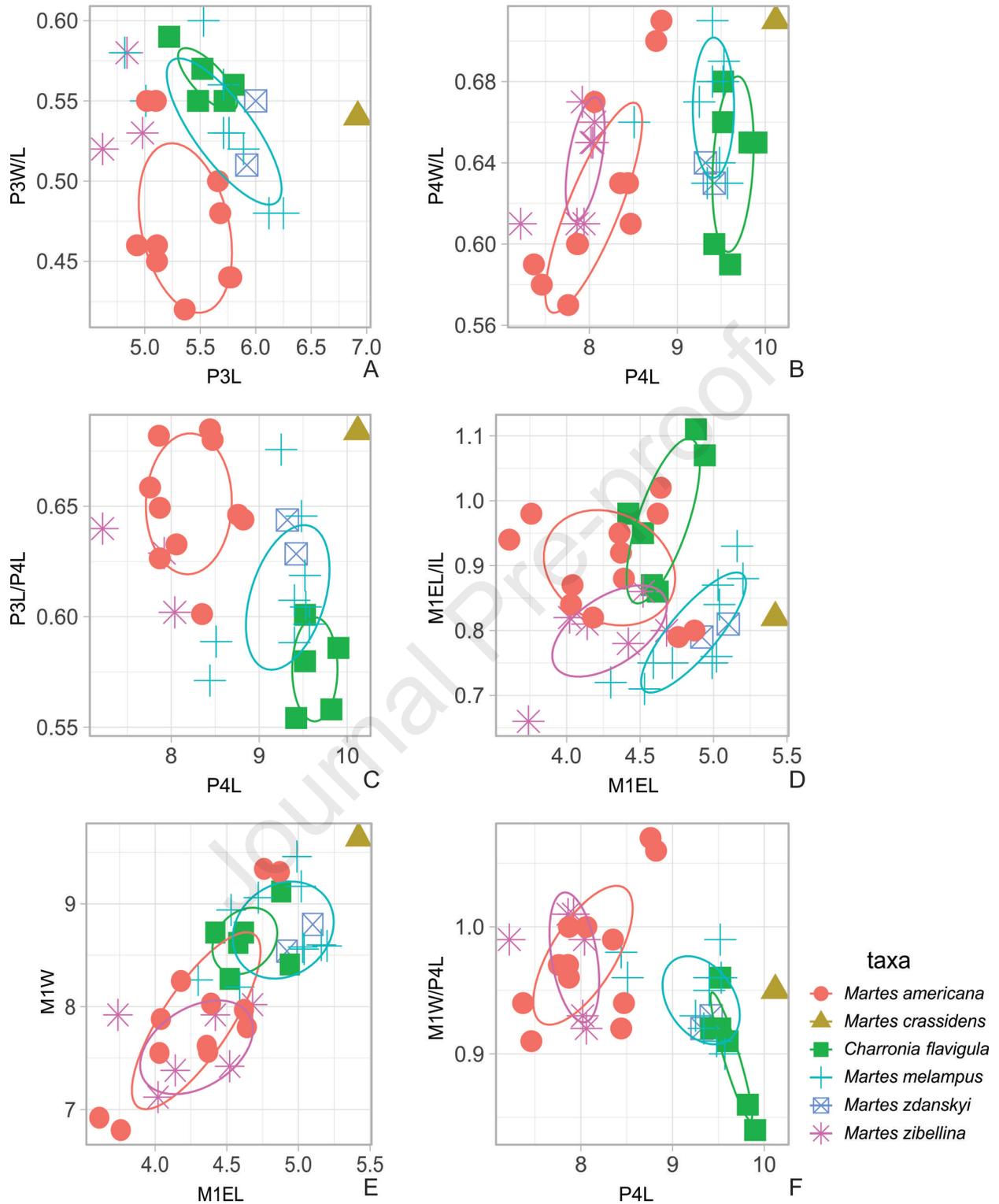


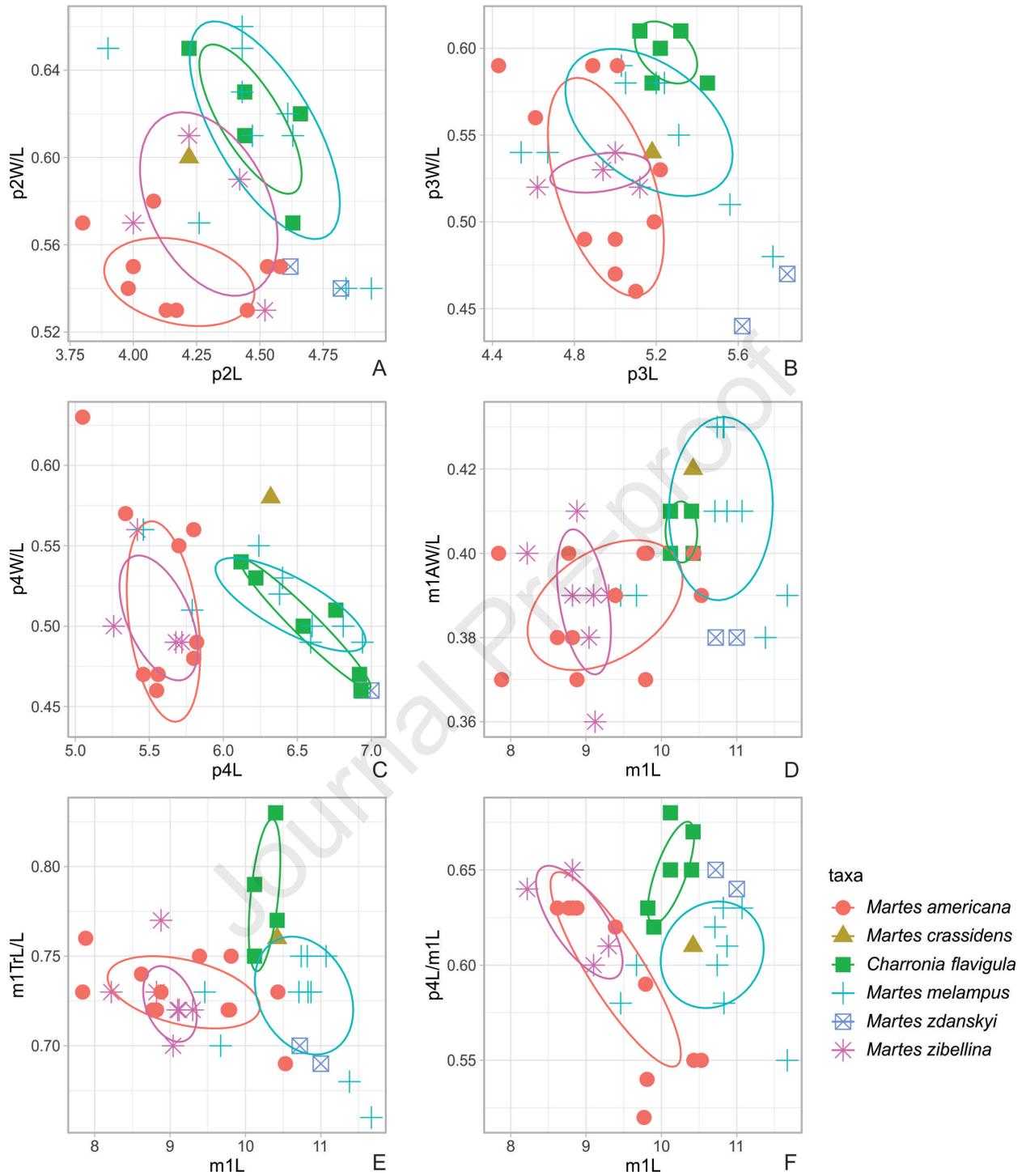
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The authors declare no Conflict of Interest.

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