# First report of leopard fossils from a limestone cave in Kenting area, southern Taiwan

Tzu-Chin Chi [Equal first author, 1, 2], Yi Gan [Equal first author, 3], Tzu-Ruei Yang [Corresp., 1, 3], Chun-Hsiang Chang [Corresp. 1]

1 Department of Geology, National Museum of Natural Science, Taichung, Taiwan

2 Department of Earth and Environmental Sciences, National Chung Cheng University, Chiayi, Taiwan

3 Department of Earth Sciences, National Cheng Kung University, Tainan, Taiwan

Corresponding Authors: Tzu-Ruei Yang, Chun-Hsiang Chang
Email address: tzrueiyang@nmns.edu.tw, cch@nmns.edu.tw

Longshia-dong Cave, a limestone cave located in the Kenting area within the Kenting National Park of southern Taiwan, yields numerous terrestrial mammalian fossils. Many of them were not reported in historical literature and are neither present in Taiwan. For instance, no historical literature mentioned leopards inhabited in Taiwan, and thus their existence remained unknown. This study describes three fossil leopard (*Panthera pardus*) teeth uncovered from Longshia-dong Cave. Two isolated lower premolars and one lower molar, respectively p3, p4 and m1, were discovered in a very small area (11×6 cm) and show a series of progressive increase in size. Thus, the three teeth should have been belonging to the same individual from the subfamily of Pantherinae. Traditional linear measurements and two-dimensional geometric morphometric analysis for the occlusal surface outlines were conducted on the fossil teeth and extant pantherines inhabited in Asia such as clouded leopards (*Neofelis nebulosa*), leopards (*Panthera pardus*), and tigers (*Panthera tigiris*). Results show that the fossil teeth are similar both in size and morphology to the teeth of extant leopards, suggesting the assignment of the fossil teeth to leopards. This study, for the first time, reported the presence of leopards in the Late Pleistocene of Taiwan. Besides, the smaller size of the fossil teeth than Chinese fossil leopards is putatively attributed to insular dwarfism or individual size variability, yet more studies are required.

# First report of leopard fossils from a limestone cave in

# Kenting area, southern Taiwan

Tzu-Chin Chi[1,2], Yi Gan[3], Tzu-Ruei Yang[1,3], Chun-Hsiang Chang[1]

1. Department of Geology, National Museum of Natural Science, 404605 Taichung, Taiwan
2. Department of Earth and Environmental Sciences, National Chung Cheng University, 621301 Chiayi County, Taiwan
3. Department of Earth Sciences, National Cheng Kung University, 701401 Tainan, Taiwan

Corresponding Authors:

Tzu-Ruei Yang

No. 1, Guanqian Rd., North Dist., Taichung City 404605, Taiwan

Email address: tzurueiyang@nmns.edu.tw

Chun-Hsiang Chang

No. 1, Guanqian Rd., North Dist., Taichung City 404605, Taiwan

Email address: cch@nmns.edu.tw; chang28@gmail.com

**Keywords:** Felidae, Morphology, *Panthera pardus*, Late Pleistocene, Geometric morphometric analysis

## Abstract

Longshia-dong Cave, a limestone cave located in the Kenting area within the Kenting National Park of southern Taiwan, yields numerous terrestrial mammalian fossils. Many of them were not reported in historical literature and are neither present in Taiwan. For instance, no historical literature mentioned leopards inhabited in Taiwan, and thus their existence remained unknown. This study describes three fossil leopard (*Panthera pardus*) teeth uncovered from Longshia-dong Cave. Two isolated lower premolars and one lower molar, respectively p3, p4 and m1, were discovered in a very small area (11×6 cm) and show a series of progressive increase in size. Thus, the three teeth should have been belonging to the same individual from the subfamily of Pantherinae. Traditional linear measurements and two-dimensional geometric morphometric analysis for the occlusal surface outlines were conducted on the fossil teeth and extant pantherines inhabited in Asia such as clouded leopards (*Neofelis nebulosa*), leopards (*Panthera pardus*), and tigers (*Panthera tigiris*). Results show that the fossil teeth are similar both in size and morphology to the teeth of extant leopards, suggesting the assignment of the fossil teeth to leopards. This study, for the first time, reported the presence of leopards in the Late Pleistocene of Taiwan. Besides, the smaller size of the fossil teeth than Chinese fossil leopards is putatively attributed to insular dwarfism or individual size variability, yet more studies are required.

## Introduction

Longshia-dong Cave (= Lobster Cave) is located in the Kenting Forest Recreation Area (KFRA) of the Kenting National Park, southernmost Taiwan (Fig. 1). The KFRA is covered with thick limestone (Hengchun Limestone) that deposited during the Middle Pleistocene (Gong &

48  Yui, 1998). A number of caves and fissures formed in the Hengchun Limestone, some of which,

49  such as Longshia-dong Cave, accumulated numerous terrestrial mammal fossils. This cave opens

50  at ca. 240 m above the present sea level and is a small tunnel inclined gently toward its inner part

51  (Kawamura et al., 2016).

52      The investigation of Longshia-dong Cave was initiated by Prof. Yoshinari Kawamura from

53  the Aichi University of Education, Japan and Dr. Chun-Hsiang Chang from the National

54  Museum of Nature Science, Taiwan (Kawamura et al., 2016). To date, fossils of Cervidae,

55  Rodentia (e.g., *Microtus* and *Hystrix*), Carnivora (three teeth; this study), *Macaca* sp., and

56  *Rhinolophus* sp. uncovered from this cave are identified (Kawamura et al., 2016). However, the

57  *Microtus* (Rodentia) is now restricted to high mountains in Taiwan and the *Hystrix* sp.

58  (Rodentia) is no longer present in Taiwan. Besides, leopard teeth were not reported in Taiwan

59  previously. These lines of evidence indicate a very different faunal setting in comparison with

60  the present one.

61      In previous excavations scientists have discovered putative Middle-Late Pleistocene big cat

62  fossils, such as *Panthera* cf. *tigris* and *Panthera* sp. from the Chochen area in southern Taiwan

63  (Fig. 1; Otsuka, 1984; Chen, 2000a; Chen, 2000b; Wei, 2007). Besides, fossil remains of

64  *Panthera tigris* have also been collected from the Penghu Channel, a N-S striking submarine

65  valley off the west coast of Taiwan (Fig. 1) (Ho et al., 1997; Asahara et al., 2015). While both of

66  these studies indicate a rich fossil record of felids in the Middle-Late Pleistocene of Taiwan, the

67  modern Felidae in Taiwan are only featured by two species, including clouded leopard (*Neofelis*

68  *nebulosa*) and leopard cat (*Prionailurus bengalensis*). Even more recently, Chiang et al. (2015)

69  presumed that the former is extinct in Taiwan, thus leaving only the latter present to our

70  knowledge.

71    Previous studies indicated the similarities of Taiwan's fauna to the Early Pleistocene fauna

72    of southern China (e.g., Otsuka & Lin, 1984; Lai, 1989; Qi et al., 1999; Chen, 2000a; Fooden &

73    Wu, 2001). The fauna of southern China probably entered Taiwan in the Late Pliocene to Early

74    Pleistocene, when Taiwan was connected with China (Lai, 1989; Chen, 2000a; Fooden & Wu,

75    2001); however, only clouded leopard was reported in Taiwan's historical record. While

76    Swinhoe (1862) had never seen a living individual, he described it as a small, short-tailed, small-

77    footed animal based on the fur specimen and named it as *Leopardus brachyurus*. Later, Swinhoe

78    (1870) replaced *L. brachyurus* with *Felis macrocelis*, but *L. brachyurus* is still the most

79    commonly used name.

80    In the excavation to Longshia-dong Cave in 2014, three teeth were collected from the same

81    horizon. A preliminary study has indicated their affinity to feline remains, though further

82    investigations are needed (Gan, 2016). This study thus aims to reveal their taxonomic affinity

83    based on traditional linear and geometric measurements. Besides, the comparison between the

84    studied material and leopard fossils from various sites of the Pleistocene in China, including the

85    Zhoukoudian site (Teilhard de Chardin & Pei, 1941) and Mentougou Bull Eye Cave (Deng et al.,

86    1999) of Beijing, Lantian (Gongwangling) of Shanxi (Hu & Qi, 1978), Anyang (Yinxu) of

87    Henan Province (Teilhard de Chardin & Young, 1936), Liucheng Cave of Guangxi Province

88    (Pei, 1987), also allows us to reveal more details.

89    Geological setting

90    The Kenting National Park is located in the Hengchun Peninsula, southernmost Taiwan

91    (Fig. 1). The Hengchun Peninsula represents the earliest stage of the Taiwanese orogeny (Huang

92    et al., 1985), and therefore many incipient thrust faults are observed. A major boundary fault, the

93    N-S striking Hengchun Fault (Fig. 1; Chen et al., 2005), divides the Hengchun Peninsula into

94  two terranes, including the Central Range in the East and the Western Foothills (Hengchun

95  Valley and West Hengchun Hill) in the West (Yen & Wu, 1986). Since the Late Pleistocene, the

96  Hengchun Peninsula was uplifted at a rate of 2-6 mm/yr (Chen et al., 2005) and thus gave rise to

97  the development of coral reef and limestone (Hengchun Limestone). Many karst caves were

98  afterward formed and harbor various fossils. A thin layer of reddish sand and gravels (Hsu, 1989;

99  Hseu et al., 2004) overlying the Hengchun Limestone was named as Eluanpi Bed in the

100  Southeast, or Taiping Formation in the West, to Longshia-dong Cave (Fig. 1).

101      Our studied area, Longshia-dong Cave, is located in the southeastern part of the Kenting

102  National Park, a national park that is featured by the karst landscape mostly contributed by the

103  Hengchun Limestone (Fig. 1). The cave opens to the East, measuring 30~40 m long, 8 m wide,

104  and about 5 m deep, and a puddle was found in the end of the cave (Kawamura et al., 2016).

105  Most of the limestone in the cave is covered by a layer of reddish sediment composed of

106  limestone pebbles and fossils, though the boundary between the reddish sediment and Hengchun

107  Limestone is unclear. A flow stone made of carbonate calcite was found 7 m away from the cave

108  entry, and the fossil-bearing sediments are found behind it. The fossil-bearing sediments are

109  characterized by a mixture of reddish sand and mud, as well as limestone pebbles, which shows a

110  great similarity to the Eluanbi Bed. Besides, a layer of blackish mud and light yellowish-red silt

111  (possibly loess) overlying the fossil-bearing sediments, based on a previous study using $^{14}$C

112  dating, is composed of recent alluvial deposits since the Holocene (Wang, 2015).

113      Since an estimation of the age for the fossil-bearing sediments was inaccessible, previous

114  studies have put emphasis on the age of formation of the Hengchun Limestone, which gave a

115  maximum estimation for the leopard fossils uncovered from the cave. The Hengchun Limestone

116  was either considered two-stage (Gong, 1982) or three-stage (Shih et al., 1989) reef formation,

117    but both studies have concluded a dating result of 500 ka, which is similar to the result arisen

118    from nannofossils (NN19, around 500 ka; Chi, 1982). Besides, another geochemical

119    chronological study has suggested a date of 325-125 ka for the age of formation of the Hengchun

120    Limstone (Gong, 1994).

121        Afterwards, Kawamura et al. (2016) offered the first estimation of the age for the fossil-

122    bearing sediments. Based on stratigraphic relationships, Kawamura et al. (2016) suggested an

123    age of the Late Pleistocene (126 to 12 ka) for the fossil-bearing sediments, which is much older

124    than the 7 ka revealed by $^{14}$C dating of the bone collagen extracted from some ruminant antlers

125    and lower jaws uncovered from the same locality. Because of the rarity and poor-preservation of

126    the leopard remains in this study, a rigorous age of the leopard remains is inaccessible. While the

127    age of the fossils requires further investigations, this study will discuss further details of the

128    leopard remains based on the temporal range from 500 to 12 ka.

129

## Materials & Methods

131        Three well-preserved whitish fossil teeth were collected from Longshia-dong cave in the

132    2014 excursion led by one of the authors (C.-H. Chang). All of them (F056584, F056585, and

133    F056586) are housed at National Museum of Natural Science, Taichung, Taiwan (NMNS) under

134    the accession numbers provided. Before excavation, we used strings to divide the cave ground

135    into a grid contributed by mostly 50×50 cm areas. The three teeth were discovered in a small

136    portion (11×6 cm) out of one of the areas and present a series of progressive increase in size;

137    thus, we believed they should have been belonging to a felid individual (Fig. 2). The felid fossil

138    teeth, based on their shape (Hillson, 2005), are assignable to p3 (F056584), p4 (F056585) and

139    m1 (F056586) from the right mandible (Fig. 2). In addition to the three felid teeth, the skulls and

140    mandibles of 17 extant specimens, including seven clouded leopards (*Neofelis nebulosa*, but one

141    of them might be Sunda clouded leopard (*Neofelis diardi*)), five leopards (*Panthera pardus*), and

142    five tigers (*Panthera tigris*), which are housed at the NMNS, Endemic Species Research

143    Institute, and Taipei Zoo, respectively, were also included in this study (see the details in the

144    Supplemental Tab. 1). Prior to our qualitative studies of the fossil and extant felid teeth

145    (Kawamura, 1992; Fukawa, 2000), we compare their morphological features to determine the

146    assignment of the fossil felid teeth (Fig. 3). Photos of all specimens were taken with a Panasonic

147    Lumix DMC-GF1 camera and a Panasonic Lumix GF1 14-45mm/F3.5-5.6 lens. For the

148    traditional linear measurements and geometric morphometric studies, these photos were

149    afterwards imported into the tpsDig 2.05 (Rohlf, 2005).

150        Traditional linear measurements were taken point-to-point; a total of 22 dental dimensions

151    including antero-posterior crown length (1, 5, 15 in Fig. 4), dorsoventral crown height (3, 7, 10,

152    13, 17, 20 in Fig. 4), width of each cusp (4, 8, 11, 14, 18, 21 in Fig. 4), anteroposterior length of

153    cusps (2, 6, 9, 12, 16, 19 in Fig. 4), and crown height at the place of carnassial notch (22 in Fig.

154    4) (Christiansen, 2008), were obtained from all specimens if accessible (a fossil individual and

155    17 extant specimens, see the details in the Supplemental Tab. 1). The three fossil felid teeth

156    belonged to the right mandible and therefore 22 dental dimensions were obtained. The 17 extant

157    specimens, on the other hand, permit the measurement of both lower right and left jaws, thus

158    contributing to a 17x22x2 data matrix (note that some dental dimensions are not available due to

159    poor preservation, see the details in the Supplemental Tab. 1).

160        The data from the aforementioned traditional linear measurements were introduced into two

161    rounds of principal component analysis (PCA) (Morrison, 1976; Dunteman, 1994), which plots

162    the data to a new coordinate system. The new coordinate system is contributed by N-1 principal

163    components, which are orthogonal to each other (Jolliffe, 2002; Hsu, 2003). All PCA in this

164    study were performed with the R package "stats" (R Core Team, 2013). In the first round of

165    PCA, 22 dental dimensions from the three teeth (p3, p4, and m1) of a mandible (either right or

166    left) are seen as a dataset. Any missing of the 22 dental dimensions from p3, p4, or m1 leads to

167    the removal of the whole dataset from the first round of PCA. Ultimately, one dataset from the

168    felid fossil, ten datasets from the seven clouded leopards, five datasets from the five leopards,

169    and nine datasets from the five tigers, were used in the first round of PCA (Fig. 5a).

170        To avoid the effect of the interspecific difference in tooth size on the first round of PCA, we

171    performed the second round of PCA with the R package "stats" for p3, p4, and m1, separately.

172    For instance, we obtained three ratios, including of protoconid length (2 in Fig. 4 and Tab. 1) to

173    crown length (1 in Fig. 4 and Tab. 1), of protoconid height (3 in Fig. 4 and Tab. 1) to crown

174    length (1 in Fig. 4 and Tab. 1), and protoconid length (2 in Fig. 4 and Tab. 1) to protoconid

175    height (3 in Fig. 4 and Tab. 1) based on the data from all available p3 (a fossil felid, 13 clouded

176    leopards, five leopards, and nine tigers). The three ratios were used for PCA analysis with the

177    package "stats." For PCA analysis (Fig. 5b), on the other hand, six ratios and seven ratios were

178    obtained based on the data from all available p4 and m1, respectively (see the details in Fig. 5)

179    and were analyzed with the package "stats" (Figs. 5c and 5d). Besides, we construct a bivariate

180    plot of the selected numbered dimensions of p3, p4, m1 (1, 4, 5, 11, 15, 21 from Tab. 1) of the

181    fossil and extant leopard specimens with the regression lines for each selected number

182    dimensions (Fig. 6).

183        In addition to the PCA analyses based on traditional linear measurements, we also

184    performed geometric morphometric analysis (Slice, 1996) because of its utility of revealing the

185    morphological differences between different groups (Zelditch et al., 1995) and the ability to

186    exclude the factor of size. All photographs were input into the program tpsUtil for building up a

187    tps file. To access the morphology of the occlusal surface of each tooth in the absence of

188    apparent landmarks, we used the "curve mode" in the program tpsDig 2.05 (accessed on Dec 1,

189    2014 from http://life.bio.sunysb.edu/morph/; (Rohlf, 2005) to place evenly distributed 150 semi-

190    landmarks around the occlusal surface on each photo (Gunz & Mitteroecker, 2013). The 150

191    semi-landmarks were then digitized from photographs using tpsDig 2.05, which converted the

192    points marked on the photographs into Cartesian x, y coordinates. After scaling and alignment of

193    the digitized semi-landmarks using generalized Procrustes analysis, a relative warp analysis

194    (RWA) was then performed on the set of specimen semi-landmarks in tpsRelw (Rohlf, 2007) to

195    unravel the morphological variation between the fossil and extant teeth. We then visualize the

196    morphological variation from RWA by plotting the relative warp axes as a PCA. Relative

197    differences are presented in the form of thin plate spline deformation grids (Figs. 7-9; Zelditch et

198    al., 2004; Tseng et al., 2010).

199

## Results

201    *Description and morphological comparison*

202        Family Felidae Fischer [von Waldheim], (1817)

203        Subfamily Pantherinae Pocock, 1917

204        Genus *Panthera* Oken, 1816

205        *Panthera pardus* (Linnaeus, 1758) (Fig. 2)

206        Based on our observation of all extant felid specimens and previous studies (Gray, 1867;

207    Christiansen & Kitchener, 2011; King, 2012), we concluded the following common dental

208    characters (Fig. 3): (1) two-rooted p3, p4 and m1; (2) p3 is   smaller than p4; (3) p4 is in a

209    similar size to m1; (4) p3, p4 has three cusps (paraconid, protoconid and hypoconid) and its

210   paraconid and hypoconid are well-developed (5) m1 has two well-developed cusps (paraconid

211   and protoconid) and undeveloped talonid. All of the aforementioned features are present in the

212   fossil teeth and thus indicate the assignment of the fossil teeth to Felidae. Moreover, the fossil

213   teeth can be further assigned to Pantherinae based on their similar size to extant pantherines.

214   Pumas (*Puma concolor*), which belong to Felinae, a sister group to Pantherinae, are the only

215   group of felines that present similar dental size; however, their current distribution (only in

216   Americas) makes the attribution of the fossil teeth to puma unlikely.

217       In previous studies (Meachen-Samuels & Van Valkenburgh, 2009), dental size is the only

218   character that was used for distinguishing different pantherines, such as lions (*Panthera leo*),

219   snow leopards (*Panthera uncia*), tigers, clouded leopards, and leopards. For instance, the dental

220   size of lions is significantly larger than the one of the fossil teeth. Moreover, the attribution of

221   the fossil teeth to snow leopards is unlikely since snow leopards are only present in high

222   mountains. However, dental size is not an indicator for the distinguishment between tigers,

223   clouded leopards, and leopards. This study, however, shows that several pantherines, including

224   clouded leopards, leopards, and tigers, can be distinguished based on three dental characters,

225   including (1) the level of p3 paraconid development, (2) the shape of p4 occlusal surface, (3) the

226   size difference between m1 paraconid and m1 protoconid (Fig. 3; Tab. 2).

227       Clouded leopards have two distinct features, including an absent paraconid of p3 (as seen in

228   all examined clouded leopards) and a well-developed protoconid of m1, while both of which are

229   absent in the fossil teeth from Longshia-dong Cave (Fig. 2). Thus, the assignment of the fossil

230   teeth from Longshia-dong Cave to clouded leopards is here excluded. On the other hand, tiger

231   teeth are characterized by a highly developed p4 paraconid, which is not seen in the fossil teeth

232   (Figs. 2, 7). Moreover, the p3 of tigers has a lower paraconid than the one of the fossil (Figs. 2,

233    7). Tigers also present a wider crown in all teeth, especially in m1, than the ones of the fossil

234    (Tab. 2).

235        The fossil pantherine teeth, in addition to their size, show many distinct features that are

236    similar to those of the extant leopards, such as the presence of p3 paraconid and the shape of

237    occlusal surface. The presence of m1 and slightly worn enamel further indicate that the fossil

238    teeth might belong to a very young adult (Stander, 1997). The presence of hollow, not fully

239    developed roots in the fossil teeth further suggests a juvenile origin (about 1~2 years old).

240    However, the gender of the fossil pantherine is uncertain because of the absence of canine teeth

241    (whose size is a key difference between male and female carnivores), the lacking of

242    morphological differences between male and female leopard teeth (Pocock, 1930), and the

243    extremely poor sample size MNI = 1 (minimum number of individuals).

244    *Traditional linear measurement*

245        While our aforementioned morphological comparison indicates the affinity of the fossil

246    teeth to leopards (*Panthera pardus*), traditional linear measurement was performed for further

247    lines of evidence. The result of the first round of PCA based on the 22 dental dimensions shows

248    a significant disparity between tigers and the others (clouded leopards and leopards) (Fig. 5a)

249    (factor loading of each component shows on Supplemental Tab. 3), although the disparity

250    between clouded leopards and leopards is inapparent. In the second round of PCA based on

251    various ratios from the dimensions of p3, p4, and m1, no pattern is indicated by the result of the

252    PCA on p3 (Fig. 5b) and the fossil teeth is not clustered by any group. However, based on the

253    result of PCA on p4 and m1 (Fig. 5c and 5d), the assignment of the fossil teeth to clouded

254    leopards is excluded.

255    While the above PCAs have potentially rules out the affinity of the fossil teeth to leopards,

256    we further conducted a comparison of the selected dental dimensions including 1, 4, 5, 11, 15, 21

257    (Tab. 1) between the fossil and five extant leopard specimens (Fig. 6). The result shows a similar

258    covariation of the p3, p4, and m1 between the fossil and five extant leopard specimens, further supporting

259    our previous inference that the three fossil teeth belonged to the same individual.

260

261    *Geometric morphometric analysis*

262    In addition to the traditional linear measurement (Fig. 5), geometric morphometric analysis

263    was also performed for further lines of evidence. In the RWA based on all third premolars (p3),

264    the first three relative warp axes accounted for 74.81% of the total variation, though no

265    morphological disparities were revealed (Fig. 7). The RWA based on all fourth premolars (p4),

266    however, shows the disparity between clouded leopards and the others in the plots of RW1 to

267    RW2 (Fig. 8a) and RW2 to RW3 (Fig. 8c). The RW2 explains 24.52% of the total shape

268    variance and relates primarily to the prominence of the mesial side toward buccal or lingual side

269    (Fig. 8f). On the other hand, the RWA based on all first molars indicates the isolation of tigers in

270    the plots of RW1 to RW2 (Fig. 9a) and RW2 to RW3 (Fig. 9c). Striking samely, the RW2 in the

271    RWA based on all first molars, which accounts for 22.67% of the total variation, is also the best

272    indicator that excludes tigers.In summary, the fossil pantherine teeth uncovered from Longshia-

273    dong Cave, based on various lines of evidence, are assignable to leopards. While the plot of p3,

274    p4, and m1 sizes of the fossil and extant leopards indicates that only the fossil m1 is

275    encompassed within the variations of the extant leopard teeth, the slope of the regression line

276    based on the three fossil teeth is similar to the ones of those based on the extant specimens. Thus,

277    the three fossil teeth were very likely from a common origin.

278 **Discussion**

279 *An integrative, qualitative method for the identification of leopard teeth*

280    Morphological comparisons have been utilized in many studies for the species identification

281 of various mammalian teeth, such as elephants (Todd, 2010), hedgehogs (Gould, 2001) and

282 moles (Van Cleef-Roders & Van Den Hoek Ostende, 2001). Despite the similarity both in size

283 and morphology of pantherine teeth (lions excluded as their teeth are apparently larger than

284 leopard teeth), several studies offered qualitative methods on the basis of the size and

285 morphology for the identification of the subfamily of Pantherinae (e.g., Hemmer, 1966). On the

286 other hand, canid teeth are much more complex than felid teeth and thus have more homologous

287 features for landmarks. Therefore, Asahara et al. (2015) have applied morphological

288 comparisons in combination with geometric morphometric analyses to canine teeth, which is an

289 integrative method that has never been performed on felid teeth. This study, for the first time,

290 demonstrates that an integration of morphological comparisons, linear measurements, and

291 geometric morphometric studies allows species identification of the subfamily of Pantherinae

292 based on teeth. Based on the integrated approach, we thus assign the studied fossil teeth

293 (F056584, F056585, and F056586) to *Panthera pardus*.

294 *Taphonomic implications for an adult origin of the fossil teeth*

295    A previous study by Stander (1997) suggested that tooth wear in leopards is a reliable

296 indicator for their ages. The eruption of permanent teeth in one to two years old leopards is

297 completed and thus are whitish and wearless. The crown tips are worn in individuals older than

298 three years old, and the tooth wear appears first on incisors, then on canines, on premolars, and

299 finally on molars. The wear is apparent on the teeth of the individuals of five or six years old.

300 Although the fossil teeth in this study only preserve p3, p4, and m1, their complete eruption

301    indicates an age older than one year. Moreover, the slight wear on their crown tips offers further

302    information that the fossil leopard should have been younger than five years old at death.

303    *A behavioral or sedimentary origin?*

304        Extant leopards tend to carry their prey to a safe, isolated location for storage (de Ruiter &

305    Berger, 2000). Many studies, based on field observation, indicated that the leopards in South

306    Africa prefer carrying their prey into their caves, thus contributing to the large number of skeletal

307    remains in many caves in South Africa (Le Roux & Skinner, 1989). In addition to the fossil

308    leopard teeth, many mammalian fossils, such as deers (*Cervus* sp.), macaques (*Macaca* sp.), and

309    hystrixes (*Hystrix* sp.), were also uncovered from Longshia-dong Cave. These mammalian

310    fossils were once considered the kills brought back by leopards. Nevertheless, a previous study

311    pointed out that the deposit in Longshia-dong Cave is a result of multiple reworkings (Wang,

312    2015). The co-occurrence of the mammalian fossils in Longshia-dong Cave probably represents

313    a fossil accumulation over thousands of years.

314        Moreover, leopards left various bite marks on prey's bones (Shi & Wu, 2011; Binford,

315    2014), but Lin (2017) examined fossil bones from Longshia-dong Cave and failed to find any

316    common bite marks. Most deer fossils from the cave are mandibles or limb bones, all of which

317    are unfavorable to leopards (Li, 2007). Thus, we suggest that the accumulation of mammalian

318    fossils in Longshia-dong Cave is very likely a result of multiple reworkings.

319    *A comparison of the fossil teeth from Longshia-dong Cave to Chinese leopard fossils*

320        Leopards are widely distributed throughout Asian and African continents, but only a few of

321    them are currently present on islands such as Java and Sri-Lanka (Pocock, 1932). No written

322    literature in Taiwan has reported the presence of leopards; however, this study reported the first

323    leopard fossils from Longshia-dong Cave and thus suggested the presence of leopards in the Late

324    Pleistocene of Taiwan.

325         Many previous studies suggested a continental origin of Taiwanese mammalian fossils

326    based on various lines of evidence (Otsuka & Lin, 1984; Lai, 1989; Qi et al., 1999; Chen, 2000a;

327    Fooden & Wu, 2001). The Late Pleistocene of China has produced numerous leopard fossils

328    from various sites, including Beijing Mentougou Niuyan Cave (Deng et al., 1999), the first and

329    thirteenth locations of Beijing Zhoukoudian Site (Pei, 1934), Shaanxi Lantian Gongwangling

330    Site (Hu & Qi, 1978), Anyang Yinxu Site (Teilhard de Chardin & Young, 1936), and Guangxi

331    Liucheng Cave (Pei, 1987) (Fig. 10). Among these reports, Deng et al. (1999) claimed that the

332    two lower first molars of the three fossil leopard teeth uncovered from Mentougou Niuyan Cave

333    are the smallest (19.3×9.2 mm and 19.5×8.5 mm) in comparison with the other Chinese fossil

334    leopard teeth. The size of the fossil teeth in our study (16.77×7.95 mm; Tab. 3), however, are

335    much smaller than the teeth reported in Deng et al. (1999). The smaller dental size can be

336    explained by three hypotheses: (1) ontogenetic variation, (2) individual size variability, and (3)

337    insular dwarfism. The first hypothesis is here precluded as both of our specimen and the

338    Mentougou Niuyan Cave specimen are permanent teeth. The second hypothesis is currently a

339    working hypothesis in the presence of only one fossil specimen. Despite the uncertainty arisen

340    from the poor sample size (N=1), the third hypothesis is an interesting explanation. Meiri et al.

341    (2005) indicated that the m1 size in carnivores randomly varies in different habitats, albeit not

342    regularly and predictably with either area or isolation. They concluded three selective forces,

343    including resource limitation, predation, and interspecific competition. Our study area, Kenting

344    National Park, has produced less various fossils than all aforementioned Chinese sites,

345    suggesting a habitat with fewer resources for carnivores. Besides, the leopard described in this

346    study is the only carnivores found in Kenting National Park to date, potentially indicating lower

347    predation pressure by other carnivores and the absence of interspecific competition. While the

348    absence of interspecific competition would have resulted in gigantism, both of the fewer

349    resources and lower predation pressure possibly contributed to the smaller size of Taiwanese

350    leopards than Chinese leopards. Yet, more specimens are required for further studies and will

351    help illuminate the smaller dental size of the Longshia-dong Cave specimen

352

## Conclusions

354        Leopards are a group of carnivores widely distributed throughout Asian and African

355    continents, yet they are no longer found in eastern Asia due to civilization. Fossils thus represent

356    the only clue indicating prehistoric leopards. While their teeth are significantly smaller than the

357    other leopard teeth compared and thus are easily identified, poorly preserved fossils hinder

358    further investigations. This study, based on an integration of morphological and geometric

359    morphometric analyses, reveals the assignment of the fossil teeth excavated from Longshia-dong

360    Cave to *Panthera pardus*, which is currently absent on Taiwan Island and suggests the presence

361    of leopards in the Late Pleistocene of Taiwan. Such a record of prehistoric leopards in Taiwan

362    thus adds up to the carnivore biodiversity of Taiwan. However, whether the *Panthera* individual

363    is aboriginal or migrated is still uncertain. Our study also found that the teeth from Longshia-

364    dong Cave belonged to a smaller individual in comparison with the fossil record from China

365    indicates the smaller size of Taiwanese leopard fossil teeth than Chinese ones. Such a smaller

366    dental size was possibly a result of individual size variability or insular dwarfism. To conclude,

367    the discovery of the leopard fossil in Taiwan opens shed some light on the origin of the Kenting

368    Fauna. Nevertheless, the insular dwarfism of, and the migration history of, the prehistoric

369    leopards in Taiwan are still speculations and thus require more specimens and studies.

370

## Acknowledgements

372        The authors would like to thank Y.- J. Chen of NMNS, S.-W. Chang of the Endemic

373    Species Research Institute, and T.-C. Chan of Taipei Zoo for their assistance in accessing the

374    specimens. We are also grateful to P.-J. Chiang for his helpful comments and J. Chen for her

375    help on illustrations. Two anonymous reviewers and Martin Sabol have helped improve this

376    study with their constrictive comments. Appreciation also goes to all members of the Taiwan-

377    Japan joint excursion in 2014. We also thank K.-C. Wang and T.-Y. Hsiao for their assistance in

378    the excursion. We also thank J.-S. Chi for proofreading. This study was supported by the grants

379    of the Ministry of Science and Technology (MOST), Taiwan (102-2116-M-178-004- to C.-H.

380    Chang and 108-2116-M-178-003-MY2 and 110-2116-M-178-002 to T.-R. Yang).

381

## References

383    Asahara M, Chang C-H, Kimura J, Son NT, and Takai M. 2015. Re-examination of the fossil

384        raccoon dog (*Nyctereutes procyonoides*) from the Penghu channel, Taiwan, and an age

385        estimation of the Penghu fauna. *Anthropological Science* 123:177-184.

386        doi:10.1537/ase.150710

387    Binford LR. 2014. *Bones: Ancient Men and Modern Myths*. Academic press, New York. 320 p.

388    Chen K-T. 2000a. On Taiwan mammalian faunas in different periods of time and related

389        problems: The background materials for Taiwan zooarchaeological studies, part 1.

390        *Bulletin of the Institute of History and Philology Academia Sinica* 71:129-198. doi:

391            10.6355/BIHPAS.200003.0129

392    Chen K-T. 2000b. On Taiwan mammalian faunas in different periods of time and related

393            problems: The background materials for Taiwan zooarchaeological studies, part 2.

394            *Bulletin of the Institute of History and Philology Academia Sinica* 71:367-457. doi:

395            10.6355/BIHPAS.200006.0367

396    Chen W-S, Lee W-C, Huang N-W, Yen I-C, Yang C-C, Yang H-C, Chen Y-C, and Sung S-H.

397            2005. Characteristics of accretionary prism of Hengchun Peninsula, southern Taiwan:

398            Holocene activity of the Hengchun fault. *Western Pacific Earth Sciences* 5:129-154. (in

399            Chinese with English abstract)

400    Chi W-R. 1982. The calcareous nannofossils of the Lichi Melange and the Kenting Melange and

401            their significance in the interpretation of plate-tectonics of the Taiwan region. *Ti-Chih*

402            *(Geology)* 4:99-114. (in Chinese with English abstract)

403    Chiang P-J, Pei KJ-C, Vaughan MR, Li C-F, Chen M-T, Liu J-N, Lin C-Y, Lin L-K, and Lai Y-

404            C. 2015. Is the clouded leopard *Neofelis nebulosa* extinct in Taiwan, and could it be

405            reintroduced? An assessment of prey and habitat. *Oryx* 49:261-269. doi:

406            10.1017/S003060531300063X

407    Choe RS, Han KS, Kim SC, U C, Ho CU, and Kang I. 2020. Late Pleistocene fauna from

408            Chongphadae Cave, Hwangju County, Democratic People's Republic of Korea.

409            *Quaternary Research* 97:42-54. doi: doi.org/10.1017/qua.2020.9

410    Christiansen P. 2008. Species distinction and evolutionary differences in the clouded leopard

411            (*Neofelis nebulosa*) and Diard's clouded leopard (*Neofelis diardi*). *Journal of*

412            *Mammalogy* 89:1435-1446. doi:10.1644/08-MAMM-A-013.1

413 Christiansen P, and Kitchener AC. 2011. A neotype of the clouded leopard (*Neofelis nebulosa*

414    Griffith 1821). *Mammalian Biology* 76:325-331. doi:10.1016/j.mambio.2010.05.002

415 de Ruiter DJ, and Berger LR. 2000. Leopards as taphonomic agents in dolomitic caves—

416    implications for bone accumulations in the hominid-bearing deposits of South Africa.

417    *Journal of Archaeological Science* 27:665-684. doi:10.1006/jasc.1999.0470

418 Deng T Huang W, and Wang H. 1999. The Late Pleistocene mammalian fossils from Niuyan

419    Cave in Mentougou, Beijing, China. *Vertebrata Palasiatica* 37:156-164.

420 Dunteman GH. 1994. *Principal Component Analysis (PCA)*. Sage Publications, Newbury Park.

421    96 p.

422 Fischer von Waldheim G. 1817. Adversaria zoologica. *Mémoires de la Société Imperiale des

423    Naturalistes de Moscou* 5:368-428.

424 Fooden J, and Wu H-Y. 2001. Systematic review of the Taiwanese Macaque, *Macaca cyclopis

425    Swinhoe, 1863. *Fieldiana Zoology* 98: 1-70.

426 Fukawa M. 2000. *Research Methods for Fossils*. Kyoritsu Shuppan, Tokyo. 388 p.(in Japanese)

427 Gan Y. 2016. Study the Late Pleistocene cat (Carnivora, Felidae) fossils from a limestone cave

428    within Kenting Area, southern Taiwan. Master Thesis. Department of Earth Sciences,

429    National Cheng Kung University Tainan. 107 p.

430 Gong S-Y. 1982. Study stratigraphic and paleoenvironmental of Hengchun Limestone. Master

431    Thesis. Department of Geology, National Taiwan University, Taipei. 60 p.

432 Gong S-Y. 1994. Pleistocene carbonate deposition in the Kueitzechiao-Oluanpi area, Hengchun,

433    Taiwan: A preliminary study. *Journal of Geological Society of China* 37:165-188

434 Gong S-Y, and Yui T-F. 1998. Meteoric diagenesis and stable isotopic compositions of the

435    Hengchun Limestone, southern Taiwan. *Journal of Geological Society of China* 41:1-24.

436    Gould GC. 2001. The phylogenetic resolving power of discrete dental morphology among extant

437       hedgehogs and the implications for their fossil record. *American Museum Novitates*

438       3340:1-52. doi:10.1206/0003-0082(2001)340<0001:TPRPOD>2.0.CO;2

439    Gray JE. 1867. Notes on the skulls of the cats (Felidae). *Proceedings of the Zoological Society of*

440       *London* 1867:258-277. doi:10.1111/j.1469-7998.1867.tb00432.x

441    Gunz P, and Mitteroecker P. 2013. Semilandmarks: a method for quantifying curves and surfaces. *Hystrix*

442    24:103-109. doi:10.4404/hystrix-24.1-6292

443

444    Hemmer H. 1966. Untersuchungen zur Stammesgeschichte der Pantherkatzen (Pantherinae). Teil

445       I. *Veröffentlichungen der Zoologischen Staatssammlung München* 11:1–121. (in German)

446    Hillson S. 2005. *Teeth*: Cambridge University Press, Cambridge. 373 p.

447    Ho C-K, Qi G-Q, and Chang C-H. 1997. A preliminary study of Late Pleistocene Carnivore

448       fossiIs from the Penghu Channel, Taiwan. *Journal of the National Taiwan Museum*

449       40:195-224. doi:10.6548/ATMB.199712_40.0007

450    Hseu Z-Y, Wang H-H, Wu S-H, and Chang I-S. 2004. Pedogenesis and classification of soils in

451       the Kenting uplifted coral reef nature reserve, Southern Taiwan. *Taiwan Journal of*

452       *Forest Science* 19:153-164.

453    Hsu C-C. 2003. Geomorphometric study of *Octopus* and *Cistopus* (Cephalopoda: Octopodidae)

454       based on landmarks of beaks. Master Thesis. National Sun Yat-sen University. 66 p.

455    Hsu M-Y. 1989. A geomorphological study of marine terraces in Taiwan. PhD Thesis.

456       Department of Geography, Chinese Culture University, Taipei. 178 p.

457    Hu C, and Qi T.. 1978. Gongwangling Pleistocene mammalian fauna of Lantian, Shaanxi.

458       *Palaeontologica Sinica ser. C* 21:1-64. (in Chinese with English abstract)

459  Huang C-Y, Cheng Y, and Jeh C. 1985. Genesis of the Kenting Formation in the Hengchun

460      Peninsula, southern Taiwan. *Ti-Chih (Geology)* 6:21-38. (in Chinese with English

461      abstract)

462  Jin C, Zheng J, Wang Y, Xu Q. 2008. The stratigraphic distribution and zoogeography of the

463      early pleistocene mammalian fauna from south China. *Acta Anthropologica Sinica*

464      27:304-317. (in Chinese with English abstract)

465  Jolliffe IT. 2002. *Principal Component Analysis.* Springer series in statistics 29. 488 p.

466  Kawamura A, Chang C-H, and Kawamura Y. 2016. Middle Pleistocene to Holocene mammal

467      faunas of the Ryukyu Islands and Taiwan: An updated review incorporating results of

468      recent research. *Quaternary international* 397:117-135. doi:10.1016/j.quaint.2015.06.044

469  Kawamura Y. 1992. Collecting technique and storage system for micro-mammalian fossils.

470      *Honyurui Kagaku (Mammalian Science)* 31:99-104.

471  King LM. 2012. Phylogeny of *Panthera,* including *P. atrox*, based on cranialmandibular

472      characters. Master Thesis. East Tennessee State University, Johnson City. 160 p.

473  Lai K-Y. 1989. The fossil record of mammals in Taiwan. Monograph of the Symposium on the

474      Geographical Origin of the Fauna of Taiwan. Taipei. p 26-49.

475  Le Roux P, and Skinner J. 1989. A note on the ecology of the leopard (*Panthera pardus*

476      Linnaeus) in the Londolozi Game Reserve, South Africa. *African Journal of Ecology*

477      27:167-171. doi:10.1111/j.1365-2028.1989.tb00940.xLi Q. 2007. Fauna analysis of

478      Zhoukoudian Tianyuan Cave human fossil site. Master Thesis. Institute of Vertebrate

479      Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing. 66 p.

480  Li X, and Deng K. 2003. Early Pleistocene carnivore fossils from Zhen'an, Shaanxi, China.

481      *Journal of Northwest University (Natural Science Edition)* 33:455-459. (in Chinese with

482      English abstract)

483    Li Y, Pei S, Tong H, Yang X, Cai Y, Liu W, and Wu X. 2013. A preliminary report on the 2011

484        excavation at Houbeishan Fuyan Cave, Daoxian, Hunan Province. *Acta Anthropologica*

485        *Sinica* 32:133-143. (in Chinese with English abstract)

486    Lin C-Y. 2017. Study on fossil deer in a limestone cave from the Late Pleistocene of Kenting

487        area, southern Taiwan. Master Thesis. Department of Life Sciences, Tunghai University,

488        Taichung. 224 p.

489    Linnaeus C. 1758. *Systema naturae*: Stockholm Laurentii Salvii.

490    Meachen-Samuels J, and Van Valkenburgh B. 2009. Craniodental indicators of prey size

491        preference in the Felidae. *Biological Journal of the Linnean Society* 96:784-799.

492        doi:10.1111/j.1095-8312.2008.01169.x

493    Meiri S, Dayan T, and Simberloff D. 2005. Area, isolation and body size evolution in insular

494        carnivores. *Ecology Letters* 8:1211-1217. doi:10.1111/j.1461-0248.2005.00825.x

495    Morrison D. 1976. The structure of multivariate observations: I. Principal components.

496        *Multivariate Statistical Methods* 2:266-301.

497    Oken, L. 1816. Okens Lehrbuch der Naturgeschichte. Dritter Theil. Zoologie. Mit viezig

498        Kupfertafeln. Zweite Abtheilung. Fleischthiere. August Schmid und Comp., Jena. 1270 p.

499    Otsuka H. 1984. Stratigraphic position of the Chochen vertebrate fauna of the Toukoushan

500        Group in the environs of the Chochen District, Southwest Taiwan, with special reference

501        to its geologic age. *Quarterly Journal of the Taiwan Museum* 37:37-55.

502        doi:10.6532/JTM.198406_37(1).0002

503    Otsuka H, and Lin C-C. 1984. Fossil rhinoceros from the Toukoushan Group in Taiwan. *Journal*

504        *of Taiwan Museum* 37:1-35.

505    Pei W. 1934. On the Carnivora from locality 1 of Choukoutien. *Paleontologia Sinica ser. C*

506        8:76-80. (in Chinese with English abstract)

507    Pei W. 1987. Carnivora, Proboscidea and Rodentia from Liucheng *Gigantopithecus* cave and

508        other caves in Guangxi. *Memoirs of Institute of Vertebrate Paleontology and*

509        *Paleoanthropology, Academia Sinica* 18:5-134.

510    Pocock R. 1917. XL.—The classification of existing Felidae. *Journal of Natural History*. p 329-

511        350. doi:10.1080/00222931709487018

512    Pocock R. 1930. The panthers and ounces of Asia. Volume II. *Journal of Bombay Natural*

513        *History Society* 34: 329-336.

514    Pocock R. 1932. The leopards of Africa. *Proceedings of the Zoological Society of London*

515        26:543-591. doi:10.1111/j.1096-3642.1932.tb01085.x

516    Qi G-Q, Ho C-K, and Chang C-H. 1999. The Pleistocene fossil suids from Chochen, Tainan,

517        southwestern Taiwan. *Collection and Research* 12:33-40.

518    R Core Team. 2013. A language and environment for statistical computing. R Foundation for

519        Statistical Computing. Vienna, Austria.

520    Rohlf FJ. 2005. tpsDig, digitize landmarks and outlines, version 2.05. *Department of Ecology*

521        *and Evolution, State University of New York at Stony Brook.*

522    Rohlf FJ. 2007. tpsRelw version 1.45. *Department of Ecology and Evolution, State University of*

523        *New York, Stony Brook.*

524    Shi M, and Wu X. 2011. The microscratch trace of animal bone surface and human behavior

525        study of Kua Hu Qiao Site in Xiaoshan District, Zhejiang Province. *Quaternary Sciences*

526        31:723-729.

527    Shih T-T, Tsai W-T, Hsu M-Y, Mezaki S, and Koba M. 1989. The study of ages and terraces of

528        coral reef in the Kenting National Park Area. Conservation Research Report of the

529        Kenting National Park Headquarters, Construction and Planning Agency, Ministry of the

530        Interior. 58 p.

531    Slice DE. 1996. Introduction to landmark methods. in (eds.) Marcus LF, Corti M, Loy A, Naylor

532        GJP, Slice DE. *Advances in Morphometrics*: Springer, Boston. pp. 113-115.

533        doi:10.1007/978-1-4757-9083-2_10

534    Stander P. 1997. Field age determination of leopards by tooth wear. *African Journal of Ecology*

535        35:156-161. doi:10.1111/j.1365-2028.1997.068-89068.x

536    Suzuki H. 1966. Skeletal remains of Hamakita Man. *Journal of the Anthropological Society of*

537        *Nippon* 74:172–174. (In Japanese)

538    Swinhoe R. 1862. On the Mammals of the island of Formosa (China). *Proceedings of the*

539        *Zoological Society of London* 30:347-368. doi:10.1111/j.1469-7998.1862.tb06539.x

540    Swinhoe R. 1870. Catalogue of the mammals of China (south of the Yangtsze) and of the island

541        of Formosa. *Proceedings of Zoological Society of London* 22:615-653.

542    Teilhard de Chardin PT, and Pei W. 1941. The fossil mammals from Locality 13 of

543        Choukoutien. *Palaeontologica Sinica ser. C* 11:1-106.

544    Teilhard de Chardin PT, and Young C. 1936. On the mammalian remains from the

545        archaeological Site of Anyang. *Palaeontologica Sinica ser. C* 12:1-78.Todd NE. 2010.

546        New phylogenetic analysis of the family Elephantidae based on cranial-dental

547        morphology. *Anatomical Record (Hoboken)* 293:74-90. doi:10.1002/ar.21010

548    Tseng JZ, Wen H, and Chen S-Q. 2010. Geometric morphometrcs analysis of cranial shape

549        among late Miocene hyaenid ecomorphologies in the Linxia Basin, Gansu, China.

550        *Vertebrata Palasiatica* 48:235-246.

551    Van Cleef-Roders JT, and van den Hoek Ostende LW. 2001. Dental morphology of *Talpa*

552        *europaea* and *Talpa occidentalis* (Mammalia: Insectivora) with a discussion of fossil

553        Talpa in the Pleistocene of Europe. *Zoologische Mededelingen* 75:51-68.

554    Wang J, Chen J, Chen Q, and Lu T. 1990. The discovery and exploitation of the resources of

555        animal fossils in Panlongdong Cave, Yunfu County, Guangdong Province. *Tropical*

556        *Geography* 10:333-339. (in Chinese with English abstract)

557    Wang K-C. 2015. Rodent fossils from late Quaternary limestone cave in Kenting area, southern

558        Taiwan. Master Thesis. Department of Earth Sciences, National Cheng Kung University,

559        Tainan. 174 p.

560    Wang L, Lin Y, Chang S, and Yuan J. 1982. Mammalian fossils found in northwest part of Huan

561        Province and their significance. *Vertebrata Palasiatica* 4:350-358. (in Chinese with

562        English abstract)

563    Wei K-Y. 2007. Quaternary mammalian fossils of Taiwan: an eclectic overview and prospects

564        for future study. in (ed.) Wei K-Y. Studies on the Quaternary Geology of Taiwan:

565        Overview and Prospect. *Special Publication of the Central Geological Survey* 18:261-

566        286.

567    Wu X, Deng X, and Zheng L. 2008. Late Pleistocene fauna at Yang'er Cave in Hunan Province.

568        *Quaternary Sciences* 28: 1114-1128. (in Chinese with English abstract)

569    Wu X, Pei S, Wu X, Qu S, Chen M, Hu Q, and Liu W. 2009. A preliminary study of the Bailong

570        Cave paleoanthropological site in Yunxi County, Hubei Province. *Acta Anthropologica*

571        *Sinica* 28:1-15. (in Chinese with English abstract)

572    Xu C, Zhang Y, Chen C, and Fang D. 1984. Human occipital bone and mammalian fossils from

573        Chaoxian, Anhui. *Acta Anthropologica Sinica* 3:202-301. (in Chinese with English

574        abstract)

575    Yen T-P, and Wu C-Y. 1986. The Pliocene and younger formations in the southern part of the

576        Hengchun Peninsula. *Ti-Chih (Geology)* 7:1-10. (in Chinese with English abstract)

577    You Y, and Qi G. 1973. New materials of Pleistocene mammals in Yuanmou, Yunnan.

578        *Vertebrata Palasiatica* 11:66-80. (in Chinese with English abstract)

579    Young C. 1935. Note on a mammalian microfauna from Yenchingkou near Wanhsien, Szechuan.

580        *Bulletin of the Geological Society of China* 14:247-248. (in Chinese with English

581        abstract)Zelditch ML, Fink WL, and Swiderski DL. 1995. Morphometrics, homology,

582        and phylogenetics: quantified characters as synapomorphies. *Systematic Biology* 44:179-

583        189. doi:10.2307/2413705

584    Zelditch ML, Lundrigan BL, and Garland Jr T. 2004. Developmental regulation of skull

585        morphology. I. Ontogenetic dynamics of variance. *Evolution & Development* 6:194-206.

586        doi:10.1111/j.1525-142X.2004.04025.x

587    Zhang Y, Long Y, Ji H, and Ding S. 1989. The Cenozoic deposits of the Yunnan region.

588        *Professional Papers on Stratigraphy and Paleontology* 7:1-21. (in Chinese)

589    Zhao L, Zhang L, Xu C, Wang X, and Cai H. 2013. New discovered Early Pleistocene mammal

590        fossils and bone artifact in Hezhang of Guizhou Plateau. *Acta Anthropologica Sinica*

591        32:477-484. (in Chinese with English abstract)

592    Zhao L, Zhang L, Du B, Nian X, Zheng Y, Zhang Z, Wang C, Wang X, and Cai H. 2016. New

593        discovery of human fossils and associated mammal fauna from Mawokou Cave in Bijie,

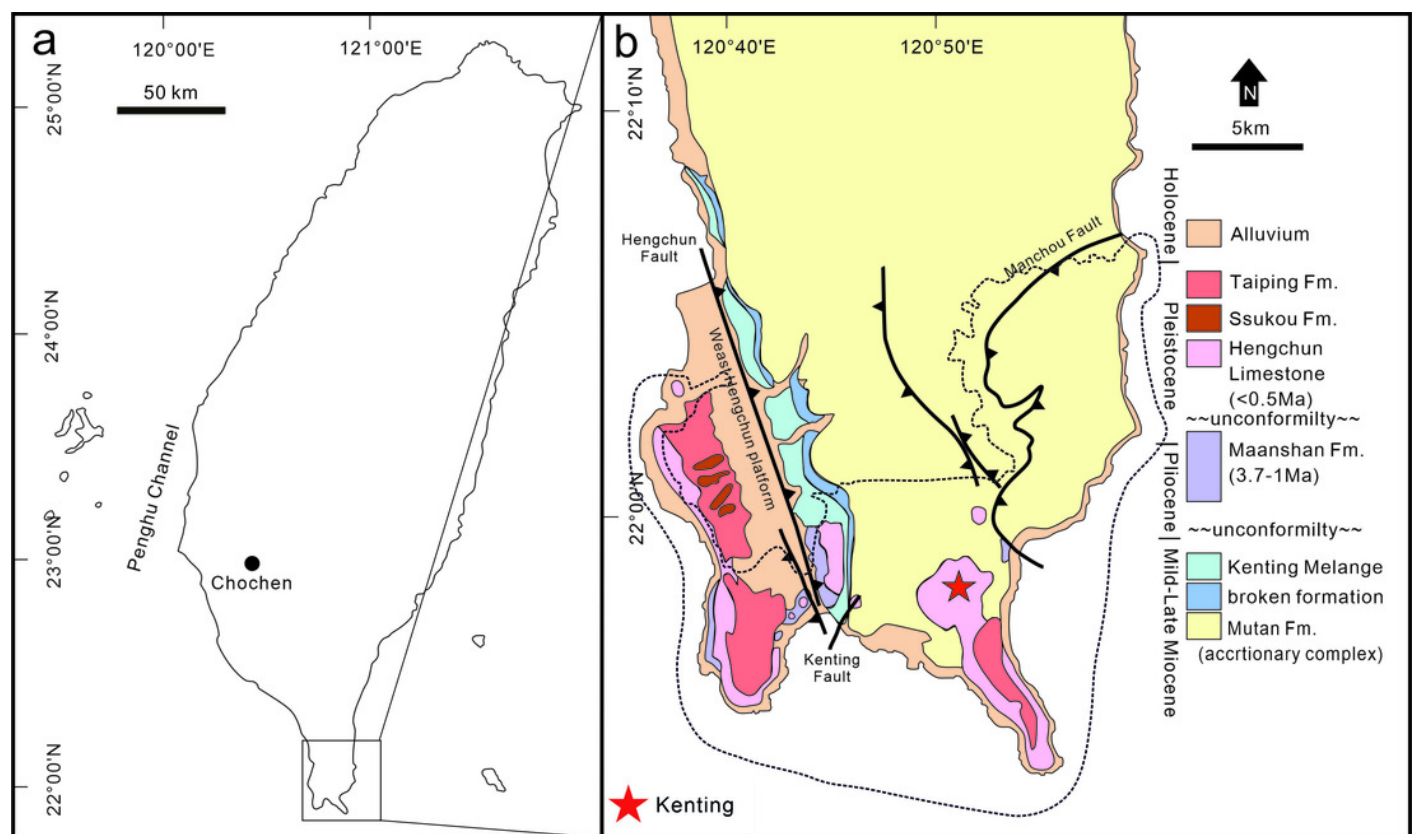
594        Guizhou Province of southern China. *Acta Anthropologica Sinica* 35:24-35. (in Chinese

595        with English abstract)

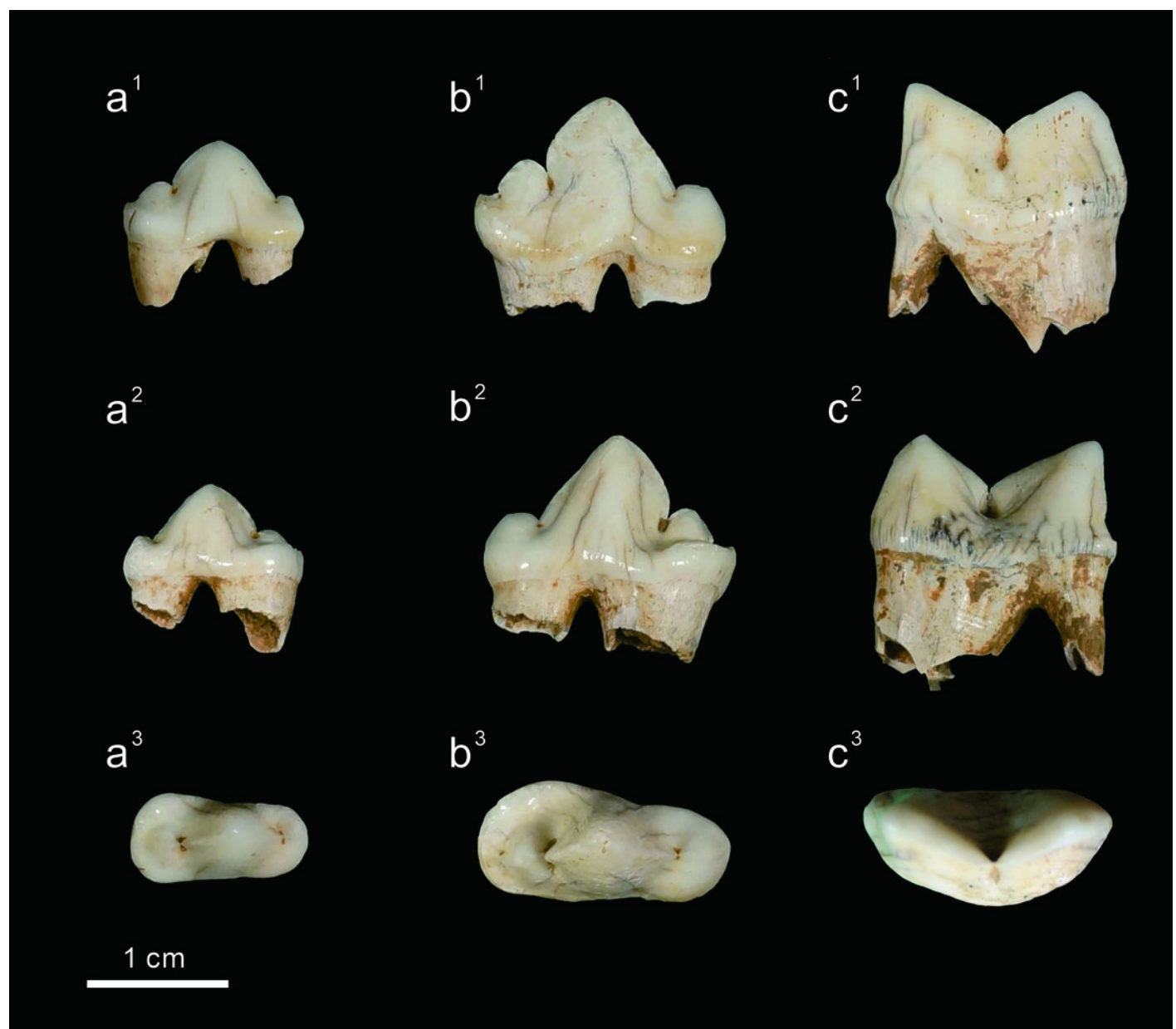
596

# Figure 1

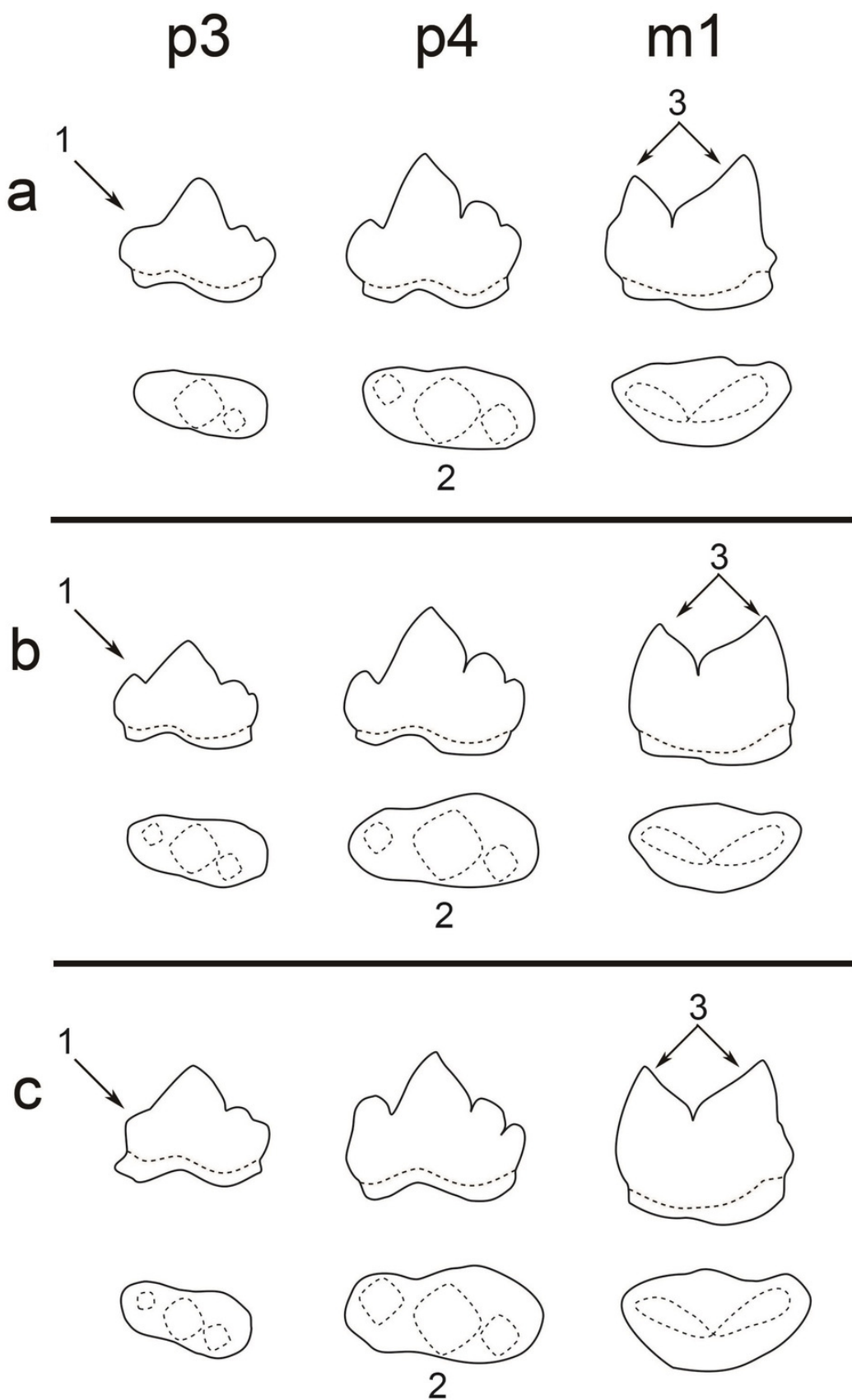
Location and geological map of the discovery site of the leopard fossils in Taiwan

A map of Taiwan shows the location of the Kenting National Park (a), and a geological map of southernmost Taiwan is presented in (b). The location of the discovery site, Longshia-dong Cave, is indicated by a red star in (b).

# Figure 2

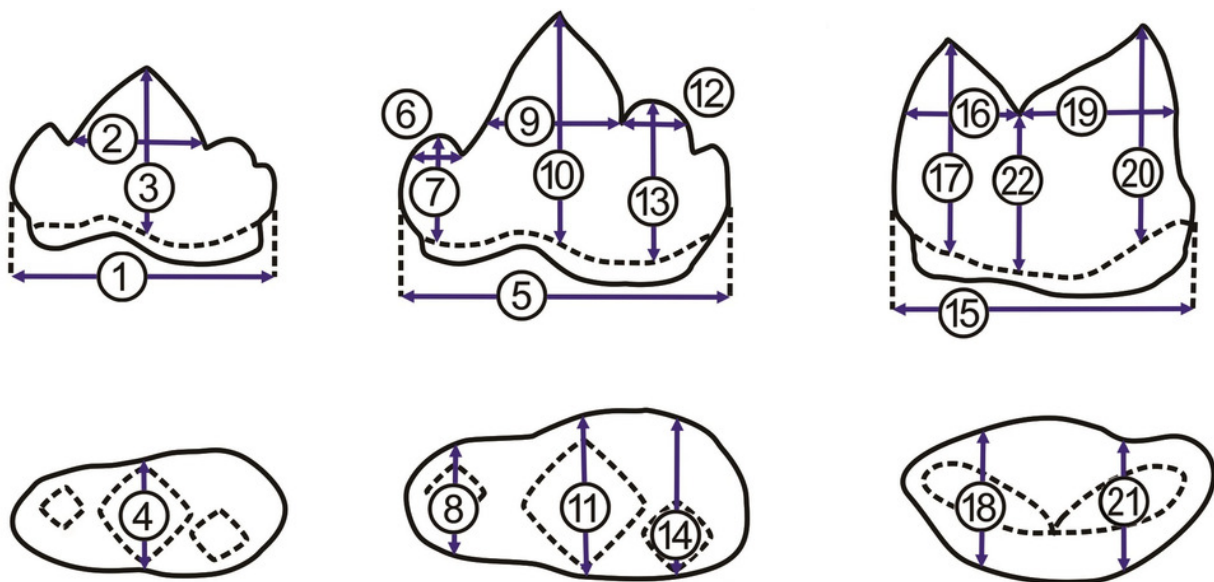
The three felid lower cheek teeth from Longshia-dong Cave

The three felid lower cheek teeth from Longshia-dong Cave, including p3 (a, F056584), p4 (b, F056585), and m1 (c, F056585), and their buccal views (1), lingual views (2), and occlusal views (3).

# Figure 3

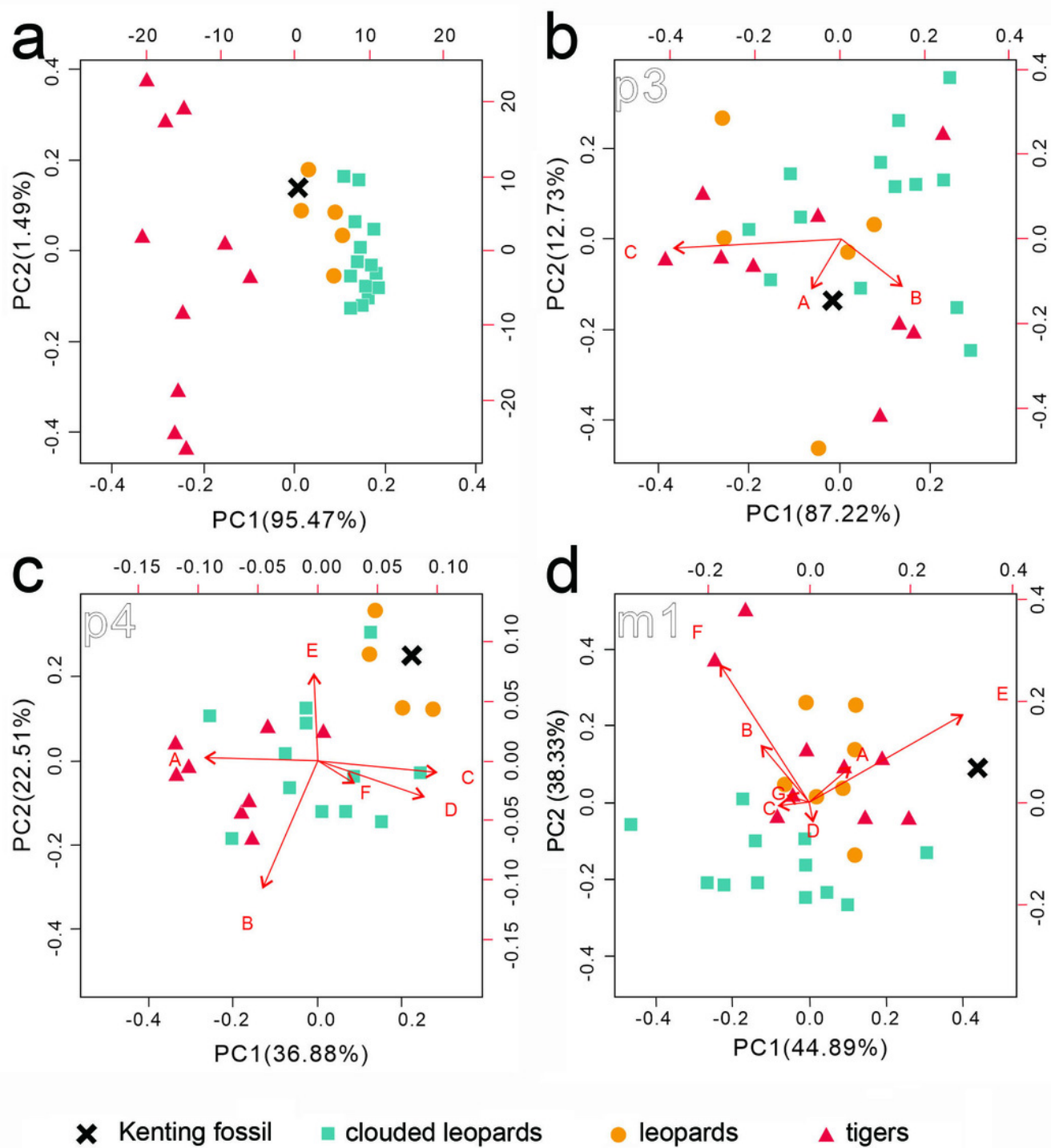
A comparison of the teeth (p3, p4, and m1) of three pantherines

A comparison of the teeth (p3, p4, and m1) of three pantherines including (a) clouded leopard, (b) leopard, and (c) tiger. Three significant characters are indicated by (1) the developmental level of p3 paraconid, (2) the shape of p4 occlusal surface (the difference between paraconid and protoconid widths), and (3) the size difference between m1 paraconid and m1 protoconid.

# Figure 4

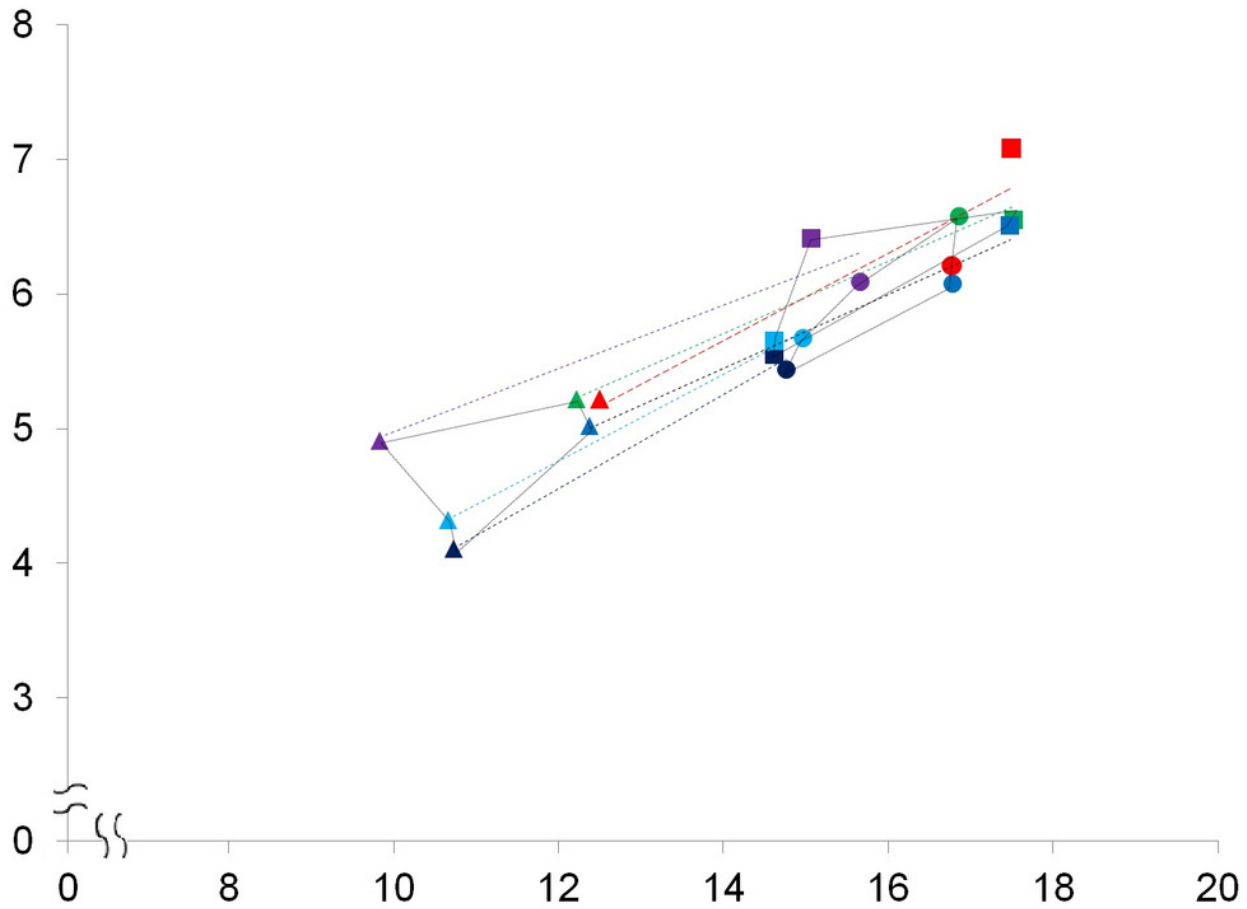
Measurements of p3, p4, and m1

Measurements of p3, p4, and m1 from the buccal side (a, from left to right) and from the occlusal side (b, from left to right). For the numbered dimensions, see Tab. 1.

# Figure 5

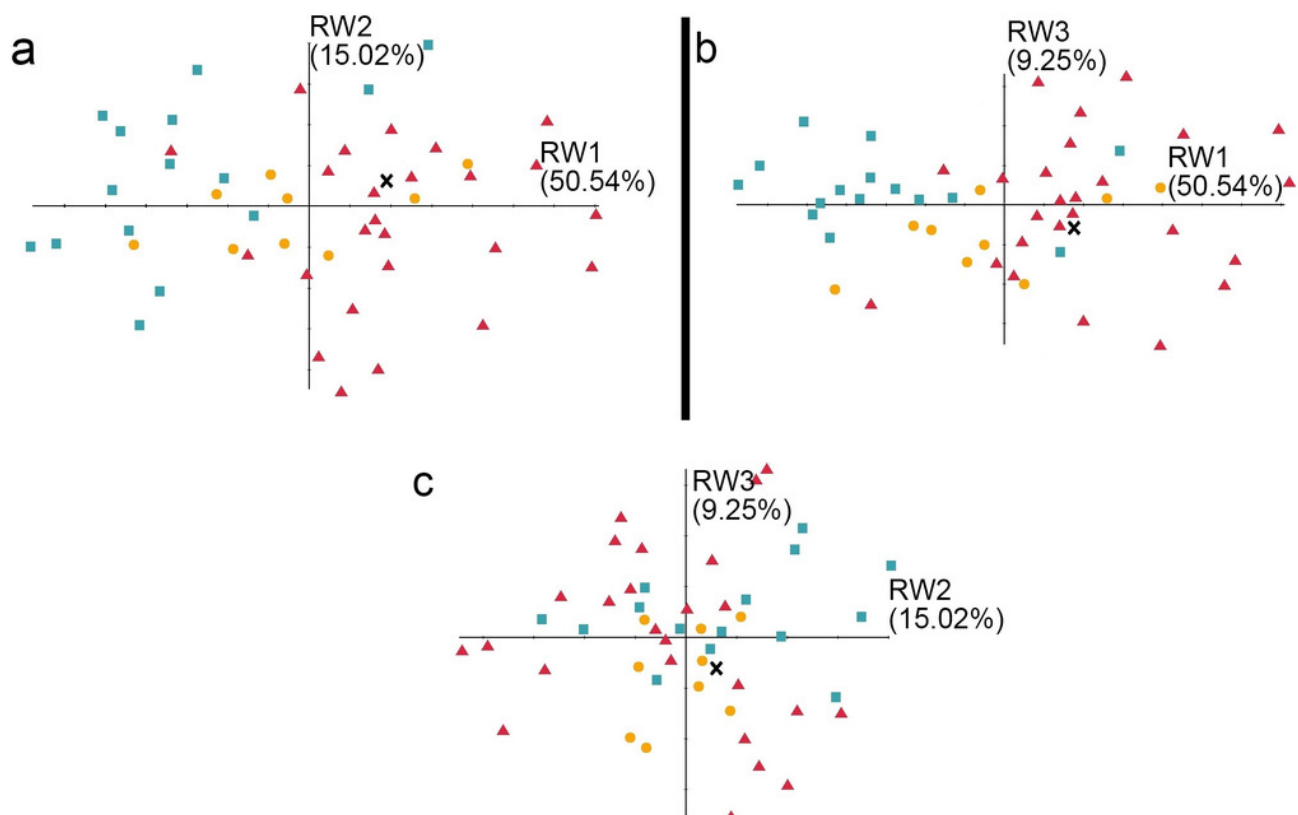
Two rounds of PCA analysis of the traditional linear measurements

The first round of PCA analysis based on all datasets is presented in (a). The second round of PCA analysis was performed for p3 (b), p4 (c), and m1 (d), separately. The result from the three ratios converted from four p3 numbered dimensions (A: 2/1, B: 3/1, C: 2/3) is shown in (b). The result from the six ratios converted from seven p4 numbered dimensions (A: 6/ 5, B: 7/5, C: 9/5, D: 10/5, E: 12/5, F: 13/5 is presented in (c). The result from the seven ratios converted from eight m1 numbered dimensions (A: 16/15, B: 17/15, C: 19/15, D: 20/15, E: 16/19, F: 17/20, G: 22/15 is shown in (d). See the details of the numbered dimensions in Fig. 3 and Tab. 1. Red triangles, *Panthera tigris*; yellow circles, *Panthera pardus*; cyan square, *Neofelis nebulosa* and *Neofelis diardi*; black cross, the studied fossil felid teeth. Red arrow represents a simplified ratio that shows the trend relating to the two principal components. Factor loadings of each principal component is indicated by the arrow length.

# Figure 6

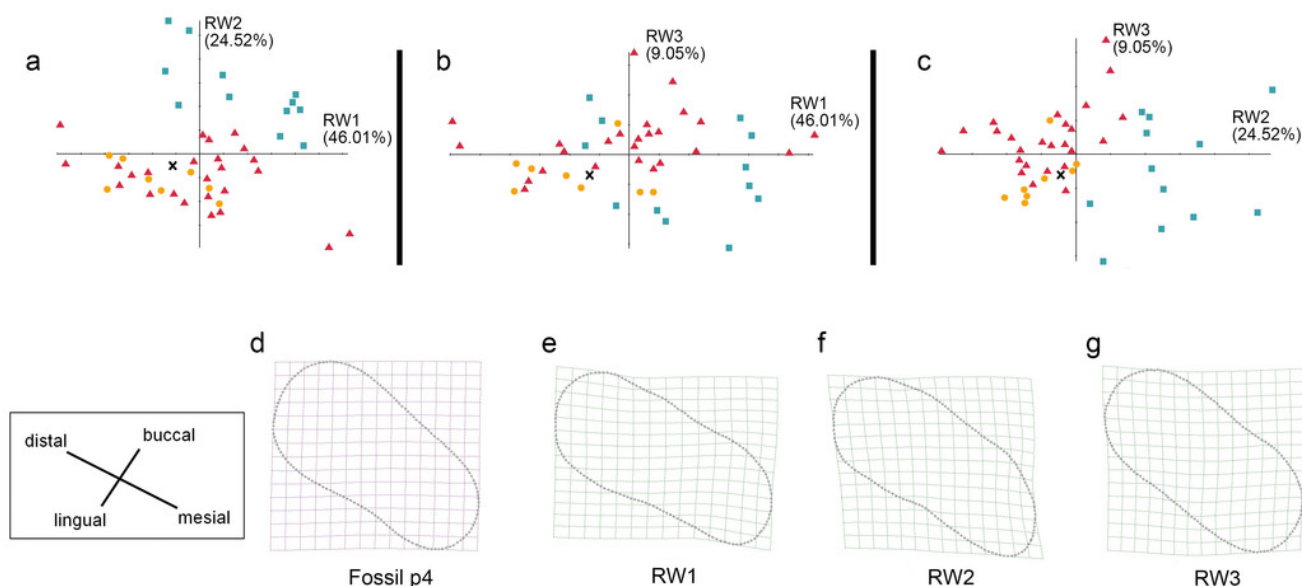
A bivariate plot of selected numbered dimensions of p3, p4, m1 of the fossil and extant leopard specimens

A bivariate plot of selected numbered dimensions (1, 4, 5, 11, 15, 21 from Tab. 1) of p3, p4, m1 of the fossil and extant leopard specimens (in mm). Dotted light blue, black, dark blue, green, and purple lines represent the regression lines for the dimensions of the five extant specimens, including the right and left sides of the specimen no. 1348-1, the right and left sides of the specimen no. 1431-1, and the left side of the specimen no. 549-1 (see Supplemental Tab. 1). The regression line for the dimensions of the fossil specimen is marked in red. Triangles, p3; squares, p4; circles, m1.

# Figure 7

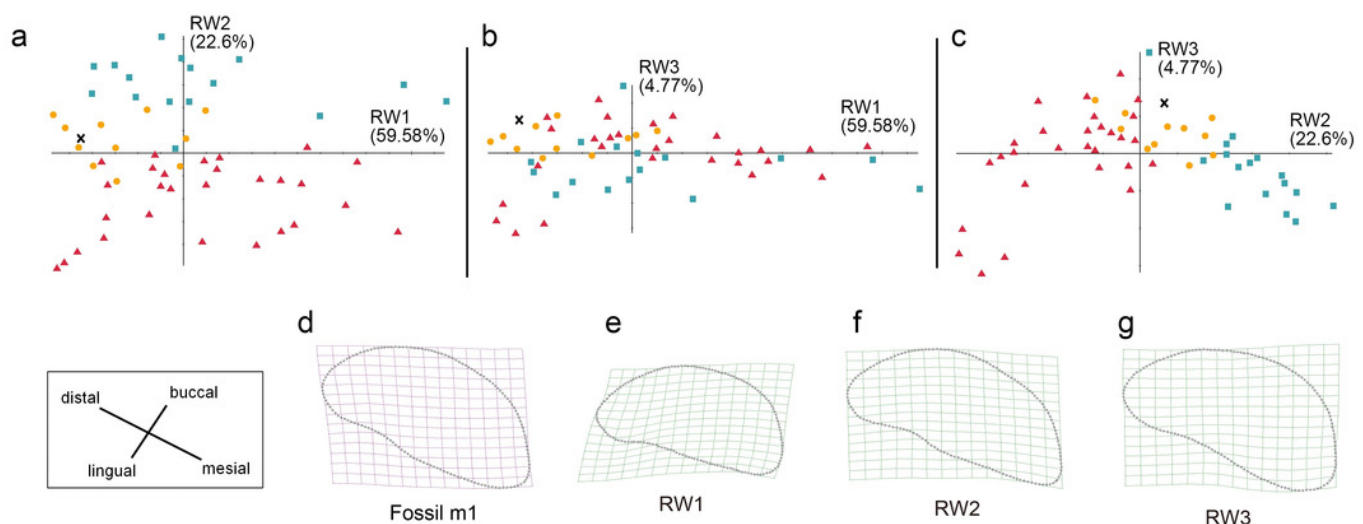
The shape variation of the occlusal surface of p3 in three pantherines

The shape variation of the occlusal surface of p3 in three pantherines, as revealed by a principal components analysis of three warp scores. (a) RW1 versus RW2; (b) RW1 versus RW3; (c) RW2 versus RW3. RW1 in a positive direction explains 50.54% variance, RW2 in a positive direction explains 15.02% variance, and RW3 in a positive direction explains 9.25% variance. Red triangles, *Panthera tigris*; yellow circles, *Panthera pardus*; cyan square, *Neofelis nebulosa* and *Neofelis diardi* ; black cross, the studied fossil felid teeth.

# Figure 8

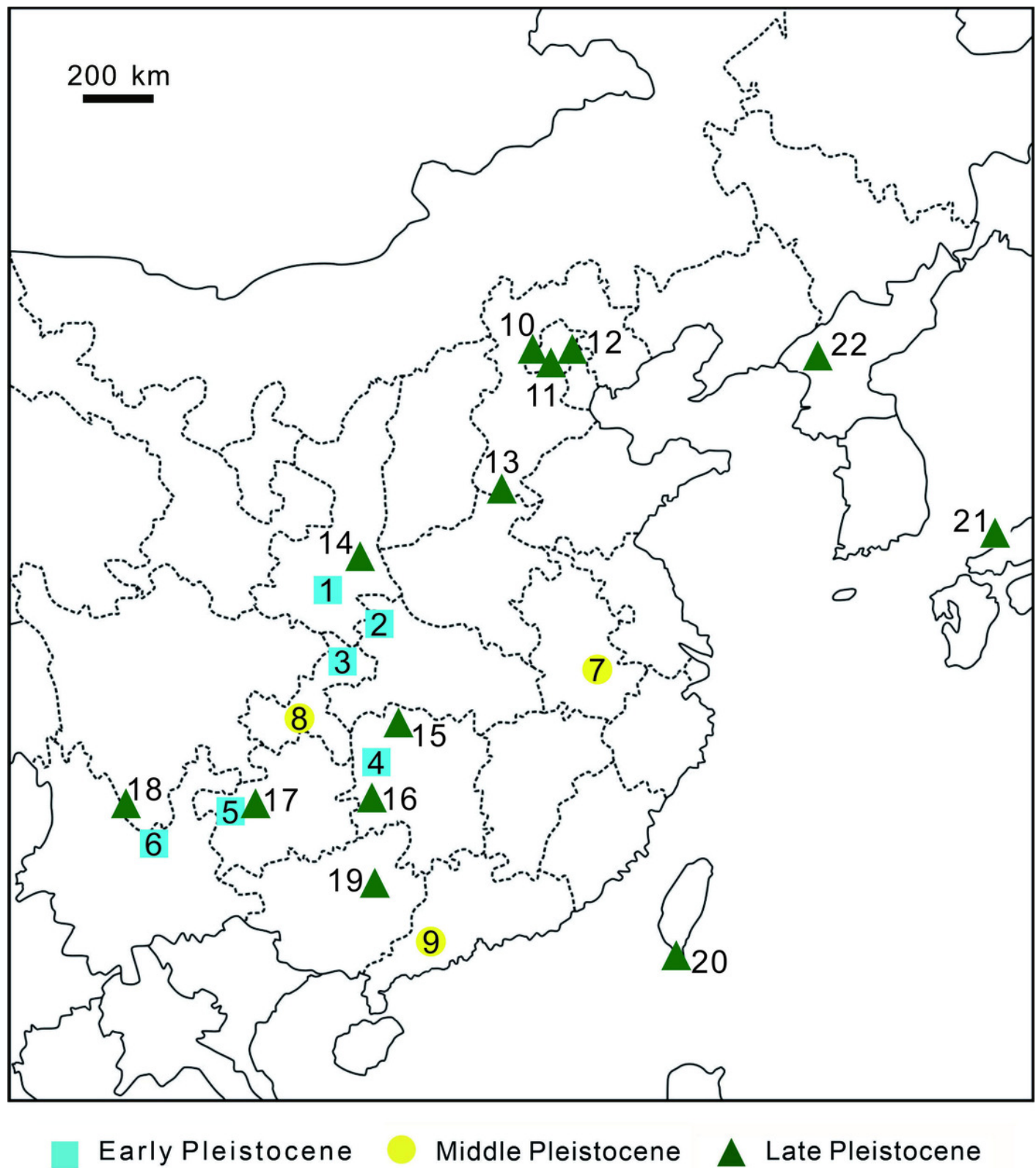
The shape variation of occlusal surface of p4 in three pantherines

The shape variation of occlusal surface of p4 in three pantherines, as revealed by a principal components analysis of warp scores. Plot of (a)RW1 versus RW2; (b) RW1 versus RW3; (c) RW2 versus RW3. Red triangles, *Panthera tigris*; yellow circles, *Panthera pardus*; cyan square, *Neofelis nebulosa and Neofelis diardi*; black cross, the studied fossil felid teeth. (d) the shape of fossil p4, (e) thin-plate spline deformation grid depicting shape variation along RW1 in a positive direction explains 46.01% variance, (f) thin-plate spline deformation grid depicting shape variation along RW2 in a positive direction explains 24.52% variance, (g) thin-plate spline deformation grid depicting shape variation along RW3 in a positive direction explains 9.05% variance.

# Figure 9

The shape variation of occlusal surface of m1 in three pantherines

The shape variation of occlusal surface of m1 in three pantherines, as revealed by a principal components analysis of warp scores. (a) RW1 versus RW2; (b) RW1 versus RW3; (c) RW2 versus RW3.Red triangles, *Panthera tigris*; yellow circles, *Panthera pardus*; cyan square, *Neofelis nebulosa and Neofelis diardi*; black cross, the studied fossil felid teeth. (d) the shape of fossil p4; (e) thin-plate spline deformation grid depicting shape variation along RW1 in a positive direction which explains 59.58% variance, (f) thin-plate spline deformation grid depicting shape variation along RW2 in a positive direction explaines 22.6% variance; (g) thin-plate spline deformation grid depicting shape variation along RW3 in a positive direction explains 4.77% variance.

# Figure 10

Discovery sites of Pleistocene leopard fossils in East Asia

Discovery sites of Pleistocene leopard fossils in East Asia. **Early Pleistocene** 1, Zhen'an, Shaanxi Province, China (Li & Deng, 2003); 2, Bailong Cave, Yunxi, Hubei Province, China (Wu et al., 2009); 3, Longgupou, Wushan County, Chongqing, China (Jin et al., 2008); 4, Cili County, Hunan Province, China (Wang et al., 1982); 5, Hezhang County, Guizhou Province, China (Zhao et al., 2013); 6, Yuanmou, Yunnan Province, China (You & Qi, 1973); **Middle Pleistocene** 7, Chaoxian, Anhui Province, China (Xu et al., 1984); 8, Yanjinggou (formerly Yenchingkou), Chongqing, China (Young, 1935); 9, Panlong Cave, Yunfu, Guangdong Province, China (Wang et al., 1990); **Late Pleistocene** 10, Niuyan Cave (= Bull Eye Cave), Mentougou, Beijing, China (Deng et al., 1999); 11, Locality 1, Zhoukoudien (formerly Choukoutien), Beijing, China (Pei, 1934); 12, Locality 13, Zhoukoudien, Beijing, China (formerly Choukoutien) (Teilhard de Chardin & Pei, 1941); 13, Anyang, Henan Province, China (Teilhard de Chardin & Yang, 1936); 14, Gongwangling, Lantian County, Shaanxi Province, China (Hu & Qi, 1978); 15, Yang'er Cave, Huatan County, Hunan Province, China (Wu et al., 2008); 16, Fuyan Cave, Daoxian, Hunan Province, China (Li et al., 2013); 17, Mawoukou Cave, Bijie, Guizhou Province, China (Zhao et al., 2016); 18, Heshang Cave, Fumin County, Yunnan Province, China (but possibly Middle Pleistocene; Zhang et al., 1989); 19, Liucheng *Gigantopithecus* Cave, Guangxi Province, China (Pei, 1987); 20, this study. 21, Lower Hamakita Formation, Honshu Island, Japan (Suzuki, 1966) 22, Chongphadae Cave, Hwangju County, Democratic People's Republic of Korea (Choe et al., 2020)

Selected dimensions of teeth

1 **Table 1** Selected dimensions of teeth

| dimension | |
|---|---|
| 1 | p3 crown length |
| 2 | p3 protoconid length |
| 3 | p3 protoconid height |
| 4 | p3 protoconid crown width |
| 5 | p4 crown length |
| 6 | p4 paraconid length |
| 7 | p4 paraconid crown height |
| 8 | p4 paraconid crown width |
| 9 | p4 potoconid length |
| 10 | p4 protoconid crown height |
| 11 | p4 protoconid width |
| 12 | p4 hypoconid length |
| 13 | p4 hypoconid height |
| 14 | p4 hypoconid crown width |
| 15 | m1 crown length |
| 16 | m1 paraconid length |
| 17 | m1 paraconid height |
| 18 | m1 paraconid width |
| 19 | m1 protoconid length |
| 20 | m1 protoconid height |
| 21 | m1 protoconid width |

| 22 | m1 carnassial notch height |
|---|---|

Morphological comparisons of three extant species and the fossil. ○, present; -, absent; △, uncertain.

1 **Table 2** Morphological comparisons of three extant species and the fossil. ○, present; -, absent;

2 △, uncertain.

|  | p3 paraconid | m1 metaconid | size comparison between the paraconid, and the protoconid, of m1 | chubby talonid on p3 and p4 | occlusal surface |
|---|---|---|---|---|---|
| Longshia-dong Cave fossils | ○ | - | similar | ○ | intermediate |
| Modern clouded leopards (*Neofelis* sp.) | - | △ | bigger protoconid | - | narrow |
| Modern tigers (*Panthera tigris*) | ○ | - | similar | ○ | intermediate |
| Modern leopards (*Panthera pardus*) | △ | - | similar | ○ | chubby |

Comparisons of dental size measurements (mm) of Longshia-dong Cave fossil to Chinese leopard fossils (expressed by length*width).

1 **Table 3** Comparisons of dental size measurements (mm) of Longshia-dong Cave fossil to

2 Chinese leopard fossils (expressed by length×width).

| | Longshia-dong Cave (Kenting, Taiwan) | Niuyan Cave (Beijing, China) | | | Zhoukoudian (Beijing, China) | | Gongwangling (Shaanxi, China) | | recent |
|---|---|---|---|---|---|---|---|---|---|
| | | V11799 | V11800 | V11801 | location 1st | location 13th | V2980 | | |
| p3 | 12.5×6.39 | 13.4×6.5 | - | - | 16.3×9 | 16×7.5 | 14.4×8 | 14.8×7.9 | 12×6.3 |
| p4 | 17.49×8.51 | 18.2×9.7 | 18.5×9.5 | - | 23.2×12 | 21×10 | 21×11.2 | 22.3×11 | 18×9.4 |
| m1 | 16.77×7.95 | 19.3×9.2 | 19.8×8.5 | 19.5×8.5 | 24×12.2 | 21×10 | 22.2×12 | 22.7×12.3 | 18.3×8.6 |