Age determination of *Palaeoloxodon huaihoensis* from Penghu Channel, Taiwan: significance of their age distribution based on fossils

Jia-Cih Kang[1], Chien-Hsiang Lin [1,2,*], Chun-Hsiang Chang [1,3*]

[1] Department of Life Science, Tunghai University, Taichung, Taiwan
[2] Biodiversity Research Center, Academia Sinica, Taipei, Taiwan
[3] Department of Geology, National Museum of Nature Science, Taichung, Taiwan

Corresponding Author:
Chien-Hsiang Lin [2*]
Chun-Hsiang Chang [3*]

Email address:
[2*] chlin.otolith@gmail.com
[3*] cch@mail.nmns.edu.tw

Abstract

Fossil teeth of *Palaeoloxodon huaihoensis* have been recovered over decades from the Penghu Channel during fisheries activities. The National Museum of Nature Science (NMNS) has a collection of such tooth material, which differs in size and morphology and likely represents ontogenetic variation and growth trajectory of various age groups of *P. huaihoensis*. However, little is known regarding *P. huaihoensis* age determination. By using teeth length, enamel thickness (ET), and plate counts, we established the age distribution of the species, which is directly derived from the extant African forest elephant *Loxodonta africana*. When measuring signs of allometric growth, we found that in both the upper and lower jaws, tooth width was correlated negatively with lamellar frequency but positively with ET. In the same age group, the number of lamellae was higher in *P. huaihoensis* than in *L. africana*. The reconstructed age distribution indicated no difference in the upper or lower jaw. Notably, the age frequency distribution of *P. huaihoensis* differed significantly from that of *Mammuthus primigenius*: *P. huaihoensis* more adult and older adult individuals in the population (median age: 33–34.5 years). This distinct pattern is speculated to be related to the harsh environmental conditions and intense interspecific competition among *P. huaihoensis* during the last ice age.

Keywords: age distribution, Pleistocene, subtropical west Pacific, elephant age group, lamellar frequency, tooth morphology, Taiwan, Penghu Channel

Introduction

40 The fossil genus *Palaeoloxodon* (Palaeoloxodontinae, Elephantidae) has been widely recorded
41 from Eurasia, Africa, and East Asia during the Late Pleistocene (Markiyama, 1924; Matsumoto,
42 1929; Osborn, 1936; Zong, 1987; Haynes, 1991). *Palaeoloxodon* has eight known species: *P.*
43 *antiquus* (Falconer & Cautley, 1847; Osborn, 1942), *P. namadicus* (Falconer & Cautley, 1847;
44 Osborn, 1924; Matsumoto, 1929), *P. falconeri* (Falconer, 1862; Busk, 1867; Vaufrey, 1929;
45 Osborn, 1942), *P. mnaidriensis* (Adams, 1870), *P. cypriotes* (Bate, 1903; Osborn 1942), *P. recki*
46 (Dietrich, 1916; Maglio, 1970; Maglio, 1973; Beden, 1979, unpublished data), *P. naumanni*
47 (Makiyama, 1924), and *P. huaihoensis* (Qi, 1999). In China and neighboring areas, records of
48 *Palaeoloxodon* are relatively abundant (Liu, 1977; Qi, 1999), and many specimens have been
49 identified as *P. namadicus, P. naumanni or P. huaihoensis* (Ho et al., 2000; Shieh et al., 2007;
50 Qi, 1999). Among the three species, *P. namadicus* is found mostly in the Nihewan Basin, China
51 (Wei, 1976). Records of *P. naumanni* are widely distributed in China and Japan but not in
52 Taiwan (Takahashi et al., 2001). *Palaeoloxodon huaihoensis* is the only known species from the
53 Penghu Channel, Taiwan (Shieh & Chang, 2007). Ho et al. (2000) stated that *P. huaihoensis* was
54 once distributed both in the China and Taiwan area during the Pleistocene (Shieh & Chang,
55 2007).
56
57 You et al. (1995) divided the Eastern China Sea into three paleobiogeographic zones in the Late
58 Pleistocene, with the north of 38°N representing *Mammuthus–Coelodonta* fauna, 28 °N - 38 °N
59 representing *Palaeoloxodon–Elaphurus davidianus* fauna, and *Ailuropoda–Stegodon* fauna to
60 south of 28°N. According to this scheme, Taiwan and the adjacent Penghu Channel should
61 belong to the *Ailuropoda–Stegodon* fauna category. However, the Penghu fauna is mainly
62 composed of *E. davidianus, Bubalus teilhardi*, and *P. huaihoensis* (Kuo, 1982; Hu & Tao, 1993;
63 Ho, 1998; Qi, 1999), which is more similar to the fauna in the Huaihe River Region, which
64 belongs to the *Palaeoloxodon–E. davidianus* fauna (You, 1995; Chen, 2000; Ho et al., 2008).
65 Studies have indicated the existence of a narrow and semiclosed sea similar to a land bridge
66 between the Yellow Sea and East Sea in the last ice age (Chen, 2000). Therefore, the
67 paleoclimate in the Pleistocene Taiwan Strait might belong to the tropical-temperate zone (Cai,
68 1999). Indeed, the so-called "Taiwan Landbridge Fauna" includes at least two distinct faunas
69 during the Middle-Late Pleistocene: one spanning from the Middle to early Late Pleistocene
70 (Chochen fauna) and one confined to the Late Pleistocene (Penghu fauna) (Chen, 2000).
71
72 The fauna of Chochen area includes several large mammals, such as *Rhinoceros sinensis*
73 *hayasakai* (Hayasakai, 1942), *Stegodon* (*Parastegodon*) *akashiensis* (Hayasakai, 1942; Shikama
74 et al., 1975; Otsuka, 1984), and *S.* (*Parastegodon*) *aurorae* (Shikama et al., 1975), but no fossils
75 of *P. huaihoensis* were found (Kuo, 1982; Ho & Qi, 1999). The Chochen fauna is believed to
76 share more affinities with that of the Huanan area in southern China than in with the mammal
77 fauna from northern China (Ho, 1998; Cai, 1999; Ho & Qi, 1999; Shieh & Chang, 2007).
78 However, the taphonomic and postmortem transportation processes of Chochen area are very
79 complex and somewhat ambiguous, which resulted in both terrestrial and marine elements in the
80 whole fauna (e.g., Lin et al., 2019). However, the composition of the Penghu fauna indicates that
81 all of it likely originated from northern China throughout the Pleistocene (Ho et al., 1997; Qi,
82 1999; Shieh & Chang, 2007).

83
84 The elephant teeth fossils provide crucial evidence about the ecosystem in the past. The tooth
85 growth patterns enables inference of the population's age distribution (Haynes, 1985) and the
86 related habitat distribution across vegetation and climate gradient (Webb, 1977; Janis, 1989;
87 Sukumar, 1992; Fox, 2000; Sukumar, 2003). However, analyses based on *Palaeoloxodon* teeth
88 have not been conducted thoroughly. Therefore, this study explored the age distribution and
89 structure of *P. huaihoensis* from Penghu Channel, Taiwan, using the teeth fossils. We defined
90 age groups with descriptions, reconstructed their age distribution and compared it with other
91 fossil species, and interpreted species distribution in the area.
92

93 ## Materials & Methods
94 **Specimens and measurements**
95 *P. huaihoensis* specimens were all dredged and recovered by fishing nets from the Penghu
96 Channel, Taiwan, as in Chang (2015). The Penghu Channel (22°40′N–23°40′N, 119°00′E–
97 120°00′E) is located in the Taiwan Strait between Penghu Island (Pescadores) and Taiwan (Fig.
98 1). A total of 221 teeth (dp4 (n = 3), M1 (13), M2 (42), and M3 (163)), including 88 jaws, were
99 available at the National Museum of Nature Science (NMNS), Taiwan for this study. Eroded and
100 abraded specimens were not analyzed (Fig. 2, Table S1)
101
102 Figure 1: Map showing the sampling area in the Penghu Channel (dash rectangle). The base map
103 was created using ArcGIS.
104
105 Figure 2: Images of *P. huaihoensis* specimens deposited at the National Museum of Nature
106 Science (NMNS). (A) Nine enamel loops complete of the lower left dp4 and erosion at both
107 ends, F027933. (B) All lamellae in wear and the lower right M1 is connected to M2, which is
108 slightly worn and lacks enamel thickness (ET), F020284. (C) Nineteen lamellae of the lower left
109 M3 in buccal view, F051590. (D)(E) The upper right and left M3 with all lamellae in wear and
110 slightly eroded at both ends, F026947. (F) Buccal surface of the lower right M3, F020284. (G)
111 Anterior 2-3 enamel loops confluent on the occlusal surface of lower right M3 from catalog
112 number F020226. (H) Lingual view of the lower right M3, F020248. All scale bars represent 5
113 cm.
114
115 We first used the plate counts to identify the position of the molar. Next, the tooth length, width,
116 and height were measured (Fig. 3), with the height taken vertically from the crown apex of the
117 plate. The enamel thickness (ET) was measured with calipers. To calculate lamellar frequency,
118 the number of complete plates at 10 cm at the crown base of both the lingual and buccal sides
119 was taken (Short, 1969; Hasegawa, 1972; Maglio, 1973; Shieh & Chang, 2007; Chang, 2010,
120 unpublished data).
121
122 Figure. 3. Measurements of an elephant tooth used in this study.
123

124 **Age determination**
125 We used the size, structure, and wear of teeth to determine the age distribution of *P. huaihoensis*
126 (Morrison-Scott, 1947; Sikes, 1966; Maglio, 1973; Lang, 1980). Thirty age groups based on
127 tooth morphology and shearing rate of deciduous teeth of African forest elephants were
128 established by Laws (1966), and this method has been widely used for the reconstruction of age
129 distribution in many elephant species (Haynes, 1991; Lister, 1999). We used this method too
130 with slight modifications. For example, Laws' method indicates that M3 has a maximum number
131 of 12 plates in *L. africana*, but in *P. huaihoensis*, as many as 22 plates can be found in M3. In
132 this case, the remaining number of plates in *P. huaihoensis* can be obtained by the rate of tooth
133 eruption of *L. africana* multiplied by the observed plates of *P. huaihoensis*. Thus, the age group
134 XX of Law's with 12 plates indicates that there will be six plates in the age groups of *P.*
135 *huaihoensis* if $(22/12) \times 6 = 11$ plates are remaining (see Table S2). Consequently, we
136 established 24 age groups defined using 88 jaws (Fig. 4).
137
138 Figure 4: Definition of age groups I–XXIV. I: dp4 all lamellae in wear, M1 slight wear
139 (specimen number: F02793); II: dp4 well worn, approximately 3-4 plates remaining; M1 first 1-2
140 lamellae in wear (F051613); III: M1 all in wear; M2 worn to enamel of first two lamellae
141 (F044264); IV: M1 first 1-2 enamel loops confluent, M2 slight wear (F020284); V: M1 well
142 worn; M2 more enamel loops showing (F051497); VI: M1 only 5-6 enamel loops left, slight
143 erosion of posterior border; M2 lamellae well formed (F051562); VII: M1 well worn, only three
144 plates remain; M2 slight erosion of anterior edge, 9-10 enamel loops complete (F027950); VIII:
145 M2 first enamel loops confluent (F044271); IX: M1 worn out; M2 well into wear showing
146 lozenges, more lamellae visible (F020247); X: M2 all except last 3 lamellae in wear (F020255);
147 XI: M2 complete, all lamellae in wear, and all enamel loops showing M2 erosion at both ends;
148 M3 lamellae well formed (F027988); XII: M2 all lamellae in wear, 15 enamel loops complete
149 (F026927); XIII: M2 only approximately 8-9 loops remain and erosion at both ends (F020287);
150 XIV: M3 worn to enamel of first lamellae and more enamel loops (F030111); XV: M2 lost; M3
151 11-12 enamel loops complete (F020278); XVI: M2 worn out; M3 no erosion of anterior border,
152 anterior 1-2 enamel loops confluent (F044257); XVII: M3 only 2 lamellae not in wear
153 (F027320); XVIII: M3 all except last lamellae in wear (F044266); XIX: M3 first 1-2 enamel
154 loops may confluent (F051487); XX-I: M3 erosion at both borders, anterior 2-3 enamel loops
155 confluent (F026942); XX-II: M3 all except last lamellae in wear (F020258); XXI-I: M3 more
156 enamel loops showing, slight erosion of the anterior border (F044270); XXI-II: M3 well worn,
157 first enamel loops may be slightly confluent (F051560); XXII-I: M3 all lamellae in wear, no
158 erosion at both ends (F044268); XXII-II: M3 erosion at both borders, anterior 2-3 enamel loops
159 confluent (F027963); XXIII-I: M3 only five complete enamel loops remain, anterior part broken
160 off (F044261); XXIII-II: anterior third of tooth missing, only five complete lamellae remain
161 (F027967); XXIV: M3 only 2-3 loops remain (F051559).
162
163 **Statistical analysis**
164 The tooth width and lamellar frequency in occlusal and buccal sides of the lower and upper jaws
165 of dp4-M3 as well as the relationship between the width and enamel thickness (ET) of lower and
166 upper jaws of dp4-M3 were plotted using R software (Core Team and Others 2013). The
167 relationship between two variables was indicated using Pearson's correlation coefficient. These

168 relationships reflect whether the concerned variables revealed an allometric growth pattern. The
169 number of lamellae throughout the lifespan was plotted against the estimated age of *P.*
170 *huaihoensis* (see above, Age determination). Moreover, *L. africana* data were used for
171 comparison (Laws, 1966).
172
173 A histogram based on the frequency distribution of specimens was established to reconstruct the
174 age distribution of *P. huaihoensis*. Unlike studies in which only the lower jaws were considered
175 (Laws, 1966), we included upper jaw specimens for comparison. A null hypothesis of the
176 distributions of upper and lower jaws was first tested using the two-sample t test. However, when
177 no significant difference between upper and lower jaws was detected, only lower jaw specimens
178 were used in subsequent analyses. A Shapiro–Wilk test was conducted to test whether the fossil
179 age distribution data were distributed normally; if not, the median for the lower jaws was
180 calculated using the Wilcoxon–Mann–Whitney test.
181
182 Finally, we compared the age distribution based on fossil remains of *P. huaihoensis* with other
183 species: the stable age distribution of fossil *Mammuthus primigenius* and *M. columbi*. A null
184 hypothesis stating the same age distribution for each population pair was analyzed using
185 Pearson's chi-square test. Here, the independence of age and the number of individuals in each
186 of the two populations were tested. The *M. columbi* and *M. primigenius* data were derived from
187 the studies of Louguet-Lefebvre (2013) and Wojtal (2001), respectively. All analyses were
188 performed using R (Core Team and Others 2013).
189

190 **Results**
191 Tooth width and lamellar frequency were negatively correlated on both the occlusal and buccal
192 sides for dp4-M3. Lamellar frequency increased when tooth width decreased in both upper and
193 lower jaws (Fig. 5a, b, d, e). By contrast, the tooth width and ET were positively correlated on
194 both the sides (Fig. 5c, f). The size range overlapped in some cases; for instance, the M2
195 overlapped with M3 in occlusal width and lamellar frequency and width and ET of the lower
196 jaw, respectively (Fig. 5d, f).
197
198 Figure 5: The relationships of various meristic measurements in the jaws of dp4-M3.
199 (A) Tooth width and lamellar frequency in the occlusal surface of the upper jaw (r = −0.558, t =
200 −7.699, p < 0.05). (B) Tooth width and lamellar frequency in the buccal side of the upper jaw (r
201 = −0.476, t = −6.201, p < 0.05). (C) Tooth width and enamel thickness (ET) of the upper jaw (r =
202 0.531, t = 7.179, p < 0.05). (D) Width and lamellar frequency in the occlusal surface of the lower
203 jaw (r = −0.649, t = −7.915, p < 0.05). (E) Width and lamellar frequency in the buccal side of the
204 lower jaw (r = −0.453, t = −7.523, p < 0.05). (F) Width and ET of the lower jaw (r = 0.457, t =
205 4.759, p < 0.05).
206
207 A summary of the various age groups derived from the tooth morphology, lamellar number, teeth
208 position, and age estimation is presented in Table 1. The number of lamellae of *P. huaihoensis*
209 was considerably higher than that of *L. africana* in the same age group (Fig. 6). Moreover, the

210 increasing rate of lamellae in *P. huaihoensis* was progressively more evident than that of *L.*
211 *africana* from M1, eventually reaching 22 lamellae in M3.
212
213 Table 1: Comparison of estimated ages derived from the lower jaw of *P. huaihoensis* and *L.*
214 *africana*. The positions of the teeth used in Laws (1966) are indicated in parentheses.
215
216 Figure 6: Differences in the relationship of the number of lamellar and age in *P. huaihoensis* and
217 *L. africana*. Data of *L. africana* are from Laws (1966).
218
219 The reconstructed age distribution of *P. huaihoensis* revealed that the age peaked at 29–36 years,
220 indicating a higher number of adult individuals (Fig. 7). Notably, the distributions of the upper
221 and lower jaws were similar (two-sample t test, $p = 0.941$, $t = 0.075$), and they possibly
222 originated from a single population (mean = 0.04). The Shapiro–Wilk test indicated a nonnormal
223 age distribution ($p < 0.05$), and using the Wilcoxon–Mann–Whitney test, the medians of lower
224 jaws indicated an age of 33–34.5 years.
225
226 Figure 7: Age distribution of *P. huaihoensis* from Penghu Channel, Taiwan. The frequency (%)
227 is based on the proportion of specimens (n).
228
229 Pearson's chi-square test revealed that *P. huaihoensis* age distribution was significantly different
230 from the stable age distribution of *M. primigenius* ($p < 0.05$, Fig. 8a) but not from that of *M.*
231 *columbi* ($p > 0.05$, Fig. 8b). *M. primigenius* mainly comprised juveniles and young-adult
232 individuals, whereas *P. huaihoensis* and *M. columbi* comprised mostly adults aged 30–40 years.
233

Discussion

235 Tooth eruption has widely been used for estimating extant elephant age (Laws, 1966; Krumery &
236 Buss, 1968; Shoshani, 1982; Roth & Shoshani, 1988). This method has also been applied to
237 fossil species—for example, the age distribution of the *Mammut* (Mastodon) (Haynes, 1985), *M.*
238 *columbi* (Saunders, 1980; Louguet-Lefebvre, 2013), and *M. primigenius* (Lister, 1999; Wojtal,
239 2001; Rountrey, 2012). However, in *P. huaihoensis*, plate count, length, ET, and lamellar
240 frequency measurements revealed substantial differences from the extant *L. africana* (e.g., Fig.
241 6).
242
243 Our age distribution for *P. huaihoensis* has a distinct pattern compared with that of *M.*
244 *primigenius* (Wojtal, 2001). In *M. primigenius*, numerous younger individuals (0–12 years) and
245 much fewer adults were found in the European Kraków Spadzista site (Fig. 8a). Such a pattern
246 represents the natural deaths of the whole population, suggesting nonselective cumulative deaths
247 in the normal environment (Klein, 1985; Haynes, 1991; Haynes & Klimowicz, 2016).
248
249 Figure 8: Comparison of the age distribution of *P. huaihoensis* with that of (A) *M. primigenius*
250 and (B) *M. columbi*.

251

252   Although the upper and lower jaws of *P. huaihoensis* suggest that these specimens originate
253   from a single population, the reconstructed age distribution indicates an older adult–dominant
254   pattern (median = 33–34.5 years). The age profile of *M. columbi* seems to be similar to that of *P.*
255   *huaihoensis* (Fig. 8b), but the living environment and taphonomic process for both species were
256   completely disparate. The Hot spring site has yielded many specimens of *M. columbi*, and this
257   areas are known to be not only essential for providing a water source for animals inhabiting
258   adjacent areas but also a natural trap with unstable sediments that preferentially traps larger adult
259   individuals (Agenbroad & Mead, 1994). This may be the reason that the inferred *M. columbi*
260   population mainly comprised adult individuals (Louguet-Lefebvre, 2013). Intense interspecific
261   competition between adults under harsh environmental conditions can cause massive death; we
262   speculate that this was the case of *P. huaihoensis*. During the last ice age, climate change-related
263   resource shortages likely resulted in sharp competition within the population of *P. huaihoensis*,
264   particularly in large adult males (Valeix et al., 2007; Ferry et al., 2016).

265

266   In addition to competition, the notable older age predominance may have been caused by
267   sampling bias because our materials were collected by bottom trawl fisheries and smaller teeth of
268   *P. huaihoensis* from younger individuals may not have been sufficiently represented. However,
269   fossils from the Penghu Channel have been collected for decades and have resulted in a massive
270   collection of a diverse fauna (e.g., Hu & Tao, 1993), including fossil remains of much smaller
271   sizes such as fragments of the tibia, vertebrae, ribs, and even a tiny lower jaw of *Homo* (Chang et
272   al., 2015) were recovered using this method. In any case, small teeth of *P. huaihoensis* would be
273   considerably represented if they existed. Therefore, the age frequency distribution suggests that
274   the area around Penghu Channel might not have been a nursery ground for *P. huaihoensis*.
275   Nevertheless, whether our material represents an equilibrium age distribution of *P. huaihoensis*
276   remains uncertain because this age distribution could have existed only in fossil species.
277   The fossil records of *P. huaihoensis* date from the Middle to Late Pleistocene (Liu, 1977; Chen,
278   2000). The species was first found in the northern part of Anhui, China (Liu, 1977). The further
279   geographical distribution includes Huaihe River Region (Cai, 1999; Ho & Qi, 1999) and
280   northern Jiangsu, China (Qian, 2017; Chen et al., 2020) (Fig. 9). In Taiwan, however, the species
281   has only been found in the Penghu Channel and never southwards; thus, it is not found in the
282   famous Chochen fauna (Kuo, 1982). Because of cold temperatures and water and food shortage,
283   animals could have migrated from higher to lower latitudes; in particular, *P. huaihoensis* could
284   have migrated southward in search of grasslands and water resources (Webb, 1977; Janis, 1989;
285   Fox, 2000), especially given that the Penghu Channel was adapted to steppe habitats during the
286   Late Pleistocene. However, possible ecological explanations, such as climate change and niche
287   competition, have yet to be explored fully. Overall, the fossil records suggest that *P. huaihoensis*
288   was distributed from northern China and to as far south as Penghu Channel in the last ice age but
289   did not migrate across the Taiwan Strait to Taiwan Island (Fig. 9).

290

Figure 9: Postulated migration direction (black arrow) of *P. huaihoensis*. The species likely originated from northern China (black pins), where fossil records are more abundant. The extension of the record in the Penghu Channel (white pin) in the last ice age is currently its southern limit. The current sea depth contour (−120 m) delineates the ancient coastline during the last ice age. The map is derived from the National Centers for Environmental Information (https://www.ngdc.noaa.gov).

Conclusions

The age distribution of such a large mammal as *P. huaihoensis*, which once inhabited the subtropical west Pacific in the Late Pleistocene, has been largely unknown. By using its fossil teeth from the Penghu Channel, we reconstructed its age distribution and defined 24 age groups by measuring the ontogenetic morphological changes in teeth length, ET, and plate counts. Compared with *M. primigenius*, *P. huaihoensis* from the Penghu Channel is distinct in having significantly more adult and older adult individuals and very few juveniles, similar instead to *M. columbi*. However, unlike taphonomic patterns of age distribution observed in the case of *M. columbi*, we speculate that environmental conditions and interspecific competition are possible causes. The fossil records further indicate that *P. huaihoensis* was mainly distributed in northern China and only extended southward in the Penghu Channel. The postulated ancient migration route of the species and the possible underlying ecological reasons would benefit from further investigation of the collection from northern China. Future studies should elucidate the exact age distribution of *P. huaihoensis* in northern China compared with that of the Penghu Channel and conduct isotope analyses to explore the possible vegetation and climatic impacts on the migration and specific age distribution recovered from the Penghu Channel.

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Figure 1

Map showing the sampling area in the Penghu Channel (dash rectangle). The base map was created using ArcGIS.

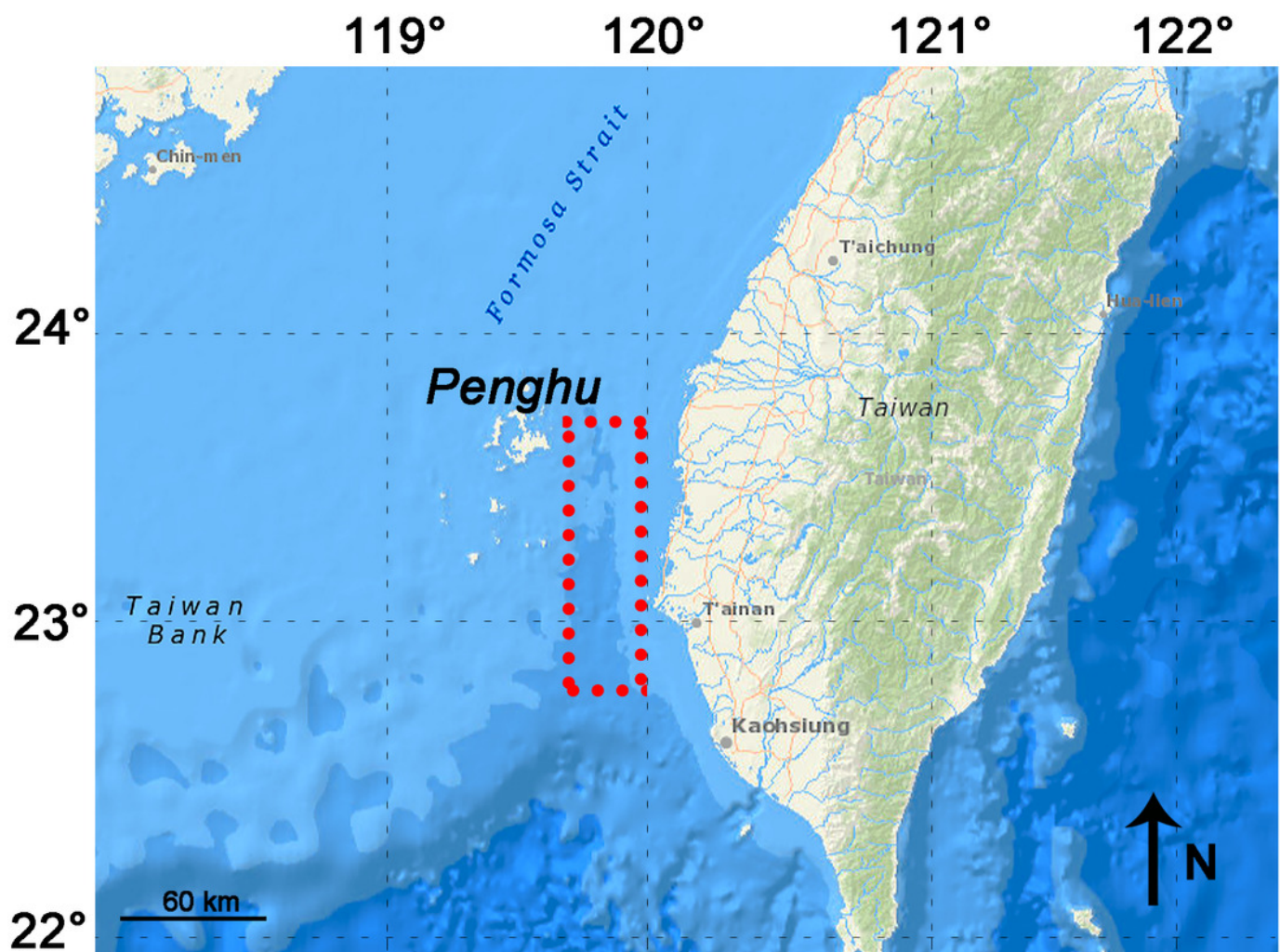



Figure 2

Images of *P. huaihoensis* specimens deposited at the National Museum of Nature Science (NMNS).

(A) Nine enamel loops complete of the lower left dp4 and erosion at both ends, F027933. (B) All lamellae in wear and the lower right M1 is connected to M2, which is slightly worn and lacks enamel thickness (ET), F020284. (C) Nineteen lamellae of the lower left M3 in buccal view, F051590. (D)(E) The upper right and left M3 with all lamellae in wear and slightly eroded at both ends, F026947. (F) Buccal surface of the lower right M3, F020284. (G) Anterior 2-3 enamel loops confluent on the occlusal surface of lower right M3 from catalog number F020226. (H) Lingual view of the lower right M3, F020248. All scale bars represent 5 cm.

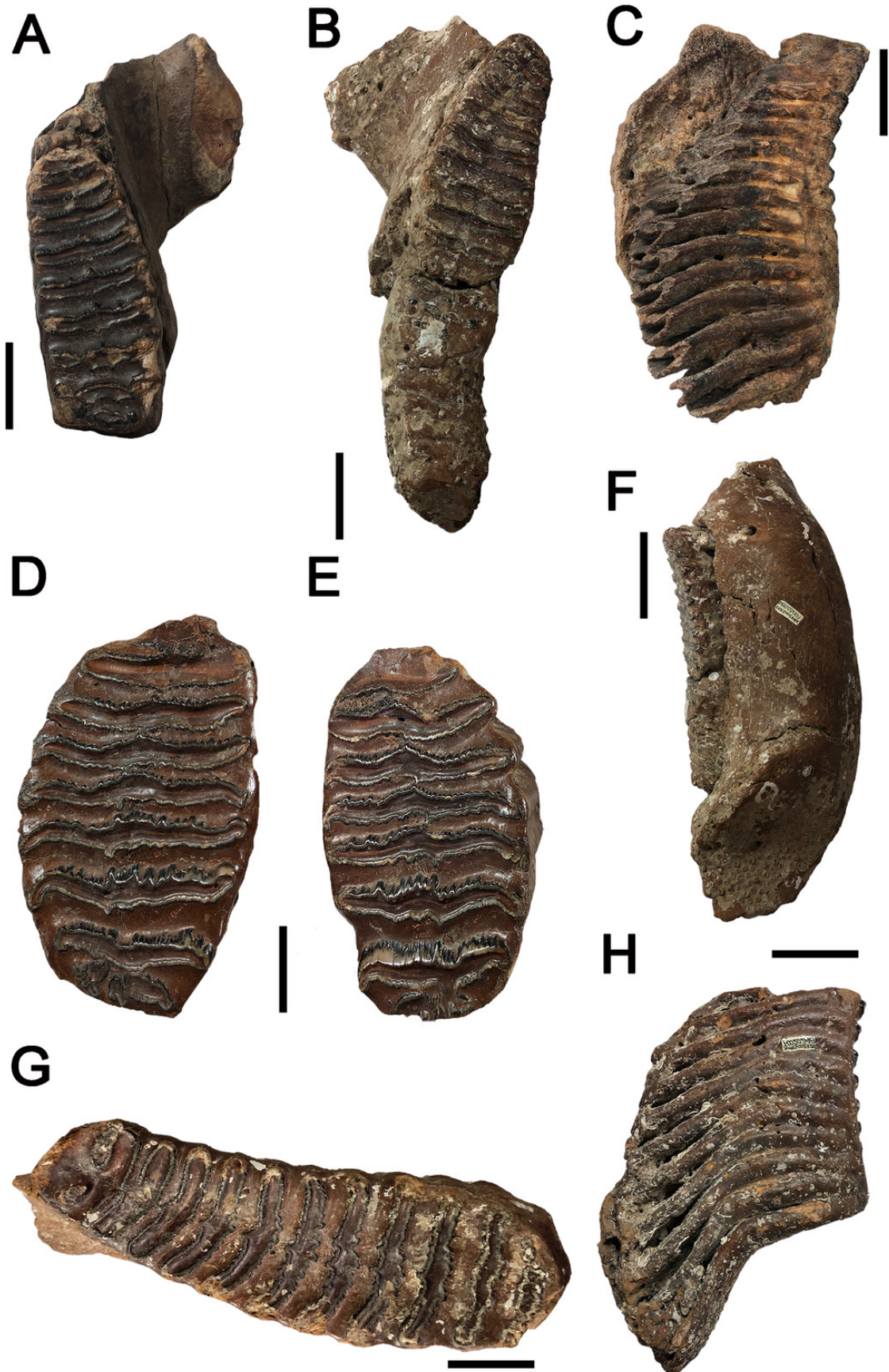



Figure 3

Measurements of an elephant tooth used in this study.

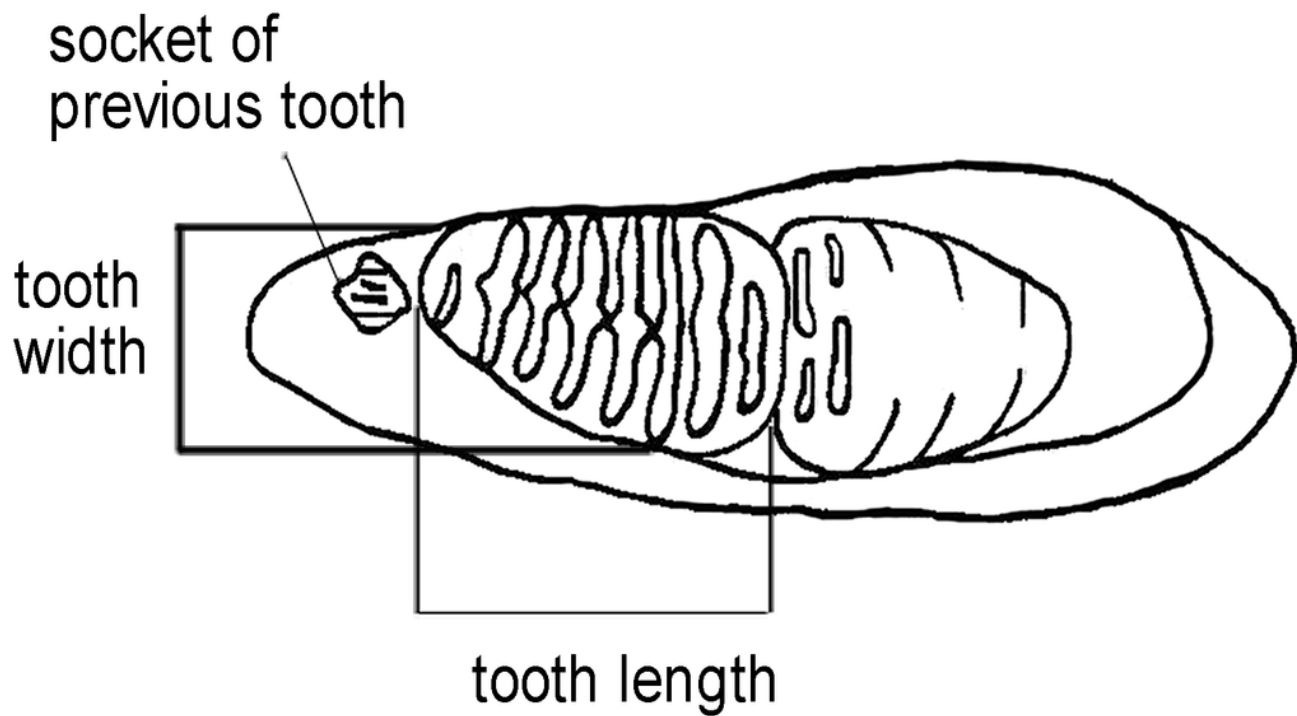



Figure 4

Definition of age groups I–XXIV.

I: dp4 all lamellae in wear, M1 slight wear (specimen number: F02793); II: dp4 well worn, approximately 3-4 plates remaining; M1 first 1-2 lamellae in wear (F051613); III: M1 all in wear; M2 worn to enamel of first two lamellae (F044264); IV: M1 first 1-2 enamel loops confluent, M2 slight wear (F020284); V: M1 well worn; M2 more enamel loops showing (F051497); VI: M1 only 5-6 enamel loops left, slight erosion of posterior border; M2 lamellae well formed (F051562); VII: M1 well worn, only three plates remain; M2 slight erosion of anterior edge, 9-10 enamel loops complete (F027950); VIII: M2 first enamel loops confluent (F044271); IX: M1 worn out; M2 well into wear showing lozenges, more lamellae visible (F020247); X: M2 all except last 3 lamellae in wear (F020255); XI: M2 complete, all lamellae in wear, and all enamel loops showing M2 erosion at both ends; M3 lamellae well formed (F027988); XII: M2 all lamellae in wear, 15 enamel loops complete (F026927); XIII: M2 only approximately 8-9 loops remain and erosion at both ends (F020287); XIV: M3 worn to enamel of first lamellae and more enamel loops (F030111); XV: M2 lost; M3 11-12 enamel loops complete (F020278); XVI: M2 worn out; M3 no erosion of anterior border, anterior 1-2 enamel loops confluent (F044257); XVII: M3 only 2 lamellae not in wear (F027320); XVIII: M3 all except last lamellae in wear (F044266); XIX: M3 first 1-2 enamel loops may confluent (F051487); XX-I: M3 erosion at both borders, anterior 2-3 enamel loops confluent (F026942); XX-II: M3 all except last lamellae in wear (F020258); XXI-I: M3 more enamel loops showing, slight erosion of the anterior border (F044270); XXI-II: M3 well worn, first enamel loops may be slightly confluent (F051560); XXII-I: M3 all lamellae in wear, no erosion at both ends (F044268); XXII-II: M3 erosion at both borders, anterior 2-3 enamel loops confluent (F027963); XXIII-I: M3 only five complete enamel loops remain, anterior part broken off (F044261); XXIII-II: anterior third of tooth missing, only five complete lamellae remain

(F027967); XXIV: M3 only 2-3 loops remain (F051559).

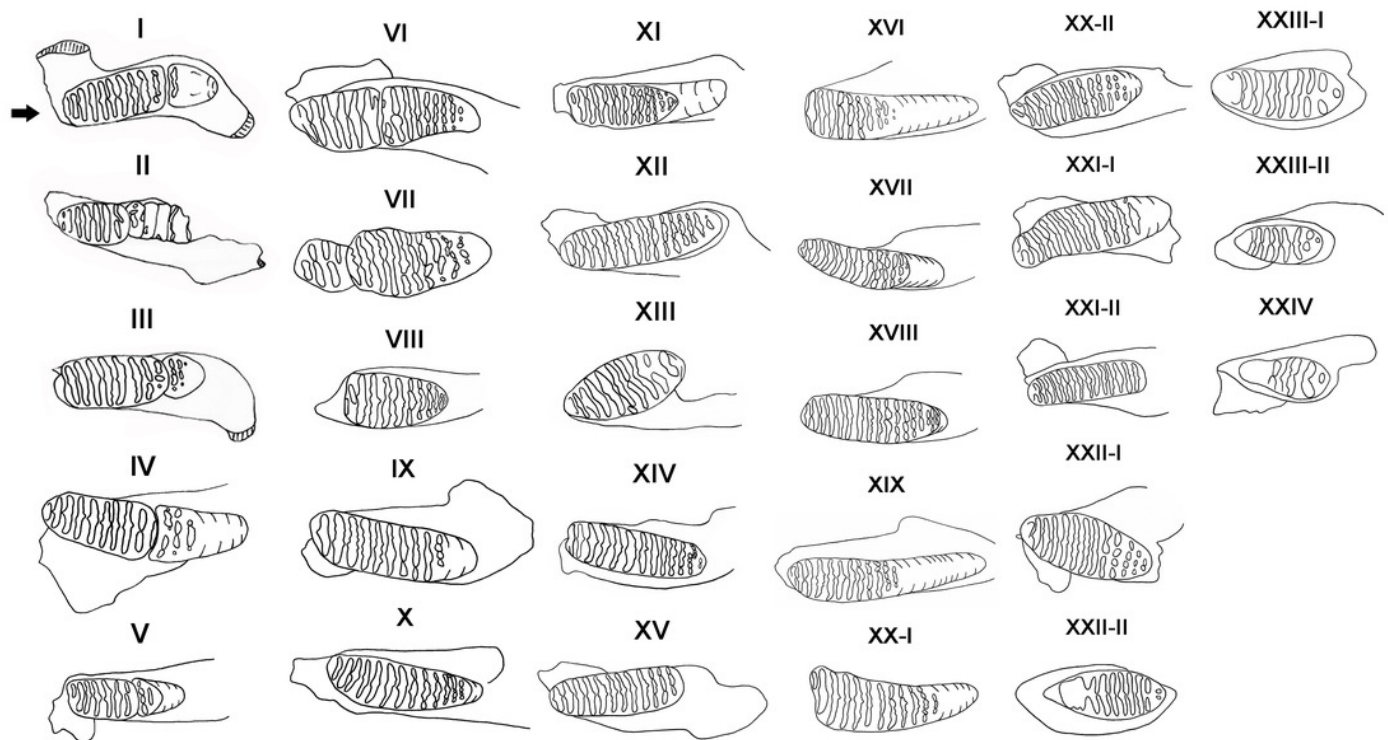



Figure 5

The relationships of various meristic measurements in the jaws of dp4-M3.

(A) Tooth width and lamellar frequency in the occlusal surface of the upper jaw (r = −0.558, t = −7.699, p < 0.05). (B) Tooth width and lamellar frequency in the buccal side of the upper jaw (r = −0.476, t = −6.201, p < 0.05). (C) Tooth width and enamel thickness (ET) of the upper jaw (r = 0.531, t = 7.179, p < 0.05). (D) Width and lamellar frequency in the occlusal surface of the lower jaw (r = −0.649, t = −7.915, p < 0.05). (E) Width and lamellar frequency in the buccal side of the lower jaw (r = −0.453, t = −7.523, p < 0.05). (F) Width and ET of the lower jaw (r = 0.457, t = 4.759, p < 0.05).

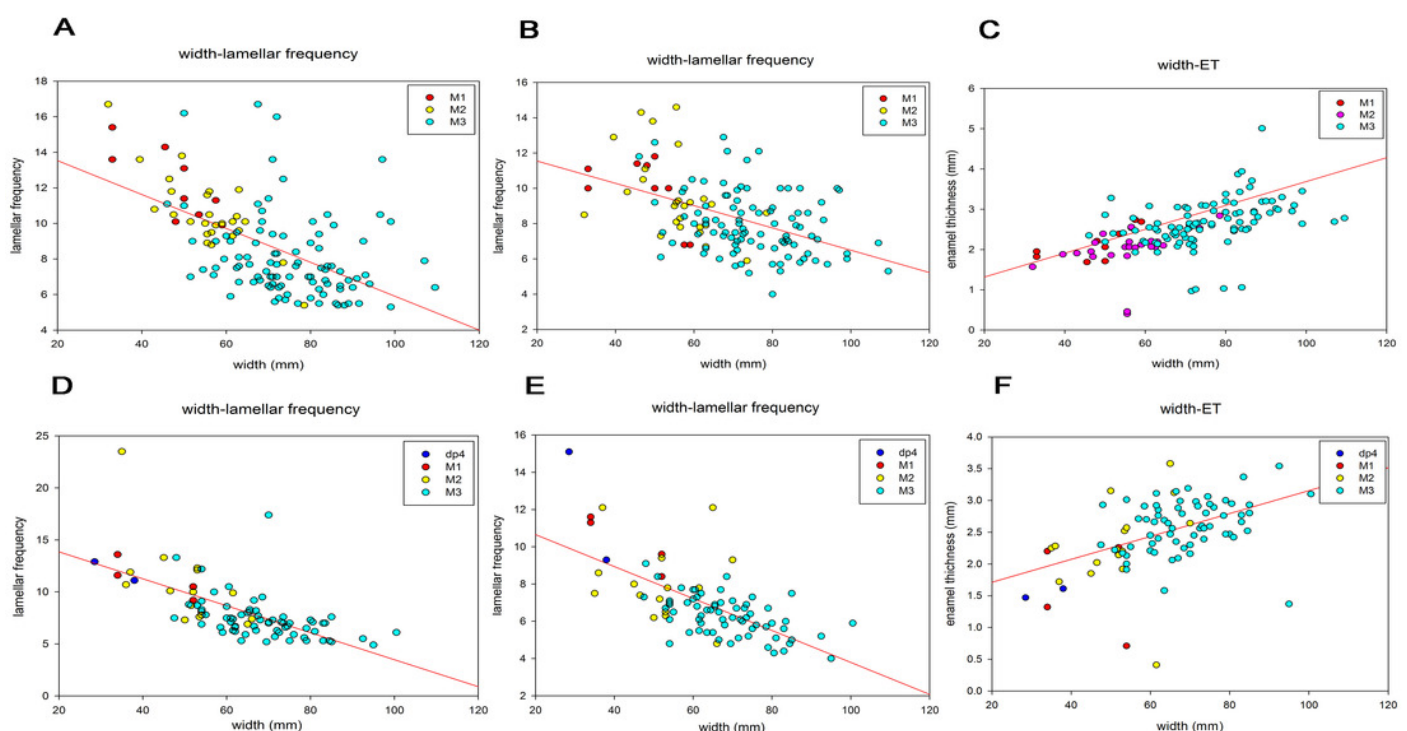



Figure 6

Differences in the relationship of the number of lamellar and age in *P. huaihoensis* and *L. africana*. Data of *L. africana* are from Laws (1966).

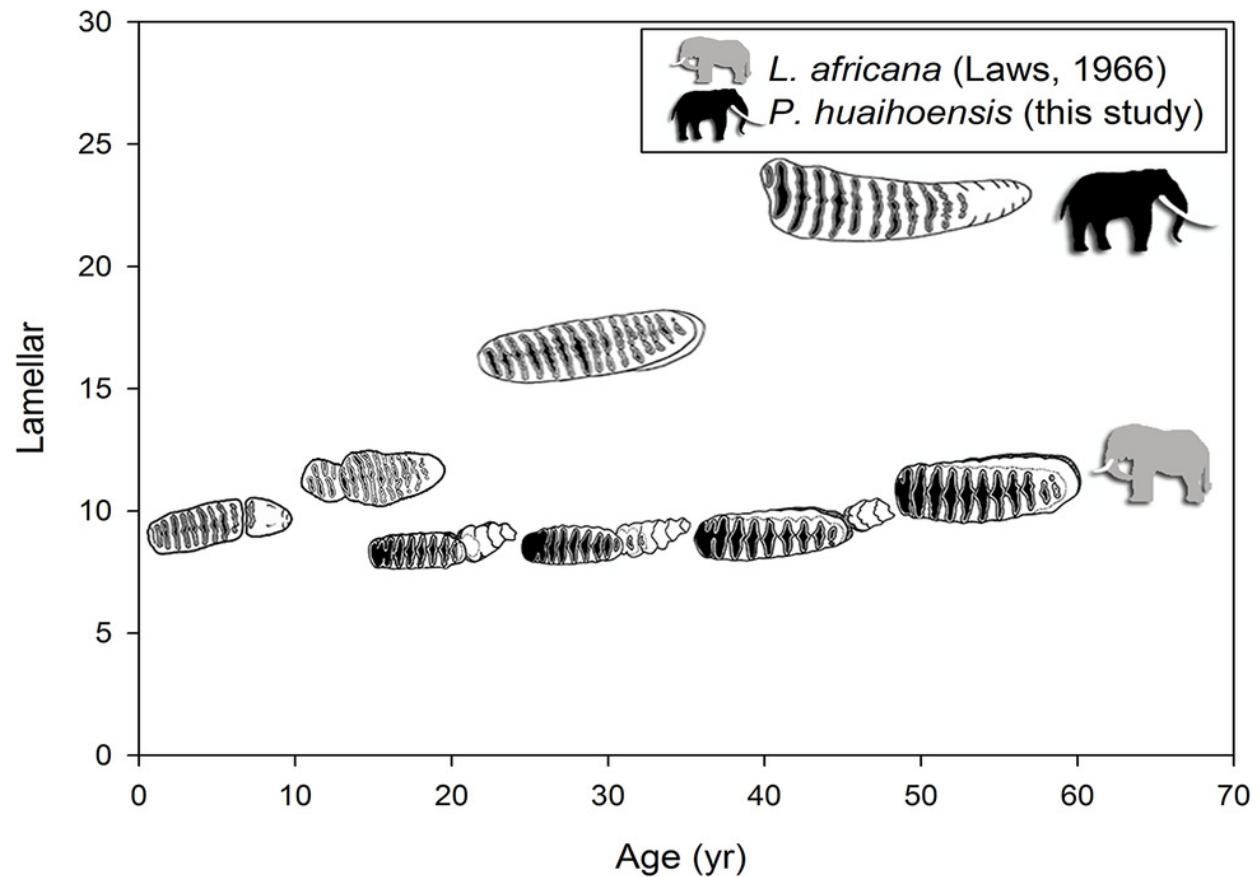



Figure 7

Age distribution of *P. huaihoensis* from Penghu Channel, Taiwan. The frequency (%) is based on the proportion of specimens (n).

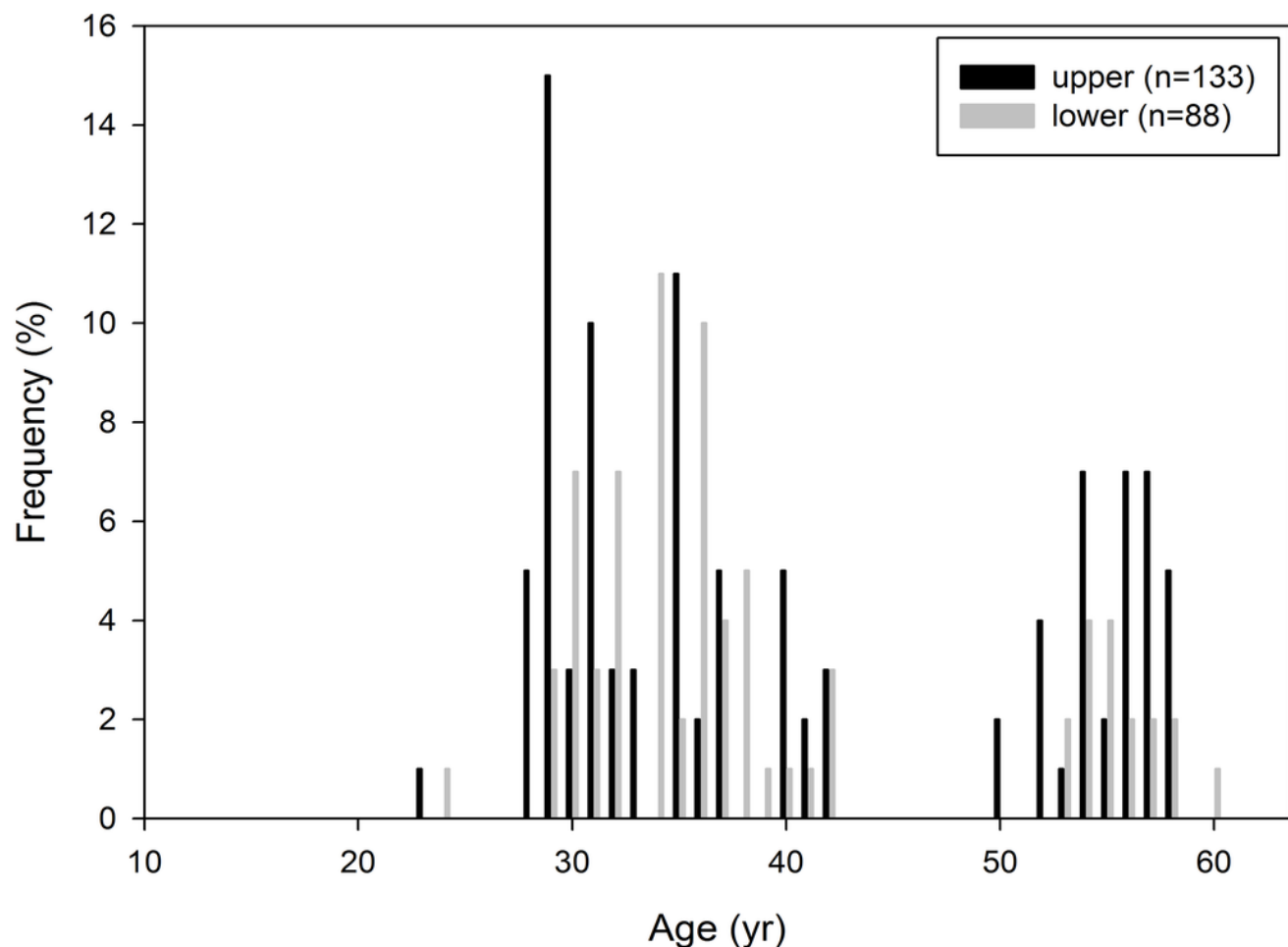



Figure 8

Comparison of the age distribution of *P. huaihoensis* with that of (A) *M. primigenius* and (B) *M. columbi*.

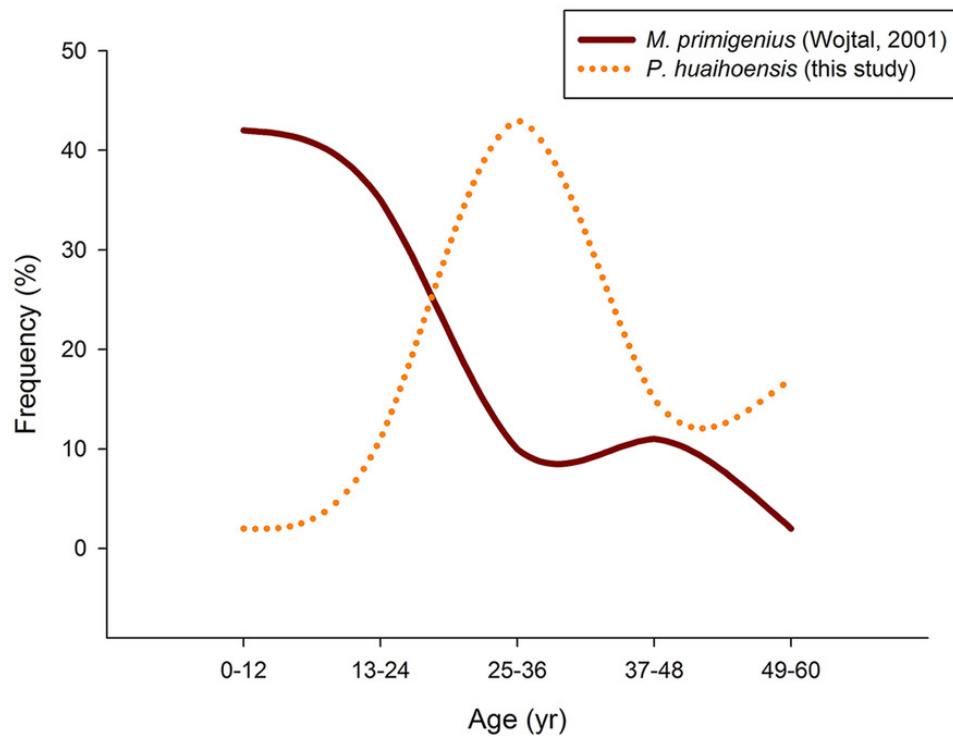
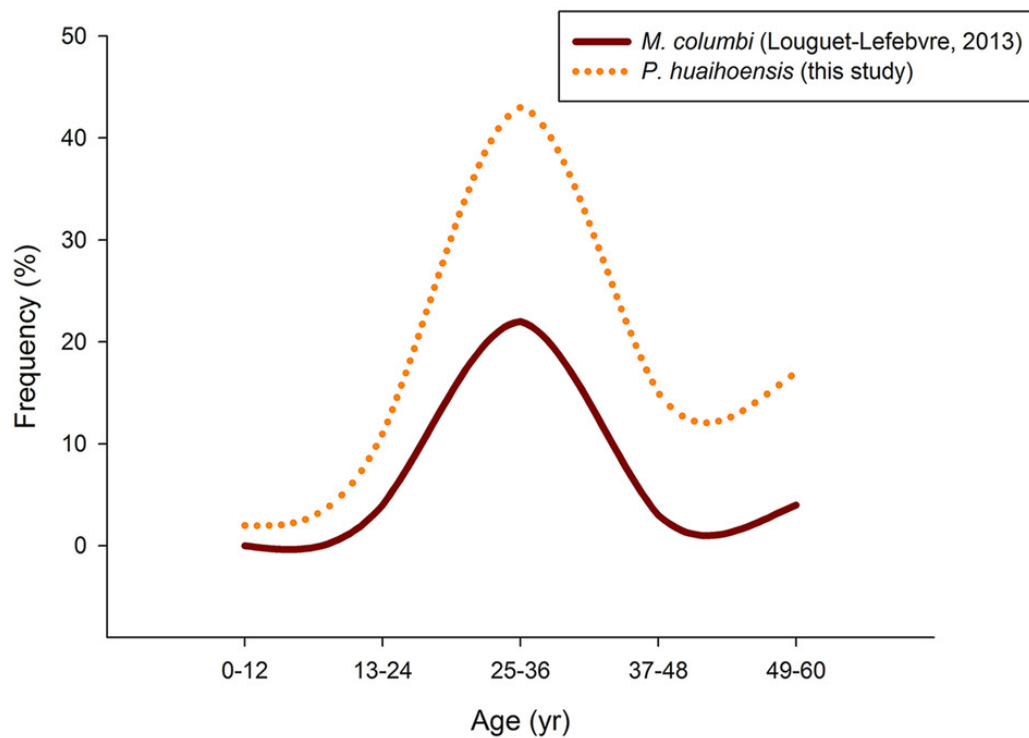
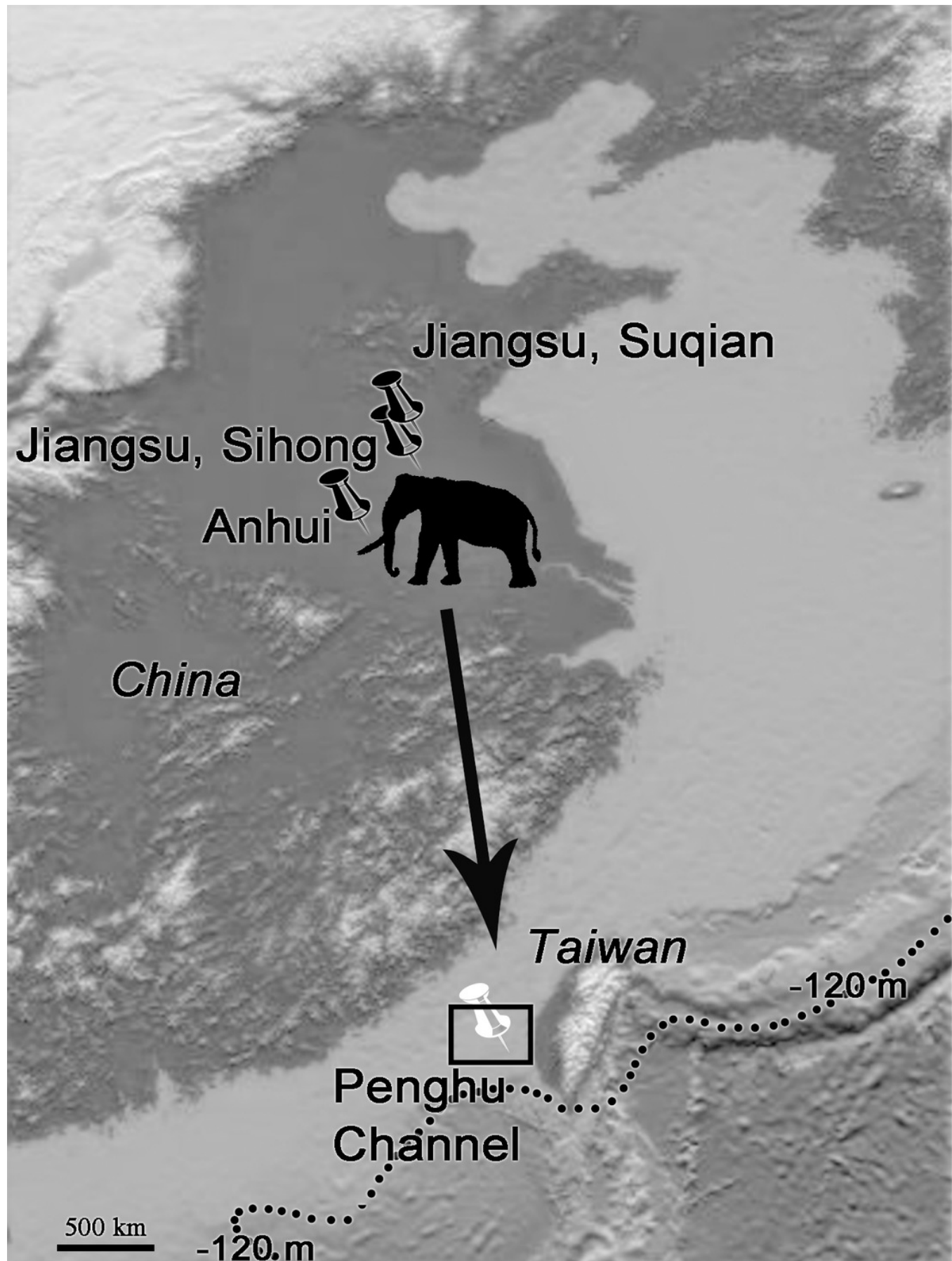



Figure 9

Postulated migration direction (black arrow) of *P. huaihoensis*. The species likely originated from northern China (black pins), where fossil records are more abundant. The extension of the record in the Penghu Channel (white pin) in the last ice age

The current sea depth contour (−120 m) delineates the ancient coastline during the last ice age. The map is derived from the National Centers for Environmental Information (https://www.ngdc.noaa.gov).

Comparison of estimated ages derived from the lower jaw of *P. huaihoensis* and *L. africana*. The positions of the teeth used in Laws (1966) are indicated in parentheses.

Tooth position	*L. africana* (from Laws, 1966)			*P. huaihoensis* (this study)		
	Age groups	No. of lamellae	Age (yrs)	Age groups	No. of lamellae	Age (yrs)
dp2	I–V	3	0–3	–	–	–
dp3	VI–X	7	4–13	–	–	–
dp4	XI–XV	9	15–24	I–IV	9	4–16
M1	XVI–XX	9	26–34	V–X	11	18–28
M2	XXI–XXV	10	36–47	XI–XVI	17	32–41
M3	XXVI–XXX	12	49–60	XVII–XXIV	22	43–57