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

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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 teeth 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* had 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.

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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

The fossil genus *Palaeoloxodon* (Palaeoloxodontinae, Elephantidae) has been widely recorded from Eurasia, Africa, and East Asia during the Late Pleistocene (Markiyama, 1924; Matsumoto, 1929; Osborn, 1936; Zong, 1987; Haynes, 1991). *Palaeoloxodon* has eight known species: *P. antiquus* (Falconer & Cautley, 1847; Osborn, 1942), *P. namadicus* (Falconer & Cautley, 1847; Osborn, 1924; Matsumoto, 1929), *P. falconeri* (Falconer, 1862; Busk, 1867; Vaufrey, 1929; Osborn, 1942), *P. mnaidriensis* (Adams, 1870), *P. cypriotes* (Bate, 1903; Osborn 1942), *P. recki* (Dietrich, 1916; Maglio, 1970; Maglio, 1973; Beden, 1979, unpublished data), *P. naumanni* (Makiyama, 1924), and *P. huaihoensis* (Qi, 1999). In China and neighboring areas, records of *Palaeoloxodon* are relatively abundant (Liu, 1977; Qi, 1999), and many specimens have been identified as *P. namadicus, P. naumanni or P. huaihoensis* (Ho et al., 2000; Shieh et al., 2007; Qi, 1999). Among the three species, *P. namadicus* is found mostly in the Nihewan Basin, China (Wei, 1976). Records of *P. naumanni* are widely distributed in China and Japan but not in Taiwan (Takahashi et al., 2001). *Palaeoloxodon huaihoensis* is the only known species from the Penghu Channel, Taiwan (Shieh & Chang, 2007). Ho et al. (2000) stated that *P. huaihoensis* was once distributed both in the China and Taiwan area during the Pleistocene (Shieh & Chang, 2007).

You et al. (1995) divided the Eastern China Sea into three paleobiogeographic zones in the Late Pleistocene, with the north of 38°N representing *Mammuthus–Coelodonta* fauna, 28 °N - 38 °N representing *Palaeoloxodon–Elaphurus davidianus* fauna, and *Ailuropoda–Stegodon* fauna to south of 28°N. According to this scheme, Taiwan and the adjacent Penghu Channel should belong to the *Ailuropoda–Stegodon* fauna category. However, the Penghu fauna is mainly composed of *E. davidianus, Bubalus teilhardi*, and *P. huaihoensis* (Kuo, 1982; Hu & Tao, 1993; Ho, 1998; Qi, 1999), which is more similar to the fauna in the Huaihe River Region, which belongs to the *Palaeoloxodon–E. davidianus* fauna (You, 1995; Chen, 2000; Ho et al., 2008). Studies have indicated the existence of a narrow and semiclosed sea similar to a land bridge between the Yellow Sea and East Sea in the last ice age (Chen, 2000). Therefore, the paleoclimate in the Pleistocene Taiwan Strait might belong to the tropical-temperate zone (Cai, 1999). Indeed, the so-called "Taiwan Landbridge Fauna" includes at least two distinct faunas during the Middle-Late Pleistocene: one spanning from the Middle to early Late Pleistocene (Chochen fauna) and one confined to the Late Pleistocene (Penghu fauna) (Chen, 2000).

The fauna of Chochen area includes several large mammals, such as *Rhinoceros sinensis hayasakai* (Hayasakai, 1942), *Stegodon* (*Parastegodon*) *akashiensis* (Hayasakai, 1942; Shikama et al., 1975; Otsuka, 1984), and *S.* (*Parastegodon*) *aurorae* (Shikama et al., 1975), but no fossils of *P. huaihoensis* were found (Kuo, 1982; Ho & Qi, 1999). The Chochen fauna is believed to share more affinities with that of the Huanan area in southern China than in with the mammal fauna from northern China (Ho, 1998; Cai, 1999; Ho & Qi, 1999; Shieh & Chang, 2007). However, the taphonomic and postmortem transportation processes of Chochen area are very complex and somewhat ambiguous, which resulted in both terrestrial and marine elements in the whole fauna (e.g., Lin et al., 2019). However, the composition of the Penghu fauna indicates that all of it likely originated from northern China throughout the Pleistocene (Ho et al., 1997; Qi, 1999; Shieh & Chang, 2007).

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

Materials & Methods

Specimens and measurements

P. huaihoensis specimens were all dredged and recovered by fishing nets from the Penghu Channel, Taiwan, as in Chang (2015). The Penghu Channel (22°40′N–23°40′N, 119°00′E–120°00′E) is located in the Taiwan Strait between Penghu Island (Pescadores) and Taiwan (Fig. 1). A total of 221 teeth (dp4 (n = 3), M1 (13), M2 (42), and M3 (163)), including 88 [illegible], were available at the National Museum of Nature Science (NMNS), Taiwan for this study. Eroded and abraded specimens were not analyzed (Fig. 2, Table S1)

Figure 1: Map showing the sampling area in the Penghu Channel ([illegible] 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.

We first used the plate counts to identify the p[illegible]on of the molar. Next, the tooth length, width, and height were measured (Fig. 3), with the height taken vertically from the crown apex of the plate. The enamel thickness (ET) was measured with calipers. To calculate lamellar frequency, the number of complete plates at 10 cm at the crown base of both the lingual and buccal sides was taken (Short, 1969; Hasegawa, 1972; Maglio, 1973; Shieh & Chang, 2007; Chang, 2010, unpublished data).

Figure. 3. Measurements of an elephant to[illegible]sed in this study.

Age determination

We used the size, structure, and wear of teeth to determine the age distribution of *P. huaihoensis* (Morrison-Scott, 1947; Sikes, 1966; Maglio, 1973; Lang, 1980). Thirty age groups based on tooth morphology and shearing rate of deciduous teeth of African forest elephants were established by Laws (1966), and this method has been widely used for the reconstruction of age distribution in many elephant species (Haynes, 1991; Lister, 1999). We used this method too with slight modifications. For example, Laws' method indicates that M3 has a maximum number of 12 plates in *L. africana*, but in *P. huaihoensis*, as many as 22 plates can be found in M3. In this case, the remaining number of plates in *P. huaihoensis* can be obtained by the rate of tooth eruption of *L. africana* multiplied by the observed plates of *P. huaihoensis*. Thus, the age group XX of Law's with 12 plates indicates that there will be six plates in the age groups of *P. huaihoensis* if $(22/12) \times 6 = 11$ plates are remaining (see Table S2). Consequently, we established 24 age groups defined using 88 jaws (Fig. 4).

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).

Statistical analysis

The tooth width and lamellar frequency in occlusal and buccal sides of the lower and upper jaws of dp4-M3 as well as the relationship between the width and enamel thickness (ET) of lower and upper jaws of dp4-M3 were plotted using R software (Core Team and Others 2013). The relationship between two variables was indicated using Pearson's correlation coefficient. These relationships reflect whether the concerned variables revealed an allometric growth pattern. The number of lamellae throughout the lifespan was plotted against the estimated age of *P. huaihoensis* (see above, Age determination). Moreover, *L. africana* data were used for comparison (Laws, 1966).

A histogram based on the frequency distribution of specimens was established to reconstruct the age distribution of *P. huaihoensis*. Unlike studies in which only the lower jaws were considered (Laws, 1966), we included upper jaw specimens for comparison. A null hypothesis of the distributions of upper and lower jaws was first tested using the two-sample t test. However, when no significant difference between upper and lower jaws was detected, only lower jaw specimens were used in subsequent analyses. A Shapiro–Wilk test was conducted to test whether the fossil age distribution data were distributed normally; if not, the median for the lower jaws was calculated using the Wilcoxon–Mann–Whitney test.

Finally, we compared the age distribution based on fossil remains of *P. huaihoensis* with other species: the stable age distribution of fossil *Mammuthus primigenius* and *M. columbi*. A null hypothesis stating the same age distribution for each population pair was analyzed using Pearson's chi-square test. Here, the independence of age and the number of individuals in each of the two populations were tested. The *M. columbi* and *M. primigenius* data were derived from the studies of Louguet-Lefebvre (2013) and Wojtal (2001), respectively. All analyses were performed using R (Core Team and Others 2013).

Results

Tooth width and lamellar frequency were negatively correlated on both the occlusal and buccal sides for dp4-M3. Lamellar frequency increased when tooth width decreased in both upper and lower jaws (Fig. 5a, b, d, e). By contrast, the tooth width and ET were positively correlated on both the sides (Fig. 5c, f). The size range overlapped in some cases; for instance, the M2 overlapped with M3 in occlusal width and lamellar frequency and width and ET of the lower jaw, respectively (Fig. 5d, f).

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 ($r = 0.457$, $t = 4.759$, $p < 0.05$).

A summary of the various age groups derived from the tooth morphology, lamellar number, teeth position, and age estimation is presented in Table 1. The number of lamellae of *P. huaihoensis* was considerably higher than that of *L. africana* in the same age group (Fig. 6). Moreover, the increasing rate of lamellae in *P. huaihoensis* was progressively more evident than that of *L. africana* from M1, eventually reaching 22 lamellae in M3.

Table 1: 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.

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).

The reconstructed age distribution of *P. huaihoensis* revealed that the age peaked at 29–36 years, indicating a higher number of adult individuals (Fig. 7). Notably, the distributions of the upper and lower jaws were similar (two-sample t test, $p = 0.941$, $t = 0.075$), and they possibly originated from a single population (mean = 0.04). The Shapiro–Wilk test indicated a nonnormal age distribution ($p < 0.05$), and using the Wilcoxon–Mann–Whitney test, the medians of lower jaws indicated an age of 33–34.5 years.

Figure 7: Age distribution of *P. huaihoensis* from Penghu Channel, Taiwan. The frequency (%) is based on the proportion of specimens (n).

Pearson's chi-square test revealed that *P. huaihoensis* age distribution was significantly different from the stable age distribution of *M. primigenius* ($p < 0.05$, Fig. 8a) but not from that of *M. columbi* ($p > 0.05$, Fig. 8b). *M. primigenius* mainly comprised juveniles and young-adult individuals, whereas *P. huaihoensis* and *M. columbi* comprised mostly adults aged 30–40 years.

Discussion

Tooth eruption has widely been used for estimating extant elephant age (Laws, 1966; Krumery & Buss, 1968; Shoshani, 1982; Roth & Shoshani, 1988). This method has also been applied to fossil species—for example, the age distribution of the *Mammut* (Mastodon) (Haynes, 1985), *M. columbi* (Saunders, 1980; Louguet-Lefebvre, 2013), and *M. primigenius* (Lister, 1999; Wojtal, 2001; Rountrey, 2012). However, in *P. huaihoensis*, plate count, length, ET, and lamellar frequency measurements revealed substantial differences from the extant *L. africana* (e.g., Fig. 6).

Our age distribution for *P. huaihoensis* has a distinct pattern compared with that of *M. primigenius* (Wojtal, 2001). In *M. primigenius*, numerous younger individuals (0–12 years) and r[illegible] fewer adults were found in the European Kraków Spadzista site (Fig. 8a). Such a p[illegible]n represents the natural deaths of the whole population, suggesting nonselective cumulative deaths in the normal environment (Klein, 1985; Haynes, 1991; Haynes & Klimowicz, 2016).

Figure 8: Comparison of the age distribution of *P. huaihoensis* with that of (A) *M. primigenius* and (B) *M. columbi*.

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

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

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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References

Adams AL. 1870. *Notes of a Naturalist in the Nile Valley and Malta: a narrative of exploration and research in connection with the natural history, Geology and archaeology of the lower Nile and Maltese Islands.* Edinburgh, UK: Edmonston and Douglas. 295

Agenbroad LD, Mead JI. 1994. The Hot Springs Mammoth Site: a Decade of Field and Laboratory Research in Paleontology, Geology, and Paleoecology, Mammoth Site of Hot Springs. South Dakota, Inc., Hot Springs. 451 DOI: doi.org/10.1086/419383

Bate DMA. 1903. Preliminary note on the discovery of a pygmy elephant in the Pleistocene of Cyprus. *Proceedings of the Royal Society of London* B197:347-60

Beden M. 1979. *Les Elephants (Loxodonta et Elephas) d 'Afrique Orientale: Systématique, Phylogénie, Intérêt Biochronologique.* D. Phil. Thesis, Université de Poitiers.

Busk G. 1867. Description of the remains of three extinct species of elephant, collected by Capt. Spratt, C. B. R. N., in the ossiferous cavern of Zebbug, in the island of Malta. Partly from the notes from the late H. Falconer, M. D. F. R. S. *Transactions of the Zoological Society of London VI (PtV)* 227-306

Cai BQ. 1999. The Later Pleistocene Fossil Mammals and the Palaeogeographical Environment of the Taiwan Strait. *Journal of Xiamen University (Arts & Social Sciences)* 4:29-33.

Chang CH. 2010. Evolution of Elephantide in the Quaternary of the Far East. D. Phil. Thesis, University College London

Chang CH, Kaifu Y, Takai M, Kono RT, Grün R, Matsu'ura S, Kinsley L, Lin LK. 2015. The first archaic Homo from Taiwan. *Nature Communications* 6:6037 DOI: 10.1038/ncomms7037

Chen X, Wu S, Wang P, Wang XB, Chao JH. 2020. A report on the Late Pleistocene vertebrate fossils from the Zhangshan locality, Suqian, Jiangsu Province. *Acta Antheropologica Sinica* 39(2):319-331 DOI: 10.16359/j.cnki.cn11-1963/q.2018.0021

Chen KT. 2000. On Taiwan Mammalian Faunas in Different Periods of Time and Related Problems: The Background Materials for Taiwan Zooarchaeological Studies: I. *Bulletin of the Institute of History and Philology Academia Sinica* 71(1):129-198

Dietrich WO. 1916. *Elephas antiquus Recki* n.f. aus dem Diluvium Deutsch- Ostafiikas. *Archives of Biology.* 4:1-80

Falconer H, Cautley PT. 1847. *Fauna Antiqua Sivalensis, being the Fossil Zoology of the Sewalik Hills in the North of India.* London: Smith, Elder and Co.

Falconer H. 1862. On Ossiferous Caves in Malta, Explored by Captain Spratt, R.N., C.B., with an account of *Elephas meletensis*, a pigmy species of fossil elephant and other remains found in them. *Parthenon* 125:780

Fatti LP, Smuts GL, Starfield AM, Spurdle AA. 1980. Age Determination in African Elephants. *Journal of Mammalogy* 61(3):547-551 DOI: doi.org/10.2307/1379852

Ferry N, Dray S, Fritz H, Valeix M. 2016. Interspecific interference competition at the resource patch scale: do large herbivores spatially avoid elephants while accessing water? *Journal of Animal Ecology* 85(6):1574–85 DOI: 10.1111/1365-2656.12582

Hasegawa Y. 1972. The Naumann's elephant, *Palaeoloxodon naumanni* (MAKIYAMA) from the late Pleistocene off Shakagahana, Shodoshima Is. In Seto Inland Sea, Japan. *Bulletin of the National Science Museum* 15(3):513-591

Hayasakai A. 1942. On the occurrence of mammalian remains in Taiwan - a preliminary summary. *Taiwan Tigaku Kizi* 13(4):95-109

Haynes G. 1985. Age Profiles in Elephant and Mammoth Bone Assemblages. *Quaternary Research* 24(3):333-345 DOI: 10.1016/0033-5894(85)90055-9

Haynes G. 1991. *Mammoths, Mastodons, and Elephants: Biology, Behavior, and the Fossil Record.* New York: Cambridge University Press. 413 DOI: 10.1002/gea.3340090506

Haynes G, Klimowicz J. 2016. The Meaning of the Mammoth Age Profile from Kraków

Spadzista Trench B+B1. In Wojtal P, Wilczynski J, Haynes G. (Eds.), A Gravettian Site in Southern Poland: Kraków Spadzista. Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Kraków, pp. 159-187
Ho CK, Qi GQ, Chang CH. 1996. A preliminary study and reconstruction of Late Pleistocene megafauna *Bubalus teilhardi Young* from the Penghu Channel. *Taiwan Annual of Taiwan Museum* 39:1-15
Ho CK, Qi GQ, Chang CH. 1997. A Preliminary Study of Late Pleistocene Carnivore FossiIs from the Penghu Channel, Taiwan. *Journal of the National Taiwan Museum* 40:195-224 DOI: 10.6548/ATMB
Ho CK. 1998. The mammalian of Penghu Channel in the Late Pleistocene. *Newsletter of Chinese Ethnology* 36:3-11
Ho CK, Qi GQ. 1999. Quaternary fauna and paleoenvironment of Penghu submarine trench of Taiwan. *Quaternary Science* 2:47-48
Ho CK, Qi GQ, Chang CH. 2000. Systematic Description and Classification of Late Pleistocene *Palaeoloxodon*. *Journal of the National Taiwan Museum* 43:49-105 DOI: 10.6548/ANTM.200012_43.0003
Ho CK, Qi GQ, Chang CH. 2008. A preliminary study of Late Pleistocene Megafauna Cervus sp. from the Penghu Channel, Taiwan. *Journal of Taiwan Museum* 61(1):1-16 DOI: 10.6532/JNTM
Hu CH, Tao HJ. 1993. *The fossil faunas of Penghu Islands, Taiwan.* Taiwan, Penghu: Penghu District Cultural Center Publications.
Janis CM. 1989. A climatic explanation for patterns of evolutionary diversity in ungulate mammals. *Palaeontology*. 32: 463-481
Klein RG. 1985. Age (mortality) profiles as a means of distinguishing hunted species from scavenged ones in Stone Age archeological sites. *Paleobiology* 8(2):151-158
Krumery WA, Buss IO. 1968. Age estimation, growth, and relationships between body dimensions of the female African elephant. *Journal of Mammalogy* 49:22-31 DOI: 10.2307/1377724
Kuo YW. 1982. Penghu fauna. *Journal of Marine Science* 27:123-132
Lang EM. 1980. Observations on growth and molar change in the African elephant. *African Journal of Ecology* 18:217-234 DOI: 10.1111/j.1365-2028.1980.tb00643.x
Laws RM. 1966. Age criteria for the African elephant. *The East African Wildlife Journal* 4:1-37 DOI: 10.1111/j.1365-2028.1966.tb00878.x
Lin CH, Chien CW, Lee SW, Chang CW. 2019. Fish fossils of Taiwan: a review and prospection. *Historical Biology* DOI: 10.1080/08912963.2019.1698563
Lister AM. 1999. Epiphyseal fusion and postcranial age determination in the woolly mammoth, *Mammuthus primigenius* (Blum.). Deinsea 6:79-88
Liu JL. 1977. *Palaeoloxodon* from Huaiyuan District, northern part of Anhui. *Vertebrata PalAsiatica* 15(4):278-286 DOI: 10.19615/j.cnki.1000-3118.1977.04.006
Louguet-Lefebvre S. 2013. The Columbian mammoths from the Upper Pleistocene of Hot Springs (South Dakota, United States). *PALEO* 24:149-171 DOI: doi.org/10.4000/paleo.2861

Maglio VJ. 1970. Early Elephantidae of Africa and tentative correlation of African Plio-Pleistocene deposits. *Nature* 225:328-332
Maglio VJ. 1973. Origin and evolution of the Elephantidae. *Transactions of the American Philosophical Society, New Series* 63:1-149 DOI: 10.2307/1006229
Makiyama J. 1924. Notes on a fossil elephant from Sahama, Totomi. *Memoirs of the College of Science. Kyoto Imperial University. Series B. Biology* 1(2):255-264
Matsumoto H. 1929. On *Loxodonta* (*Palaeoloxodon*) tokunagai MATSUMOTO, with remarks on the descent of Loxodontene elephants. *Science reports of Tohoku University. Series, 2 (Geology)* 13(1):7-9
Morrison-scott TCS. 1947. A revision of our knowledge of African elephants' teeth, with notes on forest and 'pygmy' elephants. *Proceedings of the Zoological Society of London* 117:505-527 DOI: 10.1111/j.1096-3642.1947.tb00534.x
Osborn HF. 1936. Proboscidea: a monograph on the discovery, evolution, migration and extinction of the mastodonts and elephants of the world. Moeritherioidea, Deinotherioidea, Mastodontoidea, Volume I. New York: The American Museum Press. 864
Osborn HF. 1942. Proboscidea: a monograph of the discovery, evolution, migration and extinction of the mastodonts and elephants of the world. Stegodontoidea, Elephantoidea, Volume II. New York: American Museum of Natural History. 958
Otsuka H. 1984. Stratigraphic position of the Chochen vertebrate Fauna of the Chochen District, southwest Taiwan, with special reference to its geologic age. *Journal of the National Taiwan Museum* 37(1):37-55
Qian MP, Gao TS, Jiang R, Zhu QB, Jin GD, Yu JJ, MA X, Jiang Y. 2017. The discovery of a late Pleistocene *Palaeoloxodon huaihoensis* skeleton from Sihong County in northern Jiangsu Province. *Journal of Stratigraphy* 41(2):173-178
Roth VL, Shoshani J. 1988. Dental identification and age determination in *Elephas maximus*. *Journal of Zoology (London)* 214:567-588 DOI: 10.1111/j.1469-7998.1988.tb03760.x
Rountrey AN, Fisher DC, Tikhonov AN, Kosintsev PA, Lazarev PA, Boeskorov G, Buigues B. 2012. Early tooth development, gestation, and season of birth in mammoths. *Quaternary International* 255:1-10 DOI: 10.1016/j.quaint.2011.06.006
Shieh YT, Chang CH. 2007. Study on the Proboscidea Fossils of the National Taiwan Museum. *Journal of Taiwan Museum* 60(1):33-44 DOI: 10.6532/JNTM
Short RV. 1969. Notes on the teeth and ovaries of an African elephant (*Loxodonta africana*) of known age. *Journal of Zoology (London)* 158:421-425 DOI: 10.1111/j.1469-7998.1969.tb02159.x
Shikama T, Otsuka H, Tomida Y. 1975. Fossil Proboscidea from Taiwan (I). *Science reports of the Yokohama National University, Section II, Biological and geological sciences* 22:13-35
Sikes K. 1967. The African elephant, 22: a field method for estimating age. *The Journal of Zoology* 154:235-248 DOI: 10.1111/j.1469-7998.1968.tb01661.x
Sukumar R. 1992. *The Asian Elephant: Ecology and Management.* Cambridge studies in applied ecology and resource management. Cambridge: Cambridge University Press. 272

— 2003. *The living elephants: Evolutionary ecology, behavior, and conservation.* New York: Oxford University Press. 496
Takahashi K, Namatsu K. 2000. Origin of the Japanese Proboscidea in the Plio-Pleistocene. *Earth Science (Chikyu Kagaku)* 54(4):257-267 DOI: 10.15080/agcjchikyukagaku.54.4_257
Valeix M, Chamaillé-Jammes S, Fritz H. 2007. Interference competition and temporal niche shifts: elephants and herbivore communities at waterholes. *Oecologia* 153:739-748 DOI: 10.1007/s00442-007-0764-5
Vaufrey R. 1929. Les éléphants nains des iles méditerranéennes et la question des isthmes Pléistocènes. *Archives de TInstitut de Paléontologie Humaine, Paris* 6:1-216
Webb, S.D., 1977. A history of savanna vertebrates in the new world — Part 1: North America. Annu. *Annual Review of Ecology and Systematics*. 8:355–380
Wei Q. 1976. Recent find of *Palaeoloxodon namadicus* from Nihewan Beds, NW Hebei. *Vertebrata PalAsiat* 14:53-58
Wojtal P. 2001. The woolly mammoth *(Mammuthus primigenius)* remains from the Upper Palaeolithic site Krakow Spadzista Street (B). Proceedings of the 1st International Congress. CNR, Rome 367–372
You YZ, Dong XR, Cai BQ, Sun YL. 1995. The mammalian fossils from western Taiwan strait. *Vertebrata PalAsiat* 33(3):231-237
Zong G. 1987. Note on some mammalian fossils of Yanyuan, Sichuan. *Vertehrata PalAsiatica* 25(2):137-45

Figure 1

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

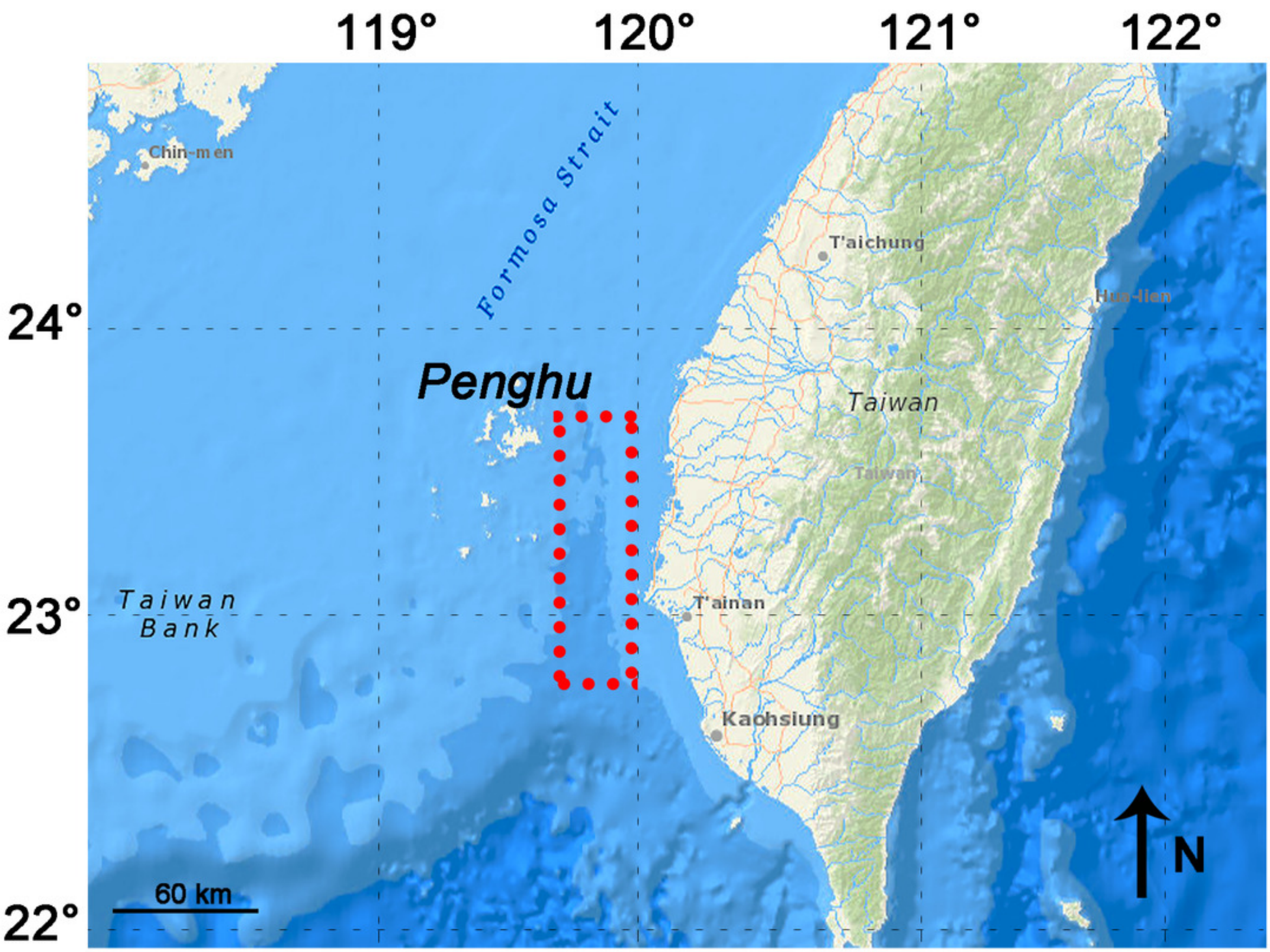


Figure 2

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.

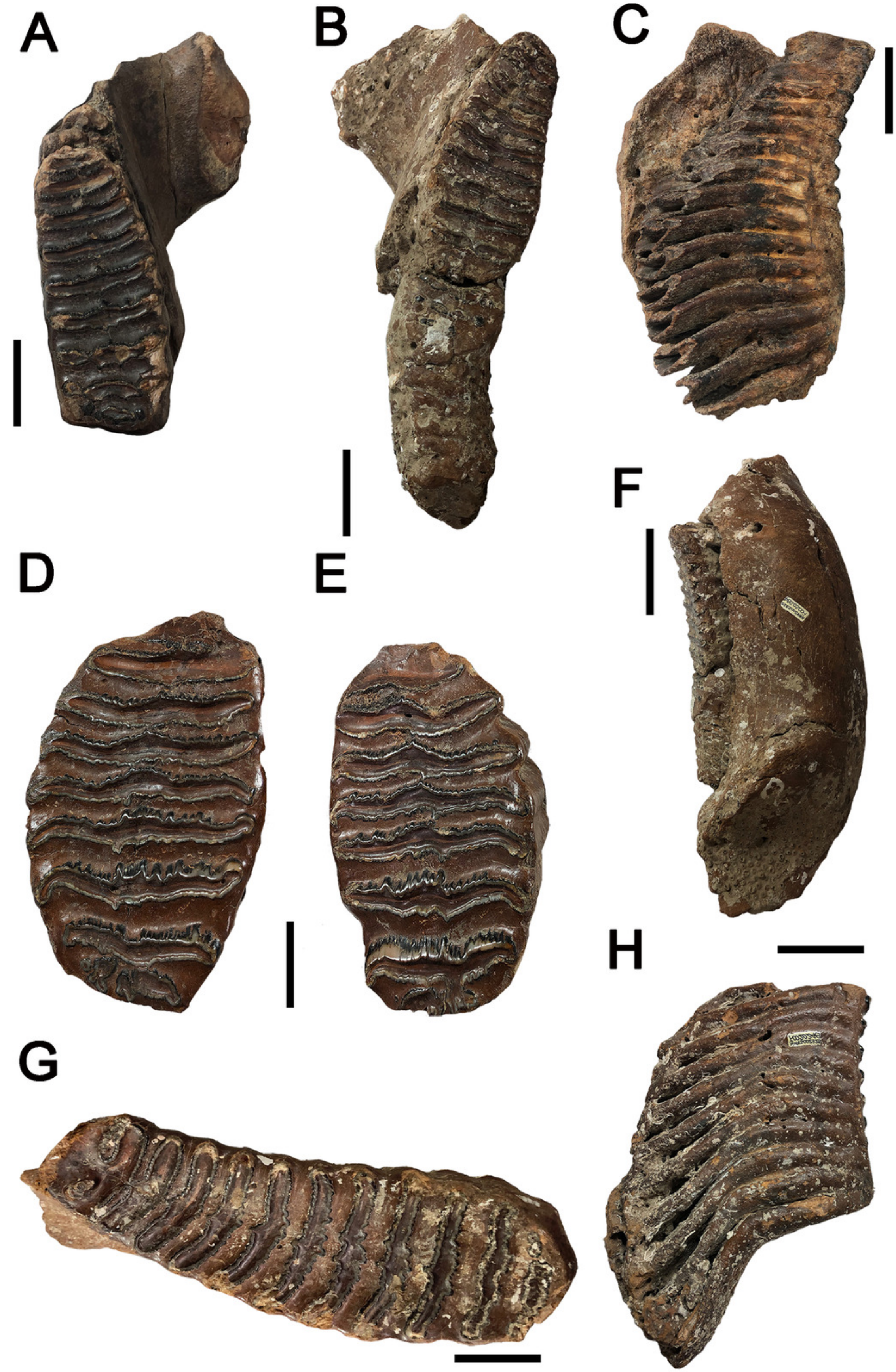

A
B
C
D
E
F
G
H

Figure 3

Measurements of an elephant tooth used in this study.

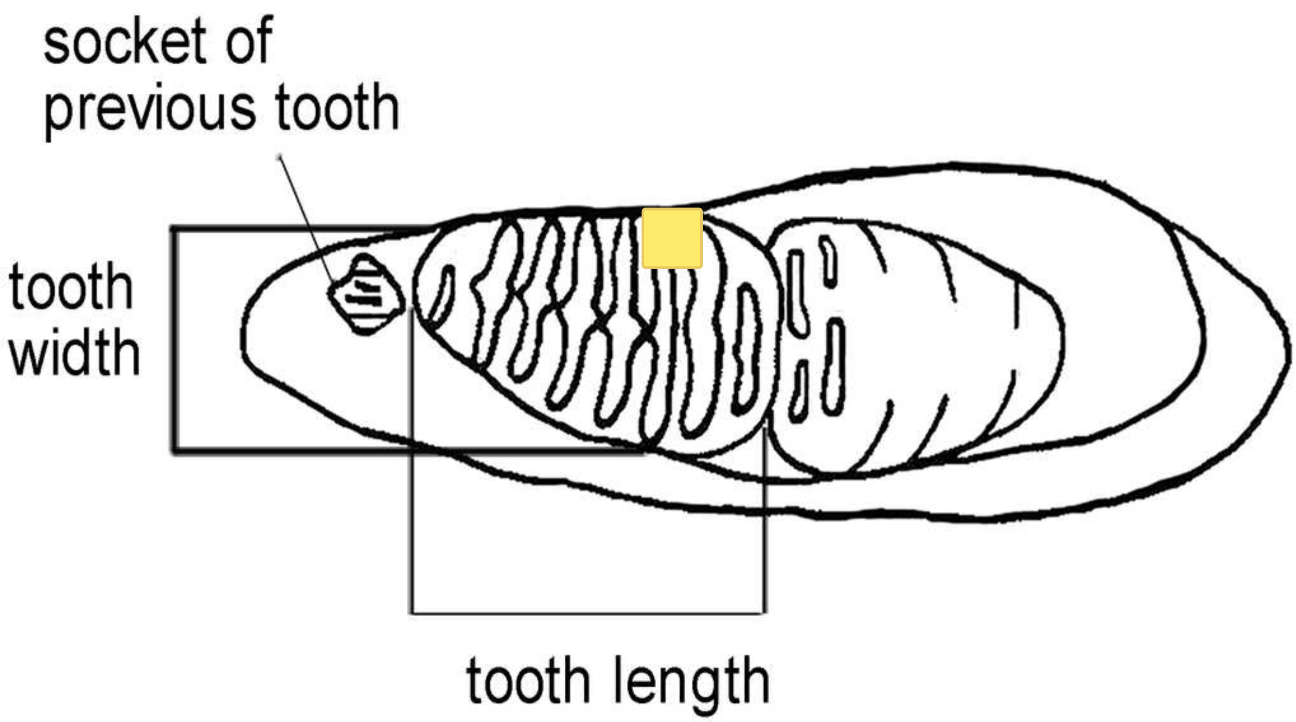


Figure 4

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).

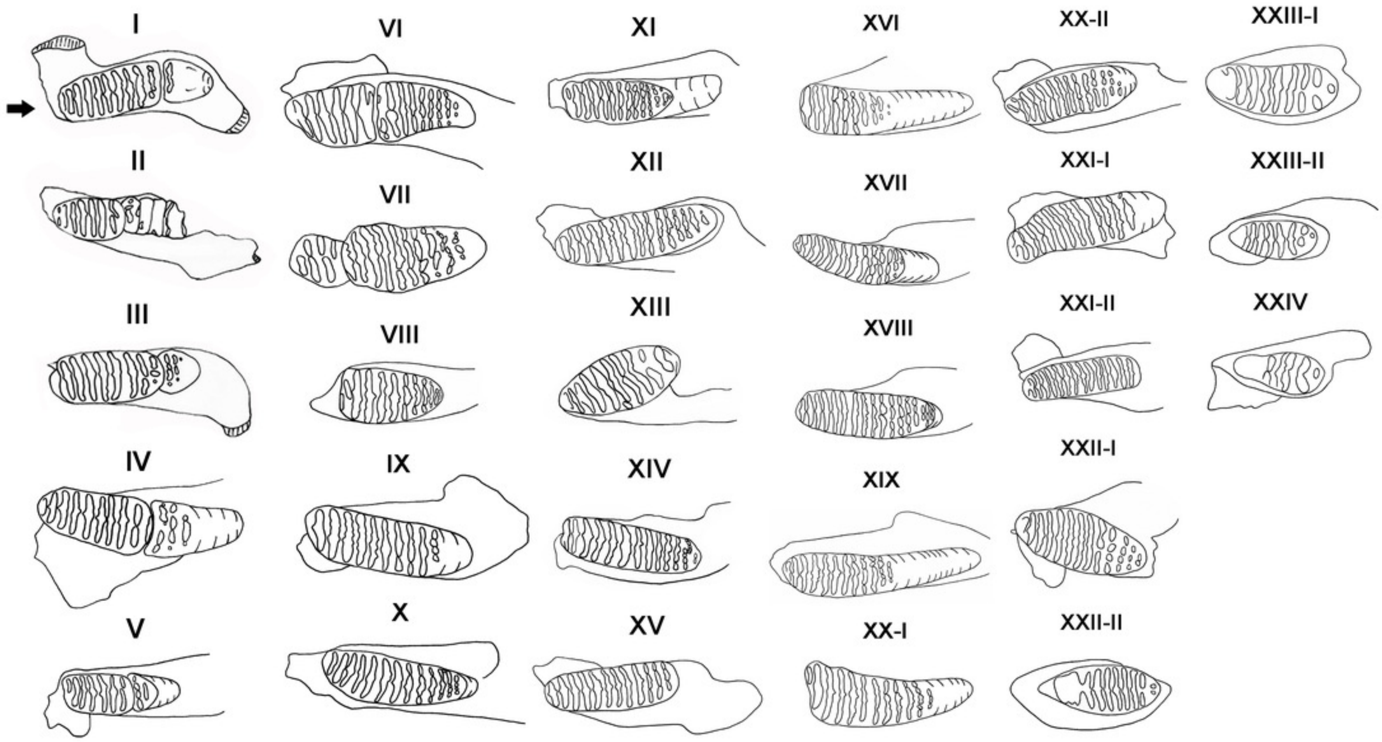


Figure 5

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 ($r = 0.457$, $t = 4.759$, $p < 0.05$).

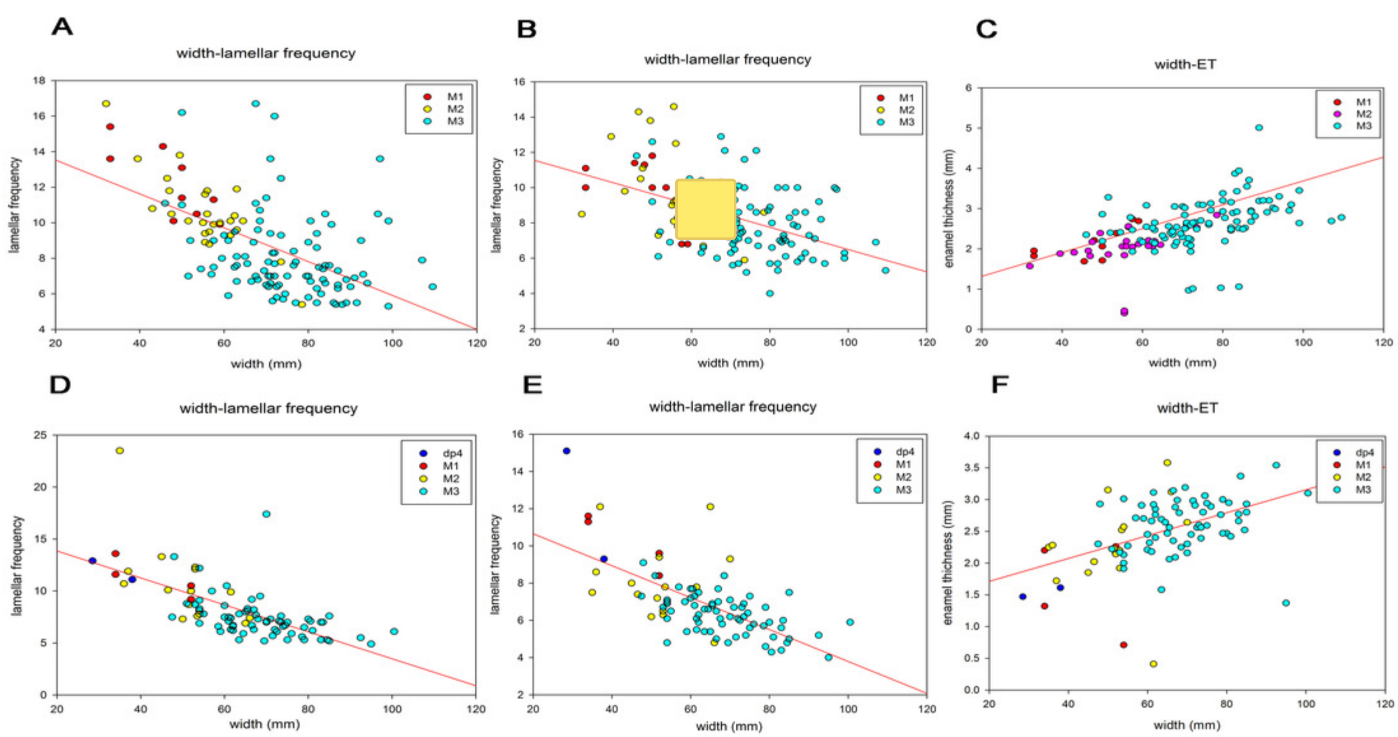


Figure 6

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).

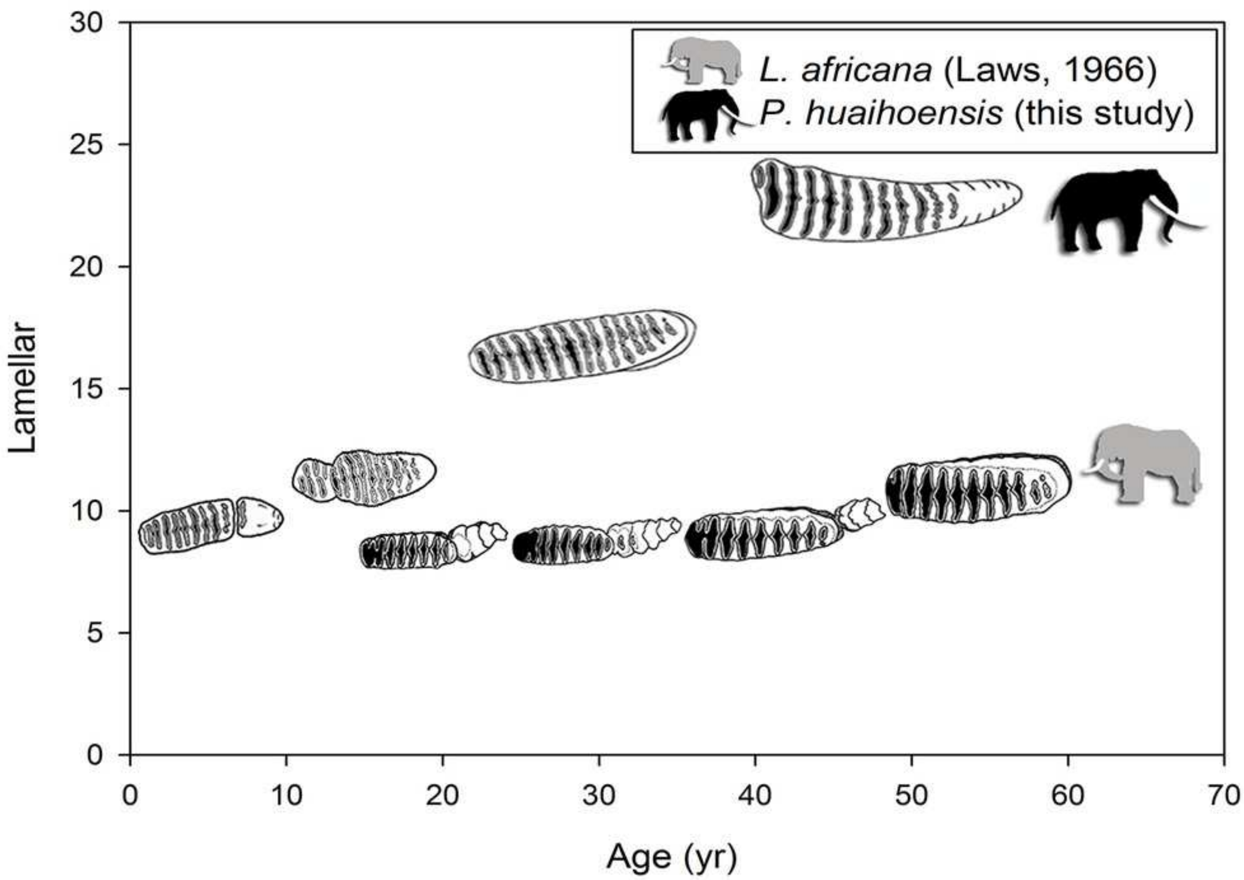


Figure 7

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

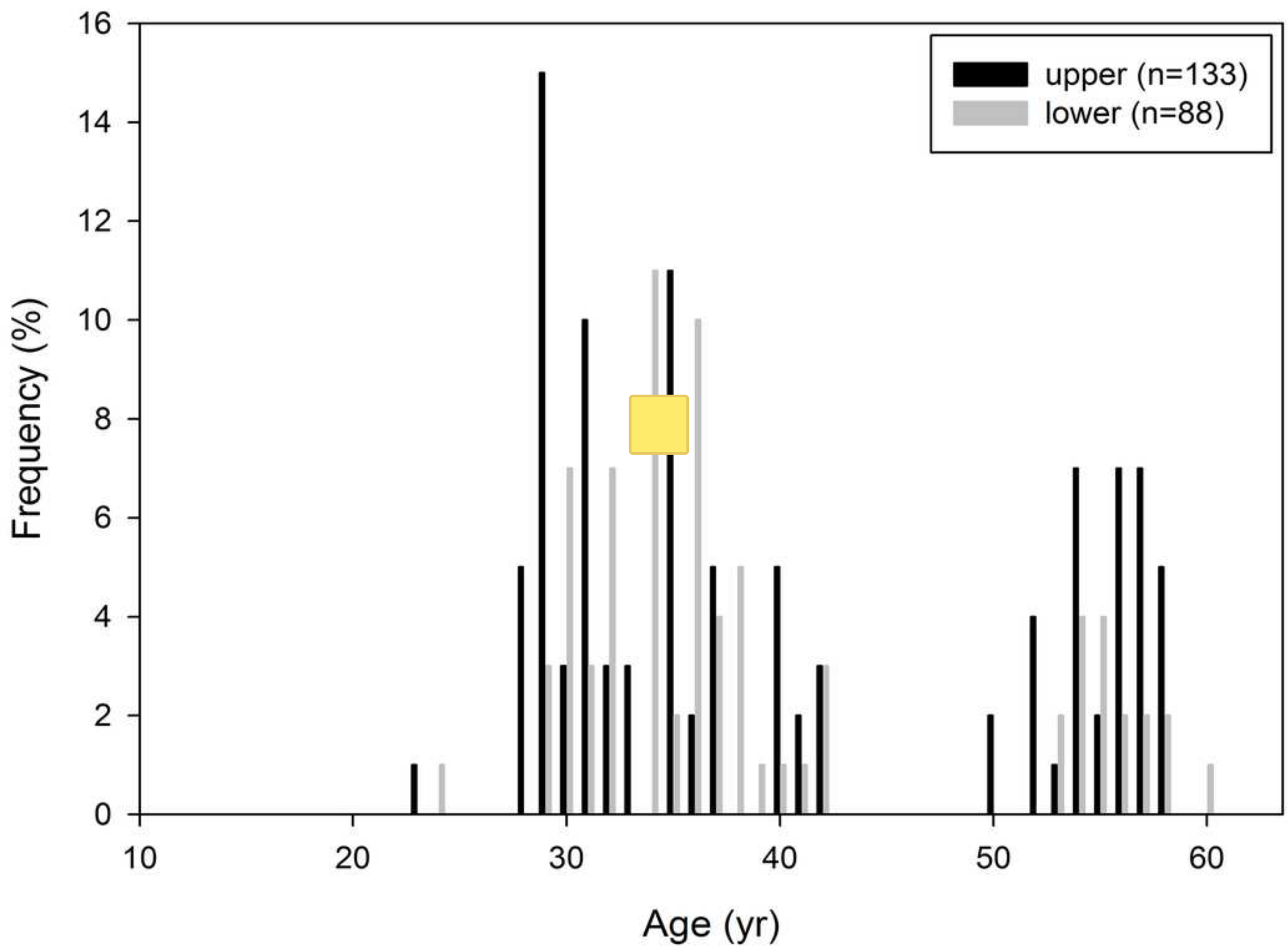
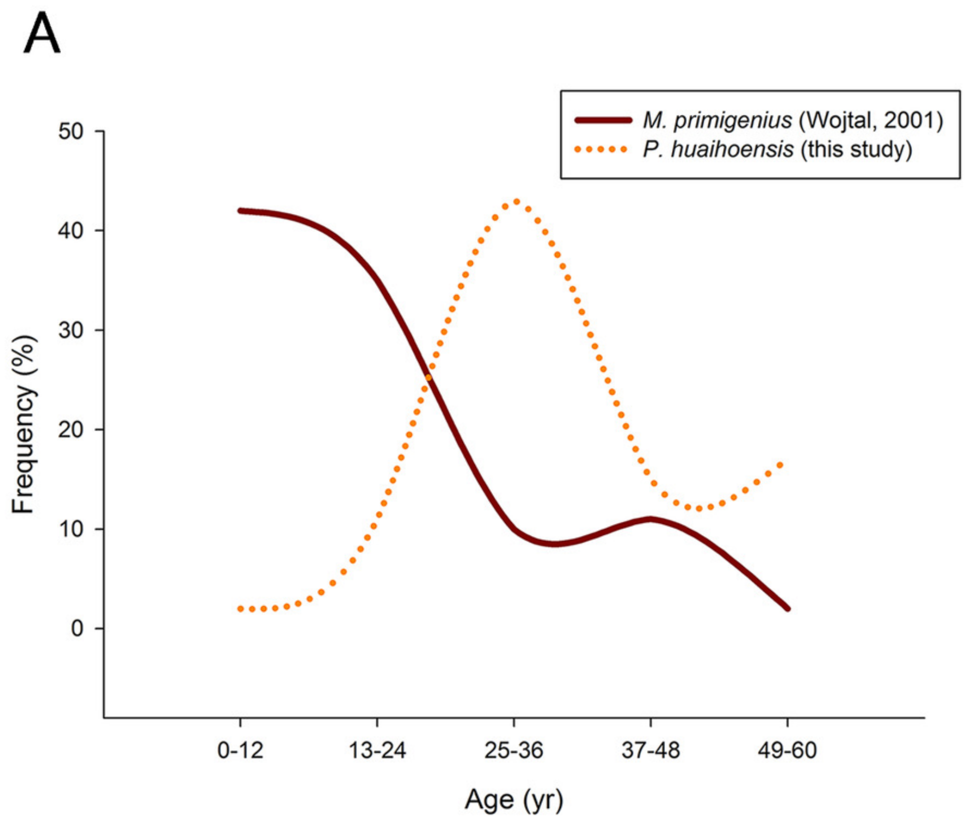


Figure 8

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


A
M. primigenius (Wojtal, 2001)
P. huaihoensis (this study)
Frequency (%)
50
40
30
20
10
0
0-12
13-24
25-36
37-48
49-60
Age (yr)

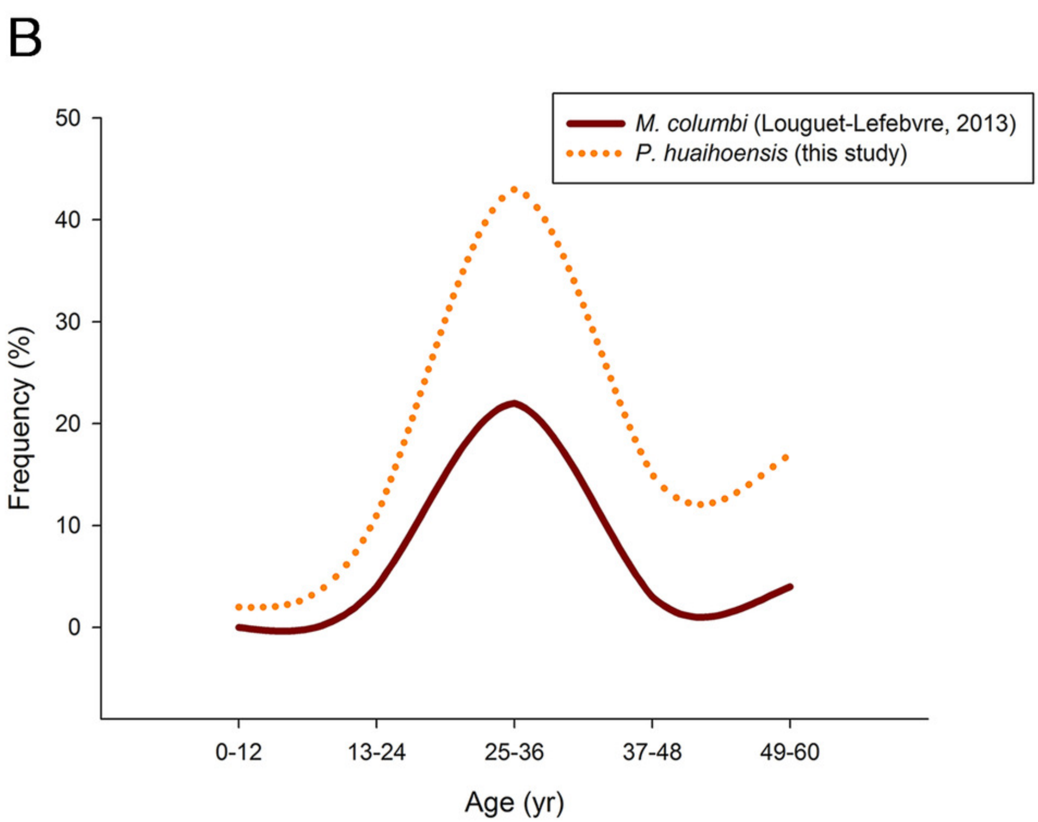

B
M. columbi (Louguet-Lefebvre, 2013)
P. huaihoensis (this study)
Frequency (%)
50
40
30
20
10
0
0-12
13-24
25-36
37-48
49-60
Age (yr)

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).

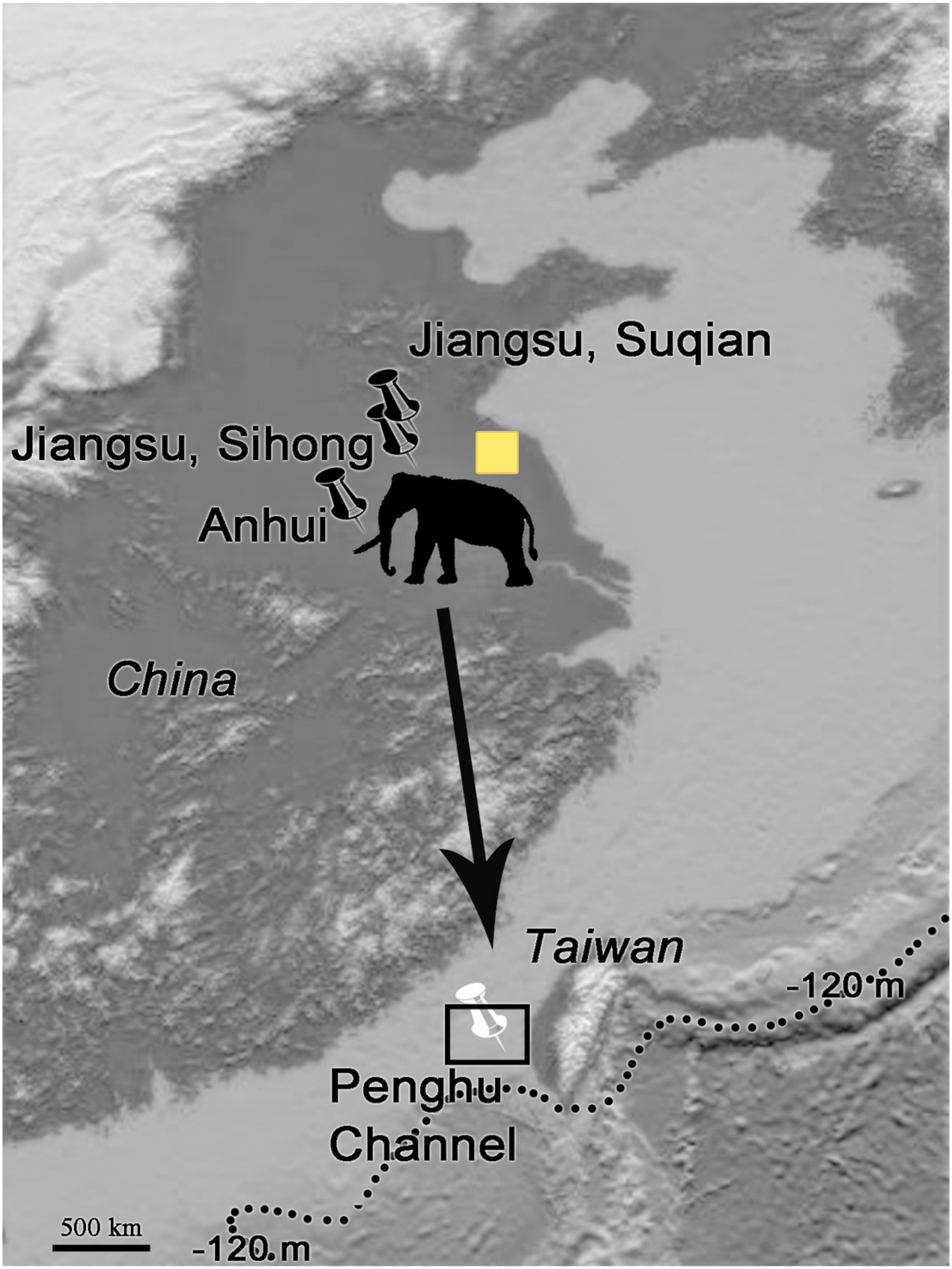

Jiangsu, Suqian
Jiangsu, Sihong
Anhui
China
Taiwan
-120 m
Penghu
Channel
500 km
-120 m

Table 1(on next page)

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

1